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

6.1 Introduction

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

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

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

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

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

6.2 Methods

TEXTURE DATA

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

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

ANALYSIS

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

The null model

If there are no biotic restrictions on the characters that species may have to be able to co-occur, distributions of species characters in communities should be statistically indistinguishable from distributions obtained when character values are assigned to communities at random. Random assignment of the observed species character values to sites is therefore the basis for an appropriate null model¹. However, constraints must be built into the null model so that statistically significant departure from it can be uniquely attributed to mechanisms incorporated in the hypothesis being tested (Strong *et al.* 1979; Tokeshi 1986; Wilson 1995).

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

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

Treatment of site species richness

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

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

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

Treatment of abundance data.

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

Treatment of common species

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

of 'convergence' due to common² species, it is necessary to effectively exclude these species from analysis.

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

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

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

where x_i = character value for species *i*;

n = number of species in the community;

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

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

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

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

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

Multiple records for the same species

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

Abundance weighting for community texture

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

1. by presence, i.e. equally;

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

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

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

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

Pooled communities

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

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

where x_i = character value for species or entity at site *i*;

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

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

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

Randomisation tests

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



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

Randomisation algorithm

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

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

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

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

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

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

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

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

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

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

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

Comparison of observed with null communities

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

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

where s = number of species and entities present in community;

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

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

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

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

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

where n = the number of communities being compared;

 $X_{T,i}$ = the mean for texture variate T in community *i*;

 \overline{x}_T = the mean of $X_{T,i}$ across all *n* communities, for variate *T*.

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

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

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

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

Binomial test for overall significance

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

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

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

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

The scope of the 'experiment' is not necessarily clear: in the case of the present study it could consist of all comparisons of community texture means with respect to one texture variate and weighting method; all tests in this chapter; all the tests done in the whole study; or even all tests carried out in the lifetime of the investigator (Fisher & van Belle 1993). The application of Bonferroni correction to achieve an experimentwise target significance of 0.05 for this chapter would require a target significance in each test of $0.05 / 1612 = 3.1 \times 10^{-5}$. For various practical and theoretical reasons, such highly significant departure from null model expectation is unlikely to be demonstrable.

An alternative approach is to ask the significance of the number of significances obtained, i.e. the probability that the significant results obtained in separate tests all represent type I errors. Problems of this type can be addressed using the binomial distribution. Given a random sample of size n from a population of which a proportion p of members possess some attribute A, the binomial distribution gives the probability that m members of the sample possess attribute A (Snedecor & Cochran 1967). In the present context, n would correspond to the number of independent tests done; A would represent significant departure from null expectation; p would be the target significance level and m the number of tests showing significance⁴.

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

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

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

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

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

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

6.3 Results

VALIDITY OF THE NULL MODEL

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

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

PATTERNS AMONG COMMUNITIES Landmass scale

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

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



(a) Tasmania / Australia / New Zealand / South America

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

(b) Tasmania / Australia



Abundance weighting method

Fig. 6.2 (continued)



Fig. 6.2 (continued)

(d) Tasmania / South America



(f) Australia / South America

Fig. 6.2 (continued)

Regional scale

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

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

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

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



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



(c) Balfour / Mathinna

Fig. 6.3 (continued)



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



(a) Southern / central / northern New Zealand

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



Fig. 6.5 (continued)

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

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

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

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



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

Local scale

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

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

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

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

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

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

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



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

(c) Ten Mile / Deer



Fig. 6.7 (continued)



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



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



(c) Ohakune / Clements

Fig. 6.9 (continued)



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

Closely matched sites from different landmasses

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

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

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

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



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



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



Fig. 6.12 (continued)

PATTERNS AMONG TEXTURE VARIATES

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

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

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

	Convergence			Divergence				
Variate	Presence	Rank	Sqrt biomass	Biomass	Presence	Rank	Sqrt biomass	Biomass
Area Shape Lobation Thickness Succulence SLW Inclination SF N P Total chl	$ \begin{array}{c} 1 (0) \\ 1 (1) \\ 1 (1) \\ 0 (0) \\ 1 (0) \\ 0 (0) \\ 1 (0) \\ 2 (1) \\ 0 (0) $	$\begin{array}{c} 0 (0) \\ 0 (0) \\ 0 (0) \\ 1 (1) \\ 0 (0) \\ 1 (0) \\ 1 (1) \\ 0 (0) \\ 0 (0) \\ 0 (0) \\ 0 (0) \\ 0 (0) \\ 0 (0) \\ 0 (0) \end{array}$	$\begin{array}{c} 0 \ (0) \\ 1 \ (1) \\ 0 \ (0) \\ 1 \ (1) \\ 3 \ (1) \\ 3 \ (2) \\ 0 \ (0) \\ 1 \ (1) \\ 0 \ (0) \\ 0 \ (0) \\ 2 \ (1) \\ 0 \ (0) \\ 0 \ (0) \end{array}$	$ \begin{array}{c} 1 (1) \\ 1 (1) \\ 1 (0) \\ 2 (0) \\ 3 (0) \\ 6 (2) \\ 0 (0) \\ 0 (0) \\ 0 (0) \\ 0 (0) \\ 1 (1) \\ 2 (1) \end{array} $	$7 (5^{**}) 0 (0) 1 (1) 1 (0) 4 (3^*) 4 (4^{**}) 0 (0) 2 (0) 9 (5^{**}) 18 (10^{**}) 10 (4^{**}) 18 (7^{*}) 18 (7^{*}) $	$8 (6^{**}) 1 (1) 1 (1) 2 (0) 0 (0) 4 (3^*) 2 (1) 1 (0) 2 (2) 17 (9^{**}) 10 (4^{**}) 15 (5^{**}) $	$\begin{array}{c} 4 (4^{**}) \\ 1 (1) \\ 0 (0) \\ 0 (0) \\ 0 (0) \\ 0 (0) \\ 1 (1) \\ 5 (2) \\ 0 (0) \\ 4 (2) \\ 5 (3^{*}) \\ 8 (2) \end{array}$	$\begin{array}{c} 3 (2) \\ 1 (1) \\ 0 (0) \\ 0 (0) \\ 0 (0) \\ 0 (0) \\ 0 (0) \\ 3 (2) \\ 0 (0) \\ 1 (0) \\ 1 (0) \\ 1 (0) \end{array}$
Height	0(0) 0(0)	0 (0) 1 (1)	5 (3*)	2 (1) 5 (2)	18 (7**) 3 (3*)	15 (5**) 3 (1)	8 (2) 0 (0)	1 (0) 0 (0)

*0.01≤*P*<0.001; ***P*<0.001 (no binomial probabilities in range 0.01≤*P*<0.05).

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

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

6.4 Discussion

COMMUNITY-LEVEL CONVERGENCE AND DIVERGENCE

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

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

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

Patterns in relation to environmental similarity

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

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

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

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

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

Factors underlying convergence and divergence

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

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

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

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

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

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

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

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

PREVIOUS STUDIES OF COMMUNITY TEXTURE CONVERGENCE

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

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

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

is unclear.

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

Analysis of variance and related tests

Schluter (1986) sought convergence ('similarity', in his terms⁵) in the morphology of finches from five continents using a modified analysis of variance with communities as `treatments' and characters of species within communities as `replicates.' A significantly low F statistic value (greater variation in morphology within than among communities on different continents) was interpreted as evidence that convergence had occurred. A variance deficit within continents would suggest overdispersion of species characters, and so, the operation of assembly rules (Pianka 1980). Significant convergence in finch body size was found, although body shape was divergent between continents.

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

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

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

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

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

Species-for-species matching

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

Null model randomisation tests

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

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

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

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

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

The present study in the context of previous work

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

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

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

CONCLUSIONS

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