10. Convergence among *Nothofagus*-dominated communities: focusing on height guilds

10.1 Introduction

In Chapters 6-9, texture convergence was sought in the entire vascular plant guild of *Nothofagus*-dominated communities. Implicit in this approach is the assumption that assembly rules apply to the entire vascular guild, causing distributions of functional attributes in different communities to converge. Assembly rules summarise the effects of interspecific interactions, such as competition, that would impose restrictions on what functional combinations of species are possible. The concept of assembly rules, and much of its associated theory, is historically associated with studies of animal community structure (Diamond 1975; Connor & Simberloff 1984; Wilson 1987; Stone & Roberts 1990). The principal mechanism assumed, by such studies, to underlie the operation of assembly rules is diffuse competition, whereby species influence one another by depleting pools of resources (particularly food) in common demand (MacArthur 1972b). Whereas diffuse competition can be readily envisaged as a factor structuring communities of motile animals, it is less applicable to plants, for which proximal interactions among sessile neighbours would be seem more likely to predominate (Aarssen 1992). If the interspecific interactions underlying plant assembly rules largely take place among neighbouring plants it follows that the individuals involved would tend to be similar in stature. Non-reciprocal interactions will, of course, occur between individuals of dissimilar stature. For example, canopy trees may profoundly influence the environment experienced by ground-layer species, whereas the reverse is less likely. However, such highly asymmetric interactions would hardly contribute to the operation of assembly rules (restricting interspecific niche overlaps), because the species involved have such dissimilar niches.

If it is true that the interspecific interactions most likely to give rise to plant community structure would involve plants of similar stature, searching for convergence (and therefore community structure) at the level of the whole plant community may be less than optimal. If assembly rules apply at all levels (‘strata’) in the vertical structure of each community (and if the other assumptions of the community convergence hypothesis are met) then convergence should be apparent between whole communities. However, if assembly rules apply for some strata but are absent or weak within others, convergence may not be readily detectable at the whole community level. This potential problem is equivalent to that highlighted by Diamond & Gilpin (1982), criticising the ‘dilution of relevant data from guilds with irrelevant data from the whole species pool’ in studies of bird community structure (Connor & Simberloff 1979). Since guild associates (members of the same guild) tend to make demands on the same units of resources (Root 1967), species interactions should be stronger within guilds than among different guilds (Pianka 1980). Consequently, niche structure (and associated patterns such as character overdispersion and community-level convergence[1]) might be more apparent at the guild than at the whole-community level.

The present chapter addresses the possibility that community structure in *Nothofagus*-dominated forests is restricted to or more pronounced within certain guilds. This is an alternative to the assumption, made in previous chapters, that community structure would apply at the level of the entire community (i.e. vascular plant guild). Using the null model randomisation tests developed in Chapters 6-9, convergence is sought within guilds corresponding to zones in the vertical forest structure. Each guild encompasses all species having a 'functional presence' in one of three such zones, and thus groups together species most likely to be involved in species interactions of the kind that might give rise to assembly rules, and so, community structure. The guilds conform approximately to the concepts of forest strata or sinusiae (Smith 1973; Wilson 1989), although the boundaries between them are arbitrary.

10.2 Methods

TEXTURE DATA

Analysis was based on 13 texture variates, comprising species values for the 12 characters listed in Section 2.3.5 and for species height, defined in Section 6.2. Although convergence is sought, in the present chapter, within height guilds, for which vertical structure is likely to be less important than at the whole-community level as a potential niche gradient, it seems possible that fine-scale differences in vertical niches could influence community structure, even within height guilds. Species height was therefore included in the analyses, as in previous chapters. Field and laboratory methods are described in Chapter 2, while details of the 17 study sites are given in Chapter 3.

DELINEATION OF GUILDS

Three guilds were defined, each comprising all species or entities 'functionally present' in one of the following classes of height above ground level: 0-1 m, 1-5 m and >5 m. A species was deemed functionally present in a guild if PSUs occurred within one of the height classes encompassed by the guild (as recorded in the field: see Section 2.3.2). In the case of species for

[1]In the present discussion, terms such as 'community structure' and 'community-level convergence' may, according to context, refer to processes or patterns at either the whole-community or guild level.

which multiple age-classes were recorded as separate entities, juvenile entities were included in a guild if PSUs of adults of the same species occurred in its height class. This was to ensure that character data for each species present in a guild as an adult would be as representative as possible of the lifetime niche of the species. It was possible for a given species or entity in a particular community to be present in more than one guild.

The three guilds were intended to correspond approximately to the ground/herb, shrub and tree strata, respectively (c.f. Wilson *et al.* 1995). However, these are primarily terms of convenience: although there clearly are guild patterns in the vertical structure of forest communities, it is unclear whether there are somewhat discrete strata, or, alternatively, niche variation is approximately continuous from ground to canopy level (Wilson 1989). The vertical boundaries imposed between the guilds defined here are arbitrary: it is not implied that they correspond to discontinuities in the distribution of species in niche space.

Texture data within guilds

Character data were obtained for each species or entity at each study site. However, no distinction between samples obtained from different height classes (i.e. guilds) was made at the measurement stage (Sections 2.3.2, 2.3.4). Therefore, site character values were retained with species when they were assigned to guilds. Abundance (photosynthetic biomass) data associated with species were, however, adjusted to take account of the relative functional abundance of species within guilds. In each guild i, a species was assigned a photosynthetic biomass a_i according to the formula:

$$a_i = \frac{\sum_{j=1}^{n} c_j \cdot p_{ij}}{n} \cdot w$$

where c_j = number of PSUs of the species recorded in quadrat j;

p_{ij} = proportion of PSUs of the species in quadrat j estimated to occur in height classes up to the highest encompassed by guild i;

n = number of quadrats sampled;

w = mean PSU dry weight for the species at the study site.

ANALYSIS

Texture convergence

Convergence in texture between corresponding guilds in different communities was sought using randomisation tests comparing observed among-community variation in texture to variation expected under a null model assigning species characters to communities at random. The null model is described fully in Section 6.2. In separate tests, texture was characterised by the distribution (test statistic $\hat{D}_T$) and mean-adjusted distribution ($\hat{D}'_T$) of each of the 13 texture variates within the guild of interest at each of the communities being compared. Tests comparing community texture means (test statistic $\bar{D}_T$) were not performed in this chapter, since it is clear from comparisons in Chapters 7 and 9 that tests based on texture means tend to yield very similar results to equivalent tests comparing texture distributions. Of the two approaches, tests based on distributions are expected to be somewhat less prone to type I errors (Section 7.1), and were therefore applied here.

Comparisons performed

Comparisons within the 0-1 m guild were performed for 31 sets of communities at the landmass, regional and local scales, while binomial tests for overall significance (Section 6.2) were applied to the results obtained for 16 independent community comparisons. The hierarchy of comparisons is described in Section 6.2 and depicted graphically in Fig. 6.1.

For the 1-5 m and >5 m guilds, it was not possible to perform the full set of community comparisons. This was the case where there were fewer than two species unique to just one of the assemblages (guilds within communities) being compared. As species in common to more than one community in a comparison were not randomised under the null model (Section 6.2), it would not be possible to demonstrate departure from the null model in such cases, rendering the comparison meaningless. Comparisons that could not be performed for this reason were, for the 1-5 m guild, ZC1/ZC2, ZN1/ZN2/ZN3; for the >5 m guild, ZC1/ZC2, ZS1/ZS2/ZS3, T1/T2/T3, T2/T3, ZS/ZC/ZN. The number of comparisons performed was therefore 29 (14 independent) for the 1-5 m guild, and 26 (15 independent) for the >5 m guild.

10.3 Results

GUILD SPECIES NUMBER

The number of species unique to each community/guild combination can influence the degree of departure from null expectation observable using the randomisation tests performed in this study. The data presented in Table 10.1 illustrate, for the seven sample comparisons discussed in detail below, general differences among guilds in the number of species or entities available for randomisation under the null model. The data are interpreted in Section 10.4.

Table 10.1 Total number of species or entities available (`free') for randomisation in tests based on the null model described in Section 6.2, for seven sample community comparisons including all species in each community, or species in one of three guilds — 0-1 m, 1-5 m and >5 m — in each community. Full names of communities identified by codes in the table are given in Section 3.2 and in subsequent text.

Comparison	Free species/entities			
	Community	0-1 m	1-5 m	>5 m
T, A, Z, S	285	261	206	97
T, Z	159	149	109	53
ZS, ZC	42	37	37	9
ZN2, ZN3	53	54	29	16
T1, A2	49	45	38	22
T2, ZN1	91	79	63	30
ZN2, SA1	98	93	64	27

Patterns among communities

For brevity, detailed results are presented only for a representative sample of the comparisons performed. For each guild, results are shown for overall comparisons among the four landmasses; for one pair of communities, well matched in their macroenvironments, at the landmass, regional and local scales; and for three well-matched sites from different landmasses.

0-1 m Guild

There is no significant convergence within the 0-1 m guild among the four landmass-scale communities (Tasmania, Australia, New Zealand and South America), when texture distributions[2] are compared (Fig. 10.1a). However the landmasses are divergent in most variates using one or more methods to weight species by their abundance. Comparing texture distributions adjusted to a constant mean, there is convergence in PSU inclination and chlorophyll *a/b* with species unweighted by abundance, and in PSU phosphorus and chlorophyll *a/b* at relatively high weighting levels. Divergence is still apparent in in PSU area, nitrogen, total

[2]Following the convention established in Chapter 9, ‘distribution’ will, unless otherwise qualified, refer to community texture distributions, not adjusted to a constant mean.

chlorophyll and (with weighting by abundance rank) chlorophyll *a/b*.

Fig. 10.1 Null model randomisation tests for convergence or divergence in texture in the 0-1 m guild (see text) 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 distributions (test statistic $\hat{D}_T$) and mean-adjusted distributions ($\hat{D}'_T$). The relative deviance R_T of among-community variation in texture is shown for each of 13 texture variates 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). 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).

The figure appears on the following page.

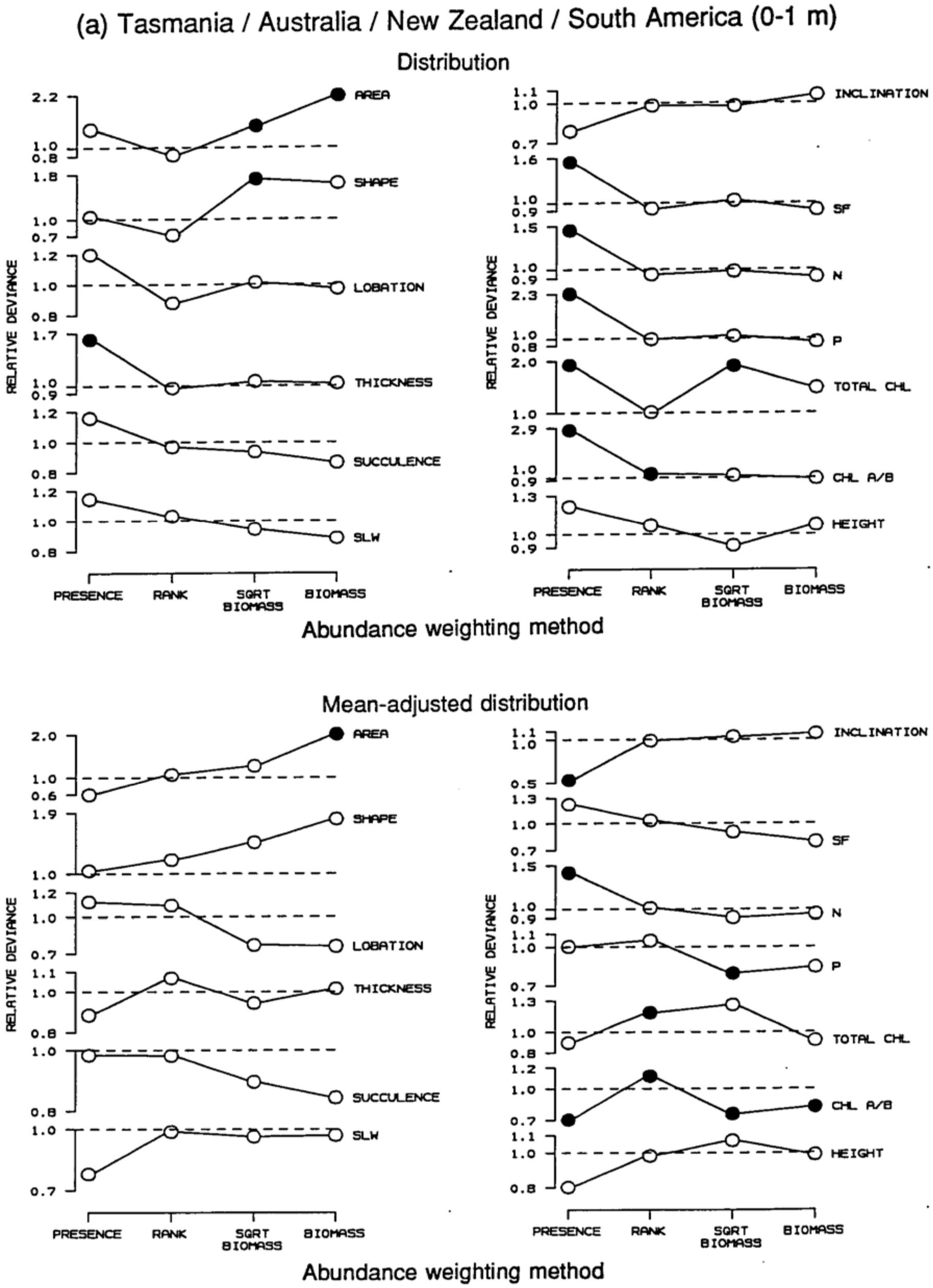

Fig. 10.1 (continued)

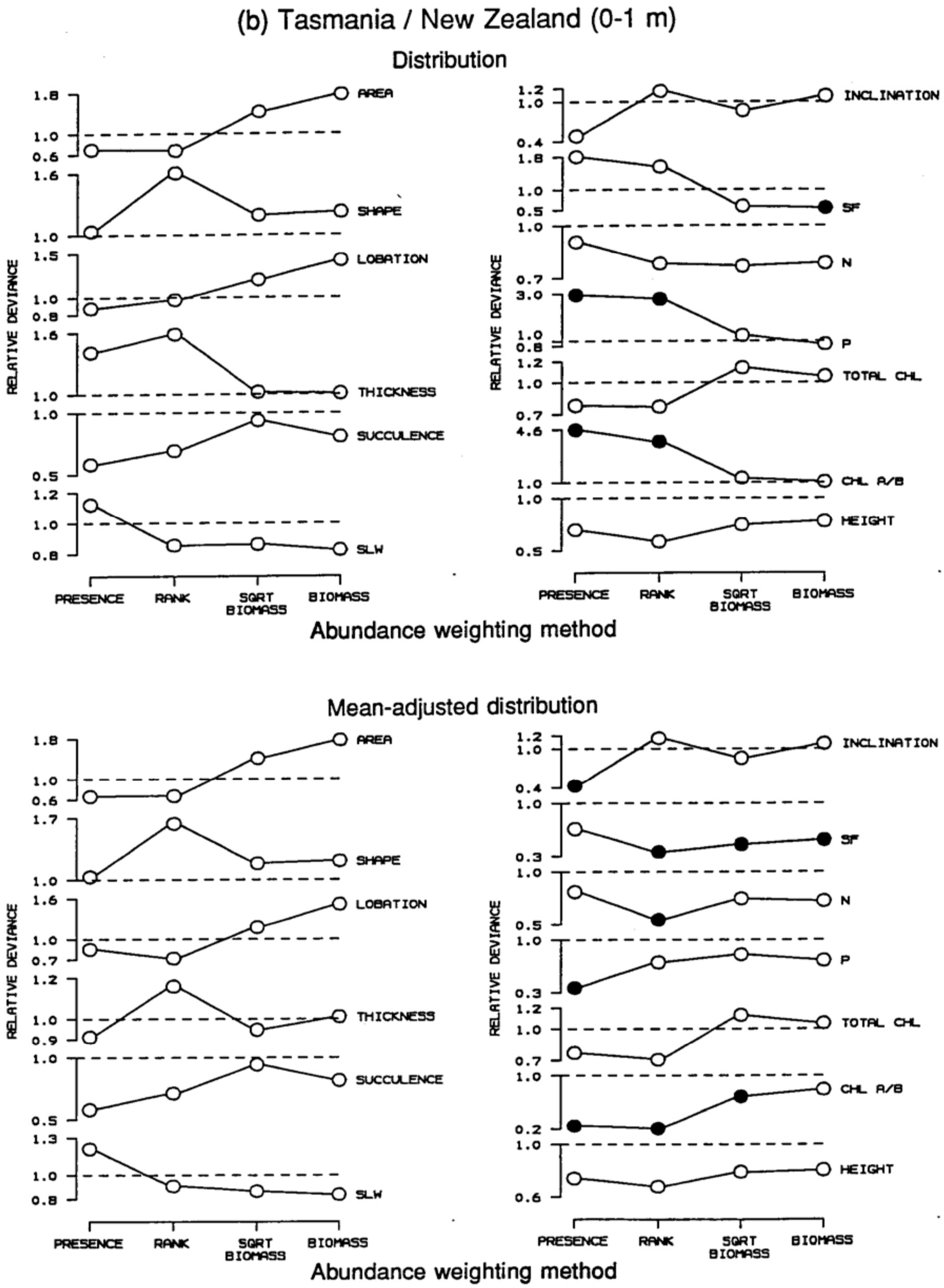

Fig. 10.1 (continued)

Tasmania and New Zealand, which were identified in Chapter 3 as being relatively similar in their environments, show significant convergence only in support fraction, with weighting by photosynthetic biomass (Fig. 10.1b). At this heavy weighting level, the convergence is likely to apply primarily to a minority of species accounting for the majority of biomass in the guild. Divergence, however, is restricted to two variates: PSU phosphorus and chlorophyll *a/b*. Mean-adjusted texture distributions are convergent for PSU inclination, nitrogen, phosphorus, chlorophyll *a/b* and support fraction, primarily at lower weighting levels. There is no divergence.

Despite being closely matched in their environments, regional-scale communities southern (ZS) and central (ZC) New Zealand show no convergence in the distributions of any texture variate in the guild under consideration (Fig. 10.2). Several variates are divergent at lower weighting levels. Comparing mean-adjusted distributions, there is convergence in PSU succulence, phosphorus content and total chlorophyll at lower weighting levels, while PSU shape is divergent with weighting by abundance rank.

Texture distributions for local-scale communities ZN2 Rotokura and ZN3 Clements are not significantly convergent in any variate (Fig. 10.3). PSU area and support fraction are divergent at higher weighting levels, while PSU chlorophyll *a/b* is divergent with species weighted equally. Mean-adjusted distributions at these sites are convergent for PSU shape, nitrogen content and total chlorophyll at lower weighting levels, while support fraction remains divergent with species weighted by their biomass values.

Results of comparisons between sites from different landmasses well matched in their environments are depicted in Fig. 10.4. T1 Balfour and A2 Cascades are significantly convergent in their distributions of PSU thickness, with weighting by photosynthetic biomass (Fig. 10.4a). Several variates show significant divergence, most notably PSU total chlorophyll content, which is divergent at all weighting levels. Comparing mean-adjusted distributions, the sites are convergent in PSU phosphorus, total chlorophyll and chlorophyll *a/b* at lower weighting levels, but divergent in PSU shape and support fraction at higher weighting levels.

Distributions of PSU nitrogen content are convergent between T2 Anne and ZN1 Ohakune, when species values are weighted by the square root of photosynthetic biomass (Fig. 10.4b). There is divergence in PSU shape and chlorophyll *a/b*. Mean-adjusted distributions are convergent for three variates: PSU lobation, nitrogen content and chlorophyll *a/b*, while there is no significant divergence.

ZN2 Rotokura and SA1 Quetrihué are convergent in biomass-weighted distributions of PSU specific weight, while PSU shape, phosphorus content and chlorophyll *a/b* are divergent at lower weighting levels (Fig. 10.4c). Comparing mean-adjusted texture distributions, there is convergence in specific weight, phosphorus content and chlorophyll *a/b*. No variate shows significant divergence.

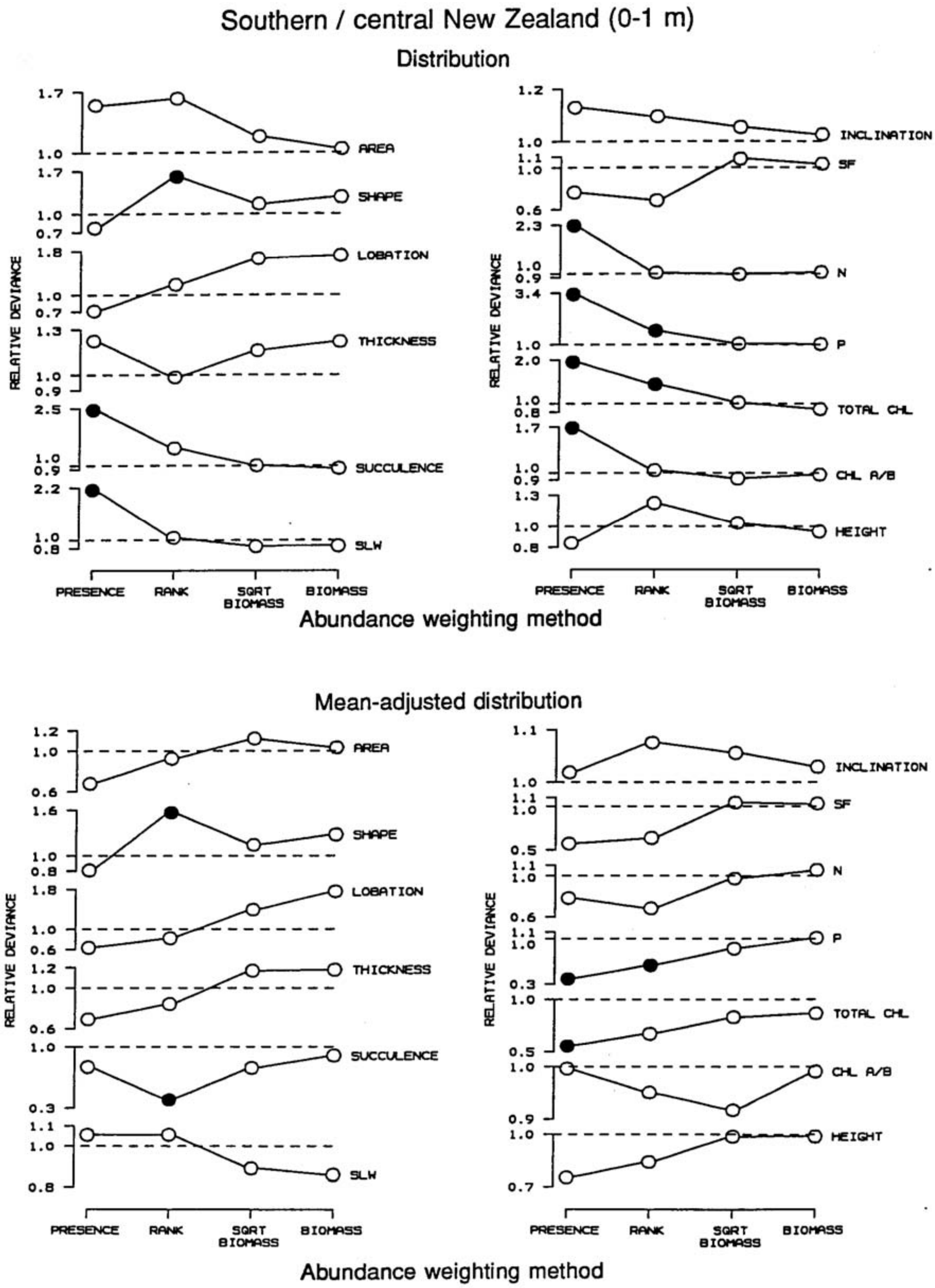

Fig. 10.2 Null model randomisation tests for convergence or divergence in texture in the 0-1 m guild between regional-scale *Nothofagus*-dominated communities southern (ZS) and central (ZC) New Zealand. Format as for Fig. 10.1.

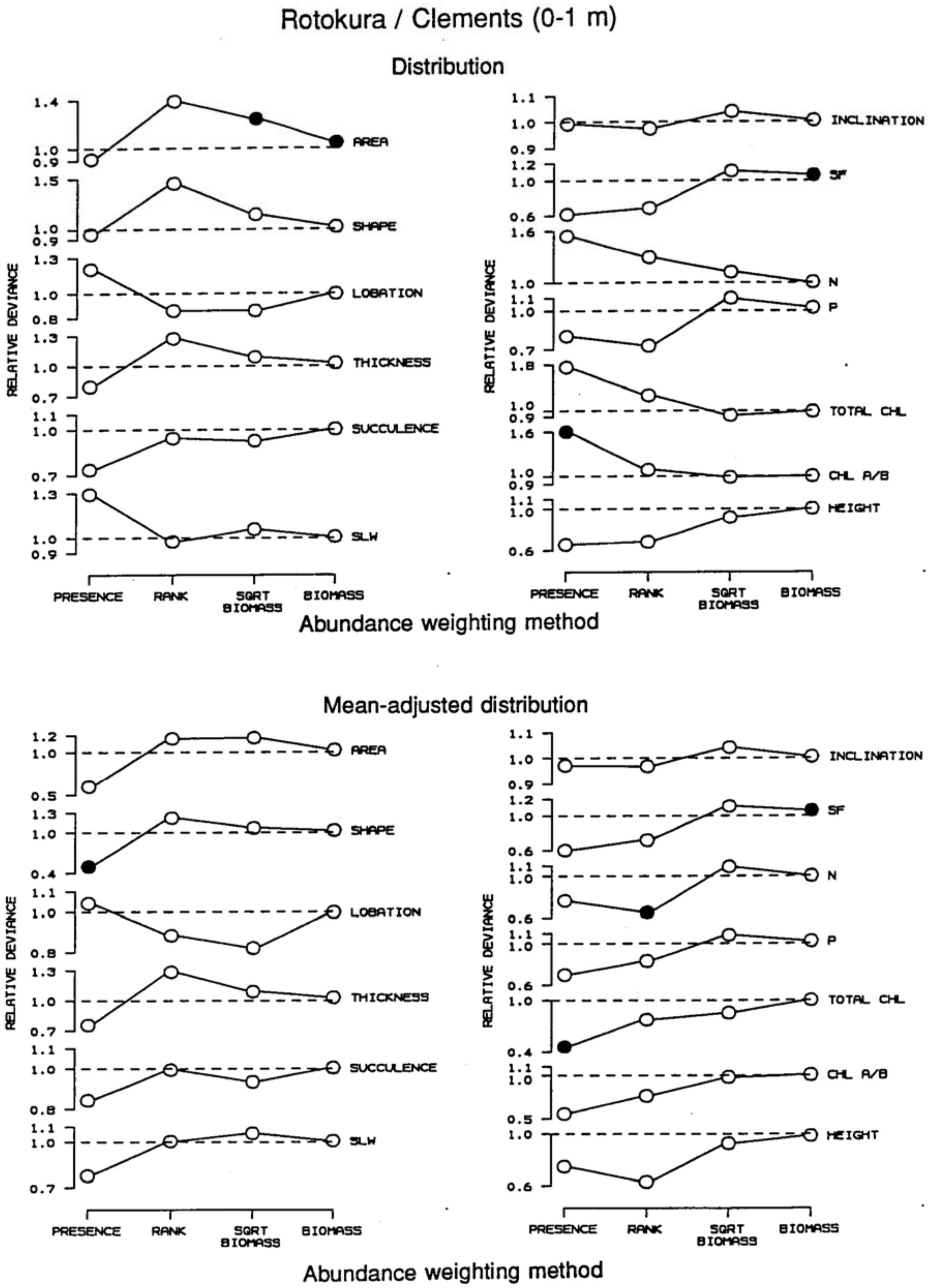

Fig. 10.3 Null model randomisation tests for convergence or divergence in texture in the 0-1 m guild between local-scale *Nothofagus*-dominated communities ZN2 Rotokura and ZN3 Clements. Format as for Fig. 10.1.

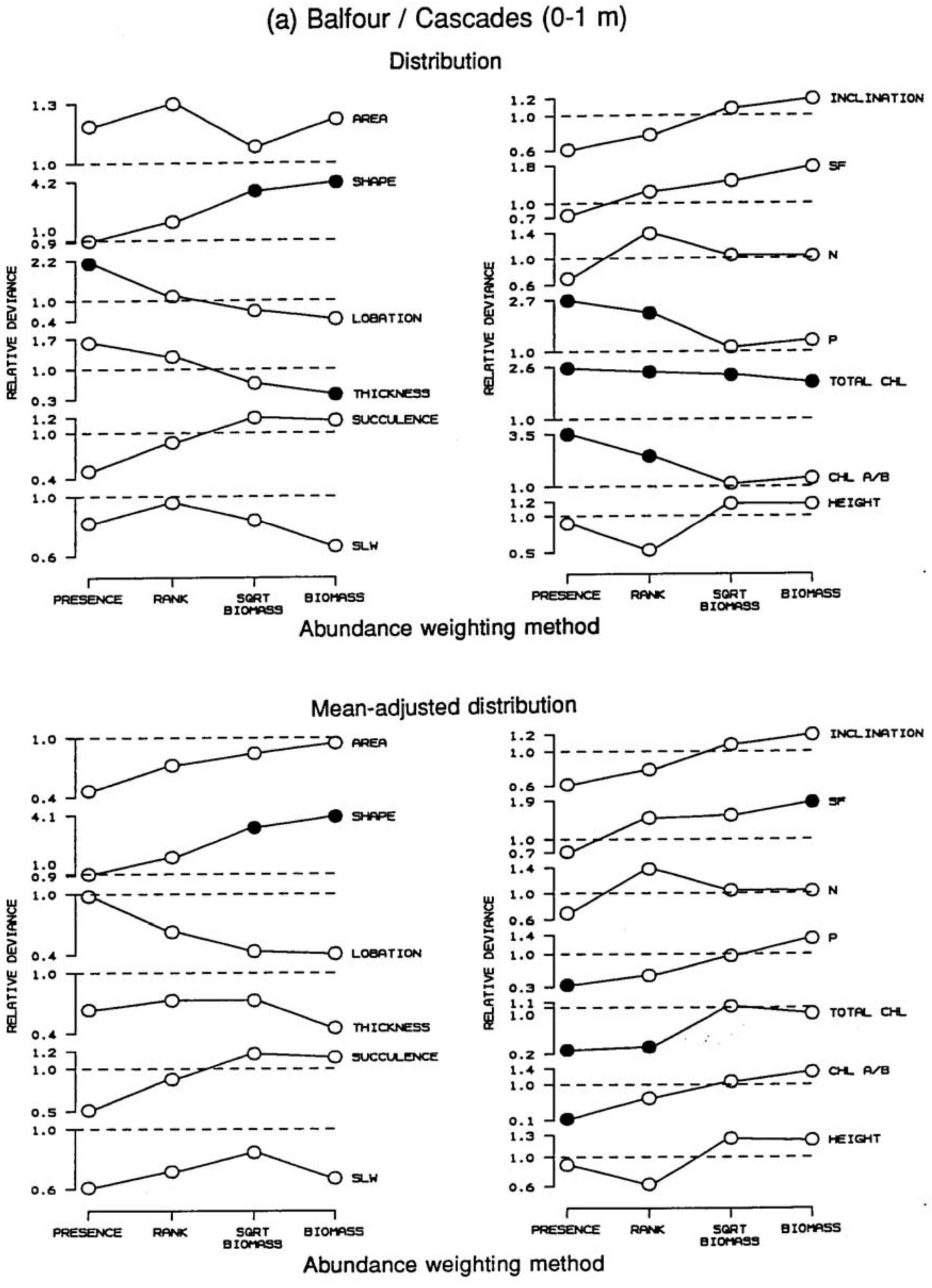

Fig. 10.4 Null model randomisation tests for convergence or divergence in texture in the 0-1 m guild between *Nothofagus*-dominated communities from different landmasses closely matched in their environments: **(a)** T1 Balfour/A2 Cascades; **(b)** T2 Anne/ZN1 Ohakune; **(c)** ZN2 Rotokura/SA1 Quetrihué. Format as for Fig. 10.1.

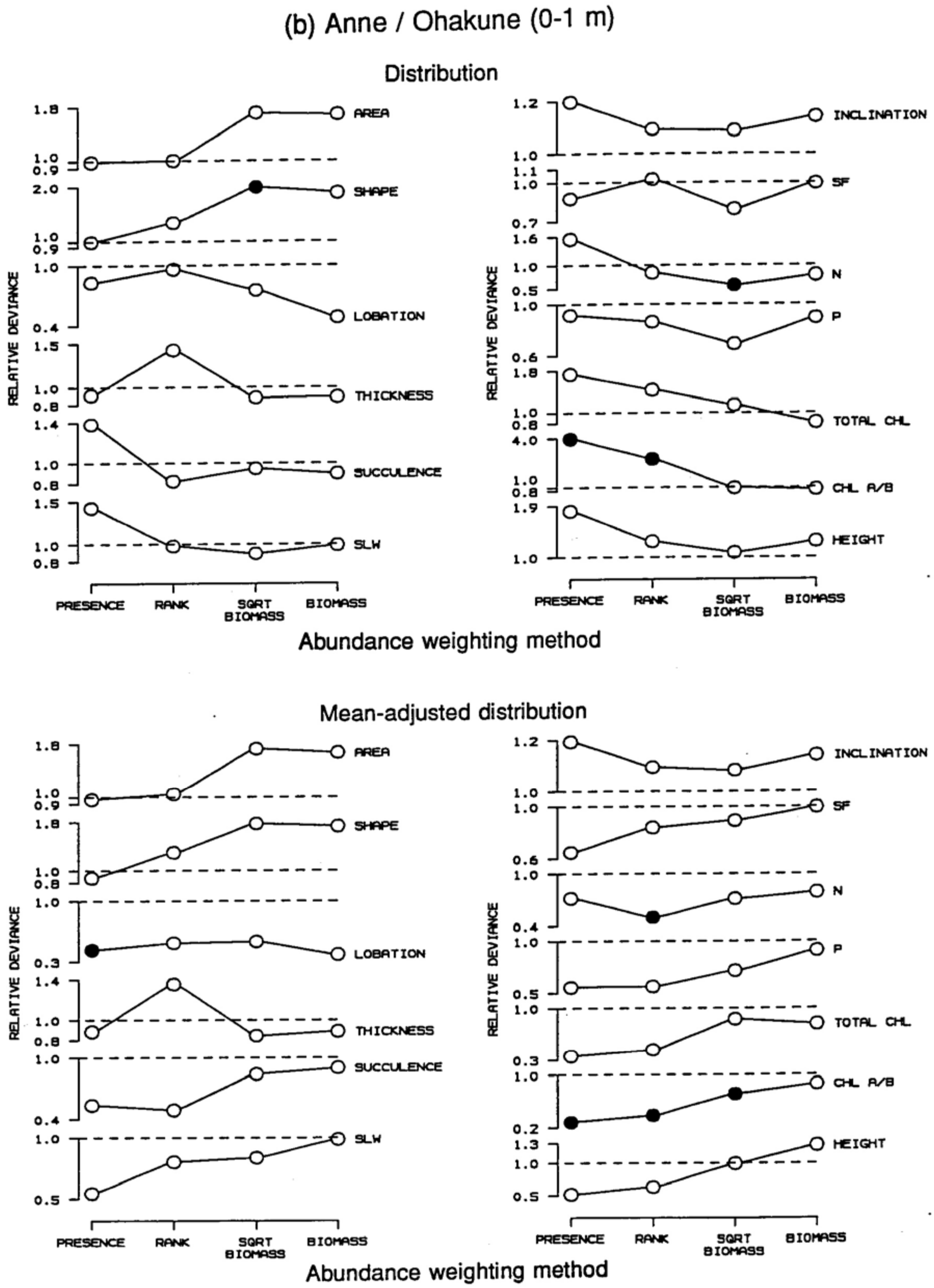

Fig. 10.4 (continued)

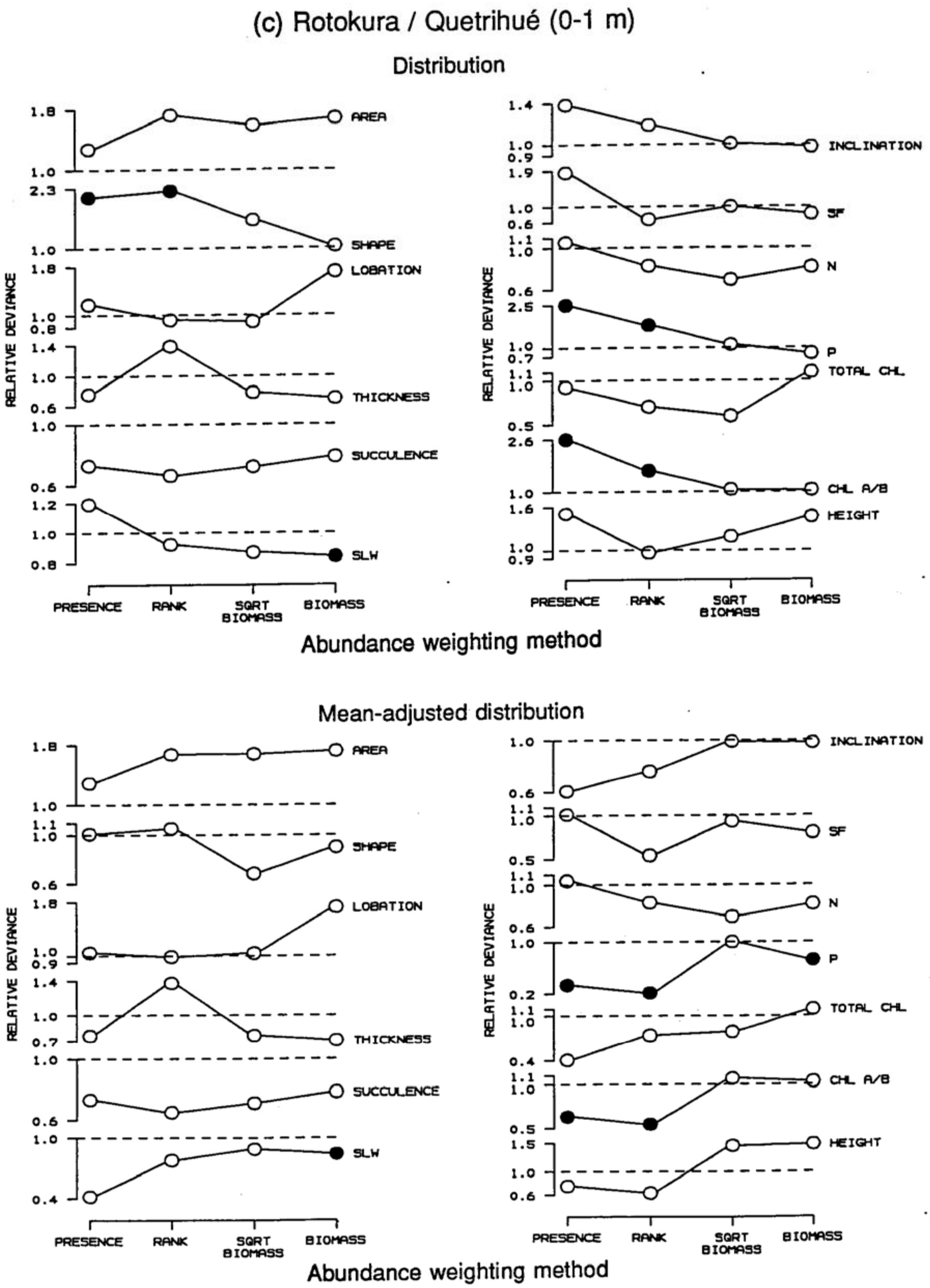

Fig. 10.4 (continued)

1-5 m Guild

Results of overall comparisons among Tasmania, Australia, New Zealand and South America for the 1-5 m guild are shown in Fig. 10.5a. Overall, patterns are similar to those obtained for the 0-1 m guild, with some changes in significance but few in the direction of departure from expectation under the null model. There is no significant convergence between texture distributions, while several variates show significant divergence, especially at lower weighting levels. For mean-adjusted distributions, there is convergence in PSU phosphorus and chlorophyll *a/b*, in both cases with species weighted by the square root of photosynthetic biomass. PSU shape and total chlorophyll, and support fraction, show significant divergence.

No convergence was detected between texture distributions in the 1-5 m guild of Tasmania and New Zealand (Fig. 10.5b). Three variates, PSU phosphorus, total chlorophyll and chlorophyll *a/b*, are divergent at low to intermediate weighting levels. Comparing mean-adjusted distributions, there is convergence in PSU inclination, phosphorus and chlorophyll *a/b*, and no divergence. These results closely match those obtained for the 0-1 m guild for the same community combination.

Southern (ZS) and central (ZC) New Zealand show no significant convergence in texture distributions, while six variates are divergent at lower weighting levels (Fig. 10.6). In comparisons of mean-adjusted distributions, however, convergence was detected in PSU area, succulence, phosphorus content, total chlorophyll, support fraction and species height. The convergence generally applies at lower weighting levels, but is significant at all levels for PSU succulence and total chlorophyll. There is no divergence between mean-adjusted distributions.

Little departure from null expectation was detected for the 1-5 m guild in comparisons of northern New Zealand sites ZN2 Rotokura and ZN3 Clements (Fig. 10.7). The only test yielding a significant result (convergence) was of mean-adjusted distributions of PSU nitrogen content, with species values weighted by abundance rank.

Comparisons of texture distributions for T1 Balfour and A2 Cascades revealed no significant convergence, while divergence was detected in PSU shape, phosphorus content, chlorophyll *a/b* and (at all weighting levels) total chlorophyll (Fig. 10.8a). Mean-adjusted distributions, by contrast, were found to be convergent in PSU lobation, thickness, specific weight, phosphorus, total chlorophyll and chlorophyll *a/b* at low or intermediate weighting levels. Divergence was confined to PSU shape, with species values weighted by photosynthetic biomass or its square root.

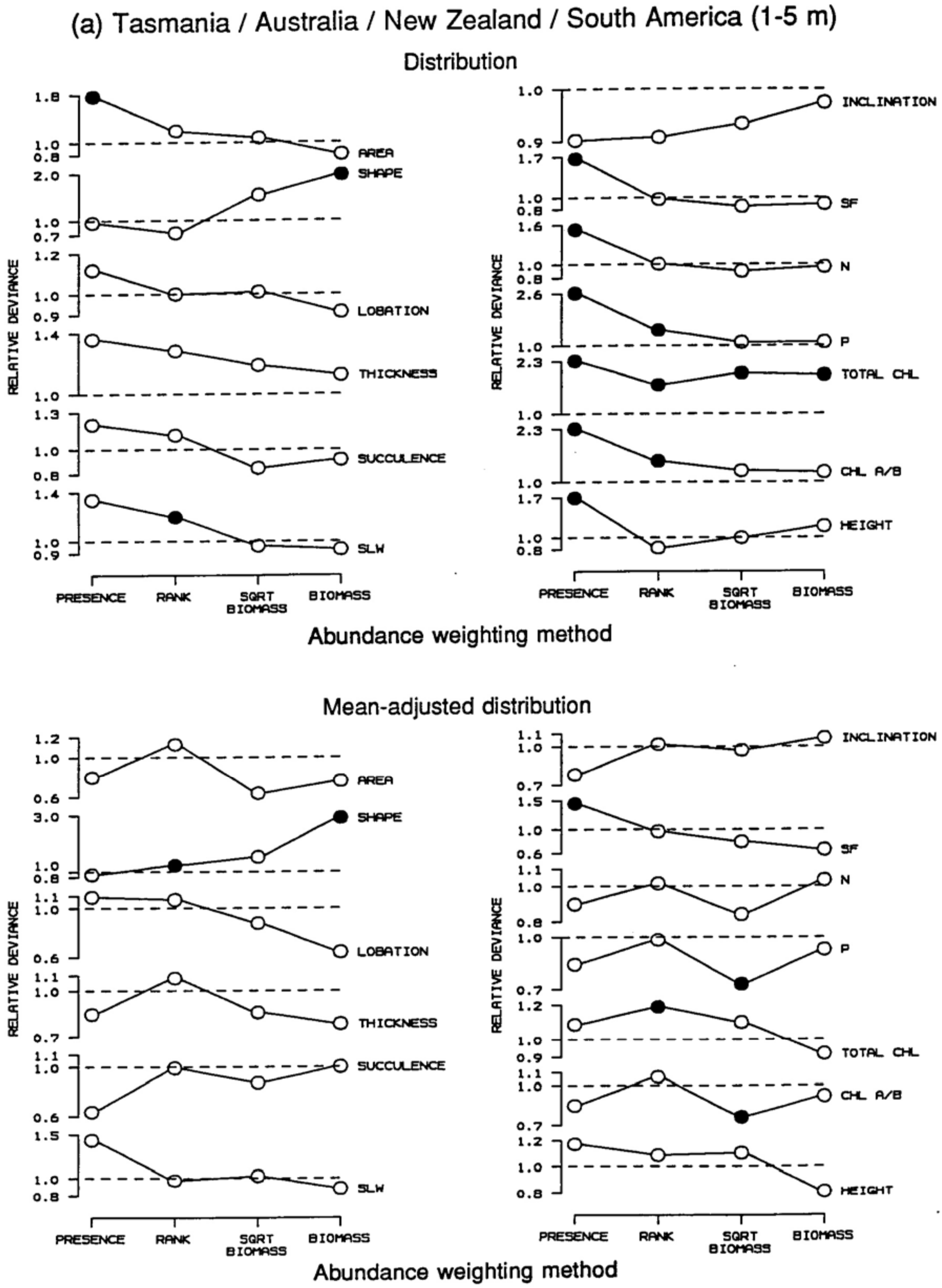

Fig. 10.5 Null model randomisation tests for convergence or divergence in texture in the 1-5 m guild between landmass-scale *Nothofagus*-dominated communities **(a)** Tasmania (T), Australia (A), New Zealand (Z) and South America (S); **(b)** Tasmania and New Zealand. Format as for Fig. 10.1.

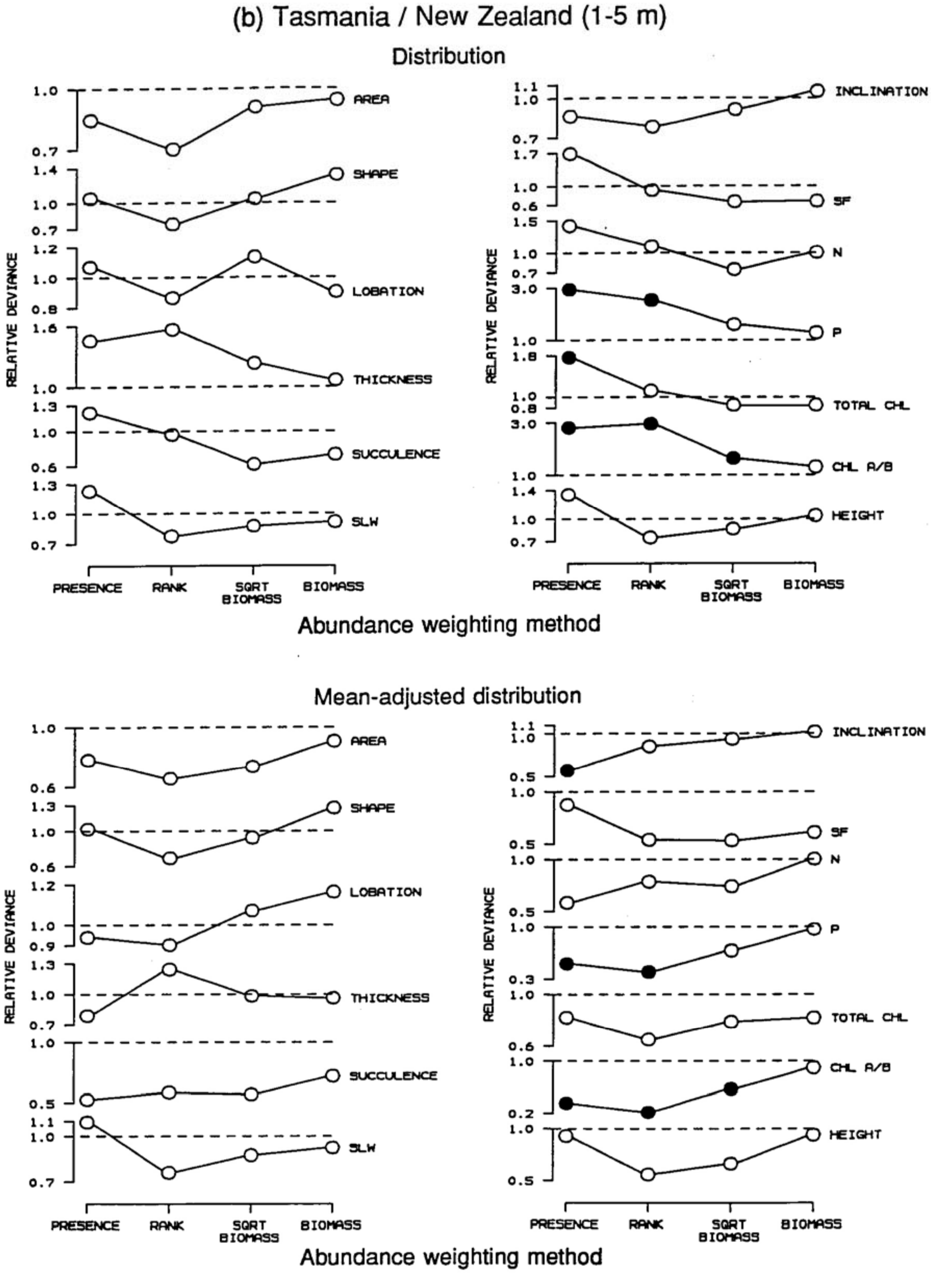

Fig. 10.5 (continued)

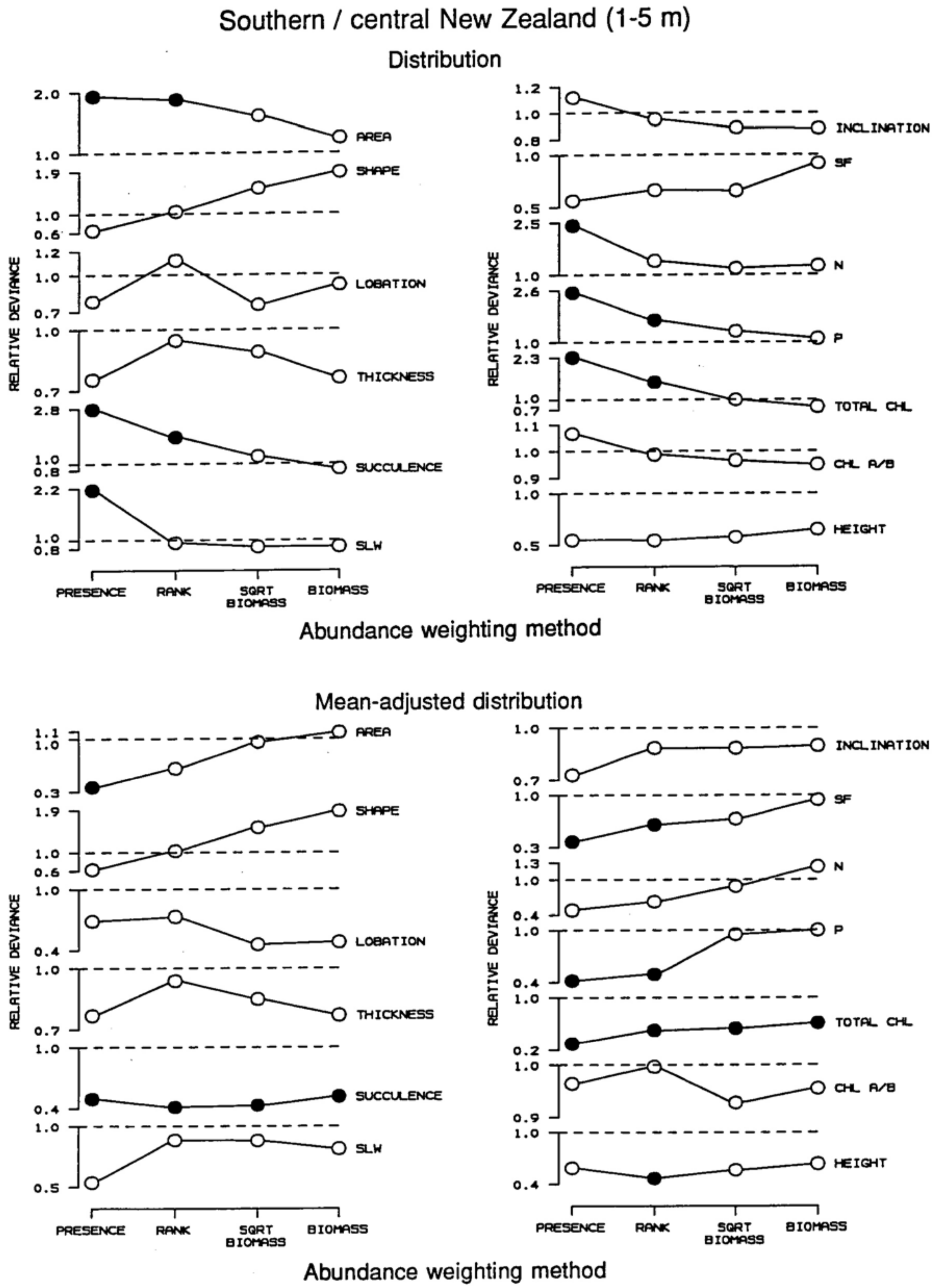

Fig. 10.6 Null model randomisation tests for convergence or divergence in texture in the 1-5 m guild between regional-scale *Nothofagus*-dominated communities southern (ZS) and central (ZC) New Zealand. Format as for Fig. 10.1.

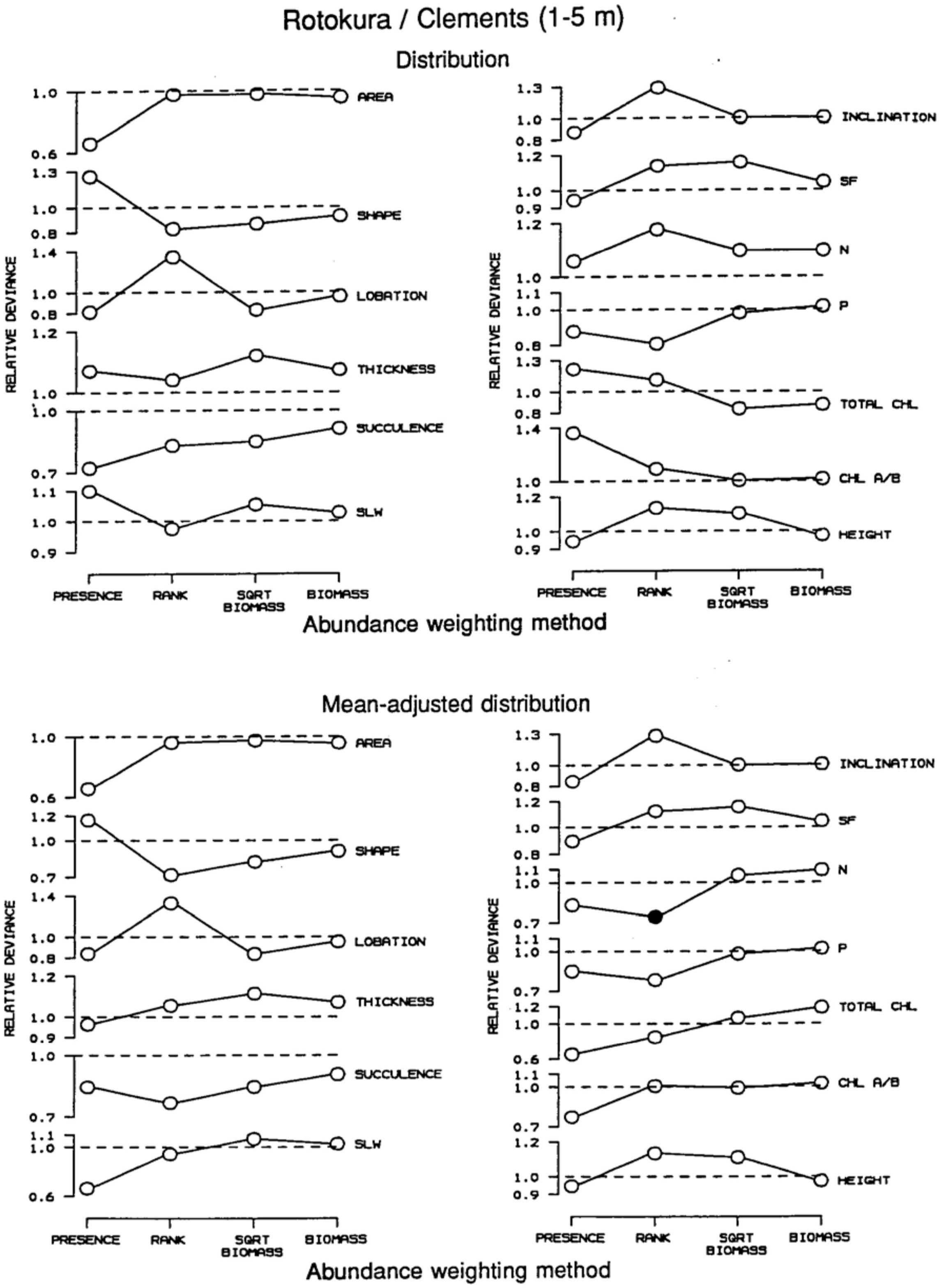

Fig. 10.7 Null model randomisation tests for convergence or divergence in texture in the 1-5 m guild between local-scale *Nothofagus*-dominated communities ZN2 Rotokura and ZN3 Clements. Format as for Fig. 10.1.

Abundance rank-weighted distributions of support fraction are convergent between T2 Anne and ZN1 Ohakune, while PSU phosphorus (weighting by species presence) and chlorophyll *a/b* (all weighting factors except biomass) are divergent (Fig. 10.8b). Mean-adjusted distributions of PSU lobation (biomass), nitrogen (abundance rank), phosphorus (presence and rank) and chlorophyll *a/b* are convergent. There is no divergence between mean-adjusted texture distributions for these sites.

Comparisons of texture distributions for ZN2 Clements and SA1 Quetrihué revealed no significant convergence, and divergence in only two variates, PSU phosphorus and chlorophyll *a/b*, with species unweighted by their abundance (Fig. 10.8c). For mean-adjusted distributions, the same two variates are convergent with species unweighted, and there is no further significant departure from the null model.

>5 m Guild

Distributions of abundance rank-weighted PSU specific weight are convergent in the >5 m guild among Tasmania, Australia, New Zealand and South America (Fig. 10.9a). The landmasses are divergent in PSU phosphorus content, total chlorophyll, chlorophyll *a/b* and species height. Mean-adjusted distributions of PSU succulence (weighting by photosynthetic biomass), chlorophyll *a/b* (presence) and support fraction (abundance rank) are convergent, but there is divergence in species height (rank and biomass weighting).

Between Tasmania and New Zealand there is convergence in distributions of PSU succulence (abundance rank weighting), while phosphorus content and chlorophyll *a/b* are divergent (Fig. 10.9b). Comparing mean-adjusted texture distributions, there is convergence in PSU area, succulence, phosphorus and chlorophyll *a/b* at lower weighting levels, and in PSU shape with species weighted by photosynthetic biomass. No significant divergence was detected between mean-adjusted distributions.

Tests comparing southern (ZS) and central (ZC) New Zealand revealed no significant departure from null model expectation, whether texture was expressed as the distribution or the mean-adjusted distribution of character values in the >5 m guild at each community (Fig. 10.10).

Distributions of PSU specific weight and chlorophyll *a/b* are convergent between ZN2 Rotokura and ZN3 Clements, with species weighted equally (Fig. 10.11). No significant divergence was detected. There is convergence in mean-adjusted distributions of PSU succulence and specific weight at lower weighting levels, while PSU shape is divergent with photosynthetic biomass as the weighting factor.

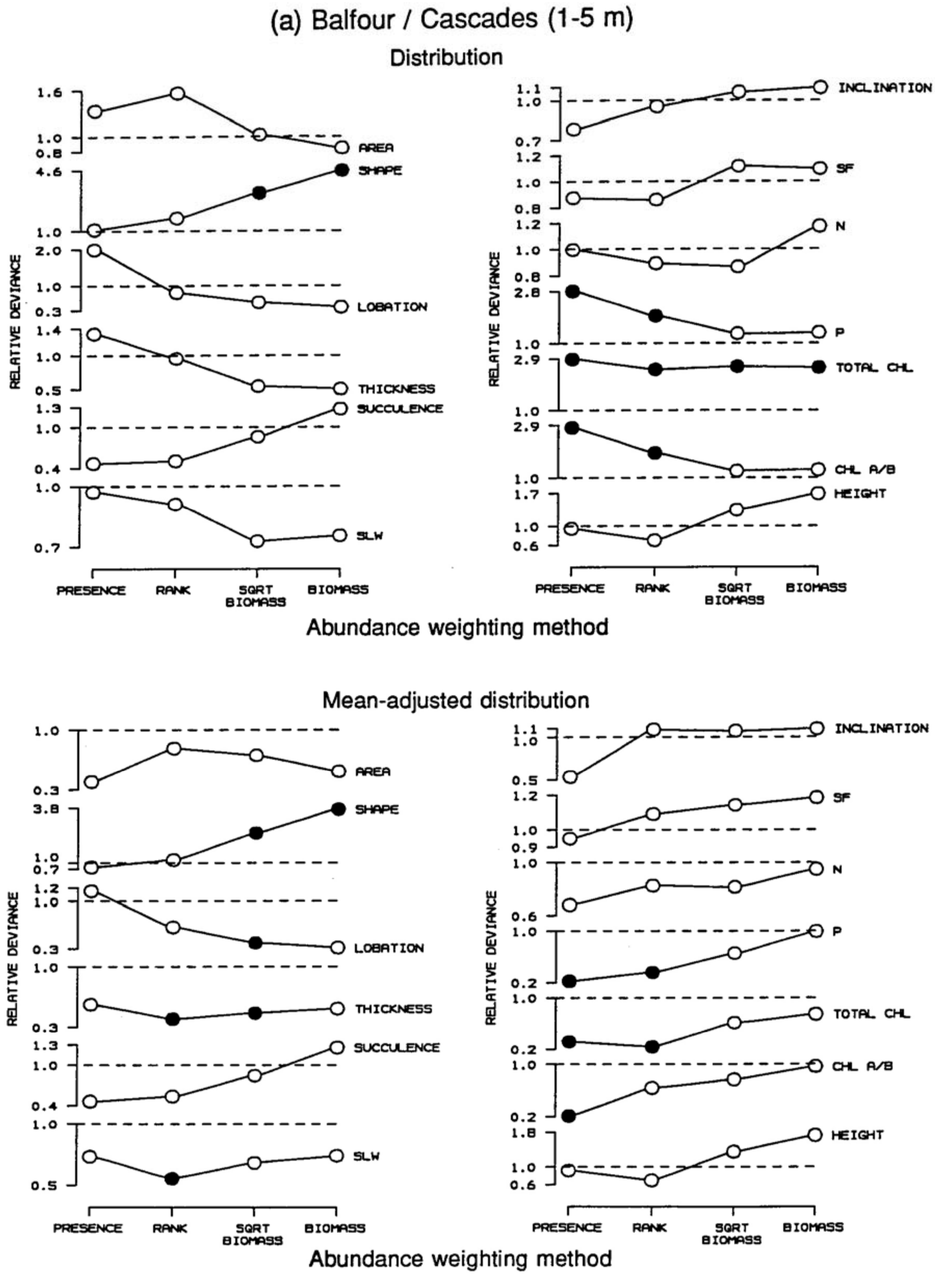

Fig. 10.8 Null model randomisation tests for convergence or divergence in texture in the 1-5 m guild between *Nothofagus*-dominated communities from different landmasses closely matched in their environments: **(a)** T1 Balfour/A2 Cascades; **(b)** T2 Anne/ZN1 Ohakune; **(c)** ZN2 Rotokura/SA1 Quetrihué. Format as for Fig. 10.1.

(b) Anne / Ohakune (1-5 m)

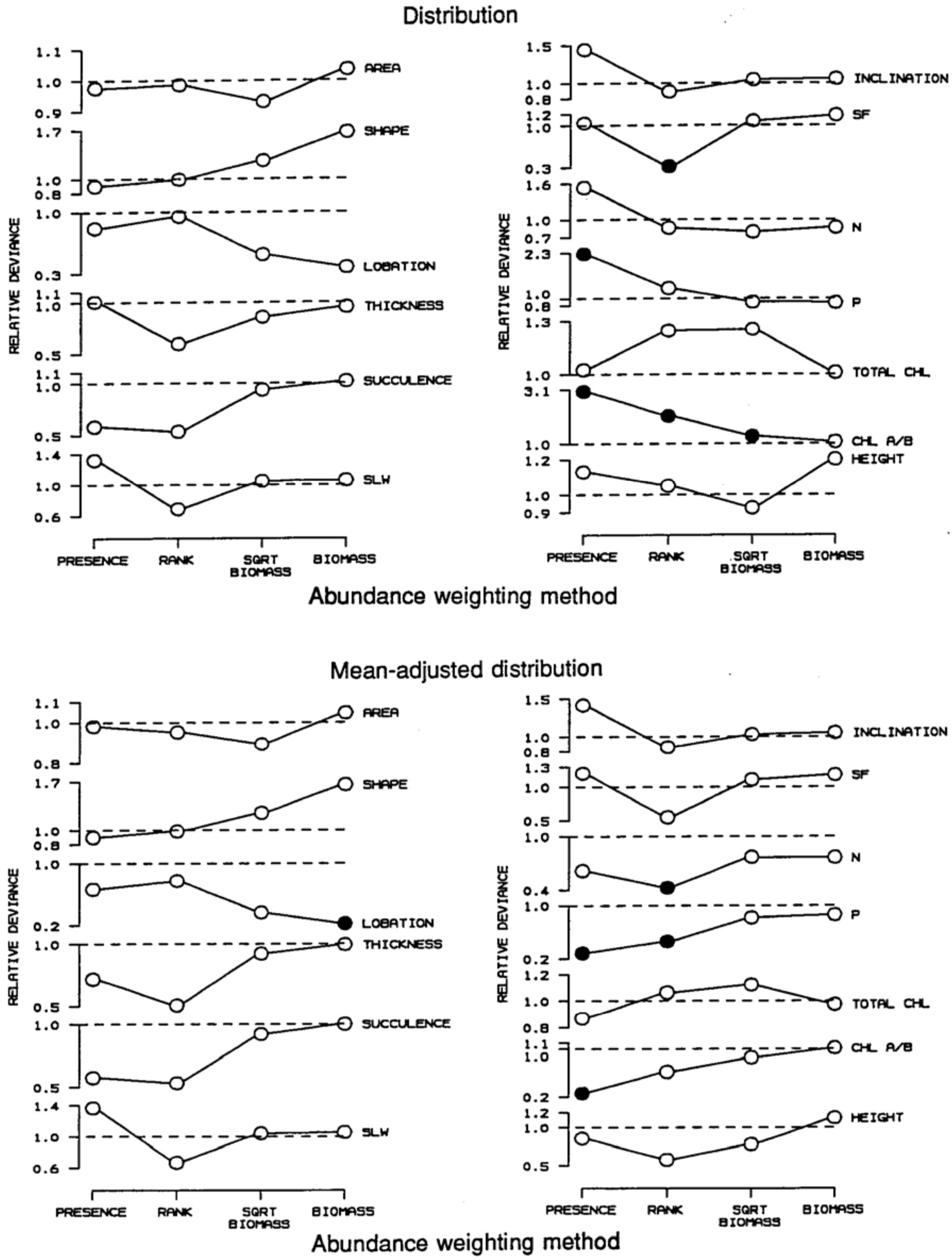

Fig. 10.8 (continued)

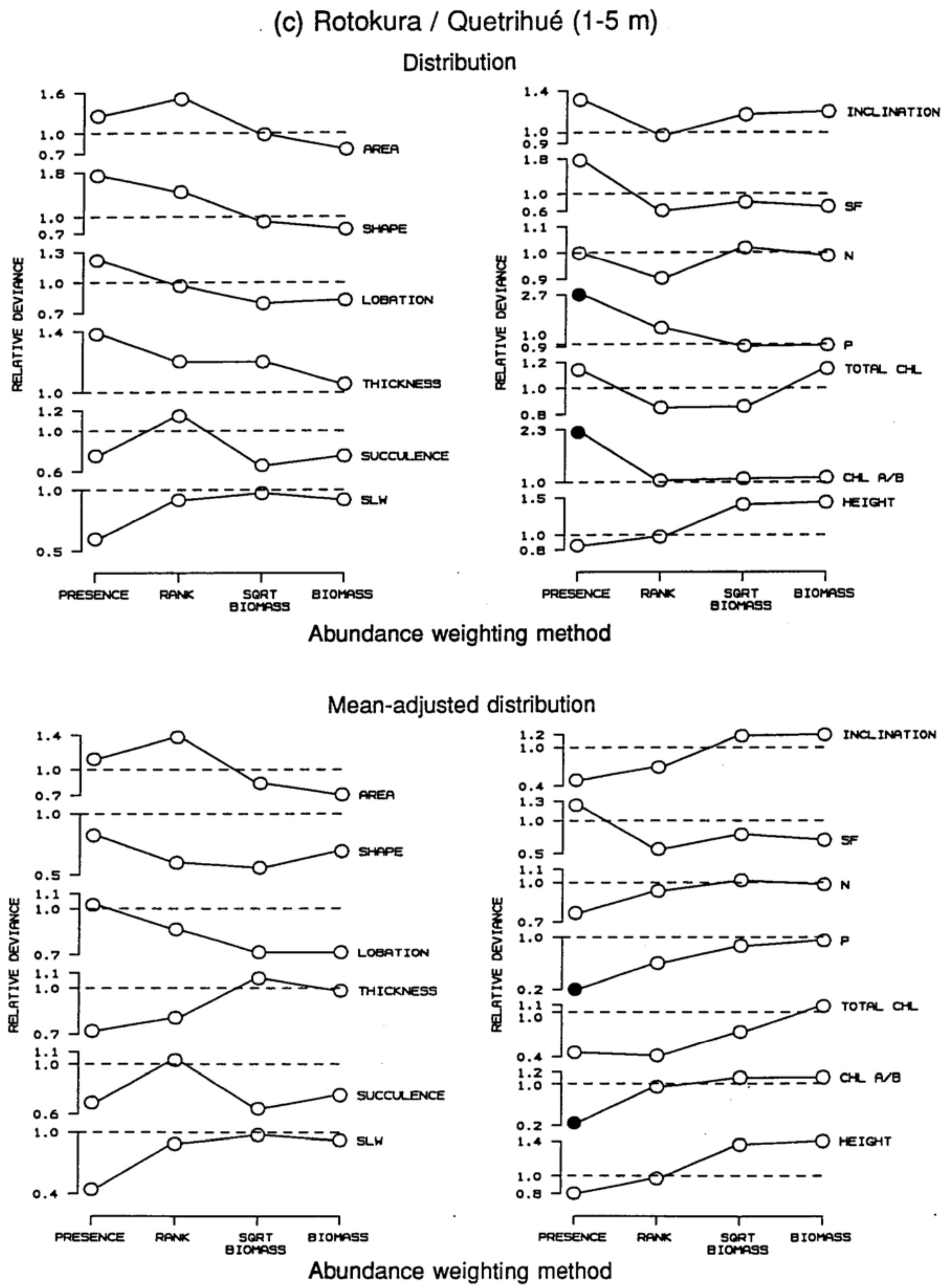

Fig. 10.8 (continued)

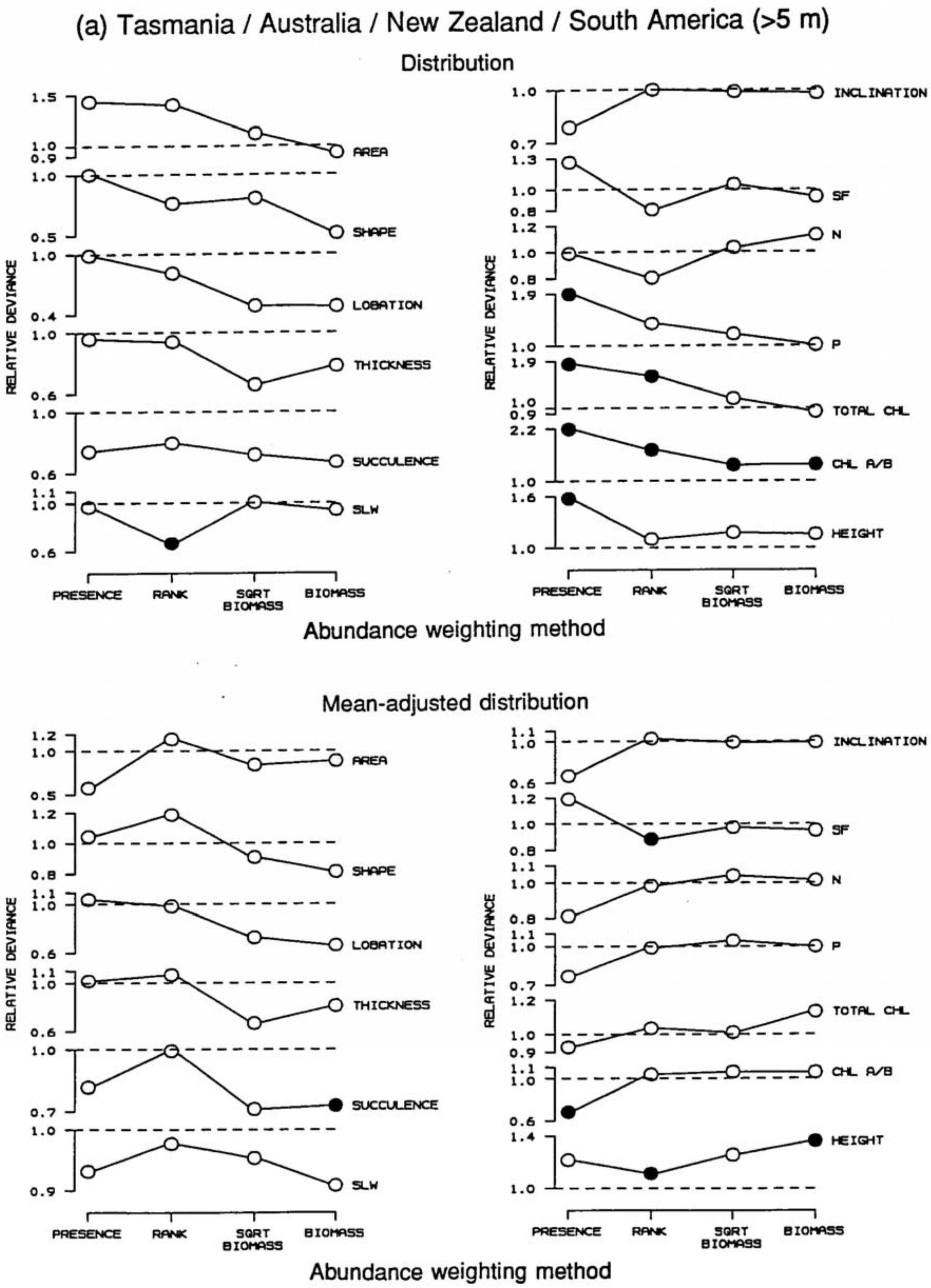

Fig. 10.9 Null model randomisation tests for convergence or divergence in texture in the >5 m guild between landmass-scale *Nothofagus*-dominated communities **(a)** Tasmania (T), Australia (A), New Zealand (Z) and South America (S); **(b)** Tasmania and New Zealand. Format as for Fig. 10.1.

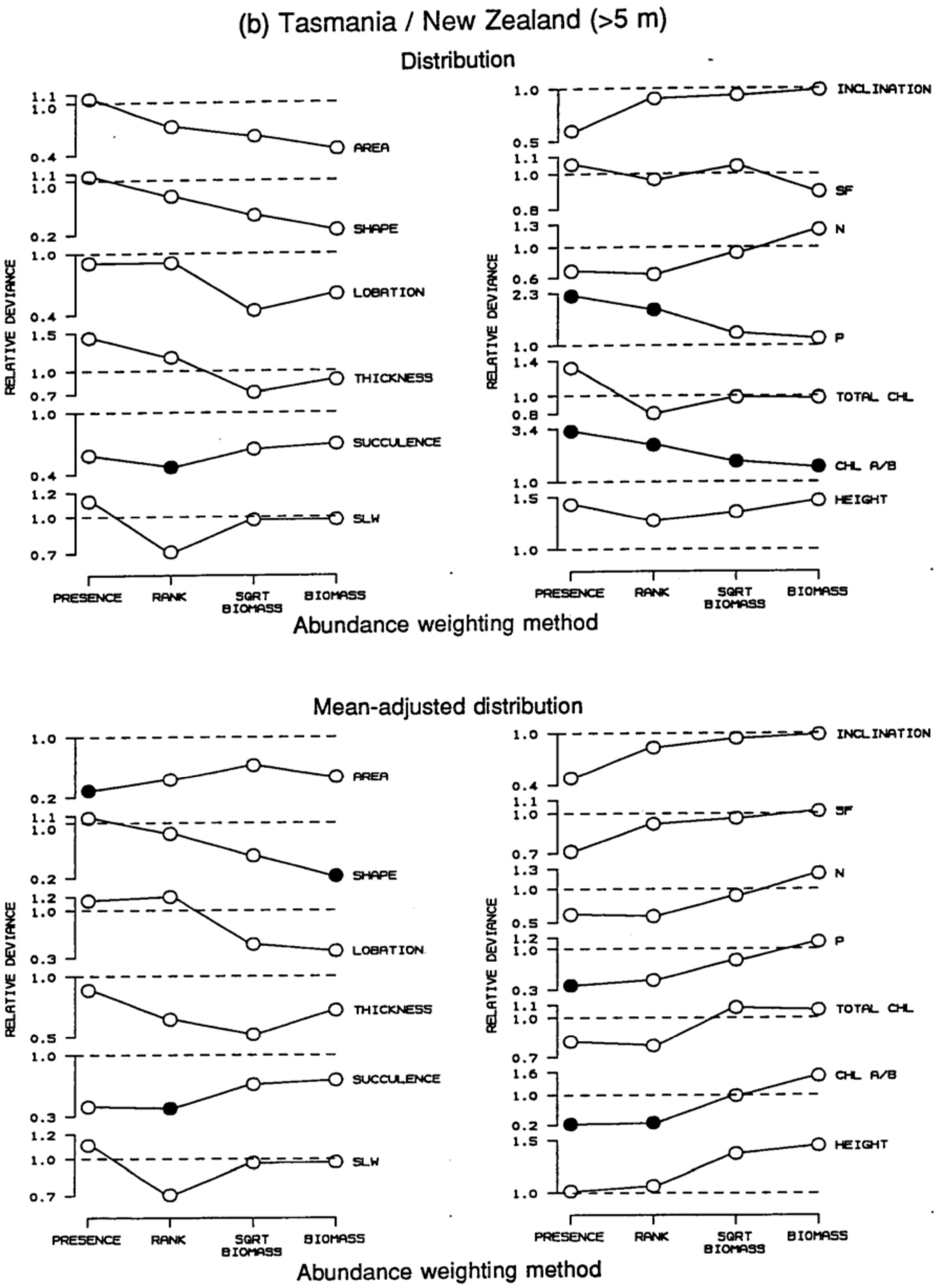

Fig. 10.9 (continued)

Only one test revealed significant departure from the null model when texture distributions for the >5 m guild at T1 Balfour and A2 Cascades were compared: there was divergence in PSU total chlorophyll with species unweighted by their abundance (Fig. 10.12a). Mean-adjusted distributions showed convergence in PSU shape, thickness, succulence, phosphorus content, total chlorophyll and chlorophyll *a/b*, primarily in the absence of abundance weighting. No significant divergence was detected.

Biomass-weighted distributions of PSU area are convergent between T2 Anne and ZN1 Ohakune, while PSU phosphorus (weighting by species presence), chlorophyll *a/b* (all weighting factors except photosynthetic biomass) and species height (biomass) are divergent (Fig. 10.12b). When mean-adjusted distributions are compared, PSU phosphorus and chlorophyll *a/b* are convergent at lower weighting levels, and there is no significant divergence.

No significant departure from the null model was observed in comparisons of texture distributions for ZN2 Rotokura and SA1 Quetrihué (Fig. 10.12c). Mean-adjusted distributions of PSU phosphorus content and total chlorophyll are, however, convergent at lower weighting levels.

PATTERNS AMONG TEXTURE VARIATES

0-1 m Guild

Although convergence among texture distributions in the 0-1 m guild was detected in a number of individual tests, the total incidence in any texture variate at any weighting level is not significant as a proportion of 16 independent community comparisons, according to binomial tests (Table 10.2). Divergence was detected more frequently, and is significant overall at some weighting levels, for the variates PSU area, shape, succulence, nitrogen content, phosphorus content, total chlorophyll, chlorophyll *a/b* and species height. In general, the divergence is significant only at lower weighting levels, although for PSU area, the incidence is significant at all weighting levels. This demonstrates that there are marked quantitative differences in foliar area in the ground strata of many of the communities sampled.

In comparisons of mean-adjusted texture distributions, the incidence of convergence is higher, and significant overall for several variates — PSU area, lobation, nitrogen content, phosphorus content, total chlorophyll, chlorophyll *a/b* and support fraction — with species weighted equally or by abundance rank. PSU phosphorus content and chlorophyll *a/b* ratio were found to be convergent in the largest number of comparisons, 12 and 13, respectively, of 31, with species values unweighted. On the basis of the close correlation between these variates, demonstrated in Chapter 9, it is likely that the very similar patterns of departure from null expectation in each may be attributed to the same underlying factor. Divergence, significant as a proportion of the tests carried out, persists for PSU area (weighting by photosynthetic biomass) and shape (square root of biomass).

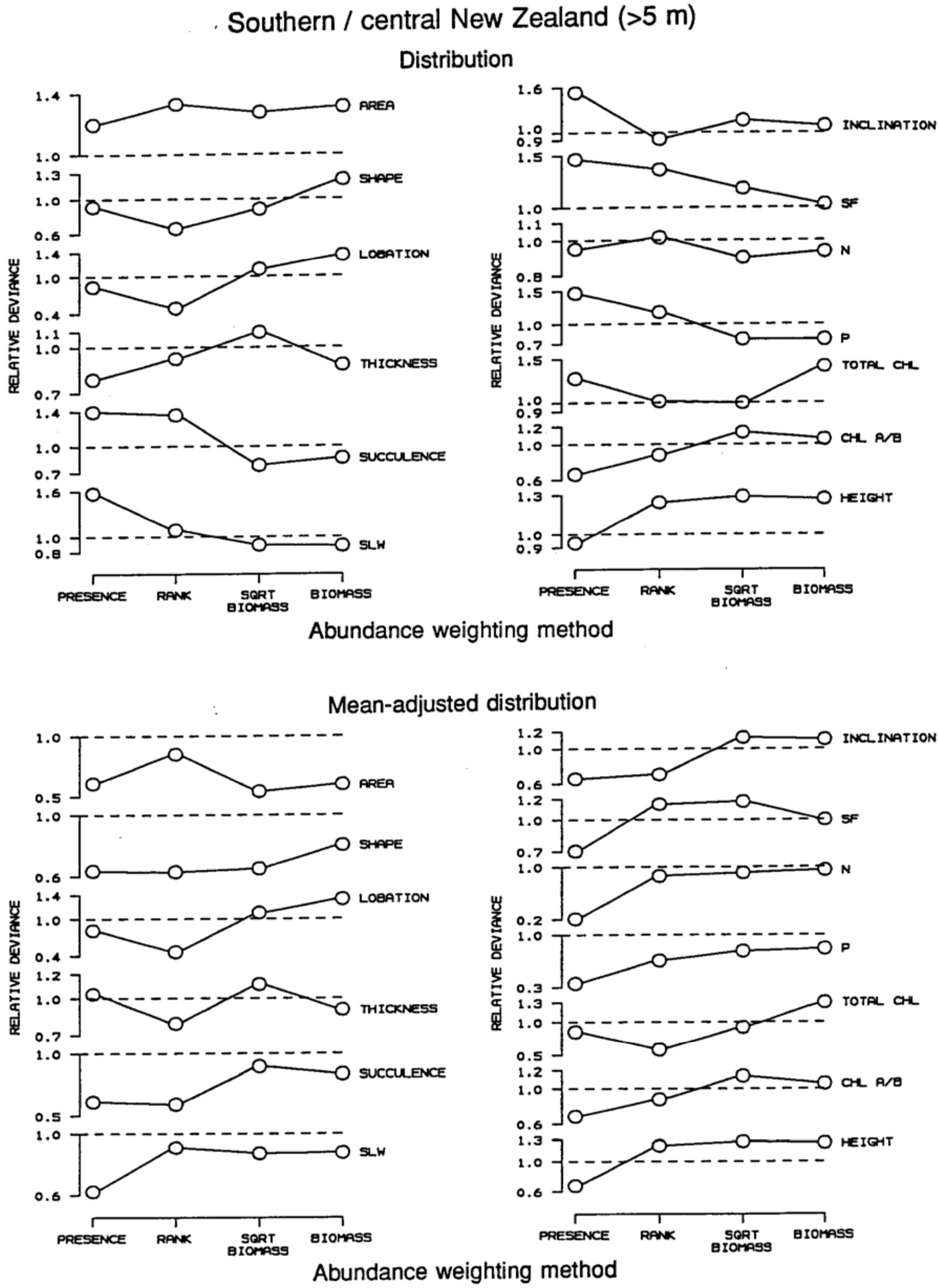

Fig. 10.10 Null model randomisation tests for convergence or divergence in texture in the >5 m guild between regional-scale *Nothofagus*-dominated communities southern (ZS) and central (ZC) New Zealand. Format as for Fig. 10.1.

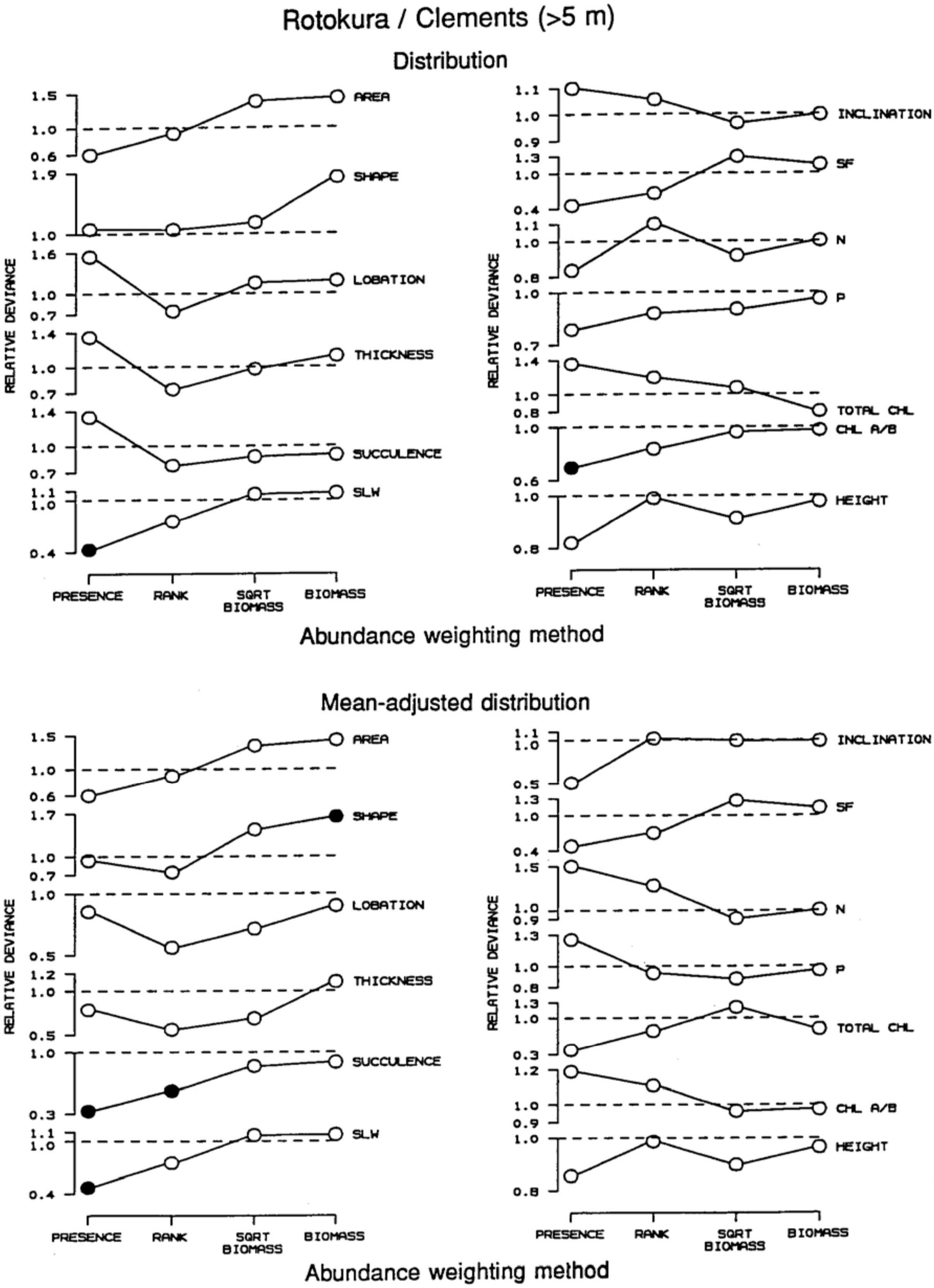

Fig. 10.11 Null model randomisation tests for convergence or divergence in texture in the >5 m guild between local-scale *Nothofagus*-dominated communities ZN2 Rotokura and ZN3 Clements. Format as for Fig. 10.1.

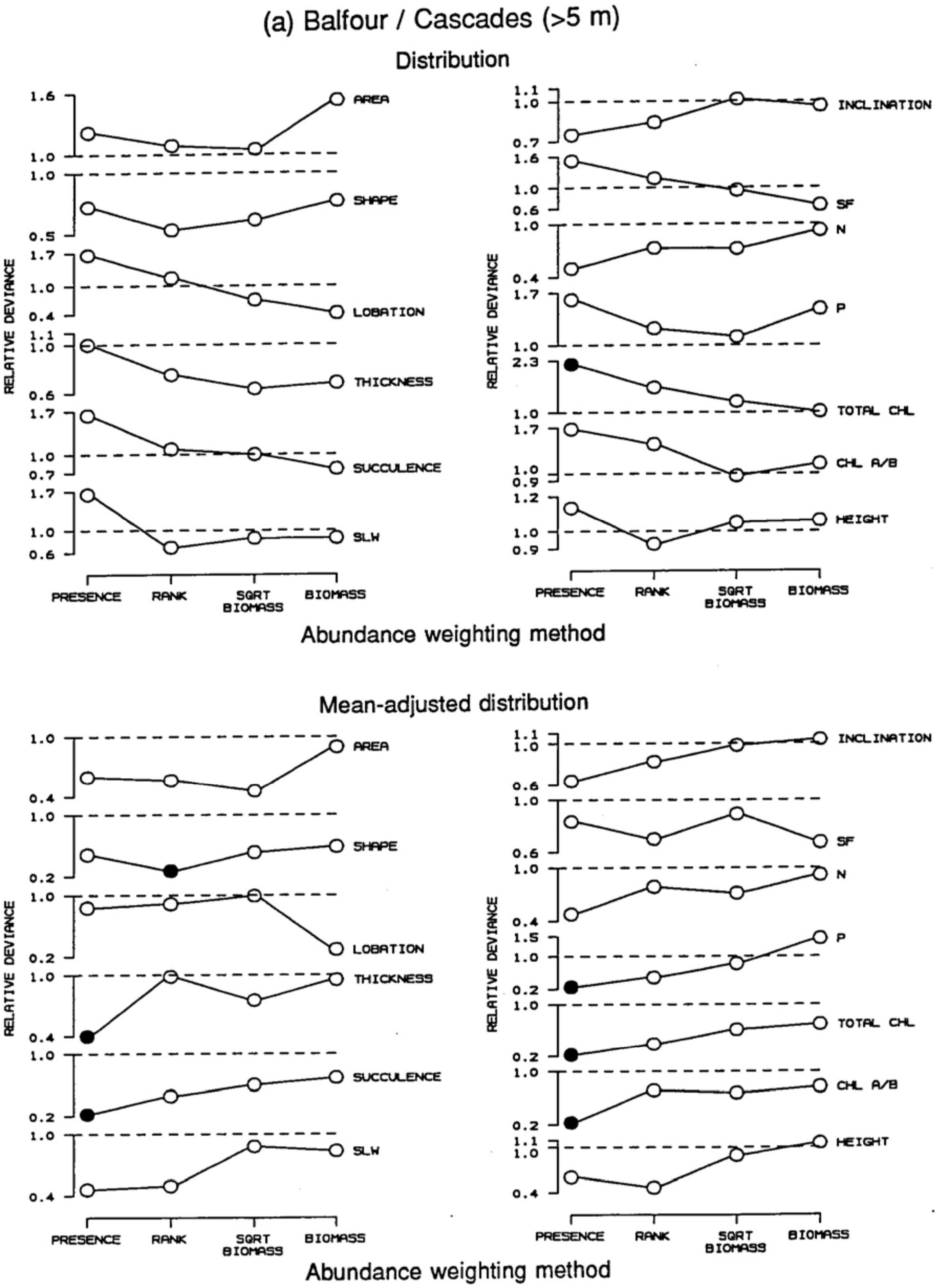

Fig. 10.12 Null model randomisation tests for convergence or divergence in texture in the >5 m guild between *Nothofagus*-dominated communities from different landmasses closely matched in their environments: **(a)** T1 Balfour/A2 Cascades; **(b)** T2 Anne/ZN1 Ohakune; **(c)** ZN2 Rotokura/SA1 Quetrihué. Format as for Fig. 10.1.

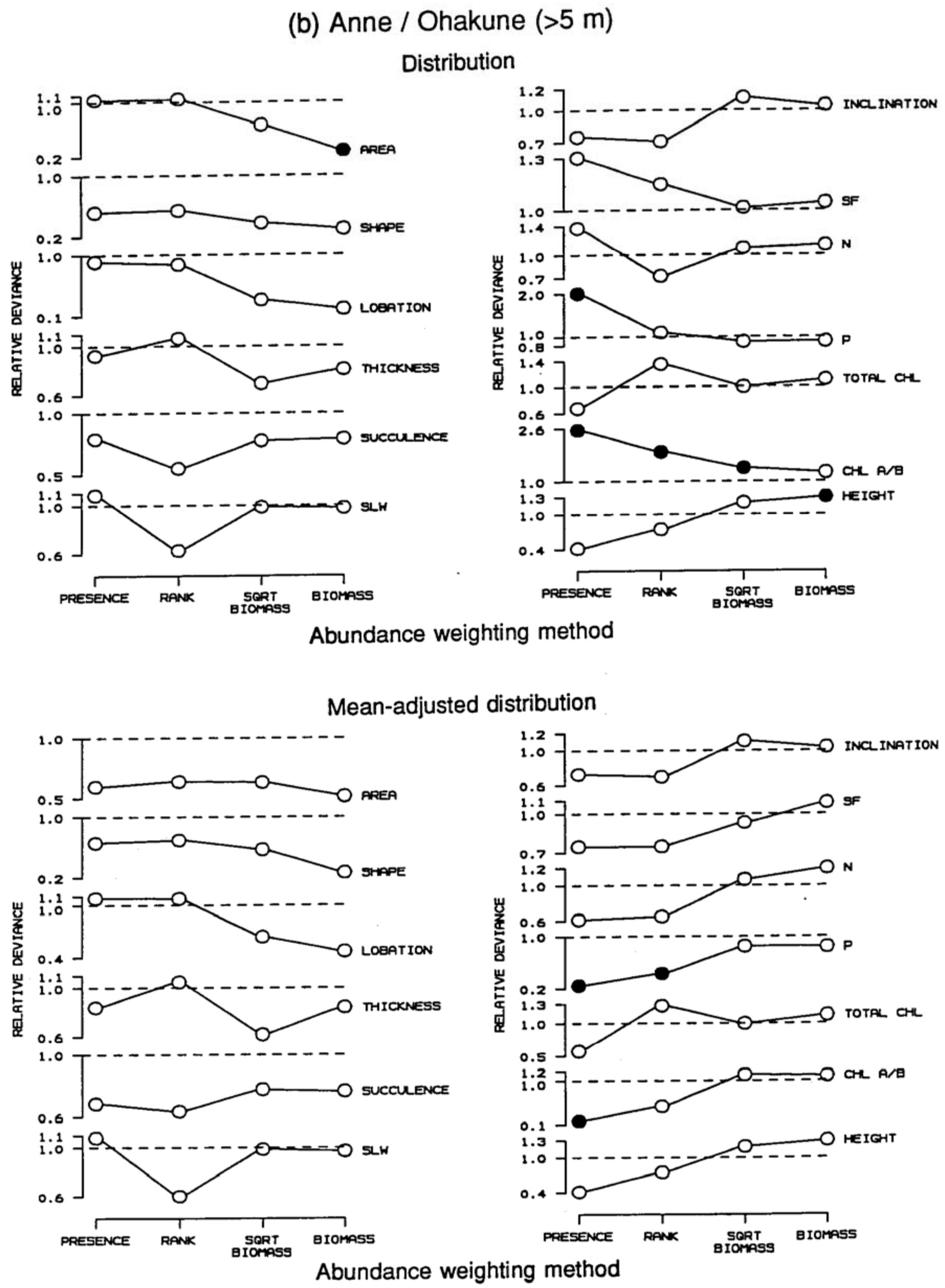

Fig. 10.12 (continued)

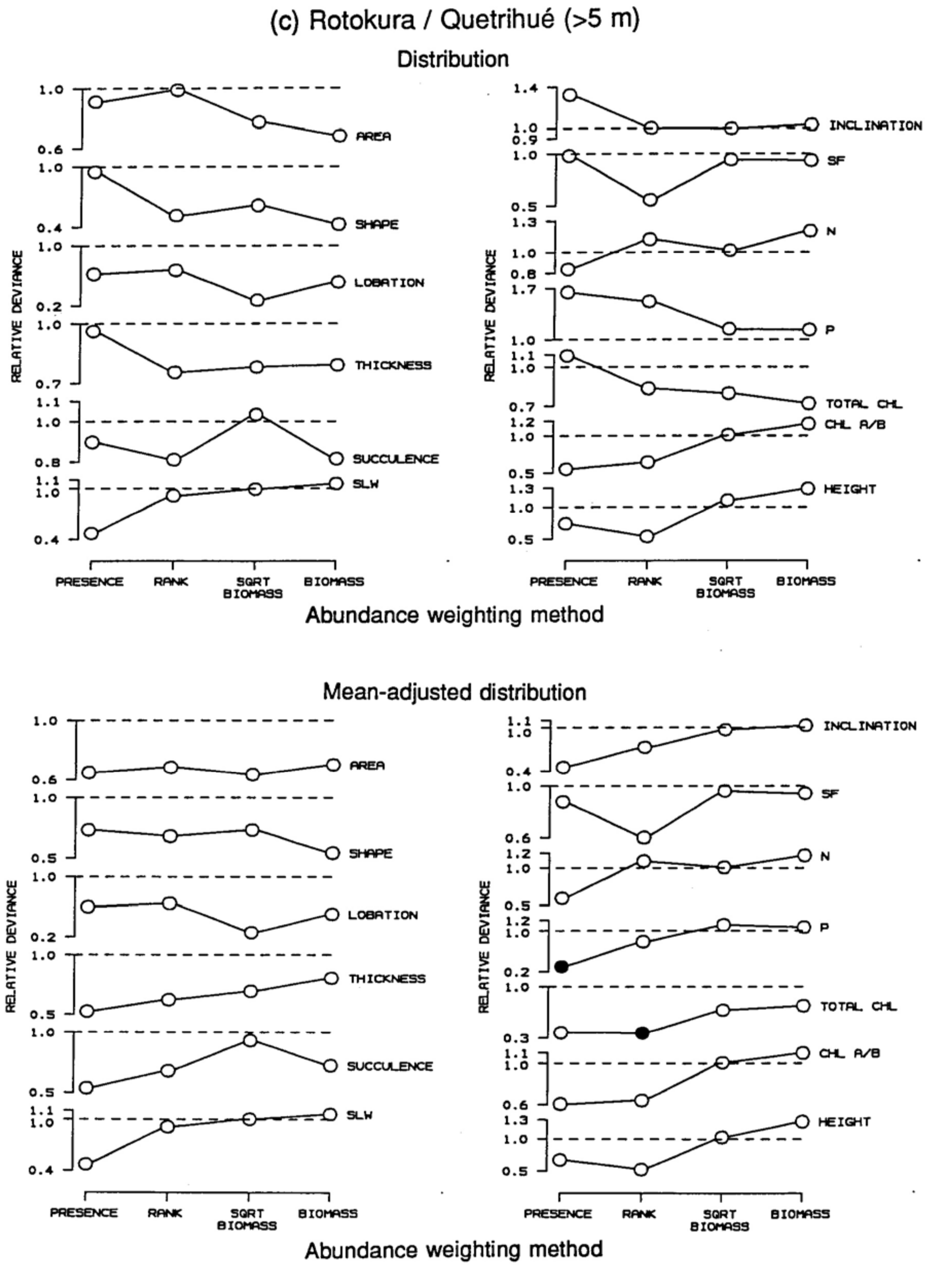

Fig. 10.12 (continued)

Table 10.2 Incidence of significant convergence or divergence in each texture variate for the 0-1 m guild among 31 community comparisons and (in parentheses) for 16 independent community comparisons (see text). Results are shown for each of four methods of weighting species values by abundance and for two methods of expressing community texture (distribution and mean-adjusted distribution). Overall significance, determined from the binomial distribution, is shown for results from the 16 independent comparisons.

	Texture Variate	Convergence				Divergence			
		Presence	Rank	Sqrt biomass	Biomass	Presence	Rank	Sqrt biomass	Biomass
Distribution	Area	0 (0)	0 (0)	0 (0)	0 (0)	5 (4**)	4 (3*)	8 (4**)	8 (4**)
	Shape	1 (1)	0 (0)	0 (0)	0 (0)	2 (1)	4 (3*)	8 (5**)	3 (1)
	Lobation	1 (1)	1 (1)	2 (1)	1 (1)	4 (2)	1 (1)	0 (0)	0 (0)
	Thickness	5 (2)	1 (1)	0 (0)	2 (1)	4 (1)	2 (1)	0 (0)	0 (0)
	Succulence	0 (0)	0 (0)	0 (0)	0 (0)	4 (4**)	0 (0)	0 (0)	0 (0)
	SLW	0 (0)	2 (2)	0 (0)	1 (0)	2 (2)	0 (0)	0 (0)	0 (0)
	Inclination	0 (0)	0 (0)	0 (0)	0 (0)	3 (1)	2 (1)	0 (0)	0 (0)
	SF	2 (1)	1 (1)	1 (1)	2 (2)	3 (0)	1 (0)	1 (1)	3 (2)
	N	0 (0)	2 (1)	1 (0)	0 (0)	12 (8**)	2 (1)	0 (0)	0 (0)
	P	0 (0)	2 (1)	1 (1)	0 (0)	19 (11**)	15 (9**)	4 (2)	2 (0)
	Total chl	0 (0)	0 (0)	0 (0)	1 (1)	10 (4**)	8 (4**)	7 (1)	2 (1)
	Chl *a/b*	1 (1)	0 (0)	0 (0)	0 (0)	21 (9**)	14 (6**)	1 (0)	1 (1)
	Height	0 (0)	0 (0)	0 (0)	1 (1)	3 (3*)	0 (0)	1 (1)	2 (2)
Mean-adjusted distribution	Area	3 (3*)	0 (0)	1 (1)	1 (1)	0 (0)	0 (0)	3 (1)	7 (4**)
	Shape	2 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (1)	6 (4**)	3 (1)
	Lobation	4 (3*)	4 (3*)	1 (0)	2 (0)	0 (0)	0 (0)	0 (0)	0 (0)
	Thickness	5 (2)	2 (1)	0 (0)	1 (1)	1 (1)	1 (1)	0 (0)	0 (0)
	Succulence	2 (2)	3 (2)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
	SLW	3 (2)	1 (1)	0 (0)	1 (0)	0 (0)	0 (0)	0 (0)	0 (0)
	Inclination	2 (1)	0 (0)	0 (0)	0 (0)	1 (0)	0 (0)	0 (0)	0 (0)
	SF	4 (2)	5 (3*)	2 (2)	2 (1)	0 (0)	0 (0)	1 (1)	4 (2)
	N	3 (3*)	8 (4**)	1 (0)	0 (0)	2 (0)	0 (0)	0 (0)	0 (0)
	P	12 (8**)	11 (7**)	1 (0)	1 (0)	1 (0)	0 (0)	2 (0)	2 (0)
	Total chl	10 (3*)	5 (1)	2 (1)	1 (1)	0 (0)	3 (2)	0 (0)	0 (0)
	Chl *a/b*	13 (7**)	11 (5**)	5 (2)	1 (0)	3 (1)	1 (0)	1 (0)	1 (1)
	Height	1 (1)	2 (1)	0 (0)	1 (0)	0 (0)	0 (0)	0 (0)	1 (1)

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

1-5 m Guild

The incidence of significant convergence among texture distributions in the 1-5 m guild is very low, and non-significant overall for each variate and weighting factor combination (Table 10.3). Divergence, by contrast, was detected in all variates, and is significant as a proportion of 14 independent comparisons for all except PSU lobation, thickness and inclination. With the exceptions of PSU area and shape the incidence of divergence in each variate is significant only at lower weighting levels.

Mean-adjusted distributions of several variates were found to be convergent in a large enough number of comparisons do be deemed significant overall. These variates are PSU area, succulence, specific weight, nitrogen content, phosphorus content, total chlorophyll, chlorophyll *a/b*, support fraction and species height. As for the 0-1 m guild, PSU phosphorus and chlorophyll *a/b* were convergent in the largest number of comparisons. The only variate showing a significant incidence of divergence is PSU shape.

Table 10.3 Incidence of significant convergence or divergence in each texture variate for the 1-5 m guild among 29 community comparisons and (in parentheses) for 14 independent community comparisons (see text). Results are shown for each of four methods of weighting species values by abundance and for two methods of expressing community texture (distribution and mean-adjusted distribution). Overall significance, determined from the binomial distribution, is shown for results from the 14 independent comparisons.

	Texture Variate	Convergence				Divergence			
		Presence	Rank	Sqrt biomass	Biomass	Presence	Rank	Sqrt biomass	Biomass
Distribution	Area	0 (0)	0 (0)	0 (0)	0 (0)	6 (2*)	5 (4***)	2 (2*)	0 (0)
	Shape	0 (0)	0 (0)	1 (1)	1 (1)	2 (2*)	3 (2*)	5 (3**)	5 (2*)
	Lobation	1 (0)	0 (0)	3 (1)	1 (1)	2 (1)	0 (0)	0 (0)	0 (0)
	Thickness	1 (1)	0 (0)	0 (0)	0 (0)	4 (0)	1 (0)	0 (0)	0 (0)
	Succulence	0 (0)	1 (1)	0 (0)	0 (0)	4 (2*)	1 (1)	0 (0)	0 (0)
	SLW	0 (0)	0 (0)	0 (0)	0 (0)	3 (2*)	3 (2*)	0 (0)	0 (0)
	Inclination	1 (1)	0 (0)	0 (0)	0 (0)	2 (0)	1 (1)	0 (0)	0 (0)
	SF	0 (0)	2 (0)	1 (0)	1 (1)	4 (2*)	2 (2*)	0 (0)	0 (0)
	N	1 (1)	1 (0)	0 (0)	0 (0)	9 (6***)	0 (0)	0 (0)	0 (0)
	P	0 (0)	1 (0)	0 (0)	0 (0)	19 (9***)	12 (7***)	3 (1)	1 (1)
	Total chl	0 (0)	0 (0)	0 (0)	0 (0)	11 (4***)	10 (4***)	6 (1)	6 (1)
	Chl *a/b*	0 (0)	1 (0)	1 (1)	0 (0)	19 (8***)	11 (4***)	3 (1)	0 (0)
	Height	0 (0)	0 (0)	0 (0)	1 (1)	4 (2*)	3 (1)	0 (0)	0 (0)
Mean-adjusted distribution	Area	2 (2*)	1 (1)	2 (1)	1 (1)	0 (0)	0 (0)	0 (0)	0 (0)
	Shape	0 (0)	1 (0)	1 (1)	0 (0)	0 (0)	2 (0)	3 (2*)	6 (3**)
	Lobation	1 (0)	1 (0)	1 (0)	1 (0)	1 (0)	0 (0)	0 (0)	0 (0)
	Thickness	2 (1)	1 (0)	1 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
	Succulence	3 (2*)	4 (3**)	3 (1)	4 (3**)	0 (0)	0 (0)	0 (0)	0 (0)
	SLW	4 (2*)	2 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
	Inclination	1 (1)	0 (0)	1 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
	SF	4 (3**)	4 (3**)	0 (0)	1 (1)	1 (0)	0 (0)	1 (1)	0 (0)
	N	3 (3**)	4 (1)	0 (0)	0 (0)	1 (0)	0 (0)	0 (0)	0 (0)
	P	16 (9***)	12 (7***)	2 (1)	0 (0)	1 (0)	0 (0)	1 (0)	0 (0)
	Total chl	7 (3**)	9 (3**)	7 (4***)	4 (3**)	0 (0)	1 (0)	0 (0)	0 (0)
	Chl *a/b*	11 (5***)	6 (3**)	5 (2*)	0 (0)	3 (1)	0 (0)	0 (0)	0 (0)
	Height	0 (0)	4 (3**)	1 (0)	2 (1)	0 (0)	2 (1)	0 (0)	0 (0)

*0.01≤*P*<0.05; **0.001≤*P*<0.01; ****P*<0.001

>5 m Guild

The number of comparisons of texture distributions for the >5 m guild in which significant convergence was detected was no higher for any variate/weighting factor combination than would be expected by chance alone, according to binomial tests (Table 10.4). Divergence was significant overall for PSU area (with weighting by presence only), phosphorus content (presence, abundance rank) and total chlorophyll (presence). The overall incidence of divergence is lower than for the 0-1 m and 1-5 m guilds. This may reflect a tendency for fewer species to be represented in the tree stratum than in the ground or intermediate strata, rather than a particularly low degree of character dissimilarity among communities (see Section 10.4).

The incidence of significant convergence between mean-adjusted texture distributions is likewise relatively low for the >5 m guild: PSU area, succulence, specific weight, phosphorus content and chlorophyll *a/b* were all found to be convergent in a larger proportion of independent community comparisons than expected on a random basis, primarily at lower abundance weighting levels. Significant divergence was detected between mean-adjusted distributions in only five tests, and is not significant overall for any variate.

Table 10.4 Incidence of significant convergence or divergence in each texture variate for the >5 m guild among 26 community comparisons and (in parentheses) for 15 independent community comparisons (see text). Results are shown for each of four methods of weighting species values by abundance and for two methods of expressing community texture (distribution and mean-adjusted distribution). Overall significance, determined from the binomial distribution, is shown for results from the 15 independent comparisons.

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

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

10.4 Discussion

COMMUNITY-LEVEL CONVERGENCE

Convergence between texture distributions was detected in each guild in a number of tests, but among an independent subset of comparisons the number of tests showing significance in the direction of convergence was no higher, for any variate/weighting level combination, than would be expected on the basis of chance (Tables 10.2-10.4). Divergence, on the other hand, was detected frequently and was significant overall for a majority of texture variates for the 0-1 m and 1-5 m guilds, though for only three variates in the case of the >5 m guild.

For each guild, mean-adjusted distributions were found to be convergent in a larger number of community comparisons, and the incidence was significant overall for a number of variates. Only three variates, PSU shape, thickness and inclination, did not show convergence, in any guild, in a significant number of independent comparisons. Of the three guilds, the highest incidence of convergence was detected in the 1-5 m guild, which would correspond primarily to the shrub stratum in many *Nothofagus*-dominated forests (Bycroft *et al.* 1993; Wilson *et al.* 1995). The lowest incidence of convergence was in the >5 m guild, the tree stratum. However, this finding may in part reflect the structure of the data set rather than the ecology of the forest canopy, a possibility that is discussed below. Divergence between mean-adjusted texture distributions, significant as a proportion of the number of tests done, was confined to two variates, PSU area and shape, and to the 0-1 m and 1-5 m guilds.

Interpretation of differences between guilds

Differences among guilds in the significance of divergence or convergence in particular variates must be interpreted with caution, as for many variates differences in the number of tests showing significant departure from the null model are marginal. For example, it is interesting to note that the incidence of significant convergence among mean-adjusted distributions of the correlated variates PSU succulence and specific weight in the 0-1 m guild was not high enough to be deemed significant overall (Table 10.1), whereas these variates showed overall significance in the other two guilds (Tables 10.2, 10.3) and across whole communities (Table 8.2). This result could be taken to imply that partitioning among species of resource gradients with which these variates might be correlated (for example, the vertical light gradient; Section 9.4) might be less pronounced in the ground stratum of some *Nothofagus*-dominated communities, than closer to the canopy. However, the proportions of independent tests showing significant convergence in these variates are similar for all three guilds; for example, for PSU succulence in the absence of abundance weighting, 2 (of 16), 2 (of 14), and 3 (of 15) independent comparisons showed significant convergence for the 0-1, 1-5 and >5 m guilds, respectively.

The relatively small number of tests that revealed significant convergence in the >5 m guild could be interpreted as evidence that interactions, such as competition, among the species (mainly trees) occurring from 5 m above ground level to the upper canopy are less intense than in the lower strata, resulting in weaker assembly rules, and a lower incidence of significant convergence between communities. However, the number of comparisons of texture distributions showing divergence is also lower than for other guilds. This is difficult to explain ecologically, since environmental differences expected to produce divergence would presumably apply equally in the upper and lower strata. It is therefore more likely that the low overall incidence of departure from the null model in the >5 m guild is related to the structure of the data in which patterns are being sought.

Guilds generally contain fewer species than whole communities. In the present study, the number of species available for randomisation under the null model is generally highest when whole communities are compared, is lower for the 0-1 m guild, lower still for the 1-5 m guild, and lowest, often by a factor of 2 or more, for the >5 m guild (Table 10.1). Under the null model, only species that do not occur in more than one of the communities being compared are randomised. This is to avoid bias due to the effects of common species on texture (see Section 6.2). The number of species randomised can affect the likelihood of detecting significant convergence. This is because it is whole texture distributions (for communities or guilds) that are expected to converge. Although character values for all species are taken into account in computing and comparing texture distributions (with the test statistics $\hat{D}_T$ and $\hat{D}'_T$), only the subset of species that are randomised can contribute to departure of the observed pattern from the null model. The randomised species comprise a sample from the population of species whose attributes make up the texture of the communities being compared. The smaller the sample, the poorer an estimate it will provide, on average, of the population it represents. This means that, where few species are available for randomisation, significant departure from the null model may not be demonstrable, even if the factors expected to produce it (assembly rules or environmental differences) apply. The low overall incidence of significant departure from the null model in both directions for the >5 m guild, may be a result, at least in part, of the generally low species numbers in this guild.

Guild versus community scale

Comparing the results of equivalent tests at the whole-community and guild scales, there is evidence that convergence not apparent at the whole-community level may sometimes be revealed within a particular guild. For example, mean-adjusted distributions of PSU succulence are convergent at all abundance weighting levels for the 1-5 m guild of the regional communities southern and central New Zealand (Fig. 10.6). Across all guilds, however, there is convergence at only one weighting level, abundance rank (Fig. 8.8b). Presumably the general non-convergence at the whole-community scale is due to an absence of significant convergence in

PSU succulence in the 0-1 m (Fig. 10.2) and >5 m (Fig. 10.10) guilds. Between the Tasmanian site T2 Anne and New Zealand site ZN1 Ohakune there is convergence in distributions of PSU nitrogen (weighting by the square root of photosynthetic biomass) in the 0-1 m guild (Fig. 10.4b), in support fraction (abundance rank) in the 1-5 m guild (Fig. 10.8b), and in PSU area (biomass) in the >5 m guild (Fig. 10.12b). None of these variates shows significant convergence (using any weighting factor) when the whole communities are compared (Fig. 7.15b).

On the other hand, convergence was sometimes detected at the whole community level, but not in any individual guild. For example, community-wide distributions of PSU succulence are convergent overall among the four landmasses, Tasmania, Australia, New Zealand and South America, when species are weighted by their photosynthetic biomass or its square root (Fig. 7.5a). Comparing the same communities within each of the three guilds, there is no significant convergence in PSU succulence (Figs. 10.1a, 10.5a, 10.9a). Similarly, convergence at the whole-community level in distributions of PSU lobation between the Tasmanian site T1 Balfour and Australian site A2 Cascades (Fig. 7.15a) was not detected in any individual guild, although trends were in the same direction (Figs. 10.4a, 10.8a, 10.12a). The observation of significant patterns at the scale of the whole community but not in individual guilds can be explained by the effects of differences in the numbers of species sampled at the two scales, as discussed above.

Over all tests, patterns of significant departure from null expectation are rather similar within guilds (Tables 10.1-10.3) to those obtained in comparisons of whole communities in Chapters 7 and 8 (Tables 7.2, 8.2). Both divergence of texture distributions and convergence of mean-adjusted distributions occur most consistently in the variates PSU area, succulence, nitrogen content, phosphorus content, total chlorophyll and chlorophyll *a/b* ratio. The total incidence of significant convergence among mean-adjusted distributions in the 0-1 m and 1-5 m guilds is similar to that observed for whole communities in Chapter 8. For the >5 m guild, somewhat less convergence was detected. In the 1-5 m guild the incidence of convergence was significant overall for three variates — support fraction, species height and PSU nitrogen content — for which the incidence of convergence in comparisons of whole communities was not significant.

In summary, tests seeking community-level convergence at the guild scale have revealed some patterns not evident at the scale of the whole community. However, the total incidence of convergence was not markedly higher for any guild than in comparisons of whole communities. Significant convergence was detected in each of the three guilds, suggesting that assembly rules may apply at all levels in the vertical forest structure, at least for some of the communities sampled. Where this is the case, no advantage would be expected from subdividing communities into guilds.

THE PRESENT STUDY IN THE CONTEXT OF PREVIOUS WORK

The concept of the guild in ecology is often (incorrectly[3]) attributed to Root (1967), whose guilds of birds were species using 'similar resources in a similar way.' The applicability of this definition to guilds of plants has been questioned, in part because it is difficult to identify resources uniquely utilised by particular groups of plants (Wilson 1989; Simberloff & Dayan 1991; Aarssen 1992). Pianka (1980) predicted that guilds would represent foci for interspecific interactions; that is, that guild associates would interact with one another more than with species from other guilds. This criterion was used as a basis for delineating the guilds in the present chapter. Each of the three guilds examined comprised species whose primary above-ground function (capture and assimilation of radiant energy through photosynthesis) was carried out in the same zone in the vertical forest structure. It was anticipated that interspecific interactions might be more intense within one or more of these guilds, than in the entire vascular community, resulting in stronger community structure, and a greater degree of community-level convergence.

Focusing on guilds rather than whole communities is a common practice in community studies, and may be motivated, as in the present study, by the assumption that community structure would be stronger within guilds (Hawkins & MacMahon 1989; Simberloff & Dayan 1991). However, few studies have tested this assumption by examining community structure at both the guild and community scales. Bycroft *et al.* (1994) sought niche limitation and guild proportionality within a *Nothofagus*-dominated community in New Zealand. Niche limitation, greater constancy in the number of species represented in adjacent quadrats than expected under a null model of random migration (Wilson *et al.* 1987), could not be demonstrated, indicating weak structure at the whole-community scale. However, guild proportionality, an expected outcome of niche limitation at the scale of individual guilds, was detected in the herb guild, one of six sinusiae examined. Using a comparable approach, Wilson *et al.* (1995) demonstrated a similar pattern in another New Zealand *Nothofagus*-dominated forest. Other studies have detected proportionality in some guilds but not others (Wilson & Roxburgh 1994), or in none of the guilds examined (Wilson 1989). In the present study, convergence in texture has been sought as evidence of community structure. A significant incidence of convergence has been detected for several texture variates both at the community scale (Chapter 8) and in each of the three guilds examined.

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[3]Root (1967) cited Schimper (1903) whose guilds (*Genossenschaften*) were functional types of plants utilising other organisms for sustenance or support.

CONCLUSIONS

Tests seeking texture convergence within guilds revealed similar patterns of departure from the null model to those obtained in Chapters 7 and 8, where comparisons were done at the whole community scale. Although it was anticipated that community structure, and therefore texture convergence, might be stronger within guilds than at the level of the whole community, there is little evidence to support this suggestion for the three guilds examined in this chapter. In a small proportion of individual comparisons, however, significant convergence was detected in one or more guilds but not at the whole-community scale. It is possible that a minor tendency for community structure to be stronger within guilds is negated by the lower effective statistical power of guild-level tests resulting from the reduced number of species that can be randomised under the null model in guild, as opposed to whole-community, comparisons.