# Community-level Convergence and Community Structure of temperate *Nothofagus* forests

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# Abstract

Assembly rules represent the integrated action of species interactions leading to non-random patterns in the distributions of species niches in the combined niche space for a community or guild, i.e. to community structure. The most likely effect of assembly rules would be to limit the degree of overlap between niches that is possible.

In the present study, assembly rules were sought by looking for two types of non-random pattern that might be expected: convergence between disjunct communities in similar environments, and character overdispersion among the species within a community or guild. Convergence was sought both in species richness and in texture – assemblage-wide spectra of species functional characters. These pattems were sought within tall, evergreen temperate rainforest dominated by *Nothofagus* species.

Species occurrence, abundance and texture data were obtained for vascular plant species occurring at 17 environmentally-matched study sites in Tasmania (3 sites), mainland Australia (2 sites), New Zealand (8 sites) and South America (Chile and Argentina, 4 sites). Texture was evaluated in terms of 13 species characters, primarily conceming the structure and function of photosynthetic units (PSUs, i.e. leaves or their functional equivalents in certain species). All questions were addressed at local, regional and landmass scales. Texture convergence and character overdispersion were sought both within whole communities and within guilds, each comprising the species present within a vertical stratum.

Evidence for possible species richness convergence was sought using a bootstrap-based method to test the null hypothesis that communities were no more dissimilar in species richness than expected on a random basis. There were cases at all scales where the null hypothesis could not be rejected, providing preliminary evidence for assembly rules.

Evidence for texture convergence was sought by comparing the observed variation in texture between communities to the variation expected under a null model in which species characters could assort randomly among communities. In separate tests, texture was expressed as the community mean, distribution or mean-adjusted distribution (in which texture distributions from different communities were adjusted arlthmetically to a common overall mean). Little convergence of texture means or distributions was detected. However, when the effects of environmental differences between sites were minimised by comparing mean-adjusted distributions, convergence was detected at all spatial scales, both within and among landmasses. This provides strong evidence for similar assembly rules in the convergent communities.

Character overdispersion was sought by comparing the variance of the spacing of species values along character axes to the variance expected under a null model drawing characters at random from a kernel density distribution. Significantly low observed variances, representing

overdispersion, were detected for a number of texture variates at all scales. There were also trends, non-significant in individual tests, but significant among communities according to binomial tests, in several variates. This provides strong evidence for the operation of assembly rules.

Both convergence and overdispersion were most pronounced in the characters PSU area, succulence, specific weight, phosphorus content, total chlorophyll content and chlorophyll *a/b* ratio. Each of these characters would be expected to be associated with the light regime. This suggests that an important mechanism underlying the assembly rules observed may be competitive niche differentiation leading to partitioning of the vertical light gradient among species.

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# Contents

# 1. General Introduction

## 1.1 Community texture

The idea of classifying plants according to their morphology has been traced to Theophrastus (371-286 BC) who recognised four growth forms among terrestrial plants (Barkman 1988). In the modern context, von Humboldt (1806) has been credited with developing the earliest classification of plant physiognomy. Following Darwin, there was much interest in identifying plant features of adaptive significance. Warming (1909) and Schimper (1903) were among the early workers who postulated an adaptive significance for morphology, and for other classes of species characters such as phenology, physiology and life-history. Raunkiaer's (1934) life-form system, still widely used today (e.g. Danin & Orshan 1990; Floret *et al.* 1990; Shmida & Werger 1992), was based on the position of the persistent apical meristem relative to the soil surface, which Raunkiaer considered of prime adaptive importance. Numerous schemes for classifying plants according to different aspects of their morphology have been developed since (e.g. Luther 1949; Danserau 1951, 1957; Hallé, Oldeman & Tomlinson 1978; Halloy 1990). Although some workers have been cautious in attributing general adaptive significance to species characters (e.g. Du Rietz 1931), most of these studies have been motivated by an assumption that the characters are meaningful functionally, that is, that they influence a species' ability to establish, grow, and reproduce in a given environment.

If the assumption of the functional significance of species characters is valid, classifications of these characters should provide a valuable basis for characterising vegetation, both for comparison among sites, environments or regions, and for prediction. Although a number of studies have been concerned primarily with the relationships between functional characteristics of vegetation and the environment (e.g. Whitehead 1954; Parsons & Moldenke 1975; Werger & Ellenbroek 1978; Bongers & Popma 1990; Smith *et al.* 1995 [see Appendix C]), vegetation has more generally been characterised by the taxonomic affinities of the species present, supplemented perhaps by the physiognomy of the dominant species (e.g. Braun-Blanquet 1932; Ellenberg 1963; Rieley & Page 1990). Knowledge of the taxonomic composition of vegetation can provide only indirect evidence for the functional adaptations of species present, to the extent that certain species, genera and to a lesser extent higher taxonomic groups may have known ecological affinities (Whittaker 1975). Comparisons of vegetation among sites and studies is constrained by a progressive reduction in floristic overlap from the local to the regional and subsequently global scale, if assemblages are characterised only by their taxonomic composition.

With the aim of promoting a less species-oriented approach to the classification of

vegetation, Barkman (1979) proposed a scheme for classifying plant communities according to texture and structure. Texture was defined as the `qualitative and quantitative composition of vegetation as to different morphological elements', while `structure' referred to the spatial configuration of these elements. This terminology was attributed to Doing (unpublished). Though the classification scheme proposed was based solely on plant morphology, Barkman (*op. cit.*) recognised that texture could also include other species characters, and even interactions between species. Further, there is no reason why the term could not be extended to apply to assemblages of organisms other than plants. In the present study `texture', or `community texture', is used to refer to assemblage-wide spectra of characters of known or potential functional importance (an assemblage is defined as any group of co-occurring species, i.e. a community or guild, as defined below). Possible examples of texture would include the frequency distribution of leaves of different sizes in the vascular plant guild of a particular community, or the spectrum of body weights of insectivorous birds encountered in a sampling area.

## 1.2 Functional groups and guilds

The terms functional group (Cummins 1973), functional type (Gitay & Noble, *in press*), adaptive syndrome (Root & Chaplin 1976), clique (Yodzis 1982) and guild (Schimper 1903) all refer to groups of functionally-related species. Each term has its own definition, and most have been ascribed more than one meaning in different studies. Several reviews have attempted to bring order to the semantic chaos (Hawkins & MacMahon 1989; Simberloff & Dayan 1991; Wilson, *in prep.*), with the result that even more definitions abound. The closely-related concepts of functional groups and guilds are most commonly invoked in the literature, and are discussed further here.

### FUNCTIONAL GROUPS

The functional groups conceived by Cummins (1973) were of invertebrate species utilising the same types of food. Later, functional groups were defined for other types of organism, the basis of classification being either the resources used (e.g. MacMahon *et al.* 1981), or both the resources and the way they are used (e.g. Cummins & Merritt 1984), a usage synonymous with guilds *sensu* Root (1967). Plant functional groups have generally been defined according to morphology or life history characteristics rather than resource use (e.g. Grime 1977; Boutin & Keddy 1993; Golluscio & Sala 1993), probably because differences in the resources used are not so obvious for plants as for animals, which have distinct feeding niches (Simberloff & Dayan 1991).

Recently Körner (1994) has advocated extension of the functional groups concept to encompass levels of biological organisation other than species, defining them as `elements that

bear a certain set of common structural and/or process features,' where the elements concerned could be, apart from species populations, higher-order biological entities such as communities or ecosystems (sic); or lower-order entities: individuals, organs, tissues, cells etc.

Functional groups have been advocated as a means of simplifying ecosystem models (Botkin 1975; Woodward 1987), or as a basis for predicting vegetation changes in response to perturbation (Boutin & Keddy 1993) or climate change (Prentice *et al.* 1992).

## GUILDS

The original guilds of Schimper (1903) were four types of plants depending on other plants in a different way: lianes, epiphytes, saprophytes and parasites. Clements (1905) used the same term to refer to groups of species migrating together. Most frequently cited, however, is the definition of Root (1967), who used the term `guild' to refer to groups of species `using a similar class of resources in a similar way.' In this context, guilds are groups of species that possess similar alpha (habitat) niches (Pickett & Bazzaz 1978). Guilds may thus represent the `basic building blocks' of communities (Hawkins & MacMahon 1989), major ecological groups that have been `molded by adaptation to the same class of resources' (Root 1967). Guild structure might be repeated in communities in similar environments, even if the species composition is not (Hawkins & MacMahon 1989; Wilson 1989). Pianka (1980) considered that guild associates (i.e. members of the same guild), making demands on the same resources, would interact with each other more than with species outside the guild, indeed, that guilds might be `arenas of intense ... competition.'

Wilson (*in prep.*) argues for a distinction between alpha guilds (of the kind envisaged by Root [1967]), and beta guilds, comprising species with a similar beta niche, i.e. geographic or environmental distribution (Pickett & Bazzaz 1978). This distinction would be valuable, since concepts of competitive exclusion, niche differentiation, species packing etc. apply solely to species overlapping in their alpha niche, and so competing for some of the same resources. There can be no competition for environmental conditions (the properties that define beta niches). Therefore beta guilds, comprising species that have similar beta niches, would lack many of the characteristics ascribed to guilds *sensu stricto* above.

As is the case with functional groups, plant guilds are rarely defined directly according to resource use, but rather in terms of species attributes that might be expected to show some correlation with niche (e.g. Cornelius *et al.* 1991). An exception is the practice of treating vertical strata or sinusiae in plant communities as guilds (e.g. Wilson 1989; Wilson *et al.* 1995), since some resources, notably light, would be partitioned among strata as envisaged by Root (1967) for guilds.

Phylogeny has often been used implicitly or explicitly as a criterion in defining guilds (Schoener 1986; Jaksi_ 1981). MacNally & Doolan (1986) have even suggested inclusion of `closely related' in the definition of guilds. The inclusion of taxonomy as a criterion for guild

membership is consistent with Root's (1967) definition to the extent that species within higher taxonomic groups are often functionally, as well as phylogenetically, distinct from species belonging to other taxa of the same rank (Whittaker 1975). Thus guilds such as `vascular plants' or `bryophytes' may fall within Root's (1967) concept.

Assignment of species to guilds or functional groups has generally been done either qualitatively on the basis of some known or inferred feature of species' ecology (e.g. food type: Root [1967], sinusia: Wilson 1989), ecology plus phylogeny (e.g. `finches:' Schluter 1986, `tropical evergreen trees:' Prentice *et al.* 1992) or, more rarely, quantitatively using multivariate techniques such as cluster analysis (Boutin & Keddy 1993), principal component analysis (Holmes *et al.* 1979) or nearest-neighbour statistics (Winemiller & Pianka 1990). Multivariate methods group together species that are relatively similar, usually in terms of a series of intercorrelated species characters. Such methods may yield a hierarchy of nested guilds (Pianka 1994), or orthogonal guilds, defined with respect to uncorrelated axes in character space, such as principal components. A new approach to guild assignment seeks `intrinsic guilds' by optimising group membership based on co-occurrence data, assuming that guild associates will tend *not* to co-occur (Wilson & Roxburgh 1994; Wilson & Whittaker 1995). This approach explicitly assumes competition-mediated guild structure and the operation of the competitive exclusion principal (Gause 1934; Hardin 1960).

TERMINOLOGY USED IN THIS STUDY

In the present study, the terms `guild' and `functional type' will be used to refer to groups of functionally-related species. This corresponds to the concepts of both functional groups and (alpha) guilds, at least as they have been applied to plants. In general, `guilds' will refer to the specific species groups used in analyses, and major community subsets (e.g. the vascular plant guild); `functional type' will be used in a more informal and general sense, principally in discussion of community structure theory.

## 1.3 Relation between guilds and texture

Like texture, guilds are a way of characterising assemblages in terms of functional attributes of the species present. The difference is that texture is evaluated across all species in an assemblage, based on their characters, and is usually expressed as a continuous variable (such as the mean for a character), whereas the guild approach divides the assemblage into categories, usually on the basis (explicit or implicit) of species characters. Grouping species into guilds implies that there would be discontinuities (the guild boundaries) in the density of species in character space. However, this is rarely even tested for, and early evidence suggests that such discontinuities do not generally occur (Harris 1979; Lawton & Rallison 1979; Hawkins &

MacMahon 1989).

Both guilds and texture have been used as a basis for comparing different communities, for example to seek community-level convergence (e.g. using guilds: Terborgh & Robinson 1986; using texture: Wilson *et al.* 1994) or to document changes in community structure in different environments (e.g. using guilds: Cowling *et al.* 1994; using texture: Smith *et al.* 1995), but if guilds do not correspond to natural functional groupings, but rather, are arbitrarily-bounded segments along a continuum of functional variation (as seems more likely), then examination of guild patterns instead of texture will merely result in a loss of information, and therefore, a sacrifice of analytical power.

The aspects of species function that most influence community structure (such as competitive ability; Grime 1977) may be better represented by syndromes of intercorrelated characters (representing the results of adaptive trade-offs, or adaptation along multiple niche axes; see below) than by individual characters. In contrast to texture, which is usually expressed in terms of single species characters, assignment of species to guilds is generally based on several species characters, or on ecological, taxonomic or distributional features that would be correlated with a range of functional characters (see above). Guilds may therefore appear a more profitable approach to the investigation of community structure than texture. This logic is erroneous: just as multivariate techniques may be used to group species into guilds based on multiple characters, so they may be used to generate `scores' for individual species; multivariate texture for an assemblage. Multivariate texture has rarely been used in the past (but see Ricklefs and Travis 1980; Wiens 1991a) but is developed in the present study (Chapter 9).

Applications of guilds in which texture cannot be substituted include those in which a unit of biological organisation intermediate between the species and whole community (or species pool) is required. In studies of community structure it may be desirable to focus on community subsets in which interspecific interactions are concentrated, since species-mediated patterns might be obscured in the whole community or species pool, in which interactions are, on average, weaker (Gilpin & Diamond 1982, 1984; Bowers & Brown 1982). In global vegetation models it is convenient to `scale-up' from species to very generalised functional groups (e.g. `tropical evergreen trees,' `cool grass/shrub;' Prentice *et al.* 1992).

## 1.4 Community structure

The nature of ecological communities is a fundamental issue in ecology. Since Clements (1904), many have considered communities as integrated, possibly discrete entities with emergent structure and function shaped by species interactions and coevolution (e.g. Drake 1990). Like Gleason (1926) others have subscribed to the view that species are distributed in an `individualistic' way in response to environmental gradients, so that `communities' observed within a habitat or area will merely represent windows onto a continuum of compositional

variation (e.g. Austin & Smith 1989).

Although there have been many studies seeking evidence for species-mediated community structure (see below), the body of accumulated evidence is small, particularly so for plant communities (Wilson 1991). The importance of interactions in structuring communities, and, indeed, the very existence of communities continues to be a subject for debate (Wilson 1991, 1994; Keddy 1993; Palmer & White 1994).

So long as the existence and nature of community structure remains unclear, it seems inappropriate to include emergent structure (or some equivalent concept) as a criterion in the definition of the community. In the present study, a reductionist definition based on that proposed by Palmer & White (1994) is adopted: a community comprises the living organisms (or some defined subset of them) present within an area or habitat. Most references to communities in this study will implicitly pertain to vascular plant communities.

## THE SPECIES NICHE

Following Hutchinson (1958) the niche of a species may be regarded as a probablistic mapping into *n*-dimensional abstract space, of its responses to *n* biotic and abiotic factors to which species respond differentially. Each species possesses a fundamental niche, comprising the range of conditions in which it can maintain a population in the absence of interference from other species. Nested within the fundamental niche is the realised niche, the conditions in which the species actually occurs, which Hutchinson (*op. cit.*) considered the outcome of interactions with other species competing for some of the same resources. A further distinction may be made between alpha or within-commmunity niches, and beta, `along gradient,' niches (Pickett & Bazzaz 1978). The axes that differentiate alpha niches will be resources, for which species can compete, while beta niches will be defined by environmental variables, for which there can be no competition.

## ASSEMBLY RULES

Competition is conventionally thought the most important interspecific interaction (Strong *et al.* 1984). Species whose fundamental niches overlap will compete for some of the same resources; if competition is sufficiently intense one species (the weaker competitor) will succumb to competitive exclusion (Gause 1934; Hardin 1960). The theory of species packing (Pianka 1975) implies that there will be a maximum degree of niche overlap — limiting similarity — at which coexistence is possible. Within an assemblage of interacting species, the result would be segregation of realised niches along ecological factor axes, in turn leading to a somewhat regular spacing (or `overdispersion') of niches in hyperspace (Pianka 1980), a form of community structure.

Other mechanisms may produce community structure. In seral vegetation the

establishment probability of certain species may be influenced by the presence (facilitation) or absence (inhibition) of species characteristic of an earlier successional stage (Connell & Slatyer 1977), producing either complementary or matching patterns in the temporal (patch scale) and spatial (landscape scale) distributions of the species concerned. Non-random patterns could also be produced by mutualistic or interdependent (e.g. predator-prey) relationships between species. In general such mechanisms would tend to promote coexistence of functionally dissimilar species with a low degree of niche overlap (Vallis 1978; Waser & Real 1979; Hunter & Aarssen 1988; Aguiar & Sala 1994).

The relative importance and even validity of the different mechanisms hypothesised to produce community structure is unclear (Wilson 1991, 1994; Keddy 1993), their action in different communities may be highly variable (Drake 1990), while different mechanisms may produce the same patterns (Colwell 1979). Consequently it is usually not possible to attribute observed patterns to specific mechanisms. Assembly rules (Diamond 1975; Drake 1990; Wilson 1991) describe the integrated effects of all mechanisms that constrain coexistence of species, or functional types of species, whether the mechanisms themselves are explicitly identified or not. Assembly rules may describe what particular combinations of species are possible, e.g. on islands (Diamond 1975), what functional types of species can (or must) co-occur (Fox & Brown 1993) or, more generally, may document non-randomness in the composition of communities, attributable to contraints on species cooccurrence (Wilson *et al.* 1995). Assembly rules represent a possible `emergent property' of communities: a detectable feature of a community not predictable from the attributes of its component species alone (Salt 1979).

Some (Keddy 1992; Weiher & Keddy 1995a,b) have included direct environmental constraints, i.e. restrictions on fundamental niche, in the definition of assembly rule, whereas the original assembly rules of Diamond (1975) were species-mediated constraints, restricting what combinations of realised niches are possible (see also Wilson 1991; Fox & Brown 1993). In the present study, only assembly rules resulting from species interactions are considered.

Assembly rules have been advocated as a key to predicting community characteristics or composition in the recent literature (Keddy 1992; Fox & Brown 1993; Weiher & Keddy 1995a,b), but such assembly rules would need to be: (1) of a general nature, applicable to more than one community and its component species; and (2) precisely defined, so that it can be formulated mathematically and incorporated in predictive models. No study to date has identified an assembly rule that satisfies both conditions.

The assembly rule concept has been invoked both to represent processes (the integrated effects all species-mediated mechanisms limiting community composition) and patterns (patterns, such as character overdispersion, arising from this process). In the present study, `assembly rules' is used as a term of convenience to refer to the sum of all processes leading to community structure.

## EVIDENCE FOR COMMUNITY STRUCTURE

Despite a wealth of theory, much of it building on the paradigm of competition-mediated niche structure established by Hutchinson, MacArthur and colleagues (Hutchinson 1958, 1959; MacArthur & Levins 1967; MacArthur & Wilson 1967; MacArthur 1972a; May & MacArthur 1972), empirical evidence for assembly rules generating community structure remains sparse (see, e.g., Simberloff 1982, 1984; Wilson 1991). The most important evidence available to date is outlined below.

### *Assembly rules in island biogeography*

Diamond (1975) coined the term `assembly rule' for non-random patterns in the distribution of bird species on islands. In particular, negative associations between species, leading to `checkerboarded' occurrence matrices, were considered evidence of competitive sorting, certain combinations being `forbidden' because of competitive exclusion among the species involved. Diamond's conclusions were questioned by Connor & Simberloff (1979) who found that the distribution of species among islands in Diamond & Marshall's (1977) data set for the New Hebrides (now Vanuatu) could not be distinguished statistically from that expected under a null model of random colonisation. Diamond & Gilpin (1982) rebutted this criticism, claiming that Connor & Simberloff's (1979) null model was excessively conservative, leading to an excess of type II statistical errors (spurious acceptance of the null hypothesis). These papers sowed the seeds for a controversy (Gilpin & Diamond 1982, 1984, 1987; Connor & Simberloff 1983, 1984; Wilson 1987; Roberts & Stone 1990; Stone & Roberts 1990, 1992; Manly 1995) that has left the status of Diamond's (1975) assembly rules in doubt. Others have sought evidence for checkerboarding and other assembly rules on islands, some claiming to find it (Schoener & Adler 1991) and others not (Wilson 1988; Wilson *et al.* 1992b). No island biogeographic assembly rules have been reported for plants.

### *Character overdispersion and niche segregation*

Since Hutchinson (1959) suggested that competition should produce a minimum viable difference in the body sizes of sympatric guild associates (birds and mammals) many have sought evidence of such differences in real communities, often claiming to find it (e.g. MacArthur 1971; Barbour 1973; May 1978). Data from 31 such studies were reanalysed by Simberloff & Boeklen (1981) against a null model drawing sizes from a uniform random distribution, showing that most claims of constant or minimum size ratios among competitors could not be supported, even at the generous tail probability level of 0.30. MacNally (1988) reanalysed some of the same data sets using a method that seeks departure from the expected distribution of body sizes given that

competitive displacement *does* occur, likewise finding little support for constant size ratios. It seems clear that overdispersion in animal body sizes due to competition represents an exception rather than a rule. (see also Tonkyn & Cole 1986; Pleasants 1994).

Studies of character overdispersion in plants have focused particularly on the phenology of species visited by the same pollinators or seed dispersers. Segregation of flowering or fruiting periods attributed to competition for an animal visitor resource has been identified in a number of studies (e.g. Snow 1965; Waser & Real 1979; Pleasants 1980; Thomson & Rusterholz 1982; Armbruster 1986; Ashton *et al.* 1988) although the conclusions of earlier studies which did not employ null model tests (e.g. Stiles 1977, 1979) are in doubt (Poole & Rathcke 1979; Rabinowitz *et al.* 1981; Fleming & Partridge 1984). Armbruster *et al.* (1994) showed using distinct evolutionary and ecological null models, that competition for pollinators had apparently produced significant (coevolution) or near-significant (ecological sorting) segregation of floral morphology among sympatric *Stylidium* species. Del Moral *et al.* (1985) found evidence of negative associations at the patch scale between morphologically-similar species in alpine grasslands, suggestive of contemporaneous competitive sorting. Cody (1986, 1991) showed segregation in growth form and leaf shape within various plant guilds, but supported only some observations with statistical tests.

*Complementary species ranges*

Complementary species ranges (species zonation) are suggestive of competition limiting the cooccurrence of species with similar requirements. Dale (1984) sought zonation of marine algae by looking for an excess of contiguities in upslope and downslope range boundaries along a water depth gradient. Among many transects, the proportion of contiguous boundaries was usually greater than the 50% expected (though significantly so for only a few transects), suggesting a moderate degree of habitat segregation.

*Niche limitation*

Limiting similarity among sympatric species would limit the number of niches (species) that can be packed into an environmentally-defined niche hypervolume. Over an environmentally homogenous area (representing one particular hypervolume) species richness per unit area should remain more constant than expected on a random basis: there should be niche limitation (Wilson *et al.* 1987). Significant niche limitation has been found in old fields (Palmer 1987), at a fine scale in lawn communities (Watkins & Wilson 1992) and in early-successional forest (Zobel *et al.* 1993).

*Guild proportionality*

As an extension of the concept of niche limitation, a community may be considered as comprising a number of regions (hypervolumes) in niche space, each occupied by the species of a different guild (MacArthur & Wilson 1967). Species packing in each hypervolume would limit the number of species that can co-occur in its respective guild. Comparing different communities in similar environments, the proportion of total species richness represented by each guild should be more constant than expected on a random basis: there would be guild proportionality (Wilson 1989). Significant guild proportionality has been demonstrated for the ground herb guild of temperate rainforest communities (Bycroft *et al.* 1993; Wilson *et al.* 1995) and for graminoid and forb guilds at the point scale in a lawn (Wilson & Roxburgh 1994). Fox & Brown (1993) identified a significant tendency for three functional groups of desert rodents to be represented by equal numbers of species in communities. This implies that there must be among-community proportionality in each of the three functional groups. Wilson (1995), however, has shown that significant departure from the null model used by Fox & Brown (*op. cit.*) (also used in a number of earlier papers) can occur even with randomised versions of the observed data, casting doubt on their finding.

In summary, there have been few unchallenged reports of assembly rules or non-random patterns in species co-occurrence that would reflect a major influence of species interactions on community structure. With the possible exception of niche differentiation among guild associates competing for the same pollinators, the paucity of evidence is particularly pronounced for plant communities.

One category of evidence for community structure was not included in the above discussion. It is community-level convergence, the primary focus of this study, and is discussed below.

## 1.5 Community-level convergence

The phenomenon of convergence in the characters of phylogenetically-unrelated species in similar, but disjunct, environments is well documented, non-controversial, and the underlying mechanism — evolutionary selection for optimal adaptations to the same environmental conditions — is well-understood (Orians & Solbrig 1977; Cody & Mooney 1978; Givnish 1984; Niemi 1985; Körner *et al.* 1989; Wiens 1989a). At the community level, we might expect many parallels in the characters of component species in similar environments, but this would not, of itself, represent community-level convergence. Community-level convergence would require the demonstration of similarity in the emergent properties of communities.

Species-level convergence implies that there are similar fundamental niches in similar environments. If overlap of fundamental niches is the primary basis for the operation of assembly rules (as justified above) it follows that similar assembly rules should operate in similar

environments, causing overdispersion of species niches in resource space. In two communities in similar environments, the distribution of realised niches (and statistics summarising the distribution, such as the mean) should be more similar than would be expected if there were no restrictions on how similar adjacent niches can be, i.e. if the niches were distributed at random (see Fig. 1.1). Such similarity, exceeding chance expectation, would represent community-level convergence. It would support the operation of assembly rules, and the validity of the underlying assumption that species interactions determine community structure.

In dissimilar environments, communities are likely to be dissimilar in their niche structure, whether assembly rules operate or not. This is because realised niches would be clustered about different means in different conditions, as illustrated in Fig. 1.2. Compared with `null' communities produced be reassignment of the observed niches to communities at random, the observed communities would be likely to exhibit `divergence,' a greater difference in their niche distributions than expected on a random basis.

How dissimilar the environments of different communities can be before convergence will no longer be detectable is dependent on a balance between the environmentally-imposed community mean and the limiting similarity between adjacent species along niche axes (which would vary in an unknown way along axes). Since these parameters can not be determined *a priori*, failure to detect convergence can always be attributed to unquantified environmental differences between the communities being compared, making the hypothesis of convergence difficult to falsify. This is a major reservation about community-level convergence as an approach to community structure (e.g. Barbour & Minnich 1990; Blondel 1991; Keeley 1992).

Convergence in niche structure could be detected by comparison of a number of measurable parameters, including species richness and community texture.

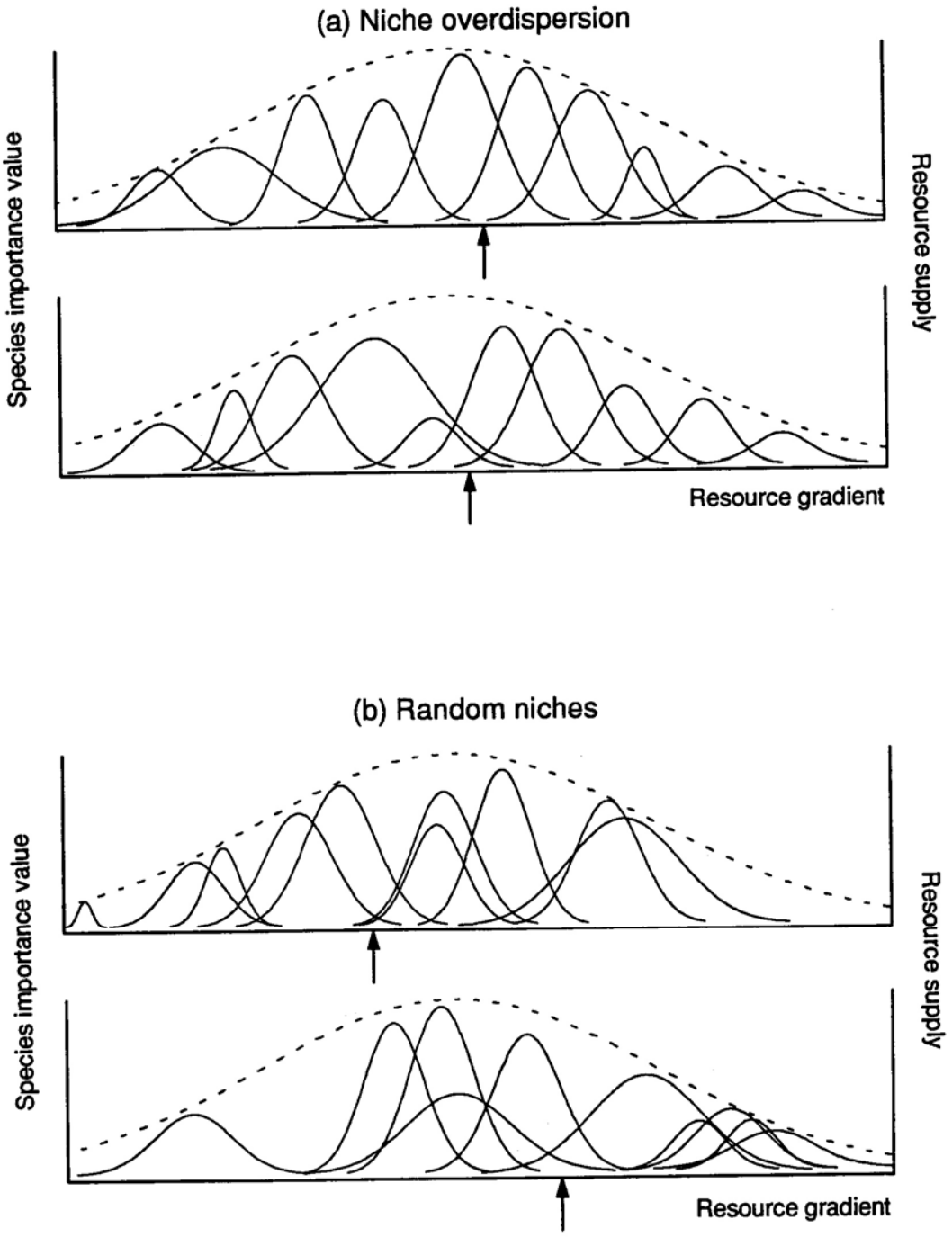



**Fig. 1.1** Convergence in niche structure between two communities in comparison to null expectation. If **(a)** assembly rules operate to produce overdispersion of species niches (solid lines) the mean niche (indicated by arrows) will be more similar between two communities with the same resource spectra (broken lines) compared with **(b)** expectation if niches are distributed at random in niche (resource) space.

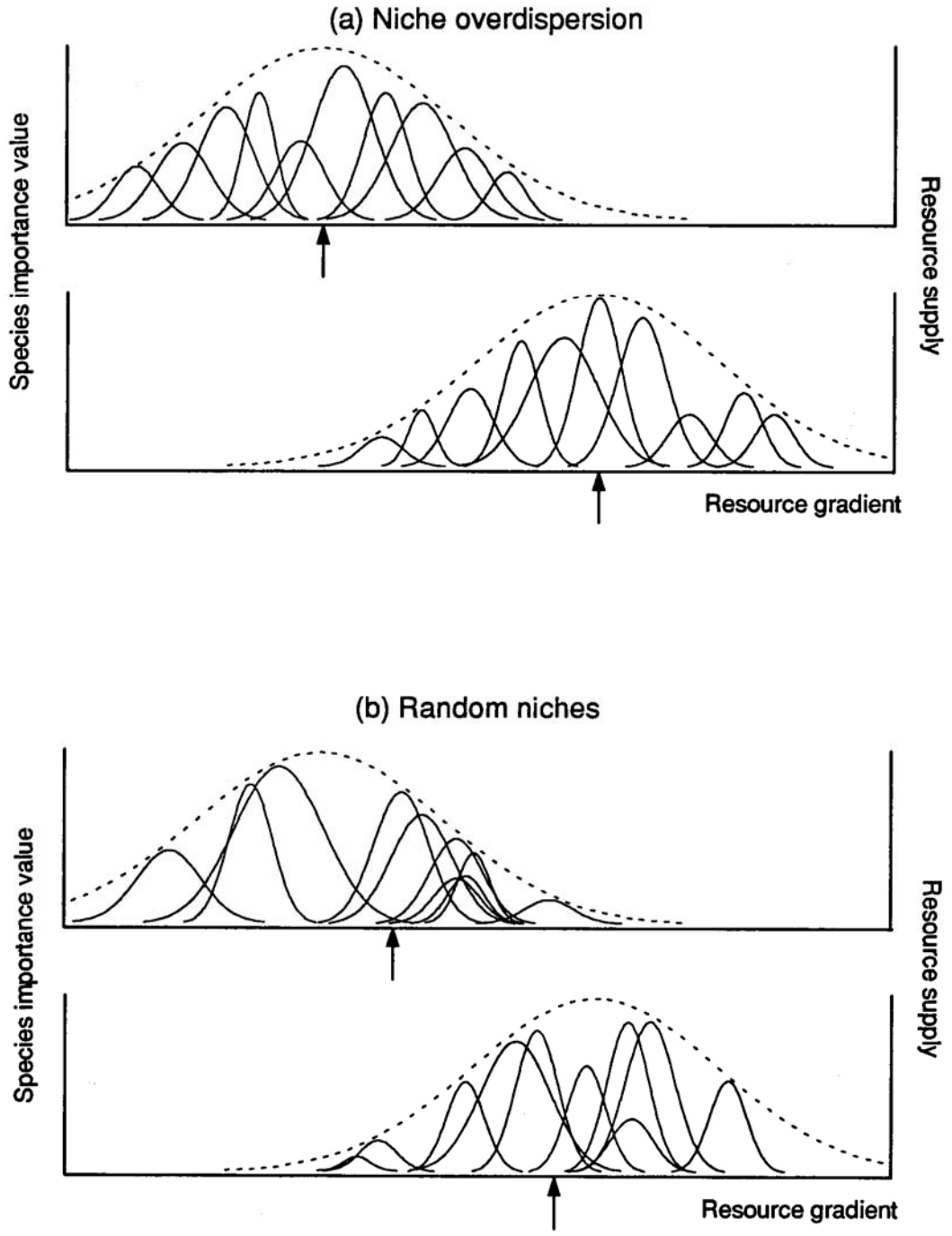



**Fig. 1.2** Non-convergence in niche structure between two communities in different environments (format as for Fig. 1.1). If different resource spectra apply in the two communities, mean niches may be as dissimilar between communities if **(a)** assembly rules produce niche overdispersion as **(b)** if niches are distributed randomly in resource space.

SPECIES RICHNESS CONVERGENCE

The concept of species packing (Pianka 1975) implies that species richness (the number of realised, alpha niches) will be limited by the dimensions of the total amount of available niche

space (the environmentally-imposed resource hypervolume) and the limiting similarity between adjacent niches in the niche space. In terms of a single limiting resource, maximum species richness is equal to the axis segment representing resources available in the environment of the community, divided by the mean limiting similarity, as illustrated in Fig. 1.3. In different communities in similar environments, the degree of species packing should be the same, resulting in convergent species richness[1].

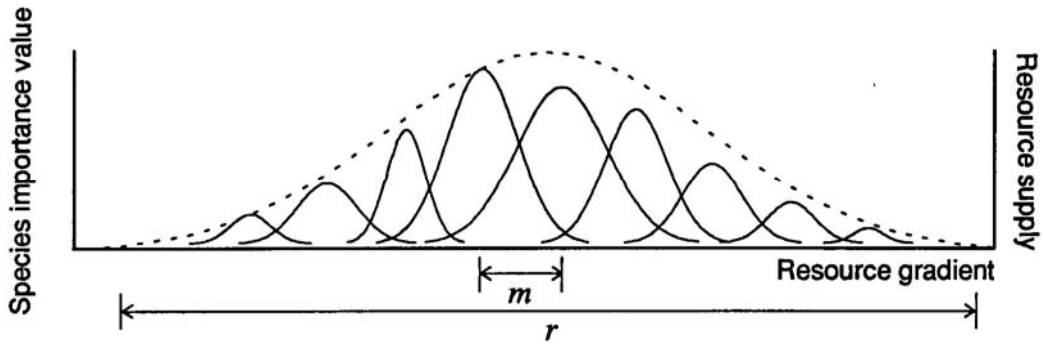



**Fig. 1.3** Species packing as a control on species richness (Format as for Fig. 1.1). If assembly rules restrict co-occurrence of similar species in communities, maximum species richness will be determined by the available resource space (*r*) divided by the mean limiting similarity (*m*) between species.

### TEXTURE CONVERGENCE

If species functional characters are substituted for niches, then the distribution of niches in resource space is replaced by texture, and a testable hypothesis is generated: community-level convergence has occurred if texture is more similar among the communities being compared, than expected on a random basis. The measure by which texture is compared in different communities could be a statistic summarising the distribution of species characters within communities (e.g. the mean: Schluter 1986; Smith *et al.* 1994 [see Appendix B]; Wilson *et al.* 1994; Chapter 6) or the distribution itself (Chapter 7).

### EVOLUTIONARY VERSUS ECOLOGICAL CONVERGENCE

In the preceding discussion, similarity in the emergent properties of communities (as reflected in

[1]The theory of species packing (Pianka 1975) implies that there should be convergence in species richness even in somewhat different environments, since a small shift in the environment would alter which species (or functional types) are present, without changing the number that can be accomodated.

non-random patterns in community species richness, texture and guild proportionality) has been termed convergence without explicit justification. Convergent objects are ones that become closer or more similar through space or time. Have `convergent' communities necessarily become more similar over time?

Some previous studies of community-level convergence were quite preoccupied with this question, seeking proof of evolutionary convergence in comparison to `ancestral communities' (Schluter 1986; Keeley 1992). In some cases, community-level convergence in species richness or texture was detected using valid statistical tests, but was referred to as `similarity,' because of uncertainty as to whether communities had become more similar *over evolutionary time* (Schluter 1986; Wiens 1989a, 1991a,b).

Significant similarity in emergent community properties need not be the product of mechanisms operating on an evolutionary time scale. The most parsimonious class of assembly rule would be based on ecological species sorting (Wilson *et al.* 1994; Smith *et al.* 1994). Species from the local pool dispersing into a patch will establish: (1) if their fundamental niches intersect the niche-space hypervolume corresponding to conditions at the site; that is, if their adaptations permit them to maintain a positive rate of population growth in the prevailing environment; and (2) if they are (a) sufficiently dissimilar from other species already present to avoid competitive exclusion, or (b) can displace similar species already present by causing them to succumb to competitive exclusion. As a community establishes in the patch, ecological species sorting will produce overdispersion of species niches and characters, the basis of community-level convergence, as developed above.

Ecological sorting will continue to operate after initial assembly of a community on an uncolonised site. Weak competitors will continue to invade but fail to establish due to exclusion by superior competitors with similar niches. Presumably there will be selective pressure upon similar species to diverge functionally, so as to enable sympatry, and thus enhance the geographic spread of their genes: they may undergo coevolutionary character displacement[2] (Connell 1980; Taper & Case 1992). Coevolutionary character displacement represents a conceptually more complex mechanism that could account for niche and character overdispersion, and provide a basis for community-level convergence.

It will not, then, be possible to determine, from observations of community structure at a single point in time, whether structure was produced by ecological species sorting alone, or by coevolutionary character displacement, integrating the effects of ecological sorting over evolutionary time (Figs. 1.4, 1.5). There is some doubt as to whether character displacement

[2]The term `character displacement' is used throughout this report in the sense of Taper & Case (1992): `the joint evolution of morphological character differences between competing species resulting from selection pressures created by the species interactions.' In this sense it refers to a process, rather than a pattern (of greater character variation among conspecifics in sympatry than in allopatry) in the sense of Connell (1980).

would be a general phenomenon in nature (Goodall 1966): the ecological amplitude of most species is sufficiently high that they come into contact with a variety of different species in different communities, with which they may share quite different parts of their fundamental niches. Any adjustment in the characters of species would at most be towards an optimum spacing among all its sympatric associates. Major character displacement along any particular niche axis seems unlikely.

In summary, significant similarity in the properties of communities could be a product of assembly rules operating over ecological time or, less certainly, evolutionary time. In either case there would be an average increase in similarity over time. The application of the `convergent' label to such communities is justified.

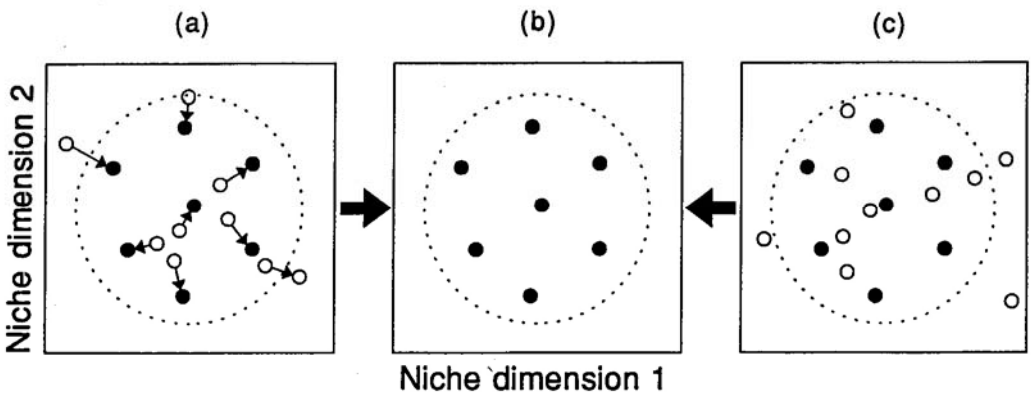



**Fig. 1.4** Two hypotheses to account for niche (or character) overdispersion in communities (two niche dimensions case). Under ecological species sorting **(c)** species from the local pool (circles) disperse onto a site, establishing only if they are adapted to the abiotic conditions (area enclosed by broken line) and sufficiently dissimilar from other species to avoid competitive exclusion. Species that satisfy both conditions (filled circles) are more regularly spaced in the niche space of the observed community **(b)** than would be expected by chance. Under coevolutionary character displacement **(a)** species that are too similar to coexist (open circles) experience selection for character divergence until coexistence is possible (filled circles).

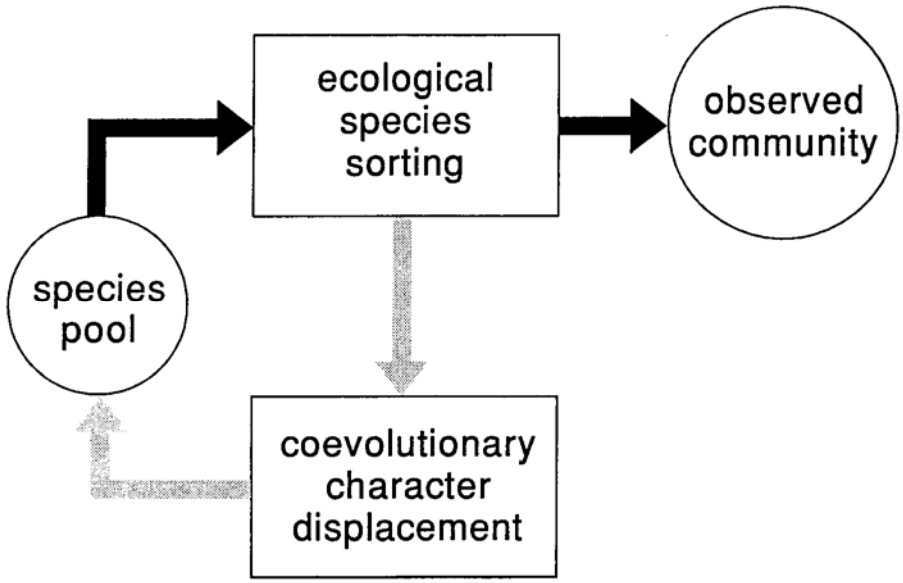



**Fig. 1.5** Relationship between ecological species sorting and coevolutionary character displacement in producing community structure. All observed communities are the result of ecological sorting from the species pool over ecological time. In evolutionary time, ecological sorting may impose selection for character displacement among functionally-similar species, thus modifying the species pool.

THE SPATIAL SCALE OF CONVERGENCE

All questions is ecology are relative to the scale at which they are asked (Wiens 1989b). Patterns produced by particular mechanisms may be apparent at some scales but not at others. Thus, for example, competing species may be negatively associated at the local scale (because overlap in their alpha niches is too high to permit coexistence) but positively associated at the regional scale (because their beta niches coincide) (Ricklefs 1987; Sherry & Holmes 1988). It has been suggested (Wiens 1989b) that controversy over the role of competition and coevolution in community assembly may be partly due to the questions having been explored at inappropriate scales.

Considerations of scale are particularly important in studies of plant community structure since plants, being non-motile in their vegetative form, interact primarily at the neighbourhood scale, comprising one plant and its immediate neighbours (Aarssen 1992). Interactions between many types of animals, by contrast, may take place over entire habitats. This means that the concept of diffuse competition in which all members of a guild affect each other simultaneously, producing the regular niche structure expected to result from competition (MacArthur 1972b), may not be readily applicable to plant communities (Aarssen 1992). The physical size of a neighbourhood is dependent on the stature of the individuals involved: for the canopy tree guild in *Nothofagus*-dominated forest, a 20 × 20 m quadrat would be expected to approximate a single neighbourhood; for the vascular epiphyte guild, a neighbourhood may comprise only a few $cm^2$.

Structure observed at the neighbourhood scale may be obscured at progressively higher sampling scales as patterns related to microenvironment, soil type, climate, disturbance history and biogeographic history become dominant.

The scale at which community structure and community-level convergence are sought has implications for both the types of mechanism involved, and the intensities of the patterns they would be expected to produce. In the present study, convergence was sought among communities at the local, regional and landmass scales. At the local scale, comparisons were between individual study sites (comprising several 20 × 20 m quadrats within a 100 × 200 m area of *Nothofagus*-dominated forest) within a radius of *c.* 60 km (a local area). Few barriers to dispersal would be expected within a local area, so local scale communities would be expected to share the same species pool. At the regional scale, comparisons were among communities characteristic of *different* regions. Regional-scale communities were either individual study sites (as described above), or comprised data pooled from several local-scale communities. Migration rates between regions might be finite but low in comparison to the local scale. Therefore, different regions within a broad biogeographic area (landmass) would share a common species pool, but evolution of regional ecotypes might also occur. Landmass-scale communities were pooled from several local- or regional-scale communities, and characterised *Nothofagus*-dominated forests for one of the four broad biogeographic areas included in the study: Tasmania, mainland Australia, New Zealand and South America. Vascular plant migration rates between landmasses would be very low, so each landmass-scale community can be regarded as having its own species pool (or several regional pools). Independent evolutionary histories would lead to different ecotypes and species on each landmass. Characteristics of each scale, and their relevance to the study of community-level convergence, are summarised in Table 1.1, and described in detail below.

While species-mediated community structure might be strongest at the neighbourhood scale, convergence may be difficult to detect at this scale, because the microenvironments perceived by individuals will be strongly affected by the shape, size and configuration of their neighbours as well as by microtopography. These factors will vary considerably between neighbourhoods, so the requirement of the convergence hypothesis, that the assemblages being compared should occur in closely similar environments, is unlikely to be met.

At the local scale, each community would comprise several (canopy tree) neighbourhoods. This means that microenvironmental differences between communities are likely to be less significant than at the neighbourhood scale: macroenvironmental parameters such as soil type and climate are more likely to distinguish communities. Macroenvironmental parameters are readily quantified, so communities with matching environments can be identified. Species interaction effects on community structure should still be apparent, although possibly less so than at the neighbourhood scale. Community composition would be determined by filtering of species from the local pool: in the absence of dispersal barriers, biogeography and

evolution could not be invoked to explain differences in composition between communities. Convergence between communities at the local scale would be the result of ecological species sorting operating to produce relatively similar niche structure in each community.

Environmental heterogeneity within regional-scale communities (if pooled from several local-scale communities) might tend to obscure community structure resulting from species interactions. Communities of neighbouring regions would share a largely common species pool, but barriers to dispersal, biogeographic history, and evolution of local ecotypes might also produce differences in composition. Convergence between regional-scale communities could be the result of ecological species sorting, coevolutionary character displacement or both types of process, producing similar niche structure in each community.

Landmass-scale communities were pooled from several regional-scale communities, and were intended to be representive of a comparable vegetation type (tall, evergreen *Nothofagus*-dominated temperate rainforest) on each landmass. Environmental heterogeneity among the component regional communities might tend to obscure community structure apparent at finer scales. There would certainly be barriers to dispersal between landmasses, resulting in different species pools. Mechanisms producing convergence between communities would almost certainly include coevolutionary character displacement, while ecological sorting from different species pools could also play a role.

**Table 1.1** Importance of species interactions and environmental variation in controlling assemblage (neighbourhood or community) composition, inter-assemblage differences in species pools, and mechanisms that would underlie convergence between assemblages at four spatial scales (see text).

| Characteristic | Scale of assemblage or comparison | | | |
|---|---|---|---|---|
| | Neighbourhood | Local | Region | Landmass |
| Expected influence of species interactions on composition | high | fairly high | moderate | possibly low |
| Expected influence of abiotic environmental variation on composition | very low | fairly low | moderate | possibly high |
| Differences in species pool between assemblages | none | none | possibly different ecotypes; possibly different species | probably different species; almost certainly different ecotypes |
| Mechanisms explaining convergence between assemblages | ecological sorting | ecological sorting | ecological sorting; possibly coevolutionary character displacement | coevolutionary character displacement; ecological sorting from different species pools |

Studies concerned with community-level convergence have been carried out in mediterranean-climate shrublands (Parsons & Moldenke 1975; Mooney *et al.* 1977; Cody *et al.* 1977; Cowling & Campbell 1980; Ricklefs and Travis 1980; Blondel *et al.* 1984), warm deserts (Orians & Solbrig 1977; Cody 1986, 1991; Wiens 1989a, 1991a,b), mangrove islands (Schluter 1990), carr wetlands (Wilson *et al.* 1994) and temperate rainforests (Smith *et al.* 1994). Schluter (1986) compared finch communities among a range of ecosystems from cold temperate desert to tropical rainforest. The generally equivocal results have led to a certain skepticism as to the utility of community-level convergence as an approach to community structure (Peet 1978; Blondel 1991; Ricklefs 1987), and to suggestions that the hypothesis of convergence may be non-testable (Barbour & Minnich 1990; Blondel *et al.* 1984; Keeley 1992).

Part of the problem has been the failure of many studies to apply statistical tests that would permit firm conclusions to be drawn. While quantitative methods and, more recently, rigorous statistical tests, have been applied to look for convergence of animal communities (Cody *et al.* 1977; Schluter 1986; Wiens 1989a, 1991a,b), investigation of the phenomenon for plant communities has generally been done by graphical or tabular comparisons of measured values (e.g. Mooney *et al.* 1977) in the absence of statistical tests.

Wilson *et al.* (1994) were the first to apply a null model randomisation approach (Crowley 1992) in a community convergence study: convergence in texture was sought between carr wetland communities in Britain and New Zealand. Smith *et al.* (1994) performed a comparable analysis to examine between-site convergence and divergence in texture within a local area. A null model is a protocol for the assembly of simulated `communities' under conditions in which the null hypothesis — an absence of assembly rules restricting the cooccurrence of functionally-similar species — is true. Although these studies detected little convergence, the use of an explicit null model permitted firm conclusions to be drawn with respect to each species character and site combination considered.

In the present study, community-level convergence is sought within a vegetation type common to four temperate regions of the southern hemisphere — *Nothofagus*-dominated temperate rainforest. This vegetation type constitutes a particularly suitable system in which to perform a study of this kind, for a number of reasons, discussed in the following section.

## 1.6 *Nothofagus*-dominated forests

Thirty-five species of *Nothofagus* (`southern beech') occur in Tasmania, the southeastern mainland of Australia, New Zealand, southern South America, New Caledonia and New Guinea. Four subgenera are recognised in the recently-revised taxonomy of the genus (Hill & Read 1991) of which one (*Brassospora*) is confined to the tropics (New Guinea and New Caledonia; 19

species) while the others occur only in the temperate zone: subspecies *Nothofagus* in South America (5 species); *Fuscospora* in New Zealand, South America and Tasmania (5 species); and *Lophozonia* in New Zealand, Tasmania and mainland Australia (6 species). *Nothofagus* is traditionally included the family Fagaceae, closely allied to Betulaceae in the order Fagales (Thorne 1983). A wealth of accumulated biogeographical and botanical data has led to proposals for the erection of a monogeneric family Nothofagaceae, possibly more closely allied to Betulaceae than Fagaceae (Romero 1986; Nixon 1989; Hill 1992).

Temperate *Nothofagus* forests are considered to represent a remnant of a formerly more widespread southern hemisphere vegetation type which has decreased in extent following cooling of southern climates in the Tertiary and Quaternary (Hill 1992). *Nothofagus* may have evolved in high southern latitudes in the southern supercontinent of Gondwana in the late Cretaceous (Hill 1992), or have migrated there following a middle Cretaceous origin in tropical areas of Western Gondwanaland (Romero 1986). Prior to the break-up of Gondwana, which began in the early Tertiary, *Nothofagus* had diversified and was present in mixed rainforest with subtropical and temperate elements then widespread in southern Australia, New Zealand, southern South America and Antarctica (Romero 1986). Apart from a possible rare transoceanic dispersal event from Australia to New Zealand during the Tertiary (Martin & Dowd 1988), there has probably been no genetic interchange of *Nothofagus* among the Gondwana fragments since the early Tertiary.

Extant species include evergreen and deciduous forest canopy trees, as well as shrubs and small trees occurring in subalpine or subantarctic scrub or vegetation of waterlogged, nutrient-deficient or semi-arid sites. In tall forests of South America, New Zealand, Tasmania and eastern Australia, *Nothofagus* typically occurs as a canopy tree 30-35 m in height with a diffuse, multi-tiered crown. Stature decreases with altitude, subalpine species sometimes adopting a stunted krummholz form above treeline (Ash 1982). Disturbance appears to influence the ecology of many *Nothofagus* species. This is notably the case in South America where *Nothofagus* species dominating seral forest developed following earthquakes, landslides or volcanic eruptions may be completely replaced by more shade-tolerant species in the absence of further disturbance (Veblen *et al.* 1981). Many species show poor regeneration under their own canopy and exhibit `advance growth' or gap-phase life histories (Wardle 1970; June & Ogden 1975; Veblen 1979; Read & Hill 1985), although Tasmanian *N. cunninghamii* can regenerate continuously under its own canopy (Read & Hill 1985, 1988). *Nothofagus*-dominated forests are typically closed rainforests with relatively simple vertical structure and low vascular plant species richness (Wardle 1984). Almost pure *Nothofagus* stands are common, even in the tropics (Ash 1982).

The present study concerns itself only with tall forests dominated by evergreen species of *Nothofagus*. These communities represent ideal subjects for the study of community-level convergence for a number of reasons, as detailed below.

1. The extant communities are derived from an ancient Gondwanan vegetation type, have a very long evolutionary history, and so may be expected to have achieved some constancy in species composition and distribution. There is little floristic overlap at the species level between communities on different land masses, thus the criterion proposed in many convergence studies that communities being compared should be `independent' phylogenetically (e.g. Cody & Mooney 1978; Orians & Paine 1983; Schluter 1986), is met.
2. In most regions, anthropogenic modification of *Nothofagus* forests has been limited, and there are pristine lowland stands in all temperate regions. By contrast, mediterranean-climate ecosystems, which have long been a focus of convergence studies (e.g. Naveh 1967; Specht 1969; Cowling & Campbell 1980; Blondel *et al.* 1984; Cowling & Witkowski 1994), have invariably suffered direct or indirect impacts from the activities of man (Barbour & Minnich 1990). Human impacts on ecosystems would almost certainly modify community structure, and would tend to obscure any convergence that might have occurred naturally, or might artifically generate `convergence' as a result of common anthropogenic impacts.
3. Temperate-zone *Nothofagus* forests, though widespread and locally dominant, have a relatively restricted distribution with respect to climate, occupying a zone between the 10 °C and 20 °C mean temperature of the warmest month (MTWM) isotherms (Ash 1982) in all temperate regions in which they occur. With respect to soils, *Nothofagus* tends to be relatively tolerant of extremes of moisture and of a moderately low nutrient supply, but the most mesic and productive sites in many regions are typically occupied by other forest types (Wardle 1991; Veblen *et al.* 1983). *N. cunninghamii* and *N. moorei* in Australia tend to be associated with more fertile sites, although this is relative to a range of soil fertilities that are generally low by world standards (Beadle 1981). Structurally, *Nothofagus* forests are similar wherever they occur, with simple vertical structure and relatively low vascular plant species richness. Close environmental matching between communities is an important assumption of the convergence hypothesis (see above), and the restricted distribution of *Nothofagus* communities along climatic gradients would help to ensure that this assumption is met.

## 1.7 Null models for hypothesis-testing in community ecology

In the present study, hypotheses were addressed by comparing an observed pattern of interest against patterns generated by a stochastic null model, simulating community assembly under conditions in which the hypothesis being addressed was false.

A null model (Harvey *et al.* 1983; Colwell & Winkler 1984) is a precise mathematical or algorithmic formulation of a null hypothesis. It represents a formula or set of rules for creating a

pattern expected under the null hypothesis, given a set of parameter values, normally taken from the real world. Null models are used in conjunction with permutation or resampling methods (Crowley 1992) to establish the significance of departure of an observed pattern from expectation under the null hypothesis.

Studies in community ecology generally seek structure in an observed data set, consistent with expectations of competition theory. For example, in occurrence data for bird species on islands, a tendency for certain species not to co-occur (negative association) might be consistent with the competition hypothesis (e.g. Diamond 1975). The alternative null hypothesis would be that bird species are distributed among islands without regard to the other species present. A null model based on the null hypothesis would describe a stochastic procedure for assigning species to islands, given certain features of the original data such as the number of species in the pool, the number of species on each island and the number of islands on which each species occurs (Connor & Simberloff 1979). Data sets generated using the null model are compared with the data observed to determine whether some pattern of interest (for example, the proportion of negative associations) is more extreme in the observed data. This pattern is quantified by a test statistic. Over many null model comparisons, the proportion of comparisons for which the value of the test statistic, calculated for the observed data, is more extreme than its value when calculated for the null model data, may be determined. This proportion (multiplied by 2 in the case of a two-tailed test) is the probability that a pattern as extreme as that observed could have arisen if the null hypothesis were true: it is the significance of departure from the null hypothesis. For example, if there are more negative associations in the observed data compared with all but 1 percent of null model data sets (and assuming a one-tailed test) there is significant ($P$=0.01) departure from the null model, and the competition hypothesis is supported.

Null model approaches have the advantage that the null hypothesis must be stated precisely, framed in terms of specific assumptions about the process being modelled. Whether or not a model is deemed `reasonable' in terms of the processes being simulated (e.g. migration) (Colwell & Winkler 1984) results obtained from its application can be clearly interpreted in the light of the model's assumptions. In contrast to traditional parametric approaches to hypothesis testing, which make complicated assumptions as to the underlying distribution from which data are drawn, null model-based tests generally permute or resample from the observed data (or a distribution derived from them), and so are free of any such assumptions (Crowley 1992).

Null model approaches have become standard in community ecology since Connor & Simberloff (1979) showed that the structure of occurrence data for birds in the New Hebrides could not be distinguished from that obtained under their null model of random migration, in contrast to claims that assembly rules were operating (Diamond 1975). Null models have been applied to search for assembly rules for species cooccurrences (Connor & Simberloff 1979; Wilson 1987, 1988; Roberts & Stone 1990; Wilson *et al.* 1992b; Manly 1995), constant or minimum body size ratios among sympatric species (Strong *et al.* 1979; Simberloff & Boeklen

1981; Tonkyn & Cole 1986), niche segregation in plants competing for animal-visitor resources (Poole & Rathcke 1979; Pleasants 1980; Cole 1981; Gleeson 1981; Thomson & Rusterholz 1982; Fleming & Partridge 1984; Armbruster 1986; Ashton *et al.* 1988; Armbruster *et al.* 1994), complementary species ranges (Dale 1984), niche limitation (Wilson *et al.* 1987; Watkins & Wilson 1992; Bycroft *et al.* 1993), guild proportionality (Wilson 1989, Bycroft *et al.* 1993; Fox & Brown 1993; Wilson & Roxburgh 1994; Wilson *et al.* 1995) and community-level convergence (Smith *et al.* 1994; Wilson *et al.* 1994).

Despite the advantages of null models, their application in community ecology has been criticised on the grounds that they are unduly conservative, giving rise to an excess of type II errors (inappropriate acceptance of the null hypothesis) and that their use is consistent with an acceptance that `randomness' has a logical primacy over `structure' in communities (Diamond & Gilpin 1982; Gilpin & Diamond 1982, 1984). For example, Gilpin & Diamond (1982, 1984) have claimed that the null model by which Connor & Simberloff (1979) sought evidence for competitive structuring of bird and bat assemblages on islands preserved too much of the structure of the observed data, resulting in a failure to reject the null hypothesis unless the effects of competition had been particularly strong (the `Narcissus effect' of Colwell & Winkler [1984]). The suggestion that non-rejection of the null hypothesis is equivalent to an acceptance that communities are assembled at random ignores the nature of the null hypothesis, which is a statistical construct and does not represent a theory to be proven: only when the null hypothesis is rejected can any valid conclusions be drawn.

## 1.8 Aims and approach of this study

The underlying hypothesis to be addressed in this study is that there are assembly rules that restrict the co-occurrence of functionally-similar species, producing community structure. Support for this general hypothesis is sought within a community type — tall, evergreen *Nothofagus*-dominated temperate rainforest — which has a number of practical and theoretical advantages for a study of this kind (Section 1.6). The overall hypothesis is addressed by seeking evidence for three types of pattern that might be expected as an outcome of the operation of assembly rules: community-level convergence in species richness; convergence in texture; and character overdispersion within communities.

The study is based on data collected at 17 sites occupied by tall evergreen *Nothofagus*-dominated forest. These sites are representative of the extant temperate distribution of this community type, encompassing four landmasses: Tasmania, mainland Australia, New Zealand and South America.

Communities were characterised by their vascular plant species richness and by texture — community-wide spectra of species characters. Texture was evaluated in terms of 13 species characters, primarily concerning the structure and function of photosynthetic units (PSUs, i.e.

leaves or their functional equivalents in certain species). PSUs are the primary above-ground functional organs of plants and so their characters would be expected to reflect evolutionary outcomes of interactions both with the abiotic environment, and with other individuals and species (Givnish 1987). This means that the texture of a community, expressed in terms of PSU characters of its component species, should be related to the niche structure of the community (Smith *et al.* 1994, 1995; Wilson *et al.* 1994). If assembly rules apply, restricting niche overlap and causing a more regular spacing of species in niche space than expected by chance, their effects should be discernable in community texture.

Texture patterns were examined both in terms of individual variates (characters) and factor analysis-derived factors, representing shared variation among them. Derived texture factors may represent better proxy variables for niche axes than individual characters because the shared character variation they summarise might correspond to variation in some underlying parameter influencing community structure (e.g. a limited resource for which there is competition among species).

All hypotheses were addressed by means of null model-based tests, comparing observed patterns of interest against patterns generated by stochastic null models, simulating community assembly in the absence of assembly rules. The null model approach was chosen in preference to traditional parametric methods, because of the greater mathematical and logical flexibility it afforded; because null model tests are free of restrictive assumptions as to the underlying distributions from which data are drawn; and because the explicit formulation of null hypotheses permitted results to be interpreted more clearly. Convergence between communities in species richness could not be sought directly using the data collected by this study. Rather, a bootstrap-based `analysis of variance' method was used to address the hypothesis that communities were more dissimilar in species richness than expected when observed quadrat richness values were distributed among communities at random, i.e. that there was divergence in species richness. If significant divergence in species richness was not detected, this was taken as preliminary evidence that convergence in species richness might have occurred (c.f. Wiens 1991a).

Texture convergence was sought by comparing observed variation in texture among communities to the variation expected under a null model in which species (or, more precisely, their observed characters) were distributed among communities at random. The null model was thus an implementation of the null hypothesis that there are no restrictions on how similar species niches (and characters correlated with niches) may be for the species to occur in sympatry. In separate tests, community texture was characterised as the community wide mean, as in previous studies (Schluter 1986; Wiens 1991a,b; Smith *et al.* 1994; Wilson *et al.* 1994), as the community-wide distribution, and as the `mean-adjusted distribution.' Comparing communities in terms of texture distributions has the advantage that none of the available character information is sacrificed (in contrast to comparisons based on a statistic summarising the distribution, such as

the mean). This could be associated with an increase in both the power and rigour of the null model test. Tests comparing mean-adjusted texture distributions (i.e. with species values adjusted arithmetically to give a constant mean in each community) were intended to focus on the component of character variation that might be primarily affected by assembly rules (the shape of the texture distribution), whilst ignoring the component primarily related to the abiotic environment (the absolute value or mean). Comparisons of mean-adjusted texture were thus intended to overcome tendencies towards `divergence' resulting from environmental differences between communities, a problem common to many studies of community-level convergence in the past (Orians & Solbrig 1977; Blondel *et al.* 1984; Barbour & Minnich 1990; Blondel 1991; Wiens 1991a).

Tests for character overdispersion asked whether the characters of species from within a community or guild were more regularly spaced along character (and therefore, potentially, niche) axes than expected under a null model of community assembly in the absence of assembly rules. Null data were drawn from a kernel density estimate of the distribution of the observed data (Silverman 1981). This is a smooth distribution approximating the shape of a frequency histogram of the observed data: it is an approximation of the underlying distribution from which the observed data are `drawn' by adaptation, phylogenetic constraints, stochastic processes and, possibly, assembly rules. The kernel function approach represents an advancement on previous studies of character overdispersion, in which null character distributions were typically drawn from the biologically-meaningless uniform distribution (Poole & Rathcke 1979; Pleasants 1980; Simberloff & Boecklen 1981), a practice that can lead to excesses of both type I and type II errors (Schoener 1984; Tonkyn & Cole 1986).

All questions were addressed at three scales — the local, regional and landmass scales — at which different patterns are likely, and different mechanisms are expected to be important in producing community structure (Ricklefs 1987; Wiens 1989b). Texture convergence and character overdispersion were also sought within height guilds, comprising all species `functionally present' within arbitrarily-bounded strata in the vertical forest structure. Species interactions are expected to be more pronounced within guilds than among them, suggesting that community structure might also be stronger at the guild scale, compared with the scale of the whole community (Pianka 1980). Searching for evidence of assembly rules within guilds may thus avoid the `dilution effect' of Gilpin & Diamond (1982, 1984), whereby structure apparent at the guild level can be obscured when `irrelevant' data from other guilds are included in the same analysis.

The hypotheses addressed in this study constitute a hierarchy (Fig. 1.6) in which specific working hypotheses (e.g. `communities A and B are convergent in the texture mean of PSU area') are tested to evaluate higher-order hypotheses (e.g. `*Nothofagus*-dominated communities exhibit community-level convergence') which, in turn, reflect on the underlying hypothesis that there are assembly rules, based on species interactions, that can produce community structure.

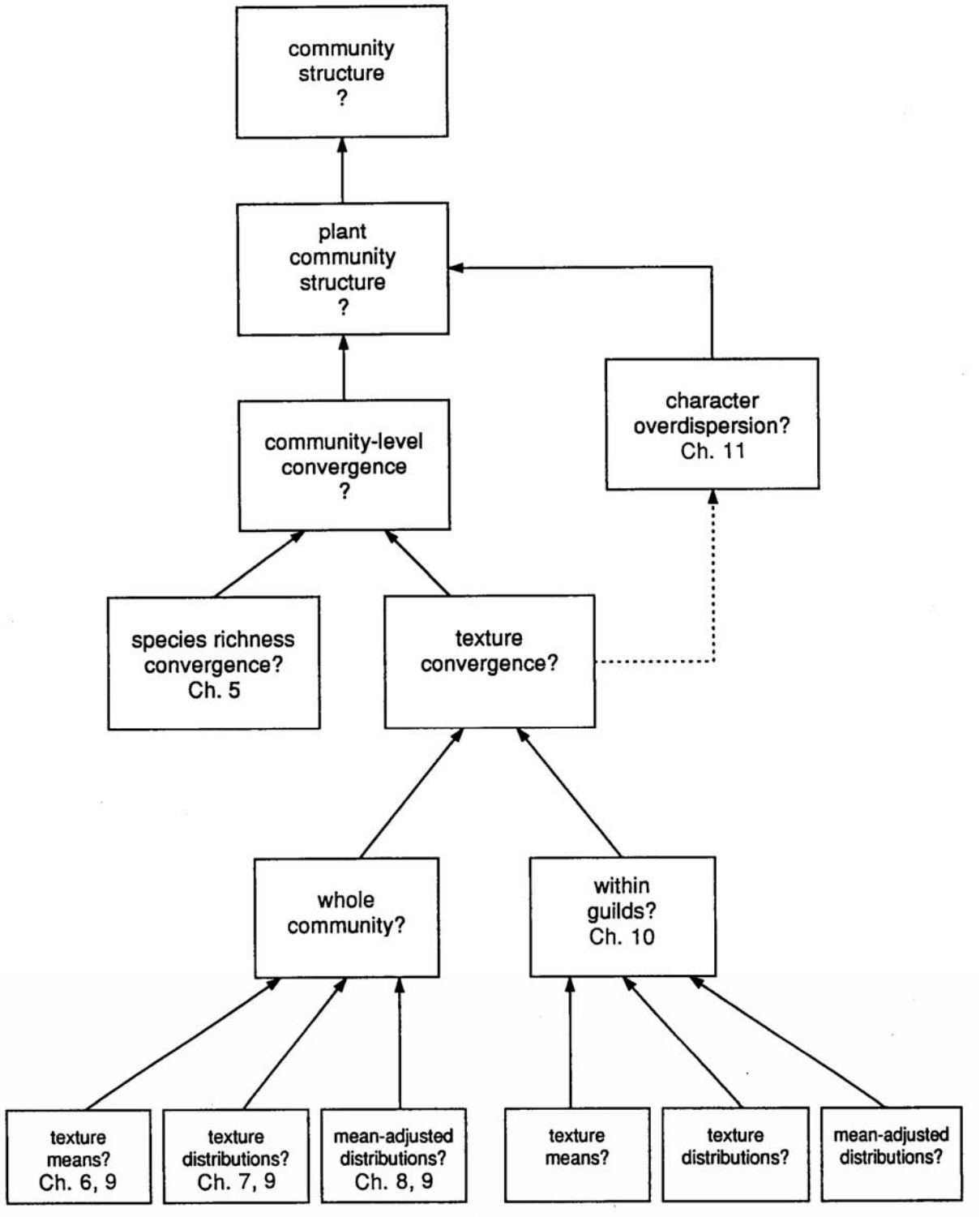



**Fig. 1.6** The hierarchy of hypotheses addressed in this study (see text), with references to relevant chapters.

# 2. Methodology for data collection

## 2.1 Introduction

In this chapter, the methodology adopted for the collection of data is described and justified. Under the heading `Rationale,' criteria for the choice of study sites are outlined. Parameters of a data set suitable for addressing the hypotheses proposed in Chapter 1 are developed with regard to practical constraints on sampling and laboratory measurement. Under the heading 'Methods,' procedures adopted for the selection of study sites, evaluation of site environmental parameters and collection and processing of species texture data are described.

## 2.2 Rationale

### 2.2.1 Site criteria

For the investigation of community-level convergence it is important that communities from similar environments be compared (see Chapter 1).

*Nothofagus* has a relatively restricted distribution with respect to major climate and soil factors. Disregarding alpine and subalpine communities, temperate-zone *Nothofagus*-dominated forests all occur within the `cool temperate or upper montane' bioclimatic zone, mean temperature of the warmest month (MTWM) *c.* 12.5-17.5 °C (Meurk 1984). The lower limit to rainfall is generally 600-1000 mm a year (Ash 1982) while competition with species dominating other forest types may impose an upper limit (Wardle 1970). In New Zealand and South America, *Nothofagus* tends to occur on soils that are relatively poor in major plant nutrients (Wardle 1984). In Tasmania and mainland Australia, *Nothofagus*-dominated forests may be associated with richer soils than other forest types, but nutrient levels are probably still comparable with those for *Nothofagus* forest in New Zealand and South America. *Nothofagus* typically grows on steeper slopes and is absent from permanently or seasonally waterlogged sites (Ash 1982).

In Australia and New Zealand, only evergreen *Nothofagus* species occur in lowland forest, but in South America there are deciduous forests dominated by *N. alpina, N. obliqua, N. pumilio* and (rarely as a forest dominant) *N. antarctica*. Deciduous trees impose substantial seasonal fluctuations in the light regime upon species growing beneath them, which would also have implications for temperature and water relations. There might be substantial microenvironmental spectra in deciduous and evergreen *Nothofagus*-dominated communities.

Tall, evergreen *Nothofagus*-dominated forest would thus represent an environmentally-restricted community type in which to seek community-level convergence. Fine control of environment would be achieved by choosing sites with similar climate and soils in different

regions. However, as temperature, rainfall and soil type vary largely independently, it might be difficult to control for all three of these parameters simultaneously. In general, climate is the most important feature controlling vegetation distribution, whereas within a climatic zone, other features such as soil type may be important (Woodward 1987). Therefore, the primary selection criterion for sites in this study was that they should have similar climates, while matching soil type (fertility) was a secondary criterion.

Climate will be affected by both latitude and altitude, temperature tending to decrease by approximately 1°C with a 150 m rise in altitude (Bureau of Meteorology 1975) and with latitude. The seasonal cycle of day-length also varies with latitude. Ideally, latitude should be standardised. Mainland Australian *Nothofagus moorei* forests occur at significantly lower latitudes than in the other temperate regions, but are restricted to high altitudes: temperatures, annual rainfall and dry season rainfall are comparable with other *Nothofagus* communities, for example, in Tasmania (Beadle 1981).

Aspect and slope have a pronounced effect on community composition and structure. North-facing slopes (in the southern hemisphere) receive more incident radiation than south-facing slopes and tend to be drier and warmer. Slope can influence water runoff, soil depth, and disturbance regimes. Shading effects of topography in narrow, steep-sided valleys can cause marked changes in light availability and temperature on a daily or seasonal basis. Restricting sites to shallow slopes would not only control the factors associated with slope, but would tend to eliminate major effects of aspect and topography as well.

In summary, close matching of the environments of different communities would be achieved if sampling were restricted to tall, evergreen *Nothofagus*-dominated forests with similar climates and, if possible, soils. Close matching would be further facilitated by standardising latitude, and choosing sites with shallow slopes.

### 2.2.2 Sampling data

To address the hypotheses of community structure proposed in Chapter 1, it is necessary to record several types of features of each community and its environment. Community-level convergence is sought in species richness and texture. A measure of species abundance is needed as a basis for weighting species in analyses. A record of the vertical structure of each community would allow analyses to focus on community subsets (vertical strata) within which species interactions might be concentrated (Wilson 1989; Pianka 1980). Finally, data are required to characterise features of the environment that might influence species responses, the operation of assembly rules and the likelihood of convergence between different communities.

Records of the number of species in each community are required to evaluate the hypothesis of community-level convergence in species richness. Comparisons are meaningful only when species richness is expressed with respect to the same sampling area (quadrat size) in different communities. This is because species richness increases in a non-linear way with area, and species-area curves can be different in different communities (Connor & McCoy 1979; Buys *et al.* 1994). For some statistical analysis, replicate data from within each community are required. Adequate degrees of freedom should be provided by sampling within five quadrats at each site.

### TEXTURE

The texture of a community is composed of a virtually infinite number of species characters. An optimum data set for the investigation of community structure will comprise characters that are:

1. relatively easy to measure. If measurements of one sample can be made relatively quickly, more samples can be measured in a given period of time. This permits evaluation both of more characters, and more replicate samples for each character.
2. of *a priori* functional importance. Only functionally important characters are likely to reflect niche distribution patterns, the underlying patterns being tested.

Leaf characters are an obvious choice: leaves constitute the primary site of photosynthesis, and their structure and function have implications for gas exchange, water potential, nutrient and energy allocation, whole-plant architecture and growth, and interactions with other organisms (Givnish 1987). Consequently leaves (and their functional equivalents) would be subject to strong selection regimes and should closely reflect evolutionary outcomes of interactions both with the abiotic environment, and with other individuals and species. Phylogenetic history may influence the way characters evolve, occasionally producing different solutions to the same adaptive problems in different species. However, assuming that natural selection leads towards optimal form and function in relation to habitat factors, then for most species, morphology and physiology will reflect niche (Parkhurst & Loucks 1972).

Some plant species possess photosynthetic organs functionally equivalent to but not homologous with the typical angiosperm simple leaf (e.g. of *Nothofagus* spp.). Such organs could include leaflets, phyllodes, pinnae etc. in different species. To enable leaf characters of a range of species to be summed and compared meaningfully, measurements were applied to functionally-equivalent photosynthetic organs on different species. The general term `photosynthetic unit' (PSU) has been applied in previous studies to such functional `leaves' (Wilson *et al.* 1994; Smith *et al.* 1994). In the present study, the PSU is defined as the minimum mobile photosynthetic structure, i.e. the smallest unit for which some independent setting of

position and angle (e.g. to optimise light reception) is apparent. In the present study, all references to `leaves' will implicitly pertain to PSUs unless a more restricted meaning is implied by the context in which the reference is made.

For many leaf characters, patterns of variation in relation to the environment have been documented. The existence of correlations between characters and environmental parameters attests to their functional significance, and many such relationships have been more closely investigated and underlying mechanisms identified. Although variation of characters with environmental parameters suggests a correlation with beta (gradient) niches, rather than alpha (resource) niches, which are of greater interest in this study, these two types of niches are related, especially for plants. For example, in the above-ground vertical structure of a forest there will be correlated gradients in several environmental (beta; e.g. temperature) and resource (alpha; e.g. light) gradients. Variation in a character (e.g. leaf specific weight) with height may (or may not) be fundamentally due to adaptation or plastic responses to only a subset of these gradients, but it may be a useful predictor for all of them.

Characters that satisfy criterion (2) above, and some functional relationships that have been hypothesised or demonstrated for them, are described below.

1. *Leaf size and shape* influence gas exchange and heat load through their effect on the thickness of the boundary layer of air of reduced velocity adjacent to the leaf surface (Taylor 1972; Givnish & Vermeij 1976; Grace 1977). Longer leaves of a given area will attract a narrower boundary layer. Similarly, lobation may significantly reduce boundary layer thickness with only a minor reduction in leaf area (Taylor 1972). Both among and within species, leaf size (area and width) tends to increase with increasing moisture and nutrient availability, and decrease with increasing irradiance (Givnish 1987). Positive relationships between mean leaf area and temperature among communities have been detected in temperate and tropical rainforests (Christophel & Greenwood 1989; Mackey 1993; Jordan & Hill 1994). There is evidence that small leaves may be advantageous in montane rainforests where reductions in root permeability at low soil temperatures can lead to physiological drought (Greller & Balasubramaniam 1988), while Woodward (1987) has suggested that mechanisms that provide protection against chilling and freezing injury to cell membranes may favour small leaves in cold climates.
2. *Leaf thickness* may be influenced by other aspects of leaf structure including mesophyll air space volume, cell size, the number of palisade cell layers, sclerophylly and succulence, which may reflect trade-offs in gas exchange, mechanical support and responses to herbivory (Björkman 1981; Gulmon & Chu 1981; Bongers & Popma 1988; Witkowski & Lamont 1991). Species tend to have thicker leaves in drier, nutrient-poorer and sunnier conditions (Loveless 1961, 1962; Beadle 1966; Grubb 1977; Medina 1984; Givnish 1987; Bongers & Popma 1988). A negative relationship between leaf thickness and nutrient availability is part

of a syndrome that has been labelled `oligotrophic xeromorphism' (Grubb 1977), which may arise through the optimisation of leaf morphology in the face of low plant nutrient levels and the energetic costs of absorbing scarce nutrients (Givnish 1984).

3. *Leaf succulence* (relative water content) may reflect osmoregulation mechanisms in plants of saline habitats (Kramer 1983) but more generally would be expected to reflect soil moisture status and humidity.
4. *Leaf specific weight* (SLW), the ratio of dry weight to area, reflects both leaf structure and photosynthetic capacity (Field & Mooney 1986) and can be a component of mathematical formulations of relative growth rate (Björkman 1981). It has been recommended as a character that may integrate the effects of canopy structure and light environment on leaf photosynthesis (Ellsworth & Reich 1993). Leaf specific weight tends to increase with irradiance and decrease with moisture and nutrient availability. It may also vary with temperature, herbivory and concentrations of atmospheric pollutants (Witkowski & Lamont 1991). A high leaf specific weight is characteristic of oligotrophic xeromorphy (see above).
5. *Leaf inclination* has implications for temperature load and light reception and may reflect leaf mechanical structure. Leaves tend to be more inclined from the horizontal at higher light intensities and lower moisture and nutrient availabilities (Sobrado & Medina 1980; Medina 1984; Givnish 1984; Hollinger 1989; Herbert & Nilson 1991). A tendency, both within and among species, and even on a single individual, for leaves to be more inclined in sunnier conditions has been explained as the result of an energetic trade-off of light reception against leaf thermal and gas exchange budgets (Givnish 1984; Hollinger 1989; Herbert & Nilson 1991).
6. *Leaf longevity* reflects a trade-off between two strategies for growth: production of `cheap' leaves which assimilate much carbon over a short period, permitting rapid growth, e.g. into light gaps or to the forest canopy; and production of more robust leaves, which photosynthesise at lower rates, but over an extended life-span (Reich *et al.* 1991). Longevity is associated with numerous leaf characters including specific weight, stomatal conductance, nitrogen and phosphorus content, net photosynthesis and support fraction (Reich *et al.* 1992).
7. *Support fraction*, is the ratio of non-leaf to total dry weight in terminal shoots. Support fraction is high in some species having divaricating stem architecture (Wilson *et al.* 1994), which is sometimes associated with long internodes and reductions in the size and number of leaves. Many understorey shrubs and juvenile trees in New Zealand exhibit divarication, which has been interpreted as an adaptation against herbivory by recently-extinct rattites (Greenwood & Atkinson 1977). Support fraction also reflects growth strategy, being correlated with leaf longevity (Reich *et al.* 1992).
8. *Stomatal density* on the abaxial surface is an important parameter governing gas exchange characteristics of leaves. Significant differences in stomatal density have been found among forest species differing in their regeneration ecology (Popma *et al.* 1992) and within species,

between sun and shade leaves (Bongers & Popma 1988).

9. *Mesophyll air space volume* influences diffusion of carbon dioxide from stomata to the sites of photosynthesis. It may limit photosynthetic rates in $C_3$ plants (Parkhurst 1986).
10. *Stomatal conductance* is a focus of the functional trade-off between carbon dioxide uptake and water loss. Stomatal conductance increases with increasing moisture availability and humidity (Givnish 1987), and with irradiance until heat load and/or leaf water potential become limiting (Cowan 1982, 1986). It is generally correlated with photosynthetic capacity (Field & Mooney 1986).
11. *Leaf absorptance* of photosynthetically-active radiation (PAR; 400-700 nm wavelength) has been shown to be related to leaf temperature and transpiration rate in plants of xeric environments (Ehleringer 1981) and to nitrogen content and photosynthetic capacity (Hollinger 1992).
12. *Mesophyll photosynthetic capacity* is the photosynthetic rate achieved under optimal conditions of temperature, humidity and carbon dioxide availability, and at saturating light intensity. Photosynthetic capacity tends to increase with increasing moisture and nutrient availability, and with irradiance (Björkman 1981; Ellsworth & Reich 1993). It is correlated with several other characters, including nitrogen content, stomatal conductance and (negatively) leaf specific weight (Reich & Walters 1994; Field & Mooney 1986; Evans 1989).
13. *Light compensation point*, i.e. the PAR level at which $CO_2$ production due to respiration balances photosynthesis, varies with photosynthetic capacity (Björkman 1981), tending to be lower in shade than in sun-associated plants, as well as in shade versus sun leaves of the same species or individuals (Bannister 1976).
14. *Leaf nitrogen and phosphorus content* are correlated with mesophyll photosynthetic capacity in $C_3$ plants (Field & Mooney 1986; Reich *et al.* 1991). Leaf nitrogen expressed on a dry weight basis has been shown to have utility as a proxy measure of photosynthetic capacity across many species (Field & Mooney 1986). This is probably a result of limitation of photosynthetic capacity by thylakoid and Calvin cycle proteins, which make up the majority of leaf nitrogen (Evans 1989).
15. *Leaf total chlorophyll content* is correlated with thylakoid nitrogen and leaf absorptance to PAR (Björkman 1981). Total chlorophyll is, however, a poor predictor of photosynthetic capacity. This is because thylakoid nitrogen declines as a proportion of total nitrogen in more sunlit, more fertile and moister environments (Evans 1989).
16. *Leaf chlorophyll* a/b *ratio* tends to decrease with irradiance (Boardman 1977; Björkman 1981; Chow *et al.* 1991; Dale & Causton 1992). This relation remains stable among different sun species, or shade species, and independent of other environmental factors, although different levels of response may exist between sun and shade species (Dale & Causton 1992).

17. *Modular hierarchy* is the number of above-ground hierarchical levels that characterise species architecture. For example, many grasses and graminoids consist of tussocks comprising several tillers, in turn divided into a number of leaves — a modular hierarchy of 3. Modular hierarchy has been recommended as a functional character which provides a link between the ultimate photosynthetic organs (leafs, leaflets, pinnae etc.) and their organisation and density (Wilson *et al.* 1994).

Not all of these characters satisfy criterion (1) above, the requirement that the characters should be straightforward to measure. Fortunately, the existence of robust correlations among many characters means that several can be omitted without significant loss of information, as justified below.

Measurement of photosynthetic capacity and light compensation point should ideally be done *in situ* and would require the use of an elaborate apparatus, for example, an infrared gas analyser (Bannister 1976). Among the many vascular species occurring in most *Nothofagus*-dominated communities this would be highly impractical. Furthermore, because conditions within the chamber in which foliage is enclosed for measurement are highly artificial, results are not always repeatable between different implementations (Chapman 1976). This would pose a problem for a study such as the present one, for which laboratory analyses must be done in several different geographical locations. Stomatal conductance is likewise inconvenient to measure, requiring a specialised apparatus. Photosynthetic capacity, light compensation point and stomatal conductance would be relatively strongly intercorrelated, all being related to light reception (Björkman 1981; Field & Mooney 1986). Leaf nitrogen content is known to be a good predictor of photosynthetic capacity, at least for $C_3$ plants (Field & Mooney 1986). This implies that leaf nitrogen content — which is more practical to measure — could be used instead of photosynthetic capacity, light compensation point and stomatal conductance, as a proxy variable for light niches.

Characters concerning the microscopic structure of leaves are time-consuming to measure because of the detailed preparation involved. Characters of this kind — stomatal density and mesophyll air space volume — would be expected to represent adaptations to $CO_2$ uptake and diffusion. Leaf size and shape characteristics should show similar relations (Givnish 1984), but have the advantage that they are more practical to measure. Therefore, microscopic characters were not included in texture as it was evaluated in this study.

Direct measurement of leaf longevity would require monitoring of plants in the field over a period of up to several years (the life-span of the longest-lived leaves). In the present study, however, most sites could be visited only once. Leaf longevity is associated with several characters (leaf specific weight, nitrogen and phosphorus content, support fraction; Reich *et al.* 1992) for which `snapshot' measurements are possible. Consequently, leaf longevity was not included in the present study.

Leaf absorptance to PAR has emerged as a useful predictor of photosynthetic capacity in some recent studies (Hollinger 1989, 1992). However, photosynthetic capacity is even more strongly predictable from leaf nitrogen content (Field & Mooney 1986), while optical measurements, which must be performed on fresh foliage, require a specialised apparatus. No advantage was seen in quantifying both leaf nitrogen and leaf absorptance to PAR. Therefore, nitrogen content alone was measured.

Modular hierarchy, though readily determined for some species (e.g. tussock-forming grasses and graminoids), is not clearly apparent for many growth forms of plants, including many shrubs and trees. It is doubtful whether a given modular hierarchy corresponds to any particular niche or niche axis (for example, a modular hierarchy of 3 might be shared by a grass, a fern and a canopy tree). It was therefore not included in the evaluation of community texture.

Following elimination of characters from the above list that are either impractical to measure, or would duplicate the role of other — more easily measured — characters as proxies for species niches, 12 characters remain. These have the advantages that can be measured relatively quickly and accurately, yet are likely to be functionally important, reflecting major aspects of species niches. The characters are listed in Section 2.3.5.

*Sampling of heteroblastic species and canopy trees*

For some species, adult and juvenile forms may exhibit significant differences in their morphology, implying that they have a different niche. This is notably the case in the New Zealand flora, for which heteroblasty (morphological and physiological differences between adults and juveniles of the same species) is characteristic (Gould 1993). Differences between juvenile and adult niche are also likely to be pronounced for canopy trees. In terms of the model for community structure developed in Chapter 1, it is the niches, rather than species *per se*, that are important in producing community structure. Therefore, juvenile and adult forms were sampled separately for canopy species, and for species in which distinct differences between juvenile and adult morphology were apparent.

SPECIES ABUNDANCE

Whether community texture in terms of a particular character (texture variate) is expressed as an index (e.g. mean among species) or as a distribution (e.g. in frequency classes), it is desirable that species of greater abundance be weighted more heavily than minor ones in evaluating it. This is because abundant species will have more effect on each other than species of low abundance, and so are more likely to exhibit non-random patterns (e.g. in their characters) which might indicate community structure (James & Boeklen 1984). A measure of species abundance is a suitable weighting factor. Photosynthetic biomass, the total dry weight of PSUs, has been recommended

(Werger & Ellenbroek 1978) as it will be correlated with production, a logical measure of a species' contribution to ecosystem functioning (e.g. nutrient cycling) and of its effect on other species. It is the only `snapshot' measure of production that can be used for all species (basal area, a useful correlate for trees, can not be meaningfully determined for many shrubs and herbs [Bonham 1989]). Photosynthetic biomass is more meaningful functionally than cover or frequency estimates, which tend to weight minor species, such as scrambling ground-layer herbs, at the expense of major ones, such as canopy trees (Smith *et al.* 1994).

Photosynthetic biomass for a species in a given area (quadrat) is the product of PSU density and mean PSU dry weight. PSU density may be determined by hierarchical enumeration of subsamples (Wilson *et al.* 1994). This is the least subjective practical method available for quantifying species abundance in terms of foliage density for large numbers of species, particularly those of high stature. Although this method has a subjective component when applied to species which do not conform to a strict modular hierarchy, values can be `transformed down' (e.g. by taking the square root) to give weighting factors in which the subjective factor is less important, certainly less so than in purely subjective measures such as percentage cover.

### VERTICAL STRUCTURE

Information relevant to the vertical structure of communities is needed to enable comparisons to focus on vertical zones (strata, or height guilds [Chapter 10]), where reciprocal species interactions are likely to be concentrated. Precise measurements at vertical scales above a few metres are difficult to make as well as time consuming, but some information would be provided by estimating the proportion of PSUs of each species occurring in each of several height classes within quadrats.

### ENVIRONMENTAL PARAMETERS

Environmental data are required to characterise abiotic influences on species responses, the operation of assembly rules and the likelihood of convergence between different communities.

#### *Climate*

The principal climatic constraints limiting the distribution of particular plant functional types are summer warmth requirements, winter cold limits and drought limits (Woodward 1987). Biologically-important differences in climate among communities would therefore be in terms of these factors, which may be characterised by the mean temperature of the warmest month, mean minimum temperature for the coldest month, annual rainfall and rainfall in the driest quarter. All these parameters would potentially vary from year to year, so long-term averages are to be

preferred.

*Soils*

For soil parameters, as for species chararacters, the explanatory value of each parameter must be weighed against time, cost and practical constraints in collecting it. The existence of strict restrictions on the importation of soil samples in New Zealand decreed that soil analyses had to be performed in the country in which samples were obtained, an additional practical constraint.

The soil nutrients most often limiting for plants are nitrogen, phosphorus and potassium (Salisbury & Ross 1985). Therefore, concentrations of these elements were determined to characterise soil nutrient status. Further parameters that are readily measured include pH, which is useful as a general measure reflecting soil aeration (and therefore drainage) and nutrient status (Russell 1950), and soil organic content, which is related to ion exchange capacity and may reflect nutrient availability, particularly of nitrogen (Russell 1950).

*Light regime*

An important aspect of the environment of the forest understorey is the irradiance regime. Because of shading by canopy trees, only a fraction of the sunlight incident at canopy level reaches the understorey. Light quality in the understorey will also be affected by preferential absorption of red and blue wavelengths by canopy trees (Salisbury & Ross 1985). Both effects result in a marked reduction in the amount of photosynthetically-active radiation available to understorey species. Light attenuation by the canopy, or its inverse, the proportion of light transmitted, is therefore an important parameter of the environment as it is perceived by the majority of species.

Ideally, measurements of canopy light transmittance should be standardised with respect to cloud conditions. In sunny conditions light fluxes are highly directional. This results in greater spatial and temporal variation in light intensity, in part because the `averaging' effect of scattering by foliage is reduced (Salminen *et al.* 1983). Therefore, it would be preferable to measure canopy light transmission consistently under overcast conditions.

### 2.2.3 Study site design

The size and structure of the study sites in which data are collected will influence the suitability of the data for addressing the hypotheses.

The smallest scale at which community-level convergence is likely to be detectable is that of the local community (see section 1.5). A local community would include several plant neighbourhoods, and would be large enough to accomodate microenvironmental (and associated

floristic) variation. A neighbourhood comprises a single individual and its immediate neighbours (Aarssen 1992), perhaps 5-6 individuals for adult *Nothofagus*. A single neighbourhood would seem appropriate as a basic sampling unit, and so the area 20 × 20 m was chosen for sampling quadrats. This area is small enough to be sampled efficiently (noticing all species, and estimating their abundance with tolerable accuracy) and in a reasonable amount of time. It is comparable to the sizes of quadrat that have previously been used to sample in forest (e.g. Foster 1988; Tonteri *et al.* 1990; Hättenschwiler & Körner 1995). A neighbourhood is also the area in which most direct species interactions would occur (Aarssen 1992) and so is a suitable scale at which to record species richness, one of the community properties for which assembly rules are predicted and sought.

*Nothofagus*-dominated forests exhibit a considerable amount of spatial heterogeneity, both as a result of microtopographic variation, and the presence of treefall gaps with associated differences in microenvironment and composition. To accomodate some of the spatial heterogeneity, and to obtain the replicate values for species richness needed for analyses, several (usually five) neighbourhood-scale quadrats were sampled at each site.

PSU densities need to be determined (by definition) on a per-area basis, and so were obtained within quadrats. All plants that appeared to be rooted within a quadrat were sampled, i.e. their PSU densities determined. In comparison with shoot presence, this had the advantage that the composition of quadrats could be precisely determined at ground level (with the exception of epiphytes, which are not rooted at ground level): projection of quadrats into higher strata is difficult in forest (Bycroft *et al.* 1993).

Most texture characters exhibit significant variation within species. Consequently a relatively large number of replicate samples (PSUs, shoots etc) are required in order to obtain an accurate estimate of the population mean for each species. Many species will be relatively rare within quadrats, but be represented more often in the whole study site (comprising several quadrats). Since the quadrats were taken to be representative of the whole study area, species samples for the evaluation of texture were taken from anywhere within the sampling area, and not necessarily only from the quadrats in which the species were recorded.

### 2.2.4 Seasonality considerations

Seasonal fluctuations in texture are to be expected, both with respect to species characters, and PSU densities. Leaf area index (LAI, the ratio of total leaf area to ground area within a sampling unit) may vary substantially between winter and summer, even in evergreen forest. Leaf concentrations of nitrogen and phosphorus would be expected to increase in summer, when translocation from woody tissues to the new shoots and buds occurs (Kramer & Kozlowski 1979), while various physical characters (e.g. succulence) would vary with leaf age, which would also have a seasonal component. To avoid bias due to seasonal variation in species characters

and PSU densities, all sites would ideally be sampled at approximately the same time of year.

## 2.3 Methods

### 2.3.1 Selection of sites

Sampling sites were sought in Tasmania, mainland Australia (`Australia,' for brevity), New Zealand and South America. These four regions are referred to as `landmasses' throughout this report. In comparison to the other landmasses, a greater number of study sites was established in New Zealand. This was in order to be able to focus on questions of community structure at the local and regional scales. In Tasmania, Australia and South America the principal aim in selecting sites was to encompass a range of tall, evergreen *Nothofagus*-dominated communities representative for each landmass. Locational, floristic and environmental data for each of the 17 study sites are presented in Chapter 3.

All sites comprised tall mature forest (average canopy height 30 m or more) dominated (at least 90% canopy cover) by one or more evergreen species of *Nothofagus*. Standardisation of climate to Meurk's (1984) `cool temperate or upper montane' bioclimatic zone (MTWM *c.* 12.5-17.5°C) was achieved by adjusting latitude and altitude, remaining within the latitudinal range 42 ± 3 °S in all landmasses except Australia (where *Nothofagus moorei* forest has a scattered montane distribution from *c.* 25 °S to 32 °S). Areas with particularly infertile soils (for example, over precambrian quartzite in Tasmania) were avoided. Steep terrain (>15° slope) and areas with impeded drainage were likewise avoided, as were narrow valleys in which shading by surrounding topography could be significant. Where slope was not negligible, southerly aspects were chosen if possible. Areas subject to human disturbance were avoided, and a buffer zone of at least 50 m was maintained, separating study sites from tracks, roads and other areas of human disturbance, as well as from sizeable natural clearings.

### 2.3.2 Field sampling

To standardise with respect to seasonal effects on texture, most sampling was done from the last month of spring (November) until the first month of Autumn (March). However, this could not be achieved for all sites and, in particular, mainland Australian sites were sampled at the beginning of spring (September-October) while some collections in southern New Zealand were made in late autumn (April-May).

## STUDY SITE LAYOUT

Sampling was carried out within a 100 × 200 m study area at each site, the long axis being aligned perpendicular to the prevailing slope (where applicable) to ensure that elevation effects within the study area would be negligible. To avoid subjectivity in the choice of sampling area, its exact position was randomised within a 200 × 400 m area where possible. Five (occasionally, when available sampling time was limited, three or four) 20 × 20 m quadrats were located within the study area by stratified randomisation. As it was intended to sample only closed forest, quadrats were repositioned (to a different random point within the study area) if a canopy opening covered more than one-third of their area.

## QUADRAT SAMPLING

In each quadrat, shoot presence of all vascular plant species was recorded. PSU densities were determined for each species present by hierarchical enumeration of subsamples. This method of counting PSUs was applied in different ways for different types of species. In the case of functional types having a distinct modular hierarchy (e.g. many graminoids, which have tussocks divided into tillers, in turn divided into individual leaves), the average number of PSUs in first-order modules was determined, then the number of first-order modules in second-order modules, and so on, finally estimating the number of highest-order modules rooted in the entire quadrat. At each level, values were obtained for several modules, on different individuals if possible, to ensure that the mean for that level was as accurate as possible. The average numbers of units at each level for a species were multiplied together and divided by quadrat area (400 $m^2$) to determine its PSU density in the quadrat. In the case of species lacking a distinct modular hierarchy a similar protocol was followed, but modules were defined arbitrarily. Binoculars were used to facilitate enumeration of PSUs for canopy trees. All PSUs of all individuals rooted (or appearing to be rooted) in the quadrat, and only those individuals, were included in the density estimates. To determine whether epiphytic species not rooted at ground level appeared to occur within the quadrat, quadrats were projected visually upwards. Adult and juvenile forms of heteroblastic species, as well as seedlings (0-2 m), saplings and subcanopy individuals (2 m to 67% of mean canopy height), and canopy individuals (above 67% of mean canopy height) of canopy species, were treated as separate entities for the purposes of PSU density estimation and texture sampling (see below).

As a record of the vertical distribution of each species, the proportion of its PSUs occurring in each of the following height classes within the quadrat was estimated visually: 0-0.3 m; 0.3-1 m; 1-2 m; 2-5 m; 5-10 m; 10-20 m; 20-30 m; 30-40 m.

The height of a representative canopy individual of each canopy species (as defined above) present in the quadrat was determined using a clinometer. Diameters at breast height

(DBH) were recorded for all canopy individuals using a diameter measuring tape. Breast height was taken at 1.6 m above ground level, except for buttressed trees, for which measurements were made just above the buttress. Soil samples were taken from the upper mineral horizon at three random points within each quadrat, and bulked to give one sample of *c.* 1 kg, representative for the quadrat. In Argentina only, soil samples from all quadrats at each site were bulked to give one sample per site. Mean slope across the quadrat (nearest 5°) was estimated using an Abney level, and aspect (nearest 5°) determined with a magnetic compass. Obvious features of the vegetation structure, composition and microtopography were noted.

### CANOPY LIGHT TRANSMISSION

To determine the proportion of incident light transmitted by the forest canopy above each quadrat, sampling of PAR quantum flux was done in the open and beneath the forest canopy. Using an electronic quantum photometer (LiCor LI-185B and similar), a light measurement was made at 2 m above ground level in an open area (e.g. large clearing or field) near the study site, at which trees and surrounding topography would have little influence on light levels. Measurements were then made at 1 m above ground level at 10 random points within each quadrat at the study site, a 1 m rule being used to position the quantum sensor at the appropriate height. A second value was then obtained in the open. At one Chilean (SC2 Antillanca) and one Argentinian site (SA2 Gutierrez), quadrat light measurements were made at 2 m as well as 1 m above ground level. This was because a dense layer of bamboo (*Chusquea* spp.) in the understorey would have reduced light levels at 1 m height significantly. Whenever possible, light transmission measurements were made at midday ±1 hr (standard time) in stable overcast conditions. At several sites, however, sampling had to be done during full sunshine. Sunflecks were avoided in these conditions. Sampling was completed as quickly as possible to avoid error due to changes in light intensity during the measurement period.

### TEXTURE SAMPLING

To evaluate community texture, shoot samples were collected for each species (or entity: see above) encountered within quadrats at each study site. Where the same species occurred in more than one quadrat at a particular site, only one collection was made. However, separate collections were made at each site regardless of whether some species had been sampled elsewhere (except in the case of occasional missing values; see below). Samples were sought within the whole study site, not just within quadrats.

PSU inclination was measured *in situ* to the nearest 5° using an Abney level or clinometer. Inclination measurements were independent of whether PSUs were erect or pendent, and independent of the position of the midrib. For each species 10 representative PSUs were

measured, from different individuals if possible.

For the evaluation of chlorophyll characters, single PSUs (or, in the case of species with very small PSUs, several PSUs) were collected from 10 different individuals of each species, or occasionally fewer if the species was of low abundance, endangered or had exceptionally large leaves. Damaged, diseased or moribund foliage, as well as new foliage not fully developed, was avoided.

To evaluate all other texture characters, 10 terminal shoots were collected from different plants if possible. The number of plants and/or shoots sampled was reduced (to the largest number practicable) in the following cases.

1. For canopy trees (mainly *Nothofagus* spp.) sampling was exceptionally time-consuming (see below). Therefore, only three trees of each species were sampled at most sites. However, three to four terminal shoots were taken from each tree, generally yielding a total of 10 samples.
2. For rare or obscure species less than 10 individuals were sampled if that number could not be found within the study area, or if collection of the full complement of samples might have placed the persistence of the local population in jeopardy. In the case of North Island New Zealand sites (ZN1 Ohakune, ZN2 Rotokura and ZN3 Clements) only one terminal shoot (to a maximum of five leaves) was allowed to be taken for mistletoe species at each site.
3. For species with exceptionally large leaves (e.g. *Cordyline indivisa*, whose mean leaf area at ZN1 Ohakune was 483 $cm^2$) as much foliage as practicable was taken.

A terminal shoot was defined as:

1. an entire tiller, for grasses and graminoids;
2. an ultimate shoot for most trees, shrubs, ferns and forbs; for consistency, the shoot was severed just below the lowest PSU remaining attached to the main axis;
3. a segment including at least 10 true leaves for certain climbing or scrambling species with persistent leaves.

In all cases, foliage not fully developed was detached from samples collected. Care was taken to sample from the upper surface or outer canopy of all plants, including trees. At most sites, a pole pruner was used to access outer canopy foliage of understorey trees, while a specially-developed canopy sampling apparatus, described below, was used to retrieve foliage of canopy trees.

APPARATUS FOR TEXTURE SAMPLING OF CANOPY TREES

Foliage samples were obtained from canopy trees using a bow-and-arrow-based apparatus developed by R. Gympel, A.J. Watkins and the author for use in the present study. A fishing reel wound with standard (12 lb breaking strain) nylon fishing line was attached to the bow. One end of the fishing line was tied to a lead-weighted arrow. To collect a foliage sample, the arrow was propelled near-vertically across the outer branches of a target tree, uncoiling the fishing line and draping it across the tree. The fishing line was then detached from the arrow and tied to one end of a 50 m length of 1.8 mm braided polyester line, at the other end of which was a 50 cm length of flexible saw wire (multi-stranded embriotic wire, designed for the amputation of bovine horns), followed by a further 50 m of braided line. The line and saw were then drawn over a branch by winding the fishing line back onto its reel, and the branch was sawn down by drawing alternately on the two ends of the line. The apparatus was used successfully at all sites sampled in this study, and was found effective to a height of approximately 40 m.

### 2.3.3 Climate parameters

For each site, values of the following climate parameters were obtained: mean temperature of the warmest month (MTWM), mean temperature of the coldest month (MTCM), mean annual temperature (MAT), annual rainfall (AR) and rainfall in the driest quarter (RDQ). Mean minimum temperatures for the coldest month, thought preferable to MTCM in characterising absolute winter cold limits, could not be obtained for South American sites. However, MTCM should be strongly correlated and was therefore used instead. For Tasmania, mainland Australia and New Zealand, climate data were obtained using the climate estimation procedures of the computer program BIOCLIM (Nix 1986; Mitchell 1991; Orr 1993). BIOCLIM interpolates among locations for which climate data are available, taking account of the position and altitude of the target point (Hutchinson 1984). This represents the best method of estimating climate for localities distant from climate recording stations. Climate data for Chilean and Argentinian sites were estimated from published records (Almeyda & Saez 1958; Anon. 1964; Putney 1970; Dimitri 1972; Veblen & Schlegel 1982), with mathematical correction for altitude and location where necessary.

### 2.3.4 Laboratory measurement

SOIL PARAMETERS

The soil parameters evaluated for each site were total nitrogen, phosphorus and potassium, pH and organic content. It was endeavoured to standardise extraction methods for all sites, to ensure

that data would be comparable. However, due to limited facilities in some of the regions visited in the course of the study, complete standardisation could not always be achieved. Analysis methods for extractions also varied, although presumably this would affect the precision of results, not their absolute values. Some analyses were performed by, or with the assistance of, staff of specialist laboratories, as follows: Soil and Plant Laboratory, Department of Primary Industry Tasmania (DPI); Forestry Department, Australian National University (ANU); Soil Fertility Service, New Zealand Pastoral Agriculture Research Institute (NZPARI); Laboratorio de Nutrición y Suelos Forestales, Instituto de Silvicultura, Universidad Austral de Chile (UAC) and Estactión Experimental Regional Agropecuaria Bariloche, Instituto Nacional de Tecnología Agropecuaria (INTA). In the following discussion, each organisation is referred to by its abbreviated code, shown in parentheses above.

Except in Argentina, where a single measurement was made on bulked soil samples from each of the two sites, separate values for each parameter were obtained for each quadrat sampled. For mainland Australian soils only, samples were also replicated at the analysis stage, three values being obtained for each quadrat from the same field sample and averaged. This was intended to improve the accuracy of overall values for each quadrat.

Descriptions of analytical methods below are from Allen (1989) unless otherwise indicated. Exact methods adopted by commercial laboratories may have differed in detail from the regimes described here in some cases.

*Nitrogen*

Nitrogen and phosphorus analyses were carried out by DPI (Tasmania); ANU (Australia); NZPARI (New Zealand); UAC (Chile) and INTA (Argentina). In Tasmania, Chile and Argentina, nitrogen was extracted using a Kjeldahl procedure. In this method, samples are digested under heat in concentrated sulphuric acid in the presence of a selenium, copper or mercury catalyst. This converts soil nitrates, nitrates and insoluble organic nitrogen compounds to ammonium (Allen 1989). In New Zealand and Australia a variation on the Kjeldahl procedure was adopted, including hydrogen peroxide is the digestion mixture. This had the advantage that phosphorus concentrations could be determined from the same digest (see below).

In Tasmania and Australia nitrogen concentrations in digests were measured by means of an automated colorimetric (indophenol blue) procedure. Ammonium in the soil extract is oxidised by sodium hypochlorate. A subsequent reaction with sodium salicylate imparts a blue colour to the solution, whose concentration, measured by spectrophotometry (absorptance at 660 nm), is proportional to the amount of nitrogen present. In Chile and Argentina, a distillation and titration method was used. Ammonium is distilled from the soil digest and received by a hydrochloric or sulphuric acid solution of known concentration, raising its pH. Titration, for example against sodium hydroxide in the presence of an indicator (phenolphthalene), allows the

ammonium-nitrogen concentration of the original solution to be determined (R. Grez, *unpublished*). An automated variation on this method was used by NZPARI to analyse New Zealand soils.

*Phosphorus*

In New Zealand and Australia, phosphorus was extracted simultaneously with nitrogen using a modified Kjeldahl procedure, as described above. In Tasmania, soils were digested under heat in concentrated nitric and perchloric acids (see `Potassium' below). In Argentina, Truog's extraction procedure was used. More soluble phosphate compounds, as well as free phosphate ions adsorbed to exchange sites in the soil are released by a dilute, buffered sulphuric acid solution. The amount of phosphorus extracted by this procedure is intermediate between total soil phosphorus and the ambient amount available for uptake by plants (Allen 1989). The values obtained cannot be compared on an equal basis with the total phosphorus values obtained at other sites.

In Tasmania, determination was done using an inductively coupled argon plasma (ICP) spectrophotometer (Jakubowski & Stuewer 1994). In Australia, New Zealand and Argentina a molybdenum blue procedure (automated, except in Argentina) was used. Dissolved phosphate in the soil extract is coupled with a molybdate reagent and a reductant (either stannous chloride or ascorbic acid) giving a blue colour whose intensity, measured by spectrophotometry (absorptance 700 nm), can be used to calculate the amount of phosphorus extracted.

Due to unforseen laboratory problems, no phosphorus values were obtained for Chilean sites.

*Potassium*

Analyses for total potassium, pH and organic content were carried out by DPI (Tasmania); UAC (Chile) and INTA (Argentina). For New Zealand and Australian sites, potassium analyses were done by the author; in Australia, with the assistance of ANU staff. Except in Argentina, extractions were done in a heated 3:1 mixture (volume basis) of concentrated nitric and perchloric acids. In Argentina extraction was done in nitric acid.

Determination of potassium concentration in extracts was by automated atomic-absorption spectrophotometry (Australia) or flame photometry (New Zealand, Chile, Argentina).

*pH*

Measurements of pH were done in distilled water using a pH meter. For New Zealand and Australian samples, a mixture of *c.* 5 g soil and 25 ml distilled water, shaken for 1 hr, was used.

*Organic content*

Organic content was estimated by loss-on-ignition at 500°C for 10 hr, except in Chile and Argentina, where a Walkley-Black carbon extraction procedure was used. Soil carbon is oxidised under heat by potassium dichromate in concentrated sulphuric acid. The resultant solution is titrated against ferrous ammonium sulphate in the presence of an indicator (diphenylamine) to determine the amount of carbon present. The chemical extraction method was considered to give a more reliable estimate of organic content for the volcanic ash-derived soils that prevail at the South American sites (R. Grez, *personal communication*). The two methods have been shown to produce an acceptable correspondence (Allen 1989).

SPECIES CHARACTERS

To ensure maintenance of field turgor, field samples were stored in plastic bags and, if possible, refrigerated (at *c.* 4°C) until laboratory measurements and drying were carried out. Storage time was kept to a minimum (generally less than two weeks). However, samples were found to remain fresh for up to two weeks if refrigerated immediately after collection.

*PSU chlorophyll content*

Chlorophyll *a* and *b* content were determined using a method adapted from Moran & Porath (1980), Moran (1982) and Inskeep & Bloom (1985) by A.J. Watkins, S.J. Clarke and the author. Leaf samples collected in the field were divided into three (occasionally two or one) replicate samples for each species. For each replicate, approximately 30 mg of macerated leaf material was introduced into a glass container. The container was weighed (1 mg precision) before and after addition of the leaf sample and the difference (the weight of the sample) recorded. Containers used were 10 ml screw-top test tubes (central and southern New Zealand sites), 10 ml soil vials (Tasmania) or 20 ml soil vials (northern New Zealand, Australia and South America). Larger glass containers (capacity *c.* 50 ml) were used for a small number of samples in Argentina. The data obtained from these were inconsistent with values elsewhere and were not used. 5 ml (for some sites, 4 ml) of N,N-dimethylformamide (DMF), retrieved with a pipette, were added to the container, the container was sealed, sheathed in aluminium foil to inhibit the entry of light, and stored, refrigerated at *c.* 4°C, for a period of 3-14 days. The resultant chlorophyll solution was analysed by spectrophotometry for absorptance in 1 cm cuvettes at wavelengths 647 nm and 664.5 nm, callibrating (to 0 absorptance) with fresh DMF. Formulae for determining chlorophyll *a* and *b* concentrations from the absorptance values are given in Section 2.3.4.

For Chilean sites, chlorophyll concentrations were measured by staff of the Laboratorio

de Nutrición y Suelos Forestales, Instituto de Silvicultura, Universidad Austral de Chile.

*Species physical characters*

For each terminal shoot sample, all leaves were detached, counted and weighed. Mean PSU fresh weight (nearest mg) for the sample was calculated and recorded. Petioles (or functional equivalents) were treated as stem, not leaf. Fresh leaves were placed with their respective stems in folded sheets of absorbent paper or newspaper, marked with a code identifying the species, replicate number, and the number of PSUs in the sample. Multiple sheets were then placed in a plant press, interleaved with corrugated aluminium sheets or corrugated cardboard to ensure adequate ventilation, and dried. Drying was achieved over incandescent light bulbs (southern and central New Zealand sites), in a drying oven at *c.* 45°C (northern New Zealand, Tasmania and South America) or in a fan-forced oven specialised for the drying of herbarium specimens (Australia). Prior to pressing, thickness was determined for one randomly selected PSU from each terminal shoot, or more than one PSU if fewer than 10 samples had been collected, giving 10 values for most species. PSU thickness was measured with a micrometer (precision 0.01 mm), avoiding the midrib (or prominent nerves of some graminoids, e.g. *Astelia* spp.) but taking no account of other veins.

Once dry, PSUs from each sample were reweighed to determine mean PSU dry weight. Dried stems were also weighed. Replicate samples for each species were pooled and 10 PSUs were selected at random for further measurements. In the case of species for which 10 or fewer PSUs had been collected, no random selection was made and all PSUs were used. PSU length and (maximum) width were determined using a ruler (nearest mm), and area using a scanning leaf area meter (LiCor Model 3100) or, for leaves narrower then 2 mm, by counting the number of 1 × 1 mm grid squares intersected by the PSU under transparent graph paper. Area was recorded to a precision of 1 $mm^2$. Length was defined as the length of a straight-line between ends of the midrib, while width was the largest distance between leaf margins perpendicular to the axis along which length was measured.

*PSU nitrogen and phosphorus content*

To determine PSU nitrogen and phosphorus concentrations, all dried PSU samples were pooled for each species and ground finely using a rotary grinder. Ground material was processed by staff of the Forestry Department, Australian National University. A Kjeldahl extraction was carried out (Allen 1989) and total nitrogen and phosphorus content (dry weight basis) determined by auto analysis.

### 2.3.5 Calculation of texture variates

MAIN CALCULATIONS

Texture was evaluated in terms of the following species characters (characters for which no units are shown are dimensionless):

1. PSU area ($cm^2$);
2. PSU shape;
3. PSU lobation;
4. PSU thickness (mm);
5. PSU succulence;
6. PSU specific weight ($g\ cm^{-2}$);
7. PSU inclination (°);
8. Support fraction;
9. PSU nitrogen content (% dry weight);
10. PSU phosphorus content (% dry weight);
11. Total PSU chlorophyll content (% dry weight);
12. PSU chlorophyll *a/b* ratio.

*Chlorophyll characters*

For each replicate, PSU chlorophyll *a* ($c_a$) and *b* ($c_b$) concentrations were calculated as a percentage of leaf dry weight using the following formulae (Inskeep & Bloom 1985):

$$c_a = \frac{v.F}{f.D}(12.7\,a_{664.5} - 2.79\,a_{647}) \times 10^{-4}$$

$$c_b = \frac{v.F}{f.D}(20.7\,a_{647} - 4.62\,a_{664.5}) \times 10^{-4}$$

where $f$ = weight of leaf sample (g);
$v$ = volume of DMF added (ml);
$a_{647}$ = absorptance at 647 nm;
$a_{664.5}$ = absorptance at 664.5 nm;
$F$ = mean species PSU fresh weight (g) (see below);
$D$ = mean species PSU dry weight (g) (see below).

From $c_a$ and $c_b$, total chlorophyll $c_t$ and chlorophyll *a/b* ratio $c_{a/b}$ could be calculated:

$$c_t = c_a + c_b$$

$$c_{a/b} = \frac{c_a}{c_b}$$

*Physical characters*

PSU shape (*h*) was calculated as the ratio of PSU length to width, i.e.

$$h = \frac{l}{w}$$

where $l$ = PSU length (mm);
$w$ = PSU width (mm).

Lobation (*b*) was determined for each replicate using the formula:

$$b = \frac{\pi . l . w}{a} \times 10^{-2}$$

where $\pi$ = 3.14159... (the ratio of the circumference to the diameter of a circle);
$a$ = PSU area ($cm^2$).

This formula expresses the ratio of the area of an ellipse with the same length and width as the sample PSU, to the area of the PSU itself. It will give the value 1 for a perfectly elliptical leaf, tending to give larger values for increasingly divided leaves, although undivided non-elliptical leaves may also yield values greater than 1.

PSU succulence (*u*) for each replicate was calculated as:

$$u = \frac{f}{d}$$

where $f$ = mean PSU fresh weight (g);
$d$ = mean PSU dry weight (g);

Support fraction (*s*) was determined for each replicate using the formula:

$$s = \frac{\sum z}{\sum d + \sum z}$$

where $\Sigma d$ = total dry weight of PSUs in terminal shoot (g);
$\Sigma z$ = total dry weight of stems in terminal shoot (g).

Species means for each character were obtained by averaging replicate values (no means had to

be calculated for PSU nitrogen or phosphorus concentrations, as only one value was obtained for each species). Prior to calculation of species means, replicate values were graphed to look for extreme values that might represent measurement or calculation errors. Where a calculation error was found, the calculation was repeated. Where a measurement error was suspected, the replicate value was discarded.

PSU specific weight (*M*) for each species was calculated as:

$$M = \frac{A}{D}$$

where $A$ = species mean PSU area ($cm^2$);
$D$ = species mean PSU dry weight (g).

TRANSFORMATIONS OF TEXTURE VARIATES

Statistical tests for skewness and kurtosis were carried out to determine whether texture variates (comprising species means for all characters from all sites) were distributed normally. A normal distribution is assumed by some parametric tests (employed in Chapter 4) and is desirable for the randomisation and bootstrap tests performed elsewhere in this study, so that test statistic values are not affected disproportionately by species with extreme character values. Tests for normality were performed with the Teddybear computer program (Wilson 1975). Variates that departed materially from a normal distribution were transformed to improve normality (Table 2.1). Only the transformed variates were used in subsequent analyses.

**Table 2.1** Transformations applied to each texture variate. The expression shown gives the transformed value from a raw species character value, *x*. ln=natural logarithm; $\sin^{-1}$=arcsine.

| Texture variate | Transformation expression |
|---|---|
| PSU area | $\ln x$ |
| PSU shape | $\ln x$ |
| PSU lobation | $\ln x$ |
| PSU thickness | $\ln x$ |
| PSU succulence | $\ln x$ |
| PSU specific weight | $\ln x$ |
| PSU inclination | $\ln x$ |
| support fraction | $\sin^{-1} x$ |
| PSU nitrogen content | $\sin^{-1} 0.01x$ |
| PSU phosphorus content | $\sin^{-1} 0.01x$ |
| total PSU chlorophyll content | $\ln x$ |
| PSU chlorophyll *a/b* ratio | $x$ |

## TREATMENT OF MISSING VALUES

Community structure is expected to arise as a result of a network of interactions, potentially among all species in a community or guild (see Chapter 1). Consequently, community structure might be reflected in the characters of all species present. Analyses seeking structure in community texture might therefore be weakened by the omission of some species from texture.

Missing species character values arose occasionally where an obscure species was found during initial survey of a quadrat, but could not be located again; where samples were damaged or became moribund due to unavoidable prolonged storage and there was no opportunity to collect replacement samples; where seedling, subcanopy/saping and/or canopy samples of canopy species were inadvertently mingled and could not be reliably distinguished *post hoc*; or where a measurement procedure yielded unreliable results.

Where missing values occurred, priority was given to revisiting the initial site, or another, similar, site, and collecting replacement samples. If collection of further samples was not possible, values for the same species from the nearest available site were used.

In rare cases, no substitute values from the same species were available. This problem arose only in respect of 10 species from sites in Chile and Argentina, for which reliable chlorophyll values could not be obtained due to unforseen laboratory problems, and for one New Zealand species (*Alepis flavida*, at ZS1 Ten Mile) for which chlorophyll solutions could not be analysed due to interference with the chlorophyll absorption peaks by other dissolved substances. To obtain estimates for total chlorophyll and chlorophyll *a/b* ratio for these species, linear models expressing these variates as combinations of the remaining 10 derived texture variates were obtained by multiple regression. All species from all sites for which there were no missing values (583 species) were used to calculate the regression models. Transformed variates were used. For each equation, a step-down procedure was performed, interatively dropping and adding terms, to find a combination including only those terms that materially influenced the mean square of the residuals (a measure of the goodness-of-fit of the regression to the observed data). This procedure results in the exclusion of parameters that do not contribute to the predictive power of the model. The resultant, `step-down,' equations are shown below (all variables transformed as in Table 2.1):

$$C_{a/b} = 0.0541H + 0.1444M - 0.2309I + 0.556S - 4.974N + 36.16P + 3.267$$

$$C_{t} = 0.3668U - 0.3126M + 1.218N - 2.6979$$

where $C_t$ = total PSU chlorophyll content;
$C_{a/b}$ = PSU chlorophyll *a/b* ratio;
$H$ = PSU shape;
$U$ = PSU succulence;
$M$ = PSU specific weight;

$I$ = PSU inclination;
$S$ = support fraction;
$N$ = PSU nitrogen content;
$P$ = PSU phosphorus content.

Fitted to the data used for the regression, the first equation has relatively poor predictive power, accounting for 29% of the variation in $C_{a/b}$. The second equation is more powerful, explaining 56% of the variation in $C_t$. Using these equations, values were calculated for the 11 species with missing values for total chlorophyll and chlorophyll *a/b*. Multiple regression was performed with the Genstat 5 computer program (Genstat 5 Committee 1987). All estimated or substituted species character values are indicated in the summarised texture data set, presented in Appendix A.

### 2.3.6 Nomenclature

Taxonomic nomenclature in this study follows Curtis (1963, 1967), Curtis & Morris (1975), Jones & Clemesha (1980) and Jarman *et al.* (1984) (Tasmania); Jones & Clemesha (1980) and Harden (1990) (Australia); Allan (1961), Moore & Edgar (1970), Brownsey *et al.* (1985) and Connor & Edgar (1987) (New Zealand); Marticorena & Quezada (1985) (Chile); and Diem (1943) and Correa (1971) (Argentina). In the case of a small number of taxa, family, genus or species designations differ between regions. In these cases, conventions adopted in New Zealand (references cited above) were observed.

### 2.3.7 Analyses

Analyses seeking evidence for community structure are described in Chapters 6-11. Except where otherwise acknowledged, all statistical analyses were performed using computer programs written by the author in the C++ programming language.

# 3. Study sites and their environments

## 3.1 Introduction

In this chapter, detailed descriptions are given of the sites at which the study was carried out. Environmental data are also presented and compared among sites. Environmental similarity is an important assumption of the hypothesis of community-level convergence (see Chapter 1). On the basis of their environments sites that are well-matched in terms of particular parameters, or all parameters, are selected for particular attention in subsequent analyses.

## 3.2 Site descriptions

Seventeen study sites, encompassing four landmasses and ten regions, were established and sampled in the course of the study. Here, general features of the floristic composition, physical structure and environment of each site are described. The sites are listed under the landmass and region in which they occur. Each is identified by a two- or three-character code and a name. The code is based on the landmass (first letter), region (second letter, if more than one site was sampled in the same region), and a number, distinguishing different sites within a region or landmass. The name is based on a geographic feature at or near the study site. For example, ZS1 Ten Mile was one of three sites in the southern region (S) of New Zealand (Z), and was situated in a patch of forest known as Ten Mile Bush. In subsequent chapters, full site names are generally used in the text, while codes alone are presented in some tables and figures.

In the descriptions below, heights given for canopy trees are averages of the values obtained for a number of representative trees. Diameters at breast height (DBH) are averages among all canopy trees of a given species encountered within quadrats. Canopy trees are defined as individuals attaining more than 67% of mean canopy height (see Chapter 2). Familial affinities are given only at the first mention of a particular genus. Nomenclatural sources and conventions are described in Section 2.3.6. The reported species richness values are the numbers of vascular plant species encountered within all quadrats sampled. The number of quadrats sampled is also given for each site, as it varies from three to five, and would have some effect on the number of species observed over the whole site. Mean quadrat species richnesses for sites are given in Chapter 5 (Table 5.1).

LANDMASS: TASMANIA (T)

The three sites sampled in Tasmania broadly encompassed the geographic distribution of

*Nothofagus cunninghamii* there (Fig. 3.1). *N. cunninghamii* is the most important dominant species of lowland to montane cool temperate rainforest in Tasmania (Jarman *et al.* 1984). The other Tasmanian *Nothofagus* species, *N. gunnii*, is a deciduous shrub or small tree confined to a restricted range of subalpine habitats, and was not sampled, as the communities it forms are of a different kind to the tall, evergreen rainforests investigated by this study. The distribution, structure, composition and general features of the ecology of Tasmanian *Nothofagus*-dominated forests are described by Beadle (1981), Howard (1981), Jackson (1983), Busby (1984), Jarman *et al.* (1984), Hill (1982), Hill & Read (1984) and Read & Hill (1985, 1988).

*Region: Northwest Tasmania*

**Site T1 Balfour**, 41° 09' S, 144° 59' E. This site was situated on the crest of a gently-sloping ridge forming the southern boundary of the Balfour Forest Reserve, at an altitude of 190 m. The forest was dominated by mature *Nothofagus cunninghamii* at an average height of 23 m and DBH 67 cm. *Atherosperma moschatum* (Monimiaceae) and *Eucryphia lucida* (Eucryphiaceae) were also present, forming an irregular subcanopy. Other major component species were *Olearia argophylla* (Compositae), *Pittosporum bicolor* (Pittosporaceae) and the tree fern *Dicksonia antarctica* (Dicksoniaceae). Regeneration of *N. cunninghamii* occurred primarily within larger treefall gaps, where *A. moschatum* regeneration tended to be more conspicuous. Twenty-three vascular plant species occurred within the three quadrats sampled. Mean slope was 5° and aspect 180° S. The geology of the area comprises a volcano-sedimentary complex of Cambrian age, the Mt Read Volcanics (Department of Mines 1976). This formation is associated with soils of high fertility, and is the most characteristic geology for *Nothofagus*-dominated forest in Tasmania (Read & Hill 1988).

*Region: Southwest Tasmania*

**Site T2 Anne**, 42° 55' S, 146° 26' E. This site occupied a terrace on the northwest-facing slope of a ridge of Mt. Anne, *c.* 600 m asl. *Nothofagus cunninghamii* was the dominant species, attaining a height of 29 m and DBH 68 cm. *Atherosperma moschatum* formed a subcanopy locally, with *Eucryphia lucida*, *Anopterus glandulosus* (Escalloniaceae), *Anodapetalum biglandulosum* (Cunoniaceae) and *Dicksonia antarctica* forming a moderately dense understorey. *N. cunninghamii* regeneration was confined to treefall gaps. Species richness (three quadrats) was 21. Mean slope was 20° and aspect 345° N. The bedrock consists of Jurassic dolerite (Department of Mines 1976).

*Region: Northeast Tasmania*

**Site T3 Mathinna**, 41° 20' S, 147° 45' E. This study site was located on the Mathinna Plains, at an altitude of 800 m. *Nothofagus cunninghamii* formed a very even canopy at a height of *c.* 22 m. The canopy trees appeared to belong predominantly to one cohort, with mean DBH 36 cm. *Phyllocladus aspleniifolius* (Podocarpaceae) occurred occasionally in the canopy, while *Atherosperma moschatum* and *Tasmannia lanceolata* (Winteraceae) were the most prominent subcanopy trees. Tree ferns, *Dicksonia antarctica*, and metre-high tussocks of *Gahnia grandis* (Cyperaceae) dominated the otherwise sparse understorey: just 20 vascular species were observed within the five quadrats sampled. Slope averaged 5° with aspect 295° W. The presence of occasional sawn stumps suggests that selective logging has taken place on a minor scale in the past. Basement rocks are mudstones and sandstones of Permian age (Prickard 1980).

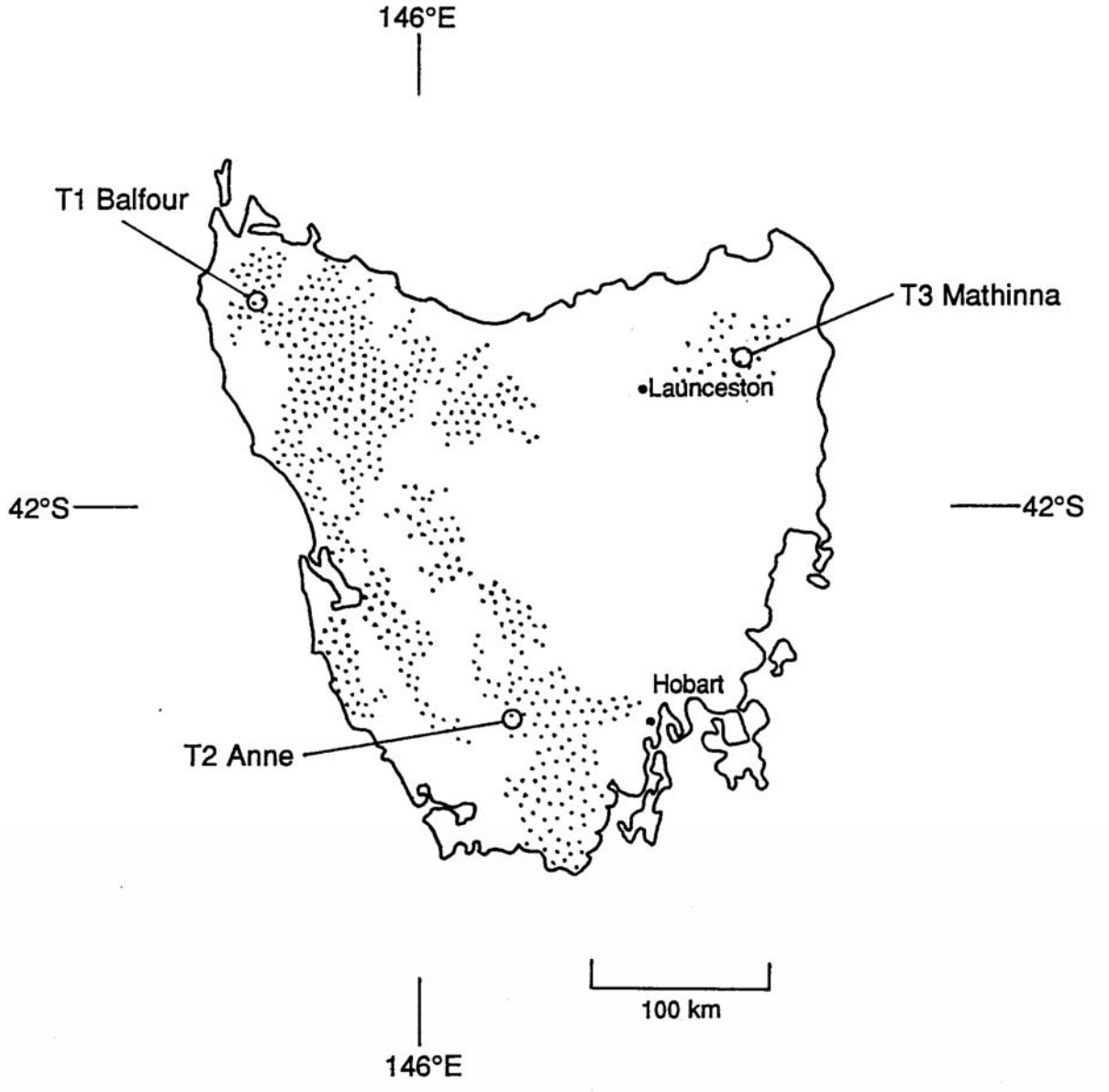



**Fig. 3.1** Locations of study sites in Tasmania, showing (shading) the approximate distribution of *Nothofagus cunninghamii*-dominated rainforest (after Davies 1964).

LANDMASS: MAINLAND AUSTRALIA (A)

In contrast to Tasmania, where *Nothofagus*-dominated rainforests are relatively abundant, *Nothofagus* has a very restricted and discontinuous distribution on mainland Australia. Both *N. cunninghamii*, which occurs at a number of localities in Victoria, and *N. moorei*, which is confined to a few isolated sites on the Great Dividing Range in northern New South Wales and southern Queensland, have probably suffered a marked contraction in their ranges as a result of decreasing rainfall in the late Palaeozoic (Hill 1994). *N. cunninghamii* rarely forms large pure stands in Victoria, but tends to occur as a codominant with *Eucalyptus* or *Acacia* species (Howard & Ashton 1978). For this reason, no Victorian sites were sampled. *N. moorei*, however, may occur as a sole canopy species, and sites dominated by this species were sampled at the southern end of its range, the Barrington Tops massif, and 200 km further north, in New England (Fig. 3.2).

Beadle (1981), Howard (1981) and Floyd (1990) describe the structure, distribution and floristic composition of *N. moorei*-dominated cool temperate rainforests. Turner (1976) has examined altitudinal gradients of texture (leaf size classes) as well as regeneration ecology in rainforest at Barrington Tops. Read & Hill (1985) investigated population size structures and regeneration of *N. moorei* at three localities, including Barrington Tops and New England.

*Region: Hunter Valley, New South Wales*

**Site A1 Lumeah**, 32° 07' S, 151° 25' E. Situated near Mt. Lumeah on the western flanks of the Barrington Tops massif, at an altitude of 930 m, this forest had a closed canopy of *Nothofagus moorei*. Canopy trees averaged 33 m in height, with DBH 80 cm. *Daphnandra* `sp. A' (Monimiaceae) also occurred at canopy level within the study site. Several other tree species made up a prominent subcanopy, including *Caldcluvia paniculosa* (Cunoniaceae), *Doryphora sassafras* (Monimiaceae), *Orites excelsa* (Proteaceae) and *Tristaniopsis collina* (Myrtaceae). The understorey was dominated by ferns, mainly *Lastreopsis decomposita* (Aspidiaceae) and *Diplazium australe* (Athyriaceae), while *Dicksonia antarctica* was associated with treefall gaps. Climbers, notably *Smilax australis* (Smilaceae) and *Palmeria scandens* (Monimiaceae), were prominent among the branches of trees. Species richness was 36 (five quadrats). Slope averaged 10° with aspect 250° W. Tertiary Basalts and Granites make up the bedrock in the area (David 1950).

*Region: New England, New South Wales*

**Site A2 Cascades**, 30° 30' S, 152° 25' E. This site was situated near The Cascades waterfall on an escarpment of the Great Dividing Range in New England National Park, altitude 1300 m.

Very mature *Nothofagus moorei* (height 28 m, DBH 71 cm) was emergent above a multispecific subcanopy including *Doryphora sassafras*, *Orites excelsa*, *Cryptocarya nova-anglica* (Lauraceae) and *Elaeocarpus holopetalus* (Elaeocarpaceae). Tree ferns, *Dicksonia antarctica*, and tussocks of *Lomandra* sp. (Xanthorrhoeaceae) were prominent in the understorey, while an unidentified graminoid (probably *Carex* sp.) was prominent within treefall gaps and patches in which thinning of the *Nothofagus* crowns permitted more light to reach the forest floor. Vascular species richness was 31 (five quadrats). Mean slope was 10°, aspect 160° S. Basement rocks in the area are Tertiary basalts and granites (David 1950).

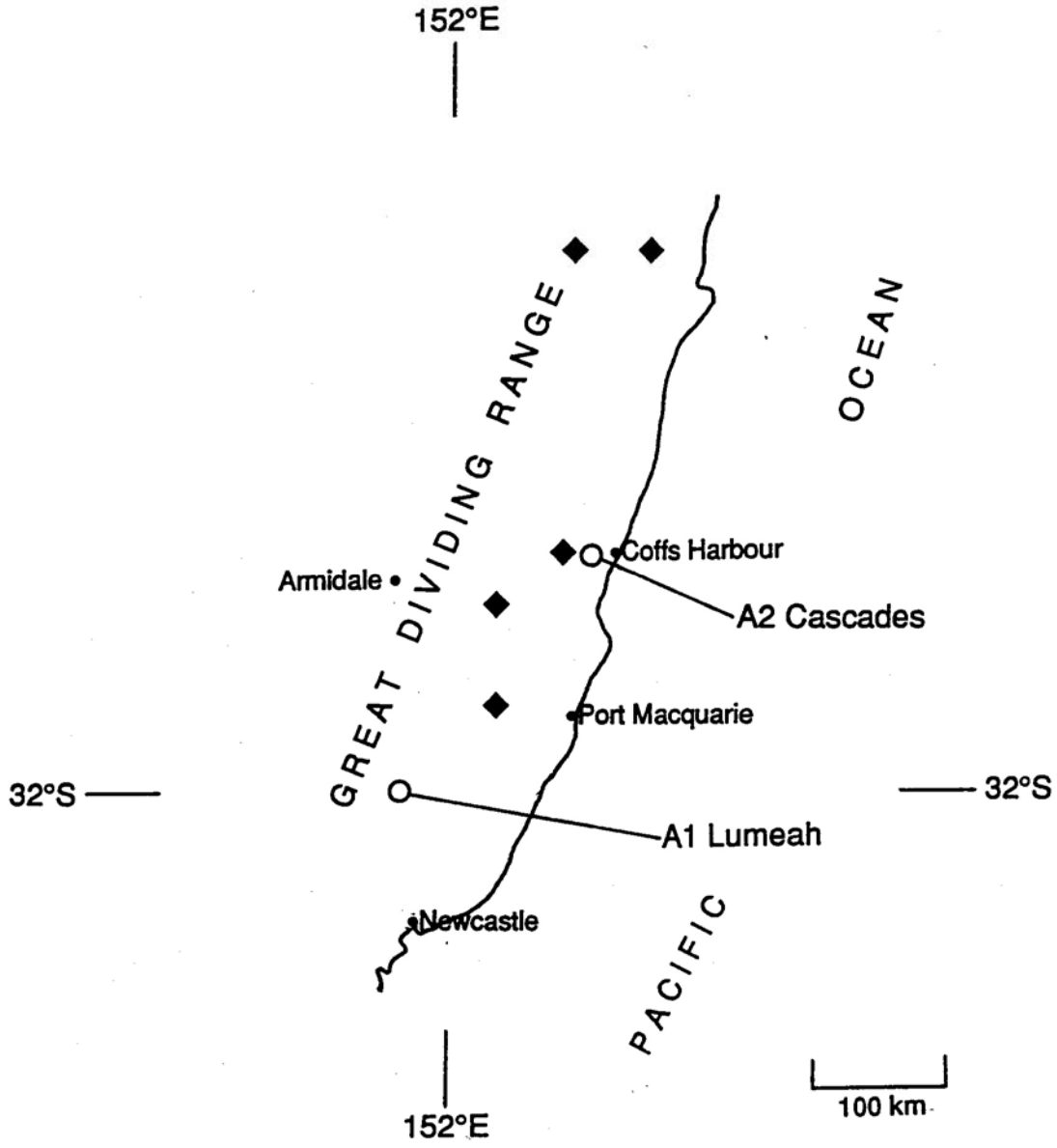



**Fig. 3.2** Locations of study sites in New South Wales, Australia, showing (diamonds) additional *Nothofagus moorei* localities (after Floyd 1990; Williams & Bale 1993).

LANDMASS: NEW ZEALAND (Z)

The five New Zealand *Nothofagus* taxa generally occur as physiognomic dominants or codominants of evergreen rainforest that is the most abundant natural vegetation type in New Zealand (Wardle 1991). *N. fusca, N. menziesii* and *N. solandri* var. *cliffortioides* are the most common taxa, and often occur together, forming a pure or almost pure *Nothofagus* canopy (Wardle 1984). *N. truncata* and *N. solandri* var. *solandri* have more restricted distributions, and were not present at any of the eight study sites sampled in New Zealand. Three geographic regions were included in the study, broadly spanning the stronghold areas of *Nothofagus* forest in New Zealand (Fig. 3.3). Several individual sites were established in each region, to provide data suitable for comparisons at the local scale (see Chapters 1, 2).

A considerable body of literature on the ecology of New Zealand *Nothofagus*-dominated forests exists, and only a representative sample is cited here. Wardle (1984) deals with the distribution and composition of the forests in some detail, also discussing regeneration dynamics, the roles of consumer organisms in *Nothofagus* ecology, and effects of exotic herbivores. Population dynamics and regeneration ecology have been examined for *N. fusca* by June & Ogden (1975, 1978); for *N. solandri* by Wardle (1970); for *N. menziesii* by Wardle (1980) and Stewart (1986); and for mixed *N. fusca-N. menziesii* forests (including that at site ZC2 Station, see below) by Stewart & Rose (1990) and Stewart *et al.* (1991). Succession and the role of disturbance in *Nothofagus* ecology was investigated by Jane (1986) and Mark *et al.* (1989), while Jane (1994) and Allen *et al.* (1994) examined effects of introduced herbivores on stand structure. Bycroft *et al.* (1993), Smith *et al.* (1994) and Wilson *et al.* (1995) have sought community structure in New Zealand *Nothofagus*-dominated forests using various approaches.

*Region: Southern New Zealand* (ZS)

**Site ZS1 Ten Mile**, 45° 17' S, 167° 48' E. This site was part of the Ten Mile Bush, a stand of *Nothofagus solandri* forest by the eastern shore of Lake Te Anau, altitude 220 m. The dominant canopy trees are ascribed to *N. solandri* var. *cliffortioides* by Wardle (1984). Their mean height and DBH were 29 m and 45 cm, respectively. *N. menziesii* also reached canopy height occasionally. A scattered small tree stratum included *Myrsine australis* (Myrsinaceae), *M. divaricata*, and *Pseudopanax crassifolius* (Araliaceae), while the well-developed shrub layer was dominated by *Neomyrtus pedunculata* (Myrtaceae) and *Coprosma* spp. (Rubiaceae). Dense regeneration of both *Nothofagus* species occurred under treefall gaps and minor canopy openings. The forest floor was characterised by luxuriant bryophyte cover, possibly reflecting somewhat poor drainage associated with the very gentle slope (5°). Thirty-three vascular plant species were observed within the five quadrats sampled. Aspect averaged 230° SW. Surface geology consists of recent gravels and till of glacial origin (New Zealand Geological Survey 1972).

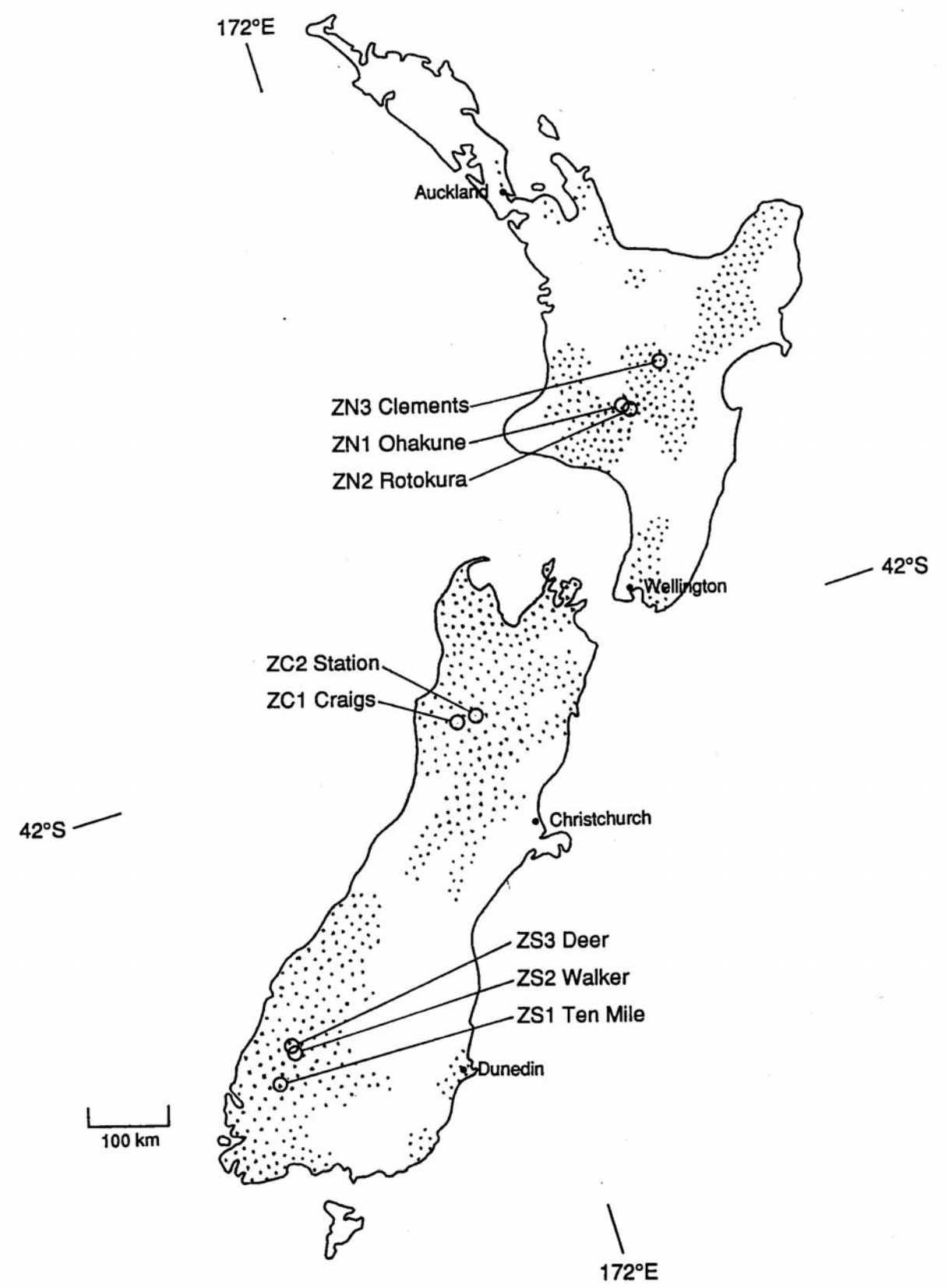



**Fig. 3.3** Locations of study sites in New Zealand, showing (shading) the approximate distribution of *Nothofagus*-dominated forests (after Wardle 1984).

**Site ZS2 Walker**, 45° 07' S, 167° 57' E. Situated near Walker Creek, on terraces above the Eglinton River, 335 m asl, this site was dominated by tall, multi-aged *Nothofagus fusca* (height 33 m, DBH 77 cm), with *N. menziesii* also present as a subcanopy or, occasionally, canopy tree. Small trees, including *Pseudowintera colorata* (Winteraceae), *Griselinia littoralis* (Griseliniaceae) and *Carpodetus serratus* (Escalloniaceae), were associated mainly with canopy openings. A dense shrub and juvenile tree layer (*Coprosma* spp., *Neomyrtus pedunculata*, *Pseudopanax* spp.) attained maximum density and diversity in treefall gaps, although *N. pedunculata* was most conspicuous beneath the closed canopy. Advance growth (very low seedlings) of *N. fusca* was ubiquitous at ground level. Ferns, notably *Polystichum vestitum* (Aspidiaceae) and *Blechnum* spp. (Blechnaceae), and tussocks of *Microlaena avennacea* (Graminiae), were associated mainly with ephemeral watercourses. Species richness was 36 (five quadrats). Slope averaged 20°, aspect 250° W. The bedrock consists of upper Mesozoic (probably Devonian) diorite, quartz diorite, granodiorite or granophyre (New Zealand Geological Survey 1972).

**Site ZS3 Deer**, 44° 59' S, 168° 00' E. This study site, near Deer Flat, was located within a *Nothofagus menziesii*-dominated community associated with gravelly river fans in the base of the Eglinton River valley, altitude 370 m. Within the study area *N. menziesii* (height 29 m, DBH 42 cm), formed an almost pure canopy except for occasional individuals of *N. fusca*, which grew on elevated ground with deeper soils. A well-developed shrub layer, dominated by *Coprosma* spp., was present, while dense regeneration of *N. menziesii* occurred mainly beneath canopy openings. A large fern, *Polystichum vestitum*, formed the principal ground cover over much of the study site. Twenty-six species occurred within the five quadrats sampled. Mean slope was 5°, aspect 200° S. Basement geology consists of Permian volcanics (New Zealand Geological Survey 1972), but alluvial deposits were present at the ground surface and probably extended to a considerable depth.

*Region: Central New Zealand* (ZC)

**Site ZC1 Craigs**, 42° 14' S, 171° 57' E. This site, near Craigs Clearing, was representative of the luxuriant rainforest characteristic of the humid western watersheds of the Southern Alps (Wardle 1984). *Nothofagus fusca* (height 28 m, DBH 43 cm) was the dominant species with *N. menziesii* (height 25 m, DBH 45 cm) forming a secondary canopy and subcanopy component. Both species were very mature and canopy openings due to fallen trees were a prominent feature of the forest. The small tree stratum included *Aristotelia serrata* (Elaeocarpaceae), *Fuchsia excorticata* (Onagraceae), *Carpodetus serratus* and *Pseudopanax crassifolius*. The shrub layer was characterised by *Pseudowintera colorata*, *Neomyrtus pedunculata* and *Coprosma* spp., while tree ferns (*Dicksonia fibrosa*) were associated with canopy gaps. A diversity of pteridophytes,

notably *Leptopteris superba* (Osmundaceae), *Cyathea colensoi* (Cyatheaceae), *Polystichum vestitum* and *Blechnum* spp., occurred at ground level, as well as tussocks of *Microlaena avennacea* and *Astelia nervosa* (Liliaceae). Epiphytic ferns, especially *Hymenophyllum* spp. (Hymenophyllaceae), were abundant. Little regeneration of *N. fusca* was observed, although seedlings and saplings of *N. menziesii* were abundant beneath canopy gaps. The climber *Muehlenbeckia australis* (Polygonaceae) was relatively common. Species richness (five quadrats) was 47. Slope averaged 10°, aspect 250° W. There was some evidence that nearby forest had been overcut in the past. Underlying geology consists of granite, granodiorite, quartz diorite, diorite or aptite of upper Mesozoic age, and is overlain by recent glacial deposits (New Zealand Geological Survey 1972).

**Site ZC2 Station**, 42° 12' S, 172° 15' E. Located in a rainshadow zone, the Maruia River valley, at an altitude of 410 m, this site contrasted markedly in structure and composition with its neighbour, described above. *Nothofagus fusca* (height 31 m, DBH 79 cm) and *N. menziesii* (height 27 m, DBH 20 cm) dominated a fairly closed canopy, *N. fusca* accounting for some 75% of total canopy cover. The understorey was sparse, mainly comprising the shrub *Neomyrtus pedunculata* and scattered individuals of *Pseudopanax crassifolius*, *Myrsine divaricata* and *Coprosma* spp. *Pseudowintera colorata* and *Griselinia littoralis* occurred beside a watercourse (Station Creek) which flowed past the study site. Regeneration of both canopy species was present at a moderate density. Fewer vascular plant species (22 species in five quadrats) were observed than at any of the other New Zealand sites sampled. The study site had negligible slope and aspect. Bedrock in the area consists of lower Quaternary marine sediments (New Zealand Geological Survey 1972), overlain by alluvial sand and silt at the study site (Stewart *et al.* 1991).

*Region: Northern New Zealand* (ZN)

**Site ZN1 Ohakune**, 39° 22' S, 175° 28' E. This site was located on a terrace at 840 m altitude on the southern slopes of Mt. Ruapehu, an intermittently active volcano. The canopy was more-or-less equally dominated by *Nothofagus solandri* var. *cliffortioides* (height 23 m, DBH 48 cm) and *N. menziesii* (height 23 m, DBH 40 cm). A single adult individual of *N. fusca* (height 16 m, DBH 30 cm) was also observed within the study area. The forest was characterised by a complex structure and high diversity of vascular taxa (63 species in five quadrats). Small tree or subcanopy species present included *Nestigis cunninghamii* (Oleaceae), *Carpodetus serratus*, *Pseudowintera colorata*, *Prumnopitys ferruginea* (Podocarpaceae) and *Podocarpus cunninghamii* (Podocarpaceae). Important shrubs were *Coprosma* spp., *Pseudopanax anomalus*, *Neomyrtus pedunculata* and *Elaeocarpus hookerianus* (Elaeocarpaceae). Pteridophytes were conspicuous both at ground-level (e.g. *Leptopteris superba*, *Polystichum vestitum*, *Blechnum* spp. and a tree fern, *Cyathea smithii*) and as epiphytes (*Asplenium flaccidum* [Aspleniaceae],

*Phymatosorus diversifolius* [Polypodiaceae], *Hymenophyllum* spp.). Several angiosperms were present as epiphytes, including *Astelia nervosa* and *Cordyline indivisa* (Agavaceae), as well as the climbers *Clematis paniculata* (Ranunculaceae), *Parsonsia capsularis* (Apocynaceae) and *Rubus schmidelioides* (Rosaceae). *Microlaena avennacea* formed the predominant ground cover. *Nothofagus solandri* and *N. menziesii* showed good regeneration in gaps, but there were few seedlings of *N. fusca*. Slope and aspect were negligible. Quaternary volcanic deposits characterise the geology (Riddolls 1987).

**Site ZN2 Rotokura**, 39° 26' S, 175° 30' E. Situated near Lake Rotokura at the base of Mt. Ruapehu to the south, altitude 680 m, this site had the highest species richness of any examined in the course of the study, a total of 65 species in five quadrats. Dominant species were *Nothofagus fusca*, which attained a height of 28 m and DBH 33 cm, and accounted for some 80% of total canopy cover; and *N. menziesii* (height 27 m, DBH 72 cm, 20% cover). An irregular understorey of small or juvenile tree species included *Carpodetus serratus*, *Aristotelia serrata*, *Pseudowintera colorata*, *Knightia excelsa* (Proteaceae) and *Prumnopitys ferruginea*. Tree ferns — *Dicksonia squarrosa*, *D. fibrosa*, *Cyathea smithii* and *C. dealbata* — formed a prominent layer in some parts of the site. Small-leaved shrubs (e.g. *Coprosma* spp., *Neomyrtus pedunculata*) were less prominent than at other New Zealand sites. One individual of the exotic shrub *Rubus fruticosus* was observed. The ground stratum was dominated by the ferns *Blechnum discolor* and *B. fluviatile* and the grass *Microlaena avennacea*. Epiphytes (e.g. *Asplenium* spp., *Hymenophyllum* spp., *Astelia nervosa*) and climbers (e.g. *Rubus schmidelioides*, *Parsonsia capsularis*) were relatively abundant. Moderate regeneration of *Nothofagus menziesii* and *N. fusca* was associated mainly with treefall gaps. Slope and aspect were negligible. A single sawn stump attested to overcutting of the forest in the past. Recent lahar constitutes the surface geology (Riddolls 1987), as at the neighbouring Ohakune site.

**Site ZN3 Clements**, 38° 58' S, 176° 10' E. This site was located off Clements Mill Road, on undulating ground on the western slopes of the Kaimanawa Range, at an altitude of 740 m. Codominant in the canopy were *Nothofagus fusca* (height 32 m, DBH 71 cm) and *N. menziesii* (height 27 m, DBH 72 cm). Canopy density was relatively variable, with numerous gaps, containing abundant regeneration of both *Nothofagus* species, being present. There were few trees below canopy level, but the shrub stratum was locally dense. The most abundant shrub species were *Neomyrtus pedunculata*, *Pseudowintera colorata* and *Coprosma* spp. Tree ferns, *Cyathea smithii* and *Dicksonia squarrosa* were common in patches, while ground cover consisted mainly of mosses, bare litter or, locally, the fern *Blechnum discolor*. Fifty-five species were observed within the five quadrats sampled. Slope averaged 5°, aspect 250° W. Lower Quaternary marine sediments comprise the predominant geology in the area (Riddolls 1987).

In South America, *Nothofagus* is distributed from 33°S to the southern tip of the continent, at 56°S. It occurs predominantly west of the Andes (i.e. in Chile), but locally also on the slopes and foothills of the Andes to the east, in Argentina (Donoso 1993). Of the nine or ten taxa described only three — the closely related *N. dombeyi, N. nitida* and *N. betuloides* — are evergreen. All three species may be dominants of temperate rainforest in the Valdivia province (*c.* 41°S) of southern central Chile, while *N. dombeyi* occurs at corresponding latitudes in northwest Patagonia, Argentina. Two study sites were established in each of these regions, one, dominated by *N. nitida*, on the Chilean Coastal Range; the others, dominated by *N. dombeyi*, on the western slopes and eastern foothills of the Andes (Fig. 3.4). A marked rainfall gradient exists from west to east across the Andes, and the three Andean communities might be expected to show corresponding differences in structure and composition. Ecological differences between the Andes and the Coastal Range have been attributed to enhanced disturbance regimes in the Andes, where volcanic eruptions, landslides and earthquakes are common (Veblen *et al.* 1981).

Donoso (1993) summarises the extensive Spanish-language literature on the structure, composition and dynamics of South American *Nothofagus*-dominated forests. Veblen *et al.* (1983) have reviewed the floristics and distribution of temperate evergreen forests in Chile and Argentina. Veblen and colleagues have also investigated stand establishment, population dynamics and interspecific interactions within various *Nothofagus*-dominated communities in Chile (Veblen *et al.* 1977a,b, 1981, 1989; Veblen 1979, 1985, 1989; Robertus *et al.* 1993) and Argentina (Veblen & Lorenz 1987; Veblen 1989; Veblen *et al.* 1989; Robertus *et al.* 1993).

*Region: Valdivia, Chile* (SC)

**Site SC1 Pelada**, 40° 12' S, 73° 26' W. This site was located at 945 m asl on top of the Cordillera Pelada, a section of the range of hills that flanks the west coast of Chile from Santiago southward to Puerto Montt. The dominant species was *Nothofagus nitida*[1], which was predominantly even-aged with a height of 20 m and mean DBH 38 cm. Stem density was extremely high, with an average of 28 canopy *N. nitida* individuals occurring in each 20 × 20 m quadrat. A few apparently older individuals with DBH up to 86 cm were present in one part of the study site. *Podocarpus nubigena* and *Saxegothaea conspicua* (both Podocarpaceae) were present as subcanopy trees, as were smaller trees and shrubs, *Laurelia philippiana* (Monimiaceae), *Amomyrtus luma* (Myrtaceae) and *Myrceugenia chrysocarpa* (Myrtaceae). *Chusquea quila* (Gramineae), a species of bamboo, was present in locally-dense thickets to a

[1]Although taken to be *N. nitida* on the basis of the leaf morphology of the canopy individuals sampled, regeneration in the area has a leaf morphology more suggestive of a hybrid between *N. nitida* and closely-related *N. betuloides* which is present nearby (C. Ramirez, *personal communication*).

height of 2-3 metres. An understorey of *Chusquea* spp. is characteristic of *Nothofagus*-dominated forests in southern central Chile (Veblen *et al.* 1977a). Ground cover included several shrub species, e.g. *Ugni candollei* (Myrtaceae), *Drimys winteri* (Winteraceae) and *Desfontainea spinosa* (Desfontaineaceae); and ferns, *Blechnum magellanicum* and *Lophosoria quadripinnata* (Lophosoriaceae). Species richness was 27 (four quadrats). Slope averaged 15°, aspect 210° SW. There was evidence of small-scale harvesting of trees and dead wood in the vicinity of the study site. Bedrock in the area consists of schist, slate, quartzite and other metamorphics of Palaeozoic age (Rojas & Subiabre 1991).

**Site SC2 Antillanca**, 40° 47' S, 72° 15' W. This site was located 5 km west of the township of Antillanca on the western slopes of the Andes, altitude *c.* 800 m. The dominant species was taken to be *Nothofagus dombeyi*[2], with average height 28 m and DBH 75 cm. A distinct subcanopy of *Saxegothaea conspicua* was present over much of the site, with bamboos *Chusquea culeou* and *C. uliginosa* forming an extremely dense understorey up to a height of 2-3 m. A number of low shrub species, for example, *Drimys winteri* var. *andina*, *Maytenus magellanica* (Celastraceae) and *Pernettya mucronata* (Ericaceae) were present at minor densities. *Hymenophyllum* spp. were abundant as epiphytes growing on tree trunks. Regeneration of *N. dombeyi* was limited to a few seedlings growing on fallen logs. Thirty-three vascular plant species were observed within the five quadrats sampled. Microtopography was quite variable and locally steep; average slope was 15°, aspect 245° SW. The geology consists of Tertiary volcanics overlain by recent volcanic ash and glacial deposits (Rojas & Subiabre 1991).

*Region: Northwest Patagonia, Argentina* (SA)

**Site SA1 Quetrihué**, 40° 51' S, 71° 37' W. Situated at the southern end of Peninsula Quetrihué, near the shore of Lake Nahuel Huapi, altitude 770 m, this site was unusual among *Nothofagus*-dominated forests in the region in lacking a bamboo understorey. The canopy trees were *N. dombeyi* (height 40 m; DBH 91 cm). A conifer, *Austrocedrus chilensis* (Cupressaceae) was also present, occasionally reaching canopy height within the study area. Common understorey trees or tall shrubs were *Luma apiculata* (Myrtaceae) and *Aristotelia chilensis*, the latter forming a distinct layer up to 3-4 m height, superficially reminiscent of that of *Chusquea* spp. within other forests in the area. Several low shrub species were present at minor densities, including *Berberis darwinii* (Berberidaceae), *Maytenus chubutensis* and *Schinus patagonicus* (Anacardiaceae). Larger canopy gaps were characterised by dense seedling and sapling growth of *N. dombeyi*.

[2]The closely-related species *N. betuloides* dominates montane forest a few km further up the Antillanca Valley (Veblen 1979). The two species are difficult to distinguish morphologically, and the canopy trees at the site could be a hybrid, or even pure *N. betuloides* (C. Ramirez, *personal communication*).

Species richness was 25 (three quadrats). Slope and aspect were negligible across the study site. Tertiary and Quaternary andesitic volcanic ashes characterise the local geology (Veblen *et al.* 1989).

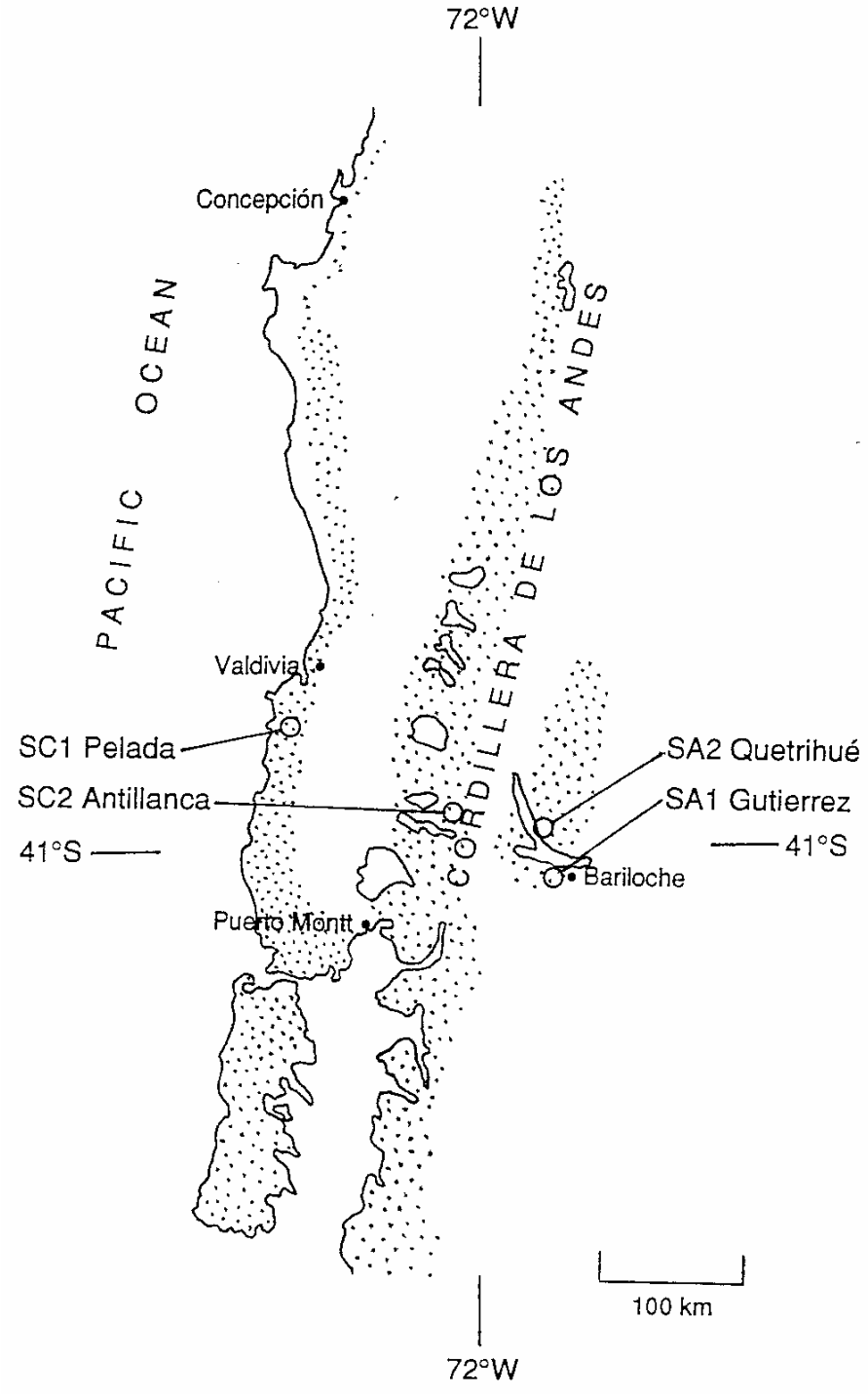



**Fig. 3.4** Locations of study sites in South America, showing (shading) the approximate distribution of *Nothofagus betuloides, N. dombeyi* and *N. nitida* in southern central Chile and northwest Patagonia, Argentina (after Donoso 1993).

**Site SA2 Gutierrez**, 41° 11' S, 71° 25' W. This site was located by Lago Gutierrez at an altitude of 810 m. An apparently even-aged stand of *Nothofagus dombeyi* (height 29 m, DBH 54 cm) formed the forest canopy. *Austrocedrus chilensis* was present occasionally as a subcanopy tree, and there was a dense understorey of bamboo, *Chusquea culeou*. Scattered low shrubs included *Berberis darwinii*, *Schinus patagonicus* and *Maytenus chubutensis*. Ground cover consisted primarily of forbs, *Osmorhiza chilensis* (Apiaceae), *Baccharis* aff. *salicifolia* (Asteraceae) and *Alstroemeria aurea* (Alstroemeriaceae). *Vicia nigricans* (Fabaceae) was relatively common twined among the branches of shrubs. Species richness was 15 (three quadrats), the lowest encountered in the present study. Mean slope was 10°, aspect 106° E. Volcanic ash comprises the surface geology in the area (L. Sancholuz, *personal communication*).

## 3.3 Comparison of site environments

An important assumption of the hypothesis of community-level convergence is that the communities being compared occur in similar environments (Orians & Paine 1983). It is not clear how great an environmental difference would be needed before a tendency towards convergence, due to overdispersion of species niches by the action of assembly rules, would be balanced by a tendency towards divergence, caused by species adaptations to different physical environments (see Section 1.5). If convergence can not be shown statistically, this could mean that there were no assembly rules, but, alternatively, it could mean that the communities were too dissimilar environmentally for convergence to be detectable, even if assembly rules did apply. While the possibility of convergence can therefore never be rejected with complete confidence (Barbour & Minnich 1990; Keeley 1992), it may be deemed unlikely if no convergence can be shown, even for communities that are very closely matched in their environmental parameters, i.e. that would seem to fulfil this assumption of the convergence hypothesis.

Community-level convergence might be expected to occur both among sites within a local area, or among disjunct sites, for example, on different landmasses. Floristic overlap is likely to be very low between landmasses, which is a technical advantage for statistical tests for convergence, which must focus on the species that are not in common between communities (see Section 6.2). However, convergence may be more difficult to demonstrate among landmasses, because the likelihood that the sites being compared have similar environments would tend to be lower.

In the following analysis, the 17 study sites are compared in terms of the major environmental parameters measured, to identify the sites, regions and landmasses for which the assumption of environmental similarity appears most likely to be met. Particular attention is given to the identification of environmentally-matched sites from different landmasses, since environmental differences are more likely to confound convergence at the landmass, than at the local, level. In subsequent chapters, this information is used to focus comparisons on

communities that are most likely to possess the preconditions to exhibit community-level convergence.

## METHODS

### *Environmental data*

The environmental data compiled for each site were climate parameters (mean temperature of the warmest month [MTWM], mean temperature of the coldest month [MTCM], mean annual temperature [MAT], annual rainfall [AR] and rainfall in the driest quarter [RDQ]), soil parameters (total potassium [K], nitrogen [N], phosphorus [P], pH and organic content [OC]) and proportional canopy light transmittance. Methods by which these data were acquired are described in Section 2.3.

### *Analysis*

To aid in the comparison of sites, principal component analysis (PCA) was carried out on the environmental parameters. PCA provides a means of concentrating the shared variation in a number of intercorrelated variables within a smaller number of uncorrelated ones, the principal components (PCs). The PCs are linear combinations of the original variables, uncorrelated with respect to the data supplied, and in rank order of the proportion of the total sample variance they explain (Manly 1994). Separate PCAs were carried out for climate data (five variates) and soil data (four variates). Phosphorus was not included in the soil PCA because no values were obtained for Chilean sites, and values for Argentina were not comparable with those obtained elsewhere (see Section 2.3.4). Variables were standardised (mean 0, standard deviation 1) prior to analysis, to ensure that they would be weighted equally in generating PCs. For both analyses, each PC with an eigenvalue $\geq 1$ was used, while remaining PCs (which would explain less variation than one of the original variables) were ignored.

Varimax factor rotation of climate and soil PCs was performed, to attempt to improve interpretability of the derived variables. Axes of the chosen PCs were `rotated' in abstract space, such that the variance of the squares of the loadings (linear coefficients on the original variables) of the new (rotated) axes was maximised. This means that, for each axis (factor), the absolute values of the loadings of some variables are maximised relative to the other variables. This can improve interpretability of the factors, which will be more more closely related to variables with large loadings than small ones. The disadvantage of factor analysis is that the rank order of explained variation in the original PCs may be lost (Manly 1994). Factor rotation did not significantly improve interpretability for the climate or soil data. Consequently, unrotated axes (the original PCs) are presented below.

PCA and factor rotation were performed with the Genstat statistical program (Genstat 5

committee 1987).

## RESULTS

### *Climate*

Climate data for each of the 17 sites are presented in Table 3.1.

**Table 3.1** Climate parameter values for all study sites, showing means among sites. MTWM=mean temperature of warmest month; MTCM=mean temperature of coldest month; MAT=mean annual temperature; AR=annual rainfall; RDQ=rainfall for driest quarter. Site codes are given in Section 3.2.

| Site | MTWM (°C) | MTCM (°C) | MAT (°C) | AR (mm) | RDQ (mm) |
|---|---|---|---|---|---|
| T1 | 15.9 | 7.8 | 11.3 | 1570 | 230 |
| T2 | 13.1 | 4.3 | 8.3 | 1790 | 330 |
| T3 | 13.3 | 3.3 | 8.1 | 1730 | 270 |
| A1 | 18.4 | 5.0 | 12.2 | 1120 | 250 |
| A2 | 17.0 | 5.9 | 11.3 | 1460 | 270 |
| ZS1 | 14.6 | 4.2 | 9.7 | 1210 | 270 |
| ZS2 | 14.4 | 3.8 | 9.4 | 1680 | 360 |
| ZS3 | 14.4 | 3.7 | 9.3 | 2400 | 490 |
| ZC1 | 15.5 | 4.2 | 10.0 | 2510 | 510 |
| ZC2 | 15.3 | 4.2 | 9.8 | 2080 | 410 |
| ZN1 | 13.2 | 3.6 | 8.5 | 1880 | 360 |
| ZN2 | 14.5 | 4.6 | 9.7 | 1250 | 240 |
| ZN3 | 14.8 | 4.3 | 9.6 | 1510 | 320 |
| SC1 | 15.0 | 7.9 | 11.3 | 4000 | 460 |
| SC2 | 12.3 | 3.5 | 7.8 | 4970 | 130 |
| SA1 | 13.5 | 6.0 | 10.2 | 1650 | 140 |
| SA2 | 12.5 | 6.5 | 10.3 | 1090 | 100 |
| mean | 14.6 | 4.9 | 9.8 | 1990 | 300 |

Loadings and percentage variation explained by the first three principal components (PC1, PC2, PC3) based on the five climate variables, are given in Table 3.2. The fourth and fifth PCs had eigenvalues <1 and were therefore not used. The loadings for each PC are the linear coefficients on the original variables from which PC scores are calculated. The importance of each variable in defining the PC is thus given by the magnitude of its loading (which is a Pearson *r* correlation coefficient between the base variable and the PC). PC1 is most strongly correlated with MAT and MTWM, and so may be interpreted as representing primarily temperature. PC2 is strongly

related to dry-season rainfall (RDQ), while PC3 corresponds to both total rainfall (AR) and winter temperatures (MTCM). Site coordinates in three-dimensional space defined by the climate PCs are shown in Fig. 3.5. Sites whose coordinates fall close together are relatively similar in terms of the climate parameters measured. The figure is interpreted below.

**Table 3.2** Loadings used to calculate principal components (PCs) from climate variables (see Table 3.1), and percentage of variation explained by each PC. Loadings >0.5 are shown in bold type.

| Variate | Loading | | |
|---|---|---|---|
| | PC1 | PC2 | PC3 |
| MTWM | **0.54** | 0.36 | 0.17 |
| MTCM | 0.47 | -0.29 | **-0.52** |
| MAT | **0.64** | 0.01 | -0.11 |
| AR | -0.26 | 0.24 | **-0.82** |
| RDQ | 0.00 | **0.85** | -0.02 |
| % variation explained | 47 | 25 | 20 |

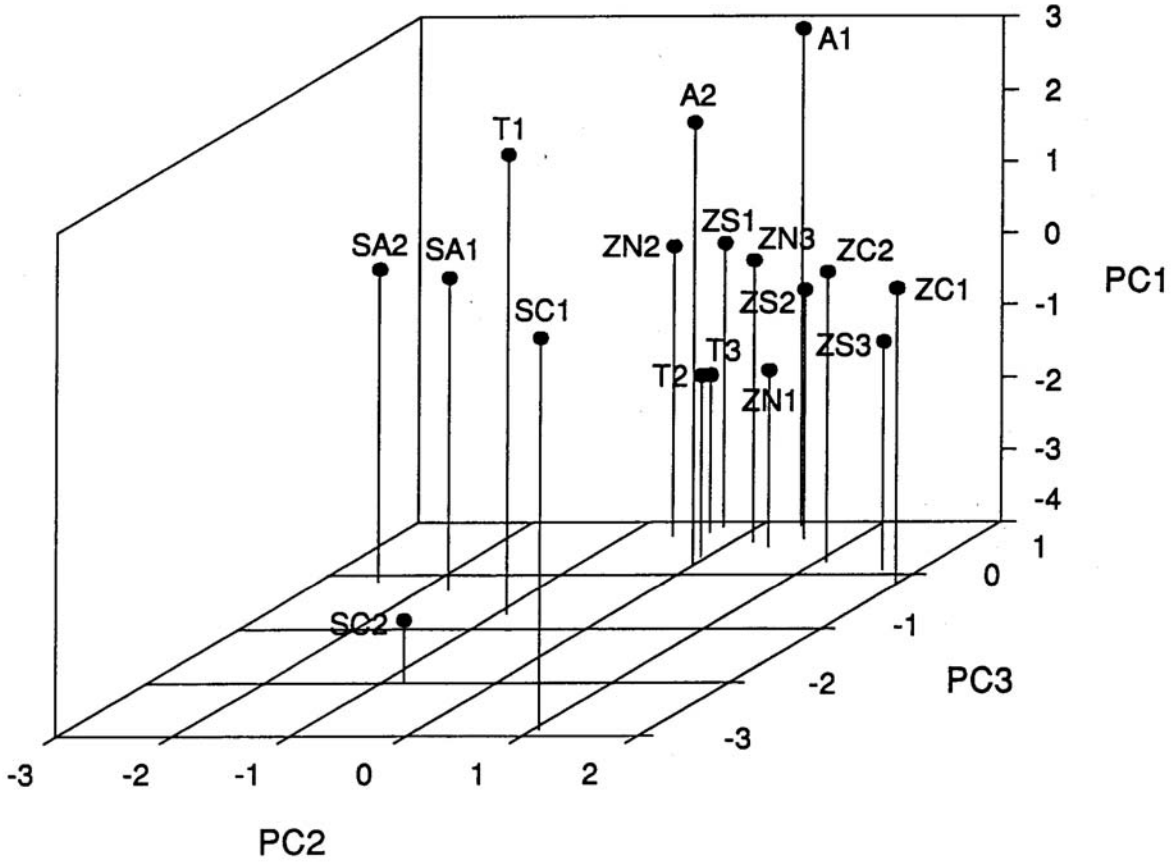



**Fig. 3.5** Site scores on the first three axes of a principal component ordination of study sites based on five climate variables (see Table 3.1). Site codes (shown beside each point) are given in Section 3.2.

*Soils*

Soil data for the study sites are given in Table 3.3.

**Table 3.3** Soil parameter values for all study sites, showing mean among sites. Site codes are given in Section 3.2. P values for sites SA1 and SA2 were obtained by a different method and are indicative only. Mean P is calculated from sites T1 to ZN3 only.

| Site | Total K (ppm) | Total N (ppm) | Total P (ppm) | pH | Organic content (%) |
|---|---|---|---|---|---|
| T1 | 1400 | 2500 | 480 | 5.3 | 25 |
| T2 | 1350 | 4800 | 420 | 4.7 | 33 |
| T3 | 2900 | 2300 | 260 | 4.0 | 15 |
| A1 | 1440 | 1000 | 2250 | 4.8 | 36 |
| A2 | 730 | 800 | 890 | 4.5 | 31 |
| ZS1 | 460 | 1700 | 180 | 4.6 | 13 |
| ZS2 | 670 | 3300 | 980 | 4.9 | 15 |
| ZS3 | 750 | 4500 | 740 | 5.2 | 18 |
| ZC1 | 880 | 3600 | 700 | 4.7 | 15 |
| ZC2 | 920 | 1800 | 420 | 4.2 | 10 |
| ZN1 | 410 | 5400 | 420 | 5.4 | 22 |
| ZN2 | 410 | 6700 | 520 | 5.4 | 26 |
| ZN3 | 400 | 3100 | 340 | 5.4 | 18 |
| SC1 | 210 | 3000 | - | 3.8 | 9 |
| SC2 | 230 | 4700 | - | 4.9 | 14 |
| SA1 | 80 | 4100 | (50) | 6.4 | 15 |
| SA2 | 90 | 3200 | (70) | 6.7 | 11 |
| mean | 780 | 3300 | 660 | 5.0 | 19 |

Loadings and percentage variation explained by the first two principal components (PC1, PC2) derived from four soil variables, are given in Table 3.4. The third and fourth PCs had eigenvalues <1 and were therefore not used. PC1 summarises variation in three variables, K, N and pH, while PC2 is primarily related to the remaining variable, organic content. Site coordinates in soil PC space are shown in Fig. 3.6, which is discussed below. Soil P is shown separately, for the sites for which P measurements were made (Fig. 3.7).

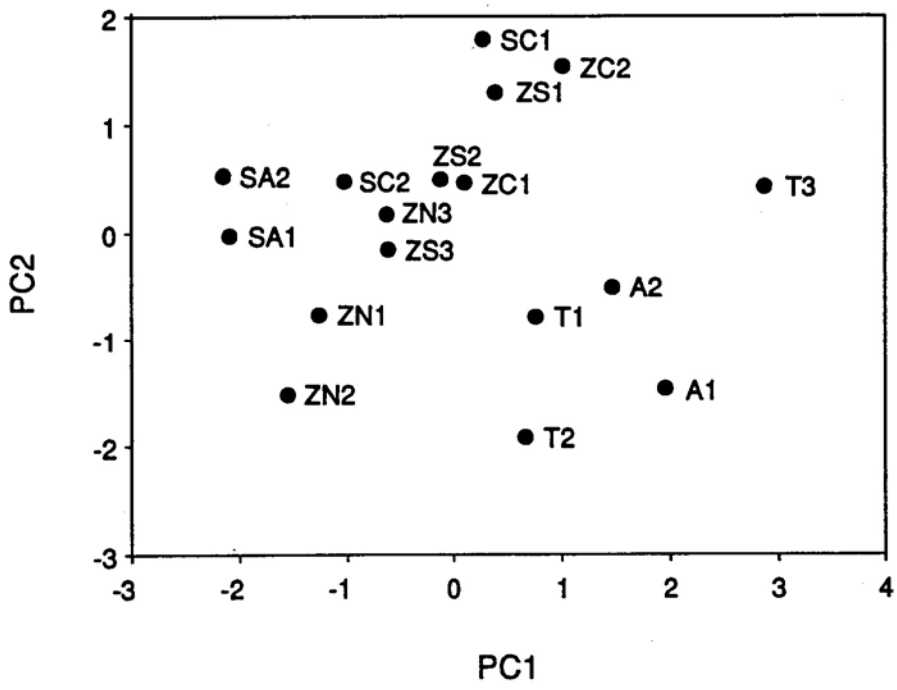



**Fig. 3.6** Site scores on the first two axes of a principal component ordination of study sites based on four soil variables (see Table 3.3; P not included in the ordination). Format as for Fig. 3.5.

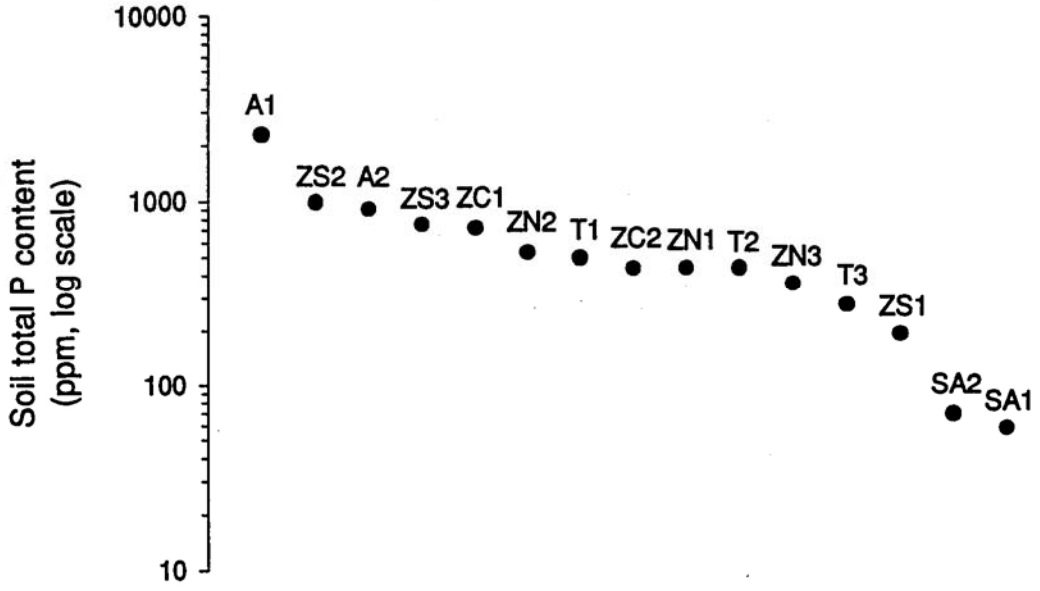



**Fig. 3.7** Soil phosphorus concentrations (log scale) at study sites. All values are total P except for SA1 and SA2, which were obtained by a different method and may be interpreted as available P (see Section 2.3.4). Format as for Fig. 3.5.

**Table 3.4** Loadings used to calculate principal components (PCs) from soil variables (see Table 3.3), and percentage of variation explained by each PC. OC=organic content. Format as for Table 3.2.

| Variate | Loading | |
|---|---|---|
| | PC1 | PC2 |
| K | **0.61** | -0.22 |
| N | **-0.50** | -0.33 |
| pH | **-0.57** | -0.28 |
| OC | 0.22 | **-0.88** |
| % variation explained | 46 | 27 |

*Light transmittance*

As anticipated, differences in light flux conditions during measurement appeared to affect canopy light transmittance values (Table 3.5). Measurements made in direct light (sunny) conditions were significantly lower than those made in diffuse light (cloudy) conditions ($P<0.001$; one-tailed *t*-test on ln-transformed site means for `sunny' versus `cloudy' sites). Only sites measured in similar light conditions can be compared. Values are presented separately for `sunny' and `cloudy' sites in Fig. 3.8, which is discussed below. Note that no light transmittance measurements were made for T2 Anne.

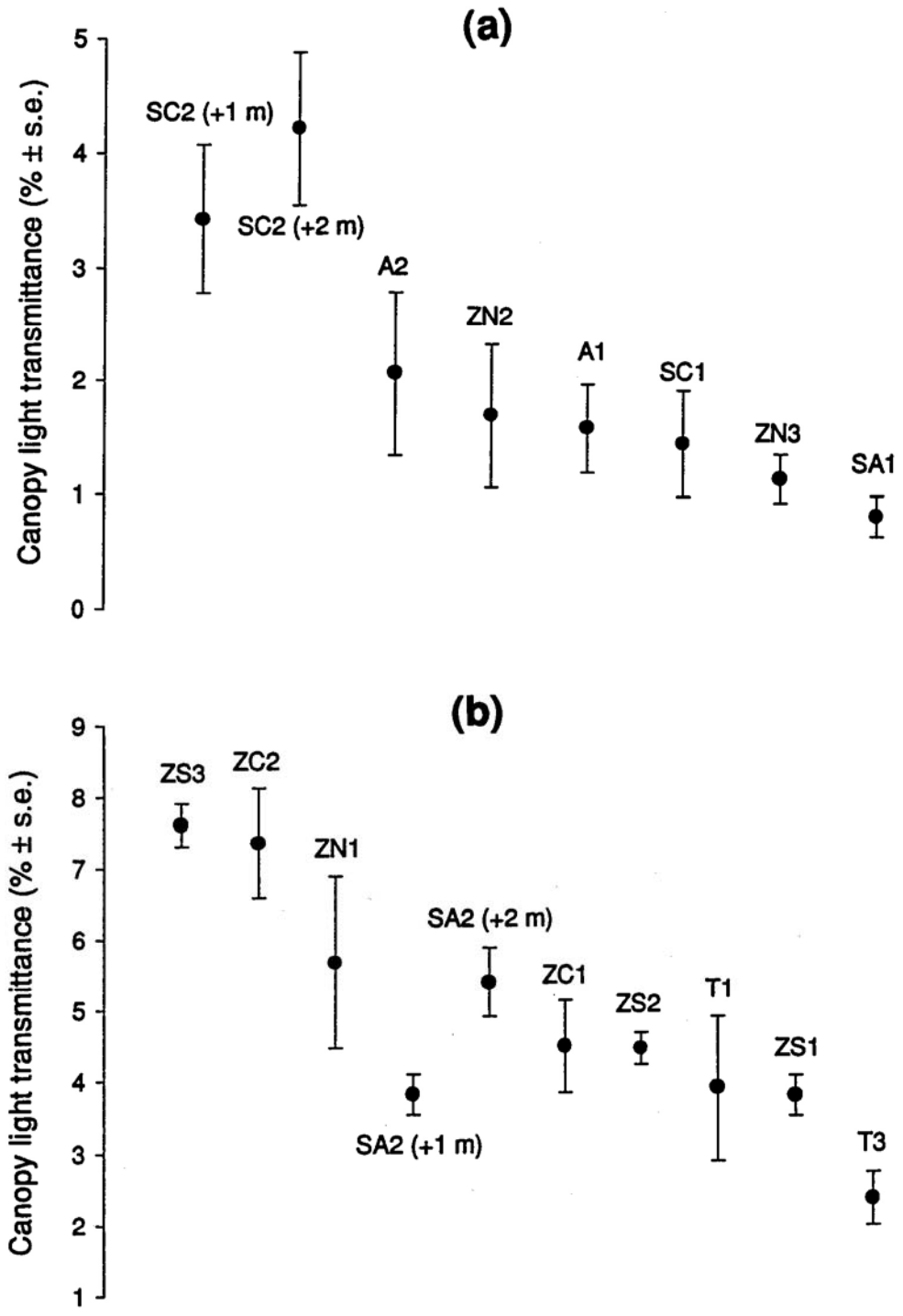



**Fig. 3.8** Mean canopy light transmittance (% of incident light at canopy level) for **(a)** sites measured during diffuse light (cloudy) conditions; **(b)** sites measured during direct light (sunny) conditions. Standard error bars ($\sigma/\sqrt{n}$; $\sigma$=standard deviation of quadrat mean values; $n$=number of quadrats sampled) are shown. Values measured at 1 m and 2 m above ground level are shown for sites SA2 and SC2; for all other sites, values are for 1 m above ground level.

**Table 3.5** Mean canopy light transmittance (% of incident light at canopy level) for study sites, showing light conditions during sampling and means among sites for `cloudy' and `sunny' sampling conditions. Values measured at 1 m and 2 m above ground level are shown for sites SA2 and SC2; for all other sites, values are for 1 m above ground level.

| Sampling conditions | Site | Transmittance (%) |
|---|---|---|
| cloudy | T1 | 3.9 |
| | T3 | 2.3 |
| | ZS1 | 3.7 |
| | ZS2 | 4.4 |
| | ZS3 | 7.6 |
| | ZC1 | 4.5 |
| | ZC2 | 7.3 |
| | ZN1 | 5.7 |
| | SA2 (+1m) | 3.8 |
| | SA2 (+2m) | 5.4 |
| | Mean* | 5.0 |
| sunny | A1 | 1.6 |
| | A2 | 2.1 |
| | ZN2 | 1.7 |
| | ZN3 | 1.1 |
| | SC1 | 1.4 |
| | SC2 (+1m) | 3.4 |
| | SC2 (+2m) | 4.2 |
| | SA1 | 0.8 |
| | Mean* | 1.8 |

*Based on values at +2m only for SA2 and SC2.

## DISCUSSION

### *Environmental variation among landmasses, regions and sites*

In terms of both climate (Fig. 3.5; Table 3.1) and soils (Figs. 3.6, 3.7; Table 3.3) sites on the same landmass tend to be more similar to each other than to sites on other landmasses, demonstating that there may be systematic environmental differences between the landmasses. In particular,

the eight New Zealand sites have rather similar scores on all three climate PCs, as well as on soil PC2. There are no clear differences in environments between the northern, central and southern regions of New Zealand. Two of the three Tasmanian sites, T2 Anne and T3 Mathinna, are very similar climatically and have relatively similar soils, although the third, T1 Balfour, experiences higher temperatures, placing it some distance away in climate space. The two Australian sites, A1 Lumeah and A2 Cascades, are relatively closely-matched in terms of both climate and soils. Argentinian sites SA1 Quetrihué and SA2 Gutierrez have similar climates and soils, but differ markedly from the Chilean sites, which experience considerably higher rainfall and (for SC2 Antillanca) low temperatures. The Chilean sites themselves differ markedly in climate, temperature and summer rainfall.

Understorey light climates, on the other hand, show no simple geographic patterns (Fig. 3.8; Table 3.5). For example, light transmittance (as measured in cloudy conditions) varies from 3.7% to 7.6% in southern New Zealand, while values in Argentina (SA2), Tasmania (T1), northern New Zealand (ZN1) and central New Zealand (ZC1, ZC2) are intermediate between these extremes.

Among the landmasses, Tasmania and New Zealand appear to be the most similar, at least in terms of climate, two Tasmanian sites, T2 Anne and T3 Mathinna, having quite similar values on PC2 (dry season rainfall) and PC3 (annual rainfall and winter temperatures) to most New Zealand sites, although PC1 (temperature) values are somewhat lower. Soil parameters tend to match for PC2 (organic content) but are somewhat higher for PC1 primarily due to higher K concentrations in the Tasmanian soils. Soil P values in Tasmania are comparable with the northern New Zealand sites. At the level of individual sites, T3 Mathinna and ZN1 Ohakune have similar climates, but rather different soils. Understorey light conditions may also be rather different at the two sites, light transmittance at Mathinna being less than half that at Ohakune. T2 Anne and Ohakune, however, are very similar climatically, and also have rather similar soils, their dissimilarity on soil PC1 being mainly due to different potassium concentrations. A comparison with respect to canopy light transmittance cannot be done, since no values were obtained for Anne.

Australian sites A1 Lumeah and A2 Cascades are exceptional both in terms of temperatures (high values on climate PC1) and soils (high values on soil PC1 associated with low N, but high P, concentrations). However, Cascades is relatively close to the Tasmanian site T1 Balfour in climate space, at least on PC1 (which accounts for almost 50% of variation in the climate parameters), and these two sites also have relatively similar soils. Comparison of these sites in terms of canopy light transmittance is not possible, as measurements were made in different light flux conditions at the two sites.

South American sites tend to be dissimilar from the other regions climatically, primarily due to differences in the amount of rainfall (especially Chile) and the seasonality of rainfall (Argentina). In terms of soils, Chilean sites have low K content and low pH, although N content

is comparable with New Zealand and Tasmania; Argentinian soils are more alkaline than those of other regions and appear to be deficient in potassium. However, SA1 Quetrihué and ZN2 Rotokura experience relatively similar climates, and are only moderately dissimilar in terms of soils (though no comparison can be made for phosphorus) and light regimes.

*Identification of environmentally-matched communities*

The above observations suggest several between-site, between-region and between-landmass comparisons that are more likely to reveal community-level convergence than others, because the communities concerned have relatively similar values for major environmental parameters.

At the landmass scale, New Zealand and Tasmania appear to be more closely matched than any other pair of the landmasses sampled. Between regions within a landmass, the northern, and particularly the southern and central regions of New Zealand exhibit little overall environmental dissimilarity. Tasmanian sites Anne and Mathinna are also closely matched, as are the Lumeah and Cascades on mainland Australia. Environmental variation among sites at the local level is generally low, with the exception of Chilean sites Pelada and Antillanca.

Best-matched sites from different landmasses are Anne (Tasmania) and Ohakune (New Zealand); Quetrihué (Argentina) and Rotokura (New Zealand); and Balfour (Tasmania) and Cascades (Australia).

Particular attention will be focused on these comparisons in interpreting the results of tests seeking community-level convergence in Chapters 6-10.

# 4. Interrelationships and vertical trends for species characters

## 4.1 Introduction

The hypothesis of convergence in community texture is that disjunct communities in similar environments will have more similar texture (community-wide spectra of species functional characters) than expected on the basis of random assortment of species characters among sites (Section 1.5). There are two important assumptions to this hypothesis. The first, that the communities under consideration occur in similar environments, was dealt with in Chapter 3, where groups of study sites with relatively similar environments were identified. The second assumption is that the species characters considered are of functional significance, that is, that they represent aspects of the adaptive strategies by which species capture resources, resist or avoid interference from other species, endure adverse environmental conditions and so maintain non-negative population growth. Convergence between communities would be caused by assembly rules, acting to produce non-random patterns — community structure — in the distribution of species niches in the abstract niche space of a community (Smith *et al.* 1994; Wilson *et al.* 1994). Only functional characters would be expected to reflect species niches, and therefore, community structure.

The above-ground vertical structure within a plant community is associated with a number of environmental and resource gradients that would be expected to influence function: light quality (spectral composition) and quantity (quantum flux), temperature, humidity, exposure to wind and type of herbivory are important examples (Cain *et al.* 1956; Smith 1973; Givnish & Vermeij 1976; Hall & Swaine 1981; Chiarello 1984). Texture, in this study, is expressed in terms of 12 species characters, primarily concerning the morphology and physiology of the PSU. The characters were chosen because they were expected, *a priori*, to be functionally important. In the present chapter, among-species trends in the vertical structure of *Nothofagus* forest are examined with respect to the 12 species characters. Although the patterns examined would primarily reflect beta niche gradients (which have no assembly rules), it seems clear that characters involved in adaptation to environmental factors will also be involved in strategies for resource capture (alpha niches; Pickett & Bazzaz 1978). Where significant vertical trends in species characters are detected, this is interpreted as evidence, supplementary to that presented in Section 2.2.2, that the characters are of functional importance, and may be related to beta and alpha niches.

It is unlikely that most functional characters will be associated uniquely with species position along one particular niche axis. Instead, many characters may represent the outcome of selective trade-offs tending to optimise responses to several biotic and abiotic environmental factors (Givnish 1987). A corollary of this is that functional species characters may themselves

be interrelated in potentially complex ways. If community-level patterns (such as texture convergence) are found with respect to several characters, it may be difficult to decide whether, at one extreme, each pattern was caused by a unique process (for example, competition for a particular resource), operating orthogonally to all others; or, at the other extreme, all the observed patterns are an outcome of the same ultimate cause. An understanding of the interactions between characters and their possible relevance to species niche responses would allow such dilemmas to be at least partly resolved. Interrelationships between species characters are examined in this chapter.

## 4.2 Methods

### SPECIES CHARACTER DATA

The 12 species characters evaluated are listed in Section 2.3.5. Measurement and calculation procedures are described in Chapter 2.

### ANALYSIS

#### *Intercorrelations between characters*

Pearson *r* correlation coefficients were calculated between each pair of species characters, using all species and entities, from all sites, for which unique, measured values were available (no substituted or predicted values). Variates were transformed as described in Section 2.3.4 (Table 2.1). Where the same species was represented by more than one record from different sites, an average for each character was calculated and used. This meant that each species was represented only once in the data set, avoiding the problems of non-independence (Jongman *et al.* 1987), which arise when multiple non-independent values (such as different measurements on the same species) are included in a sample (non-independence would tend to artificially raise the degrees of freedom, resulting in higher apparent significance levels).

#### *Vertical trends in texture*

Texture variation along vertical gradients was examined by comparing among-species character means for each landmass (Tasmania, Australia, New Zealand, South America) within each of three classes of height above ground level. These classes were intended to correspond approximately to forest strata (Smith 1973; Wilson 1989; Wilson *et al.* 1995), as follows: 0-1 m (ground/herb stratum), 1-5 m (shrub stratum) and >5 m (tree stratum). Character means for landmasses, rather than individual sites, were used as replicate observations to avoid the spatial autocorrelation that might otherwise result from floristic similarities between sites from the same landmass (Jongman *et al.* 1987). Means for each character within each height class at each study

site were calculated using transformed species (or entity[1]) values. Species were deemed to be present within a height class if PSUs of the species were recorded as occurring within the height class (see Section 2.3.2), and species represented by substituted or predicted (rather than measured) values were excluded from analysis. Site means for each height class were themselves averaged to obtain an overall value for each landmass. Significant differences in character values between height classes were sought using single-factor analysis of variance, with the four landmass means for each character/height class combination as replicates.

Analysis of variance was performed with the Teddybear computer program (Wilson 1975).

## 4.3 Results

INTERCORRELATIONS BETWEEN CHARACTERS

There are significant intercorrelations between most pairs of species characters (Table 4.1). The strongest correlations, all with $r$ values above 0.45 and significant at the 0.1% level, are among the five variates PSU succulence, total chlorophyll, phosphorus, nitrogen and specific weight (SLW), the latter tending to fall as the others increase. Support fraction is also strongly, negatively, correlated with PSU area and specific weight, and relatively strongly with nitrogen content. PSU inclination is relatively strongly associated ($r$>0.30; $P$<0.001) with several other characters: PSU specific weight, shape, lobation and (negatively) nitrogen. PSU thickness is strongly associated with PSU specific weight, and relatively strongly with PSU area and (negatively) lobation. Other pairs of characters tend to be more weakly related, having less than 10% ($r^2$) of variation in common.

VERTICAL TRENDS IN TEXTURE

Four species characters show significant vertical trends within communities (Fig. 4.1). The value of the PSU shape index decreases with height, indicating a tendency for PSUs to be longer relative to their width closer to ground level. PSU thickness, specific weight and inclination all increase with height, while succulence decreases. None of the other characters differs significantly among height classes, although most show a tendency to either decrease (nitrogen, phosphorus, total chlorophyll) or increase (area, support fraction) towards canopy level.

[1]Entity, i.e. an age or size class of a species represented by more than one such class in the data for a community (see Section 2.3.2).

**Table 4.1** Correlation matrix for 12 species characters, based on species means from 17 study sites. Species characters pertain to photosynthetic units (PSUs: see text) except for support fraction (SF). Abbreviations: SLW=specific weight; N=nitrogen content; P=phosphorus content; chl=chlorophyll (see text for full explanation).

| Variate | Chl *a/b* | Total chl | P | N | SF | Inclination | SLW | Succulence | Thickness | Lobation | Shape |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Area | 0.00 | -0.03 | -0.01 | -0.14* | -0.51*** | 0.17** | 0.16** | -0.02 | 0.31*** | 0.18** | 0.14* |
| Shape | 0.04 | -0.16* | -0.15* | -0.25*** | -0.28*** | 0.34*** | 0.35*** | -0.16** | 0.11 | -0.09 | |
| Lobation | -0.08 | -0.18** | 0.04 | -0.12 | -0.25*** | 0.33*** | 0.14* | -0.23*** | -0.35*** | | |
| Thickness | -0.03 | -0.19** | -0.10 | -0.21*** | -0.23*** | -0.09 | 0.46*** | 0.11 | | | |
| Succulence | 0.13* | 0.57*** | 0.56*** | 0.53*** | 0.21*** | -0.29*** | -0.64*** | | | | |
| SLW | -0.11 | -0.68*** | -0.49*** | -0.59*** | -0.38*** | 0.33*** | | | | | |
| Inclination | -0.16** | -0.28*** | -0.21*** | -0.32*** | -0.25*** | | | | | | |
| SF | 0.21*** | 0.21*** | 0.20** | 0.32*** | | | | | | | |
| N | 0.11 | 0.57*** | 0.64*** | | | | | | | | |
| P | 0.32*** | 0.45*** | | | | | | | | | |
| Total chl | -0.15* | | | | | | | | | | |

*$0.01 \leq P < 0.05$; **$0.001 \leq P < 0.01$; ***$P < 0.001$

## 4.4 Discussion

INTERDEPENDENCE OF SPECIES CHARACTERS

The amount of variation shared by most pairs of species characters is relatively low (Table 4.1), indicating that the characters either (1) tend to reflect species responses to different, orthogonally varying ecological factors; or (2) are of little functional importance and have a predominantly stochastic distribution. However, five characters (PSU succulence, total chlorophyll, phosphorus, nitrogen and specific weight) are quite strongly intercorrelated, while a sixth, PSU thickness, has a marked correlation with PSU specific weight. All of these characters may have a component of variation related to light availability.

Variation in leaf structure and function associated with light availability has been demonstrated both within and among species (e.g. Hollinger 1989; Popma *et al.* 1992; Ellsworth & Reich 1993; Mulkey *et al.* 1993). In general, sun leaves, and leaves of plants associated with sunny environments, are more `expensive,' with higher relative investments in mechanical, vascular and other non-photosynthetic tissues, presumably compensated for by an increased return in carbon fixation (Björkman 1981; Bongers & Popma 1988; Popma *et al.* 1992). Since non-photosynthetic tissues account for a greater proportion of leaf dry weight than in `cheaper' shade-adapted leaves, total chlorophyll content as well as concentrations of nutrients primarily associated with photosynthetic tissues — such as nitrogen and phosphorus (Evans 1989; Reich *et al.* 1991) — may be lower on a dry-weight basis (Bongers & Popma 1988; Reich & Walters 1994). Sun-adapted leaves may have multiple palisade cell layers, an adaptation that would increase the efficiency of photon capture. They may also possess a greater volume of mesophyll air space, which would enhance $CO_2$-diffusion within the denser photosynthetic tissue (Jackson 1967; Parkhurst 1986). Such anatomical differences tend to produce greater leaf thickness and dry weight per unit area (leaf specific weight) in sun- as opposed to shade-adapted leaves (Björkman 1981; Gulmon & Chu 1981; Bongers & Popma 1988). Higher mesophyll air space, as well as a greater content of sclerenchyma in sun-adapted leaves, imply that relative water content (succulence) would be lower.

Partitioning of the light gradient among species is a conspicuous aspect of above-ground structure in forests, which may be mediated by assembly rules (Wilson 1989; Wilson *et al.* 1995). PSU succulence, total chlorophyll, phosphorus content, nitrogen content, specific weight and thickness may represent different components of a character syndrome controlled by the light gradient. This possibility was taken into account in interpreting convergence in terms of these factors in Chapters 6-10.

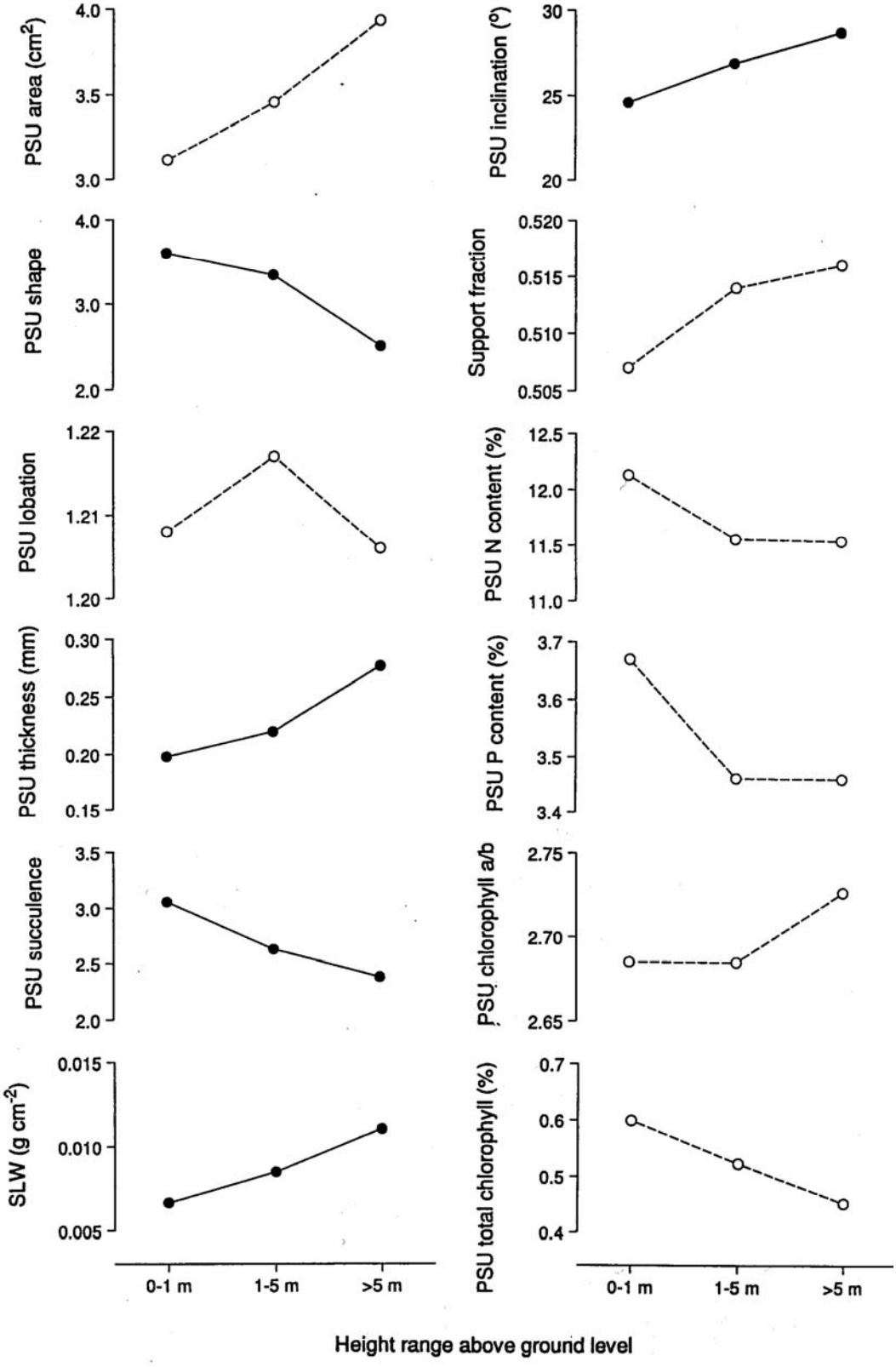



**Fig. 4.1** Mean values (all species, all sites: see text) for 12 species characters within height classes 0-1 m, 1-5 m and >5 m above ground level. Solid lines and filled points identify characters varying significantly between height classes ($P<0.05$; ANOVA of landmass means for height classes); dashed lines and open points represent characters with non-significant variation between height classes.

The primary aim of the present study is to determine whether certain communities exhibit structure in the distributions of species niches in abstract ecological space. Since niche space is defined with respect to a potentially infinite number of parameters, niches cannot be measured directly. However, attributes linked to species function, such as aspects of morphology or physiology, should be related to the underlying niche axes. In other words, structure in the distribution of species niches in ecological factor space should be reflected by structure in the distributions of species attributes in character space (Ricklefs & Travis 1980; Wiens 1991b; Weiher & Keddy 1995a; but see Laurie & Cowling 1994).

The functional importance of a species character may be assessed by examining its variation with respect to environmental variables. A close relationship between species values for a given character (e.g. leaf area) and their distributions along an environmental gradient (e.g. temperature), would suggest that the character is involved in adaptive trade-offs leading to optimal function in the conditions experienced by each species at its position along the various gradients it faces[2], i.e. in its beta niche. Whether species values for a character are determined genetically or reflect short-term plastic responses is not critical to the value of the character as a proxy variable for niches, so long as it is a reliable predictor of the environmental variable.

Is the demonstration of variation in a character along beta niche axes (for which no species-mediated restrictions on niche overlap should apply) sufficient evidence that the character will also differ among alpha niches (for which limiting similarity might apply)? The proximal effects of species interactions (the basis of assembly rules that would limit overlap of alpha niches and so produce community structure) would be to modify the microenvironments experienced by the interacting individuals. Although the objects of competition must be resources (such as light, nutrients, water and establishment sites), differences in resource spectra will be accompanied by differences in microenvironments, which should be reflected in functional species attributes. For example, in the above-ground vertical structure of a forest, there will be correlated gradients in light availability, temperature, humidity, windspeed, density of herbivores and other factors. All may influence species attributes, yet only one — light availability — directly represents a resource for which competition is likely. This means that species characters should be related to alpha, as well as beta, niches.

[2]An alternative explanation would be that the environment controls species characters directly (not via natural selection). For example, `wind-training' may be involved in producing krummholz growth forms in shrubs growing in windy alpine environments (Daubenmire 1974). It seems unlikely that the direct mechanical action of environmental forces would have played a major role in producing patterns observed for species characters in this study.

## VERTICAL TRENDS IN TEXTURE

Of the five variables exhibiting significant differences in mean character values at different heights (Fig. 4.1), three (PSU thickness, succulence and specific weight) belong to the group of highly intercorrelated variates, described above, and vary in a manner consistent with the interpretation that they represent species responses to the light gradient (Gulmon & Chu 1981; Bongers & Popma 1988; Witkowski & Lamont 1991; Ellsworth & Reich 1993). This interpretation is based on the assumption, which seems reasonable, that light availability increases towards the canopy. Patterns in PSU nitrogen, phosphorus and total chlorophyll content are not significant, but each constituent shows a tendency to occur at higher concentrations in the leaves of ground-layer plants, which is likewise consistent with the postulated light response (Björkman 1981; Field & Mooney 1986; Evans 1989; Reich *et al.* 1991).

The significant observed increase in PSU inclination with height can likewise be explained as a function of the light regime (Givnish 1984; Hollinger 1989; Herbert & Nilson 1991), which might operate via an energetic trade-off of light reception against leaf thermal and gas exchange budgets (Givnish 1984; Herbert & Nilson 1991).

The PSU shape index decreases significantly with height, suggesting that PSUs tend to become shorter relative to their width with proximity to the forest canopy. Possibly this simply reflects the relative preponderance of grasses and graminoids, with their highly elongated leaves, in the lower strata.

The observed tendency for PSU area to increase towards the canopy, though non-significant, is of interest, because it may match reports of increases in mean community leaf area with temperature, reported in some studies (Christophel & Greenwood 1989; Mackey 1993; Jordan & Hill 1994). This interpretation of the trend assumes that vertical microclimatic gradients include an increase in temperature (as may be the case in tropical rainforest; Baynton *et al.* 1965; Chiarello 1984).

## CONCLUSIONS

Covariation among the 12 species characters is relatively weak, but nevertheless significant for many character pairs. The strongest overall intercorrelations are among PSU succulence, total chlorophyll, phosphorus, nitrogen and specific weight, which may represent a syndrome of responses to the light regime.

Trends among species within the vertical structure of the communities sampled are apparent for nearly all characters, but are significant only for PSU shape (PSUs becoming less elongated with height), thichness (increasing with height), succulence (decreasing), specific weight (increasing) and inclination (increasing). In general, the patterns conform to previously published trends. They tend to vindicate the choice of these characters as proxy variables for

species niches.

# 5. Convergence and divergence in species richness among *Nothofagus*-dominated communities.

## 5.1 Introduction

A qualitative model of community assembly was described in Chapter 1. Under this model, species interactions, particularly competition, form the basis for assembly rules, which (in this model) restrict what functional types of species can co-occur within communities. Seen in terms of the niche theory of Hutchinson (1958), the effect of assembly rules is to limit how closely species niches can be packed into *n*-dimensional ecological hyperspace (MacArthur & Levins 1967). The environment also affects niches, by restricting the combinations of species attributes that are viable. While assembly rules tend to spread niches out, the environment tends to pack them together, into a niche space hypervolume of limited size (Pianka 1976). A corollary of this model is that the number of niches, and therefore species, that can occur in a community in a particular habitat will tend to be constrained. By contrast, if there were no assembly rules, an arbitrary number of species could be packed into the available niche space.

This is the basis of the concept of niche limitation, whereby the number of species encountered within sampling areas of a given size within a uniform habitat is expected to be more constant than expected by chance (Wilson *et al.* 1987; Watkins & Wilson 1992; Zobel *et al.* 1993). The same concept implies that the number of species comprising disjunct communities in similar environments should be more similar than expected by chance: the communities should exhibit convergence in species richness.

This hypothesis may be tested if a null probability distribution for among-community variation in species richness can be constructed. However, this is not a straightforward task: if the convergence hypothesis is true, species richness may be constrained (by assembly rules) not only in different communities with similar environments, but also within each community (e.g. among replicate quadrats). This means that the null distribution cannot be determined solely from species richness observations among the communities for which convergence is to be sought. Schluter (1986) overcame this problem by sampling in different types of community, that would not be expected to converge. Finch species numbers were obtained for several distinct habitats on each of five continents. An *F*-test was used to seek departure from the null hypothesis that richness within each habitat on each continent was drawn at random from an overall distribution defined by the observed pool of values. The null hypothesis was rejected when the variance in richness among continents was significantly low relative to richness among habitats, signifying that the continents were convergent, over all habitats, in species richness.

Where data from a range of habitats are not available, convergence cannot be sought directly. However, if replicate richness values are available for each community, it is possible to test the alternative hypothesis that communities are *divergent* in species richness — more dissimilar than expected on a random basis. Failure to reject the null hypothesis, that species richnesses are determined by random draws from the observed pool of values, may then be interpreted as preliminary evidence that convergence between the communities *might* have occurred. This approach was used by Wiens (1991a), who applied a Mann-Whitney *U* test to determine whether the avifaunas of North American and Australian shrub deserts were more dissimilar in species richness than expected by chance. The null hypothesis could not be rejected, and the communities were deemed `similar' in species richness.

Community species richness may be influenced by a variety of biological and physical factors of which assembly rules are but one. Biogeographic history, migration and extinction rates, frequency and severity of disturbance and the physical sizes of individuals are examples of factors that might also play a role (Whittaker 1977). Where any of these factors vary in different communities, the communities may become more dissimilar in species richness than expected by chance, i.e. they may diverge.

In the present chapter, divergence in species richness is sought among *Nothofagus*-dominated communities at the local, regional and landmass scales. A bootstrap-based test is used to test a null model under which vascular plant species richnesses are drawn at random from a pool comprising observed values for each replicate quadrat in each community being compared. The test is similar in principle to the familiar analysis of variance, asking whether richness variation among communities is significantly higher than variation among quadrats within communities. Where significant departure from the null model is observed, this is interpreted as divergence in species richness. An absence of significant divergence is taken as preliminary evidence that convergence *may* have occurred, and assembly rules might operate. However, the null hypothesis, that species richness is determined by chance, cannot then be rejected. More conclusive evidence of community-level convergence is sought in subsequent chapters comparing communities in terms of their texture.

To investigate the possibility that observed patterns in species richness are primarily the result of environment variation rather than the action of assembly rules, relationships of species richness to environmental factors are sought using regression analysis.

## 5.2 Methods

### SPECIES RICHNESS DATA

Species richness data were obtained for replicate 20 × 20 m quadrats within each of 17 study sites. Field sampling techniques and criteria for the choice of study sites are given in Section 2.3, while study sites and their environments are described and compared in Chapter 3.

## ANALYSIS

### *Bootstrap tests for divergence in species richness*

The bootstrap test employed here draws samples with replacement from a data pool comprising species richness values for each replicate quadrat from each of the communities being compared. Null model communities are assembled by assigning a bootstrap value to each replicate quadrat for each of community. The among-community variance in mean species richness for the observed data is compared with the variances obtained for each of many sets of `communities' generated under the null model, to test the hypothesis that variance among communities is no greater than would be expected if their quadrat richnesses were drawn at random from the underlying distribution. The approach is superficially analogous to analysis of variance (with communities as 'treatments', and quadrats as replicates), but does not assume that the richness data are drawn from a normal distribution (Crowley 1992). This was an advantage because the observed distribution of species richnesses was significantly skewed, even following square root-transformation.

Comparisons seeking among-community differences in species richness were carried out for communities[1] at the local, regional and landmass scales. At the landmass scale, an overall comparison among all communities, and separate comparisons for each of the six possible pairs of communities, were performed. Within each landmass, an overall comparison of all regional communities, and comparisons of each pair of communities, were carried out. For regions in which more than one site was sampled, comparisons were performed among all local communities, and all possible pairs of communities. In addition, individual sites from different landmasses that were identified as having closely-matched environments (Section 3.3), were compared. The network of comparisons is presented schematically in Fig. 5.1.

For each comparison, $10^4$ null model data sets were generated by drawing bootstrap samples (i.e. at random and with replacement) from a pool of values comprising replicate quadrat richnesses from all communities being compared. In the case of pooled communities, comprising more than one site, all quadrats from all consituent sites were treated as individual replicates. Quadrat species richness values were square root-transformed prior to analysis to compensate for skewness in their distribution.

The test statistic employed was the among-community variance in species richness, $V_r$

[1]The reader is reminded that ‘community’ is used throughout this report in a reductionist and operational sense to refer both to individual sites (local or regional communities) and pooled data from several sites within a local area (some regional communities) or region (landmass communities). A full explanation is given in Section 1.4.

$$V_r = \frac{\sum_{i=1}^{n} \left( r_i - \bar{r} \right)^2}{n}$$

where $n$ = the number of communities being compared;

$r_i$ = mean species richness (simple mean among all quadrats) for community $i$;

$\bar{r}$ = the mean of $r_i$ across all $n$ communities.

$V_r$ was calculated for each null model data set, as well as for the observed data. The significance $P$ of departure from the null model was determined as the proportion of null model data sets for which the value of $V_r$ was at least as large as for the observed data. The test was one-tailed. That is, departure from null model expectation was sought only in the direction of a variance excess in the observed communities (i.e. divergence in species richness). This was because there is no reason to expect within-site variation in quadrat richness to be *greater* than among-site variation, even if the same assembly rules apply in different communities. Only if there were a hypothesis under which this were to be expected would a two-tailed test be appropriate. A failure to reject the null hypothesis would not necessarily support the common operation of assembly rules in different communities. Rather, it would mean that this possibility could not be ruled out.

*Species richness variation with environment*

Evidence that species richness was influenced by variation in measured environmental factors was sought by multiple regression of site species richness (means of quadrat richnesses) on environmental parameters mean temperature of the warmest month (MTWM), mean temperature of the coldest month (MTCM), mean annual temperature (MAT), annual rainfall (AR), rainfall in the driest quarter (RDQ), soil total nitrogen (N) content, soil total potassium (K) content, soil total phosphorus (P) content, soil pH and soil organic content (OC). Species richness was square root transformed, while environmental parameters were transformed as shown in Table 5.1. Separate regressions were performed without Soil P, but including all 17 study sites, and with Soil P, excluding Chilean and Argentinian sites, for which no suitable Soil P values were available (Sections 2.3.4, 3.3). For each regression, an iterative step-down procedure was performed to eliminate parameters that did not explain a significant independent portion of the total among-site variation in species richness.

Simple regression was performed to determine whether species richness seemed to be be influenced by canopy light transmittance. Separate regressions were obtained for sites at which light transmittance values were obtained in ‘sunny’ (7 sites) and ‘cloudy’ (9 sites) conditions (Section 3.3).

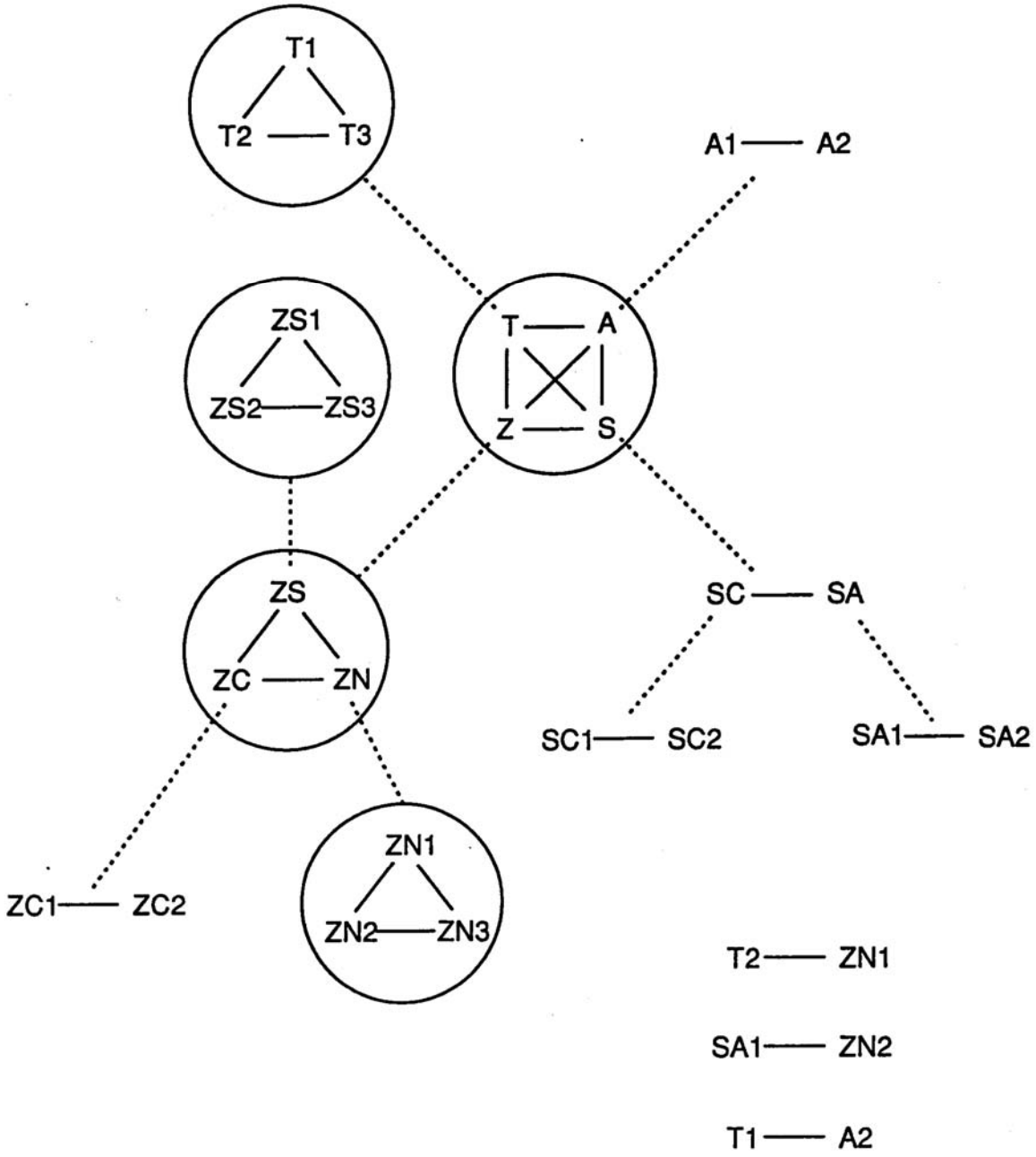



**Fig. 5.1** Schematic diagram showing comparisons (solid lines and circles) seeking divergence in species richness between landmass-, regional- and local-scale communities. Letter codes denote communities, as listed in Section 3.2. Broken lines represent spatial hierarchical relationships between communities.

**Table 5.1** Transformations applied to each environmental parameter. The expression shown gives the transformed value from a raw value, *x*. ln=natural logarithm (see text for other abbreviations).

| Environmental parameter | Transformation expression |
|---|---|
| MTWM | *x* |
| MTCM | *x* |
| MAT | *x* |
| AR | ln *x* |
| RDQ | ln *x* |
| Soil N | ln *x* |
| Soil P | ln *x* |
| Soil K | ln *x* |
| pH | *x* |
| OC | *x* |
| light (cloudy) | *x* |
| light (sunny) | ln *x* |

## 5.3 Results

TESTS FOR DIVERGENCE IN SPECIES RICHNESS

The mean number of species per 20 × 20 m quadrat for each local, regional and landmass-scale community is given in Table 5.1. Among communities at the landmass scale (Table 5.2) there is significant overall divergence in species richness. New Zealand is divergent with respect to all other landmasses. However, the hypothesis that species richness is the same for Tasmania/ Australia, Tasmania/South America and Australia/South America can not be rejected.

Comparing regional-scale communities (Table 5.3), there is overall divergence in species richness among the three Tasmanian sites, although in pairwise comparisons only T1 Balfour and T3 Mathinna have significantly different richness. Mainland Australian sites A1 Lumeah and A2 Cascades are not demonstrably divergent. Species richness differs significantly between southern (ZS), central (ZC) and northern (ZN) New Zealand, southern/northern and central/northern New Zealand are also divergent. Chilean and Argentinian communities are significantly divergent.

**Table 5.1** Vascular plant species richness for communities at the landmass-, regional- and local scales. Values are back-transformed means of square-root transformed values for each 20 × 20 m quadrat sampled in each community.

| Scale | | | | | |
|---|---|---|---|---|---|
| Landmass | | Region | | Local | |
| Community | Species | Community | Species | Community | Species |
| T | 16.2 | T1 | 17.7 | ZS1 | 14.9 |
| A | 19.5 | T2 | 16.7 | ZS2 | 19.0 |
| Z | 27.6 | T3 | 15.2 | ZS3 | 19.2 |
| S | 20.3 | A1 | 19.7 | ZC1 | 37.6 |
| | | A2 | 19.4 | ZC2 | 13.0 |
| | | ZS | 17.6 | ZN1 | 45.0 |
| | | ZC | 23.7 | ZN2 | 46.7 |
| | | ZN | 43.2 | ZN3 | 38.2 |
| | | SC | 23.3 | SC1 | 21.2 |
| | | SA | 16.2 | SC2 | 25.0 |
| | | | | SA1 | 19.0 |
| | | | | SA2 | 13.7 |

**Table 5.2** Bootstrap null model tests for divergence in species richness for landmass-scale communities Tasmania (T), mainland Australia (A), New Zealand (Z) and South America (S) (see Section 3.2). *P* shows the proportion of null model simulations in which the among-community variance in species richness is at least as large as for the observed data. Comparisons showing significant departure from null model expectation ($P<0.05$) are shown in bold type.

| Comparison | *P* | Comparison | *P* |
|---|---|---|---|
| **T,A,Z,S** | **0.026** | **A,Z** | **0.026** |
| T,A | 0.413 | A,S | 0.846 |
| **T,Z** | **0.000** | **Z,S** | **0.020** |
| T,S | 0.268 | | |

**Table 5.3** Bootstrap null model tests for divergence in species richness for regional-scale communities (codes given in Section 3.2). Format as for Table 5.2.

| Comparison | *P* | Comparison | *P* |
|---|---|---|---|
| **T1,T2,T3** | **0.032** | **ZS,ZC,ZN** | **0.000** |
| T1,T2 | 0.402 | ZS,ZC | 0.210 |
| **T1,T3** | **0.007** | **ZS,ZN** | **0.000** |
| T2,T3 | 0.114 | **ZC,ZN** | **0.001** |
| A1,A2 | 0.820 | **SC,SA** | **0.001** |

At the local scale, equality of species richness cannot not be rejected for southern New Zealand sites, either in an overall comparison of the three communities, or within each pair (Table 5.4). Central and northern New Zealand sites, on the other hand are generally divergent in species richness, with the exception of ZN1 Ohakune and ZN2 Rotokura. Chilean sites SC1 Pelada and SC2 Antillanca are divergent, as are Argentinian sites SA1 Quetrihué and SA2 Gutierrez.

**Table 5.4** Bootstrap null model tests for divergence in species richness for local scale communities (codes given in Section 3.2). Format as for Table 5.2.

| Comparison | *P* | Comparison | *P* |
|---|---|---|---|
| ZS1,ZS2,ZS3 | 0.158 | **ZN1,ZN2,ZN3** | **0.015** |
| ZS1,ZS2 | 0.103 | ZN1,ZN2 | 0.610 |
| ZS1,ZS3 | 0.091 | **ZN1,ZN3** | **0.030** |
| ZS2,ZS3 | 0.938 | **ZN2,ZN3** | **0.006** |
| **ZC1,ZC2** | **0.001** | **SC1,SC2** | **0.002** |
| | | **SA1,SA2** | **0.021** |

Of the three pairs of environmentally matched sites from different landmasses, only one, T1 Balfour/A2 Cascades does not show significant divergence in species richness (Table 5.5).

**Table 5.5** Bootstrap null model tests for divergence in species richness for sites from different landmasses with closely matched environments. Site codes are given in Section 3.2. Format as for Table 5.2.

| Comparison | *P* |
|---|---|
| T1,A2 | 0.837 |
| **T2,ZN1** | **0.001** |
| **ZN2,SA1** | **0.005** |

SPECIES RICHNESS-ENVIRONMENT RELATIONSHIPS

Step-down multiple regression of site species richness on climate and soil parameters (17 sites) revealed that species richness can be expressed as a function of two parameters, soil nitrogen content, accounting for 33% of variation in species richness ($P<0.01$) (Fig. 5.2), and MTWM, which explains a further 16% of variation ($P<0.05$). Species richness is a rising function of both explanatory variables. The whole regression accounts for 49% of among-site variation in species richness and is significant at the 1% level. Soil P was not a significant parameter of a second regression using only 13 sites but including all environmental variables; results are not presented. Species richness was not found to be significantly related to canopy light transmission, either for `cloudy' ($r^2=0.0\%$; $P=0.901$, n.s.) or `sunny' ($r^2=0.0\%$; $P=0.994$, n.s.) sites.

## 5.4 Discussion

COMMUNITY-LEVEL CONVERGENCE

The results obtained from null model comparisons provide some preliminary support for possible community-level convergence in species richness. The test used sought significant departure from the null hypothesis that species richness variation among communities was no higher than variation among quadrats within communities. This approach can demonstrate significant divergence, but is unsuitable for evaluating the significance of convergence (Section 5.1). A failure to observe divergence is interpreted here as possible evidence of convergence, but it is stressed that such conclusions are preliminary only, not being based on significant results.

For three of the six possible comparisons of one landmass with another, the hypothesis that mean quadrat species richness was the same in the *Nothofagus*-dominated communities sampled on both landmasses, could not be rejected (Table 5.2). The same was true of a number of comparisons at the regional and local scales (Tables 5.3, 5.4). A possible interpretation is that similar assembly rules apply at different sites, or within similar habitats in different regions or landmasses. Assembly rules (based on past or present species interactions, such as competition

for the same resources) would limit the allowable degree of niche overlap between co-occurring species, thus limiting the number of species that can be packed into the finite niche space provided by the environment (Pianka 1976).

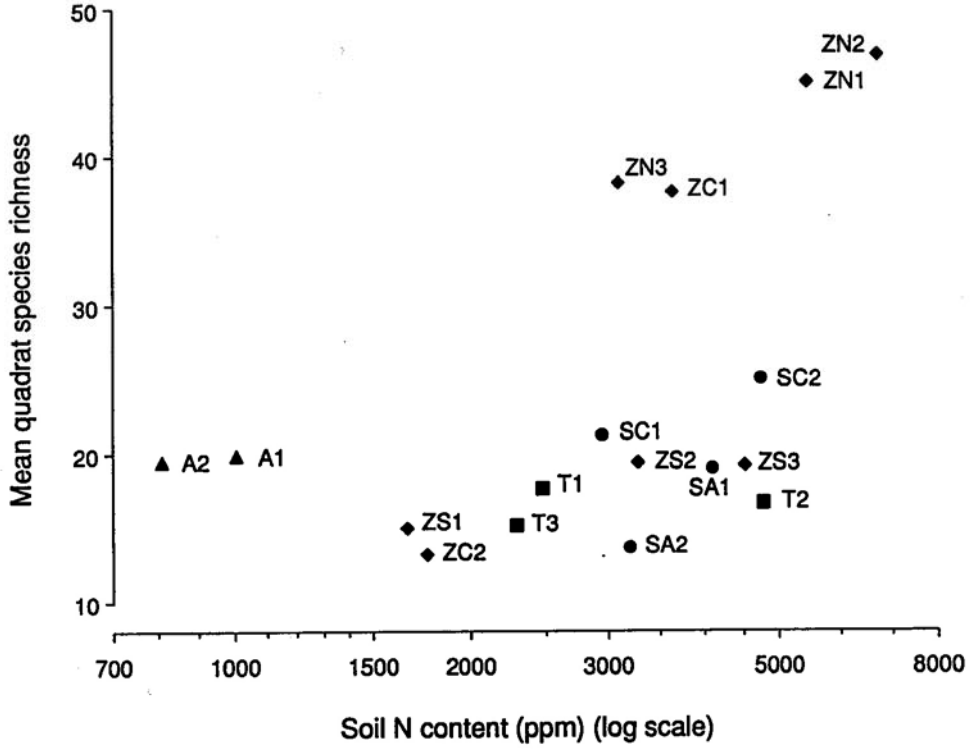



**Fig. 5.2** Relationship between site mean species richness in 20 × 20 m quadrats and soil total nitrogen content. Site codes (Section 3.2) are shown beside data points; symbols correspond to landmasses, Tasmania ( ■ ), Australia ( ▲), New Zealand ( ♦ ) or South America ( ● ).

DIVERGENCE IN SPECIES RICHNESS

Although the statistical significance of convergence in species richness could not be determined, significant divergence (greater dissimilarity in species richness between communities, than among quadrats within communities) was able to be demonstrated.

Several groups of communities at each scale were found to be divergent in species richness. What factors distinguish groups of communities showing divergence from others that do not? Environmental differences would affect species richness, because a change in the dimensions of the environmentally-determined hypervolume into which species niches are packed would alter the number of niches that can be accomodated, assuming that other relevant variables (such as the limiting similarity between adjacent species) remain unchanged (Whittaker 1977). Multiple regression revealed a tendency for species richness to increase with soil fertility

(in terms of total nitrogen content), while temperature (MTWM) significantly explained some residual variation (Section 5.3; Fig. 5.2). The observed relationship, if causal, could explain a failure for some of communities to exhibit convergence in species richness.

If significant differences in species richness have an environmental basis, then it might be expected that divergent communities would belong to groups identified as being poorly matched in their environments in Chapter 3, while non-divergent communities might be those that were found to be more similar in their environments. Such a pattern does not appear to apply at the landmass scale. The landmasses that were closest together in environmental factor space, Tasmania and New Zealand (Figs. 3.5-3.7) are significantly divergent in species richness, while *Nothofagus*-dominated communities in Australia and South America, that appear to have relatively dissimilar environments, do not differ significantly in species richness (Table 5.2).

At the regional and local scales, there is some evidence that divergence in species richness corresponds to soil factor differences. T1 Balfour and T3 Mathinna differ significantly in species richness, and are also more distantly spaced in soil space (though not in climate space) than Balfour and T2 Anne, which have comparable numbers of species (Table 5.3). Among the three regions of New Zealand, only central (ZC) and southern (ZS) New Zealand are non-divergent in species richness. Sites from these regions have relatively similar soils in comparison to those of northern New Zealand (ZN), which, notably, are generally higher in nitrogen (Table 3.3). Among northern New Zealand sites, only ZN1 Ohakune and ZN2 Rotokura do not differ significantly in species richness (Table 5.4). Compared with ZN3 Clements, Ohakune and Rotokura have more similar concentrations of potassium and nitrogen (Table 3.3).

Of the three comparisons involving sites from different landmasses, selected for being relatively similar in at least some aspects of their environments (Section 3.3), only one pair of sites, T1 Balfour and A2 Cascades, does not have a significantly different number of species per quadrat. However, these two sites are closely matched in terms of both climate and soils, whereas T2 Anne and ZN1 Ohakune may differ in soil fertility levels; ZN2 Rotokura and SA1 Quetrihué are more distantly spaced in both climate and soil space.

### RELATIONS OF OBSERVED PATTERNS TO PREVIOUSLY REPORTED TRENDS

Previous studies reveal that patterns of variation in species richness are not simple, but may be influenced by a range of factors including the physical environment (Hamilton 1975; Glenn-Lewin 1976; Carson & Pickett 1990; Smith *et al.* 1995), species morphology (Van der Maarel 1988), disturbance regimes (Connell 1978; Tilman 1982; McIntyre & Lavorel 1994), successional state (Egler 1954; Auclair & Goff 1971; Nicholson & Monk 1974; Pickett *et al.* 1987) and evolutionary and biogeographic history (Keddy 1976; Naveh & Whittaker 1979; Currie & Paquin 1987).

Different factors are likely to be important at different scales (Kolasa & Biesiadka 1984;

Ricklefs 1987). Patterns of species richness within a biogeographic region may correspond to environmental variation, for example, in soil fertility (Rice & Westoby 1983b; Van der Moezel & Bell 1989), moisture regimes (Naveh & Whittaker 1979; Margules *et al.* 1987) or temperature (Hamilton 1975; Margules *et al.* 1987). Although monotonic relationships have been found in particular studies, an overview of results from different studies suggests an absence of simple broad trends. For example, species richness has been found to increase along gradients of increasing soil fertility (Vasander 1987; Carson & Pickett 1990), but also to decrease with increasing fertility (Huston 1980; Rice & Westoby 1983b; Faber-Langendoen & Gentry 1991).

Some have suggested that the environment affects species richness by controlling primary productivity, and that the response curve may be ditonic, rising at first as productivity increases but ultimately declining as increasing competition leads to dominance by a few species (Whittaker 1977; Grime 1979). Ditonic changes in species richness have been found along gradients of moisture availability (Whittaker 1956), soil fertility (Vasander 1987), and with respect to standing crop and litter densities (Al-Mufti *et al.* 1977). If this interpretation is correct, it could explain dichotomous patterns of local and regional-scale variation in species richness among different studies.

At scales broader than the local area or biogeographic region, historical or evolutionary processes may confound effects of the physical environment on species richness (Ricklefs 1987). For example, differences in biogeographic history and the time available for evolution may explain differences in woody and herbaceous vascular diversity in shrublands of Israel, California, Chile, South Africa and Australia (Naveh & Whittaker 1979; Rice & Westoby 1983b; Cowling & Witkowski 1994).

Clear broad-scale trends of increasing species richness from high to low latitudes have been observed (Pianka 1966; Currie & Paquin 1987; Stevens 1989). Possible explanations for these trends include differences in glacial, geological and biogeographic history (Simpson 1964); an increase in spatial heterogeneity (i.e. microhabitat diversity) towards the tropics (MacArthur 1964); effects of climatic variation on species geographic ranges (Stevens 1989); and the increasing importance of interspecific competition as physical stresses decline away from the poles (Pianka 1966). It has been suggested (Currie & Paquin 1987) that gradients in available energy may underlie latitudinal trends, the total available energy being partitioned among species, limiting species richness (Odum 1975).

The diversity of factors affecting species richness, and the range of trends that have been observed, make it difficult to interpret patterns observed in the present study in terms of previous findings. There is evidence that non-convergence in species richness at the local and regional scales may be driven by differences in soil nitrogen (or associated factors) and possibly differences in temperature. Possible effects of soil nutrient status on diversity have been identified previously. However, while richness was found to increase with fertility in the present study, previously reported trends in forest and woodland vegetation have generally been in the

opposite direction (Huston 1980; Rice & Westoby 1983b; Van der Moezel & Bell 1989; Faber-Langendoen & Gentry 1991). Correlations with temperature have also been found, and these are generally positive, as in the present study (Whittaker 1956; Hamilton 1975; Margules *et al.* 1987). Temperature (as a parameter of environmental energy) may also play a role in producing latitudinal gradients in species diversity (Currie 1991); again, this trend is a positive one.

Variation in measured environmental parameters did not clearly account for divergence in species richness observed among communities at the landmass scale. Historical factors, or unquantified differences in the environments of different landmasses might play a role. For example, the low vascular plant richness of Tasmanian rainforests, observed in this study (Table 5.1), has been noted previously. A possible explanation may lie in the island's insularity coupled with the extinction of many rainforest taxa as a result of Tertiary and Quaternary climate change and Pleistocene glaciations (MacPhail *et al.* 1993).

Differences in the degree to which *Nothofagus*-dominated communities are associated with disturbance on different landmasses could account for the variation in species richness observed among landmasses. In the Andes of Chile and Argentina, many *Nothofagus* stands appear to have developed following perturbations associated with vulcanism or tectonic activity (Veblen *et al.* 1981; Veblen 1985). Veblen *et al.* (1981) suggest that succession, uninterrupted by further disturbance, would lead to replacement of *Nothofagus* by more shade-tolerant genera. Two of the study sites sampled in South America (SC1 Pelada and SA2 Gutierrez) comprised *Nothofagus* stands that were clearly even-aged, suggesting that they represent a single cohort that established following a large-scale disturbance. Species richness was low at both sites, contributing to the low overall richness value obtained for South America (Table 5.1). Although disturbance, particularly at the patch scale (June & Ogden 1975, 1978), may influence regeneration patterns in New Zealand *Nothofagus*-dominated forests (Wardle 1984; Jane 1986; Mark *et al.* 1989), it has not been regarded as a major factor influencing community persistence. Tasmanian (Read & Hill 1985, 1988) and Australian (Read & Hill 1985) *Nothofagus*-dominated forests do not seem to be dependent on allogenic disturbance, either for establishment or persistence. Effects on species richness of both disturbance intensity and time since disturbance, have been predicted (Egler 1954; Connell 1978; Pickett *et al.* 1987; Wilson *et al.* 1992a). However, empirical patterns are complex (Collins & Barber 1985), and both increases and decreases in species richness, depending on time since disturbance (Bazzaz 1975) or environments (Auclair & Goff 1971) have been observed.

## PREVIOUS STUDIES OF CONVERGENCE IN SPECIES RICHNESS

While the possibility of convergence in species richness in similar vegetation types on different continents has often been discussed (Parsons & Moldenke 1975; Whittaker 1977; Cody & Mooney 1978; Naveh & Whittaker 1979; Rice & Westoby 1983a; Fox 1995), there have been few attempts to demonstrate such convergence objectively. Examining patterns of diversity within several animal guilds, Cody *et al.* (1977) reported significant similarities in species-area curves for mediterranean-climate regions in California and Chile. Schluter (1986) detected significant convergence in species richness among finch communities from five continents.

The test employed by Schluter (*op. cit.*) was a modified analysis of variance, with continents as `treatments' and richness values from nine separate habitats, represented on each continent, as replicates. This approach is superficially similar to that employed in the present chapter, but because a range of distinct habitats was sampled on each continent, it was reasonable to apply a two-tailed test for departure from the null hypothesis that species richness was as variable among habitats within continents, as among continents. This meant that convergence (significantly lower variation among continents than among habitats) could be positively demonstrated. In the present study, replicates were randomly-located quadrats within the communities being compared. There was no basis for expecting among-quadrat variation to exceed among-site variation. Therefore a two-tailed test could not be applied, and only divergence could be positively shown.

The search for convergence in species richness among disparate communities is analogous to the study of niche limitation within communities. A model of community assembly that would lead to convergence in species richness between communities in similar environments was developed in Chapter 1 and discussed above. The same model would, of course, apply within communities, producing greater similarity in the species richness of adjacent patches than expected on the basis of random dispersal (Wilson *et al.* 1987). Niche limitation has been sought, with little success, in an agricultural field, a dune slope community and experimental diatom assemblages (Wilson *et al.* 1987); in old fields (Palmer 1987); and in *Nothofagus*-dominated forest in New Zealand (Bycroft *et al.* 1993). Significant evidence for niche limitation has been found at a fine scale in a managed lawn (Watkins & Wilson 1992) and in northern temperate forests early in succession (Zobel *et al.* 1993), providing evidence for the operation of assembly rules at a local scale.

## CONCLUSIONS

Bootstrap tests against a null model of similarity in species richness between communities have provided evidence of possible convergence in species richness at the landmass, regional and local scales. For several comparisons of *Nothofagus*-dominated communities at each scale, the

hypothesis that the communities did not differ in species richness could not be rejected at the 5% level. This suggests that assembly rules may operate in a similar way in the convergent communities, constraining the number of species that can be accomodated within the niche space determined by the environment. However, this hypothesis could not be supported statistically. An alternative interpretation is that species richness is determined by chance.

Statistically significant divergence is also apparent at all scales. Environmental matching between communities would be expected as a precondition for convergence, and there is evidence to suggest that divergence at the regional and local scales is concentrated among communities that are the most dissimilar in their environments, particularly with respect to soil factors. No such clear pattern is apparent at the landmass scale, however, suggesting that factors other than the effects of assembly rules and environment control species richness within different landmasses.

# 6. Convergence among *Nothofagus*-dominated communities: community texture means

## 6.1 Introduction

Under the model of community assembly described in Chapter 1, assembly rules mediated by species interactions would impose restrictions on the co-occurrence of functionally similar species. Similar species would tend to compete for the same resource units: if one species is a marginally stronger competitor, the others would be deprived of access to resources, and may eventually succumb to competitive exclusion (Gause 1934; Hardin 1960). At the level of a whole assemblage, the effect of assembly rules would be to spread species niches more evenly in ecological space (*sensu* Hutchinson 1958) than would be expected if there were no restrictions on the co-occurrence of similar species, and niches could be arranged at random within the total niche space delimited by the environment (Pianka 1976). Such an even, or regular, arrangement of niches in factor space has been called overdispersion (Pianka 1980). If the same assembly rules apply in the same conditions, similar overdispersion would tend to cluster species niches about the same overall mean in different communities in similar environments. This is community-level convergence (Smith *et al.* 1994; Wilson *et al.* 1994).

Species functional characters may represent or integrate one or more dimensions of species niches (Chapter 4). By extension, niche overdispersion should be reflected in species character overdispersion; and niche convergence, in texture convergence, where texture is expressed as some parameter of the community-wide distribution of a species character. One suitable parameter is the mean, which has been used previously to search for community-level convergence (Schluter 1986; Wiens 1991a; Wilson *et al.* 1994; Smith *et al.* 1994). A demonstration that community-wide means of a certain species character are convergent between different communities would lend support to the hypothesis that assembly rules operate, limiting species overlap along niche axes related to the character examined.

An objective test for community-level convergence must examine community similarity relative to expectation under the null hypothesis that there are no assembly rules restricting the co-occurrence of similar species. One approach is to define a null model, simulating community assembly under conditions in which the null hypothesis is true, and compare observed community similarity to similarity among artificial communities generated subject to the null model (Strong *et al.* 1979; Wilson *et al.* 1994). In the present chapter, randomisation tests (Crowley 1992) are applied to look for deviation from a null model under which observed species character values are reassigned to null ‘communities’ at random (within certain constraints). In

each test, community texture is characterised as the mean among species of one of 13 characters. A significantly greater similarity in texture among observed communities, than among null communities, is interpreted as evidence of texture convergence. Significant dissimilarity in texture is also sought, since environmental differences between communities would be expected to produce apparent 'divergence,' whether or not assembly rules apply (Section 1.5; Fig. 1.2).

Convergence is sought among *Nothofagus*-dominated communities at the local, regional and landmass scales. Environmental similarity between communities is an assumption of the convergence hypothesis. Therefore, particular attention is focused at each scale on communities previously identified (Chapter 3) as being closely matched in important aspects of their environments.

## 6.2 Methods

### TEXTURE DATA

Analysis was based on data for 13 species characters, the 12 listed in Section 2.3.5 and an additional variate, species height. For a given species at a given site, species height was quantified as the median height of the tallest height class in which PSUs of the species were recorded at the site (Section 2.3.2). For example, foliage of *Atherosperma moschatum* was present up to the 10-20 m height class at T1 Balfour. It was therefore assigned a species height of 15 m at that site. The variate was not intended to necessarily describe the stature of species, but rather the maximum level within the vertical forest structure in which they were 'functionally present,' as evidenced by the presence of their foliage there. Thus, for example, an understorey tree species and an epiphytic species growing beneath the forest canopy might be assigned the same species height. Environmental variation between ground and canopy level in forests may include important plant resource gradients (in particular light availability; Baynton *et al.* 1965). The positions occupied by species along these gradients, quantified as species height, might therefore reflect important aspects of realised niches.

Field and laboratory measurement regimes and criteria for the choice of study sites are described in Chapter 2. Study sites are described, and their environments compared, in Chapter 3.

### ANALYSIS

Texture convergence or divergence between communities was sought by means of randomisation tests comparing observed among-site variation in texture to variation among artificial communities generated under a null model simulating community assembly in the absence of assembly rules.

*The null model*

If there are no biotic restrictions on the characters that species may have to be able to co-occur, distributions of species characters in communities should be statistically indistinguishable from distributions obtained when character values are assigned to communities at random. Random assignment of the observed species character values to sites is therefore the basis for an appropriate null model[1]. However, constraints must be built into the null model so that statistically significant departure from it can be uniquely attributed to mechanisms incorporated in the hypothesis being tested (Strong *et al.* 1979; Tokeshi 1986; Wilson 1995).

The principal hypothesis here is that there are restrictions (assembly rules) on the combinations of species character values that are possible at each site. A corollary of this hypothesis is that communities will have more similar mean values for species characters (texture) than would be expected in the absence of such restrictions, assuming that values from all communities being compared are clustered about the same overall mean, representing an environmentally-imposed optimum. This is the hypothesis of community-level convergence. A second hypothesis is necessary, because communities might not only be more similar, but, alternatively, less similar than expected under the null model. The second hypothesis is that different communities have dissimilar environments, so that species values are clustered about different means in different communities. This is the hypothesis of `divergence' between communities. It sheds no light on the question of whether assembly rules operate in the communities being compared.

To ensure that statistically significant departure from null model expectation in a particular direction has a one-to-one correspondence with one of the above hypotheses, certain constraints must be built into the null model. These are discussed below.

Treatment of site species richness

If the number of species assigned to each randomly assembled community were allowed to vary, departure from null expectation could arise independently of convergence (or divergence) in texture. Since the mean of a random sample tends to approach the population mean as the sample size increases, communities represented by few randomly drawn values (i.e. few species) will tend to be more dissimilar in texture than communities represented by many values (species). This means that there would tend to be a link between variation in the size (number of species) of randomised communities and variation in their texture. If variation in species richness were

[1]In the following discussion it will sometimes be implied, to improve readability, that the null model assigns species, rather than their characters, to communities at random. The reader is asked to note that the null model represents random assortment of species characters, not random migration of species as taxonomic entities.

relatively low in the observed communities it would be higher, on average, in the randomised ones. As a result, randomised communities would tend to differ in texture more than the observed communities, causing departure from null expectation in the direction of convergence. Conversely, if the observed communities were relatively variable in species richness, the random communities would tend to be more similar in richness, and therefore texture, with an implication of divergence. The artifact does not arise if species number in the randomised communities is held at the values observed. Although assembly rules restricting species richness at sites (niche limitation) are a theoretical possibility (Chapter 5) they are not being sought in the present analysis. Consequently, observed site species richness was preserved in the randomised communities generated under the null model.

Treatment of abundance data.

Species abundance data (e.g. photosynthetic biomass) were used as a weighting factor in calculations of site texture means (see below). Should these data be randomised between or within sites under the null model? Site totals of species abundance (in the case of photosynthetic biomass, the photosynthetic component of standing crop) are related to productivity (Grime 1977), which is primarily a function of the physical and chemical environment. In order to distinguish the species interaction effects of interest from environmental effects, the null model must take the abiotic environment, and all factors associated with it, as given. For this reason, each randomised community was given the same total site abundance as its corresponding observed community. The observed distribution of abundance values was also retained, individual abundance values being assigned to (randomly drawn) species character values at random. Abundance values for species common to more than one of the communities being compared, however, were not randomised (see below).

Treatment of common species

Taxonomic overlap among communities would tend to increase the similarity between them. Species may be common to different communities because there are assembly rules which limit community membership to certain functional types of species, the same species having been admitted to different communities in response to the same rules. This reason would be consistent with the hypothesis being tested. An alternative explanation, however, is that certain species from the local pool are more likely to be encountered in sampling than others, for example because they are better represented in the seed pool, more readily dispersed or have wider microhabitat specificity (Rabinowitz 1981). Since it is impossible to distinguish these two causes

of 'convergence' due to common[2] species, it is necessary to effectively exclude these species from analysis.

In previous studies seeking texture convergence relative to a null model (Wilson *et al.* 1994; Smith *et al.* 1994) common species were allocated at random to communities in null model simulations, along with species confined to a single community. It was assumed that, among many randomisations, common species would have no net effect on test statistic values, and could not contribute to rejection of the null hypothesis. However, Smith *et al.* (*op. cit.*) recognised the possibility of bias when character values for common species were weighted by a measure of abundance. In each randomised community, species may become associated with any abundance value from the corresponding observed community. Assume that common species are allowed to assort randomly under the null model along with species unique to one community. Species that have a high observed abundance will be assigned lower ones, on average, in the randomised data. As a result, such species will influence texture more in the observed than in the randomised data. Abundant species common to more than one community, having similar characters and being heavily weighted, would tend to produce a low variance in texture among observed communities. However, their net effect on the among-community variance in the randomised data sets would be much lower. As a result, observed communities would tend to be found more similar than most randomised ones, even if there were no overall convergence.

While bias due to the effect of common abundant species could be pronounced when species abundance is used as a weighting factor in calculating texture, this effect is eliminated when there is no such weighting, because then each species makes the same contribution to texture in the observed and randomised data. However, even in the absence of abundance weighting, a degree of bias can occur because of differences in species richness among the communities being compared. If the community texture mean, $X$, is calculated according to the formula:

$$X = \sum \frac{x_i}{n}$$

where $x_i$ = character value for species $i$;

$n$ = number of species in the community;

then the individual contribution of a particular species, $i$, to $X$ is given by

$$c_i = \frac{x_i}{n}$$

[2]The expression 'common species' is used here to refer to a species in common to two or more communities in a particular comparison.

It is dependent on *n*, the number of species in the community in which it occurs. If a comparison involves communities that differ in species richness, and species *i* belongs to communities, in the observed data, that are relatively similar in species richness, the variance in $c_i$ in the observed data will be lower than in the randomised data (where the species is equally likely to be assigned to any particular community), with a resultant bias towards convergence. If species *i* occurs in communities that are quite different in species richness, the variance in $c_i$ will be higher in the observed than the randomised data, and there will be a bias towards divergence. This effect is only in respect of species *i*, and will tend to cancel out among all species, avoiding a strong overall bias. An overall bias is likely only if there are species that exhibit selectivity for communities with high or low species richness.

Allocating common species to communities at random in the null model, then, does not guarantee a lack of bias, whether abundance values are used to weight species characters or not. So that species occurring in more than one community in a particular comparison would neither increase nor decrease texture variation among communities in the randomised, compared with the real, data, such species were retained with their observed communities in null model randomisations. This practice ensured that species in common between communities could not produce spurious departure from the null model.

Multiple records for the same species

Adult and juvenile morphological types of some species were treated as separate entities both in field sampling and laboratory measurement. This was to ensure that character data for each species reflected as closely as possible the aggregate lifetime niche of the species in the community sampled (see Section 2.3.2). It would be unrealistic to treat multiple records for the same species as if they were different species, allocating them to null communities independently. Therefore, multiple records for the same species from the same community were allocated together in null model randomisations.

Abundance weighting for community texture

Abundant species, through their generally greater stature and population density, would be expected to have a greater overall effect on community structure than minor ones. It would therefore seem appropriate to weight community texture towards abundant species. However, the degree to which species abundance should be taken into account in calculating texture is uncertain. Therefore, several weighting methods were used to calculate community means for a character ($x_{T,i}$, see below). Species were weighted:

1. by presence, i.e. equally;

2. in proportion to their photosynthetic biomass (the mean number of PSUs per quadrat multiplied by mean PSU dry weight);
3. in proportion to the square root of photosynthetic biomass; or
4. according to abundance rank: for a community with *s* species or entities, the most abundant species (in terms of photosynthetic biomass) receives a weighting factor *s*; the next most abundant *s*-1; the next *s*-2 and so on down to 1 for the least abundant species.

If species are weighted by presence only, species of minor importance (relative abundance) in a community contribute to the overall texture value as much as more important species. There is no weighting towards more abundant species, so the test is optimised to seek convergence equally among all niches represented in the community.

Weighting by photosynthetic biomass, on the other hand, weights the most abundant species (mainly canopy trees) very heavily, so that convergence is effectively sought only among the few species accounting for the majority of standing crop. Convergence among texture means calculated using this very heavy weighting level could represent primarily the result of abiotic filtering, producing similar function in the dominant species, and not the result of biotic restrictions on niche overlap — the assembly rules being sought. Dominant species in the communities being compared may have relatively similar characters (e.g. due to selection for optimal function in similar physical environments), while minor species could have different characters, on average, to dominant ones (e.g. due to adaptation to the distinct environments of the understorey and canopy). In null model communities, characters of any species (not just abundant ones) can become associated with high abundance values. There would therefore be a tendency for observed communities (where community texture means are strongly biased towards dominant species) to be 'convergent' relative to null model communities (where texture means would be based primarily on the characters of whatever species are, by chance, allocated higher abundance values).

The square root of photosynthetic biomass and abundance rank are intermediate between these extremes, weighting abundant species more heavily, but also taking account of minor species. Abundance rank is non-parametric, in that the weighting factor is not a function of a species' individual abundance, but of its position in a rank order of abundance including all species in the community. Abundance rank may be the most 'reasonable' weighting factor to apply, taking account of the probable importance of different species in their influence on community structure, without causing an overwhelming bias towards the small number of dominant species (Smith *et al.* 1994). Convergence in texture weighted by abundance rank is unlikely to be interpretable as the sole result of abiotic filtering: biotic filtering — assembly rules mediated by species interactions — would have to have taken place for the observed communities to be significantly more similar than communities generated under the null model.

*Pooled communities*

To assemble texture data for regional and landmass scale communities it was necessary to pool values from individual sites. Where the same species (or 'entities': morphological classes of the same species) had been encountered in more than one of the sites to be pooled, records from different sites were merged mathematically to give one overall value for each. For each species character, the overall value was calculated as the arithmetic mean of transformed site values, weighting each site value by the photosynthetic biomass of the species at that site, i.e.

$$x' = \frac{\sum_{i=1}^{n}(x_i \cdot a_i)}{\sum_{i=1}^{n} a_i}$$

where $x_i$ = character value for species or entity at site $i$;
$a_i$ = photosynthetic biomass of species or entity at site $i$;
$n$ = number of sites being pooled;
$x'$ = overall character value for species or entity in the pooled community.

Weighting was applied to ensure that each overall character value for a species most strongly reflected its phenotype at sites where it was most abundant and therefore, potentially more important in its effect on community structure (see below).

Overall photosynthetic biomass values for each species in each pooled community were obtained by summing values from component sites.

*Randomisation tests*

Randomisation tests employing the null model described above were carried out to search for evidence for convergence or divergence between communities at the local, regional and landmass scales. The same combinations of communities were compared as in Chapter 5. The network of comparisons is depicted in Fig. 6.1.

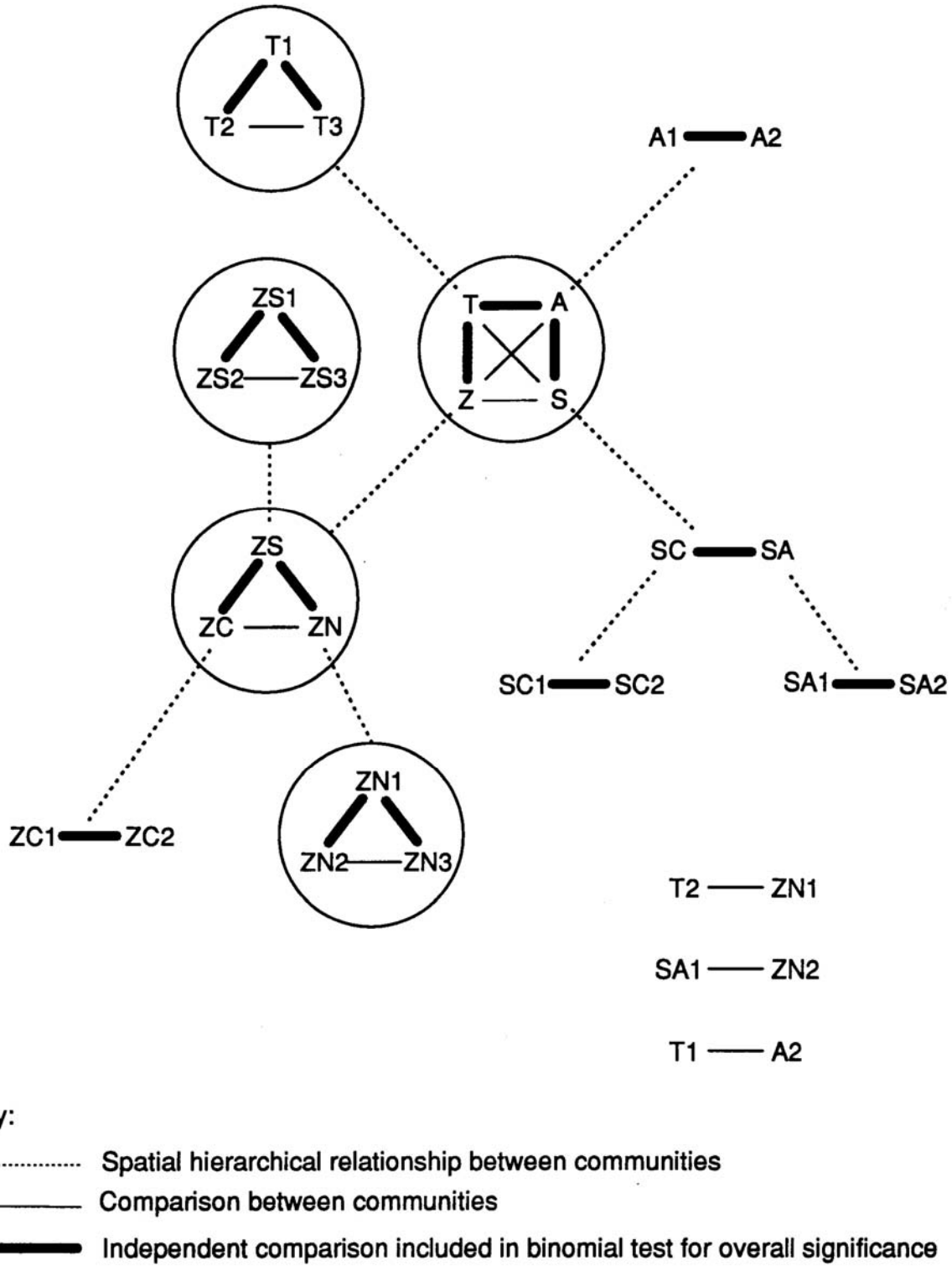



**Fig 6.1** Schematic diagram showing comparisons seeking texture convergence between landmass, regional and local scale communities. Letter codes denote communities, as listed in Section 3.2. Sixteen independent comparisons on which binomial tests for overall significance are based (see text), are highlighted.

Randomisation algorithm

To implement the null model, all species and entities recorded at the communities under consideration were pooled and reassigned to artificial communities at random, observing the following constraints, which are justified above:

1. The observed number of species in each community was preserved in the null communities.
2. Observed abundance (photosynthetic biomass) distributions, and therefore total abundance, were preserved for each community. However, abundance values were assigned to species at random, even if a species was reassigned, by chance, to the null community corresponding to that in which it was observed.
3. Species that were observed in more than one of the communities being compared were not randomised.
4. Multiple records (e.g. juvenile and adult) for the same species from a particular observed community were allocated to the same null community.

The randomisation procedure consisted of drawing species (or, more precisely, their sets of characters) at random from the combined pool and assigning them to arrays representing null communities. One community array was completely filled first, then subsequent arrays until all records from the pool had been allocated (and all communities had a full complement of species).

Because some species records were allocated, not singly, but as part of a group of records (originally pertaining to different morphological or age classes of the same species), it was necessary to reduce the probability of selecting any particular record in the group from the species pool, so that the probability of drawing the whole group was the same as that of drawing any single independent record. The probability, $P_1$, of drawing a whole multiple record from the pool, having randomly chosen one of its $m$ records, was therefore set to:

$$P_1 = \frac{1}{m}$$

A further complication was the possibility of a ‘hang-up’ (Connor & Simberloff 1979), when a set of $m$ multiple records was drawn from the pool but could not be assigned to a particular community with $s$ species or entities, because more than $s$-$m$ species had already been allocated to it. If a hang-up occurred, the randomisation was abandoned and repeated.

If multiple records were assigned with equal probability to all communities, hang-ups would be more likely for communities with a small number of species, because these are `filled up' with species records more quickly. Since randomisations were abandoned in the event of a hang-up, there would be an overall tendency for multiple records to become associated with

larger null communities (ones containing more species and entities), a potential source of bias. To avoid bias, it was necessary to make a further correction to the probability of assigning a multiple record, having drawn it from the pool, so that it was equally likely to be assigned to any community. Having chosen a multiple record (comprising *m* entities) for assignment to a community with *s* species or entities, the attempted assignment was allowed to proceed with the probability:

$$P_2 = 1 - \frac{s - m + 1}{s}$$

If not assigned, the multiple record was replaced in the pool.

To confirm that the randomisation procedure did not produce any bias towards rejection of the null hypothesis, a random variate was added to the set of 13 character variates. Each species or entity from each community being compared was assigned a real random value from the uniform distribution in the range 0-1. In the absence of bias, significant ($P$<0.05) 'convergence' or 'divergence' should be detected in the random variate in approximately 5% of tests (2.5% in each direction). After many tests, the significance of departure from this expected pattern was examined using a binomial test (see below).

Comparison of observed with null communities

Texture means $X_T$ in terms of each character $T$ were calculated for each community and each method of weighting species by abundance:

$$X_T = \frac{\sum_{i=1}^{s} (x_{T,i} \cdot w_i)}{\sum_{i=1}^{s} w_i}$$

where $s$ = number of species and entities present in community;
$x_{T,i}$ = transformed value of character $T$ for species or entity $i$;
$w_i$ = weighting factor (presence [=1], abundance rank, square root of photosynthetic biomass or photosynthetic biomass) for species or entity $i$.

Transformed (Section 2.3.5; Table 2.1) species character values $x_{T,i}$ were used. Species height values were transformed by taking the natural logarithm.

Variation among communities in texture means (evaluated separately for each species character) was quantified as the between-site deviance, $\bar{D}_T$:

$$\overline{D}_T = \sqrt{\frac{\sum_{i=1}^{n} ( X_{T,i} - \overline{X}_T )^2}{n}}$$

where $n$ = the number of communities being compared;
$X_{T,i}$ = the mean for texture variate $T$ in community $i$;
$\overline{x}_T$ = the mean of $X_{T,i}$ across all $n$ communities, for variate $T$.

For each test, 2000 null model randomisations were performed, and the test statistic $\overline{D}_T$ calculated for each randomised data set, as well as for the observed data. A low value of $\overline{D}_T$ for the observed data, relative to its mean value among randomised data sets, would indicate that the observed communities are more similar in texture, in terms of variate $T$, than expected under the null model. This may be interpreted as a tendency towards convergence. Similarly, a high value of $\overline{D}_T$ would suggest dissimilarity in texture among the observed communities, a tendency towards divergence. The strength of any tendency towards convergence or divergence was quantified as the relative deviance, $R_{\overline{D},T}$ :

$$R_{\overline{D},T} = \frac{\overline{D}_T \text{ (observed)}}{\sum \overline{D}_T \text{ (null)} / 2000}$$

$R_{\overline{D},T}$ has a value less than 1 if there is a tendency towards convergence among the observed communities in terms of texture variate $T$. A value greater than 1 corresponds to a tendency towards divergence.

The significance $P$ of departure from the null model was calculated as the proportion of randomised data sets for which $\overline{D}_T$ was at least as small (if $R_{\overline{D},T}<1$) or at least as large (if $R_{\overline{D},T}>1$)[3] as $\overline{D}_T$ for the observed communities, multiplying the result by 2 to effect a two-tailed test (Crowley 1992). Departure from null expectation was deemed significant if $P$ was found to be less than 0.05.

*Binomial test for overall significance*

In this chapter, separate randomisation tests were performed for 31 community comparisons, in terms of 13 texture variates (not including the random variate), and with four different weighting methods, making a total of 31 × 13 × 4 = 1612 separate tests. Among so many tests, an

[3] A value of $R_{\overline{D},T}$ exactly equal to 1, implying neither convergence nor divergence, would not necessitate calculation of a $P$-value.

appreciable number of significant outcomes would be expected even in the absence of systematic trends in the data set. Such inappropriate rejection of the null hypothesis is known as type I statistical error (Snedecor & Cochran 1967). At the target significance level of 0.05, 5% of tests, approximately 80, would be expected to show significant convergence or divergence by chance alone.

There are methods available for determining the overall significance of a set of statistical results. For example, Bonferroni correction divides the target significance level by the number of tests done, so that the 'experimentwise' significance level — the likelihood of a type I error in *any* of the tests — is equal to the target level (Fisher & van Belle 1993).

The scope of the 'experiment' is not necessarily clear: in the case of the present study it could consist of all comparisons of community texture means with respect to one texture variate and weighting method; all tests in this chapter; all the tests done in the whole study; or even all tests carried out in the lifetime of the investigator (Fisher & van Belle 1993). The application of Bonferroni correction to achieve an experimentwise target significance of 0.05 for this chapter would require a target significance in each test of $0.05 / 1612 = 3.1\times10^{-5}$. For various practical and theoretical reasons, such highly significant departure from null model expectation is unlikely to be demonstrable.

An alternative approach is to ask the significance of the number of significances obtained, i.e. the probability that the significant results obtained in separate tests all represent type I errors. Problems of this type can be addressed using the binomial distribution. Given a random sample of size $n$ from a population of which a proportion $p$ of members possess some attribute $A$, the binomial distribution gives the probability that $m$ members of the sample possess attribute $A$ (Snedecor & Cochran 1967). In the present context, $n$ would correspond to the number of independent tests done; $A$ would represent significant departure from null expectation; $p$ would be the target significance level and $m$ the number of tests showing significance[4].

Binomial probabilities are valid measures of overall significance only if the tests concerned are independent of each other. Clearly not all the tests carried out in this chapter are independent. It was shown in Chapter 4 that there are intercorrelations among species characters. This means that convergence or divergence between communities in terms of one texture variate, may not be independent of convergence or divergence in another. Similarly, convergence obtained using one method of weighting species characters (e.g. photosynthetic biomass) will not be independent of results obtained with another weighting method (e.g. the square root of

[4]For example, if ten independent tests for convergence or divergence are carried out at a target significance (type I error) level of 0.05 and two tests show significant departure from null model expectation, what is the probability $P$ that both significant results represent type I errors? The question is equivalent to the following: if 10 balls are drawn at random from a bag containing many balls of which 5% are red, what is the likelihood $P$ that two of the balls drawn will be red? A binomial test gives $P$=0.086.

photosynthetic biomass). There may also be non-independence in comparisons involving different sets of communities. For example, convergence between sites T1 and T2 will be statistically independent of convergence in sites T1 and T3. However, a further result showing convergence between sites T2 and T3 cannot be regarded as independent of the other two.

Separate binomial tests were carried out to determine the overall significance of (significant) convergence or divergence for each variate/weighting factor combination. Each test was applied to results obtained for a set of 16 independent community comparisons (Fig. 6.1), the largest subset of all comparisons that was possible without including non-independent tests.

A binomial test was also applied to examine the significance of departures from null expectation obtained for the random 'texture' variate. Results from all 31 community comparisons were used, since fresh random values had been generated for each comparison. A separate test of overall significance was done for each method of weighting species character values by abundance.

Binomial frequencies were calculated using a computerised implementation of the binomial expansion (Snedecor & Cochran 1967; computer program by J.B. Wilson).

## 6.3 Results

VALIDITY OF THE NULL MODEL

For each method of weighting species values by abundance, the number of tests (among-community comparisons) in which significant departure from null expectation was detected in the random texture variate, is given in Table 6.1. Given that a total of 31 comparisons was carried out among communities, occasional significance would be expected even for random values, due to type I errors. From the binomial distribution, at least three significant results in either direction (divergence or convergence) would be required for the effect to be significant overall ($P<0.05$). Divergence was detected in the random variate in one test with abundance rank or photosynthetic biomass as the weighting method. At the 5% two-tailed significance level used, the probability of detecting divergence once by chance among 31 tests is 0.543. There is therefore no evidence for bias in the null model.

**Table 6.1** The number out of 31 among-community comparisons in which community texture means calculated from random data were found to be significantly convergent or divergent ($P$<0.05) at each of four methods of weighting species values by abundance (see text).

| Weighting method | Convergence | Divergence |
|---|---|---|
| Presence | 0 | 0 |
| Abundance rank | 0 | 1 |
| Sqrt biomass | 0 | 0 |
| Biomass | 0 | 1 |

## PATTERNS AMONG COMMUNITIES

### *Landmass scale*

Little overall convergence was detected among the four landmasses, Tasmania, New Zealand, Australia and South America (Fig. 6.2a). Two texture variates, PSU succulence and specific weight, are significantly convergent with species values weighted heavily by abundance. However, this may simply reflect similar leaf attributes among the canopy (mainly *Nothofagus*) species, an interpretation consistent with the (non-significant) tendency towards convergence in several other variates, with species values weighted by photosynthetic biomass or its square root. The overall pattern is one of divergence among landmasses, several variates being significantly divergent, especially at more equitable weighting levels, i.e. when the characters of all species are materially taken into account.

The overall pattern is reflected in comparisons of individual pairs of landmasses (Fig. 6.2b-g), divergence being more common, with occasional significant convergence occurring primarily at heavy abundance weighting levels. Tasmania and New Zealand, identified (Chapter 3) as the two landmasses at which the study sites were most closely matched overall in terms of environmental factors (Fig. 6.2c), are significantly convergent only in support fraction (weighting by the square root of biomass), although PSU area, succulence, specific weight, shape, dividedness, inclination, nitrogen, height and total chlorophyll all show a non-significant tendency to be more similar than expected under the null model ($R_{\bar{D},T}$<1). This pattern applies at low as well as high weighting levels, suggesting that there is overall similarity in texture, and not merely in the characters of a few dominant species. PSU phosphorus content and chlorophyll *a/b* are, however, significantly divergent at lower weighting levels.

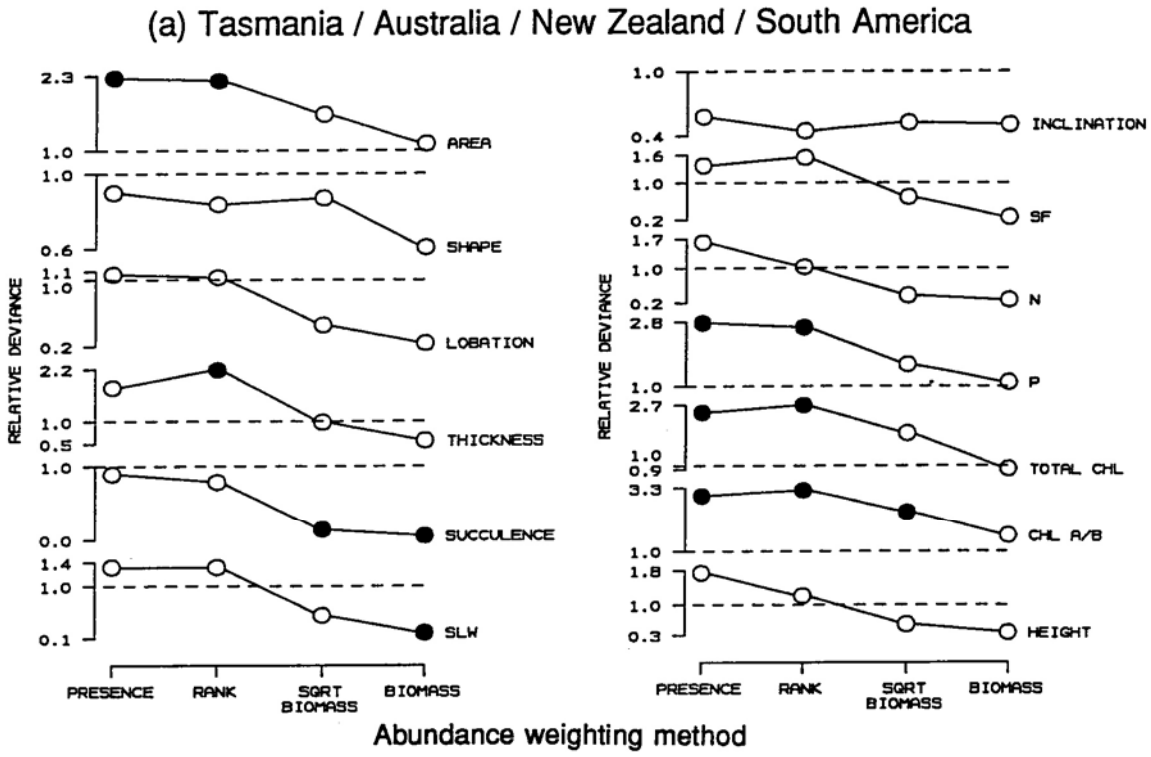



**Fig. 6.2** Null model randomisation tests for convergence or divergence in texture means between landmass-scale *Nothofagus*-dominated communities Tasmania (T), Australia (A), New Zealand (Z) and South America (S). The relative deviance $R_{\bar{D},T}$ of among-community variation in texture means is shown for each of 13 texture variates and four methods of weighting individual species values by abundance in calculations of community texture means. A value of $R_{\bar{D},T}<1$ indicates similarity in texture between communities relative to a null model simulating random community assembly (see text); $R_{\bar{D},T}>1$ indicates dissimilarity relative to the null model. Broken lines signify null model expectation ($R_{\bar{D},T}=1$). Filled symbols correspond to significant departure from the null model (convergence for $R_{\bar{D},T}<1$; divergence for $R_{\bar{D},T}>1$; $P<0.05$). Key to abbreviations: RANK=abundance rank; SQRT BIOMASS=square root of photosynthetic biomass; BIOMASS=photosynthetic biomass (see text for full explanation). Texture variates are based on PSU characters except SF (support fraction) and HEIGHT (species height). Key: SLW=specific weight; N=nitrogen content; P=phosphorus content; TOTAL CHL=total chlorophyll content; CHL A/B=chlorophyll *a/b* ratio (see text for full explanation).

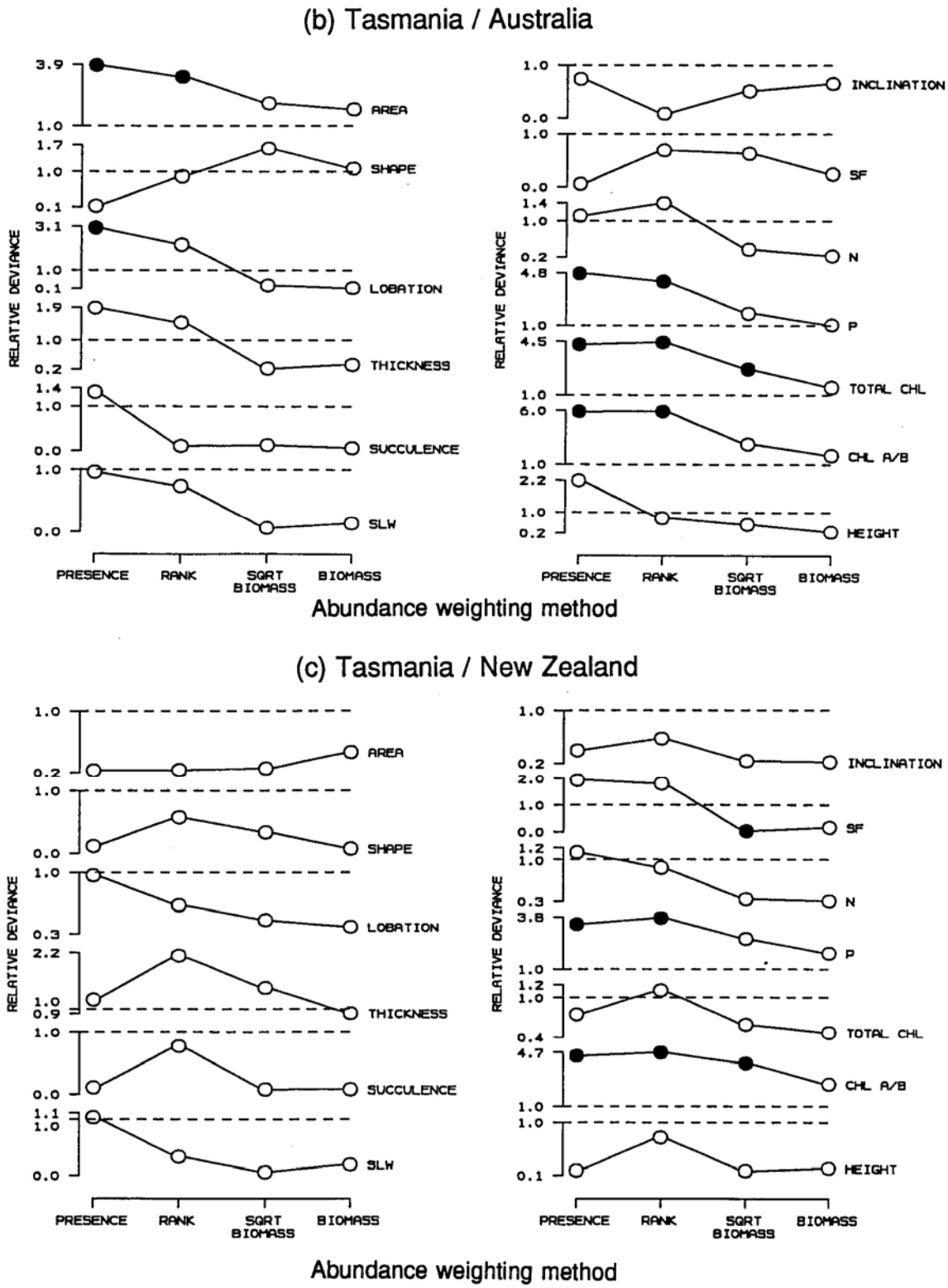



**Fig. 6.2** (continued)

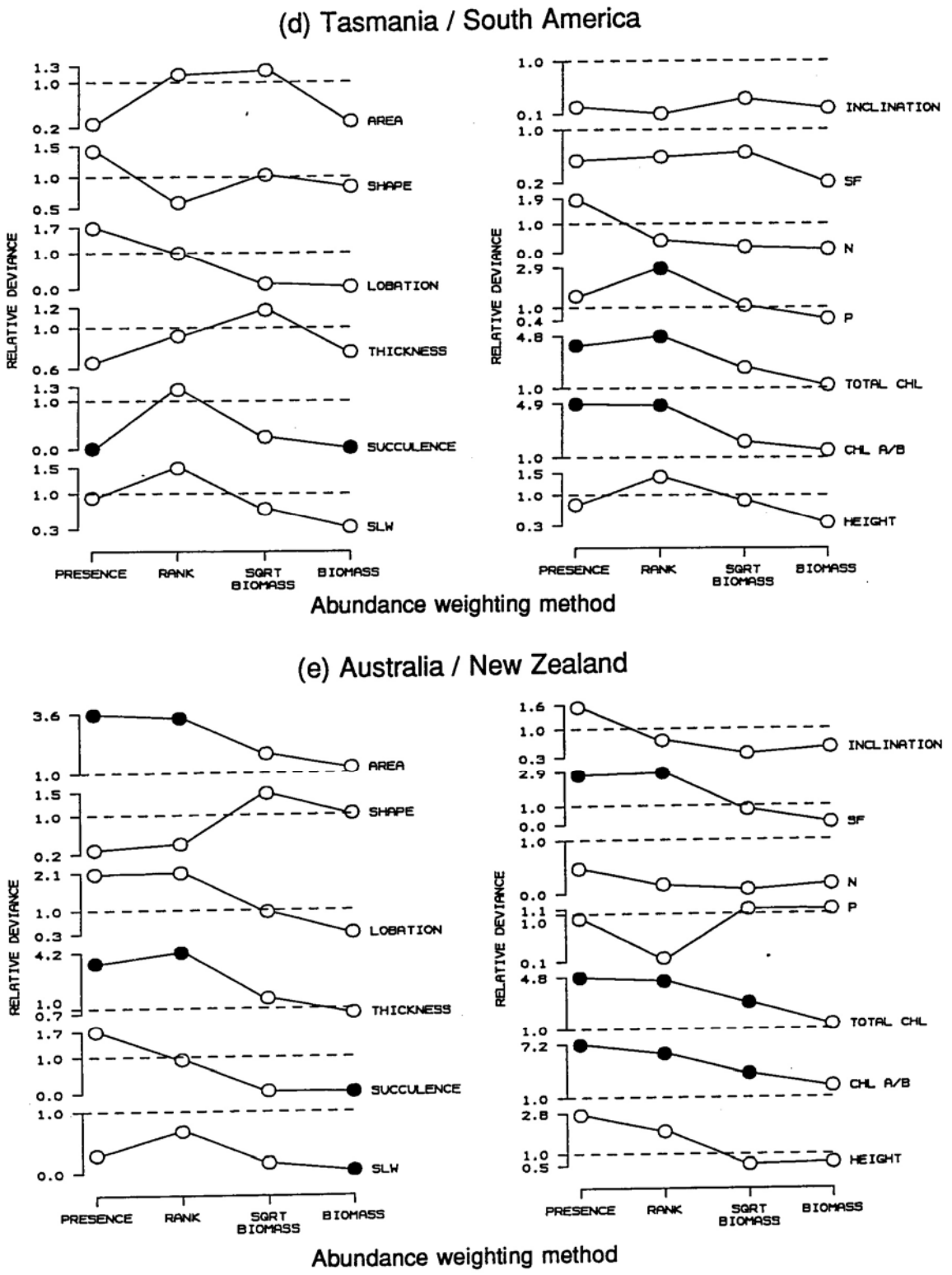



**Fig. 6.2** (continued)

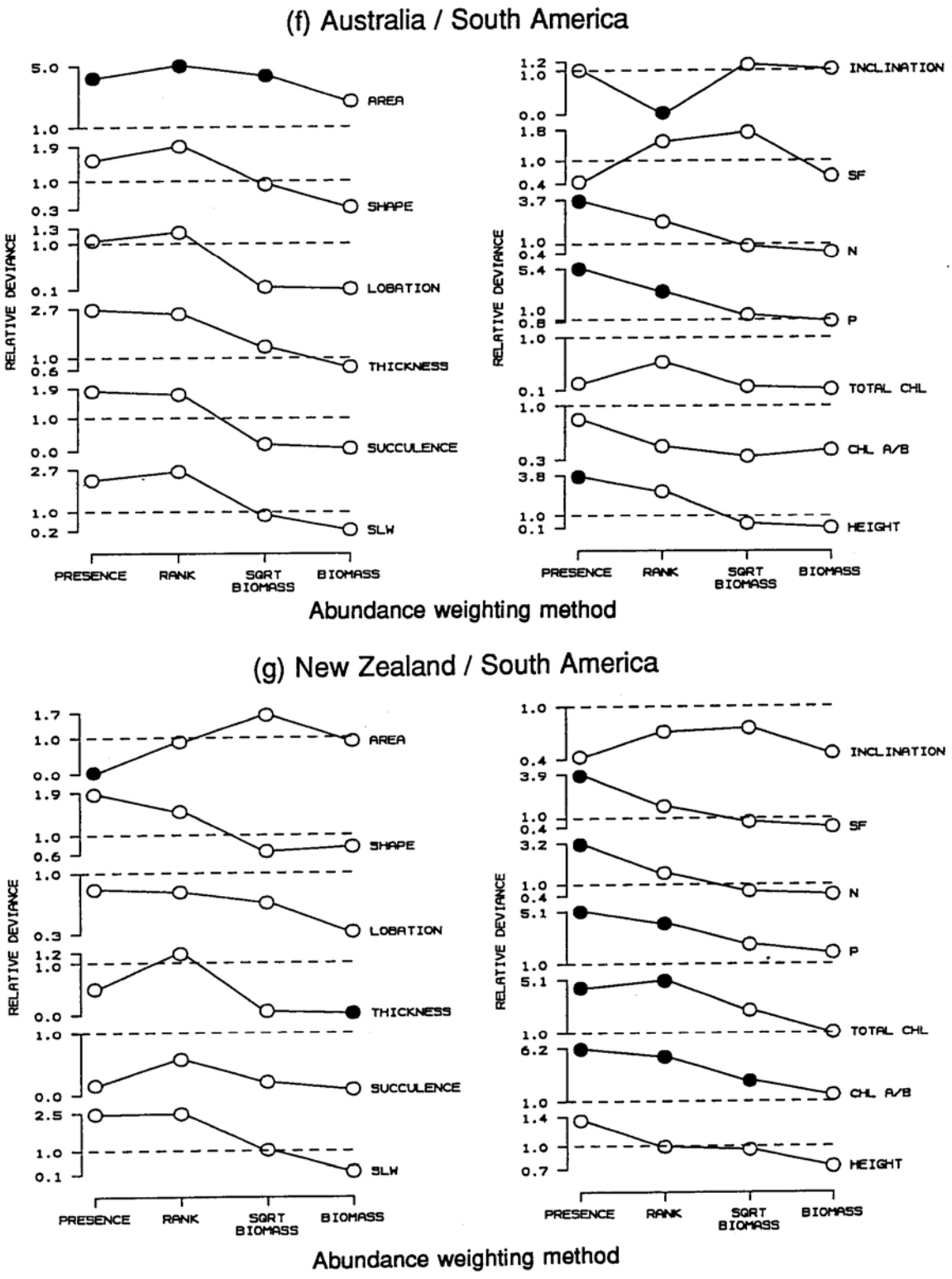



**Fig. 6.2** (continued)

*Regional scale*

The three sites from different regions of Tasmania show little convergence. In only one test, of species height with species values weighted by the square root of photosynthetic biomass, were the three communities significantly more similar to each other than would be expected if the null model were true (Fig. 6.3a). Since the principal canopy species (*Nothofagus cunninghamii*) was the same at all three sites (and could therefore not have contributed to convergence relative to the null model utilised) this must indicate a tendency for different species of relatively high abundance to occupy similar vertical positions in the understoreys of the three communities. PSU chlorophyll *a/b* ratios were significantly divergent among the three communities, when species values were weighted by the square root of photosynthetic biomass.

In pairwise comparisons of Tasmanian sites (Fig. 6.3b-d), significant convergence was detected in only two tests: for PSU shape (weighting by photosynthetic biomass) and species height (weighting by the square root of photosynthetic biomass) at T1 Balfour and T3 Mathinna, with weighting by photosynthetic biomass (Figs. 6.3c). However, Balfour and T2 Anne are significantly divergent in PSU succulence, specific weight, phosphorus content and species height at low weighting levels (Fig. 6.3b).

Australian sites A1 Lumeah and A2 Cascades are non-convergent in all texture variates (Fig. 6.4), but are significantly divergent in PSU phosphorus content (all weighting levels except photosynthetic biomass) and PSU shape (higher weighting levels).

The southern, central and northern regions of New Zealand are significantly convergent only in species height, with photosynthetic biomass or its square root as a weighting factor (Fig. 6.5a). Since there are no *Nothofagus* species that were encountered in only one of the regions, the observed similarity in species height must reflect similarity in the vertical structure of the understorey. However, species height is divergent among regions when species are weighted by abundance rank, and there is significant divergence in a further four variates: PSU succulence, phosphorus content, chlorophyll *a/b* and support fraction. With the exception of support fraction, divergence was detected at lower weighting levels, suggesting that minor species, as well as more abundant ones, may be involved in producing the dissimilarity detected between communities.

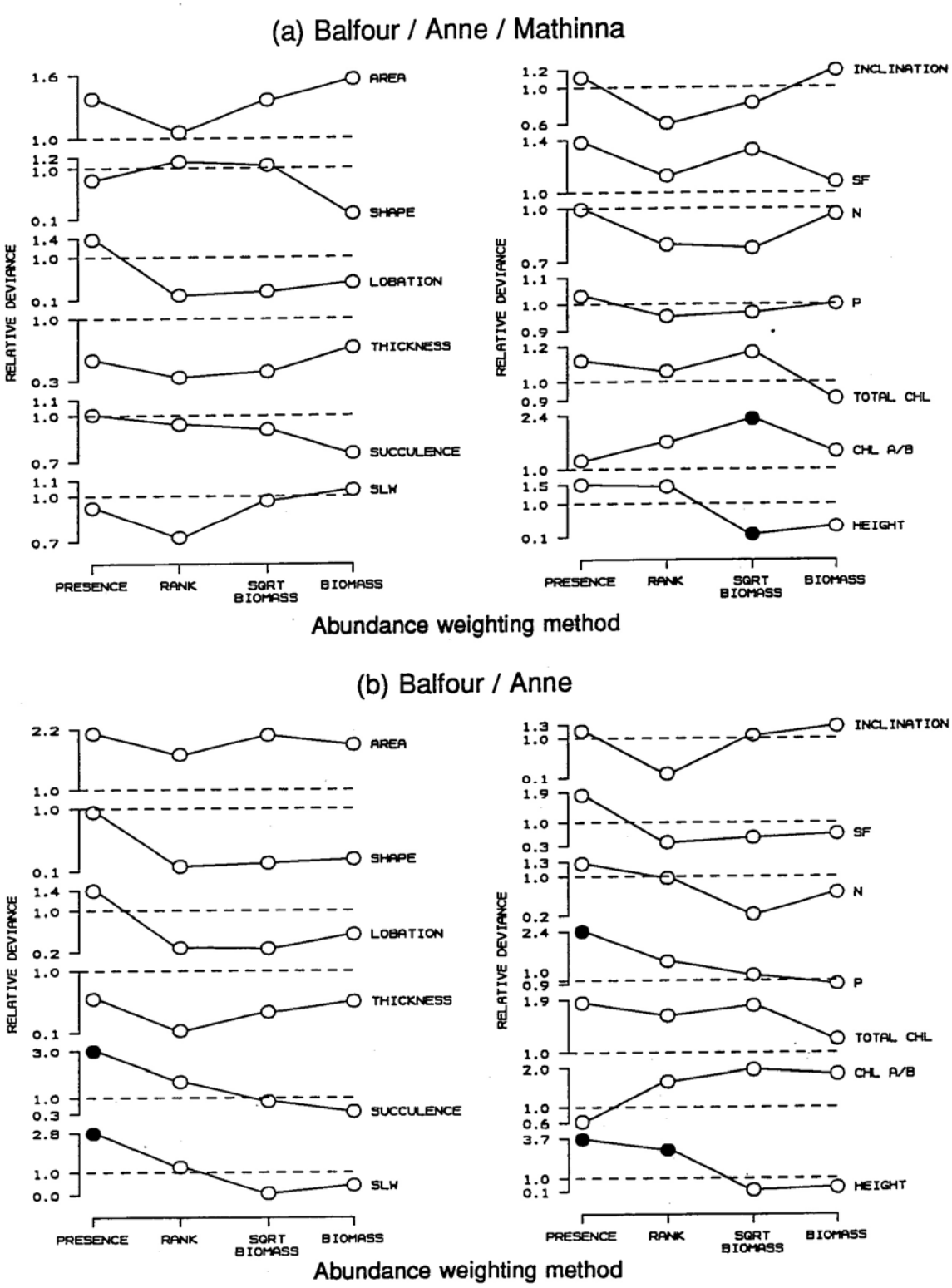



**Fig. 6.3** Null model randomisation tests for convergence or divergence in texture means between regional-scale *Nothofagus*-dominated communities T1 Balfour, T2 Anne and T3 Mathinna. Format as for Fig. 6.2.

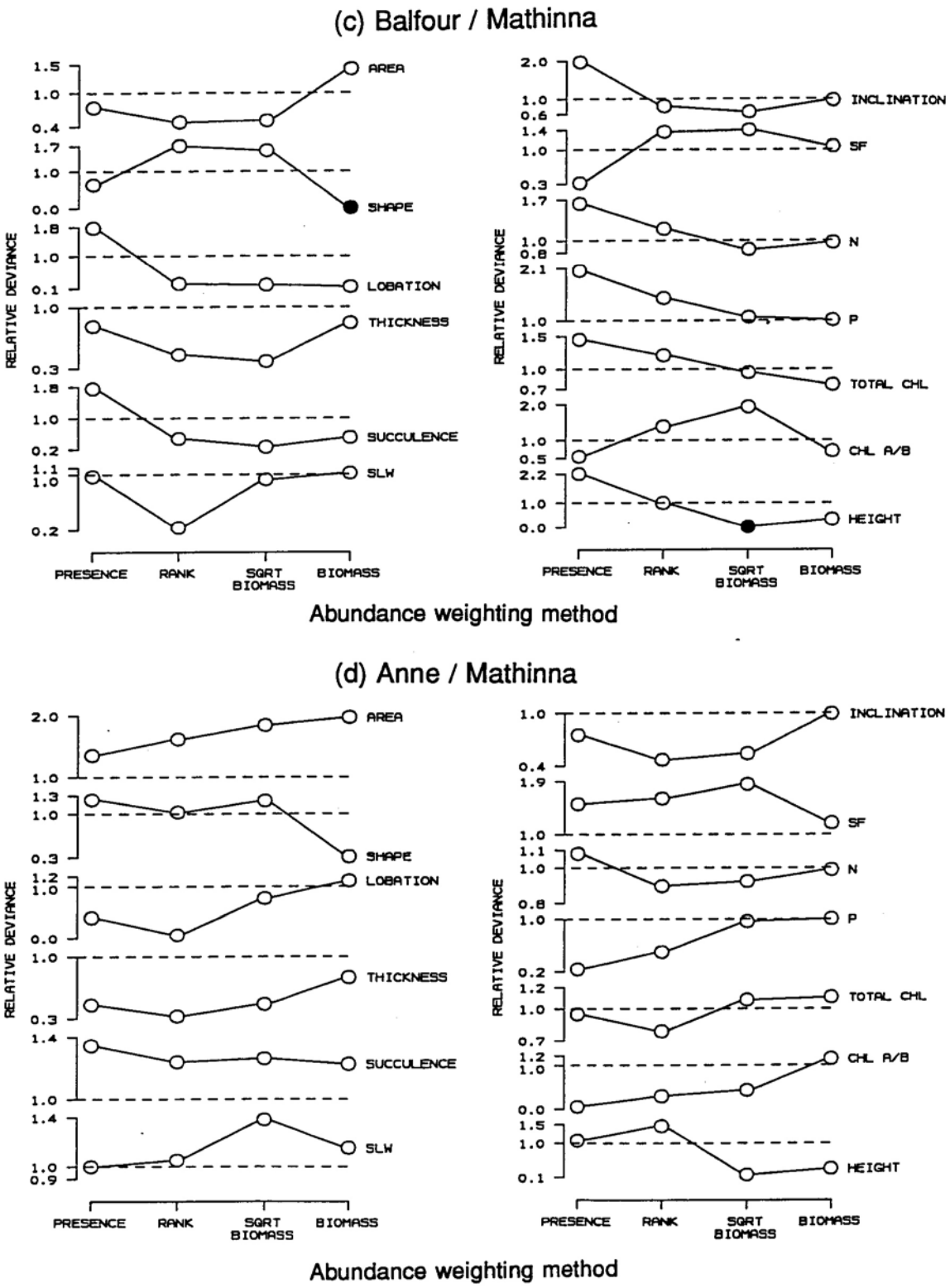



**Fig. 6.3** (continued)

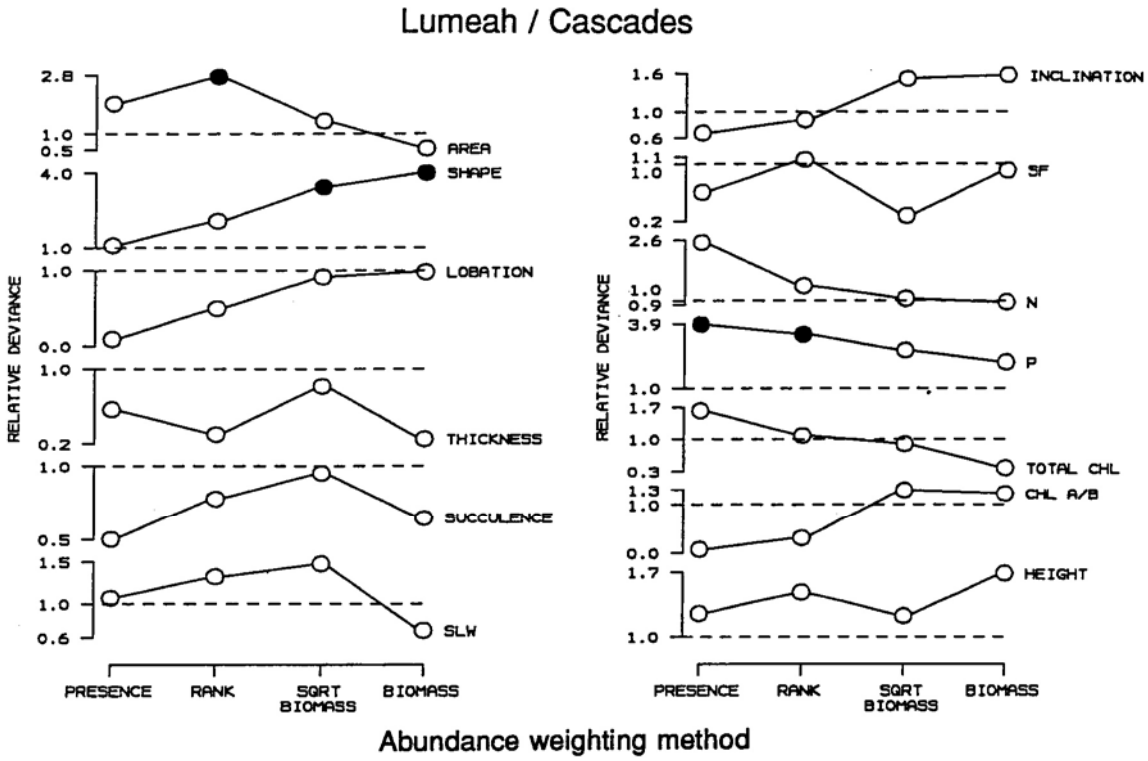



**Fig. 6.4** Null model randomisation tests for convergence or divergence in texture means between regional-scale *Nothofagus*-dominated communities A1 Lumeah and A2 Cascades. Format as for Fig. 6.2.

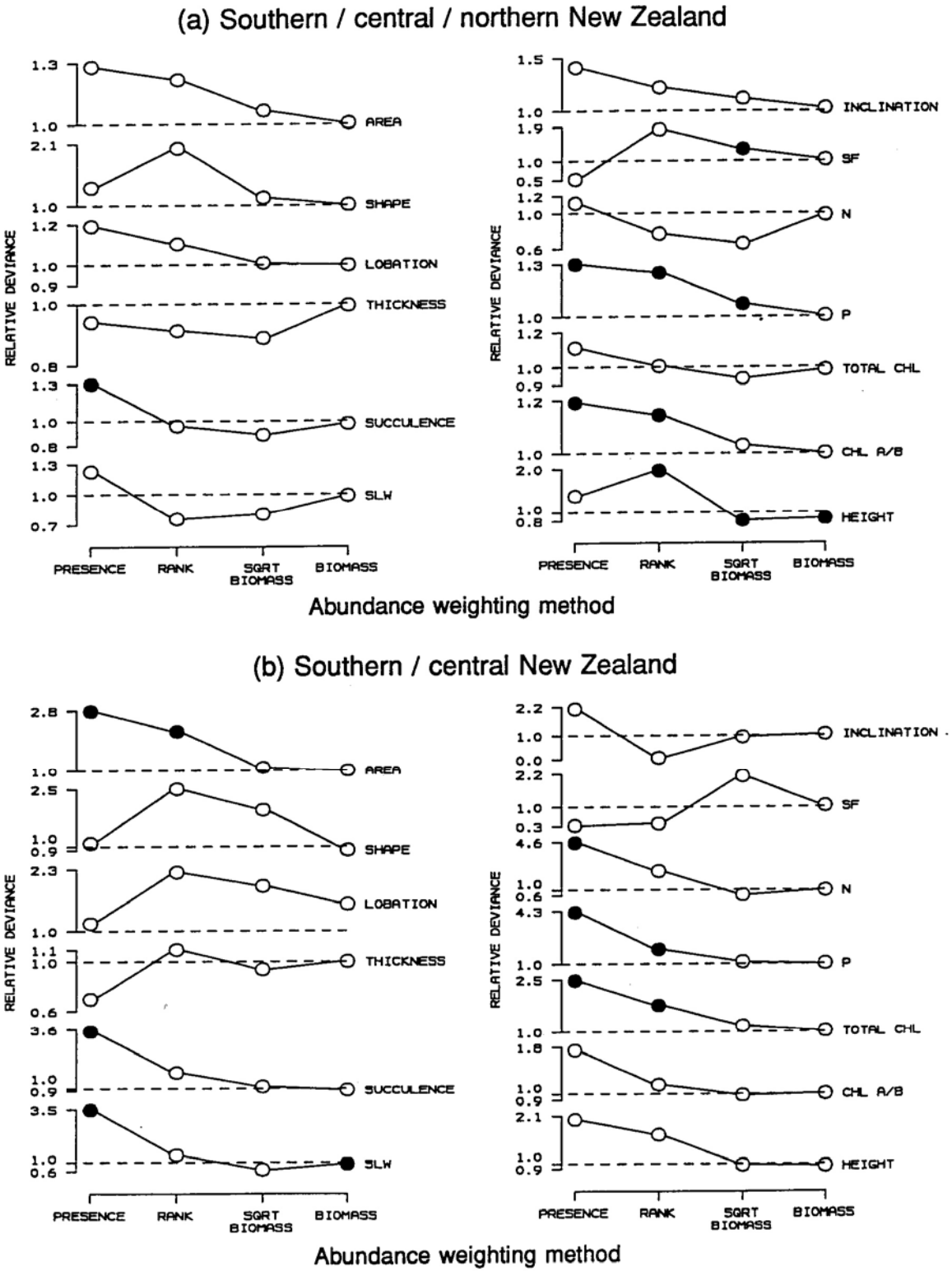



**Fig. 6.5** Null model randomisation tests for convergence or divergence in texture means between regional-scale *Nothofagus*-dominated communities southern (ZS), central (ZC) and northern (ZN) New Zealand. Format as for Fig. 6.2.

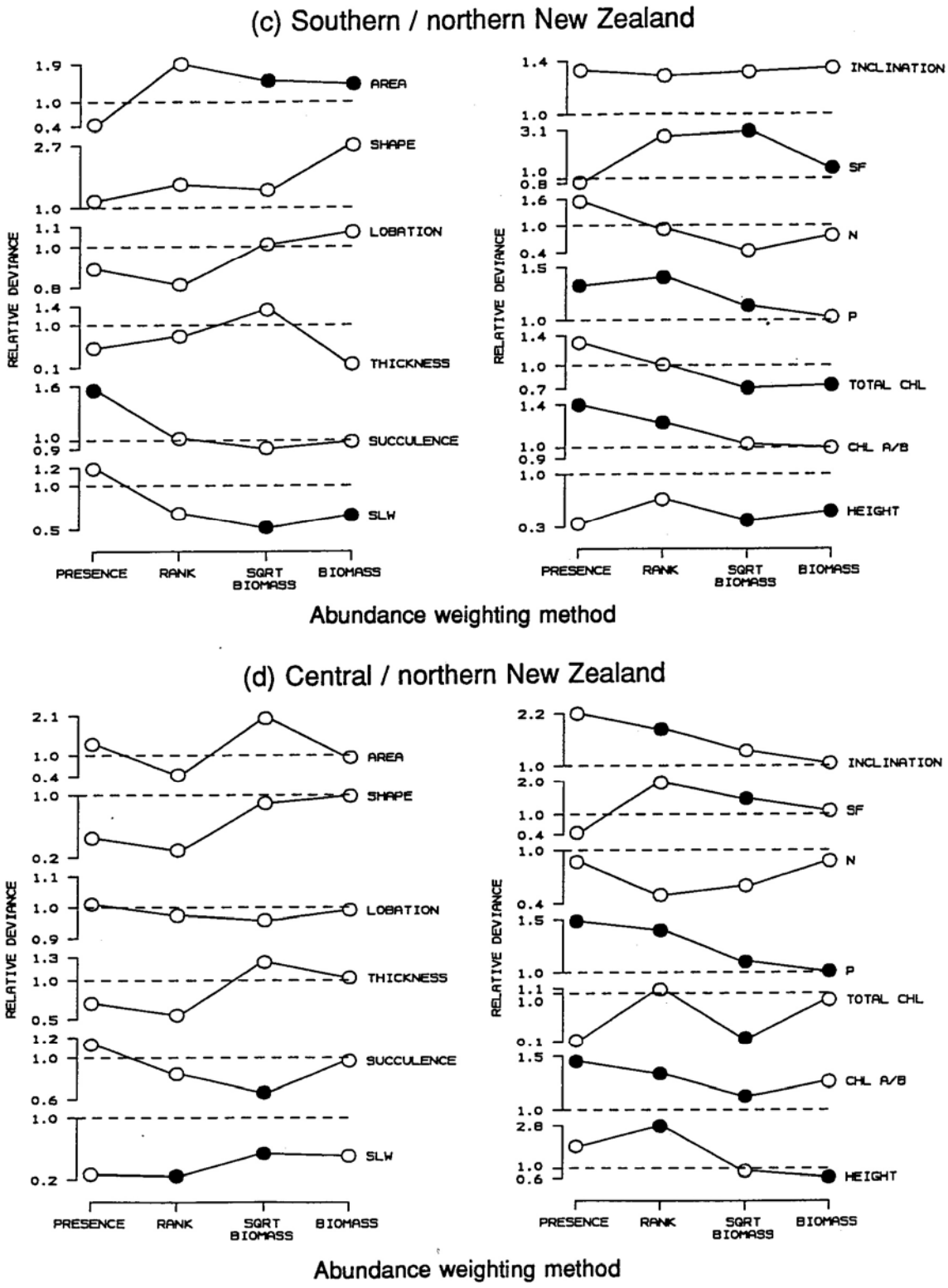



**Fig. 6.5** (continued)

Although study sites in the southern (ZS) and central (ZC) regions of New Zealand were found to be relatively similar in their macroenvironments (Chapter 3), these regional communities are divergent in several variates — PSU area, succulence, specific weight, nitrogen content, phosphorus content and total chlorophyll (Fig. 6.5b). The divergence was found only when species values were weighted by presence or abundance rank. The only test that revealed significant convergence between southern and central New Zealand was of PSU specific weight with photosynthetic biomass as the abundance weighting factor. At this very heavy weighting factor, the convergence may reflect the influence of similarity among relatively few abundant species from each community.

Southern and northern (ZN) New Zealand show significant convergence in PSU specific weight, total chlorophyll and species height (Fig. 6.5c). The convergence tends to be significant only at higher abundance weighting levels. However, PSU specific weight also shows a non-significant tendency towards convergence with weighting by abundance rank, while species height is non-significantly or significantly convergent at all weighting levels. There is significant divergence in PSU area, phosphorus content, chlorophyll *a/b* and support fraction.

PSU specific weight shows a tendency towards convergence at all abundance weighting levels between central and northern New Zealand (Fig. 6.5d). The convergence is significant at the two intermediate weighting levels. There is also convergence in PSU succulence and total chlorophyll and, with weighting by photosynthetic biomass, species height. However, several texture variates (PSU inclination, support fraction, chlorophyll *a/b* and species height) are significantly divergent at some weighting levels; PSU phosphorus content is divergent at all levels.

There is a marked degree of divergence between the pooled communities of Chile (SC) and Argentina (SA), which is significant for several of the 13 texture variates at various weighting levels (Fig. 6.6). Only PSU lobation, with species values weighted equally in determining texture means, is significantly more similar between the communities than expected under the null model. Study sites in Chile and Argentina were found to be rather dissimilar environmentally, particularly with respect to rainfall parameters (Chapter 3). The high degree of divergence seems consistent with the hypothesis that different environments have selected for different character syndromes among many of the species occurring in *Nothofagus*-dominated communities sampled in the two regions.

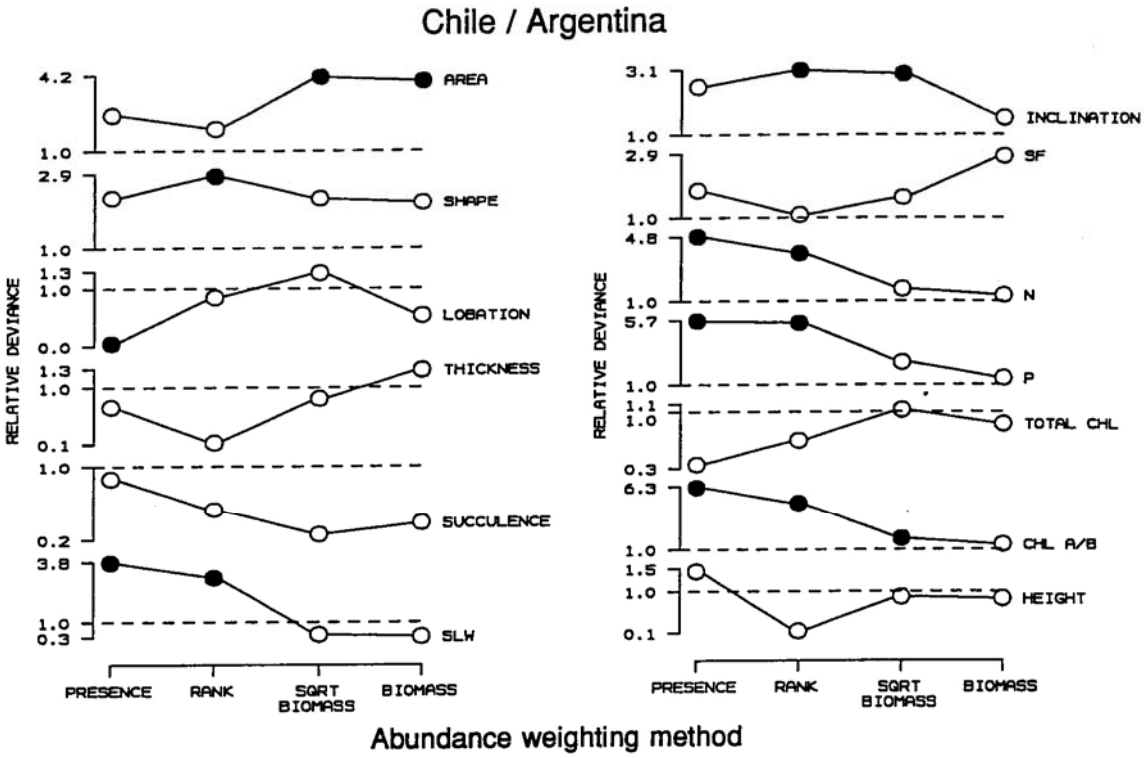



**Fig. 6.6** Null model randomisation tests for convergence or divergence in texture means between regional-scale *Nothofagus*-dominated communities of Chile (SC), and Argentina (SA). Format as for Fig. 6.2.

*Local scale*

In spite of apparent similarity in their environments (Chapter 3), there is no overall convergence among the southern New Zealand communities ZS1 Ten Mile, ZS2 Walker and ZS3 Deer (Fig. 6.7a). Three physiological parameters, PSU nitrogen, phosphorus and chlorophyll *a/b* ratio, are significantly divergent when species values are weighted equally or by abundance rank.

The overall pattern is reflected in pairwise comparisons between sites in southern New Zealand (Fig. 6.7b-d). Between Ten Mile and Walker (Fig. 6.7b), PSU shape shows a tendency towards convergence at all weighting levels, significantly so for the square root of biomass. Four variates (PSU specific weight, nitrogen, phosphorus and chlorophyll *a/b*) are divergent at low weighting levels. No significant departure from null expectation was found for any variate in a comparison of Ten Mile and Deer (Fig. 6.7c). Walker and Deer show a general tendency towards convergence in at least eight of the 13 texture variates (PSU area, shape, lobation, thickness, succulence, support fraction, PSU total chlorophyll and species height; Fig. 6.7d). However, only PSU thickness, succulence and support fraction are significantly convergent. PSU phosphorus content and chlorophyll *a/b* are divergent between these sites, when species are unweighted, or moderately weighted, by abundance.

Central New Zealand sites ZC1 Craigs and ZC2 Station are convergent in PSU thickness and specific weight (weighting by square root of biomass) and species height (abundance rank; Fig. 6.8). PSU area is also convergent with weighting by photosynthetic biomass, but is divergent at all other weighting levels. There is also some divergence in PSU lobation, total chlorophyll and, in the absence of an abundance weighting factor, species height.

Although the three study sites in northern New Zealand (ZN1 Ohakune, ZN2 Rotokura and ZN3 Clements) were found to have closely similar environments (Chapter 3), significant convergence among them was found only in community-wide means of support fraction (Fig. 6.9a). On the other hand, PSU specific weight, nitrogen content, phosphorus content, total chlorophyll and chlorophyll *a/b* all show significant divergence. The divergence is generally at low abundance weighting levels, suggesting that it is manifest across a range of species of varying abundance in the communities.

Focusing on individual pairs of sites in northern New Zealand, Ohakune and Rotokura are divergent in PSU area, specific weight and total chlorophyll (Fig. 6.9b). There is no significant convergence. Ohakune and Clements show divergence in PSU nitrogen content, total chlorophyll and chlorophyll *a/b*, although there is convergence in the latter variate when species are weighted by photosynthetic biomass (Fig. 6.9c). Species height shows an overall tendency towards similarity between the two communities, and the effect is significant at higher abundance weighting levels. Rotokura and Clements are convergent in PSU thickess, specific weight and species height, but only when photosynthetic biomass is used to weight species values in calculating site means (Fig. 6.9d). PSU area (weighting by photosynthetic biomass) and support fraction (photosynthetic biomass or its square root) show significant divergence.

The two study sites in Chile (SC1 Pelada, SC2 Antillanca) show neither significant convergence nor divergence in any variate (Fig. 6.10). PSU shape, lobation, succulence, total chlorophyll and specific weight have $R_{\bar{D},T}<1$ at all weighting levels, suggesting that there may be a tendency towards convergence in these variates which was too weak for significance to be shown.

Argentinian sites SA1 Quetrihué and SA2 Gutierrez likewise show little significant departure from the null model (Fig. 6.11). PSU shape is convergent when species values are unweighted by abundance, while support fraction is divergent at higher weighting levels.

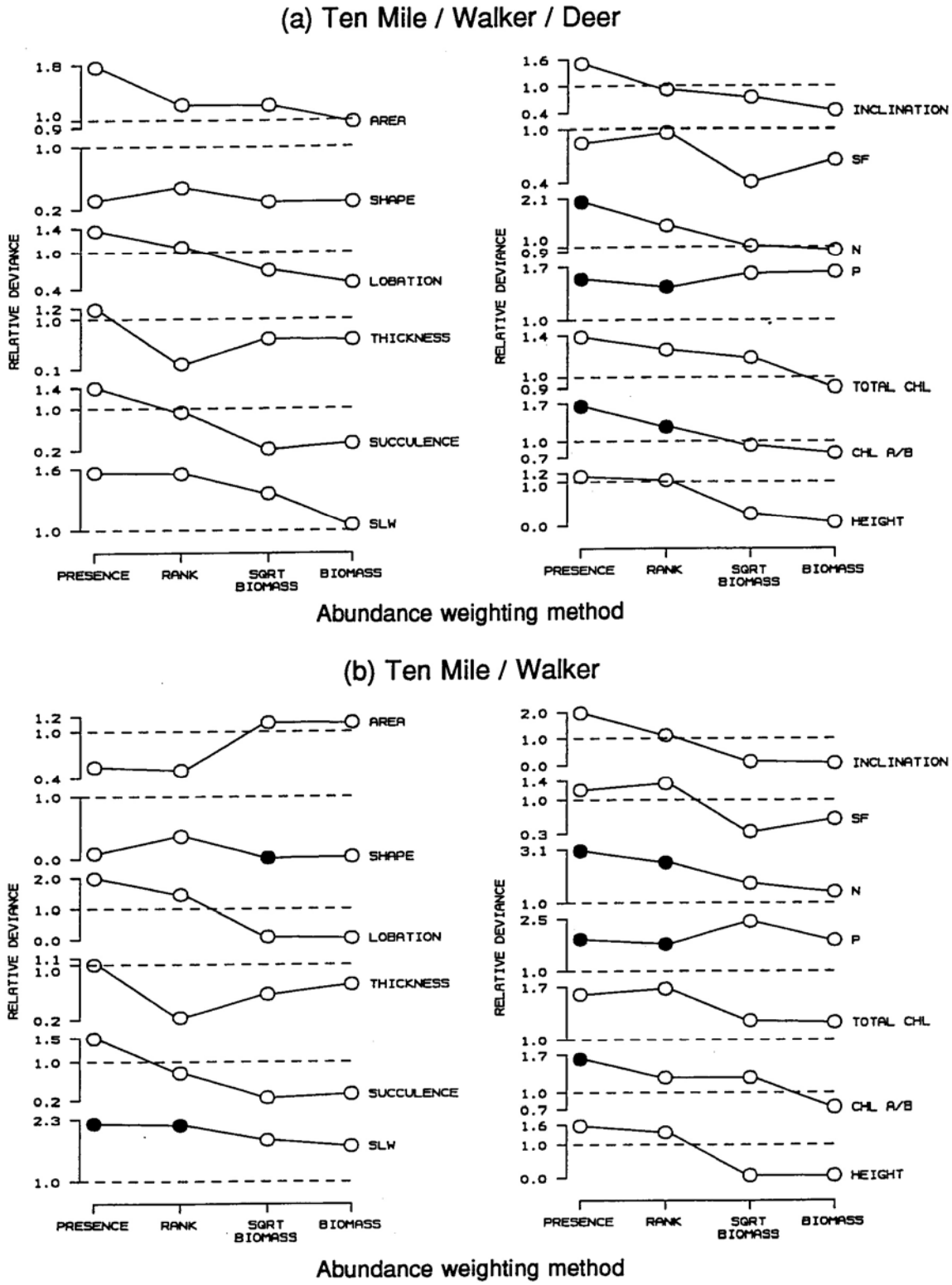



**Fig. 6.7** Null model randomisation tests for convergence or divergence in texture means between local-scale *Nothofagus*-dominated communities ZS1 Ten Mile, ZS2 Walker and ZS3 Deer. Format as for Fig. 6.2.

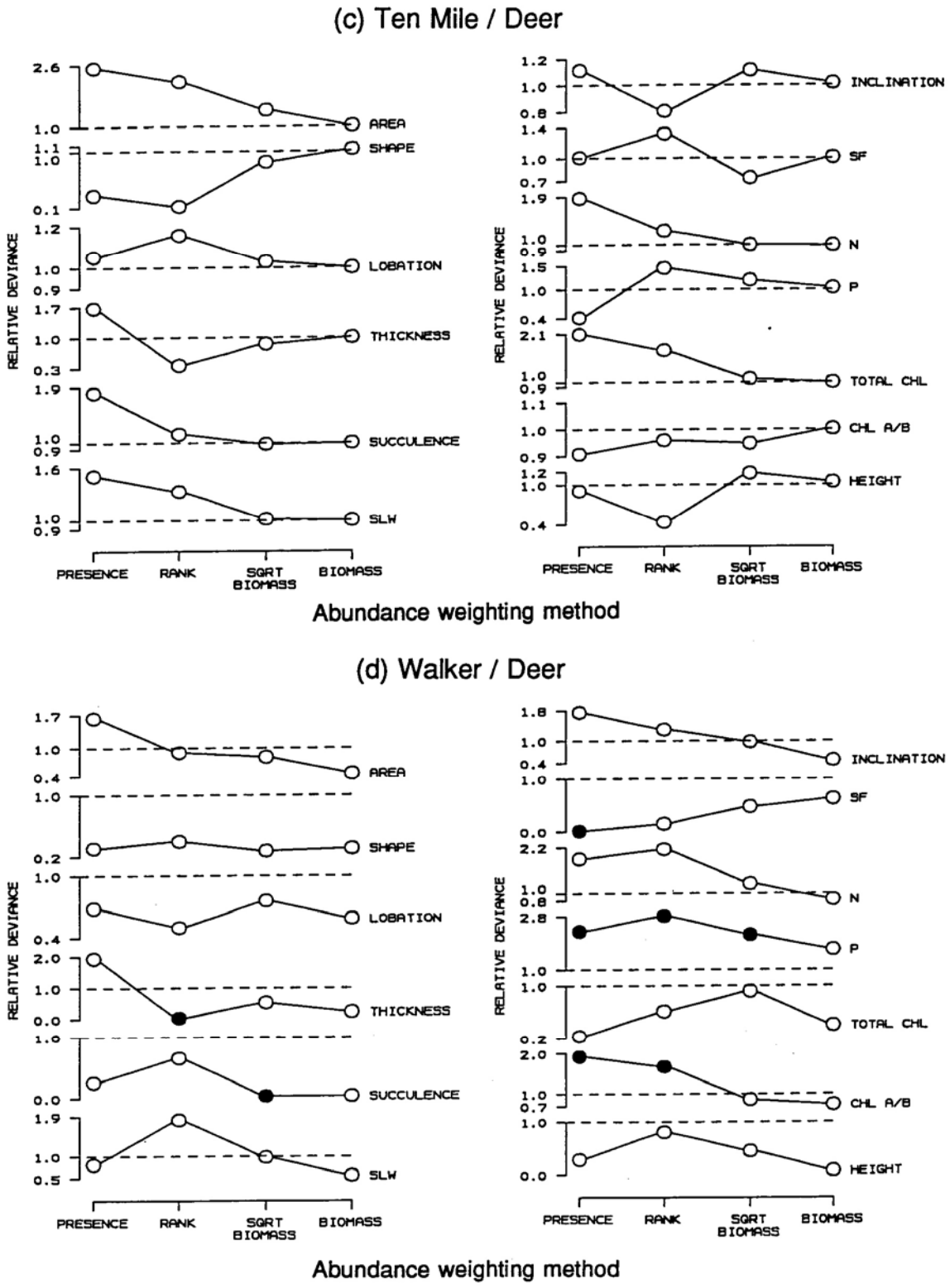



**Fig. 6.7** (continued)

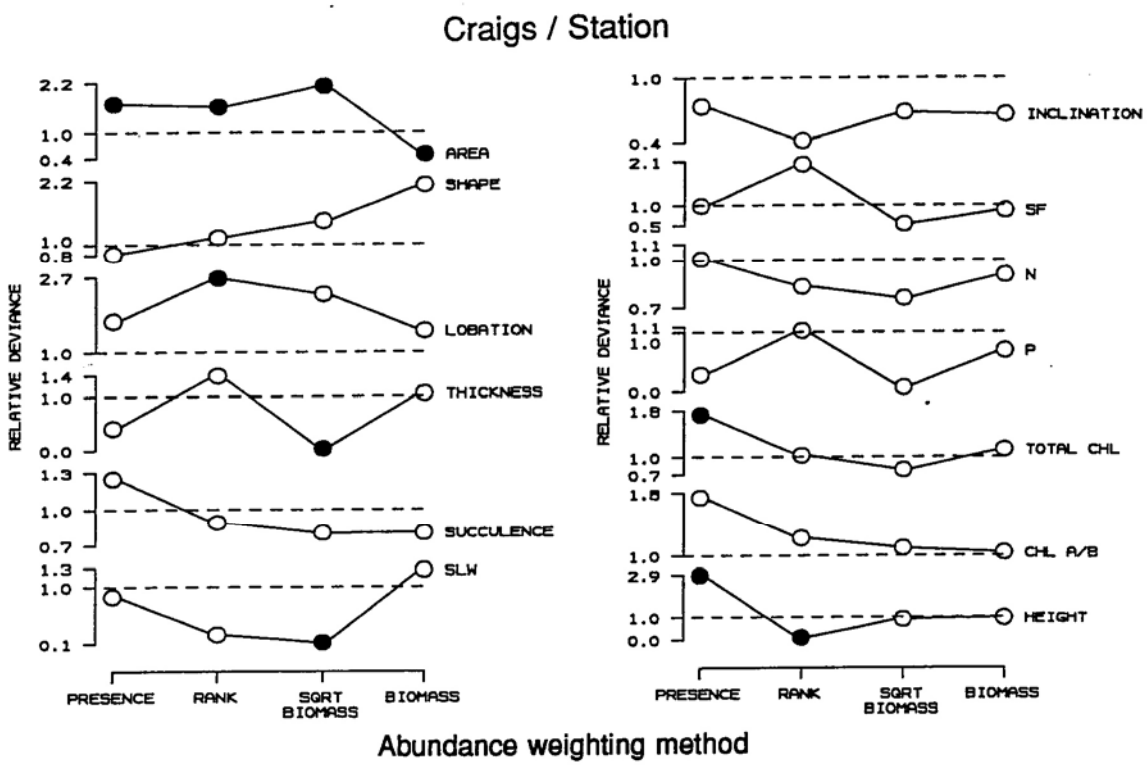



**Fig. 6.8** Null model randomisation tests for convergence or divergence in texture means between local-scale *Nothofagus*-dominated communities ZC1 Craigs and ZC2 Station. Format as for Fig. 6.2.

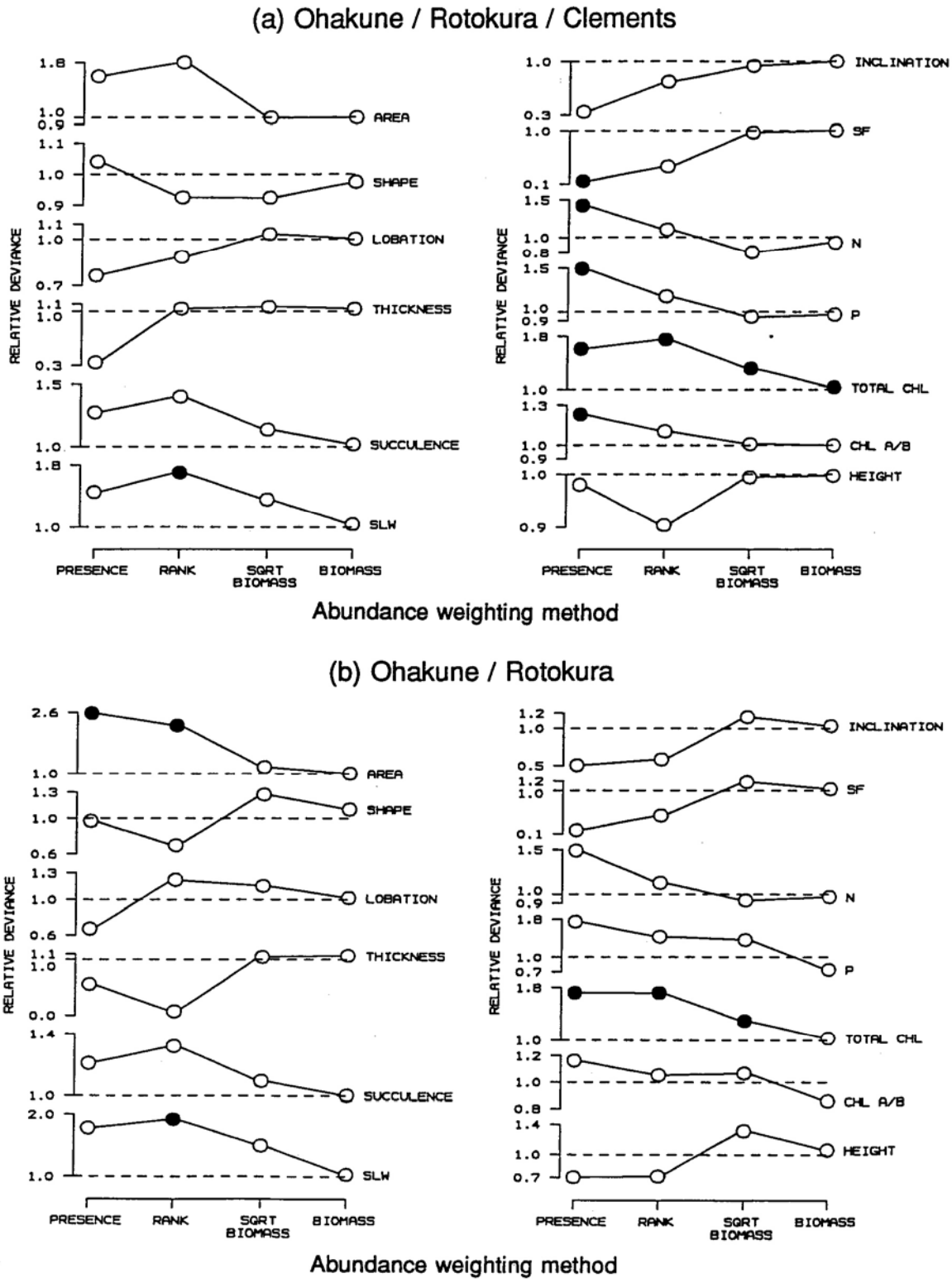



**Fig. 6.9** Null model randomisation tests for convergence or divergence in texture means between local-scale *Nothofagus*-dominated communities ZN1 Ohakune, ZN2 Rotokura and ZN3 Clements. Format as for Fig. 6.2.

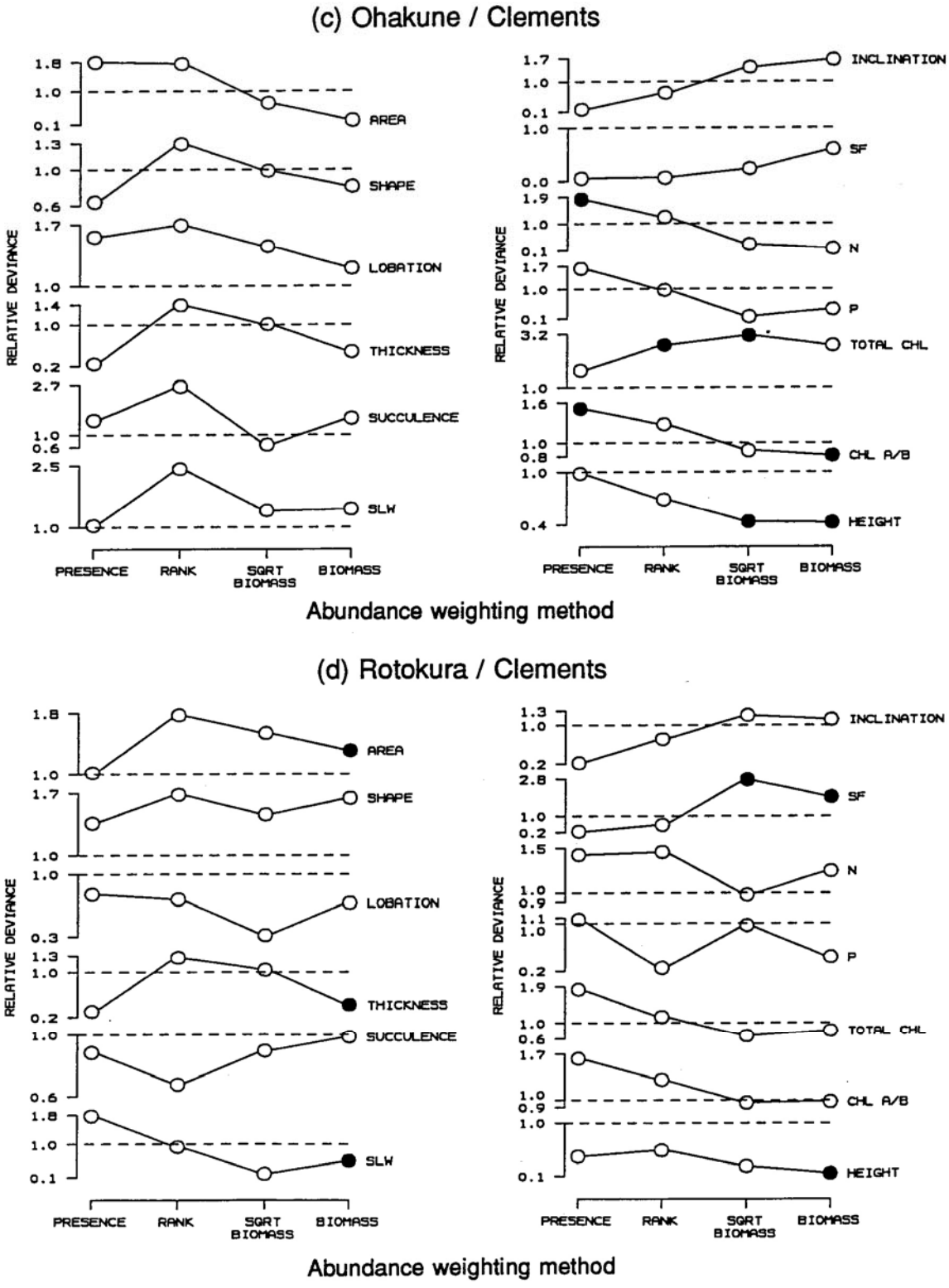



**Fig. 6.9** (continued)

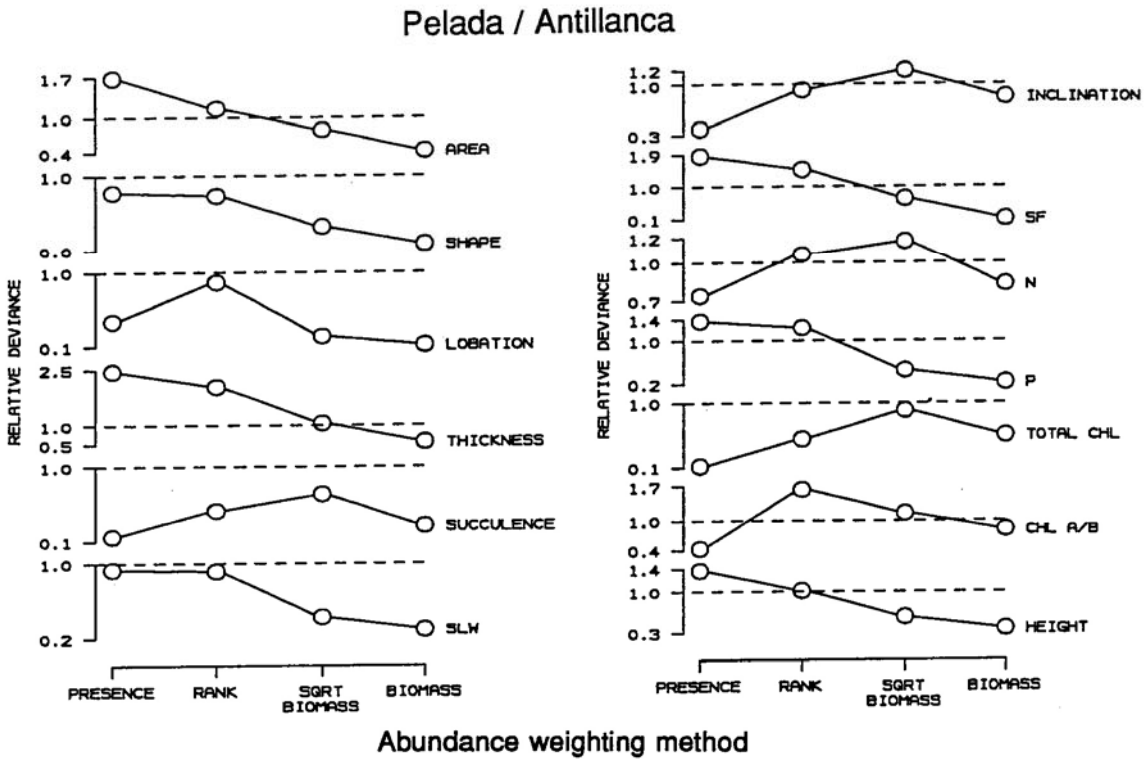



**Fig. 6.10** Null model randomisation tests for convergence or divergence in texture means between local-scale *Nothofagus*-dominated communities SC1 Pelada and SC2 Antillanca. Format as for Fig. 6.2.

*Closely matched sites from different landmasses*

Little convergence was detected in a comparison of the Tasmanian site T1 Balfour and the Australian site A2 Cascades (Fig. 6.12a). PSU specific weight was significantly convergent, but only when species values were weighted by photosynthetic biomass. Since different *Nothofagus* species are dominant at the two sites, both would be included in the convergence analysis (in contrast to comparisons in which the same species is common to more than one community; see `Treatment of common species' in Section 6.2). This means that the significant similarity at this heavy weighting level may be confined to the canopy dominants, and could have its basis in the common phylogeny of the two *Nothofagus* species concerned. Although there is no further significant convergence between the two sites, it is notable that five variates (PSU succulence, inclination, nitrogen content and height) show a tendency towards convergence ($R_{\bar{D},T}<1$) at all weighting levels, while a sixth, PSU specific weight, has $R_{\bar{D},SLW}<1$ at all weighting levels except abundance rank. The sites are significantly divergent in PSU phosphorus content, total chlorophyll and chlorophyll *a/b* at low weighting levels.

T1 Anne (Tasmania) and ZN1 Ohakune (New Zealand) are significantly convergent only in PSU inclination, in the absence of abundance weighting (Fig. 6.12b). However this variate

shows a tendency towards convergence at all weighting levels, as do PSU area, shape, lobation, thickness and support fraction. PSU nitrogen content is significantly divergent with species unweighted, and chlorophyll *a/b* is divergent at all weighting levels.

The incidence of convergence between the Argentinian site SA1 Quetrihué and ZN2 Rotokura in New Zealand is limited to two variates — PSU lobation and chlorophyll *a/b* — when species values are weighted by photosynthetic biomass (Fig. 6.12c). The result could reflect primarily similarity between the *Nothofagus* species that dominate each site. PSU phosphorus content and chlorophyll *a/b* are significantly divergent at the two lowest abundance weighting levels.

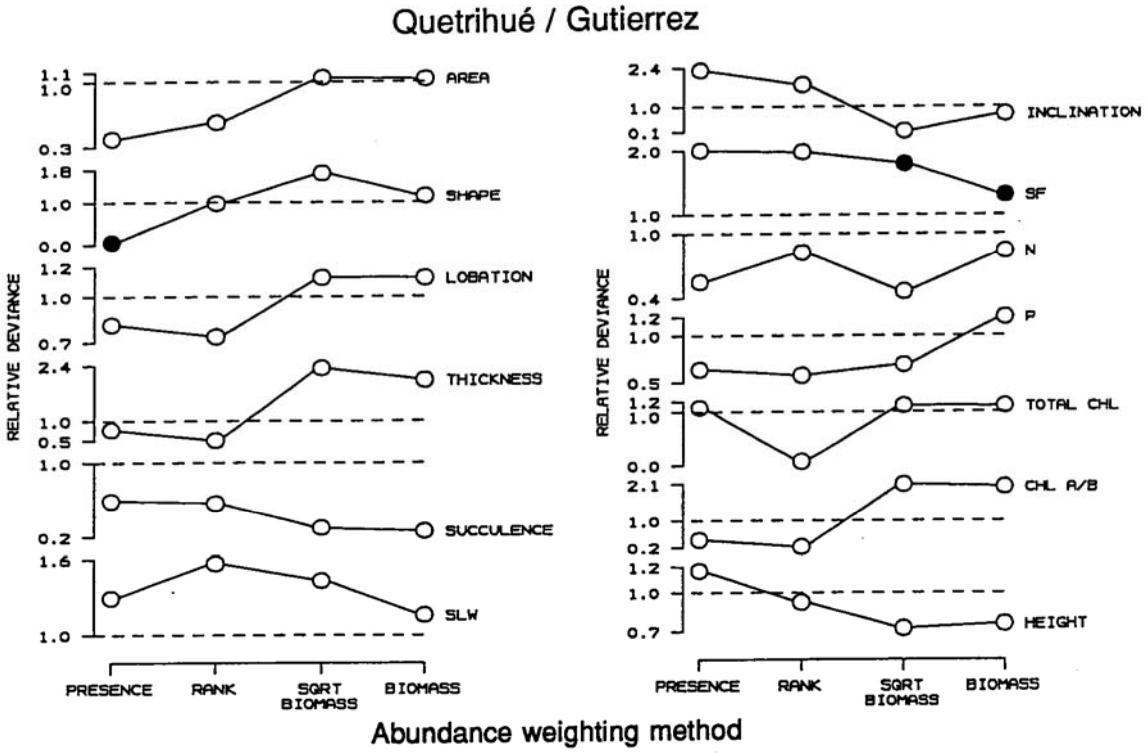



**Fig. 6.11** Null model randomisation tests for convergence or divergence in texture means between local-scale *Nothofagus*-dominated communities SA1 Quetrihué and SA2 Gutierrez. Format as for Fig. 6.2.

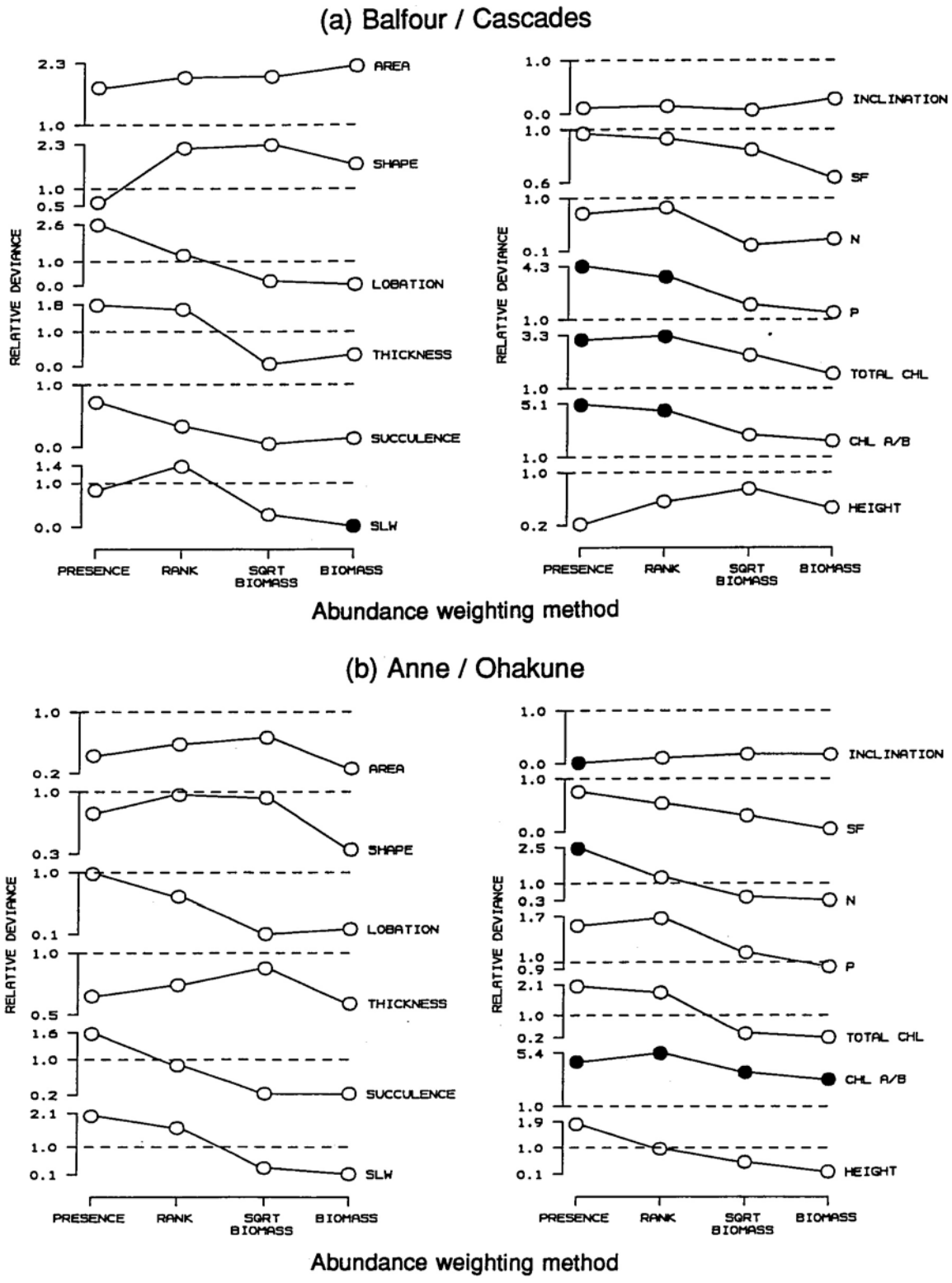



**Fig. 6.12** Null model randomisation tests for convergence or divergence in texture means between *Nothofagus*-dominated communities from different landmasses closely matched in their environments: **(a)** T1 Balfour/A2 Cascades; **(b)** T2 Anne/ZN1 Ohakune; **(c)** ZN2 Rotokura/SA1 Quetrihué. Format as for Fig. 6.2.

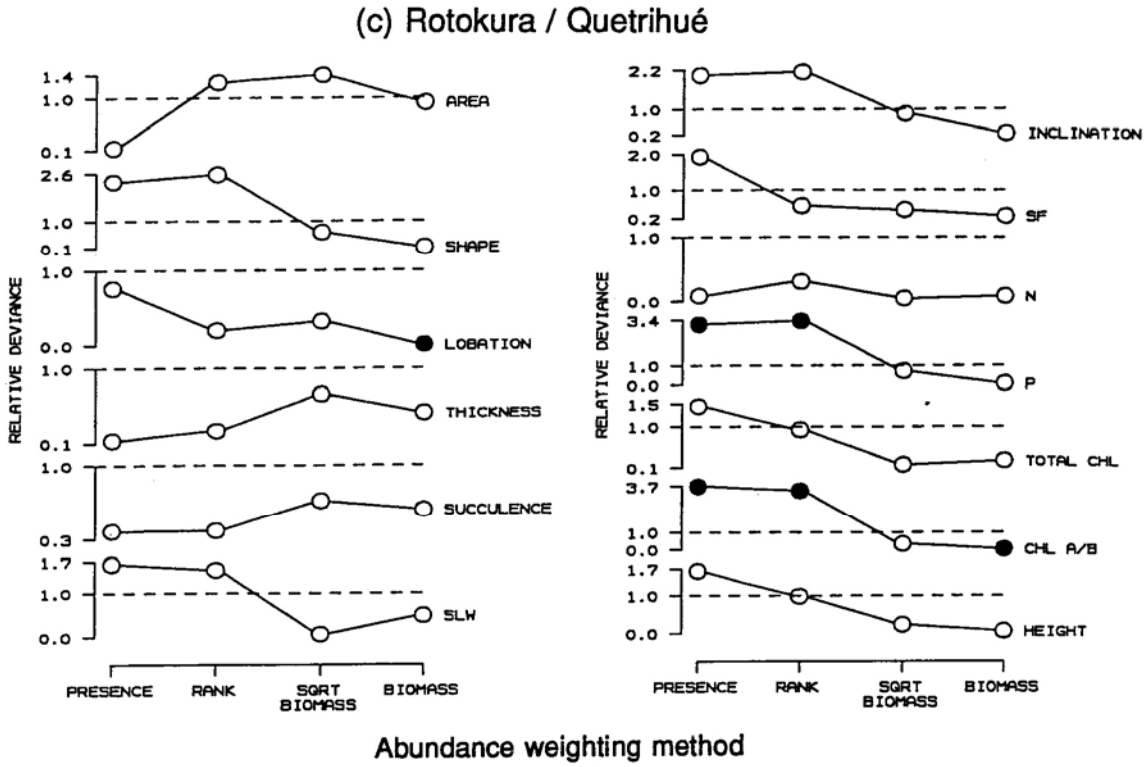



**Fig. 6.12** (continued)

PATTERNS AMONG TEXTURE VARIATES

The incidence of significant departure from the null model for each texture variate and each method of weighting species by their abundance, is shown in Table 6.2. The highest incidence of convergence is in the variates PSU specific weight, succulence, thickness and species height.

However, binomial tests of overall significance, based on 16 independent community comparisons, show that only in the case of species height, with weighting by the square root of photosynthetic biomass, is the number of tests showing significant convergence higher than the number that would be expected by chance alone (at the 5% level). This means that, although significant convergence was found in several variates in a number of comparisons, it is less than 95% certain (except in the case of species height, weighted by the square root of biomass) that the convergence detected was due to the action of assembly rules producing similar texture in different communities. It is possible, instead, that the `convergence' is a chance outcome of stochastic variation in texture, of the kind incorporated in the null model.

**Table 6.2** Incidence of significant convergence or divergence of community texture means in each texture variate at each abundance weighting method among the 31 community comparisons carried out in this chapter and (in parentheses) for 16 independent community comparisons (see Fig. 6.1). Overall significance, determined from the binomial distribution (see text), is shown for results from the 16 independent comparisons.

| Variate | Convergence | | | | Divergence | | | |
|---|---|---|---|---|---|---|---|---|
| | Presence | Rank | Sqrt biomass | Biomass | Presence | Rank | Sqrt biomass | Biomass |
| Area | 1 (0) | 0 (0) | 0 (0) | 1 (1) | 7 (5**) | 8 (6**) | 4 (4**) | 3 (2) |
| Shape | 1 (1) | 0 (0) | 1 (1) | 1 (1) | 0 (0) | 1 (1) | 1 (1) | 1 (1) |
| Lobation | 1 (1) | 0 (0) | 0 (0) | 1 (0) | 1 (1) | 1 (1) | 0 (0) | 0 (0) |
| Thickness | 0 (0) | 1 (1) | 1 (1) | 2 (0) | 1 (0) | 2 (0) | 0 (0) | 0 (0) |
| Succulence | 1 (0) | 0 (0) | 3 (1) | 3 (0) | 4 (3*) | 0 (0) | 0 (0) | 0 (0) |
| SLW | 0 (0) | 1 (0) | 3 (2) | 6 (2) | 4 (4**) | 4 (3*) | 0 (0) | 0 (0) |
| Inclination | 1 (0) | 1 (1) | 0 (0) | 0 (0) | 0 (0) | 2 (1) | 1 (1) | 0 (0) |
| SF | 2 (1) | 0 (0) | 1 (1) | 0 (0) | 2 (0) | 1 (0) | 5 (2) | 3 (2) |
| N | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 9 (5**) | 2 (2) | 0 (0) | 0 (0) |
| P | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 18 (10**) | 17 (9**) | 4 (2) | 1 (0) |
| Total chl | 0 (0) | 0 (0) | 2 (1) | 1 (1) | 10 (4**) | 10 (4**) | 5 (3*) | 1 (0) |
| Chl *a/b* | 0 (0) | 0 (0) | 0 (0) | 2 (1) | 18 (7**) | 15 (5**) | 8 (2) | 1 (0) |
| Height | 0 (0) | 1 (1) | 5 (3*) | 5 (2) | 3 (3*) | 3 (1) | 0 (0) | 0 (0) |

*$0.01 \leq P < 0.001$; **$P < 0.001$ (no binomial probabilities in range $0.01 \leq P < 0.05$).

Divergence is marked (and significant overall, based on binomial tests) in PSU area, succulence, specific weight, nitrogen content, phosphorus content, total chlorophyll, chlorophyll *a/b* and species height. There is also a relatively high incidence of divergence in support fraction, although this was not found to be significant overall. The large number of tests showing divergence supports the hypothesis that there are environmental differences between communities, and that these have caused species niches to be clustered in different regions of niche space, resulting in significant differences in community texture means.

Three variates, PSU shape, lobation and inclination, show little departure from null expectation, either in the direction of convergence or divergence.

## 6.4 Discussion

COMMUNITY-LEVEL CONVERGENCE AND DIVERGENCE

A relatively small proportion of the community comparisons carried out in terms of a particular texture variate and abundance weighting method revealed that convergence had occurred between the communities (Figs. 6.2-6.12; Table 6.2). Although convergence was found to be

significant in particular tests, binomial tests for overall significance among a subset of community comparisons revealed that only for species height, with weighting by the square root of species photosynthetic biomass, was it unlikely ($P<0.05$) that the convergence observed could be due entirely to type I errors in the individual tests (Table 6.2). It is assumed in the following discussion that significant convergence detected in individual tests is real; that is, that it supports the hypothesis of community-level convergence, stated in Section 6.1. However, it should be borne in mind that the amount of convergence detected is not significant overall, given the number of tests done, and that a proportion of the convergence detected may be due to type I errors.

Divergence was detected in most community comparisons, and was significant overall in eight of the 13 texture variates for at least one weighting factor (Figs. 6.2-6.12; Table 6.2).

*Patterns in relation to environmental similarity*

The comparatively high incidence of divergence compared with convergence suggests that environmental differences between communities have caused species niches, and characters correlated with niches, to be clustered around different optima in different communities, leading to different community texture means. Because the divergence is significant overall for many characters, the alternative hypothesis, that the texture of each community, in terms of these characters, simply represents a random set of values from the same overall distribution, is unlikely to be true.

If assembly rules apply, convergence would be expected to be more pronounced among communities that are better matched in their environments, while such communities should exhibit less divergence. Because of the small amount of convergence detected, and the possibility that many examples represent type I errors, rather than an effect of the action of assembly rules, it is difficult to determine whether such a pattern holds.

Best-matched communities showed little significant convergence, although a non-significant tendency towards similarity in a number of variates was apparent for New Zealand and Tasmania (Fig. 6.2c), whereas dissimilarity and divergence were more marked among other pairs of landmasses (Fig. 6.2b,d-g). Similarly, Balfour (Tasmania) and Cascades (Australia), one of the three pairs of sites from different landmasses identified in Chapter 3 as being relatively similar in their environments, were more similar in six texture variates at all weighting levels (except presence, for PSU specific weight) than expected under the null model (Fig. 6.12a).

Almost all `best-matched' communities were found to exhibit divergence in some variates, and there was generally no obvious tendency for divergence to be less marked among these communities, than in other comparisons at the same scale. However, Tasmania and New Zealand were found to be divergent only in PSU phosphorus and total chlorophyll, whereas other pairs of landmasses were divergent in three to five texture variates (Fig. 6.2).

In summary, there is limited evidence that similarity in climate and/or soil parameters is associated with an increased likelihood of convergence between communities, as well as a lower incidence of divergence. The pattern is not strong, however. It is possible that factors other than the macroenvironmental parameters measured differentiate communities, and that these factors have resulted in divergence in some characters, and failure for others to converge. Examples of factors that were not quantified, but that could be expected to lead to dissimilarities between communities, particularly on different landmasses, include disturbance regimes (Veblen *et al.* 1981; Barbour & Minnich 1990); adaptations and responses to different types and intensities of herbivory (Wardle *et al.* 1973; Greenwood & Atkinson 1977; Veblen *et al.* 1989; Lowman 1992), and biogeographic history coupled with phylogenetic constraints on the characters of different taxa from *Nothofagus*-dominated communities of different landmasses (Peet 1978; Blondel 1991).

*Factors underlying convergence and divergence*

The texture variates that showed the most convergence were PSU specific weight, succulence, species height and thickness (Table 6.2). With the exception of species height, these characters belong to a group that were identified as being relatively strongly intercorrelated (Section 4.3; Table 4.1) and are likely to reflect adaptations (or plastic responses) to the light regime. Species height, which was the only variate found to show convergence significant among many tests, is a measure of species position in the vertical forest structure, and so would also seem very likely to be associated with the light regime. Light is one of the plant resources most likely to be limiting in the generally mesic and eutrophic environment of a forest community (Jordan 1971). Accordingly, partitioning of the light gradient among species would seem a likely outcome of competition-mediated assembly rules, should they apply. If the same assembly rules select for similar light niches in different communities, convergence will result. It is possible that some of the convergence detected among *Nothofagus*-dominated communities, especially in terms of the six characters listed above, may reflect the operation of assembly rules for light niches.

The very low incidence of significant departure from the null model in PSU shape and lobation (Table 6.2) suggests that these characters might be of limited value as predictors of species functional responses. The paucity of divergence suggests an absence of variation with at least those aspects of the environment that differ between sites and may have produced divergence in several other characters. The low incidence of convergence suggests that coadaptation among species in terms of these characters occurs at a minor level, if at all.

Most tests showing convergence between communities compared texture means with species weighted heavily by their abundance: either photosynthetic biomass or its square root (Table 6.2). These weighting methods tend to take account primarily of the small proportion of species representing the majority of standing crop, mainly trees, which would tend to have rather

similar characters in comparison to their communities as a whole (which include functional types as diverse as graminoids, ferns, shrubs, trees, etc.). Since all species (other than those occurring in more than one community) are randomised under the null model, and the randomised species are also assigned abundances at random, abundance-weighted means of null communities may tend to be rather more variable than those of the observed communities, where the most abundant species are likely to be relatively similar in their characters. This can produce a trend towards convergence which might be primarily the result of abiotic filtering, leading to similar characters in the most abundant species, rather than biotic filtering, producing overdispersion of species characters (Section 6.2). In the case of comparisons between local-scale communities within a region, or regional communities within a landmass, such convergence would generally be among co-dominant or subcanopy species. This is because the dominant *Nothofagus* species were generally common to more than one of the communities being compared and so were not randomised (one exception is *N. nitida* at SC1 Pelada and *N. dombeyi* at SC2 Antillanca). In comparisons between landmasses, however, different species of *Nothofagus* invariably accounted for the largest share of total biomass. In the case of comparisons at the landmass scale, therefore, the possibility that the convergence observed had a phylogenetic basis cannot be discounted.

The low incidence of convergence among communities within the same region is surprising, since such communities were found to be generally the most closely matched in their environments (Chapter 3). One reason may lie in the treatment of common species in the null model. Because species occurring in more than one of the communities in a given test were not randomised, but allocated systematically to the null `communities' corresponding to those in which they were observed, such species could have no differential effect on the test statistic, $\bar{D}_T$, in the randomised, versus the observed, data. This means that the test for departure from null model expectation is effectively based only on species that do not occur in more than one of the communities being compared. In the case of communities at the local scale, which would share the same regional species pool, such species may be in the minority. For example, the three study sites in southern New Zealand, ZS1 Ten Mile, ZS2 Walker and ZS3 Deer, had 38, 41 and 30 species (entities) respectively. Because of taxonomic overlap between the assemblages, only 14, 10 and 7 species (entities) were randomised, respectively, in null model tests for convergence or divergence among them (Fig. 6.7).

Even if there are assembly rules tending to produce overdispersion of species characters within a community, this effect will be overlain by a range of other effects (e.g. phylogenic constraints, within-site spatial heterogeneity, spatial mass effect; Shmida & Ellner 1984) which, in the context of the hypothesis being tested, can be regarded as a stochastic component of texture. As the number of species (or entities) contributing to community texture decreases, the component of texture (if any) produced by assembly rules will become increasingly difficult to detect among the stochastic variation. This means that, although communities within a region

may have similar environments, and assembly rules may operate (necessary conditions for convergence to occur), convergence may be more difficult to detect because of the necessity of effectively excluding common species from the randomisation tests.

While convergence was more marked at high levels of abundance weighting, divergence was detected most frequently when species were weighted equally or according to rank order of abundance. Such dissimilarity may be due to environmental variation among communities as well as (possibly) historical differences, as described above.

## PREVIOUS STUDIES OF COMMUNITY TEXTURE CONVERGENCE

Convergence in the characters of allopatric species of similar environments has frequently been demonstrated (e.g. Orians & Solbrig 1977; Cody & Mooney 1978; Niemi 1985). Such studies show that a common physical environment may select for analogous traits within disparate phylogenetic lineages. They do not, however, show that such convergence is a general phenomenon, occurring across whole assemblages, and they shed no light on the biotic component of adaptation — the possible effects of assembly rules based on interspecific competition and other species interactions.

Convergence in spectra of species characters — texture — at the community level is of interest because it would signify not only common species adaptations to similar physical conditions, but also common responses to biotic factors. In the context of the niche space of Hutchinson (1958), filtering by the abiotic environment (Keddy 1992; Smith *et al.* 1994) would restrict species niches (and correlated characters) to a hypervolume of niche space representing limits to survival in the prevailing conditions. Assembly rules, mediated by ecological species sorting (Smith *et al.* 1994; Wilson *et al.* 1994) and/or coevolutionary character displacement (Taper & Case 1992) would cause niches (characters) to become somewhat regularly spaced in the community hypervolume. If similar environments and, accordingly, common assembly rules apply in different communities, the communities would be expected to exhibit convergence in texture.

Studies of convergence in texture between communities have usually focused on ecosystems with similar climates on different continents (e.g. Specht 1969; Naveh 1967; Parsons & Moldenke 1975; Parsons 1976; Mooney *et al.* 1977; Cody *et al.* 1977; Orians & Solbrig 1977; Cowling & Campbell 1980; Schluter 1986, 1990; Wiens 1991a,b; Keeley 1992; Cowling & Witkowsky 1994; Wilson *et al.* 1994; Montenegro & Ginocchio 1995; Arroyo *et al.* 1995). Although most studies claimed to find some convergence, few applied statistical tests to evaluate the hypothesis that community texture was more similar between communities than would be expected if species characters were drawn at random from an underlying distribution imposed by the physical environment. This means that the degree to which the findings of many convergence studies support the existence of both physical and biotic constraints on community membership,

is unclear.

A number of studies have applied rigorous tests, however. Most such studies have been of animal, rather than plant communities. Three main approaches have been adopted: (1) tests similar to analysis of variance, looking for greater overall similarity between communities in attributes of interest, than among species within communities; (2) `species-for-species matching', mapping species from various communities in the same character space and testing the hypothesis that nearest neighbours in the space will tend to be species from different communities; and (3) tests seeking similarity in texture between communities relative to random simulations generated under a null model.

*Analysis of variance and related tests*

Schluter (1986) sought convergence (`similarity', in his terms[5]) in the morphology of finches from five continents using a modified analysis of variance with communities as `treatments' and characters of species within communities as `replicates.' A significantly low *F* statistic value (greater variation in morphology within than among communities on different continents) was interpreted as evidence that convergence had occurred. A variance deficit within continents would suggest overdispersion of species characters, and so, the operation of assembly rules (Pianka 1980). Significant convergence in finch body size was found, although body shape was divergent between continents.

Both analysis of variance and a non-parametric analogue, the Mann-Whitney *U* test (Sokal & Rohlf 1969), were used by Wiens (1991a) to seek convergence in life history and behaviour traits between shrub desert avian communities in Australia and North America. Little evidence of convergence was found.

Schluter (1990) used $\chi^2$ and Kolmogorov-Smirnoff *D* tests to assess the goodness-of-fit of distributions of attributes of arthropods on mangrove islands, desert rodent communities and finches in mediterranean-climate habitats on different continents. Instead of testing for a significantly high value of the test statistic (which would be appropriate if the hypothesis that communities are more different than expected by chance were being tested), a low value was sought. Effectively these tests are equivalent to the analysis of variance approach of Schluter (1986), in that a low variance between communities, compared to the variance among species within communities, would tend to give rise to a high goodness-of-fit and hence, a low value for $\chi^2$ and *D*, signifying convergence. Significant convergence was detected for finch body sizes

[5]Schluter (1986), like some other authors (e.g. Wiens 1989, 1991a,b) reserves the term 'convergence' for instances in which there is evidence to suggest an increase in similarity over evolutionary time. In the present study, all significant similarity is termed convergence (see Section 1.5).

(data set of Schluter [1986]) but not for mangrove island arthropods; desert rodent communities were found to be non-convergent when species common to the two communities being compared were excluded from analysis.

In a study of convergence in plant growth forms, leaf attributes and reproductive strategies in mediterranean-climate communities of South Africa and Australia, Cowling & Witkowsky (1994) used the $\chi^2$ test in the opposite manner, seeking significantly high values for the test statistic, that would indicate differences between the two regions in the frequencies of species in various attribute classes. Several environmentally-matched study sites in the two regions were found to be non-significantly different in the representation of species in different classes of growth form (shrubs, graminoids and forbs), leaf size and consistence, spinescence, seed storage (one of five comparisons only) and seed dispersal. This shows that the communities being compared are non-divergent in terms of representation of several texture-based guilds (Wilson 1989; Wilson *et al.* 1995), although in the absence of tests for significant similarity (e.g. for significantly low values of $\chi^2$) the evidence for convergence must be regarded as tentative (c.f. tests for 'convergence' in Chapter 5).

*Species-for-species matching*

Ricklefs & Travis (1980) sought evidence for ecological equivalence among bird species from Californian and Chilean mediterranean-climate shrublands. The approach was to map species in a multivariate space integrating various morphological parameters, then to test for a significantly high proportion ($\chi^2$) of nearest-neighbours in the morphological space from different continents. No evidence of equivalence — species-for-species matching — was found; many species from one region had no morphological analogue in the other. The same approach was used by Wiens (1989, 1991b) to compare bird communities in Australian and North American shrub deserts in terms of morphological characters. Species from each continent were more-or-less as likely to have a morphological nearest neighbour on the same continent as on the other, providing no support for the convergence hypothesis.

*Null model randomisation tests*

Wilson *et al.* (1994) compared carr wetland communities in Britain and New Zealand in terms of five morphological characters of the vascular plant species present. Texture means in terms of these characters were calculated for each community. Differences in community texture means among the observed communities were compared with differences among randomised communities generated under a null model, to evaluate the hypothesis of convergence: that the observed communities would be more similar in texture than randomised ones. In detail, the null model was similar to that used in the present study, except in its treatment of common species:

species that occurred in more than one of the communities being compared were randomised along with other species in the null model, although different records for the same species were never assigned to the same null community. There was significant convergence in PSU width when species values were weighted by photosynthetic biomass or its square root, and also in PSU area with weighting by the square root of biomass. However, there was no convergence at low abundance weighting levels, providing little support for the operation of assembly rules.

Smith *et al.* (1994) used a similar null model to look for convergence or divergence in vascular plant texture among *Nothofagus menziesii*-dominated assemblages sampled along an altitudinal gradient in southern New Zealand. Little evidence for convergence between adjacent plots was found when species were weighted by presence only, but there was substantial convergence at higher weighting levels — abundance rank and percentage cover. The study thus provides strong evidence for assembly rules in plant communities, although a degree of bias in the null model, caused by its treatment of common species (see Section 6.2), casts some uncertainty on some results.

Guild proportionality, i.e. similarity in the relative representation of species in the same guilds in different communities, has been sought with respect to null models simulating random species migration. Where each guild is associated, explicitly or tacitly, with a particular range of niches or species characters, guild proportionality represents one type of texture convergence. Wilson (1989) compared species representation in forest sinusiae (e.g. trees, shrubs, ground-layer species, climbers and epiphytes) in adjoining plots in New Zealand temperate rainforest, finding little evidence for proportionality between plots. However, two similar studies in New Zealand *Nothofagus*-dominated forests (Bycroft *et al.* 1993; Wilson *et al.* 1995) detected significant convergence in the proportion of species comprising the ground herb guild in adjacent plots. Wilson & Roxburgh (1994) demonstrated proportionality in the graminoid and forb guilds relative to a null model at the point scale in a lawn.

Fox & Brown (1993) identified a tendency, significant relative to expectation under their null model, for three functional groups of rodents to be represented by equal numbers of species in desert communities. The same assembly rule was found to apply to communities in Nevada and the southwestern USA, signifying convergence between these communities. However, the same assembly rule also seems to apply to randomised data (Wilson 1995), shedding some doubt on its validity.

*The present study in the context of previous work*

The results obtained in the present chapter provide little evidence for the operation of assembly rules. Although significant convergence was identified in a number of individual tests, it could not be shown that the number of instances of convergence for each variate/weighting factor combination were unlikely to have arisen as a result of type I errors (exception: species height

weighted by the square root of photosynthetic biomass). In view of the small number of studies that have sought community-level convergence in plant communities using rigorous statistical tests in an appropriate manner, it remains unclear whether common species responses to a common physical and biotic environment, are likely to produce similar texture in different plant communities with similar environments.

Divergence was marked and highly significant overall for many texture variates. This suggests that there were environmental, or possibly historical, differences between communities in many of the comparisons and that these differences caused differences in the functional compositions of the communities. Where poor environmental matching exists, it is impossible to be sure whether assembly rules apply and could have produced convergence, had the environments of the communities been the same. The same problem, non-convergence potentially due to allogenic differences between communities, has plagued many convergence studies (Cowling & Campbell 1980; Blondel *et al.* 1984; Barbour & Minnich 1990; Wiens 1991a; Wilson *et al.* 1994). It is uncertain how similar the environments of different communities must be before convergence is to be expected (if assembly rules apply). This may hinder the specification of criteria by which the hypothesis of community-level convergence can be falsified (Peet 1978; Keeley 1992; Blondel 1991).

## CONCLUSIONS

On the basis of results obtained using the test for convergence in community texture means, employed in this chapter, it cannot be concluded that community-level convergence occurs between *Nothofagus*-dominated communities. The paucity of convergence even between communities with the most similar macroenvironments, as well as the observation of significant divergence between these communities, does suggest that assembly rules, if they occur at all, must have a minor influence on community structure — too weak to generate detectable convergence against a background of stochastic character variation. However, some non-significant evidence of convergence was found. In the following chapter, convergence is sought among the same communities using a slightly modified version of the same analysis, expected to be more sensitive to convergence where the effects of assembly rules are weak. It is hoped that the results obtained will enable the hypothesis of convergence to be accepted, or more clearly rejected.

# 7. Convergence among *Nothofagus*-dominated communities: community texture distributions

## 7.1 Introduction

Comparison of community texture means, in Chapter 6, revealed little evidence that the *Nothofagus*-dominated communities sampled were more similar to each other than expected under a null model simulating random community assembly. Significant convergence was detected in a number of community comparisons and in a number of texture variates (characters), but the total incidence of convergence, taking all comparisons into account, was no higher than would be expected by chance alone (except for species height, with heavy weighting of species by their abundance). There were trends towards convergence, particularly in texture variates that were expected to be of particular functional importance, and between communities closely matched in their environments; but in general, these trends were non-significant. The results of the analysis do not strongly support the hypothesis of community-level convergence. However, the possibility remains that there may be assembly rules affecting spectra of species characters in a similar way in different, environmentally-matched communities, albeit too weakly for the similarity to be found statistically significant.

Given that some weak non-random patterns do seem to exist, significant trends might be found if the statistical analysis could be refined, to make it more sensitive to convergence where the effects of assembly rules have been weak. An obvious avenue for improvement would be the way in which texture is characterised. Although the mean among species has been used to summarise community texture in several previous studies (e.g. Schluter 1986; Smith *et al.* 1994; Wilson *et al.* 1994) it has the shortcoming that it represents texture only very coarsely: much information about the distribution that it summarises is not used.

Similar assembly rules, operating in different communities, would be expected to spread species out in a generally similar (though not identical) way in niche space. This would be expected to produce similarity between communities, not only in texture means, but also in community-wide distributions of species characters. In general, similar means would imply similar distributions, and dissimilar means would imply dissimilar distributions. However, the two need not be linked. For example, the two texture distributions represented in Fig. 7.1a have the same mean but are clearly different in shape; in community 1, more species have character values in the range 2-3 than in any other class; in community 2 characters in the range 4-5 are the most popular. It is unlikely that similar assembly rules would produce texture distributions skewed in opposite directions in different communities, yet when only the mean is considered

and other information ignored, the communities are found to be very similar in texture. Another type of pattern is illustrated in Fig. 7.1b. Community 1 has a platykurtic distribution, with species values clumped about the modal (and, in this case, mean) character value, but with few very high or very low values. Community 2 has the same mean and mode, but a greater proportion of species have more extreme values, giving a relatively leptokurtic texture distribution. Once again, comparison of texture means would imply that the communities are convergent, yet differences in the distributions do not seem consistent with the operation of identical assembly rules. There are also situations in which distributions may be well-matched, but their means dissimilar. In Fig 7.1c, the two communities have distributions that are rather similar overall, but a low extreme value in Community 1 and a high one in Community 2 result in different texture means and imply that the communities are non-convergent, or even divergent, in texture.

In some cases, then, community means may poorly summarise texture, potentially leading to a failure to detect convergence where it has occurred (a type II error), or conversely, to spurious detection of convergence or divergence (type I errors). This danger would be avoided if whole distributions rather than summary statistics could be quantitatively compared. A method for comparing community texture distributions directly is developed and applied in this chapter. Although the same communities are compared as in Chapter 6, it is hoped that the use of a test statistic that quantifies similarity in the shapes of texture distributions, not just their means, will provide a more powerful test, allowing the hypothesis of community-level convergence to be be accepted, or more confidently rejected, with respect to the communities and characters considered by the study.

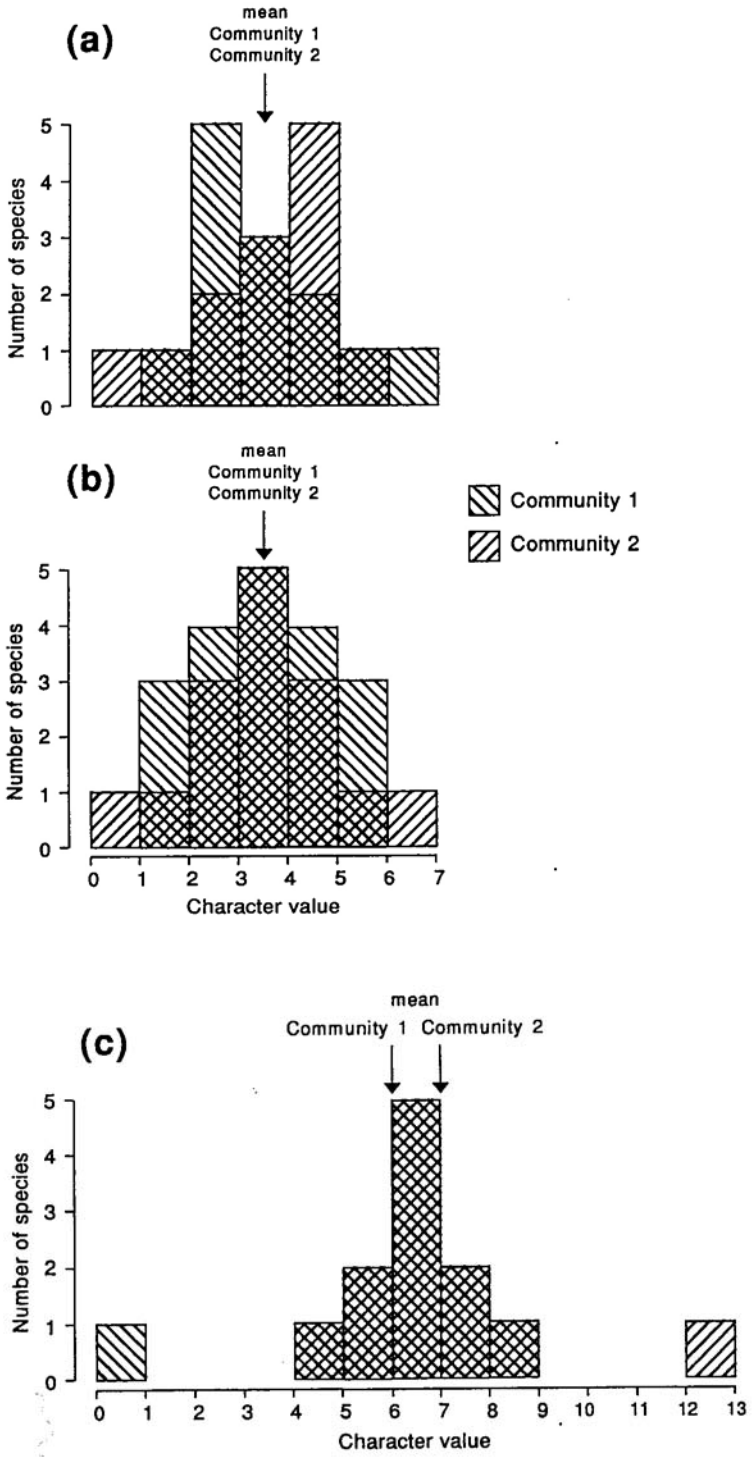



**Fig. 7.1** Possible differences in the degree of matching between texture means and distributions in different communities. In example **(a)**, Communities 1 and 2 have the same mean for a character, but the frequency distributions of the character are skewed in opposite directions. In example **(b)**, the communities have the same mean, but distributions differ in kurtosis. Communities 1 and 2 **(c)** have similar distributions for a character but single species with extreme values — low for Community 1 and high for Community 2 — result in different texture means.

## 7.2 Methods

TEXTURE DATA

Texture was evaluated in terms of 13 variates: the 12 characters listed in Section 2.3.5, in addition to species height, defined in Section 6.2. Measurement protocols for the characters are described in Chapter 2. Details of the 17 study sites are given in Chapter 3, where similarities and differences in their environments are also examined.

ANALYSIS

Convergence and divergence in texture among communities were sought using randomisation tests. These were based on a null model simulating community assembly in the absence of assembly rules. The same null model and randomisation algorithm were used as in Chapter 6: details are given in Section 6.2 and are not repeated here. The analyses of the present chapter differed with respect to the test statistic used to quantify texture similarity between communities, and in the method of weighting species by their abundance when computing their contribution to community texture.

*Representation of community texture*

Instead of representing community texture by a single value (e.g. $X_T$, the community texture mean) the complete distribution of species values, expressed as a graph of species texture contributions, was used.

The contribution of each species to the texture of its real or randomised community was based on its value for the character under investigation. In some tests, species abundance relative to other species in the same community was also included in the texture contribution. This was to take account of the possible influence of species abundance on community structure. The same four weighting factors were used as in Chapter 6; i.e. presence (all species weighted equally), abundance rank, the square root of photosynthetic biomass and photosynthetic biomass. The contribution $c_{T,i}$ of each species or entity to texture was calculated using the formula:

$$c_{T,i} = \frac{x_{T,i} \cdot w_i \cdot s}{\sum_{j=1}^{s} w_j}$$

where $s$ = number of species or entities in community;

$x_{T,i}$ = transformed value of character $T$ for species or entity $i$;

$w_i$ = weighting factor (presence [=1], abundance rank, square root of photosynthetic biomass or photosynthetic biomass) for species or entity $i$.

Species character values $x_{T,\,i}$ were transformed as described in Section 2.3.5 (Table 2.1) and Section 6.2. Note that when species are weighted by presence only, species texture contributions are equal to their character values.

The texture of each community in terms of variate $T$ was expressed by a rank-scaled texture plot, a curve obtained by plotting species texture contributions $c_{T,\,i}$ against species rank in terms of texture contributions, scaled from 0 to 1. Abscissa coordinates were thus given by:

$$\frac{r_i - 1}{s - 1}$$

where $r_i$ = rank of species (or entity) $i$ in terms of $c_{T,\,i}$ (1=highest; $s$=lowest).

Adjacent points in the texture plot were linked with a straight line (Fig. 7.2).

*Comparison of observed with null communities*

Variation in texture variate $T$ between communities was evaluated as the deviance of texture distributions, $\hat{D}_T$. For two communities this was defined as the area between rank-scaled texture plots for each community, as shown in Fig. 7.2. For comparisons of three or more communities, $\hat{D}_T$ was the mean area between texture plots for all possible pairs of the communities being compared. Areas between texture plots were determined by standard trigonometry. The value of $\hat{D}_T$ will be affected both by differences in absolute character values in the species of the communities being compared (like $\bar{D}_T$, used in Chapter 6) and by differences in the shapes of texture distributions. Its value will be lowest where the fit between distributions, expressed by rank-scaled texture plots, is high.

For each community comparison, 2000 null model randomisations were performed, calculating $\hat{D}_T$ for each randomised data set as well as for the observed data. The strength of departure from null model expectation was quantified by the relative deviance, $R_{\hat{D},T}$:

$$R_{\hat{D},T} = \frac{\hat{D}_T \text{ (observed)}}{\sum \hat{D}_T \text{ (null)} / 2000}$$

$R_{\hat{D},T}$ is exactly analogous to $R_{\bar{D},T}$, employed in Chapter 6. A value less than 1 (1 = null model expectation) represents a tendency towards convergence, while a value greater than 1 implies that there is a tendency towards divergence.

The significance $P$ of departure from the null model was calculated as the proportion of randomisations for which $\hat{D}_T$ was at least as small (if $R_{\hat{D},T}<1$) or at least as large (if $R_{\hat{D},T}>1$) in the randomised as in the observed data, multiplied by 2, since this is a two-tailed test. A target significance level of 0.05 was adopted.

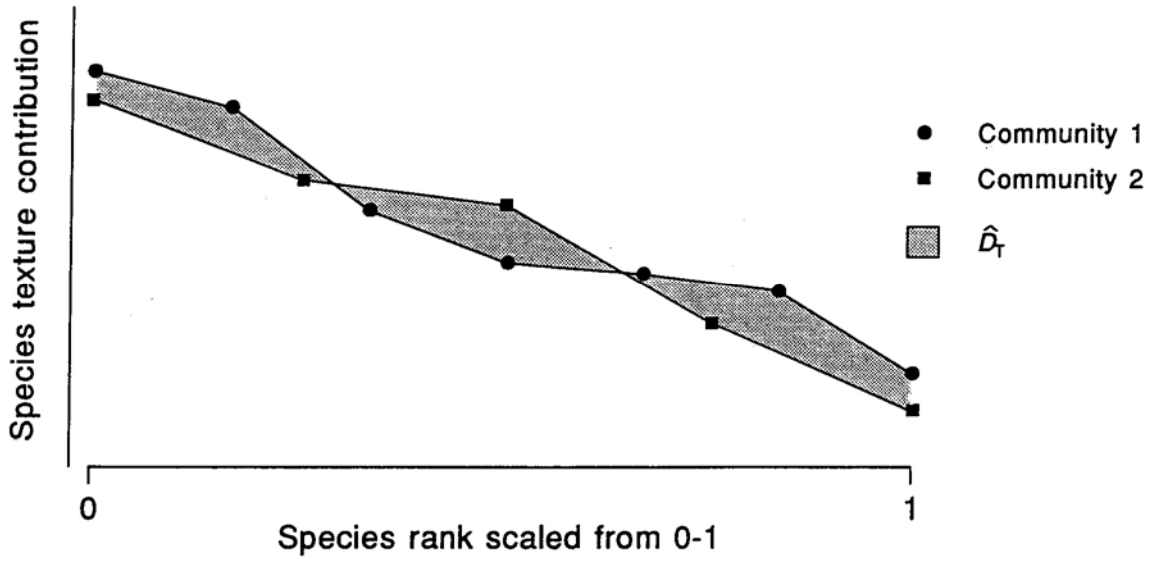



**Fig. 7.2** Example demonstrating the calculation of the deviance of texture distributions, $\hat{D}_T$, between two communities. For two communities, $\hat{D}_T$ is the area between rank-scaled texture plots for each community. Rank-scaled texture plots are produced by plotting species texture contributions in terms of a particular character and abundance weighting factor (see text) against species rank in terms of texture contributions, scaled from 0 to 1 on the abscissa.

*Comparisons performed*

Randomisation tests were performed to seek convergence or divergence in texture among 31 sets of communities at the landmass, regional and local scales, as described in Section 6.2, and depicted in Fig. 6.1.

Binomial tests for overall convergence in each texture variate/abundance weighting factor combination (methodology described in Section 6.2) were also performed, based on 16 independent community comparisons (Fig. 6.1).

As in the previous chapter, species and entities from each community were assigned values for a random variate in each comparison. This was in order to confirm, by inspection of the results obtained from comparisons of random texture, that the null model did not incorporate any hidden bias that could lead to the spurious detection of convergence or divergence. Binomial tests were applied to confirm that the random variate did not exhibit departure from null model expectation in significantly more than the 5% of tests expected by chance.

## 7.3 Results

VALIDITY OF THE NULL MODEL

The incidence of significant departure from null expectation in the random texture variate among

all 31 community comparisons is given in Table 7.1. Although significant 'convergence' was detected in two tests using species presence as the weighting factor, and 'divergence' in two tests weighting species by the square root of biomass, this incidence is not significant overall according to a binomial test ($P$=0.181). Further, the changes made in this chapter to the analysis methods of Chapter 6 do not include a change in the null model under which randomised communities were generated. The null model was found free of bias in Chapter 6 (Section 6.3; Table 6.1), and this finding is confirmed in the data of Table 7.1.

**Table 7.1** The number out of 31 among-community comparisons in which community texture distributions calculated from random data were found to be significantly convergent or divergent (community dissimilarity expressed by $\hat{\Delta}_T$ : see text; $P$<0.05) at each of four abundance weighting methods (see text).

| Weighting method | Convergence | Divergence |
|---|---|---|
| Presence | 2 | 0 |
| Abundance rank | 0 | 1 |
| Sqrt biomass | 1 | 2 |
| Biomass | 0 | 1 |

TEST STATISTIC BEHAVIOUR

Figs. 7.3 and 7.4 depict rank-scaled texture plots for three pairs of *Nothofagus*-dominated communities from this study. These examples illustrate the performance of $\hat{\Delta}_T$ as an index of dissimilarity in texture between communities. The results (relative deviance, RD and significance level $P$) of tests for convergence between texture distributions in these communities are also shown.

The three pairs of communities depicted in Fig. 7.3 have texture plots that are closely matched, both in their shapes and heights relative to the ordinate. Correspondingly, each pair was found to be significantly convergent in the texture variate shown ($R_{\hat{D},T}$<1; $P$<0.05). Note the effect of species abundance, which tends to emphasise character differences between abundant species (generally, to the left in Figs. 7.3b,c) and de-emphasise differences between minor species.

The communities compared in Fig. 7.4 have texture plots that are dissimilar in height, shape or both height and shape. As would be expected, each pair was found to be significantly divergent ($R_{\hat{D},T}$>1; $P$<0.005) in comparison to the null model communities produced by redistributing observed species values to communities at random.

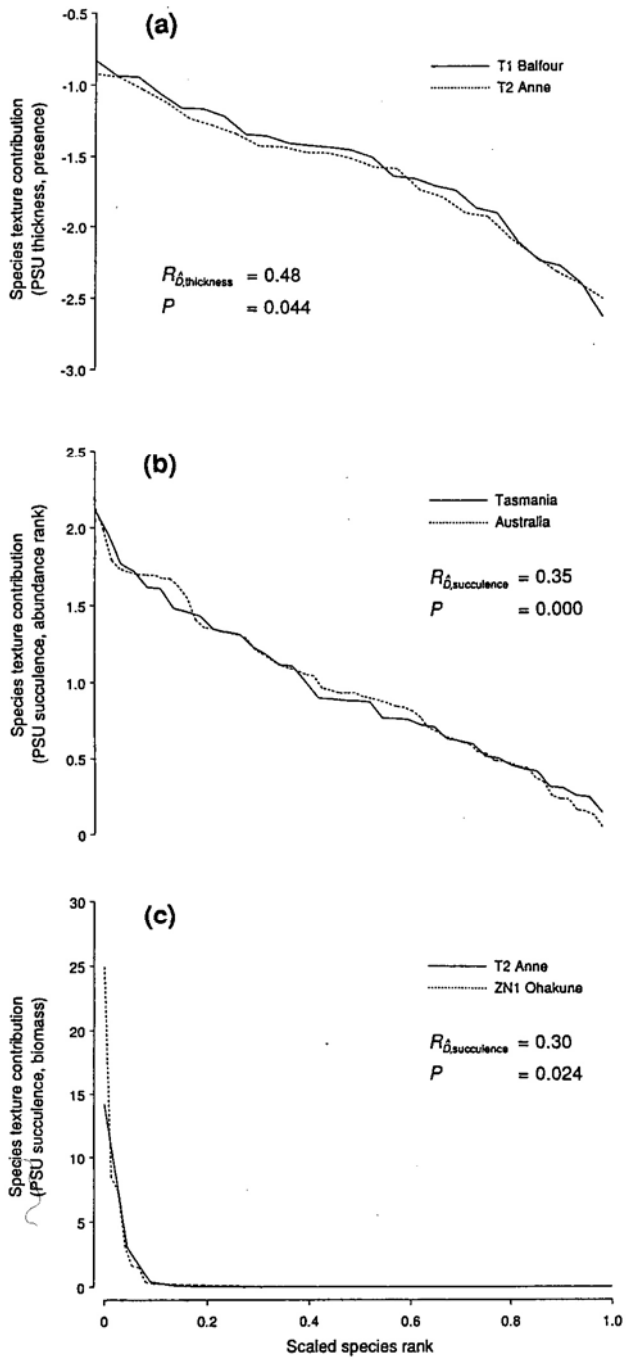



**Fig. 7.3** Rank-scaled texture plots (see Fig. 7.2) for significantly convergent *Nothofagus*-dominated communities **(a)** T1 Balfour and T2 Anne, convergence in PSU thickness with species weighted equally; **(b)** Tasmania (T) and Australia (A), convergence in PSU succulence weighted by abundance rank; **(c)** Anne and ZN1 Ohakune, convergence in PSU succulence, weighting by photosynthetic biomass. Formulae for the calculation of axis coordinates are given in the main text. Relative deviance ($R^{\wedge}_{D,T}$) and significance ($P$) values for convergence are shown on the figure.

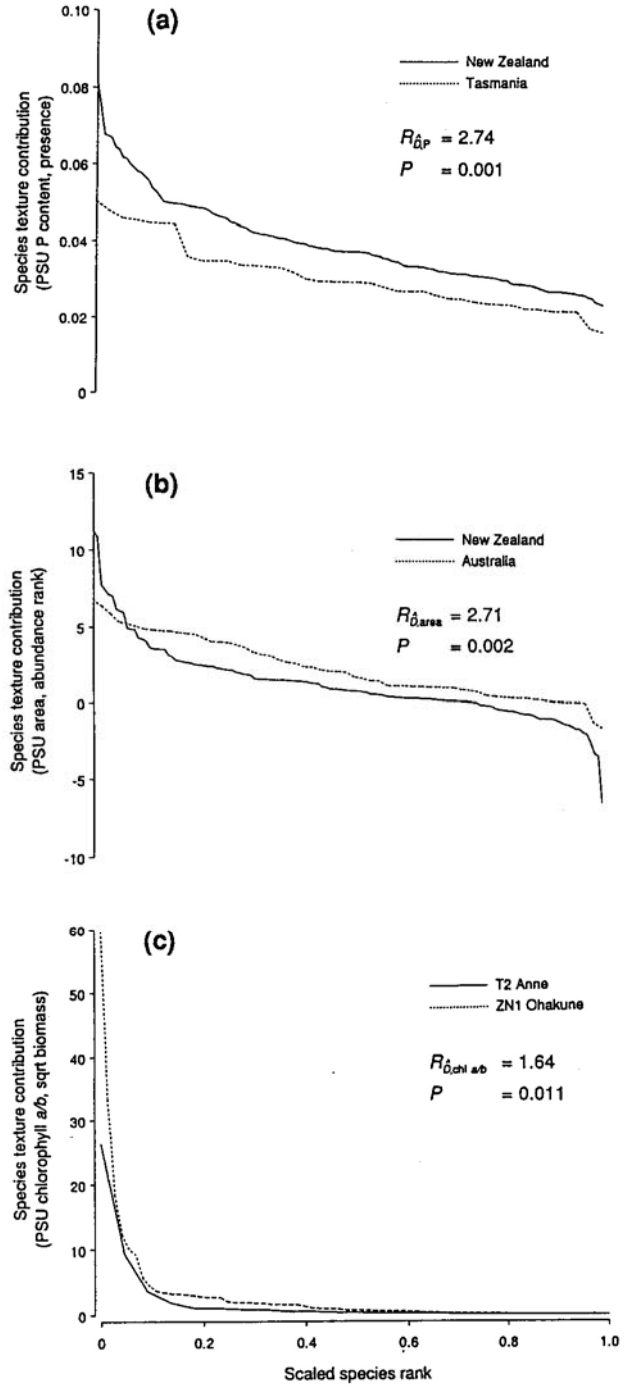



**Fig. 7.4** Rank-scaled texture plots for significantly divergent *Nothofagus*-dominated communities **(a)** New Zealand (Z) and Tasmania (T), divergence in PSU phosphorus content with species weighted equally; **(b)** New Zealand and Australia (A), divergence in PSU area weighted by abundance rank; **(c)** T2 Anne and ZN1 Ohakune, divergence in PSU chlorophyll *a/b*, weighting by the square root of photosynthetic biomass. Format as for Fig. 7.3.

## PATTERNS AMONG COMMUNITIES

### *Landmass scale*

The four landmass-scale communities of Tasmania, Australia, New Zealand and South America are significantly convergent in PSU succulence (weighting by photosynthetic biomass or its square root) and specific weight (weighting by abundance rank or biomass) (Fig. 7.5a). However, divergence was detected in all remaining variates except PSU shape, lobation and inclination, primarily with species weighted equally.

Among individual pairs of landmasses (Figs. 7.5b-g), divergence is common in a number of variates, notably PSU phosphorus content, total chlorophyll and chlorophyll *a/b*, particularly at low to intermediate abundance weighting levels. Little significant convergence was detected, although there is some convergence in PSU succulence in all comparisons except of New Zealand and South America (Fig. 7.5g). Tasmania and New Zealand, which have relatively similar macroenvironments (Chapter 3) are convergent only in PSU shape (weighting by photosynthetic biomass) and succulence (weighting by the square root of photosynthetic biomass) (Fig. 7.5c). However, divergence is also confined to two variates — phosphorus and total chlorophyll. Several variates show a non-significant tendency towards convergence ($R_{D\hat{}}$ $_{,T}$<1) at all or most weighting levels. This pattern is similar to the one observed in comparisons of texture means in Chapter 6 (Fig. 6.2c).

### *Regional scale*

Communities from three regions of Tasmania are convergent overall in PSU thickness, with species unweighted by their abundance, and in succulence, with weighting by photosynthetic biomass or its square root (Fig. 7.6a). The only test showing significant divergence was that of chlorophyll *a/b* with species weighted by abundance rank. Species height, which was found significantly convergent among abundant species when community texture means were compared (Chapter 6; Fig. 6.3a), was found non-significantly divergent using the present test, which also takes the shape of the texture distribution into account.

In pairwise comparisons of Tasmanian sites (Fig. 7.6b-d) only a few tests showed significant departure from null model expectation. All pairs of sites were found to be convergent in PSU thickness, significantly so when species were weighted by presence only (T1 Balfour/T2 Anne; Balfour/T3 Mathinna) or by the square root of photosynthetic biomass (Anne/Mathinna). PSU Lobation is convergent (weighting by abundance rank) in two comparisons. Only Balfour and Anne show significant divergence, in PSU succulence and species height at low weighting levels.

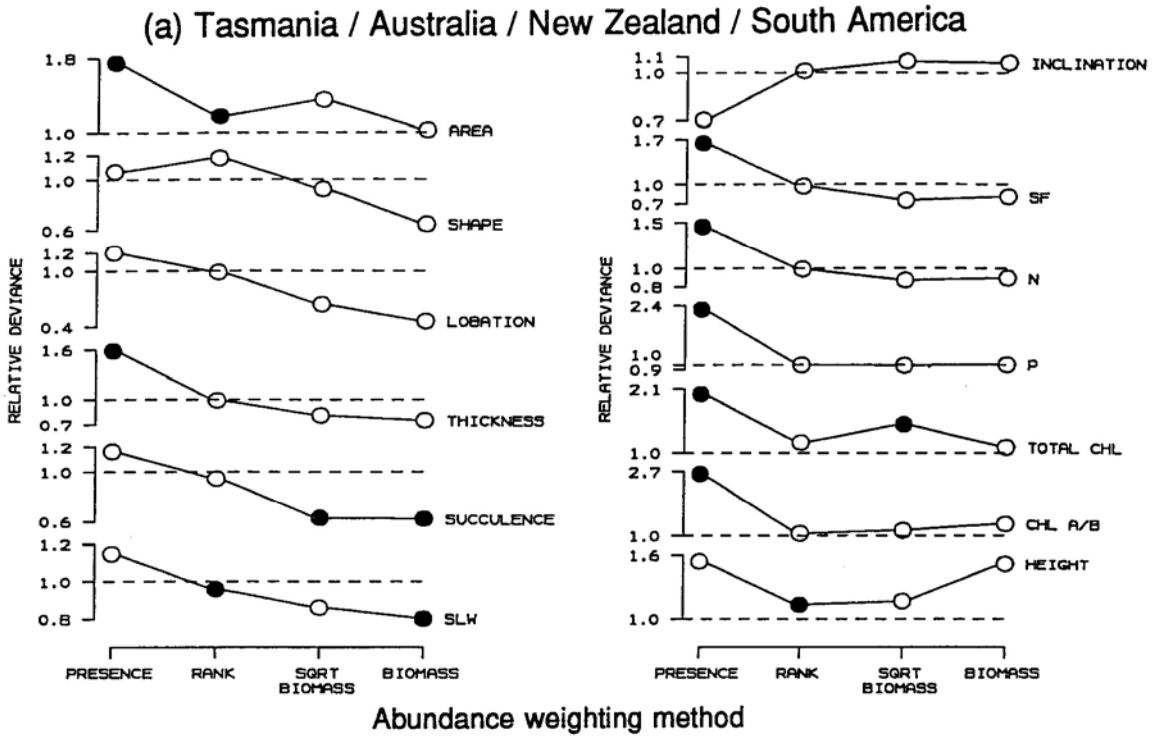



**Fig. 7.5** Null model randomisation tests for convergence or divergence in texture distributions between landmass-scale *Nothofagus*-dominated communities Tasmania (T), Australia (A), New Zealand (Z) and South America (S). The relative deviance $R_{\hat{D},T}$ of among-community variation in texture distributions is shown for each of 13 texture variates and four methods of weighting individual species values by abundance in calculations of community texture means. A value of $R_{\hat{D},T}<1$ indicates similarity in texture between communities relative to a null model simulating random community assembly (see text); $R_{\hat{D},T}>1$ indicates dissimilarity relative to the null model. Broken lines signify null model expectation ($R_{\hat{D},T}=1$). Filled symbols correspond to significant departure from the null model (convergence for $R_{\hat{D},T}<1$; divergence for $R_{\hat{D},T}>1$; $P<0.05$). Key to abbreviations: RANK=abundance rank; SQRT BIOMASS=square root of photosynthetic biomass; BIOMASS=photosynthetic biomass (see text for full explanation). Texture variates are based on PSU characters except SF (support fraction) and HEIGHT (species height). Key: SLW=specific weight; N=nitrogen content; P=phosphorus content; TOTAL CHL=total chlorophyll content; CHL A/B=chlorophyll *a/b* ratio (see text for full explanation).

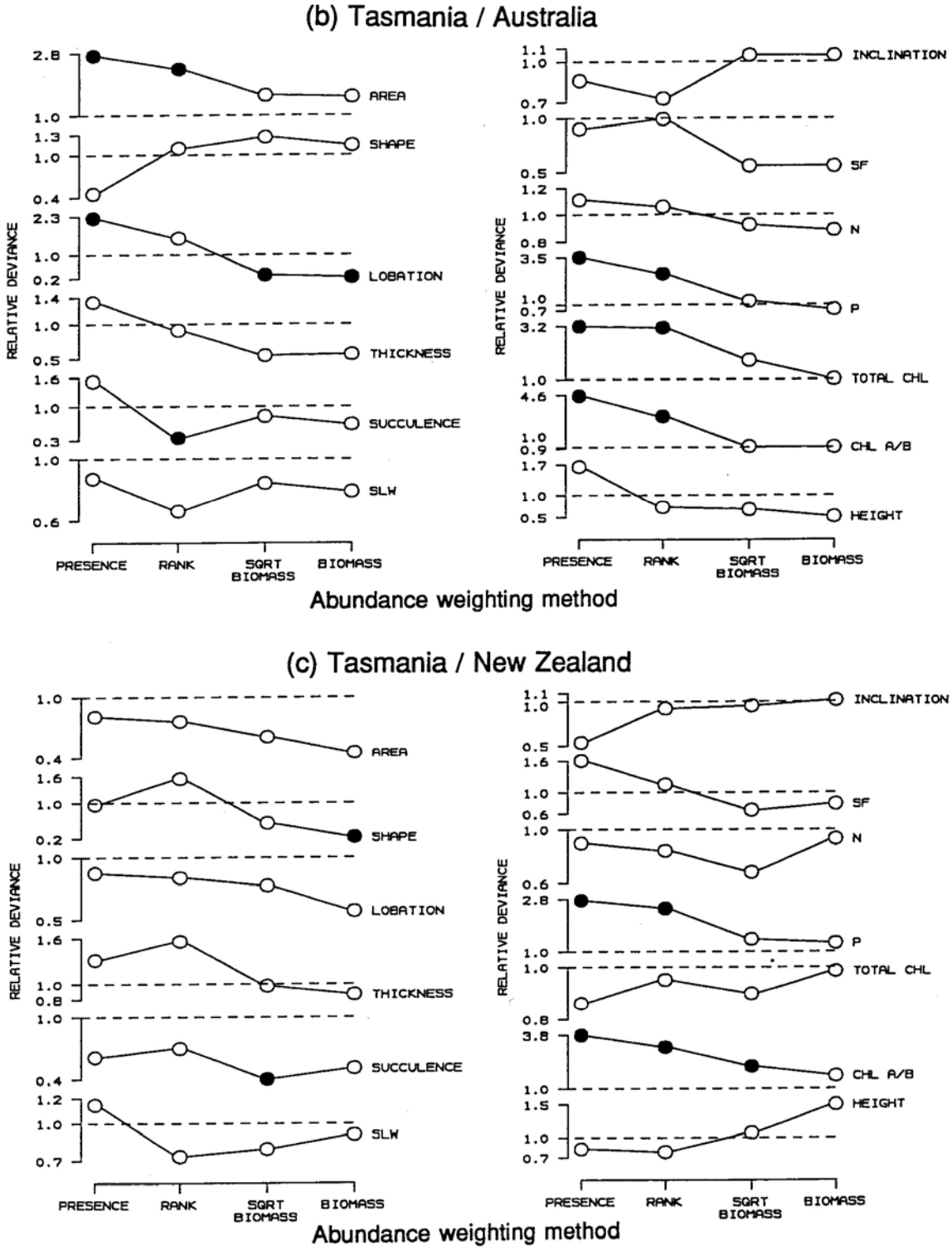



**Fig. 7.5** (continued)

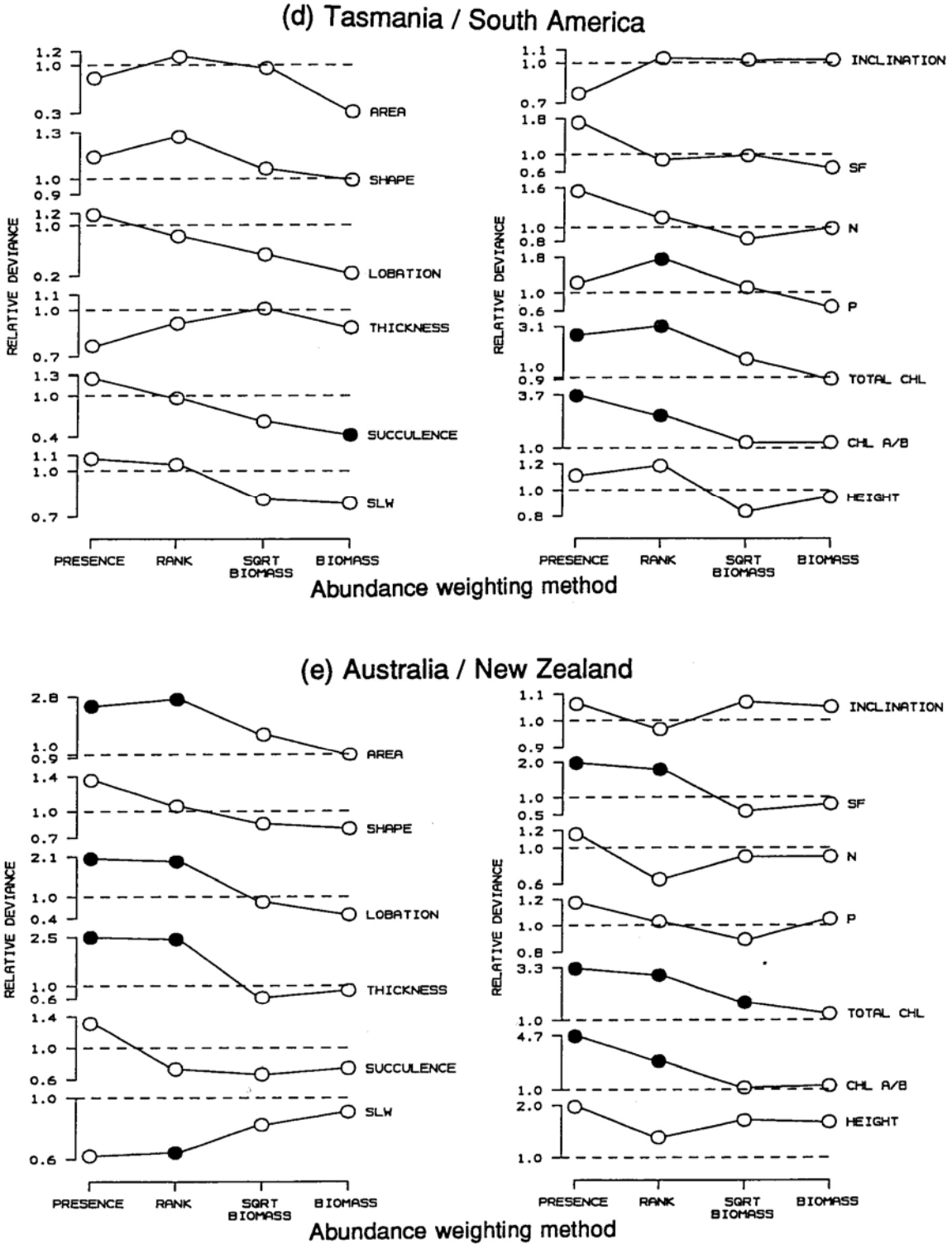



**Fig. 7.5** (continued)

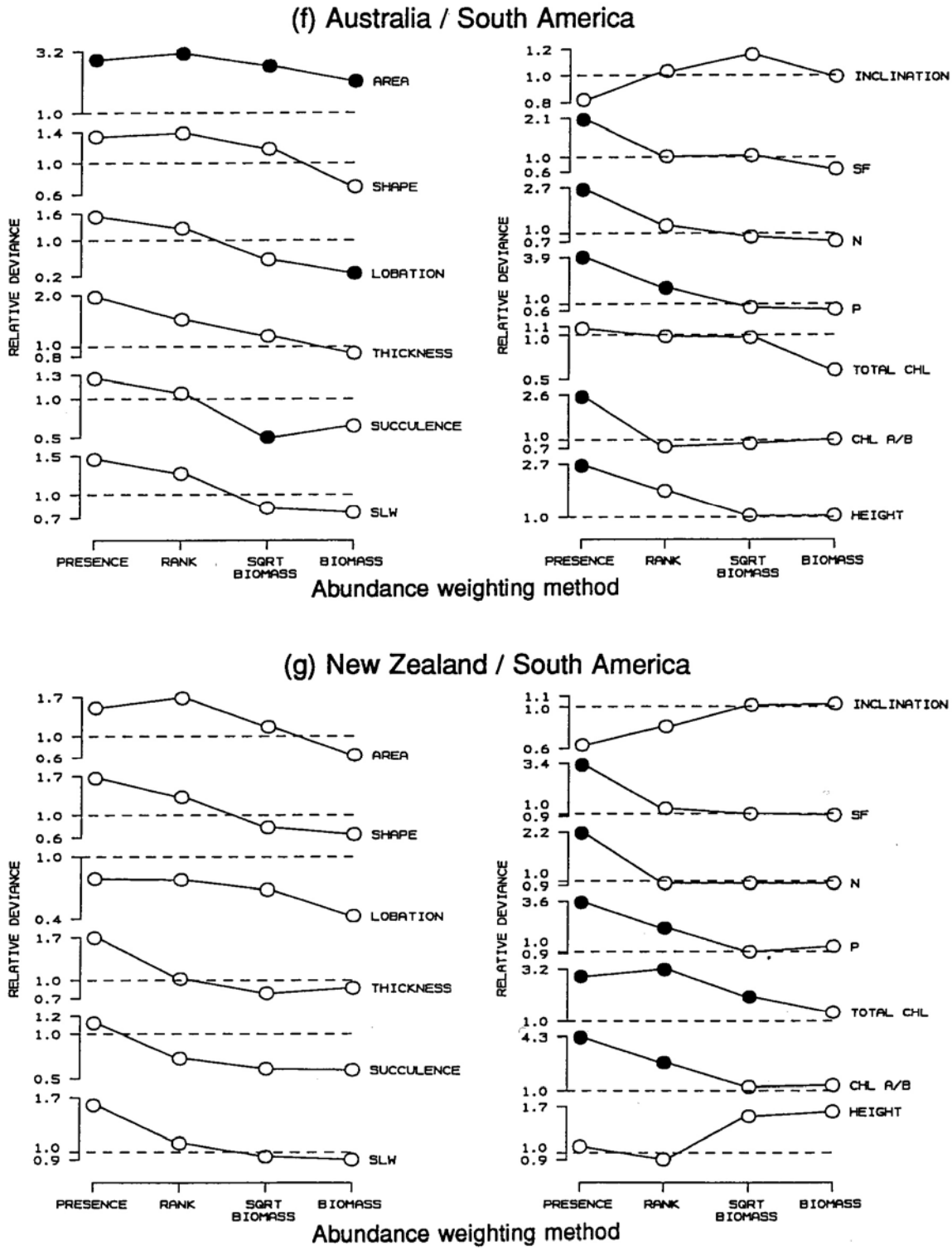



**Fig. 7.5** (continued)

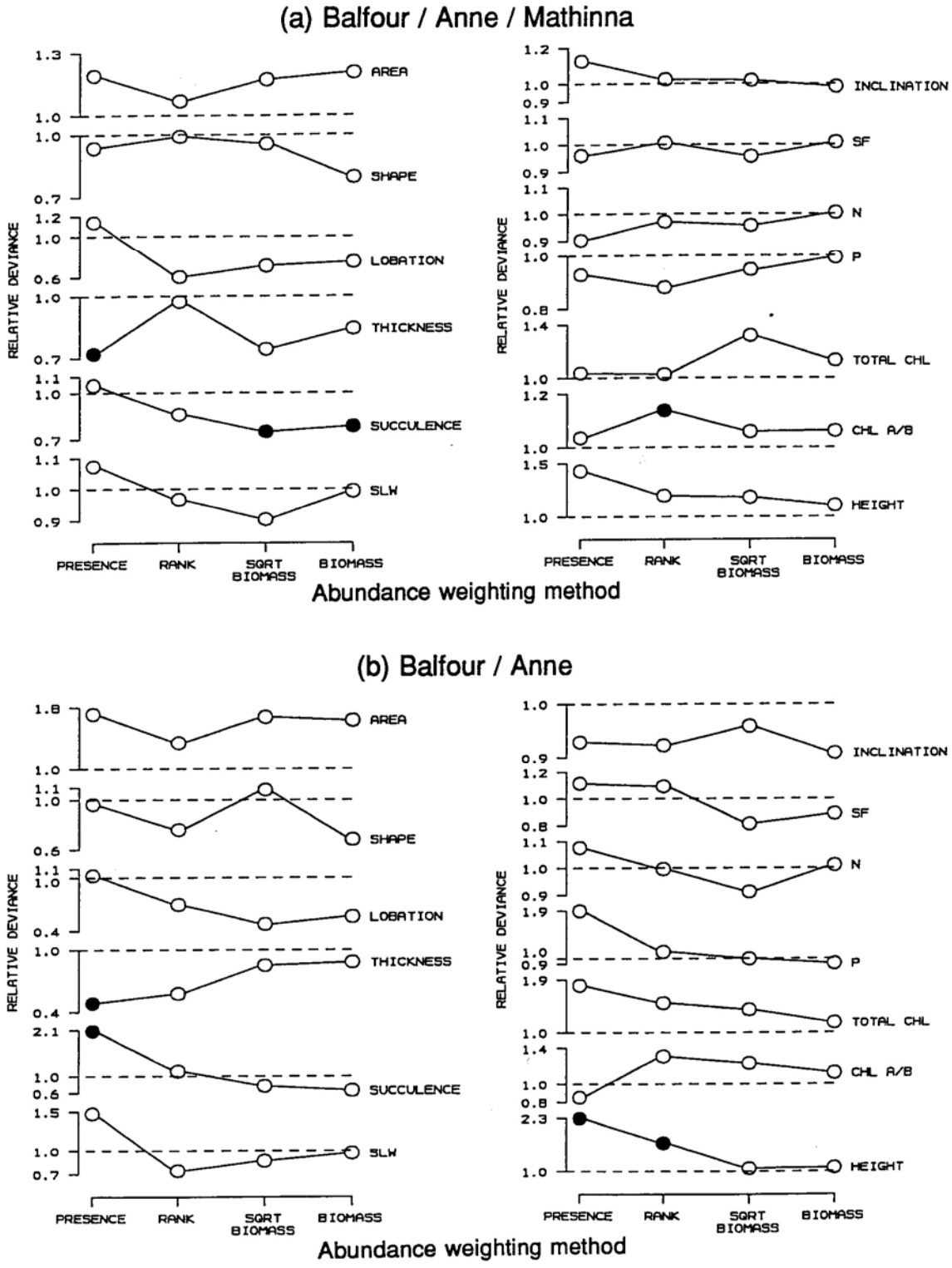



**Fig. 7.6** Null model randomisation tests for convergence or divergence in texture between regional-scale *Nothofagus*-dominated communities T1 Balfour, T2 Anne and T3 Mathinna. Format as for Fig. 7.5.

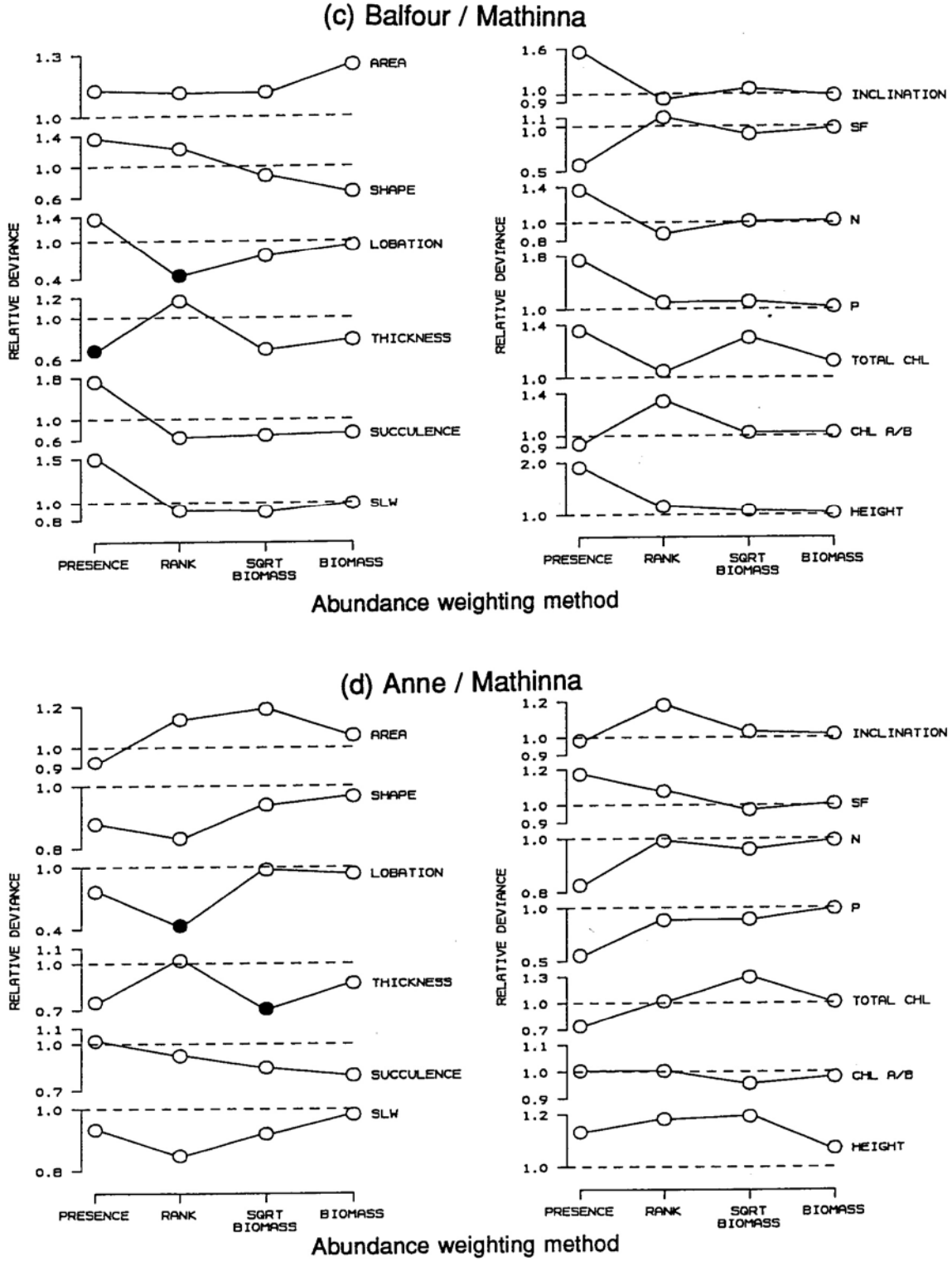



**Fig. 7.6** (continued)

Australian regional-scale communities A1 Lumeah and A2 Cascades are convergent only in PSU chlorophyll *a/b* with species unweighted by abundance, and in phosphorus content when photosynthetic biomass is used as the weighting factor (Fig. 7.7). There is divergence in PSU area, shape and (at lower weighting levels) phosphorus content.

Among the southern, central and northern regions of New Zealand, convergence was detected in PSU specific weight, nitrogen content, phosphorus content and chlorophyll *a/b*, in all cases with species values weighted by a measure of abundance (Fig. 7.8a). This is a higher incidence of convergence than was obtained when community texture means were compared, in Chapter 6 (see Fig. 6.5a). However, species height, texture means of which were convergent at higher weighting levels, is divergent when texture distributions are compared. There is also significant overall divergence in PSU shape, succulence, inclination, phosphorus content and chlorophyll *a/b* at lower weighting levels.

Pairwise comparisons of regional communities from New Zealand reveal little convergence. Despite apparently similar environments (Chapter 3), southern (ZS) and central (ZC) New Zealand appear to be the most dissimilar in texture: eight variates are significantly divergent at lower weighting levels, and there is no significant convergence (Fig. 7.8b). Southern and northern (ZN) New Zealand are convergent in PSU specific weight (weighting by abundance rank) and total chlorophyll (weighting by photosynthetic biomass or its square root), but PSU area, succulence, specific weight, phosphorus content, total chlorophyll, chlorophyll *a/b* and support fraction are divergent at various weighting levels (Fig. 7.8c). Central and northern New Zealand are convergent in PSU specific weight (weighting by abundance rank) and support fraction (photosynthetic biomass), but there is divergence at several weighting levels in PSU inclination, phosphorus content, chlorophyll *a/b* and species height (Fig. 7.8d).

Most texture variates show some divergence between *Nothofagus*-dominated communities in Chile (SC) and those in Argentina (SA; Fig. 7.9). There is no significant convergence, although PSU lobation and succulence are more similar than expected under the null model ($R_{\hat{D},T}<1$) at all weighting levels, suggesting that there may be a weak tendency towards convergence: mean community lobation was found to be convergent when all species were weighted equally (Chapter 6; Fig. 6.6).

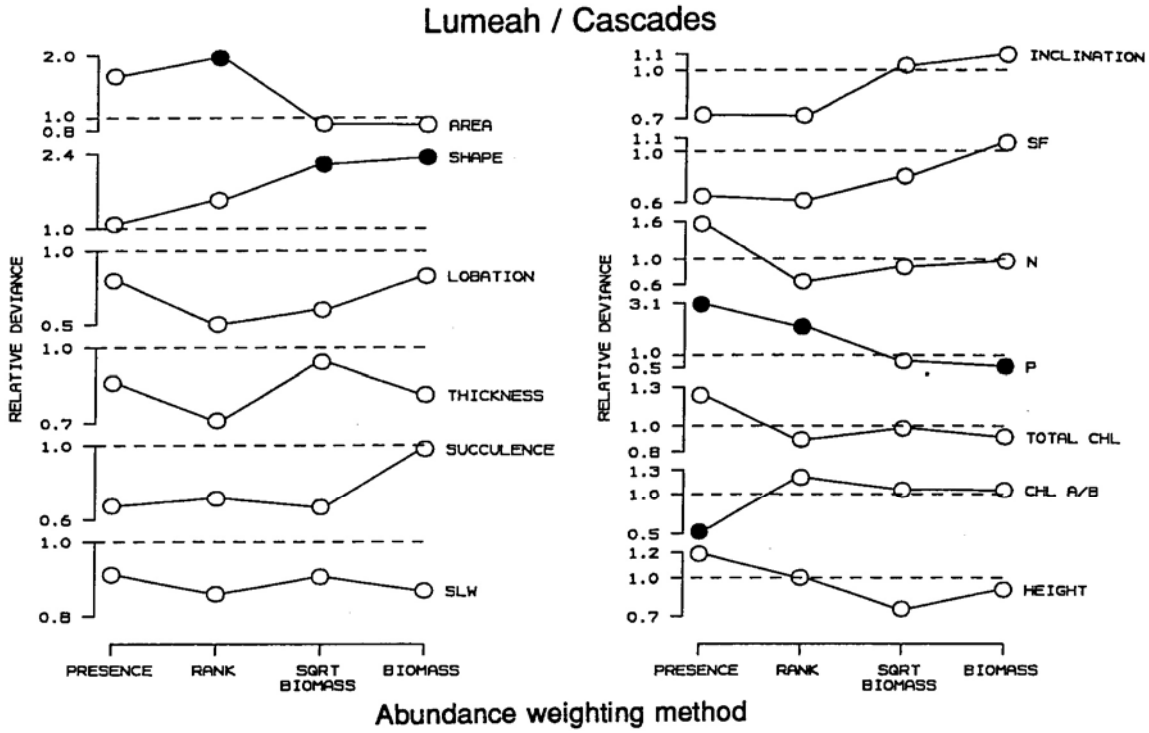



**Fig. 7.7** Null model randomisation tests for convergence or divergence in texture between regional-scale *Nothofagus*-dominated communities A1 Lumeah and A2 Cascades. Format as for Fig. 7.5.

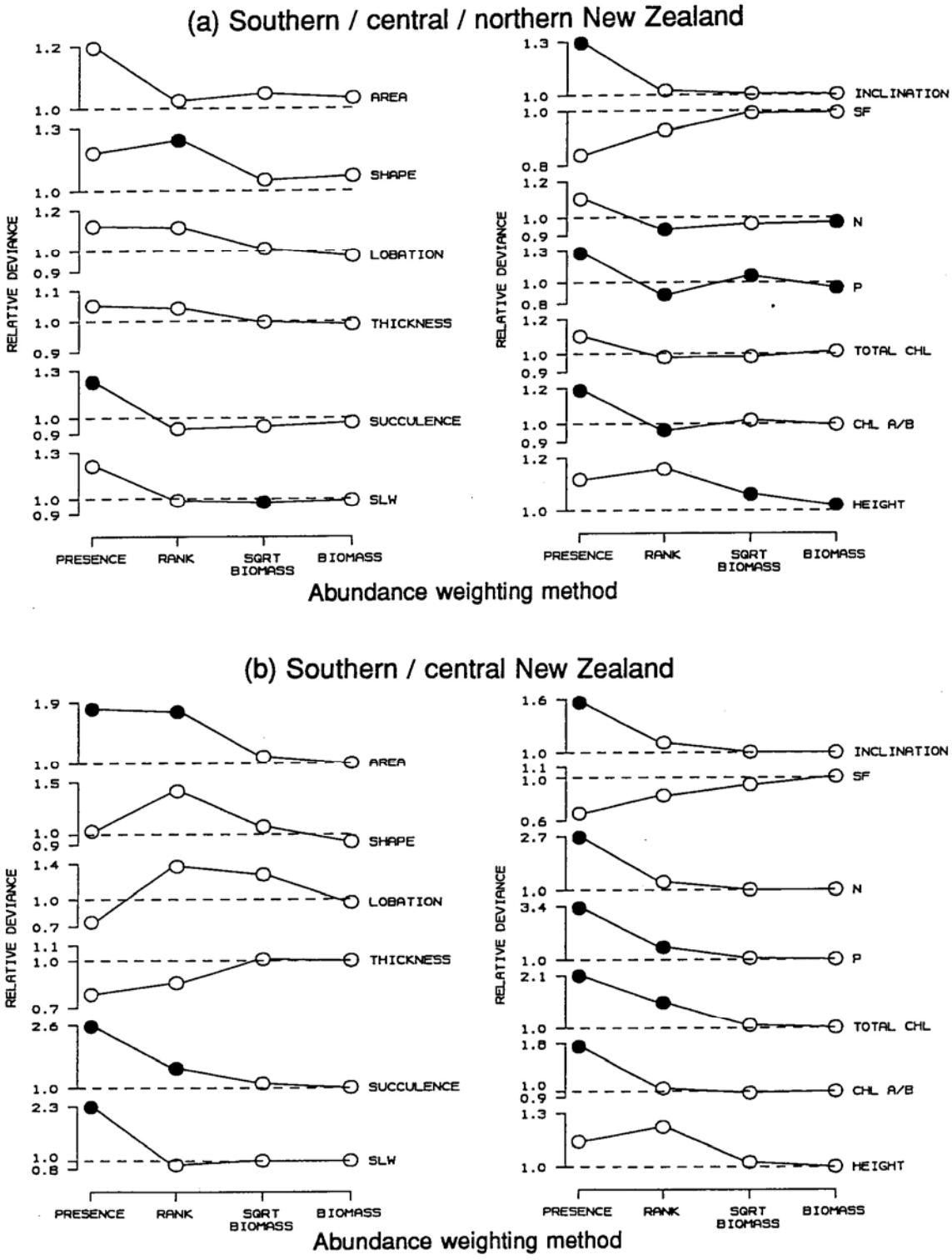



**Fig. 7.8** Null model randomisation tests for convergence or divergence in texture between regional-scale *Nothofagus*-dominated communities southern (ZS), central (ZC) and northern (ZN) New Zealand. Format as for Fig. 7.5.

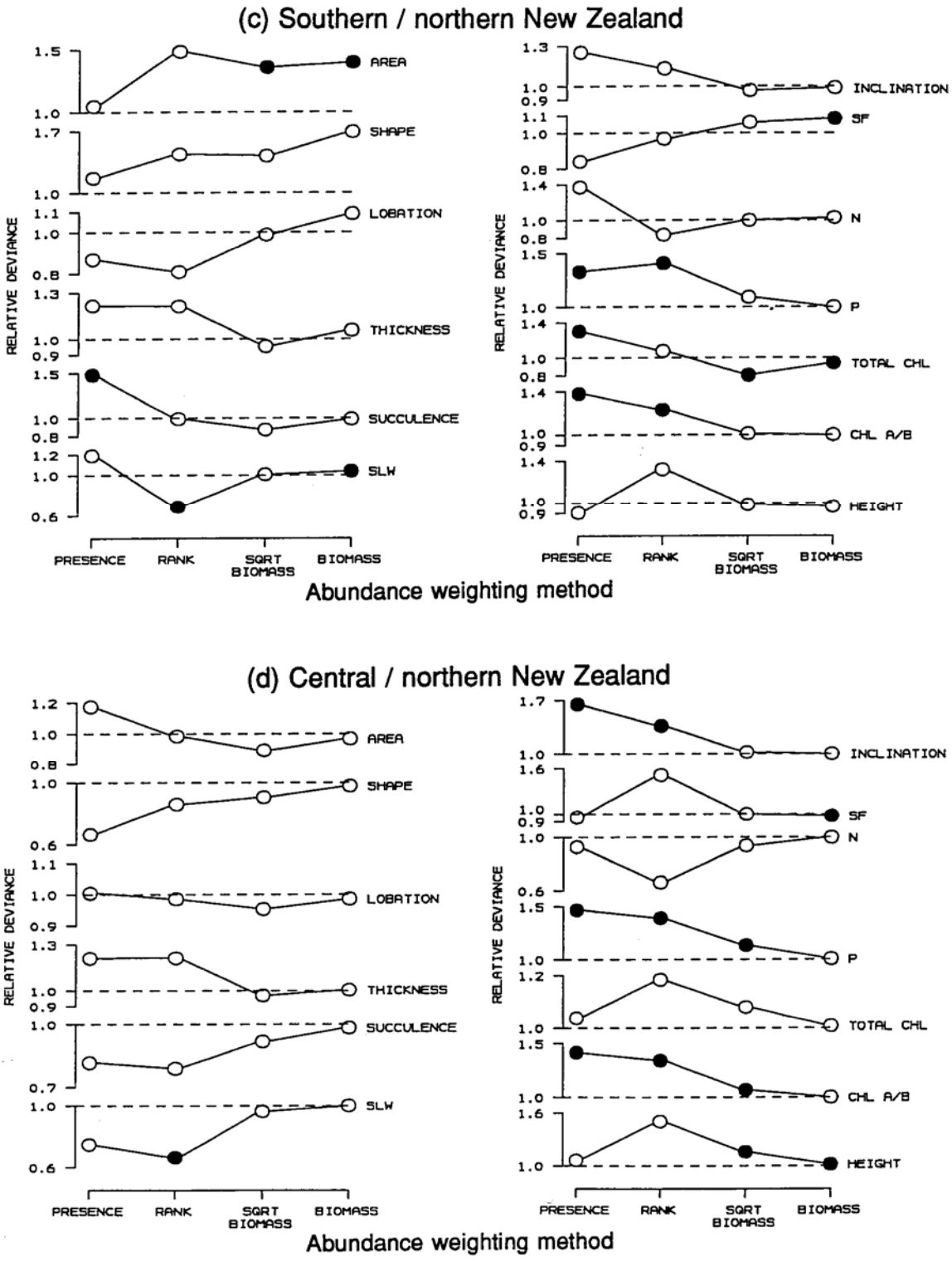



**Fig. 7.8** (continued)

*Local scale*

Southern New Zealand communities ZS1 Ten Mile, ZS2 Walker and ZS3 Deer are convergent in PSU succulence with species values weighted by abundance rank, inclination (weighting by the square root of photosynthetic biomass) and species height (photosynthetic biomass; Fig. 7.10a). This incidence of convergence is higher than was detected using the test statistic $\bar{D}_T$ in Chapter 6 (Fig. 6.7a), but still seems low, given the close environmental matching between the three communities (Chapter 3). There is divergence in PSU nitrogen and phosphorus content and chlorophyll *a/b* at low to intermediate weighting levels.

The overall pattern is reflected in comparisons of individual pairs of sites. PSU shape is convergent between Ten Mile and Walker, with species weighted by photosynthetic biomass or its square root, while species height is convergent with the square root of biomass as the weighting factor (Fig. 7.10b). PSU specific weight, nitrogen content, phosphorus content and chlorophyll *a/b* are divergent at lower weighting levels. Texture distributions at Ten Mile and Deer are consistent with null model expectation, except for PSU phosphorus content, which has a more similar distribution in each community than expected, when species values are weighted by abundance rank (Fig. 7.10c). Walker and Deer are convergent in PSU specific weight (weighting by photosynthetic biomass) but divergent in phosphorus content and chlorophyll *a/b* at low to intermediate weighting levels (Fig. 7.10d).

The two communities sampled in central New Zealand, ZC1 Craigs and ZC2 Station, are convergent in PSU specific weight (weighting by abundance rank) but divergent in area (all weighting levels except photosynthetic biomass), lobation, inclination, total chlorophyll and species height (lower weighting levels; Fig. 7.11).

The northern New Zealand communities ZN1 Ohakune, ZN2 Rotokura and ZN3 Clements were found to be closely matched in their environments in Chapter 3, yet convergence was detected in only one test — of PSU specific weight, with species values weighted by photosynthetic biomass (Fig. 7.12a). The communities are divergent in PSU nitrogen and phosphorus content, chlorophyll *a/b* with species weighted equally, and in total chlorophyll at all weighting levels.

Considering pairs of these communities, Ohakune and Rotokura show no convergence at all, but are divergent in PSU area, phosphorus content and total chlorophyll (Fig. 7.12b). Ohakune and Clements are convergent in PSU thickness (species weighted equally), specific weight (photosynthetic biomass) and chlorophyll *a/b* (photosynthetic biomass or its square root), and divergent in nitrogen content (equal weighting), total chlorophyll (abundance rank) and chlorophyll *a/b*, when species are weighted equally (Fig. 7.12c). Rotokura and Clements show the lowest incidence of departure from the null model, with convergence in PSU area and specific weight, and divergence in support fraction and species height, all at higher weighting levels (Fig.

7.12d).

As was also found in comparisons of texture means in Chapter 6 (Fig. 6.10), the Chilean sites SC1 Pelada and SC2 Antillanca show no significant departure from the null model (Fig. 7.13). While a non-significant tendency towards convergence was seen in several variates comparing community texture means, this pattern is less marked when texture distributions are compared, only PSU shape and succulence having $R_{D,T}<1$ at all weighting levels.

Argentinian communities SA1 Quetrihué and SA2 Gutierrez likewise show little significant convergence or divergence (Fig. 7.14). PSU thickness and support fraction are divergent at intermediate weighting levels, while PSU specific weight is convergent when species are weighted by the square root of photosynthetic biomass.

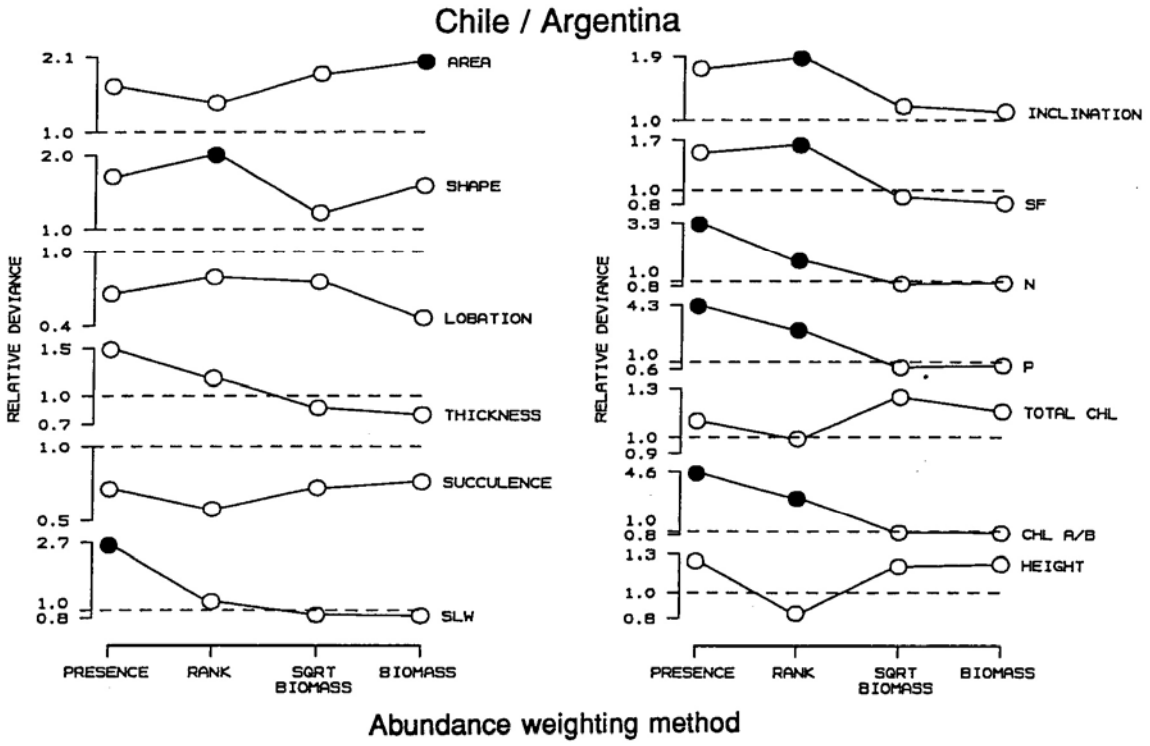



**Fig. 7.9** Null model randomisation tests for convergence or divergence in texture between regional-scale *Nothofagus*-dominated communities of Chile (SC), and Argentina (SA). Format as for Fig. 7.5.

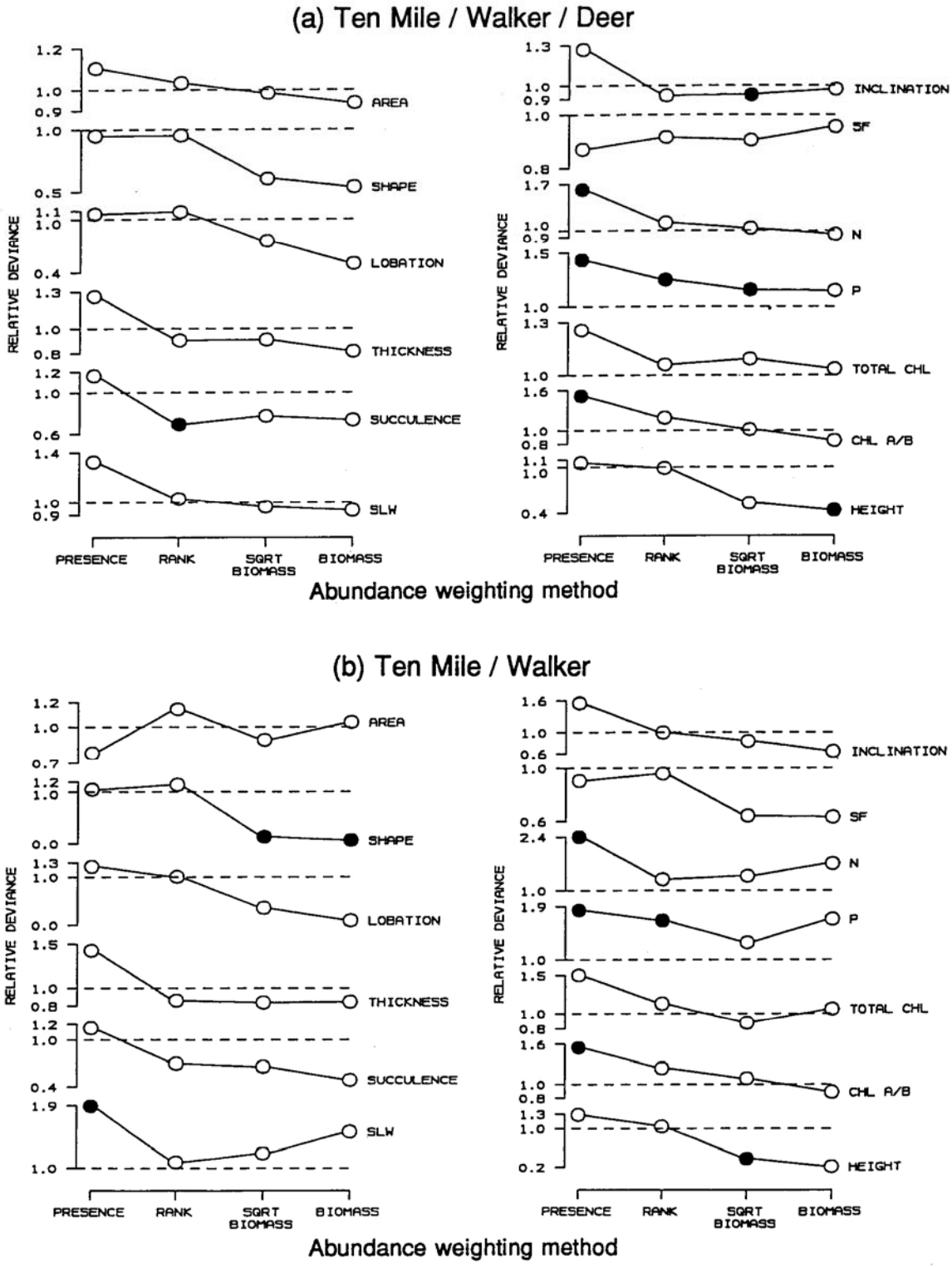
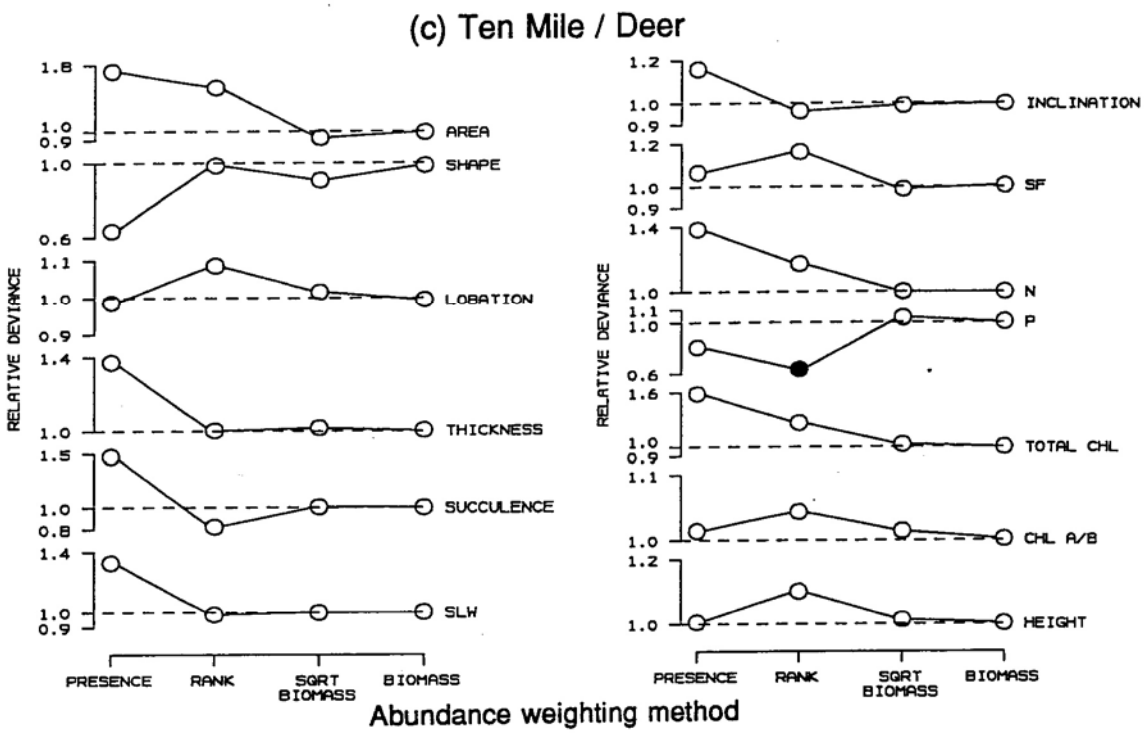



**Fig. 7.10** Null model randomisation tests for convergence or divergence in texture between local-scale *Nothofagus*-dominated communities ZS1 Ten Mile, ZS2 Walker and ZS3 Deer. Format as for Fig. 7.5.



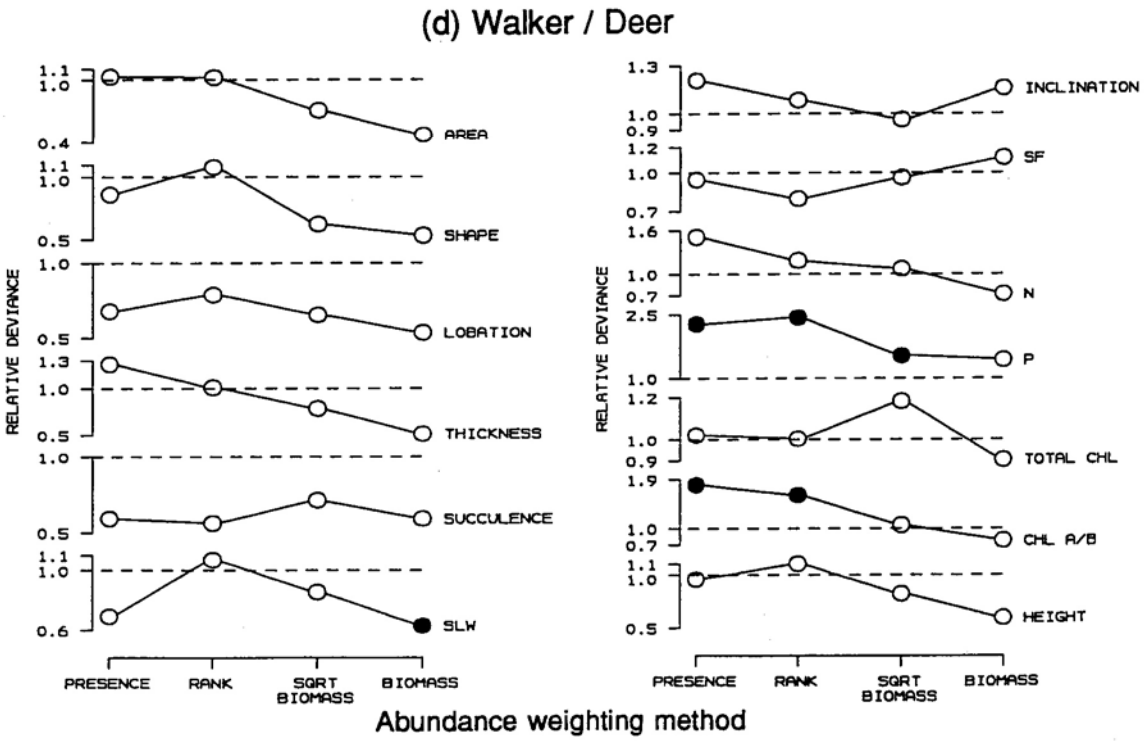




**Fig. 7.10** (continued)

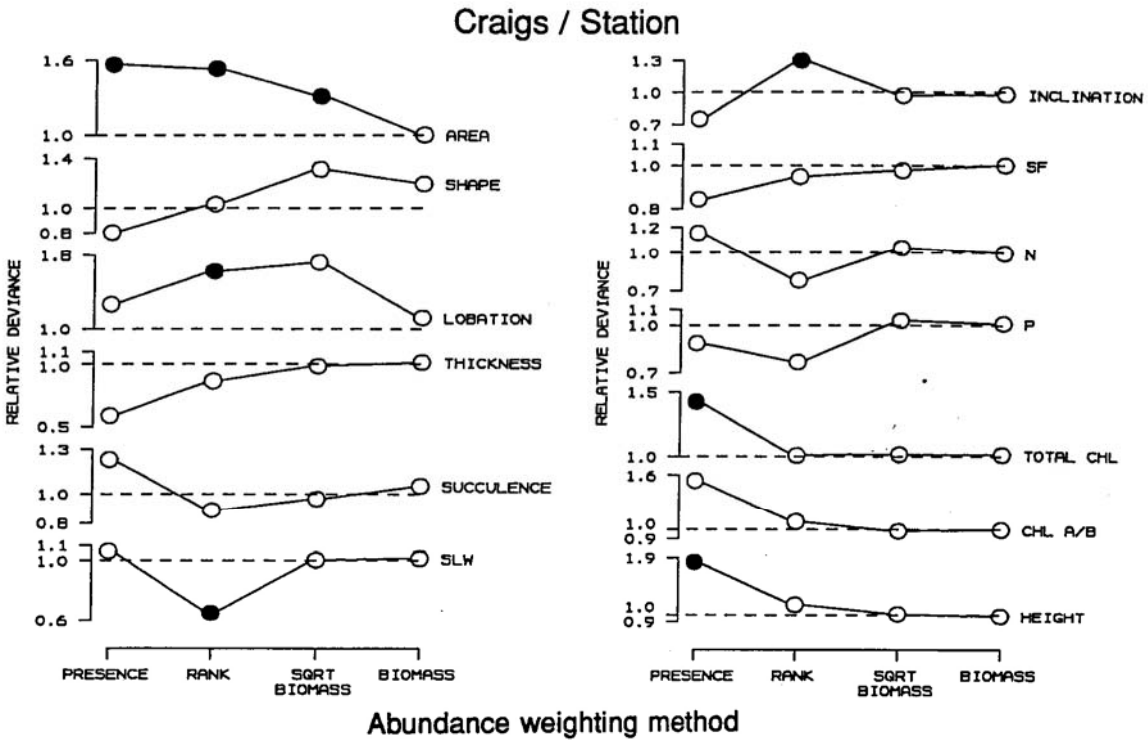



**Fig. 7.11** Null model randomisation tests for convergence or divergence in texture between local-scale *Nothofagus*-dominated communities ZC1 Craigs and ZC2 Station. Format as for Fig. 7.5.

*Closely matched sites from different landmasses*

T1 Balfour (Tasmania) and A2 Cascades (Australia) show convergence in PSU lobation at higher weighting levels, and succulence with weighting by abundance rank (Fig. 7.15a). Divergence was detected in PSU lobation, phosphorus content, total chlorophyll and chlorophyll *a/b* at low weighting levels. T2 Anne (Tasmania) and ZN1 Ohakune (New Zealand) are convergent in PSU lobation (square root of photosynthetic biomass) and succulence (photosynthetic biomass), and divergent in chlorophyll *a/b* at all weighting levels (Fig. 7.15b). Divergence is more marked than convergence between SA1 Quetrihué and SA2 Rotokura, occurring in PSU shape, phosphorus content and chlorophyll *a/b* at lower weighting levels (Fig. 7.15c). PSU shape is, however, convergent when species characters are weighted by photosynthetic biomass in community texture plots.

Comparison of whole texture distributions, as opposed to texture means, slightly increased the amount of detectable convergence between closely matched sites. Overall results are, however, very similar to those obtained in Chapter 6.

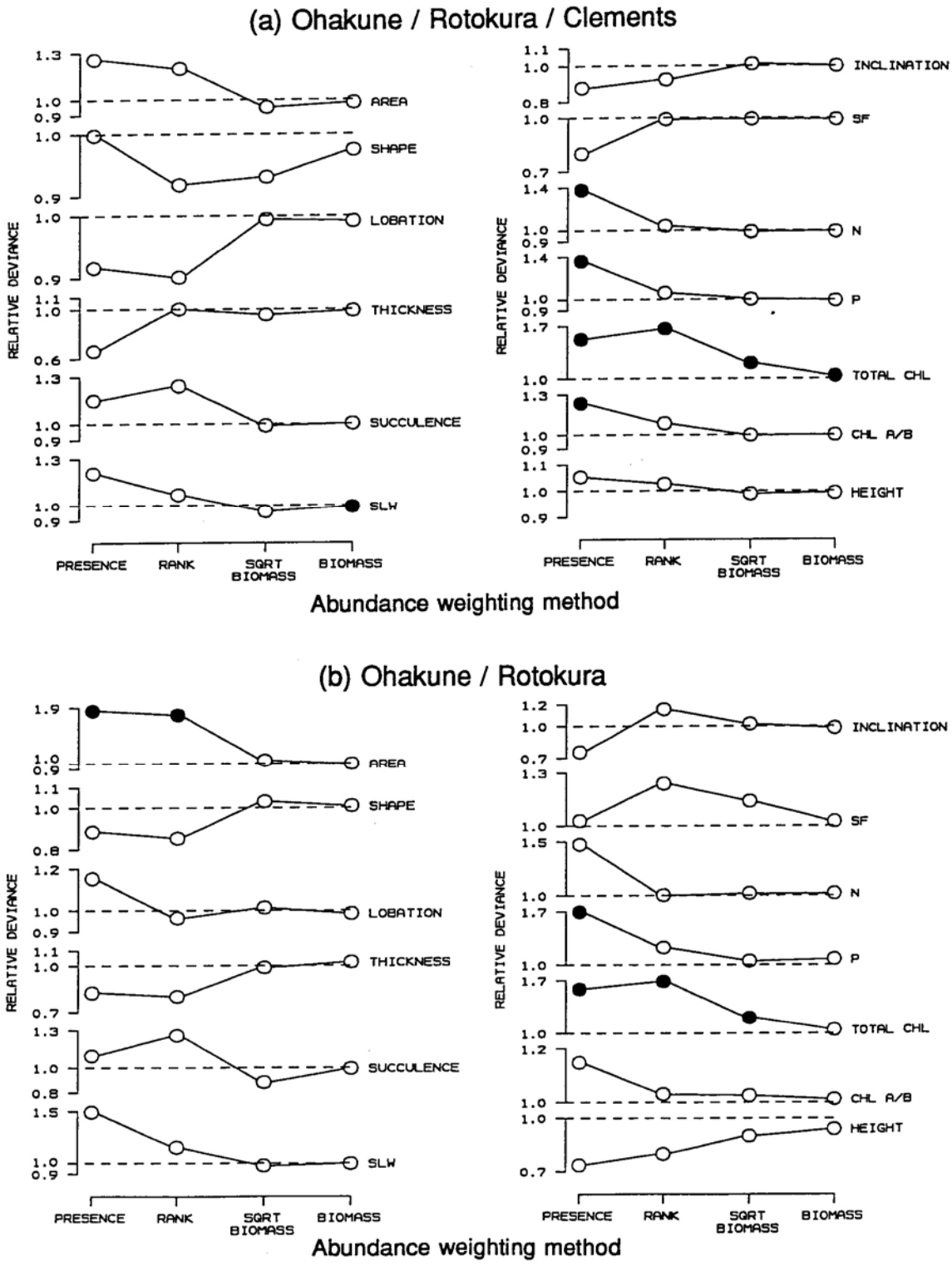



**Fig. 7.12** Null model randomisation tests for convergence or divergence in texture between local-scale *Nothofagus*-dominated communities ZN1 Ohakune, ZN2 Rotokura and ZN3 Clements. Format as for Fig. 7.5.

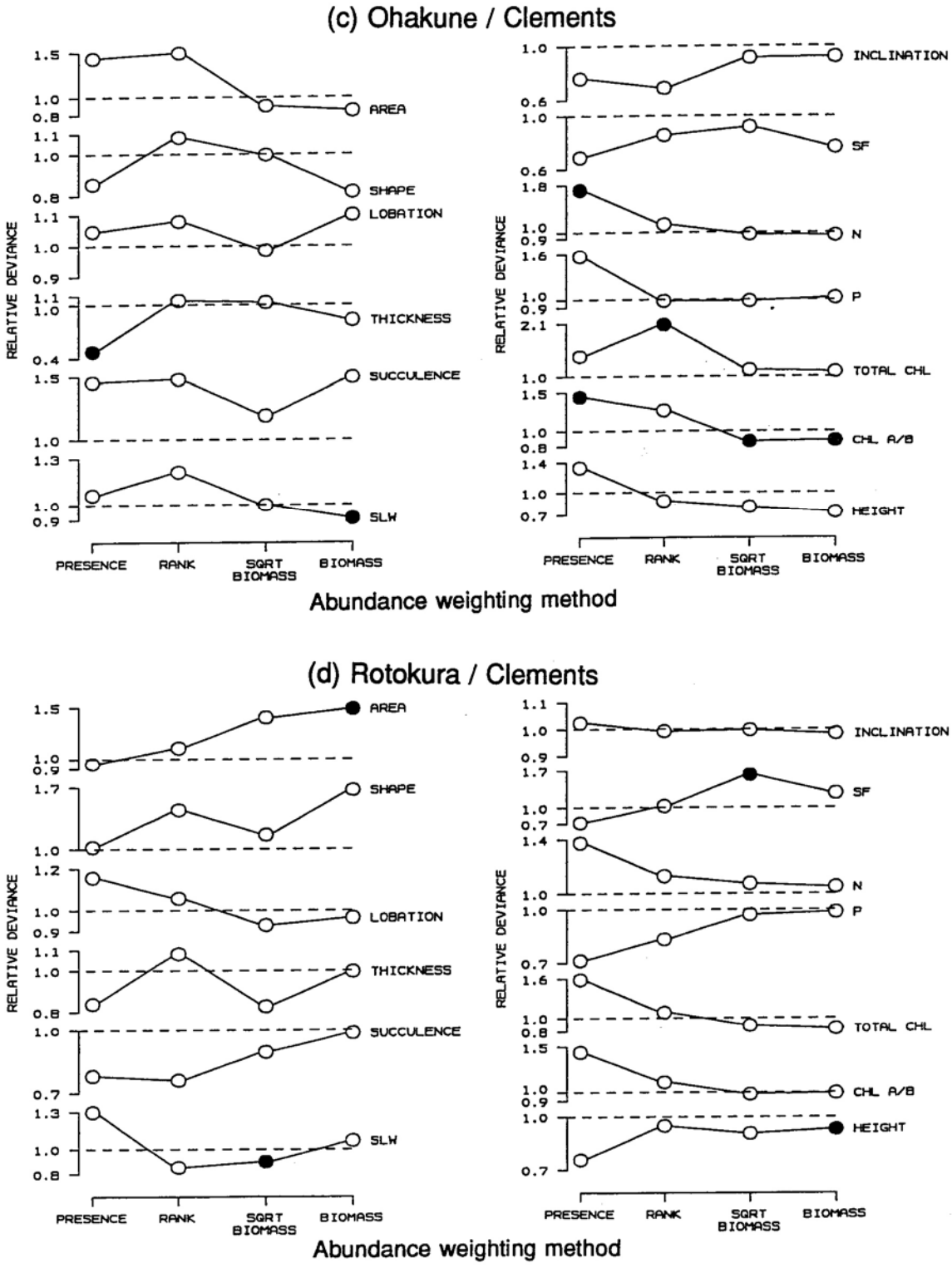



**Fig. 7.12** (continued)

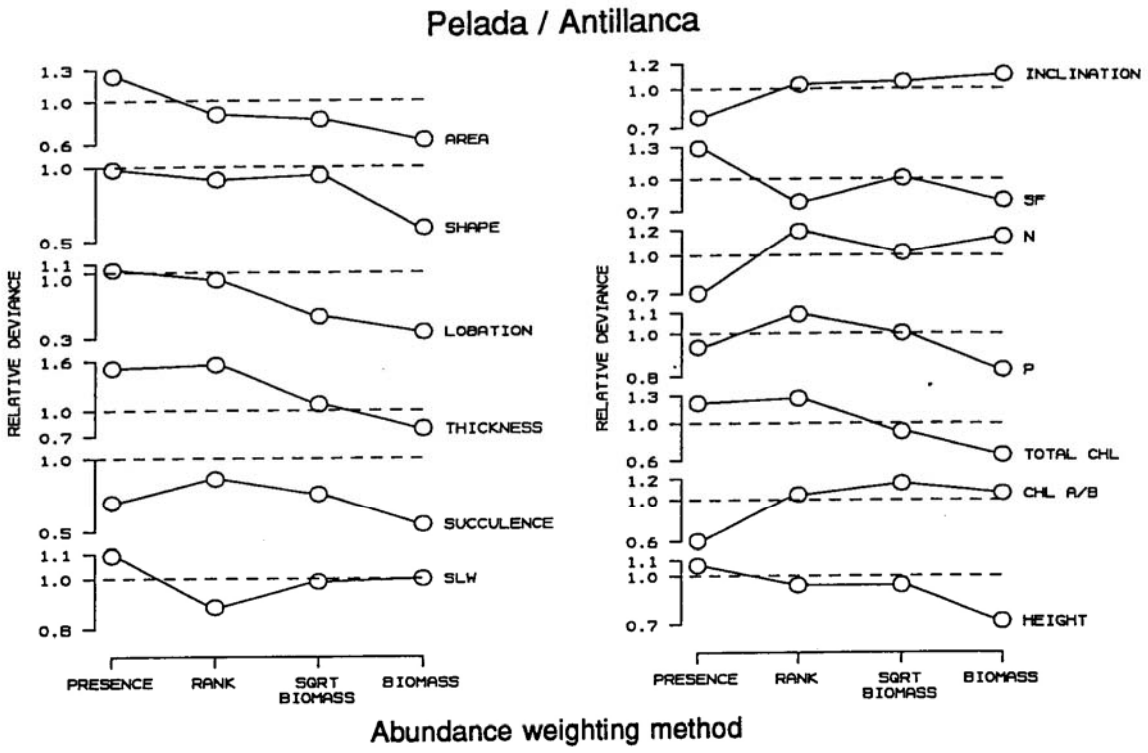



**Fig. 7.13** Null model randomisation tests for convergence or divergence in texture between local-scale *Nothofagus*-dominated communities SC1 Pelada and SC2 Antillanca. Format as for Fig. 7.5.

## PATTERNS AMONG TEXTURE VARIATES

Table 7.2 summarises the results from all comparisons as they relate to the 13 texture variates examined. The highest incidences of significant convergence are in PSU specific weight, succulence, lobation and thickness. The convergence is significant overall ($P<0.05$ according to a binomial test based on 16 independent community comparisons) for PSU thickness, when species values are unweighted by any measure of abundance. Convergence identified in all remaining variates, and at other weighting levels for PSU thickness, is not significant taking account of the number of tests done.

All texture variates show some significant divergence, although this could be shown to be significant overall only for PSU area, succulence, specific weight, nitrogen and phosphorus content, total chlorophyll, chlorophyll *a/b* and species height. Support fraction, with species weighted equally, was divergent in five comparisons, although by chance only one of these was included in the arbitrary subset of 16 independent comparisons on which the binomial test is based.

Frequencies of departure from the null model in each texture variate are generally similar to those obtained in Chapter 6, where community texture means were compared (Table 6.2).

However, there are a number of notable differences.

Although community means of PSU thickness were significantly convergent in a number of tests at higher weighting levels (Chapter 6), this variate was not found to be convergent in any comparison when species were unweighted by abundance; nor was the convergence in PSU thickness observed in Chapter 6 significant over all comparisons. Findings that distributions of PSU thickness were convergent between communities (this chapter) suggest that, although mean thickness was not sufficiently similar between communities to be found significantly convergent, distributions of this character as a whole were closely matched — sufficiently so to produce significant departure from null model expectation (e.g. Fig. 7.3a).

Conversely, species height, which was significantly convergent in 11 tests comparing abundance-weighted community means (Chapter 6), was convergent in only 3 comparisons of texture distributions (this chapter). This frequency of significance is too low to be regarded as significant over all comparisons. This implies that although community means of species height are closely matched in a number of communities, the distributions have different shapes, in some cases resulting in observed values of $\hat{D}_T$ that are not significantly lower than expected under the null model.

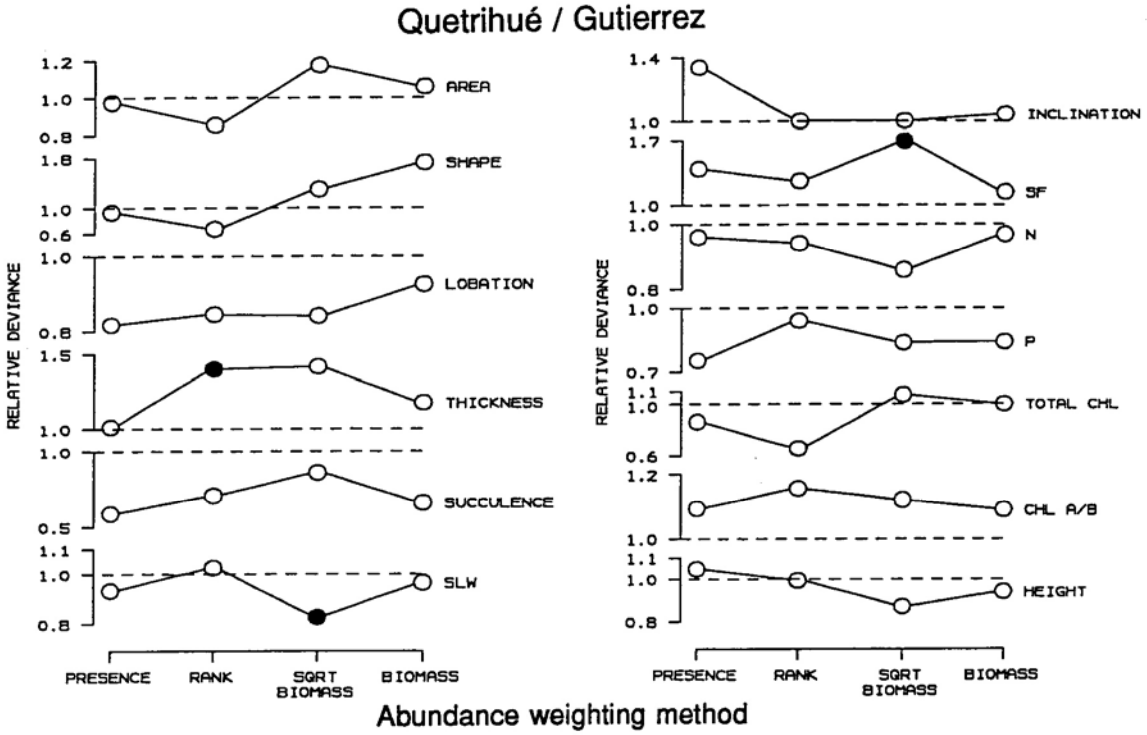



**Fig. 7.14** Null model randomisation tests for convergence or divergence in texture between local-scale *Nothofagus*-dominated communities SA1 Quetrihué and SA2 Gutierrez. Format as for Fig. 7.5.

**Table 7.2** Incidence of significant convergence or divergence of texture distributions in each texture variate at each abundance weighting method among the 31 community comparisons carried out in this chapter and (in parentheses) for 16 independent community comparisons (see Fig. 6.1). Overall significance, determined from the binomial distribution (see text), is shown for results from the 16 independent comparisons.

| Variate | Convergence | | | | Divergence | | | |
|---|---|---|---|---|---|---|---|---|
| | Presence | Rank | Sqrt biomass | Biomass | Presence | Rank | Sqrt biomass | Biomass |
| Area | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 7 (5**) | 8 (6**) | 3 (3*) | 4 (3*) |
| Shape | 0 (0) | 0 (0) | 1 (1) | 3 (2) | 1 (0) | 2 (1) | 1 (1) | 1 (1) |
| Lobation | 0 (0) | 2 (1) | 3 (1) | 3 (2) | 3 (1) | 2 (1) | 0 (0) | 0 (0) |
| Thickness | 4 (3*) | 0 (0) | 1 (0) | 0 (0) | 2 (0) | 2 (1) | 0 (0) | 0 (0) |
| Succulence | 0 (0) | 3 (1) | 4 (2) | 4 (0) | 4 (3*) | 1 (1) | 0 (0) | 0 (0) |
| SLW | 0 (0) | 5 (2) | 3 (1) | 4 (2) | 3 (3*) | 0 (0) | 0 (0) | 1 (1) |
| Inclination | 0 (0) | 0 (0) | 1 (0) | 0 (0) | 3 (1) | 3 (2) | 0 (0) | 0 (0) |
| SF | 0 (1) | 0 (1) | 0 (0) | 1 (0) | 5 (1) | 2 (1) | 2 (1) | 1 (1) |
| N | 0 (0) | 1 (0) | 0 (0) | 1 (0) | 9 (5**) | 1 (1) | 0 (0) | 0 (0) |
| P | 0 (0) | 2 (0) | 0 (0) | 2 (1) | 18 (10**) | 15 (9**) | 4 (1) | 0 (0) |
| Total chl | 0 (0) | 0 (0) | 1 (1) | 1 (1) | 11 (5**) | 9 (4**) | 5 (1) | 1 (0) |
| Chl *a/b* | 1 (0) | 1 (0) | 1 (0) | 1 (1) | 20 (9**) | 13 (5**) | 3 (1) | 1 (0) |
| Height | 0 (0) | 0 (0) | 1 (1) | 2 (0) | 3 (3*) | 2 (1) | 2 (0) | 2 (0) |

*$0.01 \leq P < 0.001$; **$P < 0.001$ (no binomial probabilities in range $0.01 \leq P < 0.05$).

## COMPARISON OF RESULTS OBTAINED WITH DIFFERENT TEST STATISTICS

Comparing Figs. 7.5-7.15 with the results of corresponding comparisons presented in Figs. 6.2-6.12, it is apparent that patterns of departure from the null model are similar, whether texture is expressed as the mean among species, or as a rank-scaled plot of the whole distribution in each community. This impression is confirmed by a quantitative comparison of results from all randomisation tests carried out using the test statistics $\bar{D}_T$ (Chapter 6) and $\hat{D}_T$ (this chapter), as shown in Table 7.3.

Values along the main diagonal of the table (highlighted) represent tests that produced the same result (i.e. significant or non-significant convergence or divergence) using both test statistics. In general, these values are high as proportions of the row and column totals, suggesting that the correspondence between the two comparison methods is high. However, in a small number of cases (six), significant convergence was detected by one method, and significant divergence by the other. Most such tests employed high abundance weighting levels (e.g. PSU specific weight for communities ZS and ZN; weighting by photosynthetic biomass; Figs. 6.5c, 7.8c). The results could reflect differences in the degree to which each test statistic is dependent

on the characters of the few most abundant species. This is because it is possible for the dominant species of a set of communities being compared to be more or less similar in their characters than overall texture. This can result in either significant convergence or divergence in texture between the same communities depending on how heavily the dominant species are weighted. Since the two test statistics utilise species abundances in a slightly different way, such differences could also occur when the same comparisons, weighting species by abundance, are carried out using a different test statistic.

More commonly, departure from the null model in a particular direction (towards convergence or divergence) was significant using one test, but not the other. Thus, of the 57 tests showing significant convergence using $\hat{D}_T$, only 10 showed significant results in the same direction using $\bar{D}_T$, but a further 37 showed non-significant convergence.

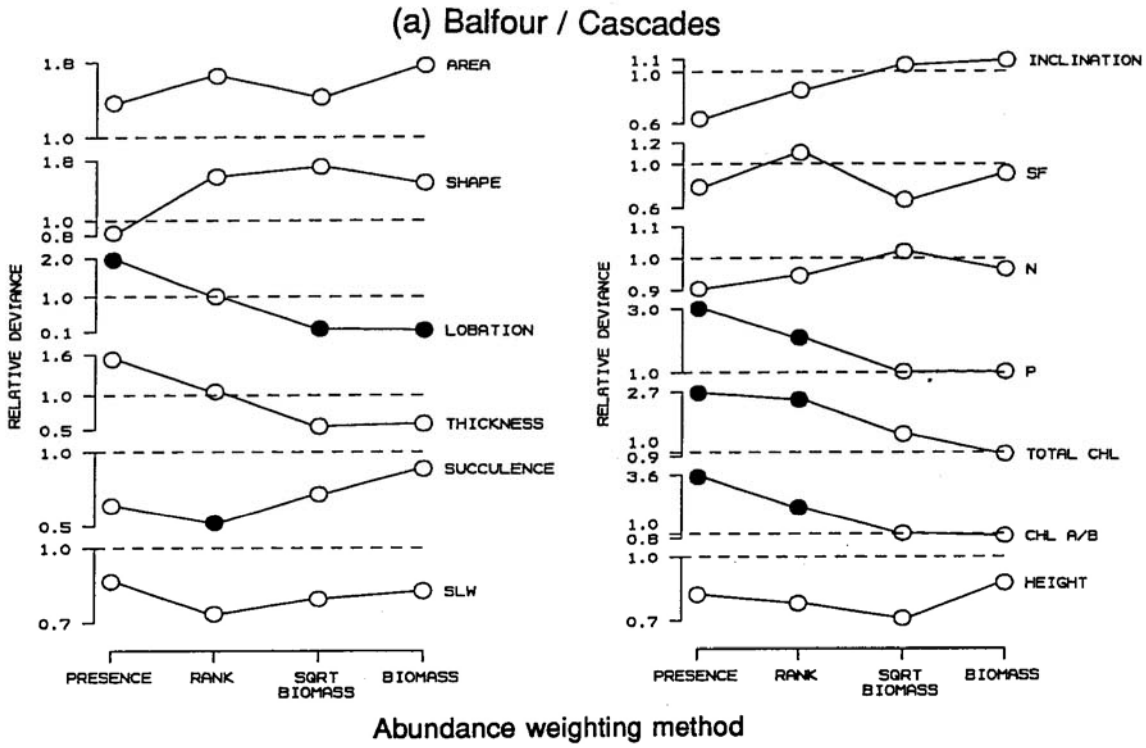



**Fig. 7.15** Null model randomisation tests for convergence or divergence in texture between *Nothofagus*-dominated communities from different landmasses closely matched in their environments: **(a)** T1 Balfour/A2 Cascades; **(b)** T2 Anne/ZN1 Ohakune; **(c)** ZN2 Rotokura/SA1 Quetrihué. Format as for Fig. 7.5.

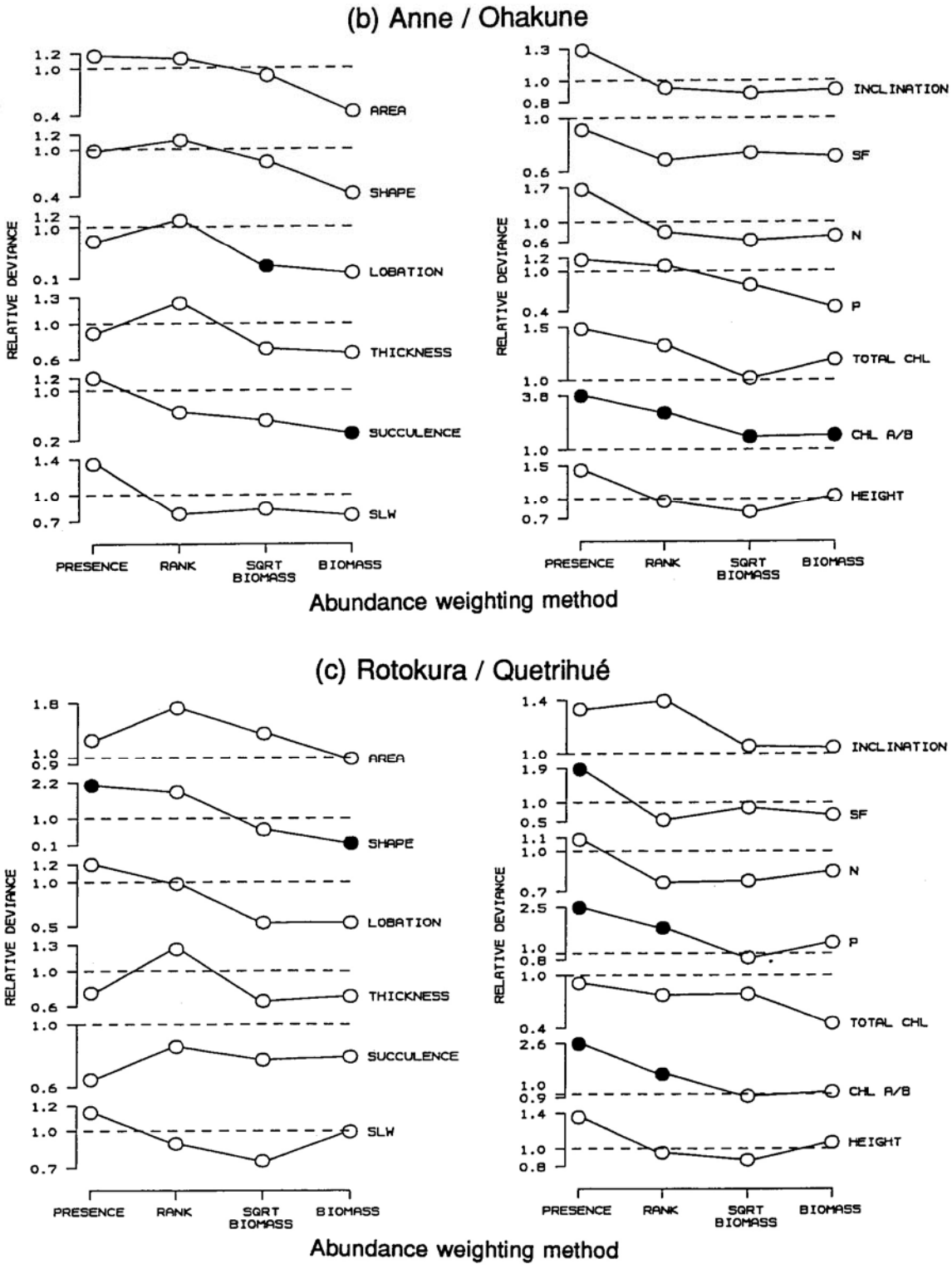



**Fig. 7.15** (continued)

**Table 7.3** Contingency table comparing results obtained in tests for community texture convergence with test statistics quantifying among-community variation in texture means ($\bar{D}_T$) and texture distributions ($\hat{D}_T$). Values shown are total numbers of tests showing significant ('sig.') or non-significant ('n.s.') convergence or divergence for 31 community comparisons, 13 texture variates and four methods of weighting species by their abundance (see text). Shading is applied to highlight the main diagonal of the table, which represents tests yielding equivalent results using both test statistics.

| | | | $\hat{D}_T$ | | | | |
|---|---|---|---|---|---|---|---|
| | | | Convergence | | Divergence | | Total |
| | | | sig.* | n.s. | sig.* | n.s. | |
| $\bar{D}_T$ | Convergence | sig.* | 10 | 20 | 4 | 14 | 48 |
| | | n.s. | 37 | 533 | 5 | 201 | 776 |
| | Divergence | sig.* | 2 | 4 | 148 | 27 | 181 |
| | | n.s. | 8 | 166 | 23 | 410 | 607 |
| | Total | | 57 | 723 | 180 | 652 | 1612 |

*$P<0.05$

It was anticipated (Section 7.1) that comparing whole texture distributions would provide a more conservative test of community convergence, because closely matched community means would not give rise to departure from the null model if distributions were non-convergent in shape (Fig. 7.1a,b). Table 7.3 shows that some 40% of the 48 comparisons showing significant convergence in texture means yielded non-significant or (in four tests) significant divergence when texture distributions were compared. For example, Tasmania and South America were found to be significantly convergent in mean PSU succulence with species weighted equally (Fig. 6.2d). However, the frequency distributions of this character in the two communities are markedly different (Fig. 7.16a), resulting in a non-significant tendency towards divergence using $\hat{D}_T$ as the test statistic (Fig. 7.5d). Similarly, Australia and South America are convergent in the abundance rank-weighted mean of PSU inclination (Fig. 6.2f) but distributions of this character within each community are sufficiently dissimilar (Fig. 7.16b) to produce a non-significant tendency towards divergence (Fig. 7.5f).

Although it was expected that comparison of texture distributions might reveal convergence between communities with different texture means (Fig. 7.1c), there were relatively few tests for which departure from the null model in the direction of divergence using $\bar{D}_T$ as the

test statistic was associated with convergence using $\hat{\Delta}_T$. Most such tests involved heavy weighting by species abundance. For example, Argentinian sites SA1 Quetrihué and SA2 Gutierrez differ in the square root of biomass-weighted mean of PSU specific weight, resulting in a non-significant tendency towards divergence using the test statistic $\bar{D}_T$ to compare the communities (Fig. 6.11). Square root of biomass-weighted distributions of the same character are, however, relatively similar (Fig. 7.16c), resulting in significant convergence using $\hat{\Delta}_T$ (Fig. 7.14).

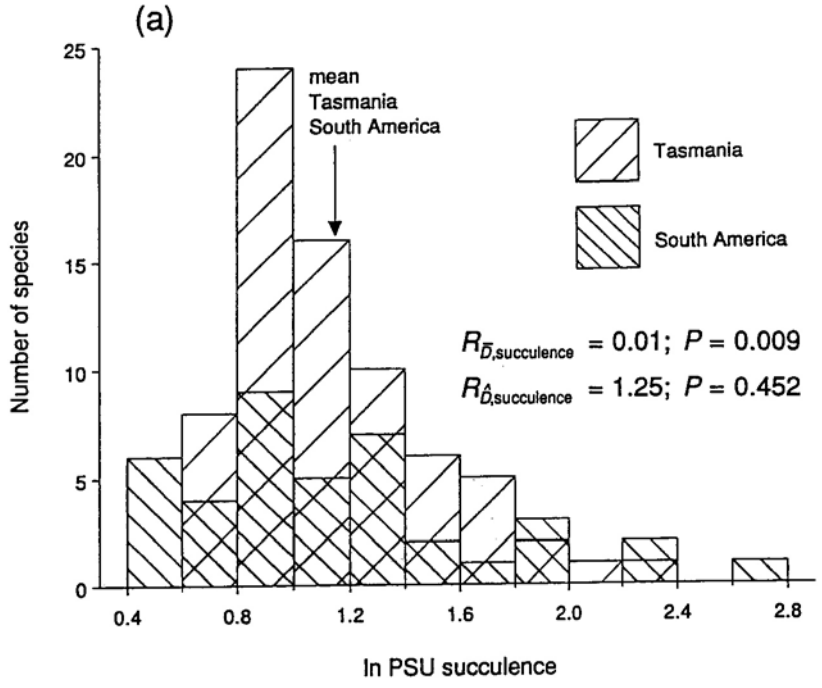



**Fig. 7.16** Frequency histograms of community texture distributions for communities showing departure from the null model in opposite directions depending on whether texture means or distributions are compared. **(a)** Tasmania (T) and South America (S), convergent in texture means of PSU succulence (no abundance weighting); non-significantly divergent in texture distributions. **(b)** Australia (A) and South America, convergent in texture means of PSU inclination (weighting by abundance rank); non-significantly divergent in texture distributions. **(c)** SA1 Quetrihué and SA2 Gutierrez, non-significantly divergent in texture means of PSU specific weight (weighting by square root of photosynthetic biomass); convergent in texture distributions. Relative deviances of texture means ($R_{\bar{D},T}$) and distributions ($R_{\hat{\Delta},T}$) and significance levels for departure from the null model (*P* for smaller tail) are shown on the figure.

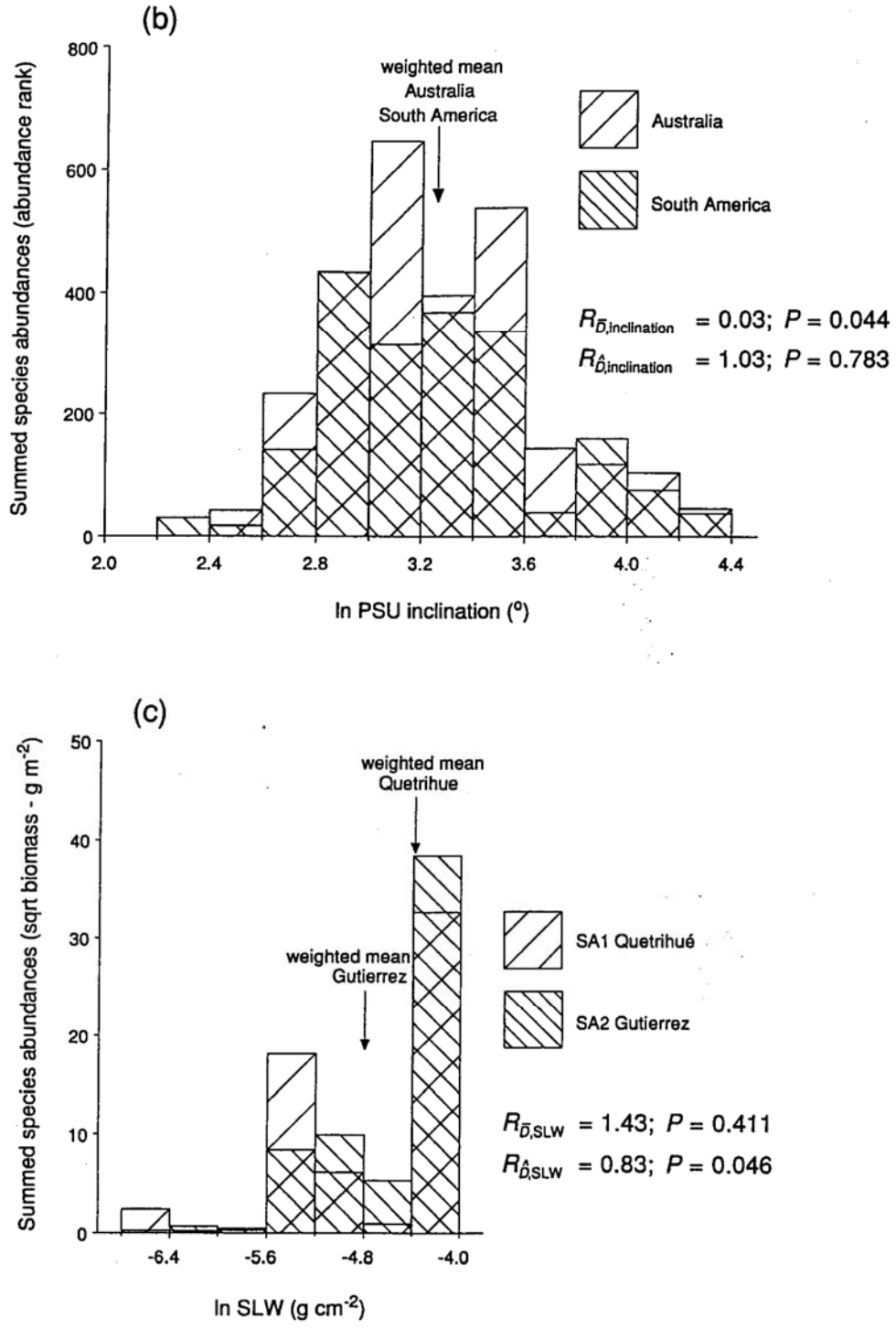



**Fig. 7.16** (continued)

## 7.4 Discussion

COMMUNITY-LEVEL CONVERGENCE AND DIVERGENCE

Significant convergence in the within-community distributions of some texture variates was found in a number of community comparisons (Figs. 7.5-7.15). Some variates were convergent when all species were weighted equally in the texture distributions. More commonly, however, the effect was significant only when species character values were weighted by a measure of abundance. Overall, however, a far higher incidence of divergence was detected, suggesting that environmental or historical differences between communities had led to overall differences in the characters of their component species.

Whereas divergence was significant over all comparisons in the majority of variates, convergence was significant only for PSU thickness, when the number of tests carried out for each variate/weighting factor combination was taken into account. Species height, which was significantly convergent overall at one weighting level for comparisons of community texture means (Chapter 6; Table 6.2) was not found to be significantly convergent overall in the present chapter, where texture distributions were compared.

It was anticipated earlier (Sections 3.3, 6.4) that convergence might tend to be concentrated among communities well-matched in climate and soil parameters, whereas divergence might be more common among communities with dissimilar macroenvironments. In fact, there was only limited evidence to support this proposition. Landmass-scale communities Tasmania and New Zealand, which were the best matched pair, in terms of their environments, of the four landmasses sampled, were convergent in two variates (Fig. 7.5c), and showed less divergence than other pairs of landmasses. On the other hand, southern and central New Zealand, which were found to be among the most similar regional scale communities (Chapter 3) showed a substantial amount of divergence and no convergence (Fig. 7.8b). Well-matched individual sites from different landmasses were found to be convergent in a slightly larger number of tests than in Chapter 6 (Fig. 7.15), but the overall pattern was similar: of little significant convergence, and divergence in some texture variates. Generally these results suggest that factors other than the climate and soil parameters by which study sites were characterised may distinguish them and lead to differences in community texture.

Generally the results, and the conclusions drawn from them, are similar to those of Chapter 6, where the comparisons were of one parameter of the community texture distribution — the mean — rather than of the distributions themselves. The overall correspondence between the results obtained in the present chapter and the previous one (Table 7.3) demonstrates that the mean is useful as a general summary statistic for community texture. However, differences in the results of some comparisons using the two approaches highlight the danger of misleading results in individual tests when only the mean of texture is considered. In some cases, departure from the null model was in opposite directions depending on which test statistic (the deviance of

means, or the deviance of distributions) was used (Fig. 7.16). By responding to differences in both the shapes of texture distributions and their means, the deviance of texture distributions, $\hat{D}_T$, used in this chapter, represents both a more conservative and more powerful index of community dissimilarity in texture.

PREVIOUS COMPARISONS OF COMMUNITY TEXTURE DISTRIBUTIONS

The notion of comparing communities in terms of frequency distributions of species morphology or growth form is not new. Numerous comparative studies have characterised communities by the relative representation of species in different growth form or life form classes (Raunkiaer 1934; Eijsink *et al.* 1978; Campbell & Werger 1988; Shmida & Werger 1992; Cowling *et al.* 1994) or classes of other texture parameters, such as leaf size or form, or reproductive traits (Raunkiaer 1934; Cody & Mooney 1978; Werger & Ellenbroek 1978; Lausi *et al.* 1989; Bongers & Popma 1990; Cowling & Witkowski 1994; Montenegro & Ginocchio 1995). Class membership may be determined qualitatively (Campbell & Werger 1988; Shmida & Werger 1992) or by quantitive measurements (Lausi *et al.* 1989; Bongers & Popma 1990), but only rarely have distributions from different communities been compared using objective numerical techniques, or conclusions drawn on the basis of statistical inference tests, such as the $\chi^2$ test of Cowling & Witkowsky (1994).

The approach of studies such as these is similar to that adopted in the present chapter to compare texture distributions of different *Nothofagus*-dominated communities. However, the rank-scaled texture plots, and the test statistic $\hat{D}_T$ used to compare them, improve on previous methods in three principal ways. Firstly, expressing texture as a plot of the texture `contributions' of all species, rather than as relative frequency histograms (e.g. Eijsink *et al.* 1978) or equivalent (e.g. Cowling *et al.* 1994), avoids the inevitable loss of information that results when species are classified into groups (the histogram bars). Secondly, previous studies have invariably used only species number as the distributional density parameter. To produce rank-scaled texture plots, species values in the present study were either unweighted (as in previous studies) or weighted by one of three measures of species abundance, in separate tests. The potentially greater influence of more abundant species on community structure was thus taken into account. Finally, by using an index, $\hat{D}_T$, that measures dissimilarity in texture distributions directly, the degree of matching between communities could be compared with expectation under an explicit null model, providing a rigorous test both for convergence — due to the combined effects of similar abiotic conditions and the operation of biotic assembly rules — or divergence, due to functional adaptation to different environments.

The test for convergence in community texture distributions, developed in this chapter, is similar in principle to tests seeking species-for-species matching, used by Ricklefs & Travis

(1980) and later by Wiens (1989, 1991b). Ricklefs & Travis (*op. cit.*) mapped bird species from disjunct mediterranean-climate regions into multivariate morphological character space and tested the hypothesis that nearest neighbours in the space would be species from different regions. The basis for the hypothesis was that similar environments, in conjunction with the operation of similar assembly rules, that might be expected to restrict the co-occurrence of species with matching morphology, would lead to similar distributions of morphological variates in each region. The hypothesis was unable to be supported statistically ($\chi^2$ test for a match between the locations of species from different communities in morphological space). As pointed out by Schluter (1990), this approach is dependent on the assumption of a one-to-one correspondence between niches of the communities (regions) being compared: significance is unlikely to be attainable where the degree of species packing, i.e. species richness, differs in the two communities, even if species characters are overdispersed as an outcome of past or present competition. The test employed here does not depend on matching species richness. All species from each community are spaced equidistantly within a constant interval on the abscissa in the texture distribution plots. A low value for $\hat{D}_T$ thus implies that there is among-community similarity in the proportions of species with particular characters, not their absolute numbers.

## CONCLUSIONS

The results obtained from tests seeking convergence in texture distributions of *Nothofagus*-dominated communities consolidate earlier conclusions drawn from comparisons of texture means. Although there is weak evidence for the operation of assembly rules, producing convergence in some characters between particular communities, the convergence is not significant as a proportion of the number of tests done, except for one character — PSU thickness — when texture is based equally on the characters of all sympatric species.

Divergence, by contrast, is marked and highly significant over all comparisons in all but five of 13 texture variates. This suggests that there are environmental or historical differences between many communities that have resulted in different overall distributions of species characters, potentially obscuring the structuring effects of assembly rules. In the following chapter, it is attempted to correct for the possible effects of environmental differences between communities, in the hope that community structure, if indeed present, may then become apparent.

# 8. Convergence among *Nothofagus*-dominated communities: mean-adjusted texture distributions

## 8.1 Introduction

Tests described in Chapters 6 and 7, comparing community-wide means and distributions of species characters among *Nothofagus*-dominated communities, have produced very limited evidence for convergence between them. However, considerable evidence for 'divergence' — significant dissilarity in texture between communities — has emerged. This divergence has been interpreted as the probable result of environmental (or other, e.g. historical) differences between communities. Where divergence is observed, the operation of species interaction-mediated assembly rules (the hypothetical basis for convergence; Wilson *et al.* 1994) can be neither confirmed nor discounted.

Abiotic and biotic factors would be expected to affect texture distributions in a different ways. Physical factors would determine what combinations of characters are functionally optimal in a given environment, and would also set outer limits to what characters are viable (Woodward 1987). Biotic factors — species interactions — might tend to restrict the co-occurrence of functionally-similar species (primarily as a result of competitive exclusion, and selection pressure to avoid it; Pianka 1975; Taper & Case 1992). This means that, while physical factors would tend to define the underlying distribution from which character values for an assemblage are 'drawn' (by adaptation and environmental filtering; Keddy 1992; Weiher & Keddy 1995a), biotic factors would accentuate the fit of actual assemblages to this expected distribution, by restricting the amount of stochastic variation that is possible. A corollary is that, over a relatively restricted environmental range, the abiotic environment might primarily determine the position of texture distributions along character axes, while the biotic environment — with its associated assembly rules — might control the shapes of the distributions. This means that if assembly rules have a similar or proportionate effect on texture distributions in different environments, it might be possible to correct for the obscuring effects of environmental differences on convergence by comparing only the shapes of texture distributions from different communities, and not their means.

Are the effects of assembly rules on texture distributions likely to be independent of environmental differences? Interspecific competition, leading to competitive exclusion (Gause 1934; Hardin 1960), is often assumed to be the most important class of species interaction defining assembly rules (Diamond 1975; Strong *et al.* 1984). Some have suggested that limits to

coexistence under competition would be determined by the size ratios of the species involved (Hutchinson 1959; MacArthur 1971; Barbour 1973; May 1978). The ratio 1:1.3 has often been invoked as a critical level of similarity in the body sizes of animals belonging to the same trophic guild (Hutchinson 1959; Ricklefs 1973; Pianka 1978). The ratio is supposed to remain constant across a wide range of animal groups and habitats (see reviews by Simberloff & Boeklen [1981]; MacNally [1988]). Analogous ratios have been suggested for plant phenological characters (Poole & Rathcke 1979; Pleasants 1980; Rabinowitz *et al.* 1981; Fleming & Partridge 1984; Armbruster *et al.* 1994). However, the evidence for constant size or character ratios has been strongly questioned (Simberloff & Boeklen 1981; MacNally 1988).

If the limiting similarity between sympatric species in terms of a particular character does, indeed, conform to a relatively constant ratio, this implies an even spacing of the logarithms of species values along character axes. The same spacing would be expected to apply even in different environments, where the mean (or optimum) character value across all sympatric species might be different. This implies that the shapes of community (or guild) texture distributions might remain relatively constant across environments, although means would be expected to change.

Constant ratios in the values of adjacent sympatric species have not previously been claimed for the morphological and physiological characters examined by the present study. For most characters, however, such a pattern seems possible, at least across the very limited environmental range spanned by the 17 *Nothofagus*-dominated study sites.

In the context of the present study, it therefore seems reasonable to erect the following hypothesis: assembly rules producing overdispersion of species characters in different communities will lead to texture distributions that are more similar in shape among communities than expected on the basis of random migration, even if environmental differences lead to a different mean. A pattern consistent with this hypothesis is illustrated in Fig. 8.1a: although Communities 1 and 2 differ in the mean character value among species, which would cause them to be found divergent using the tests of Chapters 6 and 7, similar assembly rules apply in both communities, resulting in distributions that are displaced along the abscissa, but are similar in shape. Other patterns, not supporting the above hypothesis, are also illustrated: in Fig. 8.1b, the five leftmost histogram bars match between Communities 1 and 2, but there are no species with characters above the value 9, resulting in truncation of the texture distribution for community 2 above this value. Such a pattern could arise where characters are no longer viable beyond some threshold value, for example, due to trade-offs of resource-harvesting capacity against mechanical constraints (e.g. Givnish 1987). As noted above, it is uncertain whether competition would lead to similar character ratios in different environments. By extension, texture distributions may acquire different shapes in different environments, even if assembly rules do apply: such a possibility is illustrated in Fig. 8.1c.

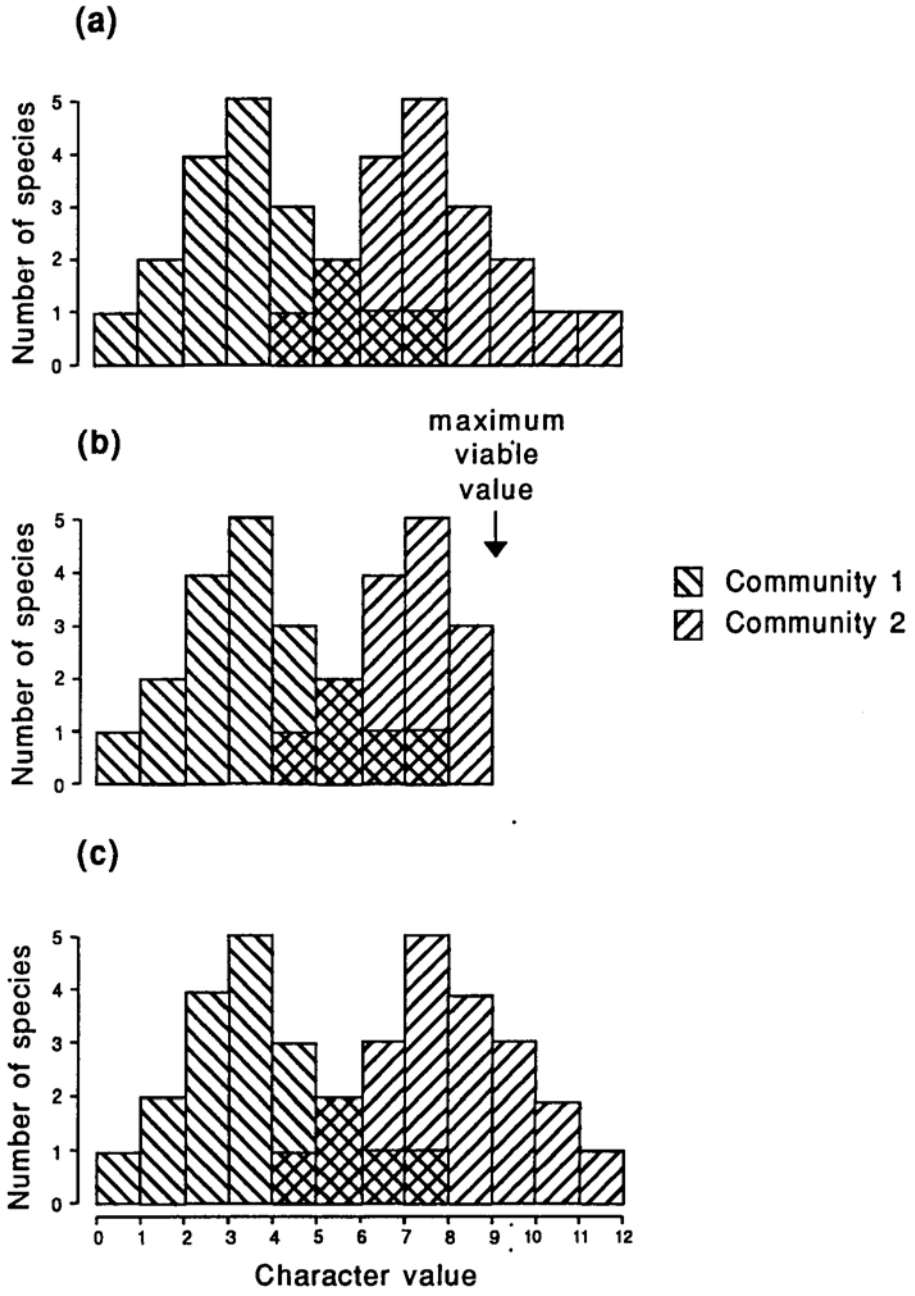



**Fig. 8.1** Possible effects of a difference in the environment (and, therefore, in community texture means) on within-community distributions of a functional species character. **(a)** Distributions in Communities 1 and 2 have the same shape (i.e. relative representation of species in character value classes), e.g. because assembly rules operate in a similar way in different environments. **(b)** Distributions are matched in shape up to a threshold value (≤9) above which the character is no longer viable. **(c)** Distributions have a different shape, e.g. because different environments cause assembly rules to work in a different way.

In the present chapter, a method is developed that may correct for environmental differences between communities, allowing convergence in their texture distributions to be detected, even if there are systematic differences in absolute species character values. The method is based on the null model developed in Chapter 6, which simulates community assembly in the absence of restrictions on the co-occurrence of functionally-similar species. The test statistic used to quantify community dissimarity is based on $\hat{D}_T$, developed in Chapter 7, which measures variation in texture distributions among communities. However, instead of responding to differences in both the shape of distributions and their means (as $\hat{D}_T$ does), the index employed in the present chapter corrects for differences in the mean, measuring variation only in the shapes of community texture distributions. A significantly low dissimilarity between communities, signifying convergence in mean-adjusted texture distributions, is taken as evidence for the operation of similar assembly rules in the communities being compared. Significantly high dissimilarity between communities is also sought. Such divergence might arise because of environmental differences between communities. However, as in previous tests (Chapters 5-7) the finding of significant divergence between communities would not constitute sufficient grounds for concluding that assembly rules did *not* operate in producing the community texture observed. This is because it is uncertain in what ways assembly rules might differ in different environments, and so, whether they could indeed produce convergent shapes, of the kind envisaged, between texture distributions in different environments.

## 8.2 Methods

### TEXTURE DATA

Analysis was based on the 12 species characters listed in Section 2.3.5, and on species height, defined in Section 6.2. Field and laboratory methods are described in Chapter 2. Study sites are described and compared in Chapter 3.

### ANALYSIS

To evaluate the hypothesis that communities were more similar in texture than expected in the absence of assembly rules, randomisation tests seeking departure from a null model were performed. The null model was developed in Chapter 6 and also used in Chapter 7. It simulates community assembly in the absence of restrictions on the co-occurrence of species with similar characters. A more comprehensive description of the null model is given in Section 6.2.

#### *Representation of community texture*

Texture was represented, as in Chapter 7, by rank-scaled texture plots of species character values.

In contrast to the approach of Chapter 7, however, all species values within each community were scaled arithmetically such that the community texture mean (with species unweighted by abundance) was the same for each of the communities being compared. This ensured that only relative differences in character values between species within each community, and not overall differences among communities, were taken into account in comparing the texture distributions of different communities.

In some tests, species values were weighted by their abundance in calculating their contribution to texture. This was to take account of the possible influence of species abundances on community structure. As in Chapters 6 and 7, four abundance weighting factors were employed: presence (all species weighted equally), abundance rank, square root of photosynthetic biomass, and photosynthetic biomass.

Species texture contributions $c'_{T,i}$ were calculated according to the formula:

$$c'_{T,i} = \frac{(x_{T,i} + \overline{X}_{T,i} - X_T) \cdot w_i \cdot s}{\sum_{j=1}^{s} w_j}$$

where $s$ = number of species or entities in community;
$x_{T,i}$ = transformed value of character $T$ for species or entity[1] $i$;
$X_T$ = the mean of the $x_{T,i}$'s for all $s$ species in the community;
$\overline{X}_T$ = the mean of the $X_T$'s for all communities being compared;
$w_i$ = weighting factor (presence [=1], abundance rank, square root of photosynthetic biomass or photosynthetic biomass) for species or entity $i$.

Species character values were transformed as described in Sections 2.3.5 (Table 2.1) and 6.2.

Texture was expressed as the mean-adjusted rank-scaled texture plot, the curve obtained by plotting species texture contributions $c'_{T,i}$ against species rank in terms of these contributions, scaled from 0 to 1 on the abscissa, and linking adjacent points with a straight line (see Fig. 8.2). Abscissa coordinates were given by:

$$\frac{r'_i - 1}{s - 1}$$

where $r'_i$ = rank of species (or entity) $i$ in terms of $c'_{T,i}$ (1=highest; $s$=lowest).

[1] 'Entities:' age or size classes of the same taxonomic species.

*Comparison of observed with null communities*

Dissimilarity in texture between communities was quantified as the deviance of mean-adjusted texture distributions, $\hat{D}'_T$. For two communities this was defined as the area between mean-adjusted rank-scaled texture plots for the two communities, as illustrated in Fig. 8.2. When three or more communities were compared, $\hat{D}'_T$ was the mean area between texture plots for all possible pairs of the communities. $\hat{D}'_T$ differs from $\hat{D}_T$, the test statistic employed in Chapter 7, in that species contributions to texture are adjusted to give a constant unweighted texture mean in all the communities being compared. This means that $\hat{D}'_T$ is an index of dissimilarity in the shape of texture distributions between communities; unlike $\hat{D}_T$, it does not respond to differences in texture means.

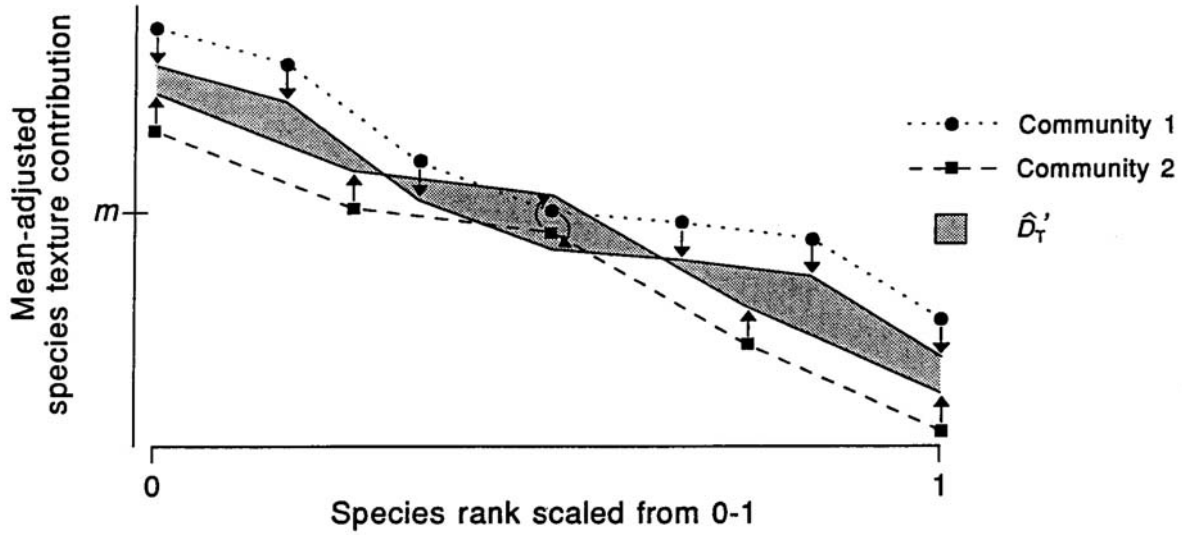



**Fig. 8.2** Example demonstrating the calculation of the deviance of mean-adjusted texture distributions, $\hat{D}'_T$, between two communities. For two communities, $\hat{D}'_T$ is the area between mean-adjusted rank-scaled texture plots for each community. These plots are produced by plotting species texture contributions in terms of a particular character and abundance weighting factor against species rank in terms of texture contribution, scaled from 0 to 1 on the abscissa. Species texture contributions are based on species character values and abundance, and are scaled arithmetically so that the mean character value (*m*, shown on the figure) is the same in each community. Arrows on the figure illustrate adjustment of species texture contributions to give the same overall mean (equal species weighting case; see text for full explanation).

For each test, 2000 sets of artificial communities were generated by randomising observed species values subject to the rules incorporated in the null model (Section 6.2). $\hat{\Delta}'_T$ was calculated for each randomised data set as well as for the observed data. The strength of departure from null model expectation was evaluated as the relative deviance, $R_{\hat{D}',T}$ :

$$R_{\hat{D}',T} = \frac{\hat{D}'_T \text{ (observed)}}{\sum \hat{D}'_T \text{ (null)} / 2000}$$

A value for $R_{\hat{D}',T}$ less than 1 (null model expectation) may be interpreted as a tendency towards convergence among the communities being compared. A value greater than 1 represents a tendency towards divergence.

The significance *P* of departure from null model expectation was given by the proportion of null model data sets for which $\hat{\Delta}'_T$ was at least as small (if $R_{\hat{D}',T}<1$) or at least as large (if $R_{\hat{D}',T}>1$) as for the observed data, multiplied by 2 to effect a two-tailed test. Departure from the null model was deemed significant if *P* was found to be below 0.05.

*Comparisons performed*

Comparisons of 31 sets of communities at the landmass, regional and local scales were performed using the analyses described above. Binomial tests for overall significance among 16 independent comparisons were performed. The hierarchy of comparisons is described in Section 6.2 and depicted in Fig. 6.1.

To confirm that the new test statistic $\hat{\Delta}'_T$ did not cause any bias towards rejection of the null hypothesis, each species and entity from each community was assigned a value at random from the uniform distribution in the range 0 to 1. 'Convergence' or 'divergence' in this random variate was sought for each community comparison, and a binomial test applied to confirm that the null hypothesis was not rejected in significantly more than the 5% of tests expected by chance.

## 8.3 Results

VALIDITY OF THE NULL MODEL

Among the 31 community combinations, communities were occasionally found to be significantly more or less similar in the random texture variate than expected under the null model: once with species unweighted by their abundance, twice with weighting by abundance rank and once with weighting by photosynthetic biomass (Table 8.1). The probabilites of obtaining these incidences by chance alone (binomial test) are 0.543 (one significant test) and 0.181 (two significant tests). There is therefore no evidence that comparison of mean-adjusted texture distributions with the index $\hat{D}'_T$ produces an intrinsic tendency to detect convergence or divergence relative to the null model.

**Table 8.1** The number out of 31 among-community comparisons in which mean-adjusted community texture distributions calculated from random data were found to be significantly convergent or divergent (community dissimilarity expressed by $\hat{D}'_T$: see text; $P<0.05$) with each of four abundance weighting methods.

| Weighting method | Convergence | Divergence |
|---|---|---|
| Presence | 1 | 0 |
| Abundance rank | 2 | 0 |
| Sqrt biomass | 0 | 0 |
| Biomass | 0 | 1 |

TEST STATISTIC BEHAVIOUR

The performance of $\hat{D}'_T$ in quantifying the correspondence between communities in terms of the shapes of their texture distributions is illustrated in Figs. 8.3 and 8.4. In Chapter 7, Landmass-scale communities New Zealand and Tasmania were found to be significantly divergent in PSU phosphorus content (species unweighted by their abundances) using $\hat{D}_T$ as an index of community dissimilarity. The reason for this appears to be a difference between the communities in the texture means for this character (Fig. 8.3a). When the mean is disregarded, and $\hat{D}'_T$ is used to compare only the shapes of the texture distributions for PSU phosphorus, the communities appear quite similar, significantly so compared with expection under the null model.

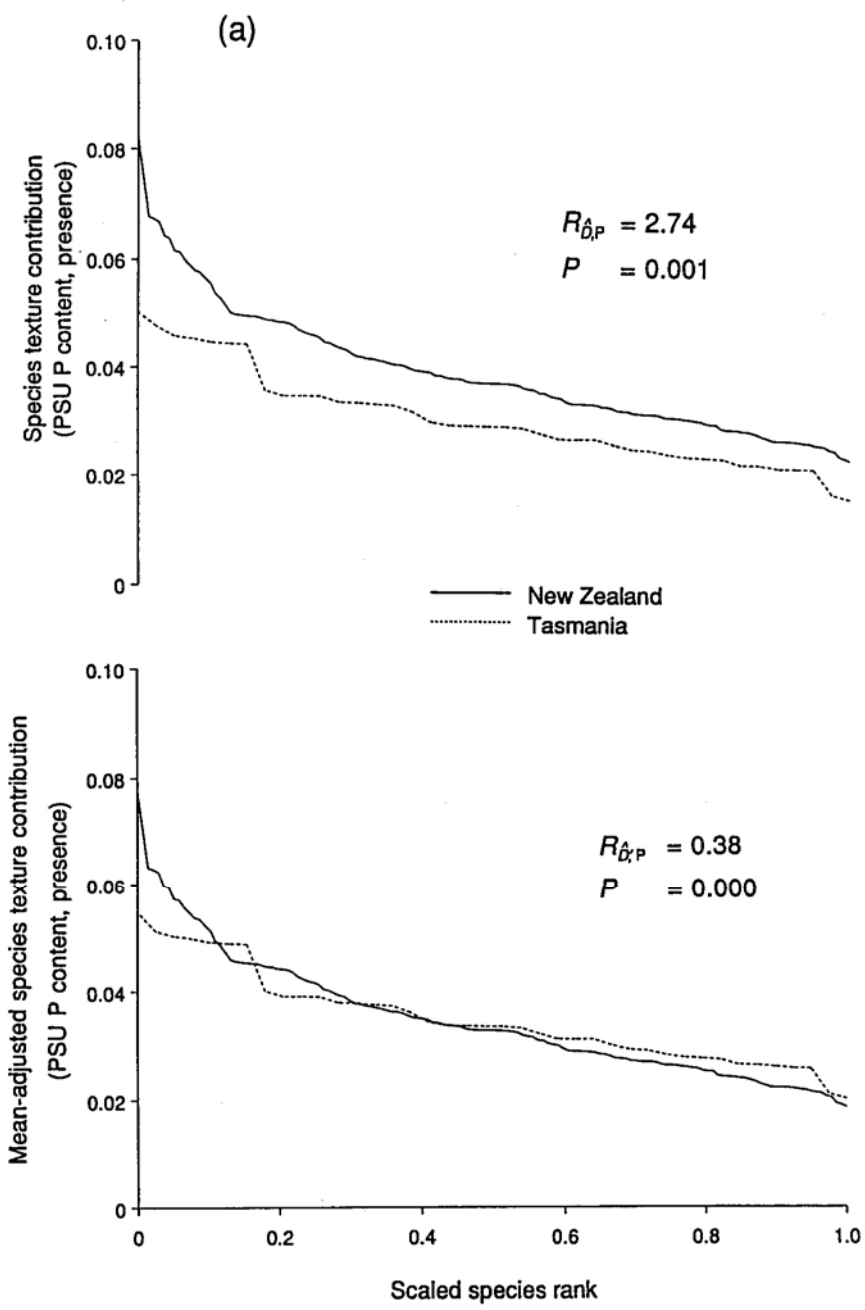



**Fig. 8.3** Rank-scaled texture plots (Fig. 7.2) and mean-adjusted rank-scaled texture plots (Fig. 8.2) for *Nothofagus*-dominated communities illustrating departure from null expectation in opposite directions using indices $\hat{D}_T$ and $\hat{D}'_T$ to compare community texture. **(a)** Tasmania (T) and New Zealand (Z), divergent in PSU thickness (species weighted equally) using $\hat{D}_T$ ; convergent using $\hat{D}'_T$; **(b)** T1 Balfour and A2 Cascades, divergent in PSU chlorophyll *a/b* (weighting by abundance rank) using $\hat{D}_T$ ; convergent using $\hat{D}'_T$. Relative deviance ($R_{\hat{D},T}$ , $R_{\hat{D}',T}$) and significance (*P*) values for convergence or divergence are shown on the figure.

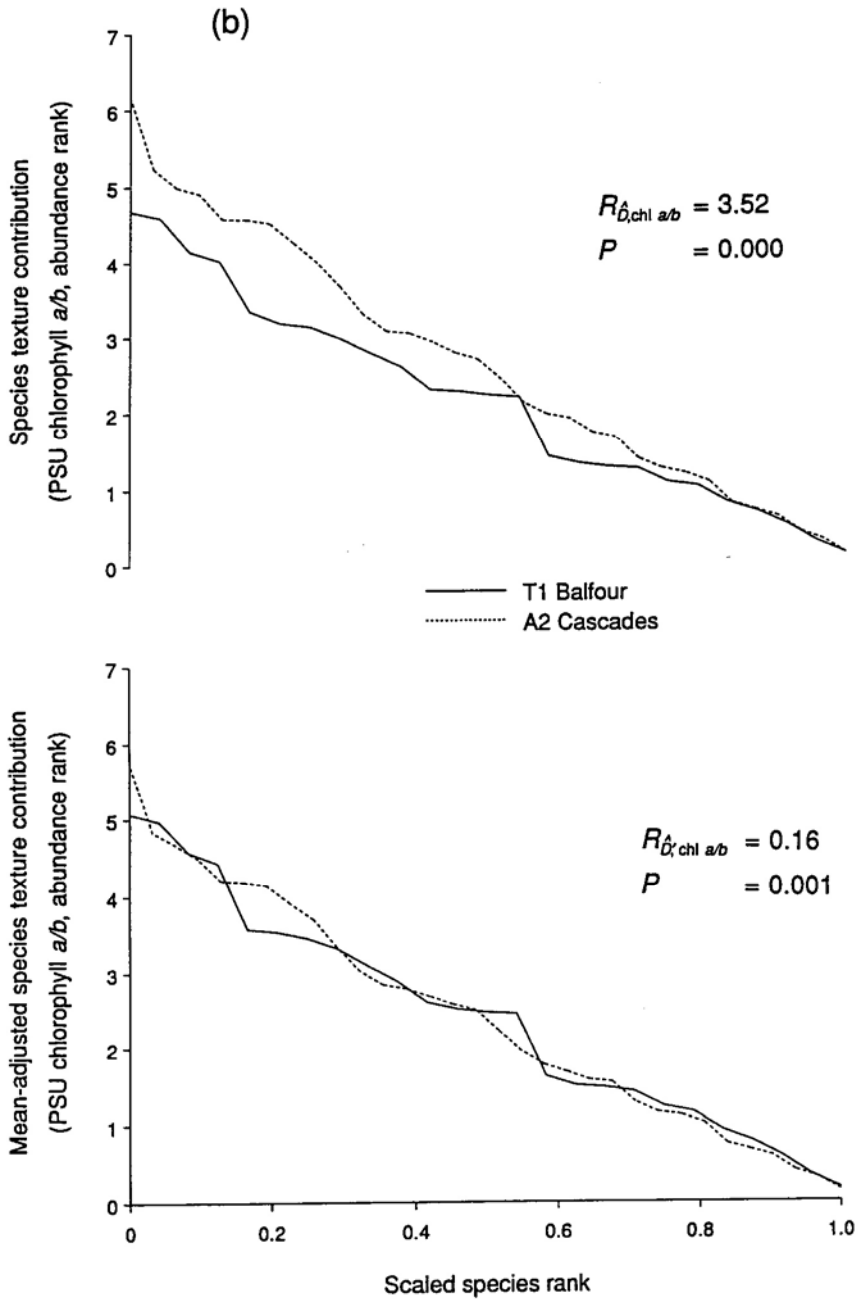



**Fig. 8.3** (continued)

Tasmanian site T1 Balfour and Australian site A2 Cascades are significantly divergent in PSU chlorophyll *a/b* when species values are weighted by abundance rank to calculate texture, and when $\hat{D}_T$ is used to compare community texture distributions (Fig. 8.3b). Using $\hat{D}'_T$ to compare mean-adjusted distributions, however, the sites are significantly convergent in chlorophyll *a/b*.

Where texture distributions differ significantly in their shapes in different communities, this may be because assembly rules are absent or weak. No convergence would then be detected by the tests used either in this chapter or in the previous one, i.e. whether or not texture means are

ignored. For example, in Chapter 7, Australia and South America were found to be significantly divergent in the distributions of species values for support fraction (Fig. 8.4a). The texture distributions are quite dissimilar in shape, though not in their means, a lower proportion of species having extremely high or low support fraction in South American than Australian *Nothofagus*-dominated communities. Consequently, significant divergence was detected once again when mean-adjusted distributions were compared using $\hat{D}'_T$.

Australian sites A1 Lumeah and A2 Cascades are significantly divergent in their distributions of PSU shape, when species are weighted by their photosynthetic biomass, and texture dissimilarity is quantified using $\hat{D}_T$ (Fig. 8.4b). Scaling of species values to give the same mean for PSU shape in the two communities does not produce a close fit between their distributions of PSU shape, and the communities remain divergent, though non-significantly so.

## PATTERNS AMONG COMMUNITIES

### *Landmass scale*

Among the four landmass-scale communities Tasmania, Australia, New Zealand and South America there is significant convergence in PSU area, with species unweighted by abundance, and in PSU thickness, succulence, specific weight and support fraction when species are weighted by some measure of abundance to determine texture contributions (Fig. 8.5a). Broadly, these results are similar to those obtained in Chapter 7, comparing non-adjusted texture distributions (Fig. 7.5a), although PSU area was found to be significantly divergent with species unweighted in the earlier analysis. In contrast to the results of Chapter 7, however, there is relatively little significant divergence when mean-adjusted texture distributions from the four landmasses are compared.

Comparing individual pairs of landmasses (Figs. 8.5b-g), there is a marked overall tendency towards convergence in many texture variates, and little significant divergence. Tasmania and Australia show the highest incidence of convergence, which is significant for PSU area, lobation, phosphorus content, total chlorophyll, chlorophyll *a/b* and species height with species weighted by presence or abundance rank (Fig. 8.5b). Tasmania and New Zealand, which were found to be most similar overall in their environments (Chapter 3) are significantly convergent in five variates at various weighting levels (Fig. 8.5c), but nearly all variates show an overall tendency towards convergence ($R_{\hat{D};T}<1$), although only a minority of tests are significant. PSU total chlorophyll, chlorophyll *a/b* and phosphorus content are significantly convergent at low weighting levels for several pairs of landmasses. By contrast, these variates tended to be found significantly or non-significantly divergent, especially at lower abundance weighting levels, when texture means (Chapter 6) or non-adjusted distributions (Chapter 7) were compared (Figs. 7.5b-g, 6.2b-g).

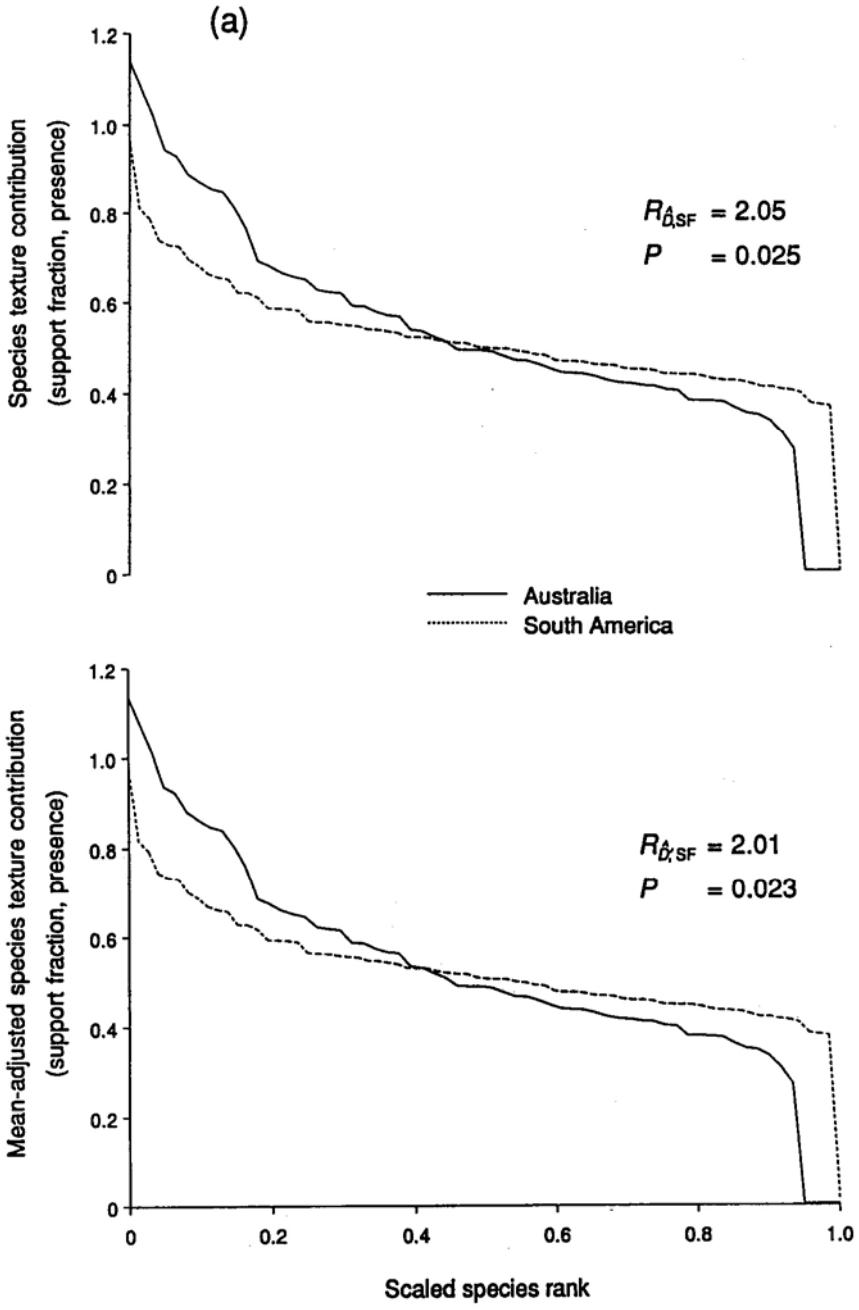



**Fig. 8.4** Rank-scaled texture plots and mean-adjusted rank-scaled texture plots for *Nothofagus*-dominated communities demonstrating divergence using both indices $\hat{D}_T$ and $\hat{D}'_T$ to compare community texture. **(a)** Australia (A) and South America (S), significant divergence in support fraction (species weighted equally) using $\hat{D}_T$ and $\hat{D}'_T$ ; **(b)** A1 Lumeah and A2 Cascades, significant divergence in PSU shape (weighting by photosynthetic biomass) using $\hat{D}_T$ , non-significant tendency towards divergence ($R_{\hat{D}',T}>1$; $P\geq 0.05$) using $\hat{D}'_T$. Format as for Fig. 8.3.

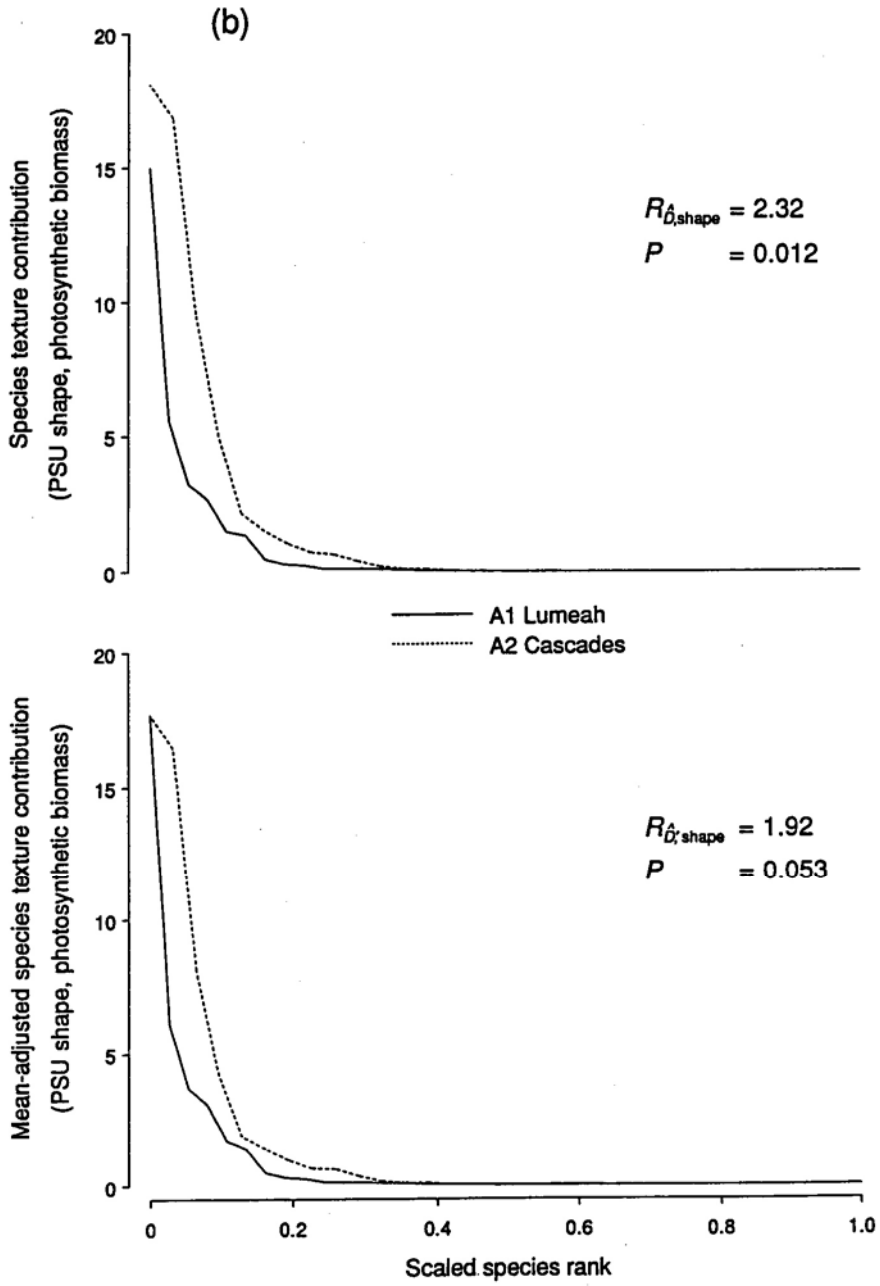



**Fig. 8.4** (continued)

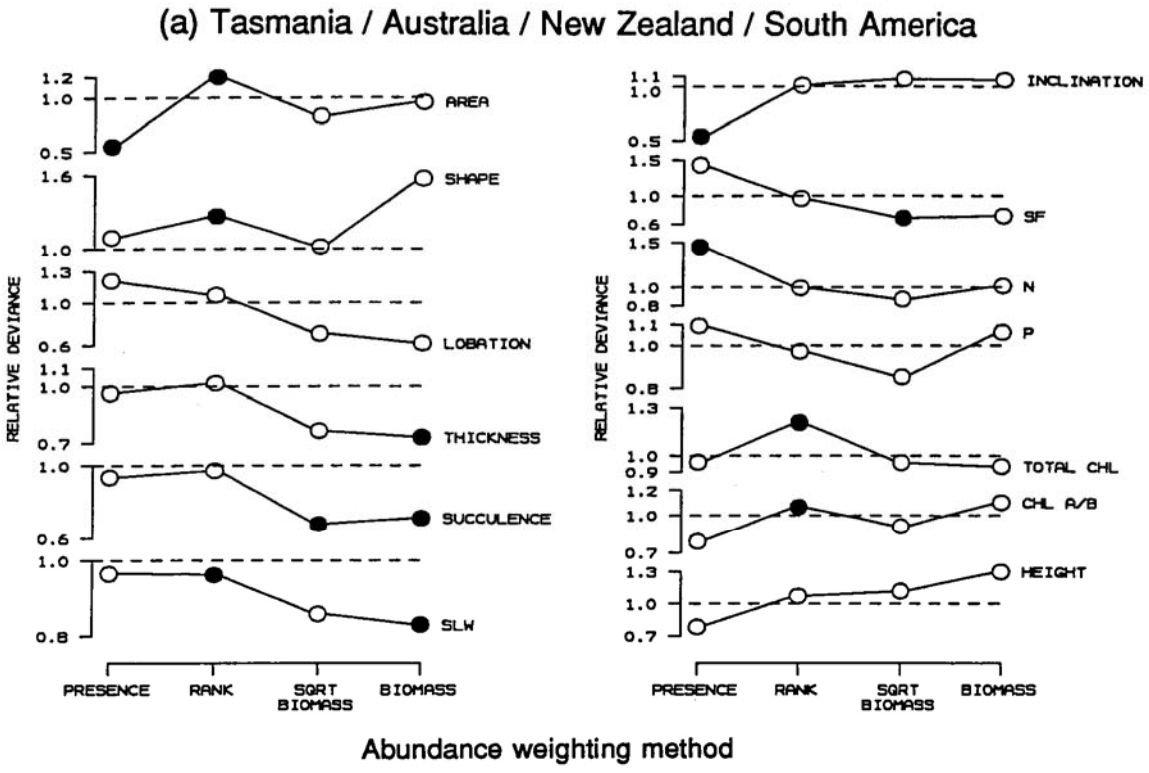



**Fig. 8.5** Null model randomisation tests for convergence or divergence in mean-adjusted texture distributions (see text) between landmass-scale *Nothofagus*-dominated communities Tasmania (T), Australia (A), New Zealand (Z) and South America (S). The relative deviance $R_{\hat{D};T}$ of among-community variation in texture distributions is shown for each of 13 texture variates and four methods of weighting individual species values by abundance in calculations of community texture means. A value of $R_{\hat{D};T}<1$ indicates similarity in texture between communities relative to a null model simulating random community assembly (see text); $R_{\hat{D};T}>1$ indicates dissimilarity relative to the null model. Broken lines signify null model expectation ($R_{\hat{D};T}=1$). Filled symbols correspond to significant departure from the null model (convergence for $R_{\hat{D};T}<1$; divergence for $R_{\hat{D};T}>1$; $P<0.05$). Key to abbreviations: RANK=abundance rank; SQRT BIOMASS=square root of photosynthetic biomass; BIOMASS=photosynthetic biomass (see text for full explanation). Texture variates are based on PSU characters except SF (support fraction) and HEIGHT (species height). Key: SLW=specific weight; N=nitrogen content; P=phosphorus content; TOTAL CHL=total chlorophyll content; CHL A/B=chlorophyll *a/b* ratio (see text for full explanation).

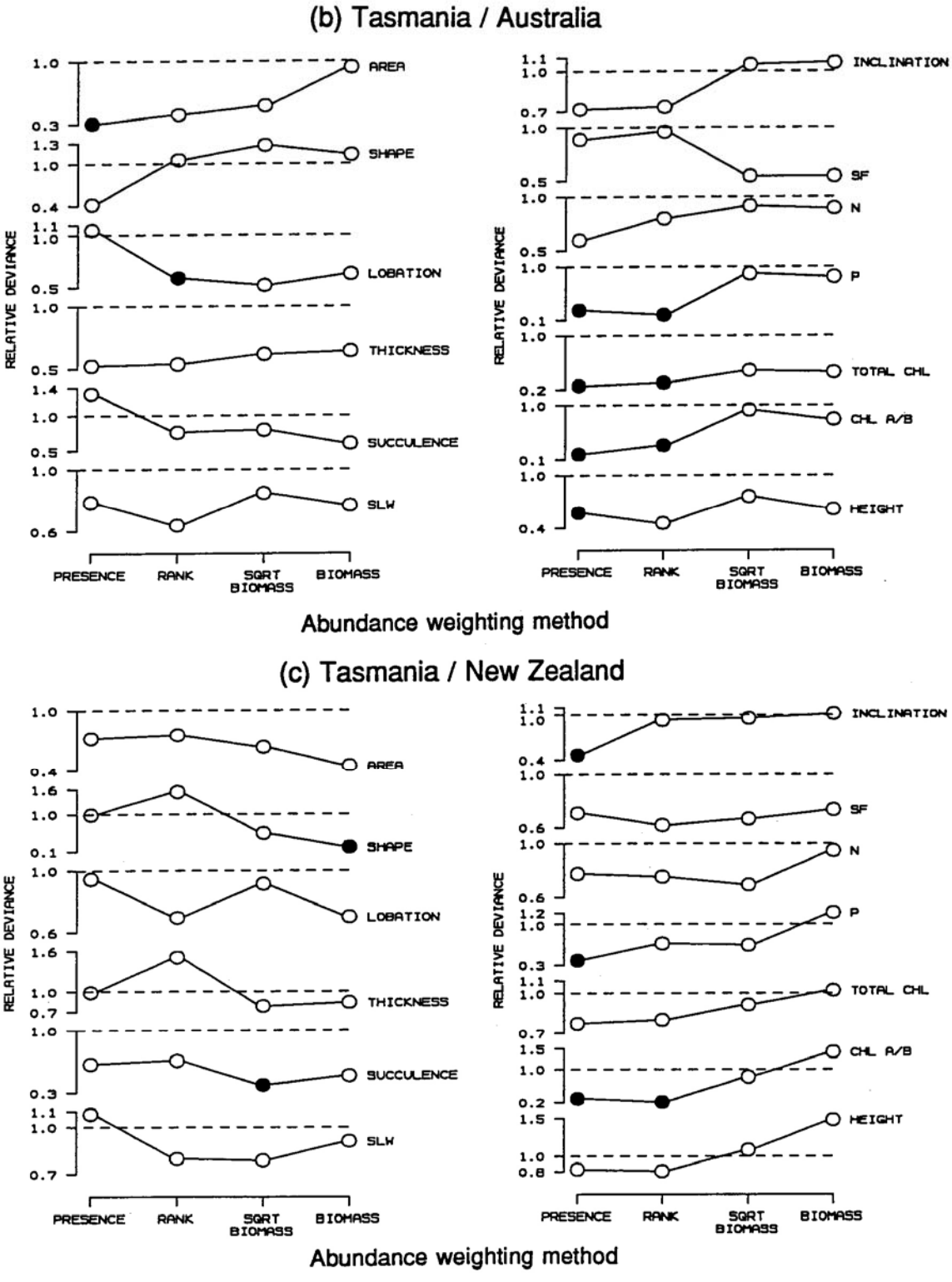



**Fig. 8.5** (continued)

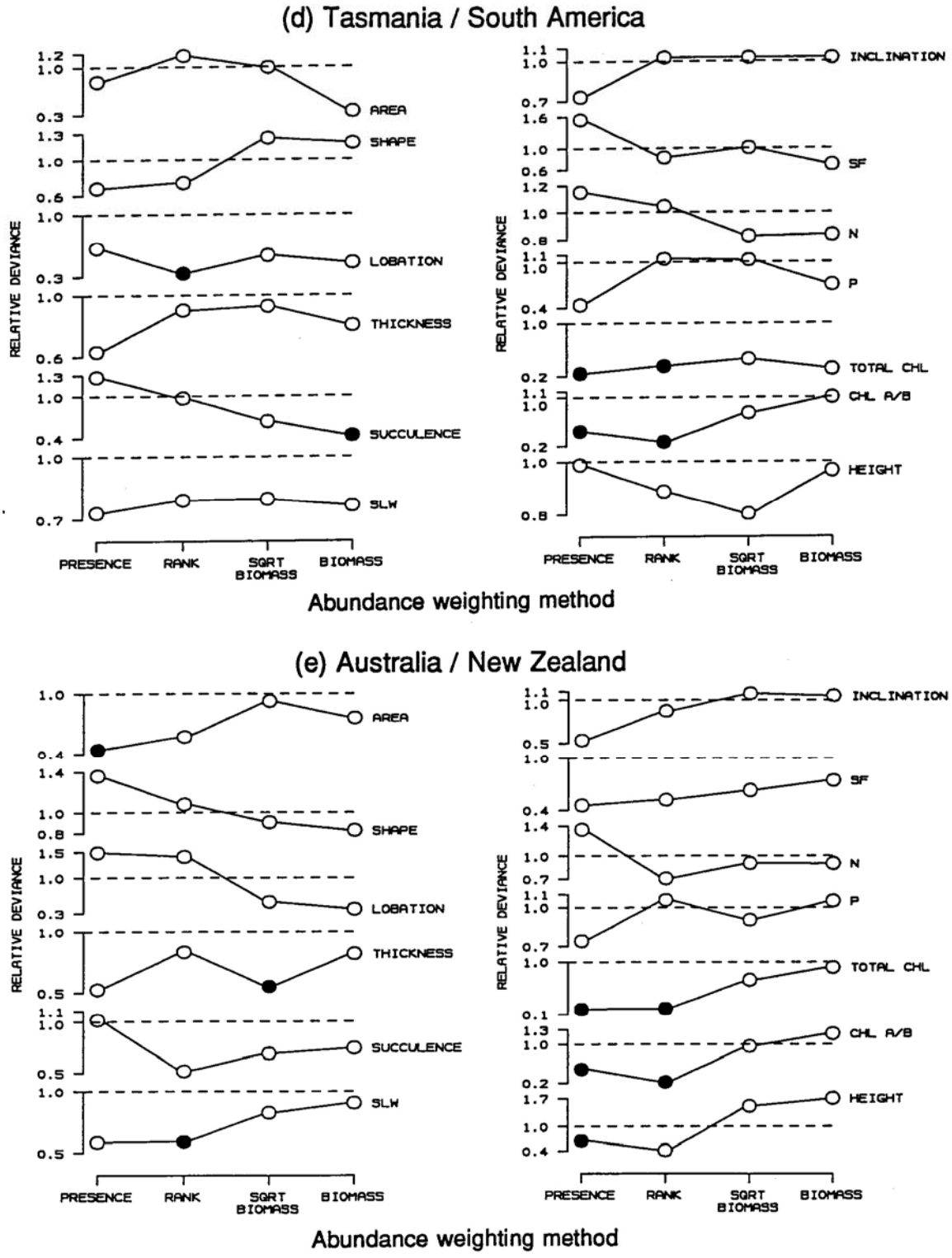



**Fig. 8.5** (continued)

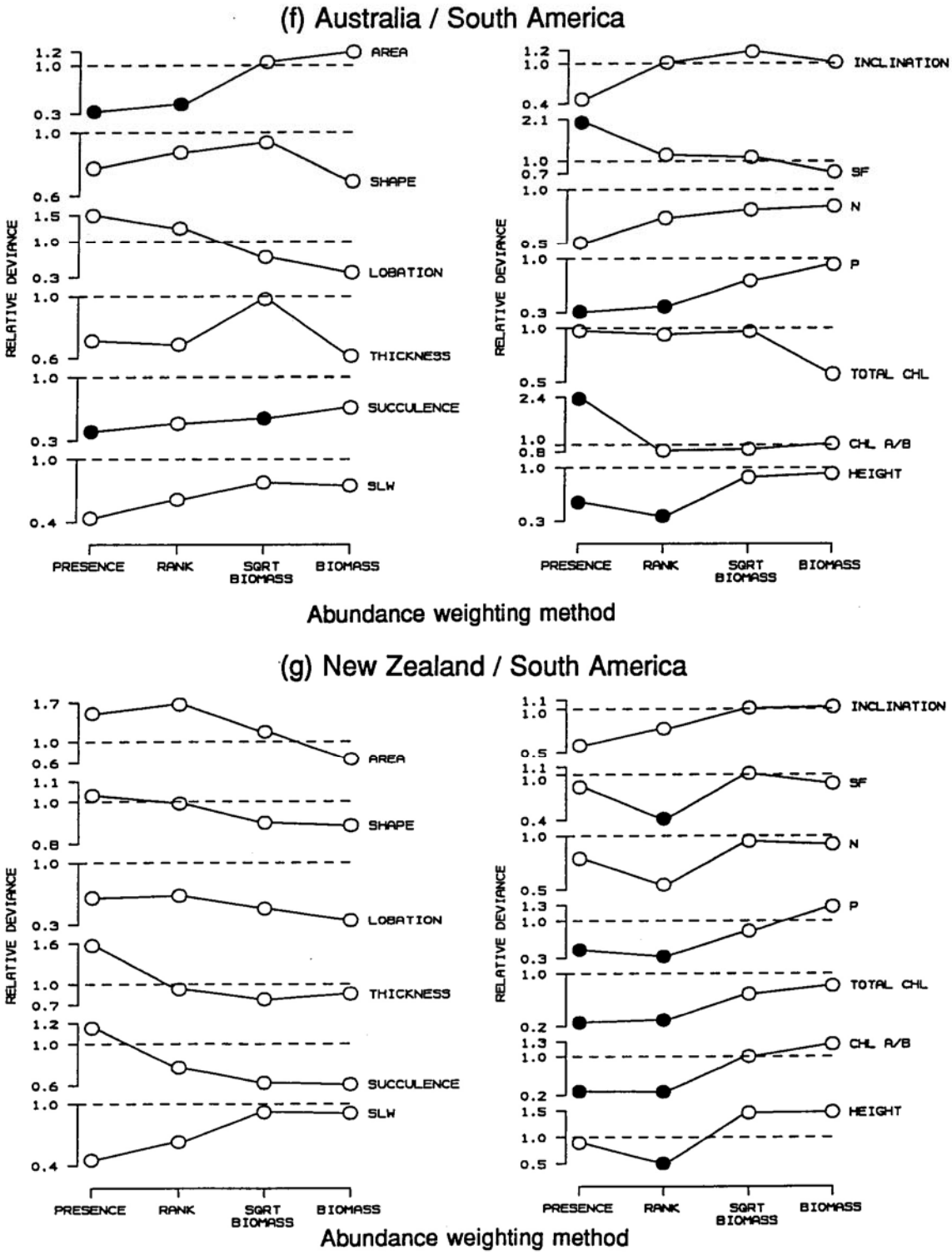



**Fig. 8.5** (continued)

*Regional scale*

Tasmanian communities T1 Balfour, T2 Anne and T3 Mathinna are significantly convergent in PSU lobation (weighting by abundance rank), thickness (presence) and total chlorophyll (presence), while there is divergence in chlorophyll *a/b* with abundance rank as the weighting method (Fig. 8.6a). The patterns are generally similar to those obtained using the test statistic $\hat{\Delta}_T$ in Chapter 7 (Fig. 7.6a). There is similarly little departure from null expectation when individual pairs of communities are compared (Fig. 8.6b-d).

The two communities sampled in Australia, A1 Lumeah and A2 Cascades, are significantly convergent in support fraction, with species weighted equally or by abundance rank, in PSU phosphorus content, at all weighting levels except photosynthetic biomass, and in chlorophyll *a/b*, with species weighted equally (Fig. 8.7). Several variates — PSU area, lobation, thickness, succulence, specific weight, nitrogen content, total chlorophyll and species height — have $R_{\hat{D};T}<1$ at all weighting levels, though this tendency towards convergence is non-significant. There is no significant divergence.

Although *Nothofagus*-dominated communities of the three regions of New Zealand are apparently quite similar in their macroenvironments (Chapter 3), no strong trend towards convergence in mean-adjusted texture distributions is apparent (Fig. 8.8a). PSU specific weight, nitrogen content, phosphorus content and chlorophyll *a/b* ratio are convergent at intermediate weighting levels, while support fraction has $R_{\hat{D};T}<1$ at all weighting levels, significantly so for abundance rank. However, there is divergence in PSU shape, phosphorus content, and chlorophyll *a/b* at various weighting levels; species height is divergent at all levels except presence. Trends are clearer among the individual pairs of communities. Southern (ZS) and central (ZC) New Zealand, considered to be the best-matched environmentally, based on data analysed in Chapter 3, show a tendency towards convergence in all variates in the absence of abundance weighting, and in most variates with weighting by abundance rank (Fig. 8.8b). The convergence is significant for PSU succulence (abundance rank), phosphorus (presence) and total chlorophyll (presence, rank). There is no significant divergence between these communities. Southern and northern (ZN) New Zealand, on the other hand, show no significant convergence, but divergence in five variates (Fig. 8.8c). Central and Northern New Zealand are significantly convergent in PSU specific weight, phosphorus content and support fraction (various weighting levels) and show no significant divergence (Fig. 8.8d). However the trend towards convergence is weaker among variates than for southern and Central New Zealand. The results contrast with those obtained for the New Zealand regions in Chapters 6 and 7, where divergence was marked and significant for many variates and in all comparisons, while relatively little convergence was observed (Figs. 6.5, 7.8).

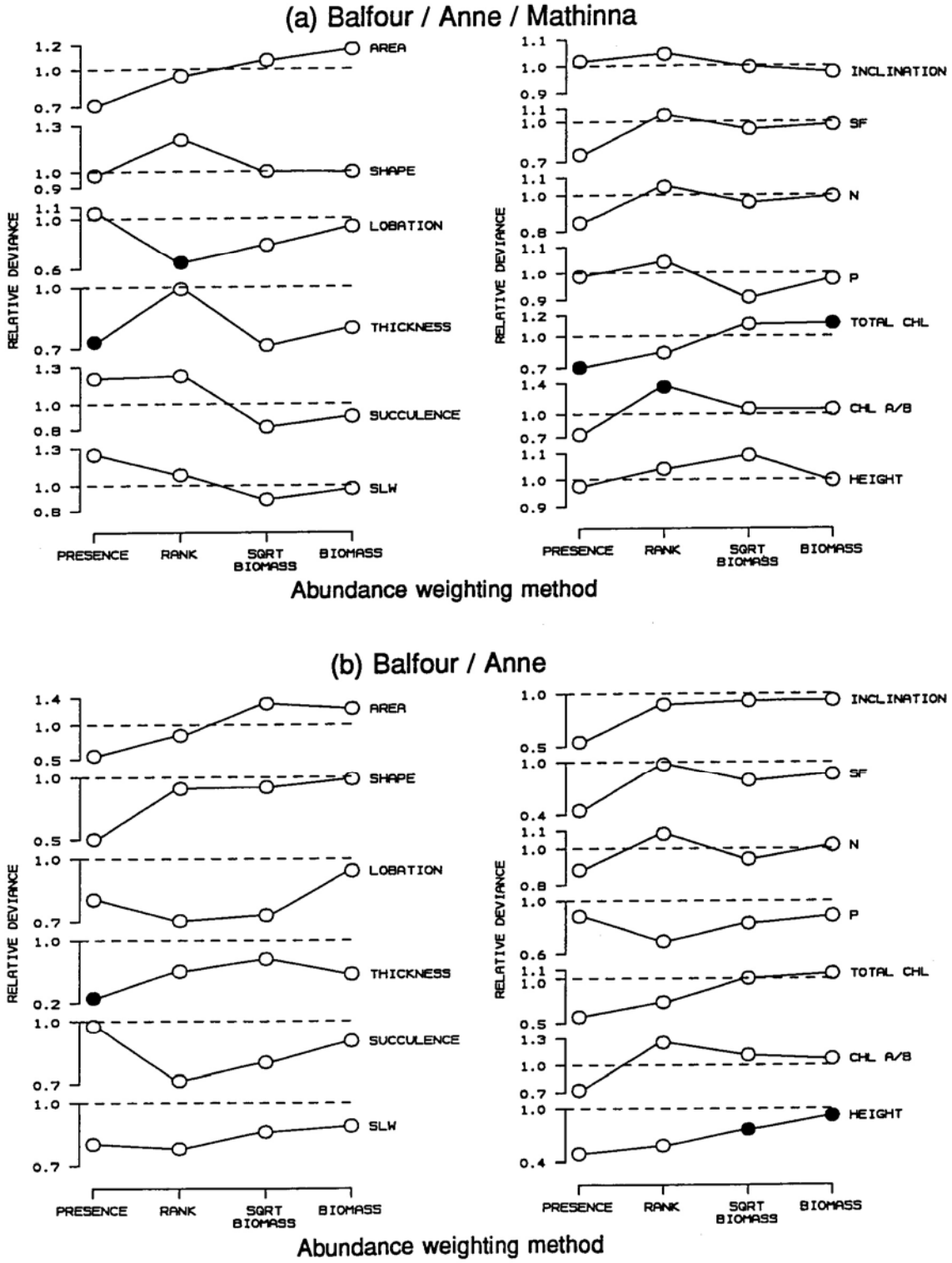
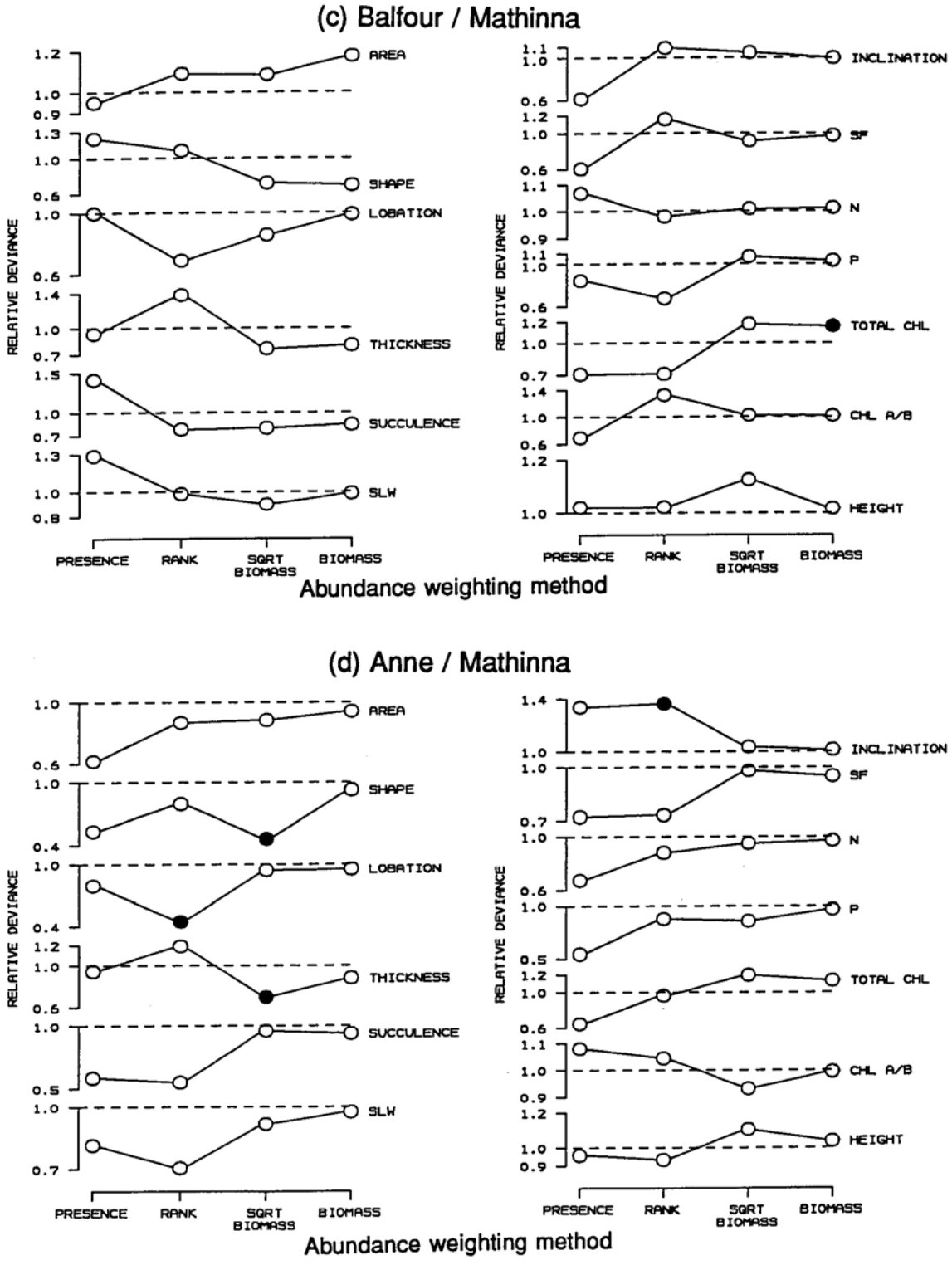



**Fig. 8.6** Null model randomisation tests for convergence or divergence in mean-adjusted texture distributions between regional-scale *Nothofagus*-dominated communities T1 Balfour, T2 Anne and T3 Mathinna. Format as for Fig. 8.5.

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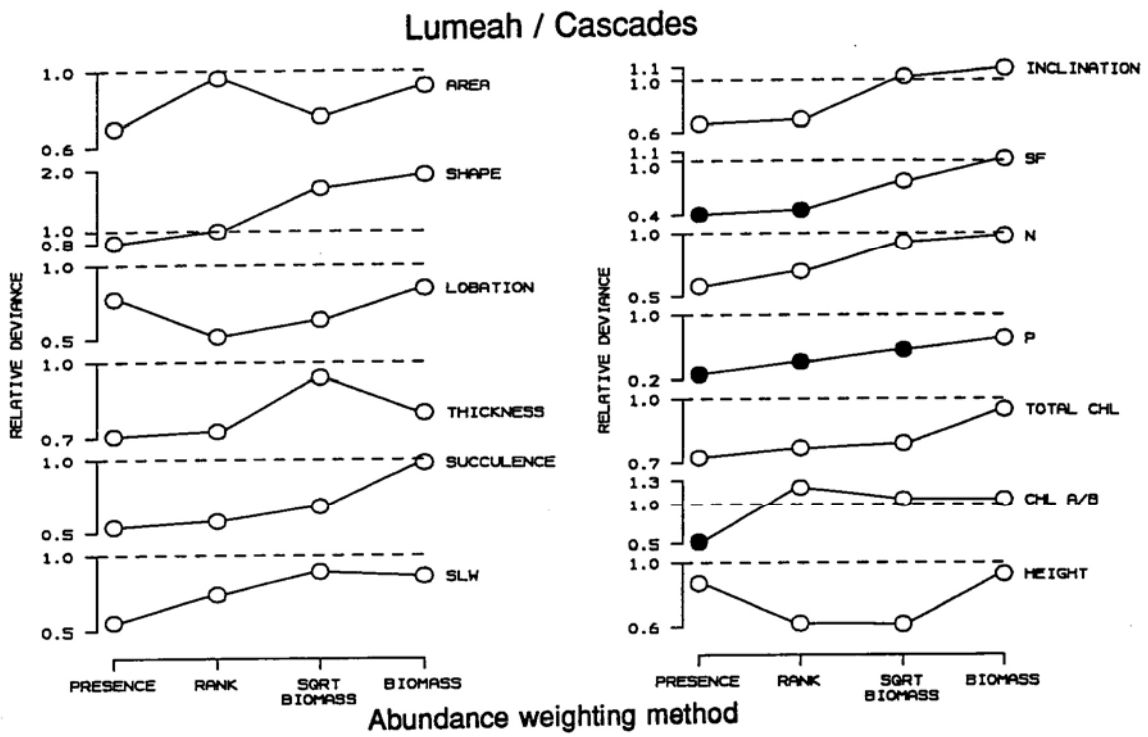



**Fig. 8.7** Null model randomisation tests for convergence or divergence in mean-adjusted texture distributions between regional-scale *Nothofagus*-dominated communities A1 Lumeah and A2 Cascades. Format as for Fig. 8.5.

Chile (SC) and Argentina (SA) are convergent in five variates — PSU succulence, specific weight, nitrogen content, phosphorus content and chlorophyll *a/b* ratio — primarily at lower weighting levels (Fig. 8.9). All variates except PSU thickness show a tendency towards convergence ($R_{\hat{D};T}<1$) when species are unweighted by their abundance. There is no divergence. By contrast, when texture was compared in terms of community means (Chapter 6) and distributions not corrected for differences in their means (Chapter 7), Chile and Argentina showed a marked degree of divergence, and virtually no significant convergence (Figs. 6.6, 7.9).

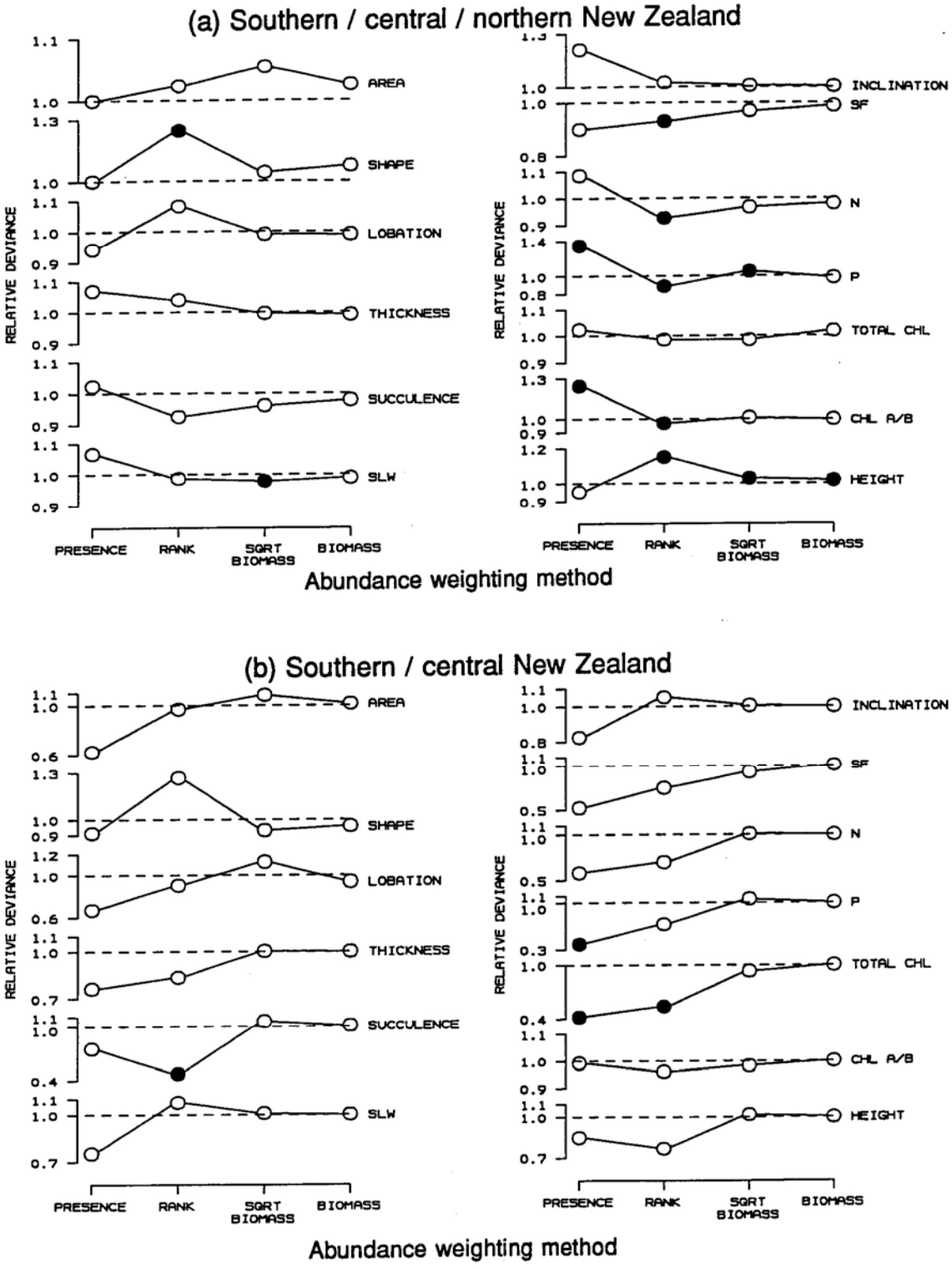



**Fig. 8.8** Null model randomisation tests for convergence or divergence in mean-adjusted texture distributions between regional-scale *Nothofagus*-dominated communities southern (ZS), central (ZC) and northern (ZN) New Zealand. Format as for Fig. 8.5.

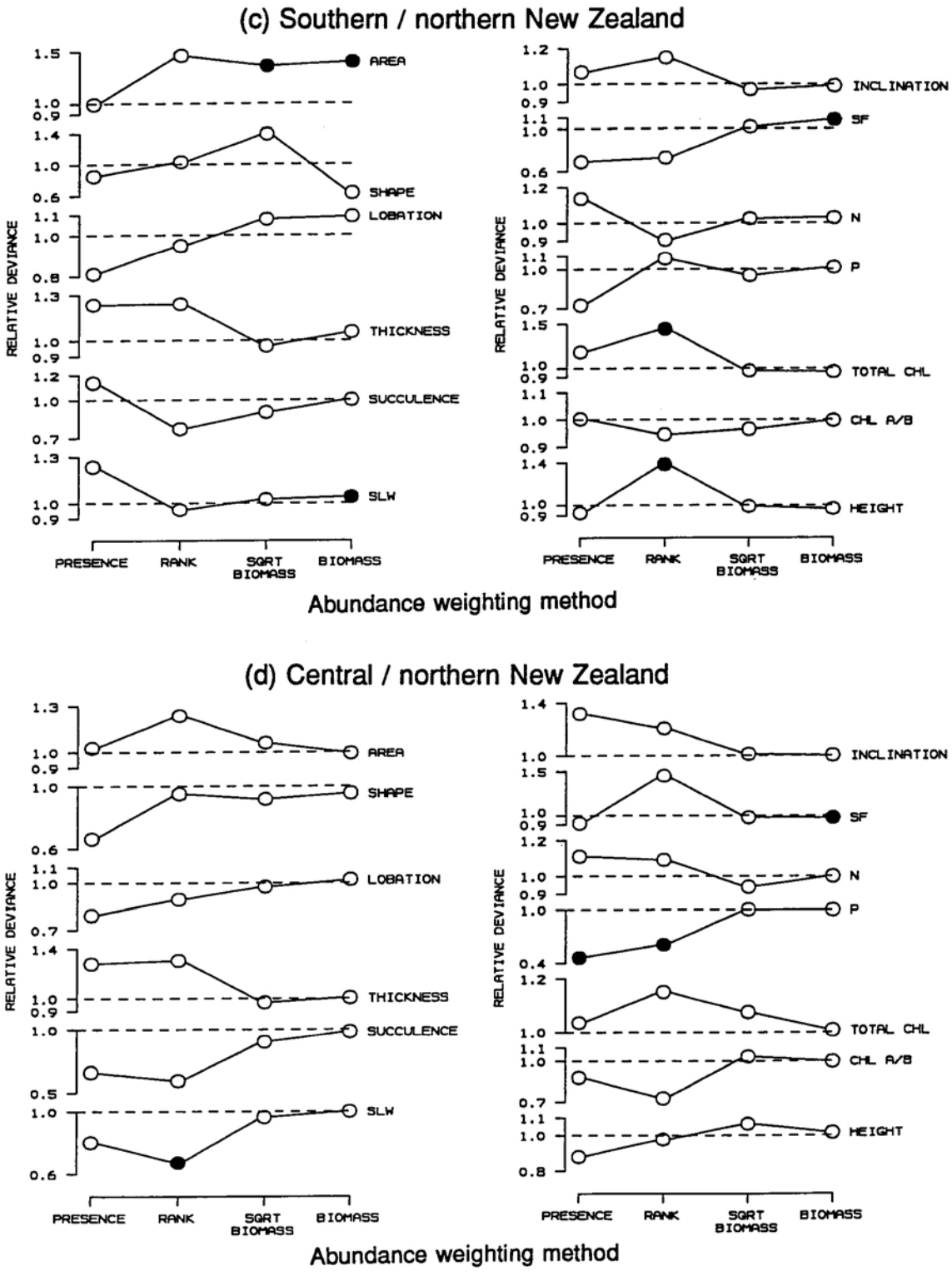



**Fig. 8.8** (continued)

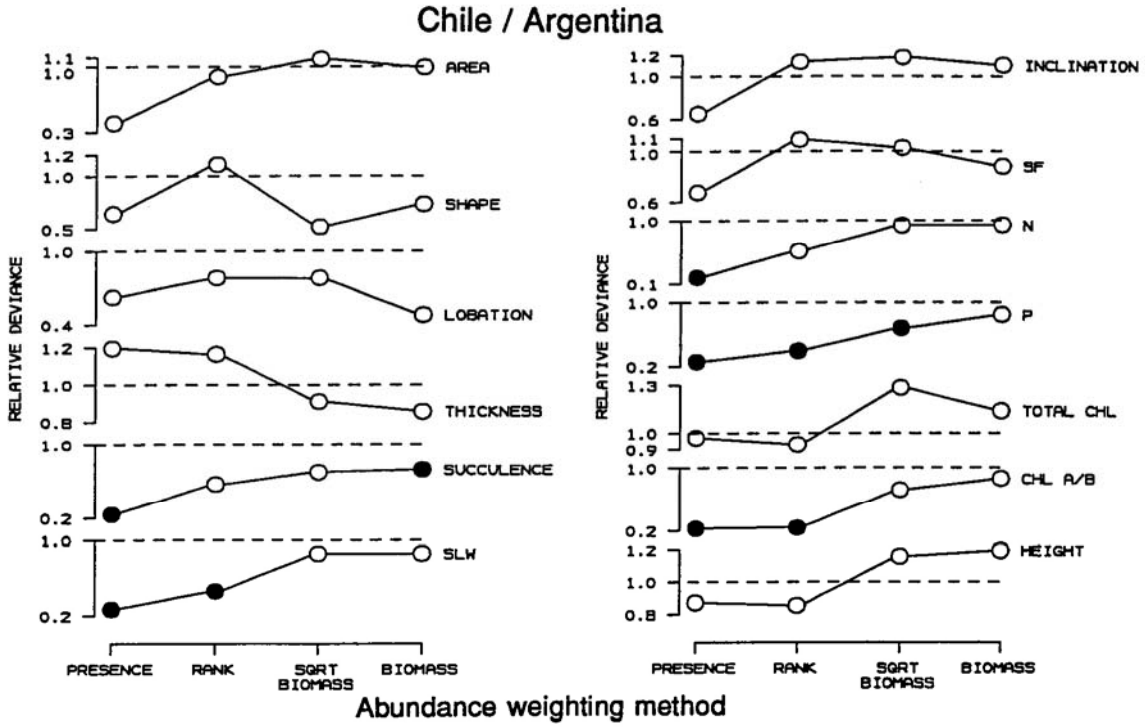



**Fig. 8.9** Null model randomisation tests for convergence or divergence in mean-adjusted texture distributions between regional-scale *Nothofagus*-dominated communities of Chile (SC), and Argentina (SA). Format as for Fig. 8.5.

*Local scale*

There is little overall departure from null model expectation among the southern New Zealand sites ZS1 Ten Mile, ZS2 Walker and ZS3 Deer (Fig. 8.10a). Ten Mile and Walker, however, show significant convergence in PSU shape, lobation, succulence, nitrogen content, phosphorus content, total chlorophyll and chlorophyll *a/b*, primarily at lower abundance weighting levels (Fig. 8.10b). The only significant divergence is in PSU thickness, with species unweighted by their abundance. Comparison of mean-adjusted texture distributions at Ten Mile and Deer (Fig. 8.10c) and at Walker and Deer (Fig. 8.10d) reveal little departure from the null model, although the six significant results are all in the direction of convergence.

Central New Zealand sites ZC1 Craigs and ZC2 Station are likewise convergent in only two variates, PSU area and chlorophyll *a/b*, both with species unweighted by their abundance (Fig. 8.11). However, this is in marked contrast to the high overall incidence of divergence observed when texture means (Chapter 6; Fig. 6.8) and non-adjusted distributions (Chapter 7; Fig. 7.11) were compared.

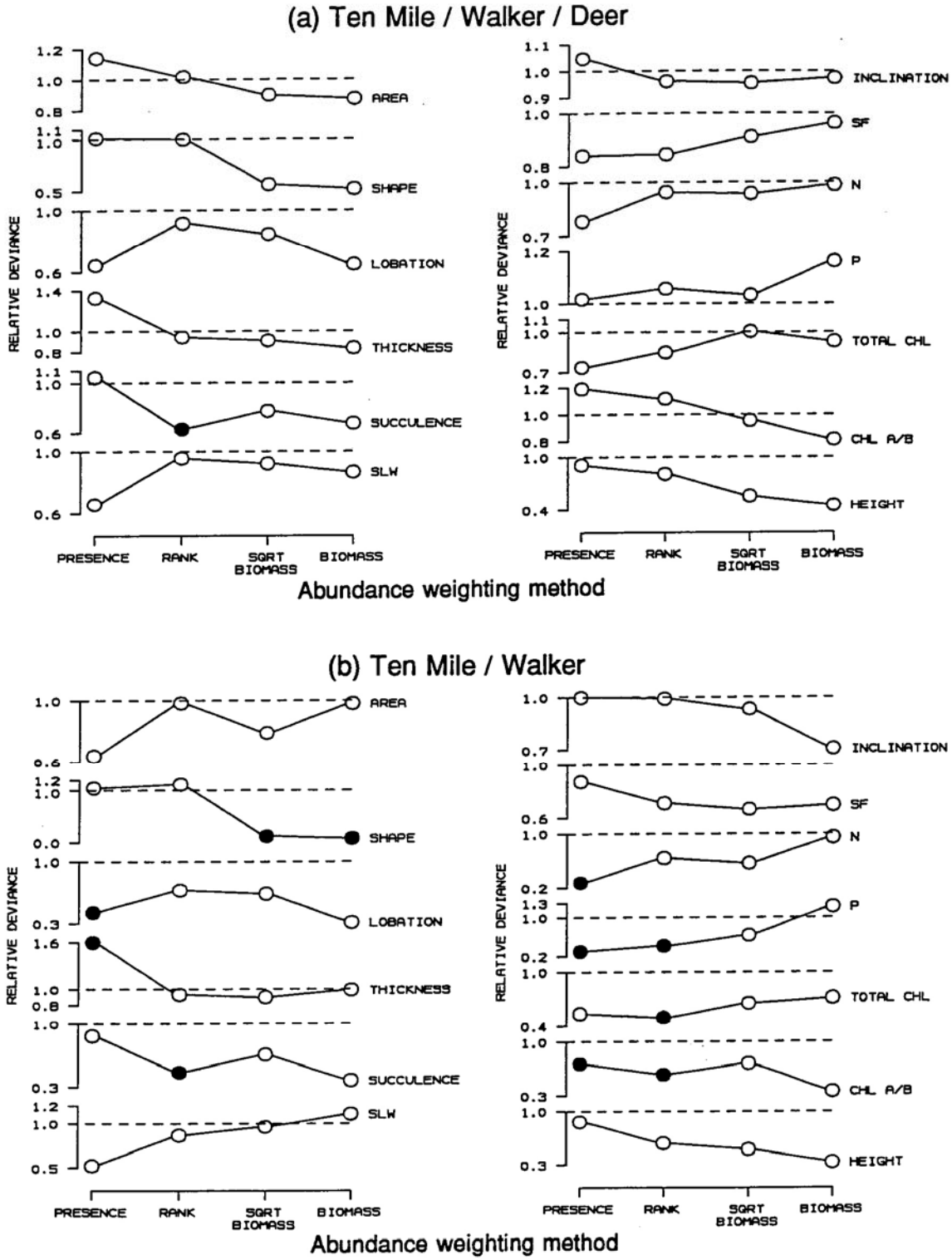
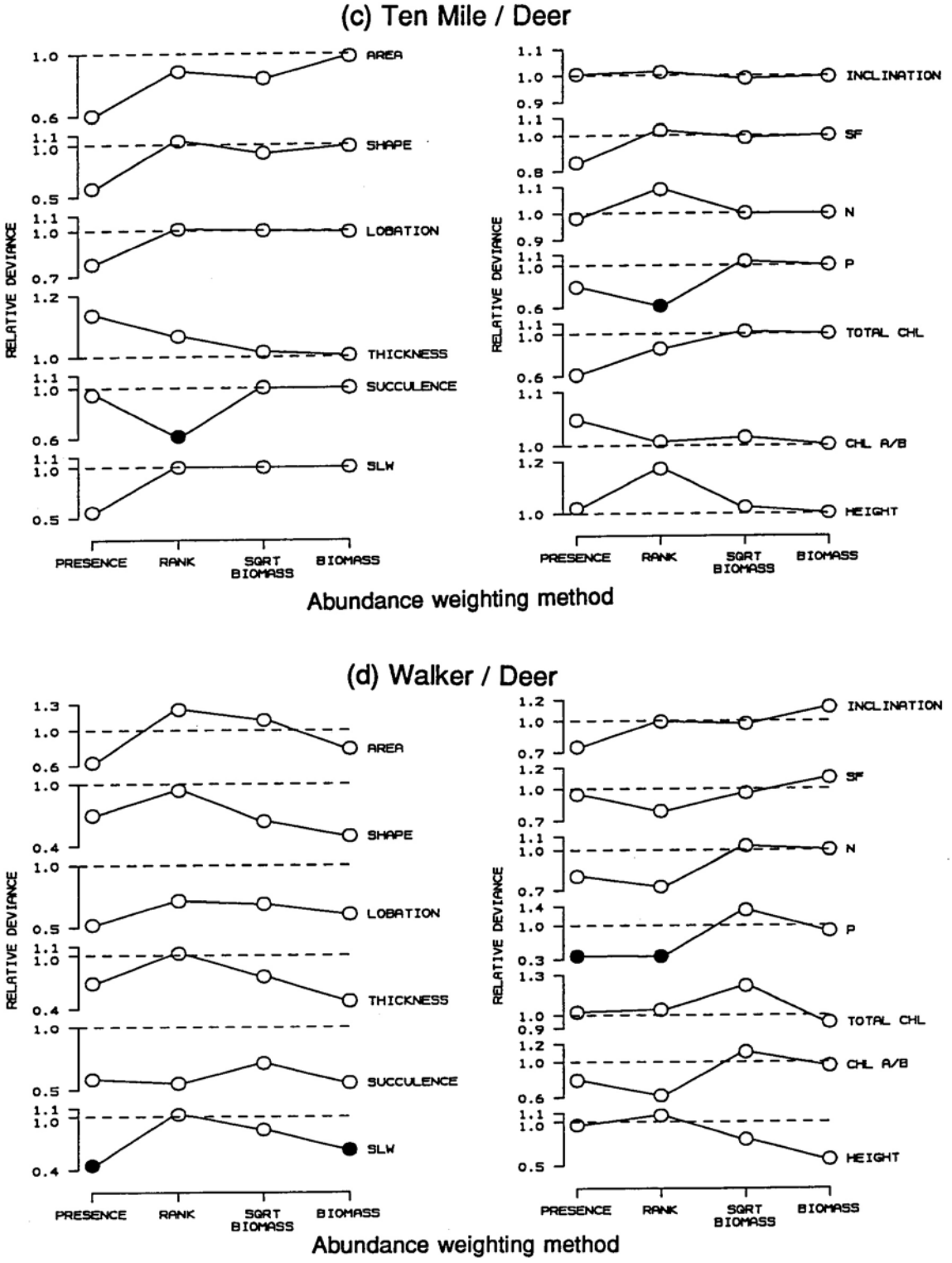



**Fig. 8.10** Null model randomisation tests for convergence or divergence in mean-adjusted texture distributions between local-scale *Nothofagus*-dominated communities ZS1 Ten Mile, ZS2 Walker and ZS3 Deer. Format as for Fig. 8.5.

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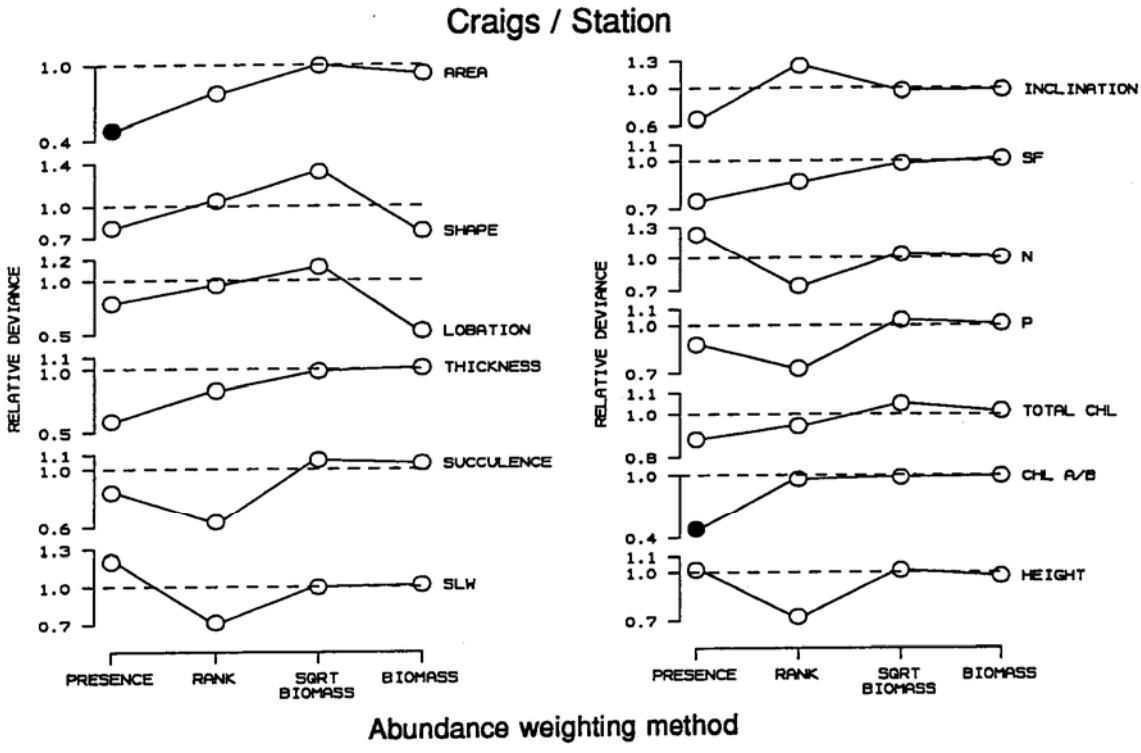



**Fig. 8.11** Null model randomisation tests for convergence or divergence in mean-adjusted texture distributions between local-scale *Nothofagus*-dominated communities ZC1 Craigs and ZC2 Station. Format as for Fig. 8.5.

Among the northern New Zealand sites ZN1 Ohakune, ZN2 Rotokura and ZN3 Clements there is convergence only in PSU thickness (species unweighted) and specific weight (weighting by photosynthetic biomass), and no divergence (Fig. 8.12a). There is likewise little departure from null expectation in pairwise comparisons of the communities. Ohakune and Rotokura show no significant convergence or divergence (Fig. 8.12b). Ohakune and Clements are convergent in five tests involving PSU thickness, specific weight and chlorophyll *a/b* (various weighting levels), and there is no divergence (Fig. 8.12c). Rotokura and Clements are convergent at one weighting level for each of the variates PSU nitrogen content, total chlorophyll and species height, but there is also divergence in PSU area, total chlorophyll and support fraction (Fig. 8.12d).

The null model could not be rejected for any variate at any abundance weighting level when the Chilean communities SC1 Pelada and SC2 Antillance were compared (Fig. 8.13). The same lack of significance was noted when these communities were compared in terms of texture means (Chapter 6; Fig. 6.10) and non-adjusted distributions (Chapter 7; Fig. 7.13).

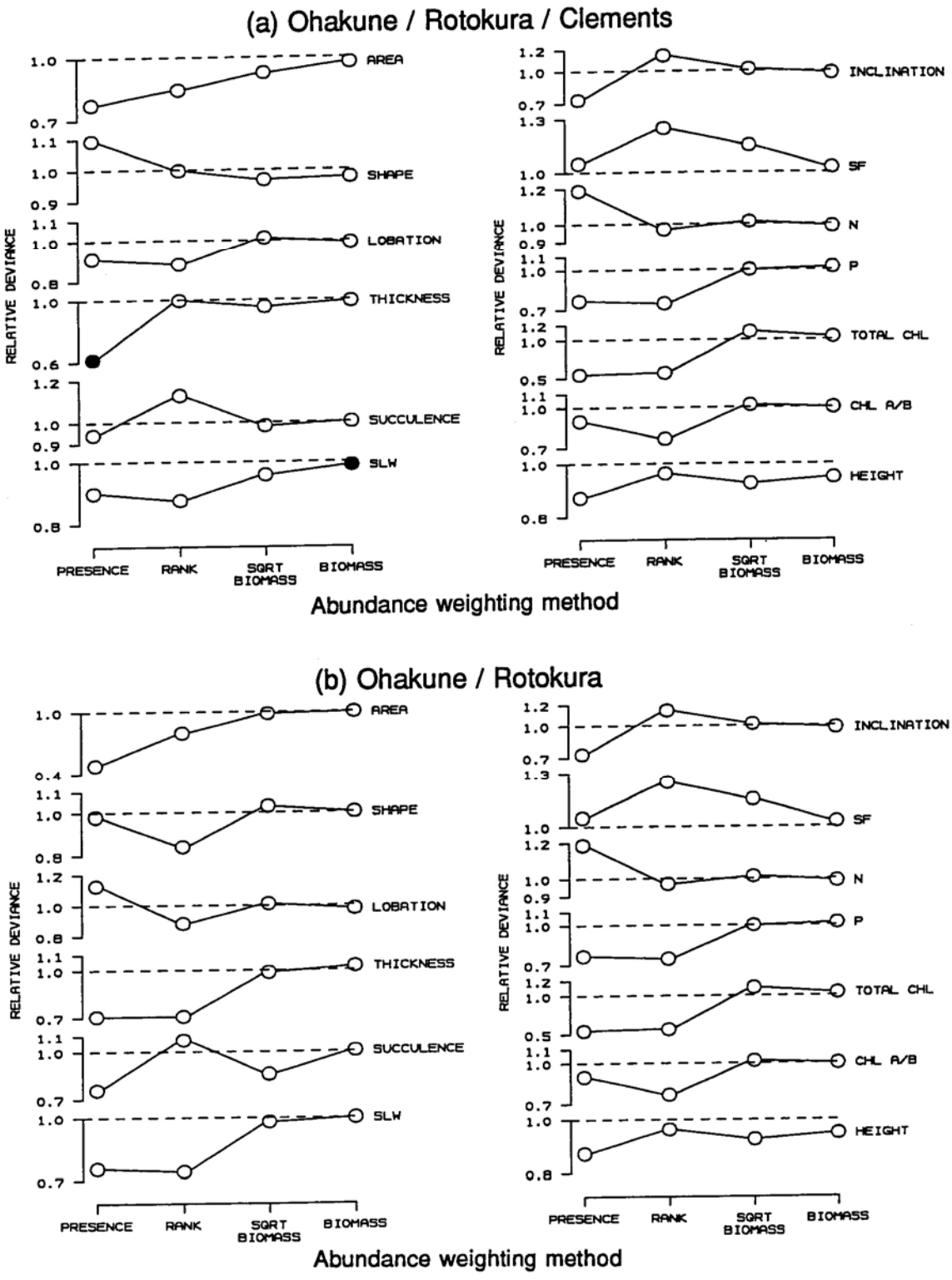



**Fig. 8.12** Null model randomisation tests for convergence or divergence in mean-adjusted texture distributions between local-scale *Nothofagus*-dominated communities ZN1 Ohakune, ZN2 Rotokura and ZN3 Clements. Format as for Fig. 8.5.

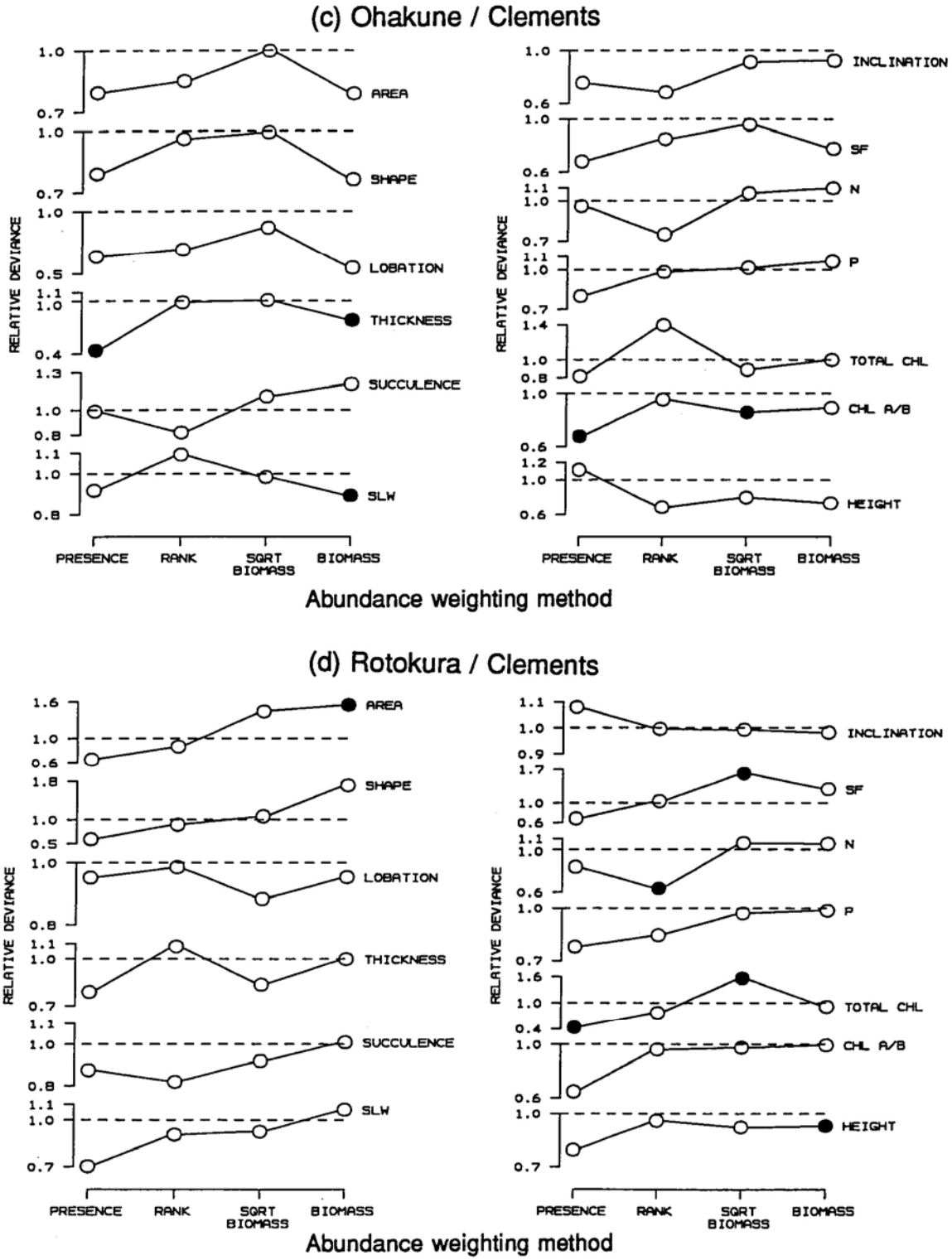



**Fig. 8.12** (continued)

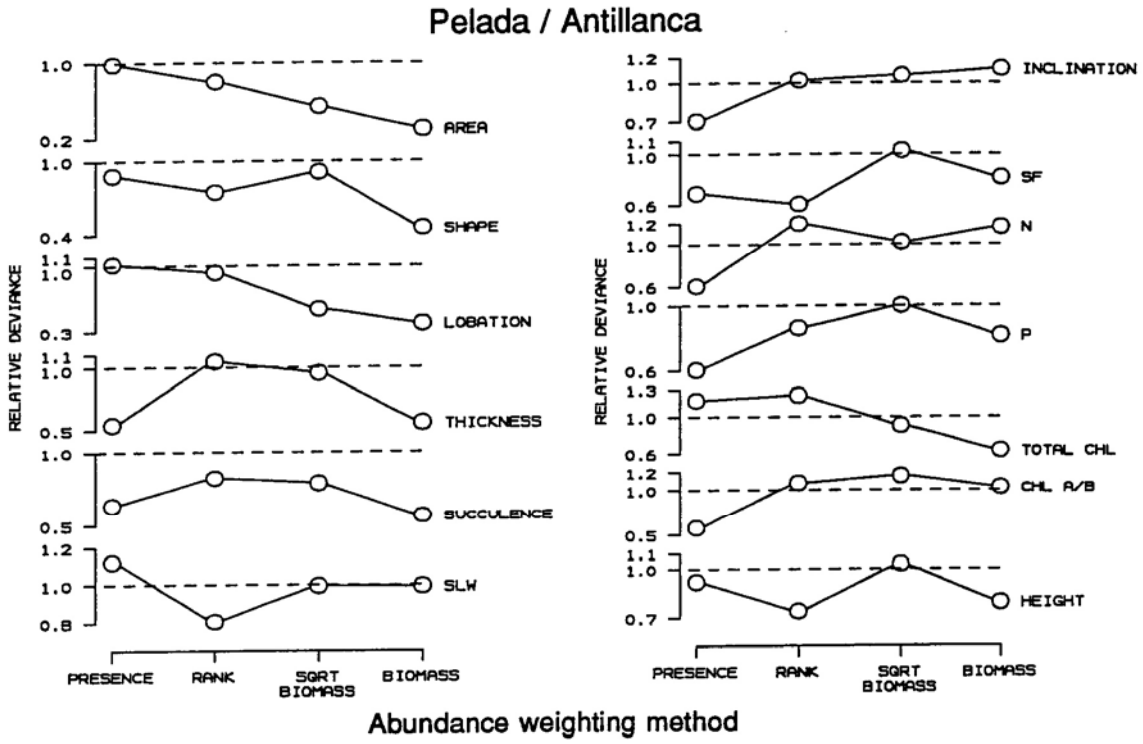



**Fig. 8.13** Null model randomisation tests for convergence or divergence in mean-adjusted texture distributions between local-scale *Nothofagus*-dominated communities SC1 Pelada and SC2 Antillanca. Format as for Fig. 8.5.

Argentinian communities SA1 Quetrihué and SA2 Gutierrez are convergent in PSU succulence and specific weight, both with species unweighted by their abundance, and divergent in PSU thickness (weighting by abundance rank) and support fraction (square root of photosynthetic biomass) (Fig. 8.14).

*Closely matched sites from different landmasses*

T1 Balfour (Tasmania) and A2 Cascades (Australia) are significantly convergent in four variates: PSU thickness, specific weight, phosphorus content, total chlorophyll and chlorophyll *a/b* (Fig. 8.15a). With the exception of PSU thickness, where the convergence is significant only with species weighted by their photosynthetic biomass or its square root, the convergence is at lower weighting levels, indicating that it spans a range of species, and not just a few dominant ones. Compared with the results obtained from comparisons of these communities in Chapters 6 (means) and 7 (distributions), the most interesting differences are with respect to the variates PSU phosphorus content, total chlorophyll content and chlorophyll *a/b*. Using the previous analyses these variates were found to be significantly divergent (Figs. 6.12a, 7.15a), rather than convergent, as here.

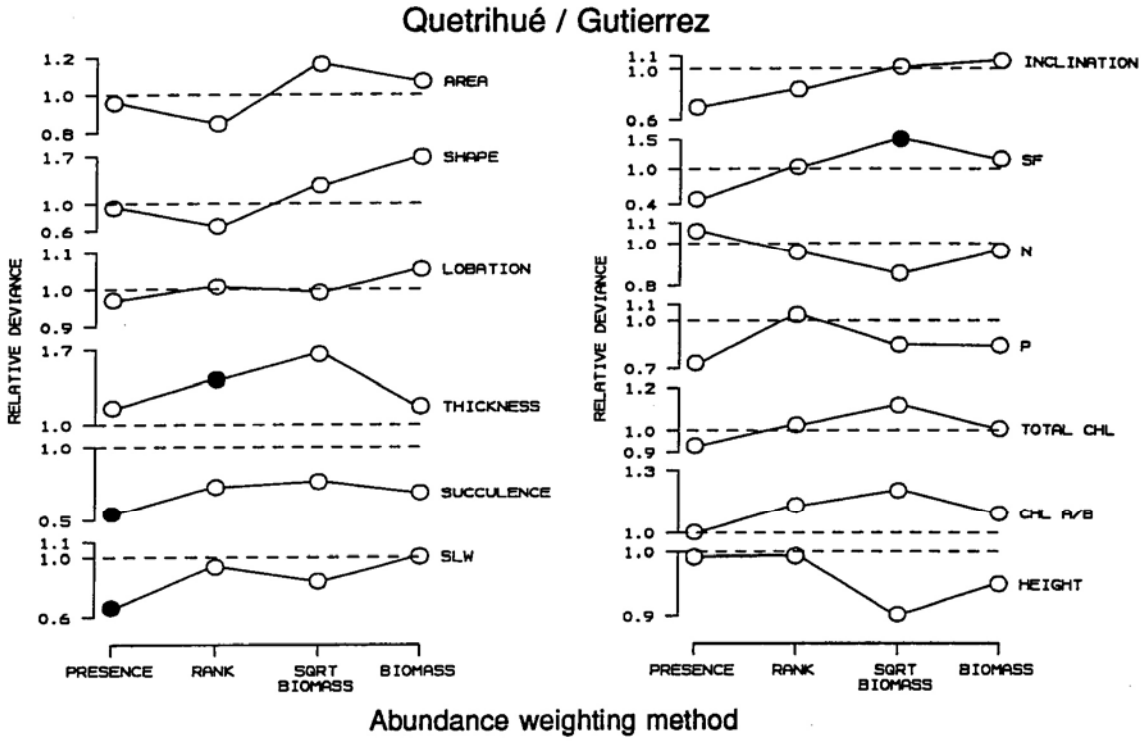



**Fig. 8.14** Null model randomisation tests for convergence or divergence in mean-adjusted texture distributions between local-scale *Nothofagus*-dominated communities SA1 Quetrihué and SA2 Gutierrez. Format as for Fig. 8.5.

There is significant convergence in PSU lobation, succulence, nitrogen content, phosphorus content, total chlorophyll and chlorophyll *a/b* between closely-matched communities from Tasmania and New Zealand, T2 Anne and ZN1 Ohakune (Fig. 8.15b). In addition, PSU specific weight, support fraction and species height show a non-significant tendency towards convergence ($R_{\hat{D};T}<1$) at all abundance weighting levels. There is no divergence. By contrast, very little significant convergence was detected between these sites in Chapters 6 and 7, while there was divergence in PSU shape, nitrogen content, phosphorus content, chlorophyll *a/b* and support fraction in either one or both of the previous analyses (Figs. 6.12b, 7.15b).

New Zealand site ZN2 Rotokura and Argentinian community SA1 Quetrihué are convergent in PSU phosphorus content (weighting by presence or abundance rank), total chlorophyll (presence) and chlorophyll *a/b* (presence) (Fig. 8.15c). Two of these variates, PSU phosphorus content and chlorophyll *a/b* ratio, were found significantly divergent when texture means and non-adjusted distributions were compared (Chapter 6: Fig. 6.12c; Chapter 7: Fig. 7.15c).

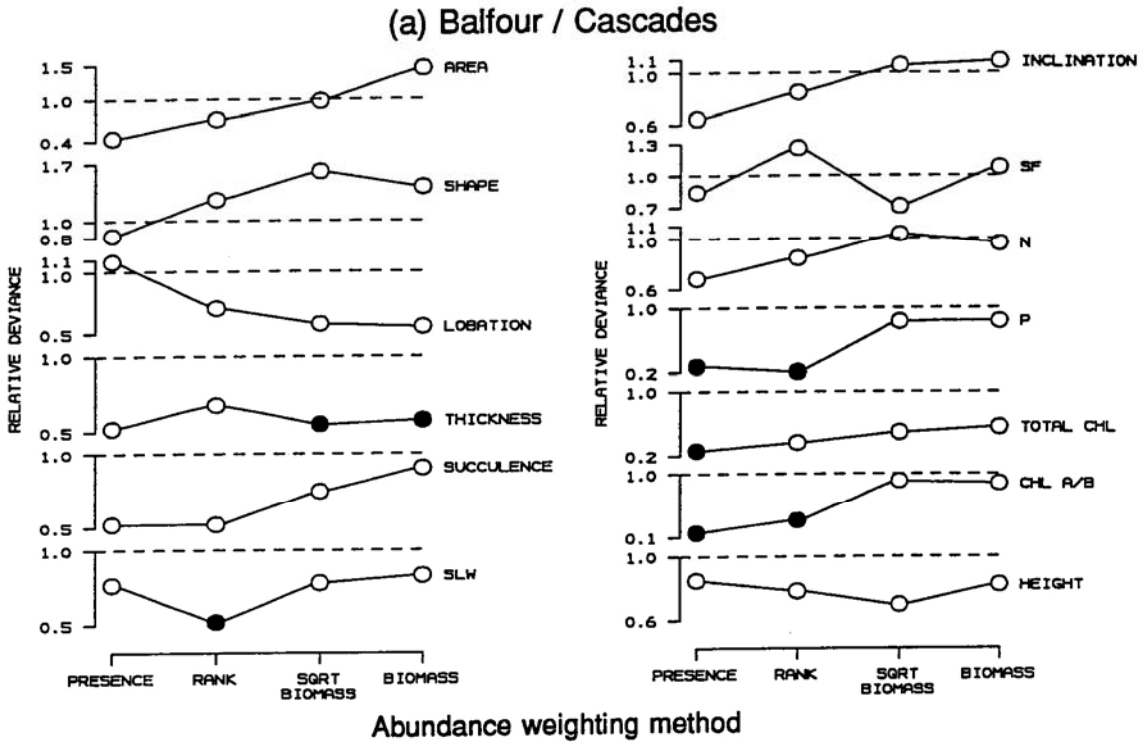



**Fig. 8.15** Null model randomisation tests for convergence or divergence in mean-adjusted texture distributions between *Nothofagus*-dominated communities from different landmasses closely matched in their environments: **(a)** T1 Balfour/A2 Cascades; **(b)** T2 Anne/ZN1 Ohakune; **(c)** ZN2 Rotokura/SA1 Quetrihué. Format as for Fig. 8.5.

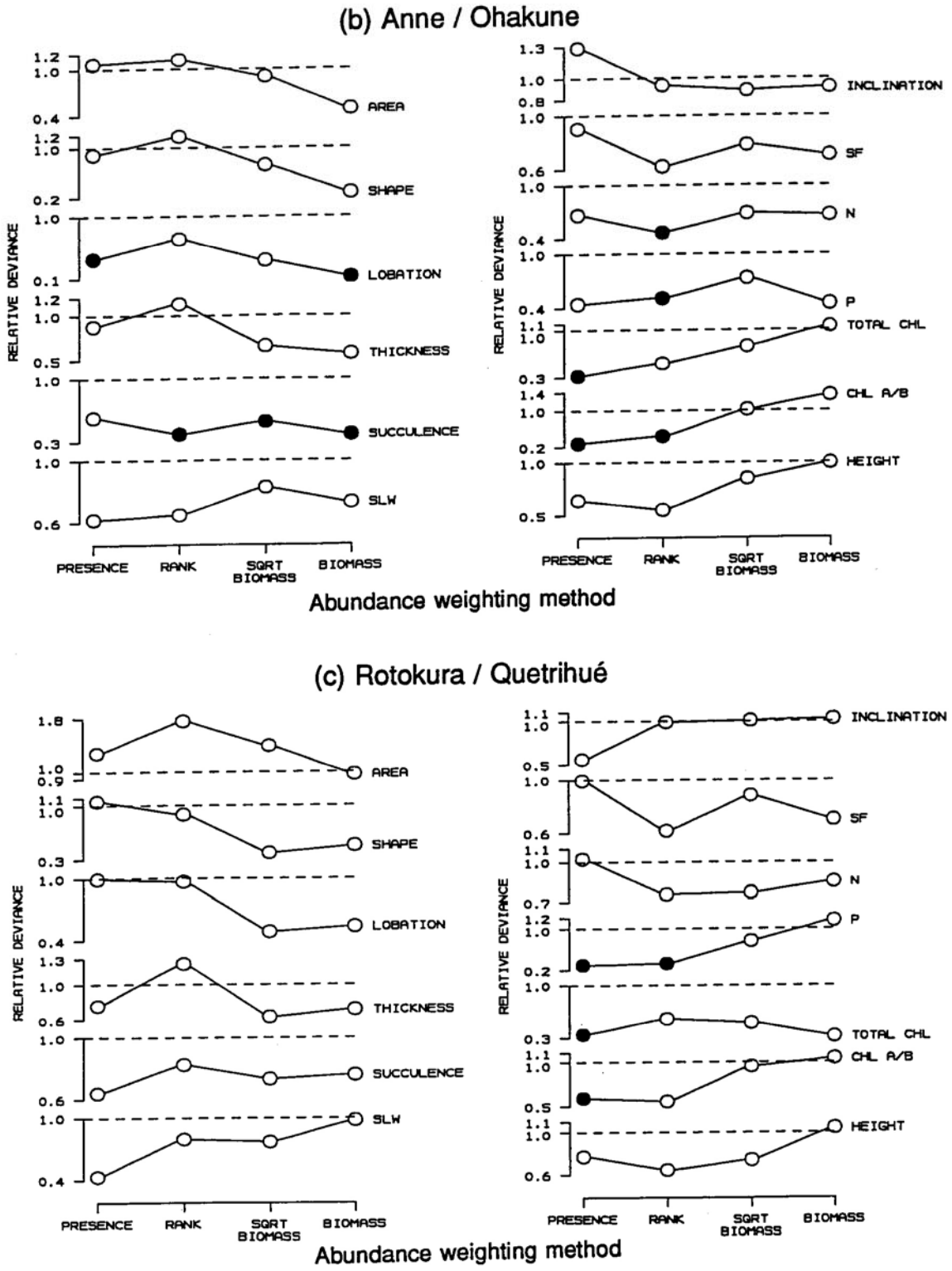



**Fig. 8.15** (continued)

## PATTERNS AMONG TEXTURE VARIATES

Table 8.2 summarises the results presented above as they relate to the 13 texture variates. All variates were significantly convergent in some tests, and for most the highest incidences were at lower weighting levels (presence or abundance rank). For six variates, PSU area, succulence, specific weight, phosphorus content, total chlorophyll content and chlorophyll *a/b* ratio, the incidence of convergence is high enough to be deemed significant overall, according to the binomial test based on the results for 16 independent community comparisons.

The highest incidences of convergence are in the variates PSU phosphorus content, total chlorophyll and chlorophyll *a/b*, which were found to be strongly divergent in the two previous chapters, comparing texture means and distributions not corrected for differences in their means (Tables 6.2, 7.2). This indicates that the distributions of these characters within communities tend to be quite similar in shape, but differ between communities in their means (see Figs 8.3a,b).There was significant divergence in one or more comparisons for all texture variates except PSU lobation, succulence and specific weight. However, for no variate, using any abundance weighting method, was the incidence of divergence high enough to be found significant overall by a binomial test. This is in marked contrast to the findings of the two previous chapters, where more than half of the variates showed divergence that was significant overall. This implies that, whereas texture means, and distributions not corrected for among-community differences in their means, are significantly different between many communities, the shapes of the distributions (disregarding the mean) are generally not sufficiently different to cause departure from the null hypothesis that species characters are drawn at random from the pooled distribution of values.

**Table 8.2** Incidence of significant convergence or divergence of mean-adjusted texture distributions for each texture variate at each abundance weighting method among the 31 community comparisons carried out in this chapter and (in parentheses) for 16 independent community comparisons (see Fig. 6.1). Overall significance, determined from the binomial distribution (see text), is shown for results from the 16 independent comparisons.

| Variate | Convergence | | | | Divergence | | | |
|---|---|---|---|---|---|---|---|---|
| | Presence | Rank | Sqrt biomass | Biomass | Presence | Rank | Sqrt biomass | Biomass |
| Area | 5 (3*) | 1 (1) | 0 (0) | 0 (0) | 0 (0) | 1 (0) | 1 (1) | 2 (1) |
| Shape | 0 (0) | 0 (0) | 2 (1) | 2 (2) | 0 (0) | 2 (0) | 0 (0) | 0 (0) |
| Lobation | 2 (1) | 4 (1) | 0 (0) | 1 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| Thickness | 4 (2) | 0 (0) | 3 (0) | 3 (1) | 1 (1) | 1 (1) | 0 (0) | 0 (0) |
| Succulence | 3 (3*) | 5 (2) | 4 (2) | 4 (1) | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| SLW | 3 (3*) | 5 (1) | 1 (0) | 4 (2) | 0 (0) | 0 (0) | 0 (0) | 1 (1) |
| Inclination | 2 (1) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 1 (0) | 0 (0) | 0 (0) |
| SF | 1 (1) | 3 (1) | 1 (0) | 1 (0) | 1 (1) | 0 (0) | 2 (1) | 1 (1) |
| N | 2 (2) | 3 (0) | 0 (0) | 0 (0) | 2 (0) | 0 (0) | 0 (0) | 0 (0) |
| P | 12 (8**) | 13 (6**) | 2 (2) | 0 (0) | 1 (0) | 0 (0) | 1 (0) | 0 (0) |
| Total chl | 10 (2) | 6 (3*) | 0 (0) | 0 (0) | 0 (0) | 2 (1) | 2 (0) | 3 (1) |
| Chl *a/b* | 13 (7**) | 10 (4**) | 1 (1) | 0 (0) | 3 (1) | 2 (0) | 0 (0) | 0 (0) |
| Height | 3 (2) | 2 (1) | 1 (1) | 2 (1) | 0 (0) | 2 (1) | 1 (0) | 1 (0) |

*$0.001 \leq P < 0.01$; **$P < 0.001$ (no binomial probabilities in range $0.01 \leq P < 0.05$).

## 8.4 Discussion

COMMUNITY-LEVEL CONVERGENCE

Direct comparison of the shapes of community texture distributions, rather than the mean alone (Chapter 6) or the shape and the mean (Chapter 7), revealed a considerable amount of convergence, significant in six variates as a proportion of the number of tests carried out (Table 8.2). In contrast to the preceding analyses, which revealed an overwhelming amount of divergence in texture between communities, tests carried out in the present chapter revealed relatively little significant convergence at any of the three spatial scales (Figs. 8.5-8.15). Although most variates showed occasional significant divergence in individual tests, the incidence was not significant for any variate, as a proportion of the number of tests done (Table 8.2).

These results suggest that comparison of community texture distributions without regard to the mean does represent an effective approach to correcting for the effects of different environments on site texture. It was anticipated that the among-community variation remaining once differences in the mean were removed (using the statistic $\hat{D}'_T$) would reflect the action of

assembly rules, and would be largely independent of the exogenous environment, at least over the narrow environmental range spanned by the *Nothofagus*-dominated communities being compared. The high incidence of convergence observed suggests that in the case of several texture variates, and among several of the communities sampled, species character values are drawn from underlying distributions, not entirely at random, but subject to certain constraints. These constraints cause the mean-adjusted distributions in different communities to be more similar than would be expected if species values were drawn at random from the same distributions, as under the null model. It is postulated that these constraints represent assembly rules, and are caused by species interactions, such as competition, which would limit the co-occurrence of species whose niches (and correlated functional characters) are too similar to prevent competitive exclusion from occurring (Hutchinson 1959; Hardin 1960; Diamond 1975).

Convergence cannot arise merely as a result of the mathematical adjustment applied to species character values in order to give the sample communities a common texture mean (Fig. 8.2). This is because convergence and divergence are sought relative to a null model. Under the null model, species character values are drawn at random (and without replacement) from the distribution obtained by pooling mean-adjusted values from all of the communities being compared in a given test. Just as adjustment to a common mean will tend to increase the absolute similarity between observed communities, so will the similarity between null model communities tend to be higher. In other words, $\hat{\Delta}'_T$ will be lower, in general, than $\hat{\Delta}_T$, but this is equally true for the observed and the randomised data. Significant convergence is detected only if $\hat{\Delta}'_T$ is lower among the observed communities than among all but 2.5% of the 2000 null model rearrangements of the observed data. The absence of significant results when random texture data are compared between communities (Table 8.1) confirms that there is no hidden bias that could lead to spurious departure from null model expectation. The convergence observed must have been produced by a real community process: it is strong evidence for the operation of species-mediated assembly rules in the *Nothofagus*-dominated communities examined by this study.

*Patterns in relation to environmental similarity*

Equalisation of community texture means using the test statistic $\hat{\Delta}'_T$ was expected to factor out the major component of variation in texture between communities related to dissimilarities in the abiotic environment. However, it seems likely that the environment would also influence the biotic component of texture (i.e. that produced by the effects of assembly rules) to some extent. This might lead to differences in the shapes of texture distributions in different environments, as illustrated, by way of example, in Figs. 8.1b-c. If so, communities having closely similar macroenvironments would be expected to exhibit more convergence, and possibly less

divergence, than communities less closely matched in their environments.

Tasmania and New Zealand, the best-matched communities at the landmass scale (Section 3.3) showed no divergence, and there was a tendency towards convergence in all variates at most abundance weighting levels, though this was significant in only six tests (Fig. 8.5c). Tasmania and Australia, though apparently more dissimilar in their environments, showed a higher incidence of significant convergence (Fig. 8.5b). At the regional scale, southern and central New Zealand showed the strongest trends towards convergence among the three regional communities from New Zealand (Fig. 8.8b). Best-matched sites from different landmasses all showed a relatively high incidence of convergence, and no significant divergence (Fig. 8.15).

In summary, a tendency is apparent for closely-matched communities to be more similar in mean-adjusted texture than combinations of communities with more dissimilar environments. This suggests that the environment does have some effect on the way assembly rules work. Texture variation due to environmental differences may tend to obscure the structure produced by assembly rules, even after differences in community texture means, which presumably reflect direct effects of the environment on species adaptations, are removed.

*Factors underlying convergence*

Of the six texture variates showing convergence that was significant overall, four (PSU succulence, specific weight, phosphorus content and total chlorophyll) belong to the syndrome of intercorrelated characters identified in Chapter 4 (Section 4.3; Table 4.2) which are likely to reflect adaptations (or plastic responses) to light availability. The other two characters showing significant convergence, PSU area and chlorophyll *a/b* ratio, though not as strongly correlated with the other characters, are also likely to exhibit variation in response to light gradients (Givnish & Vermeij 1976; Popma *et al.* 1992; Björkman 1981; Dale & Causton 1992). Variation among species in these characters, in particular PSU area, specific weight and phosphorus content, could also reflect differential nutrient uptake (Loveless 1961, 62; Grubb 1977; Medina 1984; Givnish 1987).

A possible interpretation of the convergence observed is that assembly rules operating in ecological time (through ecological species sorting) or evolutionary time (through coevolutionary character displacement) result in a partitioning of resource gradients among species (Section 1.5; Figs. 1.4, 1.5). The resource gradients may be primarily above-ground (e.g. vertical or horizontal variation in light availability) or below-ground (e.g. variation in nutrient availability with soil depth). Different species whose structure and function are similar, causing them to make demands on the same units of resources (e.g. light of the same quality and intensity), cannot coexist indefinitely. The result is that the niches and characters of sympatric species will tend to be more regularly spaced than would be expected if there were no assembly rules. This pattern is reflected in community-wide spectra of species functional characters, causing mean-adjusted

distributions of texture variates to be more similar in different communities than expected under the null model.

The spatial scale at which convergence is found to occur may shed some light on the temporal scales at which the convergence may have taken place. Different communities within a local area (such as the three communities in southern New Zealand) would share approximately the same species pool. If such communities were found to be more similar in their texture than expected on the basis of random migration (e.g. Ten Mile and Walker; Fig. 8.10b), the underlying mechanism would seem most likely to be ecological species sorting, by which contemporary competition tends to restrict the occurrence on the same site of species with overlapping niches (Section 1.5; Table 1.1). Convergence between different landmass communities, however, cannot be explained by filtering from the same species pool. Filtering from different local pools, with ecological sorting of species to give similar community texture distributions, could account for the convergence observed between individual sites on different landmasses (e.g. Tasmanian site Anne and New Zealand site Ohakune; Fig. 8.15b). Convergence was detected between pooled landmass-scale communities (e.g. Tasmania and New Zealand; Fig. 8.5c), however, is more likely to be the result of coevolutionary character displacement in the *Nothofagus*-forest flora, a consequence of repeated ecological species sorting operating at the local scale over evolutionary time (Fig. 1.5). Convergence at the intermediate regional scale (e.g. between southern and central New Zealand; Fig. 8.8b) could be explained by assembly rules operating on both ecological and evolutionary time scales. Significant convergence in mean-adjusted community texture distributions was detected at the landmass, regional and local scales, and also between individual sites on different landmasses. These results suggest that both ecological species sorting under contemporary competition, and coevolutionary character displacement integrating the effects of ecological sorting over evolutionary time, may be important in structuring *Nothofagus*-dominated communities, leading to convergence among them.

### A NEW METHOD FOR ENVIRONMENTAL CORRECTION AND ITS SIGNIFICANCE

Environmental differences between communities have often been invoked in comparative studies as possible causes of non-convergence (Orians & Solbrig 1977; Cowling & Campbell 1980; Orians & Paine 1983; Blondel *et al.* 1984; Barbour & Minnich 1990; Blondel 1991; Wiens 1991a; Keeley 1992). Differences in the abiotic or exogenous environments of communities can never be ruled out, since environments comprise an indefinite number of factors, not all of which can be quantified in any study (Keeley 1992). Consequently, when convergence between communities is sought but not found, it is always unclear whether convergence *could* have occurred, had there been closer environmental matching. As Peet (1978) points out, 'failure to observe convergence will not be a readily interpretable result.'

In the present chapter, a method was developed and applied that was intended to improve

overall interpretability, by increasing the likelihood of detecting convergence if it had, in fact, occurred. The index $\hat{\Delta}'_T$ was intended to correct for the predominant effects of environmental differences between communities, allowing convergence to be sought in the residual variation. The among-community variation remaining once differences in texture means were removed mathematically by $\hat{\Delta}'_T$ were anticipated to be primarily the result of assembly rules restricting what functional combinations of species would be possible in each community. The validity of the approach is confirmed by its success: convergence, significant as a proportion of the number of tests carried out, was detected in six texture variates. Divergence, which arose frequently in earlier tests and was attributed to differences in abiotic environments, was detected in few tests, and was not significant overall for any variate. These results show that assembly rules do operate in a similar way in different *Nothofagus*-dominated communities, producing community-wide similarities in the characters of species relative to each other, even where environmental differences are sufficiently pronounced to produce absolute differences in character spectra.

## CONCLUSIONS

Tests for convergence in mean-adjusted texture distributions revealed a significant incidence of convergence six texture variates. The convergence occurred among single study sites at the local scale, and also in communities pooled from several study sites, at the regional and landmass scales. Individual sites with relatively similar environments from different landmasses also showed a marked degree of convergence. Ten of the 13 texture variates also showed significant divergence in individual tests, but divergence was not significant overall for any variate, according to a binomial test.

The results may be interpreted as evidence for the operation of similar assembly rules in the *Nothofagus*-dominated communities examined. Although there are environmental differences between many communities, causing them so exhibit non-convergence or significant divergence when texture means are taken into account, effects of these differences on texture are largely removed when community means are arithmetically standardised using the index $\hat{\Delta}'_T$. Convergence in texture then becomes detectable, and divergence is reduced or eliminated.

# 9. Convergence among *Nothofagus*-dominated communities: derived texture factors

## 9.1 Introduction

The hypothesis of community-level convergence is that similar environments, coupled with the effects of assembly rules limiting the co-occurrence of species with similar niches, will lead to similar niche spectra in different communities (Wilson *et al.* 1995; Section 1.5). Testing this hypothesis is not completely straightforward, since niches are defined by an indefinite number of parameters and so cannot be measured directly (Hutchinson 1958; Colwell 1979). One approach is to seek similarity between communities in properties that would be determined by their niche structure; for example, species richness (Wilson *et al.* 1987; Schluter 1986; Chapter 5). Another approach is to characterise niches by measurable parameters that would be expected to show some correlation with them. This approach has been adopted in the three preceding chapters, where functional characters of species have been used as proxies for their niches, and convergence has been sought in the community-wide spectra of these characters; that is, in community texture.

The 13 characters used to characterise texture in the present study were chosen because of their assumed, or previously demonstrated, functional importance (Section 2.2.2; Chapter 4). Modes of resource capture constitute an important aspect of function (Tilman 1982), so such characters are most likely to represent useful surrogates for alpha (resource) niches. However, measured species values for a character are likely to be an outcome of adaptation to several independent or related environmental and resource parameters, as well as of other factors, such as phylogeny, random mutations and sampling errors. These factors are not necessarily independent. For example, some environmental factors (e.g. temperature) may be correlated with other environmental factors (e.g. humidity) and with certain resources (e.g. light). The hypothesis of community-level convergence makes predictions only about patterns related to finite resources for which species must compete. Where other parameters — such as environmental factors and stochastic 'noise' — are relatively important in determining what values species will have for a character, the character may tend to have a relatively poor correspondence with niche.

To maximise the likelihood of detecting convergence where it has occurred, it would be desirable to focus on the components of character variation determined only by alpha niche axes (i.e. by species responses to finite resources), disregarding other sources of variation. Multivariate ordination techniques such as principal component analysis (PCA) and factor

analysis (FA) represent one possible approach. Given a set of correlated variables, these techniques give a new set of variables (uncorrelated, in the case of PCA and some forms of FA), each summarising a component of variation in the original variables (Manly 1994). Where there are intercorrelations among the variables, the derived factors may partly summarise this shared variation. If the variables covary because of some common underlying causes (for example, characters representing different aspects of adaptation to an environmental gradient), it follows that some of the derived factors may approximate variation in the common underlying factors.

The texture variates examined in the present study are not completely independent. Significant intercorrelations were detected among most of the characters, in Chapter 4 (Table 4.1). It has been assumed that some of the shared variation might reflect common adaptations to environmental or resource factors. For example, the strongly intercorrelated variates PSU succulence, chlorophyll content, phosphorus content, nitrogen content and specific weight would all be expected to vary along gradients of light availability (Hollinger 1989; Popma *et al.* 1992; Ellsworth & Reich 1993; Mulkey *et al.* 1993). It therefore seems possible that the shared variation among them reflects adaptations, in each character, to the light regime. PCA and FA provide a method of expressing such shared variation by a reduced number of variables (the factors), which might be more strongly related to the underlying causal factors than are the base variables themselves. For example, it might be possible to summarise a component of the shared variation in the above species characters by a single derived factor. If the hypothesis that these characters covary due to parallel responses to the light regime is true, it is possible that the derived factor would show a closer relationship to light availability than do the characters themselves.

In this chapter, principal component analysis is used to identify and extract underlying components of variation in the 13 texture variates examined in previous chapters. Varimax factor rotation, a factor analysis technique, is applied in order to improve the interpretability of the derived variates (factors) in terms of the texture variates. Texture, expressed in terms of the derived factors, is compared among *Nothofagus*-dominated communities using the approaches developed in each of the previous three chapters. It is anticipated that the factors obtained may reflect underlying causes of variation in texture, including adaptation to resource spectra and environmental parameters, more closely than any of the variates from which they are derived. If community-level convergence is a reality, it should be detected in factors that reflect species responses to limiting resources, i.e., their alpha niches. Factors not related to niches, on the other hand, should show no significant convergence using the null model approach of this study.

## 9.2 Methods

TEXTURE DATA

The texture data subjected to factor analysis comprised 13 variates: the 12 listed in Section 2.3.5, in addition to species height, defined in Section 6.2. Field and laboratory methods are outlined in Chapter 2, and study sites are described in Chapter 3.

ANALYSIS

*Derivation of factors from texture variates*

Principal component analysis (PCA) was used to obtain initial derived variates based on the 13 observed ('raw') texture variates. Each texture variate (and therefore, each derived principal component) comprised values for each species or entity[1] observed at each study site, a total of 644 records (see Appendix A). Species values were transformed as described in Sections 2.3.5 (Table 2.1) and 6.2. Texture data were also standardised (to a mean of 0 and standard deviation 1), as this can result in a more even distribution of species values in the space of the derived factors.

Given data for a set of *n* variates, PCA yields a further set of *n* variates (the principal components) which are linear combinations of the original variables but are uncorrelated and in rank order of the proportion of variation in the data for which they account (Manly 1994). Where the variables supplied are appreciably intercorrelated, the first few principal components (PCs) may accomodate the majority of variation. This means that all but the first few PCs may often be ignored without a major sacrifice of explanatory power. In the present analysis, the minimum number (*m*) of principal components that explained at least 75% of the variation in each of the 13 texture variates were retained.

To improve the interpretability of the derived variates in terms of the observed species characters, varimax rotation (Cooley & Lohnes 1971) was carried out on the principal components retained once the last *n-m* had been eliminated, as described above. In this procedure, factors (initially, principal components) are mathematically 'rotated' in their multivariate space to a configuration at which the sum of the variances of the squares of the factor loadings (i.e. correlations between each factor and each of the original variables) is maximised. Kaiser normalisation of the factor loadings was first carried out, i.e. the loadings were standardised to a constant mean and standard deviation, a procedure that may give improved results. The effect of varimax rotation is to maximise some loadings while minimising others. Factors will then tend to be explained primarily by a reduced subset of the original variables, in

[1] 'Entity,' i.e. a size or age class of a species for which such classes were distinguished at certain sites.

comparison with the unrotated principal components, improving interpretability. The factors obtained by varimax rotation of principal components are still orthogonal and uncorrelated, but the rank order of explained variation characteristic of principal component analysis may be lost.

Species scores on the rotated factors were calculated by multiple regression of the factors on the original variables (Cooley & Lohnes 1971). This gave a new set of texture variates — the factors — to which tests for community convergence could be applied.

Principal component analysis and varimax rotation were carried out using the SPSS-X computer program (SPSS Inc. 1986).

*Texture convergence*

Evidence for convergence in texture between communities was sought by means of randomisation tests comparing observed among-community variation in texture to variation expected under a null model simulating random assignment of species characters to communities. The null model is described fully in Section 6.2. In separate tests, community texture was characterised by the mean (test statistic $\bar{D}_T$), distribution ($\hat{D}_T$) and mean-adjusted distribution ($\hat{D}'_T$) of each of seven factors derived by factor analysis, as described above. Randomisation tests are described fully in Sections 6.2, 7.2 and 8.2.

*Comparisons performed*

Comparisons of 31 sets of communities at the landmass, regional and local scales were performed using each of the above analyses. Binomial tests for overall significance among 16 independent comparisons were performed. The hierarchy of comparisons is described in Section 6.2 and depicted graphically in Fig. 6.1.

## 9.3 Results

DERIVATION OF TEXTURE FACTORS

Seven factors were required to achieve communalities of at least 75% for each of the 13 primary texture variates (the communality of a variable is equal to the percentage of its variation retained in the factor model; Cooley & Lohnes 1971). The communality of each variable and its loading on each of the seven factors (F1 to F7) are shown in Table 9.1. Factor loadings are equivalent to correlation coefficients (Pearson *r*) between each factor and each input variable (Cooley & Lohnes 1971). Loadings greater than 0.5, which correspond to the variables most important in defining each factor, are highlighted in the table. The proportion of the total variation in the original variables accounted for by each factor is also shown.

F1 accounts for the greatest proportion of variation in the original variables, and is related most strongly to PSU succulence, specific weight, total chlorophyll and species height. Each of the remaining six factors accounts for approximately half as much of the total variation as F1. F2 is related most strongly to PSU area and support fraction; F3 to PSU phosphorus content and chlorophyll *a/b* ratio; F4 to PSU thickness; F5 to PSU nitrogen and phosphorus content; F6 to PSU lobation and inclination; and F7 to PSU shape.

**Table 9.1** Loadings of texture variates on each of seven factors derived by varimax rotation of principal components. Loadings greater than 0.5 in magnitude are shown in bold type. Communalities of the texture variates in the factor model, and the percentage of total variation in the texture variates explained by each factor are also shown.

| Texture variate | Communality (%) | Factor loadings | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | F1 | F2 | F3 | F4 | F5 | F6 | F7 |
| Area | 76 | 0.16 | **0.71** | 0.02 | 0.29 | -0.16 | 0.34 | 0.00 |
| Shape | 90 | -0.08 | 0.16 | 0.00 | 0.07 | -0.10 | 0.16 | **0.91** |
| Lobation | 80 | -0.13 | 0.42 | 0.15 | -0.47 | -0.09 | **0.52** | -0.31 |
| Thickness | 89 | -0.12 | 0.17 | 0.04 | **0.91** | -0.07 | -0.07 | 0.03 |
| Succulence | 85 | **0.84** | 0.02 | 0.13 | 0.29 | 0.20 | -0.04 | -0.04 |
| SLW | 82 | **-0.78** | 0.18 | 0.01 | 0.29 | -0.23 | 0.13 | 0.15 |
| Inclination | 88 | -0.20 | 0.09 | -0.13 | -0.06 | -0.06 | **0.87** | 0.23 |
| SF | 88 | 0.22 | **-0.86** | 0.18 | -0.01 | -0.04 | 0.05 | -0.23 |
| N | 87 | 0.34 | -0.08 | 0.01 | -0.07 | **0.86** | -0.09 | -0.08 |
| P | 83 | 0.31 | 0.01 | **0.64** | 0.00 | **0.56** | 0.00 | -0.10 |
| Total chl | 78 | **0.81** | -0.06 | -0.17 | -0.06 | 0.29 | -0.05 | -0.08 |
| Chl *a/b* | 87 | -0.09 | -0.11 | **0.92** | 0.02 | -0.04 | -0.09 | 0.03 |
| Height | 83 | **-0.66** | -0.07 | -0.21 | 0.29 | 0.21 | 0.32 | -0.34 |
| % total variation explained | | 21.5 | 11.8 | 10.9 | 10.8 | 10.1 | 10.0 | 9.2 |

## PATTERNS AMONG COMMUNITIES

For brevity, only results from overall comparisons among the four landmasses, and for a representative sample of the comparisons done at each community scale (focusing on communities found to be closely-matched in their environments in Chapter 3) are described in detail here.

### *Landmass scale*

In a comparison of the four landmass-scale communities Tasmania, Australia, New Zealand and South America there is significant convergence in only one factor, F6 (related primarily to PSU lobation and inclination; Table 9.1), whether texture is expressed as the community mean,

distribution[2] or mean-adjusted distribution (Fig. 9.1a). The convergence in F6 is significant only at higher abundance weighting levels for comparisons of texture means or distributions, but at all levels except abundance rank (though still $R_{\hat{D};F6}<1$) for mean-adjusted distributions. Texture means and distributions are divergent at lower weighting levels for three factors, F3 (PSU phosphorus, chlorophyll *a/b*), F4 (PSU thickness) and F5 (PSU nitrogen and phosphorus). There is no significant divergence among landmasses in mean-adjusted distributions of texture factors.

Tasmania and New Zealand, the two landmass-scale communities most closely matched in their macroenvironments, show little more significant convergence (Fig. 9.1b). However, non-significant trends towards convergence are apparent for several factors, especially in comparisons of mean-adjusted distributions, for which only F4 (related to PSU thickness) shows a trend towards divergence ($R_{\hat{D};T}>1$) at any weighting level. Community means of F1 (PSU succulence, specific weight, total chlorophyll and species height) are significantly convergent with weighting by photosynthetic biomass. Distributions of F2 (PSU area, support fraction) are convergent with weighting by the square root of photosynthetic biomass. F5 (PSU nitrogen, phosphorus) is convergent when mean-adjusted distributions are compared and species values are weighted by abundance rank. F6 (PSU lobation, inclination) shows some significant convergence in texture means. Mean-adjusted distributions of F3 (PSU phosphorus, chlorophyll *a/b*) are significantly convergent at all weighting levels except biomass, while means and non-adjusted distributions are divergent at these weighting levels. There is significant divergence in no other factor.

*Regional scale*

Southern (ZS) and central (ZC) New Zealand are among the most closely matched regional scale communities in terms of their environments. However, they show significant convergence only between mean-adjusted distributions of texture factors (Fig. 9.2). Three factors, F1 (PSU succulence, specific weight, total chlorophyll and species height), F2 (PSU area, support fraction) and F3 (PSU phosphorus, chlorophyll *a/b*) are convergent at lower abundance weighting levels. Both means and distributions of F1 are divergent at lower weighting levels. Means of F2 are divergent with weighting by abundance rank, while means and distributions of F3 are divergent with species weighted by presence only. Distributions of F5 (PSU nitrogen and phosphorus) are divergent with species weighted by presence or abundance rank.

[2]In the following discussion, 'distribution' will, unless otherwise qualified, refer to community texture distributions, not adjusted to a constant mean (such distributions are compared by the index $\hat{D}_T$, described in Section 7.2).

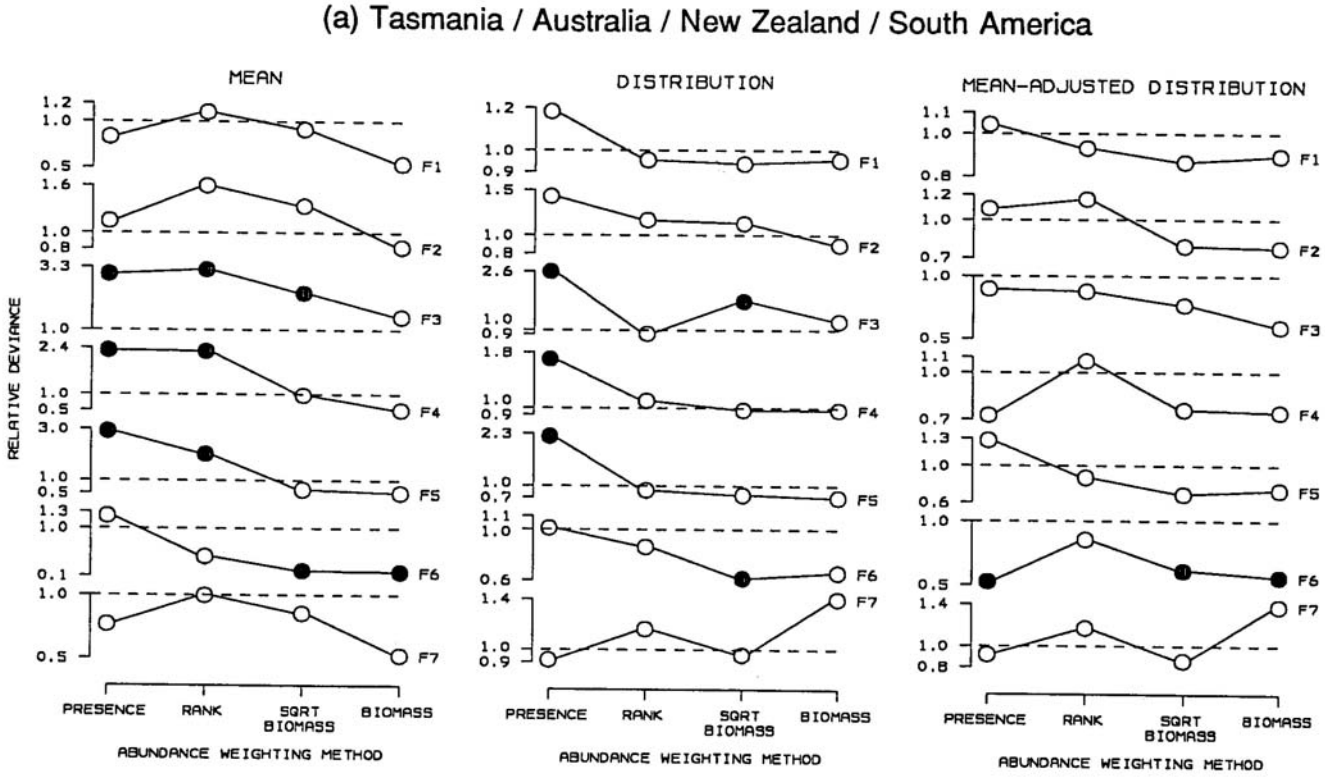



**Fig. 9.1** Null model randomisation tests for convergence or divergence in texture between landmass-scale *Nothofagus*-dominated communities **(a)** Tasmania (T), Australia (A), New Zealand (Z) and South America (S); **(b)** Tasmania and New Zealand. Results are shown from tests comparing texture means (test statistic $\bar{D}_T$), distributions ($\hat{D}_T$) and mean-adjusted distributions ($\hat{D}'_T$). The relative deviance $R_T$ of among-community variation in texture is shown for each of seven texture factors (F1-F7) and four methods of weighting individual species values by abundance in calculations of community texture. A value of $R_T<1$ indicates similarity in texture between communities relative to a null model simulating random community assembly (see text); $R_T>1$ indicates dissimilarity relative to the null model. Broken lines signify null model expectation ($R_T=1$). Filled symbols correspond to significant departure from the null model (convergence for $R_T<1$; divergence for $R_T>1$; $P<0.05$). Texture factors are derived from 13 texture variates by principal component analysis and varimax factor rotation (see text for full explanation). Key to abbreviations: RANK=abundance rank; SQRT BIOMASS=square root of photosynthetic biomass; BIOMASS=photosynthetic biomass (see text for full explanation).

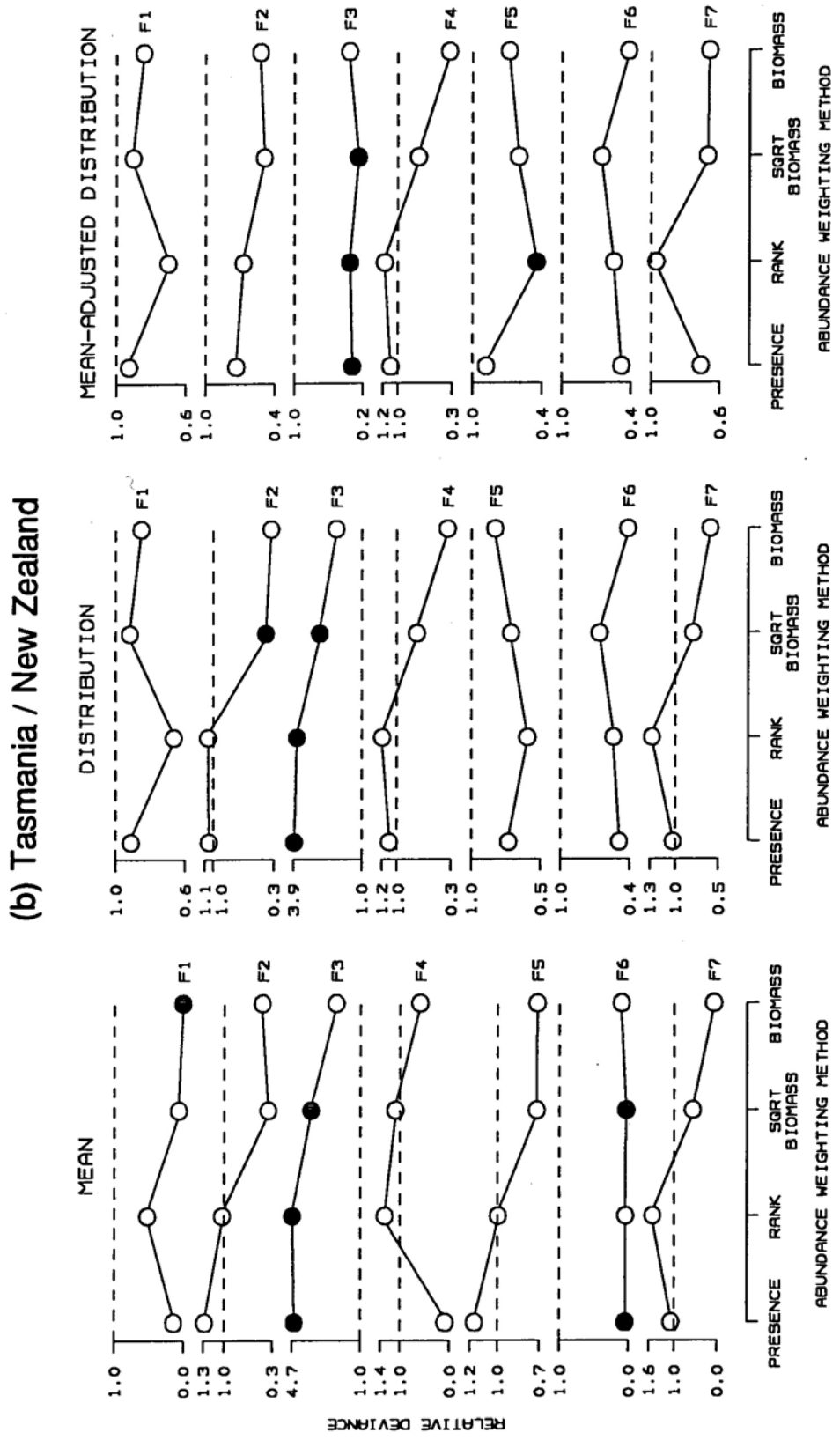



**Fig. 9.1** (continued)

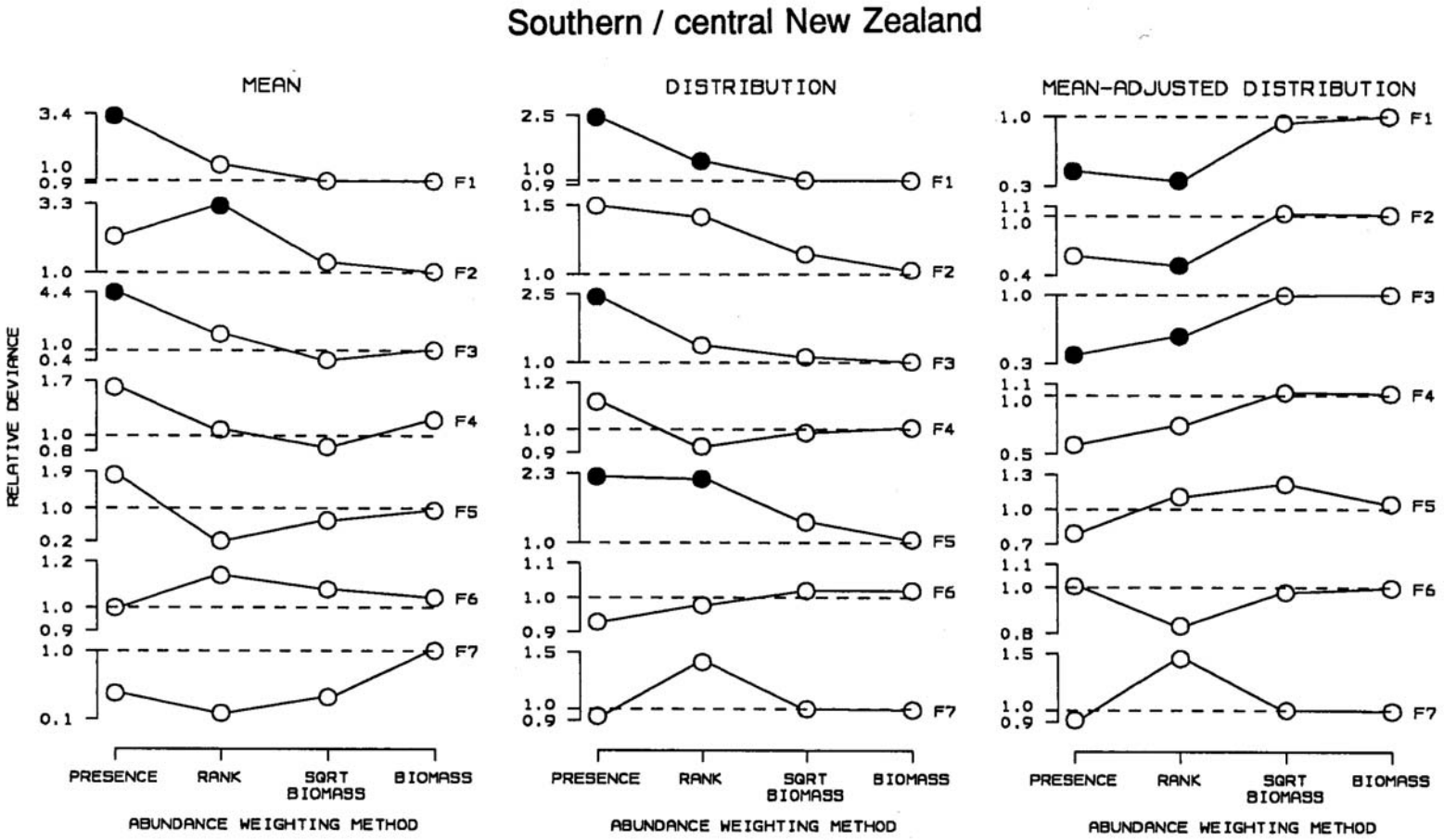



**Fig. 9.2** Null model randomisation tests for convergence or divergence in texture between regional-scale *Nothofagus*-dominated communities southern (ZS) and central (ZC) New Zealand. Format as for Fig. 9.1.

*Local scale*

Northern New Zealand sites ZN2 Rotokura and ZN3 Clements are convergent in F1 (PSU succulence, specific weight, total chlorophyll, species height) with weighting by photosynthetic biomass (mean, distribution) or its square root (mean-adjusted distribution) and for mean-adjusted distributions in F5 (PSU nitrogen, phosphorus) with weighting by abundance rank (Fig. 9.3). There is significant divergence in means and distributions of F3 (PSU phosphorus, chlorophyll *a/b*) with weighting by abundance rank, and distributions of F4 (PSU thickness) with weighting by the square root of photosynthetic biomass.

*Closely matched sites from different landmasses*

Community means of F4 (PSU thickness) at T1 Balfour and A2 Cascades are convergent when species values are weighted by the square root of photosynthetic biomass; mean-adjusted distributions of the same factor are convergent with species weighted equally (Fig. 9.4a). There is a trend towards convergence in the mean-adjusted distributions of F5 (PSU nitrogen, phosphorus) at all weighting levels, significant with species weighted equally or by the square root of biomass. Both non-adjusted and mean-adjusted distributions of F6 (PSU lobation, inclination) are convergent at higher weighting levels. Mean-adjusted distributions of F7 (PSU shape) are convergent with species weighted equally. For F3 (PSU phosphorus, chlorophyll *a/b*) there is departure from the null model in opposite directions for means and distributions (divergence), as opposed to mean-adjusted distributions (convergence); trends are significant at lower weighting levels. Notably, in comparisons of mean-adjusted texture distributions, departure from the null model is in the direction of convergence ($R_{\hat{D};T}<1$) at all weighting levels, for all factors except F2 (PSU area, support fraction) and F7.

Convergence between community texture means for T2 Anne and ZN1 Ohakune is confined to two factors, F4 (PSU thickness) and F6 (PSU lobation, inclination) at lower weighting levels (Fig. 9.4b). There is no significant convergence between distributions of texture factors. For mean-adjusted distributions, however, there is convergence in F1 (PSU succulence, specific weight, total chlorophyll, species height), F3 (PSU phosphorus, chlorophyll *a/b*) and F5 (PSU nitrogen, phosphorus) at lower weighting levels. Furthermore, all factors have $R_{\hat{D};T}<1$ (a trend towards convergence) at all weighting levels. Divergence was detected in means and distributions of F3 at all abundance weighting levels except photosynthetic biomass, and in F5 with species weighted by presence only.

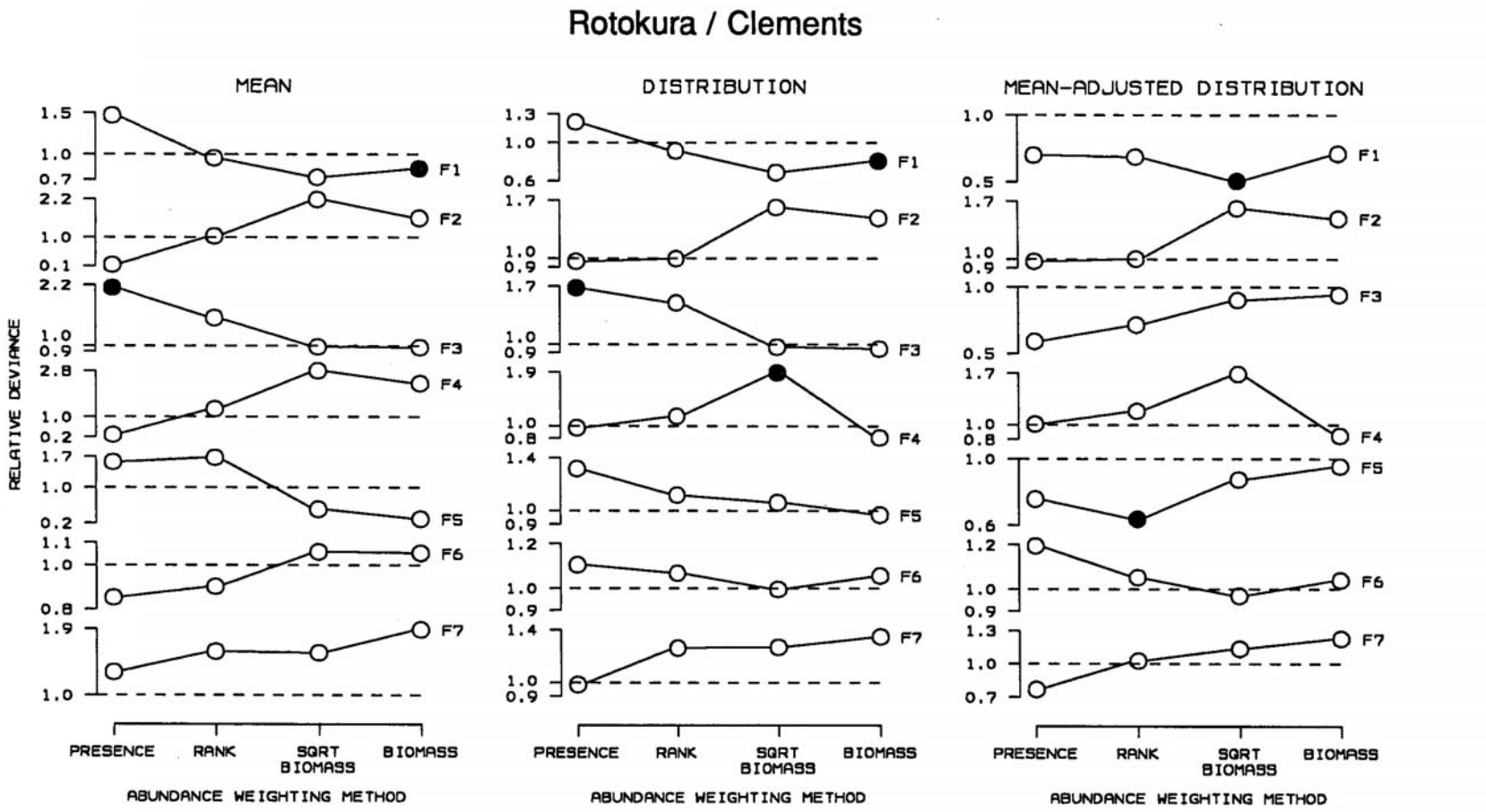



**Fig. 9.3** Null model randomisation tests for convergence or divergence in texture between local-scale *Nothofagus*-dominated communities ZN2 Rotokura and ZN3 Clements. Format as for Fig. 9.1.

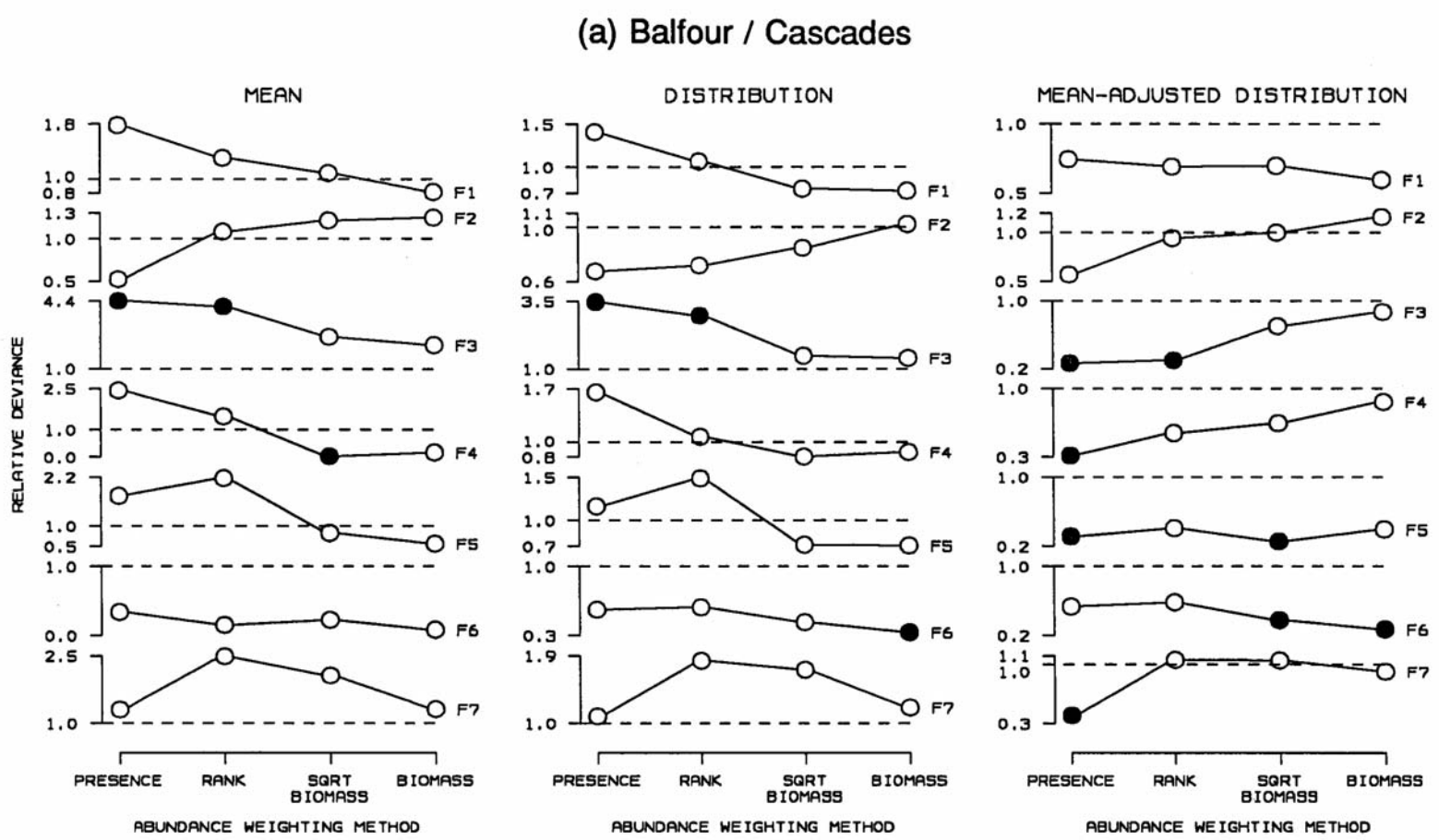



**Fig. 9.4** Null model randomisation tests for convergence or divergence in texture between *Nothofagus*-dominated communities from different landmasses closely matched in their environments: **(a)** T1 Balfour/A2 Cascades; **(b)** T2 Anne/ZN1 Ohakune; **(c)** ZN2 Rotokura/SA1 Quetrihué. Format as for Fig. 9.1.

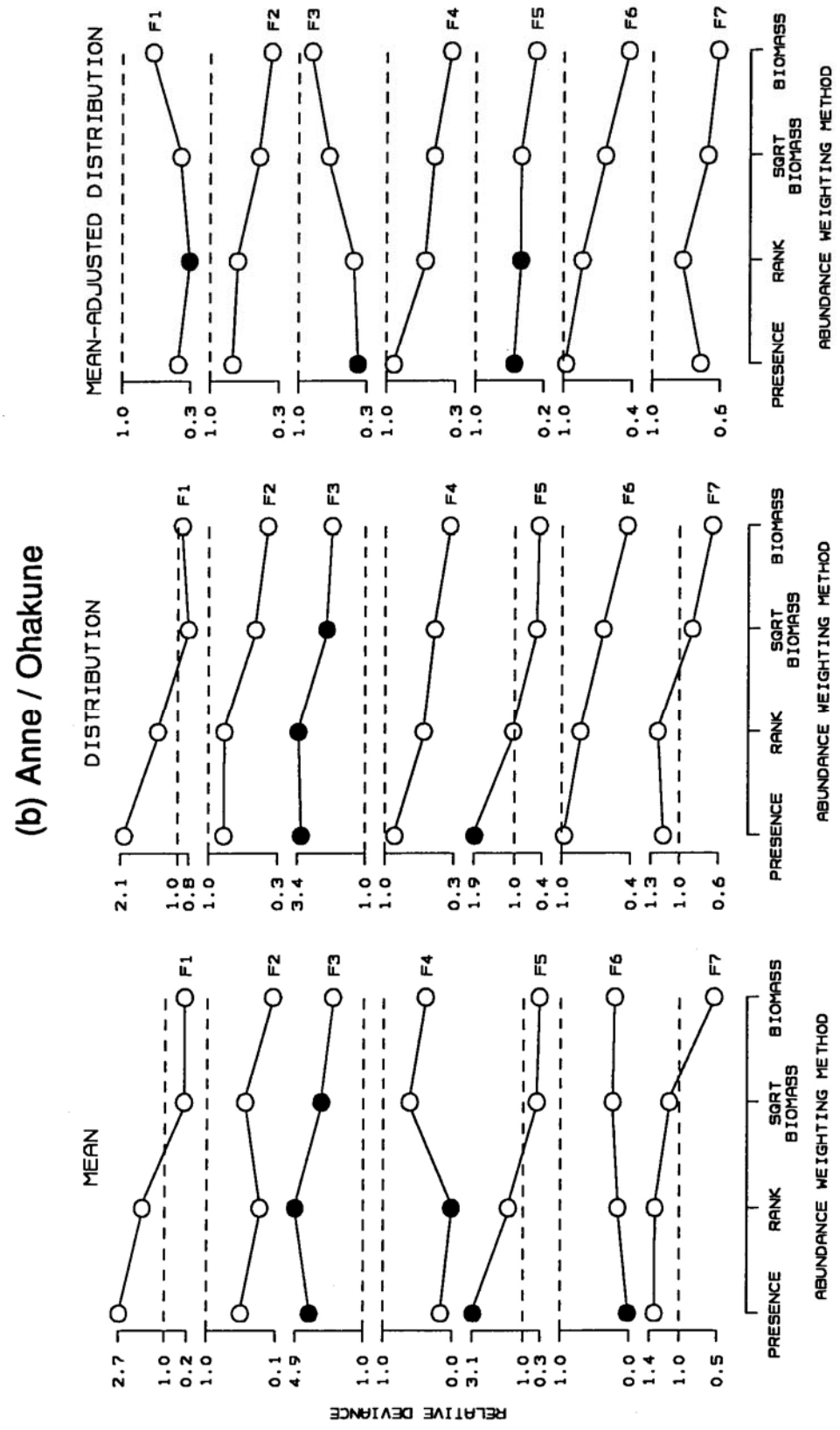



**Fig. 9.4** (continued)

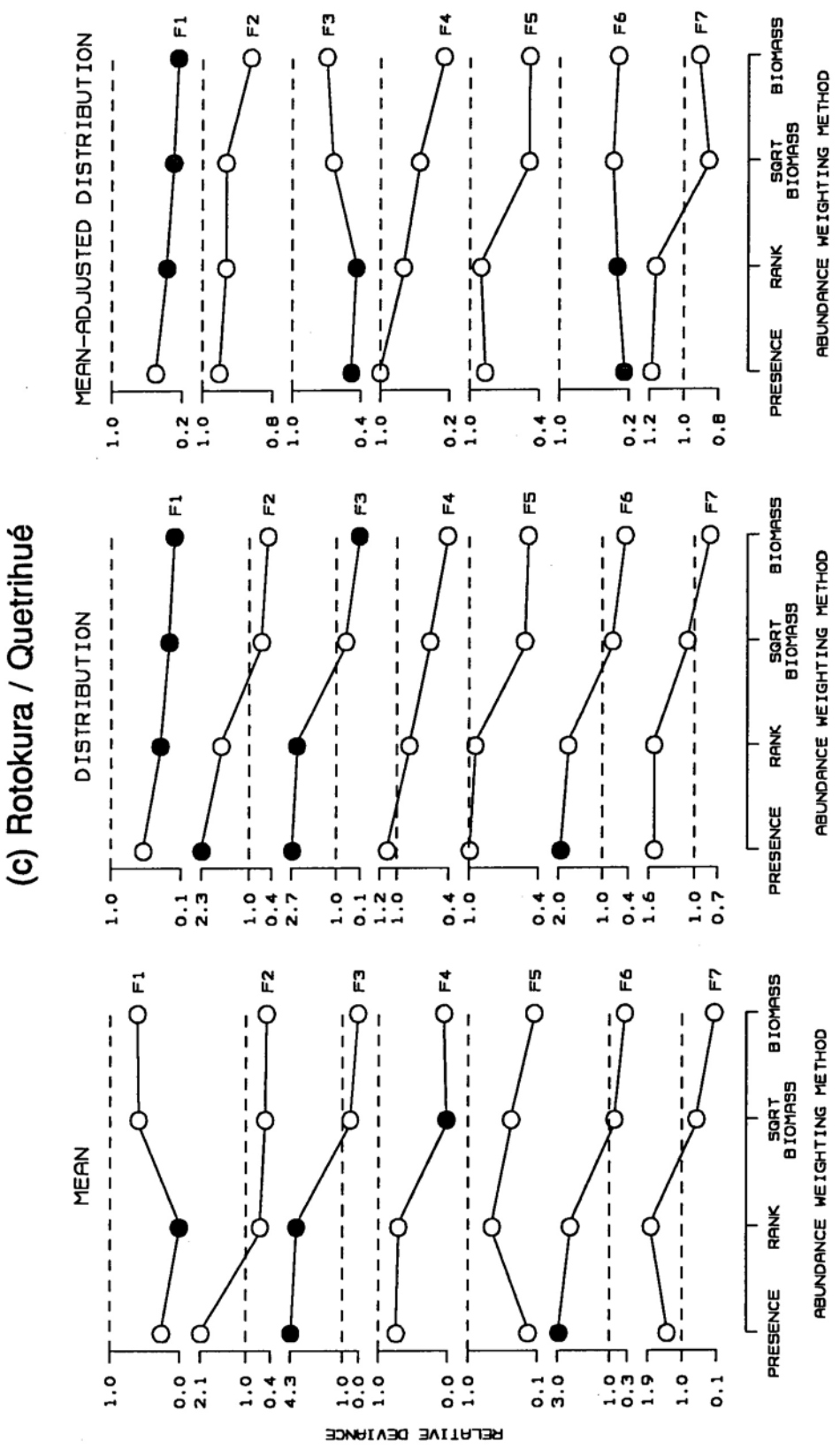



**Fig. 9.4** (continued)

Community means, distributions and mean-adjusted distributions of F1 (PSU succulence, specific weight, total chlorophyll, species height) are convergent between ZN2 Rotokura and SA1 Quetrihué, significantly so with weighting by abundance rank for means, and at all weighting levels except presence for distributions and mean-adjusted distributions (Fig. 9.4c). Means of F4 (PSU thickness) are convergent with species weighted by the square root of biomass. F3 (PSU phosphorus, chlorophyll *a/b*) is convergent when distributions (weighting by photosynthetic biomass) and mean-adjusted distributions (weighting by presence or abundance rank) are compared, but community means and distributions are divergent at lower weighting levels. A similar pattern applies to F6 (PSU lobation inclination), mean-adjusted distributions being convergent at lower weighting levels while means and distributions are divergent. Distributions of F2 (PSU area, support fraction) are divergent with species weighted equally.

### PATTERNS AMONG TEXTURE FACTORS

In comparisons of community texture means, only one factor, F1 (related to PSU succulence, specific weight, total chlorophyll and species height) showed convergence in a significantly larger number of tests than would be expected by chance: three of 16 independent community comparisons showed significant convergence in this factor when species were weighted by their photosynthetic biomass in calculating community means (Table 9.2). Divergence, by contrast, is significant overall, generally at lower abundance weighting levels, for all factors except F4 (PSU thickness) and F7 (PSU shape). The highest incidence of divergence is in F3 (PSU phosphorus, chlorophyll *a/b*).

Overall trends are similar for comparisons of texture distributions, although no factor shows convergence that is significant as a proportion of the number of tests carried out. Divergence is most marked at lower abundance weighting levels, and is significant overall for all factors except F2 (PSU area, support fraction), F6 (PSU lobation, inclination) and F7. F3, once again, was divergent in the largest number of tests.

In comparisons of mean-adjusted distributions, all factors except F6 and F7 were convergent in a significant number of tests, though only at lower weighting levels. F3, the factor most frequently divergent in comparisons of texture means and distributions, was most frequently convergent when mean-adjusted distributions were compared. F1 also shows a high incidence of convergence with species weighted by abundance rank, though the convergence was not significant overall at other weighting levels. No factor was divergent in a significant proportion of comparisons.

**Table 9.2** Incidence of significant convergence or divergence among 31 community comparisons and (in parentheses) for 16 independent community comparisons (see Fig. 6.1), in each of seven texture factors derived by factor analysis (see text). Results are shown for each of four methods of weighting species values by abundance and for each of three methods of expressing community texture (mean, distribution, mean-adjusted distribution). Overall significance, determined from the binomial distribution (see text), is shown for results from the 16 independent comparisons.

| | Factor | Convergence | | | | Divergence | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Presence | Rank | Sqrt biomass | Biomass | Presence | Rank | Sqrt biomass | Biomass |
| Mean | F1 | 0 (0) | 1 (0) | 3 (1) | 4 (3*) | 5 (4**) | 3 (2) | 1 (1) | 1 (1) |
| | F2 | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 4 (3*) | 5 (4**) | 1 (1) |
| | F3 | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 19 (8**) | 16 (6**) | 8 (2) | 0 (0) |
| | F4 | 1 (1) | 1 (0) | 3 (1) | 0 (0) | 4 (2) | 3 (1) | 0 (0) | 1 (1) |
| | F5 | 1 (1) | 0 (0) | 0 (0) | 0 (0) | 10 (6**) | 4 (3*) | 0 (0) | 0 (0) |
| | F6 | 3 (2) | 1 (1) | 3 (2) | 1 (0) | 4 (3*) | 0 (0) | 0 (0) | 1 (0) |
| | F7 | 0 (0) | 1 (1) | 1 (1) | 1 (1) | 0 (0) | 1 (1) | 2 (2) | 1 (1) |
| Distribution | F1 | 0 (0) | 3 (1) | 4 (2) | 2 (0) | 5 (4**) | 4 (3*) | 1 (1) | 0 (0) |
| | F2 | 0 (0) | 0 (0) | 1 (1) | 0 (0) | 4 (1) | 2 (1) | 2 (2) | 1 (1) |
| | F3 | 0 (0) | 0 (0) | 1 (0) | 1 (0) | 20 (9**) | 14 (6**) | 9 (3*) | 0 (0) |
| | F4 | 0 (0) | 0 (0) | 0 (0) | 1 (1) | 5 (3*) | 2 (1) | 1 (0) | 0 (0) |
| | F5 | 0 (0) | 0 (0) | 1 (0) | 0 (0) | 14 (6**) | 4 (4**) | 0 (0) | 0 (0) |
| | F6 | 0 (0) | 0 (0) | 1 (0) | 2 (1) | 2 (1) | 0 (0) | 0 (0) | 0 (0) |
| | F7 | 1 (1) | 1 (1) | 1 (0) | 1 (1) | 0 (0) | 3 (2) | 2 (2) | 1 (1) |
| Mean-adjusted distribution | F1 | 3 (1) | 11 (5**) | 5 (1) | 2 (1) | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| | F2 | 4 (3*) | 1 (1) | 2 (0) | 1 (0) | 0 (0) | 0 (0) | 1 (1) | 0 (0) |
| | F3 | 14 (7**) | 12 (6**) | 5 (2) | 0 (0) | 1 (0) | 1 (0) | 1 (0) | 0 (0) |
| | F4 | 5 (3*) | 1 (1) | 0 (0) | 1 (1) | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| | F5 | 7 (5**) | 9 (5**) | 2 (1) | 0 (0) | 2 (0) | 0 (0) | 0 (0) | 0 (0) |
| | F6 | 3 (1) | 3 (2) | 2 (0) | 3 (1) | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| | F7 | 2 (0) | 0 (0) | 1 (0) | 0 (0) | 0 (0) | 1 (0) | 0 (0) | 0 (0) |

*$0.01 \leq P < 0.001$; **$P < 0.001$ (no binomial probabilities in range $0.05 \leq P < 0.01$).

## 9.4 Discussion

COMMUNITY-LEVEL CONVERGENCE

When texture was expressed as the mean or distribution of factor values across species in each community, there was little evidence for convergence between communities. Although significant convergence was detected in a number of individual tests, the frequency of such tests was generally too low for the convergence to be deemed significant according to a binomial test (Table 9.2). Divergence, by contrast, was detected frequently, and was significant overall for all

factors except F7 (related primarily to PSU shape), when texture was expressed either as the community mean or distribution. For both ways of expressing texture, F3 (related to PSU phosphorus content and chlorophyll *a/b* ratio) showed the highest incidence of divergence.

Comparisons of mean-adjusted distributions produced quite different results: all factors except F6 (PSU lobation and inclination) and F7 were convergent in a significant number of tests at lower weighting levels, while none was significantly divergent.

Results obtained from comparisons of the factors derived in the present chapter closely reflect results obtained in Chapters 6, 7 and 8 (Tables 6.2, 7.2, 8.2) for the texture variates to which the factors are most closely related (Table 9.1). The same overall conclusions can be drawn. Environmental or historical differences may exist between many of the *Nothofagus*-dominated communities examined, resulting in significant differences between communities in means and distributions of most texture factors. Such divergence would tend to obscure convergence mediated by similar assembly rules, even if such assembly rules do apply. Mean-adjusted distributions of texture factors do show significant convergence for several sets of communities, suggesting that similar assembly rules apply in different communities, leading to community texture distributions that are similar in shape, though they differ in magnitude, arguably due to the effects of environmental or other differences between communities.

## INTERPRETATION OF TEXTURE FACTORS

The seven factors derived by principal component analysis and factor rotation of 13 texture variates are orthogonal and uncorrelated. This means that each represents an independent component of variation in the original texture data. It is possible that some factors summarise character variation produced by adaptation to limited resources — i.e. alpha niche axes. Such factors would be expected to show convergence between communities if assembly rules apply, partitioning the underlying niche space among sympatric species. Other factors might represent adaptation to aspects of the environment not correlated with resources, and therefore not subject to assembly rules. No convergence would be expected in such factors in comparison to expectation under the null model, but divergence could be observed. Some factors might also summarise 'stochastic' variation produced by various factors of minor importance. Because such variation will show (by definition) no strong trends across the data set, it will tend to be represented in the last few principal components, which account for the lowest proportions of total variation. Since six such axes were discarded prior to factor rotation, it is likely that much of the stochastic variation in the primary data set is no longer incorporated in the seven factors finally used.

All the factors except F6 and F7 showed convergence, significant as a proportion of the number of tests carried out, when mean-adjusted distributions of the factors within communities were compared (Table 9.2). This suggests that each of these factors, summarises a component of

variation in the texture data that could be related to species alpha niches. Presumably, the niche space partitioned among species is defined by resources in limited supply (Tilman 1982). It is not possible from the data in hand to identify the specific resources involved. However, some evidence is available from the factor loadings table (Table 9.1) showing which species characters are most closely related to each factor.

For example, F1 is most strongly related to the texture variates PSU succulence, specific weight, total chlorophyll and species height. Each of these characters would be expected to vary in response to light availability, while the inclusion of species height (the highest level in the canopy at which PSUs of a species were found to occur) strongly suggests a relationship to vertical structure. This implies that species scores on the factor F1 might tend to reflect their stature or (in the case of species not rooted at ground level) vertical position. Underlying resources that might be partitioned (e.g. by past or present competition) might include light or habitat space.

PSU phosphorus content has loadings >0.5 on both F3 and F5. PSU chlorophyll *a/b* ratio is also closely related to F3, suggesting that scores on this factor may reflect species adaptations to the light regime. PSU nitrogen content is highly correlated with F5, suggesting a possible association with nutrient availability (although both foliar phosphorus and nitrogen may also be correlated with irradiance; Evans 1989; Bongers & Popma 1988; Reich *et al.* 1991; Reich & Walters 1994).

### FACTORS VERSUS 'RAW' TEXTURE VARIATES

It was anticipated (in Section 9.1) that characterising texture by multivariate factors rather than simple texture variates, as was done in Chapters 6-8, might improve the sensitivity of analyses to convergence. It was expected that relevant variation related to alpha niche axes and irrelevant beta niche or stochastic variation might be partitioned into different factors by factor analysis. Factors related to alpha niche axes might then show convergence between some communities, even where the 'raw' texture variates most closely related to them might not.

In fact, the amount of significant convergence (and divergence) detected by comparisons of texture factors in this chapter is very similar to the amounts detected in corresponding texture variates in Chapters 6-8. For example, mean-adjusted distributions of F3 were found to be convergent in 14 and 12 community comparisons with species weighted by presence and abundance rank, respectively (Table 6.2). For the two variates most closely related to F3 the convergence was detected in 12 and 13 (PSU phosphorus) and 13 and 10 (PSU chlorophyll *a/b*) tests respectively (Table 8.2). In a number of cases, however, significant departure from the null model was obtained for a factor, where significant patterns could not be obtained for the texture variates most closely related to it. For example, means of F1 for landmass-scale communities Tasmania and New Zealand were found to be significantly convergent with weighting by

photosynthetic biomass (Fig. 9.1b); the four variates with loadings >0.5 on F1 — PSU succulence, specific weight, total chlorophyll and species height — all showed a tendency towards convergence ($R_{\bar{D},T}<1$) in the same comparison, but this was not significant for any of the variates (Fig. 6.2c).

In general, convergence or divergence detected in a texture factor in the present chapter, was likewise detected in one or more correlated variates in equivalent tests in previous chapters (compare, for example, Fig. 9.4a with Figs. 6.12a, 7.15a and 8.15a). The close correspondence between the results obtained using multivariate factors and 'raw' texture variates suggests that the original variates might have some association with species niches.

Seven factors were required to summarise most of the variation among the 13 texture variates (Table 9.1). This confirms that a considerable amount of variation is common to more than one of the original variates. It is likely that, in previous chapters, convergence or divergence detected in two or more variates in equivalent tests was the result of different aspects of adaptation to the same niche. For example, much of the observed variation in PSU phosphorus content and chlorophyll *a/b* ratio can be explained by a single variable, the factor F3 (Table 9.1). These two variates were often found to show similar patterns of departure from the null model (e.g. Figs. 6.2a), suggesting that they express the same niche structure. The factor F3 summarises this information, and generally shows the same patterns as both variates (e.g. Fig. 9.1a). Expressing texture by uncorrelated factors, summarising variation in the raw texture data, is parsimonious, avoiding the danger of interpreting convergence or divergence in multiple variates as independent events in cases where the same underlying mechanisms apply.

## PREVIOUS COMPARATIVE STUDIES OF MULTIVARIATE TEXTURE

The value of characterising species function by character syndromes rather than individual characters has often been recognised. In most comparative studies, however, the approach has been to group species into classes defined (explicitly or implicitly) by categories of attributes, rather than assigning them scalar values using multivariate techniques such as factor analysis. Communities may then be compared according to the relative representation of component species in different classes (e.g. Parsons 1976; Naveh & Whittaker 1979; Floret *et al.* 1990; Cornelius *et al.* 1991; Cowling *et al.* 1994; Cowling & Witkowski 1994). Class assignment may be achieved explicitly on the basis of species character data, for example, by the use of hierarchical cluster analysis methods (e.g. Parsons 1976; Jaksi & Delibes 1987; Boutin & Keddy 1993; Golluscio & Sala 1993; Guillén *et al.* 1994). More commonly, however, classes are defined *a priori* and assignment is either subjective, or based on one or more 'indicator' characters. In this case, the link between class membership and possession of specific traits is tacit. Examples include the still frequently invoked life forms of Raunkiaer (1934) (e.g. Danin & Orshan 1990; Floret *et al.* 1990; Shmida & Werger 1992), growth forms (e.g. Naveh & Whittaker

1979; Cornelius *et al.* 1991; Cowling *et al.* 1994), forest sinusiae (e.g. Smith 1973; Hubbell & Foster 1986; Wilson 1989) and animal trophic guilds (e.g. Fox 1981; Case *et al.* 1983).

Classification has the drawback that a proportion of the attribute information used as a basis for assigning species to classes is lost to subsequent analyses. In situations where detailed character data are available, scalar ordination methods (such as principal component analysis and factor analysis) have the advantage of simplifying the data (summarising many characters by fewer factors) without loss of relevant information. This characteristic is important where patterns being sought are expected to be weak, as appears likely for patterns produced by assembly rules (Simberloff 1982, 1984; Wilson 1991).

Ordination methods have been used to summarise community texture data in a small number of studies seeking community-level convergence. Ricklefs & Travis (1980) used principal component analysis to summarise morphological data for birds occupying scrub communities in North and South America. Similarities in morphological spectra between communities in Chile and California were sought by comparing the distributions of species from different regions in the multivariate space. Although a graphical comparison provided superficial evidence of morphological 'convergence,' the trend could not be confirmed statistically by nearest-neighbour analysis (see Section 7.4). Blondel *et al.* (1984) used a similar approach to look for ecomorphological convergence between bird communities of mediterranean-climate habitats in Europe and the Americas. Comparing the distributions in multivariate morphological space of species from the mediterranean-climate habitats, with species from a non-mediterranean `control' habitat, provided little evidence that the mediterranean communities were particularly well-matched. Wiens (1991b) used principal component analyses to express size and shape characteristics of Australian and North American shrub-desert birds as single variables, employing the nearest-neighbour approach of Ricklefs & Travis (1980) to test the hypothesis that each species from one continent would be most closely matched morphologically to a species from the other. The hypothesis could not be supported statistically. These studies differ from the present one in the methods used to seek convergence between communities. However, the use of ordination methods to assign morphological scores to species based on many characters is analogous to factor analysis of plant community texture data, as applied in the present chapter.

Similarity in the relative representation of species in the same guilds or functional groups in different communities, i.e. guild proportionality, has sometimes been sought as evidence for the operation of assembly rules (Wilson 1989; Bycroft *et al.* 1993; Wilson & Roxburgh 1994; Wilson *et al.* 1995; see Section 6.4). Guild proportionality is analogous to multivariate texture convergence, as carried out in the present chapter, the guilds representing (implicitly) classes of species with similar character syndromes. The primary difference between the two approaches is in the type of variable — categorical (the guilds) or scalar (factors) — by which texture is expressed.

## CONCLUSIONS

Factor analysis of texture data from *Nothofagus*-dominated communities revealed that most of the variation incorporated in the 13 texture variates (>75% of the variation in each) can be described by seven orthogonal factors. In particular, there is a high proportion of variation in common to the variates PSU succulence, specific weight, total chlorophyll content and species height; all four variates are highly correlated with the factor F1. Species scores on this factor might reflect the positions they occupy in the vertical forest structure.

Although it was expected that some of the derived factors might represent better proxies for species niches than the raw texture variates, the results of tests for community texture convergence carried out in this chapter generally consolidate rather than 'improve' the findings of Chapters 6-8. There is only very limited evidence that expressing texture by multivariate factors instead of 'raw' texture variates increased the ability of the tests to detect convergence between communities where it had occurred. It is likely that several of the 13 species characters chosen for study may show relatively strong relations to species niches; if so, extraction of factors would summarise variation shared among the character variates, but would not show a significantly improved correspondence with underlying niche axes.

# 10. Convergence among *Nothofagus*-dominated communities: focusing on height guilds

## 10.1 Introduction

In Chapters 6-9, texture convergence was sought in the entire vascular plant guild of *Nothofagus*-dominated communities. Implicit in this approach is the assumption that assembly rules apply to the entire vascular guild, causing distributions of functional attributes in different communities to converge. Assembly rules summarise the effects of interspecific interactions, such as competition, that would impose restrictions on what functional combinations of species are possible. The concept of assembly rules, and much of its associated theory, is historically associated with studies of animal community structure (Diamond 1975; Connor & Simberloff 1984; Wilson 1987; Stone & Roberts 1990). The principal mechanism assumed, by such studies, to underlie the operation of assembly rules is diffuse competition, whereby species influence one another by depleting pools of resources (particularly food) in common demand (MacArthur 1972b). Whereas diffuse competition can be readily envisaged as a factor structuring communities of motile animals, it is less applicable to plants, for which proximal interactions among sessile neighbours would be seem more likely to predominate (Aarssen 1992). If the interspecific interactions underlying plant assembly rules largely take place among neighbouring plants it follows that the individuals involved would tend to be similar in stature. Non-reciprocal interactions will, of course, occur between individuals of dissimilar stature. For example, canopy trees may profoundly influence the environment experienced by ground-layer species, whereas the reverse is less likely. However, such highly asymmetric interactions would hardly contribute to the operation of assembly rules (restricting interspecific niche overlaps), because the species involved have such dissimilar niches.

If it is true that the interspecific interactions most likely to give rise to plant community structure would involve plants of similar stature, searching for convergence (and therefore community structure) at the level of the whole plant community may be less than optimal. If assembly rules apply at all levels ('strata') in the vertical structure of each community (and if the other assumptions of the community convergence hypothesis are met) then convergence should be apparent between whole communities. However, if assembly rules apply for some strata but are absent or weak within others, convergence may not be readily detectable at the whole community level. This potential problem is equivalent to that highlighted by Diamond & Gilpin (1982), criticising the 'dilution of relevant data from guilds with irrelevant data from the whole species pool' in studies of bird community structure (Connor & Simberloff 1979). Since guild

associates (members of the same guild) tend to make demands on the same units of resources (Root 1967), species interactions should be stronger within guilds than among different guilds (Pianka 1980). Consequently, niche structure (and associated patterns such as character overdispersion and community-level convergence[1]) might be more apparent at the guild than at the whole-community level.

The present chapter addresses the possibility that community structure in *Nothofagus*-dominated forests is restricted to or more pronounced within certain guilds. This is an alternative to the assumption, made in previous chapters, that community structure would apply at the level of the entire community (i.e. vascular plant guild). Using the null model randomisation tests developed in Chapters 6-9, convergence is sought within guilds corresponding to zones in the vertical forest structure. Each guild encompasses all species having a 'functional presence' in one of three such zones, and thus groups together species most likely to be involved in species interactions of the kind that might give rise to assembly rules, and so, community structure. The guilds conform approximately to the concepts of forest strata or sinusiae (Smith 1973; Wilson 1989), although the boundaries between them are arbitrary.

## 10.2 Methods

### TEXTURE DATA

Analysis was based on 13 texture variates, comprising species values for the 12 characters listed in Section 2.3.5 and for species height, defined in Section 6.2. Although convergence is sought, in the present chapter, within height guilds, for which vertical structure is likely to be less important than at the whole-community level as a potential niche gradient, it seems possible that fine-scale differences in vertical niches could influence community structure, even within height guilds. Species height was therefore included in the analyses, as in previous chapters. Field and laboratory methods are described in Chapter 2, while details of the 17 study sites are given in Chapter 3.

### DELINEATION OF GUILDS

Three guilds were defined, each comprising all species or entities 'functionally present' in one of the following classes of height above ground level: 0-1 m, 1-5 m and >5 m. A species was deemed functionally present in a guild if PSUs occurred within one of the height classes encompassed by the guild (as recorded in the field: see Section 2.3.2). In the case of species for

[1]In the present discussion, terms such as 'community structure' and 'community-level convergence' may, according to context, refer to processes or patterns at either the whole-community or guild level.

which multiple age-classes were recorded as separate entities, juvenile entities were included in a guild if PSUs of adults of the same species occurred in its height class. This was to ensure that character data for each species present in a guild as an adult would be as representative as possible of the lifetime niche of the species. It was possible for a given species or entity in a particular community to be present in more than one guild.

The three guilds were intended to correspond approximately to the ground/herb, shrub and tree strata, respectively (c.f. Wilson *et al.* 1995). However, these are primarily terms of convenience: although there clearly are guild patterns in the vertical structure of forest communities, it is unclear whether there are somewhat discrete strata, or, alternatively, niche variation is approximately continuous from ground to canopy level (Wilson 1989). The vertical boundaries imposed between the guilds defined here are arbitrary: it is not implied that they correspond to discontinuities in the distribution of species in niche space.

*Texture data within guilds*

Character data were obtained for each species or entity at each study site. However, no distinction between samples obtained from different height classes (i.e. guilds) was made at the measurement stage (Sections 2.3.2, 2.3.4). Therefore, site character values were retained with species when they were assigned to guilds. Abundance (photosynthetic biomass) data associated with species were, however, adjusted to take account of the relative functional abundance of species within guilds. In each guild $i$, a species was assigned a photosynthetic biomass $a_i$ according to the formula:

$$a_i = \frac{\sum_{j=1}^{n} c_j \cdot p_{ij}}{n} \cdot w$$

where $c_j$ = number of PSUs of the species recorded in quadrat $j$;

$p_{ij}$ = proportion of PSUs of the species in quadrat $j$ estimated to occur in height classes up to the highest encompassed by guild $i$;

$n$ = number of quadrats sampled;

$w$ = mean PSU dry weight for the species at the study site.

ANALYSIS

*Texture convergence*

Convergence in texture between corresponding guilds in different communities was sought using randomisation tests comparing observed among-community variation in texture to variation expected under a null model assigning species characters to communities at random. The null model is described fully in Section 6.2. In separate tests, texture was characterised by the distribution (test statistic $\hat{D}_T$) and mean-adjusted distribution ($\hat{D}'_T$) of each of the 13 texture variates within the guild of interest at each of the communities being compared. Tests comparing community texture means (test statistic $\bar{D}_T$) were not performed in this chapter, since it is clear from comparisons in Chapters 7 and 9 that tests based on texture means tend to yield very similar results to equivalent tests comparing texture distributions. Of the two approaches, tests based on distributions are expected to be somewhat less prone to type I errors (Section 7.1), and were therefore applied here.

*Comparisons performed*

Comparisons within the 0-1 m guild were performed for 31 sets of communities at the landmass, regional and local scales, while binomial tests for overall significance (Section 6.2) were applied to the results obtained for 16 independent community comparisons. The hierarchy of comparisons is described in Section 6.2 and depicted graphically in Fig. 6.1.

For the 1-5 m and >5 m guilds, it was not possible to perform the full set of community comparisons. This was the case where there were fewer than two species unique to just one of the assemblages (guilds within communities) being compared. As species in common to more than one community in a comparison were not randomised under the null model (Section 6.2), it would not be possible to demonstrate departure from the null model in such cases, rendering the comparison meaningless. Comparisons that could not be performed for this reason were, for the 1-5 m guild, ZC1/ZC2, ZN1/ZN2/ZN3; for the >5 m guild, ZC1/ZC2, ZS1/ZS2/ZS3, T1/T2/T3, T2/T3, ZS/ZC/ZN. The number of comparisons performed was therefore 29 (14 independent) for the 1-5 m guild, and 26 (15 independent) for the >5 m guild.

## 10.3 Results

GUILD SPECIES NUMBER

The number of species unique to each community/guild combination can influence the degree of departure from null expectation observable using the randomisation tests performed in this study. The data presented in Table 10.1 illustrate, for the seven sample comparisons discussed in detail

below, general differences among guilds in the number of species or entities available for randomisation under the null model. The data are interpreted in Section 10.4.

**Table 10.1** Total number of species or entities available (`free') for randomisation in tests based on the null model described in Section 6.2, for seven sample community comparisons including all species in each community, or species in one of three guilds — 0-1 m, 1-5 m and >5 m — in each community. Full names of communities identified by codes in the table are given in Section 3.2 and in subsequent text.

| Comparison | Free species/entities | | | |
|---|---|---|---|---|
| | Community | 0-1 m | 1-5 m | >5 m |
| T, A, Z, S | 285 | 261 | 206 | 97 |
| T, Z | 159 | 149 | 109 | 53 |
| ZS, ZC | 42 | 37 | 37 | 9 |
| ZN2, ZN3 | 53 | 54 | 29 | 16 |
| T1, A2 | 49 | 45 | 38 | 22 |
| T2, ZN1 | 91 | 79 | 63 | 30 |
| ZN2, SA1 | 98 | 93 | 64 | 27 |

PATTERNS AMONG COMMUNITIES

For brevity, detailed results are presented only for a representative sample of the comparisons performed. For each guild, results are shown for overall comparisons among the four landmasses; for one pair of communities, well matched in their macroenvironments, at the landmass, regional and local scales; and for three well-matched sites from different landmasses.

*0-1 m Guild*

There is no significant convergence within the 0-1 m guild among the four landmass-scale communities (Tasmania, Australia, New Zealand and South America), when texture distributions[2] are compared (Fig. 10.1a). However the landmasses are divergent in most variates using one or more methods to weight species by their abundance. Comparing texture distributions adjusted to a constant mean, there is convergence in PSU inclination and chlorophyll *a/b* with species unweighted by abundance, and in PSU phosphorus and chlorophyll *a/b* at relatively high weighting levels. Divergence is still apparent in in PSU area, nitrogen, total

[2]Following the convention established in Chapter 9, ‘distribution’ will, unless otherwise qualified, refer to community texture distributions, not adjusted to a constant mean.

chlorophyll and (with weighting by abundance rank) chlorophyll *a/b*.

**Fig. 10.1** Null model randomisation tests for convergence or divergence in texture in the 0-1 m guild (see text) between landmass-scale *Nothofagus*-dominated communities **(a)** Tasmania (T), Australia (A), New Zealand (Z) and South America (S); **(b)** Tasmania and New Zealand. Results are shown from tests comparing texture distributions (test statistic $\hat{D}_T$) and mean-adjusted distributions ($\hat{D}_T'$). The relative deviance $R_T$ of among-community variation in texture is shown for each of 13 texture variates and four methods of weighting individual species values by abundance in calculations of community texture. A value of $R_T<1$ indicates similarity in texture between communities relative to a null model simulating random community assembly (see text); $R_T>1$ indicates dissimilarity relative to the null model. Broken lines signify null model expectation ($R_T=1$). Filled symbols correspond to significant departure from the null model (convergence for $R_T<1$; divergence for $R_T>1$; $P<0.05$). Key to abbreviations: RANK=abundance rank; SQRT BIOMASS=square root of photosynthetic biomass; BIOMASS=photosynthetic biomass (see text for full explanation). Texture variates are based on PSU characters except SF (support fraction) and HEIGHT (species height). Key: SLW=specific weight; N=nitrogen content; P=phosphorus content; TOTAL CHL=total chlorophyll content; CHL A/B=chlorophyll *a/b* ratio (see text for full explanation).

*The figure appears on the following page.*

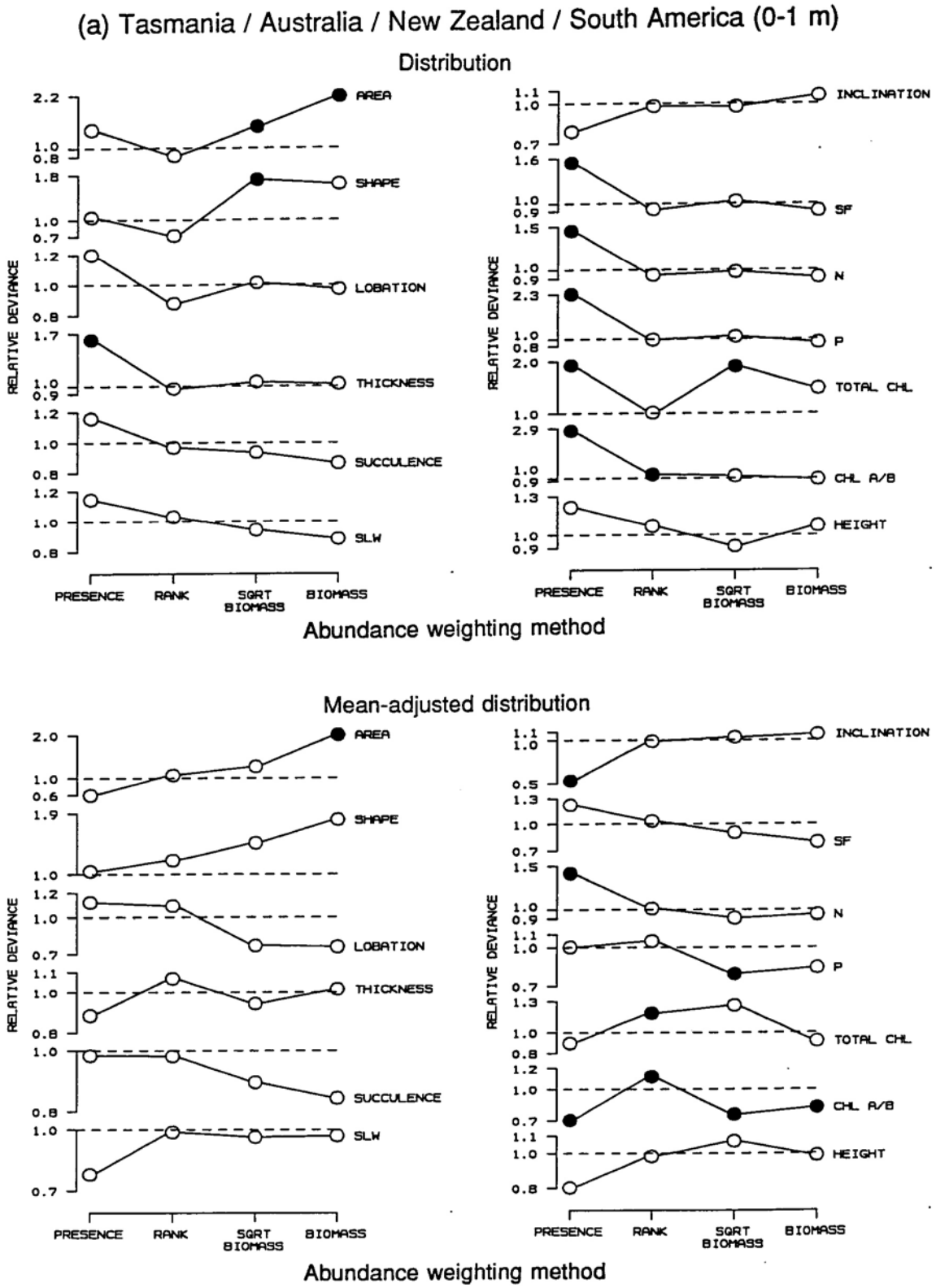



**Fig. 10.1** (continued)

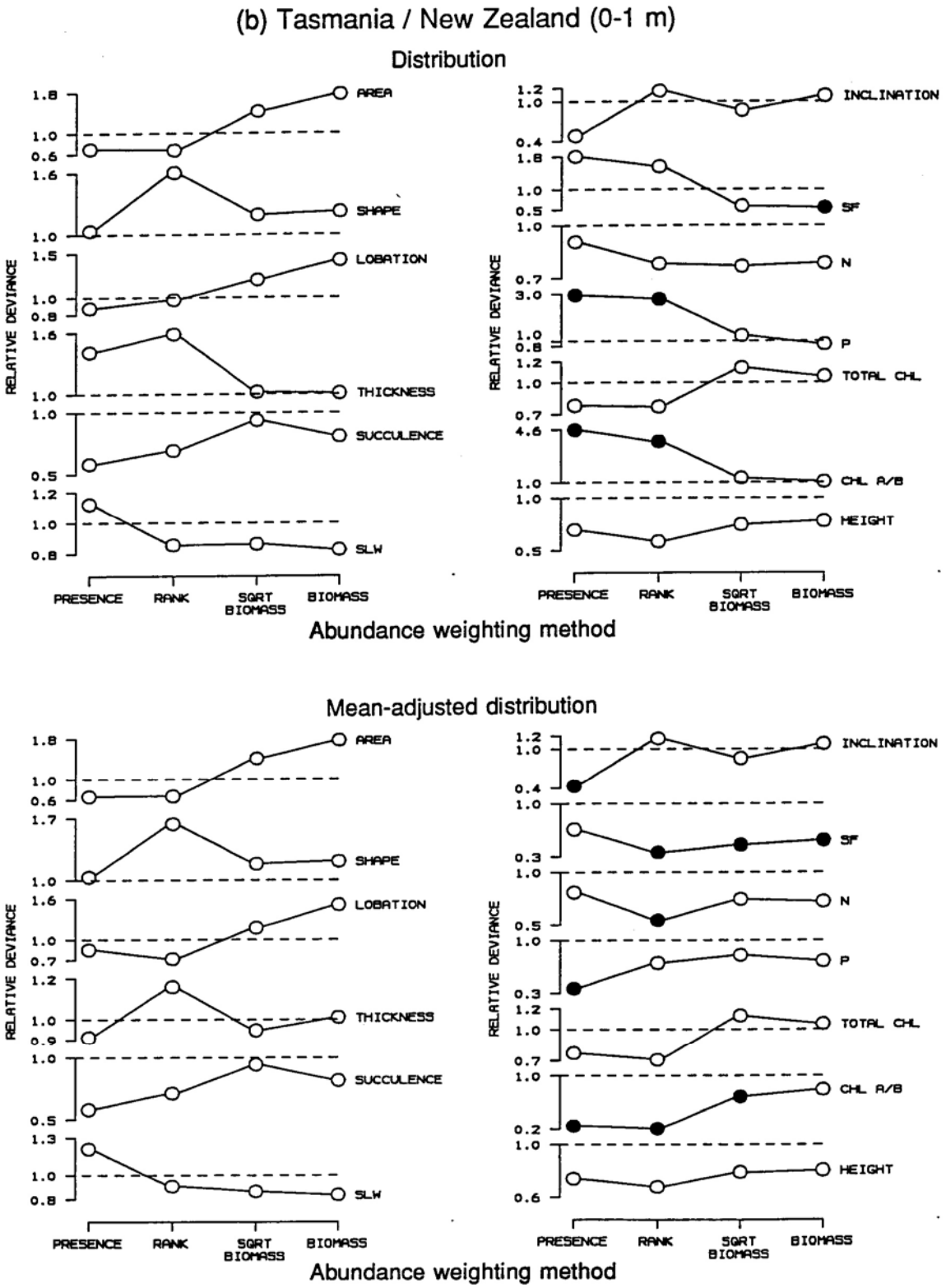



**Fig. 10.1** (continued)

Tasmania and New Zealand, which were identified in Chapter 3 as being relatively similar in their environments, show significant convergence only in support fraction, with weighting by photosynthetic biomass (Fig. 10.1b). At this heavy weighting level, the convergence is likely to apply primarily to a minority of species accounting for the majority of biomass in the guild. Divergence, however, is restricted to two variates: PSU phosphorus and chlorophyll *a/b*. Mean-adjusted texture distributions are convergent for PSU inclination, nitrogen, phosphorus, chlorophyll *a/b* and support fraction, primarily at lower weighting levels. There is no divergence.

Despite being closely matched in their environments, regional-scale communities southern (ZS) and central (ZC) New Zealand show no convergence in the distributions of any texture variate in the guild under consideration (Fig. 10.2). Several variates are divergent at lower weighting levels. Comparing mean-adjusted distributions, there is convergence in PSU succulence, phosphorus content and total chlorophyll at lower weighting levels, while PSU shape is divergent with weighting by abundance rank.

Texture distributions for local-scale communities ZN2 Rotokura and ZN3 Clements are not significantly convergent in any variate (Fig. 10.3). PSU area and support fraction are divergent at higher weighting levels, while PSU chlorophyll *a/b* is divergent with species weighted equally. Mean-adjusted distributions at these sites are convergent for PSU shape, nitrogen content and total chlorophyll at lower weighting levels, while support fraction remains divergent with species weighted by their biomass values.

Results of comparisons between sites from different landmasses well matched in their environments are depicted in Fig. 10.4. T1 Balfour and A2 Cascades are significantly convergent in their distributions of PSU thickness, with weighting by photosynthetic biomass (Fig. 10.4a). Several variates show significant divergence, most notably PSU total chlorophyll content, which is divergent at all weighting levels. Comparing mean-adjusted distributions, the sites are convergent in PSU phosphorus, total chlorophyll and chlorophyll *a/b* at lower weighting levels, but divergent in PSU shape and support fraction at higher weighting levels.

Distributions of PSU nitrogen content are convergent between T2 Anne and ZN1 Ohakune, when species values are weighted by the square root of photosynthetic biomass (Fig. 10.4b). There is divergence in PSU shape and chlorophyll *a/b*. Mean-adjusted distributions are convergent for three variates: PSU lobation, nitrogen content and chlorophyll *a/b*, while there is no significant divergence.

ZN2 Rotokura and SA1 Quetrihué are convergent in biomass-weighted distributions of PSU specific weight, while PSU shape, phosphorus content and chlorophyll *a/b* are divergent at lower weighting levels (Fig. 10.4c). Comparing mean-adjusted texture distributions, there is convergence in specific weight, phosphorus content and chlorophyll *a/b*. No variate shows significant divergence.

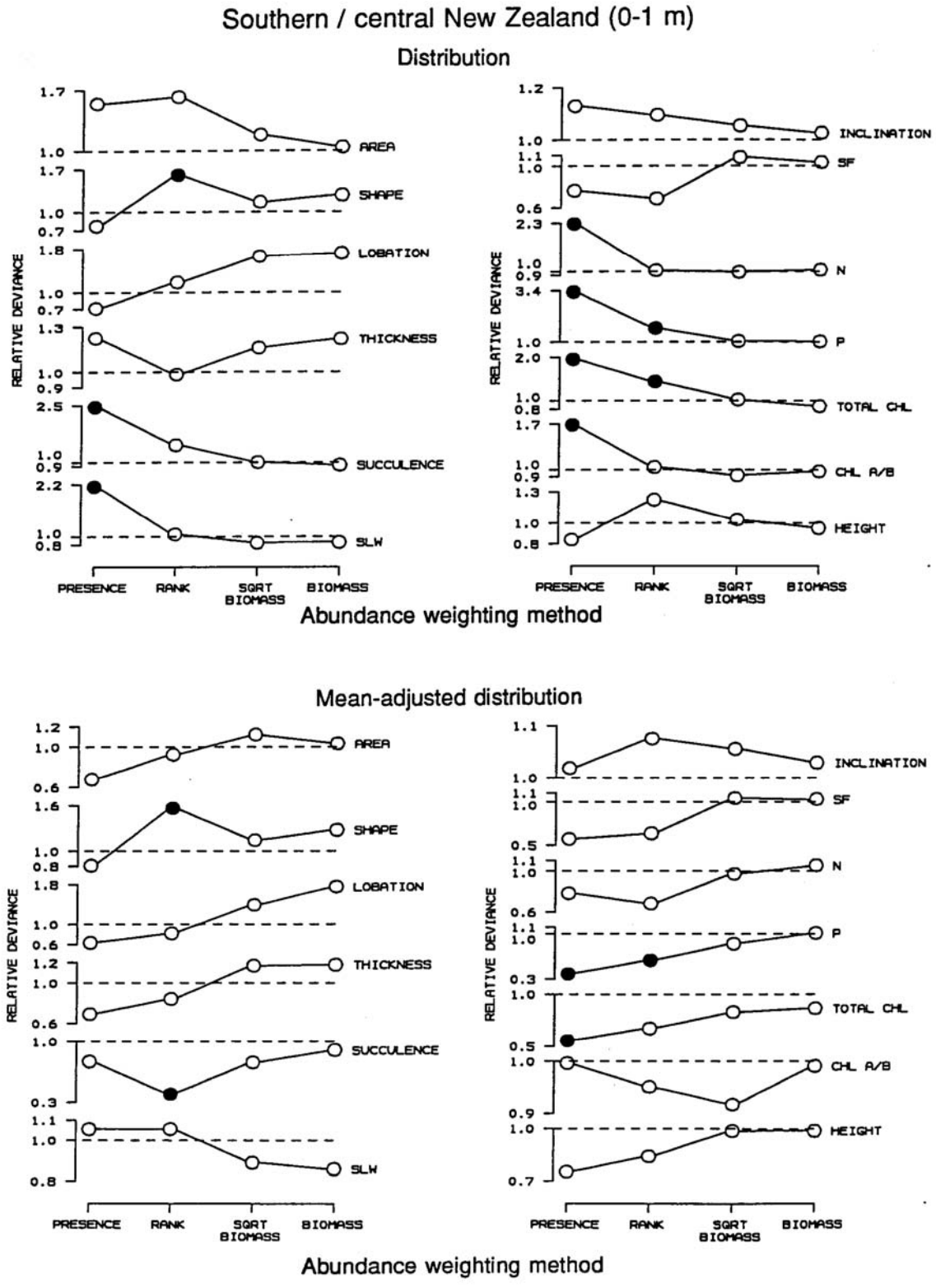



**Fig. 10.2** Null model randomisation tests for convergence or divergence in texture in the 0-1 m guild between regional-scale *Nothofagus*-dominated communities southern (ZS) and central (ZC) New Zealand. Format as for Fig. 10.1.

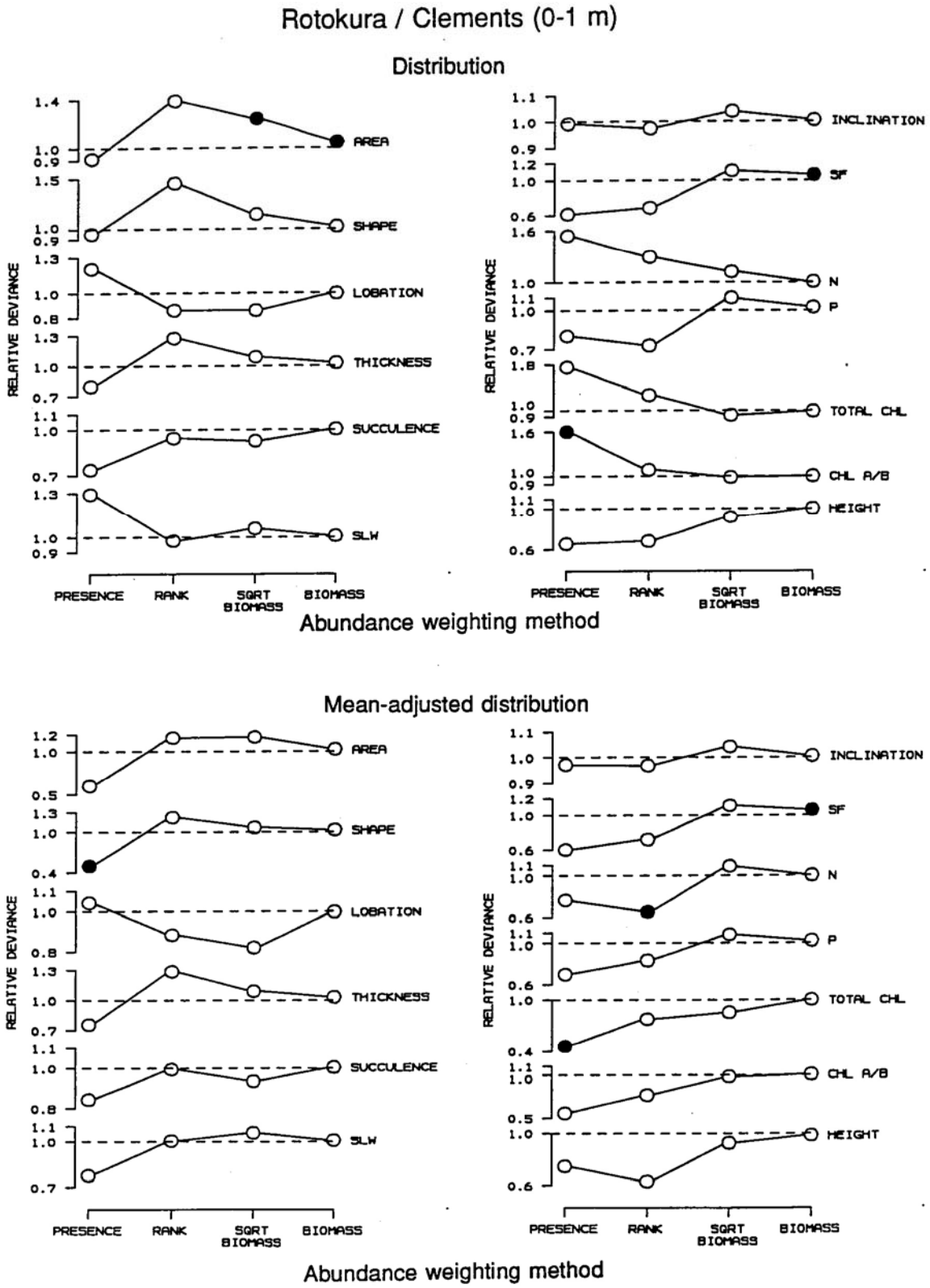



**Fig. 10.3** Null model randomisation tests for convergence or divergence in texture in the 0-1 m guild between local-scale *Nothofagus*-dominated communities ZN2 Rotokura and ZN3 Clements. Format as for Fig. 10.1.

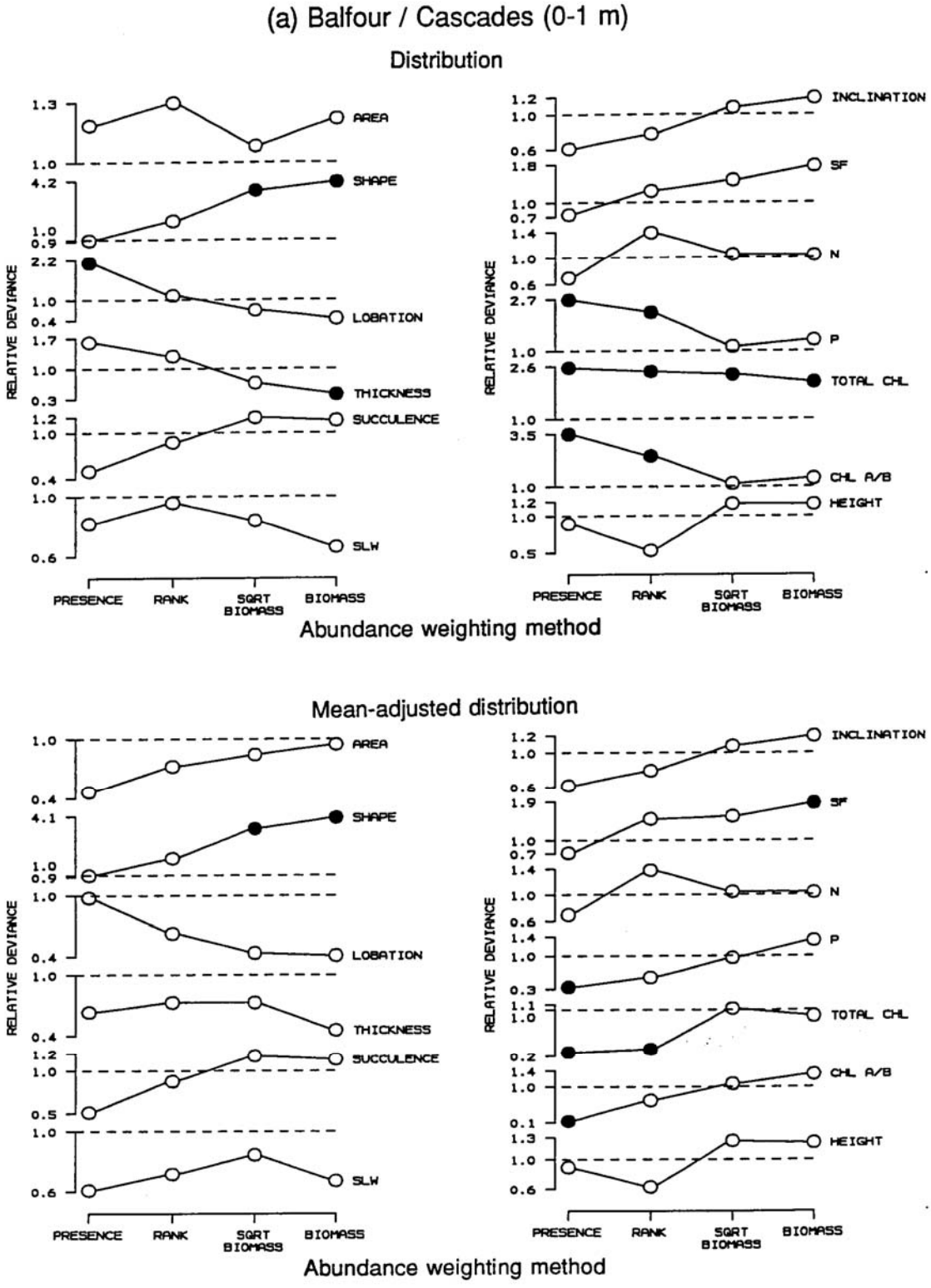



**Fig. 10.4** Null model randomisation tests for convergence or divergence in texture in the 0-1 m guild between *Nothofagus*-dominated communities from different landmasses closely matched in their environments: **(a)** T1 Balfour/A2 Cascades; **(b)** T2 Anne/ZN1 Ohakune; **(c)** ZN2 Rotokura/SA1 Quetrihué. Format as for Fig. 10.1.

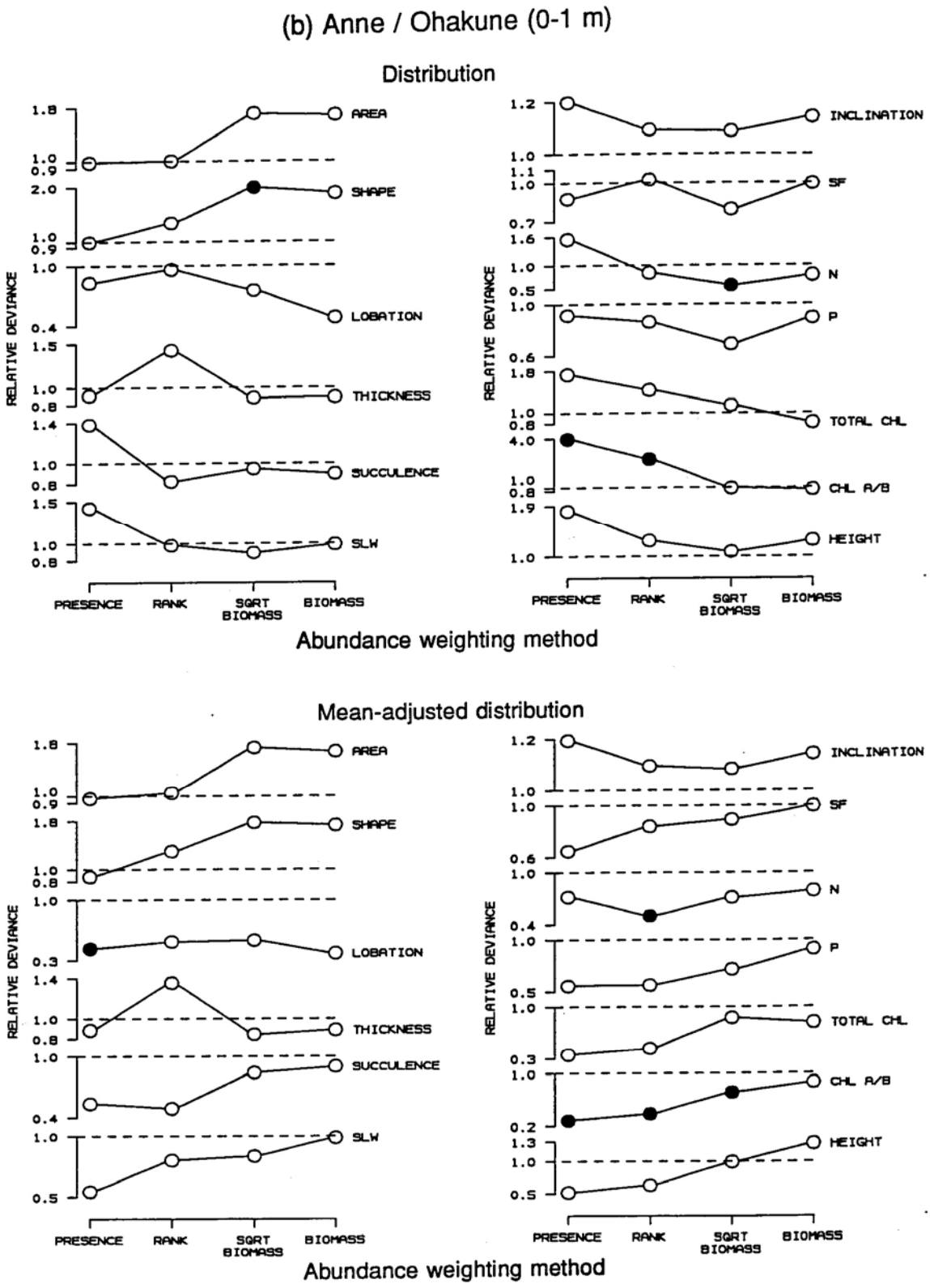



**Fig. 10.4** (continued)

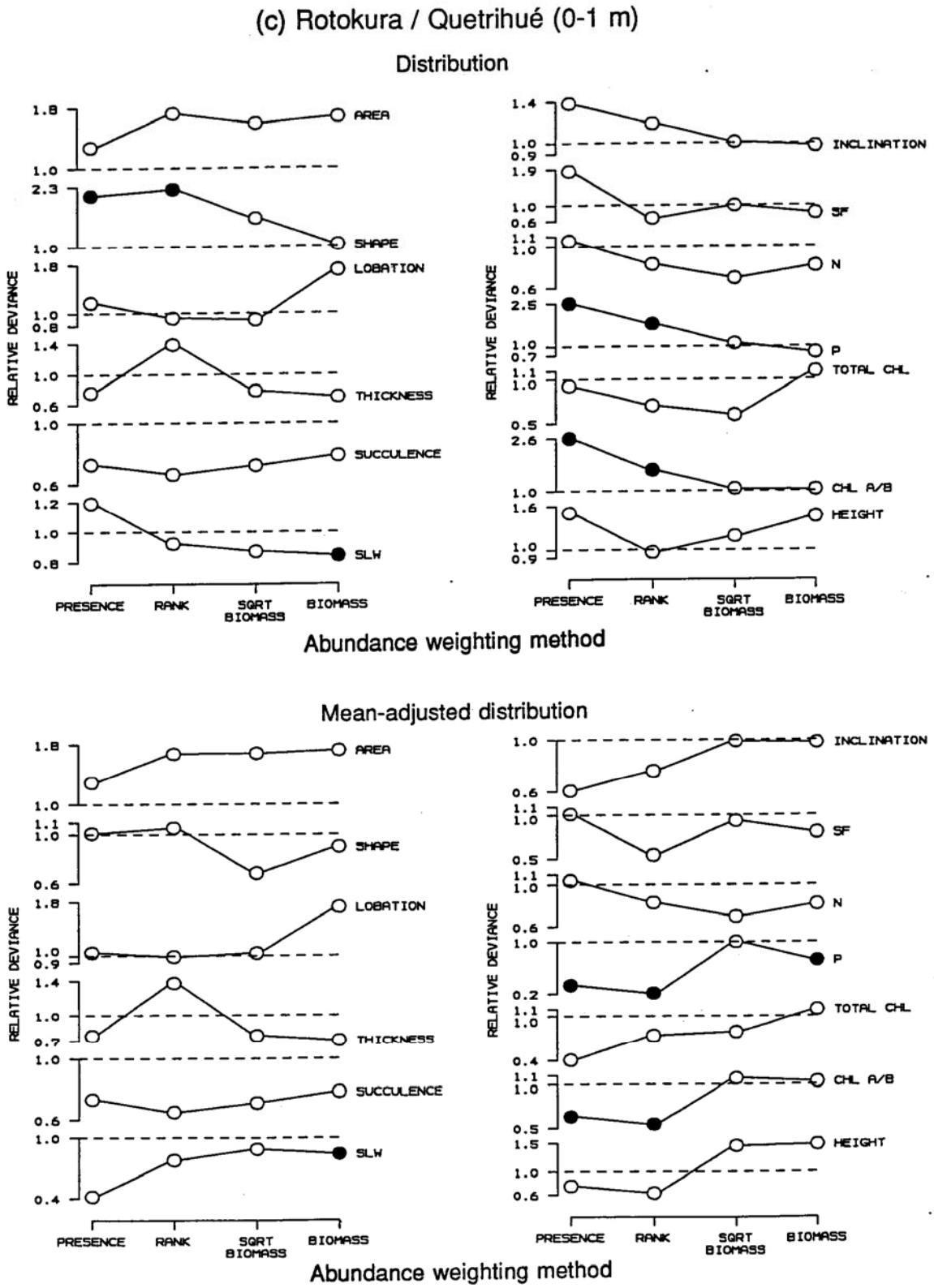



**Fig. 10.4** (continued)

*1-5 m Guild*

Results of overall comparisons among Tasmania, Australia, New Zealand and South America for the 1-5 m guild are shown in Fig. 10.5a. Overall, patterns are similar to those obtained for the 0-1 m guild, with some changes in significance but few in the direction of departure from expectation under the null model. There is no significant convergence between texture distributions, while several variates show significant divergence, especially at lower weighting levels. For mean-adjusted distributions, there is convergence in PSU phosphorus and chlorophyll *a/b*, in both cases with species weighted by the square root of photosynthetic biomass. PSU shape and total chlorophyll, and support fraction, show significant divergence.

No convergence was detected between texture distributions in the 1-5 m guild of Tasmania and New Zealand (Fig. 10.5b). Three variates, PSU phosphorus, total chlorophyll and chlorophyll *a/b*, are divergent at low to intermediate weighting levels. Comparing mean-adjusted distributions, there is convergence in PSU inclination, phosphorus and chlorophyll *a/b*, and no divergence. These results closely match those obtained for the 0-1 m guild for the same community combination.

Southern (ZS) and central (ZC) New Zealand show no significant convergence in texture distributions, while six variates are divergent at lower weighting levels (Fig. 10.6). In comparisons of mean-adjusted distributions, however, convergence was detected in PSU area, succulence, phosphorus content, total chlorophyll, support fraction and species height. The convergence generally applies at lower weighting levels, but is significant at all levels for PSU succulence and total chlorophyll. There is no divergence between mean-adjusted distributions.

Little departure from null expectation was detected for the 1-5 m guild in comparisons of northern New Zealand sites ZN2 Rotokura and ZN3 Clements (Fig. 10.7). The only test yielding a significant result (convergence) was of mean-adjusted distributions of PSU nitrogen content, with species values weighted by abundance rank.

Comparisons of texture distributions for T1 Balfour and A2 Cascades revealed no significant convergence, while divergence was detected in PSU shape, phosphorus content, chlorophyll *a/b* and (at all weighting levels) total chlorophyll (Fig. 10.8a). Mean-adjusted distributions, by contrast, were found to be convergent in PSU lobation, thickness, specific weight, phosphorus, total chlorophyll and chlorophyll *a/b* at low or intermediate weighting levels. Divergence was confined to PSU shape, with species values weighted by photosynthetic biomass or its square root.

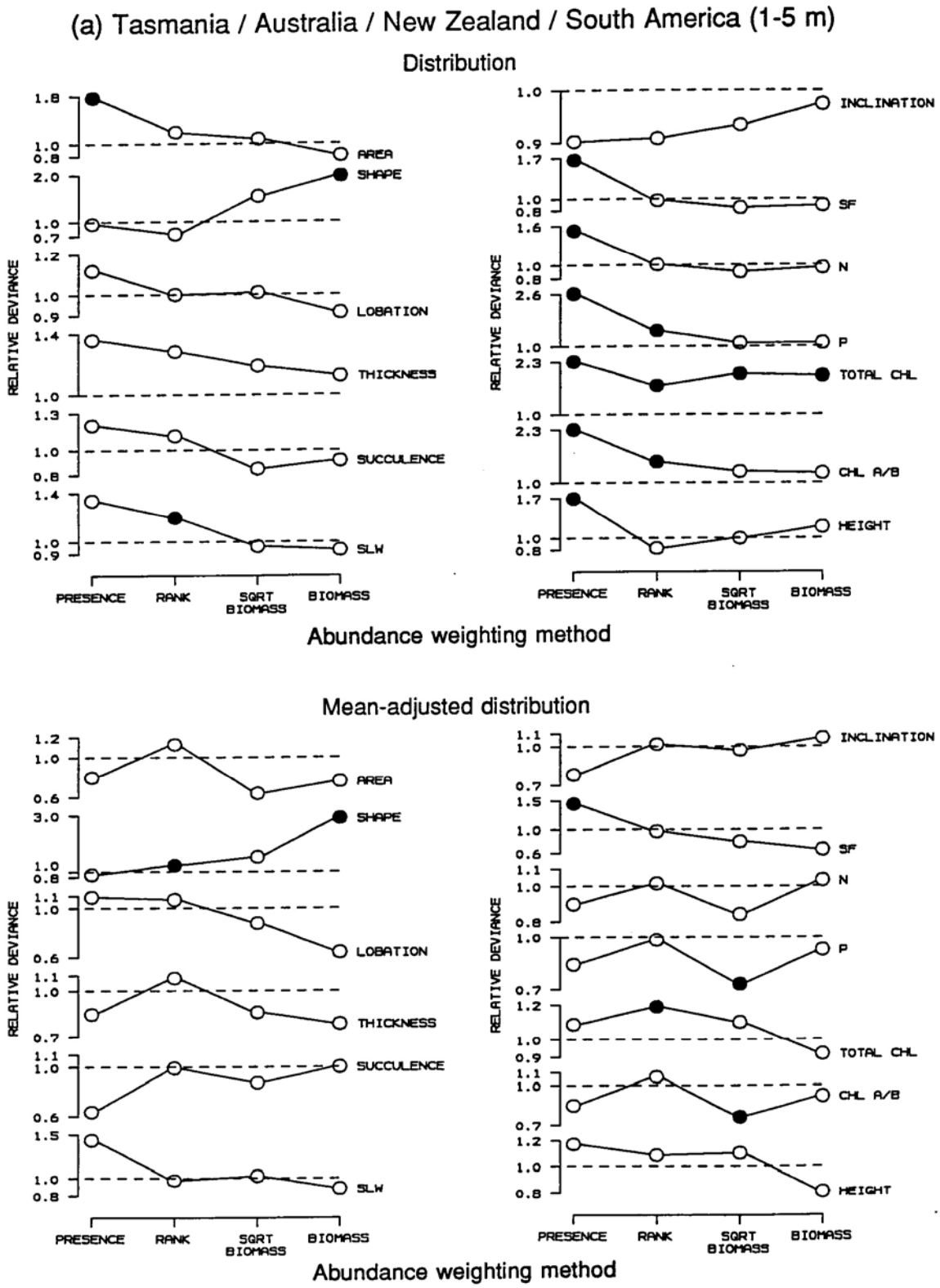
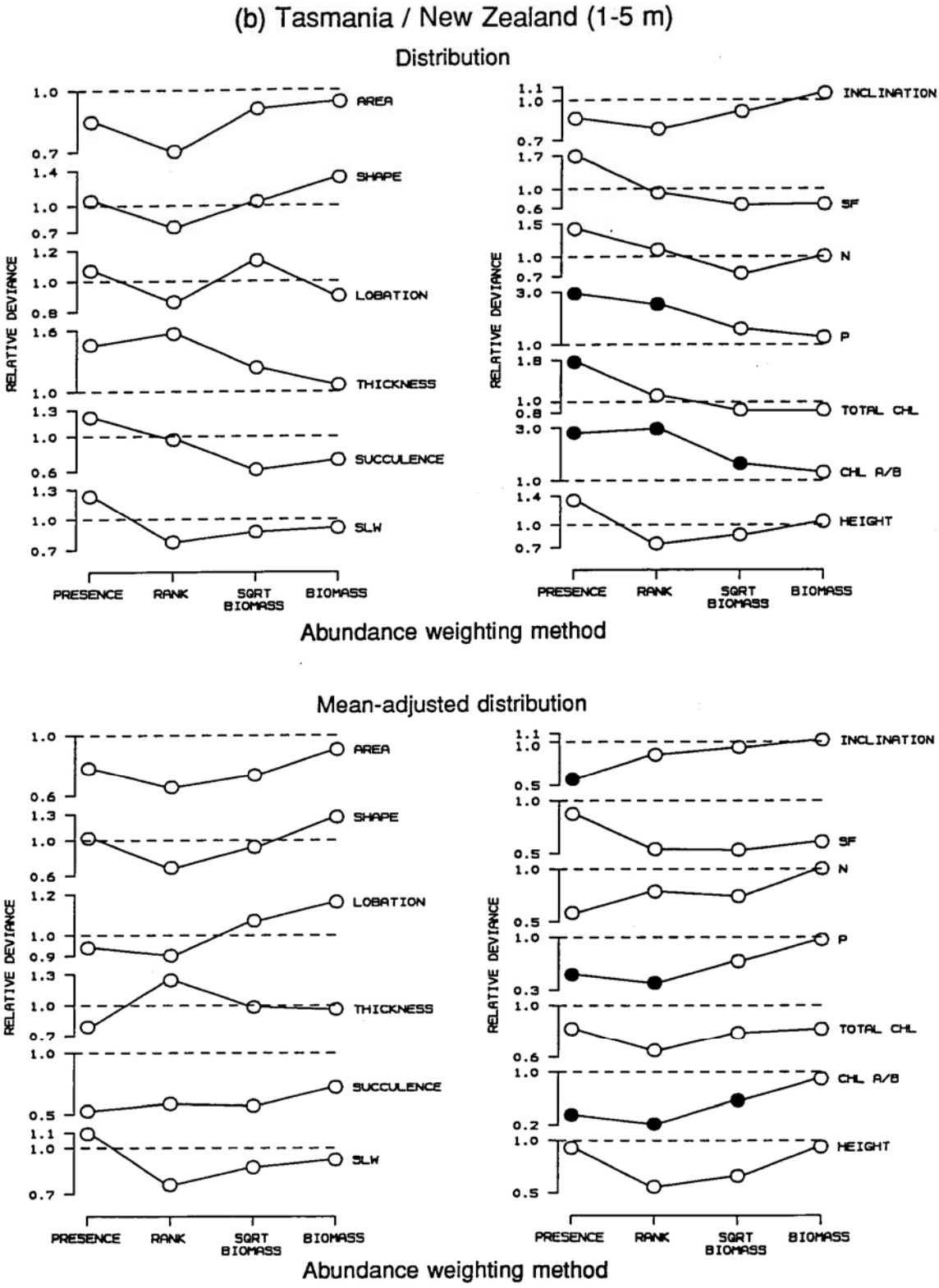



**Fig. 10.5** Null model randomisation tests for convergence or divergence in texture in the 1-5 m guild between landmass-scale *Nothofagus*-dominated communities **(a)** Tasmania (T), Australia (A), New Zealand (Z) and South America (S); **(b)** Tasmania and New Zealand. Format as for Fig. 10.1.

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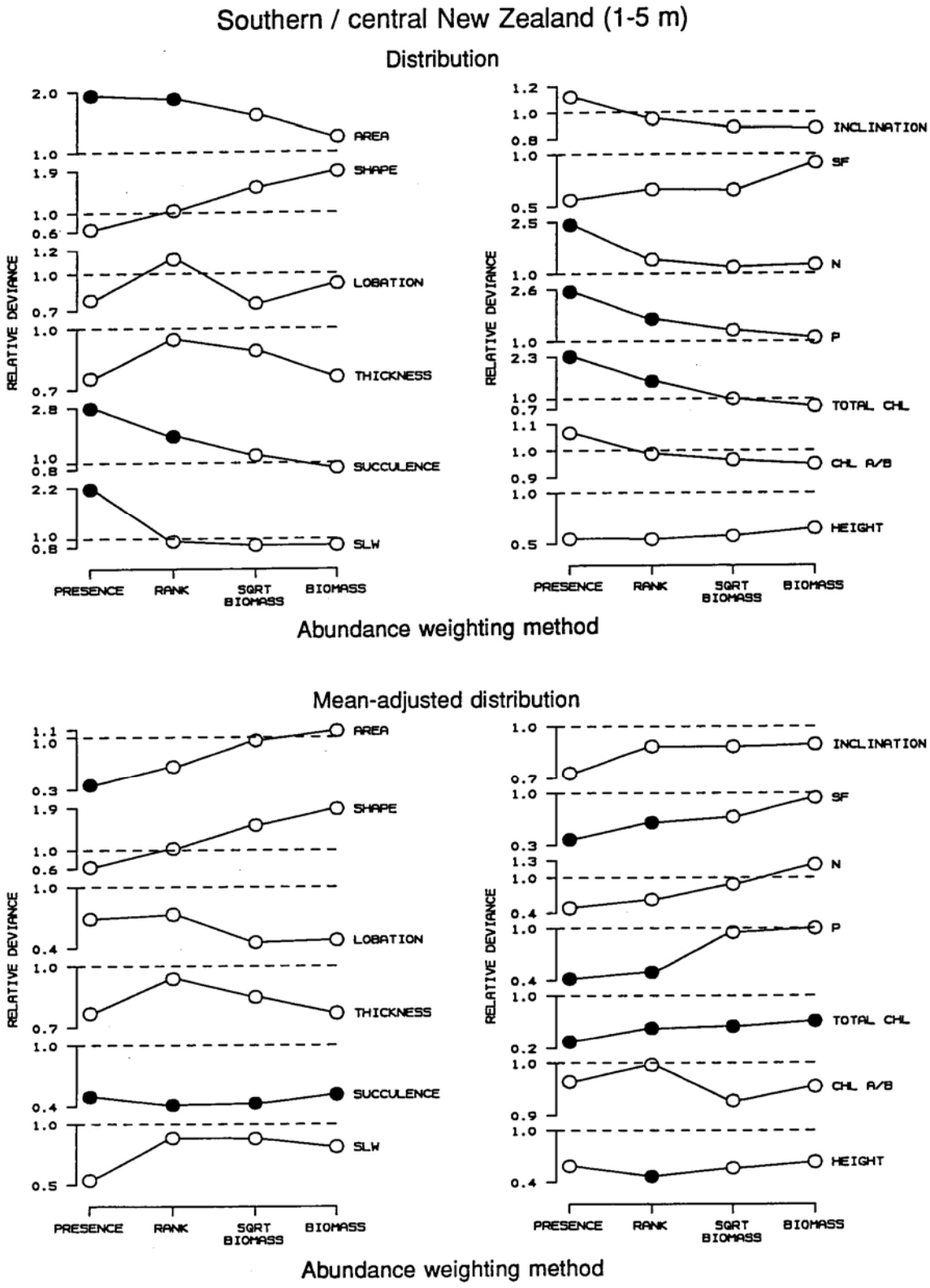



**Fig. 10.6** Null model randomisation tests for convergence or divergence in texture in the 1-5 m guild between regional-scale *Nothofagus*-dominated communities southern (ZS) and central (ZC) New Zealand. Format as for Fig. 10.1.

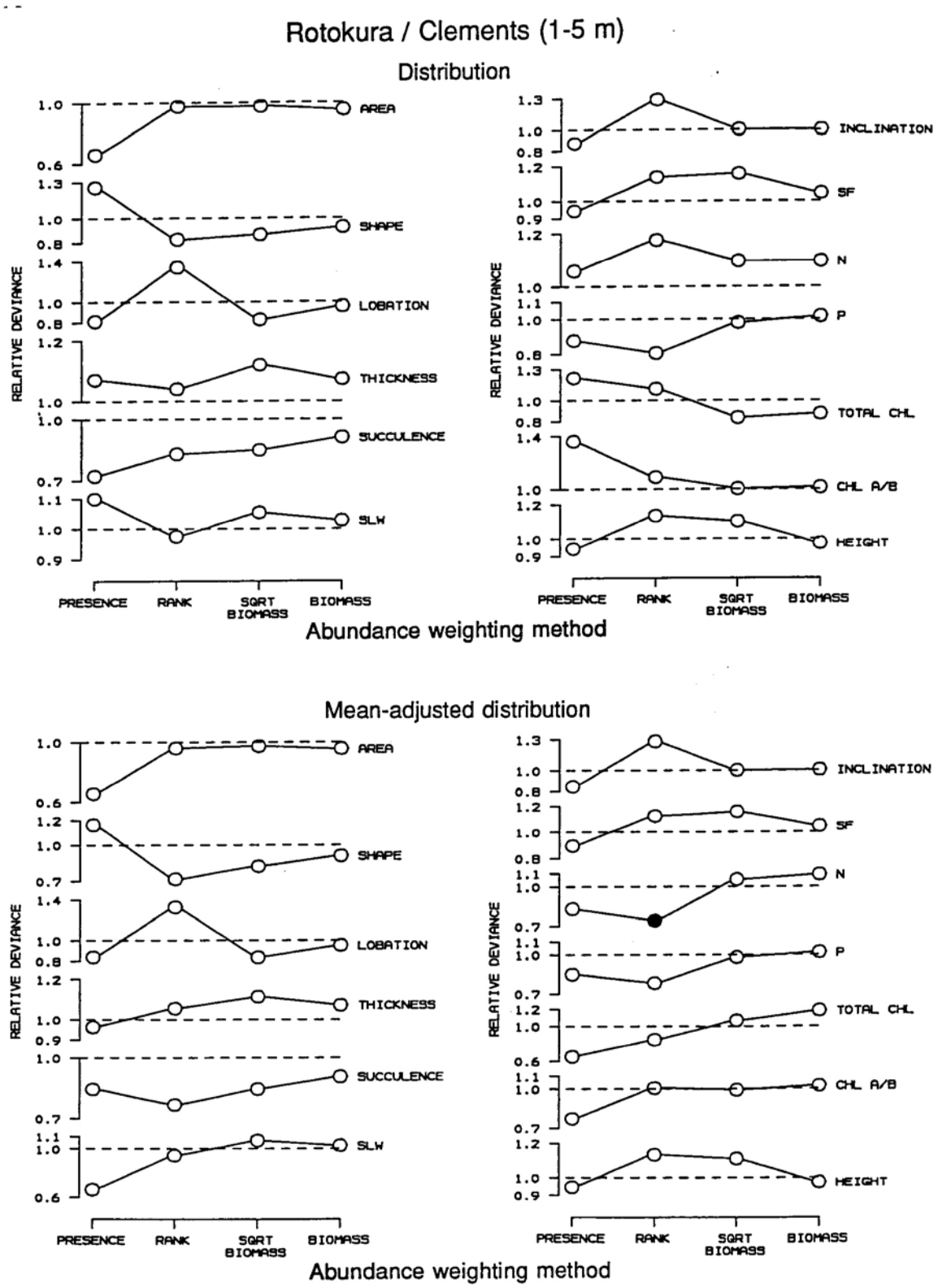



**Fig. 10.7** Null model randomisation tests for convergence or divergence in texture in the 1-5 m guild between local-scale *Nothofagus*-dominated communities ZN2 Rotokura and ZN3 Clements. Format as for Fig. 10.1.

Abundance rank-weighted distributions of support fraction are convergent between T2 Anne and ZN1 Ohakune, while PSU phosphorus (weighting by species presence) and chlorophyll *a/b* (all weighting factors except biomass) are divergent (Fig. 10.8b). Mean-adjusted distributions of PSU lobation (biomass), nitrogen (abundance rank), phosphorus (presence and rank) and chlorophyll *a/b* are convergent. There is no divergence between mean-adjusted texture distributions for these sites.

Comparisons of texture distributions for ZN2 Clements and SA1 Quetrihué revealed no significant convergence, and divergence in only two variates, PSU phosphorus and chlorophyll *a/b*, with species unweighted by their abundance (Fig. 10.8c). For mean-adjusted distributions, the same two variates are convergent with species unweighted, and there is no further significant departure from the null model.

*>5 m Guild*

Distributions of abundance rank-weighted PSU specific weight are convergent in the >5 m guild among Tasmania, Australia, New Zealand and South America (Fig. 10.9a). The landmasses are divergent in PSU phosphorus content, total chlorophyll, chlorophyll *a/b* and species height. Mean-adjusted distributions of PSU succulence (weighting by photosynthetic biomass), chlorophyll *a/b* (presence) and support fraction (abundance rank) are convergent, but there is divergence in species height (rank and biomass weighting).

Between Tasmania and New Zealand there is convergence in distributions of PSU succulence (abundance rank weighting), while phosphorus content and chlorophyll *a/b* are divergent (Fig. 10.9b). Comparing mean-adjusted texture distributions, there is convergence in PSU area, succulence, phosphorus and chlorophyll *a/b* at lower weighting levels, and in PSU shape with species weighted by photosynthetic biomass. No significant divergence was detected between mean-adjusted distributions.

Tests comparing southern (ZS) and central (ZC) New Zealand revealed no significant departure from null model expectation, whether texture was expressed as the distribution or the mean-adjusted distribution of character values in the >5 m guild at each community (Fig. 10.10).

Distributions of PSU specific weight and chlorophyll *a/b* are convergent between ZN2 Rotokura and ZN3 Clements, with species weighted equally (Fig. 10.11). No significant divergence was detected. There is convergence in mean-adjusted distributions of PSU succulence and specific weight at lower weighting levels, while PSU shape is divergent with photosynthetic biomass as the weighting factor.

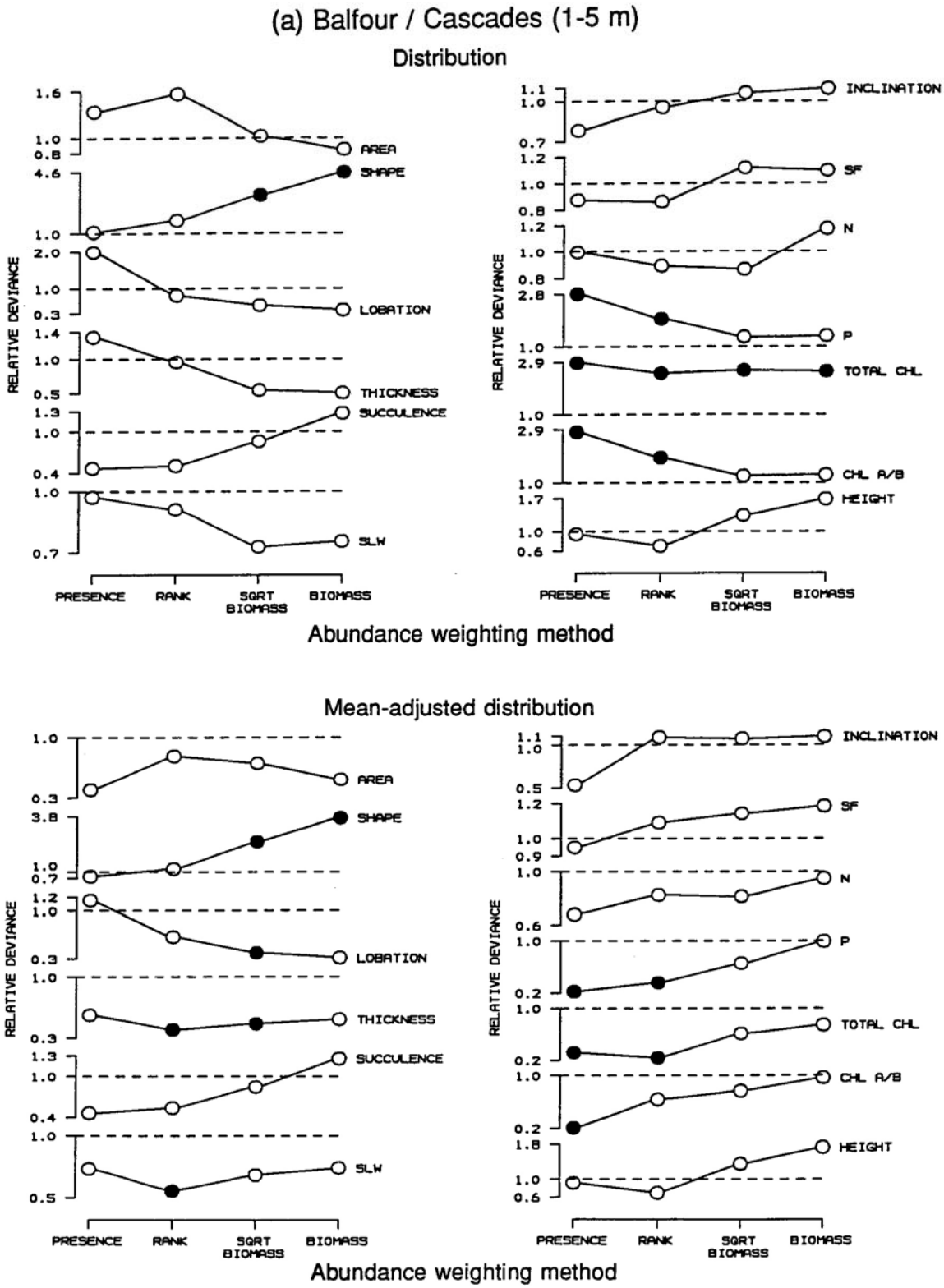



**Fig. 10.8** Null model randomisation tests for convergence or divergence in texture in the 1-5 m guild between *Nothofagus*-dominated communities from different landmasses closely matched in their environments: **(a)** T1 Balfour/A2 Cascades; **(b)** T2 Anne/ZN1 Ohakune; **(c)** ZN2 Rotokura/SA1 Quetrihué. Format as for Fig. 10.1.

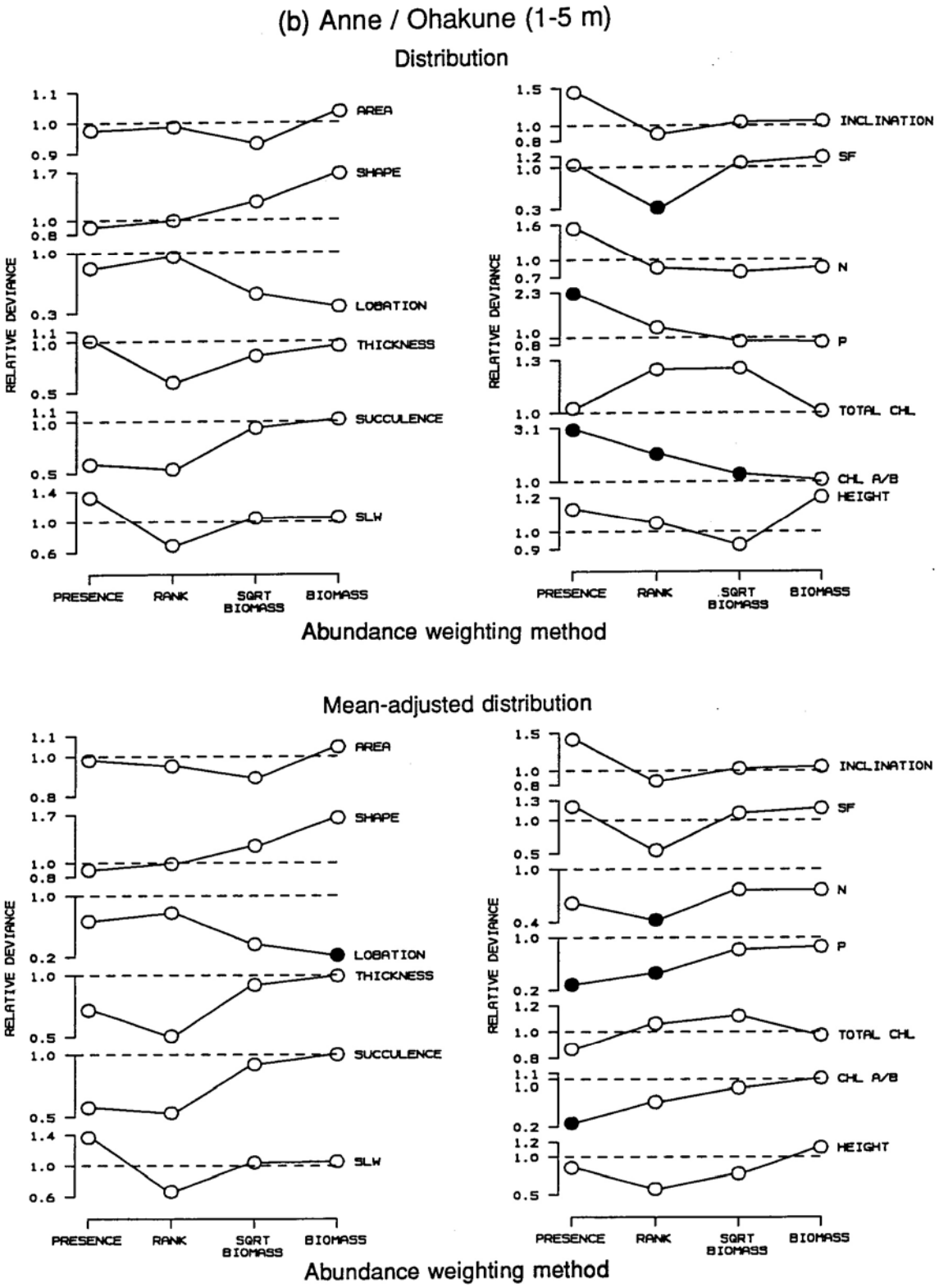
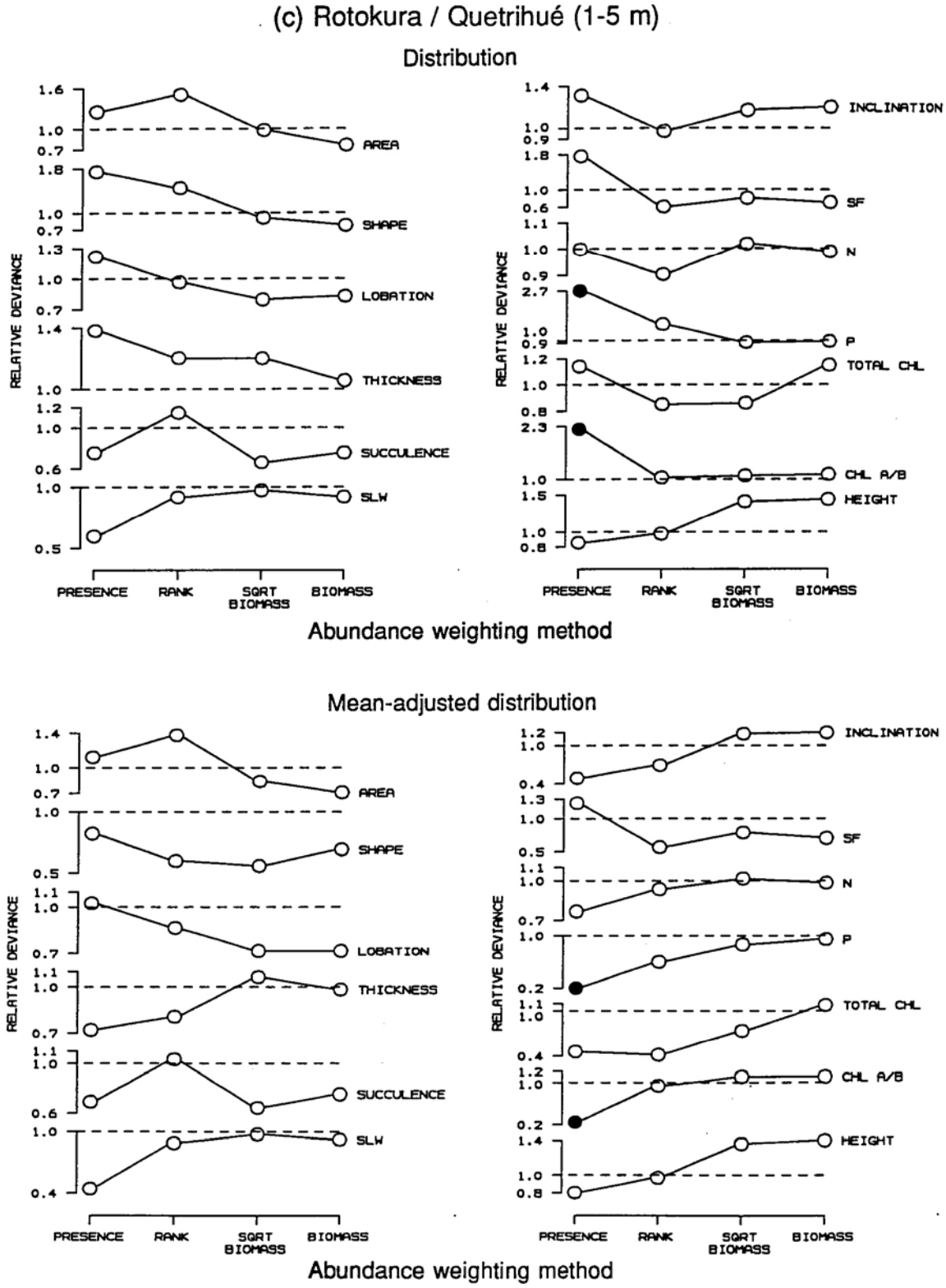



**Fig. 10.8** (continued)

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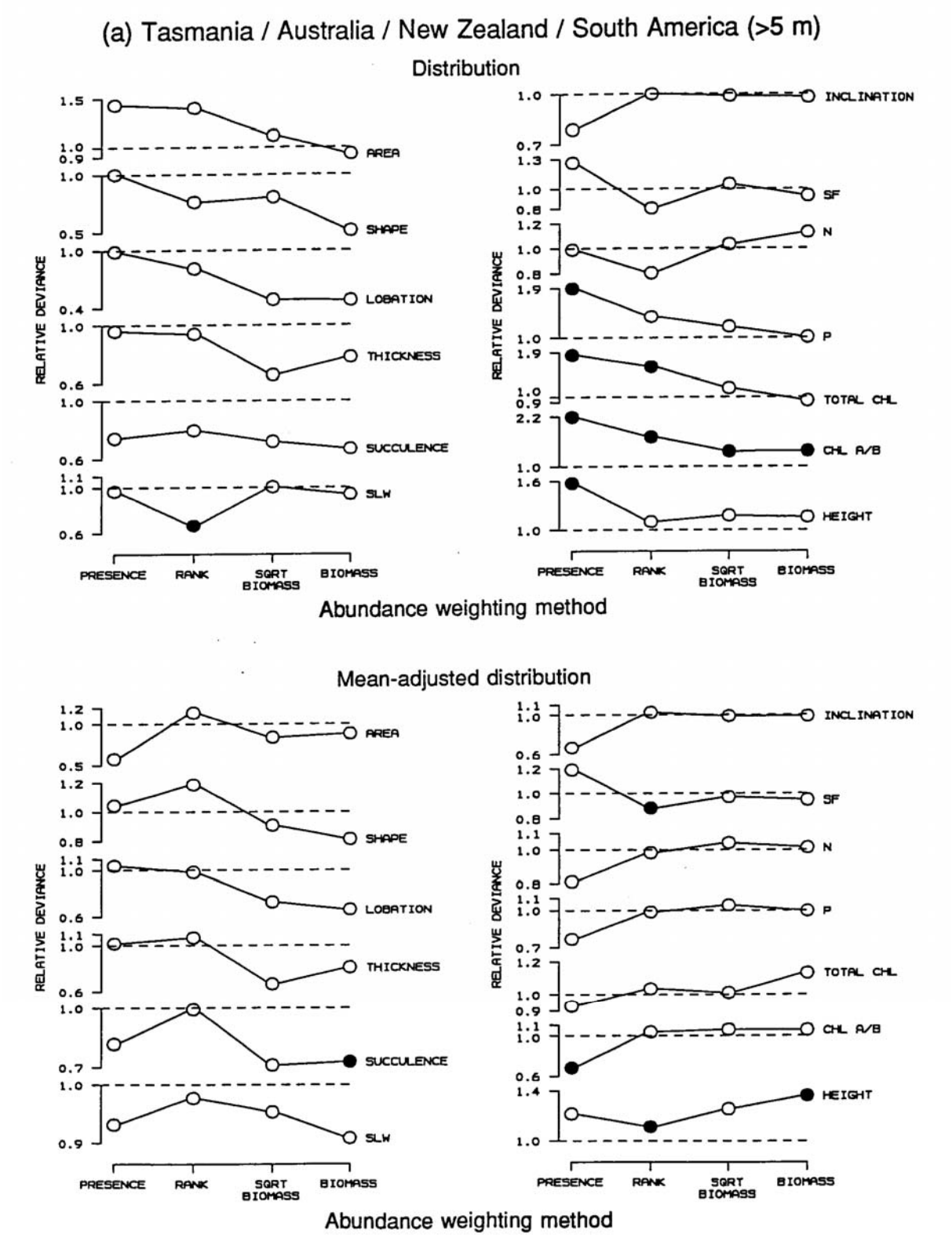


**Fig. 10.9** Null model randomisation tests for convergence or divergence in texture in the >5 m guild between landmass-scale *Nothofagus*-dominated communities **(a)** Tasmania (T), Australia (A), New Zealand (Z) and South America (S); **(b)** Tasmania and New Zealand. Format as for Fig. 10.1.

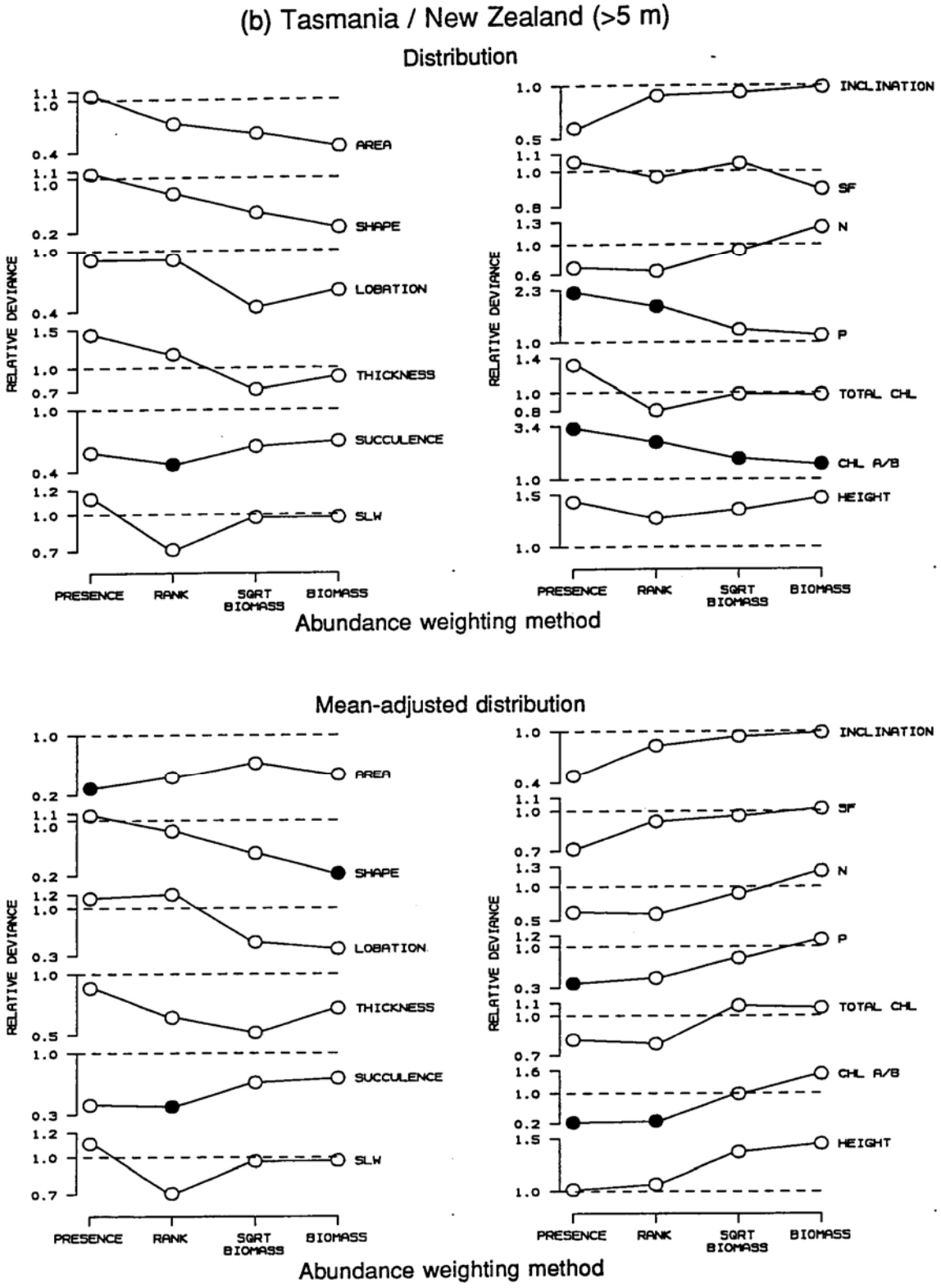


**Fig. 10.9** (continued)

Only one test revealed significant departure from the null model when texture distributions for the >5 m guild at T1 Balfour and A2 Cascades were compared: there was divergence in PSU total chlorophyll with species unweighted by their abundance (Fig. 10.12a). Mean-adjusted distributions showed convergence in PSU shape, thickness, succulence, phosphorus content, total chlorophyll and chlorophyll *a/b*, primarily in the absence of abundance weighting. No significant divergence was detected.

Biomass-weighted distributions of PSU area are convergent between T2 Anne and ZN1 Ohakune, while PSU phosphorus (weighting by species presence), chlorophyll *a/b* (all weighting factors except photosynthetic biomass) and species height (biomass) are divergent (Fig. 10.12b). When mean-adjusted distributions are compared, PSU phosphorus and chlorophyll *a/b* are convergent at lower weighting levels, and there is no significant divergence.

No significant departure from the null model was observed in comparisons of texture distributions for ZN2 Rotokura and SA1 Quetrihué (Fig. 10.12c). Mean-adjusted distributions of PSU phosphorus content and total chlorophyll are, however, convergent at lower weighting levels.

## PATTERNS AMONG TEXTURE VARIATES

### *0-1 m Guild*

Although convergence among texture distributions in the 0-1 m guild was detected in a number of individual tests, the total incidence in any texture variate at any weighting level is not significant as a proportion of 16 independent community comparisons, according to binomial tests (Table 10.2). Divergence was detected more frequently, and is significant overall at some weighting levels, for the variates PSU area, shape, succulence, nitrogen content, phosphorus content, total chlorophyll, chlorophyll *a/b* and species height. In general, the divergence is significant only at lower weighting levels, although for PSU area, the incidence is significant at all weighting levels. This demonstrates that there are marked quantitative differences in foliar area in the ground strata of many of the communities sampled.

In comparisons of mean-adjusted texture distributions, the incidence of convergence is higher, and significant overall for several variates — PSU area, lobation, nitrogen content, phosphorus content, total chlorophyll, chlorophyll *a/b* and support fraction — with species weighted equally or by abundance rank. PSU phosphorus content and chlorophyll *a/b* ratio were found to be convergent in the largest number of comparisons, 12 and 13, respectively, of 31, with species values unweighted. On the basis of the close correlation between these variates, demonstrated in Chapter 9, it is likely that the very similar patterns of departure from null expectation in each may be attributed to the same underlying factor. Divergence, significant as a proportion of the tests carried out, persists for PSU area (weighting by photosynthetic biomass) and shape (square root of biomass).

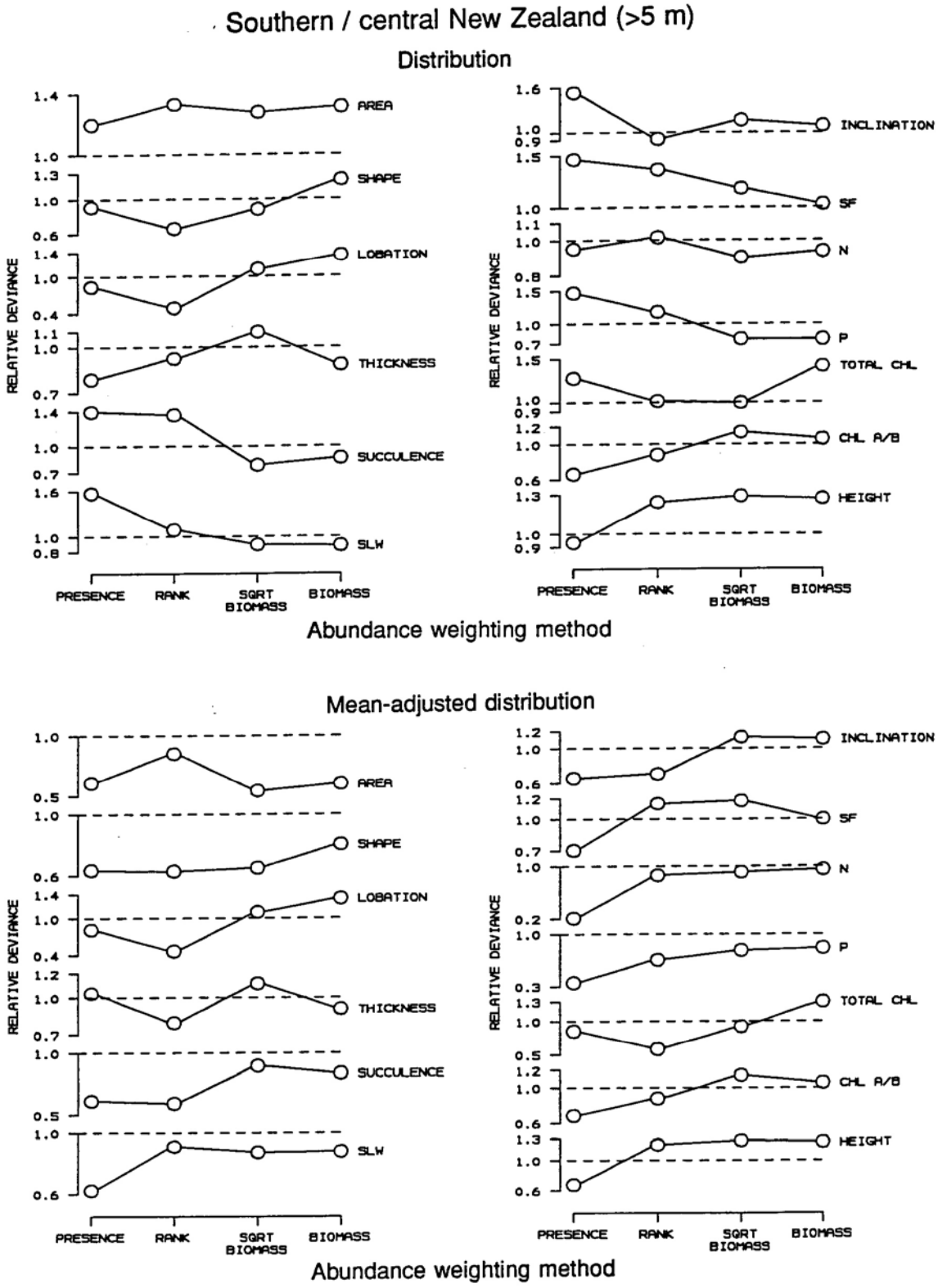


**Fig. 10.10** Null model randomisation tests for convergence or divergence in texture in the >5 m guild between regional-scale *Nothofagus*-dominated communities southern (ZS) and central (ZC) New Zealand. Format as for Fig. 10.1.

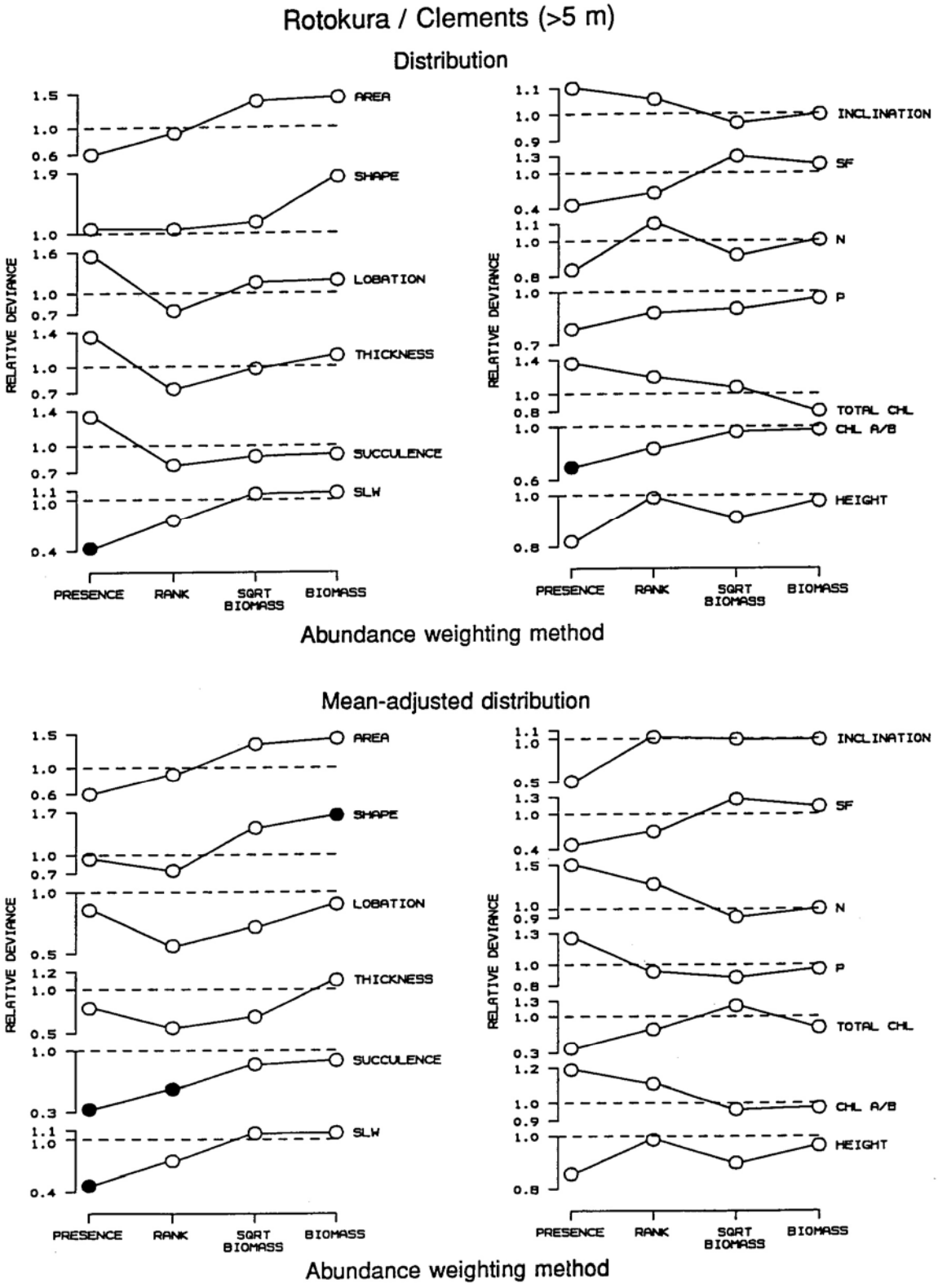


**Fig. 10.11** Null model randomisation tests for convergence or divergence in texture in the >5 m guild between local-scale *Nothofagus*-dominated communities ZN2 Rotokura and ZN3 Clements. Format as for Fig. 10.1.

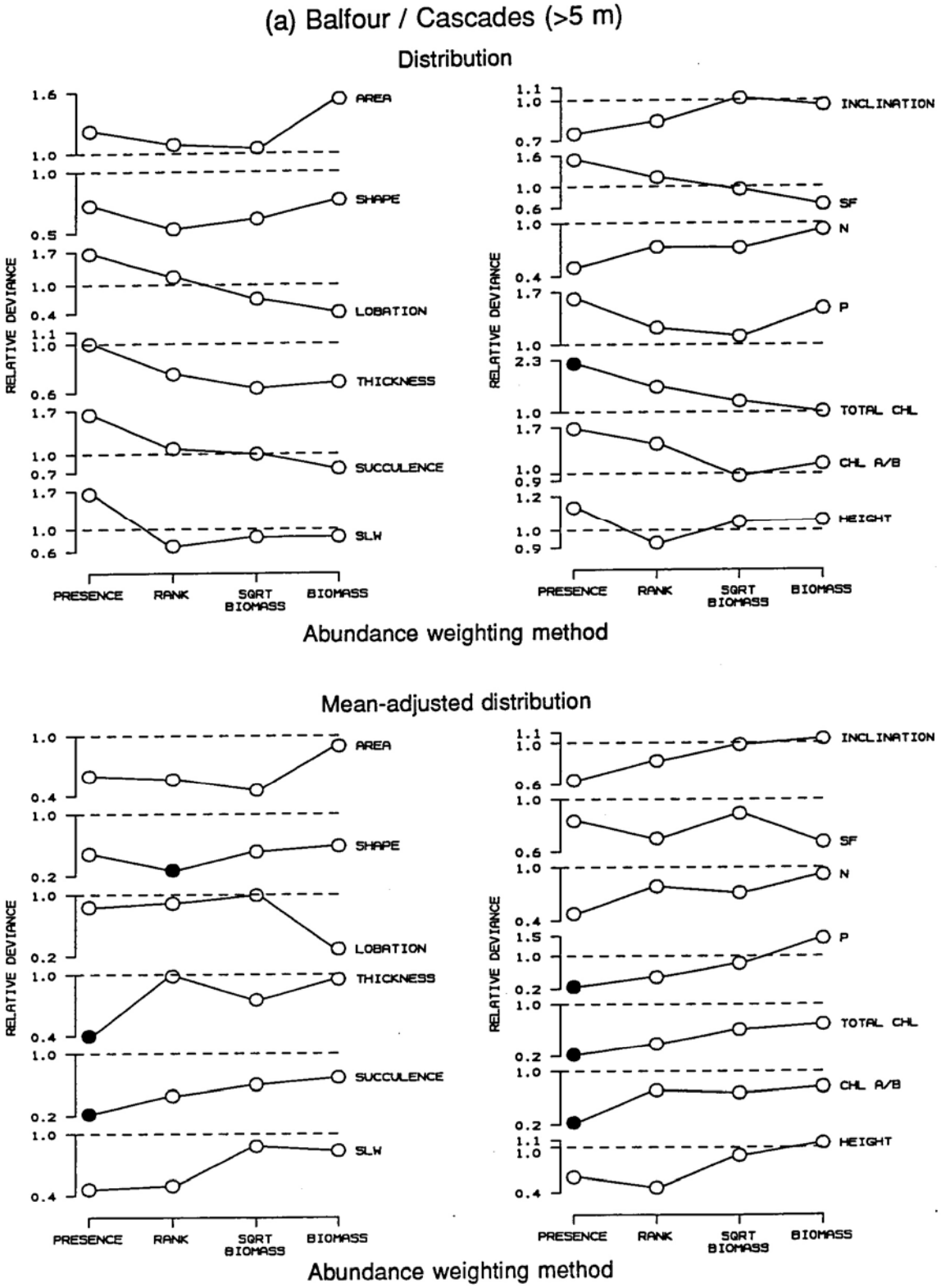


**Fig. 10.12** Null model randomisation tests for convergence or divergence in texture in the >5 m guild between *Nothofagus*-dominated communities from different landmasses closely matched in their environments: **(a)** T1 Balfour/A2 Cascades; **(b)** T2 Anne/ZN1 Ohakune; **(c)** ZN2 Rotokura/SA1 Quetrihué. Format as for Fig. 10.1.

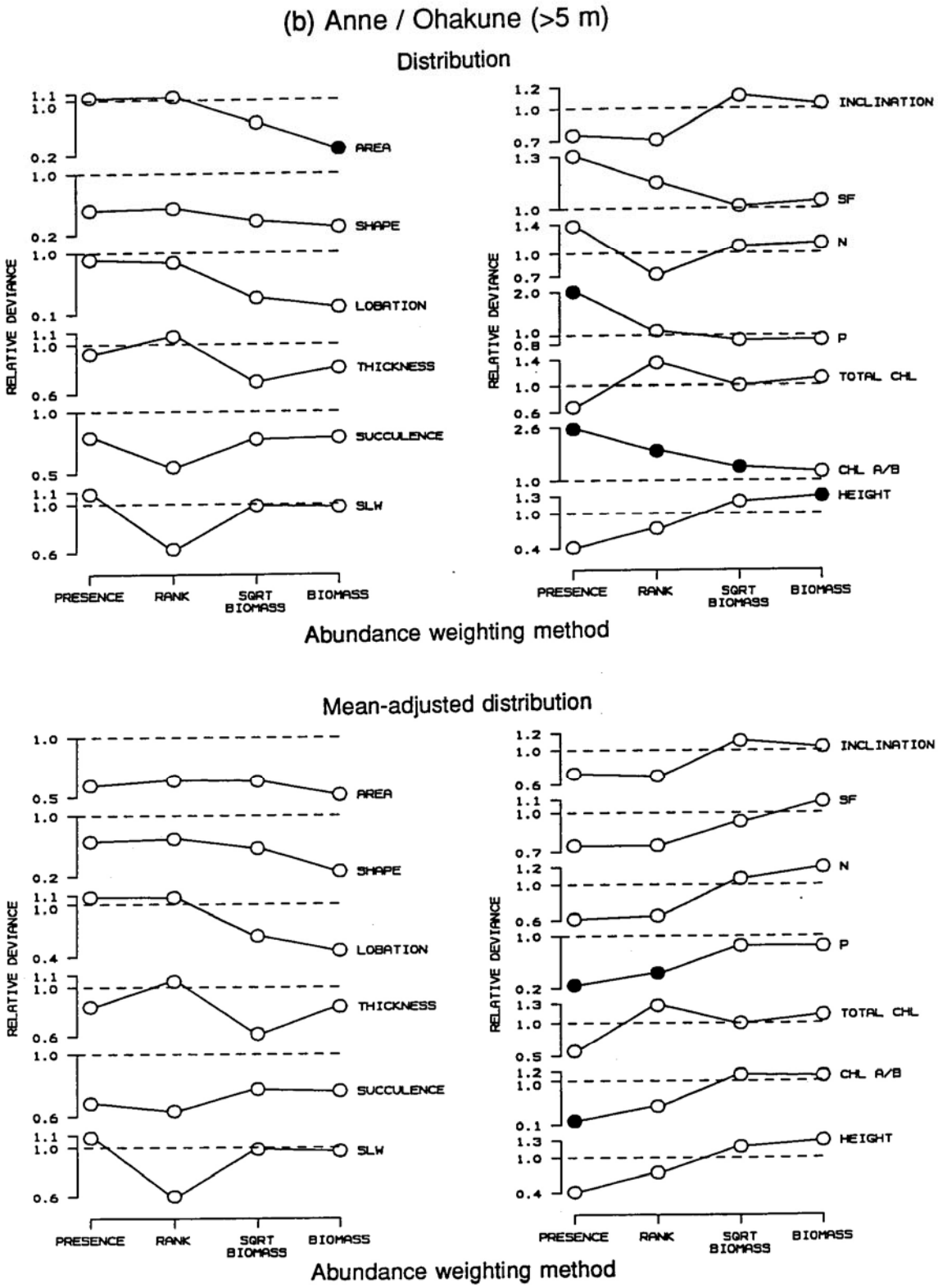


**Fig. 10.12** (continued)

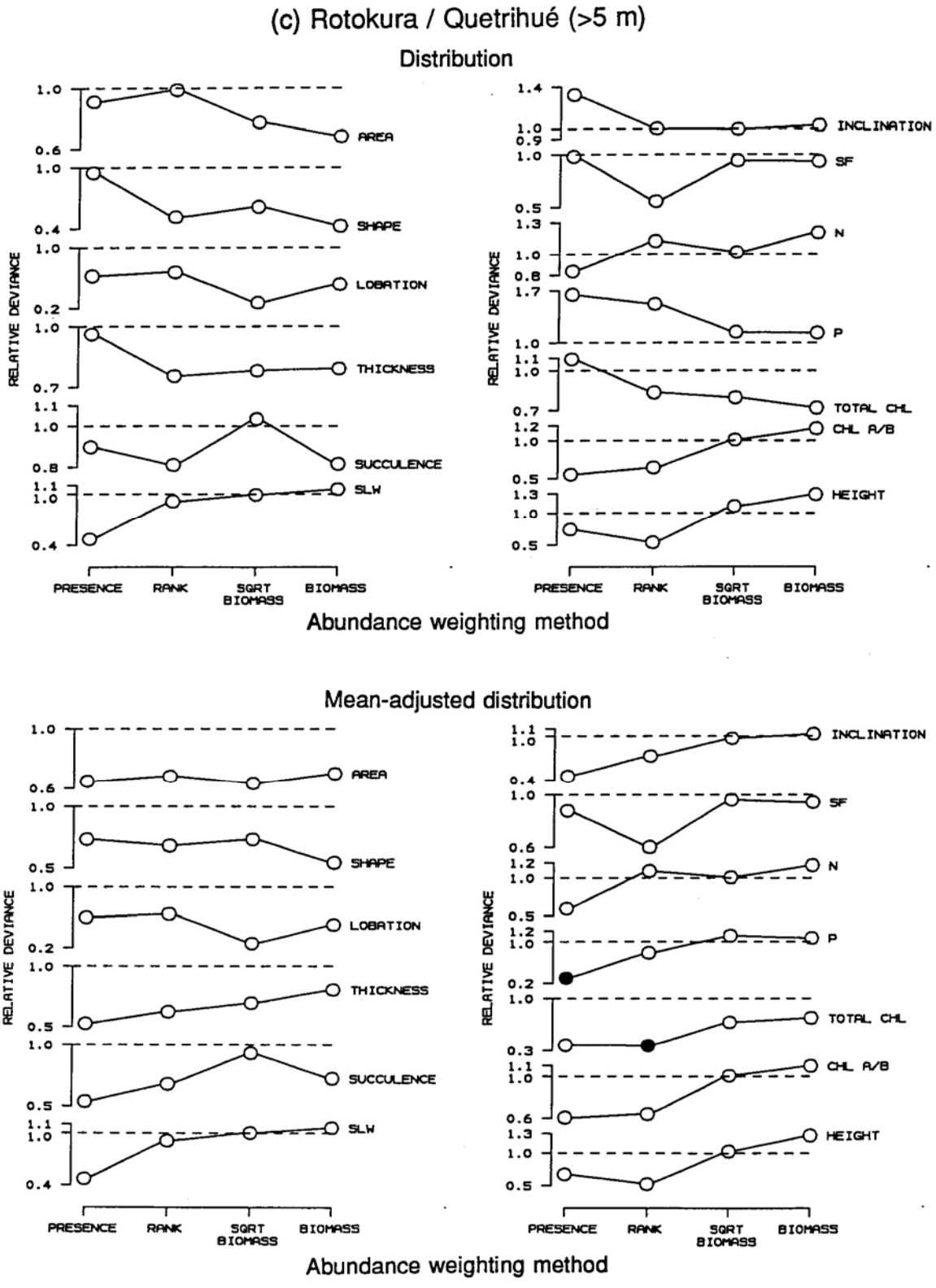


**Fig. 10.12** (continued)

**Table 10.2** Incidence of significant convergence or divergence in each texture variate for the 0-1 m guild among 31 community comparisons and (in parentheses) for 16 independent community comparisons (see text). Results are shown for each of four methods of weighting species values by abundance and for two methods of expressing community texture (distribution and mean-adjusted distribution). Overall significance, determined from the binomial distribution, is shown for results from the 16 independent comparisons.

| | Texture Variate | Convergence | | | | Divergence | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Presence | Rank | Sqrt biomass | Biomass | Presence | Rank | Sqrt biomass | Biomass |
| Distribution | Area | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 5 (4**) | 4 (3*) | 8 (4**) | 8 (4**) |
| | Shape | 1 (1) | 0 (0) | 0 (0) | 0 (0) | 2 (1) | 4 (3*) | 8 (5**) | 3 (1) |
| | Lobation | 1 (1) | 1 (1) | 2 (1) | 1 (1) | 4 (2) | 1 (1) | 0 (0) | 0 (0) |
| | Thickness | 5 (2) | 1 (1) | 0 (0) | 2 (1) | 4 (1) | 2 (1) | 0 (0) | 0 (0) |
| | Succulence | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 4 (4**) | 0 (0) | 0 (0) | 0 (0) |
| | SLW | 0 (0) | 2 (2) | 0 (0) | 1 (0) | 2 (2) | 0 (0) | 0 (0) | 0 (0) |
| | Inclination | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 3 (1) | 2 (1) | 0 (0) | 0 (0) |
| | SF | 2 (1) | 1 (1) | 1 (1) | 2 (2) | 3 (0) | 1 (0) | 1 (1) | 3 (2) |
| | N | 0 (0) | 2 (1) | 1 (0) | 0 (0) | 12 (8**) | 2 (1) | 0 (0) | 0 (0) |
| | P | 0 (0) | 2 (1) | 1 (1) | 0 (0) | 19 (11**) | 15 (9**) | 4 (2) | 2 (0) |
| | Total chl | 0 (0) | 0 (0) | 0 (0) | 1 (1) | 10 (4**) | 8 (4**) | 7 (1) | 2 (1) |
| | Chl *a*/*b* | 1 (1) | 0 (0) | 0 (0) | 0 (0) | 21 (9**) | 14 (6**) | 1 (0) | 1 (1) |
| | Height | 0 (0) | 0 (0) | 0 (0) | 1 (1) | 3 (3*) | 0 (0) | 1 (1) | 2 (2) |
| Mean-adjusted distribution | Area | 3 (3*) | 0 (0) | 1 (1) | 1 (1) | 0 (0) | 0 (0) | 3 (1) | 7 (4**) |
| | Shape | 2 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 2 (1) | 6 (4**) | 3 (1) |
| | Lobation | 4 (3*) | 4 (3*) | 1 (0) | 2 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| | Thickness | 5 (2) | 2 (1) | 0 (0) | 1 (1) | 1 (1) | 1 (1) | 0 (0) | 0 (0) |
| | Succulence | 2 (2) | 3 (2) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| | SLW | 3 (2) | 1 (1) | 0 (0) | 1 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| | Inclination | 2 (1) | 0 (0) | 0 (0) | 0 (0) | 1 (0) | 0 (0) | 0 (0) | 0 (0) |
| | SF | 4 (2) | 5 (3*) | 2 (2) | 2 (1) | 0 (0) | 0 (0) | 1 (1) | 4 (2) |
| | N | 3 (3*) | 8 (4**) | 1 (0) | 0 (0) | 2 (0) | 0 (0) | 0 (0) | 0 (0) |
| | P | 12 (8**) | 11 (7**) | 1 (0) | 1 (0) | 1 (0) | 0 (0) | 2 (0) | 2 (0) |
| | Total chl | 10 (3*) | 5 (1) | 2 (1) | 1 (1) | 0 (0) | 3 (2) | 0 (0) | 0 (0) |
| | Chl *a*/*b* | 13 (7**) | 11 (5**) | 5 (2) | 1 (0) | 3 (1) | 1 (0) | 1 (0) | 1 (1) |
| | Height | 1 (1) | 2 (1) | 0 (0) | 1 (0) | 0 (0) | 0 (0) | 0 (0) | 1 (1) |

*$0.01 \leq P < 0.001$; **$P < 0.001$ (no binomial probabilities in range $0.05 \leq P < 0.01$).

*1-5 m Guild*

The incidence of significant convergence among texture distributions in the 1-5 m guild is very low, and non-significant overall for each variate and weighting factor combination (Table 10.3). Divergence, by contrast, was detected in all variates, and is significant as a proportion of 14 independent comparisons for all except PSU lobation, thickness and inclination. With the exceptions of PSU area and shape the incidence of divergence in each variate is significant only at lower weighting levels.

Mean-adjusted distributions of several variates were found to be convergent in a large enough number of comparisons do be deemed significant overall. These variates are PSU area, succulence, specific weight, nitrogen content, phosphorus content, total chlorophyll, chlorophyll *a/b*, support fraction and species height. As for the 0-1 m guild, PSU phosphorus and chlorophyll *a/b* were convergent in the largest number of comparisons. The only variate showing a significant incidence of divergence is PSU shape.

**Table 10.3** Incidence of significant convergence or divergence in each texture variate for the 1-5 m guild among 29 community comparisons and (in parentheses) for 14 independent community comparisons (see text). Results are shown for each of four methods of weighting species values by abundance and for two methods of expressing community texture (distribution and mean-adjusted distribution). Overall significance, determined from the binomial distribution, is shown for results from the 14 independent comparisons.

| | Texture Variate | Convergence | | | | Divergence | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Presence | Rank | Sqrt biomass | Biomass | Presence | Rank | Sqrt biomass | Biomass |
| Distribution | Area | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 6 (2*) | 5 (4***) | 2 (2*) | 0 (0) |
| | Shape | 0 (0) | 0 (0) | 1 (1) | 1 (1) | 2 (2*) | 3 (2*) | 5 (3**) | 5 (2*) |
| | Lobation | 1 (0) | 0 (0) | 3 (1) | 1 (1) | 2 (1) | 0 (0) | 0 (0) | 0 (0) |
| | Thickness | 1 (1) | 0 (0) | 0 (0) | 0 (0) | 4 (0) | 1 (0) | 0 (0) | 0 (0) |
| | Succulence | 0 (0) | 1 (1) | 0 (0) | 0 (0) | 4 (2*) | 1 (1) | 0 (0) | 0 (0) |
| | SLW | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 3 (2*) | 3 (2*) | 0 (0) | 0 (0) |
| | Inclination | 1 (1) | 0 (0) | 0 (0) | 0 (0) | 2 (0) | 1 (1) | 0 (0) | 0 (0) |
| | SF | 0 (0) | 2 (0) | 1 (0) | 1 (1) | 4 (2*) | 2 (2*) | 0 (0) | 0 (0) |
| | N | 1 (1) | 1 (0) | 0 (0) | 0 (0) | 9 (6***) | 0 (0) | 0 (0) | 0 (0) |
| | P | 0 (0) | 1 (0) | 0 (0) | 0 (0) | 19 (9***) | 12 (7***) | 3 (1) | 1 (1) |
| | Total chl | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 11 (4***) | 10 (4***) | 6 (1) | 6 (1) |
| | Chl *a*/*b* | 0 (0) | 1 (0) | 1 (1) | 0 (0) | 19 (8***) | 11 (4***) | 3 (1) | 0 (0) |
| | Height | 0 (0) | 0 (0) | 0 (0) | 1 (1) | 4 (2*) | 3 (1) | 0 (0) | 0 (0) |
| Mean-adjusted distribution | Area | 2 (2*) | 1 (1) | 2 (1) | 1 (1) | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| | Shape | 0 (0) | 1 (0) | 1 (1) | 0 (0) | 0 (0) | 2 (0) | 3 (2*) | 6 (3**) |
| | Lobation | 1 (0) | 1 (0) | 1 (0) | 1 (0) | 1 (0) | 0 (0) | 0 (0) | 0 (0) |
| | Thickness | 2 (1) | 1 (0) | 1 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| | Succulence | 3 (2*) | 4 (3**) | 3 (1) | 4 (3**) | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| | SLW | 4 (2*) | 2 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| | Inclination | 1 (1) | 0 (0) | 1 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| | SF | 4 (3**) | 4 (3**) | 0 (0) | 1 (1) | 1 (0) | 0 (0) | 1 (1) | 0 (0) |
| | N | 3 (3**) | 4 (1) | 0 (0) | 0 (0) | 1 (0) | 0 (0) | 0 (0) | 0 (0) |
| | P | 16 (9***) | 12 (7***) | 2 (1) | 0 (0) | 1 (0) | 0 (0) | 1 (0) | 0 (0) |
| | Total chl | 7 (3**) | 9 (3**) | 7 (4***) | 4 (3**) | 0 (0) | 1 (0) | 0 (0) | 0 (0) |
| | Chl *a*/*b* | 11 (5***) | 6 (3**) | 5 (2*) | 0 (0) | 3 (1) | 0 (0) | 0 (0) | 0 (0) |
| | Height | 0 (0) | 4 (3**) | 1 (0) | 2 (1) | 0 (0) | 2 (1) | 0 (0) | 0 (0) |

*$0.01 \le P < 0.05$; **$0.001 \le P < 0.01$; ***$P < 0.001$

*>5 m Guild*

The number of comparisons of texture distributions for the >5 m guild in which significant convergence was detected was no higher for any variate/weighting factor combination than would be expected by chance alone, according to binomial tests (Table 10.4). Divergence was significant overall for PSU area (with weighting by presence only), phosphorus content (presence, abundance rank) and total chlorophyll (presence). The overall incidence of divergence is lower than for the 0-1 m and 1-5 m guilds. This may reflect a tendency for fewer species to be represented in the tree stratum than in the ground or intermediate strata, rather than a particularly low degree of character dissimilarity among communities (see Section 10.4).

The incidence of significant convergence between mean-adjusted texture distributions is likewise relatively low for the >5 m guild: PSU area, succulence, specific weight, phosphorus content and chlorophyll *a/b* were all found to be convergent in a larger proportion of independent community comparisons than expected on a random basis, primarily at lower abundance weighting levels. Significant divergence was detected between mean-adjusted distributions in only five tests, and is not significant overall for any variate.

**Table 10.4** Incidence of significant convergence or divergence in each texture variate for the >5 m guild among 26 community comparisons and (in parentheses) for 15 independent community comparisons (see text). Results are shown for each of four methods of weighting species values by abundance and for two methods of expressing community texture (distribution and mean-adjusted distribution). Overall significance, determined from the binomial distribution, is shown for results from the 15 independent comparisons.

| | Texture Variate | Convergence | | | | Divergence | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Presence | Rank | Sqrt biomass | Biomass | Presence | Rank | Sqrt biomass | Biomass |
| Distribution | Area | 0 (0) | 0 (0) | 0 (0) | 1 (0) | 3 (3*) | 2 (2) | 1 (1) | 0 (0) |
| | Shape | 1 (1) | 0 (0) | 0 (0) | 0 (0) | 1 (1) | 0 (0) | 0 (0) | 0 (0) |
| | Lobation | 1 (0) | 0 (0) | 1 (0) | 0 (0) | 3 (2) | 2 (1) | 1 (1) | 0 (0) |
| | Thickness | 1 (1) | 0 (0) | 0 (0) | 0 (0) | 1 (0) | 0 (0) | 0 (0) | 0 (0) |
| | Succulence | 1 (1) | 2 (2) | 2 (2) | 1 (1) | 1 (1) | 0 (0) | 0 (0) | 0 (0) |
| | SLW | 1 (0) | 3 (2) | 0 (0) | 0 (0) | 1 (1) | 0 (0) | 0 (0) | 0 (0) |
| | Inclination | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 1 (1) | 0 (0) | 0 (0) |
| | SF | 0 (0) | 1 (1) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 1 (1) | 0 (0) |
| | N | 1 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| | P | 0 (0) | 0 (0) | 2 (2) | 1 (1) | 7 (4**) | 4 (3*) | 0 (0) | 0 (0) |
| | Total chl | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 8 (3*) | 5 (1) | 0 (0) | 0 (0) |
| | Chl *a*/*b* | 1 (0) | 0 (0) | 0 (0) | 2 (1) | 7 (2) | 6 (2) | 3 (1) | 2 (1) |
| | Height | 0 (0) | 0 (0) | 0 (0) | 1 (1) | 2 (0) | 0 (0) | 0 (0) | 1 (0) |
| Mean-adjusted distribution | Area | 4 (4**) | 1 (1) | 1 (1) | 1 (1) | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| | Shape | 0 (0) | 1 (0) | 1 (0) | 1 (1) | 0 (0) | 0 (0) | 0 (0) | 1 (0) |
| | Lobation | 1 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| | Thickness | 2 (1) | 2 (2) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| | Succulence | 6 (3*) | 5 (3*) | 5 (4*) | 2 (1) | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| | SLW | 2 (1) | 5 (4**) | 1 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| | Inclination | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| | SF | 2 (2) | 1 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| | N | 1 (0) | 0 (0) | 0 (0) | 1 (0) | 0 (0) | 1 (0) | 0 (0) | 0 (0) |
| | P | 7 (3*) | 3 (2) | 2 (2) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| | Total chl | 6 (1) | 5 (2) | 1 (0) | 1 (0) | 0 (0) | 0 (0) | 1 (1) | 0 (0) |
| | Chl *a*/*b* | 8 (2) | 6 (3*) | 1 (1) | 1 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| | Height | 0 (0) | 0 (0) | 1 (0) | 0 (0) | 0 (0) | 1 (0) | 0 (0) | 1 (0) |

*$0.001 \leq P < 0.01$; **$P < 0.001$ (no binomial probabilities in range $0.01 \leq P < 0.05$).

## 10.4 Discussion

COMMUNITY-LEVEL CONVERGENCE

Convergence between texture distributions was detected in each guild in a number of tests, but among an independent subset of comparisons the number of tests showing significance in the direction of convergence was no higher, for any variate/weighting level combination, than would be expected on the basis of chance (Tables 10.2-10.4). Divergence, on the other hand, was detected frequently and was significant overall for a majority of texture variates for the 0-1 m and 1-5 m guilds, though for only three variates in the case of the >5 m guild.

For each guild, mean-adjusted distributions were found to be convergent in a larger number of community comparisons, and the incidence was significant overall for a number of variates. Only three variates, PSU shape, thickness and inclination, did not show convergence, in any guild, in a significant number of independent comparisons. Of the three guilds, the highest incidence of convergence was detected in the 1-5 m guild, which would correspond primarily to the shrub stratum in many *Nothofagus*-dominated forests (Bycroft *et al.* 1993; Wilson *et al.* 1995). The lowest incidence of convergence was in the >5 m guild, the tree stratum. However, this finding may in part reflect the structure of the data set rather than the ecology of the forest canopy, a possibility that is discussed below. Divergence between mean-adjusted texture distributions, significant as a proportion of the number of tests done, was confined to two variates, PSU area and shape, and to the 0-1 m and 1-5 m guilds.

*Interpretation of differences between guilds*

Differences among guilds in the significance of divergence or convergence in particular variates must be interpreted with caution, as for many variates differences in the number of tests showing significant departure from the null model are marginal. For example, it is interesting to note that the incidence of significant convergence among mean-adjusted distributions of the correlated variates PSU succulence and specific weight in the 0-1 m guild was not high enough to be deemed significant overall (Table 10.1), whereas these variates showed overall significance in the other two guilds (Tables 10.2, 10.3) and across whole communities (Table 8.2). This result could be taken to imply that partitioning among species of resource gradients with which these variates might be correlated (for example, the vertical light gradient; Section 9.4) might be less pronounced in the ground stratum of some *Nothofagus*-dominated communities, than closer to the canopy. However, the proportions of independent tests showing significant convergence in these variates are similar for all three guilds; for example, for PSU succulence in the absence of abundance weighting, 2 (of 16), 2 (of 14), and 3 (of 15) independent comparisons showed significant convergence for the 0-1, 1-5 and >5 m guilds, respectively.

The relatively small number of tests that revealed significant convergence in the >5 m

guild could be interpreted as evidence that interactions, such as competition, among the species (mainly trees) occurring from 5 m above ground level to the upper canopy are less intense than in the lower strata, resulting in weaker assembly rules, and a lower incidence of significant convergence between communities. However, the number of comparisons of texture distributions showing divergence is also lower than for other guilds. This is difficult to explain ecologically, since environmental differences expected to produce divergence would presumably apply equally in the upper and lower strata. It is therefore more likely that the low overall incidence of departure from the null model in the >5 m guild is related to the structure of the data in which patterns are being sought.

Guilds generally contain fewer species than whole communities. In the present study, the number of species available for randomisation under the null model is generally highest when whole communities are compared, is lower for the 0-1 m guild, lower still for the 1-5 m guild, and lowest, often by a factor of 2 or more, for the >5 m guild (Table 10.1). Under the null model, only species that do not occur in more than one of the communities being compared are randomised. This is to avoid bias due to the effects of common species on texture (see Section 6.2). The number of species randomised can affect the likelihood of detecting significant convergence. This is because it is whole texture distributions (for communities or guilds) that are expected to converge. Although character values for all species are taken into account in computing and comparing texture distributions (with the test statistics $\hat{D}_T$ and $\hat{D}'_T$), only the subset of species that are randomised can contribute to departure of the observed pattern from the null model. The randomised species comprise a sample from the population of species whose attributes make up the texture of the communities being compared. The smaller the sample, the poorer an estimate it will provide, on average, of the population it represents. This means that, where few species are available for randomisation, significant departure from the null model may not be demonstrable, even if the factors expected to produce it (assembly rules or environmental differences) apply. The low overall incidence of significant departure from the null model in both directions for the >5 m guild, may be a result, at least in part, of the generally low species numbers in this guild.

*Guild versus community scale*

Comparing the results of equivalent tests at the whole-community and guild scales, there is evidence that convergence not apparent at the whole-community level may sometimes be revealed within a particular guild. For example, mean-adjusted distributions of PSU succulence are convergent at all abundance weighting levels for the 1-5 m guild of the regional communities southern and central New Zealand (Fig. 10.6). Across all guilds, however, there is convergence at only one weighting level, abundance rank (Fig. 8.8b). Presumably the general non-convergence at the whole-community scale is due to an absence of significant convergence in

PSU succulence in the 0-1 m (Fig. 10.2) and >5 m (Fig. 10.10) guilds. Between the Tasmanian site T2 Anne and New Zealand site ZN1 Ohakune there is convergence in distributions of PSU nitrogen (weighting by the square root of photosynthetic biomass) in the 0-1 m guild (Fig. 10.4b), in support fraction (abundance rank) in the 1-5 m guild (Fig. 10.8b), and in PSU area (biomass) in the >5 m guild (Fig. 10.12b). None of these variates shows significant convergence (using any weighting factor) when the whole communities are compared (Fig. 7.15b).

On the other hand, convergence was sometimes detected at the whole community level, but not in any individual guild. For example, community-wide distributions of PSU succulence are convergent overall among the four landmasses, Tasmania, Australia, New Zealand and South America, when species are weighted by their photosynthetic biomass or its square root (Fig. 7.5a). Comparing the same communities within each of the three guilds, there is no significant convergence in PSU succulence (Figs. 10.1a, 10.5a, 10.9a). Similarly, convergence at the whole-community level in distributions of PSU lobation between the Tasmanian site T1 Balfour and Australian site A2 Cascades (Fig. 7.15a) was not detected in any individual guild, although trends were in the same direction (Figs. 10.4a, 10.8a, 10.12a). The observation of significant patterns at the scale of the whole community but not in individual guilds can be explained by the effects of differences in the numbers of species sampled at the two scales, as discussed above.

Over all tests, patterns of significant departure from null expectation are rather similar within guilds (Tables 10.1-10.3) to those obtained in comparisons of whole communities in Chapters 7 and 8 (Tables 7.2, 8.2). Both divergence of texture distributions and convergence of mean-adjusted distributions occur most consistently in the variates PSU area, succulence, nitrogen content, phosphorus content, total chlorophyll and chlorophyll *a/b* ratio. The total incidence of significant convergence among mean-adjusted distributions in the 0-1 m and 1-5 m guilds is similar to that observed for whole communities in Chapter 8. For the >5 m guild, somewhat less convergence was detected. In the 1-5 m guild the incidence of convergence was significant overall for three variates — support fraction, species height and PSU nitrogen content — for which the incidence of convergence in comparisons of whole communities was not significant.

In summary, tests seeking community-level convergence at the guild scale have revealed some patterns not evident at the scale of the whole community. However, the total incidence of convergence was not markedly higher for any guild than in comparisons of whole communities. Significant convergence was detected in each of the three guilds, suggesting that assembly rules may apply at all levels in the vertical forest structure, at least for some of the communities sampled. Where this is the case, no advantage would be expected from subdividing communities into guilds.

The concept of the guild in ecology is often (incorrectly[3]) attributed to Root (1967), whose guilds of birds were species using 'similar resources in a similar way.' The applicability of this definition to guilds of plants has been questioned, in part because it is difficult to identify resources uniquely utilised by particular groups of plants (Wilson 1989; Simberloff & Dayan 1991; Aarssen 1992). Pianka (1980) predicted that guilds would represent foci for interspecific interactions; that is, that guild associates would interact with one another more than with species from other guilds. This criterion was used as a basis for delineating the guilds in the present chapter. Each of the three guilds examined comprised species whose primary above-ground function (capture and assimilation of radiant energy through photosynthesis) was carried out in the same zone in the vertical forest structure. It was anticipated that interspecific interactions might be more intense within one or more of these guilds, than in the entire vascular community, resulting in stronger community structure, and a greater degree of community-level convergence.

Focusing on guilds rather than whole communities is a common practice in community studies, and may be motivated, as in the present study, by the assumption that community structure would be stronger within guilds (Hawkins & MacMahon 1989; Simberloff & Dayan 1991). However, few studies have tested this assumption by examining community structure at both the guild and community scales. Bycroft *et al.* (1994) sought niche limitation and guild proportionality within a *Nothofagus*-dominated community in New Zealand. Niche limitation, greater constancy in the number of species represented in adjacent quadrats than expected under a null model of random migration (Wilson *et al.* 1987), could not be demonstrated, indicating weak structure at the whole-community scale. However, guild proportionality, an expected outcome of niche limitation at the scale of individual guilds, was detected in the herb guild, one of six sinusiae examined. Using a comparable approach, Wilson *et al.* (1995) demonstrated a similar pattern in another New Zealand *Nothofagus*-dominated forest. Other studies have detected proportionality in some guilds but not others (Wilson & Roxburgh 1994), or in none of the guilds examined (Wilson 1989). In the present study, convergence in texture has been sought as evidence of community structure. A significant incidence of convergence has been detected for several texture variates both at the community scale (Chapter 8) and in each of the three guilds examined.

[3]Root (1967) cited Schimper (1903) whose guilds (*Genossenschaften*) were functional types of plants utilising other organisms for sustenance or support.

## CONCLUSIONS

Tests seeking texture convergence within guilds revealed similar patterns of departure from the null model to those obtained in Chapters 7 and 8, where comparisons were done at the whole community scale. Although it was anticipated that community structure, and therefore texture convergence, might be stronger within guilds than at the level of the whole community, there is little evidence to support this suggestion for the three guilds examined in this chapter. In a small proportion of individual comparisons, however, significant convergence was detected in one or more guilds but not at the whole-community scale. It is possible that a minor tendency for community structure to be stronger within guilds is negated by the lower effective statistical power of guild-level tests resulting from the reduced number of species that can be randomised under the null model in guild, as opposed to whole-community, comparisons.

# 11. Character overdispersion as evidence for assembly rules in *Nothofagus*-dominated communities

## 11.1 Introduction

Assembly rules represent the integrated effects of all types of species interaction on community structure (Diamond 1975; Drake 1990; Wilson 1991). Certain types of interaction, particularly competition, would tend to impose a limiting similarity on the species in a community by restricting the degree of niche overlap that is possible (MacArthur 1972b; Pianka 1976, 1980). By enforcing a degree of functional dissimilarity among species within an assemblage, such assembly rules would tend to result in niches, and correlated species characters, being more regularly spaced than would be expected if there were no such rules. Such a tendency towards regular spacing in the characters of potentially interacting species has been termed character overdispersion (Pianka 1980; Weiher & Keddy 1995a). One potential pattern that could result from overdispersion — texture convergence between communities — has already been sought in this study. Texture convergence may be expected if similar assembly rules apply in similar physical environments. While similarity in the physical environments of two communities would tend to produce broadly similar spectra of functional species characters (i.e. similar texture), restrictions on how dissimilar the characters of species in the same community may be, would accentuate the similarity — possible causing texture distributions in different communities to become more similar than would be expected if species characters could assort freely, i.e. at random (Smith *et al.* 1994; Wilson *et al.* 1994).

In previous chapters, texture convergence was sought within disjunct *Nothofagus*-dominated communities, to evaluate the hypothesis that similar assembly rules apply in different communities, producing overdispersion in their texture distributions and, in turn, convergence. Significant convergence was detected between some communities, primarily in the shapes of texture distributions, disregarding their means (Chapters 8-10). However, the predominant pattern was one of non-convergence, suggesting that assembly rules (of the kind discussed above) are absent or weak in their effects on community structure, that they operate in only some communities, or that texture differences resulting from environmental or historical differences between communities are too pronounced for convergence to be detectable, even if assembly rules do apply.

To determine whether community texture has been influenced by assembly rules, an alternative approach would be to seek character overdispersion directly; that is, to ask whether the species within a community are dispersed along character axes more regularly than would be

expected if there were no constraints on how dissimilar species must be to permit coexistence. Because this approach addresses structure at the level of the individual assemblage (community or guild), no assumptions as to the environment of the assemblage must be met. This represents an advantage over tests for community-level convergence, which depend on the assumption that the assemblages under investigation are closely matched in their environments (although the test for convergence in mean-adjusted texture distributions, developed in Chapter 8, overcomes this requirement to a limited extent).

Character overdispersion has been sought as evidence for competition-mediated character displacement in the past, both within animal (e.g. MacArthur 1971; Brown 1975; Simberloff & Boecklen 1981) and plant guilds (e.g. Snow 1965; Stiles 1977, 1979; Pleasants 1980; Armbruster *et al.* 1994). A difficulty with many such studies, however, has been in the choice of an appropriate null model and in the methods used to establish statistically significant departure from it (Tonkyn & Cole 1986; Pleasants 1990, 1994; Arita 1993). In the present chapter, character overdispersion in *Nothofagus*-dominated communities, and guilds within these communities, is sought by comparing patterns of spacing between species along character axes to expectation under a null model in which characters are drawn at random from a distribution approximating that of the observed data. If values are determined randomly, the differences between them will tend to be more variable than if there are restrictions on how similar values can be. The variance of these differences is thus a suitable index of overdispersion: here a low observed variance in the spacing between species values along character (texture) axes is interpreted as evidence for overdispersion, and therefore, for assembly rules limiting the co-occurrence of species whose characters are too similar. A kernel estimation method (Silverman 1981; Efron & Tibshirani 1993; Manly 1995b) is used to obtain a null sampling distribution that may approximate the underlying distribution from which species values are drawn in nature. This represents an advancement on previous studies of competitive displacement that have commonly drawn null species values from the biologically meaningless uniform distribution (Tonkyn & Cole 1986).

## 11.2 Methods

### TEXTURE DATA

Analysis was based on texture data comprising species values for the 12 characters described in Section 2.3.5. The variate species height, included in the analyses of Chapters 6-10, was not used in the present Chapter. This was because of its semi-categorical nature, which would lead to the artifact of distributions being found `clustered' relative to the null model, using the analysis described below. Some analyses were also performed using seven texture factors (F1-F7) derived from 'raw' texture variate data by multivariate analysis, in Chapter 9.

Field and laboratory measurement regimes and criteria for the choice of study sites are

described in Chapter 2. Study sites are described in detail in Chapter 3.

## ANALYSIS

Overdispersion in species character values within an assemblage was sought using smoothed bootstrap resampling tests, comparing the spacing of species values in the observed assemblage to spacing in artificial assemblages generated under a null model.

### *The null model*

An appropriate null model will incorporate all features of the observed data not related to the hypothesis (or hypotheses) being tested. This is to ensure that statistically significant departure from the null model in a particular direction can be uniquely interpreted as support for one of these hypotheses (Tokeshi 1986; Wilson 1995). The principal hypothesis here is that species character values will be more regularly spaced than expected in the absence of assembly rules. The physical environment at a site would be expected to determine what character values the species present may have to establish and function successfully. In the absence of assembly rules, however, no restrictions would be expected on how similar sympatric species may be. The underlying distribution of character values in nature is unlikely to be uniform, but would reflect a variety of environmental, functional and phylogenetic influences, unrelated to assembly rules (Tonkyn & Cole 1986). In order to avoid spurious rejection of the null hypothesis due to trends caused by these factors, such trends should be taken into account by the null model. This means that the null model should resample from this underlying distribution, or as close an approximation of it as can be achieved. Manly (1995b) has recommended the use of a combination of smoothed bootstrap resampling and kernel density estimation to obtain null model values from a continuous distribution based on that of the observed data.

A kernel density estimate is a continuous probability density function built by summation of $n$ Gaussian normal density curves, each with its mode at one of the $n$ values comprising the data set whose distribution is being modelled (Silverman 1981; Efron & Tibshirani 1993). The shape of the kernel density curve approximates that of a relative frequency histogram of the data. The standard deviation, $h$, of each component normal curve is known as the 'window size' and determines the smoothness of the kernel estimate (Fig. 11.1). A null model was defined, in which character values were drawn at random from a kernel density estimate of the distribution of the observed data.

Given species values $x_{T,i}$ for a character (texture variate) $T$ from an assemblages consisting of $n$ species or entities, null data sets were generated by drawing $n$ random values from a kernel density estimate of the distribution of $x_{T,i}$ values. Following Efron & Tibshirani (1993), the variance of the kernel estimate was adjusted to be equal that of the observed data. Random

(smoothed bootstrap) values $x'_{T,i}$ from the kernel density function were thus given by:

$$x'_{T,i} = X_T + \frac{x_{T,i} - X_T + h\rho}{\sqrt{1 + h^2 / \sigma_T{}^2}}$$

where $X_T$ is the mean of texture variate $T$, i.e.

$$X_T = \frac{\sum_{i=1}^{n} x_{T,i}}{n};$$

$\sigma_T$ is the standard deviation of variate $T$, i.e.

$$\sigma_T = \sqrt{\frac{\sum_{i=1}^{n} \left( x_{T,i} - X_T \right)^2}{n}}$$

and $\rho$ is a random value from the standard normal distribution. Transformed (Section 2.3.5; Table 2.1) species character values $x_{T,i}$ were used. To examine the effect of the window size $h$ on the outcome of the bootstrap tests, complete analyses, as described below, were carried out for several communities with $h$ set to each of four proportions of the observed standard deviation of character values, as follows: $0.0625\sigma_T$; $0.125\sigma_T$; $0.25\sigma_T$ and $0.5\sigma_T$. The window size chosen was found to have hardly any effect on the outcome of the tests (i.e. on the values obtained for $R_{V,T}$ and $P$, see below). Therefore, only results obtained from tests carried out with $h$=$0.25\sigma_T$ are presented.

*Bootstrap tests for over- or underdispersion*

Tests employing the null model described above were carried out to search for evidence of character overdispersion in communities at the local, regional and landmass scales, and in each of the three height guilds, defined in Chapter 10, within each community. No test was performed for assemblages comprising fewer than three species or entities (assemblages excluded from analysis for this reason were the >5 m guild for ZS2 Walker and SA2 Gutierrez). For each community and guild, separate tests were carried with respect to each of the 12 texture variates. For whole communities only, overdispersion in each of the seven derived texture factors was also sought.

Tests were two-tailed; that is, significant departure from the null model was sought both in the direction of overdispersion (a low variance in the spacing between species values along character axes) and underdispersion (a high variance). Overdispersion corresponds to regularity in the spacing of species characters, and provides support for the underlying hypothesis that there

are assembly rules which limit the co-occurrence of species with similar characters. Underdispersion corresponds to clustering of species characters and could be explained by convergence of species attributes about the same adaptive optima (Weiher & Keddy 1995) or by historically-based similarities in the characters of related species (Harvey & Pagel 1991). Although overdispersion is the pattern of primary interest in this study, both over- and underdispersion represent biologically meaningful alternatives to the null model, and a two-tailed test is therefore appropriate.

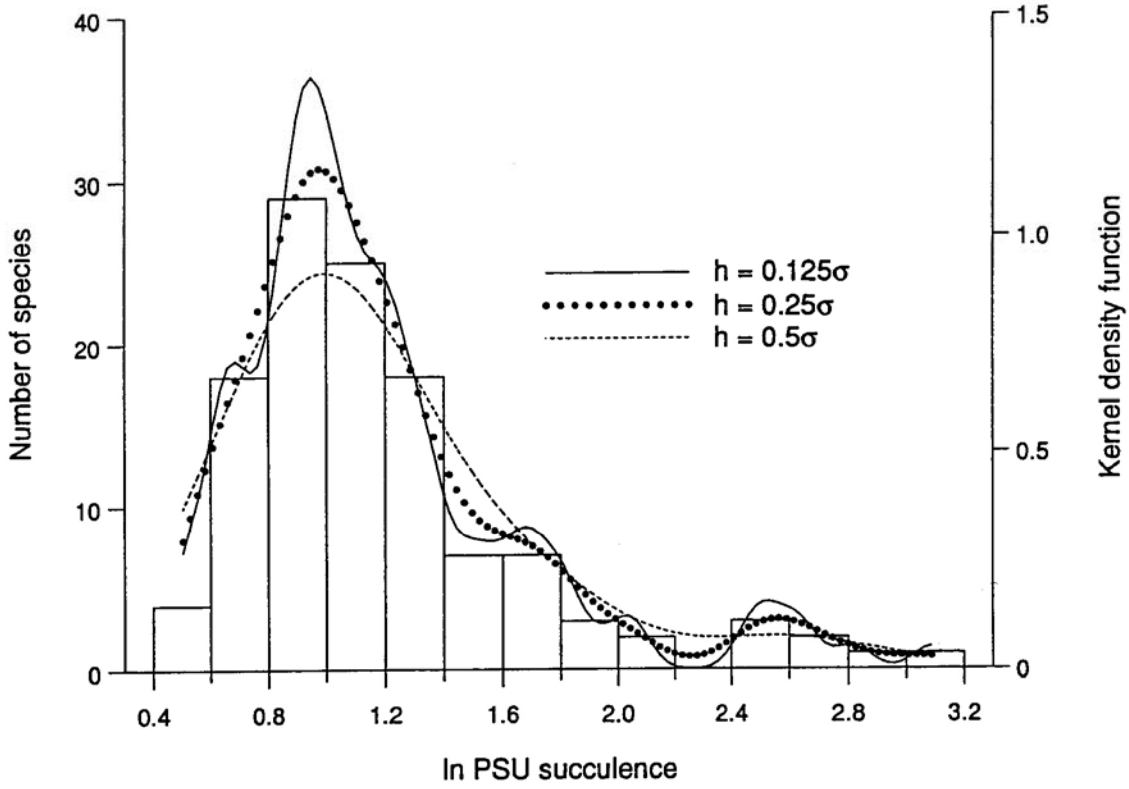


**Fig. 11.1** Comparison of the frequency distribution of a texture variate (PSU succulence, New Zealand) with kernel density functions calculated from the texture data. Each curve was calculated with the window size *h*, which controls the smoothness of the kernel estimate, set to a different proportion of the sample standard deviation, $\sigma$. All results presented in this chapter are based on analyses with $h=0.25\sigma$.

To confirm that there was no bias towards rejection of the null hypothesis in bootstrap tests, two random variates were added to the set of character variates examined in each assemblage. Each species or entity in the assemblage was assigned a real random value from a uniform distribution in the range 0-1, and a random value from the normal distribution with mean 0.5 and standard deviation 1/6 (both random variates will tend to have the same mean and range). In the absence of bias, significant ($P<0.05$) over- or underdispersion should be detected in each random variate

in approximately 5% of tests (2.5% in each direction), while the proportions of tests showing a tendency towards overdispersion ($R_{V,T}$<1; see below) and underdispersion ($R_{V,T}$>1) should be approximately the same. After many tests, the significances of departure from these expected patterns were examined using binomial tests (see below).

*Pooled communities*

To assemble data for regional communities comprising more than one site (e.g. southern New Zealand) and landmass communities (e.g. New Zealand), it was necessary to pool values from individual sites. This was done according to the protocol described in Section 6.2.

*Comparison of observed with null assemblages*

For a given texture variate (character) *T*, spacing of species values along character axes was characterised by the variance of differences in character values between adjacent species, $V_T$ (Poole & Rathcke 1979):

$$V_T = \frac{\sum_{i=1}^{n-1} (z_{T,i} - Z_T)^2}{n-1}$$

where $z_{T,i}$ is the character value difference between adjacent species ranked in ascending order of their character values, i.e.

$$z_{T,i} = x_{T,i+1} - x_{T,i} \; ; \; x_{T,i+1} \geq x_{T,i} \text{ for } i=1, 2, ..., n-1$$

and $Z_T$ is the mean of the $z_{T,i}$ values, i.e.

$$Z_T = \frac{\sum_{i=1}^{n-1} z_{T,i}}{n-1}$$

The value of $V_T$ will be lowest when species characters are very regularly spaced, increasing as the spacing becomes increasingly random, while the highest values would apply if species were highly clustered in their character values.

For each test, 2000 null model simulations were performed, and the test statistic ($V_T$) calculated for each bootstrapped (null model) data set, as well as for the observed data. A low value of $V_T$ for the observed data, relative to its mean value among bootstrapped data sets, would indicate that species characters in the observed assemblage are more regularly spaced than expected under the null model. This may be interpreted as a tendency towards overdispersion in texture variate *T*. Similarly, a high value of $V_T$ would suggest that species characters in the observed are somewhat clustered, a tendency towards underdispersion. The strength of any

tendency towards over- or underdispersion was quantified as the relative variance, $R_{V,T}$:

$$R_{V,T} = \frac{V_T \text{ (observed)}}{\sum V_T \text{ (null)} / 2000}$$

$R_{V,T}$ has a value less than 1 if there is a tendency towards overdispersion in the observed assemblage in terms of texture variate *T*. A value greater than 1 corresponds to a tendency towards underdispersion.

The significance *P* of departure from the null model was calculated as the proportion of bootstrapped data sets for which $V_T$ was at least as small (if $R_{V,T}<1$) or at least as large (if $R_{V,T}>1$) as $V_T$ for the observed data, multiplying the result by 2 to effect a two-tailed test (Crowley 1992). Departure from the null model was deemed significant if *P* was found to be less than 0.05.

*Binomial tests for overall significance*

Binomial tests were applied to determine whether the number of tests yielding significant results was higher than would be expected on a random basis. The approach was to ask whether the proportion of a set of bootstrap tests revealing significant overdispersion ($R_{V,T}<1$) or underdispersion ($R_{V,T}>1$), was higher than would be expected by chance, given a 5% likelihood of type I error in each test.

For a binomial test to be valid, it must be applied to a set of independent observations (see Section 6.2). In previous chapters, which sought convergence or divergence among pairs or groups of communities, the 'observations' were results from a subset of comparisons which were independent (Fig. 6.1). In the present chapter, it is individual assemblages, not combinations of them, that are examined by each test. Independence among the assemblages is not guaranteed. Some regional and all landmass-scale communities are derived by pooling observations from individual study sites, and so are clearly not independent of them. Even among some individual sites, there may be shared texture variation inherited from common species pools. However, the assembly process itself will be independent between sites. Assembly rules leading to overdispersion may be based exclusively on ecological species sorting, operating at the local scale, or also on coevolutionary character displacement, which would be based on past ecological sorting, and would affect local community composition via the regional species pool (Section 1.5; Figs. 1.4, 1.5). If local-scale ecological species sorting is more important than coevolutionary character displacement as a basis for assembly rules applying at the local scale, overdispersion observed at different sites within a region or landmass may be largely independent statistically. For this reason, binomial tests for overall significance were applied to the results from tests examining character dispersion at individual sites and within guilds at individual sites, but not within regional or landmass scale communities whose data were pooled from several sites.

Separate binomial tests were applied to determine the overall significance of (significant)

over- or underdispersion for each texture variate at the whole-community scale, and for each texture variate/height guild combination.

*Binomial tests for overall trends*

Overall trends in the largely non-significant results obtained in individual bootstrap tests were examined using the binomial distribution. To distinguish these binomial tests from tests for overall significance, described above, they are termed `tests for overall trends.' The approach was to ask whether the proportion of bootstrap tests whose results were in one direction (say, $R_{V,T}<1$[1]) differed significantly from the 50% expected in the absence of any systematic trends. A significant departure from chance expectation would imply the existence of a trend towards overdispersion (if $R_{V,T}<1$ in a majority of tests) or underdispersion (if $R_{V,T}>1$ in a majority of tests) among the test results examined, although the underlying mechanism may have been too weak to have produced significant results in all (or any) of the individual bootstrap tests.

Binomial tests for overall trends were applied to the results from tests examining character dispersion at individual sites, and within guilds at individual sites. To maximise the independence of the binomial `observations' (bootstrap tests) regional and landmass scale communities whose data were pooled from several sites were not included in the analyses. Separate tests were applied to the results obtained for each texture variate at the whole-community scale, and for each texture variate/guild combination.

Binomial frequencies both in tests for overall significance and tests for overall trends were calculated from the binomial expansion (Snedecor & Cochran 1967; computer program by J.B. Wilson).

*Tests for bias in bootstrap tests*

To confirm that the null model and bootstrap test algorithm did not lead to any bias towards rejection of the null hypothesis, binomial tests for overall significance and overall trends (as described above) were applied to results from bootstrap tests seeking dispersion patterns in the uniform and normal random `texture' variates (see above). Results from all 26 whole communities were used, since each community (even regional and landmass communities represented by pooled data for true texture variates) was assigned values for the random variate directly.

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[1]There were no tests in which $R_{V,T}$ was exactly equal to 1, i.e. where no tendency was detected either in the direction of over- or underdispersion. It is therefore exactly equivalent to ask whether the proportion of tests for which $R_{V,T}<1$, *or* for which $R_{V,T}>1$, differs from 50% expectation.

## 11.3 Results

VALIDITY OF THE NULL MODEL

Bootstrap tests performed on both uniform and normal random variates produced no evidence of bias (Table 11.1). No significant departure from the null model was observed in any of the 26 tests performed (corresponding to each local, regional and landmass-scale community). For both types of random variate, a slightly larger number of tests yielded high values of the relative variance (i.e. $R_{V,T}>1$, suggesting a tendency towards underdispersion) than low values ($R_{V,T}<1$). However, neither trend is significant according to binomial tests. There is therefore no evidence for bias in the null model.

**Table 11.1** Incidences of departure from null expectation in bootstrap tests for over- and underdispersion in two variates pertaining to each of 26 communities (see text), containing random values drawn from uniform and normal distributions respectively. `Binomial *P*' shows the probability of obtaining, by chance alone, incidences of the number of tests showing a tendency towards overdispersion ($R_{V,T}<1$; see text) and of the number showing a tendency towards underdispersion ($R_{V,T}>1$) at least as unequal as those observed.

| Number of tests showing pattern | Random variate | |
|---|---|---|
| | Uniform | Normal |
| Significant overdispersion | 0 | 0 |
| Significant underdispersion | 0 | 0 |
| Tendency towards overdispersion | 10 | 12 |
| Tendency towards underdispersion | 16 | 14 |
| Binomial *P* | 0.327 | 0.845 |

PATTERNS WITHIN COMMUNITIES AND GUILDS

*Communities*

Landmass-scale communities Tasmania and Australia show no significant departure from the expectation that species are dispersed randomly in character space (Figs. 11.2a, b). For New Zealand, however, there is overdispersion in PSU succulence, specific weight and total chlorophyll, and in the texture factor (F1) most closely related to these variates (Fig. 11.2c). Species values for F3 (PSU phosphorus content, chlorophyll *a/b*) are also significantly overdispersed. It is notable that all texture variates except support fraction, and all factors except F6 (PSU lobation, inclination) have $R_{V,T}<1$ — a tendency towards overdispersion. For South

America, there is no significant overdispersion; however, all texture variates and factors except support fraction show a tendency in this direction (Fig. 11.2d).

Of the three communities in Tasmania, there is significant overdispersion only at T2 Anne, for PSU thickness and its corresponding texture factor, F4 (Figs. 11.3a-c). Australian sites A1 Lumeah and A2 Cascades show no significant departure from null expectation (Figs. 11.3d, e). For the pooled regional community southern New Zealand (ZS) there is overdispersion in PSU area (Fig. 11.3f); for central New Zealand (ZC), in PSU inclination (Fig. 11.3g); and for northern New Zealand (ZN), in PSU area. All three regions of New Zealand show a strong trend towards overdispersion, with only a minority of variates having $R_{V,T}>1$. This pattern reflects that observed for New Zealand overall (Fig. 11.2c). No significant departure from null expectation is evident for SC Chile or SA Argentina (Fig. 11.3i, j).

None of the southern New Zealand sites shows significant departure from the null model (Fig. 11.4a-c). However, there appears to be a weak overall trend towards overdispersion, most notably for ZS1 Ten Mile, for which a tendency towards underdispersion ($R_{V,T}>1$) was observed only for support fraction and F1 (PSU succulence, specific weight, total chlorophyll, species height). PSU inclination values are significantly overdispersed at ZC1 Craigs, and, with the exception of F5 (PSU nitrogen, phosphorus) all variates and factors show a tendency towards overdispersion (Fig. 11.4d). No such trend is apparent for the other central New Zealand site, ZC2 Station (Fig. 11.4e). An overall trend towards overdispersion is evident among the three northern New Zealand sites (Figs. 11.4f-h). However, significant overdispersion was detected in only two tests: in PSU area at ZN1 Ohakune (Fig. 11.4f), and in PSU area and F2 (PSU area, support fraction) at ZN2 Rotokura (Fig. 11.4g). Local-scale communities sampled in Chile (Figs. 11.4i, j) and Argentina (Figs. 11.4k, l) exhibit no significant character dispersion patterns.

*Guilds*

Detailed results from bootstrap tests applied at the guild scale are presented only for the four landmass-scale communities, and for a representative subset of communities at the regional and local scales.

No significant over- or underdispersion within guilds was detected for Tasmania (Fig. 11.5a) or Australia (Fig. 11.5b). For New Zealand, however, there is overdispersion in PSU area, succulence and total chlorophyll within the 0-1 m guild (Fig. 11.5c). This pattern is similar to that observed for the whole community (Fig. 11.2c). Species values for PSU nitrogen content are significantly underdispersed in the >5 m guild for South America, the only test showing a significant result in this direction in this study (Fig. 11.5d). For all the landmass communities, except Australia, variates tend to show non-significant overdispersion (or no clear trend) for the 0-1 m and 1-5 m guilds, but underdispersion in the >5 m guild.

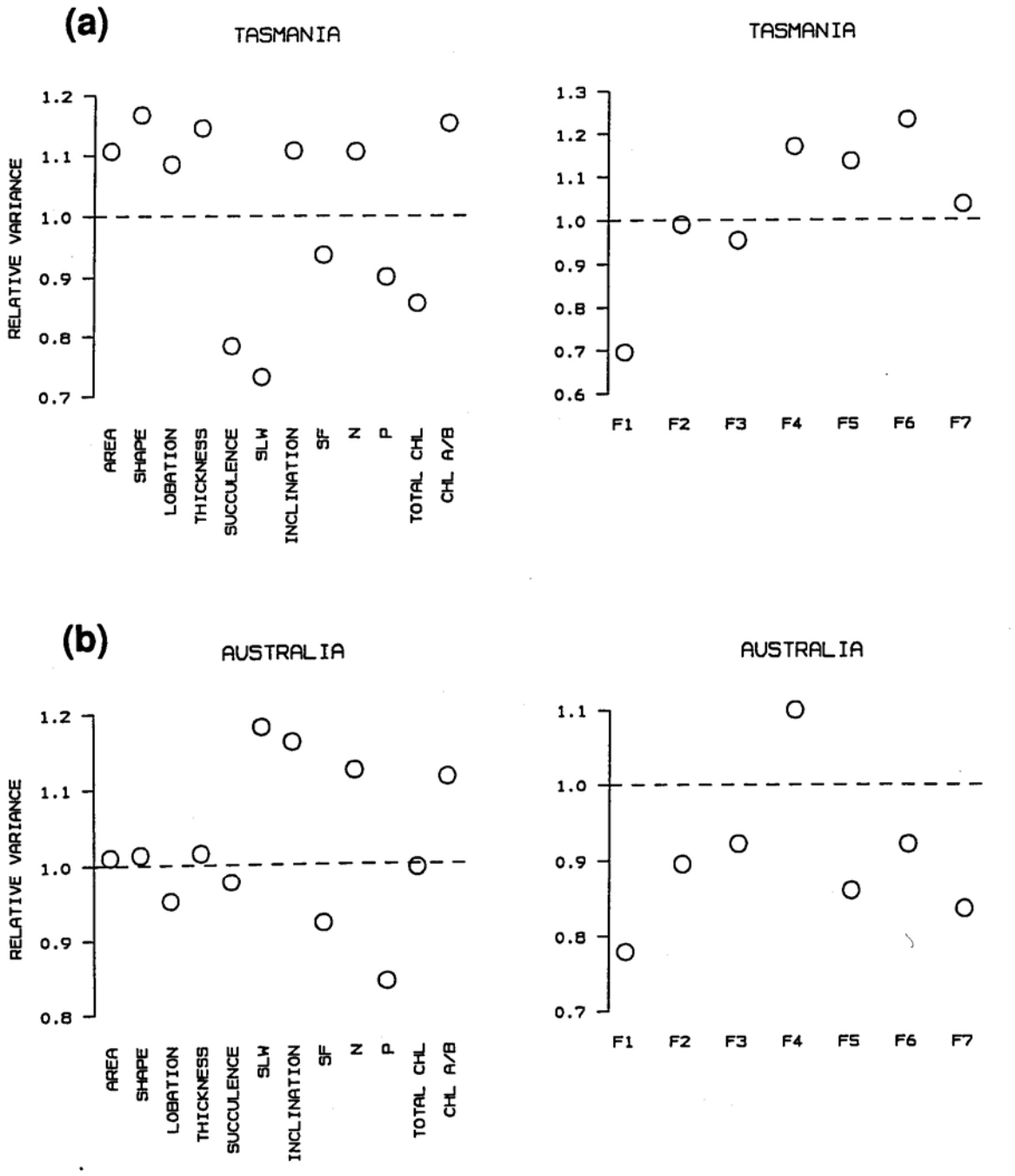


**Fig. 11.2** Smoothed bootstrap tests for over- or underdispersion in texture variates and derived factors for landmass-scale *Nothofagus*-dominated communities **(a)** Tasmania (T), **(b)** Australia (A), **(c)** New Zealand (Z) and **(d)** South America (S). The relative variance $R_{V,T}$ is an index of the strength of overdispersion ($R_{V,T}<1$) or underdispersion ($R_{V,T}>1$) relative to expectation under a stochastic null model (see text). Broken lines indicate null model expectation, $R_{V,T}=1$. Filled symbols correspond to significant departure from the null model ($P<0.05$). Texture variates (abscissa, left hand graph) are based on PSU characters except SF (support fraction). Key: SLW=specific weight; N=nitrogen content; P=phosphorus content; TOTAL CHL=total chlorophyll content; CHL A/B=chlorophyll *a/b* ratio. Texture factors F1-F7 (right hand graph) are derived from texture variates by factor analysis (see text for full explanation).

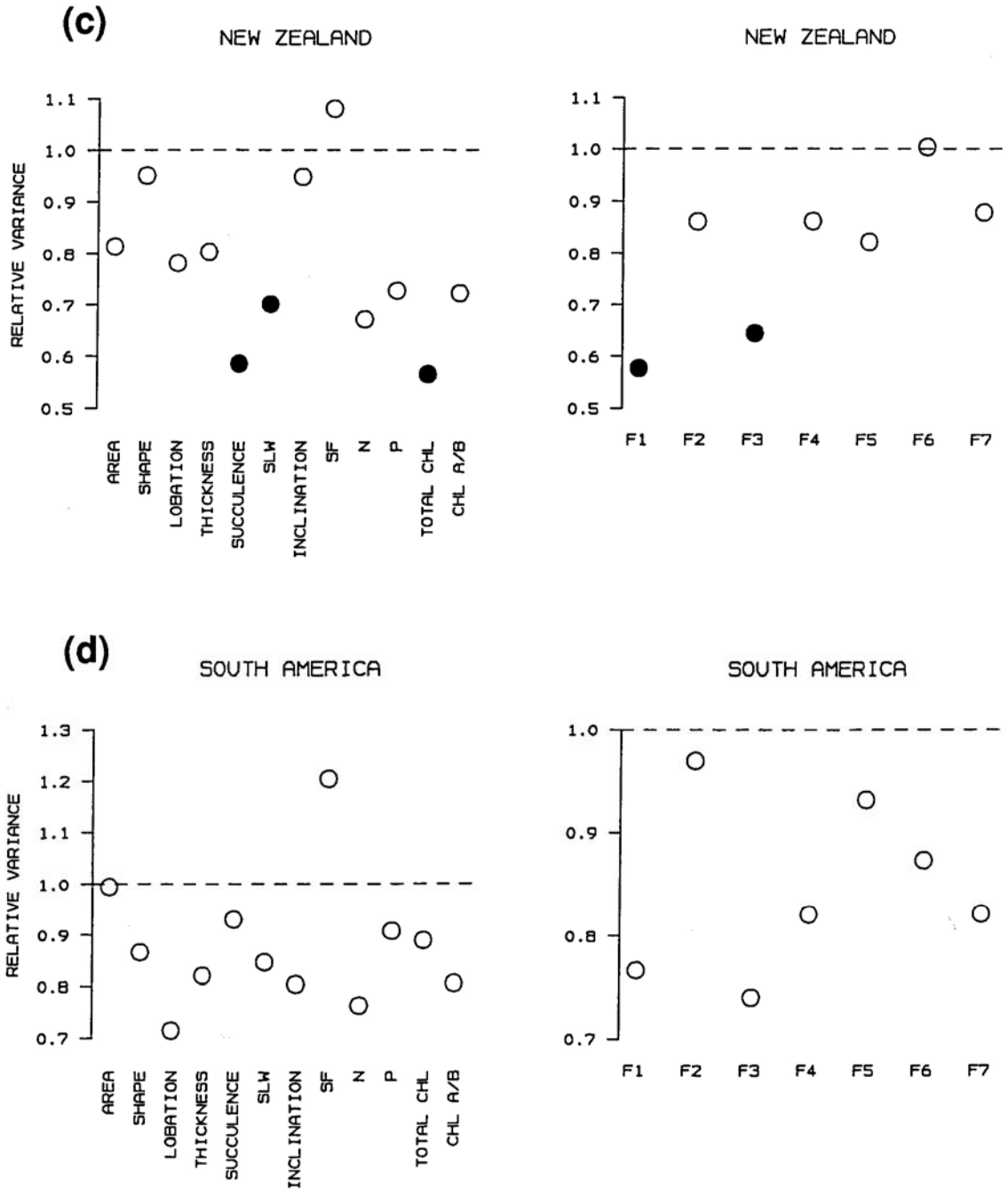


**Fig. 11.2** (continued)

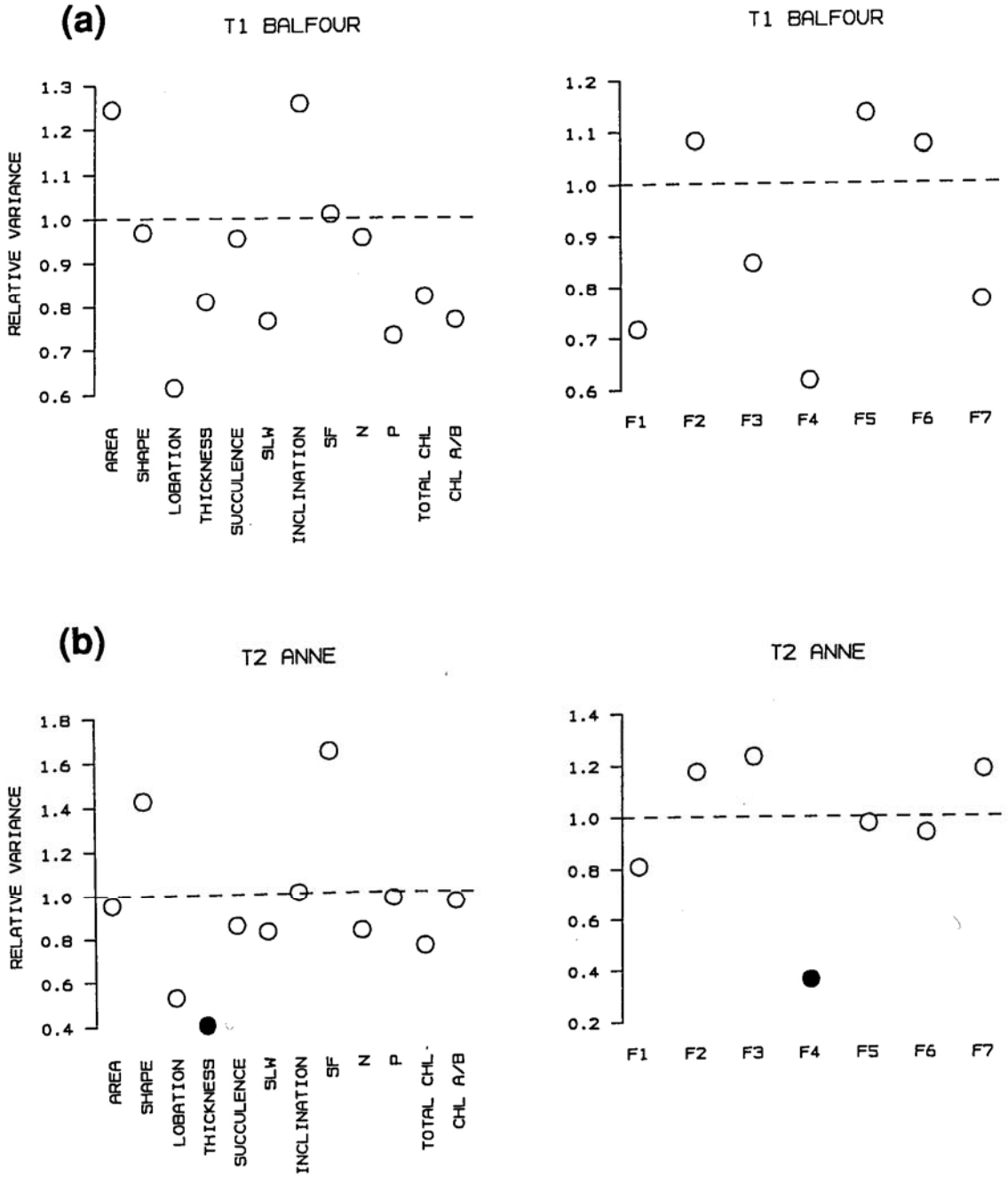


**Fig. 11.3** Smoothed bootstrap tests for over- or underdispersion in texture variates and derived factors for regional-scale *Nothofagus*-dominated communities **(a)** T1 Balfour, **(b)** T2 Anne, **(c)** T3 Mathinna, **(d)** A1 Lumeah, **(e)** A2 Cascades, **(f)** southern New Zealand (ZS), **(g)** central New Zealand (ZC), **(h)** northern New Zealand (ZN), **(i)** Chile (SC) and **(j)** Argentina (SA). Format as for Fig. 11.2.

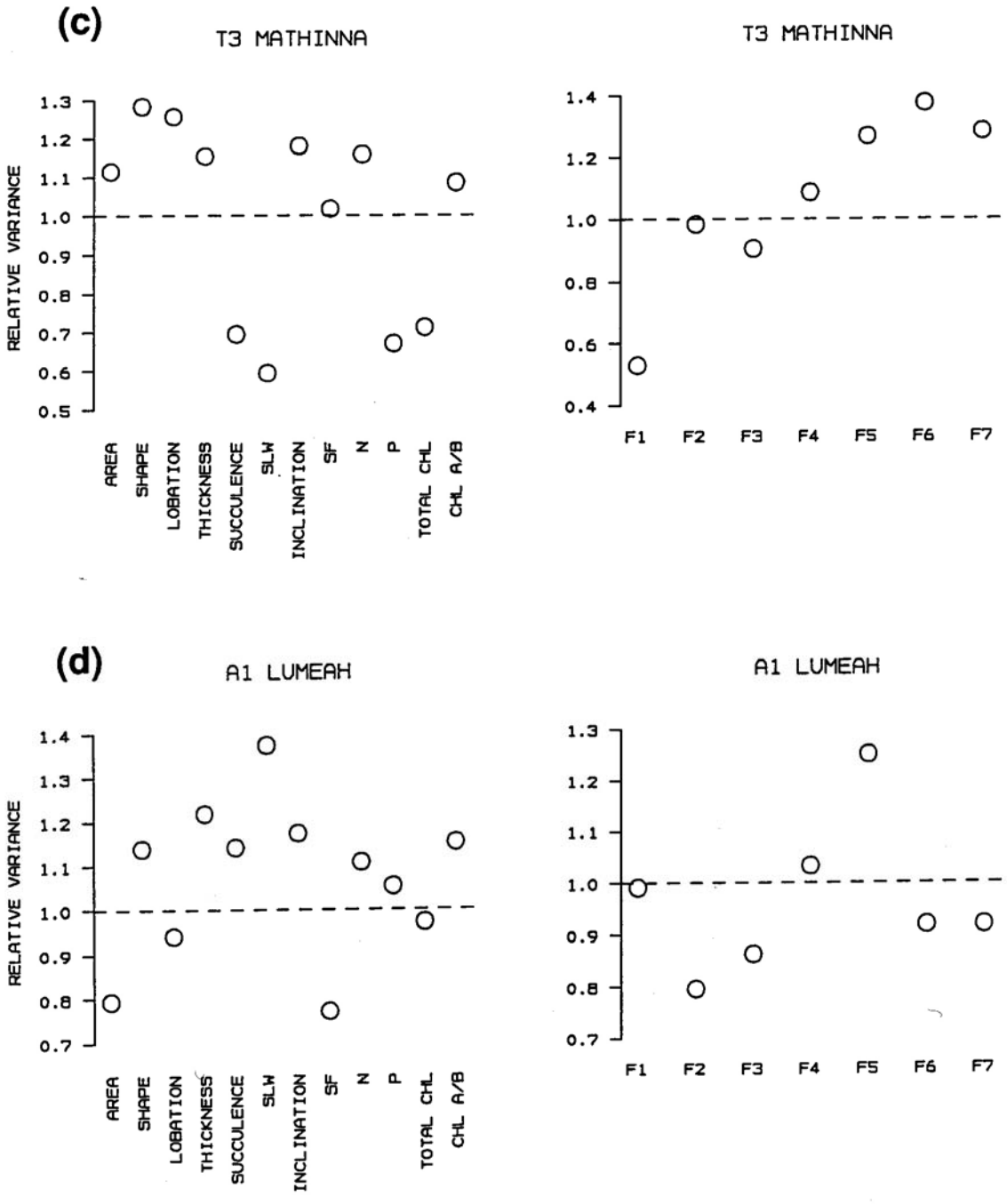


**Fig. 11.3** (continued)

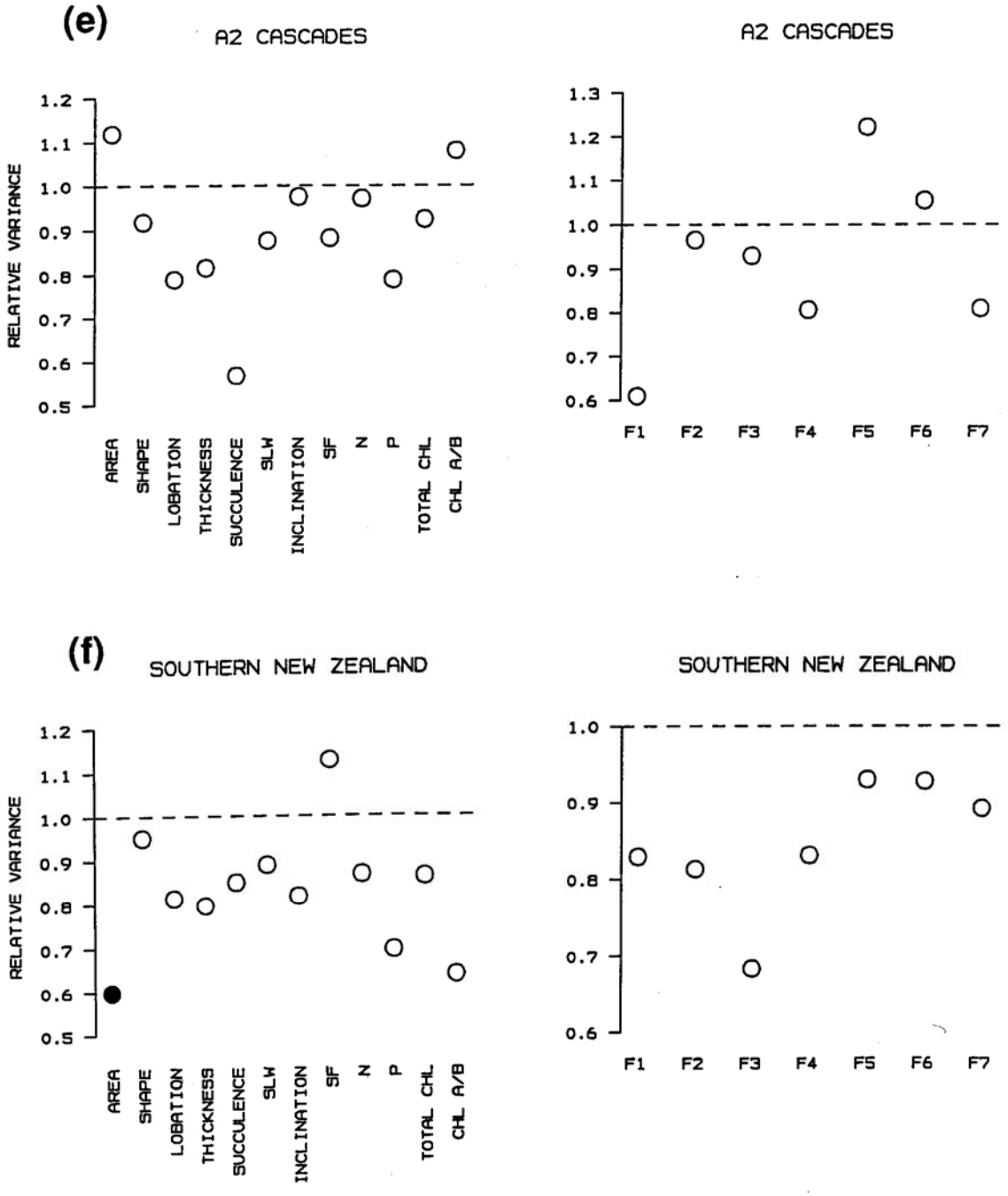


**Fig. 11.3** (continued)

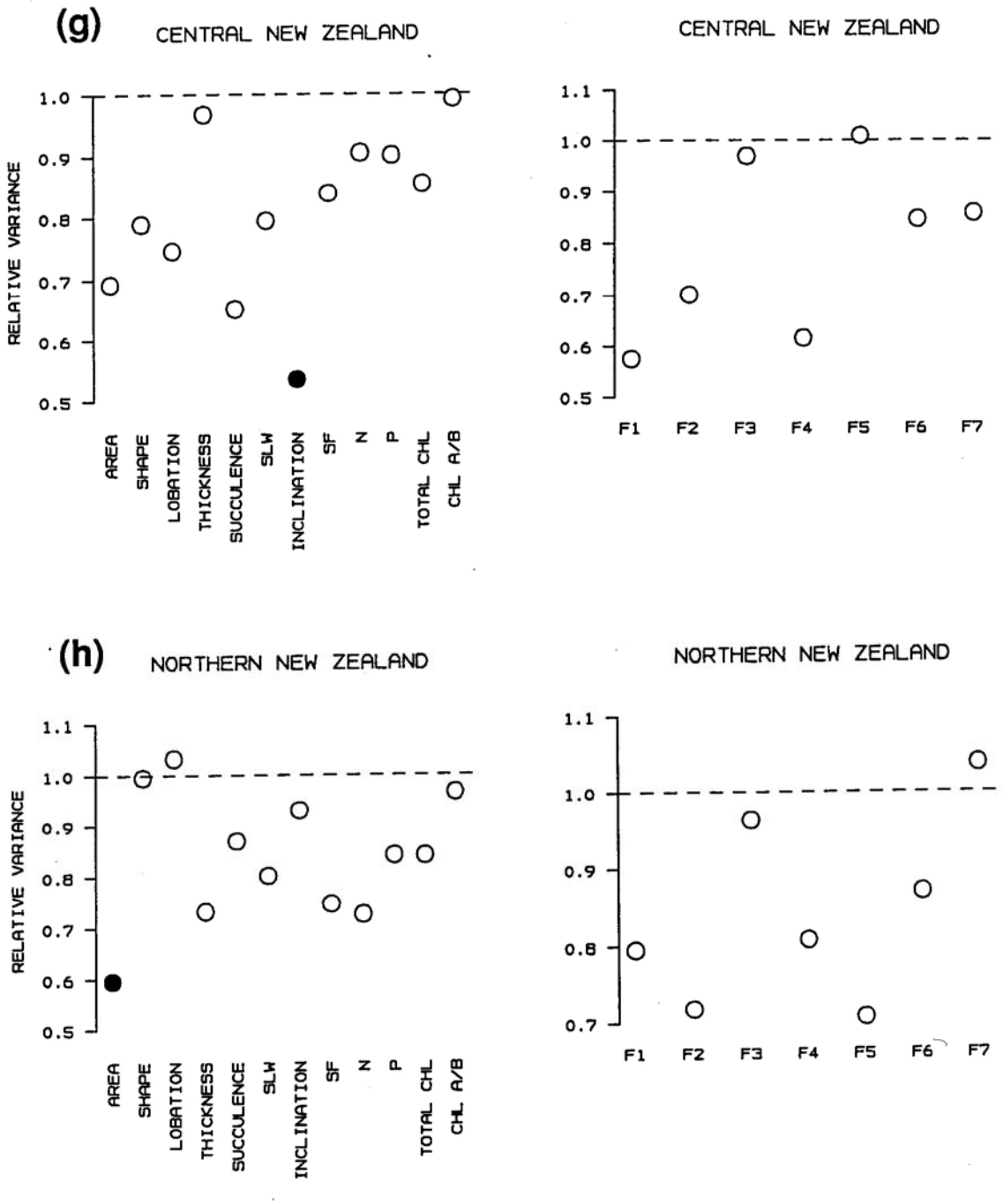


**Fig. 11.3** (continued)

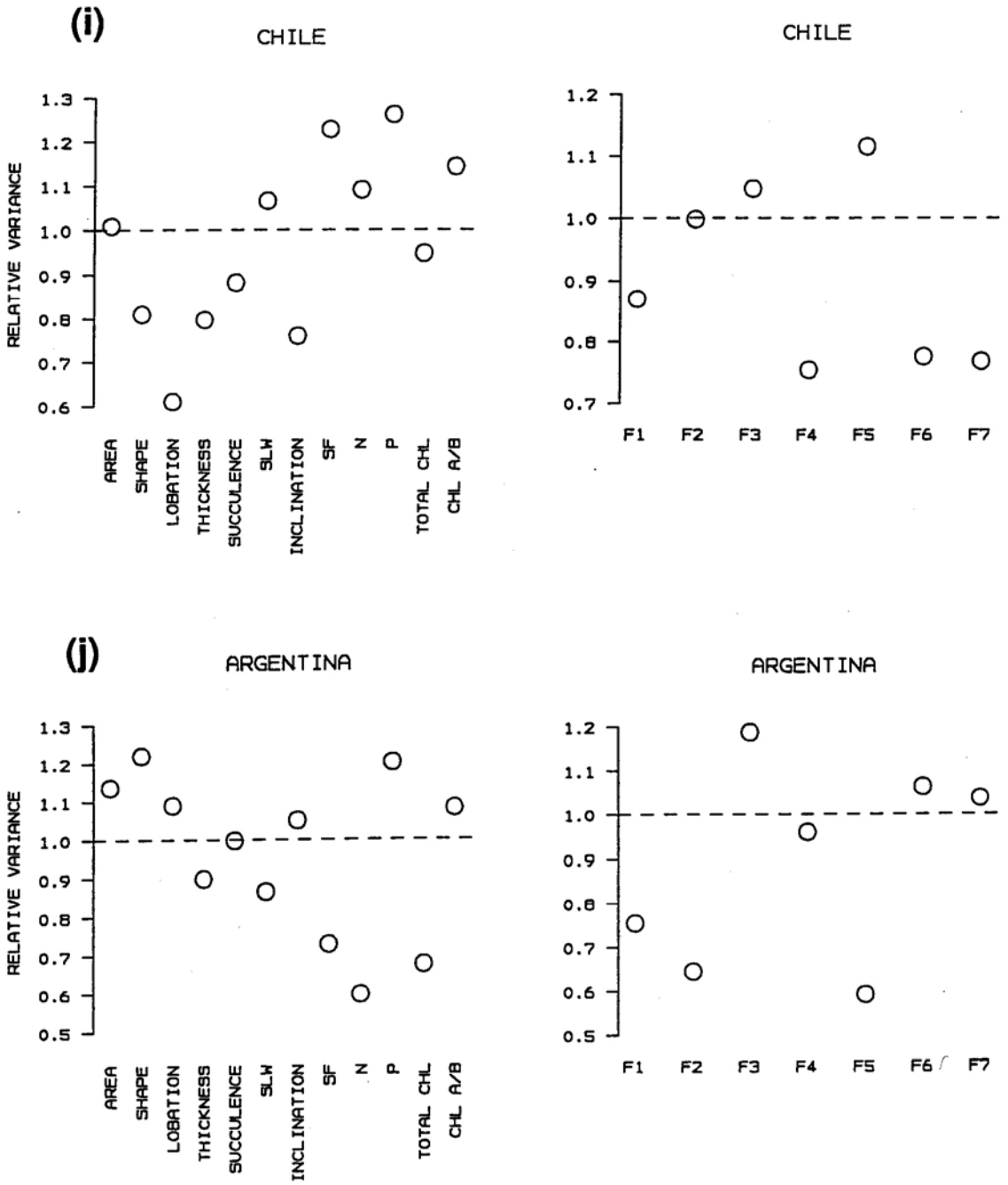


**Fig. 11.3** (continued)

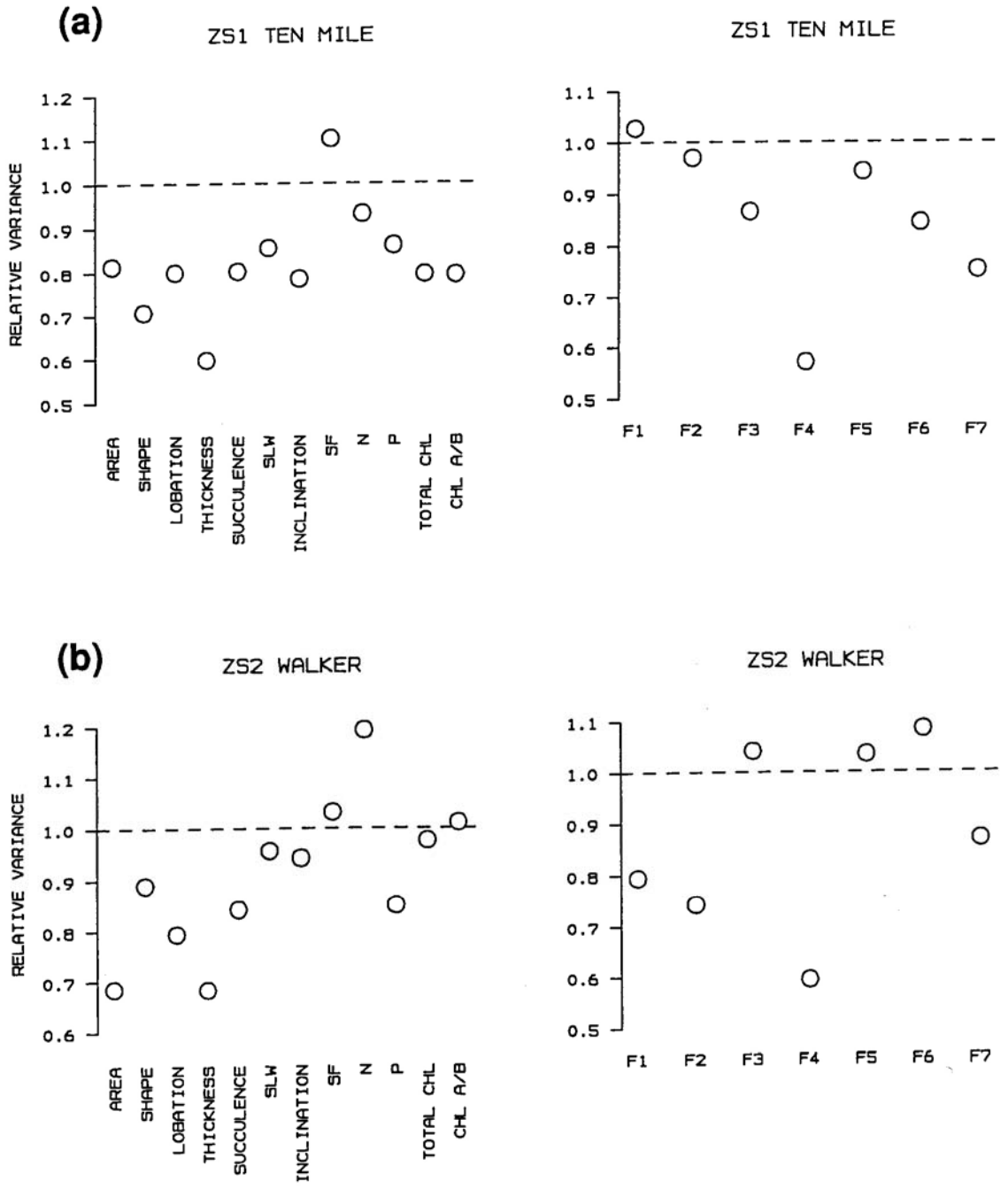


**Fig. 11.4** Smoothed bootstrap tests for over- or underdispersion in texture variates and derived factors for local-scale *Nothofagus*-dominated communities **(a)** ZS1 Ten Mile, **(b)** ZS2 Walker, **(c)** ZS3 Deer, **(d)** ZC1 Craigs, **(e)** ZC2 Station, **(f)** ZN1 Ohakune, **(g)** ZN2 Rotokura, **(h)** ZN3 Clements, **(i)** SC1 Pelada, **(j)** SC2 Antillanca, **(k)** SA1 Quetrihué and **(l)** SA2 Gutierrez. Format as for Fig. 11.2.

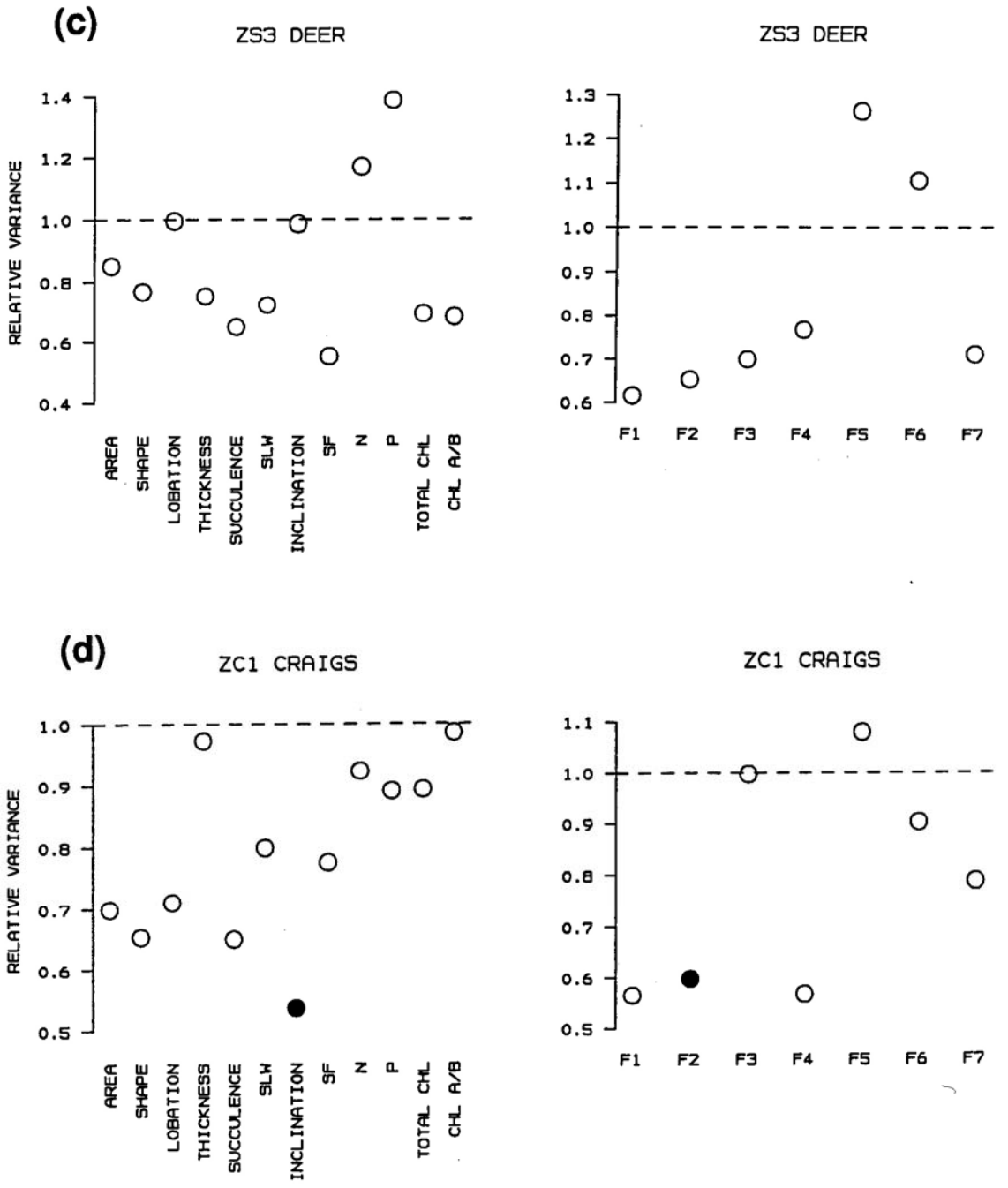


**Fig. 11.4** (continued)

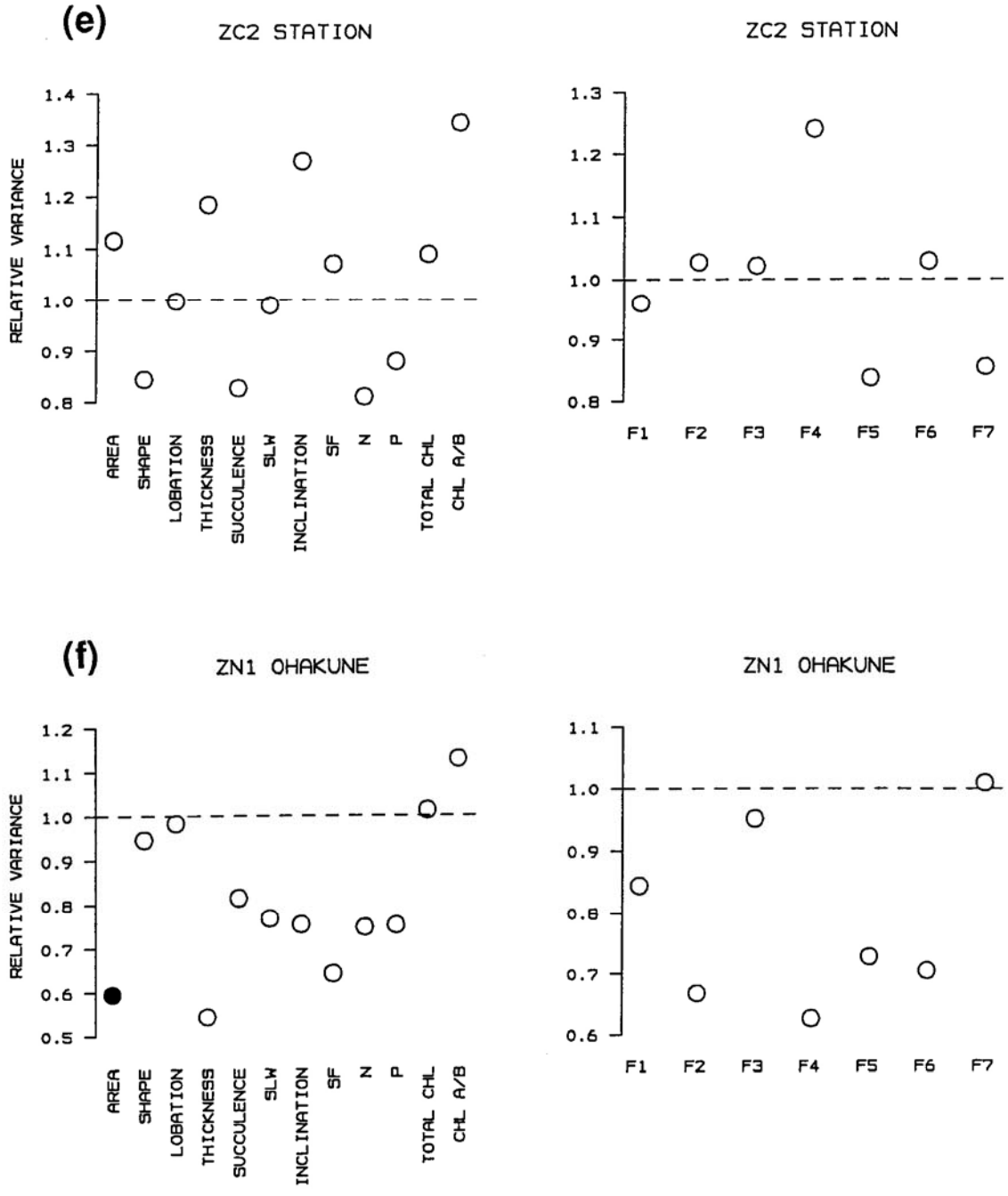


**Fig. 11.4** (continued)

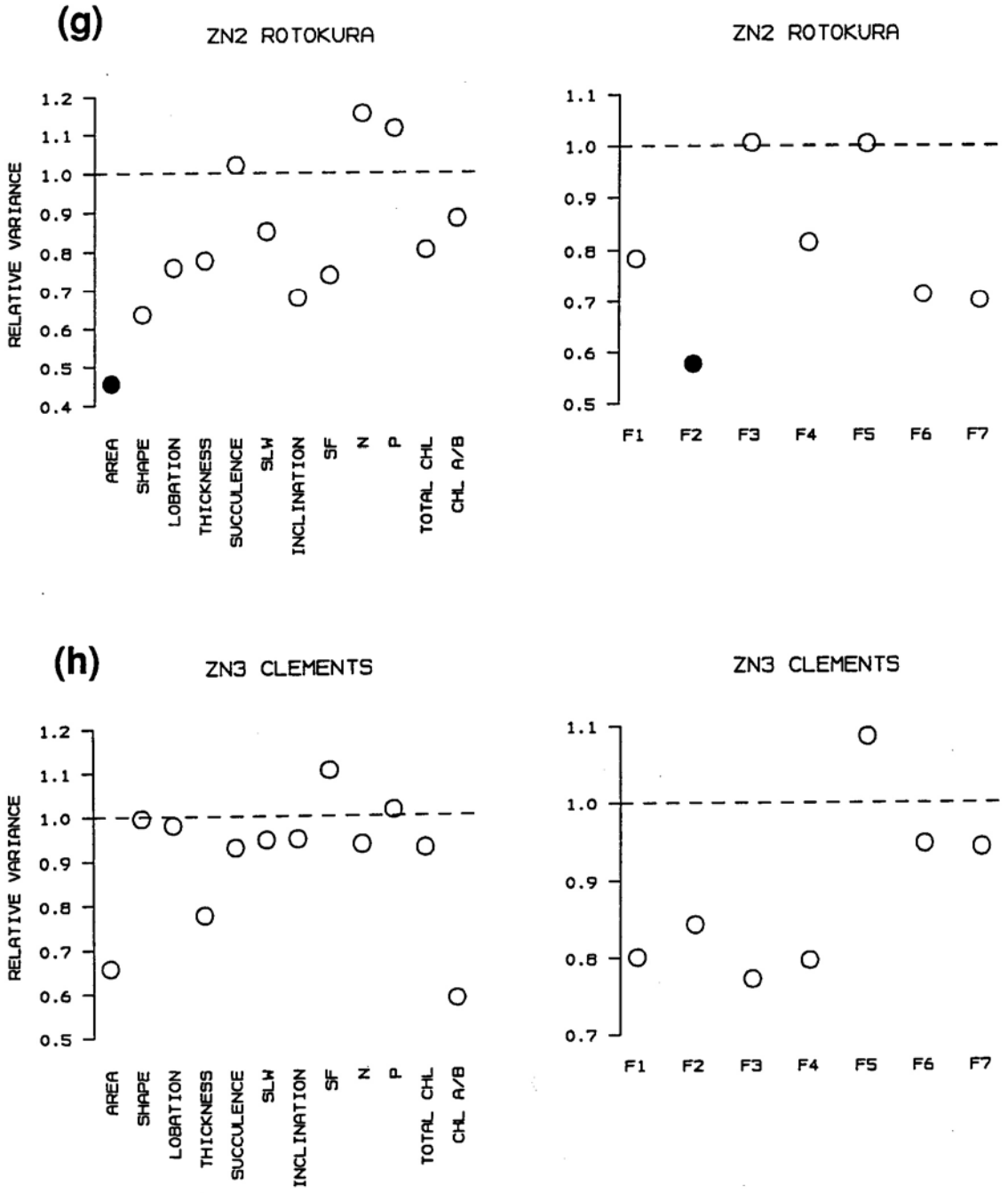


**Fig. 11.4** (continued)

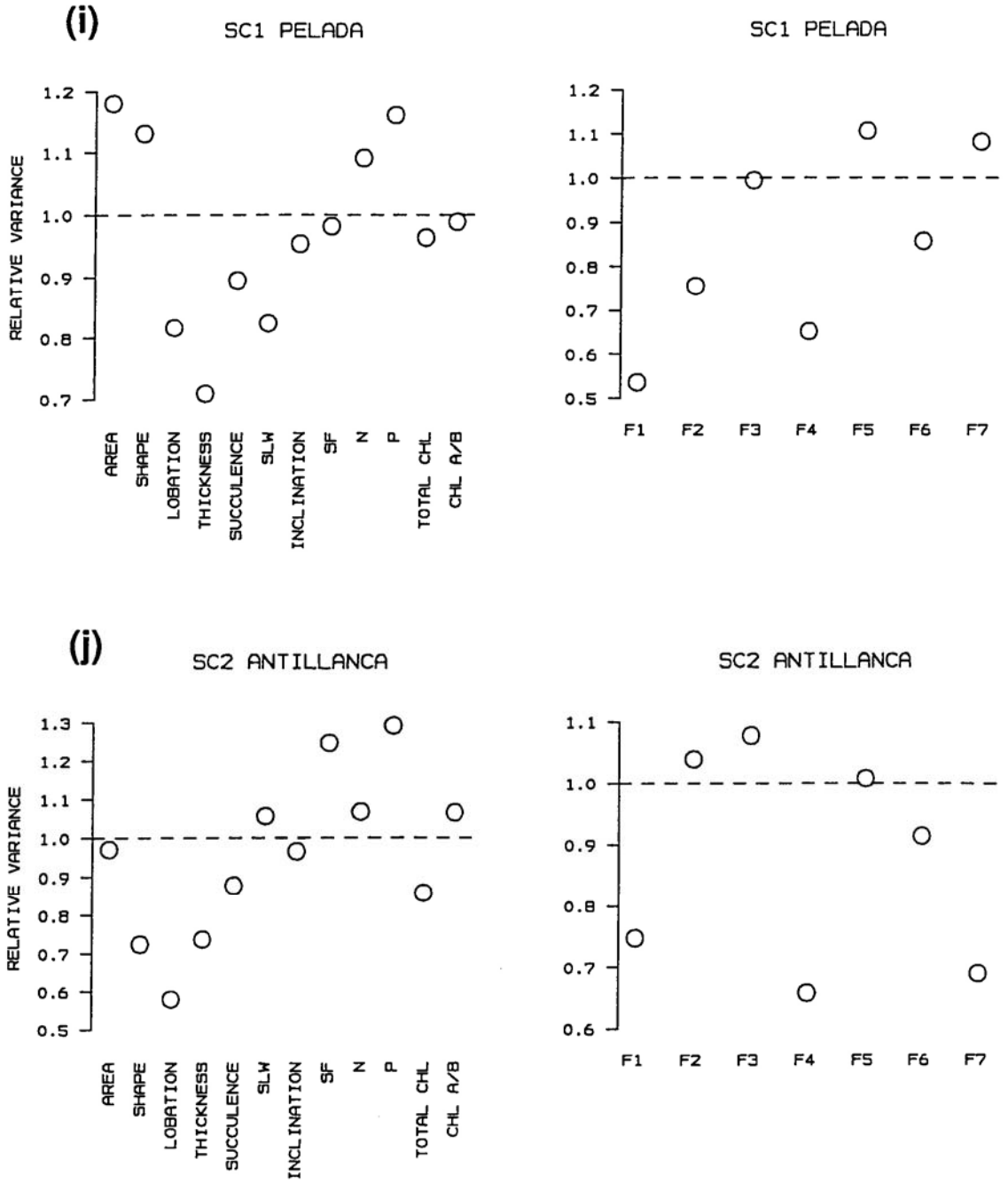


**Fig. 11.4** (continued)

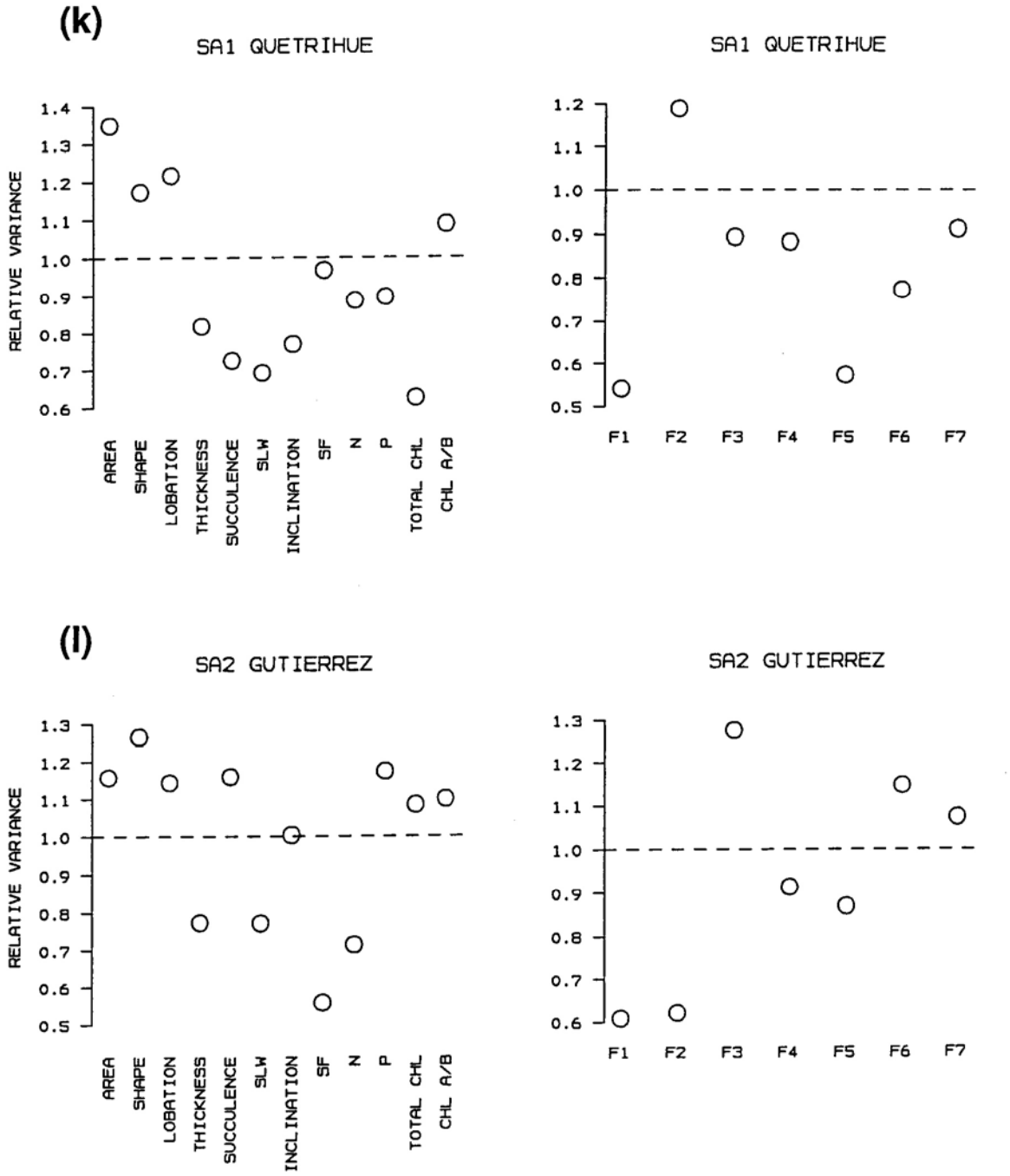


**Fig. 11.4** (continued)

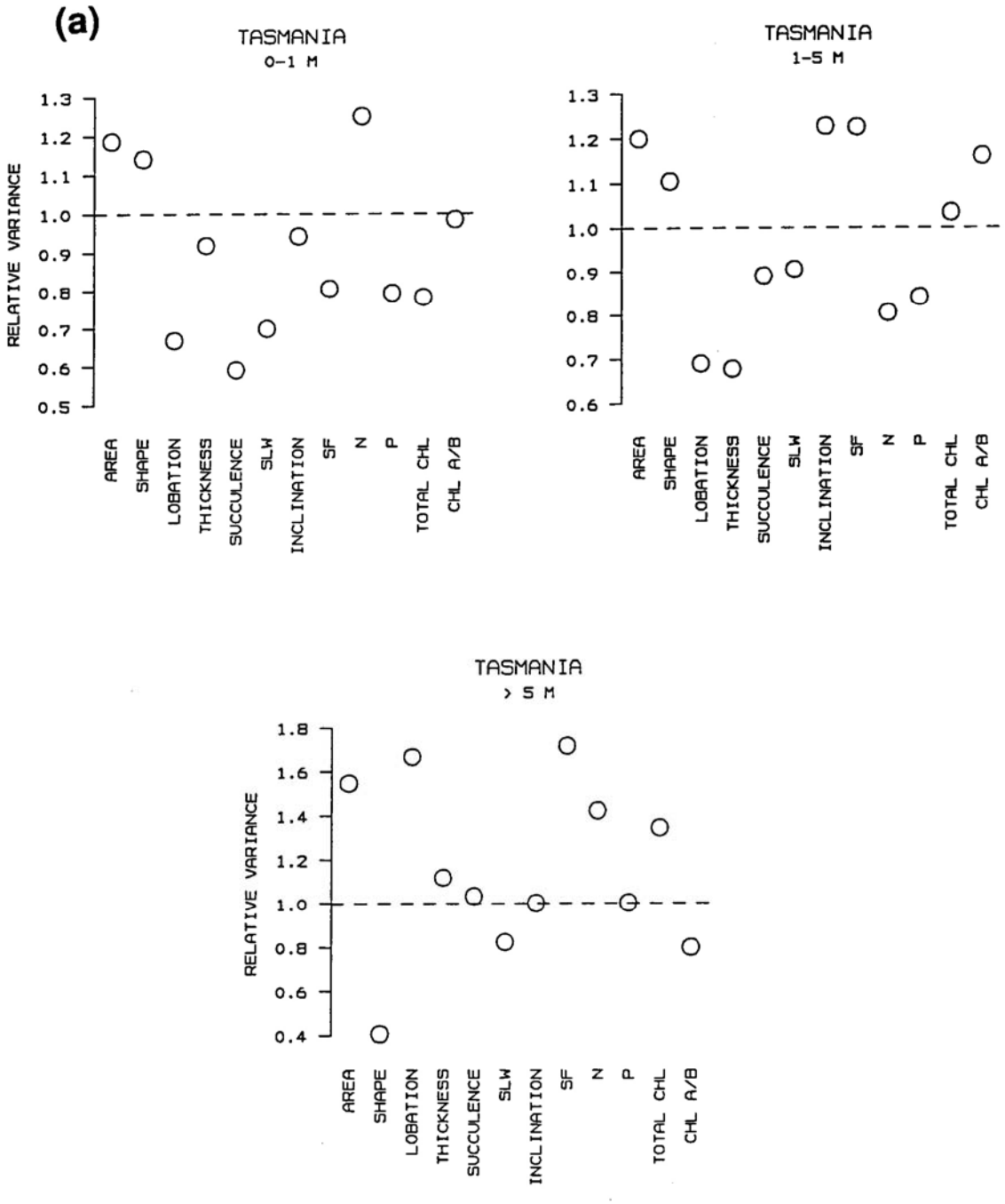


**Fig. 11.5** Smoothed bootstrap tests for over- or underdispersion in texture variates in the 0-1 m, 1-5 m and >5 m guilds (see text) of landmass-scale *Nothofagus*-dominated communities **(a)** Tasmania (T), **(b)** Australia (A), **(c)** New Zealand (Z) and **(d)** South America (S). Format as for Fig. 11.2.

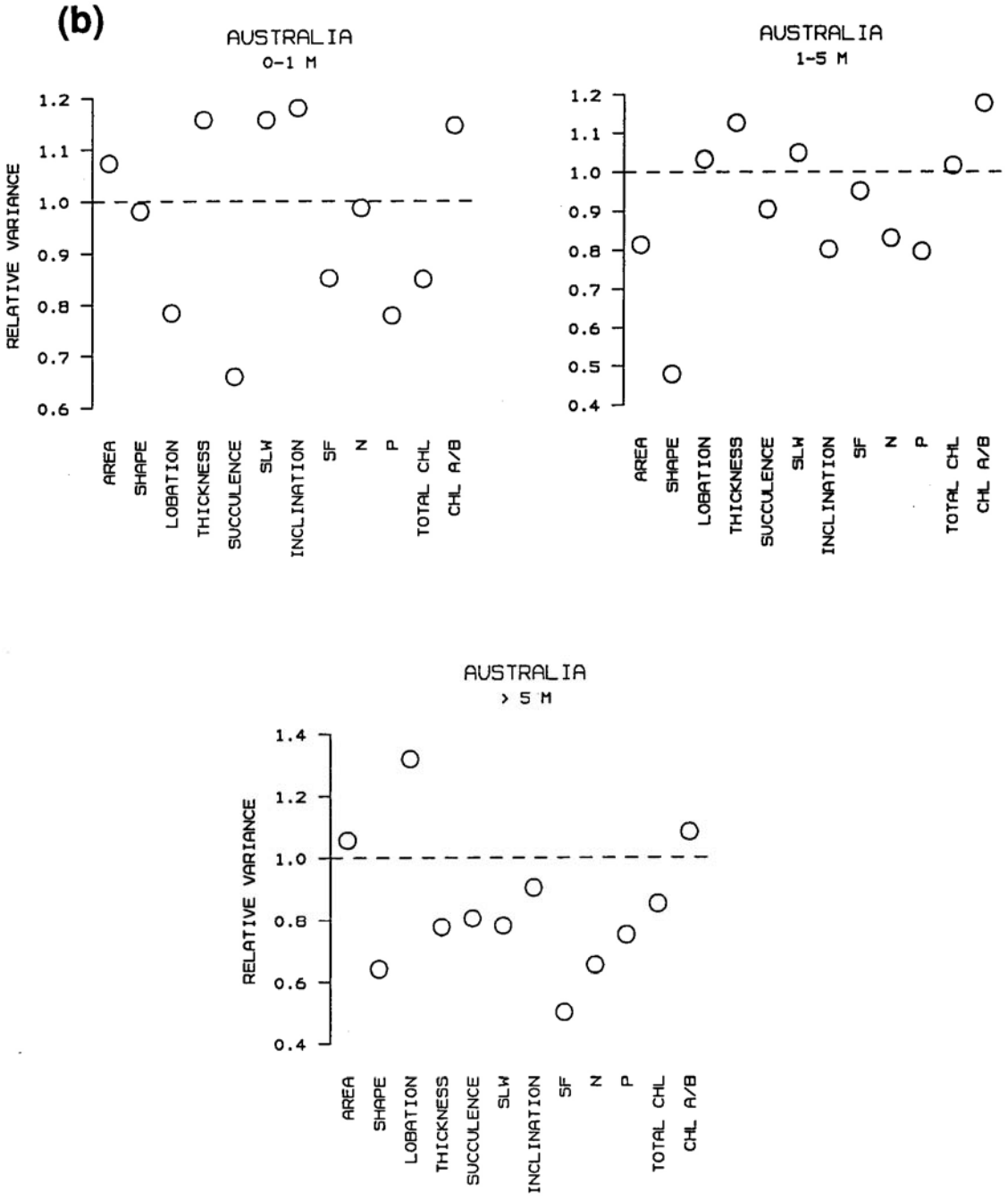


**Fig. 11.5** (continued)

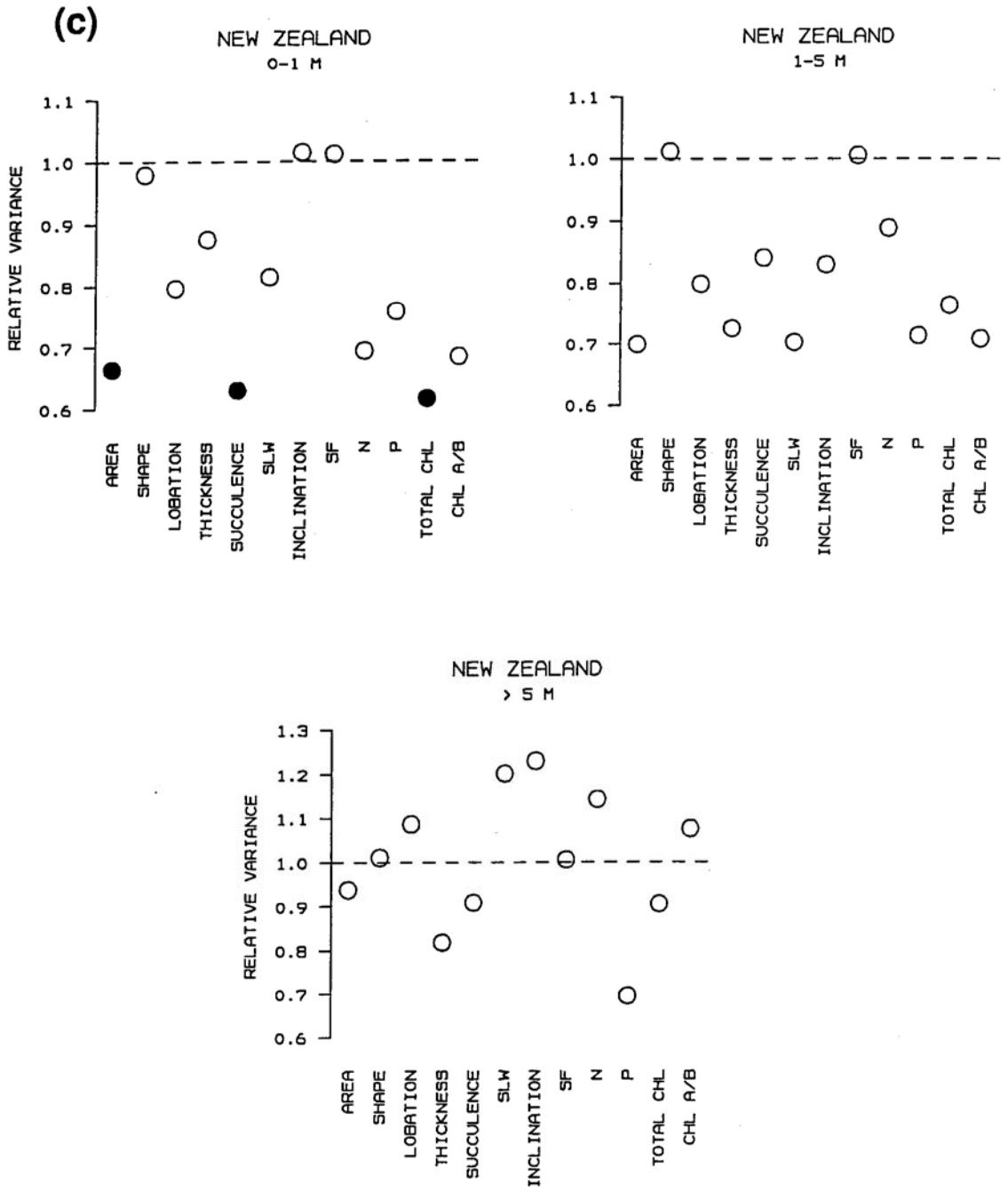


**Fig. 11.5** (continued)

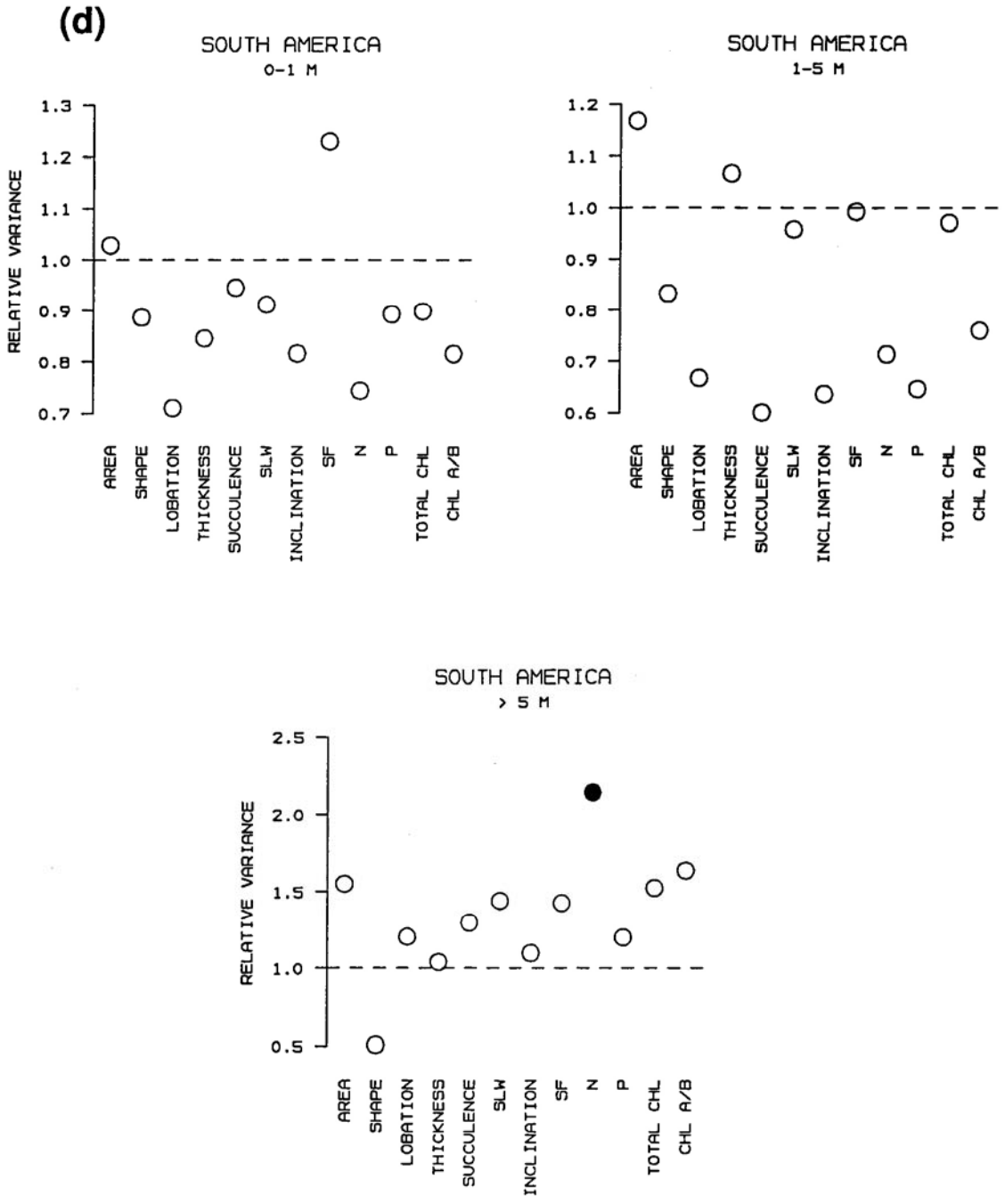


**Fig. 11.5** (continued)

Overdispersion was detected in PSU area and chlorophyll *a/b* ratios in the 0-1 m guild for southern New Zealand (ZC), and for PSU area in the 1-5 m guild (Fig. 11.6a). Most variates show a tendency towards overdispersion ($R_{V,T}$<1) in the two lower guilds, but no strong trend in either direction is apparent for the >5 m guild. Species PSU inclinations are overdispersed within the 0-1 m guild for central New Zealand, while all variates show a tendency towards overdispersion relative to null expectation (Fig. 11.6b). No strong patterns are evident for the 1-5 m and >5 m guilds, although a majority of variates have $R_{V,T}$<1 for both guilds. No significant results were obtained for guilds within the Tasmanian site T1 Balfour (Fig. 11.6c), nor for the Australian site A2 Cascades (Fig. 11.6d).

No significant departure from the null model was observed within guilds for the northern New Zealand site ZN1 Ohakune (Fig. 11.7a), although the majority of texture variates show $R_{V,T}$<1 for the 0-1 and 1-5 m guilds. For ZN2 Rotokura, there is overdispersion in PSU area for both the 0-1 m and 1-5 m guilds (Fig. 11.7b). Overdispersion was detected in the same variate for the 1-5 m guild of ZN3 Clements (Fig. 11.7c). No significant results were obtained within guilds for SA1 Quetrihué in Argentina (Fig. 11.7d).

## PATTERNS AMONG TEXTURE VARIATES

### *Communities*

Significant overdispersion was detected in a relatively small proportion of communities, and for only a subset of texture variates and factors (Table 11.2). PSU area was found to show overdispersion in four of the 26 communities examined, while for five other variates (PSU thickness, succulence, specific weight, inclination and total chlorophyll), and four factors derived from these variates (F1, F2, F3, F4) overdispersion was detected in one or two tests. The number of individual study sites showing overdispersion in any variate or factor is not significant as a proportion of the 17 examined by binomial tests for overall significance. This means that, on the basis of the data presented in Table 11.2, the proposition cannot be rejected, that the dispersion patterns observed in each variate are a chance outcome of stochastic character variation, and not of the operation of assembly rules limiting the co-occurrence of species with similar characters.

No significant underdispersion (clustering of species characters, relative to chance expectation) was detected in any variate at the whole-community scale.

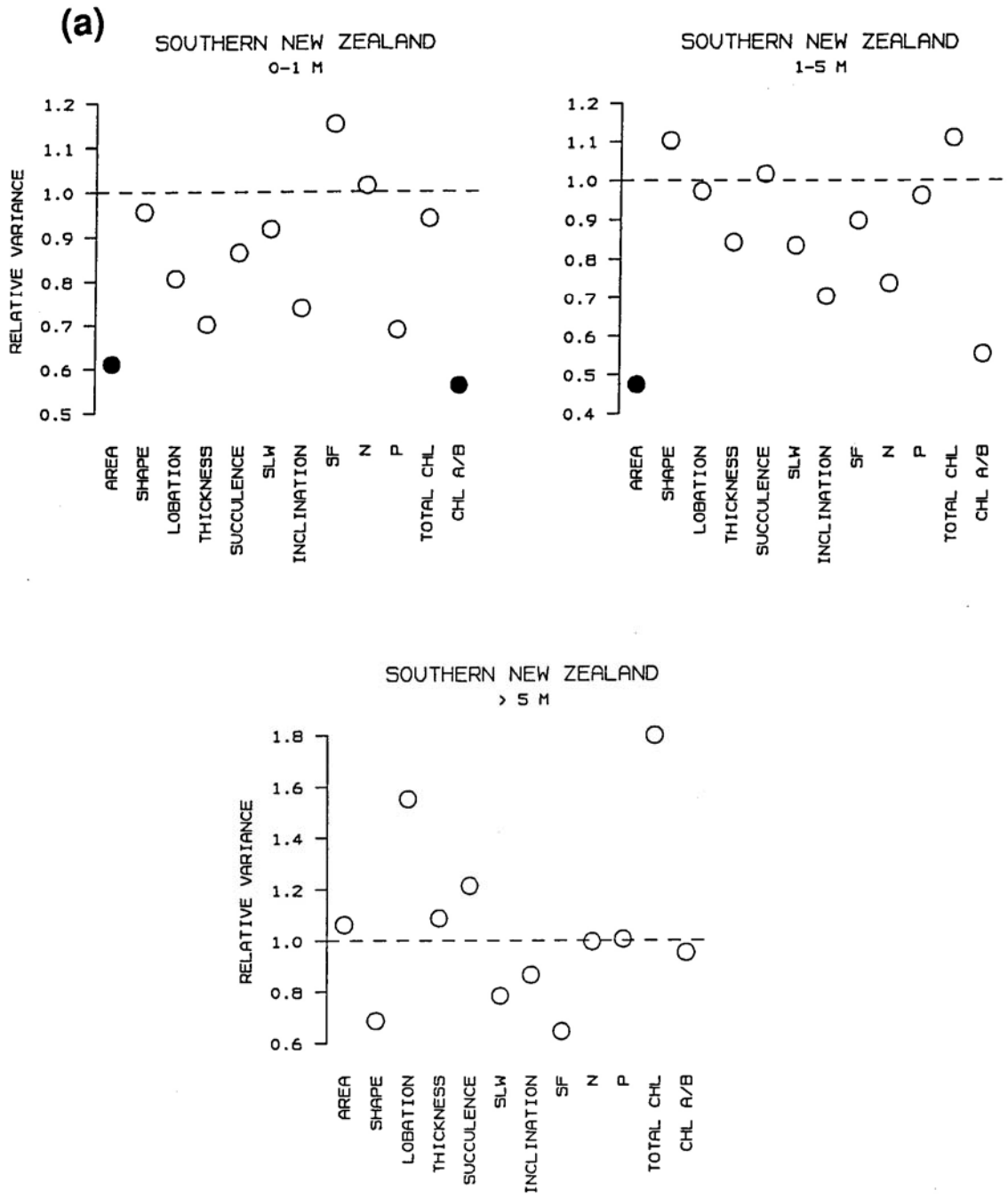


**Fig. 11.6** Smoothed bootstrap tests for over- or underdispersion in texture variates in the 0-1 m, 1-5 m and >5 m guilds (see text) of regional-scale *Nothofagus*-dominated communities **(a)** southern New Zealand (ZS), **(b)** central New Zealand (ZC), **(c)** T1 Balfour and **(d)** A2 Cascades. Format as for Fig. 11.2.

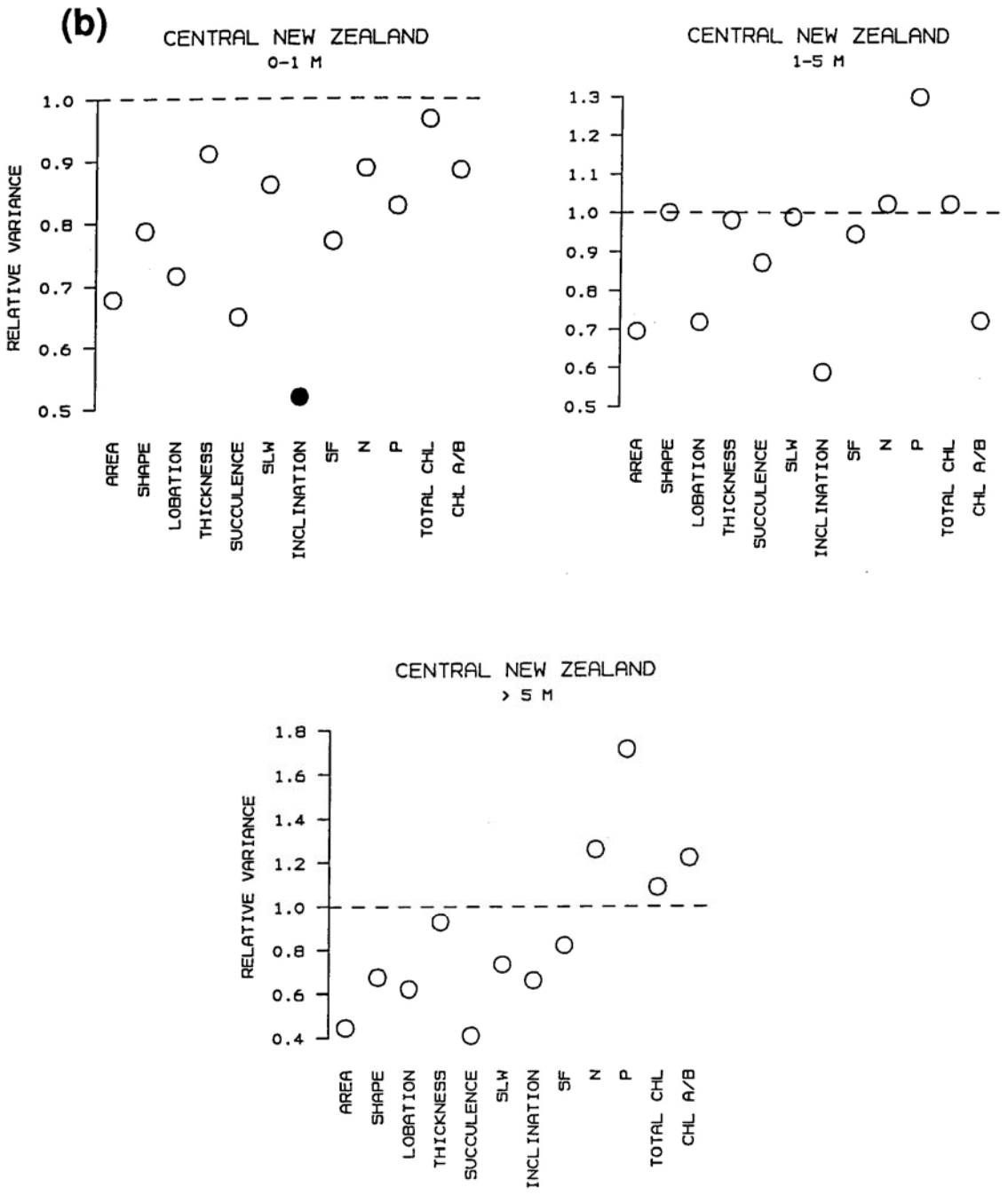


**Fig. 11.6** (continued)

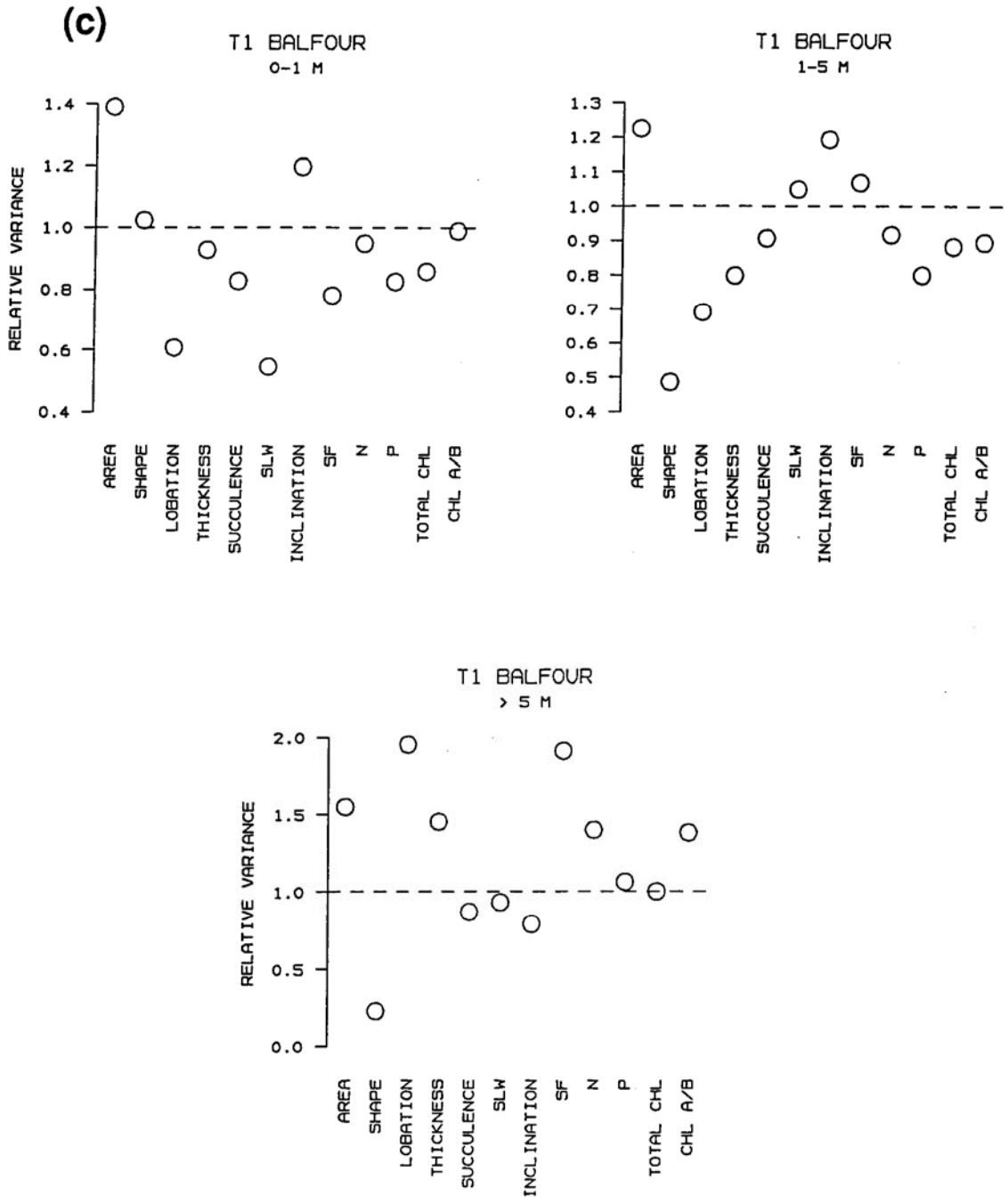


**Fig. 11.6** (continued)

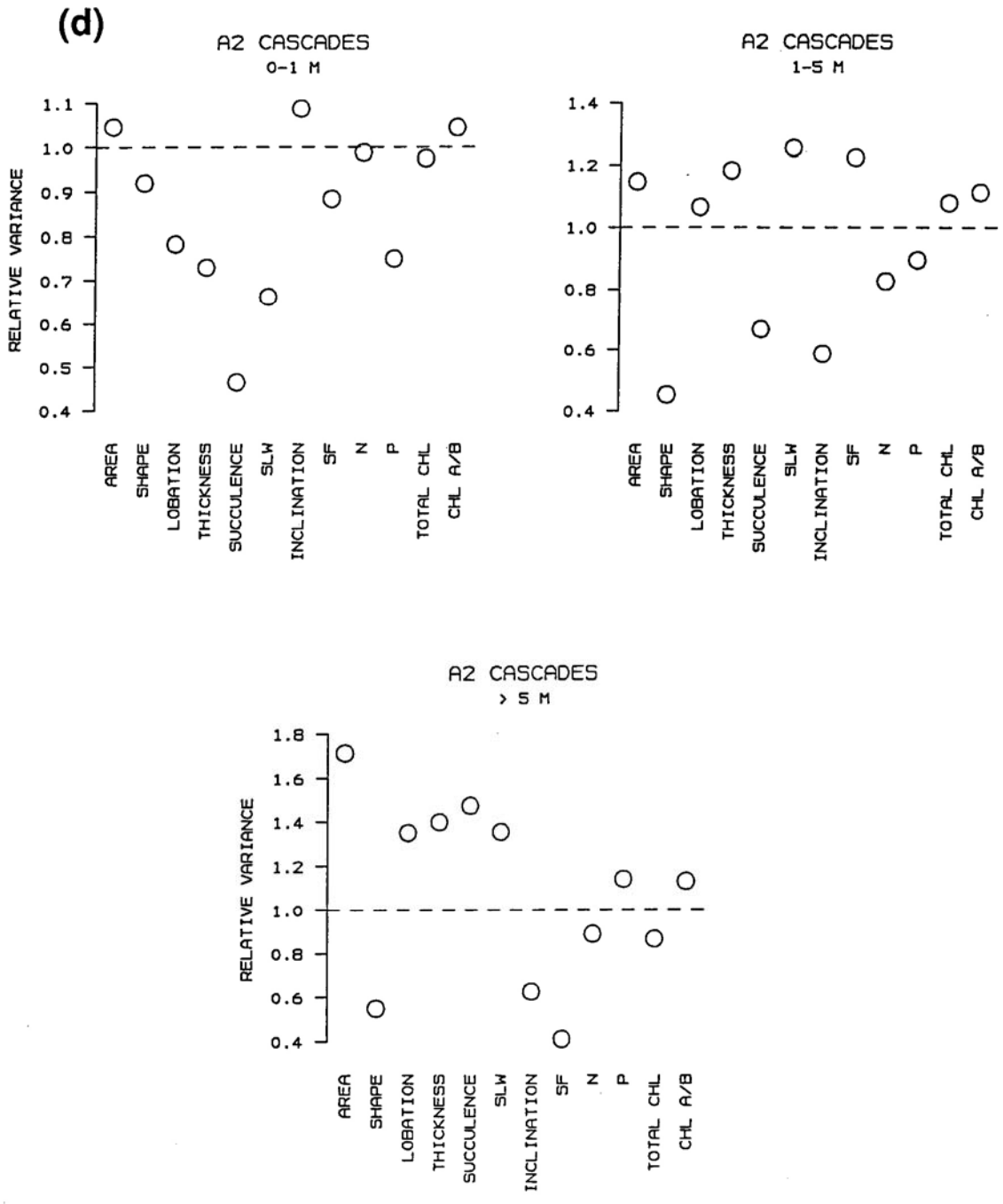


**Fig. 11.6** (continued)

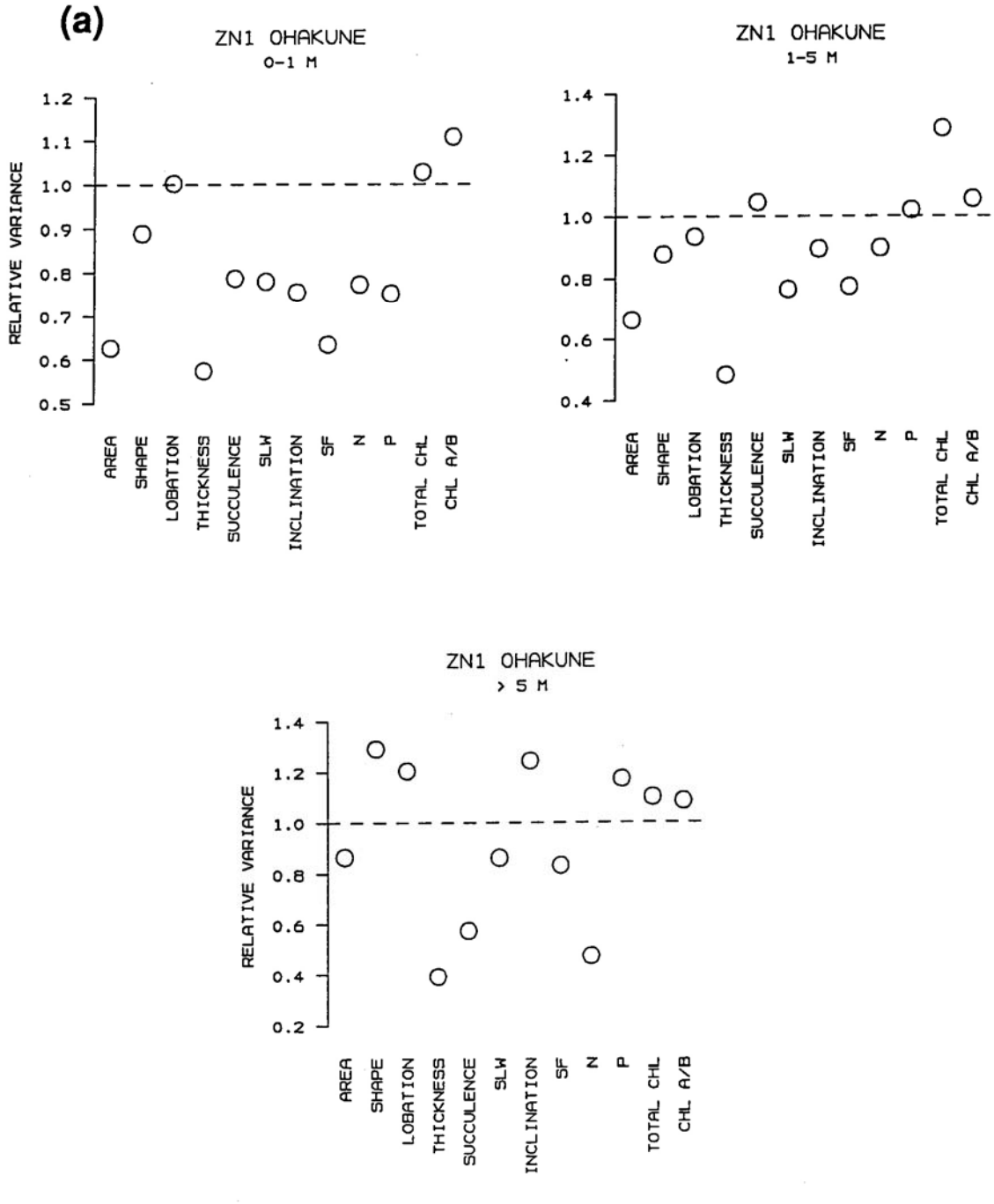


**Fig. 11.7** Smoothed bootstrap tests for over- or underdispersion in texture variates in the 0-1 m, 1-5 m and >5 m guilds (see text) of local-scale *Nothofagus*-dominated communities **(a)** ZN1 Ohakune, **(b)** ZN2 Rotokura, **(c)** ZN3 Clements and **(d)** SA1 Quetrihué. Format as for Fig. 11.2.

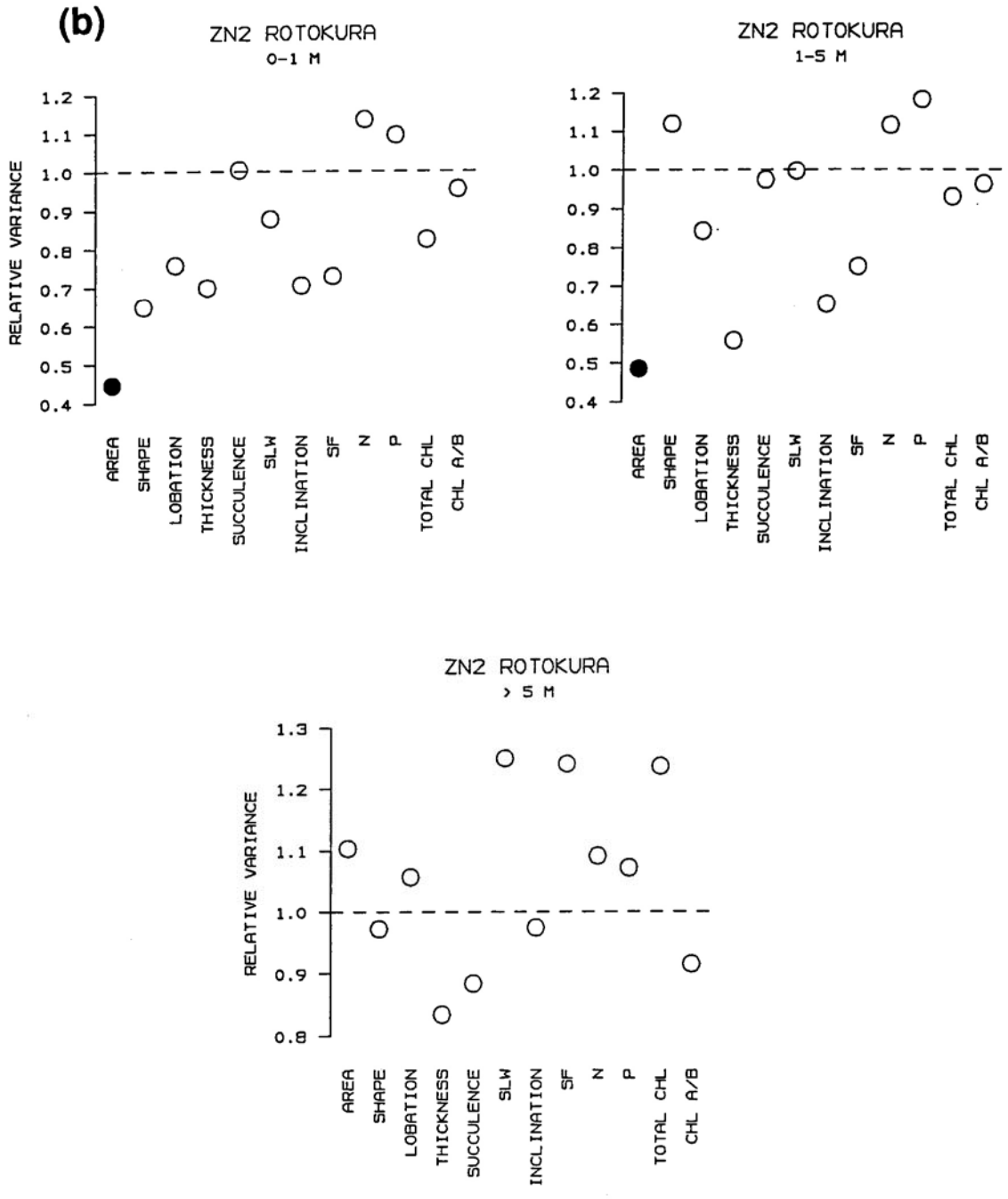


**Fig. 11.7** (continued)

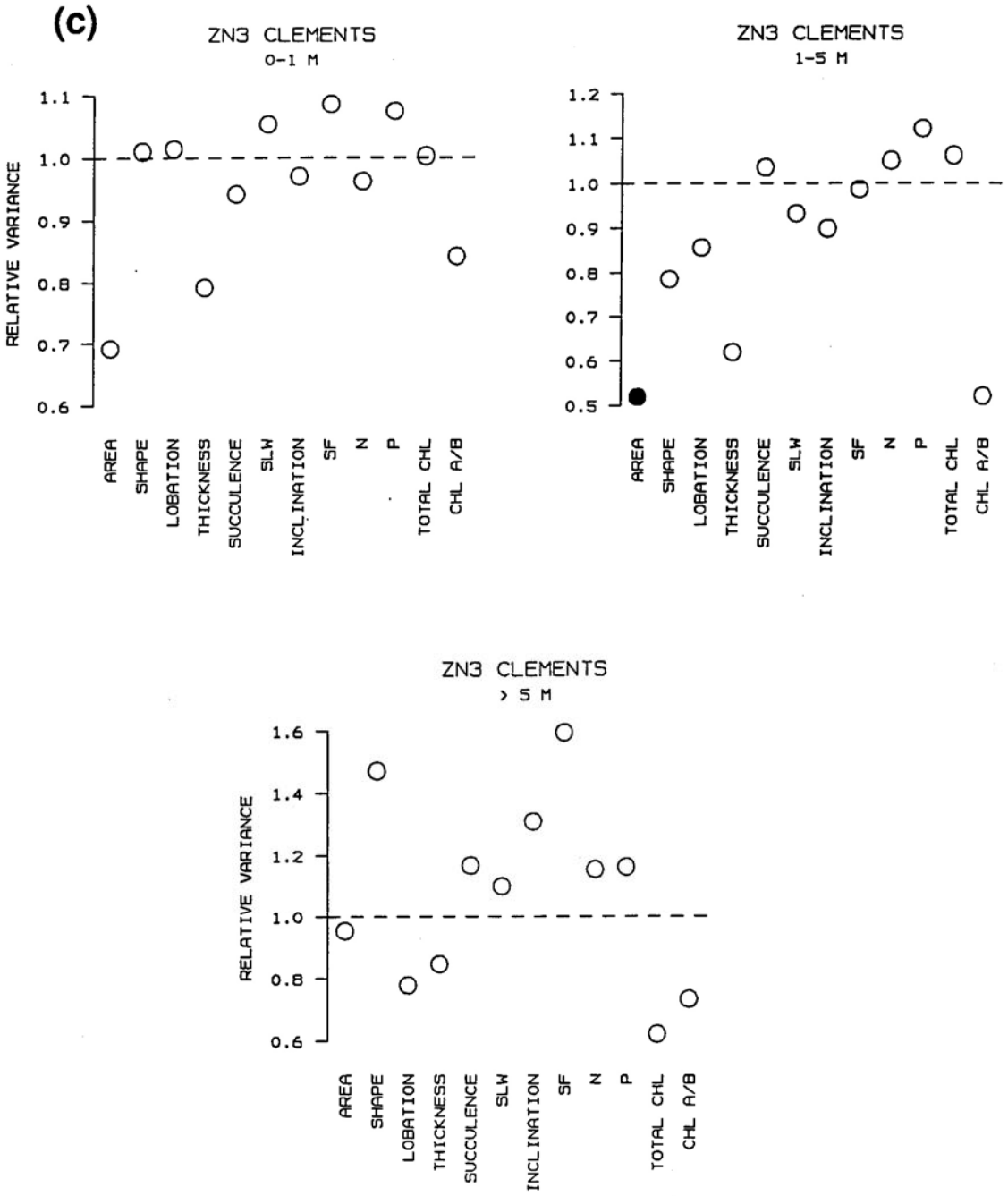


**Fig. 11.7** (continued)

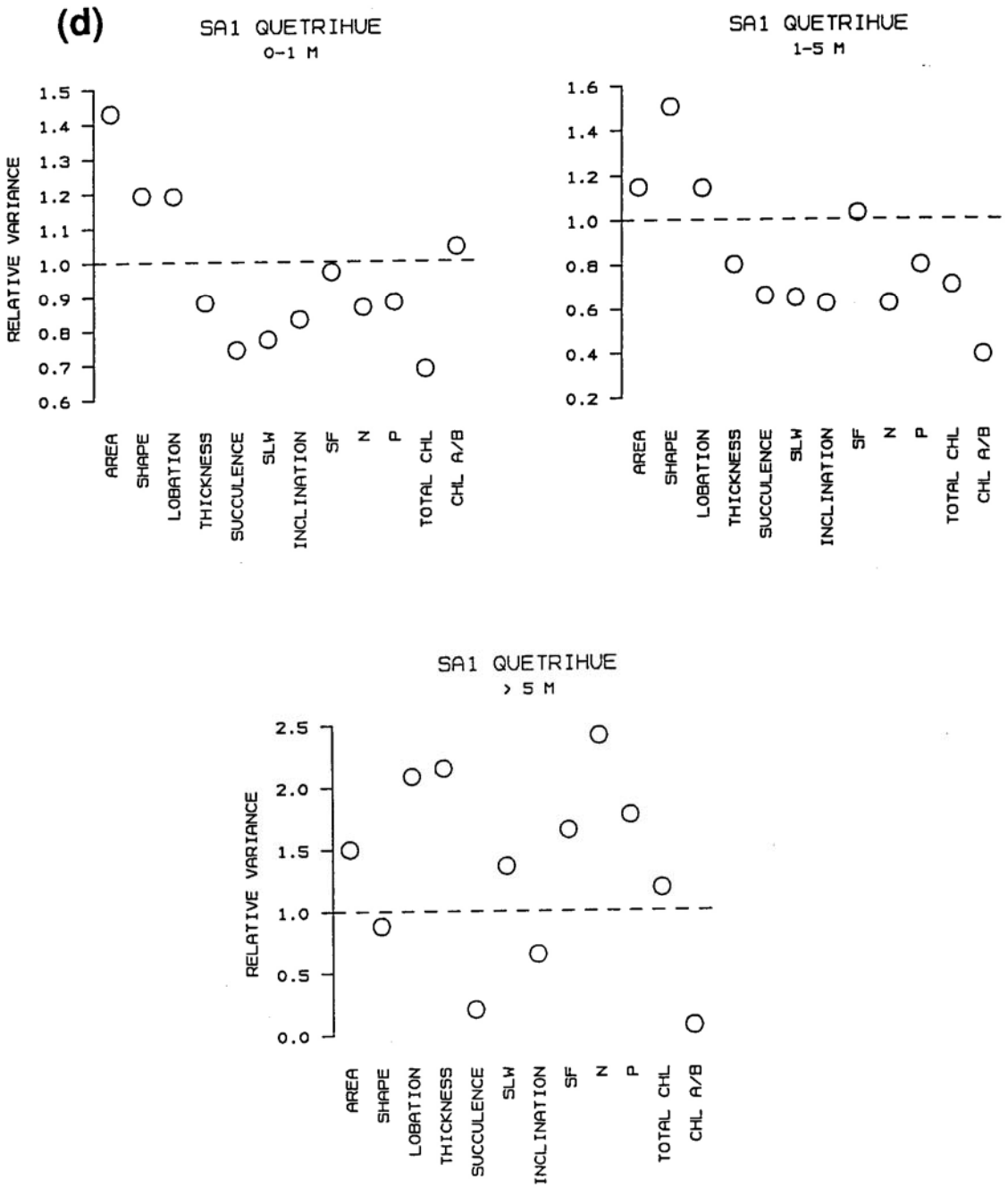


**Fig. 11.7** (continued)

**Table 11.2** Incidence of significant over- or underdispersion in each texture variate and derived texture factor among 26 local-, regional- and landmass-scale communities, and (in parentheses) among 17 of these communities, each comprising a single study site, according to smoothed bootstrap tests (see text). The incidence of significant over- or underdispersion among single study sites is not significant for any texture variate or factor at the 5% level (binomial test).

| Texture variate or factor | Overdispersed | Underdispersed |
|---|---|---|
| Area | 4 (2) | 0 (0) |
| Shape | 0 (0) | 0 (0) |
| Lobation | 0 (0) | 0 (0) |
| Thickness | 1 (1) | 0 (0) |
| Succulence | 1 (0) | 0 (0) |
| SLW | 1 (0) | 0 (0) |
| Inclination | 2 (1) | 0 (0) |
| SF | 0 (0) | 0 (0) |
| N | 0 (0) | 0 (0) |
| P | 0 (0) | 0 (0) |
| Total chl | 1 (0) | 0 (0) |
| Chl *a/b* | 0 (0) | 0 (0) |
| F1 | 1 (0) | 0 (0) |
| F2 | 2 (2) | 0 (0) |
| F3 | 1 (0) | 0 (0) |
| F4 | 1 (1) | 0 (0) |
| F5 | 0 (0) | 0 (0) |
| F6 | 0 (0) | 0 (0) |
| F7 | 0 (0) | 0 (0) |

Although the number of community/variate combinations for which significant departure from the null model could be shown is very low, some general trends were apparent (Figs. 11.2-11.4) in the relative frequencies of departure from null model expectation (whether significant or not) in each direction. Such trends within texture variates and factors are summarised in Table 11.3. For example, bootstrap tests revealed a tendency towards overdispersion ($R_{V,SLW}<1$) in PSU specific weight for 15 of the 17 communities examined. In only two communities was a tendency towards underdispersion ($R_{V,SLW}>1$) detected. From the binomial distribution, the likelihood of obtaining a frequency ratio as uneven as 15:2 by chance alone when an even ratio (8.5:8.5) is expected, is 0.013, well below the 5% target significance level. This suggests that the trend towards overdispersion in PSU specific weight across the 17 communities is the result, not

of stochastic character variation among species, but of a community process that tends to limit similarity in species characters, causing them to be more regularly spaced than expected by chance. It is suggested that this causal process may be the operation of assembly rules.

Five variates — PSU lobation, thickness, succulence, specific weight and total chlorophyll — show a significant trend towards overdispersion among the 17 individual study sites. There are also significant trends towards overdispersion for F1 (related to PSU succulence, specific weight, total chlorophyll and species height) and F4 (related to PSU thickness). Other variates and factors show little evidence for departure from randomness, although for only one variate (chlorophyll *a/b*) and one factor (F5, which is most closely related to PSU nitrogen and phosphorus content) is the frequency ratio skewed towards underdispersion.

**Table 11.3** Relative frequency of departure from null model expectation (relative deviance, $R_{V,T}$=1) in the directions of overdispersion ($R_{V,T}$<1) and underdispersion ($R_{V,T}$>1) in each texture variate and derived texture factor for 17 individual study sites, according to smoothed bootstrap tests (see text). The significance (two-tailed *P*) of a trend in either direction (binomial test for departure from the expectation of even frequencies) is shown. Data showing significant trends (*P*<0.05) appear in bold type.

| Texture variate or factor | Overdispersed | Underdispersed | *P* for trend |
|---|---|---|---|
| Area | 10 | 7 | 0.629 |
| Shape | 11 | 6 | 0.332 |
| Lobation | **14** | **3** | **0.013** |
| Thickness | **14** | **3** | **0.013** |
| Succulence | **14** | **3** | **0.013** |
| SLW | **15** | **2** | **0.002** |
| Inclination | 11 | 6 | 0.332 |
| SF | 9 | 8 | 1.000 |
| N | 10 | 7 | 0.629 |
| P | 10 | 7 | 0.629 |
| Total chl | **14** | **3** | **0.013** |
| Chl *a/b* | 8 | 9 | 1.000 |
| F1 | **16** | **1** | **0.000** |
| F2 | 12 | 5 | 0.143 |
| F3 | 11 | 6 | 0.332 |
| F4 | **14** | **3** | **0.013** |
| F5 | 6 | 11 | 0.332 |
| F6 | 10 | 7 | 0.629 |
| F7 | 12 | 5 | 0.143 |

*Guilds*

As was the case for whole communities (Table 11.2) significant departure from null expectation was observed in only a few tests at the guild scale (Table 11.4). Within the 0-1 m guild, overdispersion, significant for individual tests, was detected in PSU Area, succulence, inclination, total chlorophyll and chlorophyll *a/b*. For the 1-5 m guild there is overdispersion in PSU area and chlorophyll *a/b*, while significant departure from the null model within the >5 m guild is limited to overdispersion in PSU chlorophyll *a/b* in one community, and underdispersion in PSU nitrogen content in another. The only variate for which the incidence of overdispersion is significant as a proportion of the number of communities examined, is PSU Area, for which overdispersion was detected in the 0-1 m guild of three individual study sites.

**Table 11.4** Incidence of significant over- or underdispersion in each texture variate for the 0-1 m, 1-5 m and >5 m guilds among 26 local-, regional- and landmass-scale communities (24 for >5 m guild), and (in parentheses) among 17 of these communities (15 for >5 m guild), each comprising a single study site, according to smoothed bootstrap tests (see text). The incidence of significant over- or underdispersion among single study sites is significant only for PSU area in the 0-1 m guild ($P$<0.05 from binomial test).

| Texture variate or factor | 0-1 m Guild | | 1-5 m Guild | | >5 m Guild | |
|---|---|---|---|---|---|---|
| | Over-dispersed | Under-dispersed | Over-dispersed | Under-dispersed | Over-dispersed | Under-dispersed |
| Area | 4 (3*) | 0 (0) | 3 (2) | 0 (0) | 0 (0) | 0 (0) |
| Shape | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| Lobation | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| Thickness | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| Succulence | 1 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| SLW | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| Inclination | 2 (2) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| SF | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| N | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 1 (0) |
| P | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| Total chl | 1 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| Chl *a/b* | 2 (2) | 0 (0) | 2 (0) | 0 (0) | 1 (1) | 0 (0) |

*$P$=0.0082 (two-tailed)

Although the incidence of significant underdispersion within guilds is significant overall for only one variate, binomial tests reveal some significant trends (Table 11.5). Within the 0-1 m guild, three variates — PSU thickness, succulence and specific weight — showed a tendency towards overdispersion in a significantly large proportion of sites. Little evidence of a trend is apparent for the remaining nine variates in this guild. No trends were detected in the 1-5 m guild. In the >5 m guild there is a significant trend towards underdispersion, PSU phosphorus values showing a tendency in this direction in 12 of the 15 sites. PSU area and lobation also show possible trends towards underdispersion, though this is non-significant for both variates.

**Table 11.5** Relative frequency of departure from null model expectation (relative deviance, $R_{V,T}$=1) in the directions of overdispersion ($R_{V,T}$<1) and underdispersion ($R_{V,T}$>1) in each texture variate for the 0-1 m and 1-5 m guilds within 17 individual study sites, and the >5 m guild within 15 study sites, according to smoothed bootstrap tests (see text). The significance (two-tailed *P*) of a trend in either direction (binomial test for departure from the expectation of even frequencies) is shown. Data showing significant trends (*P*<0.05) appear in bold type.

| Texture variate | 0-1m Guild | | | 1-5m Guild | | | >5m Guild | | |
|---|---|---|---|---|---|---|---|---|---|
| | Over-dispersed | Under-dispersed | *P* for trend | Over-dispersed | Under-dispersed | *P* for trend | Over-dispersed | Under-dispersed | *P* for trend |
| Area | 7 | 10 | 0.629 | 8 | 9 | 1.000 | 4 | 11 | 0.118 |
| Shape | 9 | 8 | 1.000 | 11 | 6 | 0.332 | 10 | 5 | 0.301 |
| Lobation | 10 | 7 | 0.629 | 11 | 6 | 0.332 | 4 | 11 | 0.118 |
| Thickness | **14** | **3** | **0.013** | 11 | 6 | 0.332 | 8 | 7 | 1.000 |
| Succulence | **14** | **3** | **0.013** | 11 | 6 | 0.332 | 9 | 6 | 0.607 |
| SLW | **14** | **3** | **0.013** | 11 | 6 | 0.332 | 6 | 9 | 0.607 |
| Inclination | 8 | 9 | 1.000 | 12 | 5 | 0.143 | 7 | 8 | 1.000 |
| SF | 10 | 7 | 0.629 | 11 | 6 | 0.332 | 7 | 8 | 1.000 |
| N | 10 | 7 | 0.629 | 7 | 10 | 0.629 | 6 | 9 | 0.607 |
| P | 8 | 9 | 1.000 | 8 | 9 | 1.000 | **3** | **12** | **0.035** |
| Total chl | 10 | 7 | 0.629 | 10 | 7 | 0.629 | 5 | 10 | 0.301 |
| Chl *a/b* | 8 | 9 | 1.000 | 9 | 8 | 1.000 | 5 | 10 | 0.301 |

## 11.4 Discussion

OVERDISPERSION OF SPECIES CHARACTERS

The null hypothesis that species characters are drawn at random from some underlying distribution could be rejected for relatively few texture variates and in a minority of communities and guilds within communities (Figs. 11.2-11.7; Tables 11.2, 11.4). Only for PSU area in the 0-1

m guild was the incidence of overdispersion high enough to be deemed significant as a proportion of the number of tests carried out.

Although significant results were obtained in relatively few bootstrap tests, a number of overall trends were apparent in the (generally non-significant) results. In many communities, particularly those sampled in New Zealand, there was a tendency for species character values to be more regularly dispersed than expected on a random basis (though significantly so for only a minority of tests). This pattern was observed in communities at the landscape (e.g. New Zealand, South America; Fig. 2c-d), regional (e.g. southern, central and northern New Zealand; Fig. 3f-h) and local scales (e.g. northern New Zealand sites; Fig. 4f-h). Although the significance of these trends could not be investigated within communities (due to the non-independence of observations for different, but correlated, texture variates), binomial tests revealed some significant overall trends within variates. With the sole exception of PSU phosphorus content in the >5 m guild, significant trends were in the direction of overdispersion. These findings suggest that character dispersion patterns are not completely stochastic, but are influenced by community- or guild-level processes. The predominance of overdispersion is compatible with the hypothesis that there are assembly rules which restrict the co-occurrence of similar species, resulting in a somewhat regular spacing of species ordinates along character axes.

The amount of evidence for overdispersion detected at the guild scale was lower than at the community scale, particularly for the 1-5 m and >5 m guilds (Fig. 11.5-11.7; Tables 11.3, 11.5). However, patterns of departure from the null model in the 0-1 m guild were generally similar to those observed at the whole community level, though fewer tests gave significant results. For several communities, especially at the landscape scale (Fig. 11.5), there was a trend towards overdispersion in the 0-1 m and 1-5 m guilds, and underspersion in the >5 m guild. The trend was also apparent within variates, the only significant underdispersion being within the >5 m guild (PSU phosphorus, South America). This pattern would seem to suggest that assembly rules may have a greater controlling effect on community structure in the ground and (possibly) shrub layers than in the tree stratum. Alternatively, clustering — for example, about different adaptive optima, or among related species whose function might reflect common phylogenetic constraints — may be more pronounced in the >5 m guild, where it would tend to obscure any regularity in the spacing between species that might arise owing to the effects of assembly rules.

Of the five texture variates showing significant trends towards overdispersion among whole communities (Table 11.3), three — PSU succulence, specific weight and total chlorophyll — are closely related to factor F1, which also shows a significant trend in this direction. F1 may correspond to functional variation in response to light availability (see Section 9.4), particularly in the context of vertical structure (the texture variate species height, not examined directly in this chapter, also has a high loading on F1; see Table 9.1). The observed trend towards overdispersion in PSU thickness and its associated factor F4, might likewise be associated with the light regime (Givnish 1987; Bongers & Popma 1988; Reich *et al.* 1991) or with nutrient

uptake (Beadle 1966; Grubb 1977; Sobrado & Medina 1980). The latter alternative may be more likely, since F1 and F4 (like all the texture factors) are uncorrelated, suggesting that they may be associated with different underlying factors. A possible nutritional interpretation of the observed overdispersion is that there are assembly rules based on past or present root competition (Caldwell 1987; Caldwell *et al.* 1991), which result in partitioning of below-ground nutrient gradients among species. Resulting interspecific differences in nutrient uptake might be reflected in a somewhat regular spacing of species values for leaf thickness, which may be correlated with plant nutrient uptake.

PSU area showed the highest incidence of significant overdispersion in individual tests (although this was significant overall only for the 0-1 m guild; Table 11.4), yet did not show any significant overall trends at either the community or guild scale (Tables 11.3, 11.5). This pattern suggests that there are relatively strong assembly rules determining dispersion patterns for leaf area, but that these apply or can be detected only within certain communities (principally, regional- and local-scale communities in New Zealand), and primarily in the lower strata. Variation in leaf area has been correlated with light, nutrient and moisture regimes (Grubb *et al.* 1963; Givnish & Vermeij 1976; Grubb 1977; Hall & Swaine 1981; Chiarello 1984; Medina 1984; Givnish 1984), all of which would represent resource, as well as environmental, gradients. The overdispersion observed in PSU area could represent an outcome of assembly rules leading to partitioning of any of these resource gradients among species.

### OVERDISPERSION VERSUS TEXTURE CONVERGENCE

The hypotheses of character overdispersion within assemblages, and of texture convergence among them, are closely related. This is because texture convergence, relative to expectation under a null model of random species assortment, might be expected as an outcome of character overdispersion, if other assumptions (in particular, that of matching physical environments in the assemblages being compared) are met (Ricklefs & Travis 1980; Wiens 1991a,b; Wilson *et al.* 1994).

Disregarding significance levels in individual tests, the patterns observed at the whole-community level in the present chapter are generally consistent with the results of tests for convergence in *Nothofagus* community texture, carried out previous chapters. There were significant trends towards overdispersion in PSU lobation, thickness, succulence, specific weight and total chlorophyll (Table 11.3), while PSU area showed significant overdispersion in four communities (Table 11.2). With the exception of PSU lobation, all of these variates were convergent in a significant number of comparisons of texture distributions (Chapter 7; Table 7.2) or mean-adjusted distributions (Chapter 8; Table 8.2), with species unweighted by their abundance. Patterns in the texture factors related to these variates are similarly related. Both F1 (related to PSU succulence, specific weight and total chlorophyll) and F4 (PSU thickness)

showed a highly significant trend towards overdispersion among individual sites (Table 11.3), and were convergent in a significant number of comparisons of mean-adjusted distributions (though for F1, only with species weighted by abundance rank; Table 9.2). There was no significant overdispersion, nor strong evidence of any overall trends in this direction, for PSU phosphorus content or chlorophyll *a/b*, yet these variates showed the highest overall incidence of convergence between mean-adjusted texture distributions.

At the guild level, the observed patterns of character overdispersion bear only a weak relationship to the community-level convergence detected in previous chapters. For the 0-1 m guild, there was a significant incidence of overdispersion in PSU area (Table 11.4), while PSU thickness, succulence and specific weight showed a significant trend in this direction (Table 11.5). Of these variates, only PSU area showed a significant overall incidence of convergence among the comparisons carried out within this guild (Table 10.2). Once again, the related variates PSU phosphorus and chlorophyll *a/b* were convergent in a large number of comparisons, but showed no overdispersion that was significant overall. For the 1-5 m and >5 m guilds there was very little evidence of overdispersion, whereas significant convergence of mean-adjusted distributions was detected in a number of variates and in a significantly large number of community comparisons, in Chapter 10 (Tables 10.3, 10.4).

Given the appreciable amount of convergence detected among mean-adjusted texture distributions in different *Nothofagus*-dominated communities (Chapters 8, 9 and 10). It is perhaps somewhat surprising that the evidence for character overdispersion, obtained using direct tests in this chapter, is relatively weak. The explanation for the difference may lie in the type of distribution produced by competitive niche segregation. It has been assumed that, if assembly rules apply and impose limits on niche overlap, the amount of niche separation (and therefore, the spacing between species characters related to niches) would be of a similar magnitude for each pair of adjacent species. In other words, species values were expected to form an approximately arithmetic progression. This assumption seems reasonable, following normalisation of measured character values; for example, by taking the natural logarithm (Table 2.1). In an arithmetic progression, adjacent elements are spaced equidistantly, so that the variance ($V_T$) of the spacing between them is null. If species character values conform to a perfect arithmetic progression, highly significant overdispersion will be detected by the variance-based test (since a variance lower than zero is mathematically impossible, no bootstrapped null distribution can be more overdispersed than the observed). If, however, the limiting similarity between species changes geometrically (i.e. by multiplication) along the niche (or character) axis considered, species values will no longer be spaced equidistantly, resulting in a finite observed $V_T$. Under these conditions, it is uncertain whether the variance-based test for overdispersion would give significant results or even results in the direction expected ($R_{V,T}<1$). By contrast, the test for convergence of mean-adjusted texture distributions is based on the goodness-of-fit between the distributions (on the magnitude of $\hat{D}'_T$; Section 8.2; Fig. 8.2), and incorporates no assumptions as

to their approximate shape. This means that convergence could be detected between similar distributions, even if the component species values are overdispersed in a markedly non-arithmetic fashion.

The tests for overdispersion applied in the present chapter are analogous to tests for texture convergence with species character values weighted by presence only (Section 6.2). Convergence tests in which an abundance weighting factor (abundance rank, photosynthetic biomass, or its square root) is applied, focus on elements of community texture (the more abundant species) in which species interactions, and therefore overdispersion, might be more pronounced. It is unclear, however, how species abundance weighting could be incorporated in direct tests for overdispersion (other than by excluding species from analysis whose abundance is lower than some arbitrary threshold value), and so no attempt to do so was made.

It appears likely that the smoothed bootstrap method used to search for overdispersion is relatively conservative as an approach to seeking community structure. This is because it makes two potentially restrictive assumptions. Firstly, that the overdispersion produced by the operation of assembly rules will be essentially arithmetic in its nature (whereas overdispersion on a geometric scale can be envisaged); and secondly, that the effects of assembly rules will be sufficiently uniform to produce overdispersion across a whole assemblage (whereas the species interactions on which assembly rules would be based might be concentrated among the more abundant species). Tests seeking convergence in texture distributions between communities are free from both of these restrictions, and so may represent a more powerful approach to the detection of community structure.

## PREVIOUS STUDIES OF CHARACTER DISPERSION PATTERNS

Hutchinson (1959) proposed that competition among sympatric species competing for the same classes of food would lead to a minimum viable difference — a ratio of *c.* 1:1.3 was suggested — in their body sizes. If species packing tends to maximise resource use (Pianka 1975), while competition limits niche overlap, it follows that the ratio of the sizes of consecutive species in a rank order of body size will be relatively constant, and that species values will be evenly spaced on a logarithmic scale (Simberloff & Boecklen 1981).

Numerous studies have sought to validate this hypothesis with respect to body size or other morphological variables, for example, in communities of birds (MacArthur 1971; May 1978), fish (Barbour 1973), mammals (Brown 1975) and bees (Inouye 1977). Many early studies claimed to find constant or minimum ratios, but were deficient in that character overdispersion was not sought relative to a valid null model (Simberloff & Boecklen 1981; Tonkyn & Cole 1986; MacNally 1988). Reanalysing the data from 31 studies that had claimed evidence for minimum or constant ratios in animal sizes, Simberloff & Boecklen (1981) demonstrated that, for most data sets, the null hypothesis could not be rejected that logarithms of body sizes were drawn

at random from a uniform distribution in the same range as the observed data. The null model used by Simberloff & Boecklen (*op. cit.*) was arguably unduly simplistic (Tonkyn & Cole 1986), and the test statistics used to compare the observed and null distributions are deficient in that they are based on only a small subset of the whole distribution (Sinclair *et al.* 1985; Pleasants 1990, 1994). Consequently, it is unclear whether competitive displacement can be validly supported for these communities or not. MacNally (1988) used a different approach to seek morphological overdispersion in several types of animal community. Observed distributions of species values were compared with a geometric model of the character distributions expected, given that competitive niche segregation had occurred. There was significant deviation from the expected distribution in most cases, providing little evidence that competitive displacement had occurred.

In studies of plant communities, overdispersion of flowering and fruiting phenologies has been sought as evidence for competitive segregation of reproductive niches (e.g. Snow 1965; Waser & Real 1979; Pleasants 1980; Thomson & Rusterholz 1982; Armbruster 1986; Ashton *et al.* 1988). Phenological overlap is typically high, and recent studies have generally characterised species not only by their mean for the character of interest (as in most animal size studies, and also in the present study) but by both the mean and the variance (Gleeson 1981) or by the temporal frequency distribution of the character (Pleasants 1980; Fleming & Partridge 1984). For example, Pleasants (1980) examined temporal distributions of flowering intensity for species within guilds of bumblebee-pollinated plants to evaluate the hypothesis that the mean of pairwise overlaps in species flowering curves were lower than would be expected under a null model in which the observed curves were placed in the same growing season at random. For all but one of the guilds examined, observed overlap was lower than expected under the null model, suggesting that competition for the same pollinator species had produced niche segregation. The use of mean pairwise overlap as a test statistic in null model tests of phenological niche segregation has been criticised (Fleming & Partridge 1984) on the grounds that it focuses on interactions between nearest-neighbour species in niche space, taking no direct account of diffuse competition within the whole guild. The use of an alternative `*n*-wise' test statistic reduced or even reversed departure from the null model in a reanalysis of several data sets, suggesting that the role of competition in structuring plant reproductive guilds may be less significant than formerly supposed (Fleming & Partridge 1984). However, this question remains controversial (Fleming 1985; Pleasants 1990).

There have been relatively few studies of morphological character displacement in plants. Armbruster *et al.* (1994) studied the floral reproductive morphology of sympatric *Stylidium* species, testing the hypothesis that competition for pollinator species had led to a reduction in morphological overlap between species, in comparison to stochastic null models. Separate null models were used to evaluate hypotheses of ecological sorting and coevolutionary character displacement: significant departure was shown from the coevolutionary model, although a trend towards character segregation relative to the ecological null model was non-significant. The

observed distribution of attributes for each species from many sites was used as a pool from which values were drawn to assemble each null assemblage. This represents an advance over many previous studies of character dispersion (e.g. Pleasants 1980; Simberloff & Boecklen 1981; Fleming & Partridge 1984) which drew niches at random from a uniform distribution, an assumption unlikely to parallel nature. To test the hypotheses that competition would tend to inhibit sympatry of *Banksia* species with similar growth forms and regeneration biology, Richardson *et al.* (1995) compared the growth form diversity and regeneration biology diversity of actual assemblages with null assemblages created by by drawing species at random (though with abundance weighting) from the regional species pool. There was a significant tendency for observed assemblages to show lower growth form diversity (signifying poor differentiation of growth form niches) and lower reproductive biology diversity (poor differentiation of reproductive niches) than expected under the null model, lending little support to the competition hypothesis. Cody (1986, 1991) has examined vegetative niche segregation in a variety of shrubland and desert plant guilds, presenting several convincing examples of apparent competitive displacement. For example, morphological niches of sympatric species of Proteaceae from four South African fynbos assemblages are clearly separated when values for replicate individuals are plotted in a space defined by their leaf lengths and length:width ratios (i.e. PSU shape), although no statistical evidence for differences between species is presented.

*The present study in the context of previous work*

Although a number of previous studies, like the present one, have sought competitive displacement relative to explicit null models, there have been two common shortcomings of the tests employed. These concern the distributions from which species are drawn to create null assemblages, and the test statistics used to compare null assemblages with the observed data. In both cases, the principal danger has been an elevated likelihood of type II error, that is, of failure to reject the null hypothesis when an alternative hypothesis should be supported (the Narcissus effect of Colwell & Winkler 1984). In some situations, excessive type I errors (spurious rejection of the null hypothesis — Wilson's [1995] Jack Horner effect) are also possible (Pleasants 1990, 1994; Tonkyn & Cole 1986).

The distribution from which species values are drawn in the null model is critical to the performance of the null model test. If an inappropriate distribution is used (i.e. one that poorly approximates the natural distribution), the spacing of values in the null data may tend to be intrinsically more regular or (less likely) more clustered than in the observed data. In the former case, an excess of type II errors would be expected, in the latter, an excess of type I errors, where the hypothesis being tested is that the observed species characters are more regularly spaced than expected by chance, i.e. that there is overdispersion (Schoener 1984). In the past, null data sets have commonly been assembled from a uniform distribution in the same range as the observed

data (e.g. Poole & Rathcke 1979; Pleasants 1980; Simberloff & Boecklen 1981). However, it is unlikely that the uniform distribution represents a realistic model for distributions of species attributes in nature (Schoener 1984; Tonkyn & Cole 1986; Manly, 1995b). Tonkyn & Cole (1986) attempted to improve on this approach by drawing null body sizes from two theoretical distributions skewed towards low and intermediate values, which were considered likely to be more abundant in natural species pools, or more likely to evolve. However, the most appropriate sampling distribution will be based on the observed data (Armbruster *et al.* 1994; Manly 1995b). The kernel density estimation approach used in the present study thus represents on improvement on many previous studies: character values in the null model are drawn at random from a smooth distribution which approximates that of the data in which dispersion patterns are sought. This means that the null model is more likely to be a realistic representation of nature under conditions in which the null hypothesis (that there are no assembly rules restricting species similarity) is true, minimising the danger of the Narcissus effect.

The test statistic used to characterise dispersion patterns in the observed and null data can have an important influence on the outcome of null model tests (Fleming & Partridge 1990; Pleasants 1990, 1994; Arita 1993). Simberloff & Boecklen (1981) sought evidence for constant body size ratios by comparing the values of one or three $G_{ij}$ statistics in the observed and null model data, where $G_{ij}$ is the ratio of the *i*th-smallest to the *j*th-smallest spacing in log body size between adjacent species in rank order of size ($i<j$). A significantly high value of $G_{ij}$ in the observed data (indicating relatively similar spacing for the two pairs of species involved in the calculation for each data set) was taken as support for the competition hypothesis. This approach has the disadvantage that a potentially large proportion of the available data are ignored in calculation of the test statistics. Pleasants (1990, 1994) has also demonstrated by simulation that the tests statistics used by Simberloff & Boecklen (1981) give an unacceptably high type II error rate, and can spuriously detect overdispersion in clumped distributions. Pleasants (1990) advocates the use of a community-wide parameter as a test statistic, and suggests the mean[2] or the variance of the spacing between each pair of adjacent species along the character axis of interest (Poole & Rathcke 1979). The latter parameter was used as the test statistic ($V_T$) in the present study. It has the advantage that it is based on the dissimilarity between the pairs of species expected to be involved most strongly in competition for the niche space — those with the most similar characters. As an assemblage-wide parameter, it avoids the danger of drawing conclusions based on a non-representative subset of the whole assemblage (Pleasants 1990, 1994).

[2]'Mean' is the mean spacing between adjacent species along the character axis of interest. As Arita (1993) points out, where the null variates can have the same range as the observed data (as usually assumed), the value of 'Mean' will be identical for the observed and each null model data set, making calculation of a *P* value meaningless. 'Mean' is invalid as a community-wide index of dispersion.

While some objective evidence for competitive niche segregation has emerged from statistical analysis of character dispersion patterns within communities or guilds (Armbruster 1986; Cody 1991; Armbruster *et al.* 1994), many of the positive findings reported have been challenged on methodological grounds, and reanalysis of many data sets has led to rejection of the hypothesis that they are structured by assembly rules. The present study is one of the first in which both an appropriate null model and an appropriate test statistic have been used to seek character overdispersion, and is the first in which assembly rules for plant vegetative niches have been demonstrated using a test for overdispersion in comparison to an explicit null model.

## CONCLUSIONS

Relatively little significant evidence of overdispersion of species characters was observed within particular communities, or guilds within communities. However, there were significant trends among communities in several variates, suggesting that assembly rules apply, restricting the co-occurrence of species whose niches (and correlated characters) are too similar. The assembly rules appear to apply in some whole communities, and in the 0-1 m guild, but there is no significant evidence that they operate in the intermediate and upper forest strata. Based on the identity of the characters showing the strongest trends towards overdispersion, it seems likely that assembly rules have led to partitioning of the vertical light gradient among species, although a nutritional interpretation for the patterns is also possible.

Overall, the results obtained in this chapter provide somewhat weaker evidence for assembly rules than the convergence in mean-adjusted texture distributions identified in Chapters 8, 9 and 10. This may be a reflection of the relative power of the two approaches to seeking community structure, tests for overdispersion incorporating more restrictive assumptions as to the manner in which species would be assorted in character space.

# 12. General discussion

## 12.1 Introduction

Assembly rules (Diamond 1975; Drake 1990; Wilson 1991) represent the integrated actions of all processes, based on interspecific interactions such as competition, whose net effect would be to restrict taxonomic or functional community composition. It is often assumed that the most important overall outcome of assembly rules would be to limit the co-occurrence of species with similar niches (Pianka 1975, 1980; Simberloff & Boeklen 1981; Pleasants 1990; Wilson *et al.* 1994). The primary aim of the present study was to investigate whether natural communities, and specifically the vascular plant guild of *Nothofagus*-dominated temperate rainforests, exhibit compositional and functional structure that could be attributed to the operation of such assembly rules. This overall question was addressed via a hierarchy of hypotheses which, if supported, would in turn support the overall one (Fig. 1.6). The principal subsidiary hypotheses were of community-level convergence in species richness and texture, and of overdispersion in the functional characters of sympatric species. In the following discussion, the methods by which each hypothesis was addressed are critically examined, and their outcomes reviewed.

## 12.2 The null model approach

In the present study, each major hypotheses was addressed by comparing an observed pattern of interest against patterns generated by a stochastic null model, simulating community assembly under conditions in which the alternative hypothesis is false. Null models are widely used in objective studies of community processes (e.g. Connor & Simberloff 1979; Wilson 1989; Fox & Brown 1993; Armbruster *et al.* 1994; see reviews by Harvey *et al.* 1983; Colwell & Winkler 1984; Crowley 1992). Null model approaches have the advantage that the null hypothesis must be stated exactly, framed in terms of precise assumptions as to the process being modelled (Colwell & Winkler 1984). Null distributions are defined by resampling (with or without replacement) many times from the observed data (or a distribution defined by them), subject to the constraints of the null model. This means that, in comparison to standard parametric tests, null model tests are free of potentially restrictive assumptions as to the underlying distribution from which data are drawn, while the conceptual link between the null hypothesis and the significance or confidence value obtained as an outcome of the test is much clearer (Crowley 1992).

## BIAS IN NULL MODEL TESTS

Bias in a statistical test can occur because there is a tendency to reject the null hypothesis when it is true (a type I error) or to accept the null hypothesis when the alternative hypothesis is true (a type II error).

Because the sampling distribution for a null model test is defined on the basis of (or comprises) the observed data, data sets generated in null model simulations will tend to retain some of the observed structure. This is necessary to ensure that patterns in the data not related to the hypothesis being addressed will not produce spurious departure from the null hypothesis. However, the conservative nature of the null sampling distribution can also make departure from the null model difficult to demonstrate if the pattern of interest (e.g. convergence or overdispersion) *is* present, but is relatively weak (Wilson 1995). The result may be a tendency not to reject the null model where it is false, a type II error (Fuentes 1980; Colwell & Winkler 1984). Excessive type II error rates in null models have been termed the 'Narcissus effect' (Colwell & Winkler 1984). For example, in studies of assembly rules on islands, the biota of the island of interest plus those of neighbouring islands have been pooled to give the sampling distribution for null model tests (e.g. Connor & Simberloff 1979; Strong *et al.* 1979; Grant & Abbott 1980; Case & Siddell 1983). If competition-based assembly rules apply on each island, their effects (e.g. exclusion of some species; control of the relative frequencies of the species remaining) may be present among the pooled biota of the island group — the sampling distribution against which observed patterns were compared. This would tend to lead to underestimation of the strength of any competition-mediated patterns on particular islands (Diamond & Gilpin 1982; Colwell & Winkler 1984; Wilson 1987).

Related to the Narcissus effect — and likewise leading to a conservative outcome — is the 'dilution effect,' (Gilpin & Diamond 1982, 1984) resulting when a predicted pattern is sought in a data set that is too heterogeneous for the pattern to be distinguished relative to a stochastic null model. Gilpin & Diamond (*op. cit.*) raised this issue in relation to a study by Connor & Simberloff (1979) seeking evidence for negative associations between New Hebrides bird species, as a possible outcome of competition between them. The data set in which these patterns were sought comprised an occurrence matrix for the entire avian fauna of the island group. Gilpin & Diamond (*op. cit.*) argued that, since competition and patterns resulting from it would occur largely among species within a guild (e.g. different nectarivores) and would not be expected among species from very different guilds (e.g. owls and hummingbirds), it was unlikely for significant competition-mediated patterns to be detected at the level of the entire fauna, even if such patterns were pronounced at the level of individual guilds.

An appropriate null model will reproduce all trends in the observed data, except for patterns resulting from mechanisms implied by the hypothesis being addressed. This means that aspects of the structure of the observed data that are not related to the hypothesis being addressed

should be incorporated in the null model. A null model that does not meet this requirement is inappropriate, because there may be a tendency for departure from it to be observed even if the hypothesis being tested is false; that is, it may produce an excess of type I errors. Wilson (1995) has coined the term 'Jack Horner effect' to refer to type I errors of this kind, because the pattern in the observed data that leads to rejection of the null hypothesis is not the one predicted by the hypothesis being addressed, but rather some other pattern, typically of trivial interest. For example, in studies seeking an excess of negative species associations as evidence for assembly rules on islands (e.g. Connor & Simberloff 1979; Toft *et al.* 1982; Schoener & Adler 1991), it is important to incorporate observed island species richness in the null model, so that departure from it cannot occur merely because of observed richness differences associated with island size; similarly, observed species frequencies should be retained, so that the trivial hypothesis that species differ in rarity is not inadvertently tested (Crowder 1980; Wilson 1987).

It has been suggested that excessive type I errors can also arise as a result of using an inappropriate test statistic to characterise the pattern being sought. Pleasants (1990, 1994) demonstrated that the Jack Horner effect can occur when the indices Min and $G_{ij}$ are used as indices of character dispersion in studies of competitive displacement (e.g. Simberloff & Boecklen 1981; Boecklen & NeSmith 1985; Losos *et al.* 1989). Simulation tests with artificial data showed that random or clumped distributions could be identified by these test statistics as being more regular than expected under a null model of random dispersion. This artifact appears to be related to the fact that calculations for the indices are based on the characters of a proportion of species in each data set, and not on the whole assemblage; however, the exact basis for the problem is unclear.

### NULL MODEL TESTS IN THE PRESENT STUDY

Under the principle of parsimony, the Narcissus effect is to be preferred to the Jack Horner effect. This is because failure to reject the null hypothesis does not (or should not) result in the acceptance of any theory (Connor & Simberloff 1979). The null model does not, in general, represent a specific ecological hypothesis, but merely a set of rules for generating a reasonable probability distribution for the test statistic, given that the alternative hypothesis is false (Crowley 1992). Even if the null model were 'one of many possible competing hypotheses,' as suggested by Diamond & Gilpin (1982), failure to reject it is not statistically equivalent to supporting it. It is unclear how a hypothesis of (for example) random species migration can be tested in the absence of a corresponding null hypothesis. By contrast, the Jack Horner effect (spurious rejection of the null model) will lead to the acceptance of a specific, but manifestly false, ecological hypothesis, along with its burden of theory (Wilson 1995).

In the present study, priority was given to avoidance of the Jack Horner effect in all analyses. In some cases, this may have resulted in tests that are somewhat conservative, i.e. that

may be subject, to some extent, to the Narcissus effect. The analyses are reviewed in Sections 12.3-12.5, below.

*Trials using random data*

To confirm that null models and test statistics were free of bias (i.e. could not give rise to an excess of type I errors — the Jack Horner effect), each type of test was applied to a number of sets of artificially-generated random data. In the absence of bias, significant departure from the null model would be expected in a proportion of tests no higher than the target 5% significance level. Binomial tests were applied to confirm that this was so, and revealed no evidence of significant bias for any test (Tables 6.1, 7.1, 8.1, 11.1).

## 12.3 Species richness convergence

The possibility of convergence in species richness between communities in similar environments in different regions has often been discussed (Parsons & Moldenke 1975; Whittaker 1977; Cody & Mooney 1978; Naveh & Whittaker 1979; Rice & Westoby 1983a; Fox 1995). Convergence might be expected if there are assembly rules that restrict niche overlap, resulting in limitations on the number of niches (species) that can be packed into the corresponding niche-space hypervolumes of the communities (Pianka 1975; Section 1.5). Where objective statistical tests have been applied, however, these have generally addressed the (null) hypothesis (1) that species richness patterns are *not significantly different* among regions. For example, Cody *et al.* (1977) reported that species-area curves for bird communities of Chilean and Californian mediterranean-climate shrublands were not significantly different, while Wiens (1991a) detected no significant difference in the mean among replicate study plots in the number of bird species observed in North American and Australian shrub deserts (Mann-Whitney *U*-test). In fact, such studies do not strictly address the hypothesis (2) of community-level convergence, that regions are *more similar than expected on a random basis* (Schluter 1986; Wiens 1991b; Wilson *et al.* 1994).

Hypotheses (1) and (2) are not equivalent: the absence of significant differences in species richness predicted by hypothesis (1) could be due to convergence (resulting from the operation of assembly rules in similar environmental conditions) or merely due to an absence of strong environmental or historical differences that might lead to divergence in species richness. The correct hypothesis was tested by Schluter (1986), who applied a two-tailed *F*-test to finch species richness data for nine habitat types among five continents, demonstrating that species richness was significantly more variable among habitats than among continents. This was interpreted as evidence that community-level convergence in species richness had occurred. Convergence in the species richness of communities at a local scale has been sought as niche limitation (Wilson *et al.* 1987; Palmer 1987; Watkins & Wilson 1992; Zobel *et al.* 1993; Bycroft

*et al.* 1993). In each of these studies the observed variance in richness among plots was compared with the variance expected if species from the observed pool were distributed among plots at random (i.e. in the absence of assembly rules). A significantly low observed variance — indicating that numbers of niches (species) in each plot was more constant than expected under the null model — could be interpreted as niche limitation, although little evidence was found.

### APPROACH OF THE PRESENT STUDY

Evidence for significant convergence in species richness among communities was not sought in this study. This was because the data collected — species numbers within 5 (or occasionally fewer) replicate quadrats at each study site — do not permit the habitat × region analysis of variance approach of Schluter (1986), nor the niche limitation approach, which assumes that there are no barriers to dispersal among communities, to be applied. Instead, the hypothesis that species richness was not significantly different among communities was tested, using a bootstrap null model, in which values from the observed pool of quadrat richnesses were redistributed among communities at random (Section 5.2). A significantly high variance in richness among the observed communities, compared with null model communities, was interpreted as divergence. Where divergence was not observed, this was taken as preliminary evidence that convergence *might* have occurred, although the null hypothesis — that species richness was no more similar among sites than expected on a random basis — could not be rejected.

The test is equivalent to the Mann-Whitney *U* test of Wiens (1991a), but the bootstrap approach, resampling with replacement from the observed pool of values in the null model, may produce fewer type II errors than the non-parametric, rank based, *U*-test (Crowley 1992). Species richness values pooled from all quadrats did not quite conform to a normal distribution, even following square root transformation. Under these conditions, the bootstrap test would be expected to be marginally more rigorous (i.e. less likely to falsely reject the null hypothesis) than a standard parametric analysis of variance, which would assume that the data are distributed normally (Crowley 1992).

In a bootstrap test, drawing samples with replacement, a stable null probability distribution is achieved more slowly (i.e. after a greater number of simulations) than in a permutation test, potentially resulting in misclassification of patterns near the margin of significance (Manly 1991; Good 1994). To avoid such errors, $10^4$ null data arrangements were generated in each test, instead of 2000 as in the random permutation tests performed in other chapters.

At all scales, significant divergence in species richness was detected in about half of the comparisons performed (Tables 5.2-5.5). Among the four landmass-scale communities, three pairs — Tasmania (T)/Australia (A), Tasmania/South America (S) and Australia/South America — were not significantly divergent, leaving the possibility that there might be convergence in species richness open. At the regional scale, two pairs of Tasmanian sites (T1 Balfour/T2 Anne and T2 Anne/T3 Mathinna), the Australian sites (A1 Lumeah/A2 Cascades) and southern (ZS) and central (ZC) New Zealand were not significantly divergent. At the local scale, non-divergence was limited to all combinations of the three southern New Zealand communities (ZS1 Ten Mile, ZS2 Walker and ZS3 Deer) and northern New Zealand sites ZN1 Ohakune/ZN2 Rotokura. Of the three pairs of sites from different landmasses with closely-matching environments, only one — T1 Balfour/A2 Cascades — did not show significant divergence.

On the basis of these results, limitations on community richness imposed by assembly rules cannot be ruled out for some sets of communities. However, the alternative hypothesis, that species richness is determined by chance, or as a function of the abiotic environment cannot be rejected.

## 12.4 Texture convergence

The hypothesis of convergence in structural and functional properties of the species present in disjunct communities in similar environments has been addressed by numerous studies (e.g. Specht 1969; Naveh 1967; Parsons & Moldenke 1975; Parsons 1976; Mooney *et al.* 1977; Cody *et al.* 1977; Orians & Solbrig 1977; Cowling & Campbell 1980; Ricklefs & Travis 1980; Schluter 1986, 1990; Wiens 1989, 1991a,b; Keeley 1992; Cowling & Witkowsky 1994; Smith *et al.* 1994; Wilson *et al.* 1994; Montenegro & Ginocchio 1995). However, relatively little objective evidence for such convergence has emerged (see Section 6.4). The paucity of evidence has led a number of authors to re-examine closely the hypothesis and its assumptions, and a number of methodological and conceptual difficulties have been identified (e.g. Peet 1978; Orians & Solbrig 1983; Ricklefs 1987; Barbour & Minnich 1990; Blondel 1991). Each of the principal issues is discussed below, in relation to the methodology and results of the present study.

### WHAT PATTERNS CONSTITUTE CONVERGENCE?

It is implicit in the concept of community-level convergence that communities have become more similar over time. Because of the long time spans that are involved in evolutionary convergence, and the absence of a suitably detailed fossil record, it is generally not possible to demonstrate directly that similarity among communities has increased through evolutionary time (Schluter

1986; Wiens 1989). Recognising this problem, some authors have distinguished between community 'similarity' and 'convergence,' reserving the latter term for cases in which convergence from 'ancestral' states could be demonstrated by reference to 'related' communities in different environments (Schluter 1986; Wiens 1991a,b). Arguments for a distinction between similarity and convergence relate to an assumption that convergence could occur exclusively over evolutionary time. However, as argued in Section 1.5, unlike species- level convergence, which is necessarily an evolutionary phenomenon, community-level convergence might arise through ecological species sorting, on an ecological time scale (a possible cause for 'similarity' in Schluter's [*op. cit.*] sense). Whether coevolution is involved or not, the underlying process must be either directly or ultimately due to local-scale ecological sorting through the operation of community assembly rules (Figs. 1.4, 1.5). A distinction between similarity and convergence of communities is thus illogical, and none has been made in the present study.

### HOW SIMILAR IS SIMILAR ENOUGH?

The above question, posed by Orians & Paine (1983), alludes to the problem of deciding whether a set of communities under consideration are sufficiently similar to be deemed convergent. In earlier studies, community comparisons were largely subjective (e.g. Naveh 1967; Specht 1969; Mooney *et al.* 1970), or were quantitative (e.g. based on cluster analysis of species characters from a range of communities) but did not incorporate tests for statistical significance (e.g. Parsons & Moldenke 1975; Cowling & Campbell 1980; Blondel *et al.* 1984). Consequently, it was unclear what minimum level of similarity should be interpreted as supporting the convergence hypothesis.

In recent studies, and in the present one, this problem has been overcome by searching for statistically significant departure from a null model (Schluter 1986; Wiens 1989, 1991a,b; Smith *et al.* 1994; Wilson *et al.* 1994). Communities are deemed convergent if they are found to be significantly more similar in the attribute of interest (in the present study, in means, distributions or mean-adjusted distributions of a texture variate or derived factor) than would be expected if there were no constraints on species co-occurrences based on their characters (Section 6.2). It is not certain that this criterion will always identify communities that have converged. Where convergence has occurred, but the resulting similarity is weak, for example, owing to the confounding effects of environmental dissimilarity, significant departure from null model expectation may not be demonstrable. Non-significant tendencies towards convergence (for example, a relative deviance less than 1 among a majority of texture variates) were noted for a number of community comparisons (e.g. ZN2 Walker and ZN3 deer, Fig. 6.7d; Tasmania and Australia, Fig. 8.5b) and could possibly reflect weak convergence, or convergence partially masked by divergence attributable to allogenic community differences. While tests for texture convergence in this study may have failed to recognise convergence in some cases where the

effects of assembly rules have been weak or are masked by other patterns, this Narcissus effect is preferable to the Jack Horner effect (see Section 12.2) — spuriously recognising convergence where it has not occurred — that cannot be discounted when statistical significance tests are not applied.

## THE ASSUMPTION OF ENVIRONMENTAL SIMILARITY

An important assumption of the hypothesis of community-level convergence is that the communities under consideration have similar abiotic environments (Orians & Paine 1983; Blondel *et al.* 1991; Wiens 1991b). The environment would be expected to determine both adaptive optima and limits to the functional syndromes that species may have in order to establish populations at a particular site. Only where these parameters are closely matched in different communities, is convergence likely to be detectable.

The assumption of environmental similarity has been identified as one of the principal difficulties facing studies of community-level convergence (Orians & Paine 1983). This is because the environment comprises an indefinite number of parameters, not all of which can be quantified in any study, and not all of which can be matched between sites. If convergence is not demonstrated, differences in the environment can always be invoked as an explanation and, indeed, often are (e.g. Orians & Solbrig 1977; Cowling & Campbell 1980; Orians & Paine 1983; Blondel *et al.* 1984; Barbour & Minnich 1990; Blondel 1991; Wiens 1991a; Keeley 1992). This leaves both unsupported and untested, the hypothesis, nested within the convergence hypothesis, that there are assembly rules constraining species character values. For this reason, some authors (Barbour & Minnich 1990; Keeley 1992) has suggested that the hypothesis of community-level convergence may be an untestable one.

### *Approach of the present study*

In the present study, it was endeavoured to avoid the potential problems posed by the assumption of environmental matching, in both the data collection and analysis phases.

In the data collection phase, communities were chosen for study subject to the criterion that they should be as similar in their environments as possible. One reason for the choice of *Nothofagus*-dominated forests as a community type for study was that *Nothofagus* has a relatively restricted environmental range, and so communities with similar overall climate and soil characteristics can be found in each of the temperate regions encompassed by the genus (Ash 1982; Wardle 1984). Climatic parameters are generally considered most important in controlling vegetation distribution, whereas within a climatic zone, other features, such as soil type, may be important (Woodward 1987). Therefore, climate was standardised among study sites to the greatest extent possible. Environmental data for all study sites were collected so that the degree

of matching between sites could be assessed *a posteriori*, allowing analyses and interpretation to focus on communities particularly well-matched in their environments. Close matching between the communities sampled has two advantages. Firstly, convergence is more likely to be detectable if it has, in fact, occurred. Secondly, if convergence is not detected, the underlying hypothesis that there are assembly rules producing community structure can be more confidently rejected than would be the case if the environmental matching between communities were poor.

The hypothesis that texture might differ among communities due to (for example) poor environmental matching, was tested explicitly. Tests for departure from the null model that species (or, more precisely, their characters) are distributed among communities at random, were two-tailed; that is, departure from the null model was sought in both the directions of convergence and divergence. If convergence is detected, there is clearly no need to examine further the assumption of environmental matching: the significant departure from the null model demonstrates that the communities are sufficiently similar in their environments for detectable convergence to occur. If significant divergence is detected, this is evidence that there are environmental differences between the communities that might prevent convergence from being detectable, whether or not it has occurred. A possible alternative explanation for divergence is that it is caused by phylogenetic differences in the species pools of the divergent communities. Even if the communities have closely similar environments, differential ancestry among species in different communities, coupled with phylogenetic constraints (i.e. retention of ancestral characters) could produce significant differences in texture in comparison to the null model.

Where divergence is detected, no conclusions can be drawn as to whether similar assembly rules operate in the communities under investigation or not. Initial tests for convergence, comparing texture means (Chapter 6) and distributions (Chapter 7) in different communities revealed a marked degree of divergence, significant as a proportion of the number of tests carried out, for eight of the 13 texture variates in each type of analysis (Tables 6.2, 7.2). This suggests that, although the macroenvironments of communities were carefully standardised at the data collection stage, there was significant environmental (or other) variation among communities. Consequently, the results obtained in Chapters 6 and 7 do not allow strong conclusions to be drawn with respect to the hypothesis of community-level convergence.

Tests for convergence in mean-adjusted distributions of community texture, developed in Chapter 8, were intended to avoid the problems associated with environmental dissimilarity among communities by removing, from the convergence hypothesis, the assumption that communities would be very closely matched. Departure from the null model was based solely on differences between communities in the shapes of their texture distributions, and not on their absolute values or means. There is some theoretical basis for suggesting that the environment would affect primarily the mean of community texture, whereas assembly rules might determine the shape of the texture distribution (see Section 8.1). Therefore, tests for convergence in mean-adjusted distributions, based on the test statistic $\hat{D}'_T$, may focus on similarities in the effects of

assembly rules on texture, while ignoring among-community differences due primarily to dissimilarity in their physical environments. The validity of the approach was confirmed by its success: convergence, significant as a proportion of the number of tests performed, was detected in six texture variates and five of the seven derived factors at the whole-community level (Tables 8.2, 9.2) and also in several variates within each height guild (Tables 10.2-10.4). Divergence, by contrast, was detected in very few tests, and was not significant overall for any variate at the whole-community level (Tables 8.2, 9.2). This confirms that texture differences due to environmental differences between communities were largely eliminated by the $\hat{D}'_T$-based tests.

## THE ASSUMPTION OF PHYLOGENETIC INDEPENDENCE

In tests of community-level convergence, it is desirable that communities be relatively independent phylogenetically. This is so that functional similarity, if observed, can be attributed uniquely to convergence, and not to shared traits resulting from common phylogenies. On the other hand, if communities are too distinct phylogenetically, convergence may not be detectable (or may not even occur) as evolutionary constraints imposed by different phylogenies lead to differential adaptive solutions among communities (Peet 1978). Orians & Paine (1983) describe the criterion of phylogenetic independence thus: 'for convergence to occur, initial community composition must be reasonably distinct, but not too much so.'

Based on these considerations, comparisons in the present study were confined to the vascular plant guild. It seems likely that there would be reasonable adaptive flexibility among vascular plants, so that similar functional solutions to similar adaptive problems might be expected within disjunct floras. In *Nothofagus*-dominated communities, this assumption is evidenced by the largely distinct genera and families occupying similar 'niches' (using this term in a very general sense) on different landmasses. For example, the subcanopy and small tree strata are typically represented in Tasmania by species in the genera *Anodapetalum*, *Anopteris*, *Atherosperma*, *Eucryphia*, *Olearia*, *Pittosporum* and *Tasmannia*, in the families Cunoniaceae, Escallionaceae, Monimiaceae, Eucryphiaceae, Asteraceae and Winteraceae. In New Zealand, typical components of the same strata belong to the genera *Coprosma*, *Myrsine*, *Neomyrtus*, *Pittosporum*, *Pseudopanax* and *Pseudowintera* and to the families Rubiaceae, Myrsinaceae, Myrtaceae, Pittosporaceae, Araliaceae and Winteraceae. Presumably the generally distinct genera and families evolved to occupy broadly equivalent niches on the two landmasses following the vicariance event that led to their separation in the early Tertiary — the breakup of Gondwana (Romero 1986).

*Treatment of common species*

To reduce the danger of interpreting convergence among compositionally-overlapping communities as an outcome of assembly rules, where common phylogenetic history might be the true cause, species occurring in more than one community in any comparison were mathematically excluded from analysis. Such species were taken into account by the null model, but rather than being assigned to null communities at random, they were retained (with their observed character and abundance values) in the null community corresponding to that in which they were sampled. This meant that common species contributed equally to test statistic values in the observed and each null-model data set, and could not contribute to departure from the null model, whether in the direction of convergence or divergence (Section 6.2). By excluding species in common between communities from analysis, it was possible to perform valid comparisons among regions within a landmass, and even among sites within a local area.

This method of dealing with common[1] species represents an improvement on two previous studies of community-level convergence. Wilson *et al.* (1994) sought texture convergence among carr wetland communities in Britain and New Zealand, which had a small proportion of species in common. Smith *et al.* (1994; Appendix B) examined texture variation among adjacent plots within *Nothofagus*-dominated rainforest along an altitudinal gradient; there was substantial overlap among plots at the species level. In both studies, common species were randomised along with species confined to just one community in a particular comparison, though different records for the same species were never assigned to the same null community in any trial. Although this would be expected to cause little bias when species are unweighted by their abundance (because each species would contribute almost equally to test statistic values in the observed and each randomised data set), bias is possible when species are weighted by their abundance in calculations of community texture[2]. This is because species that have a high observed abundance would tend to be assigned a lower one in null model simulations. Abundant species common to more than one community, having similar characters and being heavily weighted, would tend to reduce texture variation among the observed communities, more, on average, than among communities generated under the null model, causing a bias towards convergence. Although this potential artifact was recognised by Smith *et al.* (1994), it was not dealt with in that paper. The analyses carried out in the present study cannot lead to such an artifact: significant convergence among communities with species in common can be explained only by similarity, exceeding chance expectation, in the characters of species that are not

[1]The expression 'common species' is used here to refer to a species in common to two or more communities in a particular comparison.

[2]A lesser degree of bias can also occur when species are unweighted by their abundance. This potential artifact is discussed in Section 6.2.

common to more than one of the communities being compared.

*Phylogenetic overlap among* Nothofagus *communities*

Although compositional overlap at the species level could not account for any of the convergence observed in the present study, the possibility that common genera, families or higher-order taxa (see above) may have had some effect on the outcome of analyses cannot be discounted. This is because species in the same genus or family may share some common ancestral traits. Consequently, where species from the same genus or family are present in different communities, these common traits may tend to contribute to similarity in community texture, whether or not the mechanism implied by the convergence hypothesis — the operation of similar assembly rules in the communities being compared — applies.

Table 12.1 summarises the degree of overlap at the family and genus levels among the *Nothofagus*-dominated communities sampled in Tasmania, Australia, New Zealand and South America. Overlap at the species level is also shown, although this is not relevant to the outcome of analyses, for the reasons explained above. Fewer than half of all families and (except between New Zealand and Tasmania) under 15% of genera in any two landmasses are common to both, although the proportions of species in shared genera and families tend to be higher (up to 75% for shared families). New Zealand and Tasmanian communities are most closely related taxonomically. Much of the phylogenetic overlap is accounted for by pteridophyte taxa — all but two of the species observed on more than one landmass are ferns.

Compositional overlap between landmasses is likely to affect convergence analyses only if species from different landmasses belonging to the same taxa have retained some common ancestral characters. Some insight into whether this is likely can be obtained by comparing variation in the characters of congeneric or confamilial species from different landmasses, with overall character variation in their genus or family. By way of example, Fig. 12.1 depicts a hierarchical classification of all species encountered in five genera (arbitrarily selected) that are shrubs and understorey trees in New Zealand, and were encountered in sampling on at least one other landmass. The classification is based on standardised, transformed species values for the 13 characters on which convergence analyses in Chapters 6-10 were based (full explanation in figure caption). It thus depicts the overall similarity between species on the basis of their characters. Generally, species from Tasmania, Australia or South America fall within or close to the range of variation of their congeners in New Zealand. This means that the congeners on different landmasses are generally quite similar in their characters. This could be the result of independent adaptation to similar niches by congeneric species, but it is likely that initial similarity due to common phylogeny has also played a role.

**Table 12.1** Compositional overlap of *Nothofagus*-dominated communities in Tasmania, Australia, New Zealand and South America based on species encountered in sampling. Data shown are the percentage of taxa (families, genera or species) from two landmasses that are common to both landmasses and (in parentheses) the percentage of species from both landmasses that belong to taxa common to both landmasses.

| Landmass | Taxonomic rank | Percentage of shared taxa (percentage of species in shared taxa) | | |
|---|---|---|---|---|
| | | South America | New Zealand | Australia |
| Tasmania | Families | 21 (43) | 47 (75) | 36 (49) |
| | Genera | 9 (26) | 28 (57) | 14 (20) |
| | Species | 0 | 5 | 6 |
| Australia | Families | 18 (36) | 33 (60) | |
| | Genera | 5 (11) | 14 (34) | |
| | Species | 0 | 1 | |
| New Zealand | Families | 36 (61) | | |
| | Genera | 13 (36) | | |
| | Species | 0 | | |

The only exception to the general pattern in Fig. 12.1 is *Aristotelia peduncularis* (Tasmania), which is more similar to two species of *Elaeocarpus* than it is to its congeners in mainland Australia, New Zealand and South America. However, *Aristotelia* and *Elaeocarpus* are confamilial (in the family Elaeocarpaceae), providing some possible evidence for character conservatism at the family level. Similar patterns to those presented in Fig. 12.1 apply for other guilds including ferns and canopy trees (results not presented). There is thus some evidence to suggest that compositional overlap, at least at the generic level, could have contributed to producing greater similarity in texture between landmass-scale communities than expected under the null model.

While phylogenetic overlap among the four landmass-scale communities is relatively limited, similarities at the genus and family levels are significantly higher among regional- and local-scale communities. For example, regional communities central (ZC) and southern (ZS) New Zealand have 20 out of 41 genera, and 19 of 32 families, in common. Some 73% of species recorded at both communities belong to shared genera, while 85% belong to shared families. Overlaps are generally of a similar magnitude at the local level. For example, southern New Zealand sites ZS1 Ten Mile and ZS2 Walker have 15 of 25 genera, and 15 of 21 families in

common; 80% of species belong to shared genera, while 86% of species are in shared families. Assuming that, at the local or regional scale, there would tend to be greater functional similarity among species within a genus or family than among genera or families, phylogenetic overlaps, rather than assembly rules, could account for, or have contributed to, the convergence observed among communities at these scales.

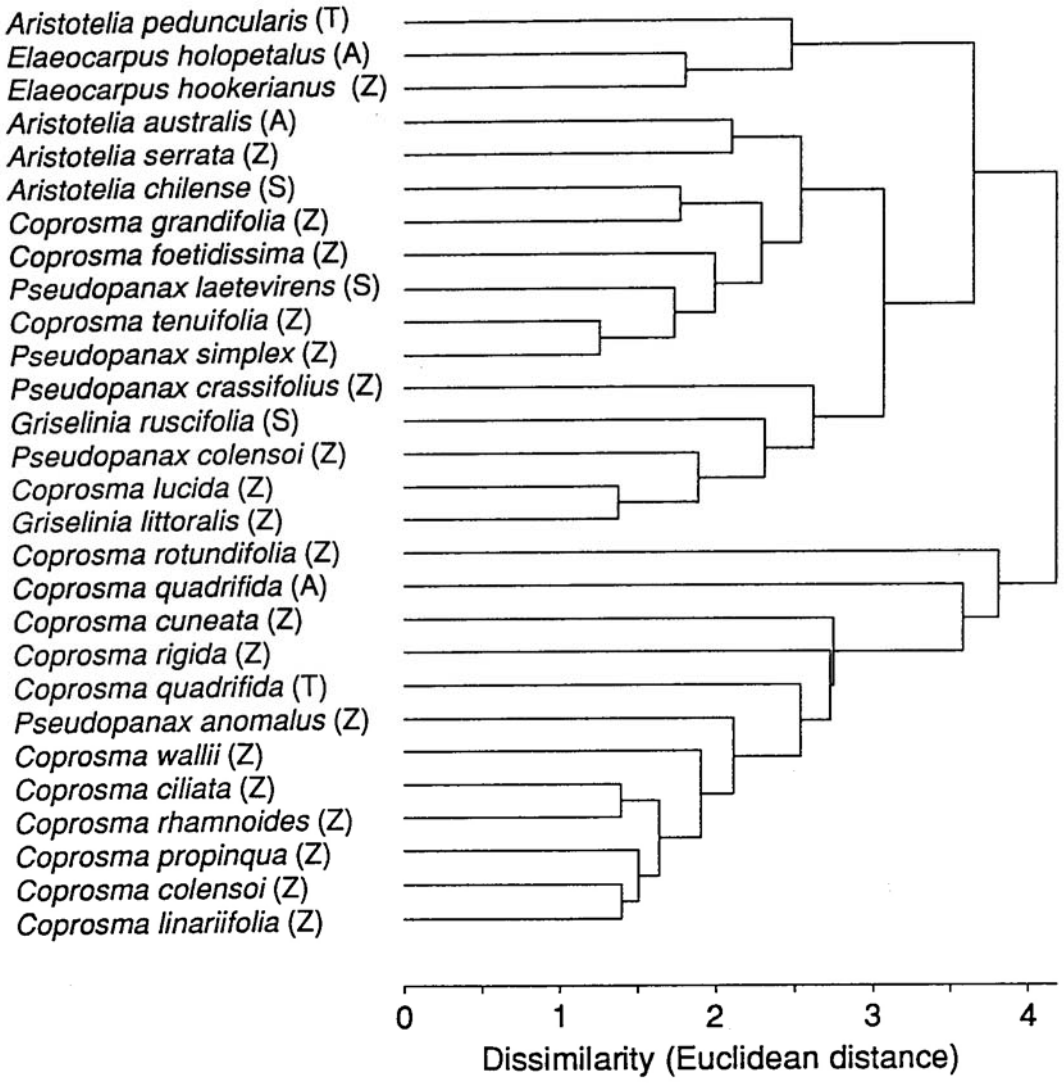


**Fig. 12.1** Functional classification by cluster analysis of species belonging to five shrub and small tree genera encountered on more than one landmass (T-Tasmania; A-Australia; Z-New Zealand; S-South America) in this study. Classification is based on transformed, standardised species values for 13 characters (the 12 listed in Section 2.3.5 and also species height, defined in Section 6.2). Character values were transformed as shown in Table 2.1 (ln-transformation for species height). Dissimilarity between species was calculated as the Euclidean distance between their coordinates in character space; agglomeration of species and species clusters was by group average linkage (Manly 1994).

*Influence of* Nothofagus

A universal source of phylogenetic non-independence among the communities examined by this study is the presence in each of one or more species of *Nothofagus*. The degree to which this will affect the outcome of a particular convergence test is dependent on the abundance weighting factor employed and on whether each *Nothofagus* species is faithful to just one of the communities being compared, or occurs in more than one community. In comparisons in which a *Nothofagus* species was present in more than one community, the species was mathematically excluded from analysis (like any other species not unique to one community; see above) and could not contribute to departure from the null model. Most comparisons among local-scale and regional-scale communities were of this kind. In comparisons (including all of those among different landmasses, and a few among regions or within a local area) of communities containing different *Nothofagus* species, similarity in the characters of these species could contribute to the detection of a tendency towards convergence. However, this effect would be minimal in the absence of abundance weighting (i.e. weighting by species presence [=1] only), since each *Nothofagus* record would contribute to the test statistic value only as much as every other species or entity unique to one community in the comparison (e.g. *Nothofagus* accounted for 5 out of 86 species or entities randomised in tests comparing the landmass communities Tasmania and Australia). Only where a weighting factor, particularly photosynthetic biomass or its square root, was applied (Section 6.2), would it be likely for similarities in the characters of different *Nothofagus* species (which generally accounted for the majority of total photosynthetic biomass at the whole-community level) to primarily account for the detection of significant convergence. It does not appear that this potential source of bias accounts for much of the observed convergence. Convergence, significant as a proportion of the number of tests carried out, was detected primarily at low weighting levels (presence or abundance rank), where *Nothofagus* alone is unlikely to lead to the detection of significant convergence (Tables 8.2, 9.2, 10.2-10.4). There were numerous comparisons in which convergence was detected at higher weighting levels, yet *Nothofagus* was not included in the calculation of texture (because the same species occurred in more than one of the communities being compared), or was included in only one community, and so could not cause a bias towards convergence (e.g. southern/northern New Zealand [Fig. 6.5c]; ZN2 Rotokura/ZN3 Clements [Fig. 7.12d]; Chile/Argentina [Fig. 8.9]).

OPTIMISATION OF NULL MODEL TESTS

Texture convergence was sought by randomisation tests comparing observed variation in texture among communities, to the variation expected under a null model of random species assortment. Where the observed variation in texture among communities was significantly low (indicating that the communities were more similar than expected under the null model, in the spectra of

species characters represented) it was concluded that convergence must have occurred (Section 6.2). Communities were compared in terms of their means for texture variates (Chapter 6, 9) and also in terms of community wide distributions of species characters, either adjusted to a common mean among communities (Chapters 8, 9, 10), or not (Chapters 7, 9, 10).

The null model developed in Chapter 6 and used in all subsequent tests of community texture convergence (Chapters 6-10) was carefully formulated to avoid any danger of the Jack Horner effect. For example, to avoid detecting departure from the null model due to differences among communities in species number, the observed numbers of species and entities at each site were retained in the null data. For similar reasons, species abundance distributions within communities were retained in the randomisations. To avoid the danger of interpreting convergence among compositionally-overlapping communities as an outcome of assembly rules, where common phylogenetic history might be the true cause, species occurring in more than one community in any comparison were mathematically excluded from analysis (see above). By excluding common species from analysis, it was possible to perform valid comparisons among regions within a landmass, and even among sites within a local area.

The possibility of the dilution effect (Gilpin & Diamond 1982, 1984), leading to incorrect acceptance of the null hypothesis in tests for convergence and character overdispersion at the whole-community level, was recognised. For this reason, convergence (Chapter 10) and overdispersion (Chapter 11) were also sought within each of three height guilds. It was anticipated that species interactions might be stronger among the members of each of these guilds than in the community as a whole (conforming to this criterion of Pianka [1980]), and that significant departure from null models excluding the expected effects of assembly rules might therefore be more likely. In practice, null hypotheses were rejected with similar frequency at the whole-community and guild scales, suggesting either that assembly rules are equally important, in their effects on community structure, at both scales, or that the guild classification was an inappropriate one (compare Tables 8.2 and 10.2-10.5; Tables 11.3 and 11.5).

In separate series of convergence tests, texture was characterised as the community-wide mean of a texture variate (Chapter 6) and the community-wide distribution (Chapter 7, 8). The mean has commonly been used as a summary statistic for community texture in the past (e.g. Schluter 1986; Bongers & Popma 1990; Wiens 1991a,b; Smith *et al.* 1994, 1995; Wilson *et al.* 1994). However, it has the disadvantage that it represents texture somewhat coarsely: not all of the information about the distribution it summarises is utilised. In studies of texture convergence, the result could be a failure to recognise convergence where it has occurred (a type II error) or the spurious detection of `convergence' where it has not (a type I error). Type II errors could result where similar assembly rules have produced similar texture distributions in the communities being compared, but texture means do not match owing to stochastic differences (Fig. 7.1c). Type I errors could occur where texture distributions in the communities being compared are skewed in opposite directions, but have similar means (Fig. 7.1a), or differ in kurtosis (Fig. 7.1b).

It is unlikely that matching assembly rules in different communities would produce such differences in the shapes texture of distributions, yet convergence could be detected if communities were compared only on the basis of their means. Comparison of texture distributions directly uses more of the available texture information, and so is less likely to lead to incorrect acceptance or rejection of the null hypothesis.

## INTERPRETATION OF OBSERVED PATTERNS

Tests for convergence in community texture means (Chapter 6, 9) and distributions not adjusted to a constant among-community mean (Chapter 7, 9, 10) revealed little evidence that communities were more similar in texture than expected under the null model. Rather, there was a marked degree of divergence, both among communities (Tables 6.2, 7.2, 9.2) and within height guilds within communities (Table 10.2-10.4), suggesting that differences in the environments of communities on different landmasses (e.g. Fig. 7.5a), regions (e.g. Fig. 7.8b) and even in the same local area (e.g. Fig. 7.10a) had caused ecological filtering (*sensu* Keddy 1992), evolutionary selection, or plastic responses leading to different overall spectra of species characters in each community. Significant convergence was detected in a number of individual tests, but binomial tests showed that the overall incidence (among 16 independent community comparisons) was significant only for texture means of species height (with species values weighted by the square root of photosynthetic biomass in calculations of texture means), biomass-weighted means of the derived texture factor F1 (related to PSU succulence, specific weight, total chlorophyll and species height) and unweighted distributions of PSU thickness. For all other variates or factors there was a 2.5% or higher likelihood that all of the convergence observed was due to chance alone. This means that comparisons of community texture means and distributions were able to provide little support for the hypothesis that *Nothofagus*-dominated communities are subject to assembly rules.

The test for convergence or divergence in mean-adjusted distributions, based on the index $\hat{D}'_T$ (Fig. 8.2), was developed in an attempt to remove from analysis among-community texture variation due to the effects of differences in the physical environment. By responding to differences in the shapes of community texture distributions, independently of their absolute values or means, the test was intended to focus on the component of variation in texture that would be primarily affected by assembly rules, if, indeed, such rules apply (Chapter 8).

In comparisons of mean-adjusted distributions, divergence was detected in a small number of tests. At the whole-community scale, this number was not significant overall in any variate or factor according to binomial tests (Table 8.2, 9.2). Within the 0-1 m guild, there was a significant overall incidence of divergence in PSU area and shape, and in the 1-5 m guild in PSU shape, in each case solely with weighting of species values by photosynthetic biomass or its square root (Tables 10.2-10.4). At both the whole-community and guild levels, the incidence of

divergence among mean-adjusted distributions was markedly lower than among means or distributions. This provides some evidence for the success of $\hat{D}_T'$ in removing the effects on texture of environmental differences between communities.

Convergence of mean-adjusted texture was detected among most communities examined, at all three spatial scales, and at both the whole-community and guild levels. Among whole communities, the incidence of convergence was significant overall for six of 13 texture variates (Table 8.2) and five of seven derived texture factors (Table 9.2). The highest overall incidence of convergence was in the 1-5 m guild, where all but four texture variates showed such a pattern (Table 10.3). In general, convergence was most marked in the absence of species weighting, or with species weighted only by abundance rank, which does not cause the outcome of tests to depend strongly on similarity in the characters of the most abundant species. This demonstrates that the convergence among communities tends to be based on the characters of many or most of the vascular species present, not merely the few accounting for the majority of biomass, which might be expected to have a disproportionate influence on community structure.

The high, and highly significant, incidence of convergence among mean-adjusted texture distributions of both whole communities and guilds within communities, provides strong evidence for the operation of assembly rules. The convergence cannot arise merely because species character values in different communities are drawn from the same underlying distribution (which would reflect a variety of environmental, functional and phylogenetic influences, not necessarily related to assembly rules; Tonkyn & Cole 1986), because by permuting the observed character values (species) among sites, the null model itself draws values from an estimate of the common underlying distribution. Departure from the null model can arise only if texture distributions in different communities are *more* similar than 97.5% of communities generated by the null model. This suggests that there are forces that govern community membership, in addition to the abiotic factors whose effects may be seen in the general pool of character values. These forces are interpreted here as assembly rules, whose probable effect is to limit the co-occurrence of species whose niches and characters are too similar.

## 12.5 Character overdispersion

Non-random patterns in the distributions of the characters of sympatric species are regarded as an important class of evidence for assembly rules (Hutchinson 1959; Pianka 1980; Weiher & Keddy 1995a). Overdispersion of species characters is a possible result of assembly rules: because of restrictions on how similar species may be to co-occur, species values may become more regularly spaced along character (niche) axes than expected on a random basis. Character overdispersion is a basis for the hypothesis of texture convergence (Smith *et al.* 1994; Wilson *et al.* 1994; Section 1.5). There has been much discussion as to the methodology by which character overdispersion should be sought. While earlier studies often lacked a clear null

hypothesis and appropriate significance tests (e.g. MacArthur 1971; Barbour 1973; Brown 1975; Inouye 1977; May 1978), most recent studies have addressed the hypothesis that character values (e.g. size or shape characteristics of animals; plant flowering or seeding times; flower morphology) are more regularly dispersed than expected under the null hypothesis that there are no restrictions on how similar species' characters may be (e.g. Simberloff & Boecklen 1981; Pleasants 1980; Armbruster *et al.* 1994; see Section 11.4). However, there has been disagreement as to the parameters of an appropriate null model, and as to the test statistics by which observed and null data distributions should be characterised to seek departure from null expectation (Fleming & Partridge 1984; Tonkyn & Cole 1986; MacNally 1988; Pleasants 1990, 1994; Arita 1993).

In Chapter 11, character overdispersion among the species occurring in the same community or guild was sought by comparing variability in the spacing of species values along character (or multivariate factor) axes (test statistic $V_T$), to the variability expected if species characters were determined at random. Under the null model, species values were drawn from a smoothed kernel function approximation of the distribution of the observed data. This represents an advancement over previous studies drawing values from the biologically-meaningless uniform distribution (Poole & Rathcke 1979; Pleasants 1980; Simberloff & Boecklen 1981) or from a theoretical distribution not related to the underlying distribution of the observed species values (Tonkyn & Cole 1986).

The use of an inappropriate sampling distribution can give both type I and type II errors, depending upon the hypothesis being tested, and the manner in which the observed and null distributions vary (Tonkyn & Cole 1986; Wilson 1995). Schoener (1984) has suggested that resampling from the uniform distribution in the same range as the observed data (e.g. Simberloff & Boecklen 1981) will tend to give an excess of type II errors (the Narcissus effect) when overdispersion is being sought. This is because character distributions in nature are generally modal, with many intermediate values and few extreme ones. This means that the variance of the spacing between character values in nature will tend to be higher than when values are drawn from a uniform distribution, in which all values within the sampling range are equally likely. Since overdispersion is characterised by a low variance in the spacing between values, a null model based on the uniform distribution will be rejected only where the observed overdispersion is especially pronounced. The kernel function-based null model used in Chapter 11 is free from this potential problem, because the probability of drawing a null character value in a certain range is approximately proportional to the relative frequency of observed values in that range. If intermediate values are more common than extreme ones in the observed data (suggesting that, for biological reasons, such values are more likely to occur in nature, given the environment and the history of the assemblage sampled), random intermediate values are more likely than random extreme ones in each null model data set.

Although the kernel function-based null model avoids excessive type II errors related to

the factors outlined above, it could be argued that the observed distribution of character values will reflect the actions both of biological and phylogenetic mechanisms not incorporated in the hypothesis being tested, and (if the hypothesis is true) of assembly rules. Modelling null distributions on the observed distribution will incorporate both sources of variation, with the result that some of the structure produced by assembly rules may be preserved in null model data sets. This would tend to make the null model difficult to reject unless overdispersion is pronounced — a Narcissus effect (c.f. Fuentes 1980; Gilpin & Diamond 1984). The magnitude of this effect will depend on the relative importance of assembly rules, tending to space species characters out, and of other processes, which might tend to cluster species together (about the same adaptive optima, or, in the case of phylogenetic constraints, about ancestral character values). The generally weak trends towards overdispersion identified in previous studies (e.g. MacNally 1988; Simberloff & Boecklen 1981; Fleming & Partridge 1984), suggest that the effects of assembly rules will be weak relative to other effects. If so, null data sets drawn from the relatively smooth kernel estimates used will incorporate little species interaction-mediated structure, and Narcissus effects will be minor.

The test statistic $V_T$ used to quantify character dispersion patterns in the present study has been recommended because it is based on the dissimilarity between adjacent species in character space (Pleasants 1990, 1994). Assuming that species characters are close proxies for alpha niches, reciprocal interactions — particularly competition — would be expected to be most pronounced among adjacent species (Pianka 1975). As an assemblage-wide parameter, $V_T$ is preferable to statistics based only on the characters of a few species pairs (such as Min and $G_{ij}$ of Simberloff & Boecklen [1981]; see Section 12.2). However, by focusing on pairs of species most likely to interact, it avoids the dilution effect of statistics such as the `overlap index' of Fleming & Partridge (1984), which is based on the dissimilarities between all possible pairs of species in the community, not all of which are likely to be involved in strong reciprocal interactions (Pleasants 1990, 1994).

### INTERPRETATION OF OBSERVED PATTERNS

Relatively little significant overdispersion was detected in individual assemblages, and, with the exception of PSU area in the 0-1 m guild (Table 11.4), the number of assemblages in which significant overdispersion was detected in any given variate appeared to be no greater than would be expected by chance alone, at the 5% target significance level (Tables 11.2, 11.4).

However, a marked, though only occasionally significant, overall trend towards overdispersion (relative variance less than 1) was apparent for several communities and variates. For example, species values for all but one of the 13 texture variates were overdispersed at the whole-community scale in New Zealand, although this effect was significant only for PSU succulence, specific weight and total chlorophyll (Fig. 11.2c). Among all 17 regional- or local-

scale communities comprising a single study site, at least 14 exhibited overdispersion (whether significant or not) in the variates PSU lobation, thickness, succulence, specific weight and total chlorophyll, and in the derived factors F1 and F4 (Table 11.3). This incidence is significantly higher than would be expected as a result of type I errors in the individual tests. It therefore provides overall support for the hypothesis that there are assembly rules which limit the co-occurrence of species with similar niches, resulting in a somewhat regular spacing of species in niche (and associated character) space.

## 12.6 Integration of results

Each of the three principal approaches seeking evidence for community structure in this study has yielded some evidence to support the overall hypothesis that species-mediated assembly rules operate in *Nothofagus*-dominated communities. However, some qualifications apply. Convergence in species richness among communities has not been shown conclusively. Rather, about half of all communities compared could not be shown to be divergent, suggesting that convergence among them could have occurred, although the patterns observed are also consistent with quadrat species richnesses having been drawn at random from observed pools of observations. Significant convergence in community texture has been shown, but it is possible that phylogenetic similarities between communities at the genus and higher taxonomic levels may account for a proportion of this convergence, especially at the regional and local scales, where phylogentic overlap is high. It is unlikely that the observed convergence, which was significant overall primarily at low abundance weighting levels, is due to common dominance by *Nothofagus* in each of the sites. Departure from null expectation was less pronounced in tests of character overdispersion than in tests of community-level convergence. However, some significant trends were identified. These cannot be explained as the result of any phylogenetic or methodological artifact, and so represent strong evidence for the operation of assembly rules.

### ECOLOGICAL INTERPRETATION OF OBSERVED PATTERNS

The central question in the present study has been whether evidence for the operation of assembly rules — species interaction-mediated restrictions on community composition — could be discerned in quantifiable community patterns. The question as to what specific mechanisms might underlie such assembly rules, as have been demonstrated by this study, is a considerably more exacting one. This question has rarely been addressed directly, and this study did not attempt to do so. However, some evidence of possible mechanisms is implied by the identities of the characters for which the strongest non-random patterns were demonstrated.

Factor F1 was found to be convergent in a significant number of community comparisons (mean-adjusted texture distributions; Table 9.2), and also showed overdispersion in a significant

number of communities (Table 11.3). The four texture variates closely correlated ($r$>0.5; Table 9.1) with F1, PSU succulence, specific weight, total chlorophyll and species height, showed similar patterns to this factor at the whole community level (Table 8.2), and also within some guilds (Tables 10.2-10.4, 11.5). The identities of the characters related to F1, especially species height, suggest a relationship to the light regime, and particularly, to vertical structure (Björkman 1981; Field & Mooney 1986; Ellsworth & Reich 1993; Witkowski & Lamont 1991). This interpretation is consistent with trends observed for three of these characters in Chapter 4: among all species sampled, PSU succulence and total chlorophyll decreased (significantly for succulence) with height above ground level, while specific weight showed a significant increase (Fig. 4.1). A possible ecological interpretation of the observed convergence and overdispersion is as follows. Light quality (spectral composition) and quantity (quantum flux) are factors governing plant distributions and may be particularly important in forest ecosystems (Smith 1973). The attributes of species will determine over what range along this gradient they can function, i.e. will determine fundamental niche — the full range of environmental conditions in which species can establish, grow and reproduce in the absence of interference from other species. Among-species differences in competitive ability at any point along these gradients will govern which species can maintain populations in a community, i.e. will determine realised niches. In general, overlap of realised niches will be limited by competitive exclusion, resulting in a somewhat regular spacing of species along the light, and vertical, gradient (Pianka 1980). This niche pattern is reflected in species characters such as leaf specific weight, chlorophyll content and species height, and is detected as departure of the observed distributions of these characters from distributions generated by null models which assume no restrictions on how similar the characters of co-occurring species (and their realised niches) may be.

Mean-adjusted distributions of PSU area were convergent in a significant number of tests both at the whole community level (Table 8.2) and in all three guilds (Tables 10.2-10.4). While a significant overall incidence of overdispersion was detected only in the 0-1 m guild (Table 11.4), PSU area also showed significant overdispersion in four of 26 communities, although this was not significant according to a binomial test (Table 11.2). Leaf area has been found to vary along gradients of light quantity and quality, nutrient status and moisture availability (Grubb *et al.* 1963; Givnish & Vermeij 1976; Grubb 1977; Hall & Swaine 1981; Chiarello 1984; Medina 1984; Givnish 1984). This implies that the convergence and overdispersion observed could reflect partitioning of either of these three niche (resource) gradients among species. A non-significant tendency for PSU area to increase with height above ground level was identified in Chapter 4 (Fig. 4.1), and suggests that the vertical light gradient may, once again, be involved.

Although the texture factor F3, and its correlated variates PSU phosphorus content and chlorophyll *a/b* ratio, did not show any significant trends towards overdispersion within communities, mean-adjusted distributions of these variates were convergent in the greatest number of community comparisons, at both the whole-community (Table 8.2) and guild scales

(Tables 10.2-10.4). This implies that there are similarities, exceeding chance expectation, in the distributions of these characters among species in different *Nothofagus*-dominated communities. Chlorophyll *a/b* ratios may be closely related to light reception (Boardman 1977; Björkman 1981; Chow *et al.* 1991). Plant phosphorus concentrations might reflect soil nutrient status, but may also be related to photosynthetic responses (Evans 1989; Reich *et al.* 1991). The shared component of variation in PSU phosphorus content and chlorophyll *a/b* accomodated by F3 seems more likely to reflect responses to the light regime, since chlorophyll *a/b* has been shown to be largely independent of soil nutrient status, at least within a species (Dale & Causton 1992).

Factor F4 showed significant convergence and overdispersion at the whole-community scale (Tables 9.2, 11.3), while the strongly-correlated texture variate PSU thickness also showed a significant trend towards overdispersion in the 0-1 m guild (Table 11.5). Leaf thickness may be related to light reception (Givnish 1987; Bongers & Popma 1988; Reich *et al.* 1991), or to plant nutrient status (Beadle 1966; Grubb 1977; Sobrado & Medina 1980).

Convergence in F5 was detected in a significant number of community comparisons (Table 9.2). It is most closely related to PSU nitrogen content and phosphorus content, suggesting that species values for F5 may be related to nutrient uptake. Overdispersion or convergence among communities in nutrient-related characters could result if competition for below-ground resources results in partitioning of root space among species (Caldwell 1987; Caldwell *et al.* 1991). Associated differences in nutrient uptake might be reflected in species above-ground characters, causing them to exhibit overdispersion within assemblages, and convergence among them.

In summary, patterns supporting hypotheses of assembly rules were revealed most strongly in texture variates and derived factors that are most likely to reflect plant responses and adaptations to light availability. This finding may be related to the types of characters (principally leaf attributes) quantified, but also suggests that competitive partitioning of light gradients, particularly within the vertical forest structure, may be the most important mechanism underlying the assembly rules detected. A lesser amount of convergence and overdispersion was detected in texture variates that could be related to nutritional niches. This suggests that competitive partitioning of below-ground nutrient gradients may also have contributed to some of the patterns observed.

Assembly rules concerning vertical forest structure have been identified previously: Bycroft *et al.* (1993) and Wilson *et al.* (1995) detected significant guild proportionality in the ground herb guild in different southern New Zealand *Nothofagus*-dominated communities. Guild proportionality (similar proportional representation of species in a guild in comparison to a null model of random species assortment) is expected as a result of assembly rules restricting guild membership. Results of the present study demonstrate related patterns possibly produced by similar assembly rules.

## ASSEMBLY RULES: EVOLUTION OR ECOLOGY?

In Chapter 1, two related hypotheses were proposed to account for non-random patterns in the distributions of sympatric species in niche space. In an ecological time frame, and at the local scale, ecological species sorting might limit the establishment of species from the pool migrating onto a site. Only species with sufficiently dissimilar niches (characters) can co-occur: immigrants must either assume an unoccupied region of niche space, or displace weaker competitors already present (Fig. 1.4). In an evolutionary time frame, and at the regional or landmass scale, repeated ecological species sorting at many sites will give rise to selection pressure for similar species in the pool to diverge in their characters until coexistence becomes possible: there would be coevolutionary character displacement (Fig. 1.4). The hypotheses are related because both have local-scale ecological sorting as their basis (Fig. 1.5).

Community-level convergence and character overdispersion have generally been thought of as evolutionary phenomena — as outcomes of coevolutionary character displacement (Hutchinson 1959; Simberloff & Boecklen 1981; Orians & Solbrig 1983; Blondel *et al.* 1984; Schluter 1986). However, it is clear that both patterns could result solely from ecological sorting (Ricklefs 1987; Smith *et al.* 1994; Armbruster *et al.* 1994). Because ecological sorting would operate at very local scales (though its effects might also be detected regionally) whereas coevolutionary character displacement would operate at scales up to those at which gene flows are restricted by dispersal barriers, the scale at which community-level convergence or overdispersion is observed can shed some light on the relative importance of ecological and evolutionary processes in producing the observed patterns.

Both texture convergence and character overdispersion were detected at all spatial scales examined. For example, convergence was detected between landmass-scale communities Tasmania and New Zealand (Figs. 8.5c, 9.1b), regional-scale communities southern and central New Zealand (Figs. 8.8b, 9.2) and local-scale communities ZN2 Rotokura and ZN3 Clements (Figs. 8.12d, 9.3). There was significant overdispersion for New Zealand as a whole (PSU succulence; specific weight and total chlorophyll; Fig. 11.2c); in the regional community southern New Zealand (PSU area; Fig. 11.3f) and in the local community T2 Anne (Fig. 11.3b). At the local scale, communities would share the same species pool; independent coevolution in the communities being compared is unlikely, because on an evolutionary time scale barriers to dispersal would be insignificant. Therefore, overdispersion in, or texture convergence among, communities at the local scale would almost certainly be the result of ecological species sorting alone. At the landmass scale, each community (in the present study, comprising pooled data from several study sites) has its own species pool (or several regional species pools), so overdispersion or convergence is more likely to be an outcome of coevolutionary character displacement within each *Nothofagus*-forest flora, integrating the effects of local-scale ecological species sorting over evolutionary time. However, ecological sorting from different species pools, in the absence of

coevolution, could also explain the convergence observed. At the regional scale, overdispersion and convergence could be due to ecological sorting, coevolution within regional pools, or a combination of both processes.

In summary, significant evidence of assembly rules was gathered at each of the three spatial scales considered. This suggests that the assembly rules may operate both through local scale ecological sorting of species, and possibly (though not certainly) through coevolutionary character displacement, integrating the effects of ecological sorting over evolutionary time.

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# Appendix A. Species character data

Species character (texture) data from each study site are presented in this appendix. Values are shown for each species, or age/size class of a species (`entity'), for the characters PSU thickness (*Thick*, mm), PSU area (*Area*, $cm^2$), PSU inclination (*Inclin*, ° from horizontal), PSU succulence (*Succ*, no units), PSU specific weight (*SLW*, g $cm^{-2}$), PSU shape (*Shape*, no units), PSU chlorophyll *a/b* ratio (*Chl* a/b, no units), PSU total chlorophyll content (*Chl*, % of dry weight), PSU nitrogen content (*N*, % of dry weight), support fraction (*SF*, no units), PSU phosphorus content (*P*, % of dry weight) and PSU lobation (*Lobe*, no units). Measurement and calculation protocols for these characters are described in Chapter 2. The 17 study sites are described in Chapter 3. Nomenclatural sources are listed in Section 2.3.6. Arbitrary `field names' are shown for species not positively identified.

Key to age/size classes:
- A = adults;
- C = canopy individuals (>67% of mean canopy height);
- J = juveniles or seedlings (<2 m height);
- S = subcanopy individuals or saplings (2 m to 67% of mean canopy height).

† Identifies values substituted from another record for the same species or predicted using a multiple regression model (some chlorophyll values only: see Section 2.3.5). When shown beside a species name, the symbol indicates that all character values were substituted from another record.

| **Site T1 Balfour** | *Thick* | *Area* | *Inclin* | *Succ* | *SLW* | *Shape* | *Chl* a/b | *Chl* | *N* | *SF* | *P* | *Lobe* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Aristotelia peduncularis* | 0.19 | 4.70 | 31 | 2.61 | 0.0060 | 2.64 | 1.69 | 0.79 | 1.40 | 0.37 | 0.049 | 1.10 |
| *Asplenium bulbiferum* | 0.34 | 4.15 | 46 | 3.74 | 0.0083 | 3.48 | 2.29 | 0.36 | 0.92 | 0.13 | 0.113 | 1.47 |
| *Asplenium flaccidum* | 0.44 | 10.30 | 50 | 4.70 | 0.0129 | 2.76 | 2.27 | 0.46 | 1.28 | 0.18 | 0.120 | 4.21 |
| *Atherosperma moschatum* | 0.29 | 10.50 | 26 | 2.70 | 0.0081 | 2.08 | 2.18 | 0.40 | 1.59 | 0.35 | 0.064 | 1.26 |
| *Blechnum watsii* | 0.31 | 6.96 | 18 | 1.91 | 0.0098 | 2.63 | 2.16 | 0.27 | 1.05 | 0.05 | 0.067 | 0.95 |
| *Cenarrhenes nitida* | 0.39 | 22.50 | 23 | 2.40 | 0.0129 | 4.10 | 2.71 | 0.23 | 0.62 | 0.18 | 0.028 | 1.30 |
| *Coprosma quadrifida* | 0.12 | 0.19 | 16 | 2.67 | 0.0068 | 3.51 | 2.43 | 0.44 | 2.18 | 0.39 | 0.120 | 0.94 |
| *Ctenopteris heterophylla* | 0.23 | 7.34 | 34 | 3.13 | 0.0108 | 4.86 | 2.33 | 0.33 | 1.09 | 0.00 | 0.085 | 4.46 |
| *Dicksonia antarctica* | 0.15 | 2.03 | 27 | 2.29 | 0.0095 | 4.76 | 1.97 | 0.45 | 2.04 | 0.14 | 0.078 | 1.08 |
| *Eucryphia lucida* | 0.26 | 3.07 | 18 | 2.40 | 0.0099 | 2.82 | 2.14 | 0.34 | 0.82 | 0.33 | 0.045 | 0.96 |
| *Grammitis billardieri* | 0.18 | 1.44 | 36 | 2.61 | 0.0072 | 11.46 | 2.30 | 0.34 | 1.24 | 0.00 | 0.071 | 1.01 |
| *Histiopteris incisa* | 0.15 | 4.27 | 15 | 4.39 | 0.0023 | 3.45 | 2.08 | 0.58 | 2.16 | 0.15 | 0.101 | 1.15 |
| *Hymenophyllum flabellatum* | 0.10 | 9.74 | 76 | 2.66 | 0.0035 | 2.00 | 2.05 | 0.45 | 1.06 | 0.26 | 0.085 | 1.94 |
| *Hymenophyllum peltatum*† | 0.09 | 0.73 | 34 | 1.93 | 0.0077 | 2.47 | 1.69 | 0.65 | 0.92 | 0.27 | 0.085 | 3.81 |
| *Hymenophyllum rarum* | 0.07 | 2.69 | 40 | 1.71† | 0.0019† | 2.94 | 1.92† | 0.39† | 1.19† | 0.29† | 0.045† | 2.66 |
| *Hypolepis rugosula* | 0.17 | 8.59 | 21 | 4.04 | 0.0016 | 2.95 | 2.03 | 0.65 | 1.94 | 0.17 | 0.137 | 1.84 |
| *Nothofagus cunninghamii* (C) | 0.39 | 0.53 | 36 | 2.07 | 0.0167 | 1.37 | 2.15 | 0.25 | 1.20 | 0.28 | 0.058 | 1.06 |
| *Nothofagus cunninghamii* (S) | 0.24 | 0.69 | 32 | 1.96 | 0.0104 | 1.52 | 1.94 | 0.40 | 1.24 | 0.36 | 0.051 | 1.12 |
| *Nothofagus cunninghamii* (J) | 0.22 | 0.70 | 15 | 2.04 | 0.0074 | 1.42 | 1.77 | 0.37 | 1.20 | 0.32 | 0.059 | 0.97 |
| *Olearia argophylla* | 0.31 | 26.30 | 20 | 2.53 | 0.0098 | 3.00 | 2.64 | 0.32 | 1.42 | 0.21 | 0.083 | 1.20 |
| *Phymatosorus diversifolius* | 0.26 | 21.80 | 42 | 3.54 | 0.0076 | 9.18 | 3.10 | 0.27 | 1.01 | 0.48 | 0.045 | 0.99 |
| *Pimelia drupacea* | 0.19 | 1.66 | 16 | 3.60 | 0.0061 | 3.76 | 1.94 | 1.46 | 2.22 | 0.34 | 0.101 | 0.97 |
| *Pittosporum bicolor* | 0.24 | 2.43 | 31 | 2.03 | 0.0123 | 6.55 | 2.12 | 0.27 | 1.06 | 0.33 | 0.108 | 1.02 |
| *Trochocarpa* aff. *cunninghamii* | 0.24 | 0.44 | 34 | 1.65 | 0.0125 | 2.99 | 2.01 | 0.31 | 1.03 | 0.51 | 0.025 | 1.02 |
| *Uncinia* sp. 1† | 0.11 | 0.20 | 28 | 3.44 | 0.0069 | 150.70 | 1.99 | 0.82 | 1.92 | 0.18 | 0.128 | 1.27 |

| **Site T2 Anne** | *Thick* | *Area* | *Inclin* | *Succ* | *SLW* | *Shape* | *Chl* a/b | *Chl* | *N* | *SF* | *P* | *Lobe* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Acianthus viridis*† | 0.17 | 0.73 | 11 | 13.70 | 0.0016 | 1.26 | 3.83 | 0.73 | 0.44 | 0.89 | 0.209 | 0.96 |
| *Anodapetalum biglandulosum* | 0.29 | 3.29 | 25 | 2.73 | 0.0084 | 2.54 | 2.02 | 0.44 | 0.91 | 0.37 | 0.053 | 1.14 |
| *Anopteris glandulosus* | 0.40 | 18.60 | 32 | 3.76 | 0.0144 | 6.22 | 2.49 | 0.33 | 0.66 | 0.24 | 0.048 | 1.34 |
| *Atherosperma moschatum* | 0.32 | 7.75 | 30 | 3.20 | 0.0074 | 3.04 | 2.10 | 0.58 | 1.55 | 0.34 | 0.096 | 1.22 |
| *Blechnum watsii* | 0.36 | 9.81 | 21 | 4.00 | 0.0093 | 2.81 | 1.93 | 0.73 | 1.30 | 0.05 | 0.071 | 0.99 |
| *Corybas* sp. | 0.23 | 0.84 | 17 | 10.20 | 0.0029 | 0.95 | 2.39 | 1.31 | 1.98 | 0.29 | 0.268 | 0.86 |
| *Dicksonia antarctica* | 0.14 | 1.27 | 30 | 2.95 | 0.0072 | 4.49 | 1.78 | 0.65 | 2.16 | 0.15 | 0.135 | 1.16 |
| *Eucryphia lucida* | 0.23 | 2.64 | 24 | 2.09 | 0.0106 | 3.70 | 2.27 | 0.31 | 0.80 | 0.36 | 0.081 | 0.94 |
| *Grammitis billardieri* | 0.18 | 1.92 | 31 | 2.59 | 0.0059 | 21.43 | 2.02 | 0.42 | 1.11 | 0.00 | 0.070 | 1.28 |
| *Histiopteris incisa* | 0.15 | 4.20 | 22 | 7.67 | 0.0011 | 2.59 | 1.81 | 1.74 | 3.69 | 0.18 | 0.283 | 1.35 |
| *Hydrocotyle* sp. | 0.20 | 0.56 | 26 | 7.27 | 0.0030 | 0.56 | 2.29 | 1.03 | 2.34 | 0.51 | 0.199 | 0.62 |
| *Hymenophyllum australe* | 0.08 | 1.11 | 32 | 2.80 | 0.0030 | 2.14 | 1.61 | 0.78 | 1.83 | 0.40 | 0.110 | 2.67 |
| *Hymenophyllum peltatum* | 0.09 | 0.73 | 31 | 1.93 | 0.0077 | 2.47 | 1.69 | 0.65 | 1.33 | 0.27 | 0.116 | 3.81 |
| *Hymenophyllum rarum* | 0.10 | 1.50 | 32 | 1.86 | 0.0046 | 3.03 | 1.54 | 0.61 | 1.28 | 0.23 | 0.093 | 2.63 |
| *Hypolepis rugosula* | 0.11 | 5.19 | 38 | 5.69 | 0.0008 | 2.48 | 1.76 | 1.34 | 3.45 | 0.16 | 0.210 | 1.31 |
| *Nothofagus cunninghamii* (C)† | 0.39 | 0.53 | 36 | 2.07 | 0.0167 | 1.37 | 2.15 | 0.25 | 1.20 | 0.28 | 0.058 | 1.06 |
| *Nothofagus cunninghamii* (S) | 0.24 | 0.50 | 41 | 1.97 | 0.0125 | 1.40 | 1.72 | 0.43 | 1.08 | 0.35 | 0.089 | 1.13 |
| *Nothofagus cunninghamii* (J) | 0.26 | 0.50 | 18 | 1.97 | 0.0120 | 1.16 | 1.85 | 0.38 | 1.05 | 0.41 | 0.042 | 1.08 |
| *Pittosporum bicolor* | 0.28 | 2.04 | 30 | 2.51 | 0.0106 | 4.66 | 2.14 | 0.38 | 1.22 | 0.34 | 0.058 | 1.08 |
| *Polystichum proliferum* | 0.22 | 5.96 | 12 | 2.72 | 0.0065 | 3.53 | 2.16 | 0.52 | 1.50 | 0.17 | 0.112 | 1.21 |
| *Pterostylis* sp. 1† | 0.24 | 2.42 | 18 | 10.60 | 0.0025 | 2.12 | 2.41 | 0.77 | 3.07 | 0.24 | 0.253 | 1.03 |
| *Trochocarpa* aff. *cunninghamii* | 0.21 | 0.28 | 27 | 2.01 | 0.0104 | 3.86 | 2.04 | 0.39 | 1.09 | 0.42 | 0.026 | 0.96 |
| *Uncinia* sp. 2 | 0.12 | 0.14 | 26 | 4.15 | 0.0082 | 159.80 | 2.06 | 0.82 | 1.57 | 0.25 | 0.120 | 1.49 |

| **Site T3 Mathinna** | *Thick* | *Area* | *Inclin* | *Succ* | *SLW* | *Shape* | *Chl* a/b | *Chl* | *N* | *SF* | *P* | *Lobe* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Acianthus viridis* | 0.17 | 0.73 | 11 | 13.70 | 0.0016 | 1.26 | 3.83 | 0.73 | 0.44 | 0.89 | 0.209 | 0.96 |
| *Atherosperma moschatum* | 0.28 | 15.20 | 32 | 2.91 | 0.0064 | 2.20 | 2.07 | 0.54 | 1.78 | 0.29 | 0.090 | 1.33 |
| *Blechnum watsii* | 0.37 | 14.20 | 14 | 3.50 | 0.0097 | 3.63 | 1.72 | 0.76 | 1.29 | 0.07 | 0.046 | 0.95 |
| *Corybas* sp. | 0.26 | 1.29 | 16 | 8.96 | 0.0027 | 0.94 | 2.43 | 0.89 | 3.32 | 0.35 | 0.218 | 0.89 |
| *Cyathodes glauca* | 0.19 | 0.24 | 24 | 1.74 | 0.0174 | 8.86 | 2.05 | 0.37 | 1.26 | 0.39 | 0.066 | 1.05 |
| *Dicksonia antarctica* | 0.14 | 3.47 | 30 | 2.21 | 0.0080 | 4.78 | 1.84 | 0.52 | 2.37 | 0.15 | 0.090 | 1.22 |
| *Drymophylla cyanocarpa* | 0.10 | 0.67 | 15 | 6.09 | 0.0016 | 4.81 | 2.01 | 1.22 | 3.39 | 0.51 | 0.197 | 0.92 |
| *Gahnia grandis* | 0.28 | 90.20 | 40 | 1.76 | 0.0157 | 391.30 | 2.27 | 0.27 | 0.71 | 0.00 | 0.045 | 1.04 |
| *Grammitis billardieri* | 0.19 | 1.22 | 23 | 2.71 | 0.0067 | 12.44 | 2.00 | 0.47 | 1.59 | 0.00 | 0.108 | 1.30 |
| *Histiopteris incisa* | 0.14 | 3.41 | 14 | 6.36 | 0.0016 | 2.22 | 1.90 | 1.22 | 3.41 | 0.16 | 0.206 | 1.30 |
| *Hymenophyllum peltatum* | 0.01 | 0.87 | 14 | 1.25 | 0.0080 | 3.00 | 1.71 | 0.44 | 1.05 | 0.23 | 0.073 | 3.39 |
| *Hymenophyllum rarum* | 0.04 | 1.14 | 34 | 1.71 | 0.0045 | 2.38 | 2.18 | 0.64 | 1.15 | 0.29 | 0.090 | 2.58 |
| *Hypolepis rugosula* | 0.22 | 7.56 | 15 | 5.65 | 0.0016 | 2.24 | 1.90 | 0.97 | 3.03 | 0.12 | 0.257 | 1.41 |
| *Nothofagus cunninghamii* (C) | 0.38 | 0.68 | 35 | 2.10 | 0.0190 | 1.35 | 2.20 | 0.23 | 1.47 | 0.24 | 0.125 | 1.09 |
| *Nothofagus cunninghamii* (S) | 0.22 | 0.85 | 22 | 2.16 | 0.0080 | 1.43 | 1.75 | 0.54 | 1.43 | 0.28 | 0.131 | 1.15 |
| *Nothofagus cunninghamii* (J) | 0.22 | 0.69 | 15 | 1.99 | 0.0087 | 1.48 | 1.79 | 0.41 | 1.14 | 0.24 | 0.107 | 0.97 |
| *Phyllocladus aspleniifolius* (C) | 0.56 | 1.45 | 42 | 1.49 | 0.0298 | 2.25 | 1.90 | 0.26 | 0.96 | 0.25 | 0.062 | 1.26 |
| *Phyllocladus aspleniifolius* (S) | 0.38 | 3.37 | 33 | 1.89 | 0.0172 | 2.63 | 1.83 | 0.42 | 1.04 | 0.32 | 0.057 | 1.45 |
| *Phymatosorus diversifolius* | 0.29 | 34.50 | 41 | 3.88 | 0.0078 | 7.26 | 2.02 | 0.55 | 1.22 | 0.55 | 0.061 | 1.07 |
| *Pittosporum bicolor* | 0.21 | 2.34 | 20 | 2.41 | 0.0075 | 5.92 | 2.09 | 0.47 | 1.34 | 0.18 | 0.079 | 0.98 |
| *Pterostylis* sp. 1 | 0.24 | 2.42 | 18 | 10.60 | 0.0025 | 2.12 | 2.41 | 0.77 | 3.07 | 0.24 | 0.253 | 1.03 |
| *Tasmannia lanceolata* | 0.31 | 14.40 | 17 | 3.45 | 0.0082 | 3.81 | 2.23 | 0.50 | 1.35 | 0.17 | 0.089 | 1.23 |
| *Uncinia* sp. 1 | 0.11 | 0.20 | 28 | 3.44 | 0.0069 | 150.70 | 1.99 | 0.82 | 1.92 | 0.18 | 0.128 | 1.27 |

| **Site A1 Lumeah** | *Thick* | *Area* | *Inclin* | *Succ* | *SLW* | *Shape* | *Chl* a/b | *Chl* | *N* | *SF* | *P* | *Lobe* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Acmena smithii* | 0.32 | 15.11 | 22 | 2.53 | 0.0092 | 2.49 | 2.31 | 0.71 | 1.21 | 0.18 | 0.147 | 1.27 |
| *Adiantum formosum* | 0.07 | 0.48 | 20 | 2.66 | 0.0023 | 1.90 | 1.92 | 1.75 | 2.65 | 0.19 | 0.223 | 0.99 |
| *Arthropteris tenella* | 0.22 | 6.28 | 68 | 3.14 | 0.0042 | 6.19 | 2.68 | 0.70 | 1.81 | 0.16 | 0.194 | 1.22 |
| *Caldcluvia paniculosa* | 0.29 | 35.70 | 20 | 2.56 | 0.0099 | 2.45 | 2.56 | 0.63 | 1.02 | 0.12 | 0.170 | 1.10 |
| *Cephalaria cephalobotrys* | 0.20 | 8.63 | 36 | 2.86 | 0.0071 | 2.05 | 2.39 | 0.94 | 1.43 | 0.73 | 0.141 | 1.13 |
| *Citriobatus pauciflorus* | 0.15 | 0.18 | 22 | 2.36 | 0.0077 | 1.39 | 2.88 | 0.63 | 1.65 | 0.60 | 0.154 | 1.03 |
| *Cryptocarya foveolata* | 0.29 | 11.14 | 30 | 2.07 | 0.0101 | 2.06 | 3.21 | 0.41 | 1.72 | 0.23 | 0.204 | 1.11 |
| *Cryptocarya glaucescens* | 0.22 | 23.74 | 29 | 2.42 | 0.0095 | 2.94 | 2.55 | 0.37 | 1.36 | 0.23 | 0.185 | 1.07 |
| *Daphnandra* sp. A | 0.25 | 22.39 | 26 | 3.33 | 0.0042 | 2.74 | 2.94 | 0.80 | 2.01 | 0.30 | 0.232 | 1.20 |
| *Dennstaedtia davallioides* | 0.10 | 4.05 | 16 | 4.73 | 0.0013 | 2.59 | 2.34 | 1.55 | 3.15 | 0.17 | 0.272 | 1.21 |

| **A1 Lumeah** (continued) | *Thick* | *Area* | *Inclin* | *Succ* | *SLW* | *Shape* | *Chl* a/b | *Chl* | *N* | *SF* | *P* | *Lobe* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Dicksonia antarctica* | 0.16 | 2.13 | 13 | 2.20 | 0.0116 | 3.86 | 2.76 | 0.52 | 1.64 | 0.13 | 0.324 | 1.13 |
| *Dioscorea transversa* | 0.14 | 24.06 | 20 | 4.14 | 0.0022 | 1.86 | 2.49 | 1.83 | 3.06 | 0.56 | 0.227 | 1.08 |
| *Diplazium australe* | 0.14 | 3.74 | 16 | 5.37 | 0.0022 | 2.71 | 2.49 | 1.66 | 3.50 | 0.16 | 0.233 | 1.10 |
| *Diploglottis australis* | 0.20 | 172.40 | 15 | 2.12 | 0.0037 | 2.81 | 2.61 | 0.90 | 1.96 | 0.18 | 0.217 | 1.02 |
| *Doryphora sassafras* | 0.36 | 18.18 | 25 | 2.76 | 0.0094 | 2.35 | 2.95 | 0.60 | 1.46 | 0.23 | 0.128 | 1.16 |
| *Lastreopsis decomposita* | 0.14 | 1.78 | 15 | 2.51 | 0.0062 | 3.25 | 2.16 | 1.17 | 2.74 | 0.13 | 0.188 | 1.08 |
| *Lomandra* c.f. *longifolia* | 0.42 | 43.91 | 50 | 2.99 | 0.0320 | 93.00 | 2.55 | 1.12 | 0.99 | 0.00 | 0.084 | 1.07 |
| *Microsorum scandens* | 0.24 | 7.84 | 42 | 4.51 | 0.0054 | 8.70 | 2.60 | 1.30 | 2.24 | 0.40 | 0.411 | 1.15 |
| *Nothofagus moorei* (C) | 0.37 | 9.11 | 25 | 1.93 | 0.0175 | 1.91 | 2.64 | 0.36 | 1.39 | 0.39 | 0.137 | 1.15 |
| *Nothofagus moorei* (S) | 0.35 | 11.77 | 25 | 1.97 | 0.0162 | 2.38 | 2.64 | 0.37 | 1.12 | 0.29 | 0.122 | 1.12 |
| *Orites excelsa* | 0.28 | 43.92 | 45 | 2.17 | 0.0079 | 5.63 | 2.43 | 0.59 | 0.83 | 0.13 | 0.065 | 1.16 |
| *Palmeria scandens* | 0.27 | 26.07 | 19 | 3.52 | 0.0050 | 2.15 | 2.50 | 1.33 | 1.88 | 0.21 | 0.227 | 1.07 |
| *Pandorea pandorana* (A) | 0.16 | 7.70 | 35 | 5.11 | 0.0031 | 2.60 | 2.73 | 1.57 | 2.94 | 0.83 | 0.415 | 1.25 |
| *Pandorea pandorana* (J) | 0.04 | 0.17 | 12 | 3.10 | 0.0023 | 1.67 | 2.52 | 1.50 | 2.61 | 0.60 | 0.309 | 1.33 |
| *Parsonsia straminea* | 0.20 | 11.68 | 42 | 3.66 | 0.0027 | 2.97 | 2.58 | 1.19 | 2.27 | 0.38 | 0.177 | 0.95 |
| *Pellaea falcata* var. *falcata* | 0.29 | 1.62 | 18 | 3.04 | 0.0093 | 4.60 | 2.60 | 1.20 | 2.18 | 0.16 | 0.222 | 0.87 |
| *Polystichum proliferum* | 0.22 | 7.87 | 11 | 2.64 | 0.0060 | 3.44 | 3.02 | 0.55 | 1.86 | 0.21 | 0.276 | 1.31 |
| *Pyrrosia rupestris* | 0.83 | 0.84 | 56 | 1.76 | 0.0748 | 4.86 | 2.40 | 0.06 | 0.24 | 0.14 | 0.154 | 1.61 |
| *Smilax australis* | 0.41 | 23.48 | 20 | 2.21 | 0.0116 | 1.65 | 2.69 | 0.67 | 1.20 | 0.34 | 0.094 | 1.08 |
| *Synoum glandulosum* | 0.26 | 24.11 | 21 | 3.48 | 0.0062 | 3.51 | 2.66 | 0.75 | 1.96 | 0.14 | 0.213 | 1.15 |
| *Tasmannia insipida* | 0.30 | 13.55 | 35 | 2.46 | 0.0105 | 2.90 | 3.03 | 0.53 | 1.12 | 0.17 | 0.159 | 1.20 |
| *Tmesipteris ovata* | 0.22 | 0.16 | 54 | 5.76 | 0.0049 | 4.35 | 2.30 | 1.19 | 1.95 | 0.26 | 0.802 | 1.01 |
| *Tristaniopsis collina* | 0.30 | 10.58 | 30 | 2.47 | 0.0097 | 3.09 | 2.67 | 0.61 | 1.31 | 0.10 | 0.272 | 1.23 |
| Graminoid no. 1 | 0.42 | 140.50 | 62 | 2.21 | 0.0506 | 143.90 | 2.53 | 0.63 | 0.78 | 0.00 | 0.094 | 1.30 |
| Pteridophyte | 0.25 | 0.81 | 44 | 3.23 | 0.0056 | 2.25 | 2.61 | 0.78 | 2.01 | 0.48 | 0.224 | 0.92 |
| Shrub no. 1 | 0.36 | 48.87 | 20 | 2.52 | 0.0116 | 2.23 | 2.81 | 0.69 | 1.32 | 0.12 | 0.125 | 1.10 |
| Shrub no. 2 | 0.34 | 40.92 | 31 | 2.24 | 0.0099 | 2.32 | 2.51 | 0.65 | 1.02 | 0.22 | 0.100 | 1.10 |
| Shrub no. 3 | 0.32 | 24.12 | 24 | 2.98 | 0.0104 | 4.05 | 2.60 | 0.52 | 1.19 | 0.14 | 0.202 | 1.22 |

| **Site A2 Cascades** | *Thick* | *Area* | *Inclin* | *Succ* | *SLW* | *Shape* | *Chl* a/b | *Chl* | *N* | *SF* | *P* | *Lobe* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Alyxia ruscifolia* | 0.31 | 1.20 | 28 | 2.06 | 0.0142 | 2.21 | 2.82 | 0.47 | 1.08 | 0.25 | 0.081 | 1.25 |
| *Aristotelia australasica* | 0.23 | 17.85 | 19 | 2.99 | 0.0037 | 2.47 | 2.11 | 1.23 | 2.36 | 0.35 | 0.242 | 1.16 |
| *Blechnum watsii* | 0.31 | 7.40 | 17 | 2.79 | 0.0090 | 3.52 | 2.43 | 0.62 | 1.09 | 0.11 | 0.069 | 0.98 |
| *Coprosma quadrifida* | 0.07 | 0.07 | 13 | 2.67 | 0.0049 | 1.65 | 2.53 | 1.50 | 1.94 | 0.65 | 0.152 | 0.95 |
| *Cordyline stricta* | 0.29 | 24.68 | 17 | 2.49 | 0.0185 | 14.74 | 2.52 | 0.82 | 1.44 | 0.19 | 0.101 | 1.44 |
| *Cryptocarya nova-anglica* | 0.28 | 10.70 | 22 | 2.10 | 0.0116 | 2.32 | 2.66 | 0.43 | 1.32 | 0.24 | 0.101 | 1.11 |
| *Denhamia moorei* | 0.27 | 3.12 | 15 | 2.39 | 0.0081 | 3.32 | 2.88 | 0.57 | 1.42 | 0.23 | 0.101 | 1.14 |
| *Dicksonia antarctica* | 0.15 | 1.76 | 25 | 2.60 | 0.0076 | 3.87 | 2.52 | 0.94 | 1.97 | 0.15 | 0.185 | 1.07 |
| *Diplazium australe* | 0.17 | 2.98 | 28 | 5.02 | 0.0022 | 2.48 | 2.50 | 0.58 | 2.20 | 0.18 | 0.259 | 1.16 |
| *Doryphora sassafras* | 0.35 | 8.64 | 26 | 2.33 | 0.0124 | 2.05 | 2.61 | 0.57 | 1.37 | 0.19 | 0.102 | 1.15 |
| *Elaeocarpus holopetalus* | 0.37 | 4.26 | 22 | 1.96 | 0.0133 | 2.38 | 1.42 | 0.62 | 0.97 | 0.19 | 0.084 | 1.07 |
| *Hibbertia scandens* | 0.33 | 8.73 | 34 | 4.18 | 0.0042 | 3.90 | 2.74 | 1.07 | 1.65 | 0.37 | 0.112 | 1.22 |
| *Hyrocotyle pedicellosa* | 0.39 | 7.67 | 22 | 9.36 | 0.0042 | 0.49 | 2.65 | 1.32 | 2.55 | 0.37 | 0.211 | 0.52 |
| *Lastreopsis decomposita* | 0.18 | 1.52 | 25 | 2.51 | 0.0069 | 3.30 | 2.37 | 0.69 | 1.60 | 0.12 | 0.153 | 1.33 |
| *Lomandra* sp. | 0.48 | 36.79 | 51 | 2.89 | 0.0382 | 134.00 | 2.60 | 0.99 | 1.30 | 0.00 | 0.108 | 1.21 |
| *Luzuriaga* sp. | 0.34 | 7.46 | 18 | 3.31 | 0.0090 | 2.83 | 2.60 | 0.97 | 1.67 | 0.08 | 0.110 | 1.14 |
| *Nothofagus moorei* (C) | 0.30 | 6.08 | 30 | 1.60 | 0.0163 | 2.18 | 3.18 | 0.34 | 1.43 | 0.18 | 0.130 | 1.12 |
| *Orites excelsa* (A) | 0.27 | 13.89 | 33 | 2.17 | 0.0112 | 5.85 | 2.70 | 0.47 | 0.98 | 0.18 | 0.060 | 1.13 |
| *Orites excelsa* (J) | 0.18 | 3.33 | 20 | 2.05 | 0.0082 | 4.85 | 2.65 | 0.51 | 0.56 | 0.16 | 0.063 | 1.34 |
| *Pandorea pandorana* (J)† | 0.06 | 0.42 | 20 | 2.58 | 0.0017 | 1.49 | 2.52 | 1.25 | 1.84 | 0.53 | 0.208 | 1.20 |
| *Parsonsia brownii* | 0.28 | 6.40 | 35 | 2.83 | 0.0065 | 3.75 | 2.97 | 0.85 | 2.54 | 0.31 | 0.159 | 1.20 |
| *Petermannia cirrosa* | 0.32 | 9.09 | 24 | 3.30 | 0.0099 | 2.69 | 2.21 | 0.49 | 1.13 | 0.58 | 0.074 | 1.09 |
| *Phymatosorus diversifolius* | 0.27 | 21.47 | 33 | 3.67 | 0.0084 | 9.57 | 2.60 | 0.62 | 0.74 | 0.41 | 0.084 | 1.04 |
| *Polyphlebium venosum* | 0.06 | 1.59 | 53 | 3.13 | 0.0016 | 2.27 | 2.43 | 0.81 | 0.48 | 0.00 | 0.209 | 2.45 |
| *Pyrrosia rupestris* | 0.55 | 0.96 | 61 | 2.75 | 0.0490 | 2.27 | 2.55 | 0.28 | 1.02 | 0.27 | 0.168 | 1.28 |
| *Trochocarpa* sp. A | 0.27 | 1.14 | 26 | 1.84 | 0.0128 | 4.26 | 2.79 | 0.54 | 1.20 | 0.34 | 0.058 | 1.07 |
| *Uncinia* sp. 3 | 0.17 | 4.09 | 46 | 3.37 | 0.0062 | 235.40 | 3.00 | 0.95 | 1.50 | 0.31 | 0.100 | 0.93 |
| Climber no. 1 | 0.27 | 21.32 | 29 | 3.09 | 0.0064 | 2.23 | 2.27 | 0.69 | 0.91 | 0.14 | 0.149 | 1.23 |
| Climber no. 2 | 0.28 | 1.48 | 41 | 5.24 | 0.0043 | 2.08 | 2.43 | 0.84 | 1.46 | 0.53 | 0.258 | 1.01 |
| Epiphyte | 0.47 | 11.51 | 70 | 1.70 | 0.0293 | 5.24 | 2.56 | 0.35 | 1.58 | 0.78 | 0.145 | 1.15 |
| Graminoid no. 2 | 0.30 | 8.28 | 34 | 3.07 | 0.0073 | 175.70 | 2.88 | 0.80 | 1.37 | 0.64 | 0.115 | 0.93 |
| Shrub no. 4 | 0.22 | 18.79 | 28 | 1.79 | 0.0092 | 3.31 | 3.43 | 0.33 | 1.27 | 0.22 | 0.095 | 1.12 |

| **Site ZS1 Ten Mile** | *Thick* | *Area* | *Inclin* | *Succ* | *SLW* | *Shape* | *Chl* a/b | *Chl* | *N* | *SF* | *P* | *Lobe* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Alepis flavida* | 0.40 | 2.84 | 60 | 2.60 | 0.0203 | 2.54 | 2.46† | 1.66† | 1.24 | 0.42 | 0.177 | 1.09 |
| *Aristotelia serrata* (J) | 0.11 | 17.81 | 18 | 2.58 | 0.0066 | 1.63 | 3.18 | 0.44 | 1.69 | 0.49 | 0.167 | 1.08 |
| *Asplenium flaccidum* | 0.43 | 38.43 | 45 | 3.69 | 0.0223 | 5.07 | 2.95 | 0.46 | 1.53 | 0.18 | 0.339 | 4.00 |
| *Blechnum discolor* | 0.15 | 297.00 | 24 | 1.74 | 0.0147 | 7.56 | 2.85 | 0.30 | 1.13 | 0.15 | 0.137 | 1.72 |
| *Carpodetus serratus* (J) | 0.12 | 2.04 | 16 | 2.30 | 0.0061 | 1.40 | 3.27 | 0.33 | 1.24 | 0.58 | 0.099 | 1.12 |
| *Coprosma ciliata* | 0.15 | 0.21 | 18 | 3.49 | 0.0065 | 2.58 | 3.04 | 0.62 | 1.37 | 0.39 | 0.122 | 1.09 |
| *Coprosma colensoi* | 0.12 | 0.35 | 19 | 2.48 | 0.0054 | 3.42 | 3.30 | 0.39 | 1.40 | 0.47 | 0.132 | 1.12 |
| *Coprosma foetidissima* | 0.12 | 1.79 | 20 | 3.46 | 0.0059 | 2.71 | 3.04 | 0.65 | 1.63 | 0.49 | 0.142 | 1.36 |
| *Coprosma linariifolia* | 0.14 | 0.42 | 22 | 1.83 | 0.0107 | 7.44 | 3.37 | 0.25 | 1.17 | 0.45 | 0.100 | 0.85 |
| *Coprosma lucida* | 0.35 | 25.30 | 35 | 4.01 | 0.0088 | 2.52 | 3.23 | 0.53 | 1.20 | 0.39 | 0.108 | 1.18 |
| *Coprosma rhamnoides* | 0.08 | 0.22 | 11 | 2.32 | 0.0040 | 3.10 | 3.05 | 0.59 | 1.39 | 0.50 | 0.123 | 1.10 |
| *Ctenopteris heterophylla* | 0.26 | 7.07 | 27 | 2.12 | 0.0231 | 4.99 | 3.03 | 0.21 | 0.82 | 0.00 | 0.145 | 6.65 |
| *Earina autumnalis* | 0.29 | 1.82 | 35 | 3.26 | 0.0160 | 19.20 | 2.78 | 0.44 | 1.04 | 0.33 | 0.151 | 1.01 |
| *Elaeocarpus hookerianus* (J) | 0.12 | 0.54 | 17 | 1.95 | 0.0094 | 2.80 | 1.78 | 0.61 | 1.55 | 0.61 | 0.110 | 1.33 |
| *Grammitis billardieri* | 0.16 | 1.08 | 18 | 2.16 | 0.0135 | 17.04 | 2.87 | 0.26 | 1.31 | 0.00 | 0.145 | 1.12 |
| *Hymenophyllum flabellatum*† | 0.10 | 9.23 | 66 | 2.36 | 0.0043 | 2.65 | 2.17 | 0.44 | 0.69 | 0.31 | 0.114 | 1.79 |
| *Hymenophyllum multifidum* | 0.05 | 2.74 | 37 | 1.33 | 0.0118 | 1.69 | 2.93 | 0.35 | 1.01 | 0.28 | 0.105 | 3.33 |
| *Hymenophyllum rarum* | 0.05 | 1.71 | 55 | 2.03 | 0.0048 | 2.20 | 2.77 | 0.36 | 0.86 | 0.27 | 0.089 | 1.95 |
| *Hymenophyllum sanguinolentum* | 0.04 | 2.53 | 34 | 1.56 | 0.0156 | 1.89 | 2.79 | 0.36 | 1.08 | 0.34 | 0.132 | 3.76 |
| *Microlaena avennacea* | 0.15 | 21.71 | 14 | 2.44 | 0.0095 | 39.62 | 3.23 | 0.32 | 0.86 | 0.14 | 0.069 | 1.53 |
| *Myrsine australis* | 0.14 | 6.06 | 20 | 2.68 | 0.0072 | 2.27 | 3.23 | 0.33 | 0.97 | 0.22 | 0.095 | 1.27 |
| *Myrsine divaricata* | 0.14 | 0.45 | 18 | 2.29 | 0.0080 | 1.28 | 3.07 | 0.48 | 1.59 | 0.70 | 0.126 | 1.20 |
| *Neomyrtus pedunculata* | 0.15 | 0.27 | 20 | 1.92 | 0.0173 | 1.37 | 3.40 | 0.32 | 1.07 | 0.57 | 0.090 | 1.21 |
| *Nothofagus menziesii* (C) | 0.30 | 0.72 | 26 | 1.89 | 0.0200 | 1.30 | 4.10 | 0.24 | 1.57 | 0.36 | 0.238 | 1.13 |
| *Nothofagus menziesii* (S) | 0.21 | 0.92 | 25 | 1.87 | 0.0132 | 1.22 | 3.23 | 0.28 | 1.23 | 0.17 | 0.139 | 1.21 |
| *Nothofagus menziesii* (J) | 0.18 | 0.74 | 21 | 1.94 | 0.0130 | 1.21 | 3.34 | 0.36 | 1.21 | 0.17 | 0.137 | 1.24 |
| *Nothofagus solandri* (C) | 0.33 | 0.33 | 33 | 1.86 | 0.0283 | 1.83 | 3.83 | 0.21 | 1.21 | 0.41 | 0.112 | 1.20 |
| *Nothofagus solandri* (S) | 0.17 | 0.74 | 19 | 2.11 | 0.0100 | 1.39 | 3.19 | 0.37 | 1.15 | 0.18 | 0.110 | 1.05 |
| *Nothofagus solandri* (J) | 0.15 | 0.59 | 16 | 2.15 | 0.0088 | 1.43 | 3.21 | 0.37 | 1.10 | 0.25 | 0.119 | 1.08 |
| *Phymatosorus diversifolius* | 0.24 | 45.14 | 31 | 3.03 | 0.0089 | 5.52 | 3.15 | 0.43 | 1.15 | 0.68 | 0.135 | 1.51 |
| *Polystichum vestitum* | 0.20 | 1.54 | 22 | 2.15 | 0.0110 | 3.36 | 2.89 | 0.31 | 1.28 | 0.15 | 0.119 | 1.41 |
| *Prumnopitys ferruginea* (J) | 0.08 | 0.26 | 18 | 2.30 | 0.0103 | 7.66 | 2.97 | 0.37 | 1.06 | 0.27 | 0.086 | 0.86 |
| *Pseudopanax crassifolius* (A) | 0.49 | 23.58 | 60 | 2.45 | 0.0189 | 9.05 | 2.99 | 0.33 | 0.99 | 0.16 | 0.100 | 1.24 |
| *Pseudopanax crassifolius* (J) | 0.29 | 13.81 | 50 | 2.12 | 0.0438 | 43.37 | 2.69 | 0.32 | 0.61 | 0.19 | 0.070 | 1.14 |
| *Pseudopanax simplex* | 0.18 | 9.79 | 25 | 2.65 | 0.0068 | 2.56 | 3.00 | 0.50 | 1.26 | 0.37 | 0.105 | 1.10 |
| *Pyrrosia elaeagnifolia* | 0.48 | 3.27 | 42 | 4.75 | 0.0166 | 1.86 | 2.89† | 0.29† | 0.54 | 0.45 | 0.152 | 1.14 |
| *Rubus australis* | 0.16 | 1.93 | 15 | 2.47 | 0.0047 | 1.32 | 2.88 | 0.61 | 1.35 | 0.37 | 0.111 | 1.32 |
| *Uncinia uncinata* | 0.16 | 9.03 | 42 | 2.15 | 0.0065 | 102.30 | 5.00† | 0.25† | 0.71 | 0.12 | 0.066 | 0.91 |

| **Site ZS2 Walker** | *Thick* | *Area* | *Inclin* | *Succ* | *SLW* | *Shape* | *Chl* a/b | *Chl* | *N* | *SF* | *P* | *Lobe* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Aristotelia serrata* (J) | 0.14 | 25.73 | 27 | 3.36 | 0.0057 | 1.41 | 3.06 | 0.74 | 1.68 | 0.40 | 0.290 | 1.22 |
| *Asplenium flaccidum* | 0.40 | 8.73 | 65 | 3.61 | 0.0017 | 3.32 | 3.12 | 0.62 | 1.62 | 0.13 | 0.219 | 6.25 |
| *Blechnum chambersii* | 0.16 | 71.87 | 30 | 2.99 | 0.0090 | 6.01 | 2.82 | 0.82 | 1.96 | 0.00 | 0.246 | 1.88 |
| *Blechnum discolor* | 0.18 | 57.73 | 26 | 1.66 | 0.0106 | 3.15 | 4.46 | 0.29 | 1.12 | 0.14 | 0.210 | 1.44 |
| *Blechnum fluviatile* | 0.18 | 0.54 | 16 | 3.81 | 0.0065 | 1.38 | 4.13 | 0.72 | 1.61 | 0.32 | 0.501 | 1.12 |
| *Blechnum procerum* | 0.24 | 6.06 | 29 | 2.24 | 0.0106 | 3.09 | 4.43 | 0.37 | 0.92 | 0.10 | 0.191 | 1.05 |
| *Carpodetus serratus* (J) | 0.14 | 4.63 | 14 | 2.53 | 0.0058 | 1.32 | 4.57 | 0.49 | 1.57 | 0.32 | 0.164 | 0.90 |
| *Coprosma ciliata* | 0.18 | 0.18 | 9 | 2.65 | 0.0081 | 2.14 | 4.48 | 0.46 | 1.39 | 0.45 | 0.214 | 0.96 |
| *Coprosma colensoi* | 0.15 | 0.37 | 23 | 2.77 | 0.0069 | 3.93 | 3.46 | 0.62 | 1.65 | 0.53 | 0.156 | 0.89 |
| *Coprosma foetidissima* | 0.21 | 1.44 | 26 | 3.20 | 0.0022 | 2.20 | 3.31 | 0.46 | 1.49 | 0.77 | 0.239 | 1.18 |
| *Coprosma linariifolius* | 0.18 | 0.36 | 16 | 2.38 | 0.0087 | 7.35 | 3.44 | 0.38 | 1.21 | 0.39 | 0.178 | 0.85 |
| *Coprosma lucida* | 0.35 | 26.91 | 20 | 4.04 | 0.0077 | 2.35 | 4.71 | 0.50 | 1.42 | 0.27 | 0.149 | 1.19 |
| *Coprosma* aff. *propinqua* | 0.18 | 0.17 | 24 | 1.91 | 0.0099 | 2.86 | 4.76 | 0.22 | 1.21 | 0.53 | 0.157 | 0.97 |
| *Coprosma rhamnoides* | 0.11 | 0.22 | 12 | 2.64 | 0.0059 | 3.11 | 4.66 | 0.56 | 1.61 | 0.66 | 0.165 | 1.02 |
| *Coprosma rigida* | 0.15 | 0.21 | 24 | 2.58 | 0.0090 | 1.96 | 4.42 | 0.45 | 1.79 | 0.81 | 0.200 | 0.91 |
| *Coprosma rotundifolia* | 0.14 | 2.20 | 14 | 2.98 | 0.0039 | 1.16 | 5.01 | 0.67 | 2.26 | 0.64 | 0.260 | 0.97 |
| *Grammitis billardieri* | 0.21 | 1.48 | 29 | 2.59 | 0.0131 | 14.72 | 4.20 | 0.32 | 1.17 | 0.00 | 0.170 | 1.25 |
| *Griselinia littoralis* (J) | 0.41 | 18.61 | 18 | 4.41 | 0.0098 | 1.58 | 4.04 | 0.45 | 0.88 | 0.31 | 0.134 | 1.04 |
| *Hymenophyllum multifidum* | 0.05† | 2.21 | 22 | 1.43 | 0.0211 | 2.32 | 4.12 | 0.29 | 1.08 | 0.24 | 0.142 | 3.92 |
| *Hymenophyllum sanguinolentum* | 0.04† | 2.93 | 32 | 1.45 | 0.0166 | 1.94 | 4.07 | 0.44 | 1.26 | 0.27 | 0.154 | 2.46 |
| *Microlaena avennacea* | 0.16 | 26.01 | 30 | 3.05 | 0.0114 | 46.15 | 4.66 | 0.70 | 1.30 | 0.33 | 0.283 | 1.57 |
| *Myrsine divaricata* | 0.15 | 0.44 | 24 | 2.71 | 0.0084 | 1.15 | 4.61 | 0.48 | 1.64 | 0.78 | 0.157 | 1.21 |
| *Neomyrtus pedunculata* | 0.16 | 0.25 | 15 | 1.58 | 0.0097 | 1.29 | 4.33 | 0.27 | 1.34 | 0.73 | 0.194 | 0.96 |
| *Nothofagus fusca* (C)† | 0.21 | 2.59 | 34 | 2.08 | 0.0099 | 1.78 | 4.24 | 0.39 | 1.96 | 0.25 | 0.250 | 1.19 |

| **ZS2 Walker** (continued) | *Thick* | *Area* | *Inclin* | *Succ* | *SLW* | *Shape* | *Chl* a/b | *Chl* | *N* | *SF* | *P* | *Lobe* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Nothofagus fusca* (S) | 0.16 | 2.34 | 13 | 2.05 | 0.0085 | 1.26 | 3.47 | 0.43 | 1.66 | 0.35 | 0.252 | 1.16 |
| *Nothofagus fusca (J)* | 0.14 | 2.12 | 13 | 2.07 | 0.0061 | 1.30 | 3.34 | 0.45 | 1.48 | 0.35 | 0.221 | 1.09 |
| *Nothofagus fusca* × *solandri* (J) | 0.14 | 1.09 | 22 | 2.09 | 0.0068 | 1.18 | 3.21 | 0.41 | 1.33 | 0.30 | 0.167 | 1.09 |
| *Nothofagus menziesii* (C) | 0.30 | 0.48 | 29 | 1.83 | 0.0201 | 1.18 | 5.37 | 0.24 | 1.44 | 0.33 | 0.250 | 1.37 |
| *Nothofagus menziesii* (S) | 0.23 | 0.90 | 20 | 1.71 | 0.0135 | 1.19 | 3.44 | 0.34 | 1.23 | 0.22 | 0.208 | 1.20 |
| *Nothofagus menziesii* (J) | 0.20 | 0.69 | 16 | 1.92 | 0.0162 | 1.18 | 3.57 | 0.36 | 1.40 | 0.25 | 0.195 | 1.27 |
| *Polystichum vestitum* | 0.20 | 4.07 | 16 | 2.84 | 0.0067 | 3.95 | 4.09 | 0.54 | 1.96 | 0.17 | 0.401 | 1.58 |
| *Pseudopanax crassifolius* (J) | 0.55 | 28.53 | 25 | 2.17 | 0.0365 | 42.59 | 3.69 | 0.22 | 0.53 | 0.17 | 0.121 | 1.08 |
| *Pseudopanax simplex* (A) | 0.20 | 3.87 | 12 | 3.25 | 0.0049 | 1.99 | 4.28 | 0.53 | 1.33 | 0.53 | 0.116 | 1.13 |
| *Pseudopanax simplex* (J) | 0.22 | 1.69 | 23 | 2.29 | 0.0058 | 3.04 | 4.38 | 0.45 | 1.27 | 0.64 | 0.138 | 2.98 |
| *Pseudowintera colorata* | 0.28 | 12.38 | 27 | 2.99 | 0.0081 | 2.33 | 3.11 | 0.45 | 1.61 | 0.28 | 0.185 | 1.07 |
| *Rubus cissoides* | 0.19 | 19.33 | 26 | 2.25 | 0.0057 | 1.87 | 2.80 | 0.36 | 1.44 | 0.39 | 0.194 | 1.14 |
| *Rubus schmidelioides* | 0.13 | 3.45 | 41 | 2.04 | 0.0053 | 5.18 | 2.96 | 0.54 | 1.97 | 0.73 | 0.230 | 1.28 |
| *Schefflera digitata* (J) | 0.22 | 28.95 | 33 | 4.12 | 0.0047 | 2.37 | 3.81 | 0.80 | 2.29 | 0.39 | 0.301 | 1.17 |
| *Uncinia silvestris*† | 0.13 | 2.72 | 22 | 3.10 | 0.0041 | 214.80 | 3.41 | 0.55 | 1.09 | 0.30 | 0.238 | 0.90 |
| *Uncinia uncinata* | 0.19 | 19.77 | 30 | 2.92 | 0.0077 | 106.40 | 5.00 | 0.34 | 0.90 | 0.20 | 0.258 | 1.00 |
| *Uncinia gracilenta* | 0.16 | 4.39 | 17 | 2.66 | 0.0058 | 153.40 | 4.16 | 0.34 | 1.00 | 0.23 | 0.176 | 0.79 |

| **Site ZS3 Deer** | *Thick* | *Area* | *Inclin* | *Succ* | *SLW* | *Shape* | *Chl* a/b | *Chl* | *N* | *SF* | *P* | *Lobe* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Asplenium flaccidum* | 0.38 | 9.19 | 70 | 3.62 | 0.0166 | 3.94 | 2.97 | 0.53 | 1.78 | 0.26 | 0.331 | 5.02 |
| *Blechnum penna-marina* | 0.15 | 6.68 | 19 | 2.48 | 0.0094 | 8.91 | 3.29 | 0.43 | 1.52 | 0.16 | 0.217 | 2.03 |
| *Carpodetus serratus* (J) | 0.14 | 2.34 | 19 | 2.19 | 0.0047 | 1.45 | 4.27 | 0.66 | 1.93 | 0.42 | 0.264 | 1.16 |
| *Coprosma ciliata* | 0.18 | 0.13 | 9 † | 2.49 | 0.0102 | 2.26 | 3.56 | 0.44 | 1.57 | 0.45 | 0.163 | 0.99 |
| *Coprosma colensoi* | 0.20 | 0.29 | 23 † | 2.33 | 0.0090 | 3.18 | 3.48 | 0.41 | 1.39 | 0.49 | 0.138 | 1.35 |
| *Coprosma* aff. *colensoi* | 0.16 | 0.34 | 24 | 2.62 | 0.0065 | 1.87 | 3.78 | 0.42 | 1.79 | 0.58 | 0.238 | 0.97 |
| *Coprosma cuneata* | 0.19 | 0.15 | 15 | 2.51 | 0.0070 | 4.05 | 5.04 | 0.44 | 1.11 | 0.35 | 0.189 | 0.90 |
| *Coprosma foetidissima* | 0.27 | 2.15 | 14 | 3.78 | 0.0052 | 2.46 | 4.86 | 0.66 | 1.93 | 0.38 | 0.250 | 1.04 |
| *Coprosma rhamnoides* | 0.13 | 0.27 | 27 | 2.85 | 0.0038 | 2.11 | 4.81 | 0.63 | 1.78 | 0.57 | 0.212 | 0.96 |
| *Grammitis billardieri* | 0.19 | 1.04 | 32 | 2.60 | 0.0078 | 15.89 | 5.21 | 0.13 | 1.36 | 0.00 | 0.286 | 1.17 |
| *Griselinia littoralis* (J) | 0.50 | 10.00 | 18 | 3.45 | 0.0117 | 1.45 | 3.28 | 0.26 | 0.64 | 0.35 | 0.142 | 0.99 |
| *Hymenophyllum multifidum* | 0.05† | 7.10 | 18 | 1.59 | 0.0082 | 1.87 | 4.27 | 0.35 | 0.98 | 0.25 | 0.118 | 2.11 |
| *Hymenophyllum sanguinolentum* | 0.04† | 6.47 | 33 | 1.64 | 0.0127 | 2.09 | 4.52 | 0.34 | 1.12 | 0.27 | 0.149 | 3.19 |
| *Myrsine divaricata* | 0.18 | 0.53 | 24 | 2.46 | 0.0085 | 1.34 | 3.16 | 0.41 | 1.60 | 0.63 | 0.186 | 1.16 |
| *Nertera dichondrifolia* | 0.14 | 0.34 | 12 | 2.59 | 0.0063 | 1.07 | 4.37 | 0.47 | 1.51 | 0.52 | 0.314 | 1.06 |
| *Nothofagus fusca* (C) | 0.21 | 2.90 | 30 | 2.12 | 0.0113 | 1.55 | 3.69 | 0.39 | 1.60 | 0.22 | 0.356 | 1.15 |
| *Nothofagus fusca* (S) | 0.18 | 2.62 | 12 | 2.05 | 0.0080 | 1.31 | 3.43 | 0.50 | 1.51 | 0.22 | 0.232 | 1.10 |
| *Nothofagus fusca* (J) | 0.16 | 2.16 | 22 | 2.11 | 0.0068 | 1.25 | 3.21 | 0.48 | 1.37 | 0.25 | 0.213 | 1.16 |
| *Nothofagus menziesii* (C) | 0.30 | 0.48 | 29 | 1.83 | 0.0201 | 1.18 | 5.37 | 0.24 | 1.44 | 0.33 | 0.250 | 1.37 |
| *Nothofagus menziesii* (S) | 0.22 | 0.57 | 17 | 1.84 | 0.0177 | 1.07 | 3.47 | 0.36 | 1.43 | 0.19 | 0.206 | 1.33 |
| *Nothofagus menziesii* (J) | 0.21 | 0.74 | 28 | 1.83 | 0.0134 | 1.23 | 3.45 | 0.40 | 1.32 | 0.21 | 0.219 | 1.31 |
| *Phyllocladus aspleniifolius* var. *alpinus* | 0.46 | 1.66 | 46 | 1.96 | 0.0166 | 2.57 | 4.09 | 0.28 | 0.87 | 0.21 | 0.159 | 1.26 |
| *Podocarpus cunninghamii* | 0.31 | 0.59 | 34 | 1.88 | 0.0225 | 7.14 | 4.89 | 0.14 | 0.57 | 0.20 | 0.154 | 1.35 |
| *Polystichum vestitum* | 0.24 | 3.57 | 12 | 1.77 | 0.0138 | 4.18 | 3.08 | 0.38 | 1.53 | 0.31 | 0.361 | 1.55 |
| *Pseudopanax anomalus* | 0.18 | 0.61 | 32 | 2.31 | 0.0074 | 1.11 | 3.24 | 0.46 | 1.60 | 0.58 | 0.229 | 1.07 |
| *Pseudopanax crassifolius* (J) | 0.59 | 28.90 | 41 | 2.19 | 0.0428 | 53.58 | 2.72 | 0.26 | 0.62 | 0.19 | 0.092 | 1.12 |
| *Pseudowintera colorata* | 0.37 | 14.80 | 16 | 2.54 | 0.0149 | 2.03 | 3.11 | 0.27 | 1.10 | 0.32 | 0.128 | 1.08 |
| *Rubus schmidelioides* | 0.15 | 2.09 | 36 | 2.02 | 0.0097 | 5.76 | 2.69 | 0.41 | 1.59 | 0.28 | 0.213 | 1.35 |
| *Uncinia uncinata* | 0.21 | 12.30 | 24 | 2.92† | 0.0123† | 95.23 | 3.84† | 0.36† | 0.83† | 0.20† | 0.209† | 2.21 |
| *Uncinia silvestris* | 0.13 | 2.72 | 22 | 3.10 | 0.0041 | 214.80 | 3.41 | 0.55 | 1.09 | 0.30 | 0.238 | 0.90 |

| **Site ZC1 Craigs** | *Thick* | *Area* | *Inclin* | *Succ* | *SLW* | *Shape* | *Chl* a/b | *Chl* | *N* | *SF* | *P* | *Lobe* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Acianthus fornicatus* | 0.24 | 3.76 | 17 | 16.70 | 0.0013 | 1.34 | 3.91 | 1.08 | 4.67 | 0.59 | 0.444 | 1.34 |
| *Aristotelia serrata* | 0.13 | 31.85 | 16 | 3.45 | 0.0037 | 1.62 | 2.41 | 0.80 | 1.97 | 0.40 | 0.310 | 1.19 |
| *Asplenium bulbiferum* | 0.19 | 3.61 | 20 | 4.43 | 0.0035 | 2.99 | 4.21 | 0.62 | 2.13 | 0.20 | 0.413 | 2.42 |
| *Asplenium flaccidum* | 0.45 | 15.70 | 45 | 3.81 | 0.0315 | 5.74 | 4.00 | 0.56 | 1.31 | 0.21 | 0.333 | 7.97 |
| *Astelia nervosa* | 0.52 | 230.51 | 36 | 4.36 | 0.0293 | 34.83 | 3.15 | 0.40 | 0.93 | 0.00 | 0.177 | 1.15 |
| *Blechnum* c.f. *capense* | 0.18 | 21.78 | 25 | 2.57 | 0.0071 | 7.86 | 2.94 | 0.67 | 1.14 | 0.23 | 0.321 | 1.03 |
| *Blechnum colensoi* | 0.38 | 196.03 | 36 | 3.49 | 0.0098 | 2.73 | 3.97 | 0.49 | 1.12 | 0.13 | 0.362 | 1.73 |
| *Blechnum discolor* | 0.23 | 263.10 | 33 | 2.80 | 0.0138 | 6.02 | 3.95 | 0.47 | 0.92 | 0.18 | 0.164 | 1.79 |
| *Blechnum fluviatile* | 0.16 | 0.69 | 15 | 4.27 | 0.0062 | 1.26 | 4.21 | 0.47 | 1.87 | 0.32 | 0.319 | 1.15 |
| *Blechnum minus* | 0.27 | 8.88 | 19 | 3.27 | 0.0086 | 3.15 | 3.69 | 0.50 | 1.06 | 0.12 | 0.124 | 1.01 |

| **ZC1 Craigs** (continued) | *Thick* | *Area* | *Inclin* | *Succ* | *SLW* | *Shape* | *Chl* a/b | *Chl* | *N* | *SF* | *P* | *Lobe* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Carpodetus serratus* (A) | 0.13 | 3.52 | 16 | 2.91 | 0.0048 | 1.40 | 3.07 | 0.83 | 1.76 | 0.54 | 0.363 | 1.05 |
| *Carpodetus serratus* (J)† | 0.13 | 3.52 | 16 | 2.91 | 0.0048 | 1.40 | 3.07 | 0.83 | 1.76 | 0.54 | 0.363 | 1.05 |
| *Coprosma ciliata* | 0.14 | 0.17 | 17 | 2.71 | 0.0062 | 2.32 | 4.30 | 0.49 | 1.92 | 0.47 | 0.270 | 0.86 |
| *Coprosma foetidissima* | 0.21 | 1.45 | 25 | 4.59 | 0.0052 | 1.98 | 4.17 | 0.61 | 1.76 | 0.46 | 0.240 | 1.23 |
| *Coprosma rhamnoides* | 0.10 | 0.20 | 16 | 2.42 | 0.0046 | 2.41 | 4.28 | 0.53 | 1.62 | 0.57 | 0.226 | 0.98 |
| *Coprosma rotundifolia* | 0.11 | 1.04 | 16 | 3.36 | 0.0034 | 1.39 | 5.01† | 0.76† | 2.36 | 0.65 | 0.461 | 0.93 |
| *Corybas trilobus* | 0.31 | 2.67 | 17 | 20.10 | 0.0014 | 0.70 | 4.31 | 1.19 | 2.52 | 0.45 | 0.626 | 0.96 |
| *Cyathea colensoi* | 0.14 | 1.99 | 14 | 3.27 | 0.0070 | 3.26 | 3.99 | 0.69 | 2.24 | 0.17 | 0.221 | 1.55 |
| *Dicksonia fibrosa* | 0.17 | 1.00 | 17 | 2.52 | 0.0093 | 3.71 | 4.16 | 0.57 | 1.80 | 0.16 | 0.227 | 1.40 |
| *Fuchsia excorticata* | 0.21 | 18.31 | 22 | 5.63 | 0.0038 | 2.44 | 4.33 | 0.68 | 2.03 | 0.19 | 0.378 | 1.18 |
| *Grammitis billardieri* | 0.24 | 2.41 | 36 | 2.73 | 0.0090 | 16.39 | 3.63 | 0.38 | 0.94 | 0.00 | 0.141 | 1.49 |
| *Griselinia littoralis* (A)† | 0.39 | 28.09 | 26 | 4.12 | 0.0068 | 1.63 | 3.34 | 0.53 | 1.17 | 0.31 | 0.162 | 1.01 |
| *Griselinia littoralis* (J) | 0.39 | 28.09 | 26 | 4.12 | 0.0068 | 1.63 | 3.34 | 0.53 | 1.17 | 0.31 | 0.162 | 1.01 |
| *Histiopteris incisa* | 0.17 | 5.61 | 20 | 6.66 | 0.0024 | 2.51 | 3.04 | 1.46 | 2.94 | 0.18 | 0.390 | 1.67 |
| *Hymenophyllum flabellatum* | 0.10 | 9.23 | 66 | 2.36 | 0.0043 | 2.65 | 2.17 | 0.44 | 0.69 | 0.31 | 0.114 | 1.79 |
| *Hymenophyllum multifidum* | 0.06 | 1.71 | 33 | 2.11 | 0.0165 | 2.42 | 3.66 | 0.53 | 0.95 | 0.19† | 0.105 | 7.97 |
| *Hymenophyllum sanguinolentum* | 0.08 | 7.10 | 40 | 2.19 | 0.0121 | 1.66 | 3.86 | 0.60 | 1.10 | 0.18† | 0.151 | 5.16 |
| *Leptopteris superba* | 0.14 | 1.78 | 24 | 2.61 | 0.0227 | 4.74 | 3.64 | 0.66 | 1.99 | 0.33 | 0.274 | 4.23 |
| *Microlaena avennacea* | 0.15 | 10.86 | 37 | 2.95 | 0.0218 | 54.56 | 4.16 | 0.50 | 0.94 | 0.29 | 0.302 | 2.90 |
| *Muehlenbeckia australis* | 0.11 | 3.62 | 16 | 6.34 | 0.0011 | 1.22 | 4.55 | 1.44 | 2.77 | 0.69 | 0.452 | 0.98 |
| *Myrsine divaricata* | 0.15 | 0.31 | 12 | 2.76 | 0.0106 | 1.14 | 3.05 | 0.74 | 1.53 | 0.76 | 0.151 | 1.24 |
| *Neomyrtus pedunculata* | 0.13 | 0.20 | 21 | 1.79 | 0.0077 | 1.43 | 3.53 | 0.26 | 1.11 | 0.75 | 0.146 | 1.28 |
| *Nertera dichondrifolia* | 0.16 | 0.34 | 17 | 5.05 | 0.0036 | 1.12 | 4.26 | 0.78 | 1.92 | 0.54 | 0.405 | 0.92 |
| *Nothofagus fusca* (C) | 0.23 | 4.92 | 32 † | 2.12 | 0.0100 | 1.42 | 2.98 | 0.32 | 1.77 | 0.25 | 0.325 | 1.23 |
| *Nothofagus fusca* (S) | 0.17 | 3.36 | 21 | 2.22 | 0.0068 | 1.43 | 2.80 | 0.59 | 1.48 | 0.44 | 0.211 | 1.20 |
| *Nothofagus fusca* (J) | 0.15 | 2.16 | 15 † | 2.47 | 0.0057 | 1.22 | 3.26 | 0.39 | 1.29 | 0.32 | 0.164 | 1.20 |
| *Nothofagus menziesii* (C) | 0.29 | 0.30 | 28 | 1.68 | 0.0263 | 1.20 | 5.22 | 0.23 | 1.37 | 0.32 | 0.267 | 1.42 |
| *Nothofagus menziesii* (S) | 0.22 | 0.87 | 25 | 1.84 | 0.0092 | 1.08 | 3.40 | 0.41 | 1.28 | 0.33 | 0.178 | 0.95 |
| *Nothofagus menziesii* (J) | 0.18 | 0.84 | 21 | 2.40 | 0.0066 | 1.28 | 4.18 | 0.47 | 1.15 | 0.32 | 0.168 | 1.24 |
| *Parsonsia capsularis* | 0.25 | 2.26 | 30 | 3.69 | 0.0099 | 13.85 | 4.15 | 0.72 | 1.93 | 0.53 | 0.323 | 1.18 |
| *Pneumatopteris pennigera* | 0.17 | 9.20 | 16 | 4.28 | 0.0036 | 5.59 | 2.43 | 0.87 | 2.09 | 0.34 | 0.332 | 1.29 |
| *Polystichum vestitum* | 0.22 | 4.32 | 17 | 2.71 | 0.0086 | 4.17 | 3.88 | 0.56 | 1.79 | 0.20 | 0.295 | 1.82 |
| *Prumnopitys ferruginea* (J) | 0.19 | 0.23 | 29 | 2.53 | 0.0167 | 7.12 | 2.83 | 0.44 | 0.83 | 0.30 | 0.132 | 0.90 |
| *Pseudopanax anomalus* | 0.14 | 0.48 | 17 | 2.27 | 0.0059 | 1.18 | 3.04 | 0.57 | 1.56 | 0.78 | 0.210 | 1.09 |
| *Pseudopanax crassifolius* (A) | 0.56 | 24.40 | 40 | 2.67 | 0.0190 | 6.98 | 4.42 | 0.39 | 1.20 | 0.13 | 0.126 | 1.11 |
| *Pseudopanax crassifolius* (J) | 0.54 | 42.33 | 18 | 2.42 | 0.0345 | 52.36 | 4.13 | 0.13 | 0.70 | 0.22 | 0.127 | 1.21 |
| *Pseudowintera colorata* | 0.30 | 8.57 | 14 | 2.82 | 0.0113 | 1.91 | 3.80 | 0.31 | 1.45 | 0.31 | 0.199 | 1.10 |
| *Pterostylis graminea* | 0.17 | 6.06 | 19 | 13.80 | 0.0020 | 13.07 | 3.26 | 1.22 | 3.23 | 0.46 | 0.671 | 1.41 |
| *Rubus cissoides* | 0.20 | 17.03 | 18 | 2.24 | 0.0064 | 2.21 | 2.67 | 0.44 | 1.55 | 0.41 | 0.145 | 1.21 |
| *Rubus schmidelioides* | 0.19 | 2.79 | 44 | 2.19 | 0.0098 | 3.83 | 2.61 | 0.46 | 1.63 | 0.39 | 0.188 | 1.29 |
| *Schefflera digitata* (A) | 0.18 | 13.33 | 18 | 5.88 | 0.0044 | 2.98 | 2.97 | 1.73 | 1.75 | 0.23 | 0.213 | 1.09 |
| *Schefflera digitata* (J)† | 0.18 | 13.33 | 18 | 5.88 | 0.0044 | 2.98 | 2.97 | 1.73 | 1.75 | 0.23 | 0.213 | 1.09 |
| *Uncinia distans* | 0.21 | 2.95 | 33 | 3.33 | 0.0110 | 138.70 | 4.39 | 0.42 | 1.00 | 0.21 | 0.289 | 1.57 |
| *Uncinia gracilenta* | 0.17 | 1.92 | 27 | 2.87 | 0.0148 | 188.80 | 3.40 | 0.55 | 1.06 | 0.41 | 0.252 | 1.19 |
| *Uncinia uncinata* | 0.24 | 14.60 | 22 | 2.71 | 0.0106 | 92.65 | 4.54 | 0.34 | 0.75 | 0.16 | 0.266 | 1.09 |

| **Site ZC2 Station** | *Thick* | *Area* | *Inclin* | *Succ* | *SLW* | *Shape* | *Chl* a/b | *Chl* | *N* | *SF* | *P* | *Lobe* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Chiloglottis cornuta* | 0.26 | 2.80 | 21 | 12.20 | 0.0038 | 2.79 | 4.38 | 0.53 | 3.60 | 0.30 | 0.559 | 1.14 |
| *Coprosma ciliata* | 0.18 | 0.20 | 16 | 2.44 | 0.0056 | 2.13 | 4.47 | 0.41 | 1.67 | 0.68 | 0.253 | 0.88 |
| *Coprosma cuneata* | 0.12 | 0.06 | 20 | 2.55 | 0.0069 | 4.24 | 4.51 | 0.38 | 1.22 | 0.47 | 0.203 | 0.81 |
| *Coprosma rhamnoides* | 0.11 | 0.15 | 19 | 2.65 | 0.0058 | 2.05 | 4.43 | 0.46 | 1.72 | 0.59 | 0.241 | 1.03 |
| *Grammitis billardieri* | 0.24 | 1.12 | 42 | 2.33 | 0.0099 | 14.16 | 3.70 | 0.30 | 1.16 | 0.00 | 0.157 | 1.24 |
| *Griselinia littoralis* (J) | 0.41 | 5.93 | 21 | 3.60 | 0.0130 | 1.39 | 4.40 | 0.42 | 0.69 | 0.27 | 0.159 | 0.99 |
| *Histiopteris incisa* | 0.13 | 1.49 | 17 | 6.78 | 0.0016 | 2.17 | 3.87 | 1.10 | 2.93 | 0.17 | 0.497 | 1.31 |
| *Hymenophyllum pulcherrimum* | 0.13 | 7.06 | 28 | 2.19 | 0.0089 | 1.88 | 3.75 | 0.47 | 1.21 | 0.27 | 0.188 | 2.39 |
| *Hymenophyllum sanguinolentum* | 0.04 | 3.91 | 50 | 2.20 | 0.0100 | 2.01 | 2.69 | 0.58 | 2.49 | 0.33 | 0.422 | 4.10 |
| *Muehlenbeckia australis* | 0.11† | 3.62† | 16 † | 6.34† | 0.0011† | 1.22† | 5.91 | 1.39 | 2.77† | 0.69† | 0.452† | 0.98† |
| *Myrsine divaricata* | 0.19 | 0.36 | 16 | 3.17 | 0.0075 | 1.11 | 3.08 | 0.62 | 1.62 | 0.72 | 0.259 | 1.20 |
| *Neomyrtus pedunculata* | 0.21 | 0.22 | 15 | 2.28 | 0.0115 | 1.33 | 3.53 | 0.36 | 1.06 | 0.64 | 0.191 | 1.19 |
| *Nertera dichondrifolia* | 0.17 | 0.21 | 13 | 4.38 | 0.0050 | 0.93 | 4.39 | 1.22 | 2.36 | 0.55 | 0.390 | 1.01 |
| *Nothofagus fusca* (C) | 0.23 | 4.07 | 32 | 1.95 | 0.0128 | 1.42 | 2.91 | 0.36 | 1.42 | 0.22 | 0.313 | 1.20 |
| *Nothofagus fusca* (S) | 0.17 | 3.96 | 15 | 1.83 | 0.0070 | 1.33 | 3.21 | 0.40 | 1.41 | 0.27 | 0.240 | 1.25 |
| *Nothofagus fusca* (J) | 0.16 | 2.22 | 23 | 2.58 | 0.0068 | 1.27 | 3.58 | 0.54 | 1.34 | 0.39 | 0.195 | 1.25 |
| *Nothofagus fusca* × *solandri* (J) | 0.15† | 0.59† | 16 † | 2.15† | 0.0088† | 1.43† | 3.30 | 0.36 | 1.10† | 0.25† | 0.119† | 1.08† |

| **ZC2 Station** (continued) | *Thick* | *Area* | *Inclin* | *Succ* | *SLW* | *Shape* | *Chl* a/b | *Chl* | *N* | *SF* | *P* | *Lobe* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Nothofagus menziesii* (C) | 0.24 | 0.68 | 28 | 1.77 | 0.0147 | 1.33 | 4.57 | 0.25 | 0.96 | 0.26 | 0.221 | 1.22 |
| *Nothofagus menziesii* (S) | 0.22 | 0.65 | 26 | 1.88 | 0.0141 | 1.21 | 3.40† | 0.42† | 1.09 | 0.31 | 0.205 | 1.25 |
| *Nothofagus menziesii* (J) | 0.20 | 0.70 | 20 | 1.98 | 0.0096 | 1.20 | 4.43 | 0.37 | 1.13 | 0.40 | 0.237 | 1.19 |
| *Polystichum vestitum* | 0.22 | 1.03 | 16 | 2.58 | 0.0098 | 3.16 | 3.51 | 0.43 | 1.39 | 0.20 | 0.369 | 2.04 |
| *Pseudopanax anomalus* | 0.17 | 0.34 | 24 | 2.86 | 0.0064 | 1.68 | 4.18 | 0.56 | 1.56 | 0.80 | 0.243 | 1.19 |
| *Pseudopanax crassifolius* (A) | 0.56 | 14.40 | 26 | 2.62 | 0.0190 | 7.14 | 4.42† | 0.38† | 0.86 | 0.12 | 0.089 | 1.18 |
| *Pseudopanax crassifolius* (J) | 0.50 | 24.70 | 24 | 2.18 | 0.0410 | 54.40 | 2.76 | 0.33 | 0.60 | 0.16 | 0.084 | 0.97 |
| *Pseudowintera colorata* | 0.31 | 12.40 | 18 | 2.75 | 0.0077 | 1.87 | 3.75 | 0.23 | 1.40 | 0.24 | 0.160 | 1.15 |
| *Uncinia silvestris* | 0.15 | 1.71 | 35 | 2.54 | 0.0082 | 137.60 | 4.48 | 0.48 | 1.19 | 0.29 | 0.245 | 0.83 |
| *Uncinia uncinata* | 0.24 | 12.00 | 37 | 2.65 | 0.0082 | 99.09 | 4.57 | 0.39 | 1.04 | 0.21 | 0.401 | 0.87 |

| **Site ZN1 Ohakune** | *Thick* | *Area* | *Inclin* | *Succ* | *SLW* | *Shape* | *Chl* a/b | *Chl* | *N* | *SF* | *P* | *Lobe* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Acaena anserinifolia* | 0.08 | 0.23 | 15 | 3.18 | 0.0031 | 2.34 | 2.34 | 0.92 | 2.64 | 0.55 | 0.164 | 1.19 |
| *Aristotelia serrata* | 0.24 | 33.00 | 44 | 2.84 | 0.0057 | 1.62 | 2.44 | 0.52 | 1.72 | 0.19 | 0.156 | 1.08 |
| *Asplenium flaccidum* | 0.65 | 35.60 | 81 | 3.27 | 0.0254 | 3.70 | 2.81 | 0.33 | 1.01 | 0.14 | 0.139 | 6.70 |
| *Astelia nervosa* | 0.45 | 512.00 | 29 | 3.95 | 0.0400 | 48.21 | 3.16 | 0.28 | 0.76 | 0.00 | 0.081 | 1.07 |
| *Blechnum discolor* | 0.22 | 302.00 | 35 | 2.61 | 0.0160 | 6.43 | 2.80 | 0.45 | 0.84 | 0.00 | 0.065 | 1.66 |
| *Blechnum fluviatile* | 0.12 | 0.51 | 9 | 3.61 | 0.0039 | 1.35 | 2.24 | 0.90 | 4.06 | 0.30 | 0.131 | 0.95 |
| *Blechnum penna-marina* | 0.17 | 4.55 | 32 | 4.82 | 0.0067 | 8.23 | 2.88 | 0.55 | 3.58 | 0.18 | 0.278 | 1.81 |
| *Blechnum procerum* | 0.27 | 7.68 | 16 | 3.10 | 0.0091 | 2.34 | 2.55 | 0.53 | 1.39 | 0.07 | 0.097 | 0.99 |
| *Cardamine debilis* | 0.14 | 0.18 | 9 | 7.72 | 0.0025 | 0.78 | 2.65 | 1.26 | 6.32 | 0.61 | 0.381 | 0.86 |
| *Carpodetus serratus* | 0.20 | 2.41 | 24 | 2.81 | 0.0066 | 1.38 | 2.71 | 0.54 | 2.79 | 0.31 | 0.180 | 0.87 |
| *Chiloglottis cornuta* | 0.29 | 4.26 | 11 | 12.50 | 0.0026 | 2.28 | 2.89 | 1.05 | 4.97 | 0.13 | 0.279 | 1.06 |
| *Clematis paniculata* (A) | 0.41 | 17.50 | 32 | 3.38 | 0.0127 | 2.25 | 2.88 | 0.41 | 2.03 | 0.29 | 0.094 | 0.99 |
| *Clematis paniculata* (J) | 0.24 | 2.78 | 64 | 4.45 | 0.0058 | 2.99 | 2.75 | 0.79 | 2.69 | 0.73 | 0.268 | 1.32 |
| *Coprosma ciliata* | 0.16 | 0.13 | 14 | 2.90 | 0.0076 | 2.15 | 2.71 | 0.46 | 2.50 | 0.59 | 0.181 | 1.03 |
| *Coprosma colensoi* | 0.16 | 0.25 | 18 | 3.01 | 0.0044 | 6.55 | 2.75 | 0.62 | 3.09 | 0.50 | 0.160 | 0.98 |
| *Coprosma foetidissima* | 0.23 | 1.56 | 9 | 4.94 | 0.0042 | 1.72 | 3.05 | 0.70 | 2.36 | 0.34 | 0.196 | 0.99 |
| *Coprosma rhamnoides* | 0.15 | 0.19 | 28 | 2.21 | 0.0051 | 1.43 | 2.88 | 0.43 | 1.79 | 0.81 | 0.103 | 0.94 |
| *Coprosma tenuifolia* | 0.20 | 8.18 | 20 | 3.10 | 0.0033 | 2.51 | 3.08 | 0.44 | 2.07 | 0.21 | 0.122 | 1.00 |
| *Cordyline indivisa* | 0.50 | 483.00 | 38 | 2.32 | 0.0305 | 8.53 | 3.28 | 0.15 | 1.20 | 0.00 | 0.111 | 1.16 |
| *Corybas trilobus* | 0.43 | 3.50 | 11 | 24.90 | 0.0017 | 0.40 | 2.70 | 1.90 | 9.28 | 0.22 | 0.334 | 0.53 |
| *Ctenopteris heterophylla* | 0.19 | 7.78 | 60 | 1.91 | 0.0197 | 6.07 | 2.52 | 0.18 | 2.09 | 0.00 | 0.113 | 2.84 |
| *Cyathea smithii* | 0.13 | 2.38 | 23 | 2.23 | 0.0073 | 3.13 | 2.32 | 0.53 | 2.87 | 0.15 | 0.106 | 1.05 |
| *Cyathodes fasciculata* | 0.10 | 0.15 | 17 | 1.82 | 0.0079 | 6.99 | 2.72 | 0.33 | 2.63 | 0.29 | 0.106 | 1.12 |
| *Dacrydium cupressinum* (S)† | 0.19 | 0.01 | 34 | 1.86 | 0.0314 | 9.36 | 2.76 | 0.30 | 1.04 | 0.62 | 0.070 | 1.54 |
| *Dacrydium cupressinum* (J) | 0.19 | 0.01 | 34 | 1.86 | 0.0314 | 9.36 | 2.76 | 0.30 | 1.04 | 0.62 | 0.070 | 1.54 |
| *Dicksonia fibrosa* | 0.20 | 1.39 | 34 | 2.16 | 0.0148 | 3.53 | 2.76 | 0.41 | 2.01 | 0.13 | 0.109 | 1.10 |
| *Elaeocarpus hookerianus* (A) | 0.32 | 8.34 | 38 | 1.97 | 0.0186 | 3.70 | 1.14 | 0.51 | 0.87 | 0.22 | 0.070 | 1.20 |
| *Elaeocarpus hookerianus* (J) | 0.18 | 0.46 | 34 | 2.01 | 0.0066 | 3.61 | 1.19 | 0.75 | 2.25 | 0.64 | 0.104 | 1.41 |
| *Grammitis billardieri* | 0.18 | 1.57 | 26 | 2.40 | 0.0053 | 14.26 | 2.71 | 0.43 | 2.85 | 0.00 | 0.095 | 1.13 |
| *Griselinia littoralis* | 0.48 | 19.40 | 33 | 2.91 | 0.0100 | 1.48 | 3.19 | 0.30 | 0.90 | 0.26 | 0.084 | 0.91 |
| *Histiopteris incisa* | 0.13 | 0.62 | 17 | 6.78 | 0.0019 | 1.96 | 2.35 | 1.25 | 20.50 | 0.29 | 0.441 | 0.95 |
| *Hydrocotyle americana* | 0.12 | 0.24 | 16 | 4.88 | 0.0039 | 0.78 | 2.78 | 0.71 | 6.02 | 0.56 | 0.229 | 0.87 |
| *Hymenophyllum multifidum* | 0.01 | 5.47 | 52 | 1.56 | 0.0073 | 1.85 | 2.52 | 0.23 | 2.81 | 0.23 | 0.109 | 2.25 |
| *Hymenophyllum pulcherrimum* | 0.01 | 19.50 | 81 | 2.31 | 0.0063 | 2.96 | 1.88 | 0.57 | 2.52 | 0.28 | 0.166 | 3.13 |
| *Hymenophyllum rarum* | 0.02 | 2.74 | 63 | 1.66 | 0.0048 | 2.40 | 1.28 | 0.58 | 1.23 | 0.13 | 0.075 | 1.84 |
| *Hymenophyllum sanguinolentum* | 0.02 | 5.61 | 51 | 1.65 | 0.0059 | 1.93 | 2.43 | 0.30 | 2.49 | 0.29 | 0.123 | 2.70 |
| *Lagenifera strangulata* | 0.20 | 0.72 | 14 | 6.54 | 0.0029 | 1.00 | 2.60 | 0.90 | 7.02 | 0.38 | 0.255 | 1.09 |
| *Leptopteris superba* | 0.04 | 4.00 | 23 | 2.79 | 0.0095 | 5.56 | 2.64 | 0.39 | 1.48 | 0.33 | 0.132 | 1.37 |
| *Luzula* aff. *picta* | 0.12 | 1.45 | 39 | 4.88 | 0.0050 | 80.45 | 2.75 | 0.81 | 5.20 | 0.29 | 0.211 | 1.11 |
| *Lycopodium varium* | 0.23 | 0.10 | 30 | 3.07 | 0.0086 | 10.70 | 2.30 | 0.54 | 1.36 | 0.46 | 0.099 | 0.82 |
| *Microlaena avennacea* | 0.16 | 33.00 | 56 | 2.83 | 0.0078 | 47.09 | 2.68 | 0.54 | 1.19 | 0.31 | 0.080 | 1.03 |
| *Muehlenbeckia australis* | 0.12 | 0.69 | 20 | 4.57 | 0.0027 | 1.19 | 2.41 | 1.08 | 17.30 | 0.84 | 0.355 | 1.04 |
| *Myrsine divaricata* | 0.18 | 0.40 | 14 | 3.16 | 0.0061 | 1.24 | 2.58 | 0.52 | 2.97 | 0.72 | 0.151 | 0.98 |
| *Neomyrtus pedunculata* | 0.23 | 0.15 | 16 | 2.09 | 0.0110 | 2.07 | 2.88 | 0.36 | 2.38 | 0.65 | 0.087 | 1.19 |
| *Nertera dichondrifolia* | 0.14 | 0.25 | 19 | 4.17 | 0.0061 | 1.14 | 2.55 | 0.73 | 1.96 | 0.50 | 0.146 | 0.92 |
| *Nestigis cunninghamii* | 0.39 | 14.30 | 22 | 1.83 | 0.0157 | 4.19 | 2.69 | 0.33 | 1.14 | 0.14 | 0.080 | 1.02 |
| *Nothofagus fusca* (C) | 0.21 | 2.54 | 20 | 1.95 | 0.0106 | 1.42 | 2.28 | 0.42 | 1.93 | 0.29 | 0.126 | 1.10 |
| *Nothofagus fusca* (S) | 0.18 | 2.77 | 26 | 2.30 | 0.0094 | 1.24 | 2.43 | 0.60 | 1.44 | 0.23 | 0.126 | 1.11 |
| *Nothofagus fusca* (J) | 0.14 | 1.67 | 20 | 2.01 | 0.0062 | 1.24 | 2.77 | 0.33 | 1.04 | 0.28 | 0.100 | 1.12 |
| *Nothofagus menziesii* (C) | 0.28 | 0.57 | 28 | 1.81 | 0.0179 | 1.18 | 3.58 | 0.22 | 1.60 | 0.29 | 0.116 | 1.03 |
| *Nothofagus menziesii* (S) | 0.24 | 0.61 | 38 | 1.91 | 0.0153 | 1.07 | 2.96 | 0.32 | 1.14 | 0.28 | 0.085 | 0.99 |
| *Nothofagus menziesii* (J) | 0.21 | 1.07 | 20 | 2.03 | 0.0098 | 1.12 | 2.79 | 0.42 | 1.37 | 0.28 | 0.095 | 1.10 |

| **ZN1 Ohakune** (continued) | *Thick* | *Area* | *Inclin* | *Succ* | *SLW* | *Shape* | *Chl* a/b | *Chl* | *N* | *SF* | *P* | *Lobe* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Nothofagus solandri* (C) | 0.31 | 0.37 | 44 | 1.83 | 0.0174 | 1.68 | 3.47 | 0.22 | 1.75 | 0.32 | 0.098 | 0.97 |
| *Nothofagus solandri* (S) | 0.20 | 0.48 | 26 | 2.02 | 0.0099 | 1.35 | 2.77 | 0.33 | 1.59 | 0.25 | 0.099 | 0.96 |
| *Nothofagus solandri* (J) | 0.17 | 0.46 | 11 | 2.45 | 0.0060 | 1.22 | 2.74 | 0.43 | 1.28 | 0.34 | 0.107 | 0.92 |
| *Parsonsia capsularis* | 0.17 | 2.00 | 25 | 3.32 | 0.0055 | 18.02 | 2.64 | 0.73 | 2.64 | 0.53 | 0.236 | 0.99 |
| *Phymatosorus diversifolius* | 0.29 | 72.00 | 36 | 2.65 | 0.0157 | 2.02 | 2.80 | 0.34 | 1.06 | 0.49 | 0.128 | 3.34 |
| *Podocarpus cunninghamii* (A) | 0.41 | 1.34 | 34 | 1.96 | 0.0183 | 7.70 | 2.91 | 0.15 | 0.79 | 0.34 | 0.077 | 1.10 |
| *Podocarpus cunninghamii* (J)† | 0.41 | 1.34 | 34 | 1.96 | 0.0183 | 7.70 | 2.91 | 0.15 | 0.79 | 0.34 | 0.077 | 1.10 |
| *Polystichum vestitum* | 0.16 | 3.92 | 28 | 2.62 | 0.0064 | 3.66 | 2.33 | 0.60 | 2.36 | 0.15 | 0.154 | 1.39 |
| *Prumnopitys ferruginea* (S) | 0.31 | 0.34 | 22 | 2.32 | 0.0127 | 7.17 | 2.61 | 0.35 | 1.23 | 0.39 | 0.097 | 0.85 |
| *Prumnopitys ferruginea* (J) | 0.18 | 0.19 | 23 | 2.61 | 0.0091 | 9.00 | 2.63 | 0.40 | 1.26 | 0.33 | 0.080 | 0.84 |
| *Prumnopitys taxifolia* (S) | 0.28 | 0.11 | 21 † | 2.09 | 0.0178 | 7.67 | 2.84† | 0.42† | 1.13 | 0.52 | 0.066 | 0.65 |
| *Pseudopanax anomalus* | 0.25 | 0.24 | 13 | 2.63 | 0.0119 | 1.48 | 2.69 | 0.26 | 1.18 | 0.87 | 0.057 | 1.04 |
| *Pseudopanax crassifolius* (J) | 0.78 | 35.70 | 34 | 2.25 | 0.0362 | 59.62 | 2.35 | 0.30 | 0.83 | 0.25 | 0.062 | 1.00 |
| *Pseudowintera colorata* | 0.28 | 10.00 | 12 | 2.17 | 0.0107 | 3.09 | 2.79 | 0.26 | 1.84 | 0.23 | 0.104 | 1.02 |
| *Pterostylis* sp. 2† | 0.28 | 6.04 | 13 | 12.60 | 0.0033 | 3.05 | 3.22 | 1.23 | 2.18 | 0.29 | 0.247 | 1.04 |
| *Rubus schmidelioides* | 0.28 | 7.35 | 30 | 1.93 | 0.0141 | 9.54 | 2.35 | 0.36 | 1.80 | 0.35 | 0.082 | 0.99 |
| *Schefflera digitata* (J)† | 0.20 | 12.00 | 12 | 5.66 | 0.0028 | 2.22 | 2.94 | 1.63 | 1.98 | 0.31 | 0.156 | 1.25 |
| *Sonchus oleraceus* | 0.13 | 3.17 | 22 | 9.09 | 0.0008 | 1.10 | 3.21 | 1.00 | 2.99 | 0.48 | 0.159 | 1.20 |
| *Stellaria parviflora* | 0.12 | 0.16 | 32 | 7.62 | 0.0018 | 1.08 | 2.93 | 0.94 | 19.20 | 0.53 | 0.281 | 0.92 |
| *Uncinia filiformis* | 0.16 | 2.49 | 28 | 2.74 | 0.0076 | 226.90 | 2.64 | 0.55 | 1.12 | 0.24 | 0.058 | 0.78 |
| *Uncinia uncinata* | 0.15 | 9.86 | 35 | 2.56 | 0.0100 | 100.40 | 3.42 | 0.30 | 1.23 | 0.18 | 0.071 | 0.94 |
| *Uncinia viridis* | 0.18 | 2.71 | 34 | 2.72 | 0.0087 | 109.70 | 2.53 | 0.48 | 0.37 | 0.30 | 0.035 | 1.08 |

| **Site ZN2 Rotokura** | *Thick* | *Area* | *Inclin* | *Succ* | *SLW* | *Shape* | *Chl* a/b | *Chl* | *N* | *SF* | *P* | *Lobe* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Aristotelia serrata* | 0.19 | 34.80 | 24 | 3.40 | 0.0042 | 1.53 | 2.59 | 0.78 | 1.72 | 0.19 | 0.117 | 1.12 |
| *Asplenium bulbiferum* | 0.13 | 6.80 | 26 | 6.24 | 0.0037 | 3.02 | 2.67 | 1.03 | 1.90 | 0.30 | 0.143 | 1.40 |
| *Asplenium flaccidum* | 0.58 | 54.40 | 68 | 3.84 | 0.0258 | 3.40 | 2.79 | 0.47 | 1.06 | 0.14 | 0.122 | 6.93 |
| *Asplenium polyodon* | 0.21 | 5.08 | 44 | 2.28 | 0.0070 | 3.26 | 2.84 | 0.57 | 1.14 | 0.22 | 0.070 | 1.45 |
| *Astelia nervosa* | 0.52 | 273.00 | 42 | 3.63 | 0.0427 | 58.35 | 3.04 | 0.25 | 0.84 | 0.00 | 0.108 | 0.84 |
| *Blechnum colensoi* | 0.37 | 160.00 | 14 | 3.49 | 0.0090 | 3.15 | 2.58 | 0.80 | 1.27 | 0.07 | 0.059 | 1.86 |
| *Blechnum discolor* | 0.21 | 374.00 | 29 | 2.70 | 0.0169 | 7.36 | 2.86 | 0.55 | 0.76 | 0.14 | 0.053 | 1.90 |
| *Blechnum fluviatile* | 0.14 | 0.93 | 17 | 4.79 | 0.0032 | 1.72 | 2.76 | 1.15 | 1.77 | 0.42 | 0.117 | 1.04 |
| *Blechnum* sp. 1 | 0.16 | 49.80 | 40 | 2.66 | 0.0052 | 6.52 | 2.69 | 0.81 | 1.17 | 0.32 | 0.055 | 1.09 |
| *Cardamine debilis* | 0.14 | 0.27 | 17 | 8.41 | 0.0021 | 0.99 | 2.97 | 1.60 | 2.24 | 0.64 | 0.169 | 1.51 |
| *Carpodetus serratus* | 0.17 | 5.19 | 18 | 3.38 | 0.0029 | 1.31 | 3.04 | 0.67 | 1.50 | 0.33 | 0.115 | 0.97 |
| *Clematis paniculata* (J) | 0.27 | 7.10 | 20 | 5.90 | 0.0044 | 5.37 | 2.97 | 1.19 | 1.75 | 0.41 | 0.123 | 1.18 |
| *Coprosma ciliata* | 0.23 | 0.18 | 18 | 3.07 | 0.0058 | 2.71 | 3.20 | 0.71 | 1.50 | 0.49 | 0.104 | 1.02 |
| *Coprosma grandifolia* | 0.27 | 37.20 | 15 | 3.70 | 0.0065 | 2.21 | 3.29 | 0.76 | 1.45 | 0.25 | 0.069 | 1.28 |
| *Coprosma propinqua* | 0.17 | 0.39 | 14 | 4.46 | 0.0067 | 3.82 | 3.16 | 0.80 | 1.56 | 0.26 | 0.098 | 0.93 |
| *Coprosma rhamnoides* | 0.14 | 0.19 | 20 | 2.86 | 0.0061 | 1.55 | 3.04 | 0.77 | 1.67 | 0.55 | 0.101 | 1.03 |
| *Coprosma tenuifolia* | 0.22 | 8.87 | 27 | 3.44 | 0.0055 | 2.55 | 3.10 | 0.65 | 1.49 | 0.31 | 0.092 | 0.98 |
| *Corybas trilobus* | 0.37 | 3.11 | 18 | 22.10 | 0.0016 | 0.44 | 2.75 | 1.79 | 2.96 | 0.36 | 0.516 | 0.65 |
| *Cyathea dealbata* | 0.12 | 4.66 | 42 | 2.44 | 0.0089 | 4.35 | 2.80 | 0.67 | 1.59 | 0.13 | 0.068 | 1.29 |
| *Cyathea smithii* | 0.11 | 2.20 | 32 | 2.54 | 0.0065 | 3.46 | 2.70 | 0.73 | 1.62 | 0.16 | 0.070 | 1.10 |
| *Cyathodes fasciculata* | 0.12 | 0.32 | 19 | 2.37 | 0.0057 | 6.47 | 3.06 | 0.64 | 1.20 | 0.33 | 0.074 | 0.88 |
| *Dicksonia fibrosa* | 0.13 | 1.51 | 32 | 2.39 | 0.0073 | 3.52 | 3.13 | 0.35 | 1.97 | 0.15 | 0.095 | 1.17 |
| *Dicksonia squarrosa* | 0.14 | 2.74 | 37 | 2.48 | 0.0076 | 3.88 | 3.06 | 0.58 | 1.41 | 0.16 | 0.073 | 1.32 |
| *Earina autumnalis* | 0.19 | 1.57 | 52 | 2.51 | 0.0105 | 44.54 | 2.93 | 0.58 | 1.10 | 0.21 | 0.086 | 0.90 |
| *Elaeocarpus hookerianus* (J) | 0.15 | 0.86 | 19 | 2.22 | 0.0088 | 7.87 | 1.88 | 0.75 | 1.11 | 0.64 | 0.059 | 0.84 |
| *Grammitis billardieri* | 0.22 | 1.25 | 28 | 2.64 | 0.0086 | 16.57 | 2.85 | 0.64 | 1.07 | 0.00 | 0.090 | 1.13 |
| *Griselinia littoralis* | 0.37 | 20.40 | 21 | 3.98 | 0.0083 | 1.58 | 3.12 | 0.51 | 1.05 | 0.40 | 0.086 | 1.10 |
| *Hedycarya arborea* | 0.28 | 9.32 | 30 | 3.98 | 0.0057 | 3.41 | 3.01 | 0.82 | 5.18 | 0.60 | 0.310 | 1.21 |
| *Histiopteris incisa* | 0.14 | 5.84 | 23 | 6.62 | 0.0013 | 2.79 | 2.87 | 1.53 | 21.00 | 0.15 | 0.220 | 1.40 |
| *Hydrocotyle moschata* | 0.16 | 1.36 | 9 | 5.92 | 0.0034 | 0.86 | 2.70 | 1.27 | 2.10 | 0.50 | 0.148 | 1.30 |
| *Hymenophyllum flabellatum* | 0.04 | 7.02 | 76 | 2.76 | 0.0024 | 1.89 | 2.69 | 0.69 | 1.09 | 0.34 | 0.088 | 1.65 |
| *Hymenophyllum multifidum* | 0.02 | 4.66 | 78 | 1.76 | 0.0061 | 1.52 | 2.51 | 0.47 | 1.03 | 0.20 | 0.066 | 2.17 |
| *Hymenophyllum rarum* | 0.02 | 1.13 | 36 | 1.80 | 0.0033 | 2.33 | 2.81 | 0.55 | 0.97 | 0.39 | 0.097 | 2.00 |
| *Hymenophyllum sanguinolentum* | 0.02 | 4.74 | 54 | 1.78 | 0.0077 | 1.60 | 2.75 | 0.36 | 0.85 | 0.38 | 0.071 | 2.09 |
| *Knightia excelsa* (J) | 0.16 | 22.00 | 23 | 2.56 | 0.0047 | 6.80 | 1.58 | 0.86 | 1.07 | 0.24 | 0.056 | 1.10 |
| *Lagenifera strangulata* | 0.20 | 0.71 | 16 | 6.90 | 0.0027 | 1.04 | 3.21 | 0.93 | 1.87 | 0.54 | 0.124 | 0.96 |
| *Leptopteris hymenophylloides* | 0.02 | 9.28 | 27 | 2.77 | 0.0037 | 2.92 | 2.71 | 0.50 | 1.69 | 0.17 | 0.130 | 1.63 |
| *Microlaena avennacea* | 0.18 | 42.50 | 48 | 2.88 | 0.0075 | 51.49 | 3.12 | 0.60 | 1.00 | 0.32 | 0.065 | 0.99 |
| *Muehlenbeckia complexa* | 0.14 | 1.05 | 16 | 7.02 | 0.0023 | 1.03 | 3.20 | 2.03 | 3.53 | 0.67 | 0.241 | 1.19 |

| **ZN2 Rotokura** (continued) | *Thick* | *Area* | *Inclin* | *Succ* | *SLW* | *Shape* | *Chl* a/b | *Chl* | *N* | *SF* | *P* | *Lobe* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Myrsine divaricata* | 0.18 | 0.39 | 19 | 3.12 | 0.0062 | 1.35 | 2.82 | 0.67 | 1.23 | 0.83 | 0.092 | 1.13 |
| *Neomyrtus pedunculata* | 0.21 | 0.26 | 16 | 2.48 | 0.0073 | 1.86 | 3.12 | 0.47 | 1.03 | 0.49 | 0.059 | 1.09 |
| *Nothofagus fusca* (C) | 0.23 | 3.62 | 39 | 2.66 | 0.0090 | 1.43 | 3.40 | 0.45 | 1.58 | 0.17 | 0.123 | 1.15 |
| *Nothofagus fusca* (S) | 0.16 | 3.41 | 26 | 2.67 | 0.0060 | 1.45 | 2.92 | 0.63 | 1.44 | 0.18 | 0.090 | 1.20 |
| *Nothofagus fusca* (J) | 0.15 | 1.64 | 24 | 2.73 | 0.0056 | 1.27 | 2.82 | 0.48 | 1.22 | 0.22 | 0.086 | 1.22 |
| *Nothofagus menziesii* (C) | 0.28 | 0.57 | 36 | 1.94 | 0.0206 | 1.24 | 3.45 | 0.30 | 1.36 | 0.34 | 0.080 | 1.19 |
| *Nothofagus menziesii* (S) | 0.22 | 0.93 | 22 | 1.88 | 0.0138 | 1.21 | 3.14 | 0.44 | 1.17 | 0.28 | 0.070 | 1.15 |
| *Nothofagus menziesii* (J) | 0.21 | 1.13 | 15 | 2.05 | 0.0113 | 1.20 | 2.93 | 0.55 | 1.14 | 0.28 | 0.079 | 1.19 |
| *Nothofagus solandri* (J) | 0.15 | 0.78 | 22 | 2.69 | 0.0054 | 1.29 | 2.98 | 0.60 | 1.12 | 0.23 | 0.072 | 1.03 |
| *Parsonsia capsularis* | 0.18 | 1.64 | 18 | 4.09 | 0.0055 | 17.80 | 3.10 | 1.13 | 2.19 | 0.58 | 0.196 | 1.17 |
| *Phymatosorus diversifolius* | 0.31 | 64.30 | 38 | 4.82 | 0.0072 | 2.04 | 2.81 | 0.70 | 1.25 | 0.55 | 0.116 | 2.41 |
| *Pittosporum tenuifolium* | 0.17 | 7.98 | 34 | 3.35 | 0.0034 | 2.01 | 2.87 | 0.76 | 1.14 | 0.19 | 0.111 | 1.07 |
| *Polystichum vestitum* | 0.20 | 5.74 | 16 | 4.05 | 0.0053 | 2.75 | 2.85 | 0.88 | 1.63 | 0.16 | 0.116 | 1.47 |
| *Prumnopitys ferruginea* (S) | 0.29 | 0.42 | 22 | 2.47 | 0.0122 | 7.08 | 3.10 | 0.39 | 0.91 | 0.40 | 0.068 | 0.93 |
| *Prumnopitys ferruginea* (J) | 0.22 | 0.33 | 19 | 2.83 | 0.0090 | 7.41 | 2.87 | 0.50 | 0.96 | 0.37 | 0.076 | 0.88 |
| *Prumnopitys taxifolia* (J) | 0.13 | 0.15 | 21 | 2.36 | 0.0056 | 7.67 | 2.84 | 0.47 | 0.98 | 0.57 | 0.065 | 0.78 |
| *Pseudopanax anomalus* | 0.17 | 0.25 | 16 | 2.78 | 0.0085 | 1.40 | 3.10 | 0.60 | 1.28 | 0.84 | 0.094 | 1.23 |
| *Pseudopanax crassifolius* (A) | 0.60 | 44.20 | 22 | 2.74 | 0.0194 | 8.22 | 2.84 | 0.27 | 0.86 | 0.15 | 0.057 | 1.21 |
| *Pseudopanax crassifolius* (J) | 0.55 | 26.80 | 21 | 2.49 | 0.0262 | 55.59 | 2.64 | 0.27 | 0.53 | 0.35 | 0.034 | 0.99 |
| *Pseudowintera colorata* | 0.32 | 12.50 | 14 | 2.85 | 0.0093 | 2.99 | 2.85 | 0.31 | 1.23 | 0.24 | 0.068 | 1.06 |
| *Pterostylis* aff. *montana* | 0.23 | 10.40 | 50 | 14.00 | 0.0023 | 13.43 | 2.81 | 1.17 | 1.55 | 0.31 | 0.244 | 1.01 |
| *Pyrrosia elaeagnifolia* | 1.25 | 2.75 | 31 | 5.55 | 0.0231 | 2.57 | 2.89 | 0.34 | 0.75 | 0.26 | 0.135 | 1.05 |
| *Rubus fruticosus* | 0.21 | 24.00 | 20 | 2.52 | 0.0046 | 1.50 | 2.65 | 1.12 | 1.76 | 0.41 | 0.081 | 1.12 |
| *Rubus schmidelioides* | 0.15 | 6.80 | 28 | 1.98 | 0.0061 | 11.80 | 2.77 | 0.51 | 1.14 | 0.49 | 0.079 | 1.01 |
| *Schefflera digitata* | 0.20 | 12.00 | 12 | 5.66 | 0.0028 | 2.22 | 2.94 | 1.63 | 1.98 | 0.31 | 0.156 | 1.25 |
| *Sonchus oleraceus*† | 0.13 | 3.17 | 22 | 9.09 | 0.0008 | 1.10 | 3.21 | 1.00 | 2.99 | 0.48 | 0.159 | 1.20 |
| *Stellaria parviflora* | 0.11 | 0.23 | 32 | 11.00 | 0.0014 | 0.98 | 3.00 | 0.91 | 1.84 | 0.45 | 0.244 | 1.00 |
| *Uncinia filiformis* | 0.16 | 3.41 | 40 | 2.68 | 0.0073 | 237.20 | 3.01 | 0.60 | 1.16 | 0.34 | 0.122 | 0.88 |
| *Uncinia* aff. *leptostachya* | 0.19 | 5.84 | 53 | 2.51 | 0.0084 | 173.60 | 3.12 | 0.51 | 1.15 | 0.36 | 0.068 | 0.88 |
| *Uncinia rupestris* | 0.15 | 1.47 | 26 | 3.08 | 0.0084 | 186.30 | 2.85 | 0.85 | 1.29 | 0.25 | 0.091 | 0.90 |
| *Uncinia uncinata* | 0.22 | 12.80 | 36 | 2.93 | 0.0060 | 97.24 | 3.28 | 0.46 | 0.86 | 0.27 | 0.054 | 0.88 |
| *Uncinia viridis* | 0.17 | 3.73 | 34 | 2.87 | 0.0060 | 115.70 | 2.99 | 0.76 | 1.22 | 0.30 | 0.083 | 0.92 |

| **Site ZN3 Clements** | *Thick* | *Area* | *Inclin* | *Succ* | *SLW* | *Shape* | *Chl* a/b | *Chl* | *N* | *SF* | *P* | *Lobe* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Aristotelia serrata* | 0.11 | 2.35 | 34 | 3.06 | 0.0027 | 1.60 | 3.01 | 0.57 | 1.38 | 0.66 | 0.147 | 1.10 |
| *Asplenium flaccidum* | 0.45 | 38.10 | 80 | 4.83 | 0.0340 | 5.04 | 2.80 | 0.64 | 0.98 | 0.20 | 0.128 | 4.21 |
| *Asplenium polyodon* | 0.24 | 2.58 | 44 | 2.58 | 0.0162 | 3.75 | 2.97 | 0.46 | 1.95 | 0.26 | 0.240 | 1.21 |
| *Astelia solandri* | 0.42 | 96.10 | 34 | 3.48 | 0.0370 | 67.45 | 2.77 | 0.26 | 0.49 | 0.00 | 0.052 | 1.07 |
| *Blechnum discolor* | 0.22 | 315.00 | 42 | 2.68 | 0.0160 | 5.87 | 2.92 | 0.46 | 0.49 | 0.08 | 0.039 | 1.69 |
| *Blechnum fluviatile* | 0.10 | 0.60 | 14 | 3.49 | 0.0027 | 1.18 | 2.92 | 0.74 | 1.40 | 0.31 | 0.100 | 0.95 |
| *Blechnum procerum* | 0.12 | 3.40 | 24 | 2.22 | 0.0045 | 2.53 | 2.96 | 0.36 | 0.98 | 0.10 | 0.057 | 1.04 |
| *Blechnum vulcanicum* | 0.18 | 36.80 | 40 | 3.87 | 0.0062 | 2.28 | 2.91 | 0.46 | 1.40 | 0.16 | 0.139 | 1.39 |
| *Carpodetus serratus* | 0.18 | 4.19 | 24 | 3.27 | 0.0071 | 1.51 | 3.07 | 0.75 | 1.59 | 0.32 | 0.127 | 1.03 |
| *Coprosma banksii* | 0.21 | 0.29 | 10 | 2.91 | 0.0072 | 5.63 | 3.07 | 0.68 | 1.13 | 0.64 | 0.073 | 0.88 |
| *Coprosma foetidissima* | 0.21 | 1.40 | 15 | 4.44 | 0.0040 | 2.02 | 2.98 | 0.93 | 1.59 | 0.29 | 0.099 | 1.06 |
| *Coprosma linariifolia* | 0.11 | 0.13 | 13 | 3.04 | 0.0074 | 9.68 | 3.14 | 0.72 | 1.41 | 0.54 | 0.091 | 0.92 |
| *Coprosma lucida* | 0.33 | 21.00 | 29 | 3.60 | 0.0084 | 2.33 | 3.05 | 0.59 | 0.98 | 0.27 | 0.068 | 1.03 |
| *Coprosma rhamnoides* | 0.12 | 0.13 | 23 | 2.52 | 0.0047 | 1.59 | 3.33 | 0.71 | 0.23 | 0.79 | 0.023 | 1.04 |
| *Coprosma tenuifolia* | 0.19 | 5.10 | 20 | 2.65 | 0.0091 | 2.57 | 3.12 | 0.48 | 0.83 | 0.21 | 0.055 | 1.08 |
| *Coprosma wallii* | 0.19 | 0.23 | 15 | 2.92 | 0.0058 | 2.49 | 3.01 | 0.77 | 1.38 | 0.56 | 0.088 | 0.93 |
| *Corybas trilobus* | 0.33 | 1.63 | 14 | 16.00 | 0.0023 | 0.41 | 2.60 | 1.67 | 2.53 | 0.39 | 0.192 | 0.76 |
| *Ctenopteris heterophylla* | 0.21 | 10.80 | 60 | 2.22 | 0.0210 | 5.22 | 3.04 | 0.13 | 0.77 | 0.08 | 0.077 | 3.91 |
| *Cyathea smithii* | 0.11 | 2.82 | 19 | 2.35 | 0.0054 | 3.45 | 2.70 | 0.66 | 1.43 | 0.13 | 0.068 | 1.23 |
| *Dicksonia squarrosa* | 0.14 | 3.62 | 24 | 2.71 | 0.0059 | 3.18 | 2.92 | 0.67 | 1.53 | 0.13 | 0.125 | 1.21 |
| *Earina mucronata* | 0.26 | 2.00 | 31 | 2.40 | 0.0130 | 35.43 | 3.17 | 0.43 | 1.21 | 0.27 | 0.098 | 0.96 |
| *Grammitis billardieri* | 0.28 | 2.06 | 50 | 2.82 | 0.0078 | 18.06 | 2.69 | 0.51 | 0.85 | 0.00 | 0.077 | 1.11 |
| *Griselinia littoralis* (A)† | 0.41 | 23.70 | 20 | 3.01 | 0.0073 | 1.60 | 3.24 | 0.29 | 0.54 | 0.21 | 0.043 | 1.03 |
| *Griselinia littoralis* (J) | 0.41 | 23.70 | 20 | 3.01 | 0.0073 | 1.60 | 3.24 | 0.29 | 0.54 | 0.21 | 0.043 | 1.03 |
| *Histiopteris incisa* | 0.15 | 5.17 | 26 | 5.85 | 0.0032 | 2.68 | 3.11 | 0.94 | 2.04 | 0.16 | 0.172 | 1.48 |
| *Hydrocotyle disecta* | 0.15 | 0.64 | 13 | 5.91 | 0.0032 | 0.88 | 2.97 | 0.89 | 2.16 | 0.55 | 0.138 | 1.41 |
| *Hymenophyllum flabellatum* | 0.02 | 7.88 | 74 | 2.02 | 0.0056 | 2.25 | 2.64 | 0.49 | 0.91 | 0.35 | 0.075 | 1.76 |
| *Hymenophyllum multifidum* | 0.02 | 8.12 | 30 | 1.69 | 0.0085 | 1.44 | 2.83 | 0.45 | 0.95 | 0.27 | 0.063 | 2.19 |
| *Hymenophyllum rarum* | 0.02 | 1.49 | 70 | 1.69 | 0.0038 | 2.12 | 2.66 | 0.32 | 0.76 | 0.15 | 0.057 | 1.45 |

| **ZN3 Clements** (continued) | *Thick* | *Area* | *Inclin* | *Succ* | *SLW* | *Shape* | *Chl* a/b | *Chl* | *N* | *SF* | *P* | *Lobe* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Hymenophyllum villosum* | 0.02 | 8.66 | 53 | 1.66 | 0.0066 | 1.65 | 2.88 | 0.46 | 1.12 | 0.26 | 0.080 | 2.91 |
| *Lagenifera strangulata* | 0.14 | 0.47 | 12 | 4.20 | 0.0029 | 1.01 | 2.94 | 0.76 | 1.51 | 0.58 | 0.100 | 0.98 |
| *Leptopteris hymenophylloides* | 0.08 | 8.50 | 33 | 2.76 | 0.0056 | 3.44 | 2.94 | 0.43 | 1.60 | 0.23 | 0.126 | 1.56 |
| *Microlaena avennacea* | 0.14 | 20.10 | 30 | 2.74 | 0.0063 | 45.87 | 3.28 | 0.63 | 1.00 | 0.32 | 0.072 | 0.96 |
| *Muehlenbeckia complexa* | 0.13 | 0.47 | 21 | 6.53 | 0.0025 | 1.03 | 3.21 | 1.56 | 2.65 | 0.89 | 0.220 | 0.99 |
| *Neomyrtus pedunculata* | 0.18 | 0.12 | 11 | 2.17 | 0.0099 | 1.67 | 3.32 | 0.42 | 0.91 | 0.58 | 0.047 | 1.05 |
| *Nertera depressa* | 0.15 | 0.16 | 16 | 5.26 | 0.0036 | 1.16 | 3.08 | 0.68 | 1.59 | 0.53 | 0.137 | 0.93 |
| *Nertera dichondrifolia* | 0.15 | 0.24 | 14 | 5.04 | 0.0041 | 1.05 | 2.87 | 1.13 | 1.60 | 0.49 | 0.126 | 0.94 |
| *Nothofagus fusca* (C) | 0.23 | 2.73 | 32 | 2.19 | 0.0123 | 1.57 | 3.67 | 0.40 | 1.50 | 0.20 | 0.106 | 1.13 |
| *Nothofagus fusca* (S) | 0.17 | 1.97 | 22 | 2.53 | 0.0071 | 1.24 | 3.35 | 0.50 | 1.34 | 0.31 | 0.100 | 1.09 |
| *Nothofagus fusca* (J) | 0.14 | 1.84 | 15 | 2.60 | 0.0048 | 1.16 | 3.22 | 0.51 | 1.17 | 0.36 | 0.089 | 1.05 |
| *Nothofagus menziesii* (C) | 0.29 | 0.48 | 24 | 2.16 | 0.0157 | 1.09 | 4.32 | 0.24 | 1.46 | 0.27 | 0.102 | 1.07 |
| *Nothofagus menziesii* (S) | 0.24 | 1.43 | 30 | 2.03 | 0.0088 | 1.18 | 3.15 | 0.45 | 5.06 | 0.31 | 0.310 | 1.11 |
| *Nothofagus menziesii* (J) | 0.22 | 0.98 | 15 | 2.15 | 0.0101 | 1.16 | 3.09 | 0.57 | 1.15 | 0.26 | 0.087 | 1.06 |
| *Paesia scaberula* | 0.13 | 3.24 | 28 | 3.07 | 0.0072 | 1.97 | 2.99 | 0.62 | 1.14 | 0.16 | 0.118 | 2.36 |
| *Parsonsia heterophylla* | 0.21 | 5.10 | 31 | 4.75 | 0.0057 | 10.27 | 3.13 | 0.56 | 1.45 | 0.64 | 0.082 | 1.12 |
| *Peraxilla colensoi* | 0.40 | 5.84 | 56 | 3.42 | 0.0198 | 2.04 | 3.04 | 0.58 | 1.27 | 0.15 | 0.146 | 1.49 |
| *Phymatosorus diversifolius* | 0.32 | 82.40 | 54 | 3.84 | 0.0071 | 1.63 | 3.03 | 0.35 | 0.86 | 0.41 | 0.095 | 2.32 |
| *Polystichum vestitum* | 0.20 | 2.58 | 15 | 3.74 | 0.0086 | 3.45 | 2.73 | 0.80 | 1.62 | 0.29 | 0.143 | 1.16 |
| *Pseudopanax anomalus* | 0.17 | 0.44 | 17 | 2.68 | 0.0049 | 1.35 | 3.18 | 0.48 | 1.23 | 0.80 | 0.076 | 0.98 |
| *Pseudopanax simplex* | 0.25 | 4.10 | 22 | 3.07 | 0.0085 | 2.30 | 3.07 | 0.71 | 1.30 | 0.32 | 0.114 | 1.13 |
| *Pseudopanax crassifolius* (A) | 0.51 | 24.80 | 42 | 2.61 | 0.0163 | 7.96 | 3.08 | 0.34 | 0.77 | 0.16 | 0.059 | 1.29 |
| *Pseudopanax crassifolius* (J) | 0.31 | 19.50 | 17 | 1.99 | 0.0397 | 51.77 | 2.87 | 0.20 | 0.60 | 0.15 | 0.036 | 0.91 |
| *Pseudowintera colorata* | 0.30 | 10.90 | 17 | 2.72 | 0.0117 | 2.45 | 2.86 | 0.37 | 1.19 | 0.27 | 0.072 | 1.07 |
| *Pterostylis* sp. 2 | 0.28 | 6.04 | 13 | 12.60 | 0.0033 | 3.05 | 3.22 | 1.23 | 2.18 | 0.29 | 0.247 | 1.04 |
| *Pyrrosia elaeagnifolia* | 1.18 | 3.59 | 34 | 4.05 | 0.0364 | 3.03 | 2.91 | 0.18 | 0.58 | 0.26 | 0.066 | 1.19 |
| *Rubus schmidelioides* | 0.18 | 6.01 | 13 | 2.28 | 0.0106 | 8.56 | 2.98 | 0.44 | 1.33 | 0.40 | 0.094 | 1.02 |
| *Sonchus olearaceus* | 0.11 | 5.15 | 28 | 11.80 | 0.0012 | 1.48 | 3.01 | 2.13 | 1.77 | 0.45 | 0.119 | 1.78 |
| *Tmesipteris tannensis* | 0.30 | 0.10 | 78 | 3.89 | 0.0063 | 7.48 | 2.51 | 0.40 | 0.43 | 0.64 | 0.062 | 1.03 |
| *Uncinia filiformis* | 0.18 | 2.51 | 28 | 2.69 | 0.0081 | 222.90 | 3.33 | 0.60 | 1.06 | 0.42 | 0.062 | 0.89 |
| *Uncinia viridis* | 0.17 | 3.12 | 23 | 2.93 | 0.0049 | 120.80 | 3.24 | 0.47 | 0.89 | 0.26 | 0.069 | 0.94 |
| *Uncinia zotovii* | 0.20 | 4.69 | 42 | 2.96 | 0.0062 | 91.00 | 3.26 | 0.57 | 1.08 | 0.36 | 0.081 | 0.85 |

| **Site SC1 Pelada** | *Thick* | *Area* | *Inclin* | *Succ* | *SLW* | *Shape* | *Chl* a/b | *Chl* | *N* | *SF* | *P* | *Lobe* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Amomyrtus luma* | 0.30 | 2.44 | 23 | 2.62 | 0.0100 | 2.06 | 2.20 | 0.42 | 1.03 | 0.15 | 0.065 | 1.12 |
| *Asteranthera ovata* | 0.36 | 1.70 | 33 | 4.65 | 0.0045 | 1.36 | 2.73 | 1.04 | 0.98 | 0.37 | 0.088 | 0.90 |
| *Azara lanceolata* | 0.14 | 1.70 | 12 | 3.59 | 0.0021 | 2.95 | 2.69† | 5.53† | 1.61 | 0.18 | 0.116 | 1.05 |
| *Berberis linearifolia* | 0.35 | 1.61 | 12 | 2.95 | 0.0102 | 6.85 | 2.19 | 0.65 | 1.48 | 0.25 | 0.129 | 1.00 |
| *Blechnum magellanicum* | 0.33 | 3.92 | 30 | 3.76 | 0.0094 | 4.47 | 2.13 | 0.72 | 0.95 | 0.13 | 0.066 | 1.06 |
| *Chusquea quila* | 0.10 | 4.73 | 40 | 2.74 | 0.0029 | 11.73 | 2.60† | 3.53† | 2.11 | 0.50 | 0.127 | 1.12 |
| *Desfontainia spinosa* | 0.35 | 15.70 | 16 | 3.33 | 0.0068 | 2.08 | 2.05 | 0.54 | 0.84 | 0.17 | 0.065 | 1.28 |
| *Drimys winteri* | 0.33 | 20.60 | 19 | 2.89 | 0.0118 | 2.90 | 2.07 | 0.35 | 0.86 | 0.16 | 0.048 | 1.12 |
| *Gaultheria phillyreifolia* | 0.30 | 0.95 | 27 | 2.94 | 0.0091 | 3.35 | 3.41 | 0.56 | 0.83 | 0.18 | 0.056 | 1.10 |
| *Grammitis magellanica* | 0.22 | 1.72 | 67 | 2.16 | 0.0104 | 12.24 | 2.15 | 0.37 | 0.91 | 0.00 | 0.064 | 1.29 |
| *Greigia landbeckii* | 0.43 | 30.10 | 29 | 3.48 | 0.0126 | 38.26 | 2.42 | 0.61 | 1.16 | 0.29 | 0.083 | 1.19 |
| *Hymenophyllum dentatum* | 0.04 | 5.16 | 73 | 1.82 | 0.0097 | 2.31 | 2.29 | 0.52 | 0.74 | 0.28 | 0.050 | 1.77 |
| *Hymenophyllum krauseanum* | 0.05 | 1.87 | 58 | 1.79 | 0.0081 | 1.99 | 2.80 | 0.58 | 0.82 | 0.26 | 0.049 | 2.42 |
| *Hymenophyllum pectinatum* | 0.06 | 6.66 | 77 | 2.03 | 0.0080 | 2.55 | 2.05 | 0.41 | 0.63 | 0.30 | 0.040 | 1.51 |
| *Hymenophyllum plicatum* | 0.06 | 7.23 | 61 | 2.27 | 0.0084 | 1.59 | 2.29 | 0.43 | 0.81 | 0.22 | 0.063 | 1.52 |
| *Laurelia philippiana* | 0.43 | 15.60 | 24 | 3.75 | 0.0104 | 2.41 | 2.59 | 0.87 | 1.72 | 0.21 | 0.111 | 1.12 |
| *Lophosoria quadripinnata* | 0.17 | 5.53 | 26 | 2.41 | 0.0064 | 3.76 | 2.12† | 2.06† | 1.46 | 0.13 | 0.079 | 1.50 |
| *Luzuriaga polyphylla* | 0.24 | 0.65 | 22 | 5.44 | 0.0033 | 3.19 | 1.94 | 1.15 | 1.27 | 0.18 | 0.074 | 0.95 |
| *Mitraria coccinea* | 0.34 | 1.51 | 14 | 5.71 | 0.0046 | 2.49 | 2.38 | 1.12 | 1.39 | 0.18 | 0.108 | 1.04 |
| *Myrceugenia chrysocarpa* | 0.57 | 4.01 | 26 | 2.82 | 0.0188 | 2.90 | 1.77 | 0.43 | 0.99 | 0.14 | 0.082 | 1.09 |
| *Nothofagus nitida* (C) | 0.40 | 1.14 | 36 | 2.10 | 0.0192 | 1.66 | 1.95 | 0.32 | 0.99 | 0.25 | 0.075 | 1.18 |
| *Nothofagus nitida* (J) | 0.27 | 2.05 | 22 | 2.36 | 0.0102 | 1.60 | 2.39 | 0.41 | 0.88 | 0.21 | 0.065 | 1.06 |
| *Philesia magellanica* | 0.41 | 1.23 | 28 | 3.68 | 0.0116 | 3.90 | 2.01 | 0.60 | 0.86 | 0.19 | 0.071 | 0.95 |
| *Podocarpus nubigena* | 0.34 | 0.87 | 37 | 2.42 | 0.0137 | 8.24 | 2.40 | 0.47 | 0.91 | 0.21 | 0.066 | 0.85 |
| *Pseudopanax laetevirens* | 0.19 | 2.55 | 16 | 3.63 | 0.0044 | 3.27 | 2.39 | 0.95 | 1.18 | 0.31 | 0.092 | 1.11 |
| *Ribes magellanicum* | 0.13 | 6.46 | 19 | 5.94 | 0.0024 | 0.89 | 2.31 | 1.35 | 1.82 | 0.19 | 0.140 | 1.44 |
| *Saxegothaea conspicua* | 0.21 | 0.51 | 27 | 2.53 | 0.0100 | 7.88 | 2.18† | 1.88† | 0.91 | 0.22 | 0.065 | 0.96 |
| *Ugni candollei* | 0.37 | 2.26 | 33 | 3.40 | 0.0099 | 2.17 | 2.41 | 0.47 | 0.91 | 0.20 | 0.068 | 1.05 |

| **Site SC2 Antillanca** | *Thick* | *Area* | *Inclin* | *Succ* | *SLW* | *Shape* | *Chl* a/b | *Chl* | *N* | *SF* | *P* | *Lobe* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Asplenium dareoides* | 0.20 | 4.28 | 32 | 3.13 | 0.0084 | 1.69 | 2.31 | 0.80 | 1.49 | 0.13 | 0.097 | 2.40 |
| *Asteranthera ovata* | 0.35 | 1.15 | 23 | 4.69 | 0.0055 | 1.37 | 2.73† | 1.05† | 1.47 | 0.30 | 0.125 | 0.80 |
| *Azara lanceolata* | 0.13 | 1.08 | 26 | 3.13 | 0.0035 | 2.50 | 2.37† | 3.57† | 1.68 | 0.21 | 0.109 | 1.05 |
| *Blechnum magellanicum* | 0.33 | 8.61 | 23 | 3.20 | 0.0075 | 7.22 | 2.19 | 0.51 | 0.91 | 0.17 | 0.082 | 0.99 |
| *Chusquea culeou* | 0.10 | 2.89 | 60 | 2.22 | 0.0048 | 11.96 | 3.73† | 0.94† | 1.93 | 0.60 | 0.105 | 1.10 |
| *Chusquea uliginosa* | 0.12 | 4.44 | 29 | 2.33 | 0.0052 | 14.21 | 2.47† | 2.37† | 1.79 | 0.44 | 0.096 | 1.06 |
| *Desfontainia spinosa* | 0.31 | 8.41 | 23 | 3.41 | 0.0065 | 2.19 | 2.32 | 0.54 | 0.90 | 0.18 | 0.081 | 1.35 |
| *Drimys winteri* var. *andina* | 0.29 | 12.00 | 20 | 3.27 | 0.0091 | 3.16 | 2.42 | 0.69 | 1.07 | 0.19 | 0.075 | 1.08 |
| *Grammitis magellanica* | 0.23 | 0.81 | 29 | 2.65 | 0.0100 | 9.74 | 2.13 | 0.69 | 1.00 | 0.00 | 0.085 | 1.06 |
| *Greigia landbeckii* | 0.37 | 25.80 | 34 | 4.02 | 0.0134 | 27.77 | 2.51 | 0.81 | 0.98 | 0.12 | 0.068 | 1.26 |
| *Griselinia ruscifolia* | 0.36 | 2.51 | 19 | 3.24 | 0.0095 | 4.31 | 2.43 | 0.34 | 0.71 | 0.19 | 0.069 | 1.15 |
| *Hymenophyllum dentatum* | 0.06 | 2.14 | 56 | 2.33 | 0.0038 | 1.51 | 2.24 | 0.66 | 0.97 | 0.33 | 0.067 | 1.40 |
| *Hymenophyllum krauseanum* | 0.05 | 2.28 | 46 | 2.44 | 0.0061 | 1.86 | 2.80† | 0.79† | 0.95 | 0.20 | 0.060 | 3.33 |
| *Hymenophyllum* aff. *krauseanum* | 0.05 | 0.73 | 64 | 2.09 | 0.0049 | 1.25 | 2.16 | 0.44 | 0.79 | 0.19 | 0.057 | 1.51 |
| *Hymenophyllum pectinatum* | 0.08 | 5.60 | 68 | 2.00 | 0.0056 | 2.58 | 2.12 | 0.41 | 0.79 | 0.20 | 0.060 | 1.58 |
| *Hymenophyllum plicatum* var. *plicatum* | 0.04 | 6.86 | 54 | 2.12 | 0.0078 | 1.31 | 2.43 | 0.55 | 1.01 | 0.18 | 0.084 | 1.74 |
| *Hymenophyllum* aff. *plicatum* | 0.06 | 10.00 | 27 | 2.36 | 0.0071 | 1.23 | 2.28† | 2.03† | 1.29 | 0.41 | 0.089 | 2.77 |
| *Laurelia philippiana* (J) | 0.30 | 10.60 | 17 | 4.14 | 0.0057 | 2.27 | 2.33 | 0.77 | 1.38 | 0.16 | 0.094 | 1.18 |
| *Luzuriaga radicans* | 0.28 | 0.64 | 21 | 4.53 | 0.0073 | 4.45 | 2.44 | 0.98 | 1.40 | 0.18 | 0.137 | 1.08 |
| *Lycopodium aff. paniculatum* | 0.08 | 0.01 | 45 | 2.60 | 0.0065 | 10.50 | 2.39 | 0.56 | 1.22 | 0.68 | 0.085 | 1.05 |
| *Maytenus magellanica* | 0.41 | 6.90 | 24 | 2.86 | 0.0119 | 3.68 | 2.31 | 0.50 | 0.93 | 0.18 | 0.071 | 1.17 |
| *Myoschilos oblonga* | 0.17 | 1.23 | 25 | 4.54 | 0.0048 | 6.75 | 1.87 | 0.62 | 1.62 | 0.23 | 0.368 | 0.90 |
| *Myrceugenia chrysocarpa* | 0.43 | 4.77 | 21 | 2.37 | 0.0140 | 2.46 | 1.92 | 0.46 | 1.02 | 0.11 | 0.091 | 1.04 |
| *Nertera granadensis* | 0.19 | 0.36 | 14 | 5.50 | 0.0032 | 1.30 | 2.30 | 0.96 | 1.58 | 0.37 | 0.093 | 1.09 |
| *Nothofagus dombeyi* (C) | 0.30 | 0.73 | 45 | 2.04 | 0.0154 | 1.67 | 2.26 | 0.46 | 1.22 | 0.22 | 0.079 | 1.19 |
| *Nothofagus dombeyi* (J) | 0.19 | 1.15 | 20 | 2.10 | 0.0083 | 2.01 | 2.76† | 0.60† | 1.03 | 0.24 | 0.076 | 1.08 |
| *Pernettya mucronata* | 0.31 | 0.52 | 24 | 2.64 | 0.0148 | 3.01 | 2.01 | 0.41 | 0.85 | 0.17 | 0.051 | 1.03 |
| *Philesia magellanica* | 0.40 | 1.12 | 15 | 3.03 | 0.0149 | 4.03 | 2.37 | 0.58 | 0.86 | 0.24 | 0.064 | 0.99 |
| *Podocarpus nubigena* (J) | 0.23 | 0.54 | 23 | 2.47 | 0.0109 | 10.98 | 2.27 | 0.56 | 0.82 | 0.26 | 0.069 | 1.00 |
| *Pseudopanax laetevirens* | 0.20 | 4.57 | 22 | 3.50 | 0.0042 | 2.55 | 2.28 | 0.79 | 1.26 | 0.26 | 0.125 | 1.04 |
| *Saxegothaea conspicua* | 0.24 | 0.25 | 45 | 2.21 | 0.0137 | 8.26 | 2.05† | 1.36† | 1.00 | 0.22 | 0.073 | 0.79 |
| *Serpyllopsis caespitosa* | 0.05 | 0.17 | 54 | 2.44 | 0.0078 | 2.77 | 2.15 | 0.79 | 0.69 | 0.31 | 0.056 | 1.40 |
| *Uncinia erinacea* | 0.14 | 2.04 | 36 | 3.16 | 0.0044 | 131.00 | 2.63 | 0.75 | 1.17 | 0.22 | 0.118 | 0.88 |
| *Valeriana* sp. | 0.28 | 7.91 | 21 | 10.40 | 0.0016 | 1.32 | 1.72 | 0.69 | 1.80 | 0.44 | 0.134 | 0.67 |

| **Site SA1 Quetrihué** | *Thick* | *Area* | *Inclin* | *Succ* | *SLW* | *Shape* | *Chl* a/b | *Chl* | *N* | *SF* | *P* | *Lobe* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Acaena ovalifolia* | 0.12 | 1.39 | 15 | 3.36 | 0.0033 | 2.25 | 3.14 | 0.96 | 2.17 | 0.34 | 0.186 | 1.00 |
| *Adenocaulon chilense* | 0.15 | 20.90 | 18 | 4.54 | 0.0026 | 2.01 | 2.85 | 0.75 | 1.31 | 0.34 | 0.260 | 1.00 |
| *Alstroemeria aurea* | 0.18 | 7.09 | 38 | 8.28 | 0.0013 | 4.08 | 5.38† | 0.30† | 1.71 | 0.11 | 0.150 | 1.14 |
| *Aristotelia chilensis* | 0.20 | 31.30 | 14 | 2.87 | 0.0053 | 2.08 | 3.02 | 0.89 | 1.63 | 0.21 | 0.200 | 1.06 |
| *Austrocedrus chilensis* | 0.35 | 1.68 | 27 | 2.48 | 0.0080 | 3.01 | 3.12 | 0.56 | 1.10 | 0.26 | 0.136 | 2.93 |
| *Azara microphylla* | 0.18 | 1.01 | 18 | 2.64 | 0.0049 | 1.55 | 3.14 | 0.85 | 1.76 | 0.23 | 0.152 | 0.94 |
| *Baccharis* aff. *salicifolia* | 0.22 | 7.55 | 16 | 3.25 | 0.0046 | 3.09 | 3.03 | 0.94 | 1.43 | 0.22 | 0.110 | 1.17 |
| *Berberis darwinii* | 0.30 | 2.36 | 20 | 2.37 | 0.0092 | 1.80 | 3.20 | 0.49 | 1.07 | 0.23 | 0.124 | 1.14 |
| *Blechnum auriculatum* | 0.17 | 0.77 | 14 | 3.67 | 0.0051 | 2.58 | 2.19† | 3.89† | 1.48 | 0.16 | 0.062 | 0.87 |
| *Carex* sp. | 0.17 | 17.90 | 34 | 3.14 | 0.0051 | 69.56 | 3.64 | 0.56 | 1.03 | 0.19 | 0.159 | 0.97 |
| *Cynanchum diemii* | 0.15 | 5.87 | 26 | 3.22 | 0.0037 | 3.63 | 3.34 | 1.08 | 2.03 | 0.37 | 0.184 | 0.95 |
| *Hymenophyllum* aff. *dentatum* | 0.03 | 6.00 | 31 | 2.00 | 0.0131 | 1.83 | 2.11† | 1.29† | 1.16 | 0.27 | 0.084 | 1.49 |
| *Loasa acerifolia* | 0.18 | 10.10 | 26 | 6.33 | 0.0028 | 1.21 | 3.07 | 0.94 | 1.51 | 0.27 | 0.213 | 1.28 |
| *Luma apiculata* | 0.39 | 2.66 | 20 | 2.88 | 0.0124 | 1.49 | 2.85 | 0.51 | 1.15 | 0.19 | 0.086 | 1.07 |
| *Maytenus chubutensis* | 0.35 | 0.60 | 20 | 2.41 | 0.0134 | 1.95 | 3.12 | 0.50 | 1.13 | 0.28 | 0.092 | 1.11 |
| *Mutisia decurrens* | 0.17 | 4.63 | 22 | 3.84 | 0.0040 | 4.99 | 2.93† | 0.87† | 1.42 | 0.20 | 0.172 | 0.96 |
| *Nothofagus dombeyi* (C) | 0.31 | 0.88 | 38 | 1.97 | 0.0177 | 2.22 | 3.40† | 0.34† | 1.43 | 0.20 | 0.100 | 1.09 |
| *Nothofagus dombeyi* (S) | 0.24 | 2.88 | 22 | 2.30 | 0.0085 | 1.88 | 2.64† | 0.67† | 1.43 | 0.24 | 0.081 | 1.14 |
| *Nothofagus dombeyi* (J) | 0.20 | 2.25 | 17 | 2.31 | 0.0059 | 1.55 | 2.64 | 0.67 | 1.17 | 0.25 | 0.091 | 1.17 |
| *Osmorhiza chilensis* | 0.09 | 2.10 | 22 | 4.87 | 0.0020 | 1.80 | 4.87† | 0.60† | 2.31 | 0.52 | 0.199 | 1.46 |
| *Pseudopanax laetevirens* | 0.20 | 4.43 | 10 | 3.50 | 0.0052 | 2.96 | 3.10 | 0.71 | 1.39 | 0.30 | 0.137 | 1.09 |
| *Rhaphithamnus cyanocarpus* | 0.23 | 1.43 | 24 | 2.42 | 0.0074 | 1.77 | 3.40 | 0.55 | 1.42 | 0.31 | 0.081 | 1.06 |
| *Ribes magellanicum* | 0.17 | 22.40 | 38 | 3.82 | 0.0034 | 1.01 | 3.35† | 0.83† | 1.92 | 0.24 | 0.305 | 1.28 |
| *Rosa rubiginosa* | 0.10 | 2.43 | 18 | 2.52 | 0.0027 | 1.25 | 3.21 | 0.59 | 1.41 | 0.40 | 0.107 | 1.02 |
| *Schinus patagonicus* | 0.24 | 4.71 | 24 | 2.49 | 0.0087 | 1.74 | 3.34 | 0.53 | 1.34 | 0.26 | 0.123 | 1.13 |
| *Solanum valdivianum* | 0.14 | 16.80 | 19 | 6.71 | 0.0013 | 2.02 | 3.02 | 1.51 | 2.36 | 0.16 | 0.115 | 1.02 |
| *Vicia nigricans* | 0.11 | 1.91 | 42 | 5.44 | 0.0015 | 2.54 | 3.30 | 1.22 | 3.10 | 0.40 | 0.173 | 1.01 |

| **Site SA2 Gutierrez** | *Thick* | *Area* | *Inclin* | *Succ* | *SLW* | *Shape* | *Chl* a/b | *Chl* | *N* | *SF* | *P* | *Lobe* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Alstroemeria aurea* | 0.17 | 7.58 | 24 | 7.38 | 0.0017 | 4.87 | 5.38 | 0.27 | 1.78 | 0.31 | 0.207 | 1.16 |
| *Aristotelia chilensis* | 0.21 | 29.50 | 14 | 3.10 | 0.0042 | 1.74 | 3.16 | 1.11 | 1.55 | 0.22 | 0.143 | 1.10 |
| *Austrocedrus chilensis* (S)† | 0.40 | 2.69 | 33 | 2.58 | 0.0060 | 2.77 | 2.64 | 0.62 | 1.26 | 0.23 | 0.130 | 2.25 |
| *Austrocedrus chilensis* (J) | 0.40 | 2.69 | 33 | 2.58 | 0.0060 | 2.77 | 2.64 | 0.62 | 1.26 | 0.23 | 0.130 | 2.25 |
| *Baccharis* aff. *salicifolia* | 0.22 | 5.46 | 18 | 3.61 | 0.0054 | 5.08 | 3.10 | 1.04 | 1.41 | 0.14 | 0.158 | 1.16 |
| *Berberis darwinii* | 0.32 | 1.66 | 28 | 2.33 | 0.0104 | 1.71 | 2.84 | 0.44 | 0.93 | 0.26 | 0.083 | 1.11 |
| *Chusquea culeou* | 0.09 | 4.36 | 29 | 2.15 | 0.0043 | 13.42 | 3.73 | 0.91 | 1.62 | 0.44 | 0.101 | 1.00 |
| *Maytenus chubutensis* | 0.36 | 0.66 | 27 | 2.62 | 0.0138 | 1.82 | 1.40 | 0.37 | 1.00 | 0.23 | 0.105 | 0.99 |
| *Mutisia decurrens* | 0.12 | 9.03 | 38 | 3.76 | 0.0024 | 4.99 | 2.93 | 0.85 | 1.38 | 0.22 | 0.187 | 0.96 |
| *Nothofagus dombeyi* (C) | 0.31 | 1.44 | 32 | 1.99 | 0.0141 | 2.04 | 3.40 | 0.34 | 1.24 | 0.28 | 0.090 | 1.13 |
| *Nothofagus dombeyi* (J) | 0.21 | 2.28 | 17 | 2.32 | 0.0056 | 1.83 | 2.88 | 0.65 | 1.09 | 0.29 | 0.110 | 1.16 |
| *Osmorhiza chilensis* | 0.08 | 2.86 | 24 | 3.94 | 0.0012 | 1.64 | 4.87 | 0.49 | 2.18 | 0.53 | 0.209 | 1.40 |
| *Ribes magellanicum* | 0.16 | 28.10 | 20 | 3.76 | 0.0033 | 0.82 | 3.35 | 0.82 | 1.84 | 0.29 | 0.245 | 1.18 |
| *Rosa rubiginosa* | 0.09 | 2.16 | 14 | 2.48 | 0.0021 | 1.38 | 3.34 | 0.93 | 1.52 | 0.40 | 0.133 | 1.00 |
| *Schinus patagonicus* | 0.22 | 3.76 | 19 | 2.88 | 0.0077 | 1.95 | 3.45 | 0.65 | 1.63 | 0.27 | 0.215 | 1.14 |
| *Vicia nigricans* | 0.12 | 2.35 | 22 | 5.37 | 0.0016 | 2.86 | 2.25 | 1.32 | 2.60 | 0.38 | 0.168 | 0.98 |
| *Viola maculata* | 0.22 | 7.79 | 38 | 5.37 | 0.0030 | 1.05 | 3.58 | 0.81 | 1.72 | 0.27 | 0.126 | 0.97 |