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

8.1 Introduction

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

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

Are the effects of assembly rules on texture distributions likely to be independent of environmental differences? Interspecific competition, leading to competitive exclusion (Gause 1934; Hardin 1960), is often assumed to be the most important class of species interaction defining assembly rules (Diamond 1975; Strong *et al.* 1984). Some have suggested that limits to coexistence under competition would be determined by the size ratios of the species involved (Hutchinson 1959; MacArthur 1971; Barbour 1973; May 1978). The ratio 1:1.3 has often been invoked as a critical level of similarity in the body sizes of animals belonging to the same trophic guild (Hutchinson 1959; Ricklefs 1973; Pianka 1978). The ratio is supposed to remain constant across a wide range of animal groups and habitats (see reviews by Simberloff & Boeklen [1981]; MacNally [1988]). Analogous ratios have been suggested for plant phenological characters (Poole & Rathcke 1979; Pleasants 1980; Rabinowitz *et al.* 1981; Fleming & Partridge 1984; Armbruster *et al.* 1994). However, the evidence for constant size or character ratios has been strongly questioned (Simberloff & Boeklen 1981; MacNally 1988).

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

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

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

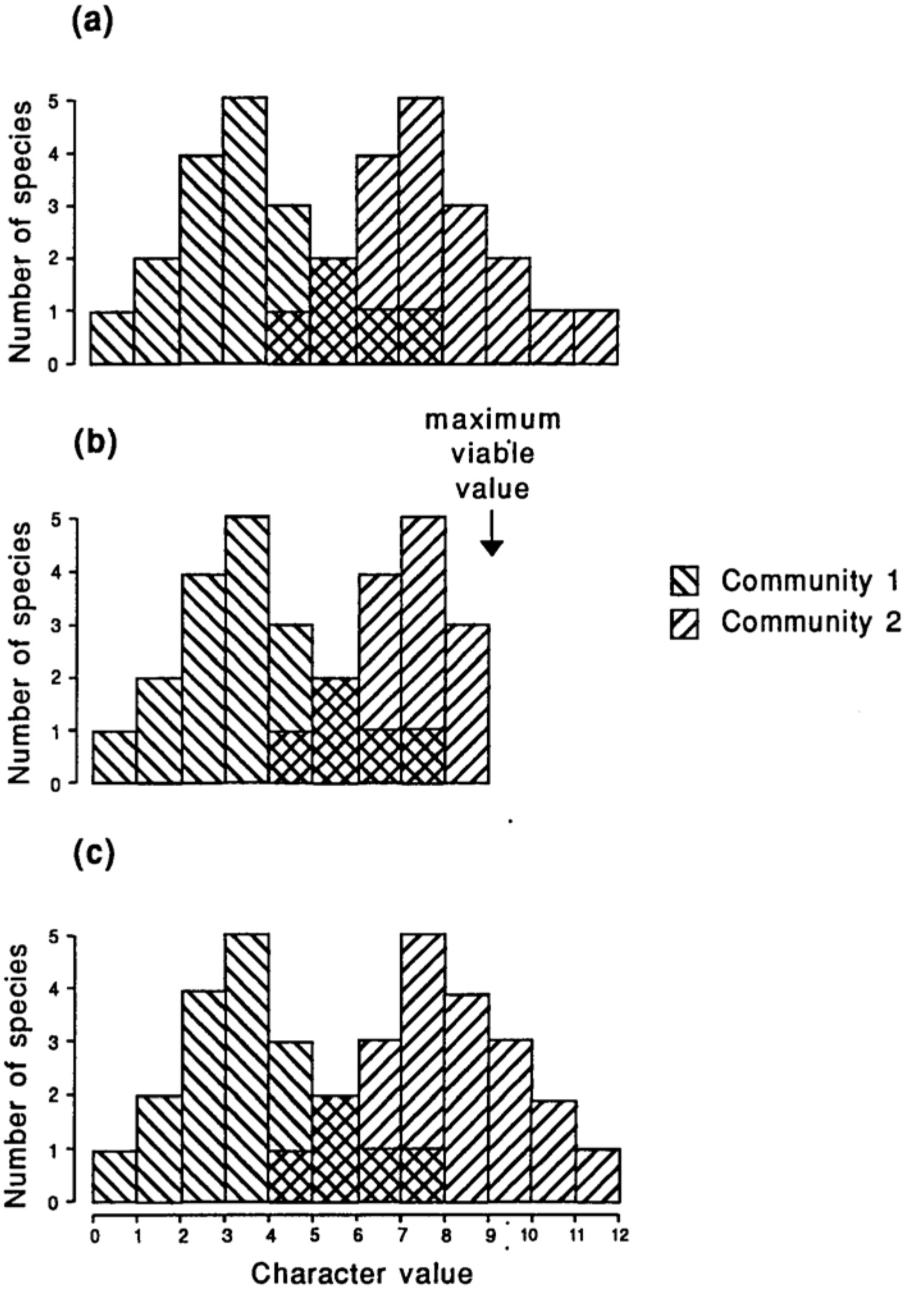


Fig. 8.1 Possible effects of a difference in the environment (and, therefore, in community texture means) on within-community distributions of a functional species character. **(a)** Distributions in Communities 1 and 2 have the same shape (i.e. relative representation of species in character value classes),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

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

8.2 Methods

TEXTURE DATA

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

ANALYSIS

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

Representation of community texture

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

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

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

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

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

where s = number of species or entities in community;

$x_{T,i}$ = transformed value of character T for species or entity[1] i;

X_T = the mean of the $x_{T,i}$'s for all s species in the community;

$\overline{X}_T$ = the mean of the X_T's for all communities being compared;

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

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

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

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

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

---

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

Comparison of observed with null communities

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

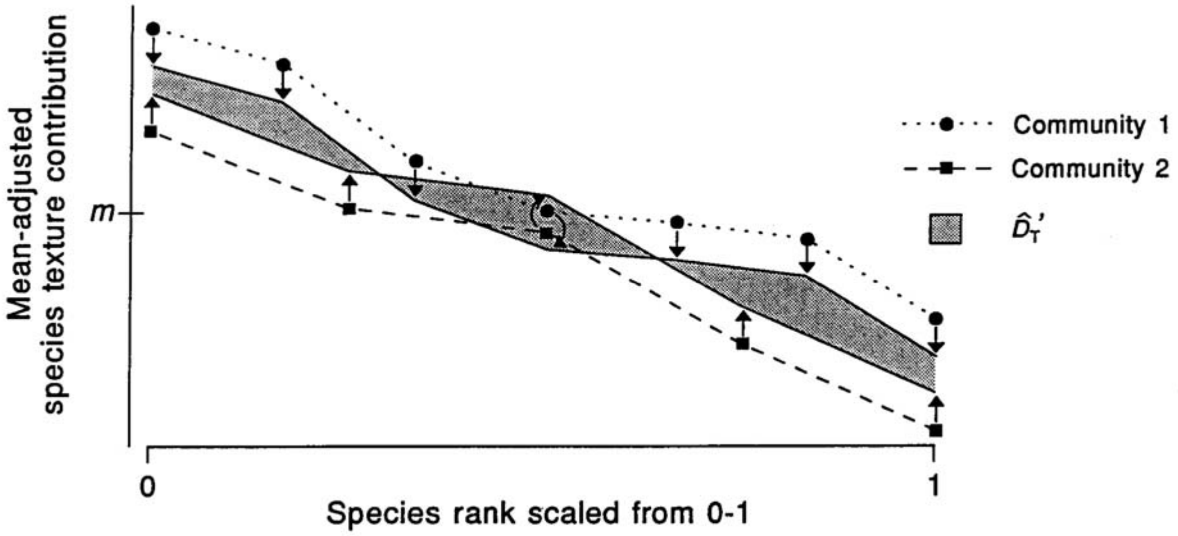


Fig. 8.2 Example demonstrating the calculation of the deviance of mean-adjusted texture distributions, $\hat{D}'_T$, between two communities. For two communities, $\hat{D}'_T$ is the area between mean-adjusted rank-scaled texture plots for each community. These plots are produced by plotting species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

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

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

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

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

Comparisons performed

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

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

8.3 Results

VALIDITY OF THE NULL MODEL

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

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

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

TEST STATISTIC BEHAVIOUR

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

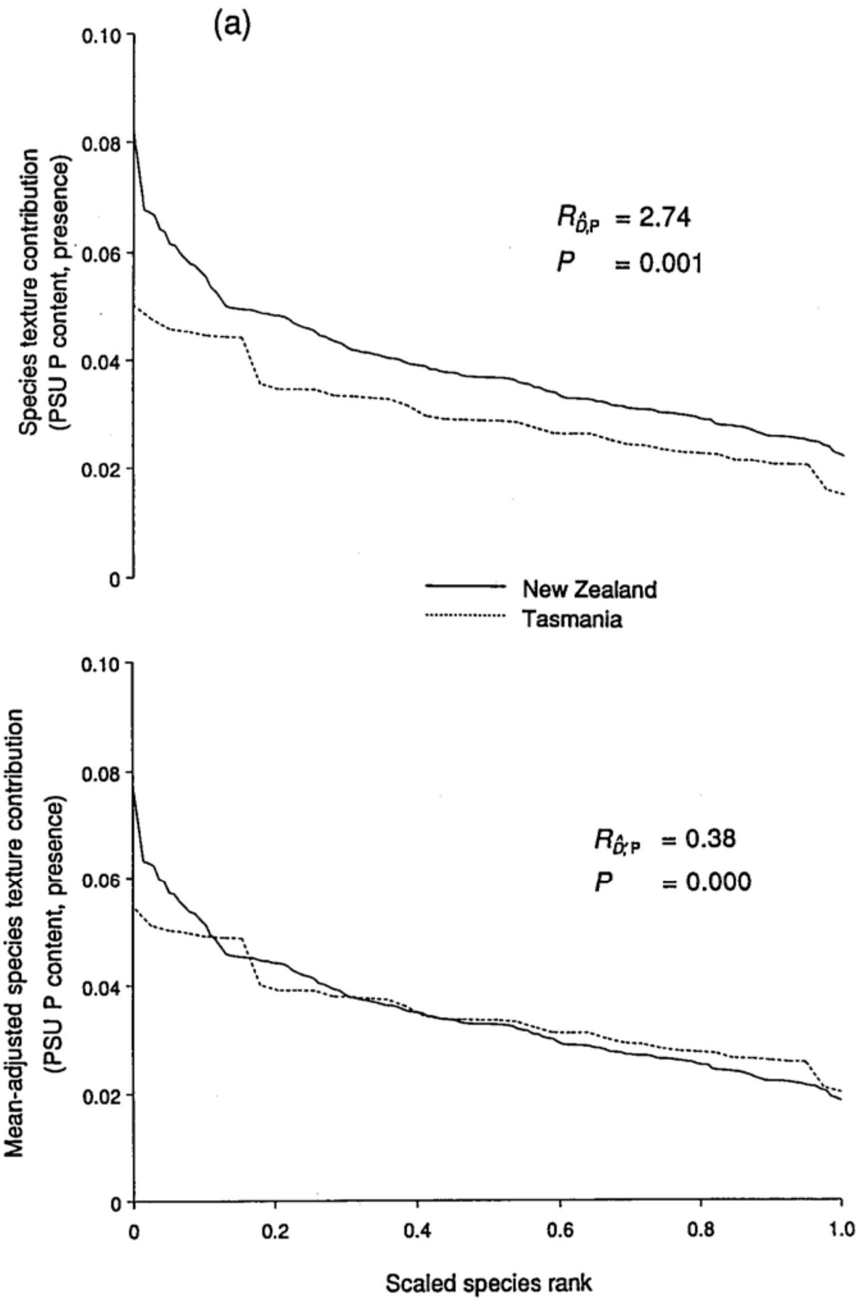


Fig. 8.3 Rank-scaled texture plots (Fig. 7.2) and mean-adjusted rank-scaled texture plots (Fig. 8.2) for *Nothofagus*-dominated communities illustrating departure from null expectation in opposite directions using indices $\hat{D}_T$ and $\hat{D}'_T$ to compare community texture. **(a)** Tasmania (T)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

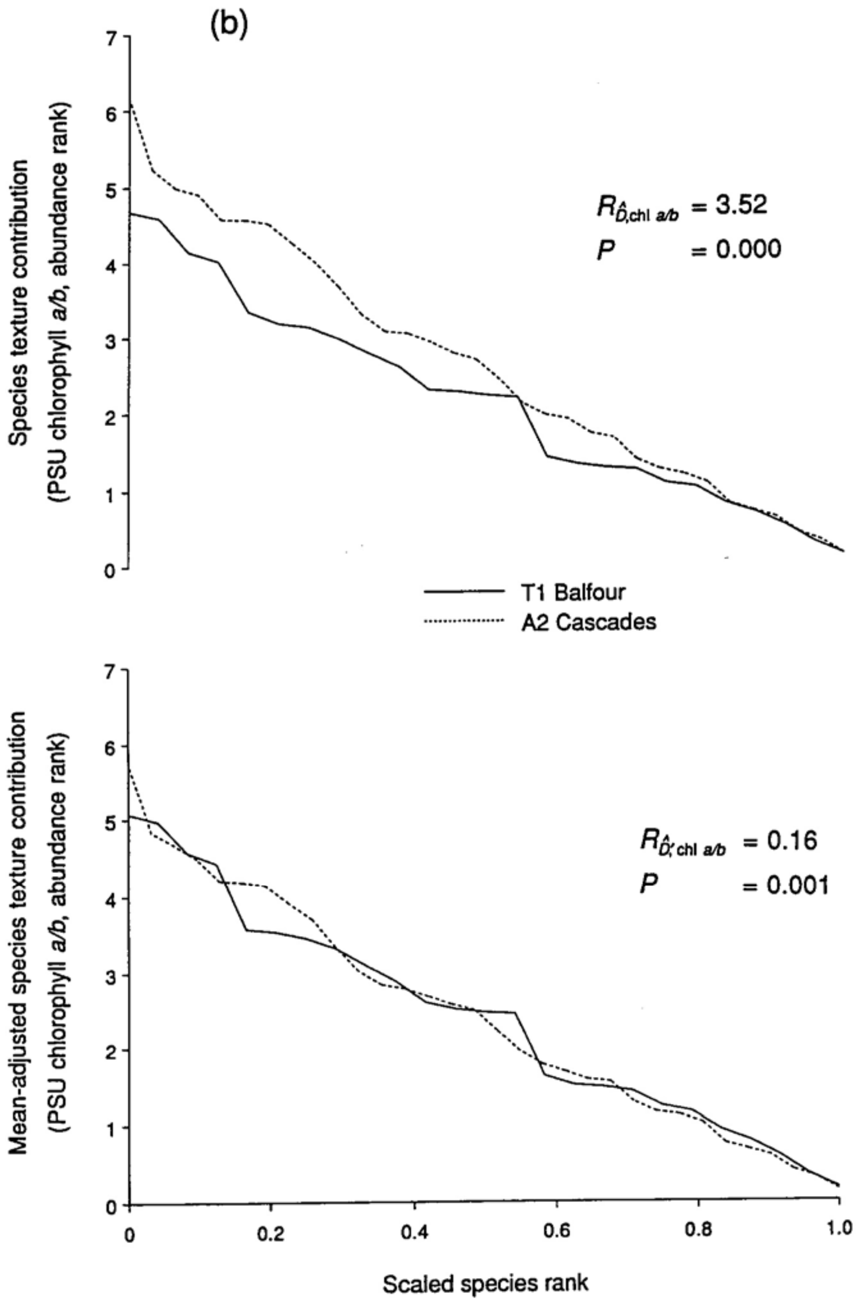


Fig. 8.3 (continued)

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

Where texture distributions differ significantly in their shapes in different communities, this may be because assembly rules are absent or weak. No convergence would then be detected by the tests used either in this chapter or in the previous one, i.e. whether or not texture means are ignored. For example, in Chapter 7, Australia and South America were found to be significantly divergent in the distributions of species values for support fraction (Fig. 8.4a). The texture distributions are quite dissimilar in shape, though not in their means, a lower proportion of species having extremely high or low support fraction in South American than Australian *Nothofagus*-dominated communities. Consequently, significant divergence was detected once again when mean-adjusted distributions were compared using $\hat{D}'_T$.

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

PATTERNS AMONG COMMUNITIES

Landmass scale

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

Comparing individual pairs of landmasses (Figs. 8.5b-g), there is a marked overall tendency towards convergence in many texture variates, and little significant divergence. Tasmania and Australia show the highest incidence of convergence, which is significant for PSU area, lobation, phosphorus content, total chlorophyll, chlorophyll *a/b* and species height with species weighted by presence or abundance rank (Fig. 8.5b). Tasmania and New Zealand, which were found to be most similar overall in their environments (Chapter 3) are significantly convergent in five variates at various weighting levels (Fig. 8.5c), but nearly all variates show an overall tendency towards convergence ($R_{\hat{D}';T}<1$), although only a minority of tests are significant. PSU total chlorophyll, chlorophyll *a/b* and phosphorus content are significantly convergent at low weighting levels for several pairs of landmasses. By contrast, these variates tended to be found significantly or non-significantly divergent, especially at lower abundance weighting levels, when texture means (Chapter 6) or non-adjusted distributions (Chapter 7) were compared (Figs. 7.5b-g, 6.2b-g).

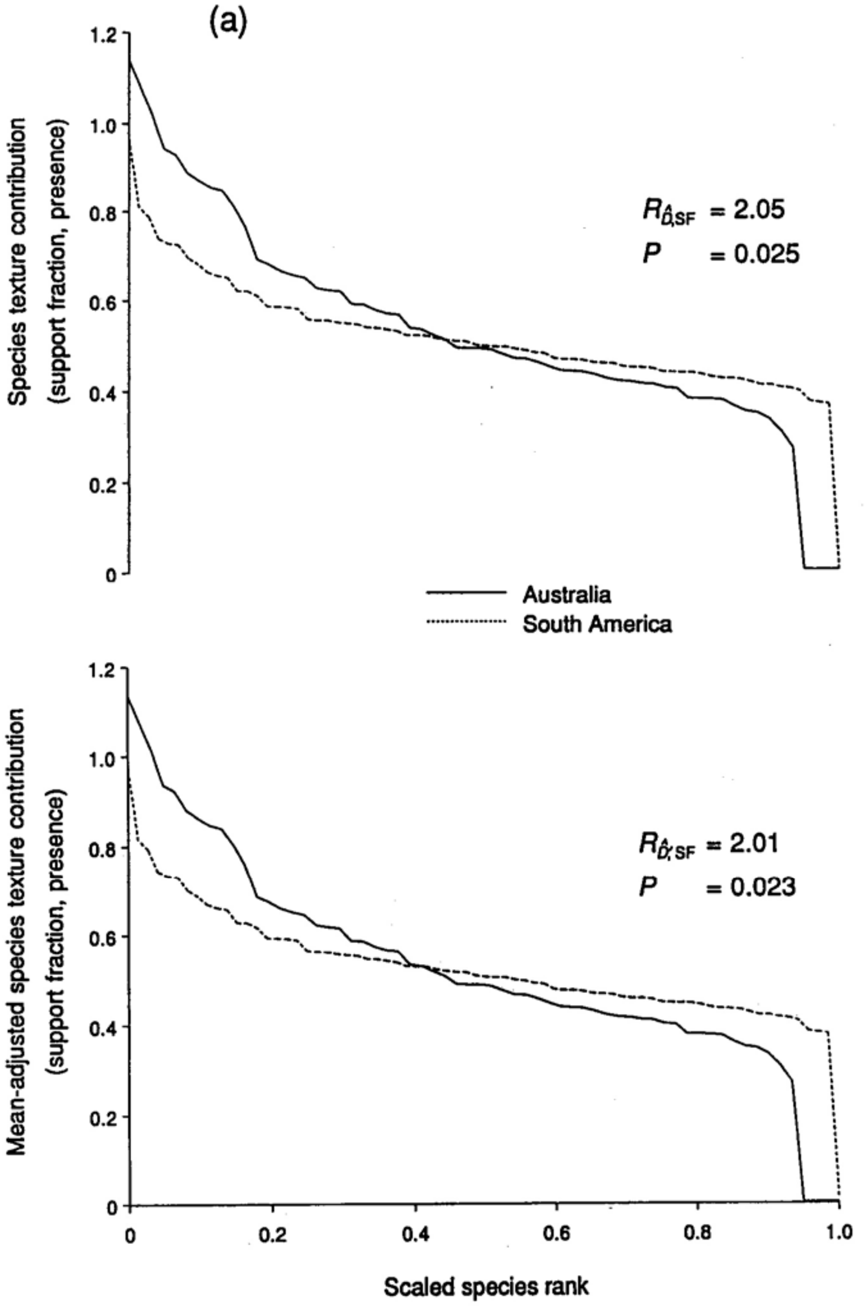


Fig. 8.4 Rank-scaled texture plots and mean-adjusted rank-scaled texture plots for *Nothofagus*-dominated communities demonstrating divergence using both indices $\hat{D}_T$ and $\hat{D}'_T$ to compare community texture. **(a)** Australia (A) and South America (S), significant divergence in support fraction (species weighted equally) using $\hat{D}_T$ and $\hat{D}'_T$; **(b)** A1 Lumeah and A2 Cascades, significant divergence in PSU shape (weighting by photosynthetic biomass) using $\hat{D}_T$, non-significant tendency towards divergence ($R_{\hat{D}';T}>1$; $P\geq0.05$) using $\hat{D}'_T$. Format as for Fig. 8.3.

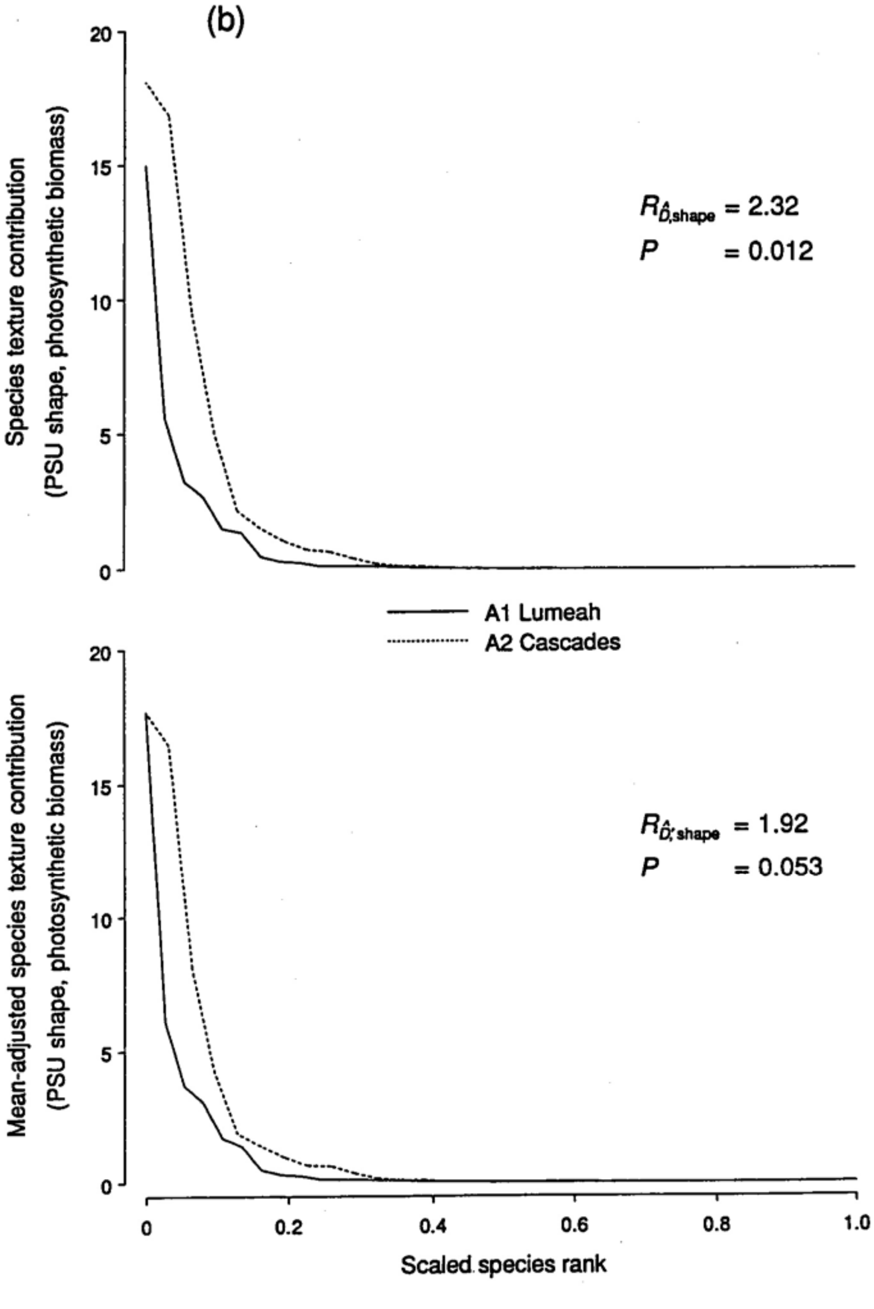


Fig. 8.4 (continued)

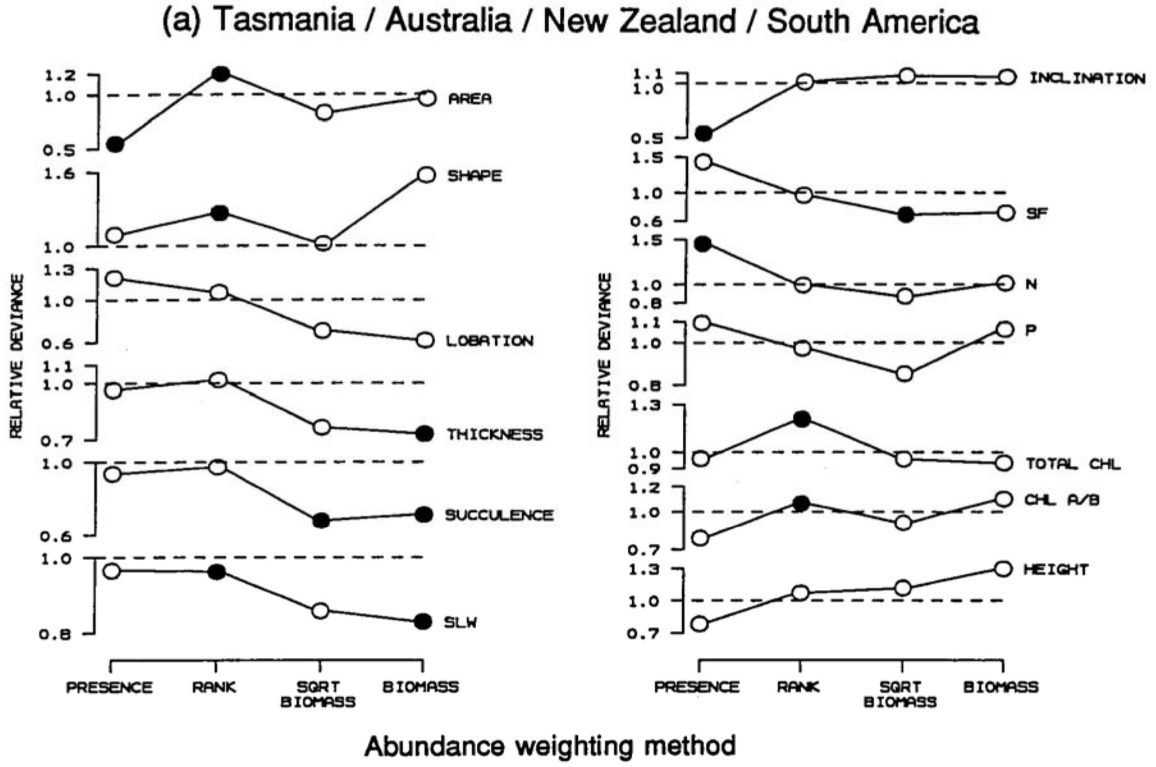
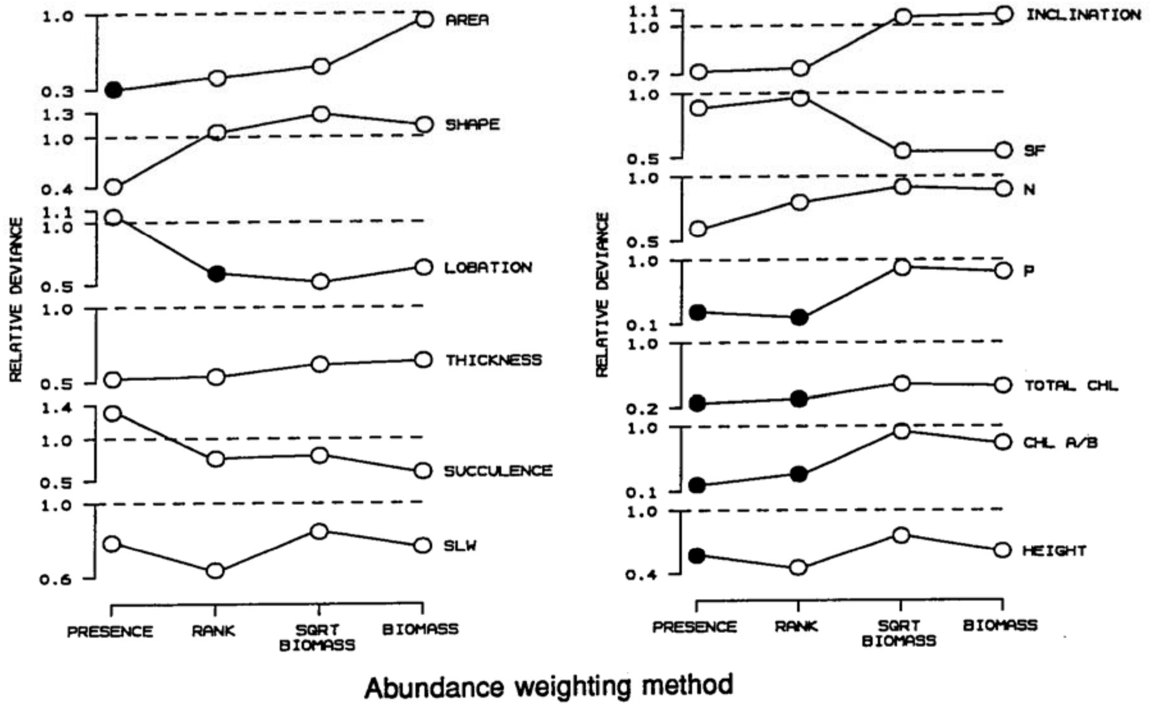


Fig. 8.5 Null model randomisation tests for convergence or divergence in mean-adjusted texture distributions (see text) between landmass-scale *Nothofagus*-dominated communities Tasmania (T), Australia (A), New Zealand (Z) and South America (S). The relative deviance $R_{\hat{D}';T}$ of among-community variation in texture distributions is shown for each of 13 texture variates and four methods of weighting individual species values by abundance in calculations of community texture means. A value of $R_{\hat{D}';T}<1$ indicates similarity in texture between communities relative to a null model simulating random community assembly (see text); $R_{\hat{D}';T}>1$ indicates dissimilarity relative to the null model. Broken lines signify null model expectation ($R_{\hat{D}';T}=1$). Filled symbols correspond to significant departure from the null model (convergence for $R_{\hat{D}';T}<1$; divergence for $R_{\hat{D}';T}>1$; $P<0.05$). Key to abbreviations: RANK=abundance rank; SQRT BIOMASS=square root of photosynthetic biomass; BIOMASS=photosynthetic biomass (see text for full explanation). Texture variates are based on PSU characters except SF (support fraction) and HEIGHT (species height). Key: SLW=specific weight; N=nitrogen content; P=phosphorus content; TOTAL CHL=total chlorophyll content; CHL A/B=chlorophyll *a/b* ratio (see text for full explanation).

(b) Tasmania / Australia



(c) Tasmania / New Zealand

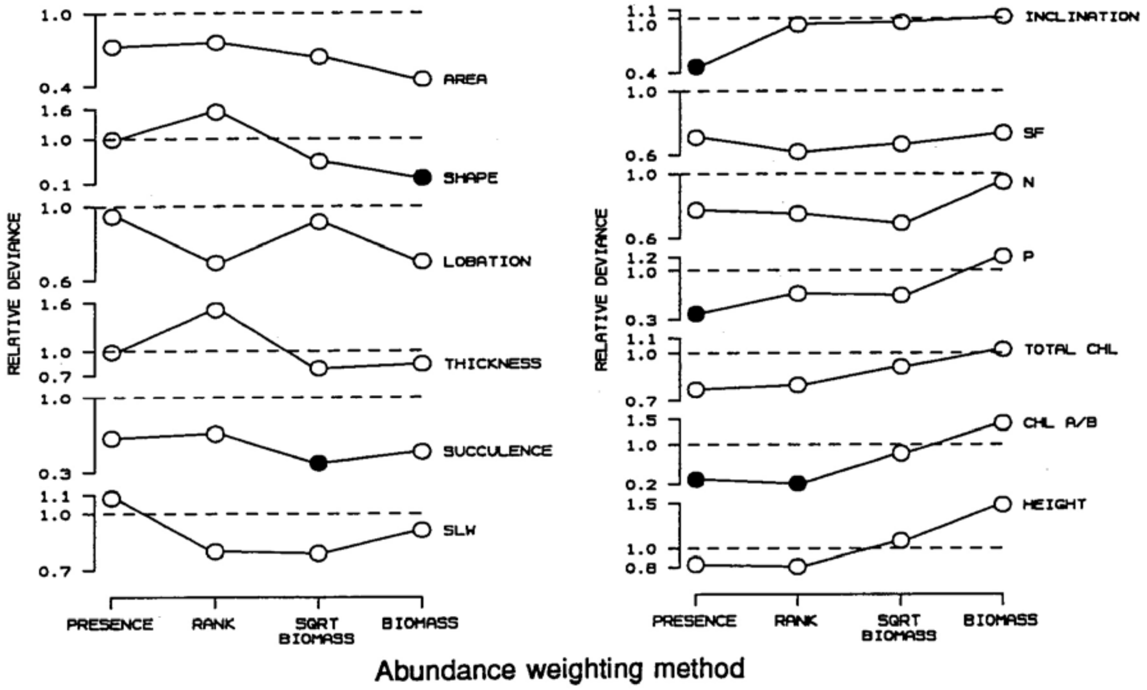
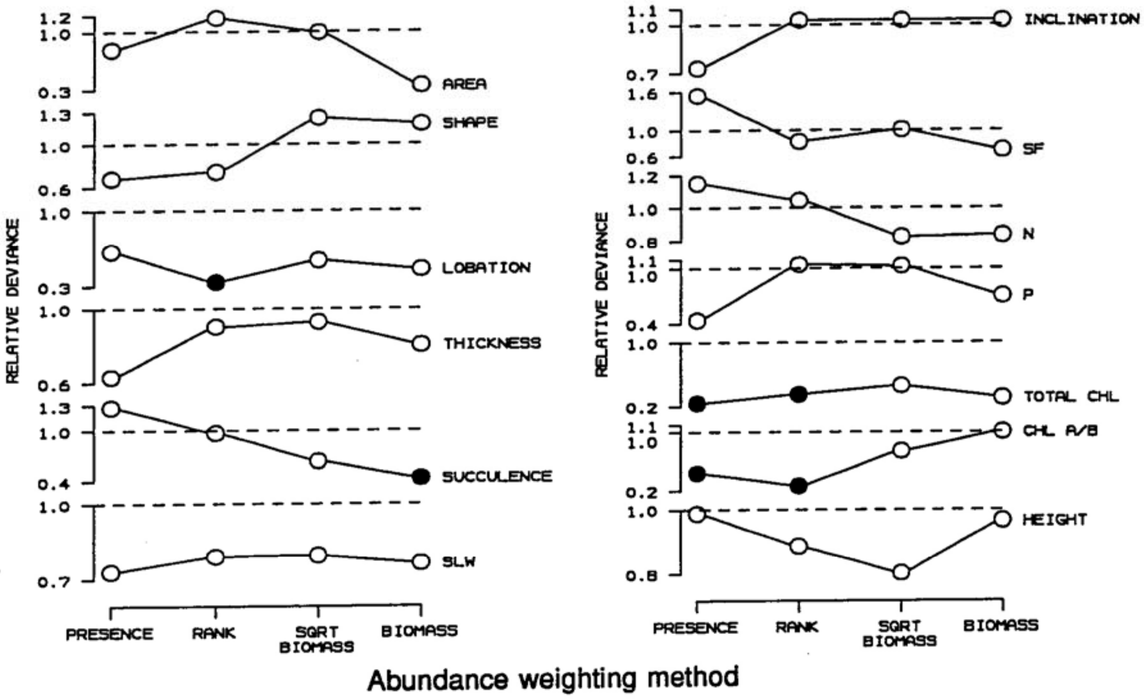


Fig. 8.5 (continued)

(d) Tasmania / South America



(e) Australia / New Zealand

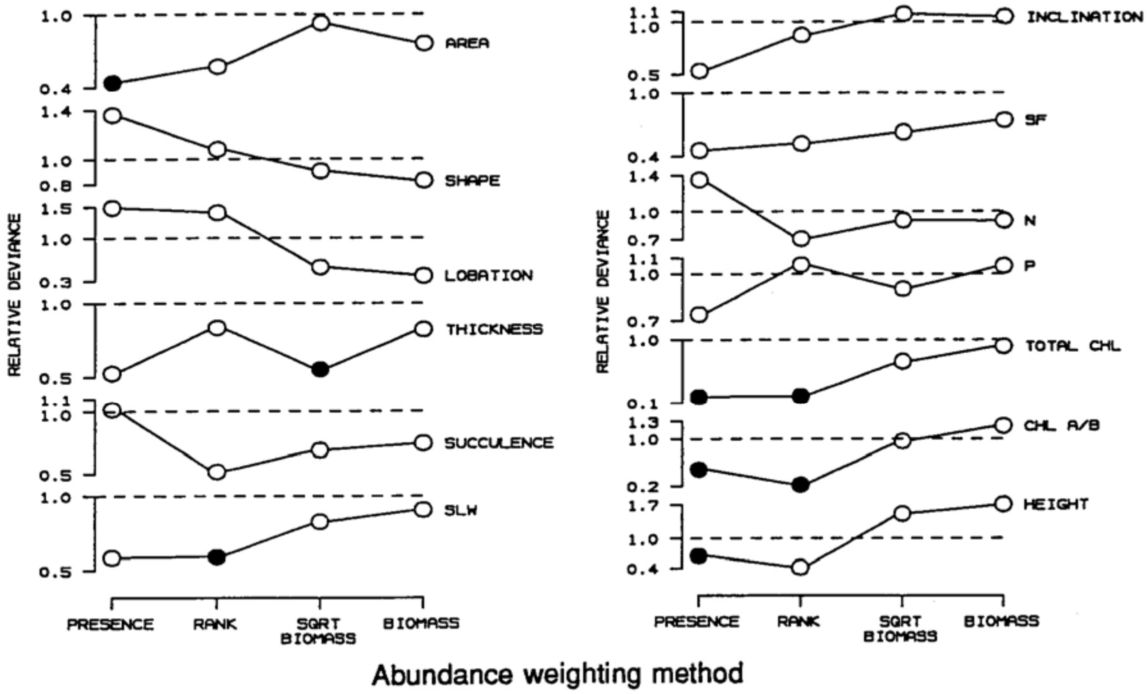
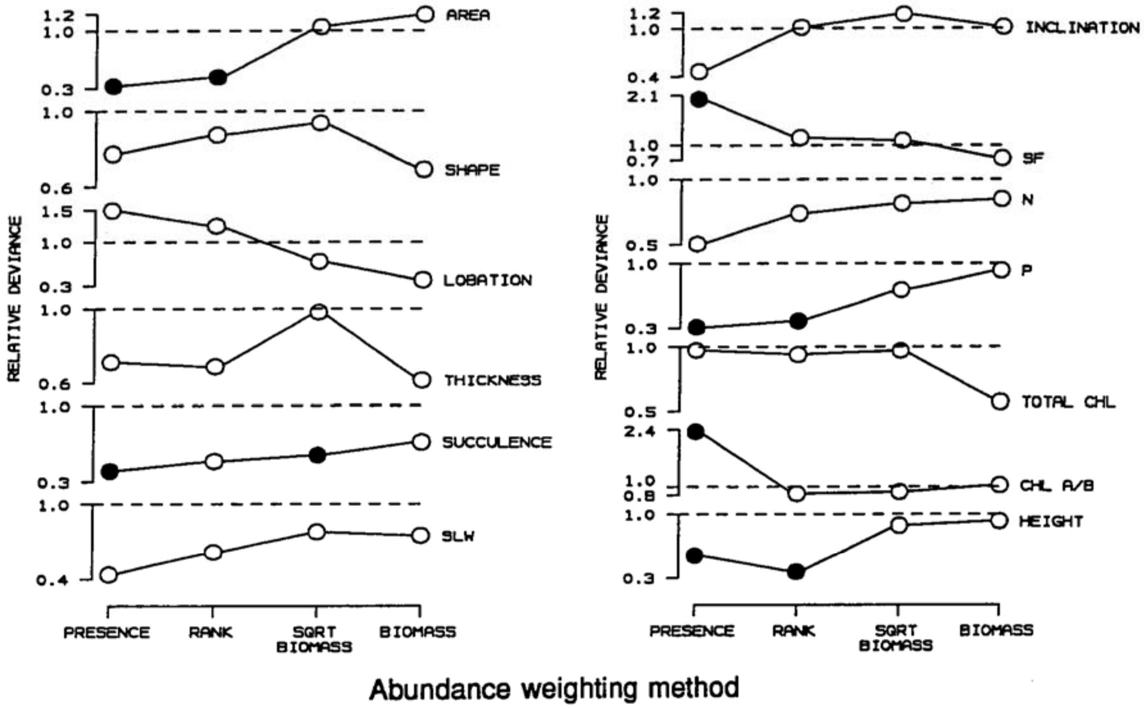


Fig. 8.5 (continued)

(f) Australia / South America



(g) New Zealand / South America

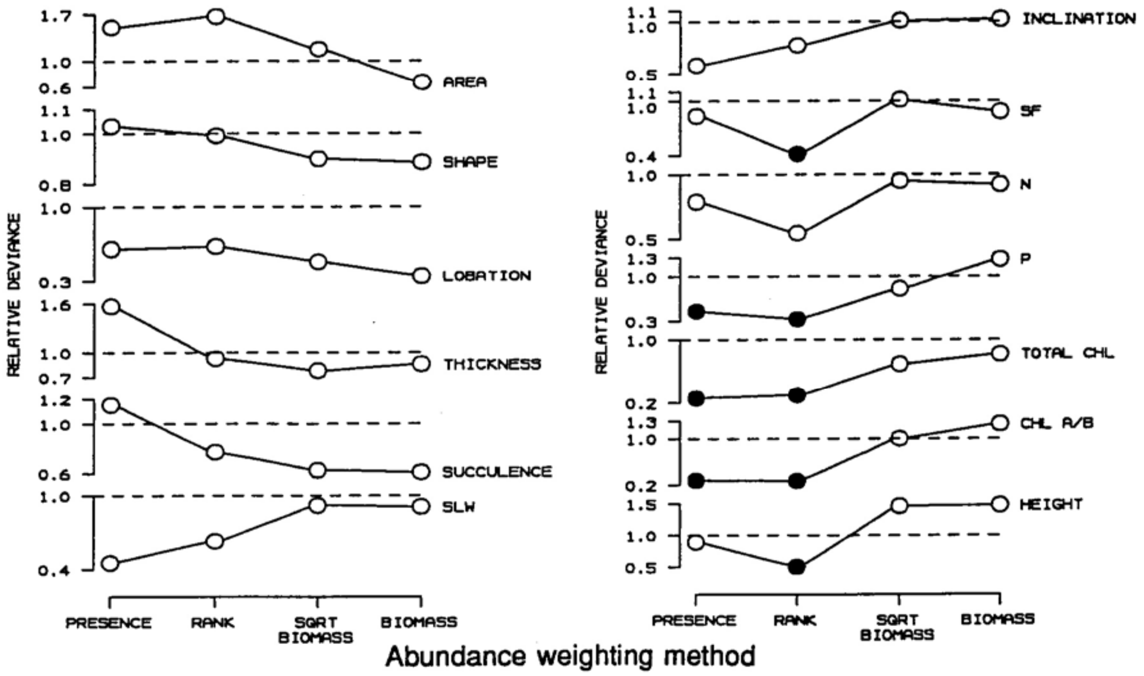


Fig. 8.5 (continued)

Regional scale

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

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

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

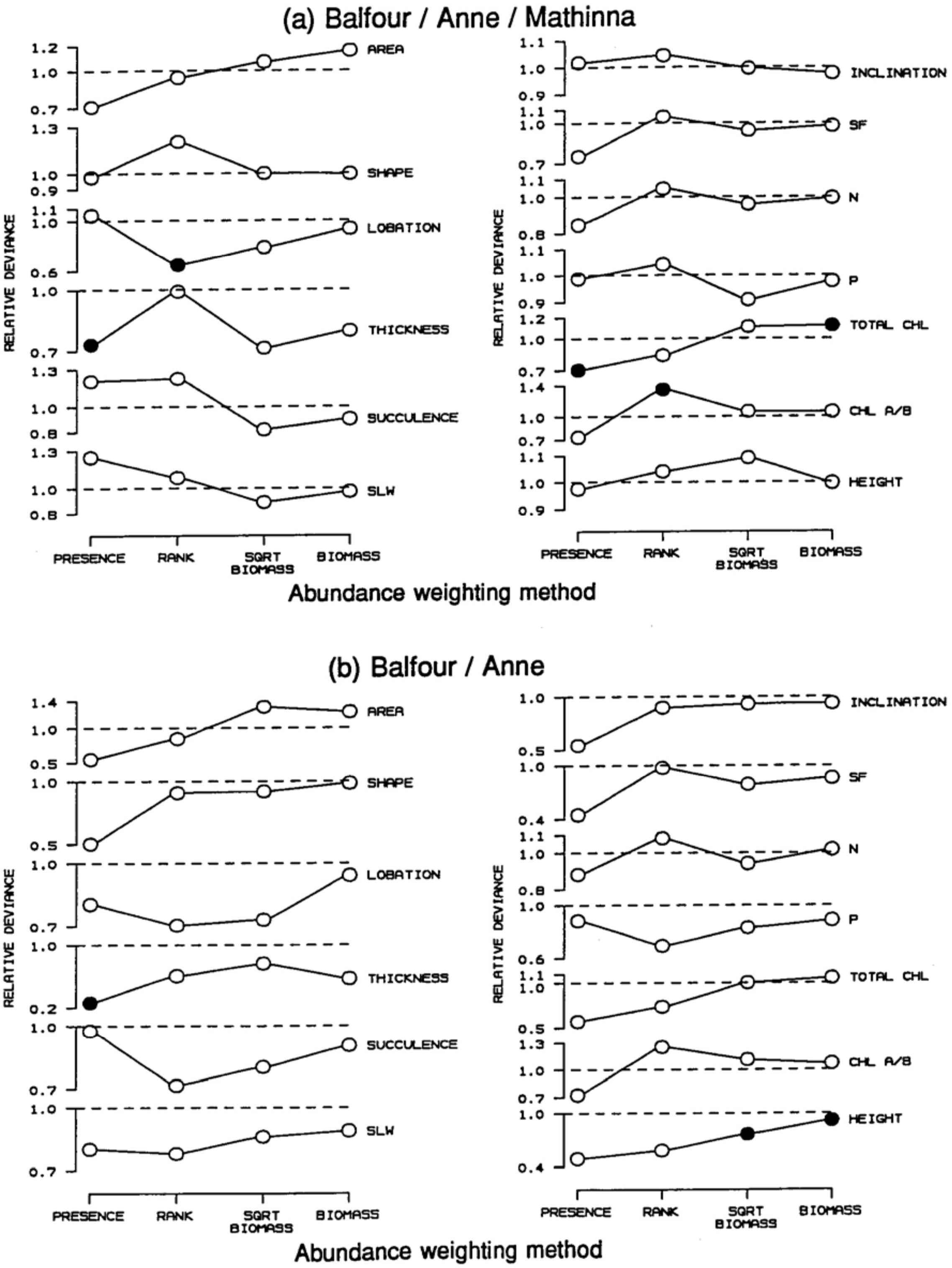
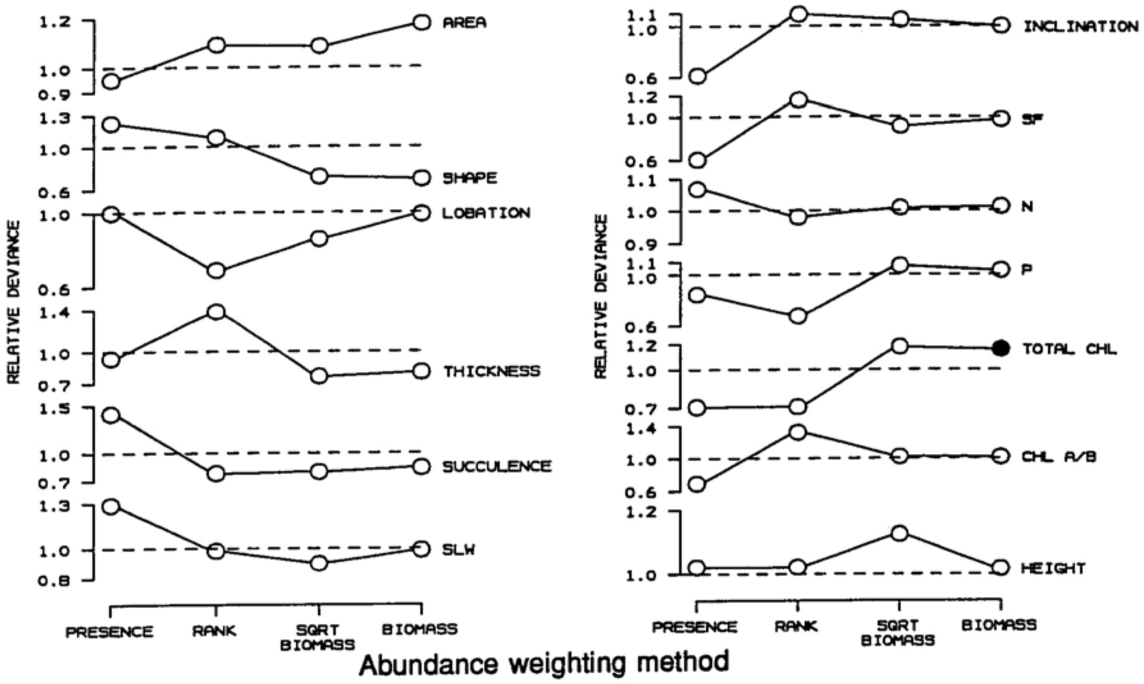


Fig. 8.6 Null model randomisation tests for convergence or divergence in mean-adjusted texture distributions between regional-scale *Nothofagus*-dominated communities T1 Balfour, T2 Anne and T3 Mathinna. Format as for Fig. 8.5.

(c) Balfour / Mathinna



(d) Anne / Mathinna

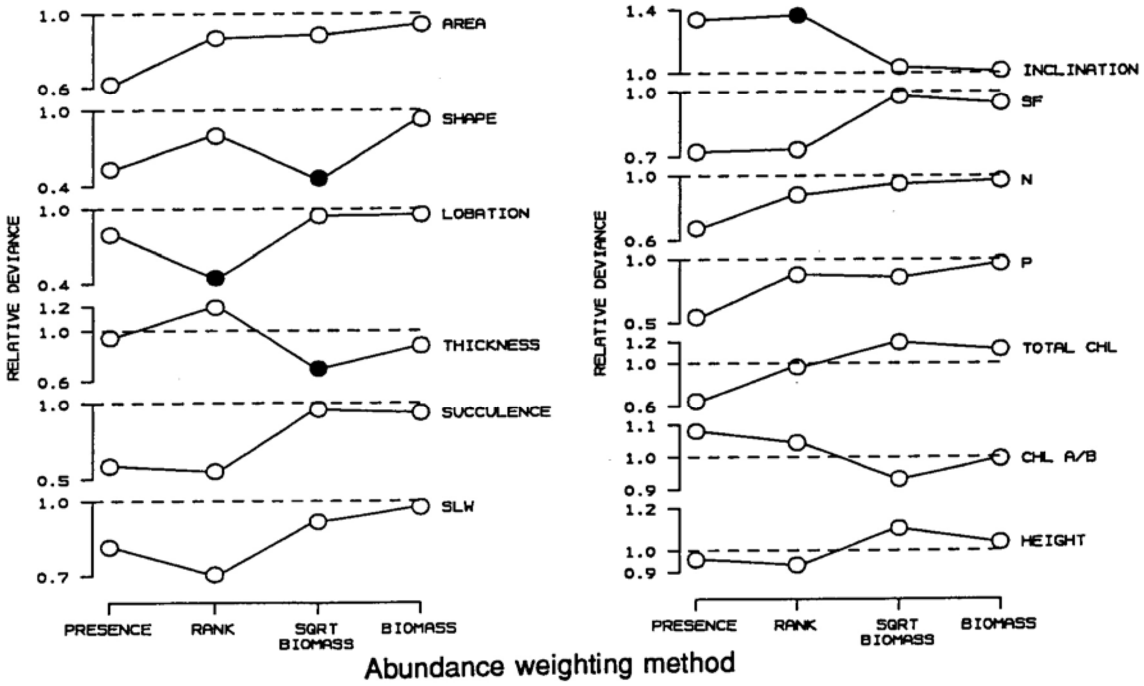


Fig. 8.6 (continued)

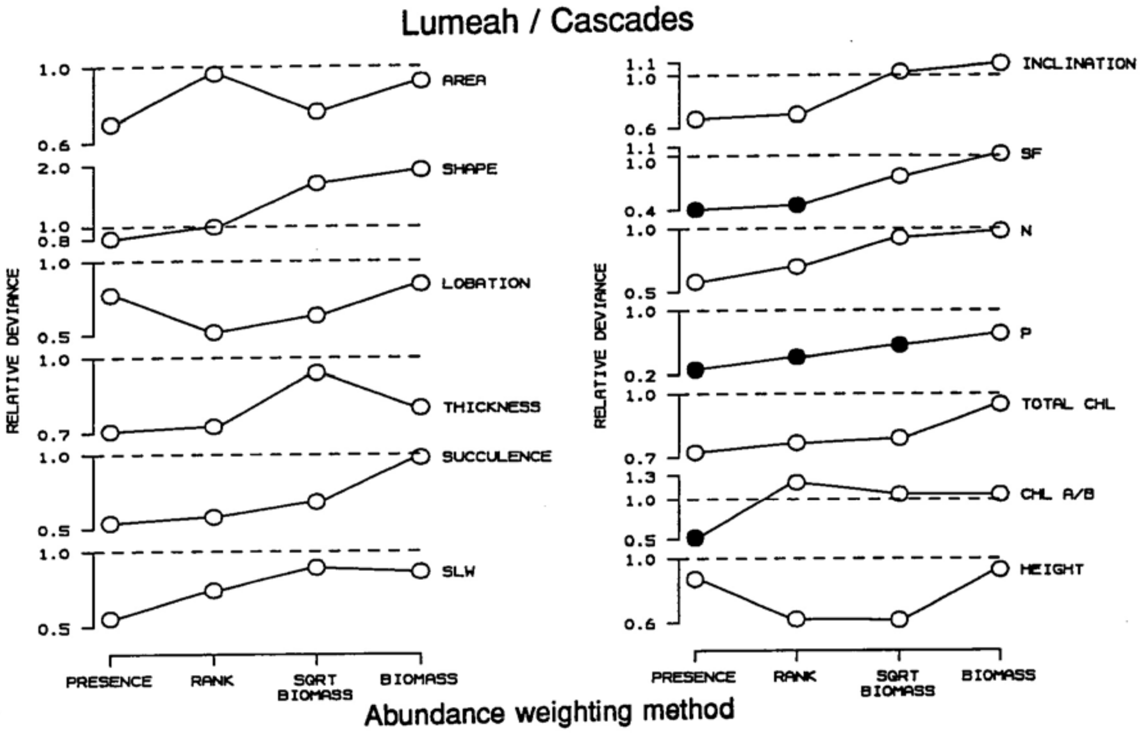
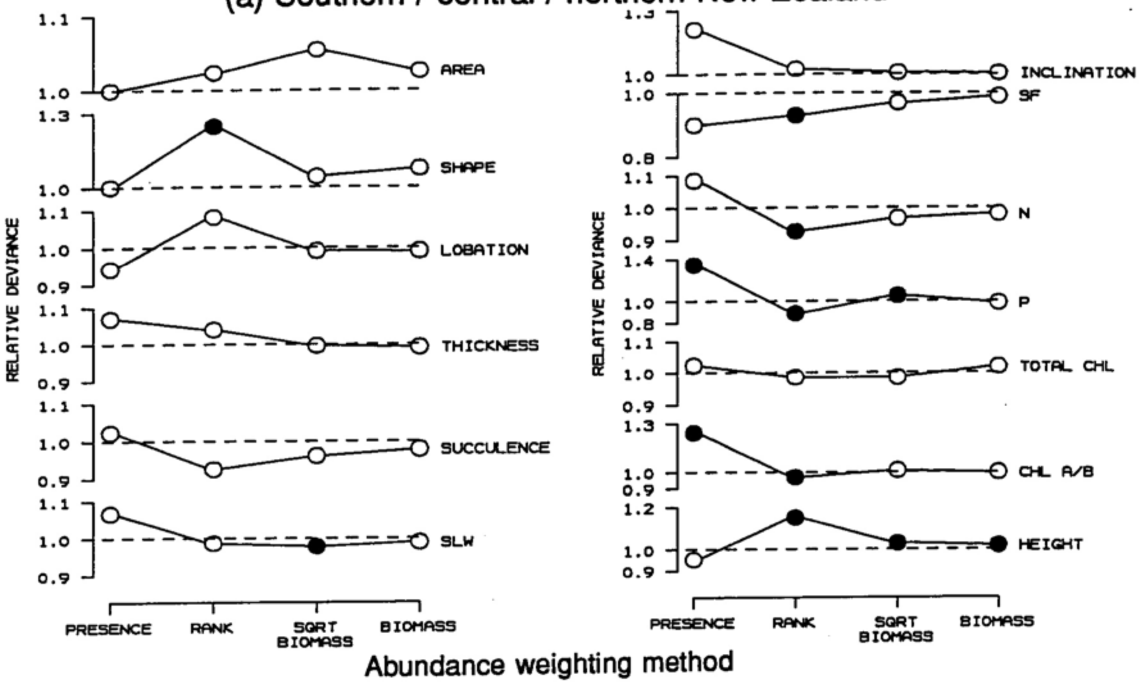


Fig. 8.7 Null model randomisation tests for convergence or divergence in mean-adjusted texture distributions between regional-scale *Nothofagus*-dominated communities A1 Lumeah and A2 Cascades. Format as for Fig. 8.5.

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

(a) Southern / central / northern New Zealand



(b) Southern / central New Zealand

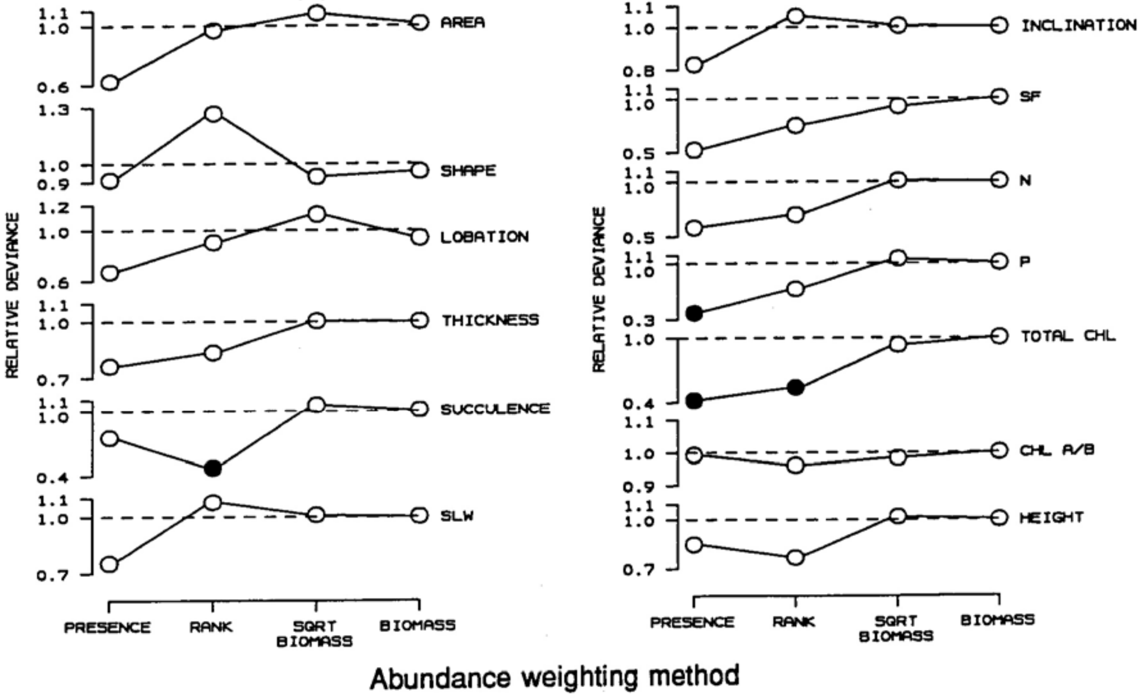
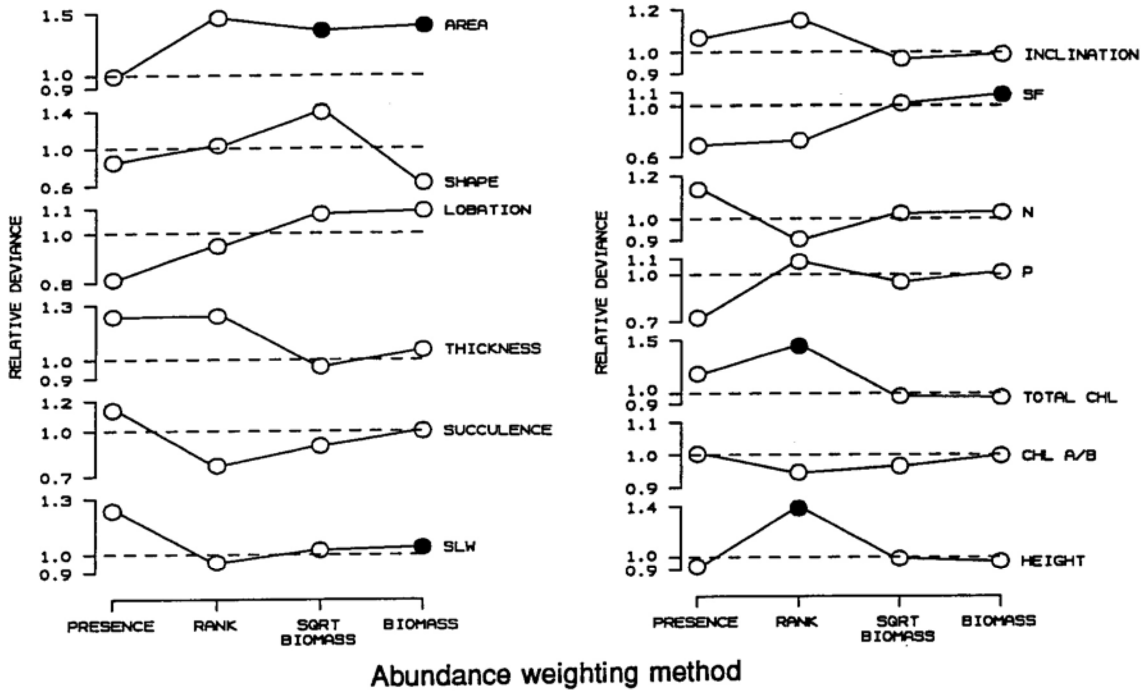


Fig. 8.8 Null model randomisation tests for convergence or divergence in mean-adjusted texture distributions between regional-scale *Nothofagus*-dominated communities southern (ZS), central (ZC) and northern (ZN) New Zealand. Format as for Fig. 8.5.

(c) Southern / northern New Zealand



(d) Central / northern New Zealand

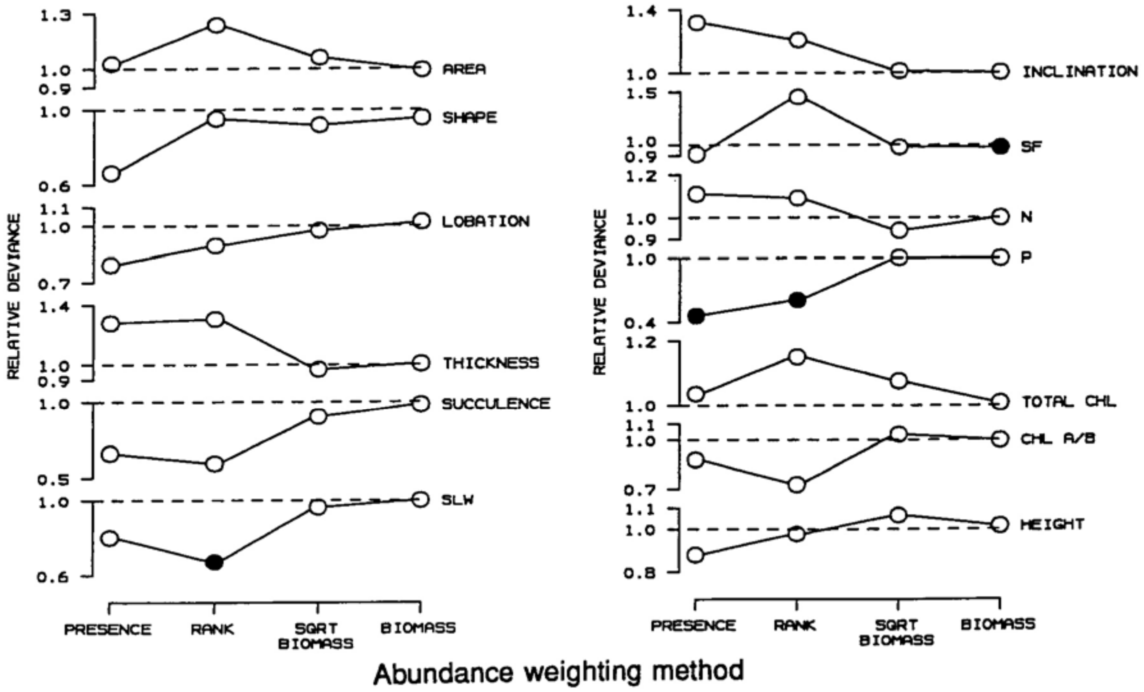


Fig. 8.8 (continued)

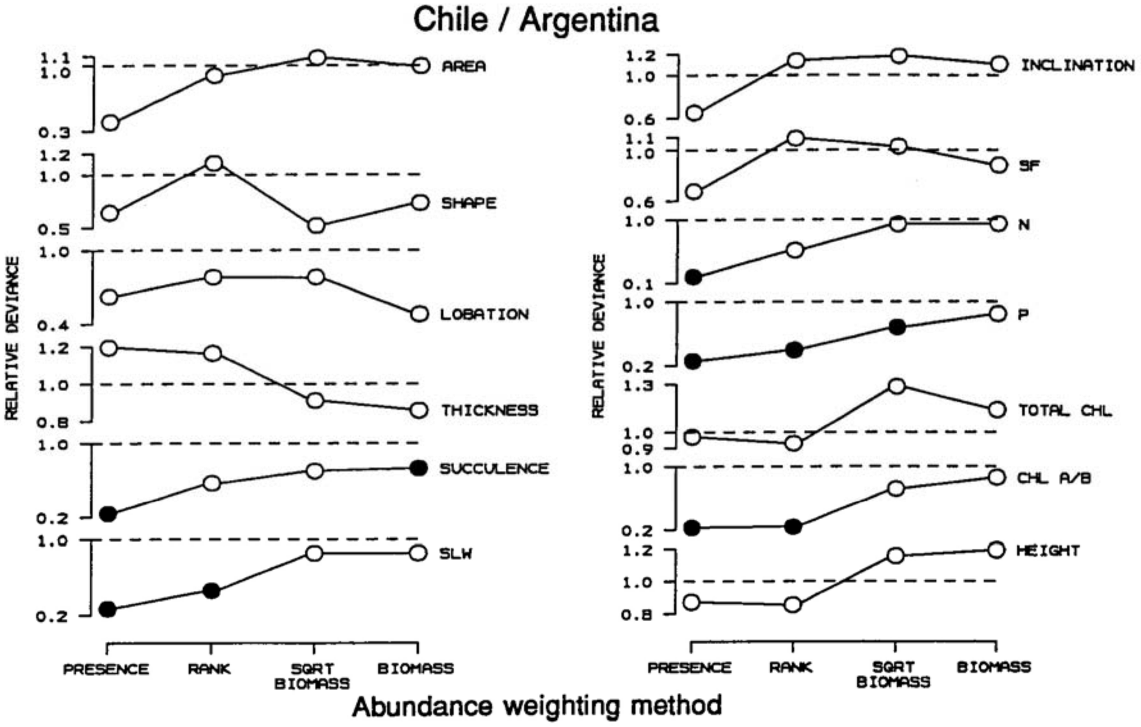


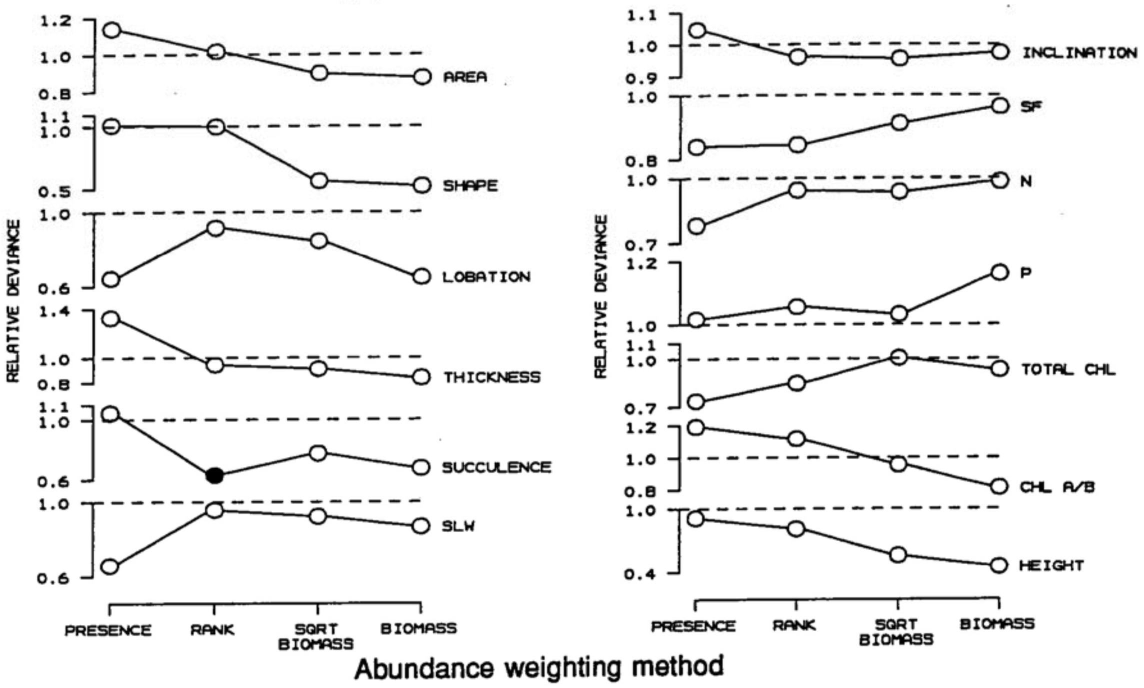
Fig. 8.9 Null model randomisation tests for convergence or divergence in mean-adjusted texture distributions between regional-scale *Nothofagus*-dominated communities of Chile (SC), and Argentina (SA). Format as for Fig. 8.5.

Local scale

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

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

(a) Ten Mile / Walker / Deer



(b) Ten Mile / Walker

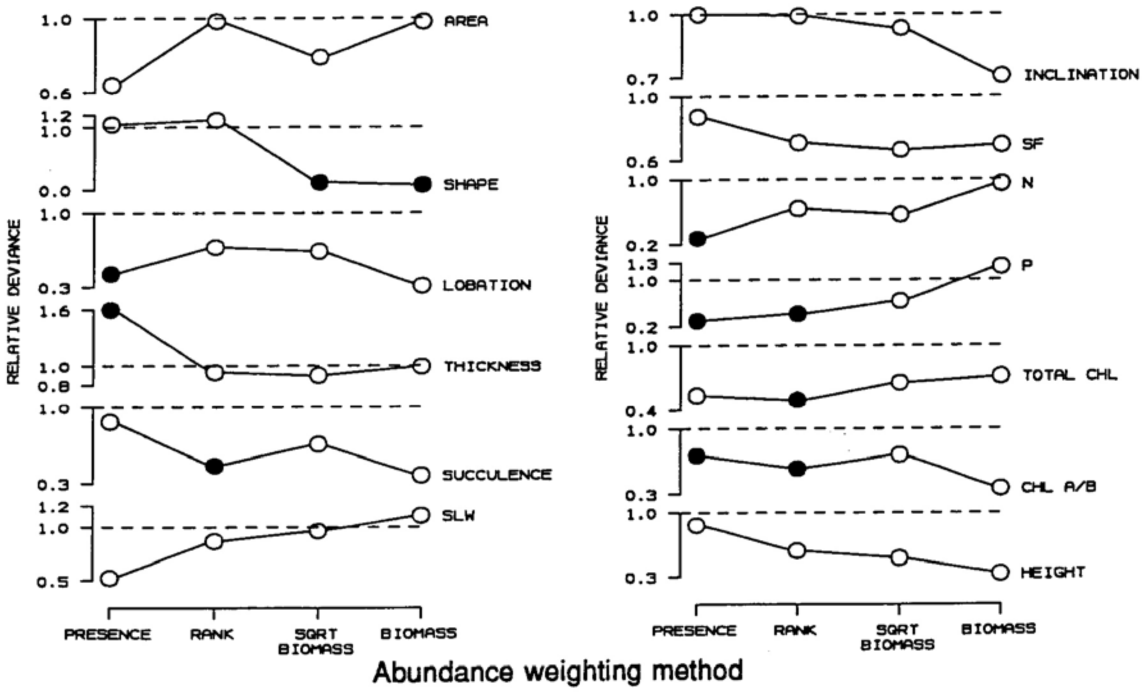
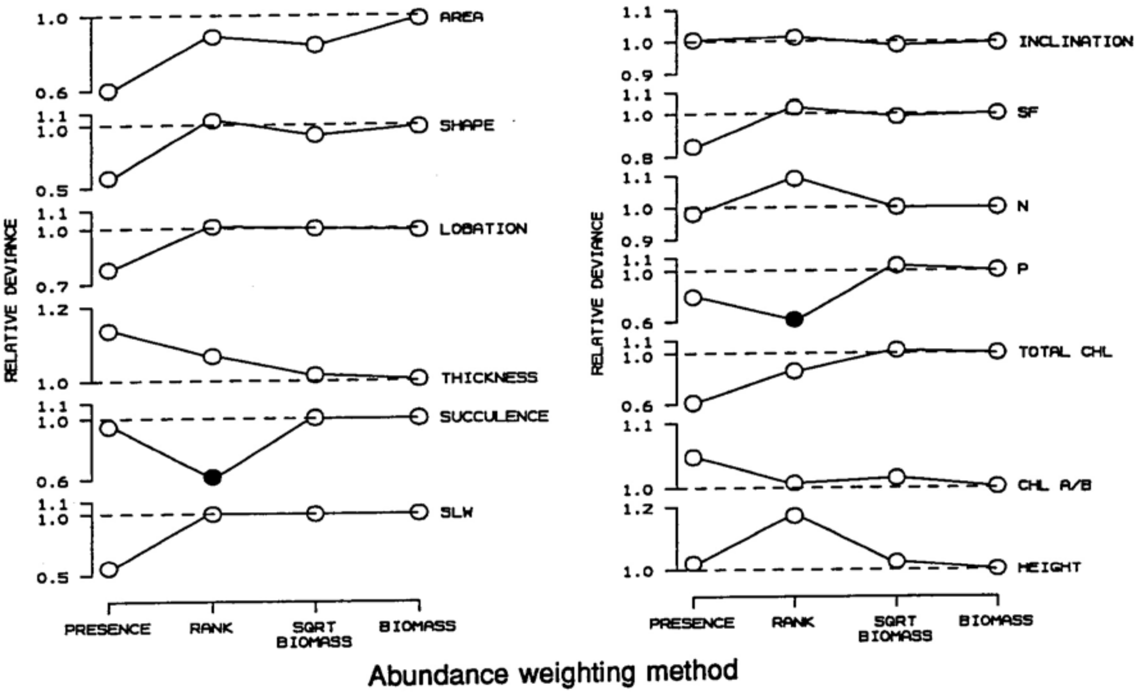


Fig. 8.10 Null model randomisation tests for convergence or divergence in mean-adjusted texture distributions between local-scale *Nothofagus*-dominated communities ZS1 Ten Mile, ZS2 Walker and ZS3 Deer. Format as for Fig. 8.5.

(c) Ten Mile / Deer



(d) Walker / Deer

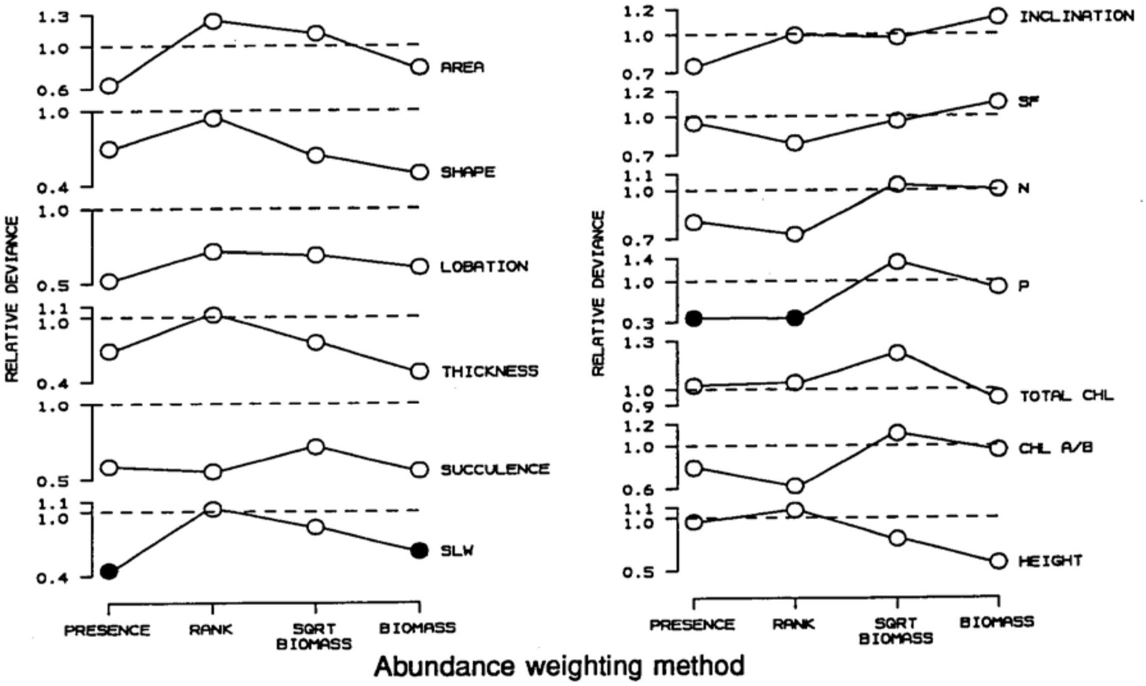


Fig. 8.10 (continued)

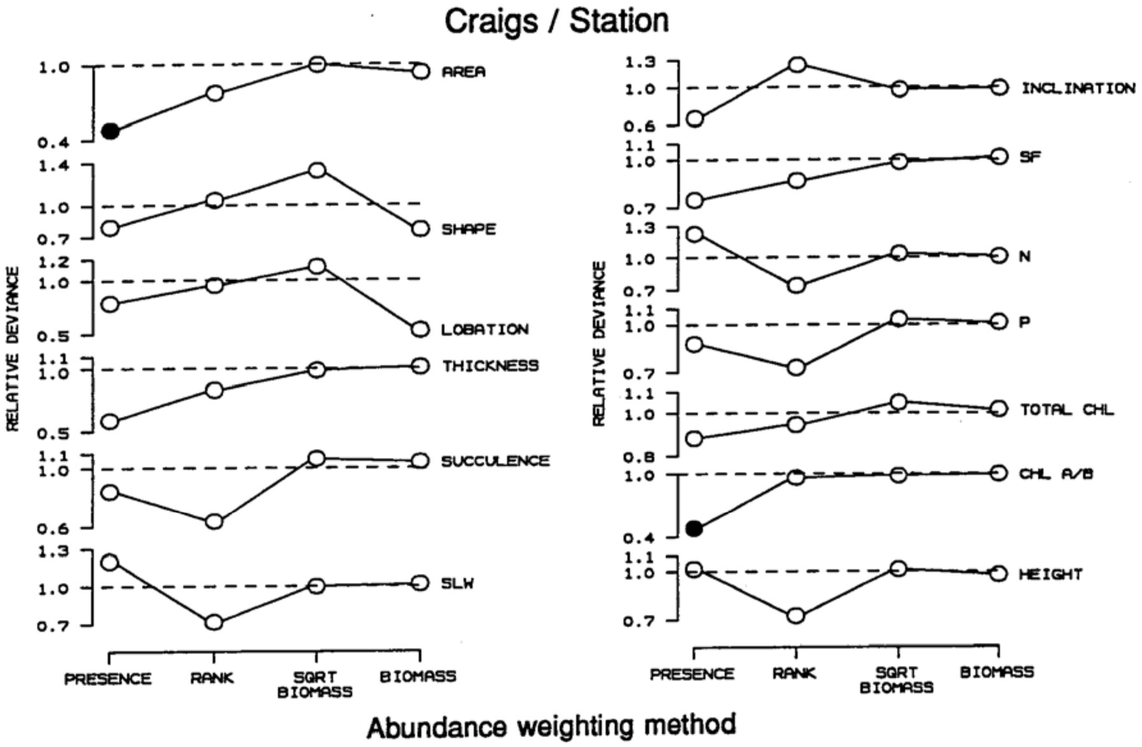
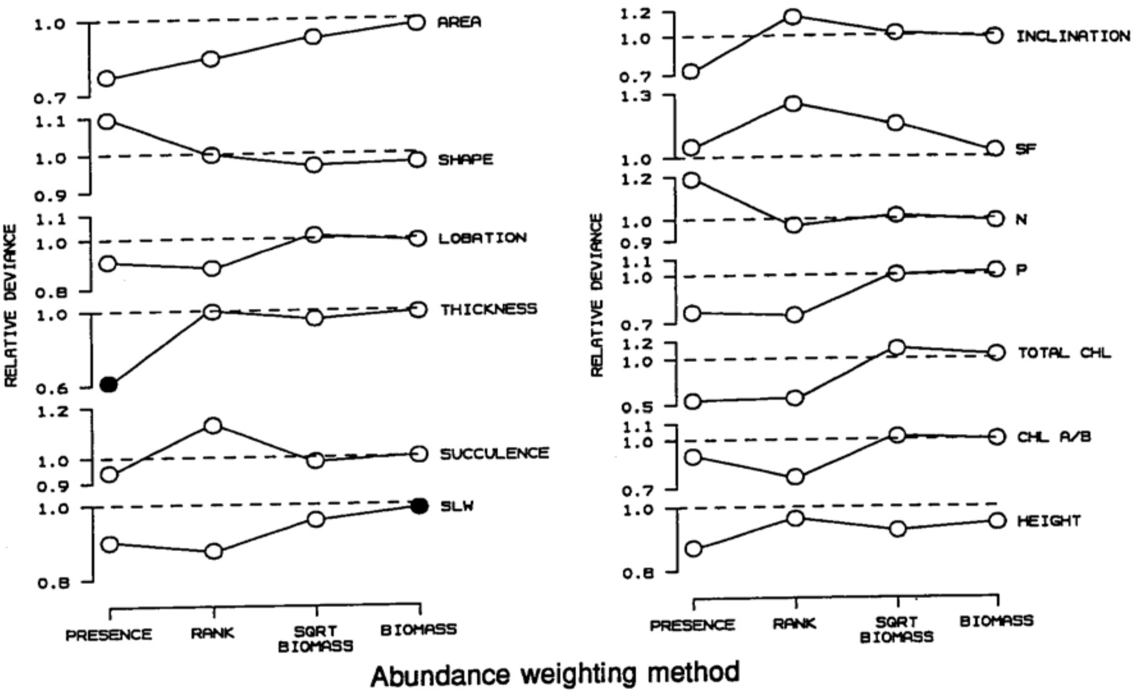


Fig. 8.11 Null model randomisation tests for convergence or divergence in mean-adjusted texture distributions between local-scale *Nothofagus*-dominated communities ZC1 Craigs and ZC2 Station. Format as for Fig. 8.5.

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

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

(a) Ohakune / Rotokura / Clements



(b) Ohakune / Rotokura

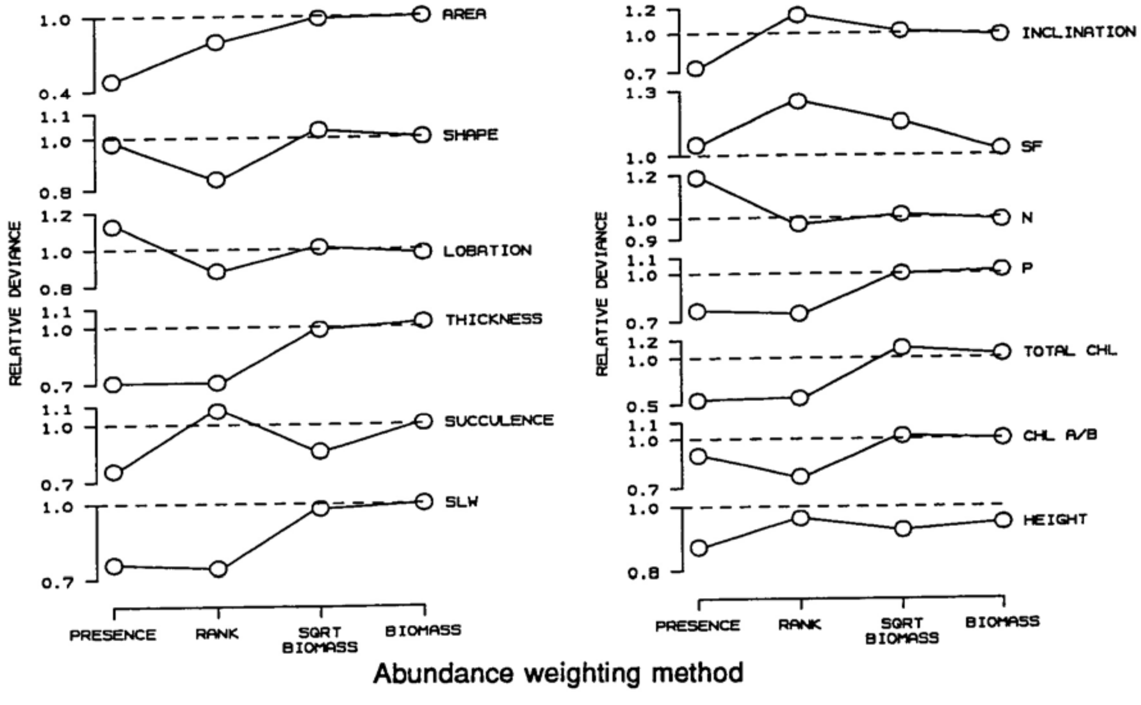
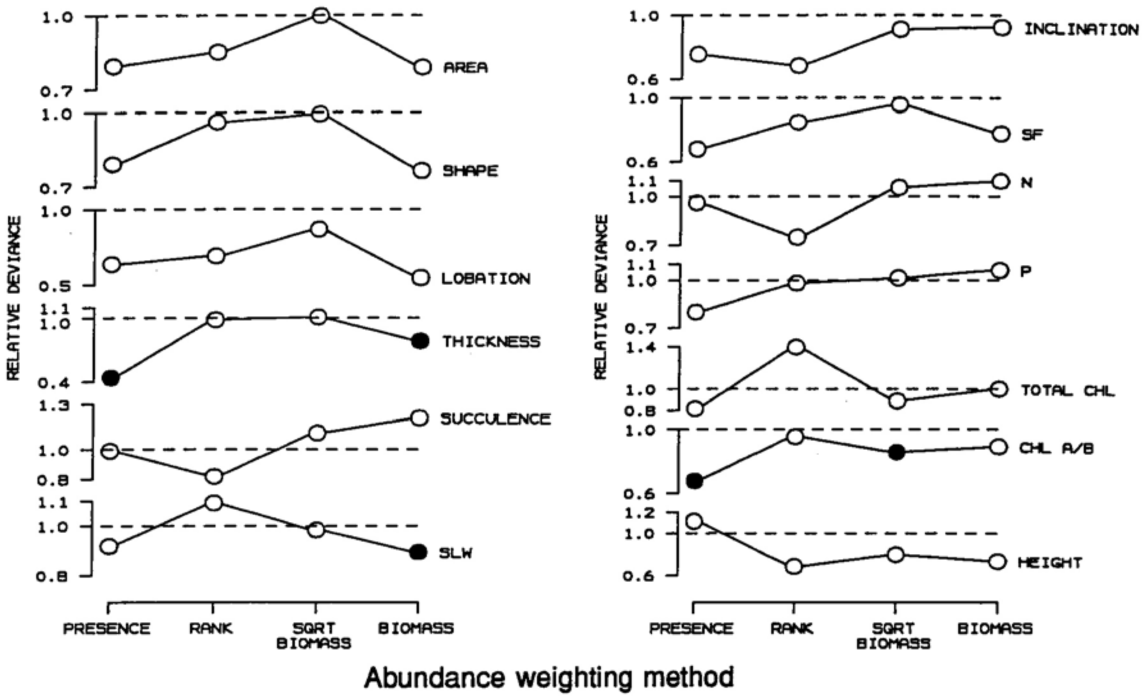


Fig. 8.12 Null model randomisation tests for convergence or divergence in mean-adjusted texture distributions between local-scale *Nothofagus*-dominated communities ZN1 Ohakune, ZN2 Rotokura and ZN3 Clements. Format as for Fig. 8.5.


(c) Ohakune / Clements

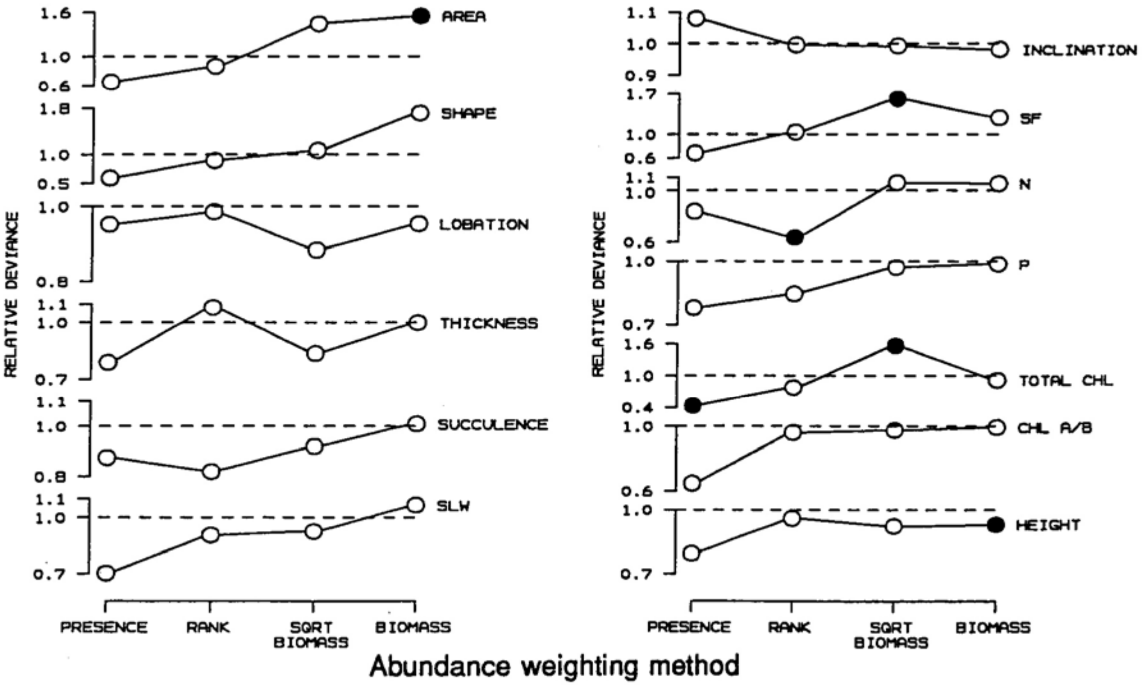

(d) Rotokura / Clements

Fig. 8.12 (continued)

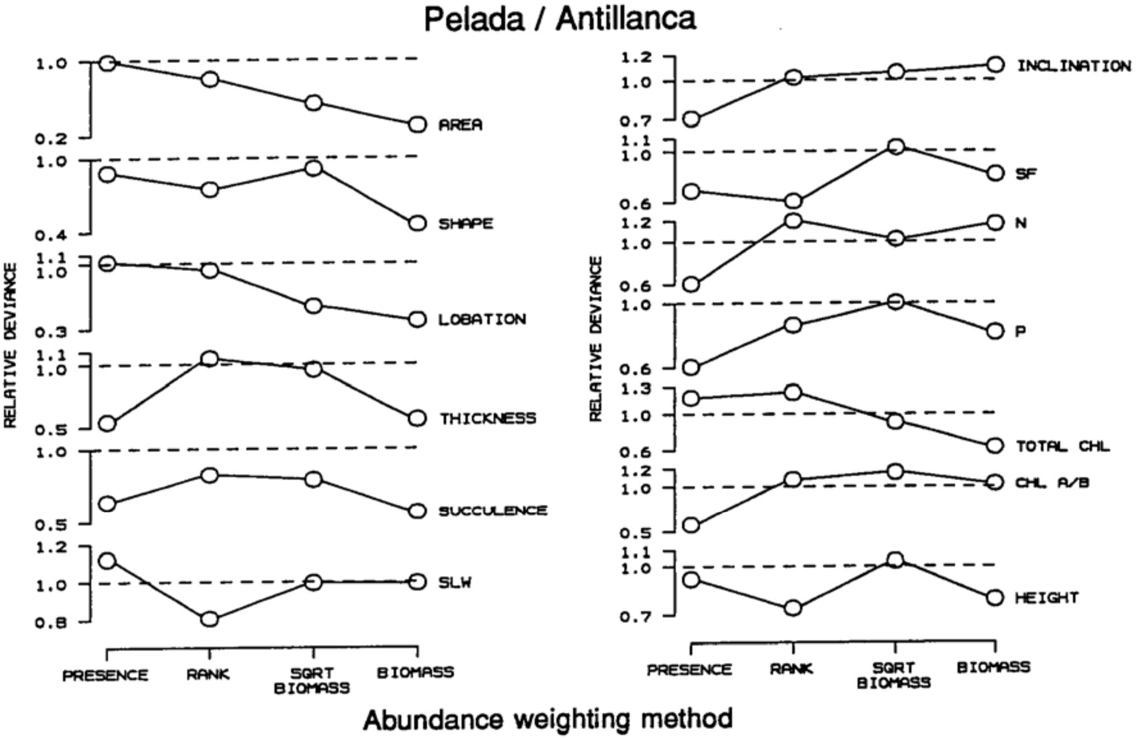


Fig. 8.13 Null model randomisation tests for convergence or divergence in mean-adjusted texture distributions between local-scale *Nothofagus*-dominated communities SC1 Pelada and SC2 Antillanca. Format as for Fig. 8.5.

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

Closely matched sites from different landmasses

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

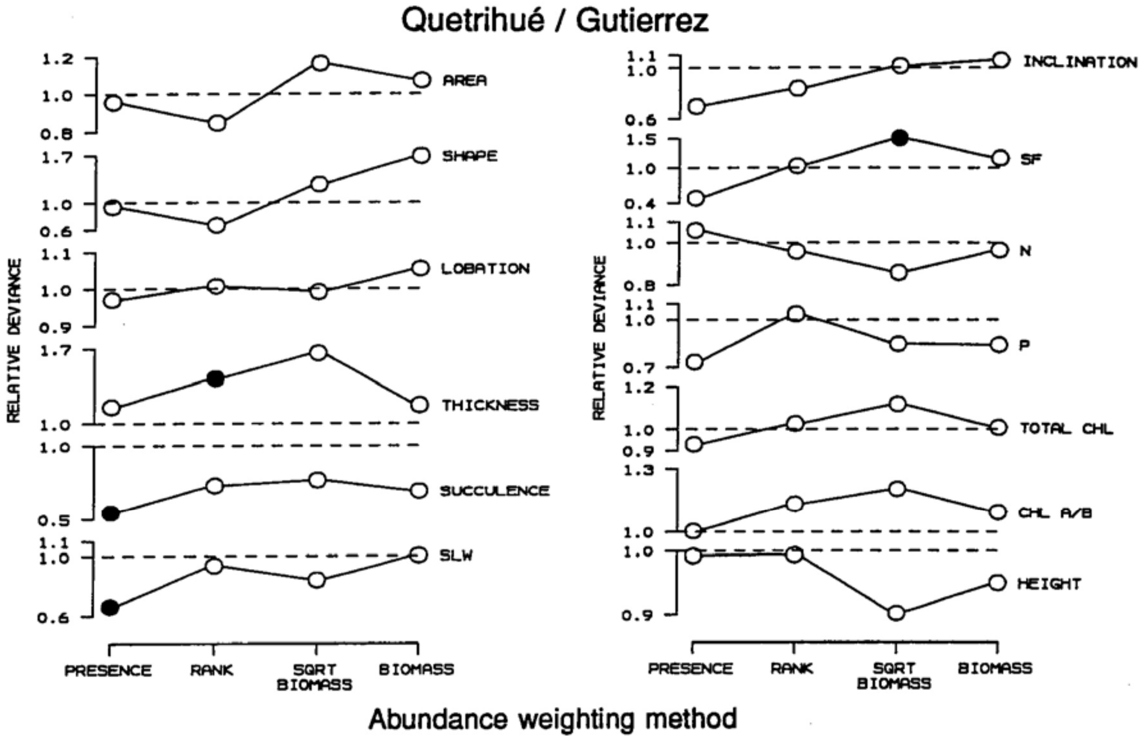


Fig. 8.14 Null model randomisation tests for convergence or divergence in mean-adjusted texture distributions between local-scale *Nothofagus*-dominated communities SA1 Quetrihué and SA2 Gutierrez. Format as for Fig. 8.5.

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

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

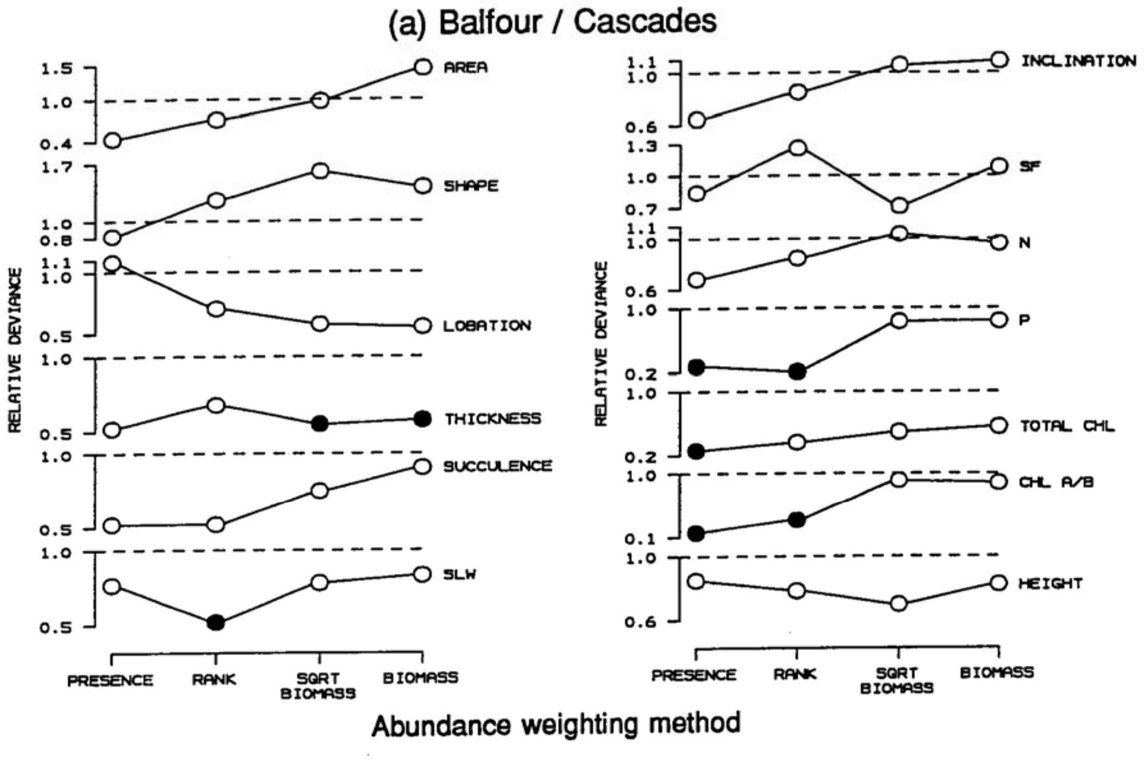
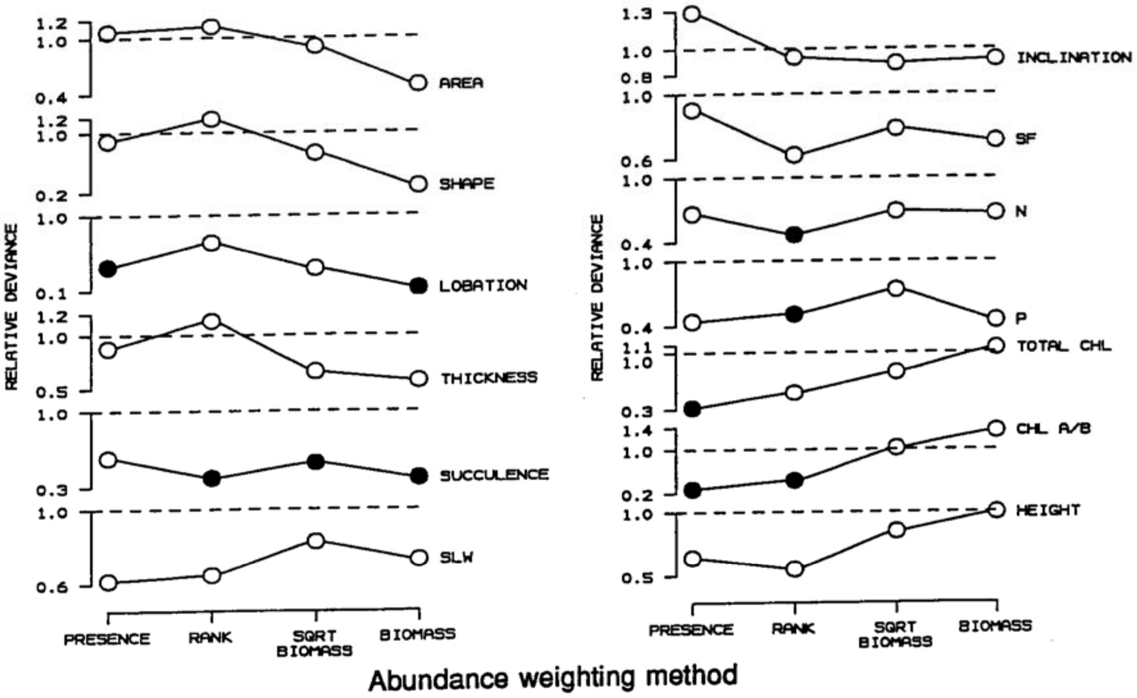


Fig. 8.15 Null model randomisation tests for convergence or divergence in mean-adjusted texture distributions between *Nothofagus*-dominated communities from different landmasses closely matched in their environments: **(a)** T1 Balfour/A2 Cascades; **(b)** T2 Anne/ZN1 Ohakune; **(c)** ZN2 Rotokura/SA1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

(b) Anne / Ohakune



(c) Rotokura / Quetrihué

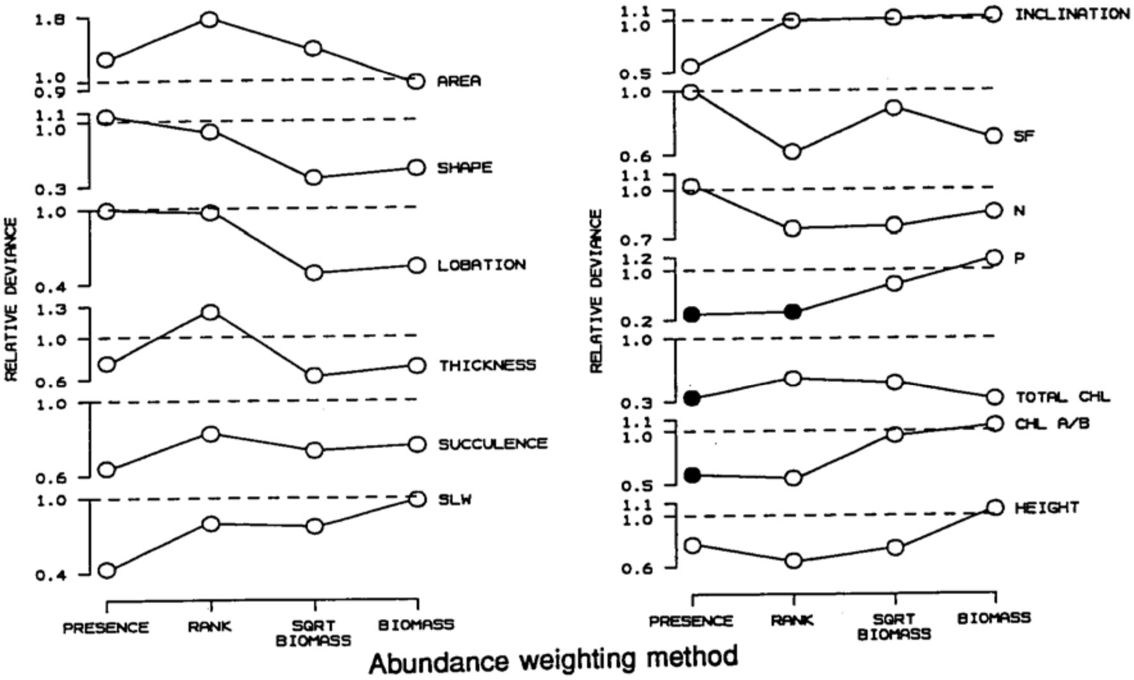


Fig. 8.15 (continued)

PATTERNS AMONG TEXTURE VARIATES

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

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

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

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

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

8.4 Discussion

COMMUNITY-LEVEL CONVERGENCE

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

These results suggest that comparison of community texture distributions without regard to the mean does represent an effective approach to correcting for the effects of different environments on site texture. It was anticipated that the among-community variation remaining once differences in the mean were removed (using the statistic $\hat{D}'_T$) would reflect the action of assembly rules, and would be largely independent of the exogenous environment, at least over the narrow environmental range spanned by the *Nothofagus*-dominated communities being compared. The high incidence of convergence observed suggests that in the case of several texture variates, and among several of the communities sampled, species character values are drawn from underlying distributions, not entirely at random, but subject to certain constraints. These constraints cause the mean-adjusted distributions in different communities to be more similar than would be expected if species values were drawn at random from the same distributions, as under the null model. It is postulated that these constraints represent assembly rules, and are caused by species interactions, such as competition, which would limit the co-occurrence of species whose niches (and correlated functional characters) are too similar to prevent competitive exclusion from occurring (Hutchinson 1959; Hardin 1960; Diamond 1975).

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

Patterns in relation to environmental similarity

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

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

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

Factors underlying convergence

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

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

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

A NEW METHOD FOR ENVIRONMENTAL CORRECTION AND ITS SIGNIFICANCE

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

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

CONCLUSIONS

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

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