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

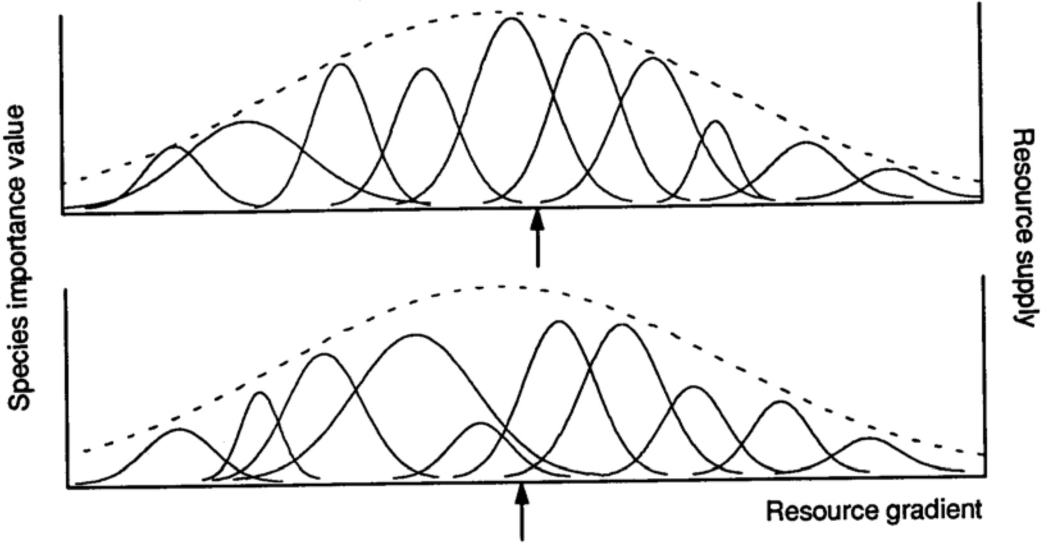
The phenomenon of convergence in the characters of phylogenetically-unrelated species in similar, but disjunct, environments is well documented, non-controversial, and the underlying mechanism — evolutionary selection for optimal adaptations to the same environmental conditions — is well-understood (Orians & 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.

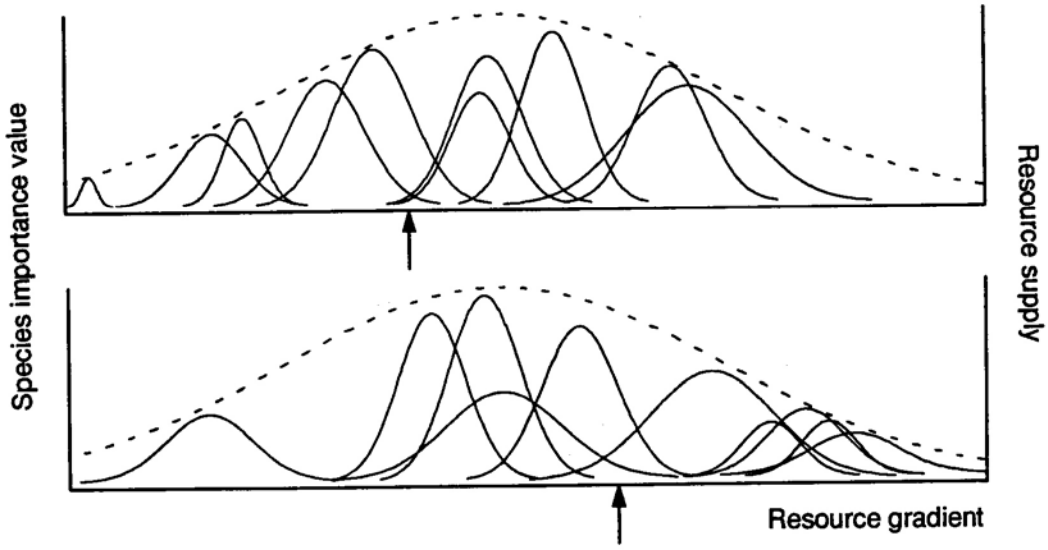
In dissimilar environments, communities are likely to be dissimilar in their niche structure, whether assembly rules operate or not. This is because realised niches would be clustered about different means in different conditions, as illustrated in Fig. 1.2. Compared with `null' communities produced 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.



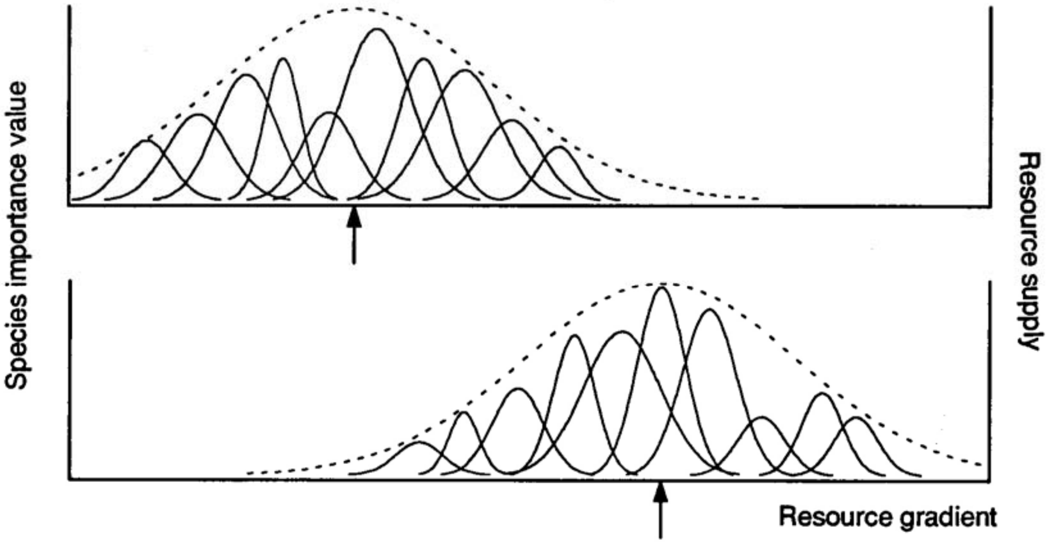
(a) Niche overdispersion



(b) Random niches

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.

(a) Niche overdispersion



(b) Random niches

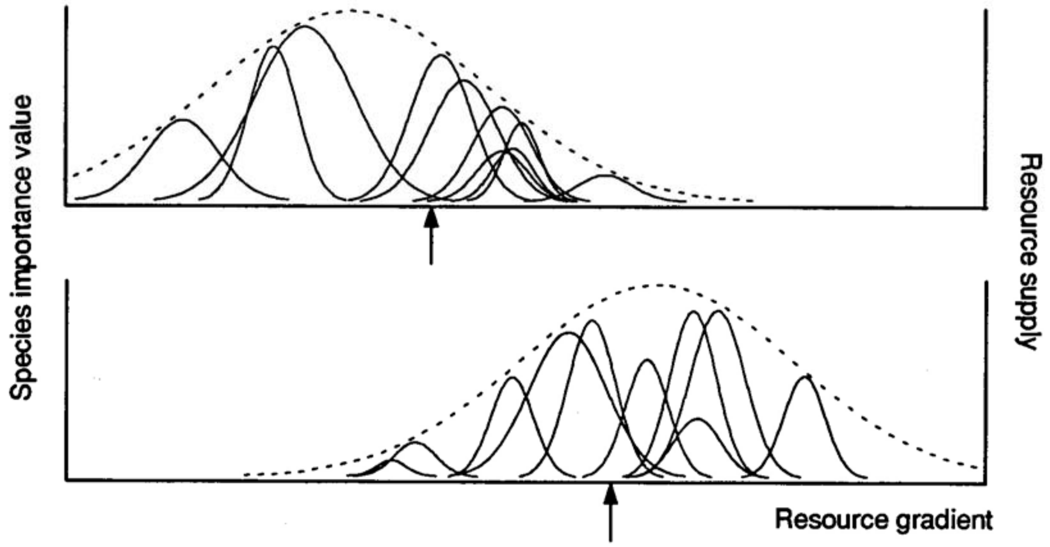


Fig. 1.2 Non-convergence in niche structure between two communities in different environments (format as for Fig. 1.1). If different resource spectra apply in the two communities, mean niches may be as dissimilar between communities if **(a)** assembly rules produce niche overdispersion as **(b)** if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

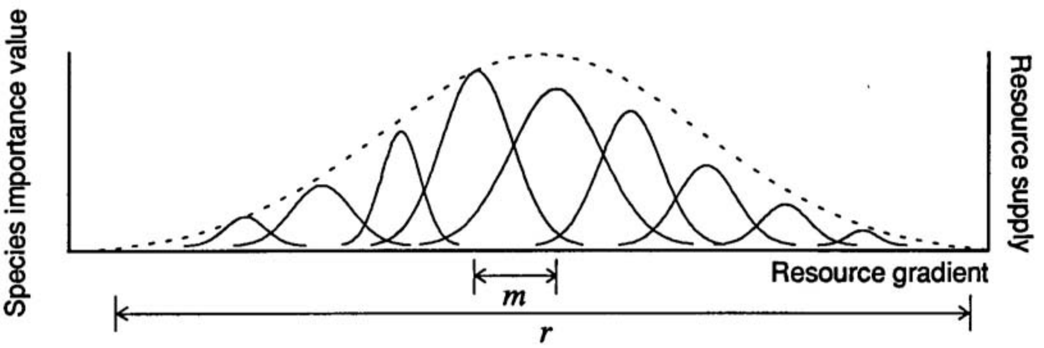


Fig. 1.3 Species packing as a control on species richness (Format as for Fig. 1.1). If assembly rules restrict co-occurrence of similar species in communities, maximum species richness will be determined by the available resource space (*r*) divided by the mean limiting similarity (*m*) between species.

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

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[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

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[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.

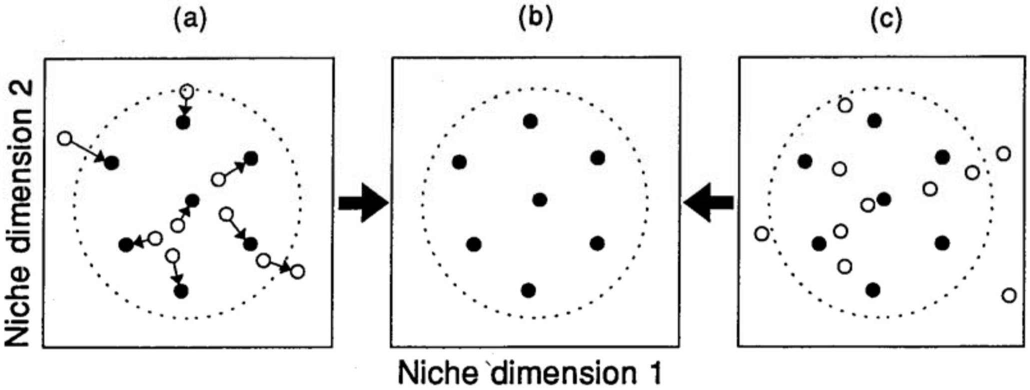

Fig. 1.4 Two hypotheses to account for niche (or character) overdispersion in communities (two niche dimensions case). Under ecological species sorting **(c)** species from the local pool (circles) disperse onto a site, establishing only if they are adapted to the abiotic conditions (area enclosed by 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).

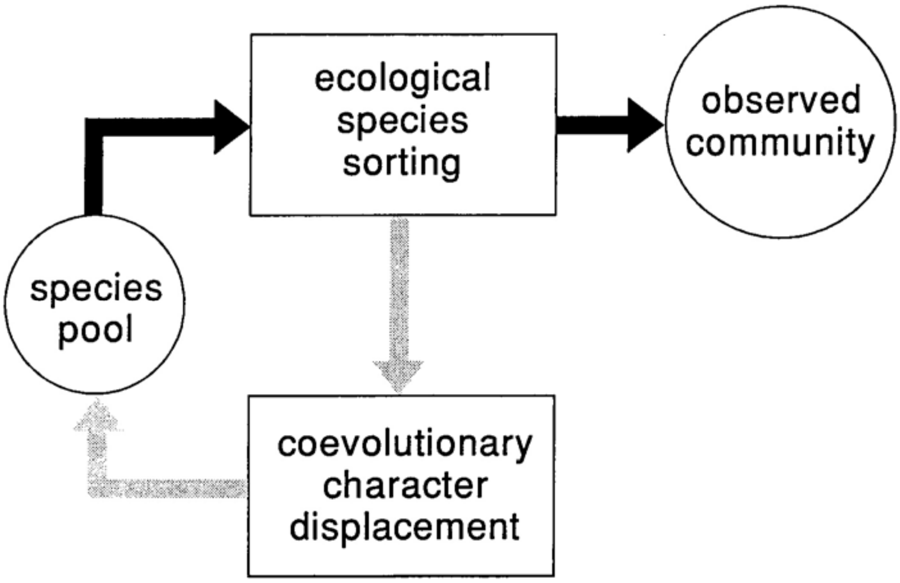

Fig. 1.5 Relationship between ecological species sorting and coevolutionary character displacement in producing community structure. All observed communities are the result of ecological sorting from the species pool over ecological time. In evolutionary time, ecological sorting may impose selection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

PREVIOUS STUDIES OF COMMUNITY-LEVEL CONVERGENCE

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.

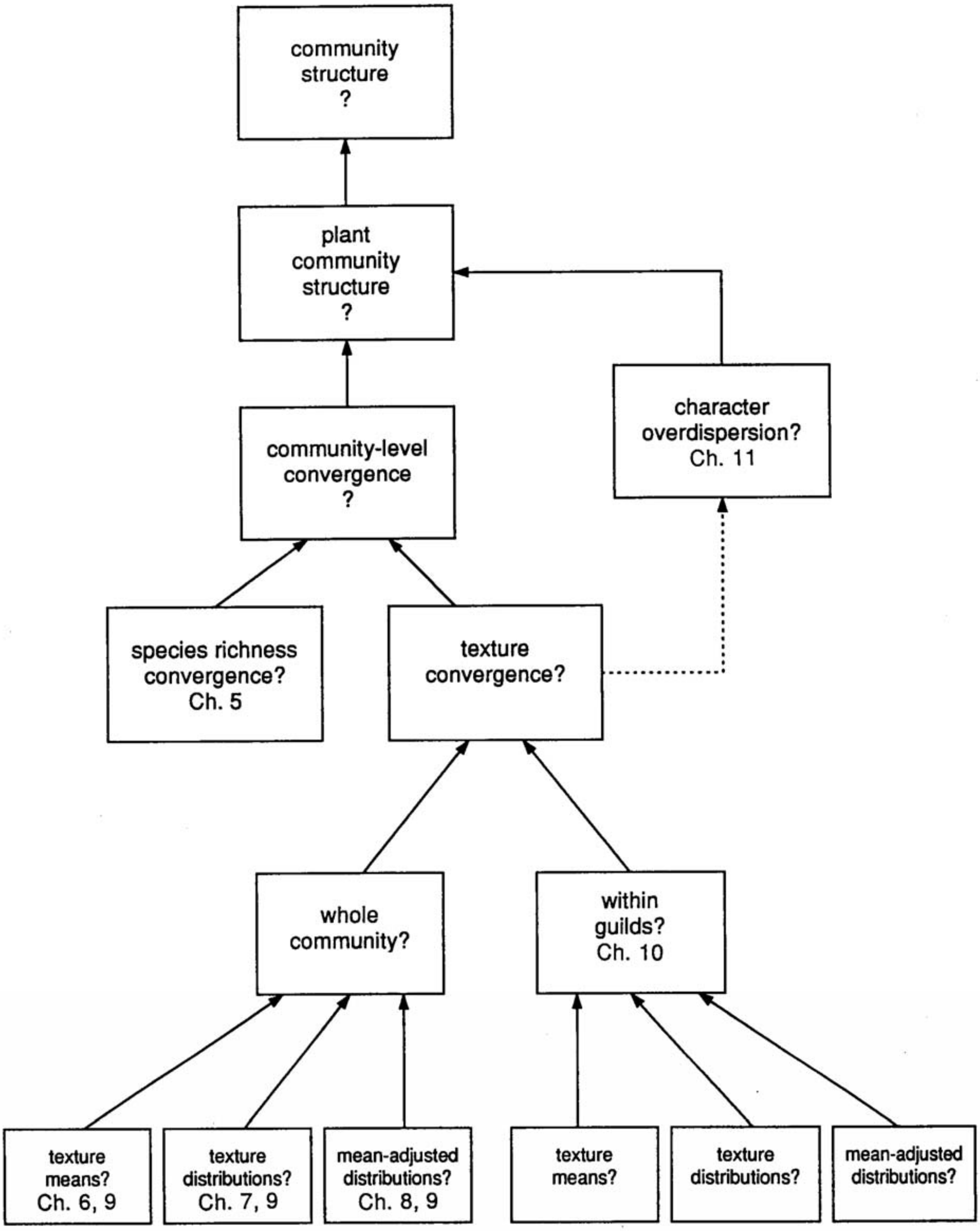

Fig. 1.6 The hierarchy of hypotheses addressed in this study (see text), with references to relevant chapters.