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.

INTERPRETATION OF OBSERVED PATTERNS

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

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[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.

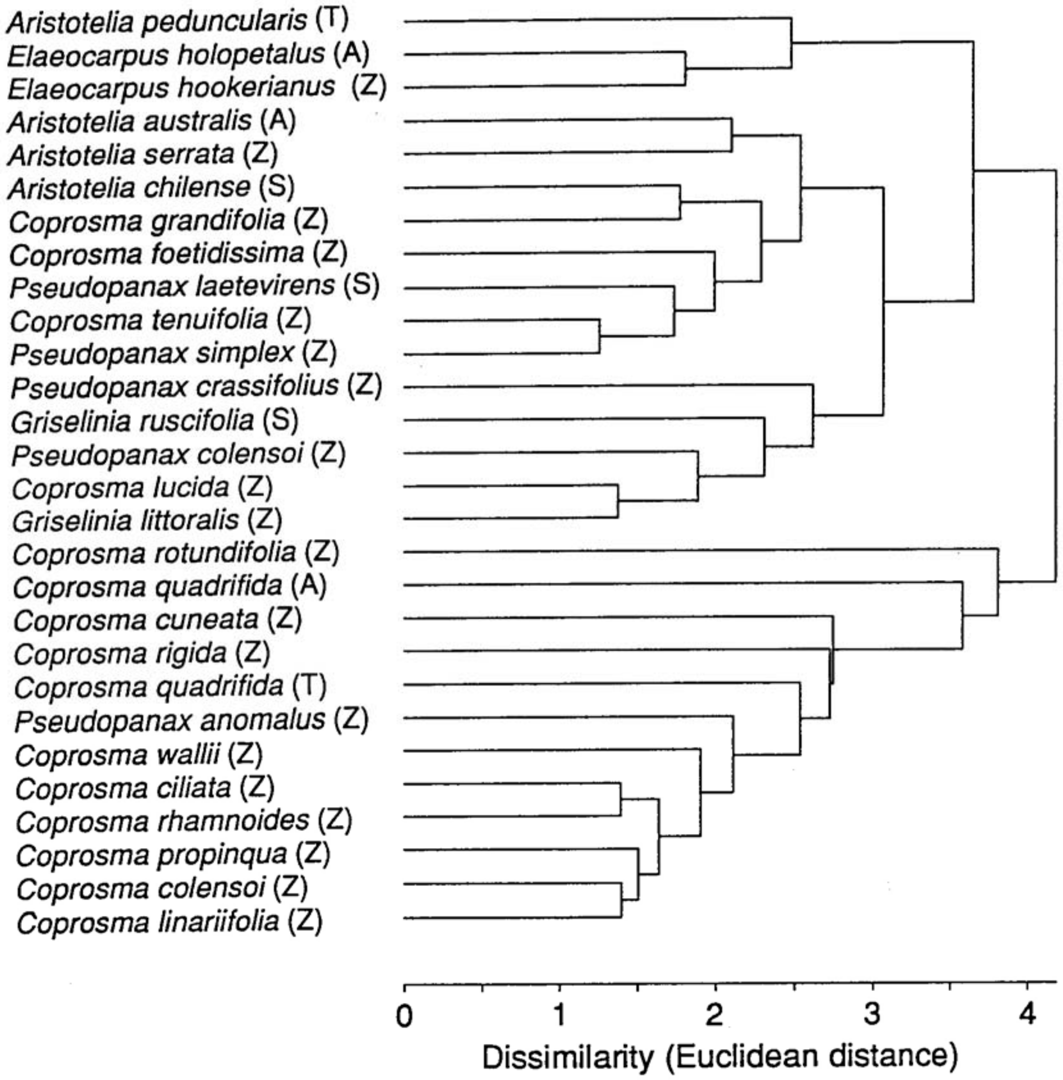

Fig. 12.1 Functional classification by cluster analysis of species belonging to five shrub and small tree genera encountered on more than one landmass (T-Tasmania; A-Australia; Z-New Zealand; S-South America) in this study. Classification is based on transformed, standardised species values for 13 characters (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.