9. Convergence among *Nothofagus*-dominated communities: derived texture factors

9.1 Introduction

The hypothesis of community-level convergence is that similar environments, coupled with the effects of assembly rules limiting the co-occurrence of species with similar niches, will lead to similar niche spectra in different communities (Wilson *et al.* 1995; Section 1.5). Testing this hypothesis is not completely straightforward, since niches are defined by an indefinite number of parameters and so cannot be measured directly (Hutchinson 1958; Colwell 1979). One approach is to seek similarity between communities in properties that would be determined by their niche structure; for example, species richness (Wilson *et al.* 1987; Schluter 1986; Chapter 5). Another approach is to characterise niches by measurable parameters that would be expected to show some correlation with them. This approach has been adopted in the three preceding chapters, where functional characters of species have been used as proxies for their niches, and convergence has been sought in the community-wide spectra of these characters; that is, in community texture.

The 13 characters used to characterise texture in the present study were chosen because of their assumed, or previously demonstrated, functional importance (Section 2.2.2; Chapter 4). Modes of resource capture constitute an important aspect of function (Tilman 1982), so such characters are most likely to represent useful surrogates for alpha (resource) niches. However, measured species values for a character are likely to be an outcome of adaptation to several independent or related environmental and resource parameters, as well as of other factors, such as phylogeny, random mutations and sampling errors. These factors are not necessarily independent. For example, some environmental factors (e.g. temperature) may be correlated with other environmental factors (e.g. humidity) and with certain resources (e.g. light). The hypothesis of community-level convergence makes predictions only about patterns related to finite resources for which species must compete. Where other parameters — such as environmental factors and stochastic ‘noise’ — are relatively important in determining what values species will have for a character, the character may tend to have a relatively poor correspondence with niche.

To maximise the likelihood of detecting convergence where it has occurred, it would be desirable to focus on the components of character variation determined only by alpha niche axes (i.e. by species responses to finite resources), disregarding other sources of variation. Multivariate ordination techniques such as principal component analysis (PCA) and factor analysis (FA) represent one possible approach. Given a set of correlated variables, these techniques give a new set of variables (uncorrelated, in the case of PCA and some forms of FA), each summarising a component of variation in the original variables (Manly 1994). Where there are intercorrelations among the variables, the derived factors may partly summarise this shared variation. If the variables covary because of some common underlying causes (for example, characters representing different aspects of adaptation to an environmental gradient), it follows that some of the derived factors may approximate variation in the common underlying factors.

The texture variates examined in the present study are not completely independent. Significant intercorrelations were detected among most of the characters, in Chapter 4 (Table 4.1). It has been assumed that some of the shared variation might reflect common adaptations to environmental or resource factors. For example, the strongly intercorrelated variates PSU succulence, chlorophyll content, phosphorus content, nitrogen content and specific weight would all be expected to vary along gradients of light availability (Hollinger 1989; Popma *et al.* 1992; Ellsworth & Reich 1993; Mulkey *et al.* 1993). It therefore seems possible that the shared variation among them reflects adaptations, in each character, to the light regime. PCA and FA provide a method of expressing such shared variation by a reduced number of variables (the factors), which might be more strongly related to the underlying causal factors than are the base variables themselves. For example, it might be possible to summarise a component of the shared variation in the above species characters by a single derived factor. If the hypothesis that these characters covary due to parallel responses to the light regime is true, it is possible that the derived factor would show a closer relationship to light availability than do the characters themselves.

In this chapter, principal component analysis is used to identify and extract underlying components of variation in the 13 texture variates examined in previous chapters. Varimax factor rotation, a factor analysis technique, is applied in order to improve the interpretability of the derived variates (factors) in terms of the texture variates. Texture, expressed in terms of the derived factors, is compared among *Nothofagus*-dominated communities using the approaches developed in each of the previous three chapters. It is anticipated that the factors obtained may reflect underlying causes of variation in texture, including adaptation to resource spectra and environmental parameters, more closely than any of the variates from which they are derived. If community-level convergence is a reality, it should be detected in factors that reflect species responses to limiting resources, i.e., their alpha niches. Factors not related to niches, on the other hand, should show no significant convergence using the null model approach of this study.

9.2 Methods

TEXTURE DATA

The texture data subjected to factor analysis comprised 13 variates: the 12 listed in Section 2.3.5, in addition to species height, defined in Section 6.2. Field and laboratory methods are outlined in Chapter 2, and study sites are described in Chapter 3.

ANALYSIS

Derivation of factors from texture variates

Principal component analysis (PCA) was used to obtain initial derived variates based on the 13 observed ('raw') texture variates. Each texture variate (and therefore, each derived principal component) comprised values for each species or entity[1] observed at each study site, a total of 644 records (see Appendix A). Species values were transformed as described in Sections 2.3.5 (Table 2.1) and 6.2. Texture data were also standardised (to a mean of 0 and standard deviation 1), as this can result in a more even distribution of species values in the space of the derived factors.

Given data for a set of n variates, PCA yields a further set of n variates (the principal components) which are linear combinations of the original variables but are uncorrelated and in rank order of the proportion of variation in the data for which they account (Manly 1994). Where the variables supplied are appreciably intercorrelated, the first few principal components (PCs) may accomodate the majority of variation. This means that all but the first few PCs may often be ignored without a major sacrifice of explanatory power. In the present analysis, the minimum number (m) of principal components that explained at least 75% of the variation in each of the 13 texture variates were retained.

To improve the interpretability of the derived variates in terms of the observed species characters, varimax rotation (Cooley & Lohnes 1971) was carried out on the principal components retained once the last n-m had been eliminated, as described above. In this procedure, factors (initially, principal components) are mathematically 'rotated' in their multivariate space to a configuration at which the sum of the variances of the squares of the factor loadings (i.e. correlations between each factor and each of the original variables) is maximised. Kaiser normalisation of the factor loadings was first carried out, i.e. the loadings were standardised to a constant mean and standard deviation, a procedure that may give improved results. The effect of varimax rotation is to maximise some loadings while minimising others. Factors will then tend to be explained primarily by a reduced subset of the original variables, in

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[1] 'Entity,' i.e. a size or age class of a species for which such classes were distinguished at certain sites.

comparison with the unrotated principal components, improving interpretability. The factors obtained by varimax rotation of principal components are still orthogonal and uncorrelated, but the rank order of explained variation characteristic of principal component analysis may be lost.

Species scores on the rotated factors were calculated by multiple regression of the factors on the original variables (Cooley & Lohnes 1971). This gave a new set of texture variates — the factors — to which tests for community convergence could be applied.

Principal component analysis and varimax rotation were carried out using the SPSS-X computer program (SPSS Inc. 1986).

Texture convergence

Evidence for convergence in texture between communities was sought by means of randomisation tests comparing observed among-community variation in texture to variation expected under a null model simulating random assignment of species characters to communities. The null model is described fully in Section 6.2. In separate tests, community texture was characterised by the mean (test statistic $\bar{D}_T$), distribution ($\hat{D}_T$) and mean-adjusted distribution ($\hat{D}'_T$) of each of seven factors derived by factor analysis, as described above. Randomisation tests are described fully in Sections 6.2, 7.2 and 8.2.

Comparisons performed

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

9.3 Results

DERIVATION OF TEXTURE FACTORS

Seven factors were required to achieve communalities of at least 75% for each of the 13 primary texture variates (the communality of a variable is equal to the percentage of its variation retained in the factor model; Cooley & Lohnes 1971). The communality of each variable and its loading on each of the seven factors (F1 to F7) are shown in Table 9.1. Factor loadings are equivalent to correlation coefficients (Pearson *r*) between each factor and each input variable (Cooley & Lohnes 1971). Loadings greater than 0.5, which correspond to the variables most important in defining each factor, are highlighted in the table. The proportion of the total variation in the original variables accounted for by each factor is also shown.

F1 accounts for the greatest proportion of variation in the original variables, and is related most strongly to PSU succulence, specific weight, total chlorophyll and species height. Each of the remaining six factors accounts for approximately half as much of the total variation as F1. F2 is related most strongly to PSU area and support fraction; F3 to PSU phosphorus content and chlorophyll *a/b* ratio; F4 to PSU thickness; F5 to PSU nitrogen and phosphorus content; F6 to PSU lobation and inclination; and F7 to PSU shape.

Table 9.1 Loadings of texture variates on each of seven factors derived by varimax rotation of principal components. Loadings greater than 0.5 in magnitude are shown in bold type. Communalities of the texture variates in the factor model, and the percentage of total variation in the texture variates explained by each factor are also shown.

Texture variate	Communality (%)	Factor loadings						
		F1	F2	F3	F4	F5	F6	F7
Area	76	0.16	**0.71**	0.02	0.29	-0.16	0.34	0.00
Shape	90	-0.08	0.16	0.00	0.07	-0.10	0.16	**0.91**
Lobation	80	-0.13	0.42	0.15	-0.47	-0.09	**0.52**	-0.31
Thickness	89	-0.12	0.17	0.04	**0.91**	-0.07	-0.07	0.03
Succulence	85	**0.84**	0.02	0.13	0.29	0.20	-0.04	-0.04
SLW	82	**-0.78**	0.18	0.01	0.29	-0.23	0.13	0.15
Inclination	88	-0.20	0.09	-0.13	-0.06	-0.06	**0.87**	0.23
SF	88	0.22	**-0.86**	0.18	-0.01	-0.04	0.05	-0.23
N	87	0.34	-0.08	0.01	-0.07	**0.86**	-0.09	-0.08
P	83	0.31	0.01	**0.64**	0.00	**0.56**	0.00	-0.10
Total chl	78	**0.81**	-0.06	-0.17	-0.06	0.29	-0.05	-0.08
Chl *a/b*	87	-0.09	-0.11	**0.92**	0.02	-0.04	-0.09	0.03
Height	83	**-0.66**	-0.07	-0.21	0.29	0.21	0.32	-0.34
% total variation explained		21.5	11.8	10.9	10.8	10.1	10.0	9.2

PATTERNS AMONG COMMUNITIES

For brevity, only results from overall comparisons among the four landmasses, and for a representative sample of the comparisons done at each community scale (focusing on communities found to be closely-matched in their environments in Chapter 3) are described in detail here.

Landmass scale

In a comparison of the four landmass-scale communities Tasmania, Australia, New Zealand and South America there is significant convergence in only one factor, F6 (related primarily to PSU lobation and inclination; Table 9.1), whether texture is expressed as the community mean, distribution[2] or mean-adjusted distribution (Fig. 9.1a). The convergence in F6 is significant only at higher abundance weighting levels for comparisons of texture means or distributions, but at all levels except abundance rank (though still $R_{\hat{D}';F6}<1$) for mean-adjusted distributions. Texture means and distributions are divergent at lower weighting levels for three factors, F3 (PSU phosphorus, chlorophyll *a/b*), F4 (PSU thickness) and F5 (PSU nitrogen and phosphorus). There is no significant divergence among landmasses in mean-adjusted distributions of texture factors.

Tasmania and New Zealand, the two landmass-scale communities most closely matched in their macroenvironments, show little more significant convergence (Fig. 9.1b). However, non-significant trends towards convergence are apparent for several factors, especially in comparisons of mean-adjusted distributions, for which only F4 (related to PSU thickness) shows a trend towards divergence ($R_{\hat{D}';T}>1$) at any weighting level. Community means of F1 (PSU succulence, specific weight, total chlorophyll and species height) are significantly convergent with weighting by photosynthetic biomass. Distributions of F2 (PSU area, support fraction) are convergent with weighting by the square root of photosynthetic biomass. F5 (PSU nitrogen, phosphorus) is convergent when mean-adjusted distributions are compared and species values are weighted by abundance rank. F6 (PSU lobation, inclination) shows some significant convergence in texture means. Mean-adjusted distributions of F3 (PSU phosphorus, chlorophyll *a/b*) are significantly convergent at all weighting levels except biomass, while means and non-adjusted distributions are divergent at these weighting levels. There is significant divergence in no other factor.

Regional scale

Southern (ZS) and central (ZC) New Zealand are among the most closely matched regional scale communities in terms of their environments. However, they show significant convergence only between mean-adjusted distributions of texture factors (Fig. 9.2). Three factors, F1 (PSU succulence, specific weight, total chlorophyll and species height), F2 (PSU area, support fraction) and F3 (PSU phosphorus, chlorophyll *a/b*) are convergent at lower abundance weighting levels. Both means and distributions of F1 are divergent at lower weighting levels. Means of F2 are divergent with weighting by abundance rank, while means and distributions of F3 are divergent with species weighted by presence only. Distributions of F5 (PSU nitrogen and phosphorus) are divergent with species weighted by presence or abundance rank.

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[2] In the following discussion, ‘distribution’ will, unless otherwise qualified, refer to community texture distributions, not adjusted to a constant mean (such distributions are compared by the index $\hat{D}_T$, described in Section 7.2).

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

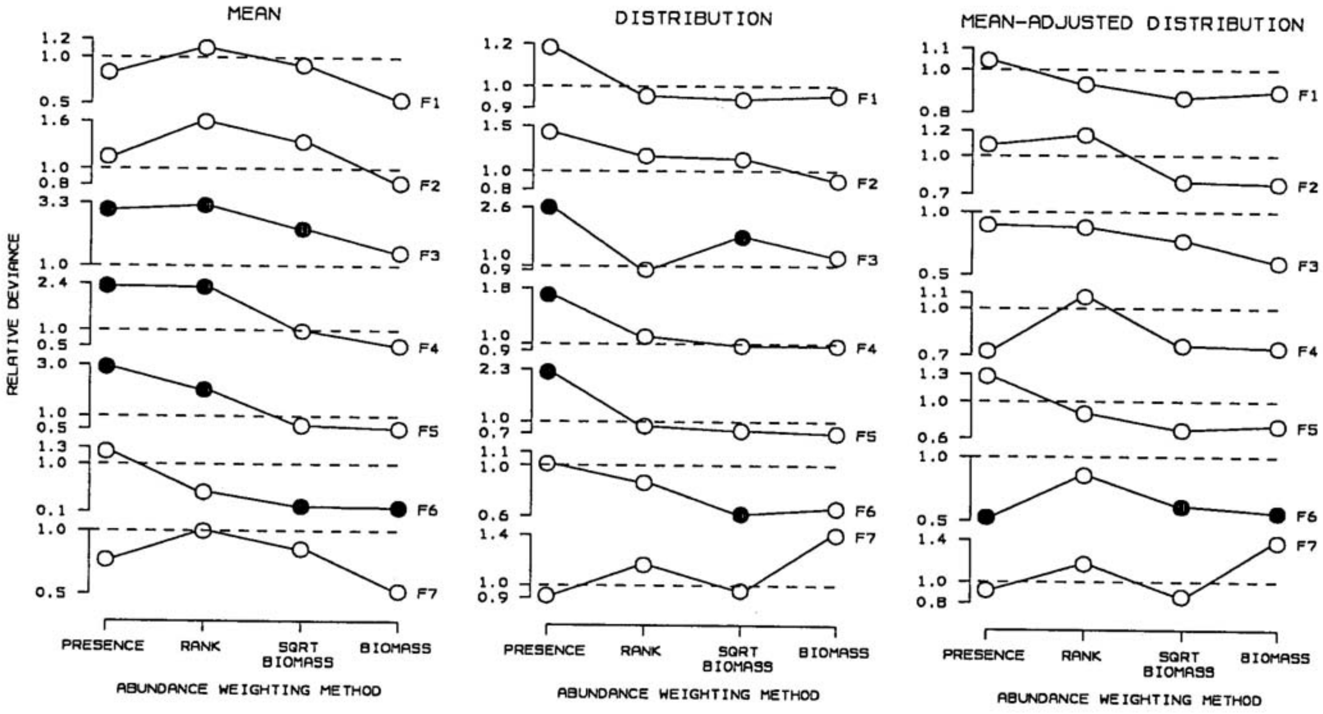

Fig. 9.1 Null model randomisation tests for convergence or divergence in texture between landmass-scale *Nothofagus*-dominated communities **(a)** Tasmania (T), Australia (A), New Zealand (Z) and South America (S); **(b)** Tasmania and New Zealand. Results are shown from tests comparing texture means (test statistic $\bar{D}_T$), distributions ($\hat{D}_T$) and mean-adjusted distributions ($\hat{D}'_T$). The relative deviance R_T of among-community variation in texture is shown for each of seven texture factors (F1-F7) and four methods of weighting individual species values by abundance in calculations of community texture. A value of $R_T<1$ indicates similarity in texture between communities relative to a null model simulating random community assembly (see text); $R_T>1$ indicates dissimilarity relative to the null model. Broken lines signify null model expectation ($R_T=1$). Filled symbols correspond to significant departure from the null model (convergence for $R_T<1$; divergence for $R_T>1$; $P<0.05$). Texture factors are derived from 13 texture variates by principal component analysis and varimax factor rotation (see text for full explanation). Key to abbreviations: RANK=abundance rank; SQRT BIOMASS=square root of photosynthetic biomass; BIOMASS=photosynthetic biomass (see text for full explanation).

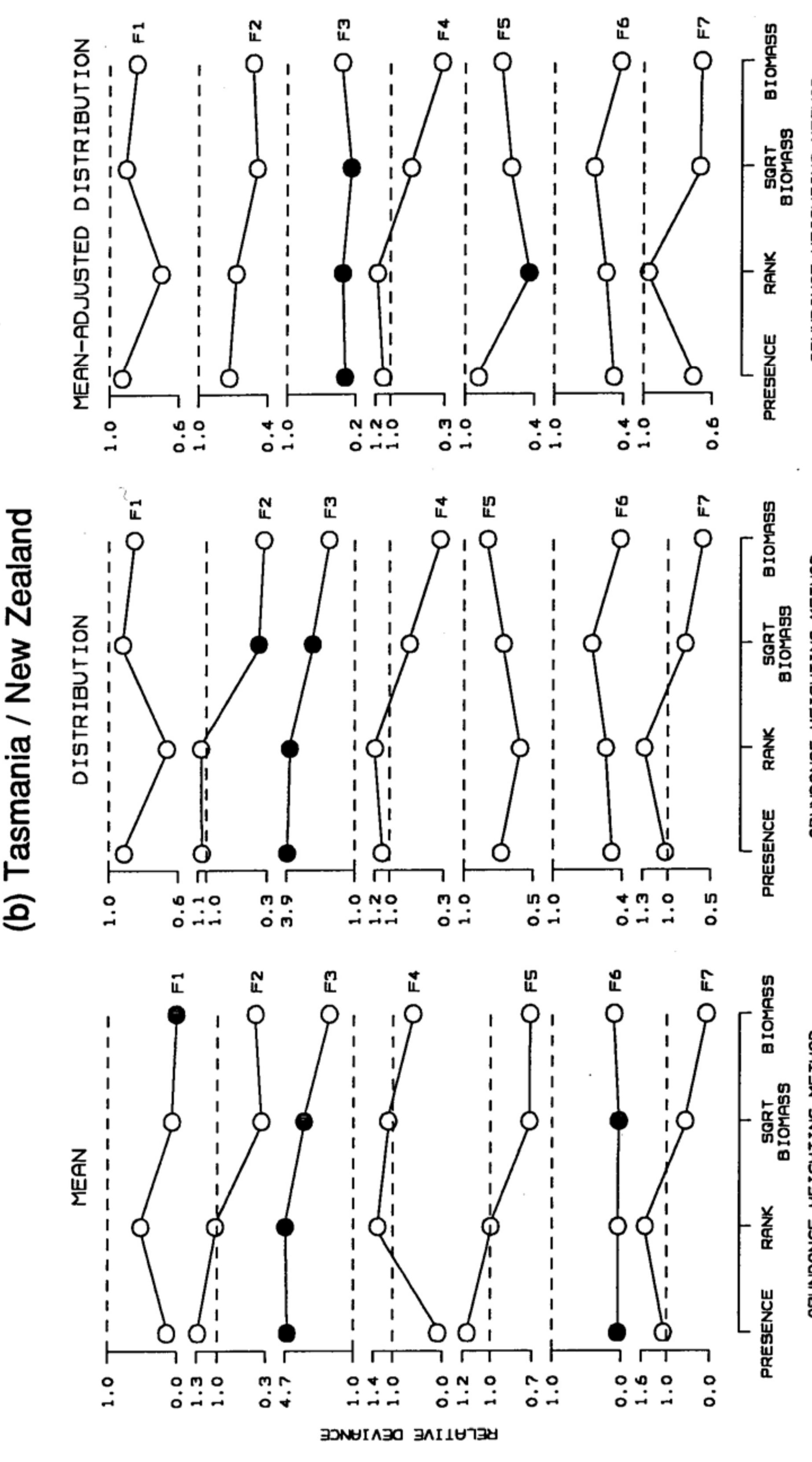

Fig. 9.1 (continued)

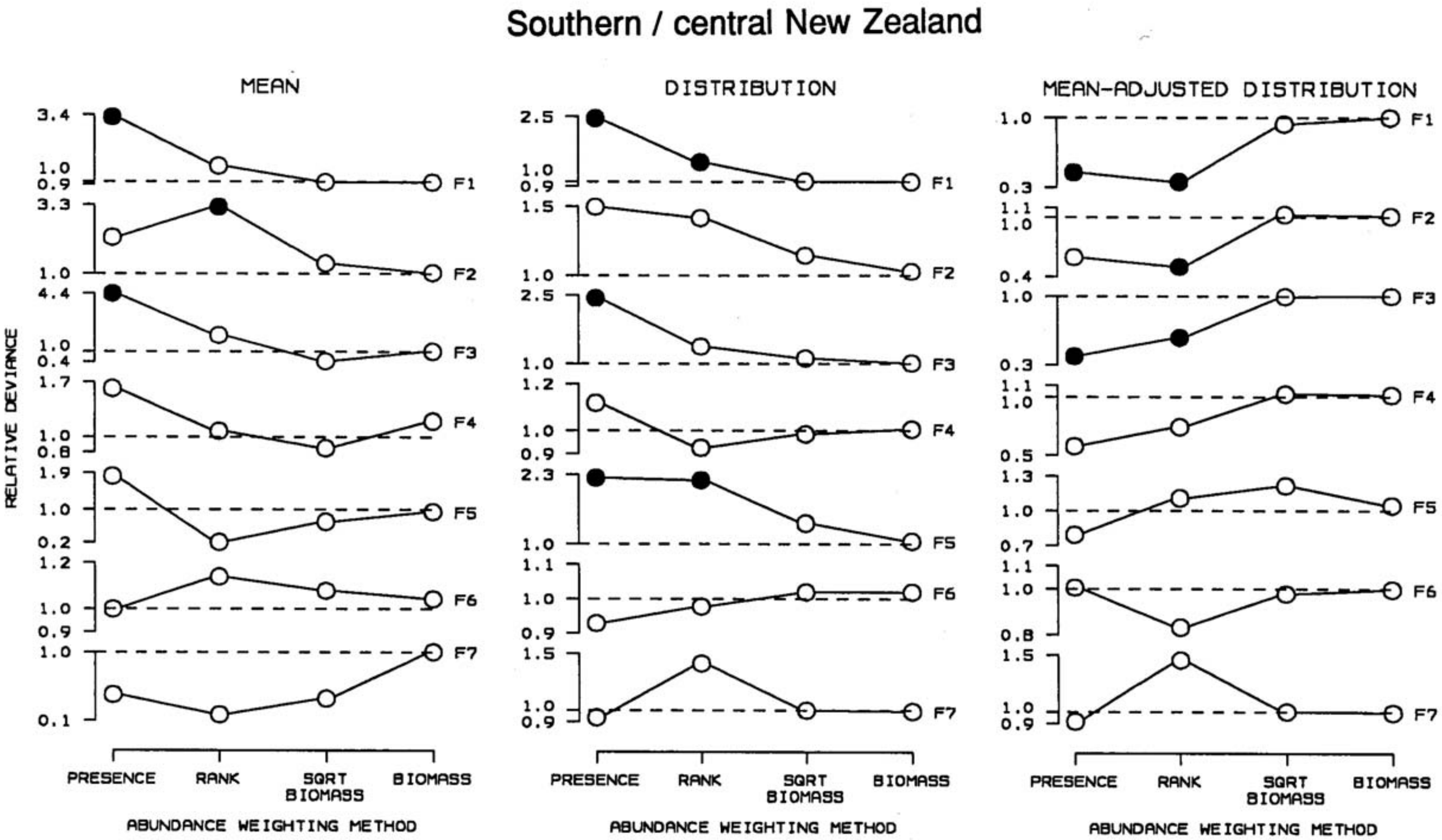

Fig. 9.2 Null model randomisation tests for convergence or divergence in texture between regional-scale *Nothofagus*-dominated communities southern (ZS) and central (ZC) New Zealand. Format as for Fig. 9.1.

Local scale

Northern New Zealand sites ZN2 Rotokura and ZN3 Clements are convergent in F1 (PSU succulence, specific weight, total chlorophyll, species height) with weighting by photosynthetic biomass (mean, distribution) or its square root (mean-adjusted distribution) and for mean-adjusted distributions in F5 (PSU nitrogen, phosphorus) with weighting by abundance rank (Fig. 9.3). There is significant divergence in means and distributions of F3 (PSU phosphorus, chlorophyll *a/b*) with weighting by abundance rank, and distributions of F4 (PSU thickness) with weighting by the square root of photosynthetic biomass.

Closely matched sites from different landmasses

Community means of F4 (PSU thickness) at T1 Balfour and A2 Cascades are convergent when species values are weighted by the square root of photosynthetic biomass; mean-adjusted distributions of the same factor are convergent with species weighted equally (Fig. 9.4a). There is a trend towards convergence in the mean-adjusted distributions of F5 (PSU nitrogen, phosphorus) at all weighting levels, significant with species weighted equally or by the square root of biomass. Both non-adjusted and mean-adjusted distributions of F6 (PSU lobation, inclination) are convergent at higher weighting levels. Mean-adjusted distributions of F7 (PSU shape) are convergent with species weighted equally. For F3 (PSU phosphorus, chlorophyll *a/b*) there is departure from the null model in opposite directions for means and distributions (divergence), as opposed to mean-adjusted distributions (convergence); trends are significant at lower weighting levels. Notably, in comparisons of mean-adjusted texture distributions, departure from the null model is in the direction of convergence ($R_{\hat{D}';T}<1$) at all weighting levels, for all factors except F2 (PSU area, support fraction) and F7.

Convergence between community texture means for T2 Anne and ZN1 Ohakune is confined to two factors, F4 (PSU thickness) and F6 (PSU lobation, inclination) at lower weighting levels (Fig. 9.4b). There is no significant convergence between distributions of texture factors. For mean-adjusted distributions, however, there is convergence in F1 (PSU succulence, specific weight, total chlorophyll, species height), F3 (PSU phosphorus, chlorophyll *a/b*) and F5 (PSU nitrogen, phosphorus) at lower weighting levels. Furthermore, all factors have $R_{\hat{D}';T}<1$ (a trend towards convergence) at all weighting levels. Divergence was detected in means and distributions of F3 at all abundance weighting levels except photosynthetic biomass, and in F5 with species weighted by presence only.

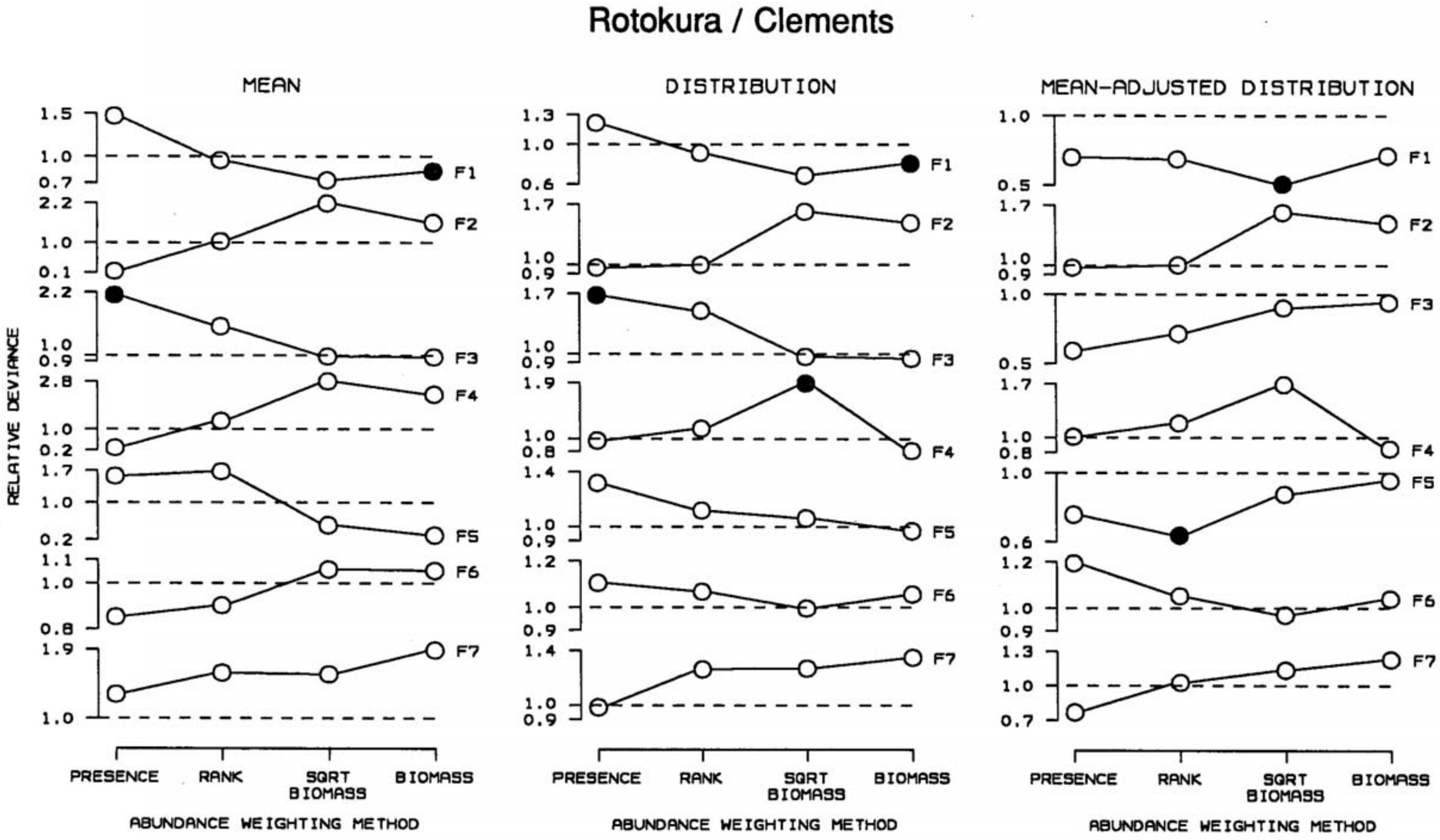

Fig. 9.3 Null model randomisation tests for convergence or divergence in texture between local-scale *Nothofagus*-dominated communities ZN2 Rotokura and ZN3 Clements. Format as for Fig. 9.1.

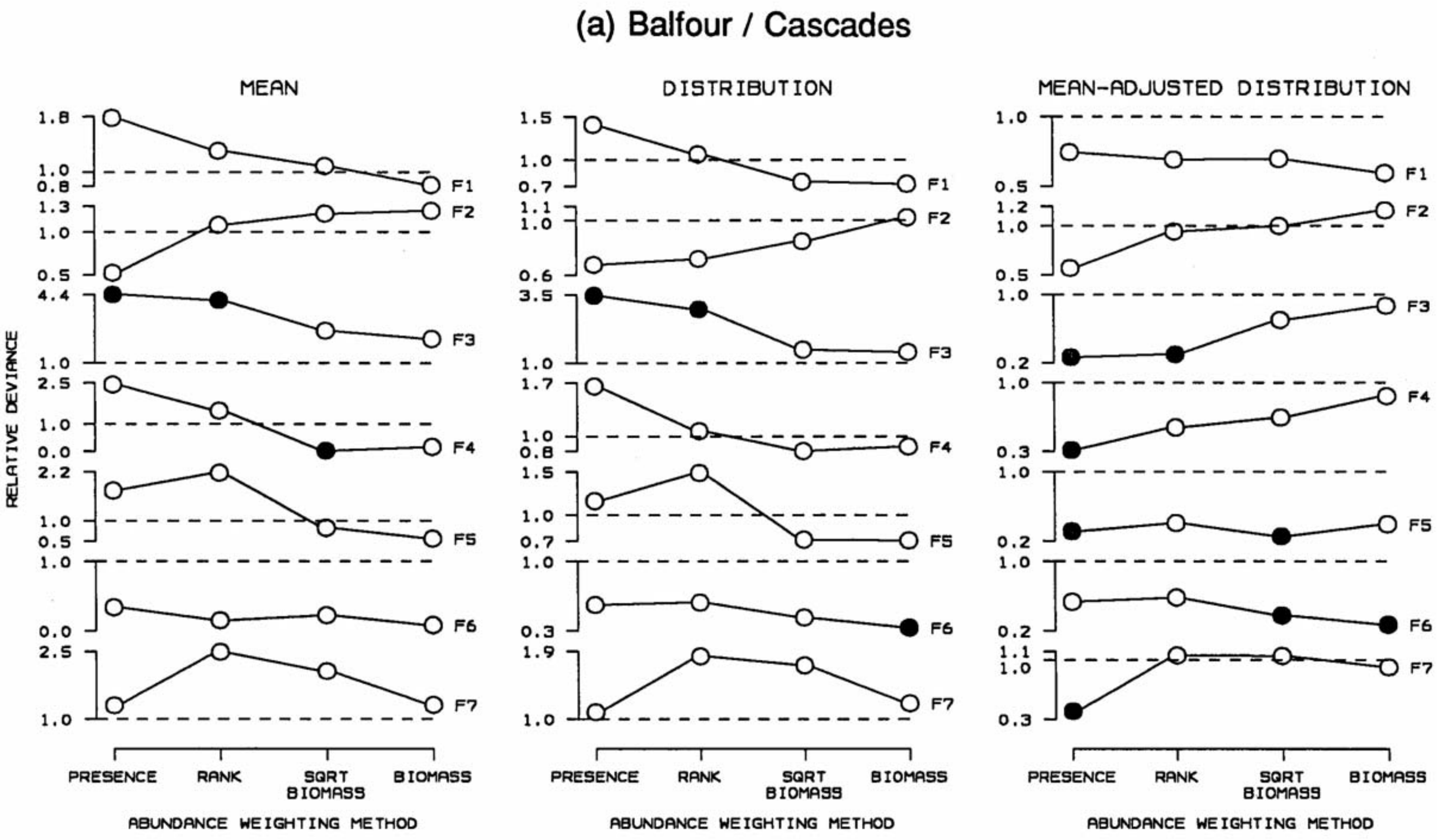

Fig. 9.4 Null model randomisation tests for convergence or divergence in texture between *Nothofagus*-dominated communities from different landmasses closely matched in their environments: **(a)** T1 Balfour/A2 Cascades; **(b)** T2 Anne/ZN1 Ohakune; **(c)** ZN2 Rotokura/SA1 Quetrihué. Format as for Fig. 9.1.

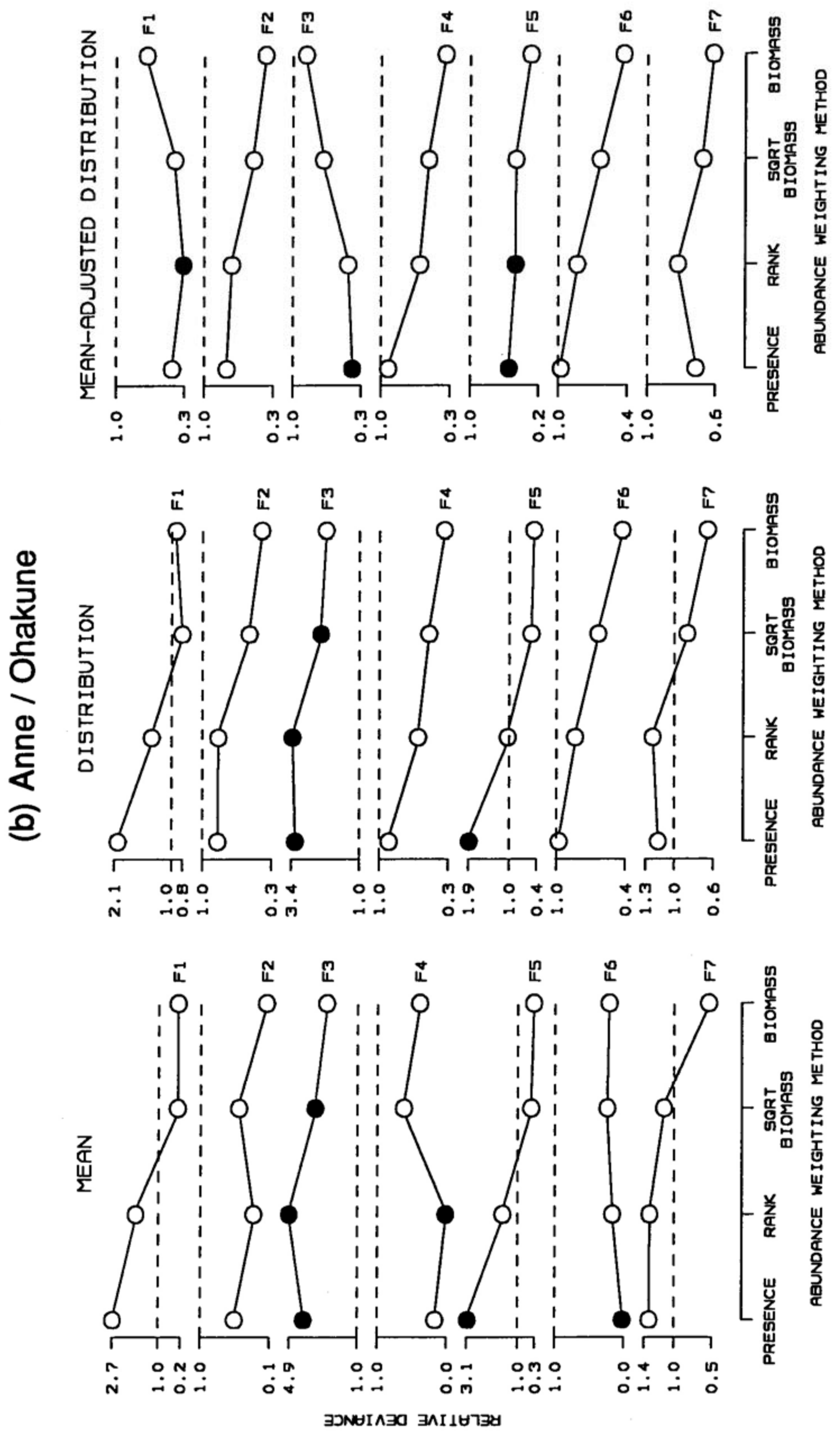

Fig. 9.4 (continued)

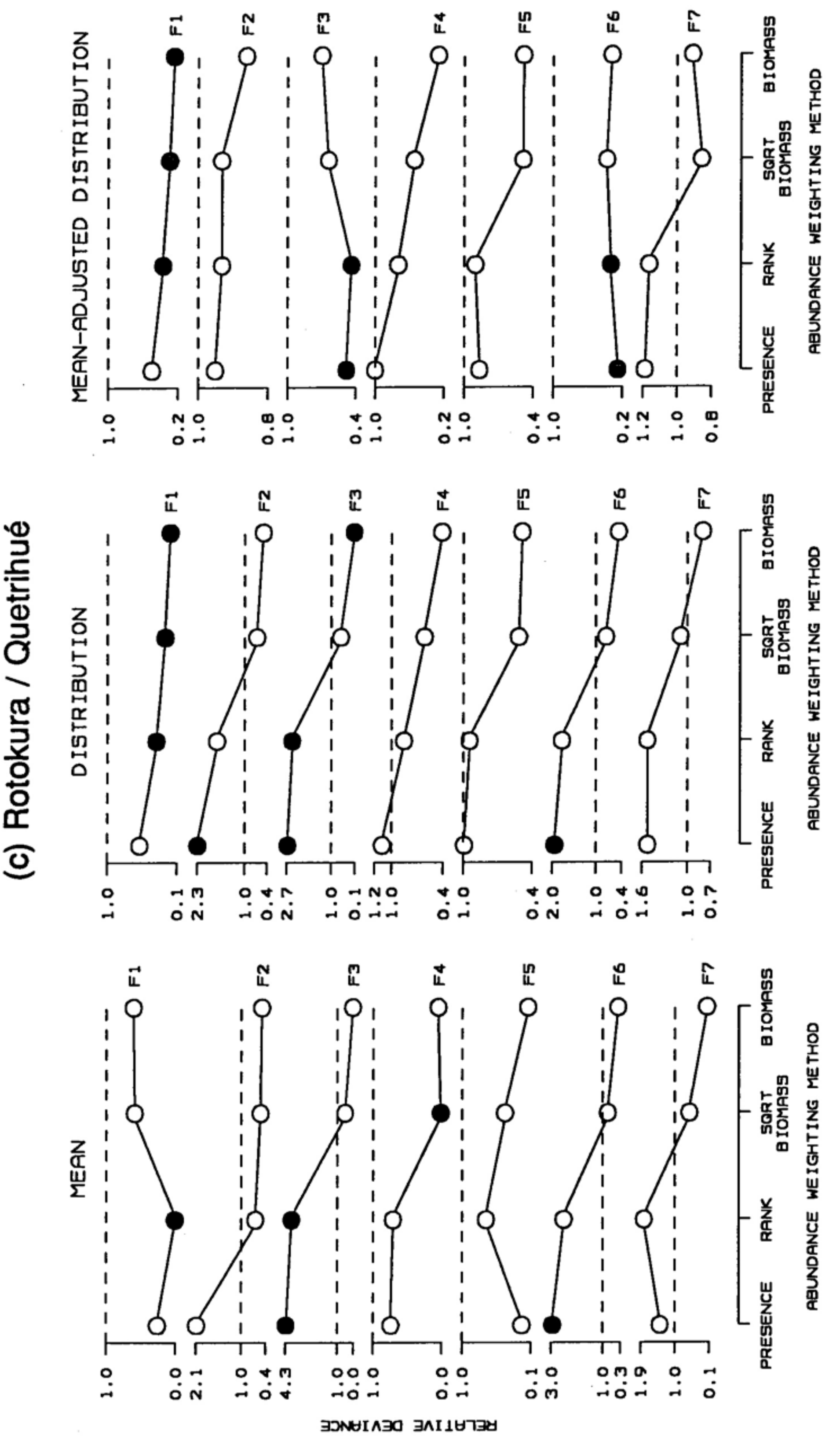

Fig. 9.4 (continued)

Community means, distributions and mean-adjusted distributions of F1 (PSU succulence, specific weight, total chlorophyll, species height) are convergent between ZN2 Rotokura and SA1 Quetrihué, significantly so with weighting by abundance rank for means, and at all weighting levels except presence for distributions and mean-adjusted distributions (Fig. 9.4c). Means of F4 (PSU thickness) are convergent with species weighted by the square root of biomass. F3 (PSU phosphorus, chlorophyll *a/b*) is convergent when distributions (weighting by photosynthetic biomass) and mean-adjusted distributions (weighting by presence or abundance rank) are compared, but community means and distributions are divergent at lower weighting levels. A similar pattern applies to F6 (PSU lobation inclination), mean-adjusted distributions being convergent at lower weighting levels while means and distributions are divergent. Distributions of F2 (PSU area, support fraction) are divergent with species weighted equally.

PATTERNS AMONG TEXTURE FACTORS

In comparisons of community texture means, only one factor, F1 (related to PSU succulence, specific weight, total chlorophyll and species height) showed convergence in a significantly larger number of tests than would be expected by chance: three of 16 independent community comparisons showed significant convergence in this factor when species were weighted by their photosynthetic biomass in calculating community means (Table 9.2). Divergence, by contrast, is significant overall, generally at lower abundance weighting levels, for all factors except F4 (PSU thickness) and F7 (PSU shape). The highest incidence of divergence is in F3 (PSU phosphorus, chlorophyll *a/b*).

Overall trends are similar for comparisons of texture distributions, although no factor shows convergence that is significant as a proportion of the number of tests carried out. Divergence is most marked at lower abundance weighting levels, and is significant overall for all factors except F2 (PSU area, support fraction), F6 (PSU lobation, inclination) and F7. F3, once again, was divergent in the largest number of tests.

In comparisons of mean-adjusted distributions, all factors except F6 and F7 were convergent in a significant number of tests, though only at lower weighting levels. F3, the factor most frequently divergent in comparisons of texture means and distributions, was most frequently convergent when mean-adjusted distributions were compared. F1 also shows a high incidence of convergence with species weighted by abundance rank, though the convergence was not significant overall at other weighting levels. No factor was divergent in a significant proportion of comparisons.

Table 9.2 Incidence of significant convergence or divergence among 31 community comparisons and (in parentheses) for 16 independent community comparisons (see Fig. 6.1), in each of seven texture factors derived by factor analysis (see text). Results are shown for each of four methods of weighting species values by abundance and for each of three methods of expressing community texture (mean, distribution, mean-adjusted distribution). Overall significance, determined from the binomial distribution (see text), is shown for results from the 16 independent comparisons.

	Factor	Convergence				Divergence			
		Presence	Rank	Sqrt biomass	Biomass	Presence	Rank	Sqrt biomass	Biomass
Mean	F1	0 (0)	1 (0)	3 (1)	4 (3*)	5 (4**)	3 (2)	1 (1)	1 (1)
	F2	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	4 (3*)	5 (4**)	1 (1)
	F3	0 (0)	0 (0)	0 (0)	0 (0)	19 (8**)	16 (6**)	8 (2)	0 (0)
	F4	1 (1)	1 (0)	3 (1)	0 (0)	4 (2)	3 (1)	0 (0)	1 (1)
	F5	1 (1)	0 (0)	0 (0)	0 (0)	10 (6**)	4 (3*)	0 (0)	0 (0)
	F6	3 (2)	1 (1)	3 (2)	1 (0)	4 (3*)	0 (0)	0 (0)	1 (0)
	F7	0 (0)	1 (1)	1 (1)	1 (1)	0 (0)	1 (1)	2 (2)	1 (1)
Distribution	F1	0 (0)	3 (1)	4 (2)	2 (0)	5 (4**)	4 (3*)	1 (1)	0 (0)
	F2	0 (0)	0 (0)	1 (1)	0 (0)	4 (1)	2 (1)	2 (2)	1 (1)
	F3	0 (0)	0 (0)	1 (0)	1 (0)	20 (9**)	14 (6**)	9 (3*)	0 (0)
	F4	0 (0)	0 (0)	0 (0)	1 (1)	5 (3*)	2 (1)	1 (0)	0 (0)
	F5	0 (0)	0 (0)	1 (0)	0 (0)	14 (6**)	4 (4**)	0 (0)	0 (0)
	F6	0 (0)	0 (0)	1 (0)	2 (1)	2 (1)	0 (0)	0 (0)	0 (0)
	F7	1 (1)	1 (1)	1 (0)	1 (1)	0 (0)	3 (2)	2 (2)	1 (1)
Mean-adjusted distribution	F1	3 (1)	11 (5**)	5 (1)	2 (1)	0 (0)	0 (0)	0 (0)	0 (0)
	F2	4 (3*)	1 (1)	2 (0)	1 (0)	0 (0)	0 (0)	1 (1)	0 (0)
	F3	14 (7**)	12 (6**)	5 (2)	0 (0)	1 (0)	1 (0)	1 (0)	0 (0)
	F4	5 (3*)	1 (1)	0 (0)	1 (1)	0 (0)	0 (0)	0 (0)	0 (0)
	F5	7 (5**)	9 (5**)	2 (1)	0 (0)	2 (0)	0 (0)	0 (0)	0 (0)
	F6	3 (1)	3 (2)	2 (0)	3 (1)	0 (0)	0 (0)	0 (0)	0 (0)
	F7	2 (0)	0 (0)	1 (0)	0 (0)	0 (0)	1 (0)	0 (0)	0 (0)

*$0.01\le P<0.001$; **$P<0.001$ (no binomial probabilities in range $0.05\le P<0.01$).

9.4 Discussion

COMMUNITY-LEVEL CONVERGENCE

When texture was expressed as the mean or distribution of factor values across species in each community, there was little evidence for convergence between communities. Although significant convergence was detected in a number of individual tests, the frequency of such tests was generally too low for the convergence to be deemed significant according to a binomial test (Table 9.2). Divergence, by contrast, was detected frequently, and was significant overall for all factors except F7 (related primarily to PSU shape), when texture was expressed either as the community mean or distribution. For both ways of expressing texture, F3 (related to PSU phosphorus content and chlorophyll *a/b* ratio) showed the highest incidence of divergence.

Comparisons of mean-adjusted distributions produced quite different results: all factors except F6 (PSU lobation and inclination) and F7 were convergent in a significant number of tests at lower weighting levels, while none was significantly divergent.

Results obtained from comparisons of the factors derived in the present chapter closely reflect results obtained in Chapters 6, 7 and 8 (Tables 6.2, 7.2, 8.2) for the texture variates to which the factors are most closely related (Table 9.1). The same overall conclusions can be drawn. Environmental or historical differences may exist between many of the *Nothofagus*-dominated communities examined, resulting in significant differences between communities in means and distributions of most texture factors. Such divergence would tend to obscure convergence mediated by similar assembly rules, even if such assembly rules do apply. Mean-adjusted distributions of texture factors do show significant convergence for several sets of communities, suggesting that similar assembly rules apply in different communities, leading to community texture distributions that are similar in shape, though they differ in magnitude, arguably due to the effects of environmental or other differences between communities.

INTERPRETATION OF TEXTURE FACTORS

The seven factors derived by principal component analysis and factor rotation of 13 texture variates are orthogonal and uncorrelated. This means that each represents an independent component of variation in the original texture data. It is possible that some factors summarise character variation produced by adaptation to limited resources — i.e. alpha niche axes. Such factors would be expected to show convergence between communities if assembly rules apply, partitioning the underlying niche space among sympatric species. Other factors might represent adaptation to aspects of the environment not correlated with resources, and therefore not subject to assembly rules. No convergence would be expected in such factors in comparison to expectation under the null model, but divergence could be observed. Some factors might also summarise ‘stochastic’ variation produced by various factors of minor importance. Because such variation will show (by definition) no strong trends across the data set, it will tend to be represented in the last few principal components, which account for the lowest proportions of total variation. Since six such axes were discarded prior to factor rotation, it is likely that much of the stochastic variation in the primary data set is no longer incorporated in the seven factors finally used.

All the factors except F6 and F7 showed convergence, significant as a proportion of the number of tests carried out, when mean-adjusted distributions of the factors within communities were compared (Table 9.2). This suggests that each of these factors, summarises a component of variation in the texture data that could be related to species alpha niches. Presumably, the niche space partitioned among species is defined by resources in limited supply (Tilman 1982). It is not possible from the data in hand to identify the specific resources involved. However, some evidence is available from the factor loadings table (Table 9.1) showing which species characters are most closely related to each factor.

For example, F1 is most strongly related to the texture variates PSU succulence, specific weight, total chlorophyll and species height. Each of these characters would be expected to vary in response to light availability, while the inclusion of species height (the highest level in the canopy at which PSUs of a species were found to occur) strongly suggests a relationship to vertical structure. This implies that species scores on the factor F1 might tend to reflect their stature or (in the case of species not rooted at ground level) vertical position. Underlying resources that might be partitioned (e.g. by past or present competition) might include light or habitat space.

PSU phosphorus content has loadings >0.5 on both F3 and F5. PSU chlorophyll *a/b* ratio is also closely related to F3, suggesting that scores on this factor may reflect species adaptations to the light regime. PSU nitrogen content is highly correlated with F5, suggesting a possible association with nutrient availability (although both foliar phosphorus and nitrogen may also be correlated with irradiance; Evans 1989; Bongers & Popma 1988; Reich *et al.* 1991; Reich & Walters 1994).

FACTORS VERSUS 'RAW' TEXTURE VARIATES

It was anticipated (in Section 9.1) that characterising texture by multivariate factors rather than simple texture variates, as was done in Chapters 6-8, might improve the sensitivity of analyses to convergence. It was expected that relevant variation related to alpha niche axes and irrelevant beta niche or stochastic variation might be partitioned into different factors by factor analysis. Factors related to alpha niche axes might then show convergence between some communities, even where the 'raw' texture variates most closely related to them might not.

In fact, the amount of significant convergence (and divergence) detected by comparisons of texture factors in this chapter is very similar to the amounts detected in corresponding texture variates in Chapters 6-8. For example, mean-adjusted distributions of F3 were found to be convergent in 14 and 12 community comparisons with species weighted by presence and abundance rank, respectively (Table 6.2). For the two variates most closely related to F3 the convergence was detected in 12 and 13 (PSU phosphorus) and 13 and 10 (PSU chlorophyll *a/b*) tests respectively (Table 8.2). In a number of cases, however, significant departure from the null model was obtained for a factor, where significant patterns could not be obtained for the texture variates most closely related to it. For example, means of F1 for landmass-scale communities Tasmania and New Zealand were found to be significantly convergent with weighting by photosynthetic biomass (Fig. 9.1b); the four variates with loadings >0.5 on F1 — PSU succulence, specific weight, total chlorophyll and species height — all showed a tendency towards convergence ($R_{\bar{D},T}<1$) in the same comparison, but this was not significant for any of the variates (Fig. 6.2c).

In general, convergence or divergence detected in a texture factor in the present chapter, was likewise detected in one or more correlated variates in equivalent tests in previous chapters (compare, for example, Fig. 9.4a with Figs. 6.12a, 7.15a and 8.15a). The close correspondence between the results obtained using multivariate factors and 'raw' texture variates suggests that the original variates might have some association with species niches.

Seven factors were required to summarise most of the variation among the 13 texture variates (Table 9.1). This confirms that a considerable amount of variation is common to more than one of the original variates. It is likely that, in previous chapters, convergence or divergence detected in two or more variates in equivalent tests was the result of different aspects of adaptation to the same niche. For example, much of the observed variation in PSU phosphorus content and chlorophyll *a/b* ratio can be explained by a single variable, the factor F3 (Table 9.1). These two variates were often found to show similar patterns of departure from the null model (e.g. Figs. 6.2a), suggesting that they express the same niche structure. The factor F3 summarises this information, and generally shows the same patterns as both variates (e.g. Fig. 9.1a). Expressing texture by uncorrelated factors, summarising variation in the raw texture data, is parsimonious, avoiding the danger of interpreting convergence or divergence in multiple variates as independent events in cases where the same underlying mechanisms apply.

PREVIOUS COMPARATIVE STUDIES OF MULTIVARIATE TEXTURE

The value of characterising species function by character syndromes rather than individual characters has often been recognised. In most comparative studies, however, the approach has been to group species into classes defined (explicitly or implicitly) by categories of attributes, rather than assigning them scalar values using multivariate techniques such as factor analysis. Communities may then be compared according to the relative representation of component species in different classes (e.g. Parsons 1976; Naveh & Whittaker 1979; Floret *et al.* 1990; Cornelius *et al.* 1991; Cowling *et al.* 1994; Cowling & Witkowski 1994). Class assignment may be achieved explicitly on the basis of species character data, for example, by the use of hierarchical cluster analysis methods (e.g. Parsons 1976; Jaksi & Delibes 1987; Boutin & Keddy 1993; Golluscio & Sala 1993; Guillén *et al.* 1994). More commonly, however, classes are defined *a priori* and assignment is either subjective, or based on one or more 'indicator' characters. In this case, the link between class membership and possession of specific traits is tacit. Examples include the still frequently invoked life forms of Raunkiaer (1934) (e.g. Danin & Orshan 1990; Floret *et al.* 1990; Shmida & Werger 1992), growth forms (e.g. Naveh & Whittaker

1979; Cornelius *et al.* 1991; Cowling *et al.* 1994), forest sinusiae (e.g. Smith 1973; Hubbell & Foster 1986; Wilson 1989) and animal trophic guilds (e.g. Fox 1981; Case *et al.* 1983).

Classification has the drawback that a proportion of the attribute information used as a basis for assigning species to classes is lost to subsequent analyses. In situations where detailed character data are available, scalar ordination methods (such as principal component analysis and factor analysis) have the advantage of simplifying the data (summarising many characters by fewer factors) without loss of relevant information. This characteristic is important where patterns being sought are expected to be weak, as appears likely for patterns produced by assembly rules (Simberloff 1982, 1984; Wilson 1991).

Ordination methods have been used to summarise community texture data in a small number of studies seeking community-level convergence. Ricklefs & Travis (1980) used principal component analysis to summarise morphological data for birds occupying scrub communities in North and South America. Similarities in morphological spectra between communities in Chile and California were sought by comparing the distributions of species from different regions in the multivariate space. Although a graphical comparison provided superficial evidence of morphological ‘convergence,’ the trend could not be confirmed statistically by nearest-neighbour analysis (see Section 7.4). Blondel *et al.* (1984) used a similar approach to look for ecomorphological convergence between bird communities of mediterranean-climate habitats in Europe and the Americas. Comparing the distributions in multivariate morphological space of species from the mediterranean-climate habitats, with species from a non-mediterranean `control' habitat, provided little evidence that the mediterranean communities were particularly well-matched. Wiens (1991b) used principal component analyses to express size and shape characteristics of Australian and North American shrub-desert birds as single variables, employing the nearest-neighbour approach of Ricklefs & Travis (1980) to test the hypothesis that each species from one continent would be most closely matched morphologically to a species from the other. The hypothesis could not be supported statistically. These studies differ from the present one in the methods used to seek convergence between communities. However, the use of ordination methods to assign morphological scores to species based on many characters is analogous to factor analysis of plant community texture data, as applied in the present chapter.

Similarity in the relative representation of species in the same guilds or functional groups in different communities, i.e. guild proportionality, has sometimes been sought as evidence for the operation of assembly rules (Wilson 1989; Bycroft *et al.* 1993; Wilson & Roxburgh 1994; Wilson *et al.* 1995; see Section 6.4). Guild proportionality is analogous to multivariate texture convergence, as carried out in the present chapter, the guilds representing (implicitly) classes of species with similar character syndromes. The primary difference between the two approaches is in the type of variable — categorical (the guilds) or scalar (factors) — by which texture is expressed.

CONCLUSIONS

Factor analysis of texture data from *Nothofagus*-dominated communities revealed that most of the variation incorporated in the 13 texture variates (>75% of the variation in each) can be described by seven orthogonal factors. In particular, there is a high proportion of variation in common to the variates PSU succulence, specific weight, total chlorophyll content and species height; all four variates are highly correlated with the factor F1. Species scores on this factor might reflect the positions they occupy in the vertical forest structure.

Although it was expected that some of the derived factors might represent better proxies for species niches than the raw texture variates, the results of tests for community texture convergence carried out in this chapter generally consolidate rather than ‘improve’ the findings of Chapters 6-8. There is only very limited evidence that expressing texture by multivariate factors instead of ‘raw’ texture variates increased the ability of the tests to detect convergence between communities where it had occurred. It is likely that several of the 13 species characters chosen for study may show relatively strong relations to species niches; if so, extraction of factors would summarise variation shared among the character variates, but would not show a significantly improved correspondence with underlying niche axes.