4. Interrelationships and vertical trends for species characters

4.1 Introduction

The hypothesis of convergence in community texture is that disjunct communities in similar environments will have more similar texture (community-wide spectra of species functional characters) than expected on the basis of random assortment of species characters among sites (Section 1.5). There are two important assumptions to this hypothesis. The first, that the communities under consideration occur in similar environments, was dealt with in Chapter 3, where groups of study sites with relatively similar environments were identified. The second assumption is that the species characters considered are of functional significance, that is, that they represent aspects of the adaptive strategies by which species capture resources, resist or avoid interference from other species, endure adverse environmental conditions and so maintain non-negative population growth. Convergence between communities would be caused by assembly rules, acting to produce non-random patterns — community structure — in the distribution of species niches in the abstract niche space of a community (Smith *et al.* 1994; Wilson *et al.* 1994). Only functional characters would be expected to reflect species niches, and therefore, community structure.

The above-ground vertical structure within a plant community is associated with a number of environmental and resource gradients that would be expected to influence function: light quality (spectral composition) and quantity (quantum flux), temperature, humidity, exposure to wind and type of herbivory are important examples (Cain *et al.* 1956; Smith 1973; Givnish & Vermeij 1976; Hall & Swaine 1981; Chiarello 1984). Texture, in this study, is expressed in terms of 12 species characters, primarily concerning the morphology and physiology of the PSU. The characters were chosen because they were expected, *a priori*, to be functionally important. In the present chapter, among-species trends in the vertical structure of *Nothofagus* forest are examined with respect to the 12 species characters. Although the patterns examined would primarily reflect beta niche gradients (which have no assembly rules), it seems clear that characters involved in adaptation to environmental factors will also be involved in strategies for resource capture (alpha niches; Pickett & Bazzaz 1978). Where significant vertical trends in species characters are detected, this is interpreted as evidence, supplementary to that presented in Section 2.2.2, that the characters are of functional importance, and may be related to beta and alpha niches.

It is unlikely that most functional characters will be associated uniquely with species position along one particular niche axis. Instead, many characters may represent the outcome of selective trade-offs tending to optimise responses to several biotic and abiotic environmental factors (Givnish 1987). A corollary of this is that functional species characters may themselves be interrelated in potentially complex ways. If community-level patterns (such as texture convergence) are found with respect to several characters, it may be difficult to decide whether, at one extreme, each pattern was caused by a unique process (for example, competition for a particular resource), operating orthogonally to all others; or, at the other extreme, all the observed patterns are an outcome of the same ultimate cause. An understanding of the interactions between characters and their possible relevance to species niche responses would allow such dilemmas to be at least partly resolved. Interrelationships between species characters are examined in this chapter.

4.2 Methods

SPECIES CHARACTER DATA

The 12 species characters evaluated are listed in Section 2.3.5. Measurement and calculation procedures are described in Chapter 2.

ANALYSIS

Intercorrelations between characters

Pearson *r* correlation coefficients were calculated between each pair of species characters, using all species and entities, from all sites, for which unique, measured values were available (no substituted or predicted values). Variates were transformed as described in Section 2.3.4 (Table 2.1). Where the same species was represented by more than one record from different sites, an average for each character was calculated and used. This meant that each species was represented only once in the data set, avoiding the problems of non-independence (Jongman *et al.* 1987), which arise when multiple non-independent values (such as different measurements on the same species) are included in a sample (non-independence would tend to artificially raise the degrees of freedom, resulting in higher apparent significance levels).

Vertical trends in texture

Texture variation along vertical gradients was examined by comparing among-species character means for each landmass (Tasmania, Australia, New Zealand, South America) within each of three classes of height above ground level. These classes were intended to correspond approximately to forest strata (Smith 1973; Wilson 1989; Wilson *et al.* 1995), as follows: 0-1 m (ground/herb stratum), 1-5 m (shrub stratum) and >5 m (tree stratum). Character means for landmasses, rather than individual sites, were used as replicate observations to avoid the spatial autocorrelation that might otherwise result from floristic similarities between sites from the same landmass (Jongman *et al.* 1987). Means for each character within each height class at each study site were calculated using transformed species (or entity[1]) values. Species were deemed to be present within a height class if PSUs of the species were recorded as occurring within the height class (see Section 2.3.2), and species represented by substituted or predicted (rather than measured) values were excluded from analysis. Site means for each height class were themselves averaged to obtain an overall value for each landmass. Significant differences in character values between height classes were sought using single-factor analysis of variance, with the four landmass means for each character/height class combination as replicates.

Analysis of variance was performed with the Teddybear computer program (Wilson 1975).

4.3 Results

INTERCORRELATIONS BETWEEN CHARACTERS

There are significant intercorrelations between most pairs of species characters (Table 4.1). The strongest correlations, all with r values above 0.45 and significant at the 0.1% level, are among the five variates PSU succulence, total chlorophyll, phosphorus, nitrogen and specific weight (SLW), the latter tending to fall as the others increase. Support fraction is also strongly, negatively, correlated with PSU area and specific weight, and relatively strongly with nitrogen content. PSU inclination is relatively strongly associated ($r>0.30$; $P<0.001$) with several other characters: PSU specific weight, shape, lobation and (negatively) nitrogen. PSU thickness is strongly associated with PSU specific weight, and relatively strongly with PSU area and (negatively) lobation. Other pairs of characters tend to be more weakly related, having less than 10% (r^2) of variation in common.

VERTICAL TRENDS IN TEXTURE

Four species characters show significant vertical trends within communities (Fig. 4.1). The value of the PSU shape index decreases with height, indicating a tendency for PSUs to be longer relative to their width closer to ground level. PSU thickness, specific weight and inclination all increase with height, while succulence decreases. None of the other characters differs significantly among height classes, although most show a tendency to either decrease (nitrogen, phosphorus, total chlorophyll) or increase (area, support fraction) towards canopy level.

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[1] Entity, i.e. an age or size class of a species represented by more than one such class in the data for a community (see Section 2.3.2).

Table 4.1 Correlation matrix for 12 species characters, based on species means from 17 study sites. Species characters pertain to photosynthetic units (PSUs: see text) except for support fraction (SF). Abbreviations: SLW=specific weight; N=nitrogen content; P=phosphorus content; chl=chlorophyll (see text for full explanation).

Variate	Chl *a*/*b*	Total chl	P	N	SF	Inclination	SLW	Succulence	Thickness	Lobation	Shape
Area	0.00	-0.03	-0.01	-0.14*	-0.51***	0.17**	0.16**	-0.02	0.31***	0.18**	0.14*
Shape	0.04	-0.16*	-0.15*	-0.25***	-0.28***	0.34***	0.35***	-0.16**	0.11	-0.09	
Lobation	-0.08	-0.18**	0.04	-0.12	-0.25***	0.33***	0.14*	-0.23***	-0.35***		
Thickness	-0.03	-0.19**	-0.10	-0.21***	-0.23***	-0.09	0.46***	0.11			
Succulence	0.13*	0.57***	0.56***	0.53***	0.21***	-0.29***	-0.64***				
SLW	-0.11	-0.68***	-0.49***	-0.59***	-0.38***	0.33***					
Inclination	-0.16**	-0.28***	-0.21***	-0.32***	-0.25***						
SF	0.21***	0.21***	0.20**	0.32***							
N	0.11	0.57***	0.64***								
P	0.32***	0.45***									
Total chl	-0.15*										

$^*0.01 \le P < 0.05$; $^{**}0.001 \le P < 0.01$; $^{***}P < 0.001$

4.4 Discussion

INTERDEPENDENCE OF SPECIES CHARACTERS

The amount of variation shared by most pairs of species characters is relatively low (Table 4.1), indicating that the characters either (1) tend to reflect species responses to different, orthogonally varying ecological factors; or (2) are of little functional importance and have a predominantly stochastic distribution. However, five characters (PSU succulence, total chlorophyll, phosphorus, nitrogen and specific weight) are quite strongly intercorrelated, while a sixth, PSU thickness, has a marked correlation with PSU specific weight. All of these characters may have a component of variation related to light availability.

Variation in leaf structure and function associated with light availability has been demonstrated both within and among species (e.g. Hollinger 1989; Popma *et al.* 1992; Ellsworth & Reich 1993; Mulkey *et al.* 1993). In general, sun leaves, and leaves of plants associated with sunny environments, are more `expensive,' with higher relative investments in mechanical, vascular and other non-photosynthetic tissues, presumably compensated for by an increased return in carbon fixation (Björkman 1981; Bongers & Popma 1988; Popma *et al.* 1992). Since non-photosynthetic tissues account for a greater proportion of leaf dry weight than in `cheaper' shade-adapted leaves, total chlorophyll content as well as concentrations of nutrients primarily associated with photosynthetic tissues — such as nitrogen and phosphorus (Evans 1989; Reich *et al.* 1991) — may be lower on a dry-weight basis (Bongers & Popma 1988; Reich & Walters 1994). Sun-adapted leaves may have multiple palisade cell layers, an adaptation that would increase the efficiency of photon capture. They may also possess a greater volume of mesophyll air space, which would enhance CO_2-diffusion within the denser photosynthetic tissue (Jackson 1967; Parkhurst 1986). Such anatomical differences tend to produce greater leaf thickness and dry weight per unit area (leaf specific weight) in sun- as opposed to shade-adapted leaves (Björkman 1981; Gulmon & Chu 1981; Bongers & Popma 1988). Higher mesophyll air space, as well as a greater content of sclerenchyma in sun-adapted leaves, imply that relative water content (succulence) would be lower.

Partitioning of the light gradient among species is a conspicuous aspect of above-ground structure in forests, which may be mediated by assembly rules (Wilson 1989; Wilson *et al.* 1995). PSU succulence, total chlorophyll, phosphorus content, nitrogen content, specific weight and thickness may represent different components of a character syndrome controlled by the light gradient. This possibility was taken into account in interpreting convergence in terms of these factors in Chapters 6-10.

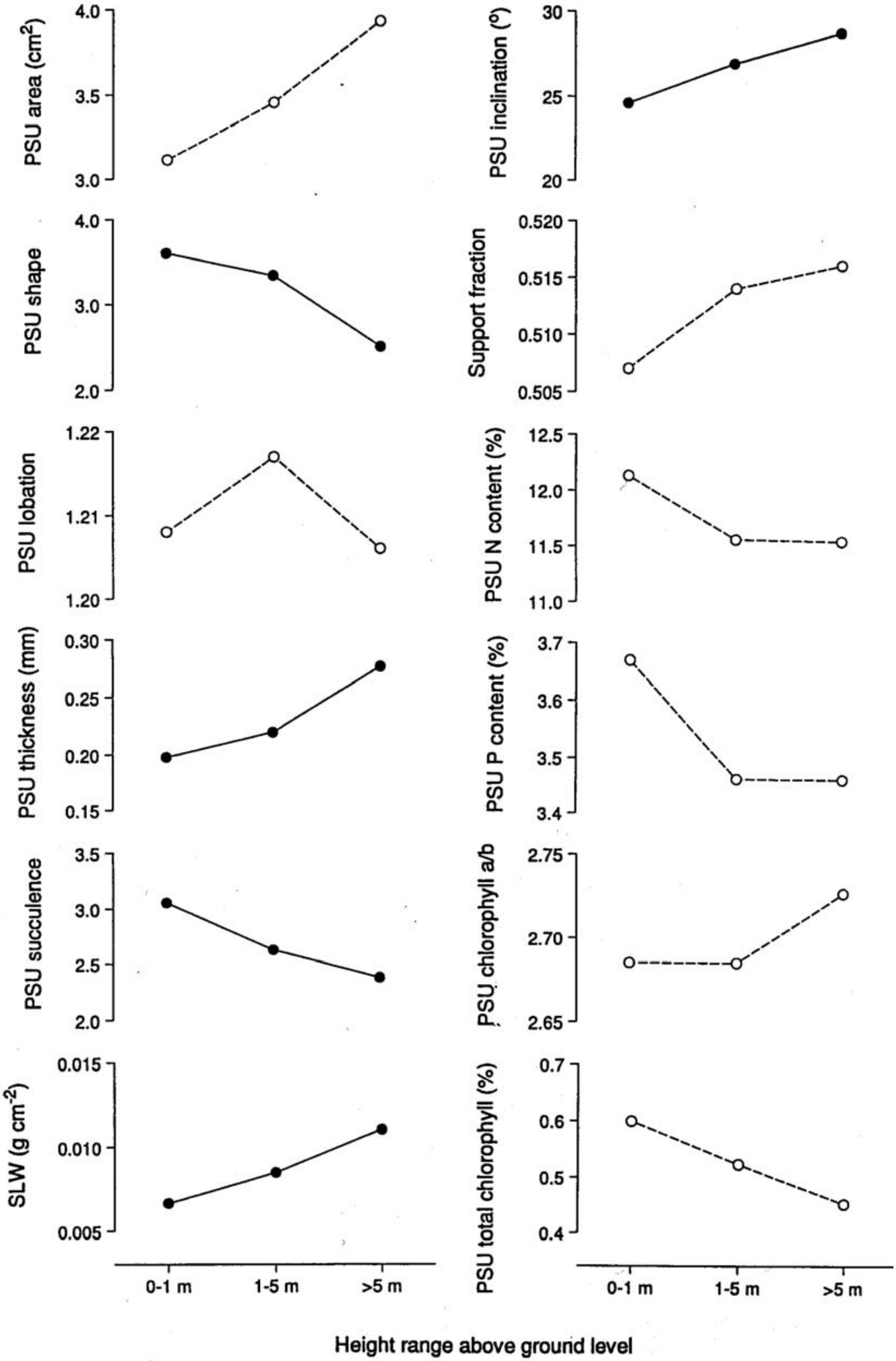

Fig. 4.1 Mean values (all species, all sites: see text) for 12 species characters within height classes 0-1 m, 1-5 m and >5 m above ground level. Solid lines and filled points identify characters varying significantly between height classes (*P*<0.05; ANOVA of landmass means for height classes); dashed lines and open points represent characters with non-significant variation between height classes.

FUNCTIONAL SIGNIFICANCE OF SPECIES CHARACTERS

The primary aim of the present study is to determine whether certain communities exhibit structure in the distributions of species niches in abstract ecological space. Since niche space is defined with respect to a potentially infinite number of parameters, niches cannot be measured directly. However, attributes linked to species function, such as aspects of morphology or physiology, should be related to the underlying niche axes. In other words, structure in the distribution of species niches in ecological factor space should be reflected by structure in the distributions of species attributes in character space (Ricklefs & Travis 1980; Wiens 1991b; Weiher & Keddy 1995a; but see Laurie & Cowling 1994).

The functional importance of a species character may be assessed by examining its variation with respect to environmental variables. A close relationship between species values for a given character (e.g. leaf area) and their distributions along an environmental gradient (e.g. temperature), would suggest that the character is involved in adaptive trade-offs leading to optimal function in the conditions experienced by each species at its position along the various gradients it faces[2], i.e. in its beta niche. Whether species values for a character are determined genetically or reflect short-term plastic responses is not critical to the value of the character as a proxy variable for niches, so long as it is a reliable predictor of the environmental variable.

Is the demonstration of variation in a character along beta niche axes (for which no species-mediated restrictions on niche overlap should apply) sufficient evidence that the character will also differ among alpha niches (for which limiting similarity might apply)? The proximal effects of species interactions (the basis of assembly rules that would limit overlap of alpha niches and so produce community structure) would be to modify the microenvironments experienced by the interacting individuals. Although the objects of competition must be resources (such as light, nutrients, water and establishment sites), differences in resource spectra will be accompanied by differences in microenvironments, which should be reflected in functional species attributes. For example, in the above-ground vertical structure of a forest, there will be correlated gradients in light availability, temperature, humidity, windspeed, density of herbivores and other factors. All may influence species attributes, yet only one — light availability — directly represents a resource for which competition is likely. This means that species characters should be related to alpha, as well as beta, niches.

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[2] An alternative explanation would be that the environment controls species characters directly (not via natural selection). For example, `wind-training' may be involved in producing krummholz growth forms in shrubs growing in windy alpine environments (Daubenmire 1974). It seems unlikely that the direct mechanical action of environmental forces would have played a major role in producing patterns observed for species characters in this study.

VERTICAL TRENDS IN TEXTURE

Of the five variables exhibiting significant differences in mean character values at different heights (Fig. 4.1), three (PSU thickness, succulence and specific weight) belong to the group of highly intercorrelated variates, described above, and vary in a manner consistent with the interpretation that they represent species responses to the light gradient (Gulmon & Chu 1981; Bongers & Popma 1988; Witkowski & Lamont 1991; Ellsworth & Reich 1993). This interpretation is based on the assumption, which seems reasonable, that light availability increases towards the canopy. Patterns in PSU nitrogen, phosphorus and total chlorophyll content are not significant, but each constituent shows a tendency to occur at higher concentrations in the leaves of ground-layer plants, which is likewise consistent with the postulated light response (Björkman 1981; Field & Mooney 1986; Evans 1989; Reich *et al.* 1991).

The significant observed increase in PSU inclination with height can likewise be explained as a function of the light regime (Givnish 1984; Hollinger 1989; Herbert & Nilson 1991), which might operate via an energetic trade-off of light reception against leaf thermal and gas exchange budgets (Givnish 1984; Herbert & Nilson 1991).

The PSU shape index decreases significantly with height, suggesting that PSUs tend to become shorter relative to their width with proximity to the forest canopy. Possibly this simply reflects the relative preponderance of grasses and graminoids, with their highly elongated leaves, in the lower strata.

The observed tendency for PSU area to increase towards the canopy, though non-significant, is of interest, because it may match reports of increases in mean community leaf area with temperature, reported in some studies (Christophel & Greenwood 1989; Mackey 1993; Jordan & Hill 1994). This interpretation of the trend assumes that vertical microclimatic gradients include an increase in temperature (as may be the case in tropical rainforest; Baynton *et al.* 1965; Chiarello 1984).

CONCLUSIONS

Covariation among the 12 species characters is relatively weak, but nevertheless significant for many character pairs. The strongest overall intercorrelations are among PSU succulence, total chlorophyll, phosphorus, nitrogen and specific weight, which may represent a syndrome of responses to the light regime.

Trends among species within the vertical structure of the communities sampled are apparent for nearly all characters, but are significant only for PSU shape (PSUs becoming less elongated with height), thichness (increasing with height), succulence (decreasing), specific weight (increasing) and inclination (increasing). In general, the patterns conform to previously published trends. They tend to vindicate the choice of these characters as proxy variables for species niches.