5. Convergence and divergence in species richness among *Nothofagus*-dominated communities.

5.1 Introduction

A qualitative model of community assembly was described in Chapter 1. Under this model, species interactions, particularly competition, form the basis for assembly rules, which (in this model) restrict what functional types of species can co-occur within communities. Seen in terms of the niche theory of Hutchinson (1958), the effect of assembly rules is to limit how closely species niches can be packed into *n*-dimensional ecological hyperspace (MacArthur & Levins 1967). The environment also affects niches, by restricting the combinations of species attributes that are viable. While assembly rules tend to spread niches out, the environment tends to pack them together, into a niche space hypervolume of limited size (Pianka 1976). A corollary of this model is that the number of niches, and therefore species, that can occur in a community in a particular habitat will tend to be constrained. By contrast, if there were no assembly rules, an arbitrary number of species could be packed into the available niche space.

This is the basis of the concept of niche limitation, whereby the number of species encountered within sampling areas of a given size within a uniform habitat is expected to be more constant than expected by chance (Wilson *et al.* 1987; Watkins & Wilson 1992; Zobel *et al.* 1993). The same concept implies that the number of species comprising disjunct communities in similar environments should be more similar than expected by chance: the communities should exhibit convergence in species richness.

This hypothesis may be tested if a null probability distribution for among-community variation in species richness can be constructed. However, this is not a straightforward task: if the convergence hypothesis is true, species richness may be constrained (by assembly rules) not only in different communities with similar environments, but also within each community (e.g. among replicate quadrats). This means that the null distribution cannot be determined solely from species richness observations among the communities for which convergence is to be sought. Schluter (1986) overcame this problem by sampling in different types of community, that would not be expected to converge. Finch species numbers were obtained for several distinct habitats on each of five continents. An *F*-test was used to seek departure from the null hypothesis that richness within each habitat on each continent was drawn at random from an overall distribution defined by the observed pool of values. The null hypothesis was rejected when the variance in richness among continents was significantly low relative to richness among habitats, signifying that the continents were convergent, over all habitats, in species richness.

Where data from a range of habitats are not available, convergence cannot be sought directly. However, if replicate richness values are available for each community, it is possible to test the alternative hypothesis that communities are *divergent* in species richness — more dissimilar than expected on a random basis. Failure to reject the null hypothesis, that species richnesses are determined by random draws from the observed pool of values, may then be interpreted as preliminary evidence that convergence between the communities *might* have occurred. This approach was used by Wiens (1991a), who applied a Mann-Whitney *U* test to determine whether the avifaunas of North American and Australian shrub deserts were more dissimilar in species richness than expected by chance. The null hypothesis could not be rejected, and the communities were deemed `similar' in species richness.

Community species richness may be influenced by a variety of biological and physical factors of which assembly rules are but one. Biogeographic history, migration and extinction rates, frequency and severity of disturbance and the physical sizes of individuals are examples of factors that might also play a role (Whittaker 1977). Where any of these factors vary in different communities, the communities may become more dissimilar in species richness than expected by chance, i.e. they may diverge.

In the present chapter, divergence in species richness is sought among *Nothofagus*-dominated communities at the local, regional and landmass scales. A bootstrap-based test is used to test a null model under which vascular plant species richnesses are drawn at random from a pool comprising observed values for each replicate quadrat in each community being compared. The test is similar in principle to the familiar analysis of variance, asking whether richness variation among communities is significantly higher than variation among quadrats within communities. Where significant departure from the null model is observed, this is interpreted as divergence in species richness. An absence of significant divergence is taken as preliminary evidence that convergence *may* have occurred, and assembly rules might operate. However, the null hypothesis, that species richness is determined by chance, cannot then be rejected. More conclusive evidence of community-level convergence is sought in subsequent chapters comparing communities in terms of their texture.

To investigate the possibility that observed patterns in species richness are primarily the result of environment variation rather than the action of assembly rules, relationships of species richness to environmental factors are sought using regression analysis.

5.2 Methods

SPECIES RICHNESS DATA

Species richness data were obtained for replicate 20 × 20 m quadrats within each of 17 study sites. Field sampling techniques and criteria for the choice of study sites are given in Section 2.3, while study sites and their environments are described and compared in Chapter 3.

ANALYSIS

Bootstrap tests for divergence in species richness

The bootstrap test employed here draws samples with replacement from a data pool comprising species richness values for each replicate quadrat from each of the communities being compared. Null model communities are assembled by assigning a bootstrap value to each replicate quadrat for each of community. The among-community variance in mean species richness for the observed data is compared with the variances obtained for each of many sets of `communities' generated under the null model, to test the hypothesis that variance among communities is no greater than would be expected if their quadrat richnesses were drawn at random from the underlying distribution. The approach is superficially analogous to analysis of variance (with communities as 'treatments', and quadrats as replicates), but does not assume that the richness data are drawn from a normal distribution (Crowley 1992). This was an advantage because the observed distribution of species richnesses was significantly skewed, even following square root-transformation.

Comparisons seeking among-community differences in species richness were carried out for communities[1] at the local, regional and landmass scales. At the landmass scale, an overall comparison among all communities, and separate comparisons for each of the six possible pairs of communities, were performed. Within each landmass, an overall comparison of all regional communities, and comparisons of each pair of communities, were carried out. For regions in which more than one site was sampled, comparisons were performed among all local communities, and all possible pairs of communities. In addition, individual sites from different landmasses that were identified as having closely-matched environments (Section 3.3), were compared. The network of comparisons is presented schematically in Fig. 5.1.

For each comparison, 10^4 null model data sets were generated by drawing bootstrap samples (i.e. at random and with replacement) from a pool of values comprising replicate quadrat richnesses from all communities being compared. In the case of pooled communities, comprising more than one site, all quadrats from all consituent sites were treated as individual replicates. Quadrat species richness values were square root-transformed prior to analysis to compensate for skewness in their distribution.

The test statistic employed was the among-community variance in species richness, V_r

[1]The reader is reminded that ‘community’ is used throughout this report in a reductionist and operational sense to refer both to individual sites (local or regional communities) and pooled data from several sites within a local area (some regional communities) or region (landmass communities). A full explanation is given in Section 1.4.

$$V_r = \frac{\sum_{i=1}^{n} \left(r_i - \bar{r} \right)^2}{n}$$

where n = the number of communities being compared;

r_i = mean species richness (simple mean among all quadrats) for community i;

$\bar{r}$ = the mean of r_i across all n communities.

V_r was calculated for each null model data set, as well as for the observed data. The significance P of departure from the null model was determined as the proportion of null model data sets for which the value of V_r was at least as large as for the observed data. The test was one-tailed. That is, departure from null model expectation was sought only in the direction of a variance excess in the observed communities (i.e. divergence in species richness). This was because there is no reason to expect within-site variation in quadrat richness to be *greater* than among-site variation, even if the same assembly rules apply in different communities. Only if there were a hypothesis under which this were to be expected would a two-tailed test be appropriate. A failure to reject the null hypothesis would not necessarily support the common operation of assembly rules in different communities. Rather, it would mean that this possibility could not be ruled out.

Species richness variation with environment

Evidence that species richness was influenced by variation in measured environmental factors was sought by multiple regression of site species richness (means of quadrat richnesses) on environmental parameters mean temperature of the warmest month (MTWM), mean temperature of the coldest month (MTCM), mean annual temperature (MAT), annual rainfall (AR), rainfall in the driest quarter (RDQ), soil total nitrogen (N) content, soil total potassium (K) content, soil total phosphorus (P) content, soil pH and soil organic content (OC). Species richness was square root transformed, while environmental parameters were transformed as shown in Table 5.1. Separate regressions were performed without Soil P, but including all 17 study sites, and with Soil P, excluding Chilean and Argentinian sites, for which no suitable Soil P values were available (Sections 2.3.4, 3.3). For each regression, an iterative step-down procedure was performed to eliminate parameters that did not explain a significant independent portion of the total among-site variation in species richness.

Simple regression was performed to determine whether species richness seemed to be be influenced by canopy light transmittance. Separate regressions were obtained for sites at which light transmittance values were obtained in ‘sunny’ (7 sites) and ‘cloudy’ (9 sites) conditions (Section 3.3).

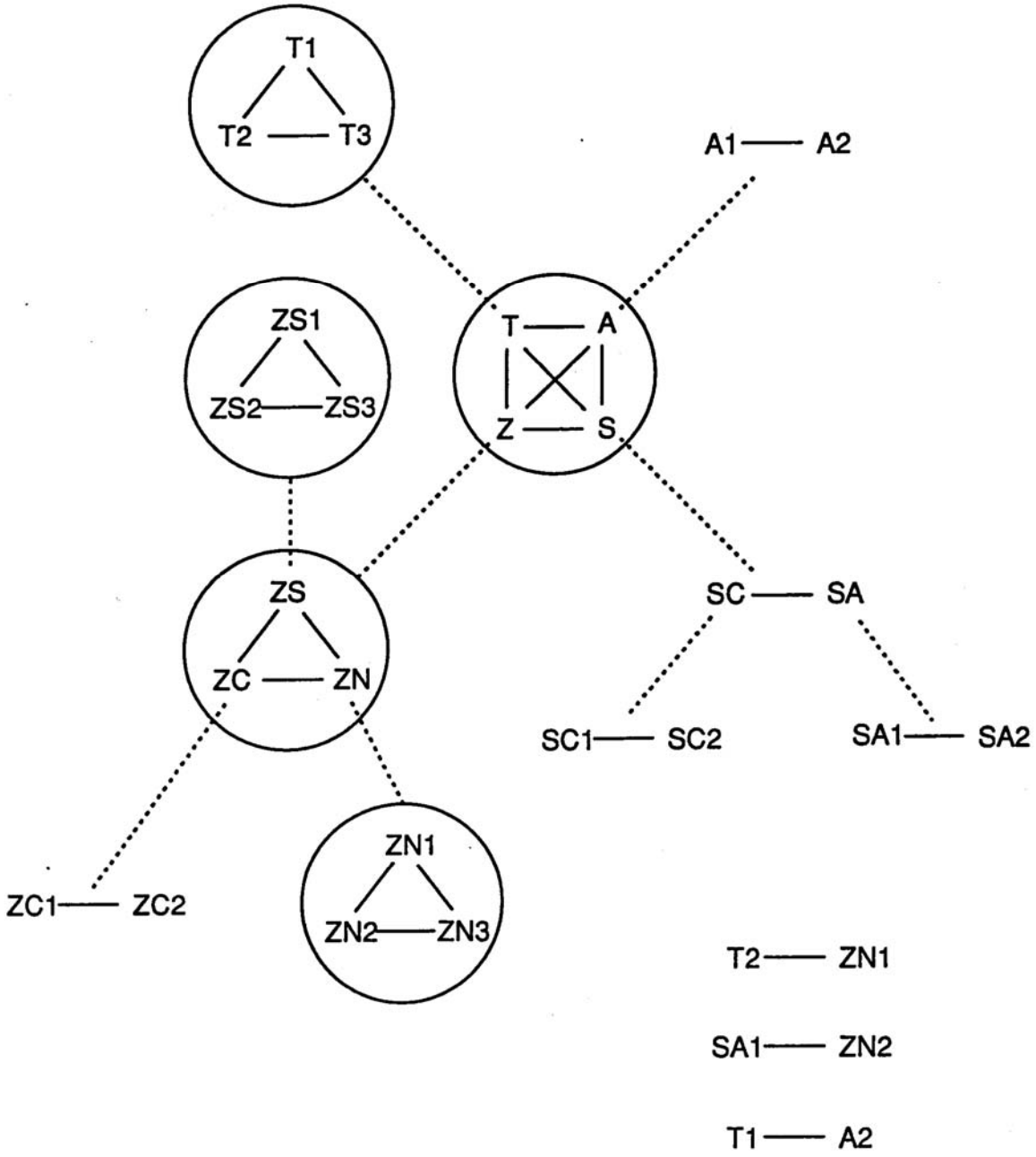

Fig. 5.1 Schematic diagram showing comparisons (solid lines and circles) seeking divergence in species richness between landmass-, regional- and local-scale communities. Letter codes denote communities, as listed in Section 3.2. Broken lines represent spatial hierarchical relationships between communities.

Table 5.1 Transformations applied to each environmental parameter. The expression shown gives the transformed value from a raw value, *x*. ln=natural logarithm (see text for other abbreviations).

Environmental parameter	Transformation expression
MTWM	*x*
MTCM	*x*
MAT	*x*
AR	ln *x*
RDQ	ln *x*
Soil N	ln *x*
Soil P	ln *x*
Soil K	ln *x*
pH	*x*
OC	*x*
light (cloudy)	*x*
light (sunny)	ln *x*

5.3 Results

TESTS FOR DIVERGENCE IN SPECIES RICHNESS

The mean number of species per 20 × 20 m quadrat for each local, regional and landmass-scale community is given in Table 5.1. Among communities at the landmass scale (Table 5.2) there is significant overall divergence in species richness. New Zealand is divergent with respect to all other landmasses. However, the hypothesis that species richness is the same for Tasmania/ Australia, Tasmania/South America and Australia/South America can not be rejected.

Comparing regional-scale communities (Table 5.3), there is overall divergence in species richness among the three Tasmanian sites, although in pairwise comparisons only T1 Balfour and T3 Mathinna have significantly different richness. Mainland Australian sites A1 Lumeah and A2 Cascades are not demonstrably divergent. Species richness differs significantly between southern (ZS), central (ZC) and northern (ZN) New Zealand, southern/northern and central/northern New Zealand are also divergent. Chilean and Argentinian communities are significantly divergent.

Table 5.1 Vascular plant species richness for communities at the landmass-, regional- and local scales. Values are back-transformed means of square-root transformed values for each 20 × 20 m quadrat sampled in each community.

Scale					
Landmass		Region		Local	
Community	Species	Community	Species	Community	Species
T	16.2	T1	17.7	ZS1	14.9
A	19.5	T2	16.7	ZS2	19.0
Z	27.6	T3	15.2	ZS3	19.2
S	20.3	A1	19.7	ZC1	37.6
		A2	19.4	ZC2	13.0
		ZS	17.6	ZN1	45.0
		ZC	23.7	ZN2	46.7
		ZN	43.2	ZN3	38.2
		SC	23.3	SC1	21.2
		SA	16.2	SC2	25.0
				SA1	19.0
				SA2	13.7

Table 5.2 Bootstrap null model tests for divergence in species richness for landmass-scale communities Tasmania (T), mainland Australia (A), New Zealand (Z) and South America (S) (see Section 3.2). *P* shows the proportion of null model simulations in which the among-community variance in species richness is at least as large as for the observed data. Comparisons showing significant departure from null model expectation ($P<0.05$) are shown in bold type.

Comparison	*P*	Comparison	*P*
T,A,Z,S	**0.026**	**A,Z**	**0.026**
T,A	0.413	A,S	0.846
T,Z	**0.000**	**Z,S**	**0.020**
T,S	0.268		

Table 5.3 Bootstrap null model tests for divergence in species richness for regional-scale communities (codes given in Section 3.2). Format as for Table 5.2.

Comparison	*P*	Comparison	*P*
T1,T2,T3	**0.032**	**ZS,ZC,ZN**	**0.000**
T1,T2	0.402	ZS,ZC	0.210
T1,T3	**0.007**	**ZS,ZN**	**0.000**
T2,T3	0.114	**ZC,ZN**	**0.001**
A1,A2	0.820	**SC,SA**	**0.001**

At the local scale, equality of species richness cannot not be rejected for southern New Zealand sites, either in an overall comparison of the three communities, or within each pair (Table 5.4). Central and northern New Zealand sites, on the other hand are generally divergent in species richness, with the exception of ZN1 Ohakune and ZN2 Rotokura. Chilean sites SC1 Pelada and SC2 Antillanca are divergent, as are Argentinian sites SA1 Quetrihué and SA2 Gutierrez.

Table 5.4 Bootstrap null model tests for divergence in species richness for local scale communities (codes given in Section 3.2). Format as for Table 5.2.

Comparison	*P*	Comparison	*P*
ZS1,ZS2,ZS3	0.158	**ZN1,ZN2,ZN3**	**0.015**
ZS1,ZS2	0.103	ZN1,ZN2	0.610
ZS1,ZS3	0.091	**ZN1,ZN3**	**0.030**
ZS2,ZS3	0.938	**ZN2,ZN3**	**0.006**
ZC1,ZC2	**0.001**	**SC1,SC2**	**0.002**
		SA1,SA2	**0.021**

Of the three pairs of environmentally matched sites from different landmasses, only one, T1 Balfour/A2 Cascades does not show significant divergence in species richness (Table 5.5).

Table 5.5 Bootstrap null model tests for divergence in species richness for sites from different landmasses with closely matched environments. Site codes are given in Section 3.2. Format as for Table 5.2.

Comparison	*P*
T1,A2	0.837
T2,ZN1	**0.001**
ZN2,SA1	**0.005**

SPECIES RICHNESS-ENVIRONMENT RELATIONSHIPS

Step-down multiple regression of site species richness on climate and soil parameters (17 sites) revealed that species richness can be expressed as a function of two parameters, soil nitrogen content, accounting for 33% of variation in species richness ($P<0.01$) (Fig. 5.2), and MTWM, which explains a further 16% of variation ($P<0.05$). Species richness is a rising function of both explanatory variables. The whole regression accounts for 49% of among-site variation in species richness and is significant at the 1% level. Soil P was not a significant parameter of a second regression using only 13 sites but including all environmental variables; results are not presented. Species richness was not found to be significantly related to canopy light transmission, either for `cloudy' ($r^2=0.0\%$; $P=0.901$, n.s.) or `sunny' ($r^2=0.0\%$; $P=0.994$, n.s.) sites.

5.4 Discussion

COMMUNITY-LEVEL CONVERGENCE

The results obtained from null model comparisons provide some preliminary support for possible community-level convergence in species richness. The test used sought significant departure from the null hypothesis that species richness variation among communities was no higher than variation among quadrats within communities. This approach can demonstrate significant divergence, but is unsuitable for evaluating the significance of convergence (Section 5.1). A failure to observe divergence is interpreted here as possible evidence of convergence, but it is stressed that such conclusions are preliminary only, not being based on significant results.

For three of the six possible comparisons of one landmass with another, the hypothesis that mean quadrat species richness was the same in the *Nothofagus*-dominated communities sampled on both landmasses, could not be rejected (Table 5.2). The same was true of a number of comparisons at the regional and local scales (Tables 5.3, 5.4). A possible interpretation is that similar assembly rules apply at different sites, or within similar habitats in different regions or landmasses. Assembly rules (based on past or present species interactions, such as competition

for the same resources) would limit the allowable degree of niche overlap between co-occurring species, thus limiting the number of species that can be packed into the finite niche space provided by the environment (Pianka 1976).

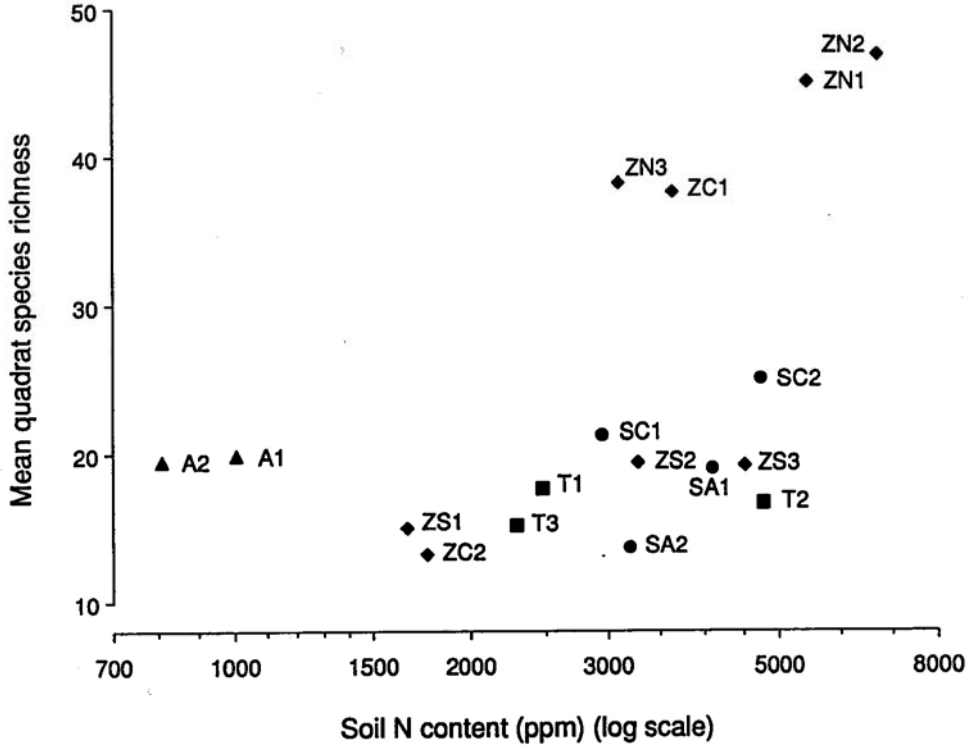

Fig. 5.2 Relationship between site mean species richness in 20 × 20 m quadrats and soil total nitrogen content. Site codes (Section 3.2) are shown beside data points; symbols correspond to landmasses, Tasmania (■), Australia (▲), New Zealand (♦) or South America (●).

DIVERGENCE IN SPECIES RICHNESS

Although the statistical significance of convergence in species richness could not be determined, significant divergence (greater dissimilarity in species richness between communities, than among quadrats within communities) was able to be demonstrated.

Several groups of communities at each scale were found to be divergent in species richness. What factors distinguish groups of communities showing divergence from others that do not? Environmental differences would affect species richness, because a change in the dimensions of the environmentally-determined hypervolume into which species niches are packed would alter the number of niches that can be accomodated, assuming that other relevant variables (such as the limiting similarity between adjacent species) remain unchanged (Whittaker 1977). Multiple regression revealed a tendency for species richness to increase with soil fertility

(in terms of total nitrogen content), while temperature (MTWM) significantly explained some residual variation (Section 5.3; Fig. 5.2). The observed relationship, if causal, could explain a failure for some of communities to exhibit convergence in species richness.

If significant differences in species richness have an environmental basis, then it might be expected that divergent communities would belong to groups identified as being poorly matched in their environments in Chapter 3, while non-divergent communities might be those that were found to be more similar in their environments. Such a pattern does not appear to apply at the landmass scale. The landmasses that were closest together in environmental factor space, Tasmania and New Zealand (Figs. 3.5-3.7) are significantly divergent in species richness, while *Nothofagus*-dominated communities in Australia and South America, that appear to have relatively dissimilar environments, do not differ significantly in species richness (Table 5.2).

At the regional and local scales, there is some evidence that divergence in species richness corresponds to soil factor differences. T1 Balfour and T3 Mathinna differ significantly in species richness, and are also more distantly spaced in soil space (though not in climate space) than Balfour and T2 Anne, which have comparable numbers of species (Table 5.3). Among the three regions of New Zealand, only central (ZC) and southern (ZS) New Zealand are non-divergent in species richness. Sites from these regions have relatively similar soils in comparison to those of northern New Zealand (ZN), which, notably, are generally higher in nitrogen (Table 3.3). Among northern New Zealand sites, only ZN1 Ohakune and ZN2 Rotokura do not differ significantly in species richness (Table 5.4). Compared with ZN3 Clements, Ohakune and Rotokura have more similar concentrations of potassium and nitrogen (Table 3.3).

Of the three comparisons involving sites from different landmasses, selected for being relatively similar in at least some aspects of their environments (Section 3.3), only one pair of sites, T1 Balfour and A2 Cascades, does not have a significantly different number of species per quadrat. However, these two sites are closely matched in terms of both climate and soils, whereas T2 Anne and ZN1 Ohakune may differ in soil fertility levels; ZN2 Rotokura and SA1 Quetrihué are more distantly spaced in both climate and soil space.

RELATIONS OF OBSERVED PATTERNS TO PREVIOUSLY REPORTED TRENDS

Previous studies reveal that patterns of variation in species richness are not simple, but may be influenced by a range of factors including the physical environment (Hamilton 1975; Glenn-Lewin 1976; Carson & Pickett 1990; Smith *et al.* 1995), species morphology (Van der Maarel 1988), disturbance regimes (Connell 1978; Tilman 1982; McIntyre & Lavorel 1994), successional state (Egler 1954; Auclair & Goff 1971; Nicholson & Monk 1974; Pickett *et al.* 1987) and evolutionary and biogeographic history (Keddy 1976; Naveh & Whittaker 1979; Currie & Paquin 1987).

Different factors are likely to be important at different scales (Kolasa & Biesiadka 1984;

Ricklefs 1987). Patterns of species richness within a biogeographic region may correspond to environmental variation, for example, in soil fertility (Rice & Westoby 1983b; Van der Moezel & Bell 1989), moisture regimes (Naveh & Whittaker 1979; Margules *et al.* 1987) or temperature (Hamilton 1975; Margules *et al.* 1987). Although monotonic relationships have been found in particular studies, an overview of results from different studies suggests an absence of simple broad trends. For example, species richness has been found to increase along gradients of increasing soil fertility (Vasander 1987; Carson & Pickett 1990), but also to decrease with increasing fertility (Huston 1980; Rice & Westoby 1983b; Faber-Langendoen & Gentry 1991).

Some have suggested that the environment affects species richness by controlling primary productivity, and that the response curve may be ditonic, rising at first as productivity increases but ultimately declining as increasing competition leads to dominance by a few species (Whittaker 1977; Grime 1979). Ditonic changes in species richness have been found along gradients of moisture availability (Whittaker 1956), soil fertility (Vasander 1987), and with respect to standing crop and litter densities (Al-Mufti *et al.* 1977). If this interpretation is correct, it could explain dichotomous patterns of local and regional-scale variation in species richness among different studies.

At scales broader than the local area or biogeographic region, historical or evolutionary processes may confound effects of the physical environment on species richness (Ricklefs 1987). For example, differences in biogeographic history and the time available for evolution may explain differences in woody and herbaceous vascular diversity in shrublands of Israel, California, Chile, South Africa and Australia (Naveh & Whittaker 1979; Rice & Westoby 1983b; Cowling & Witkowski 1994).

Clear broad-scale trends of increasing species richness from high to low latitudes have been observed (Pianka 1966; Currie & Paquin 1987; Stevens 1989). Possible explanations for these trends include differences in glacial, geological and biogeographic history (Simpson 1964); an increase in spatial heterogeneity (i.e. microhabitat diversity) towards the tropics (MacArthur 1964); effects of climatic variation on species geographic ranges (Stevens 1989); and the increasing importance of interspecific competition as physical stresses decline away from the poles (Pianka 1966). It has been suggested (Currie & Paquin 1987) that gradients in available energy may underlie latitudinal trends, the total available energy being partitioned among species, limiting species richness (Odum 1975).

The diversity of factors affecting species richness, and the range of trends that have been observed, make it difficult to interpret patterns observed in the present study in terms of previous findings. There is evidence that non-convergence in species richness at the local and regional scales may be driven by differences in soil nitrogen (or associated factors) and possibly differences in temperature. Possible effects of soil nutrient status on diversity have been identified previously. However, while richness was found to increase with fertility in the present study, previously reported trends in forest and woodland vegetation have generally been in the

opposite direction (Huston 1980; Rice & Westoby 1983b; Van der Moezel & Bell 1989; Faber-Langendoen & Gentry 1991). Correlations with temperature have also been found, and these are generally positive, as in the present study (Whittaker 1956; Hamilton 1975; Margules *et al.* 1987). Temperature (as a parameter of environmental energy) may also play a role in producing latitudinal gradients in species diversity (Currie 1991); again, this trend is a positive one.

Variation in measured environmental parameters did not clearly account for divergence in species richness observed among communities at the landmass scale. Historical factors, or unquantified differences in the environments of different landmasses might play a role. For example, the low vascular plant richness of Tasmanian rainforests, observed in this study (Table 5.1), has been noted previously. A possible explanation may lie in the island's insularity coupled with the extinction of many rainforest taxa as a result of Tertiary and Quaternary climate change and Pleistocene glaciations (MacPhail *et al.* 1993).

Differences in the degree to which *Nothofagus*-dominated communities are associated with disturbance on different landmasses could account for the variation in species richness observed among landmasses. In the Andes of Chile and Argentina, many *Nothofagus* stands appear to have developed following perturbations associated with vulcanism or tectonic activity (Veblen *et al.* 1981; Veblen 1985). Veblen *et al.* (1981) suggest that succession, uninterrupted by further disturbance, would lead to replacement of *Nothofagus* by more shade-tolerant genera. Two of the study sites sampled in South America (SC1 Pelada and SA2 Gutierrez) comprised *Nothofagus* stands that were clearly even-aged, suggesting that they represent a single cohort that established following a large-scale disturbance. Species richness was low at both sites, contributing to the low overall richness value obtained for South America (Table 5.1). Although disturbance, particularly at the patch scale (June & Ogden 1975, 1978), may influence regeneration patterns in New Zealand *Nothofagus*-dominated forests (Wardle 1984; Jane 1986; Mark *et al.* 1989), it has not been regarded as a major factor influencing community persistence. Tasmanian (Read & Hill 1985, 1988) and Australian (Read & Hill 1985) *Nothofagus*-dominated forests do not seem to be dependent on allogenic disturbance, either for establishment or persistence. Effects on species richness of both disturbance intensity and time since disturbance, have been predicted (Egler 1954; Connell 1978; Pickett *et al.* 1987; Wilson *et al.* 1992a). However, empirical patterns are complex (Collins & Barber 1985), and both increases and decreases in species richness, depending on time since disturbance (Bazzaz 1975) or environments (Auclair & Goff 1971) have been observed.

PREVIOUS STUDIES OF CONVERGENCE IN SPECIES RICHNESS

While the possibility of convergence in species richness in similar vegetation types on different continents has often been discussed (Parsons & Moldenke 1975; Whittaker 1977; Cody & Mooney 1978; Naveh & Whittaker 1979; Rice & Westoby 1983a; Fox 1995), there have been few attempts to demonstrate such convergence objectively. Examining patterns of diversity within several animal guilds, Cody *et al.* (1977) reported significant similarities in species-area curves for mediterranean-climate regions in California and Chile. Schluter (1986) detected significant convergence in species richness among finch communities from five continents.

The test employed by Schluter (*op. cit.*) was a modified analysis of variance, with continents as `treatments' and richness values from nine separate habitats, represented on each continent, as replicates. This approach is superficially similar to that employed in the present chapter, but because a range of distinct habitats was sampled on each continent, it was reasonable to apply a two-tailed test for departure from the null hypothesis that species richness was as variable among habitats within continents, as among continents. This meant that convergence (significantly lower variation among continents than among habitats) could be positively demonstrated. In the present study, replicates were randomly-located quadrats within the communities being compared. There was no basis for expecting among-quadrat variation to exceed among-site variation. Therefore a two-tailed test could not be applied, and only divergence could be positively shown.

The search for convergence in species richness among disparate communities is analogous to the study of niche limitation within communities. A model of community assembly that would lead to convergence in species richness between communities in similar environments was developed in Chapter 1 and discussed above. The same model would, of course, apply within communities, producing greater similarity in the species richness of adjacent patches than expected on the basis of random dispersal (Wilson *et al.* 1987). Niche limitation has been sought, with little success, in an agricultural field, a dune slope community and experimental diatom assemblages (Wilson *et al.* 1987); in old fields (Palmer 1987); and in *Nothofagus*-dominated forest in New Zealand (Bycroft *et al.* 1993). Significant evidence for niche limitation has been found at a fine scale in a managed lawn (Watkins & Wilson 1992) and in northern temperate forests early in succession (Zobel *et al.* 1993), providing evidence for the operation of assembly rules at a local scale.

CONCLUSIONS

Bootstrap tests against a null model of similarity in species richness between communities have provided evidence of possible convergence in species richness at the landmass, regional and local scales. For several comparisons of *Nothofagus*-dominated communities at each scale, the

hypothesis that the communities did not differ in species richness could not be rejected at the 5% level. This suggests that assembly rules may operate in a similar way in the convergent communities, constraining the number of species that can be accomodated within the niche space determined by the environment. However, this hypothesis could not be supported statistically. An alternative interpretation is that species richness is determined by chance.

Statistically significant divergence is also apparent at all scales. Environmental matching between communities would be expected as a precondition for convergence, and there is evidence to suggest that divergence at the regional and local scales is concentrated among communities that are the most dissimilar in their environments, particularly with respect to soil factors. No such clear pattern is apparent at the landmass scale, however, suggesting that factors other than the effects of assembly rules and environment control species richness within different landmasses.