11. Character overdispersion as evidence for assembly rules in *Nothofagus*-dominated communities

11.1 Introduction

Assembly rules represent the integrated effects of all types of species interaction on community structure (Diamond 1975; Drake 1990; Wilson 1991). Certain types of interaction, particularly competition, would tend to impose a limiting similarity on the species in a community by restricting the degree of niche overlap that is possible (MacArthur 1972b; Pianka 1976, 1980). By enforcing a degree of functional dissimilarity among species within an assemblage, such assembly rules would tend to result in niches, and correlated species characters, being more regularly spaced than would be expected if there were no such rules. Such a tendency towards regular spacing in the characters of potentially interacting species has been termed character overdispersion (Pianka 1980; Weiher & Keddy 1995a). One potential pattern that could result from overdispersion — texture convergence between communities — has already been sought in this study. Texture convergence may be expected if similar assembly rules apply in similar physical environments. While similarity in the physical environments of two communities would tend to produce broadly similar spectra of functional species characters (i.e. similar texture), restrictions on how dissimilar the characters of species in the same community may be, would accentuate the similarity — possible causing texture distributions in different communities to become more similar than would be expected if species characters could assort freely, i.e. at random (Smith *et al.* 1994; Wilson *et al.* 1994).

In previous chapters, texture convergence was sought within disjunct *Nothofagus*-dominated communities, to evaluate the hypothesis that similar assembly rules apply in different communities, producing overdispersion in their texture distributions and, in turn, convergence. Significant convergence was detected between some communities, primarily in the shapes of texture distributions, disregarding their means (Chapters 8-10). However, the predominant pattern was one of non-convergence, suggesting that assembly rules (of the kind discussed above) are absent or weak in their effects on community structure, that they operate in only some communities, or that texture differences resulting from environmental or historical differences between communities are too pronounced for convergence to be detectable, even if assembly rules do apply.

To determine whether community texture has been influenced by assembly rules, an alternative approach would be to seek character overdispersion directly; that is, to ask whether the species within a community are dispersed along character axes more regularly than would be expected if there were no constraints on how dissimilar species must be to permit coexistence. Because this approach addresses structure at the level of the individual assemblage (community or guild), no assumptions as to the environment of the assemblage must be met. This represents an advantage over tests for community-level convergence, which depend on the assumption that the assemblages under investigation are closely matched in their environments (although the test for convergence in mean-adjusted texture distributions, developed in Chapter 8, overcomes this requirement to a limited extent).

Character overdispersion has been sought as evidence for competition-mediated character displacement in the past, both within animal (e.g. MacArthur 1971; Brown 1975; Simberloff & Boecklen 1981) and plant guilds (e.g. Snow 1965; Stiles 1977, 1979; Pleasants 1980; Armbruster *et al.* 1994). A difficulty with many such studies, however, has been in the choice of an appropriate null model and in the methods used to establish statistically significant departure from it (Tonkyn & Cole 1986; Pleasants 1990, 1994; Arita 1993). In the present chapter, character overdispersion in *Nothofagus*-dominated communities, and guilds within these communities, is sought by comparing patterns of spacing between species along character axes to expectation under a null model in which characters are drawn at random from a distribution approximating that of the observed data. If values are determined randomly, the differences between them will tend to be more variable than if there are restrictions on how similar values can be. The variance of these differences is thus a suitable index of overdispersion: here a low observed variance in the spacing between species values along character (texture) axes is interpreted as evidence for overdispersion, and therefore, for assembly rules limiting the co-occurrence of species whose characters are too similar. A kernel estimation method (Silverman 1981; Efron & Tibshirani 1993; Manly 1995b) is used to obtain a null sampling distribution that may approximate the underlying distribution from which species values are drawn in nature. This represents an advancement on previous studies of competitive displacement that have commonly drawn null species values from the biologically meaningless uniform distribution (Tonkyn & Cole 1986).

11.2 Methods

TEXTURE DATA

Analysis was based on texture data comprising species values for the 12 characters described in Section 2.3.5. The variate species height, included in the analyses of Chapters 6-10, was not used in the present Chapter. This was because of its semi-categorical nature, which would lead to the artifact of distributions being found `clustered' relative to the null model, using the analysis described below. Some analyses were also performed using seven texture factors (F1-F7) derived from ‘raw’ texture variate data by multivariate analysis, in Chapter 9.

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

ANALYSIS

Overdispersion in species character values within an assemblage was sought using smoothed bootstrap resampling tests, comparing the spacing of species values in the observed assemblage to spacing in artificial assemblages generated under a null model.

The null model

An appropriate null model will incorporate all features of the observed data not related to the hypothesis (or hypotheses) being tested. This is to ensure that statistically significant departure from the null model in a particular direction can be uniquely interpreted as support for one of these hypotheses (Tokeshi 1986; Wilson 1995). The principal hypothesis here is that species character values will be more regularly spaced than expected in the absence of assembly rules. The physical environment at a site would be expected to determine what character values the species present may have to establish and function successfully. In the absence of assembly rules, however, no restrictions would be expected on how similar sympatric species may be. The underlying distribution of character values in nature is unlikely to be uniform, but would reflect a variety of environmental, functional and phylogenetic influences, unrelated to assembly rules (Tonkyn & Cole 1986). In order to avoid spurious rejection of the null hypothesis due to trends caused by these factors, such trends should be taken into account by the null model. This means that the null model should resample from this underlying distribution, or as close an approximation of it as can be achieved. Manly (1995b) has recommended the use of a combination of smoothed bootstrap resampling and kernel density estimation to obtain null model values from a continuous distribution based on that of the observed data.

A kernel density estimate is a continuous probability density function built by summation of n Gaussian normal density curves, each with its mode at one of the n values comprising the data set whose distribution is being modelled (Silverman 1981; Efron & Tibshirani 1993). The shape of the kernel density curve approximates that of a relative frequency histogram of the data. The standard deviation, h, of each component normal curve is known as the ‘window size’ and determines the smoothness of the kernel estimate (Fig. 11.1). A null model was defined, in which character values were drawn at random from a kernel density estimate of the distribution of the observed data.

Given species values $x_{T,i}$ for a character (texture variate) T from an assemblages consisting of n species or entities, null data sets were generated by drawing n random values from a kernel density estimate of the distribution of $x_{T,i}$ values. Following Efron & Tibshirani (1993), the variance of the kernel estimate was adjusted to be equal that of the observed data. Random (smoothed bootstrap) values $x'_{T,i}$ from the kernel density function were thus given by:

$$x'_{T,i} = X_T + \frac{x_{T,i} - X_T + h\rho}{\sqrt{1 + h^2 / \sigma_T^{\,2}}}$$

where X_T is the mean of texture variate T, i.e.

$$X_T = \frac{\sum_{i=1}^{n} x_{T,i}}{n};$$

σ_T is the standard deviation of variate T, i.e.

$$\sigma_T = \sqrt{\frac{\sum_{i=1}^{n} \left(x_{T,i} - X_T \right)^2}{n}}$$

and ρ is a random value from the standard normal distribution. Transformed (Section 2.3.5; Table 2.1) species character values $x_{T,i}$ were used. To examine the effect of the window size h on the outcome of the bootstrap tests, complete analyses, as described below, were carried out for several communities with h set to each of four proportions of the observed standard deviation of character values, as follows: $0.0625\sigma_T$; $0.125\sigma_T$; $0.25\sigma_T$ and $0.5\sigma_T$. The window size chosen was found to have hardly any effect on the outcome of the tests (i.e. on the values obtained for $R_{V,T}$ and P, see below). Therefore, only results obtained from tests carried out with $h=0.25\sigma_T$ are presented.

Bootstrap tests for over- or underdispersion

Tests employing the null model described above were carried out to search for evidence of character overdispersion in communities at the local, regional and landmass scales, and in each of the three height guilds, defined in Chapter 10, within each community. No test was performed for assemblages comprising fewer than three species or entities (assemblages excluded from analysis for this reason were the >5 m guild for ZS2 Walker and SA2 Gutierrez). For each community and guild, separate tests were carried with respect to each of the 12 texture variates. For whole communities only, overdispersion in each of the seven derived texture factors was also sought.

Tests were two-tailed; that is, significant departure from the null model was sought both in the direction of overdispersion (a low variance in the spacing between species values along character axes) and underdispersion (a high variance). Overdispersion corresponds to regularity in the spacing of species characters, and provides support for the underlying hypothesis that there are assembly rules which limit the co-occurrence of species with similar characters. Underdispersion corresponds to clustering of species characters and could be explained by convergence of species attributes about the same adaptive optima (Weiher & Keddy 1995) or by historically-based similarities in the characters of related species (Harvey & Pagel 1991). Although overdispersion is the pattern of primary interest in this study, both over- and underdispersion represent biologically meaningful alternatives to the null model, and a two-tailed test is therefore appropriate.

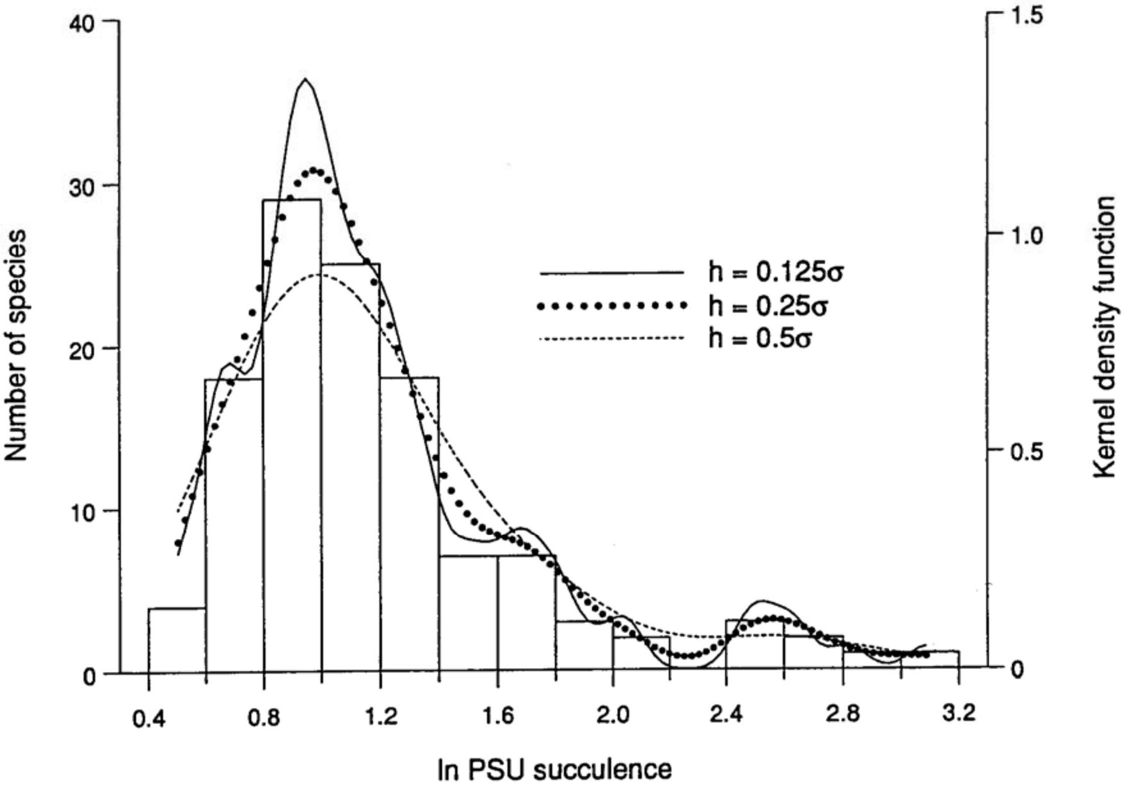

Fig. 11.1 Comparison of the frequency distribution of a texture variate (PSU succulence, New Zealand) with kernel density functions calculated from the texture data. Each curve was calculated with the window size *h*, which controls the smoothness of the kernel estimate, set to a different proportion of the sample standard deviation, σ. All results presented in this chapter are based on analyses with h=0.25σ.

To confirm that there was no bias towards rejection of the null hypothesis in bootstrap tests, two random variates were added to the set of character variates examined in each assemblage. Each species or entity in the assemblage was assigned a real random value from a uniform distribution in the range 0-1, and a random value from the normal distribution with mean 0.5 and standard deviation 1/6 (both random variates will tend to have the same mean and range). In the absence of bias, significant ($P<0.05$) over- or underdispersion should be detected in each random variate in approximately 5% of tests (2.5% in each direction), while the proportions of tests showing a tendency towards overdispersion ($R_{V,T}<1$; see below) and underdispersion ($R_{V,T}>1$) should be approximately the same. After many tests, the significances of departure from these expected patterns were examined using binomial tests (see below).

Pooled communities

To assemble data for regional communities comprising more than one site (e.g. southern New Zealand) and landmass communities (e.g. New Zealand), it was necessary to pool values from individual sites. This was done according to the protocol described in Section 6.2.

Comparison of observed with null assemblages

For a given texture variate (character) *T*, spacing of species values along character axes was characterised by the variance of differences in character values between adjacent species, V_T (Poole & Rathcke 1979):

$$V_T = \frac{\sum_{i=1}^{n-1} (z_{T,i} - Z_T)^2}{n-1}$$

where $z_{T,i}$ is the character value difference between adjacent species ranked in ascending order of their character values, i.e.

$$z_{T,i} = x_{T,i+1} - x_{T,i} \; ; \; x_{T,i+1} \geq x_{T,i} \text{ for } i=1, 2, ..., n-1$$

and Z_T is the mean of the $z_{T,\,i}$ values, i.e.

$$Z_T = \frac{\sum_{i=1}^{n-1} z_{T,i}}{n-1}$$

The value of V_T will be lowest when species characters are very regularly spaced, increasing as the spacing becomes increasingly random, while the highest values would apply if species were highly clustered in their character values.

For each test, 2000 null model simulations were performed, and the test statistic (V_T) calculated for each bootstrapped (null model) data set, as well as for the observed data. A low value of V_T for the observed data, relative to its mean value among bootstrapped data sets, would indicate that species characters in the observed assemblage are more regularly spaced than expected under the null model. This may be interpreted as a tendency towards overdispersion in texture variate *T*. Similarly, a high value of V_T would suggest that species characters in the observed are somewhat clustered, a tendency towards underdispersion. The strength of any tendency towards over- or underdispersion was quantified as the relative variance, $R_{V,T}$:

$$R_{V,T} = \frac{V_T \text{ (observed)}}{\sum V_T \text{ (null)} / 2000}$$

$R_{V,T}$ has a value less than 1 if there is a tendency towards overdispersion in the observed assemblage in terms of texture variate T. A value greater than 1 corresponds to a tendency towards underdispersion.

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

Binomial tests for overall significance

Binomial tests were applied to determine whether the number of tests yielding significant results was higher than would be expected on a random basis. The approach was to ask whether the proportion of a set of bootstrap tests revealing significant overdispersion ($R_{V,T}<1$) or underdispersion ($R_{V,T}>1$), was higher than would be expected by chance, given a 5% likelihood of type I error in each test.

For a binomial test to be valid, it must be applied to a set of independent observations (see Section 6.2). In previous chapters, which sought convergence or divergence among pairs or groups of communities, the ‘observations’ were results from a subset of comparisons which were independent (Fig. 6.1). In the present chapter, it is individual assemblages, not combinations of them, that are examined by each test. Independence among the assemblages is not guaranteed. Some regional and all landmass-scale communities are derived by pooling observations from individual study sites, and so are clearly not independent of them. Even among some individual sites, there may be shared texture variation inherited from common species pools. However, the assembly process itself will be independent between sites. Assembly rules leading to overdispersion may be based exclusively on ecological species sorting, operating at the local scale, or also on coevolutionary character displacement, which would be based on past ecological sorting, and would affect local community composition via the regional species pool (Section 1.5; Figs. 1.4, 1.5). If local-scale ecological species sorting is more important than coevolutionary character displacement as a basis for assembly rules applying at the local scale, overdispersion observed at different sites within a region or landmass may be largely independent statistically. For this reason, binomial tests for overall significance were applied to the results from tests examining character dispersion at individual sites and within guilds at individual sites, but not within regional or landmass scale communities whose data were pooled from several sites.

Separate binomial tests were applied to determine the overall significance of (significant) over- or underdispersion for each texture variate at the whole-community scale, and for each texture variate/height guild combination.

Binomial tests for overall trends

Overall trends in the largely non-significant results obtained in individual bootstrap tests were examined using the binomial distribution. To distinguish these binomial tests from tests for overall significance, described above, they are termed `tests for overall trends.' The approach was to ask whether the proportion of bootstrap tests whose results were in one direction (say, $R_{V,T}<1$[1]) differed significantly from the 50% expected in the absence of any systematic trends. A significant departure from chance expectation would imply the existence of a trend towards overdispersion (if $R_{V,T}<1$ in a majority of tests) or underdispersion (if $R_{V,T}>1$ in a majority of tests) among the test results examined, although the underlying mechanism may have been too weak to have produced significant results in all (or any) of the individual bootstrap tests.

Binomial tests for overall trends were applied to the results from tests examining character dispersion at individual sites, and within guilds at individual sites. To maximise the independence of the binomial `observations' (bootstrap tests) regional and landmass scale communities whose data were pooled from several sites were not included in the analyses. Separate tests were applied to the results obtained for each texture variate at the whole-community scale, and for each texture variate/guild combination.

Binomial frequencies both in tests for overall significance and tests for overall trends were calculated from the binomial expansion (Snedecor & Cochran 1967; computer program by J.B. Wilson).

Tests for bias in bootstrap tests

To confirm that the null model and bootstrap test algorithm did not lead to any bias towards rejection of the null hypothesis, binomial tests for overall significance and overall trends (as described above) were applied to results from bootstrap tests seeking dispersion patterns in the uniform and normal random `texture' variates (see above). Results from all 26 whole communities were used, since each community (even regional and landmass communities represented by pooled data for true texture variates) was assigned values for the random variate directly.

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[1] There were no tests in which $R_{V,T}$ was exactly equal to 1, i.e. where no tendency was detected either in the direction of over- or underdispersion. It is therefore exactly equivalent to ask whether the proportion of tests for which $R_{V,T}<1$, *or* for which $R_{V,T}>1$, differs from 50% expectation.

11.3 Results

VALIDITY OF THE NULL MODEL

Bootstrap tests performed on both uniform and normal random variates produced no evidence of bias (Table 11.1). No significant departure from the null model was observed in any of the 26 tests performed (corresponding to each local, regional and landmass-scale community). For both types of random variate, a slightly larger number of tests yielded high values of the relative variance (i.e. $R_{V,T}>1$, suggesting a tendency towards underdispersion) than low values ($R_{V,T}<1$). However, neither trend is significant according to binomial tests. There is therefore no evidence for bias in the null model.

Table 11.1 Incidences of departure from null expectation in bootstrap tests for over- and underdispersion in two variates pertaining to each of 26 communities (see text), containing random values drawn from uniform and normal distributions respectively. `Binomial *P*' shows the probability of obtaining, by chance alone, incidences of the number of tests showing a tendency towards overdispersion ($R_{V,T}<1$; see text) and of the number showing a tendency towards underdispersion ($R_{V,T}>1$) at least as unequal as those observed.

Number of tests showing pattern	Random variate	
	Uniform	Normal
Significant overdispersion	0	0
Significant underdispersion	0	0
Tendency towards overdispersion	10	12
Tendency towards underdispersion	16	14
Binomial *P*	0.327	0.845

PATTERNS WITHIN COMMUNITIES AND GUILDS

Communities

Landmass-scale communities Tasmania and Australia show no significant departure from the expectation that species are dispersed randomly in character space (Figs. 11.2a, b). For New Zealand, however, there is overdispersion in PSU succulence, specific weight and total chlorophyll, and in the texture factor (F1) most closely related to these variates (Fig. 11.2c). Species values for F3 (PSU phosphorus content, chlorophyll *a/b*) are also significantly overdispersed. It is notable that all texture variates except support fraction, and all factors except F6 (PSU lobation, inclination) have $R_{V,T}<1$ — a tendency towards overdispersion. For South

America, there is no significant overdispersion; however, all texture variates and factors except support fraction show a tendency in this direction (Fig. 11.2d).

Of the three communities in Tasmania, there is significant overdispersion only at T2 Anne, for PSU thickness and its corresponding texture factor, F4 (Figs. 11.3a-c). Australian sites A1 Lumeah and A2 Cascades show no significant departure from null expectation (Figs. 11.3d, e). For the pooled regional community southern New Zealand (ZS) there is overdispersion in PSU area (Fig. 11.3f); for central New Zealand (ZC), in PSU inclination (Fig. 11.3g); and for northern New Zealand (ZN), in PSU area. All three regions of New Zealand show a strong trend towards overdispersion, with only a minority of variates having $R_{V,T}>1$. This pattern reflects that observed for New Zealand overall (Fig. 11.2c). No significant departure from null expectation is evident for SC Chile or SA Argentina (Fig. 11.3i, j).

None of the southern New Zealand sites shows significant departure from the null model (Fig. 11.4a-c). However, there appears to be a weak overall trend towards overdispersion, most notably for ZS1 Ten Mile, for which a tendency towards underdispersion ($R_{V,T}>1$) was observed only for support fraction and F1 (PSU succulence, specific weight, total chlorophyll, species height). PSU inclination values are significantly overdispersed at ZC1 Craigs, and, with the exception of F5 (PSU nitrogen, phosphorus) all variates and factors show a tendency towards overdispersion (Fig. 11.4d). No such trend is apparent for the other central New Zealand site, ZC2 Station (Fig. 11.4e). An overall trend towards overdispersion is evident among the three northern New Zealand sites (Figs. 11.4f-h). However, significant overdispersion was detected in only two tests: in PSU area at ZN1 Ohakune (Fig. 11.4f), and in PSU area and F2 (PSU area, support fraction) at ZN2 Rotokura (Fig. 11.4g). Local-scale communities sampled in Chile (Figs. 11.4i, j) and Argentina (Figs. 11.4k, l) exhibit no significant character dispersion patterns.

Guilds

Detailed results from bootstrap tests applied at the guild scale are presented only for the four landmass-scale communities, and for a representative subset of communities at the regional and local scales.

No significant over- or underdispersion within guilds was detected for Tasmania (Fig. 11.5a) or Australia (Fig. 11.5b). For New Zealand, however, there is overdispersion in PSU area, succulence and total chlorophyll within the 0-1 m guild (Fig. 11.5c). This pattern is similar to that observed for the whole community (Fig. 11.2c). Species values for PSU nitrogen content are significantly underdispersed in the >5 m guild for South America, the only test showing a significant result in this direction in this study (Fig. 11.5d). For all the landmass communities, except Australia, variates tend to show non-significant overdispersion (or no clear trend) for the 0-1 m and 1-5 m guilds, but underdispersion in the >5 m guild.

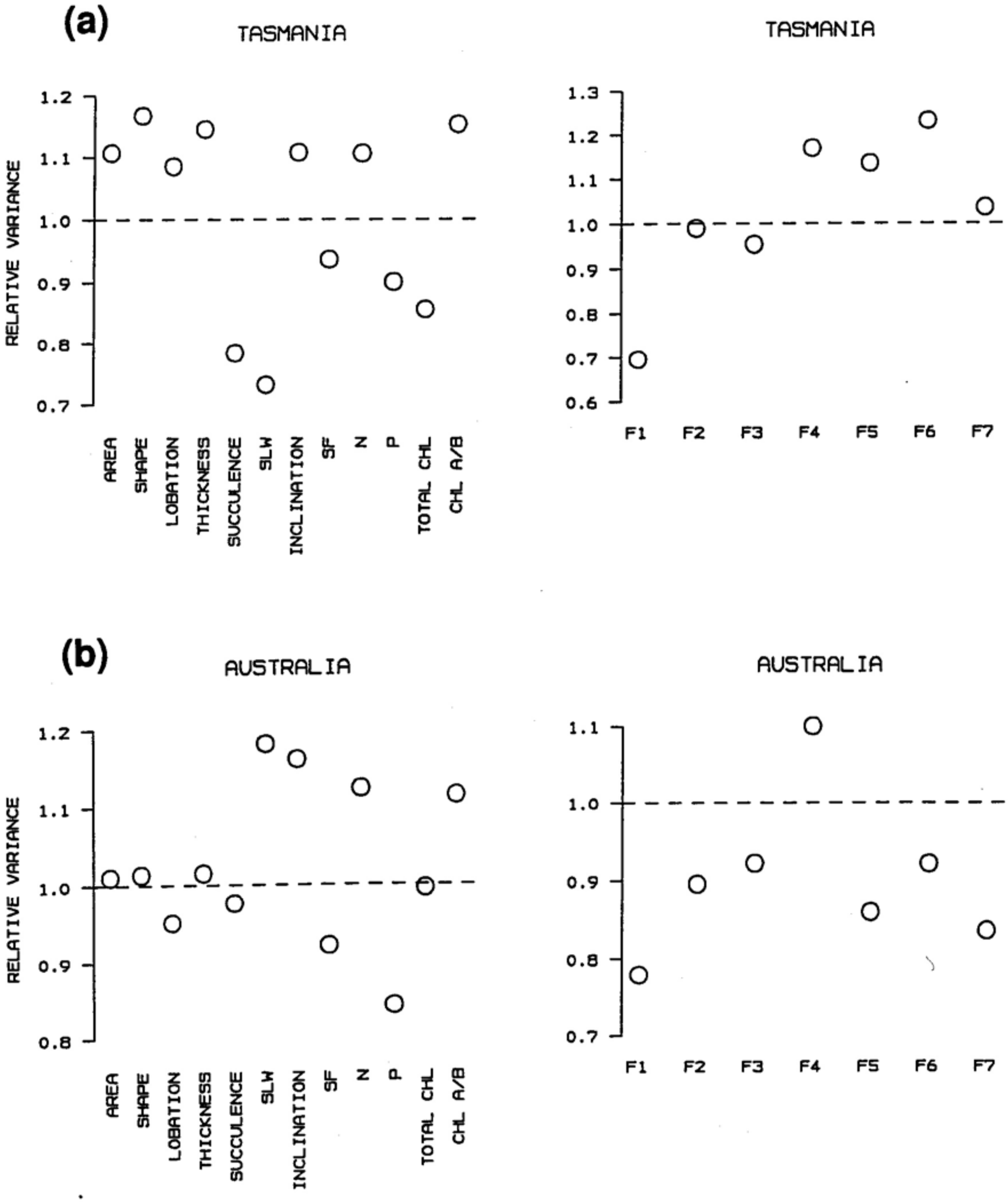
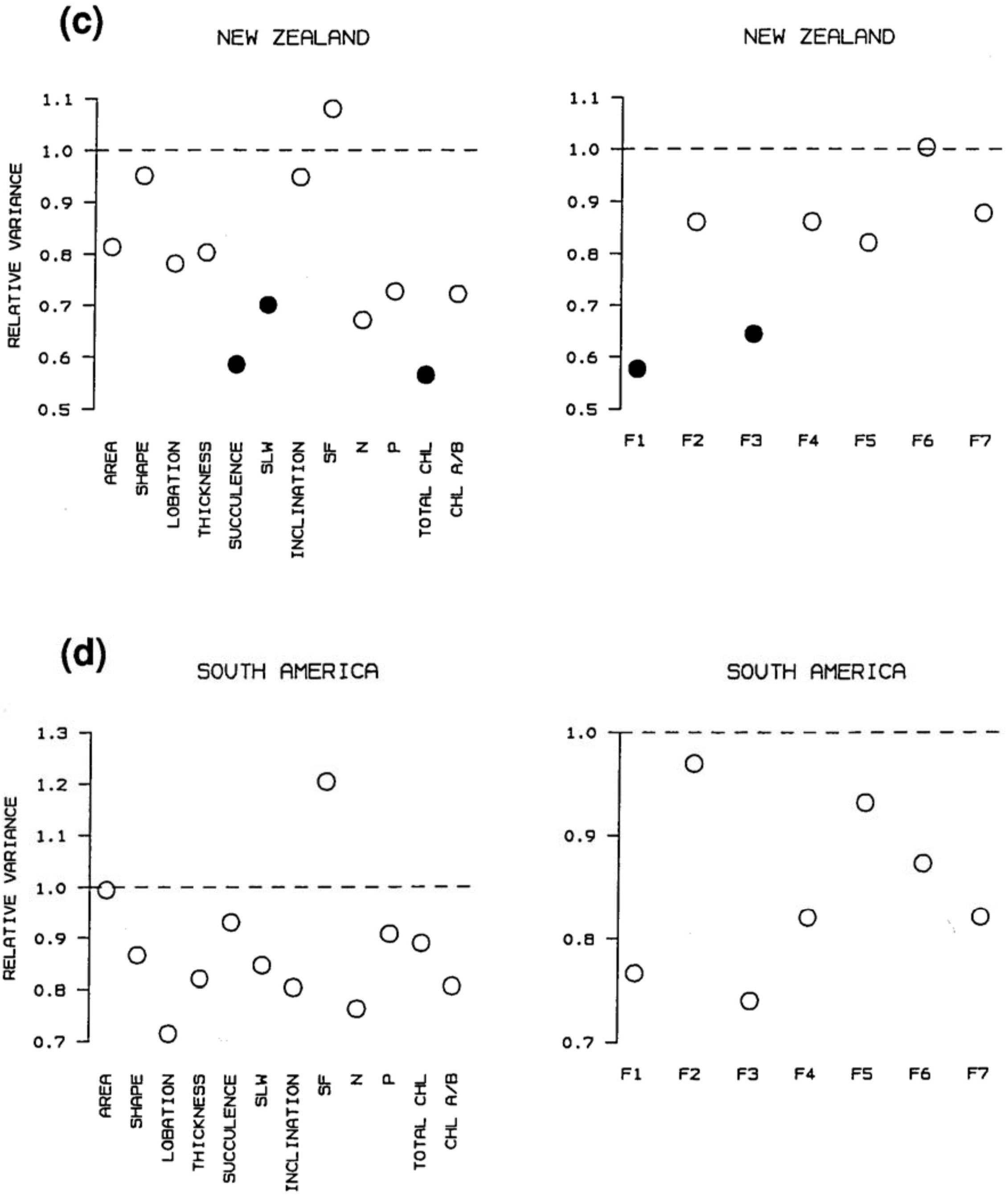


Fig. 11.2 Smoothed bootstrap tests for over- or underdispersion in texture variates and derived factors for landmass-scale *Nothofagus*-dominated communities **(a)** Tasmania (T), **(b)** Australia (A), **(c)** New Zealand (Z) and **(d)** South America (S). The relative variance $R_{V,T}$ is an index of the strength of overdispersion ($R_{V,T}<1$) or underdispersion ($R_{V,T}>1$) relative to expectation under a stochastic null model (see text). Broken lines indicate null model expectation, $R_{V,T}=1$. Filled symbols correspond to significant departure from the null model ($P<0.05$). Texture variates (abscissa, left hand graph) are based on PSU characters except SF (support fraction). Key: SLW=specific weight; N=nitrogen content; P=phosphorus content; TOTAL CHL=total chlorophyll content; CHL A/B=chlorophyll *a/b* ratio. Texture factors F1-F7 (right hand graph) are derived from texture variates by factor analysis (see text for full explanation).



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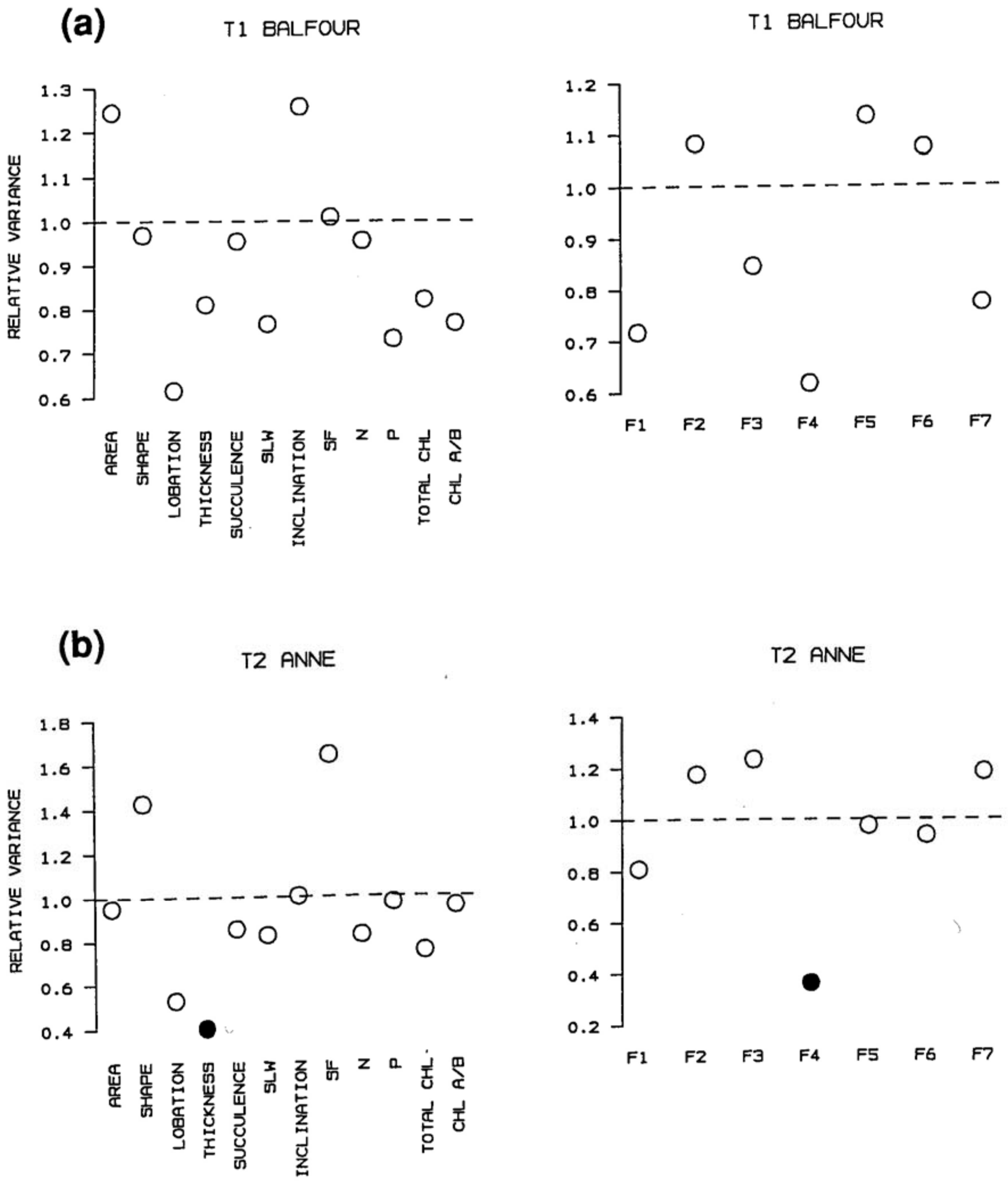
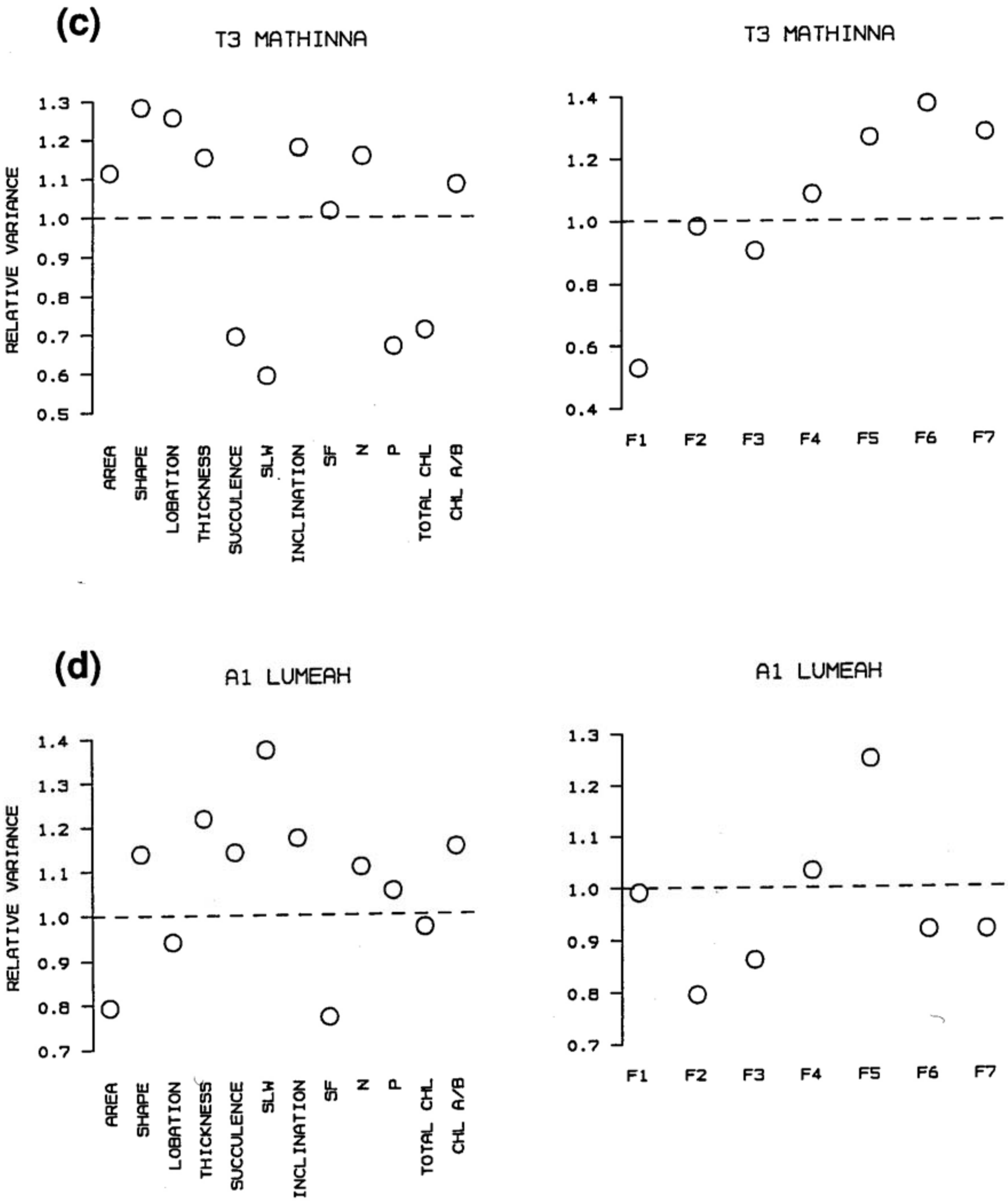


Fig. 11.3 Smoothed bootstrap tests for over- or underdispersion in texture variates and derived factors for regional-scale *Nothofagus*-dominated communities **(a)** T1 Balfour, **(b)** T2 Anne, **(c)** T3 Mathinna, **(d)** A1 Lumeah, **(e)** A2 Cascades, **(f)** southern New Zealand (ZS), **(g)** central New Zealand (ZC), **(h)** northern New Zealand (ZN), **(i)** Chile (SC) and **(j)** Argentina (SA). Format as for Fig. 11.2.



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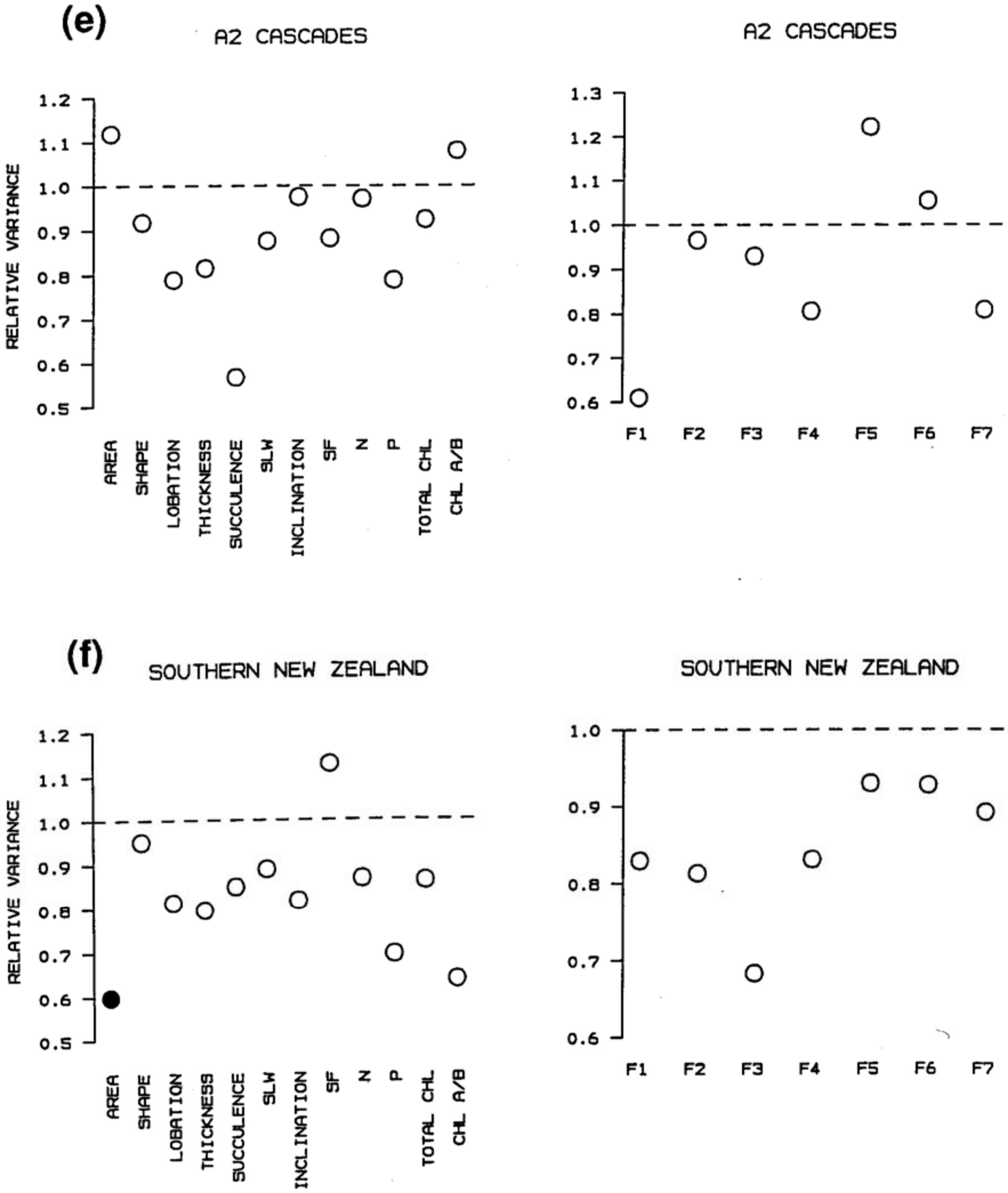

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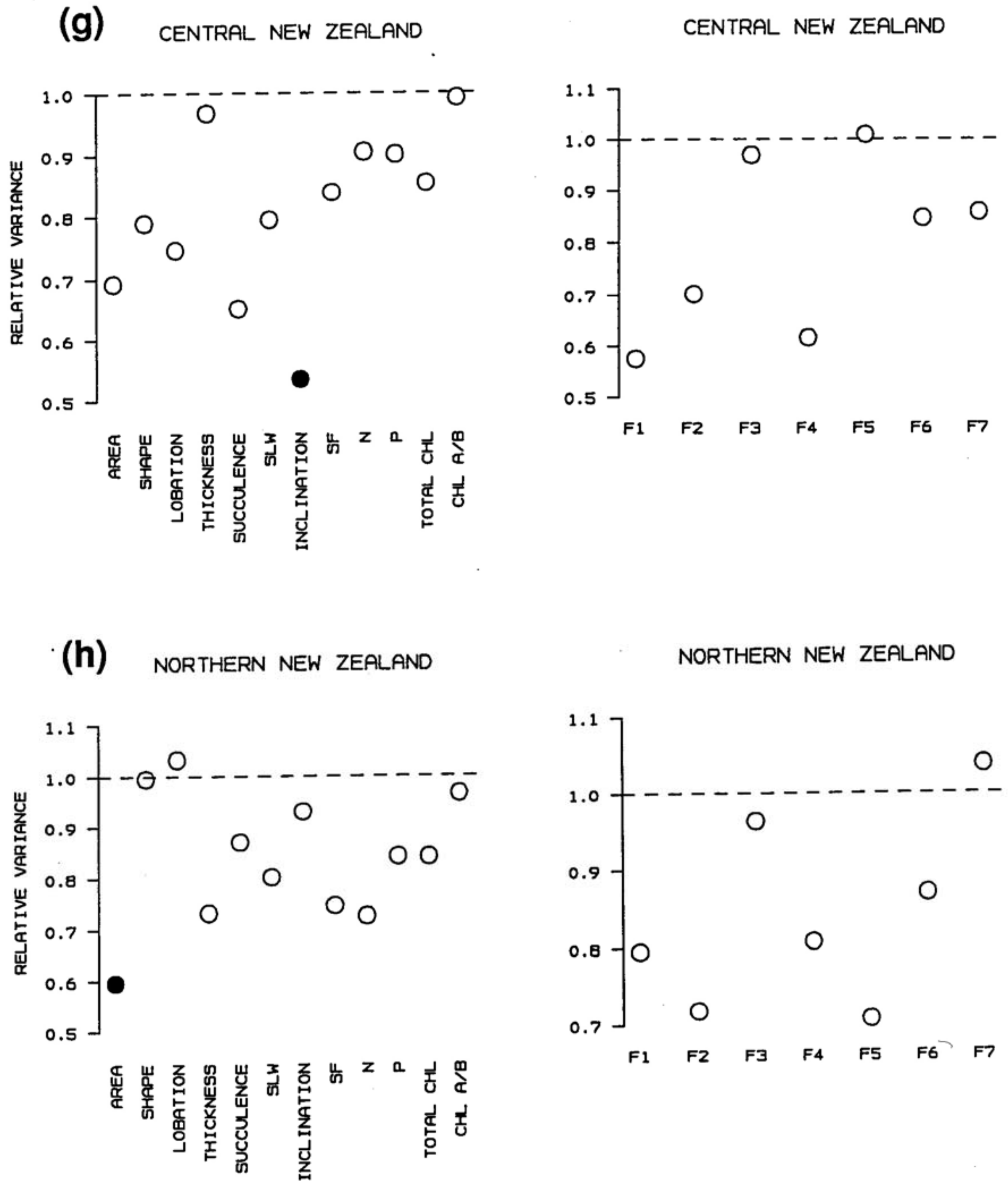

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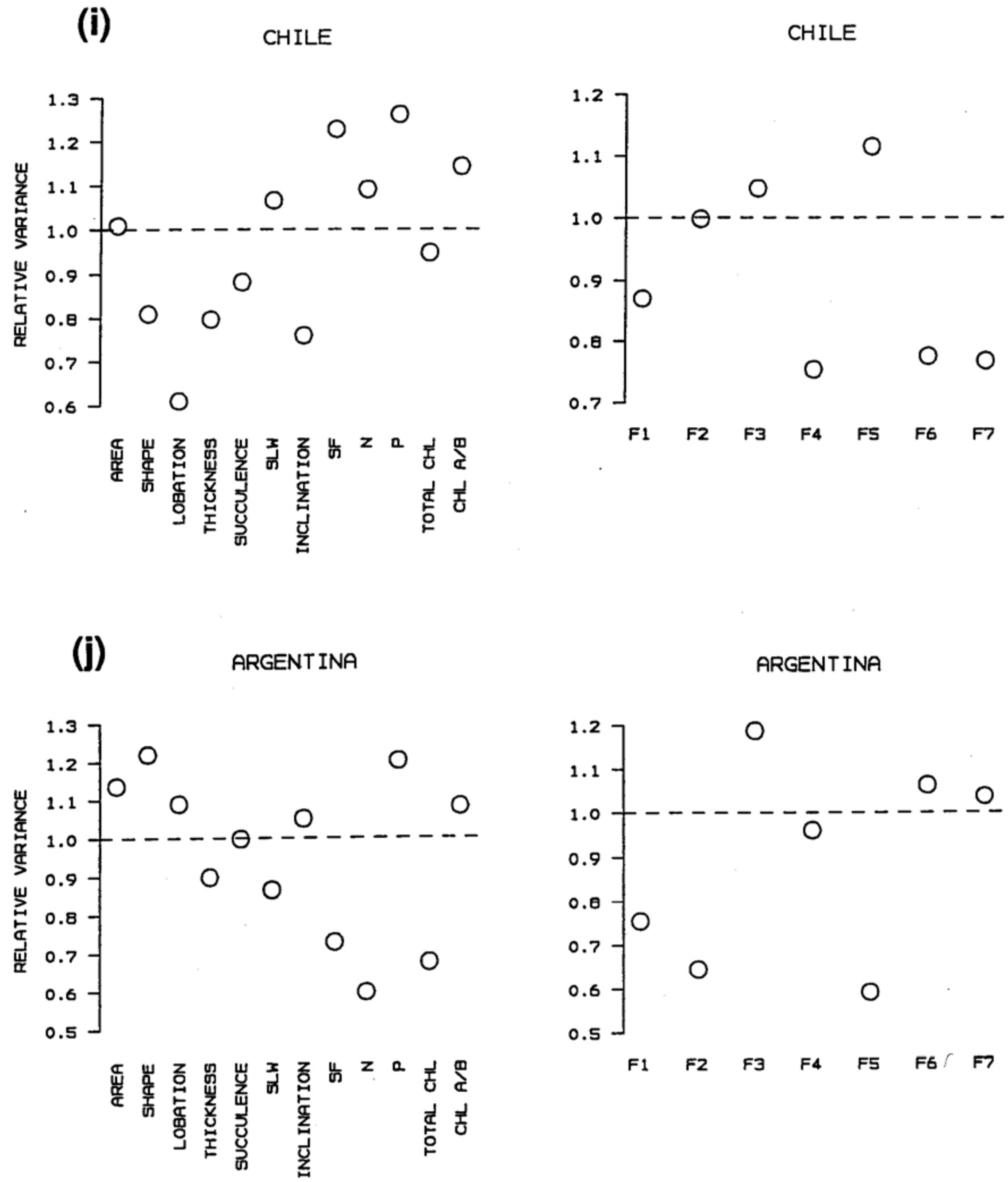

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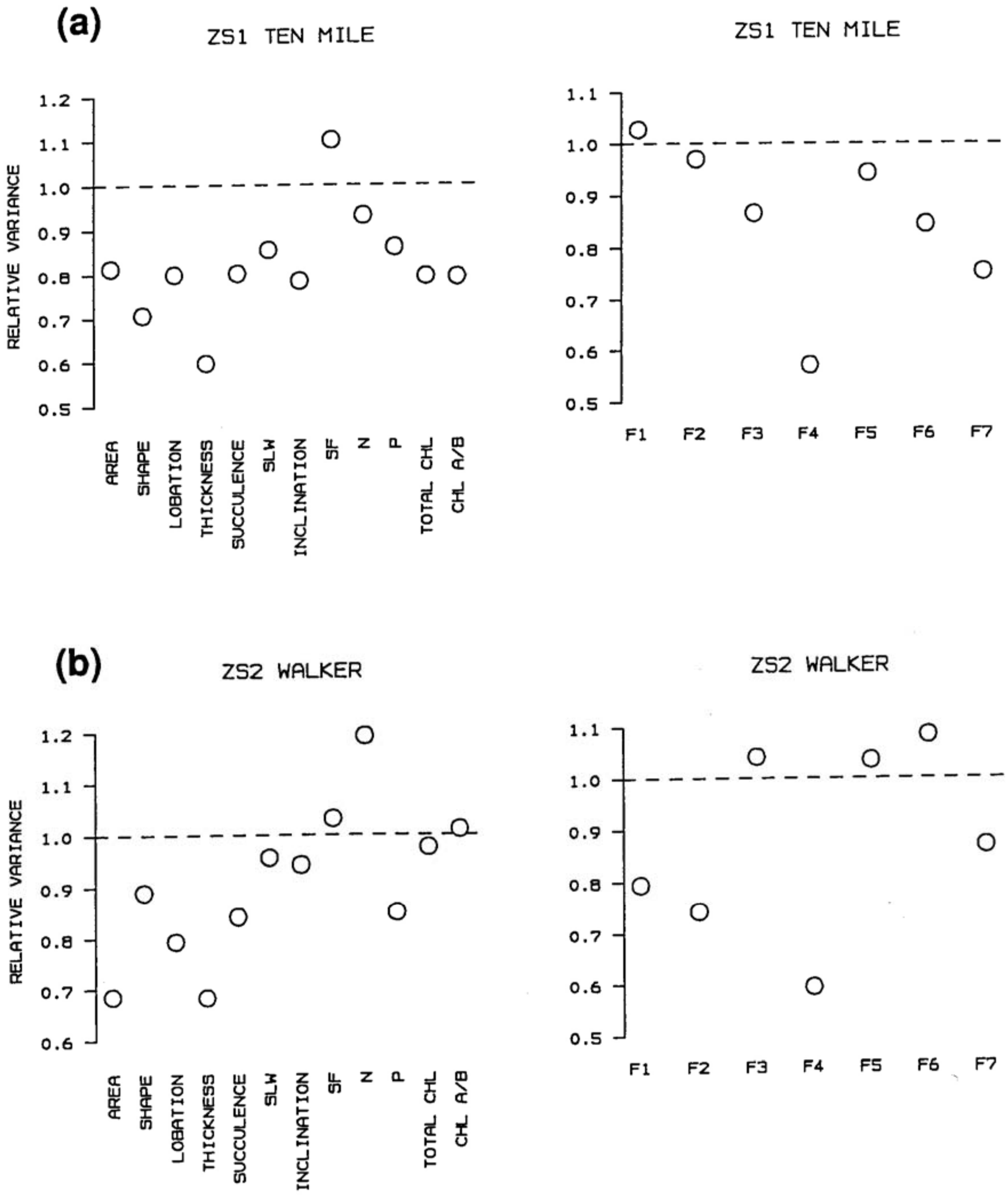
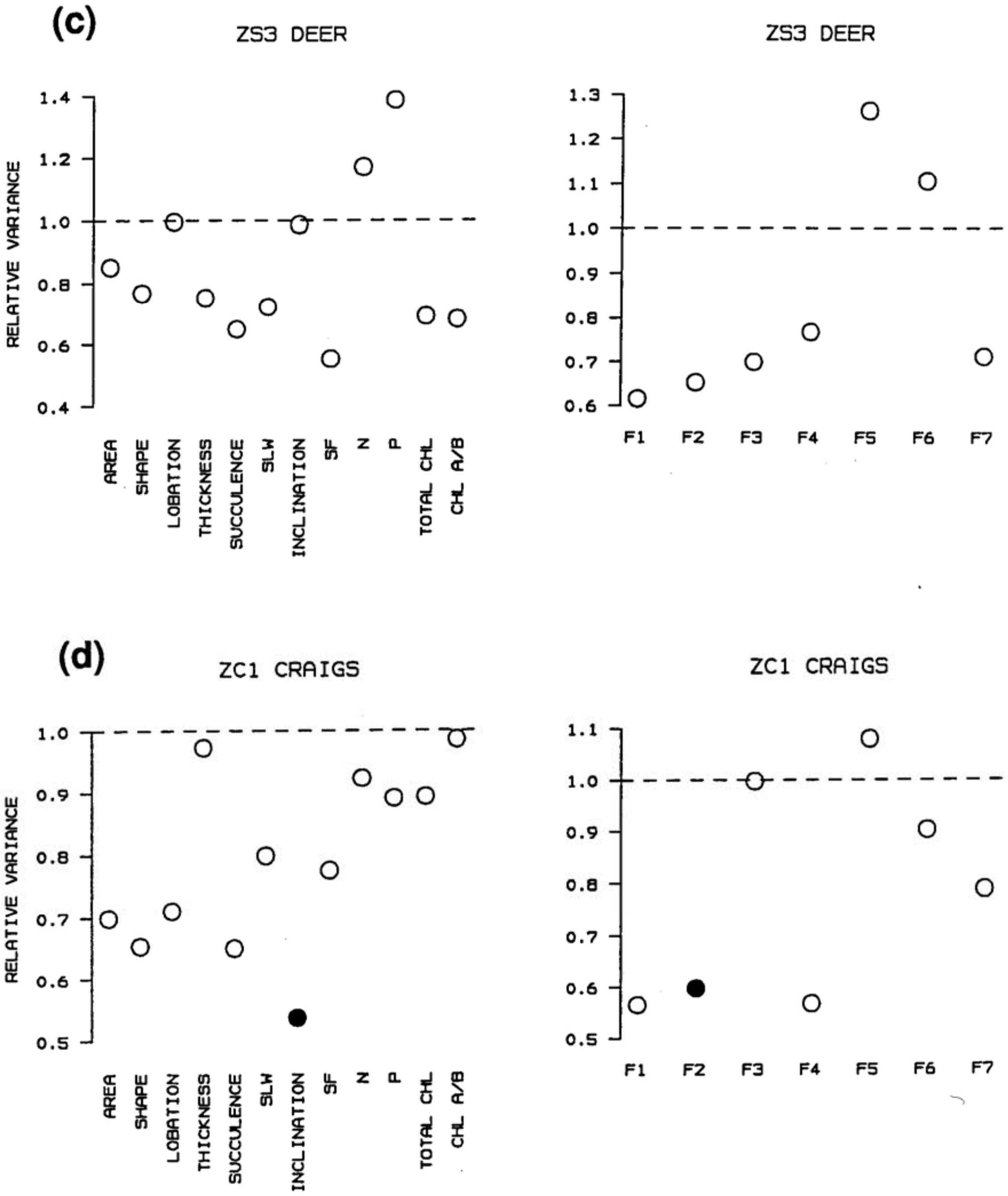


Fig. 11.4 Smoothed bootstrap tests for over- or underdispersion in texture variates and derived factors for local-scale *Nothofagus*-dominated communities **(a)** ZS1 Ten Mile, **(b)** ZS2 Walker, **(c)** ZS3 Deer, **(d)** ZC1 Craigs, **(e)** ZC2 Station, **(f)** ZN1 Ohakune, **(g)** ZN2 Rotokura, **(h)** ZN3 Clements, **(i)** SC1 Pelada, **(j)** SC2 Antillanca, **(k)** SA1 Quetrihué and **(l)** SA2 Gutierrez. Format as for Fig. 11.2.



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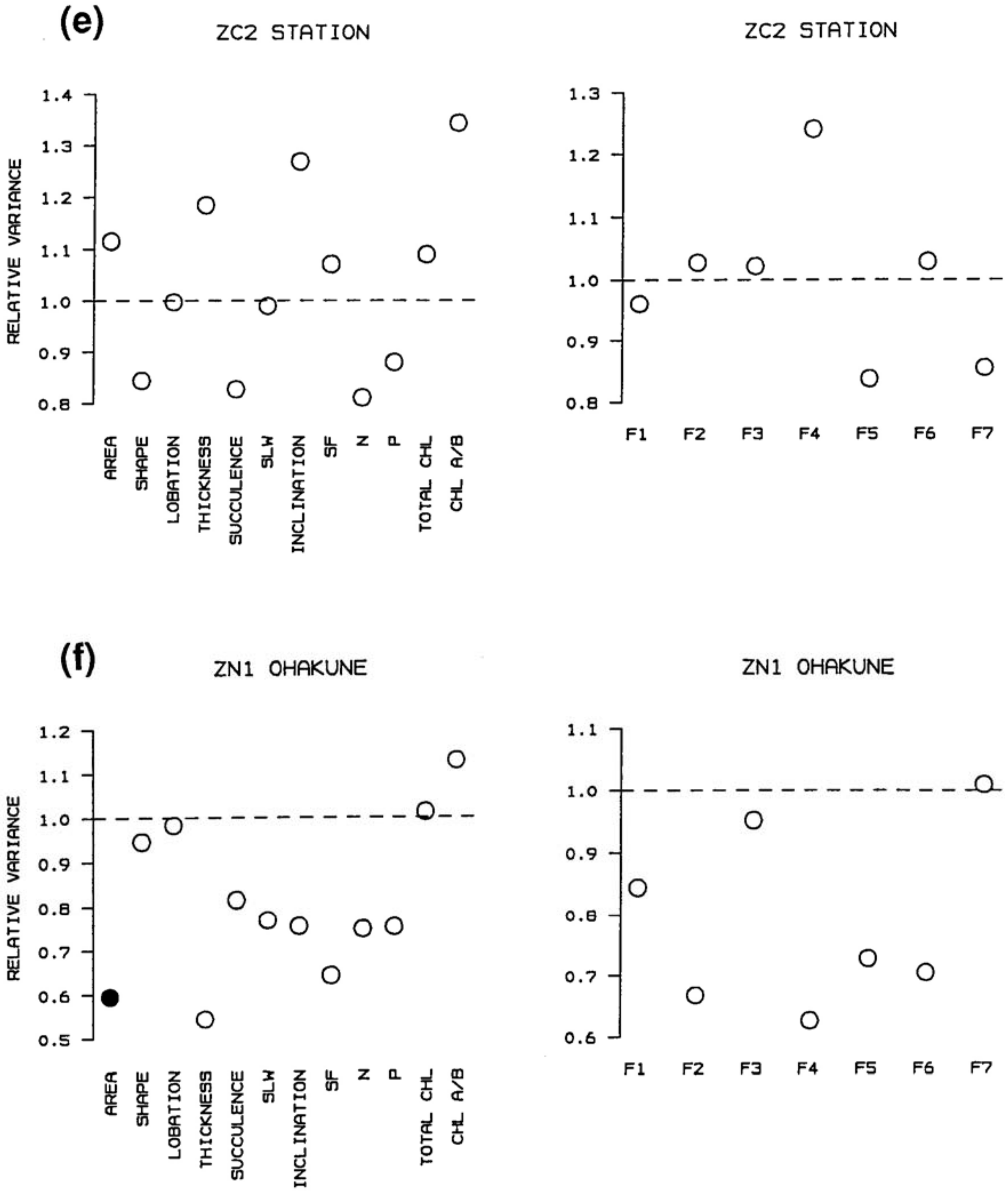

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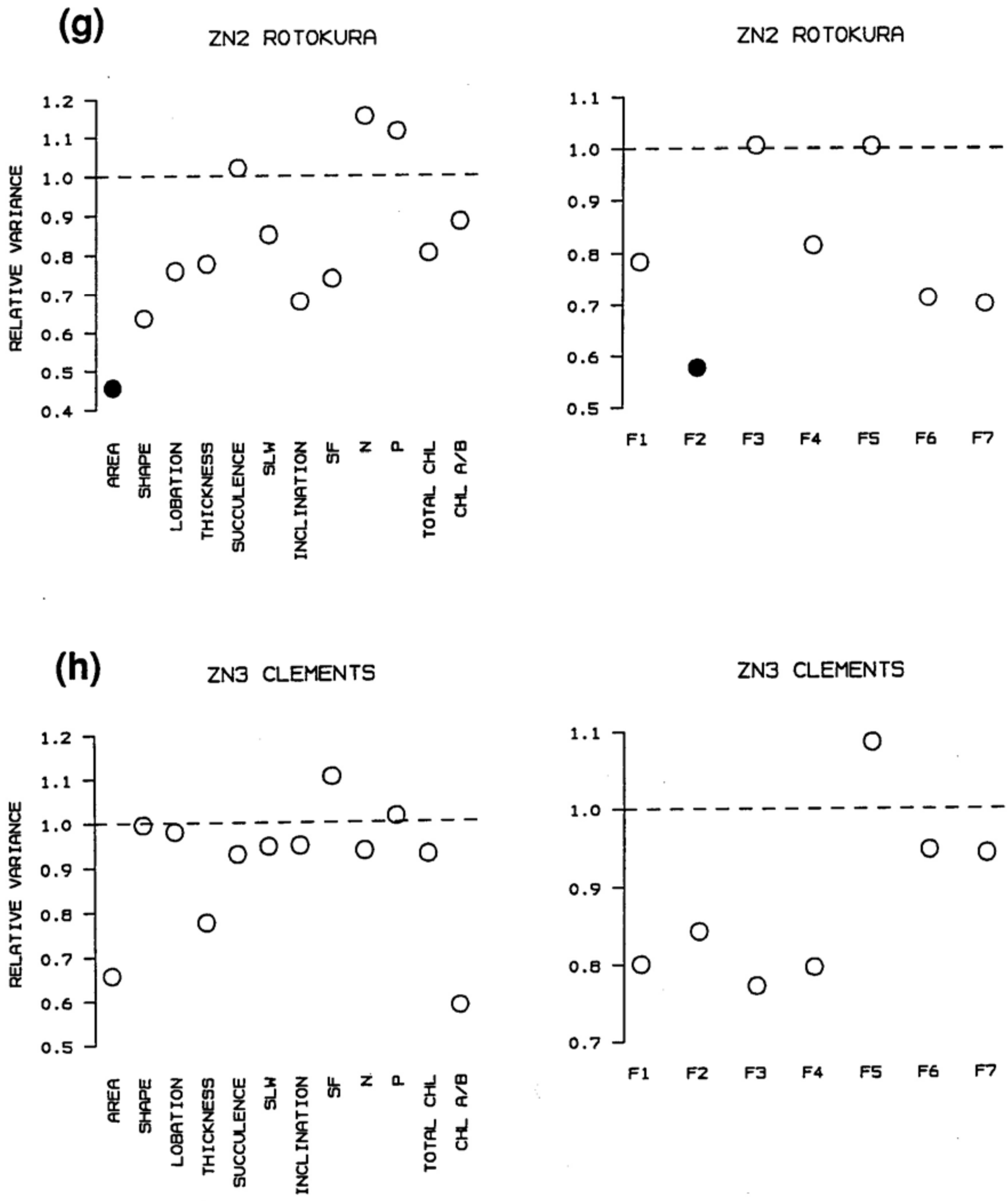

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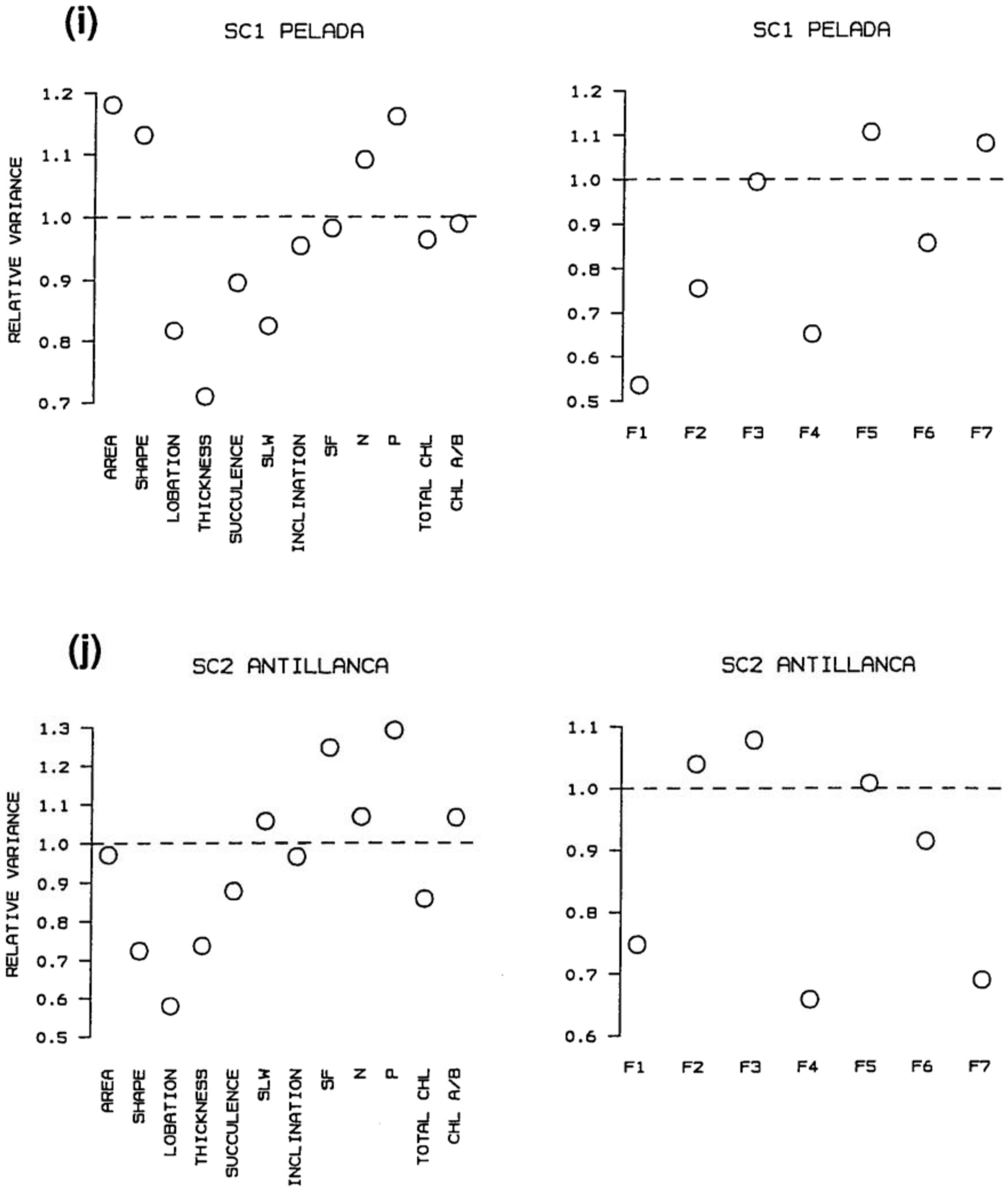

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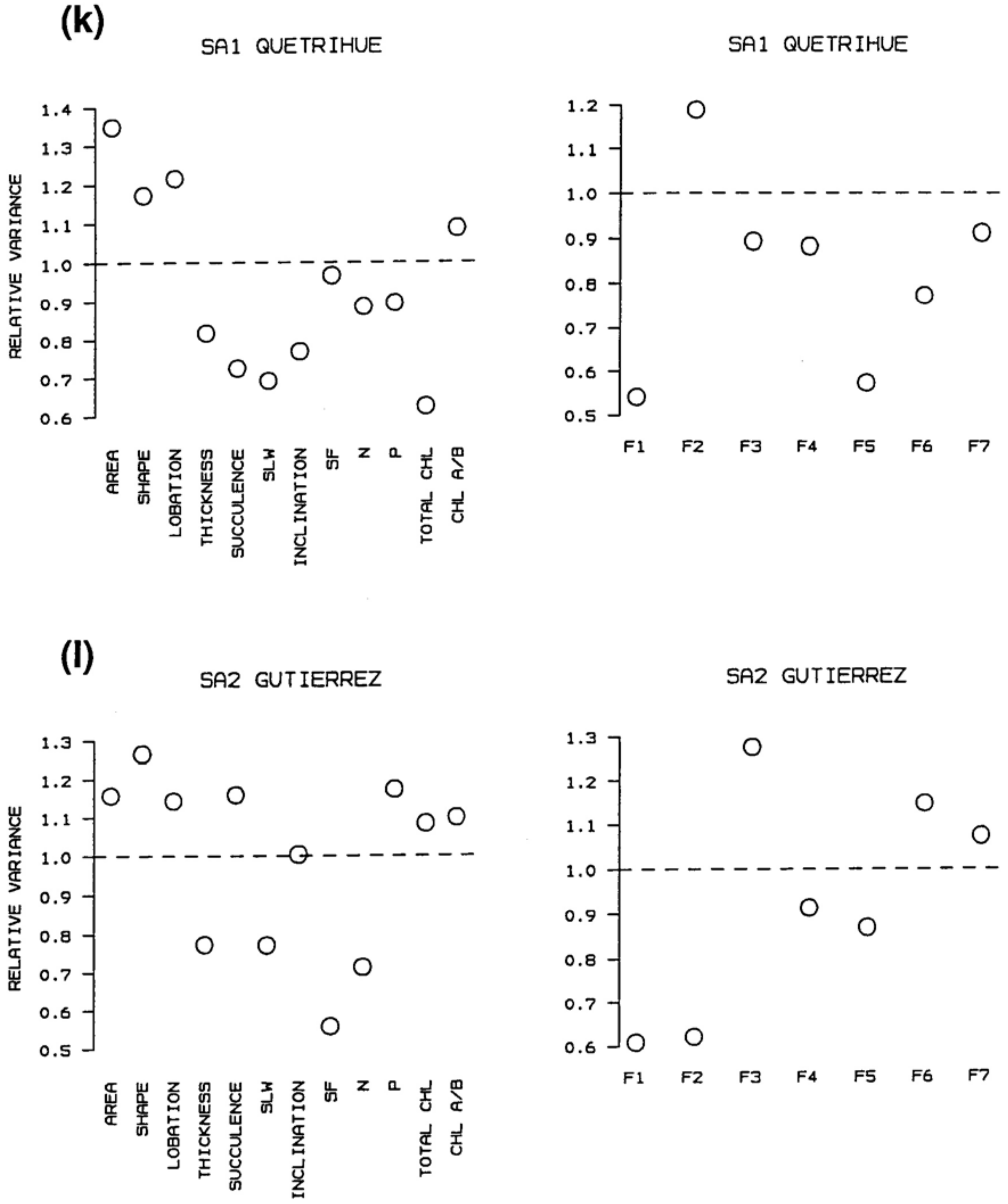

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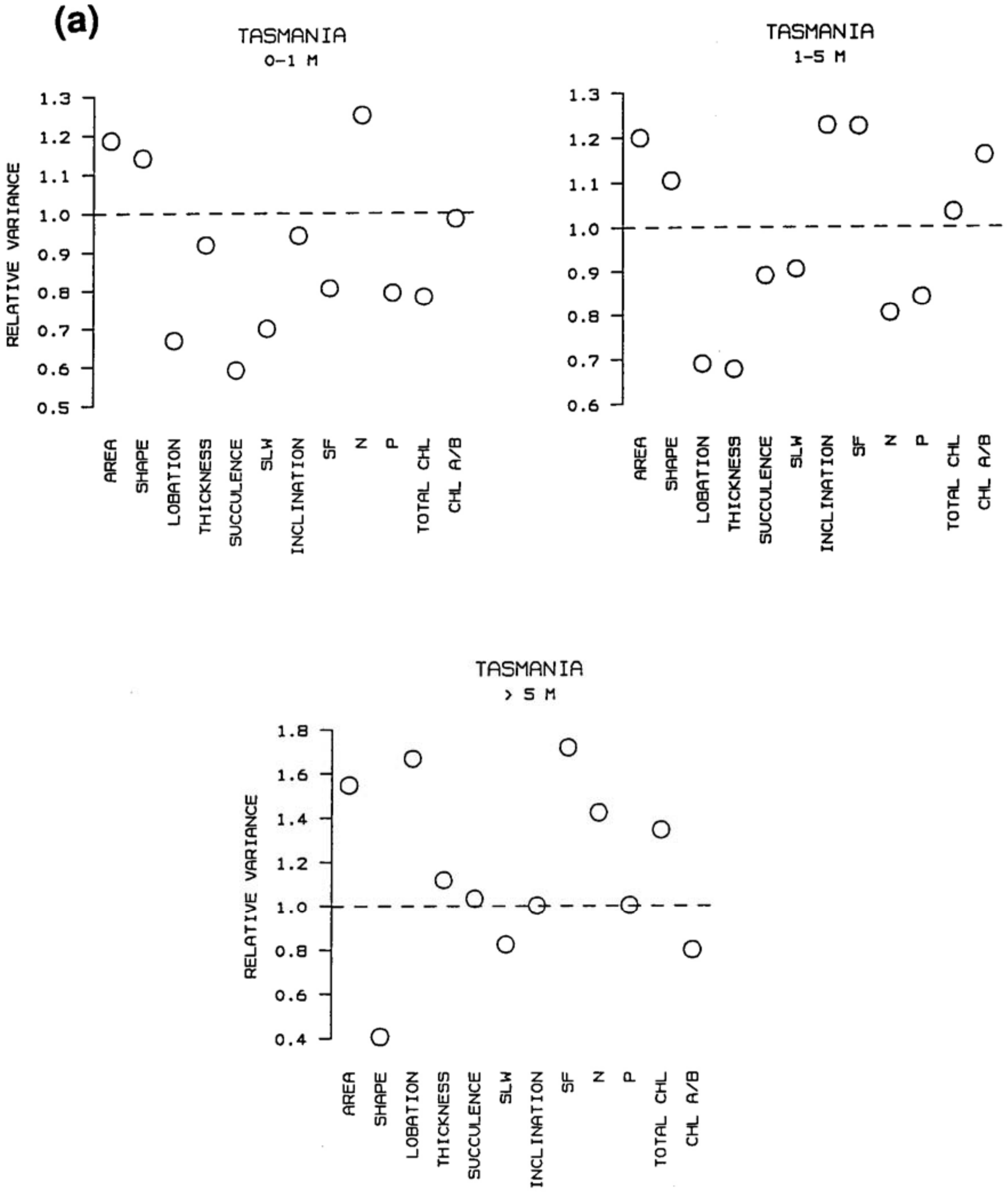

Fig. 11.5 Smoothed bootstrap tests for over- or underdispersion in texture variates in the 0-1 m, 1-5 m and >5 m guilds (see text) of landmass-scale *Nothofagus*-dominated communities **(a)** Tasmania (T), **(b)** Australia (A), **(c)** New Zealand (Z) and **(d)** South America (S). Format as for Fig. 11.2.

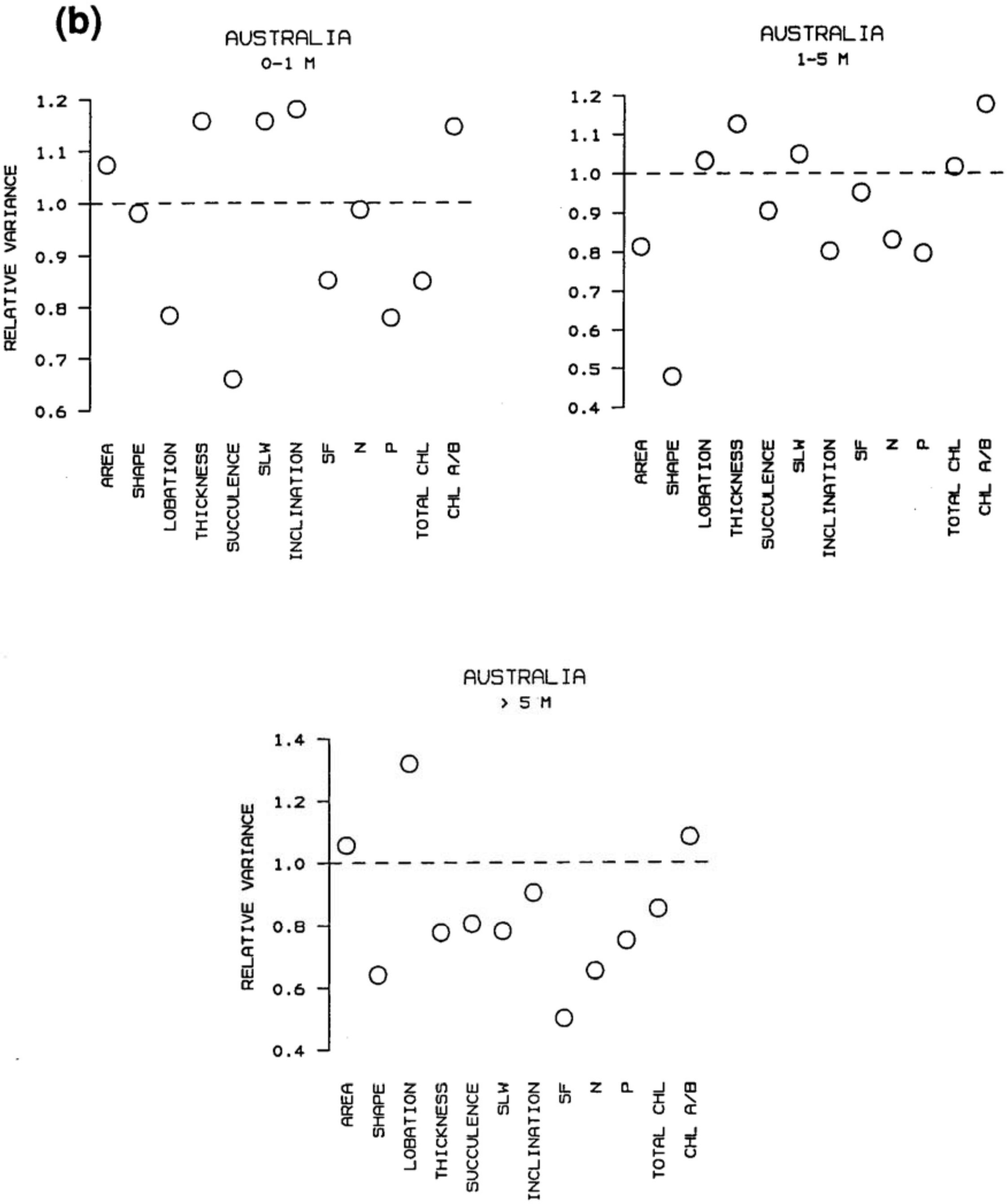

Fig. 11.5 (continued)

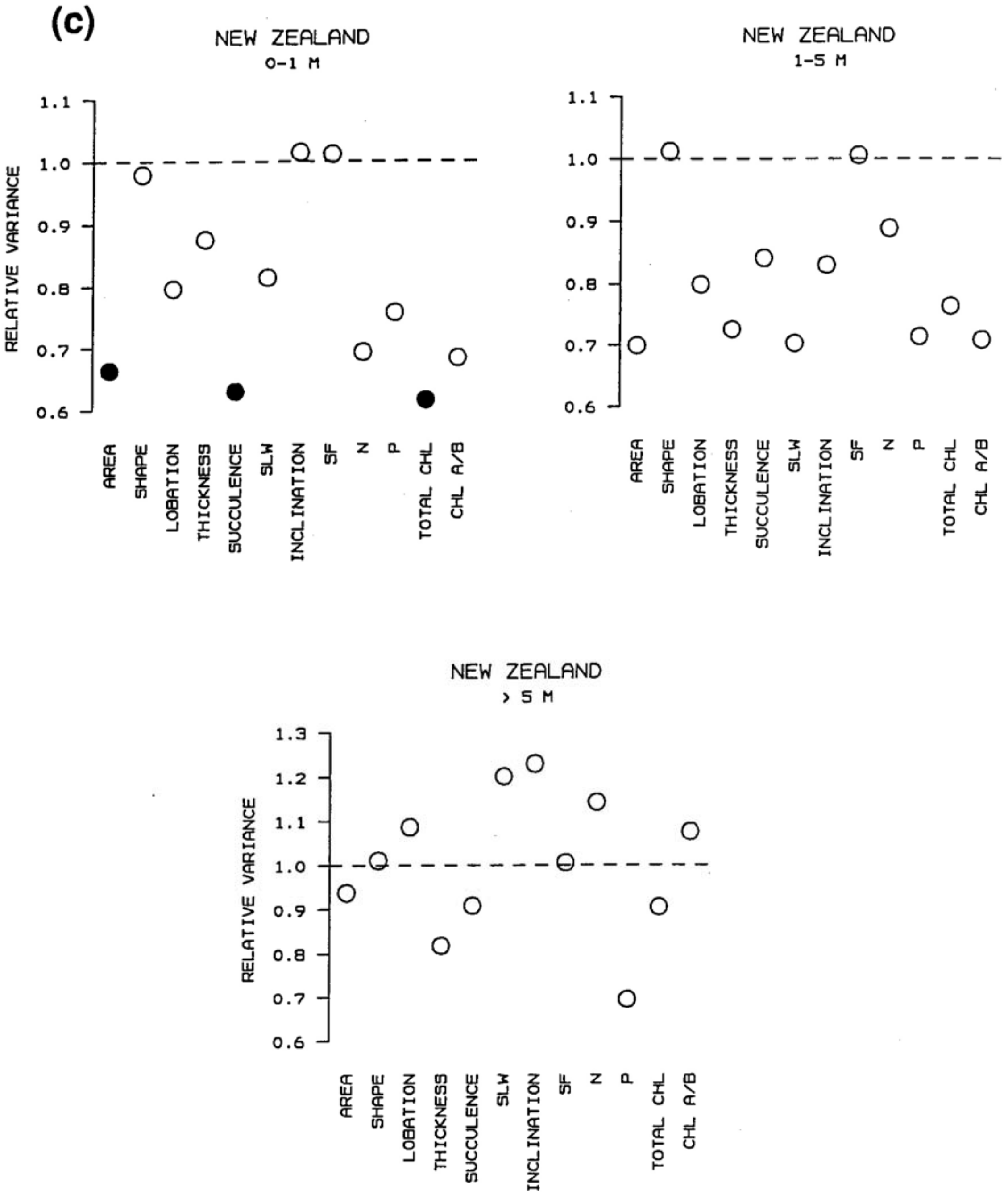

Fig. 11.5 (continued)

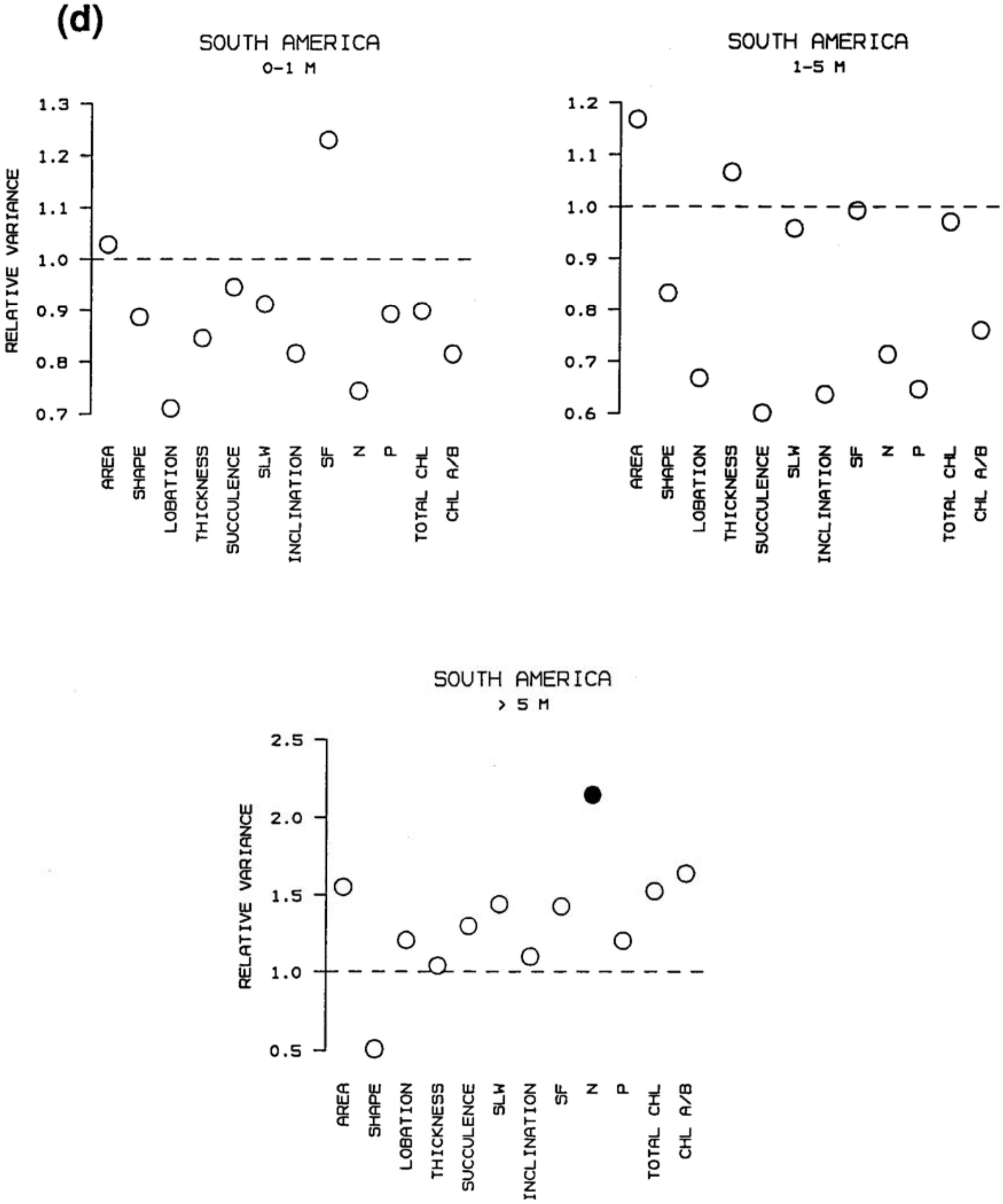

Fig. 11.5 (continued)

Overdispersion was detected in PSU area and chlorophyll *a/b* ratios in the 0-1 m guild for southern New Zealand (ZC), and for PSU area in the 1-5 m guild (Fig. 11.6a). Most variates show a tendency towards overdispersion ($R_{V,T}<1$) in the two lower guilds, but no strong trend in either direction is apparent for the >5 m guild. Species PSU inclinations are overdispersed within the 0-1 m guild for central New Zealand, while all variates show a tendency towards overdispersion relative to null expectation (Fig. 11.6b). No strong patterns are evident for the 1-5 m and >5 m guilds, although a majority of variates have $R_{V,T}<1$ for both guilds. No significant results were obtained for guilds within the Tasmanian site T1 Balfour (Fig. 11.6c), nor for the Australian site A2 Cascades (Fig. 11.6d).

No significant departure from the null model was observed within guilds for the northern New Zealand site ZN1 Ohakune (Fig. 11.7a), although the majority of texture variates show $R_{V,T}<1$ for the 0-1 and 1-5 m guilds. For ZN2 Rotokura, there is overdispersion in PSU area for both the 0-1 m and 1-5 m guilds (Fig. 11.7b). Overdispersion was detected in the same variate for the 1-5 m guild of ZN3 Clements (Fig. 11.7c). No significant results were obtained within guilds for SA1 Quetrihué in Argentina (Fig. 11.7d).

PATTERNS AMONG TEXTURE VARIATES

Communities

Significant overdispersion was detected in a relatively small proportion of communities, and for only a subset of texture variates and factors (Table 11.2). PSU area was found to show overdispersion in four of the 26 communities examined, while for five other variates (PSU thickness, succulence, specific weight, inclination and total chlorophyll), and four factors derived from these variates (F1, F2, F3, F4) overdispersion was detected in one or two tests. The number of individual study sites showing overdispersion in any variate or factor is not significant as a proportion of the 17 examined by binomial tests for overall significance. This means that, on the basis of the data presented in Table 11.2, the proposition cannot be rejected, that the dispersion patterns observed in each variate are a chance outcome of stochastic character variation, and not of the operation of assembly rules limiting the co-occurrence of species with similar characters.

No significant underdispersion (clustering of species characters, relative to chance expectation) was detected in any variate at the whole-community scale.

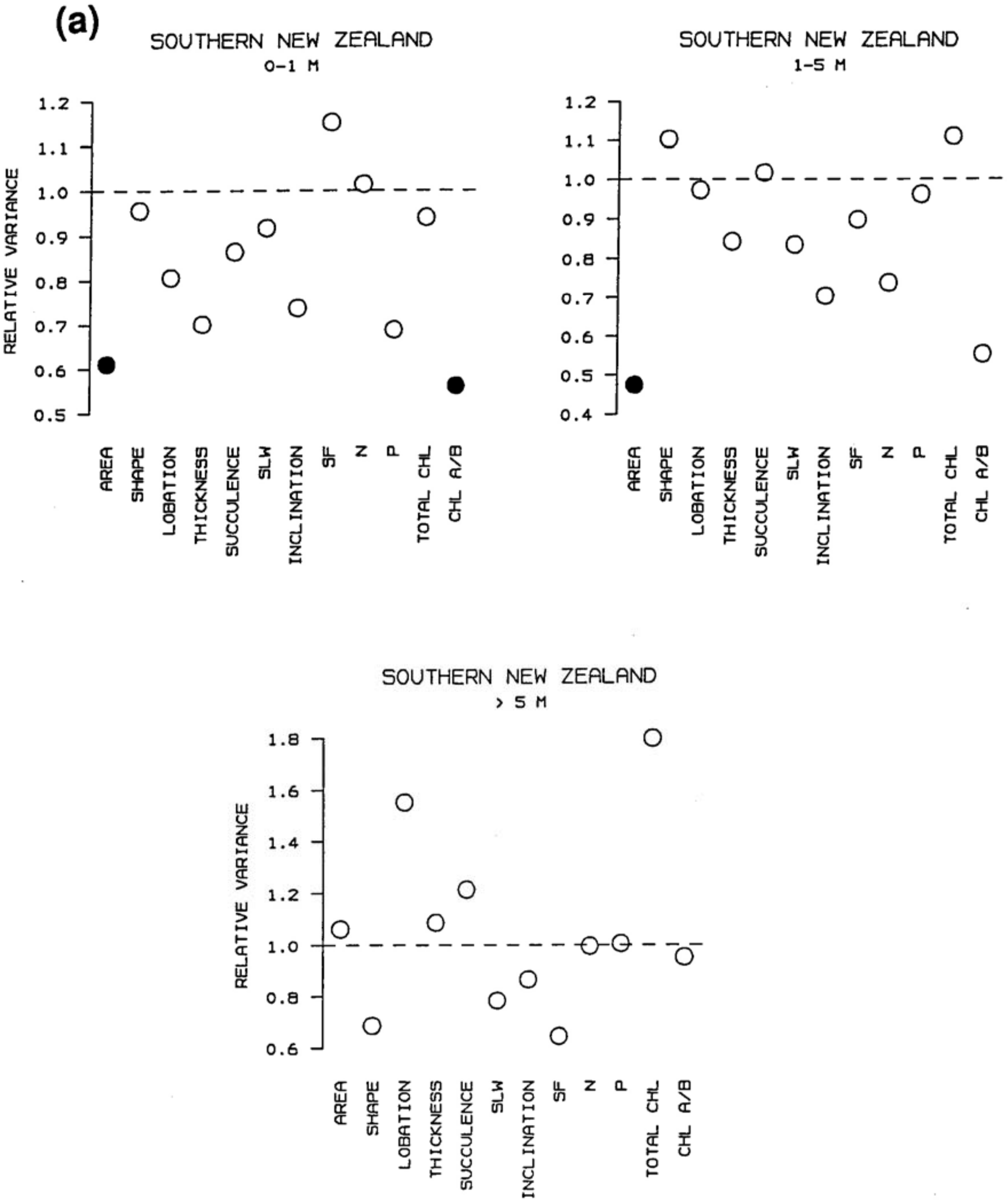

Fig. 11.6 Smoothed bootstrap tests for over- or underdispersion in texture variates in the 0-1 m, 1-5 m and >5 m guilds (see text) of regional-scale *Nothofagus*-dominated communities **(a)** southern New Zealand (ZS), **(b)** central New Zealand (ZC), **(c)** T1 Balfour and **(d)** A2 Cascades. Format as for Fig. 11.2.

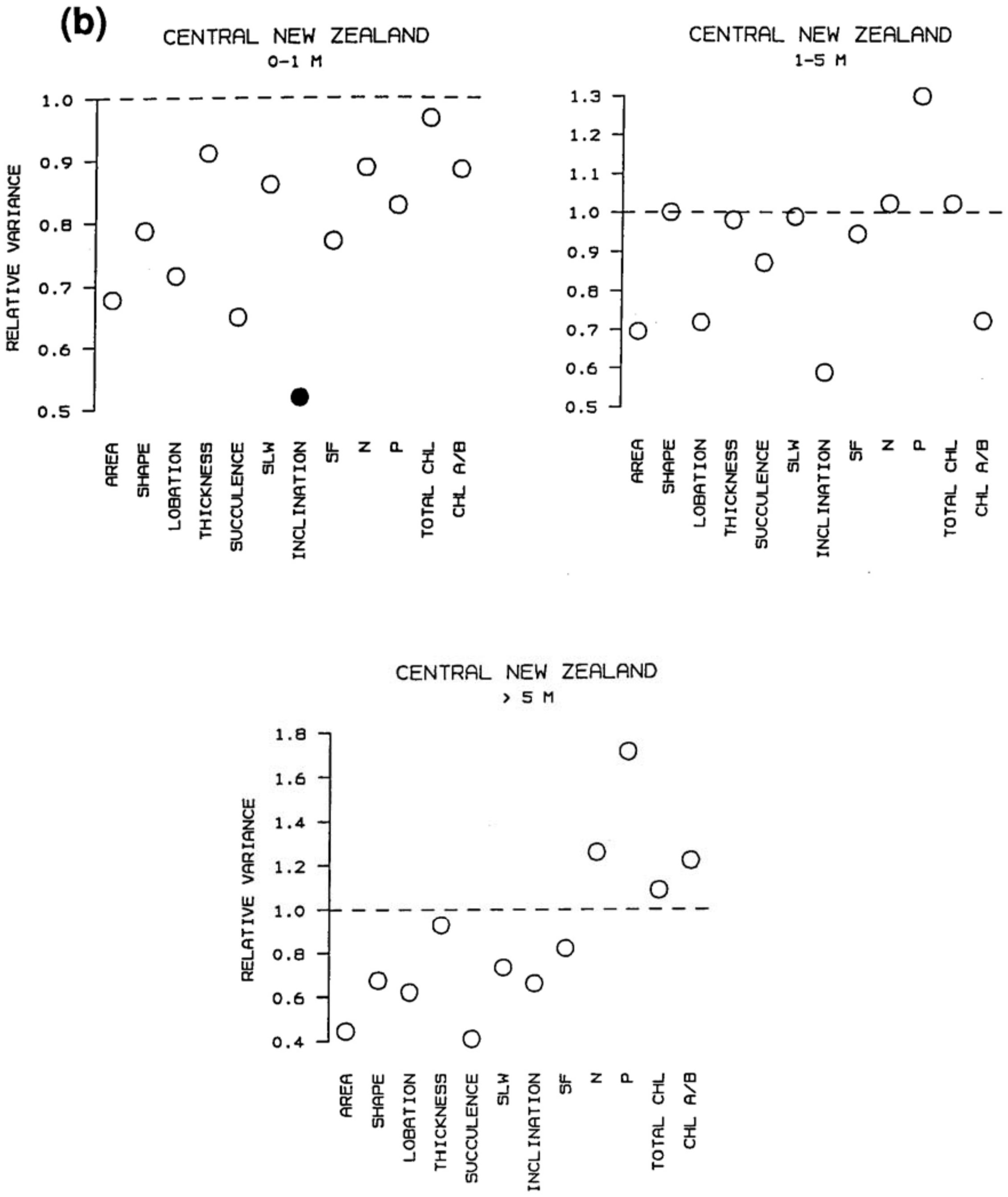

Fig. 11.6 (continued)

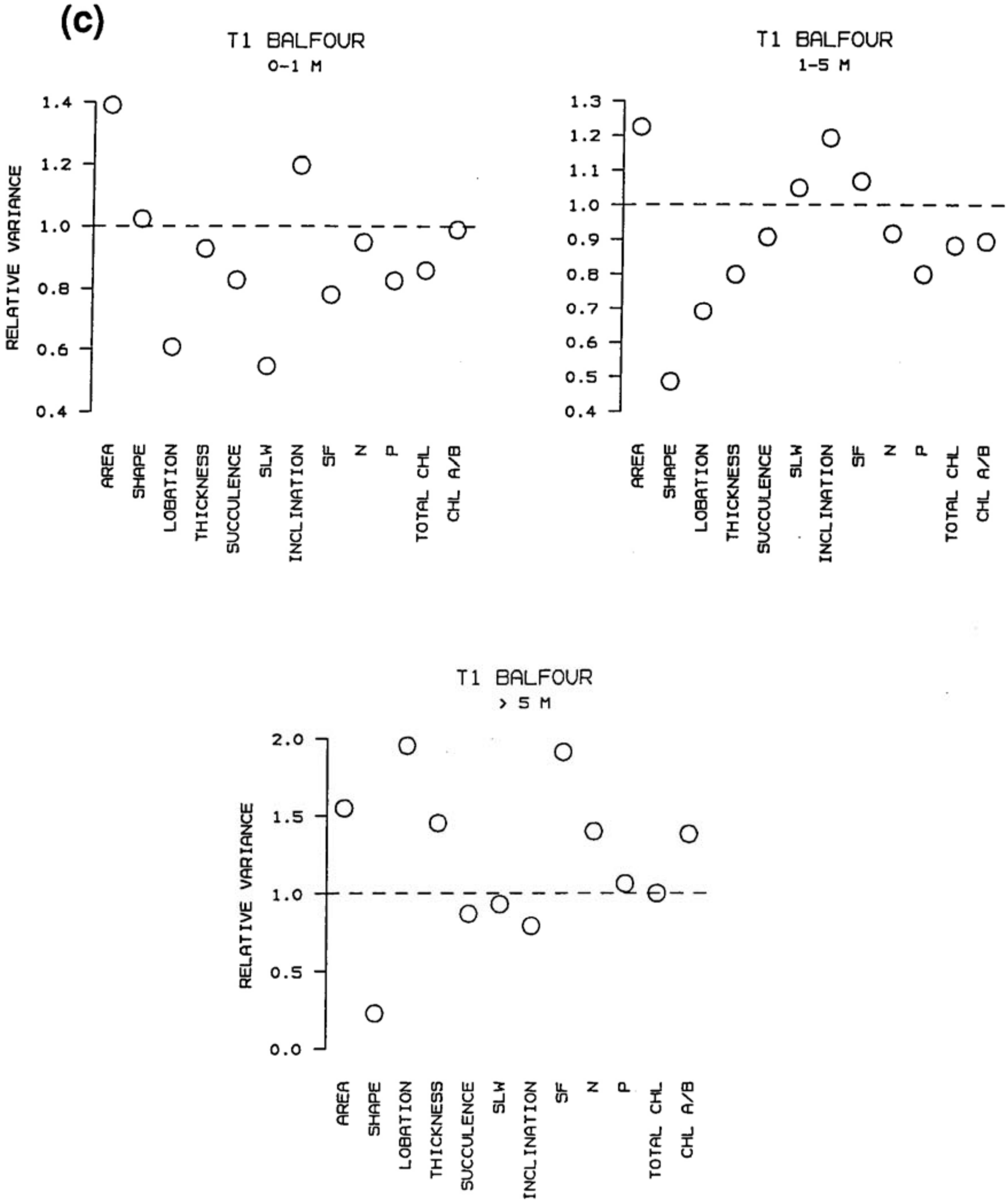

Fig. 11.6 (continued)

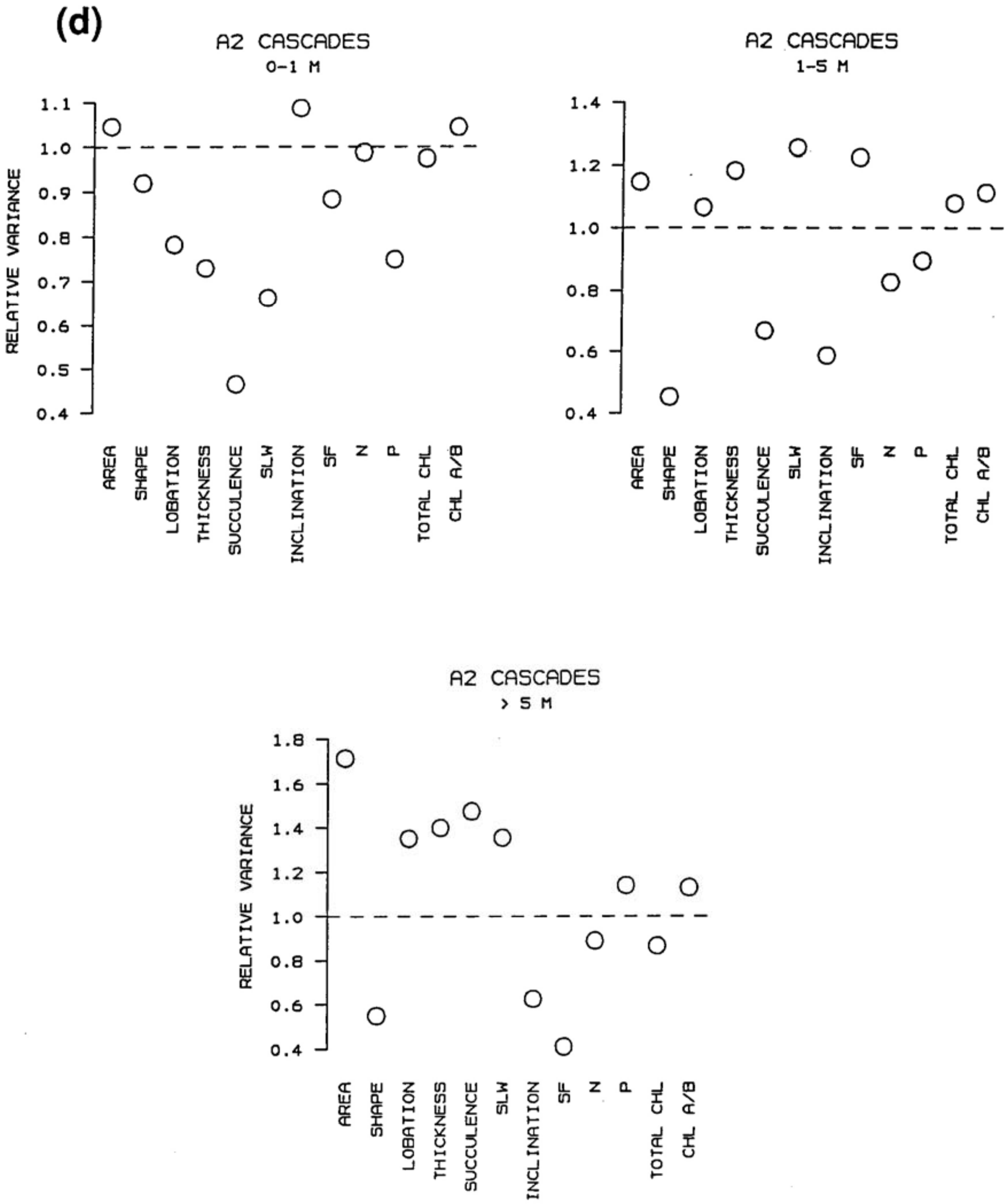

Fig. 11.6 (continued)

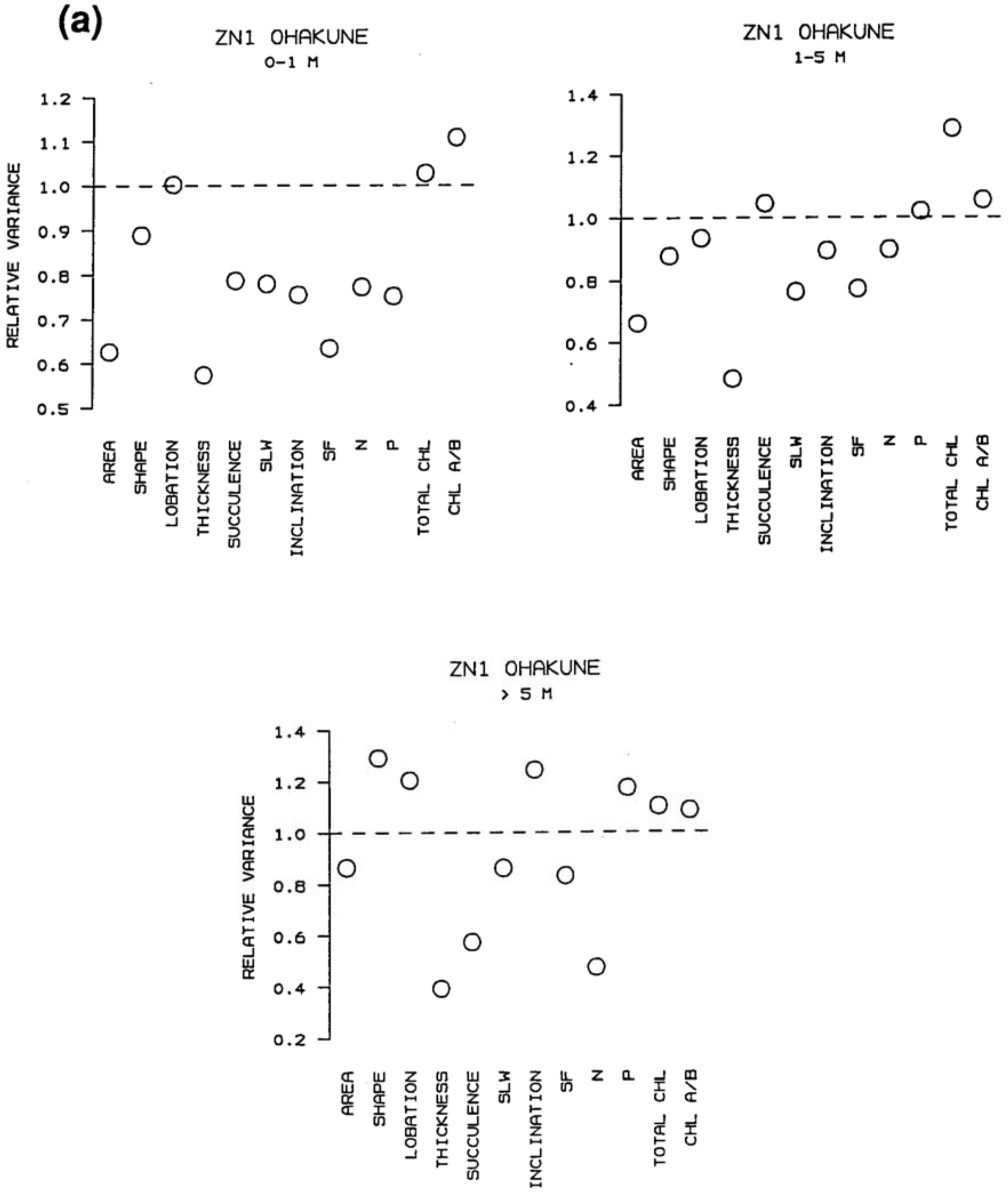

Fig. 11.7 Smoothed bootstrap tests for over- or underdispersion in texture variates in the 0-1 m, 1-5 m and >5 m guilds (see text) of local-scale *Nothofagus*-dominated communities **(a)** ZN1 Ohakune, **(b)** ZN2 Rotokura, **(c)** ZN3 Clements and **(d)** SA1 Quetrihué. Format as for Fig. 11.2.

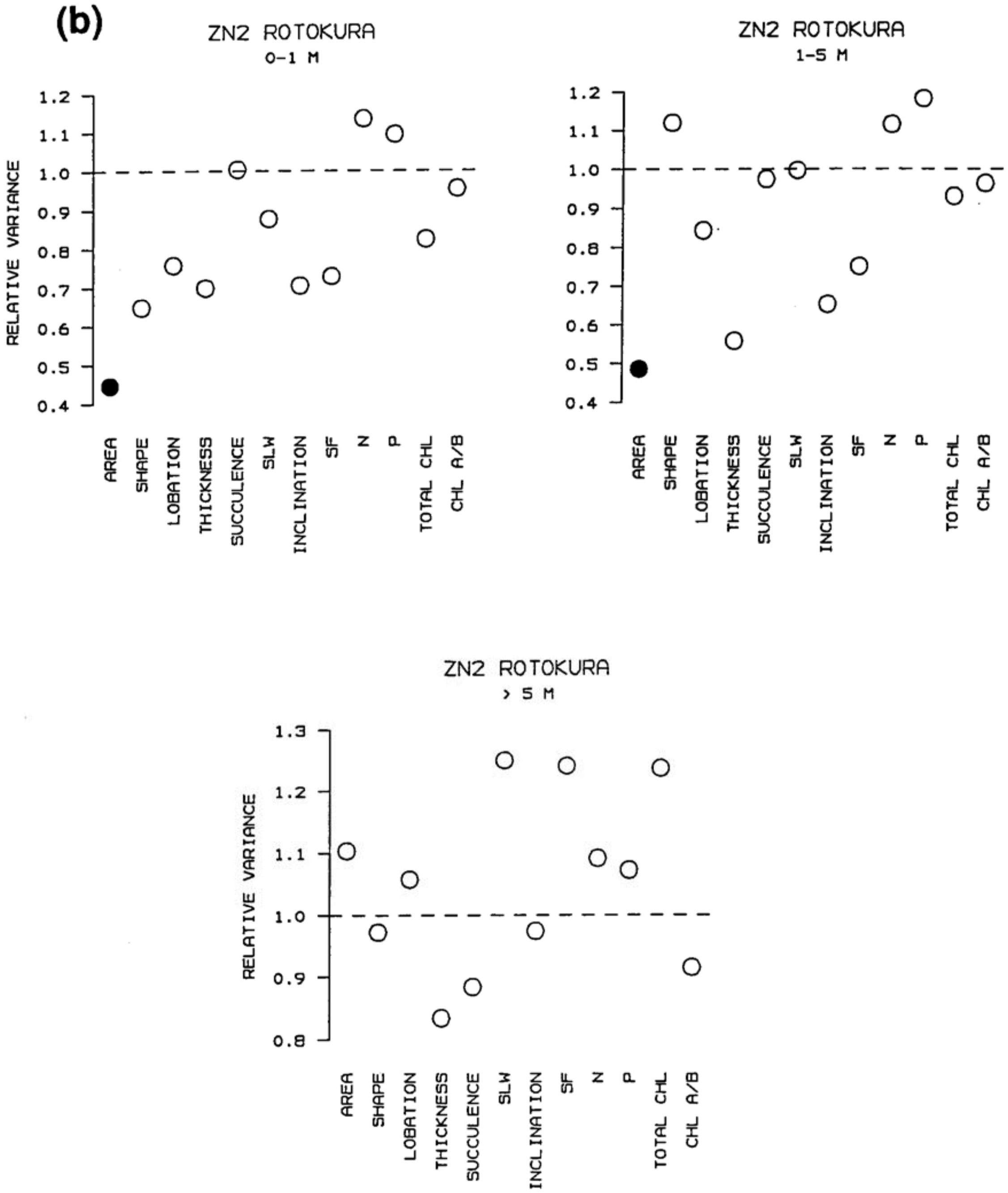

Fig. 11.7 (continued)

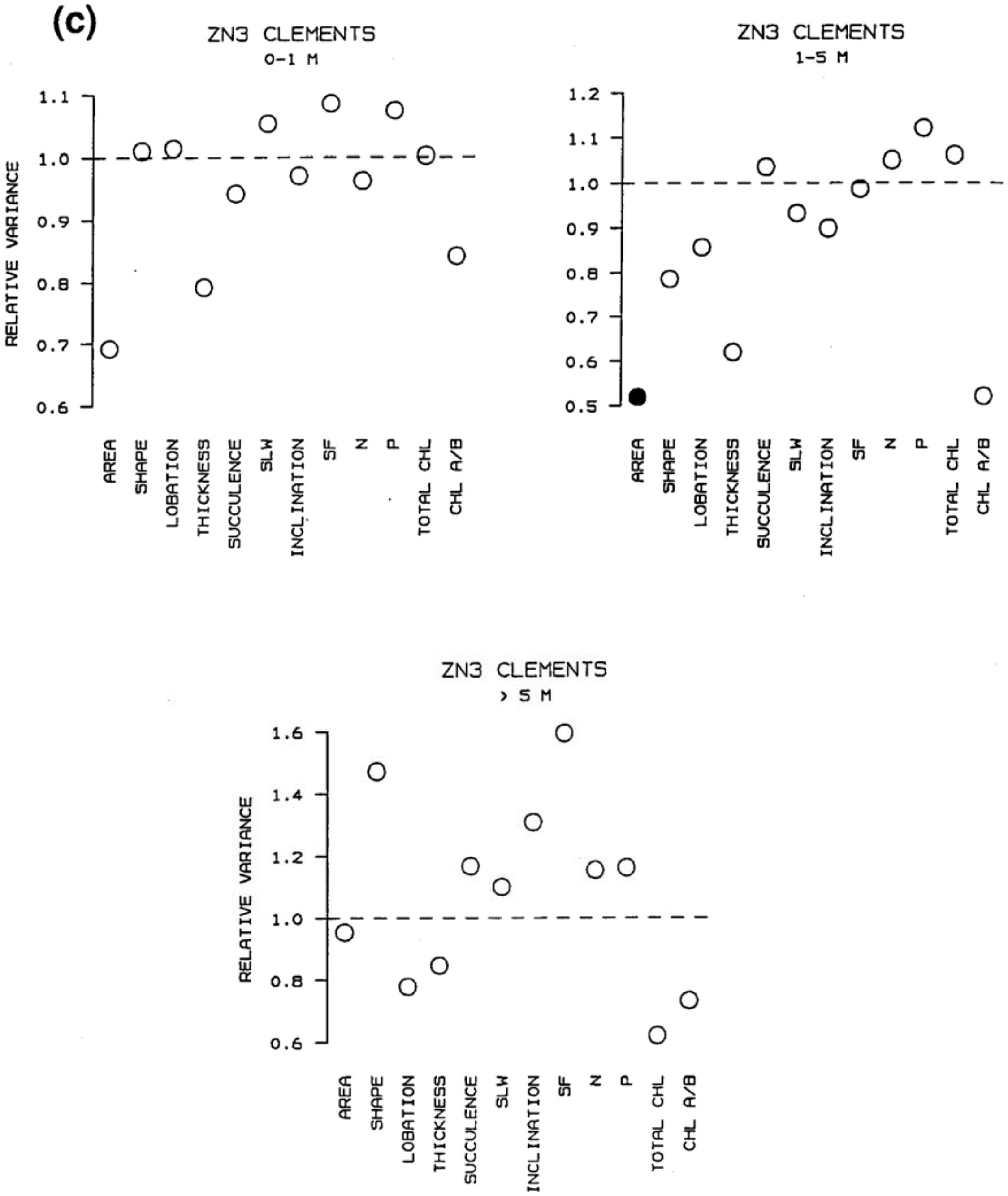

Fig. 11.7 (continued)

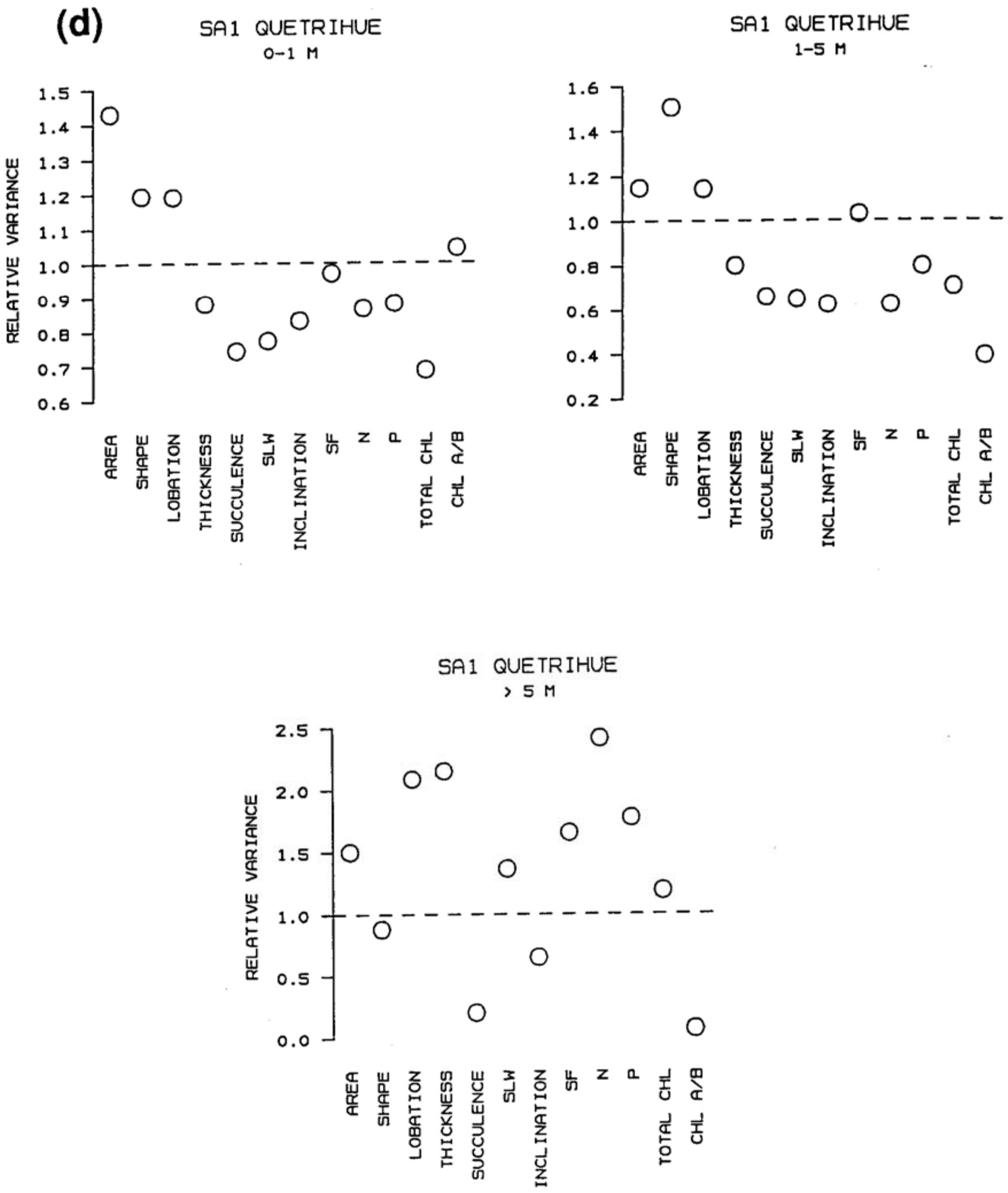

Fig. 11.7 (continued)

Table 11.2 Incidence of significant over- or underdispersion in each texture variate and derived texture factor among 26 local-, regional- and landmass-scale communities, and (in parentheses) among 17 of these communities, each comprising a single study site, according to smoothed bootstrap tests (see text). The incidence of significant over- or underdispersion among single study sites is not significant for any texture variate or factor at the 5% level (binomial test).

Texture variate or factor	Overdispersed	Underdispersed
Area	4 (2)	0 (0)
Shape	0 (0)	0 (0)
Lobation	0 (0)	0 (0)
Thickness	1 (1)	0 (0)
Succulence	1 (0)	0 (0)
SLW	1 (0)	0 (0)
Inclination	2 (1)	0 (0)
SF	0 (0)	0 (0)
N	0 (0)	0 (0)
P	0 (0)	0 (0)
Total chl	1 (0)	0 (0)
Chl *a/b*	0 (0)	0 (0)
F1	1 (0)	0 (0)
F2	2 (2)	0 (0)
F3	1 (0)	0 (0)
F4	1 (1)	0 (0)
F5	0 (0)	0 (0)
F6	0 (0)	0 (0)
F7	0 (0)	0 (0)

Although the number of community/variate combinations for which significant departure from the null model could be shown is very low, some general trends were apparent (Figs. 11.2-11.4) in the relative frequencies of departure from null model expectation (whether significant or not) in each direction. Such trends within texture variates and factors are summarised in Table 11.3. For example, bootstrap tests revealed a tendency towards overdispersion ($R_{V,SLW}<1$) in PSU specific weight for 15 of the 17 communities examined. In only two communities was a tendency towards underdispersion ($R_{V,SLW}>1$) detected. From the binomial distribution, the likelihood of obtaining a frequency ratio as uneven as 15:2 by chance alone when an even ratio (8.5:8.5) is expected, is 0.013, well below the 5% target significance level. This suggests that the trend towards overdispersion in PSU specific weight across the 17 communities is the result, not of stochastic character variation among species, but of a community process that tends to limit similarity in species characters, causing them to be more regularly spaced than expected by chance. It is suggested that this causal process may be the operation of assembly rules.

Five variates — PSU lobation, thickness, succulence, specific weight and total chlorophyll — show a significant trend towards overdispersion among the 17 individual study sites. There are also significant trends towards overdispersion for F1 (related to PSU succulence, specific weight, total chlorophyll and species height) and F4 (related to PSU thickness). Other variates and factors show little evidence for departure from randomness, although for only one variate (chlorophyll *a/b*) and one factor (F5, which is most closely related to PSU nitrogen and phosphorus content) is the frequency ratio skewed towards underdispersion.

Table 11.3 Relative frequency of departure from null model expectation (relative deviance, $R_{V,T}$=1) in the directions of overdispersion ($R_{V,T}$<1) and underdispersion ($R_{V,T}$>1) in each texture variate and derived texture factor for 17 individual study sites, according to smoothed bootstrap tests (see text). The significance (two-tailed *P*) of a trend in either direction (binomial test for departure from the expectation of even frequencies) is shown. Data showing significant trends (*P*<0.05) appear in bold type.

Texture variate or factor	Overdispersed	Underdispersed	*P* for trend
Area	10	7	0.629
Shape	11	6	0.332
Lobation	**14**	**3**	**0.013**
Thickness	**14**	**3**	**0.013**
Succulence	**14**	**3**	**0.013**
SLW	**15**	**2**	**0.002**
Inclination	11	6	0.332
SF	9	8	1.000
N	10	7	0.629
P	10	7	0.629
Total chl	**14**	**3**	**0.013**
Chl *a/b*	8	9	1.000
F1	**16**	**1**	**0.000**
F2	12	5	0.143
F3	11	6	0.332
F4	**14**	**3**	**0.013**
F5	6	11	0.332
F6	10	7	0.629
F7	12	5	0.143

Guilds

As was the case for whole communities (Table 11.2) significant departure from null expectation was observed in only a few tests at the guild scale (Table 11.4). Within the 0-1 m guild, overdispersion, significant for individual tests, was detected in PSU Area, succulence, inclination, total chlorophyll and chlorophyll *a/b*. For the 1-5 m guild there is overdispersion in PSU area and chlorophyll *a/b*, while significant departure from the null model within the >5 m guild is limited to overdispersion in PSU chlorophyll *a/b* in one community, and underdispersion in PSU nitrogen content in another. The only variate for which the incidence of overdispersion is significant as a proportion of the number of communities examined, is PSU Area, for which overdispersion was detected in the 0-1 m guild of three individual study sites.

Table 11.4 Incidence of significant over- or underdispersion in each texture variate for the 0-1 m, 1-5 m and >5 m guilds among 26 local-, regional- and landmass-scale communities (24 for >5 m guild), and (in parentheses) among 17 of these communities (15 for >5 m guild), each comprising a single study site, according to smoothed bootstrap tests (see text). The incidence of significant over- or underdispersion among single study sites is significant only for PSU area in the 0-1 m guild ($P<0.05$ from binomial test).

Texture variate or factor	0-1 m Guild		1-5 m Guild		>5 m Guild	
	Over-dispersed	Under-dispersed	Over-dispersed	Under-dispersed	Over-dispersed	Under-dispersed
Area	4 (3*)	0 (0)	3 (2)	0 (0)	0 (0)	0 (0)
Shape	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Lobation	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Thickness	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Succulence	1 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
SLW	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Inclination	2 (2)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
SF	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
N	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (0)
P	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Total chl	1 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Chl *a/b*	2 (2)	0 (0)	2 (0)	0 (0)	1 (1)	0 (0)

*P=0.0082 (two-tailed)

Although the incidence of significant underdispersion within guilds is significant overall for only one variate, binomial tests reveal some significant trends (Table 11.5). Within the 0-1 m guild, three variates — PSU thickness, succulence and specific weight — showed a tendency towards overdispersion in a significantly large proportion of sites. Little evidence of a trend is apparent for the remaining nine variates in this guild. No trends were detected in the 1-5 m guild. In the >5 m guild there is a significant trend towards underdispersion, PSU phosphorus values showing a tendency in this direction in 12 of the 15 sites. PSU area and lobation also show possible trends towards underdispersion, though this is non-significant for both variates.

Table 11.5 Relative frequency of departure from null model expectation (relative deviance, $R_{V,T}$=1) in the directions of overdispersion ($R_{V,T}$<1) and underdispersion ($R_{V,T}$>1) in each texture variate for the 0-1 m and 1-5 m guilds within 17 individual study sites, and the >5 m guild within 15 study sites, according to smoothed bootstrap tests (see text). The significance (two-tailed *P*) of a trend in either direction (binomial test for departure from the expectation of even frequencies) is shown. Data showing significant trends (*P*<0.05) appear in bold type.

Texture variate	0-1m Guild			1-5m Guild			>5m Guild		
	Over-dispersed	Under-dispersed	*P* for trend	Over-dispersed	Under-dispersed	*P* for trend	Over-dispersed	Under-dispersed	*P* for trend
Area	7	10	0.629	8	9	1.000	4	11	0.118
Shape	9	8	1.000	11	6	0.332	10	5	0.301
Lobation	10	7	0.629	11	6	0.332	4	11	0.118
Thickness	**14**	**3**	**0.013**	11	6	0.332	8	7	1.000
Succulence	**14**	**3**	**0.013**	11	6	0.332	9	6	0.607
SLW	**14**	**3**	**0.013**	11	6	0.332	6	9	0.607
Inclination	8	9	1.000	12	5	0.143	7	8	1.000
SF	10	7	0.629	11	6	0.332	7	8	1.000
N	10	7	0.629	7	10	0.629	6	9	0.607
P	8	9	1.000	8	9	1.000	**3**	**12**	**0.035**
Total chl	10	7	0.629	10	7	0.629	5	10	0.301
Chl *a/b*	8	9	1.000	9	8	1.000	5	10	0.301

11.4 Discussion

OVERDISPERSION OF SPECIES CHARACTERS

The null hypothesis that species characters are drawn at random from some underlying distribution could be rejected for relatively few texture variates and in a minority of communities and guilds within communities (Figs. 11.2-11.7; Tables 11.2, 11.4). Only for PSU area in the 0-1 m guild was the incidence of overdispersion high enough to be deemed significant as a proportion of the number of tests carried out.

Although significant results were obtained in relatively few bootstrap tests, a number of overall trends were apparent in the (generally non-significant) results. In many communities, particularly those sampled in New Zealand, there was a tendency for species character values to be more regularly dispersed than expected on a random basis (though significantly so for only a minority of tests). This pattern was observed in communities at the landscape (e.g. New Zealand, South America; Fig. 2c-d), regional (e.g. southern, central and northern New Zealand; Fig. 3f-h) and local scales (e.g. northern New Zealand sites; Fig. 4f-h). Although the significance of these trends could not be investigated within communities (due to the non-independence of observations for different, but correlated, texture variates), binomial tests revealed some significant overall trends within variates. With the sole exception of PSU phosphorus content in the >5 m guild, significant trends were in the direction of overdispersion. These findings suggest that character dispersion patterns are not completely stochastic, but are influenced by community- or guild-level processes. The predominance of overdispersion is compatible with the hypothesis that there are assembly rules which restrict the co-occurrence of similar species, resulting in a somewhat regular spacing of species ordinates along character axes.

The amount of evidence for overdispersion detected at the guild scale was lower than at the community scale, particularly for the 1-5 m and >5 m guilds (Fig. 11.5-11.7; Tables 11.3, 11.5). However, patterns of departure from the null model in the 0-1 m guild were generally similar to those observed at the whole community level, though fewer tests gave significant results. For several communities, especially at the landscape scale (Fig. 11.5), there was a trend towards overdispersion in the 0-1 m and 1-5 m guilds, and underspersion in the >5 m guild. The trend was also apparent within variates, the only significant underdispersion being within the >5 m guild (PSU phosphorus, South America). This pattern would seem to suggest that assembly rules may have a greater controlling effect on community structure in the ground and (possibly) shrub layers than in the tree stratum. Alternatively, clustering — for example, about different adaptive optima, or among related species whose function might reflect common phylogenetic constraints — may be more pronounced in the >5 m guild, where it would tend to obscure any regularity in the spacing between species that might arise owing to the effects of assembly rules.

Of the five texture variates showing significant trends towards overdispersion among whole communities (Table 11.3), three — PSU succulence, specific weight and total chlorophyll — are closely related to factor F1, which also shows a significant trend in this direction. F1 may correspond to functional variation in response to light availability (see Section 9.4), particularly in the context of vertical structure (the texture variate species height, not examined directly in this chapter, also has a high loading on F1; see Table 9.1). The observed trend towards overdispersion in PSU thickness and its associated factor F4, might likewise be associated with the light regime (Givnish 1987; Bongers & Popma 1988; Reich *et al.* 1991) or with nutrient uptake (Beadle 1966; Grubb 1977; Sobrado & Medina 1980). The latter alternative may be more likely, since F1 and F4 (like all the texture factors) are uncorrelated, suggesting that they may be associated with different underlying factors. A possible nutritional interpretation of the observed overdispersion is that there are assembly rules based on past or present root competition (Caldwell 1987; Caldwell *et al.* 1991), which result in partitioning of below-ground nutrient gradients among species. Resulting interspecific differences in nutrient uptake might be reflected in a somewhat regular spacing of species values for leaf thickness, which may be correlated with plant nutrient uptake.

PSU area showed the highest incidence of significant overdispersion in individual tests (although this was significant overall only for the 0-1 m guild; Table 11.4), yet did not show any significant overall trends at either the community or guild scale (Tables 11.3, 11.5). This pattern suggests that there are relatively strong assembly rules determining dispersion patterns for leaf area, but that these apply or can be detected only within certain communities (principally, regional- and local-scale communities in New Zealand), and primarily in the lower strata. Variation in leaf area has been correlated with light, nutrient and moisture regimes (Grubb *et al.* 1963; Givnish & Vermeij 1976; Grubb 1977; Hall & Swaine 1981; Chiarello 1984; Medina 1984; Givnish 1984), all of which would represent resource, as well as environmental, gradients. The overdispersion observed in PSU area could represent an outcome of assembly rules leading to partitioning of any of these resource gradients among species.

OVERDISPERSION VERSUS TEXTURE CONVERGENCE

The hypotheses of character overdispersion within assemblages, and of texture convergence among them, are closely related. This is because texture convergence, relative to expectation under a null model of random species assortment, might be expected as an outcome of character overdispersion, if other assumptions (in particular, that of matching physical environments in the assemblages being compared) are met (Ricklefs & Travis 1980; Wiens 1991a,b; Wilson *et al.* 1994).

Disregarding significance levels in individual tests, the patterns observed at the whole-community level in the present chapter are generally consistent with the results of tests for convergence in *Nothofagus* community texture, carried out previous chapters. There were significant trends towards overdispersion in PSU lobation, thickness, succulence, specific weight and total chlorophyll (Table 11.3), while PSU area showed significant overdispersion in four communities (Table 11.2). With the exception of PSU lobation, all of these variates were convergent in a significant number of comparisons of texture distributions (Chapter 7; Table 7.2) or mean-adjusted distributions (Chapter 8; Table 8.2), with species unweighted by their abundance. Patterns in the texture factors related to these variates are similarly related. Both F1 (related to PSU succulence, specific weight and total chlorophyll) and F4 (PSU thickness) showed a highly significant trend towards overdispersion among individual sites (Table 11.3), and were convergent in a significant number of comparisons of mean-adjusted distributions (though for F1, only with species weighted by abundance rank; Table 9.2). There was no significant overdispersion, nor strong evidence of any overall trends in this direction, for PSU phosphorus content or chlorophyll *a/b*, yet these variates showed the highest overall incidence of convergence between mean-adjusted texture distributions.

At the guild level, the observed patterns of character overdispersion bear only a weak relationship to the community-level convergence detected in previous chapters. For the 0-1 m guild, there was a significant incidence of overdispersion in PSU area (Table 11.4), while PSU thickness, succulence and specific weight showed a significant trend in this direction (Table 11.5). Of these variates, only PSU area showed a significant overall incidence of convergence among the comparisons carried out within this guild (Table 10.2). Once again, the related variates PSU phosphorus and chlorophyll *a/b* were convergent in a large number of comparisons, but showed no overdispersion that was significant overall. For the 1-5 m and >5 m guilds there was very little evidence of overdispersion, whereas significant convergence of mean-adjusted distributions was detected in a number of variates and in a significantly large number of community comparisons, in Chapter 10 (Tables 10.3, 10.4).

Given the appreciable amount of convergence detected among mean-adjusted texture distributions in different *Nothofagus*-dominated communities (Chapters 8, 9 and 10). It is perhaps somewhat surprising that the evidence for character overdispersion, obtained using direct tests in this chapter, is relatively weak. The explanation for the difference may lie in the type of distribution produced by competitive niche segregation. It has been assumed that, if assembly rules apply and impose limits on niche overlap, the amount of niche separation (and therefore, the spacing between species characters related to niches) would be of a similar magnitude for each pair of adjacent species. In other words, species values were expected to form an approximately arithmetic progression. This assumption seems reasonable, following normalisation of measured character values; for example, by taking the natural logarithm (Table 2.1). In an arithmetic progression, adjacent elements are spaced equidistantly, so that the variance (V_T) of the spacing between them is null. If species character values conform to a perfect arithmetic progression, highly significant overdispersion will be detected by the variance-based test (since a variance lower than zero is mathematically impossible, no bootstrapped null distribution can be more overdispersed than the observed). If, however, the limiting similarity between species changes geometrically (i.e. by multiplication) along the niche (or character) axis considered, species values will no longer be spaced equidistantly, resulting in a finite observed V_T. Under these conditions, it is uncertain whether the variance-based test for overdispersion would give significant results or even results in the direction expected ($R_{V,T}<1$). By contrast, the test for convergence of mean-adjusted texture distributions is based on the goodness-of-fit between the distributions (on the magnitude of $\hat{D}'_T$; Section 8.2; Fig. 8.2), and incorporates no assumptions as to their approximate shape. This means that convergence could be detected between similar distributions, even if the component species values are overdispersed in a markedly non-arithmetic fashion.

The tests for overdispersion applied in the present chapter are analogous to tests for texture convergence with species character values weighted by presence only (Section 6.2). Convergence tests in which an abundance weighting factor (abundance rank, photosynthetic biomass, or its square root) is applied, focus on elements of community texture (the more abundant species) in which species interactions, and therefore overdispersion, might be more pronounced. It is unclear, however, how species abundance weighting could be incorporated in direct tests for overdispersion (other than by excluding species from analysis whose abundance is lower than some arbitrary threshold value), and so no attempt to do so was made.

It appears likely that the smoothed bootstrap method used to search for overdispersion is relatively conservative as an approach to seeking community structure. This is because it makes two potentially restrictive assumptions. Firstly, that the overdispersion produced by the operation of assembly rules will be essentially arithmetic in its nature (whereas overdispersion on a geometric scale can be envisaged); and secondly, that the effects of assembly rules will be sufficiently uniform to produce overdispersion across a whole assemblage (whereas the species interactions on which assembly rules would be based might be concentrated among the more abundant species). Tests seeking convergence in texture distributions between communities are free from both of these restrictions, and so may represent a more powerful approach to the detection of community structure.

PREVIOUS STUDIES OF CHARACTER DISPERSION PATTERNS

Hutchinson (1959) proposed that competition among sympatric species competing for the same classes of food would lead to a minimum viable difference — a ratio of *c.* 1:1.3 was suggested — in their body sizes. If species packing tends to maximise resource use (Pianka 1975), while competition limits niche overlap, it follows that the ratio of the sizes of consecutive species in a rank order of body size will be relatively constant, and that species values will be evenly spaced on a logarithmic scale (Simberloff & Boecklen 1981).

Numerous studies have sought to validate this hypothesis with respect to body size or other morphological variables, for example, in communities of birds (MacArthur 1971; May 1978), fish (Barbour 1973), mammals (Brown 1975) and bees (Inouye 1977). Many early studies claimed to find constant or minimum ratios, but were deficient in that character overdispersion was not sought relative to a valid null model (Simberloff & Boecklen 1981; Tonkyn & Cole 1986; MacNally 1988). Reanalysing the data from 31 studies that had claimed evidence for minimum or constant ratios in animal sizes, Simberloff & Boecklen (1981) demonstrated that, for most data sets, the null hypothesis could not be rejected that logarithms of body sizes were drawn at random from a uniform distribution in the same range as the observed data. The null model used by Simberloff & Boecklen (*op. cit.*) was arguably unduly simplistic (Tonkyn & Cole 1986), and the test statistics used to compare the observed and null distributions are deficient in that they are based on only a small subset of the whole distribution (Sinclair *et al.* 1985; Pleasants 1990, 1994). Consequently, it is unclear whether competitive displacement can be validly supported for these communities or not. MacNally (1988) used a different approach to seek morphological overdispersion in several types of animal community. Observed distributions of species values were compared with a geometric model of the character distributions expected, given that competitive niche segregation had occurred. There was significant deviation from the expected distribution in most cases, providing little evidence that competitive displacement had occurred.

In studies of plant communities, overdispersion of flowering and fruiting phenologies has been sought as evidence for competitive segregation of reproductive niches (e.g. Snow 1965; Waser & Real 1979; Pleasants 1980; Thomson & Rusterholz 1982; Armbruster 1986; Ashton *et al.* 1988). Phenological overlap is typically high, and recent studies have generally characterised species not only by their mean for the character of interest (as in most animal size studies, and also in the present study) but by both the mean and the variance (Gleeson 1981) or by the temporal frequency distribution of the character (Pleasants 1980; Fleming & Partridge 1984). For example, Pleasants (1980) examined temporal distributions of flowering intensity for species within guilds of bumblebee-pollinated plants to evaluate the hypothesis that the mean of pairwise overlaps in species flowering curves were lower than would be expected under a null model in which the observed curves were placed in the same growing season at random. For all but one of the guilds examined, observed overlap was lower than expected under the null model, suggesting that competition for the same pollinator species had produced niche segregation. The use of mean pairwise overlap as a test statistic in null model tests of phenological niche segregation has been criticised (Fleming & Partridge 1984) on the grounds that it focuses on interactions between nearest-neighbour species in niche space, taking no direct account of diffuse competition within the whole guild. The use of an alternative `*n*-wise' test statistic reduced or even reversed departure from the null model in a reanalysis of several data sets, suggesting that the role of competition in structuring plant reproductive guilds may be less significant than formerly supposed (Fleming & Partridge 1984). However, this question remains controversial (Fleming 1985; Pleasants 1990).

There have been relatively few studies of morphological character displacement in plants. Armbruster *et al.* (1994) studied the floral reproductive morphology of sympatric *Stylidium* species, testing the hypothesis that competition for pollinator species had led to a reduction in morphological overlap between species, in comparison to stochastic null models. Separate null models were used to evaluate hypotheses of ecological sorting and coevolutionary character displacement: significant departure was shown from the coevolutionary model, although a trend towards character segregation relative to the ecological null model was non-significant. The observed distribution of attributes for each species from many sites was used as a pool from which values were drawn to assemble each null assemblage. This represents an advance over many previous studies of character dispersion (e.g. Pleasants 1980; Simberloff & Boecklen 1981; Fleming & Partridge 1984) which drew niches at random from a uniform distribution, an assumption unlikely to parallel nature. To test the hypotheses that competition would tend to inhibit sympatry of *Banksia* species with similar growth forms and regeneration biology, Richardson *et al.* (1995) compared the growth form diversity and regeneration biology diversity of actual assemblages with null assemblages created by by drawing species at random (though with abundance weighting) from the regional species pool. There was a significant tendency for observed assemblages to show lower growth form diversity (signifying poor differentiation of growth form niches) and lower reproductive biology diversity (poor differentiation of reproductive niches) than expected under the null model, lending little support to the competition hypothesis. Cody (1986, 1991) has examined vegetative niche segregation in a variety of shrubland and desert plant guilds, presenting several convincing examples of apparent competitive displacement. For example, morphological niches of sympatric species of Proteaceae from four South African fynbos assemblages are clearly separated when values for replicate individuals are plotted in a space defined by their leaf lengths and length:width ratios (i.e. PSU shape), although no statistical evidence for differences between species is presented.

The present study in the context of previous work

Although a number of previous studies, like the present one, have sought competitive displacement relative to explicit null models, there have been two common shortcomings of the tests employed. These concern the distributions from which species are drawn to create null assemblages, and the test statistics used to compare null assemblages with the observed data. In both cases, the principal danger has been an elevated likelihood of type II error, that is, of failure to reject the null hypothesis when an alternative hypothesis should be supported (the Narcissus effect of Colwell & Winkler 1984). In some situations, excessive type I errors (spurious rejection of the null hypothesis — Wilson's [1995] Jack Horner effect) are also possible (Pleasants 1990, 1994; Tonkyn & Cole 1986).

The distribution from which species values are drawn in the null model is critical to the performance of the null model test. If an inappropriate distribution is used (i.e. one that poorly approximates the natural distribution), the spacing of values in the null data may tend to be intrinsically more regular or (less likely) more clustered than in the observed data. In the former case, an excess of type II errors would be expected, in the latter, an excess of type I errors, where the hypothesis being tested is that the observed species characters are more regularly spaced than expected by chance, i.e. that there is overdispersion (Schoener 1984). In the past, null data sets have commonly been assembled from a uniform distribution in the same range as the observed data (e.g. Poole & Rathcke 1979; Pleasants 1980; Simberloff & Boecklen 1981). However, it is unlikely that the uniform distribution represents a realistic model for distributions of species attributes in nature (Schoener 1984; Tonkyn & Cole 1986; Manly, 1995b). Tonkyn & Cole (1986) attempted to improve on this approach by drawing null body sizes from two theoretical distributions skewed towards low and intermediate values, which were considered likely to be more abundant in natural species pools, or more likely to evolve. However, the most appropriate sampling distribution will be based on the observed data (Armbruster *et al.* 1994; Manly 1995b). The kernel density estimation approach used in the present study thus represents on improvement on many previous studies: character values in the null model are drawn at random from a smooth distribution which approximates that of the data in which dispersion patterns are sought. This means that the null model is more likely to be a realistic representation of nature under conditions in which the null hypothesis (that there are no assembly rules restricting species similarity) is true, minimising the danger of the Narcissus effect.

The test statistic used to characterise dispersion patterns in the observed and null data can have an important influence on the outcome of null model tests (Fleming & Partridge 1990; Pleasants 1990, 1994; Arita 1993). Simberloff & Boecklen (1981) sought evidence for constant body size ratios by comparing the values of one or three G_{ij} statistics in the observed and null model data, where G_{ij} is the ratio of the ith-smallest to the jth-smallest spacing in log body size between adjacent species in rank order of size ($i<j$). A significantly high value of G_{ij} in the observed data (indicating relatively similar spacing for the two pairs of species involved in the calculation for each data set) was taken as support for the competition hypothesis. This approach has the disadvantage that a potentially large proportion of the available data are ignored in calculation of the test statistics. Pleasants (1990, 1994) has also demonstrated by simulation that the tests statistics used by Simberloff & Boecklen (1981) give an unacceptably high type II error rate, and can spuriously detect overdispersion in clumped distributions. Pleasants (1990) advocates the use of a community-wide parameter as a test statistic, and suggests the mean[2] or the variance of the spacing between each pair of adjacent species along the character axis of interest (Poole & Rathcke 1979). The latter parameter was used as the test statistic (V_T) in the present study. It has the advantage that it is based on the dissimilarity between the pairs of species expected to be involved most strongly in competition for the niche space — those with the most similar characters. As an assemblage-wide parameter, it avoids the danger of drawing conclusions based on a non-representative subset of the whole assemblage (Pleasants 1990, 1994).

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[2] 'Mean' is the mean spacing between adjacent species along the character axis of interest. As Arita (1993) points out, where the null variates can have the same range as the observed data (as usually assumed), the value of 'Mean' will be identical for the observed and each null model data set, making calculation of a P value meaningless. 'Mean' is invalid as a community-wide index of dispersion.

While some objective evidence for competitive niche segregation has emerged from statistical analysis of character dispersion patterns within communities or guilds (Armbruster 1986; Cody 1991; Armbruster *et al.* 1994), many of the positive findings reported have been challenged on methodological grounds, and reanalysis of many data sets has led to rejection of the hypothesis that they are structured by assembly rules. The present study is one of the first in which both an appropriate null model and an appropriate test statistic have been used to seek character overdispersion, and is the first in which assembly rules for plant vegetative niches have been demonstrated using a test for overdispersion in comparison to an explicit null model.

CONCLUSIONS

Relatively little significant evidence of overdispersion of species characters was observed within particular communities, or guilds within communities. However, there were significant trends among communities in several variates, suggesting that assembly rules apply, restricting the co-occurrence of species whose niches (and correlated characters) are too similar. The assembly rules appear to apply in some whole communities, and in the 0-1 m guild, but there is no significant evidence that they operate in the intermediate and upper forest strata. Based on the identity of the characters showing the strongest trends towards overdispersion, it seems likely that assembly rules have led to partitioning of the vertical light gradient among species, although a nutritional interpretation for the patterns is also possible.

Overall, the results obtained in this chapter provide somewhat weaker evidence for assembly rules than the convergence in mean-adjusted texture distributions identified in Chapters 8, 9 and 10. This may be a reflection of the relative power of the two approaches to seeking community structure, tests for overdispersion incorporating more restrictive assumptions as to the manner in which species would be assorted in character space.