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

7.1 Introduction

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

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

Similar assembly rules, operating in different communities, would be expected to spread species out in a generally similar (though not identical) way in niche space. This would be expected to produce similarity between communities, not only in texture means, but also in community-wide distributions of species characters. In general, similar means would imply similar distributions, and dissimilar means would imply dissimilar distributions. However, the two need not be linked. For example, the two texture distributions represented in Fig. 7.1a have the same mean but are clearly different in shape; in community 1, more species have character values in the range 2-3 than in any other class; in community 2 characters in the range 4-5 are the most popular. It is unlikely that similar assembly rules would produce texture distributions skewed in opposite directions in different communities, yet when only the mean is considered and other information ignored, the communities are found to be very similar in texture. Another type of pattern is illustrated in Fig. 7.1b. Community 1 has a platykurtic distribution, with species values clumped about the modal (and, in this case, mean) character value, but with few very high or very low values. Community 2 has the same mean and mode, but a greater proportion of species have more extreme values, giving a relatively leptokurtic texture distribution. Once again, comparison of texture means would imply that the communities are convergent, yet differences in the distributions do not seem consistent with the operation of identical assembly rules. There are also situations in which distributions may be well-matched, but their means dissimilar. In Fig 7.1c, the two communities have distributions that are rather similar overall, but a low extreme value in Community 1 and a high one in Community 2 result in different texture means and imply that the communities are non-convergent, or even divergent, in texture.

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

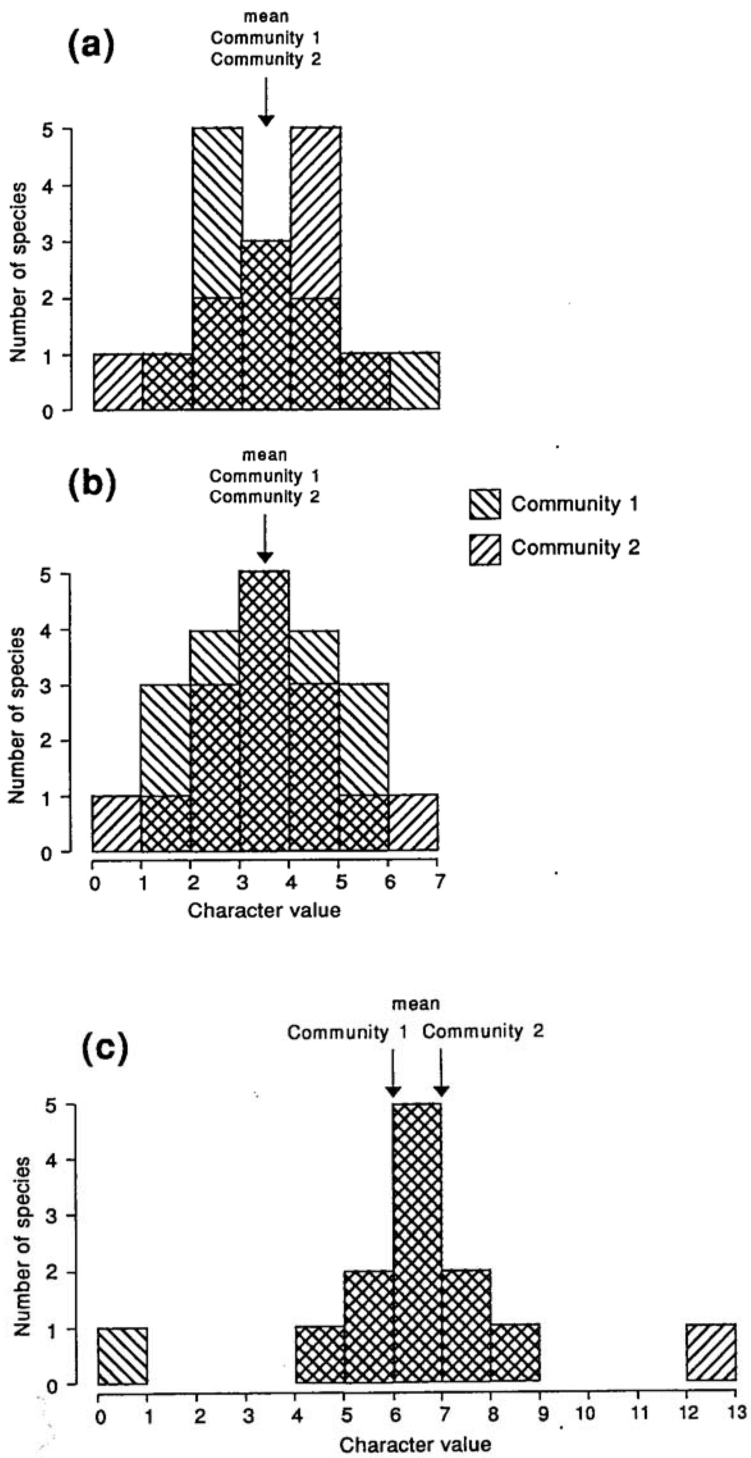


Fig. 7.1 Possible differences in the degree of matching between texture means and distributions in different communities. In example **(a)**, Communities 1 and 2 have the same mean for a character, but the frequency distributions of the character are skewed in opposite directions. In example **(b)**,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

7.2 Methods

TEXTURE DATA

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

ANALYSIS

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

Representation of community texture

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

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

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

where s = number of species or entities in community;

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

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

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

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

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

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

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

Comparison of observed with null communities

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

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

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

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

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

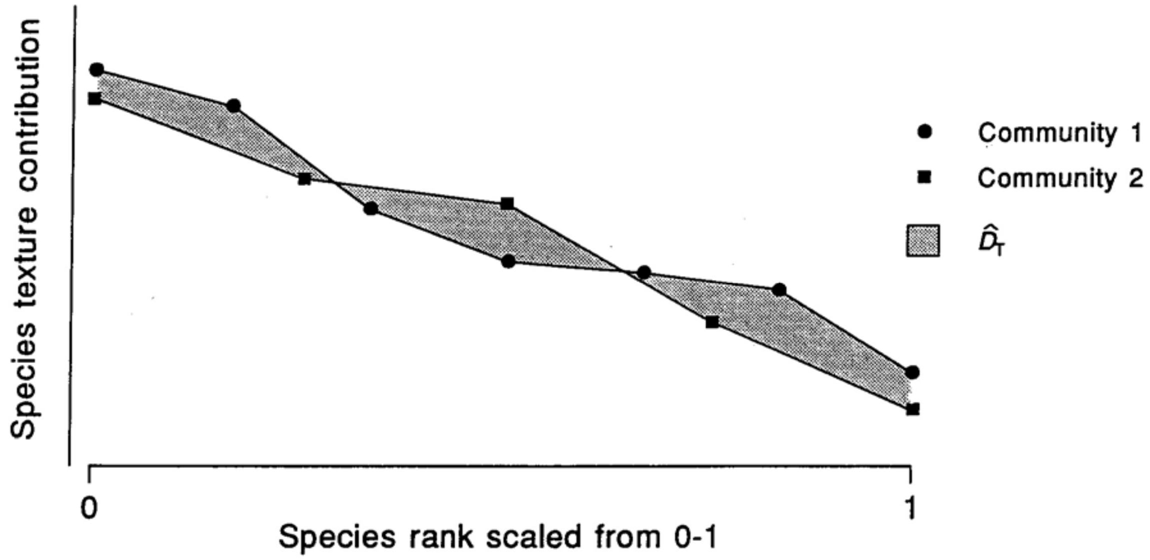


Fig. 7.2 Example demonstrating the calculation of the deviance of texture distributions, $\hat{D}_T$, between two communities. For two communities, $\hat{D}_T$ is the area between rank-scaled texture plots for each community. Rank-scaled texture plots are produced by plotting species texture contributions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

Comparisons performed

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

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

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

7.3 Results

VALIDITY OF THE NULL MODEL

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

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

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

TEST STATISTIC BEHAVIOUR

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

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

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

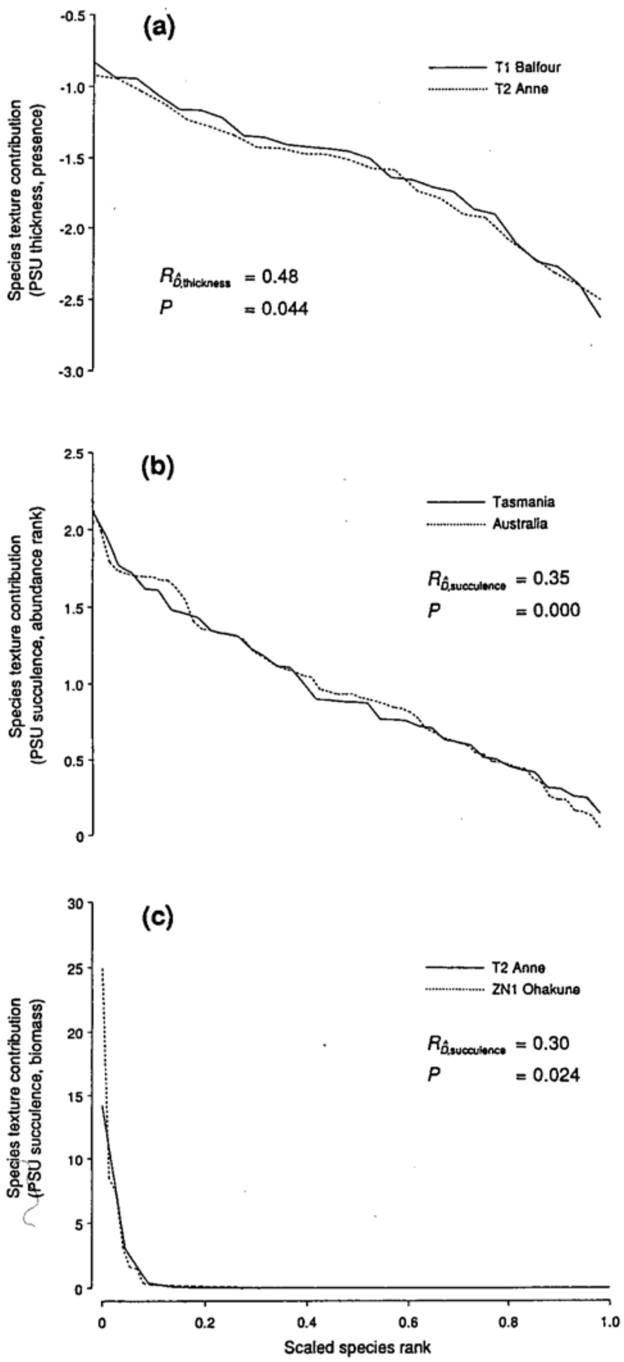


Fig. 7.3 Rank-scaled texture plots (see Fig. 7.2) for significantly convergent *Nothofagus*-dominated communities **(a)** T1 Balfour and T2 Anne, convergence in PSU thickness with species weighted equally; **(b)** Tasmania (T) and Australia (A), convergence in PSU succulence weighted by abundance rank;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

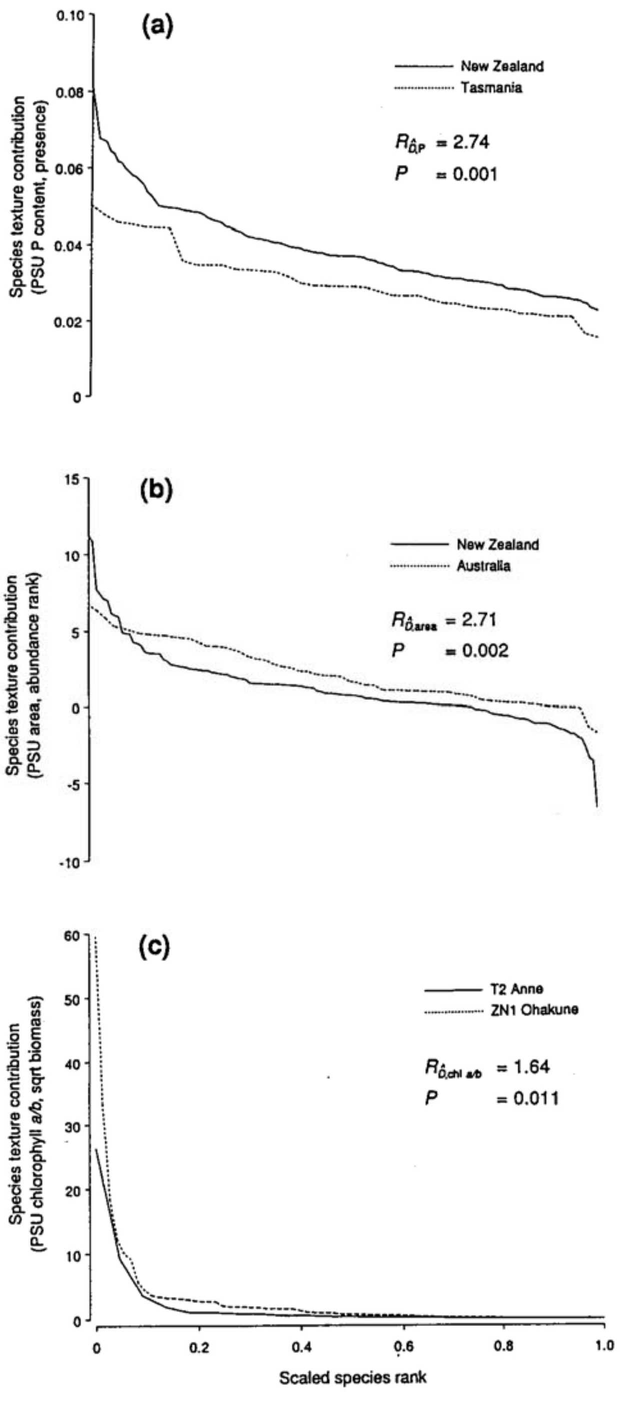


Fig. 7.4 Rank-scaled texture plots for significantly divergent *Nothofagus*-dominated communities **(a)** New Zealand (Z) and Tasmania (T), divergence in PSU phosphorus content with species weighted equally; **(b)** New Zealand and Australia (A), divergence in PSU area weighted by abundance rank; **(c)**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

PATTERNS AMONG COMMUNITIES

Landmass scale

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

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

Regional scale

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

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

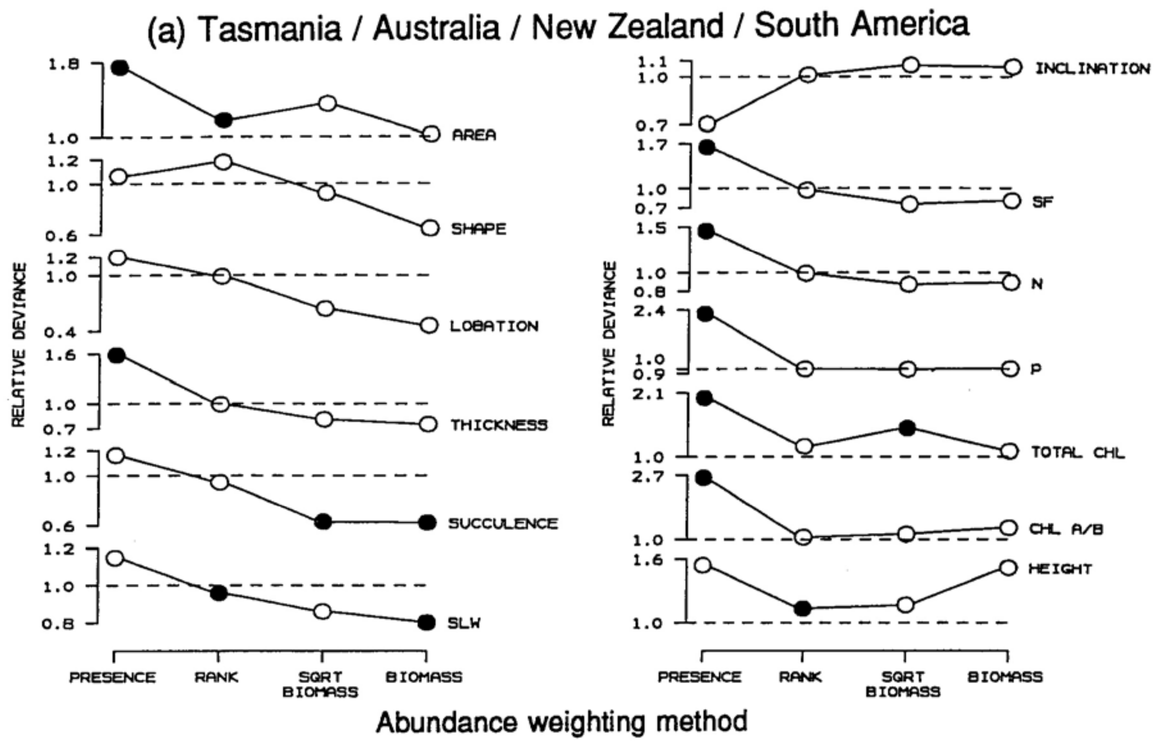


Fig. 7.5 Null model randomisation tests for convergence or divergence in texture distributions between landmass-scale *Nothofagus*-dominated communities Tasmania (T), Australia (A), New Zealand (Z) and South America (S). The relative deviance $R_{\hat{D},T}$ of among-community variation in texture distributions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

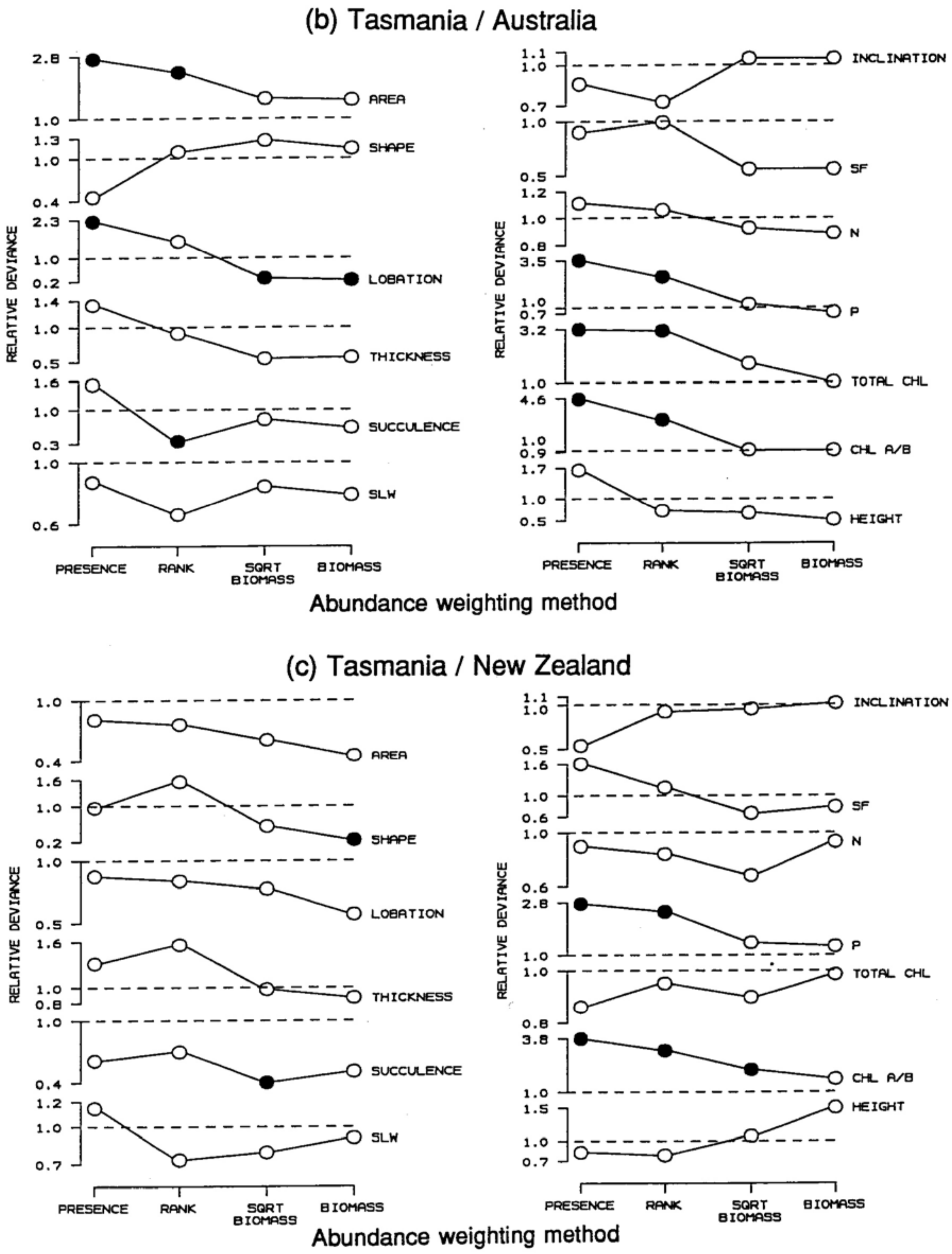
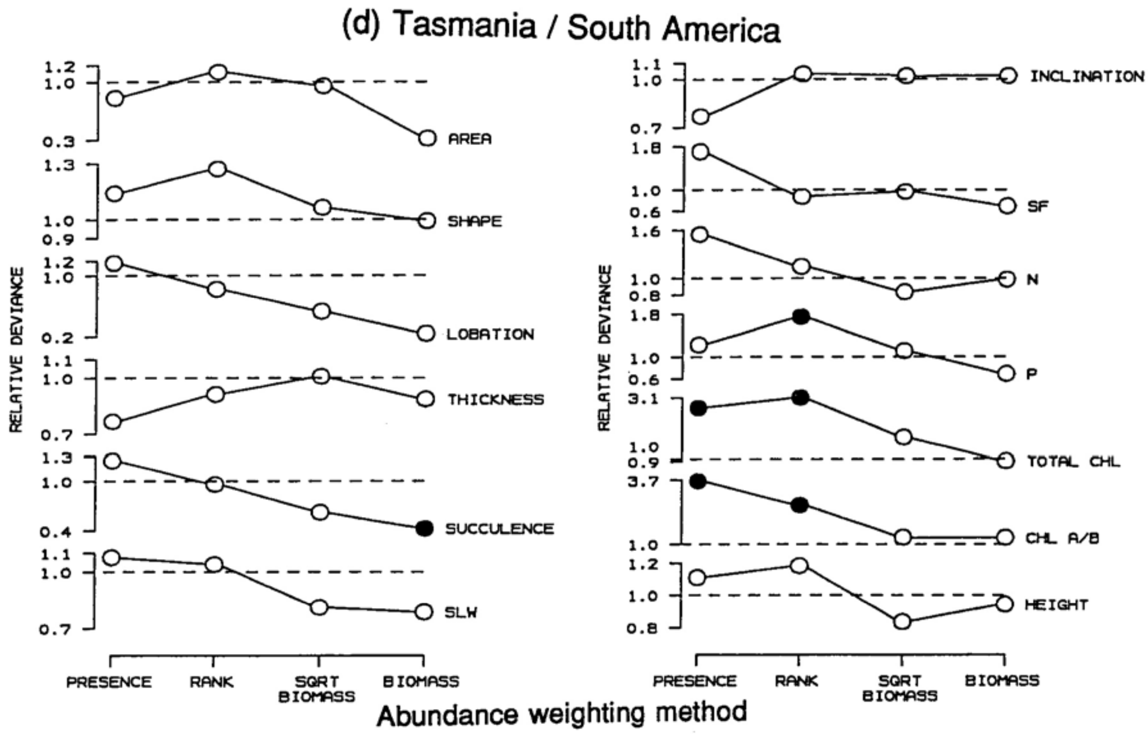
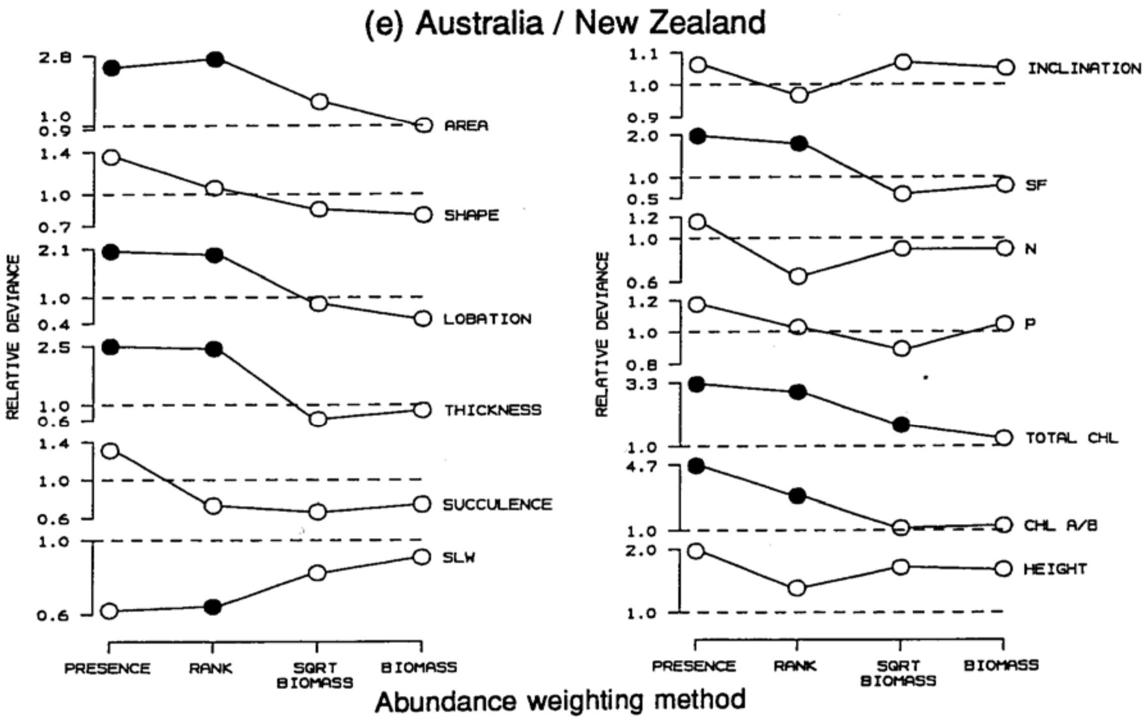


Fig. 7.5 (continued)





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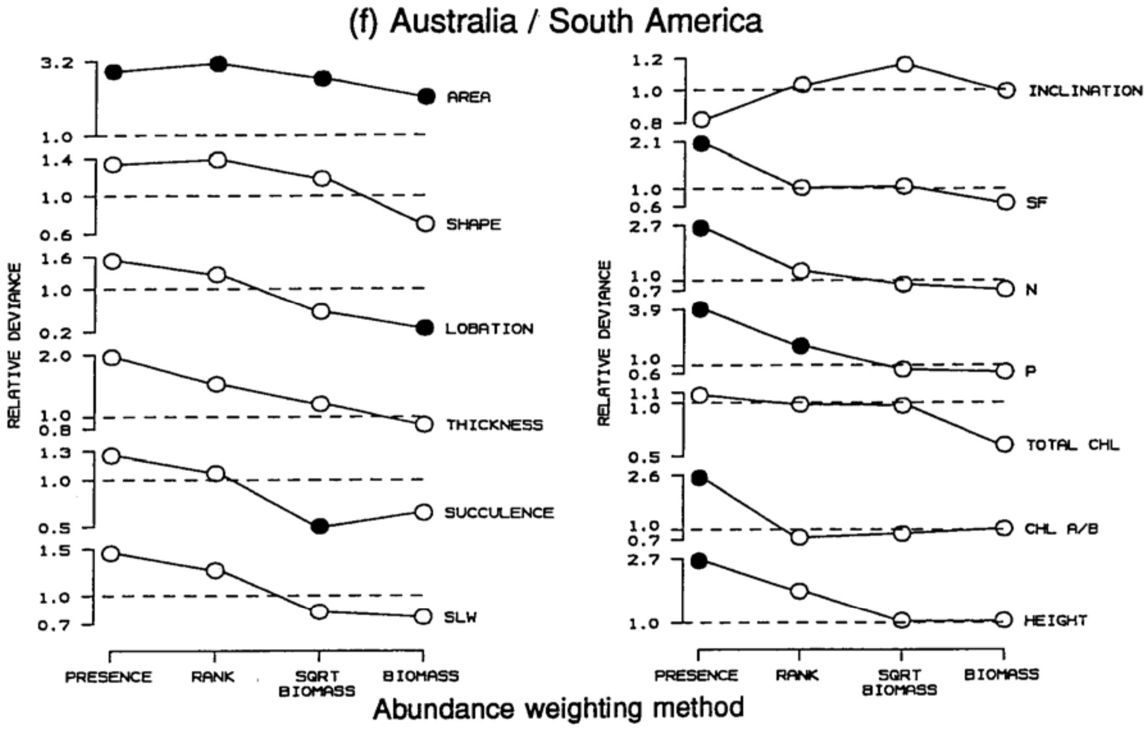

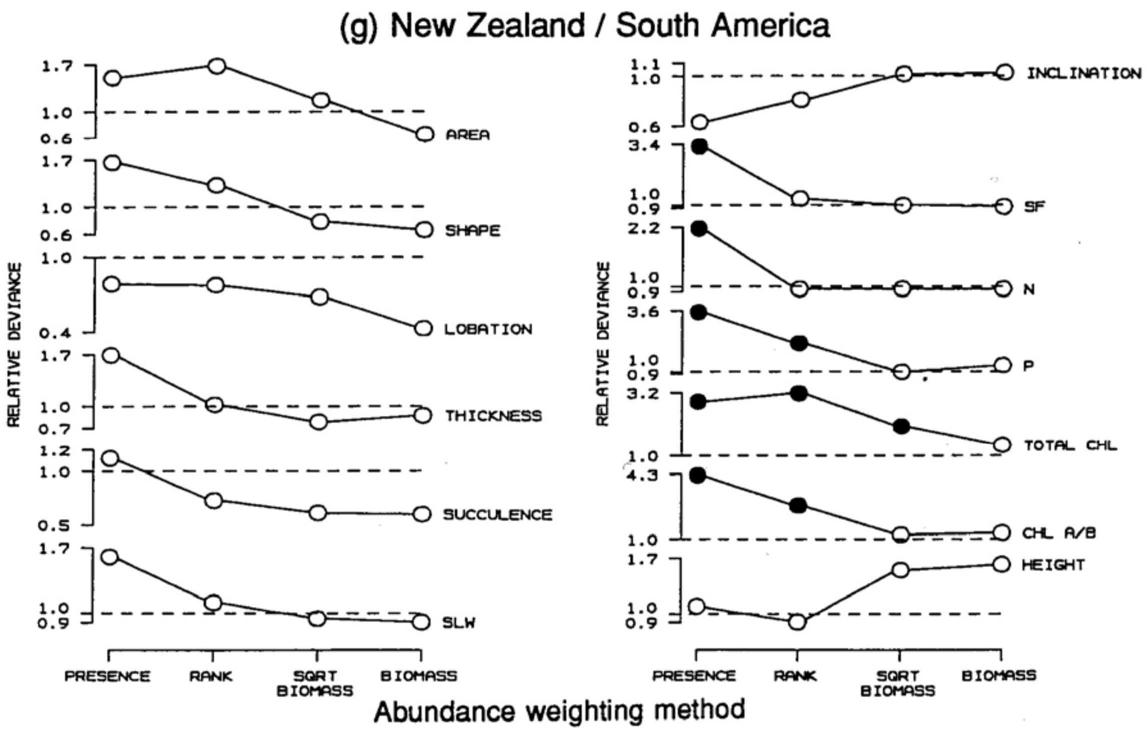

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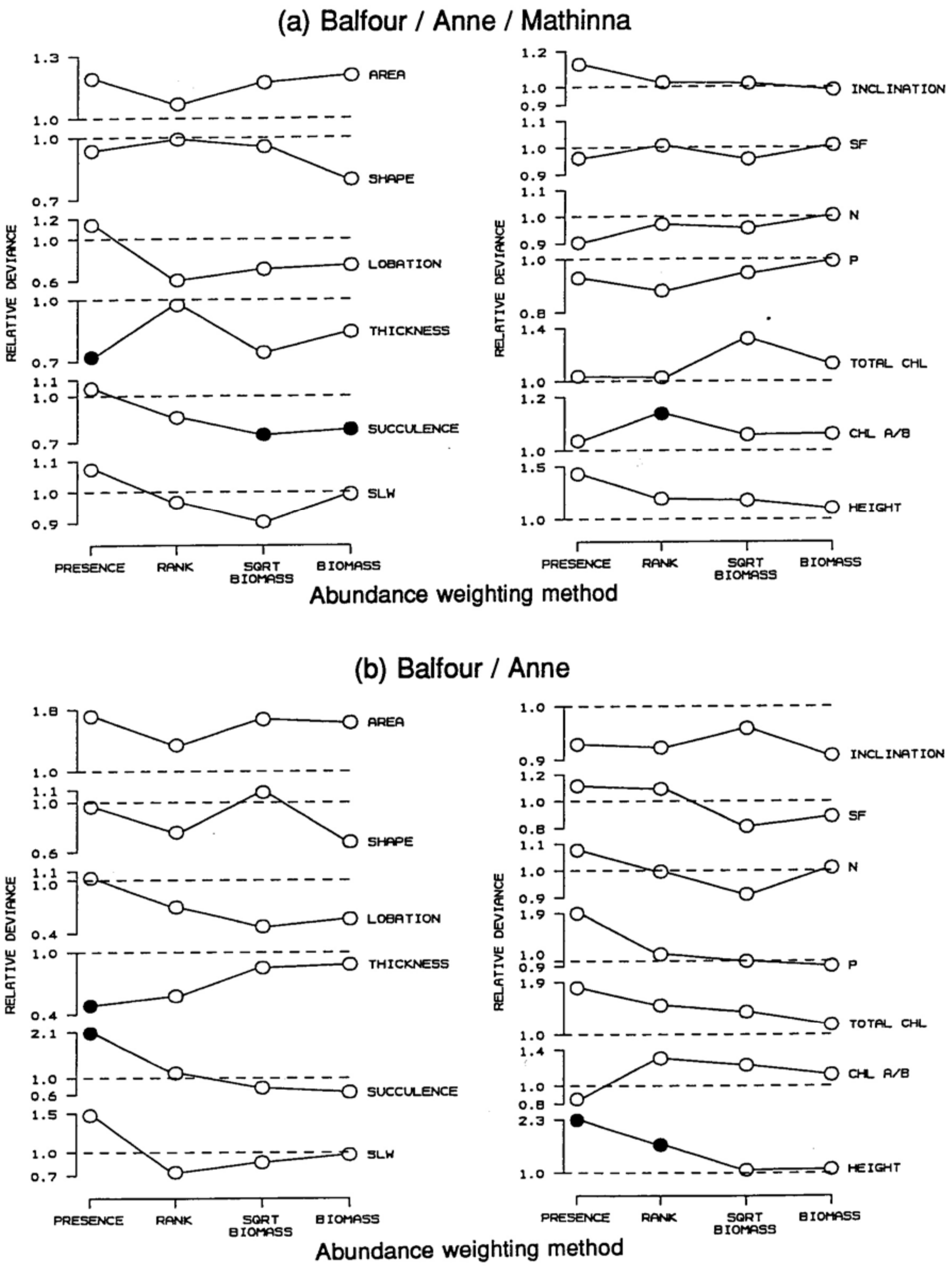
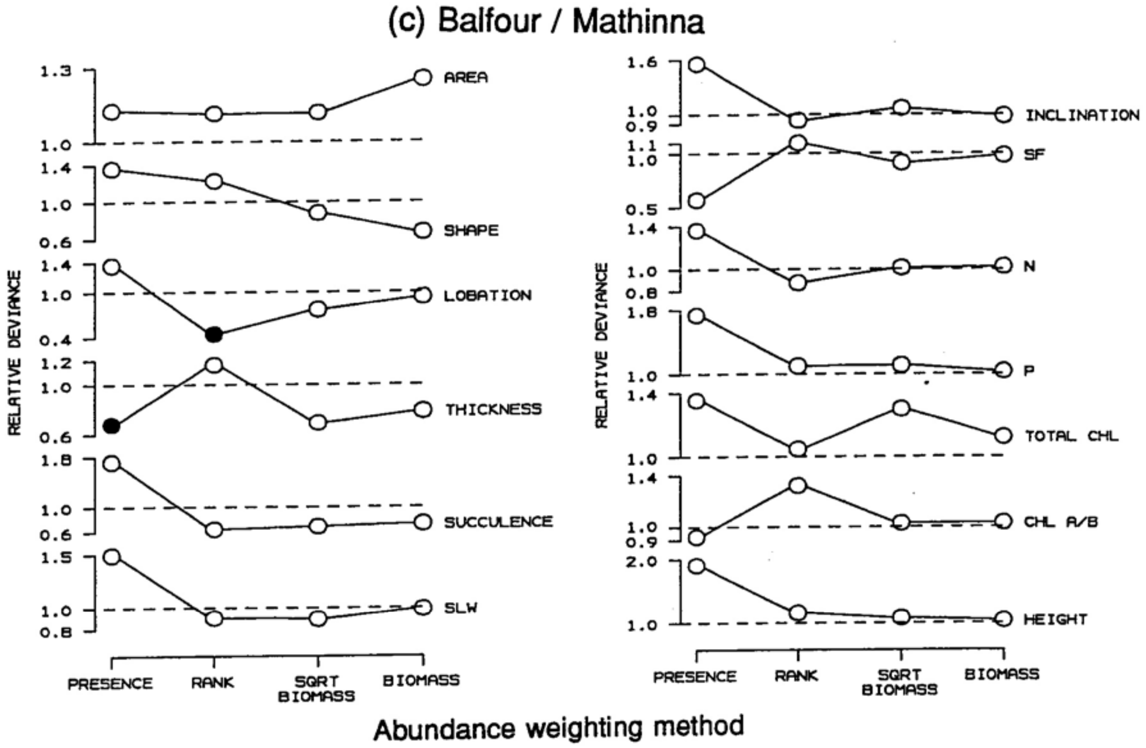


Fig. 7.6 Null model randomisation tests for convergence or divergence in texture between regional-scale *Nothofagus*-dominated communities T1 Balfour, T2 Anne and T3 Mathinna. Format as for Fig. 7.5.



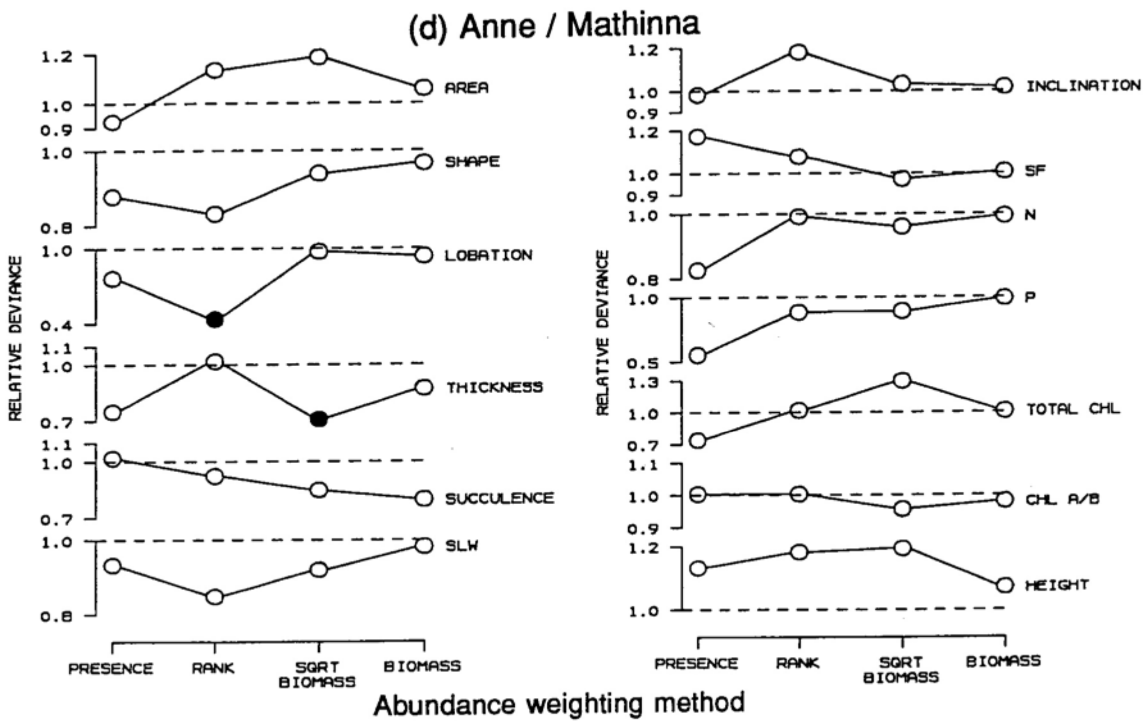


Fig. 7.6 (continued)

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

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

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

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

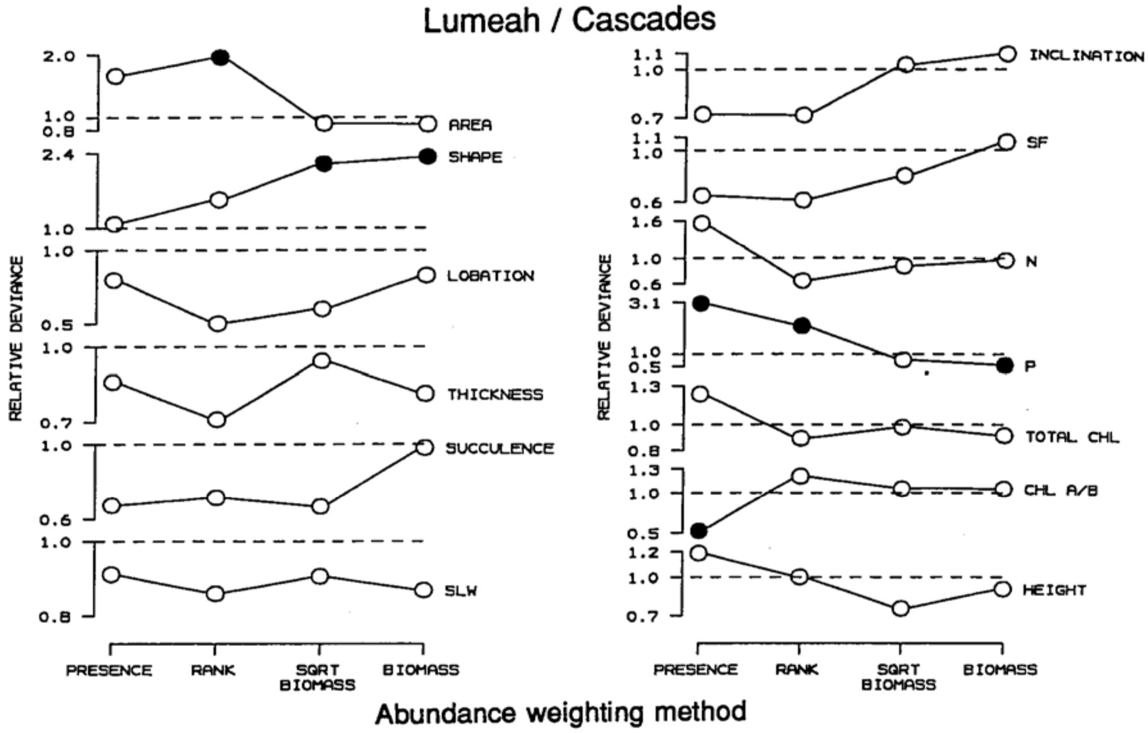


Fig. 7.7 Null model randomisation tests for convergence or divergence in texture between regional-scale *Nothofagus*-dominated communities A1 Lumeah and A2 Cascades. Format as for Fig. 7.5.

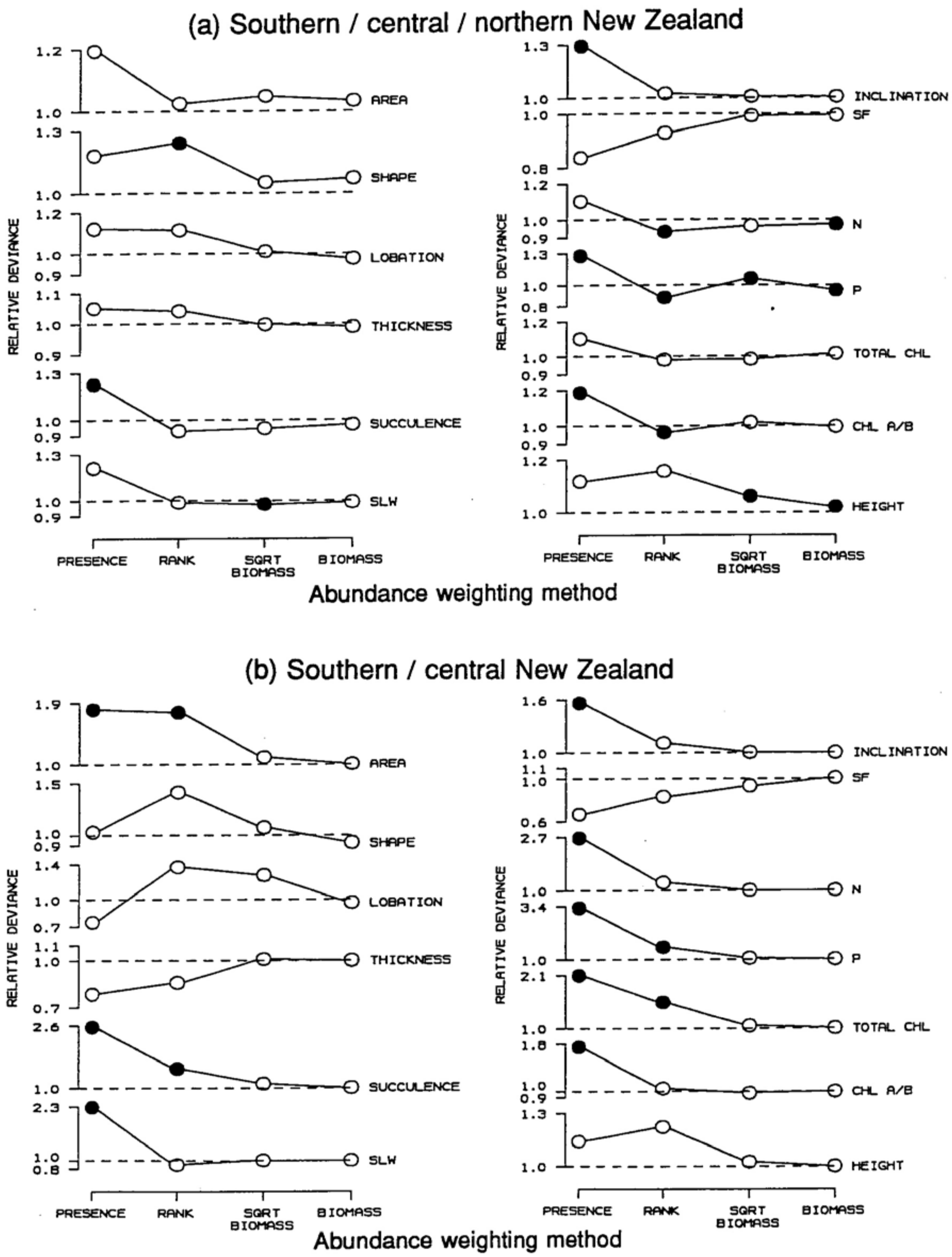
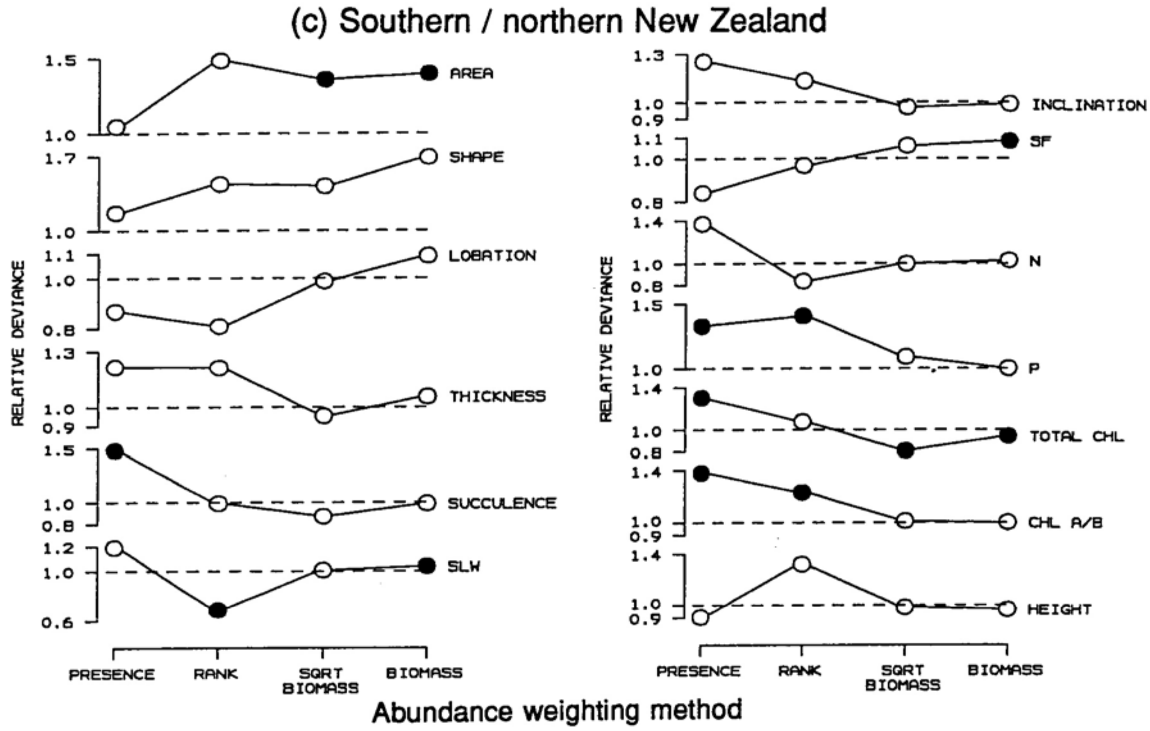


Fig. 7.8 Null model randomisation tests for convergence or divergence in texture between regional-scale *Nothofagus*-dominated communities southern (ZS), central (ZC) and northern (ZN) New Zealand. Format as for Fig. 7.5.



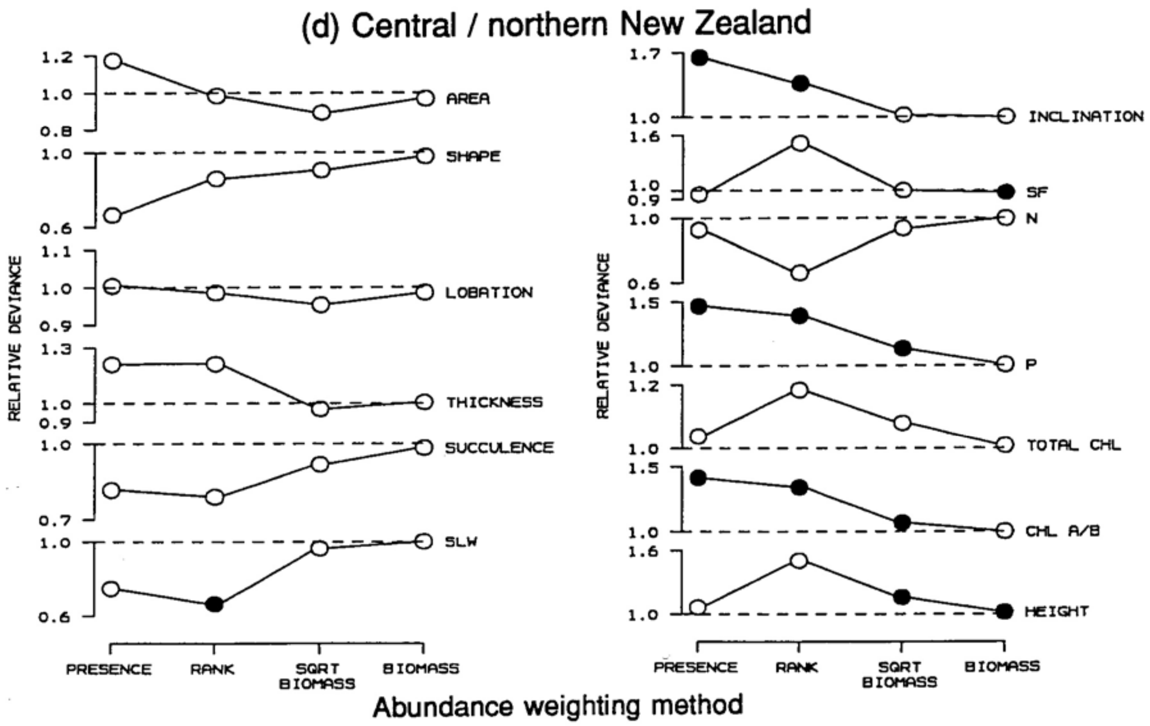


Fig. 7.8 (continued)

Local scale

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

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

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

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

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

7.12d).

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

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

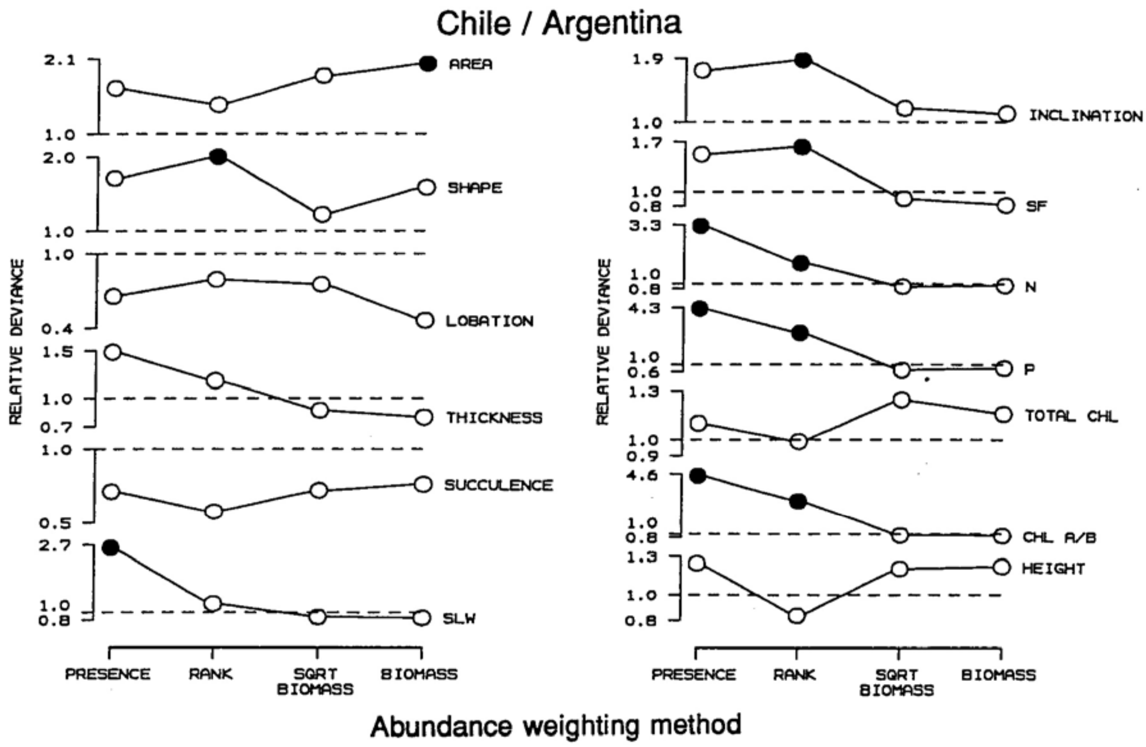


Fig. 7.9 Null model randomisation tests for convergence or divergence in texture between regional-scale *Nothofagus*-dominated communities of Chile (SC), and Argentina (SA). Format as for Fig. 7.5.

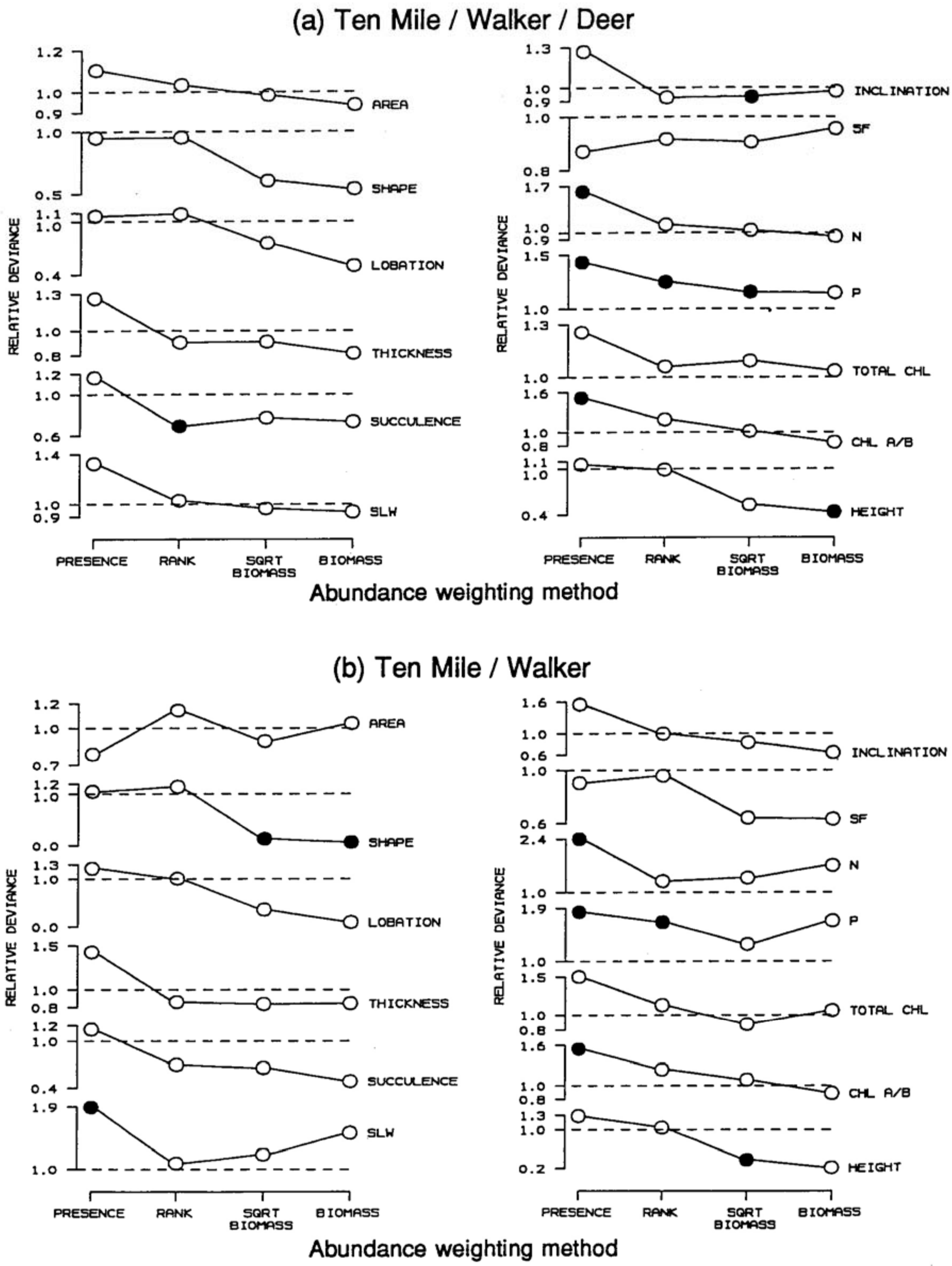
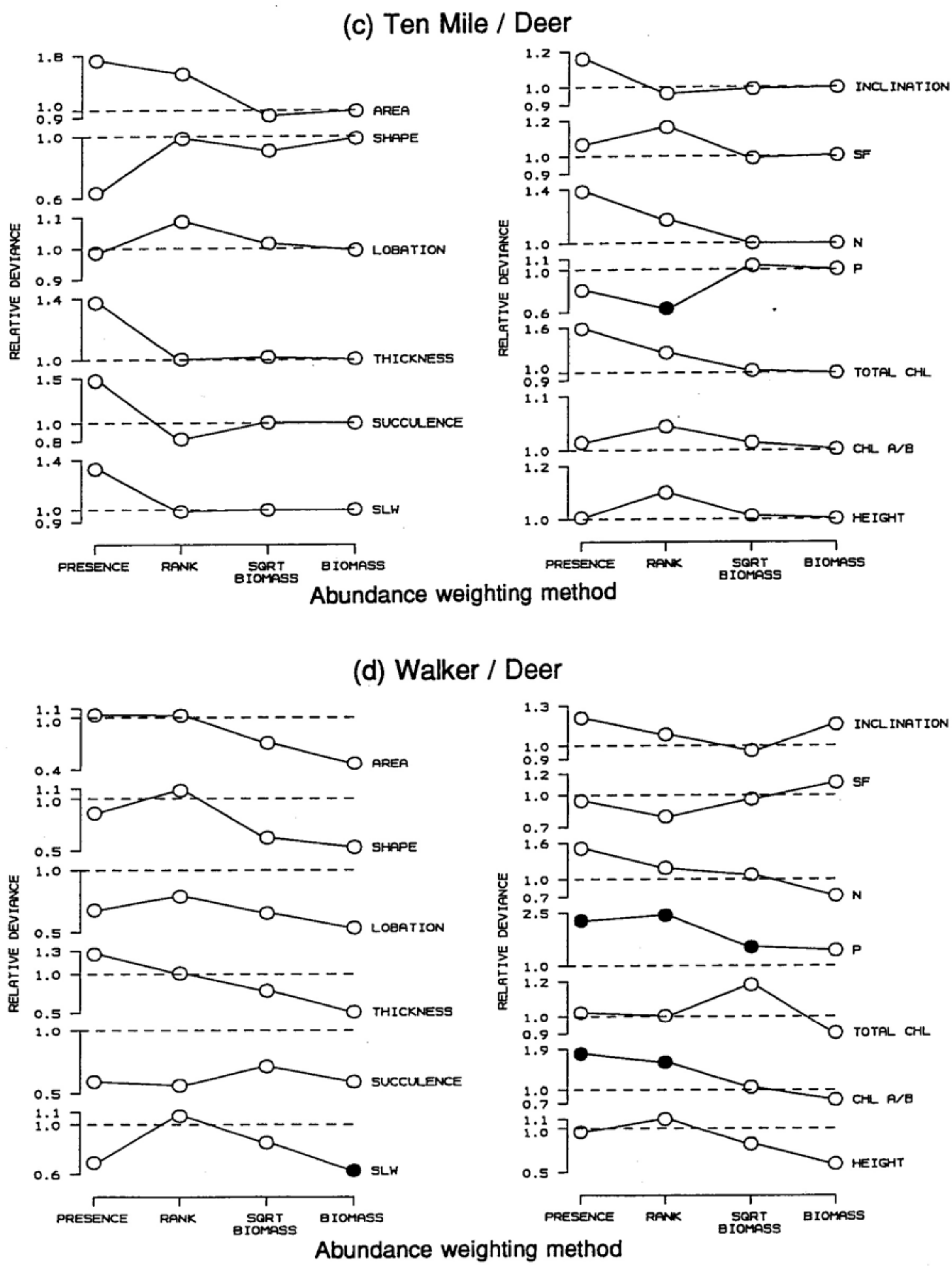


Fig. 7.10 Null model randomisation tests for convergence or divergence in texture between local-scale *Nothofagus*-dominated communities ZS1 Ten Mile, ZS2 Walker and ZS3 Deer. Format as for Fig. 7.5.



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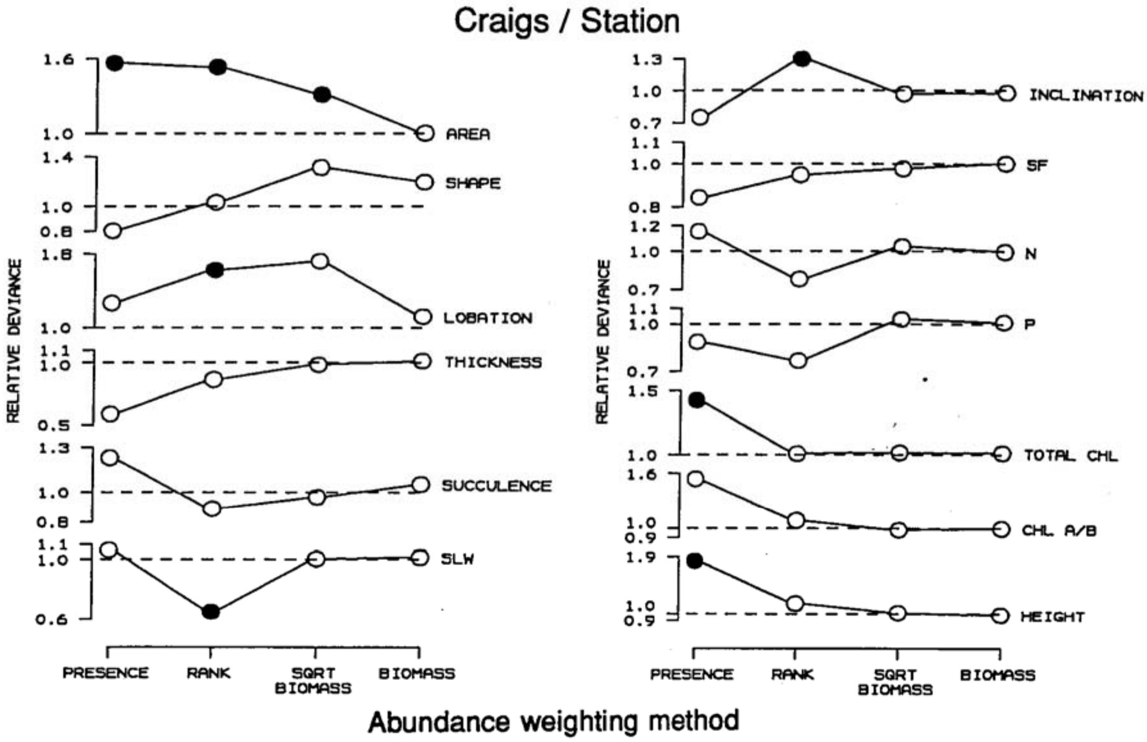


Fig. 7.11 Null model randomisation tests for convergence or divergence in texture between local-scale *Nothofagus*-dominated communities ZC1 Craigs and ZC2 Station. Format as for Fig. 7.5.

Closely matched sites from different landmasses

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

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

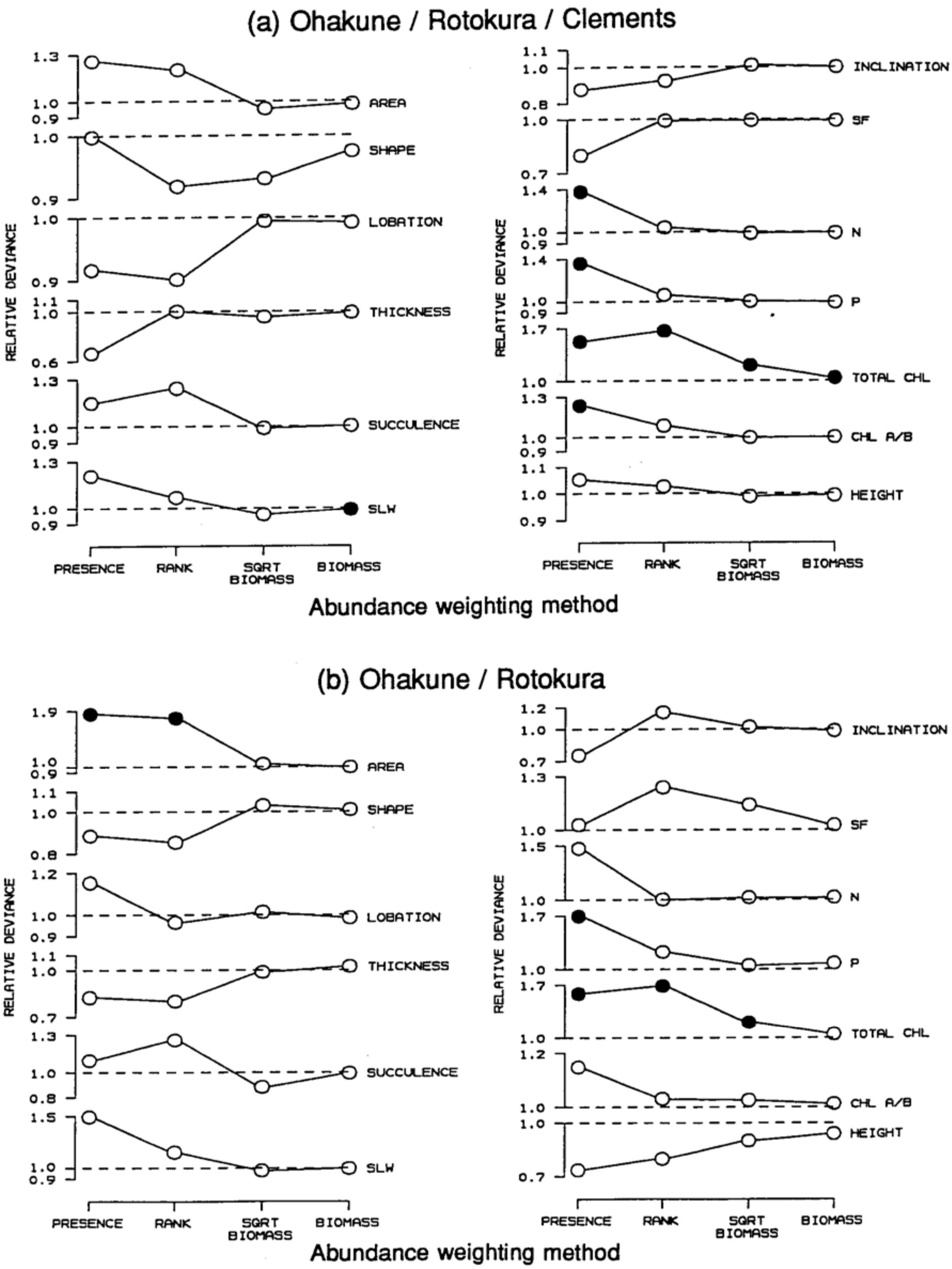
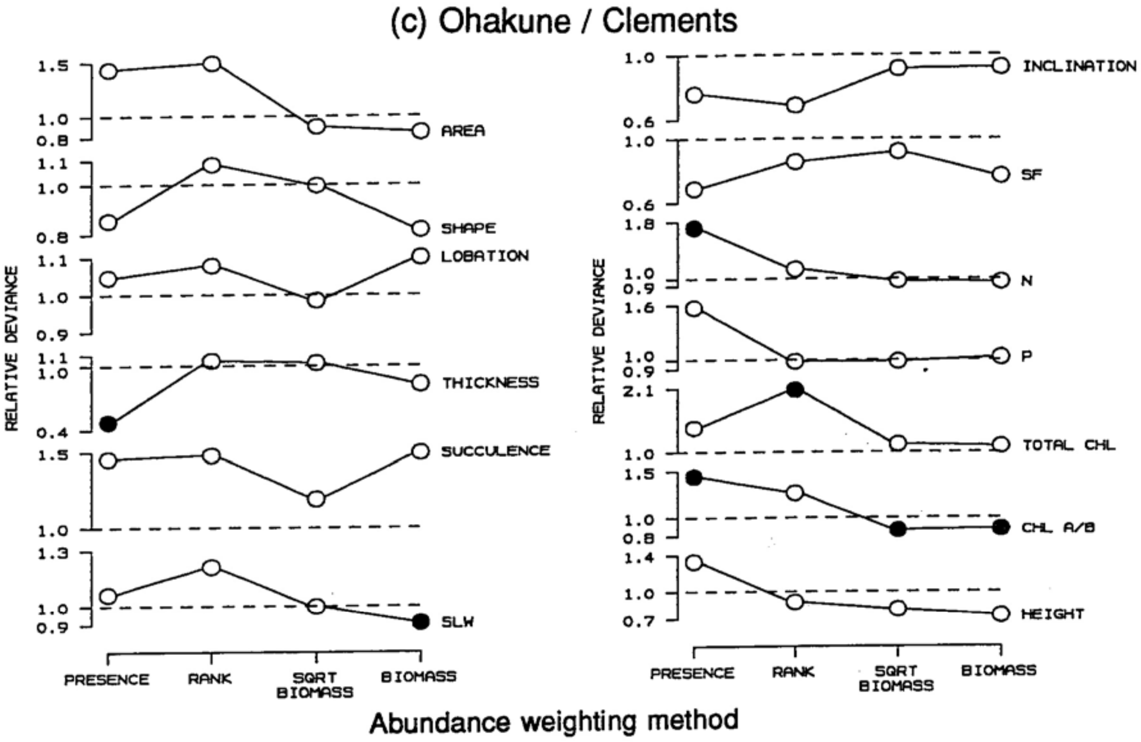


Fig. 7.12 Null model randomisation tests for convergence or divergence in texture between local-scale *Nothofagus*-dominated communities ZN1 Ohakune, ZN2 Rotokura and ZN3 Clements. Format as for Fig. 7.5.



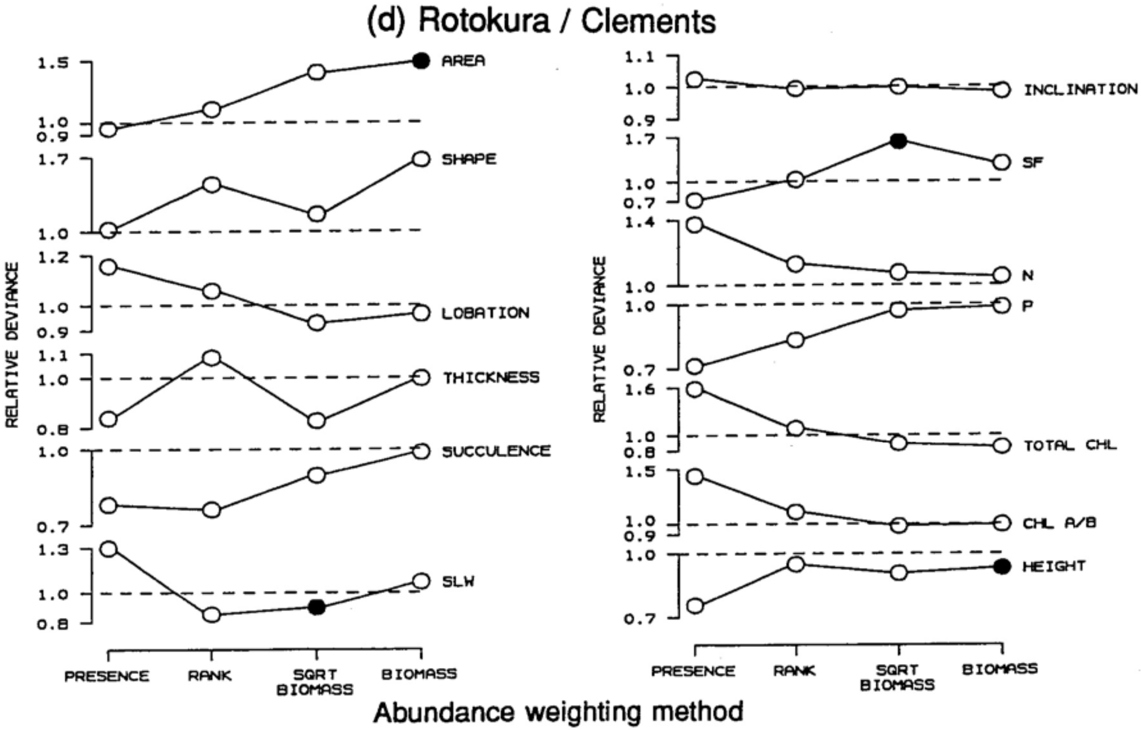


Fig. 7.12 (continued)

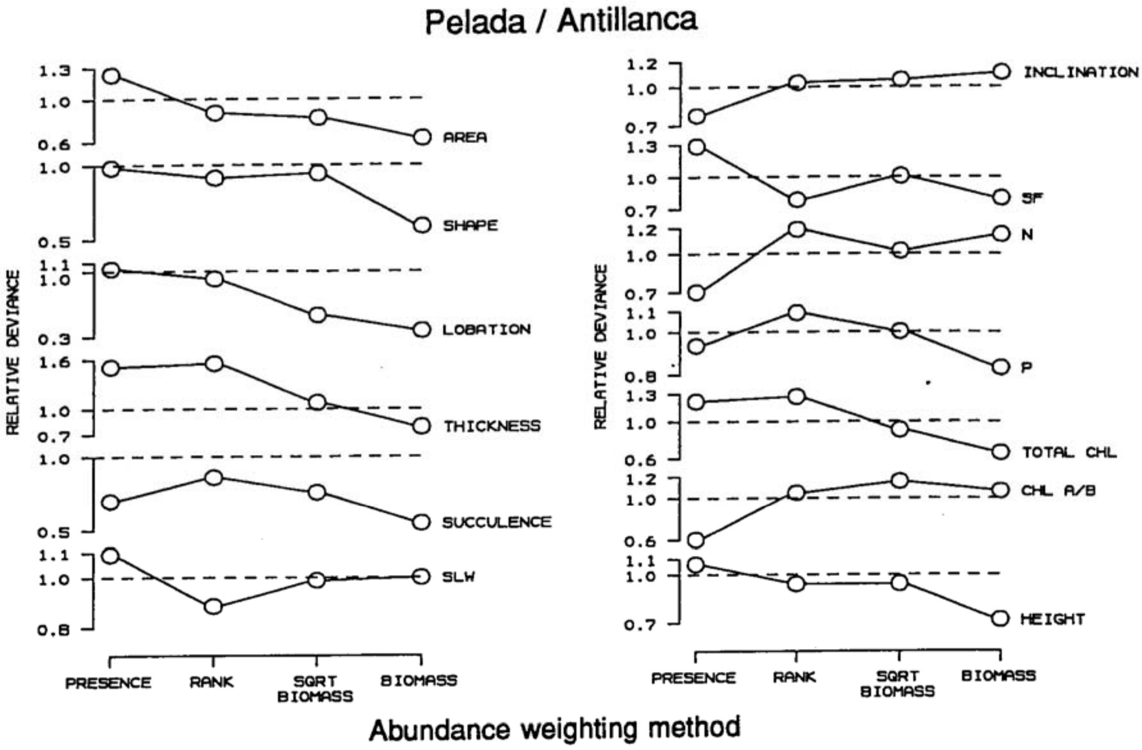


Fig. 7.13 Null model randomisation tests for convergence or divergence in texture between local-scale *Nothofagus*-dominated communities SC1 Pelada and SC2 Antillanca. Format as for Fig. 7.5.

PATTERNS AMONG TEXTURE VARIATES

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

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

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

However, there are a number of notable differences.

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

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

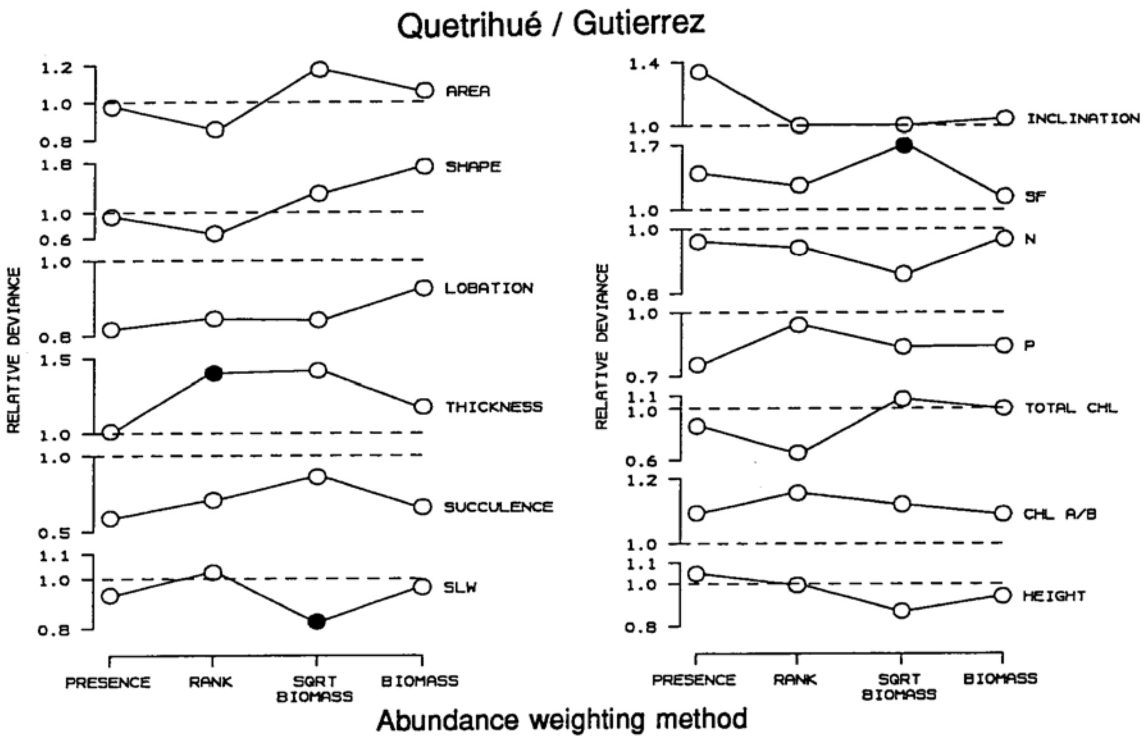


Fig. 7.14 Null model randomisation tests for convergence or divergence in texture between local-scale *Nothofagus*-dominated communities SA1 Quetrihué and SA2 Gutierrez. Format as for Fig. 7.5.

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

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

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

COMPARISON OF RESULTS OBTAINED WITH DIFFERENT TEST STATISTICS

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

Values along the main diagonal of the table (highlighted) represent tests that produced the same result (i.e. significant or non-significant convergence or divergence) using both test statistics. In general, these values are high as proportions of the row and column totals, suggesting that the correspondence between the two comparison methods is high. However, in a small number of cases (six), significant convergence was detected by one method, and significant divergence by the other. Most such tests employed high abundance weighting levels (e.g. PSU specific weight for communities ZS and ZN; weighting by photosynthetic biomass; Figs. 6.5c, 7.8c). The results could reflect differences in the degree to which each test statistic is dependent on the characters of the few most abundant species. This is because it is possible for the dominant species of a set of communities being compared to be more or less similar in their characters than overall texture. This can result in either significant convergence or divergence in texture between the same communities depending on how heavily the dominant species are weighted. Since the two test statistics utilise species abundances in a slightly different way, such differences could also occur when the same comparisons, weighting species by abundance, are carried out using a different test statistic.

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

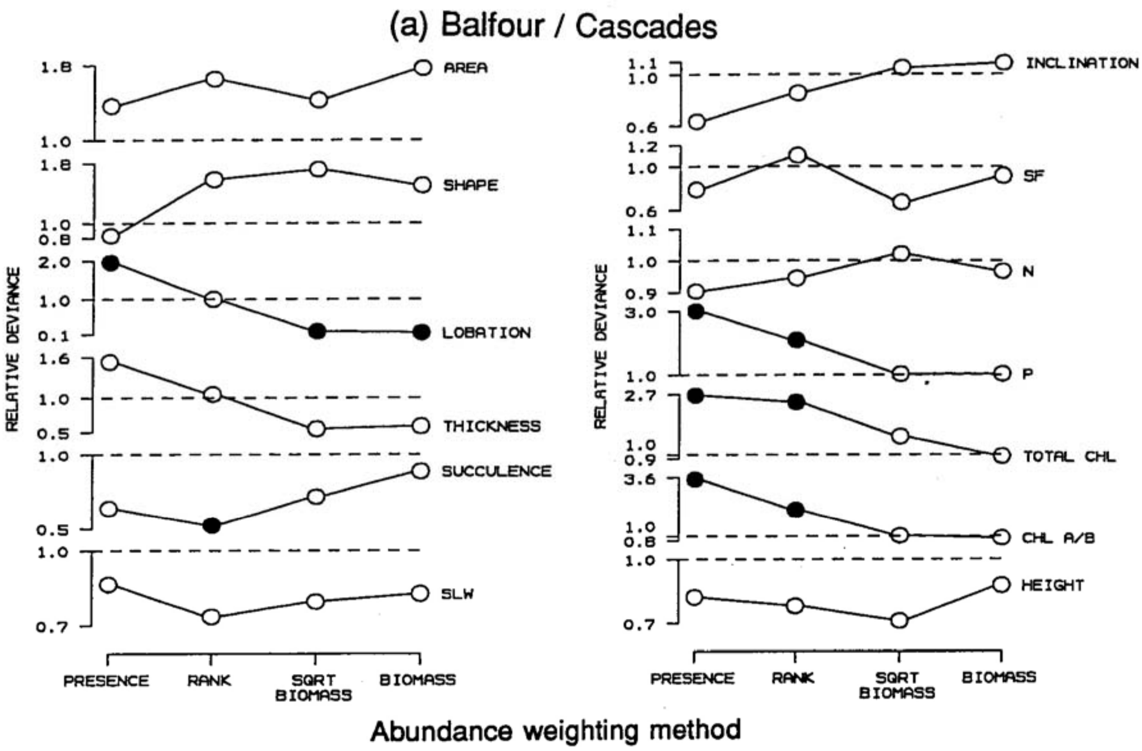


Fig. 7.15 Null model randomisation tests for convergence or divergence in texture between *Nothofagus*-dominated communities from different landmasses closely matched in their environments: **(a)** T1 Balfour/A2 Cascades; **(b)** T2 Anne/ZN1 Ohakune; **(c)** ZN2 Rotokura/SA1 Quetrihué. Format as for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

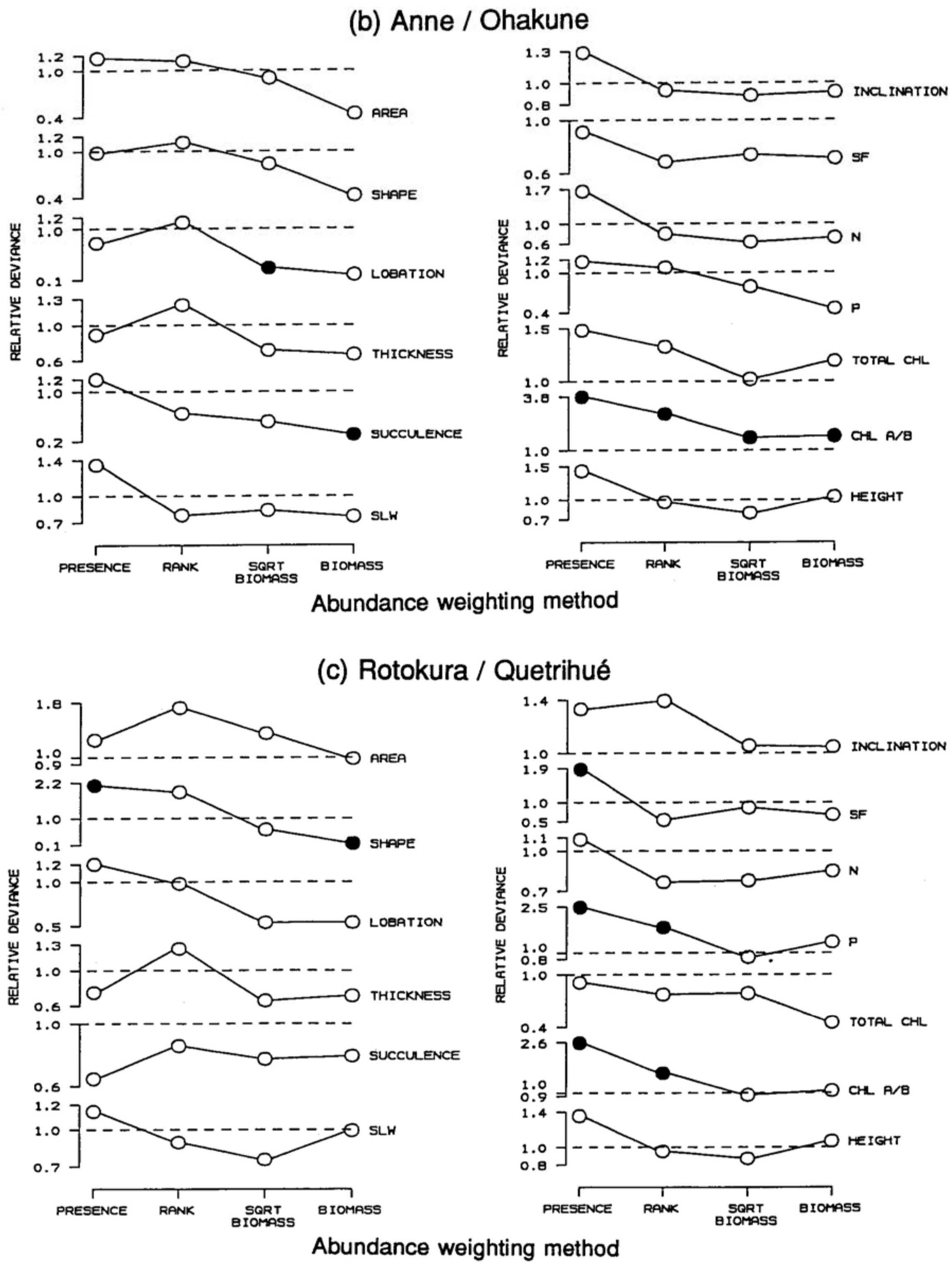


Fig. 7.15 (continued)

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

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

*P<0.05

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

Although it was expected that comparison of texture distributions might reveal convergence between communities with different texture means (Fig. 7.1c), there were relatively few tests for which departure from the null model in the direction of divergence using $\bar{D}_T$ as the test statistic was associated with convergence using $\hat{D}_T$. Most such tests involved heavy weighting by species abundance. For example, Argentinian sites SA1 Quetrihué and SA2 Gutierrez differ in the square root of biomass-weighted mean of PSU specific weight, resulting in a non-significant tendency towards divergence using the test statistic $\bar{D}_T$ to compare the communities (Fig. 6.11). Square root of biomass-weighted distributions of the same character are, however, relatively similar (Fig. 7.16c), resulting in significant convergence using $\hat{D}_T$ (Fig. 7.14).

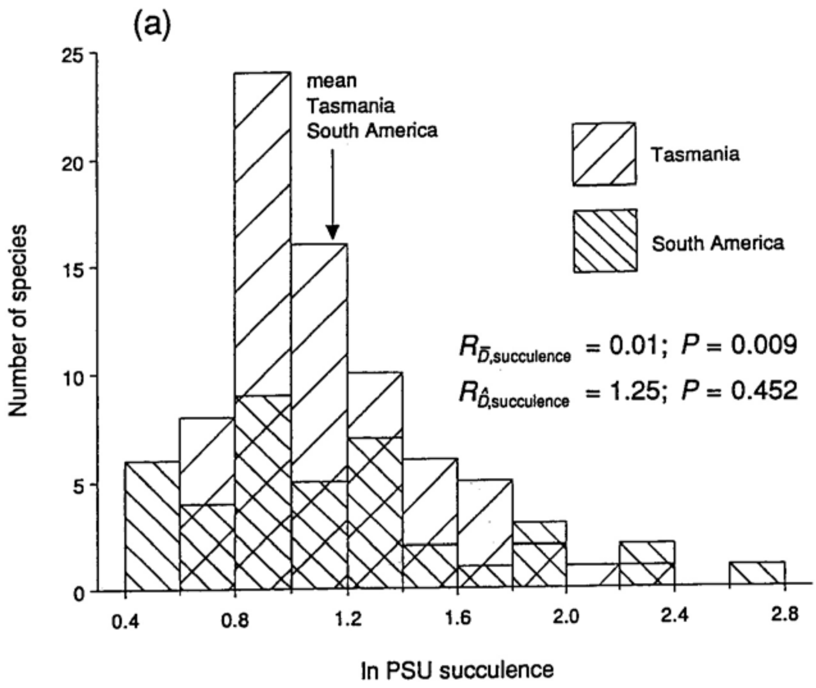
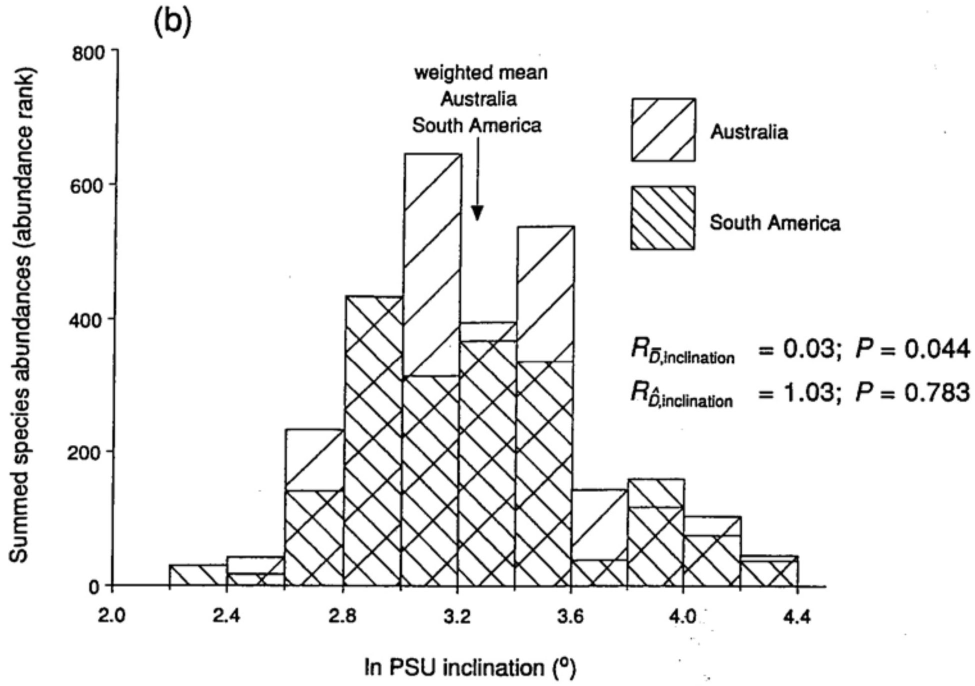


Fig. 7.16 Frequency histograms of community texture distributions for communities showing departure from the null model in opposite directions depending on whether texture means or distributions are compared. **(a)** Tasmania (T) and South America (S), convergent in texture means of PSU succulence (no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



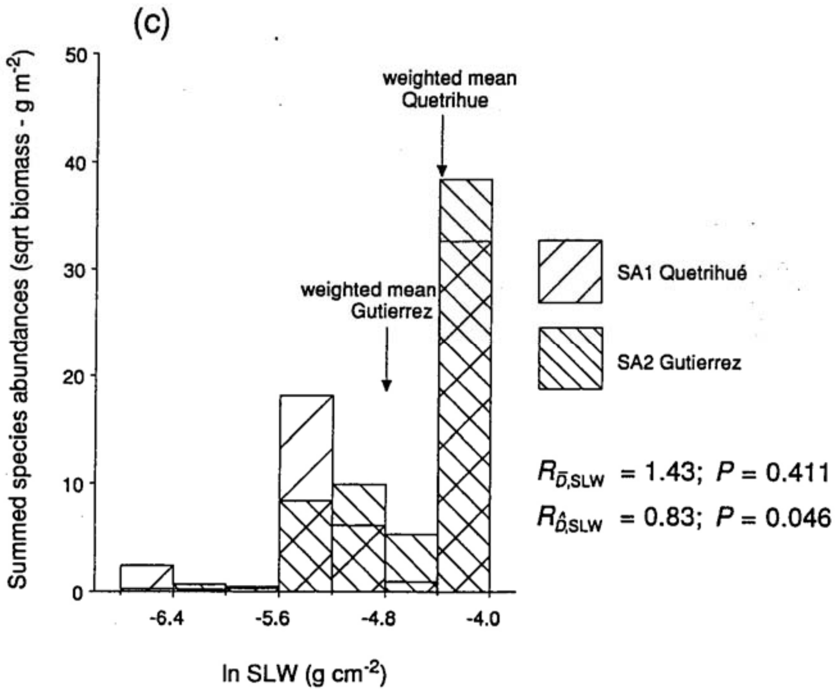


Fig. 7.16 (continued)

7.4 Discussion

COMMUNITY-LEVEL CONVERGENCE AND DIVERGENCE

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

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

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

Generally the results, and the conclusions drawn from them, are similar to those of Chapter 6, where the comparisons were of one parameter of the community texture distribution — the mean — rather than of the distributions themselves. The overall correspondence between the results obtained in the present chapter and the previous one (Table 7.3) demonstrates that the mean is useful as a general summary statistic for community texture. However, differences in the results of some comparisons using the two approaches highlight the danger of misleading results in individual tests when only the mean of texture is considered. In some cases, departure from the null model was in opposite directions depending on which test statistic (the deviance of means, or the deviance of distributions) was used (Fig. 7.16). By responding to differences in both the shapes of texture distributions and their means, the deviance of texture distributions, $\hat{D}_T$, used in this chapter, represents both a more conservative and more powerful index of community dissimilarity in texture.

PREVIOUS COMPARISONS OF COMMUNITY TEXTURE DISTRIBUTIONS

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

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

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

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

Conclusions

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

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