

VEGETATION TEXTURE AS AN APPROACH TO COMMUNITY STRUCTURE: COMMUNITY-LEVEL CONVERGENCE IN A NEW ZEALAND TEMPERATE RAINFOREST

Summary: Functional convergence of different communities in similar environments would be expected as an outcome of the operation of 'assembly rules'. At an ecological level, competitive exclusion would restrict the co-occurrence of species with similar niches. Repetition of competitive sorting on an evolutionary time scale might lead to character displacement. Either process would ultimately lead to species niches being more regularly arranged in ecological factor space than expected on a random basis, with the consequence that the niche structure of different communities in similar environments would converge.

We assessed the applicability of this model of community structure by comparing vegetation between study sites spaced in altitude 20 m apart along a continuous gradient in South Westland low-altitude conifer/broad-leaved forest, with respect to seven variates of vegetation texture primarily concerning the morphology of the photosynthetic unit (PSU). We employed a null model that assigns observed species to sites at random, as would be expected in the absence of assembly rules for the communities, comparing observed variation in texture to variation under the null model to look for convergence or divergence and to determine statistical significance.

Significant convergence between adjacent sites was found in all variates when species weighted either by percentage cover or cover rank were used to calculate site texture means, but convergence was less pronounced among groups of five or 10 consecutive sites. Significant divergence occurred at the five-site level (three variates) using cover rank as a weighting factor and at the two-, five- and 10-site levels (five variates) when no weighting factor was used. Overall, divergence was more pronounced among sets of sites spanning a wider range in altitude, which seemed consistent with the presence of an environmental gradient along the transect, although a DCA ordination of site floristics failed to reveal a simple altitudinal trend.

This study is the first to seek community-level convergence within a local area and the first to find statistically significant convergence between vegetation patches.

Keywords: Altitudinal gradient; assembly rules; coevolution; community-level convergence; community structure; competitive exclusion; null model; photosynthetic unit; randomisation test; temperate rainforest; vegetation texture.

Introduction

The composition of vegetation in a local area may be interpreted as the result of a two-phase 'filtering-out' of taxa from local species pools. The first filter is the abiotic environment, and admits only those species that are viable with respect to climatic and edaphic conditions at the site. The second filter is the biotic environment, and encompasses the species interactions whose net effect, competitive exclusion, is to restrict the co-occurrence of species whose fundamental niches overlap (MacArthur and Levins, 1964). Competitive exclusion is implicit in the concept of 'assembly rules' (Diamond, 1975;

Drake, 1990; Wilson, 1991). Although interspecific competition is conventionally regarded as the main process limiting coexistence of similar species (e.g., Aarssen, 1992), other forms of interference, such as allelopathy, would be expected to have a similar effect.

The niche of a species population within a community may be regarded as a region in n -dimensional space, with axes representing the biotic and abiotic factors to which populations in the community respond differentially (Colwell and Fuentes, 1975). In this context, a community may be expected to consist of an assortment of species populations whose niches are restricted to a specific

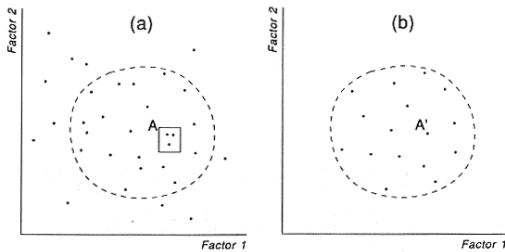


Figure 1: Conceptual distributions of species niches (represented by dots) in two-dimensional ecological factor space for a hypothetical species pool and a hypothetical community assembled from this pool. The broken line encloses an area (or, for n -dimensional space, a hypervolume) representing the environment of the community. Species from the local pool (Fig. 1a) with niches falling outside this region are excluded from the community (Fig. 1b). Competitive sorting of species with similar niches (e.g., boxed cluster A in Fig. 1a) determines which ones can establish in the stable community (A' in Fig. 1b) and results in more regular spacing of species niches in the community than expected for a random selection from the species pool.

volume of ecological factor space, determined by the environment, and more regularly spaced within that volume than would be expected in the absence of competitive exclusion. Regular spacing tends to cluster means of niche parameters in the different communities around the same values, causing the communities to converge. The same result is expected if communities are seen as assemblages of coevolved species (Roughgarden, 1983), rather than ecologically assembled entities as implied above: adaptation to the abiotic environment restricts niches to a specific hypervolume in factor space, while character displacement under the influence of competition (Brown and Wilson, 1956) causes regular spacing of niche optima.

This process may be illustrated schematically. Fig. 1a depicts modes of niche distributions for all species from a hypothetical local species pool, in two-dimensional factor space. Fig. 1b depicts realised niches for a community derived from the same pool. Species whose niches are external to the area encompassed by the broken line, representing the local environment, are excluded. Competitive sorting governs which species out of those with similar fundamental niches (such as the boxed cluster marked A in Fig. 1a) establish in the stable community (species A' in Fig. 1b). The niches represented in the resulting community are more regularly spaced than expected for a random

selection from the local species pool. In an evolutionary time frame, species belonging to cluster A undergo selection for traits that make them sufficiently different to coexist in the stable community. Again, the result is a more regular spacing of niche optima than expected on a random basis.

We examined the validity of the above model of community structure by looking for evidence of convergence in vegetation texture among a series of temperate rainforest sites. Texture, defined as "the qualitative and quantitative composition of vegetation as to different morphological elements" (Barkman, 1979), can provide a measurable surrogate for niche position in factor space. We focused on seven texture variates primarily concerning the form of the photosynthetic unit (PSU) which, as a primary site of photosynthesis, gas exchange, water loss and nutrient and energy allocation, is fundamental in determining plant niches (Givnish, 1987).

We sampled 10 sites spanning 15 km in distance and spaced 20 m apart in altitude on a continuous elevational gradient. Elevation is known to be the major factor controlling vegetation composition in Westland conifer/broad-leaved forests (Reif and Allen, 1988). Therefore, we expected to find more evidence of convergence between adjacent pairs of sites, than among consecutive groups of five sites, or among all 10 sites, based on the assumption that adjacent sites would be more closely matched with respect to environment.

To look for convergence, we utilised a test which compares observed variation in species characters (texture) among sites to variation under a null model in which the observed species are allocated to sites at random; that is, with no restrictions on the co-occurrence of species with similar niches. If, among many randomisations, observed between-site variation was consistently lower than variation under the null model, we could conclude that there was convergence in texture among the vegetation patches being compared.

Methods

Study Area

The study was carried out in the Jackson River Valley in South Westland, New Zealand, latitude 44° 05' S; longitude 168° 40' E. Annual rainfall is 4663 mm and mean temperature 10.9°C at the nearest climate station of Jackson Bay (New Zealand Meteorological Service, 1983). Study sites

were restricted to the northern slopes of the river valley, on flat or gently sloping ground with a southerly to easterly aspect. The vegetation consists of low-altitude conifer/broad-leaved forest (Wardle, 1991, pp. 126-132) dominated by rimu (*Dacrydium cupressinum*¹), kahikatea (*Dacrycarpus dacrydioides*), kamahi (*Weinmannia racemosa*) and silver beech (*Nothofagus menziesii*). It has not been subjected to anthropogenic modification except for browsing by introduced red deer (*Cervus elaphus* L.) and possibly brush-tailed possums (*Trichosurus vulpecula* Kerr), although possum populations in the area are small and there was little evidence of their presence at sampling sites. The effect of deer in the area would be to increase the abundance of sclerophyllous and unpalatable shrubs in the understorey, at the expense of more palatable and succulent shrubs and herbs, such as *Polystichum vestitum*, *Griselinia littoralis* and *Coprosma* spp. (Wardle, Hayward and Herbert, 1973). Nevertheless, deer numbers have been considerably reduced in the last 20 years and little evidence of recent browsing was observed during this study.

Substrates in the area are generally yellow-brown earths, podsolised on steeper country away from the river (Soil Bureau, D.S.I.R., 1968, pp. 121, 139, 153). These soils are relatively freely-draining and are characteristic of high-rainfall areas (During, 1967). However, site 1 (at 5 m altitude) was sited on a recent gley, and site 2 (25 m) occurred within a waterlogged kahikatea carr (Wilson, Agnew and Partridge, 1994). The underlying geology consists of undifferentiated sedimentary and metamorphic rock of Lower Palaeozoic or Precambrian age (Mutch and McKellar, 1964).

Field sampling

Study sites were located at 20 m intervals in altitude along the valley, the lowest (site 1) occurring at 5 m elevation, and the highest (site 10) at 185 m. One 10 x 10 m quadrat was positioned within each site, the exact position of the quadrat being randomised within a 25 x 25 m area to avoid inadvertent bias in its placement. At each site the presence of all vascular plant species rooted in or overhanging the quadrat was recorded. A percentage cover value was also obtained for each of the species, based on independent subjective estimates by five observers. Foliage of all species encountered was collected. Multiple collections were made of a species if differences in leaf morphology between sites

seemed possible. In the case of species exhibiting heteroblasty (e.g., *Pseudopanax crassifolius*) juvenile and adult forms were treated as separate species, and sampled accordingly.

Laboratory measurement

The photosynthetic unit (PSU) of each species was defined as the organ most closely analogous functionally to a simple leaf. It was taken to be the leaf for species with simple leaves, a leaflet for species with compound leaves, or a flattened photosynthetic stem (phylloclade) in the case of *Phyllocladus aspleniifolius* var. *alpinus* in which the true leaves of adults are reduced to vestigial scales. In the case of ferns with divided laminae, the PSU was defined as the highest order pinna that did not fuse with adjacent pinnae distal of the rachis. Values of seven morphological characters were obtained for each species, for each site in which it was collected, as described below. These values were used to construct texture variates, containing 'average' values across all species in each site of each of the morphological characters measured.

PSU length:

the maximum longitudinal dimension of the PSU. Values were log transformed for analysis.

PSU width:

the maximum latitudinal dimension of the PSU, log transformed.

PSU thickness:

measured in the field using a micrometer (the midrib was avoided).

PSU area:

obtained using a scanning leaf area meter, log transformed.

Specific PSU [leaf] weight (SLW):

the ratio of PSU dry weight to area, log transformed.

PSU succulence:

approximated as the ratio of PSU thickness to SLW, log transformed. This ratio (the inverse of density; Witkowski and Lamont, 1991) will not be a perfect correlate of true succulence (the ratio of wet to dry weight) because leaf thickness is a function of both air and water content. However, it is likely to be an adequate estimate.

Photosynthetic fraction:

the proportion of photosynthetic material (PSUs) in terminating shoots. A terminating shoot was defined as a shoot distal of the lowest leaf remaining attached

¹ Nomenclature follows Connor and Edgar (1987) and references therein.

to the main stem. The value was obtained as the ratio of dry weight of PSUs to total dry weight per terminating shoot.

Analysis

Our analysis was based on the null hypothesis that variation in texture between the communities under investigation did not differ from that expected on a random basis, that is, in the absence of assembly rules restricting what morphological types of species can co-occur. We defined and implemented a null model that reassigned the observed species to sites at random, subject to certain constraints, as described below, and compared observed between-site variation in each texture variate, to variation under the null model, for each of many randomisations. This enabled us to determine the direction of departure from the null model (whether towards convergence or divergence), and to estimate statistical significance.

Between-site variation in a given texture variate ' i ' for a group of n sites, was estimated as D_i , the mean sum-of-squares of site deviances from the overall mean, defined as follows:

$$D_i = \frac{\sum_{j=1}^n (x_{ij} - \bar{x}_i)^2}{n}$$

where x_{ij} = the (weighted) mean value of variate i at site j ;
 \bar{x}_i = the mean of x_{ij} across all n sites, for variate i .

In calculating x_{ij} all species could be weighted equally, weighted in proportion to their abundance (percentage cover) as recorded in the field, or weighted by cover rank, that is, according to an arithmetic ranking of species from least to most abundant (see below). If species are weighted equally, species of low abundance in a site contribute as much to mean site texture values as more important species. This may be unrealistic in terms of the processes we assume would structure communities, implying that all species affect each other equally, regardless of their relative abundance. In effect, there is a bias towards minor, possibly stochastic components of the texture; this may tend to obscure any real convergence, or artificially imply divergence. Weighting species by percentage cover would seem to be more appropriate, but has the

disadvantage of giving very heavy weight to the canopy dominants. This may indicate convergence where it exists only among a small subset of the total flora present, whose texture is more likely to be merely a reflection of species adaptations to the abiotic environment than of species interactions leading to niche differentiation. Using cover rank as a weighting factor may represent a suitable compromise. For a site with species richness r , the most abundant species (in terms of percentage cover) receives a weighting factor of r ; the next most abundant $r-1$; the next $r-2$ and so on down to 1 for the least abundant species. Cover rank thus takes species abundance into account, without causing an overwhelming bias towards a small number of dominant species.

In execution of the null model, the species observed at the n sites under consideration were pooled and reassigned to the sites at random, observing the following constraints:

1. Species richness was preserved for each site. This was to ensure that similarity exceeding that expected under the null model could only arise as a result of convergence in texture, not species richness.
2. Species abundance (percentage cover) values were retained with sites rather than allocated at random across sites. The sum of species abundance values at a site ('total site abundance') is related to productivity, which is primarily a function of the physical and chemical environment. In order to distinguish species interaction effects from environmental effects the null model must take the abiotic environment, and any factors associated with it, as fixed. Therefore, total site abundances should be held at the values observed, and this was achieved by retaining observed abundance values with sites in the randomisations, while assigning species to abundance values at random.
3. No species was assigned to a site more than once in each randomisation.

Randomisations were performed using the algorithm of Wilson (1987). To determine whether observed texture differed from that expected under the null model, the value of the test statistic calculated using the observed data, $D_{i,obs}$, was compared with the values, $D_{i,rand}$, obtained for each of 2000 randomisations, to yield F_c , the proportion of data arrangements yielding values of $D_{i,rand}$ at least as small as $D_{i,obs}$:

$$F_c = \frac{\text{Count}(D_{i,rand} \leq D_{i,obs})}{2000}$$

and F_d , the proportion of data arrangements yielding values of $D_{i,rand}$ at least as great as $D_{i,obs}$:

$$F_d = \frac{\text{Count}(D_{i,rand} \geq D_{i,obs})}{2000}$$

A value of F_c below 0.5 indicates a trend towards convergence; a value of F_d less than 0.5 indicates a trend towards divergence. Significance was calculated by multiplying the smaller of F_c and F_d (the proportion in the smaller tail in the frequency distribution of $D_{i,rand}$ values) by 2 (to effect a two-tailed test), giving the P -value directly (Crowley, 1992).

Comparisons were performed between each of the nine possible consecutive pairs of sites (5 and 25 m, 25 and 45 m, ..., 165 and 185 m), and between the lower five sites (5, 25, 45, 65 and 85 m), the upper five sites (105, 125, 145, 165 and 185 m), and the full set of 10 sites.

In addition to the randomisation tests, detrended correspondence analysis (DCA) ordinations (Hill and Gauch, 1980) were performed on species presence and percentage cover data, to determine whether the gradient in altitude along the transect was reflected in site floristics.

Results

Species richness per site varied from 26 to 48 with a mean of 35. Mean overlap in species composition between adjacent sites was 61 percent. At least five and on average eight species were not in common between adjacent sites. Seven species occurred in all 10 sites.

Figs. 2-4 show incidences of convergence or divergence in the seven texture variates (at $P < 0.05$), for all consecutive pairs of sites, the lowest and highest five sites, and all 10 sites, when species were weighted equally (Fig. 2), weighted by percentage cover (Fig. 3) or weighted according to cover rank (Fig. 4). A summary of the results of consecutive-pair comparisons is presented in Table 1.

With species weighted equally, significant convergence is rare, arising in only two consecutive-pair comparisons, which may not be significant with respect to the number of tests done (see *Discussion*). Significant divergence, on the other hand, occurs between various pairs of sites in five of the seven variates, and among the lower five sites, and all 10 sites, in respect of PSU width and area.

With species weighted by percentage cover,

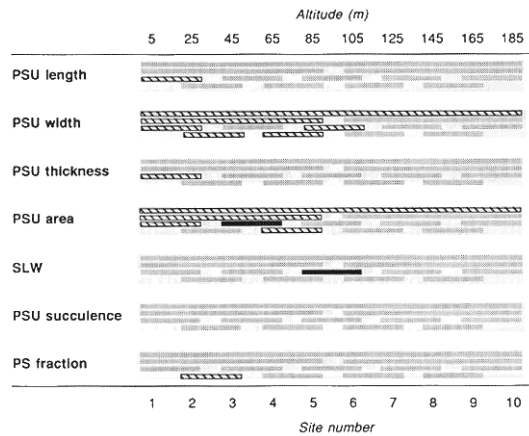


Figure 2: Significant convergence (■), divergence (▨) or no significant difference (□) in seven variates of vegetation texture ($P < 0.05$) among groups of 10 (top line for each variate), five (second line) or two (third and fourth lines) sites along an elevational gradient in South Westland low-altitude conifer/broad-leaved forest, with species weighted equally to calculate site texture means. Results are based on comparison of site mean texture values (see text) from the observed species \times site matrix, with values from each of 2000 matrices generated by a null model of random community assembly.

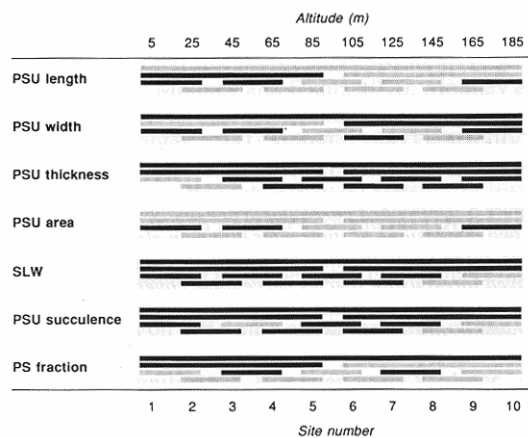


Figure 3: Significant convergence (■) or no significant difference (□) in vegetation texture ($P < 0.05$) along an elevational gradient, with species weighted by percentage cover to calculate site texture means (see Fig. 2).

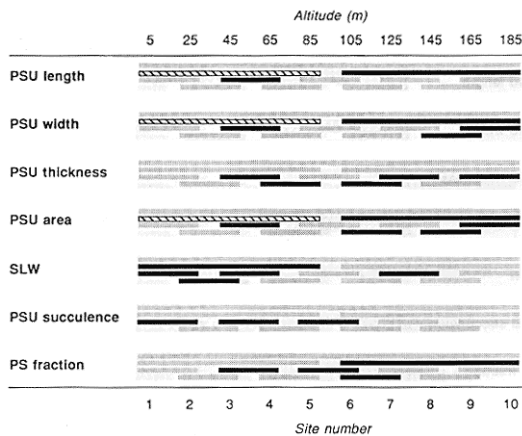


Figure 4: Significant convergence (■), divergence (▨) or no significant difference (□) in vegetation texture ($P < 0.05$) along an elevational gradient, with species weighted by cover rank (see text) to calculate site texture means (see Fig. 2).

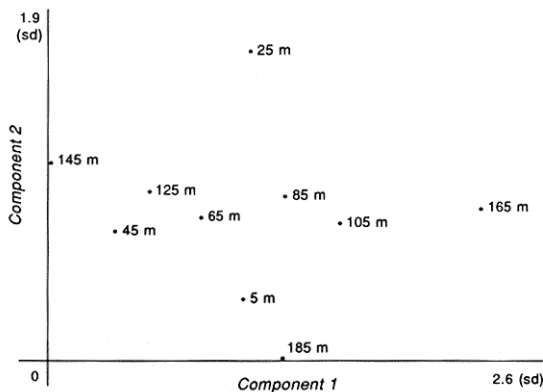


Figure 5: Detrended correspondence analysis ordination in two dimensions of study sites along an elevational gradient in South Westland low-altitude conifer/broad-leaved forest using species percentage cover data. "sd" = standard deviation (Hill and Gauch, 1980). Site elevations are shown on the figure.

convergence is marked, occurring significantly in more than half of all the consecutive-pair comparisons, and in all variates. At the five-site or 10-site level there is significant convergence in all variates except PSU area. There is no significant divergence.

Table 1: Number (and percentage) of instances of significant convergence and divergence (at $P < 0.05$) in vegetation texture between adjacent sites 20 metres apart in altitude in South Westland low-altitude conifer/broad-leaved forest, with species weighted equally, by percentage cover or by cover rank (see text) to calculate site texture means. Values are based on 63 comparisons (9 pairs of sites \times 7 texture variates) presented in Figs. 2-4.

Weighting factor	Convergence	Divergence
Equal weighting	2 (3%)	9 (14%)
Percentage cover	32 (51%)	0 (0%)
Cover rank	23 (37%)	0 (0%)

With species weighted by cover rank, there is some significant convergence in all variates at the two-site level, and in all variates except PSU succulence at the five-site level. None of the variates show significant convergence across all 10 sites. Significant divergence is evident in respect of three variates - PSU length, width and area - among the lower five sites.

Fig. 5 depicts the two-component DCA ordination of species percentage cover within study sites. Although four sites (45-105 m) fall in order along the horizontal axis (component 1), ordination values are not generally related to altitudinal position, indicating that the effect of altitude on floristics along the transect is not a simple one. The results of DCA using species presence/absence only were similar and are not shown.

Discussion

If there are assembly rules for the communities we examined, and if consecutive sites fall along a continuous environmental gradient, we may expect to find two contrasting trends in community structure along the gradient: convergence, due to ecological and/or coevolutionary species sorting (see Introduction); and divergence, due to changes in the physical environment with altitude. Convergence should be most apparent between adjacent sites which are more closely matched in environment, than within series of sites (we analysed two sets of five and the set of all 10) spanning a wider range in altitude. Divergence should be more apparent at the 10- or five-site level than at the two-site level.

With species weighted equally there was little evidence of convergence; among 63 possible comparisons of consecutive pairs of sites (9 pairs \times

7 variates), only two (or 3 percent) showed significant convergence (Table 1). Since we expect deviation from the null model as a result of type I errors in up to 5 percent of comparisons, this cannot be regarded as significant overall. By contrast, when species were weighted by percentage cover (Fig. 3), significant convergence occurred in 51 percent of two-site comparisons.

This high incidence of convergence is encouraging but must be interpreted as applying primarily to the canopy tree guild, which accounts for the larger proportion of total percentage cover but only a small proportion of the species represented in the sites. This increases the possibility that the convergence represents morphological similarity as a result of similar adaptations to the physical environment in the canopy, rather than restrictions on community assembly.

Weighting species by cover rank takes account of their relative importance without causing as strong a bias towards the canopy species. Using this method there was a 37 percent incidence of significant convergence among two-site comparisons. Not all the comparisons can be regarded as independent; some of the variates (for example PSU length and area) may be correlated, while succulence is derived directly from SLW and thickness. If apparently significant convergence occurred in certain variates as a result of type I errors, other correlated variates could show convergence. However, the putative convergence occurs in all the variates (Fig. 2) and at this high frequency is clearly significant. Sites 3 and 4 (45 and 65 m) show significant convergence in all variates, which further suggests that the observed convergence is ecological.

There was much less evidence of divergence than convergence. With species weighted equally, significant divergence arose at the 10- and five-site levels for two variates and in nine two-site comparisons among five variates (Fig. 2). However, as noted above, this weighting method is ecologically questionable. Cover rank is more conservative in this regard, and using this weighting method significant divergence was found only among the lower five sites in three variates (Fig. 4). Sites 1 and 2 (5 and 25 m) differ from each other and all the other sites in substrate, so it is not surprising that the divergence observed using both weighting methods was concentrated in the lower half of the transect. Overall, divergence is more marked at the five- and 10-site levels than the two-site level, which is consistent with expectations, although DCA results (Fig. 5) failed to support the existence of a simple environmental gradient

corresponding to altitude.

Convergence cannot arise in our analysis as a result of overlap in species occurrences in the sites being compared, when all species are weighted equally to calculate texture means. This is because species that are common to the sites being compared will contribute to the magnitude of the test statistic equally in observed and randomised data sets, so that differences in the test statistic value in observed versus randomised data will be based only on the species that are not common between sites.

When weighting is by cover rank or percentage cover, more abundant species will affect the test statistic value more in the real data than, on average, in the randomised data, because all species have an equal chance of receiving a high abundance value in the randomised data. Thus, species of high abundance which occur at more than one of the sites being compared, such as *Nothofagus menziesii*, which occurred at all sites, may tend to augment test statistic values in the real data more than in the randomised data (where they are less likely to be given a high weighting factor) artificially enhancing the likelihood of detecting convergence. This effect will be more pronounced using percentage cover as a weighting factor than cover rank. Since convergence was more marked in this study when a weighting factor was used, and was most apparent using proportional cover as the weighting factor, it seems possible that part of the convergence detected is a result of this analytical artifact.

Previous investigations of community-level convergence have generally focused on apparent similarities between ecosystems of similar climates in different parts of the world. The profusion of studies in mediterranean-climate ecosystems (e.g., Specht, 1969; Mooney and Dunn, 1970; Mooney *et al.*, 1970; Parsons and Moldenke, 1975; Mooney *et al.*, 1977; Fuentes, 1981; Shmida, 1981) generally concluded that there was convergence, but failed to support their results with statistical tests.

Comparable studies in other ecosystems (Orians and Solbrig, 1977; Cody, 1986, 1991) are similarly deficient. Schluter (1986) detected convergence in morphology and species richness between finch communities on different continents using within-versus between-community analysis of variance to determine significance. In a later study Schluter (1990) found significant convergence in trophic guild structure of mangrove island arthropods and body size of desert rodents using standard test statistics (chi-squared and Kolmogorov-Smirnov *D*). Wiens (1991a,b) used a similar approach to compare bird morphology in shrub deserts of Australia and North America but found no

convergence. Wilson *et al.* (1994) used a randomisation test similar to ours to look for convergence between carr communities in Britain and New Zealand, but found only weak evidence of convergence. We have stronger evidence for convergence. Our study is thus the second ever to utilise a statistical test to search for community-level convergence between plant assemblages, and the first to detect it.

Ours is also the first study in either plant or animal ecology to look for convergence within a local area, where the possibility exists for marked overlap in species composition between the plots being compared. Previous workers have been concerned primarily with evolutionary convergence and have avoided communities with species or even higher-order taxa in common because of the danger of detecting similarity resulting not from convergence, but from parallel evolution of allopatric lineages from the same phylogenetic stock (Orians and Solbrig, 1977). We do not seek to distinguish evolutionary from ecological convergence, since both are products of the same process of competitive species assortment. For this reason, coevolutionary character displacement has been described as the "ghost of competition past" (Connell, 1980).

The analysis of vegetation texture to look for convergence between sites within a vegetation type is similar in concept to the search for guild proportionality (Wilson, 1989; Wilson and Roxburgh, 1994), i.e., relative constancy in the proportion of species represented in different guilds (e.g., forest *sinusiae*), among sites with similar habitats. Guild proportionality, like texture convergence, is expected as a result of competitive exclusion. Wilson (1989) employed a randomisation test similar to ours to investigate guild proportionality in New Zealand low-altitude conifer/broad-leaved forest, detecting significant constancy only in the canopy and combined canopy/small tree guilds, which was interpreted as an artifact resulting from the relationship between canopy tree size and plot size.

Keeley (1992) suggested that community-level convergence might be a non-testable hypothesis, yet several recent studies (Schluter, 1986, 1990; Wiens, 1991a,b; Wilson *et al.*, *in press*), like the present one, have employed rigorous statistical tests of the hypothesis of convergence. We have evidence to support the hypothesis for plant communities: several of the vegetation plots examined were more similar to each other in terms of various morphological characteristics of the species present than expected under a null model of random species assortment. An ecological interpretation of this is

that species from the local pool assort themselves into communities according to certain constraints (assembly rules) which limit membership to species that are sufficiently dissimilar from each other to avoid competitive exclusion. Communities in similar environments (e.g., sites closely matched in altitude along our transect) are assembled according to the same rules so that the species present at different sites tend to have similar characteristics whether or not their taxonomic identities are the same.

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