

COMMUNITY STRUCTURE (NICHE LIMITATION AND GUILD PROPORTIONALITY) IN RELATION TO THE EFFECT OF SPATIAL SCALE, IN A *NOTHOFAGUS* FOREST SAMPLED WITH A CIRCULAR TRANSECT

Summary: A *Nothofagus-dominated* rainforest in eastern Fiordland, New Zealand, was sampled by shoot frequency in contiguous 1 x 1 m quadrats, along a topologically-circular transect. The data were analysed at five scales up to 5 x 1 m, to search for assembly rules, i.e., generalised restrictions on species co-occurrences. There was no evidence of niche limitation in terms of the whole community, at any scale examined. Rather, variance in species richness was greater than expected from a null model, suggesting environmental heterogeneity. This conclusion was confirmed by using a patch-model. Guild structure was examined in terms of synusiae, based on vertical stratification. The proportion of species in a quadrat that were from the Herb guild was significantly more constant than expected under the null model. However, using a patch-model this effect was reduced, and no longer significant. This suggests pools of species adapted to different micro-environments, but with parallel guild composition. Liane guild proportions were more variable than predicted by the null model; although this effect was not significant, it parallels reports from other South Island forests. The work confirms conclusions from previous work, that plant assembly rules are to be found only at small spatial scales. Processes leading to high and low variance in species richness and in guild proportions are discussed. Selection of a uniform site in the present work, and use of a patch-model, make it less likely that effects are due to environmental or historical effects. The use of guild proportionality as the criterion eliminates the effect of limitation on the number of individuals that can co-occur locally.

Keywords: Assembly rules; community structure; guild; guild proportionality; herb guild; liane; niche limitation; spatial scale.

Introduction

In recent years, the very existence of community structure, in the sense of assembly rules limiting species' coexistence, has been in question (Drake, 1990; Wilson, 1991; Keddy, 1993; Dale, 1994; Wilson, 1994). However, significant evidence for assembly rules has recently been obtained. Rules that operate in terms of species richness have been found at small scales in lawn communities (Watkins and Wilson, 1992; Wilson, Roxburgh and Watkins, 1992), and rules that operate in terms of guild representation have been found both in lawns (Wilson and Roxburgh, 1994) and in forest (Wilson, Allen and Lee, *in press*).

These initial reports raise questions of what types of community such assembly rules operate in, how consistently, and at what spatial scales.

We therefore sampled a rainforest, dominated by *Nothofagus* species, in south-western New Zealand. All questions in ecology are dependent on the spatial scale at which they are asked (O'Neill *et*

al., 1986). However, it is becoming clear that evidence for plant community structure can be found mainly, perhaps only, at a small spatial scale (Watkins and Wilson, 1992; Wilson and Roxburgh, 1994). We therefore used as the basic quadrat size the smallest we considered practicable: 1 x 1 m. In order to enable examination of the data at several spatial scales from one dataset, we used the sampling technique of contiguous quadrats. Previous work using this technique has suffered problems at the ends of the transects, where complete blocks cannot be made. We overcame this problem by using a transect that was topologically circular. This also facilitates the application of a patch-model (Watkins and Wilson, 1992).

We analysed for assembly rules in terms of niche limitation, examining variance in species richness. Such a rule would be based on a limit to the number of species that can coexist locally (Wilson, Gitay and Agnew, 1987), evidenced by a reduced variance in quadrat richness, compared to a null model.

We also analysed for guild proportionality. The concept is based on Pianka's (1980, 1988) theory of guilds as groups of species that compete more with each other than with species in other guilds. Species exclusion will therefore tend to occur within guilds, and species representation from different guilds will therefore tend to be relatively constant (Wilson, 1989; Fox, 1989). Evidence for this would be a reduced variance in guild proportions, compared to a null model.

Methods

Study site

The study site was in the valley of Borland Burn (South Branch), eastern Fiordland, South Island, New Zealand, 45° 46' S 167° 02' E, at c. 260 m a.s.l. The area comprised a gentle slope (14° from horizontal) to the east (800 from true north). Mean annual temperature is c. 8°C (N.Z. Meteorological Service, 1985a), and rainfall c. 1500 mm yr⁻¹ (N.Z. Meteorological Service, 1985b).

The vegetation is mixed beech-podocarp forest, dominant trees being the southern beeches *Nothofagus menziesii* and *N. solandri* var. *cliffortioides*, with gymnosperms *Dacrydium cupressium*, *Phyllocladus asplenifolius* var. *alpinus* and *Prumnopitys ferruginea* (for nomenclature see Connor and Edgar, 1987). The major shrubs are *Neomyrtus pedunculata* and *Coprosma* species, and the most abundant herb *Blechnum discolor*.

Sampling

An area was selected for sampling without obvious major disturbance, or environmental or vegetational discontinuity. Within it, 402 quadrats, each 1 x 1 m, were placed contiguously to form a topological circle. Shoot presence/absence of vascular plant species, and the maximum height of each species, were recorded in each quadrat. The percentage cover of the major herb species, *Blechnum discolor*, was recorded as the mean of subjective estimates by two observers.

In analysis, individuals less than 10% of their adult height in the area, where that height was 2 m or more, were regarded as juveniles.

The guilds used were synusiae, widely recognised as the ecological groups in forest. They were defined here according to the potential adult habit of the species in the area: Canopy tree (height > 20 m), Small-tree (6 - 20 m), Shrub (1 - 6 m, woody), Herb (> 0.1 m, herbaceous), Ground (< 0.1 m, herbaceous), Liane (ground-rooted, not self-supporting), and epiphyte (rooted > 1 m above ground).

Analysis

Two methods of analysis were used. In both, the expected variance under the null model, and significance, were determined by a randomisation test, using 2000 randomisations, and effecting a 2-tailed test (Crowley, 1992).

All analyses were performed at a range of quadrat sizes, from the basic 1 x 1 m up to 5 x 1 m, by adding records from adjacent quadrats to create larger ones, taking the mean over all possible starting points (Wilson *et al.*, 1987). The use of a circular transect allowed these larger quadrats to be formed around the circle, eliminating the problems found at the end of straight transects, when there are too few original units left to make a complete larger unit.

There were two methods of analysis:

Niche limitation

A low variance in quadrat richness can result from niche limitation (Wilson *et al.*, 1987), i.e., limitations to species coexistence caused by the number of species being limited by the number of niches available (Ricklefs, 1987).

The null model takes as fixed the observed frequency of each species, but allocates these species occurrences at random to quadrats, independently for each species (Wilson *et al.*, 1987).

The observed and expected variances were compared with index RV_r (relative variance in richness):

$$RV_r = \frac{\text{observed variance in quadrat richness}}{\text{variance in quadrat richness expected under the null model}}$$

RV_r takes the value 1.0 under the null model, and < 1.0 when quadrat richness is less variable than this (Wilson *et al.*, 1992), indicating an assembly rule. $RV_r > 1.0$ is most likely to be due to environmental variation.

Analyses were performed both including all occurrences of species (i.e., including juveniles), and also excluding species present in a quadrat only as juveniles.

Guild proportionality

A low variance in guild proportions can result from limitations to species coexistence based on guild membership (Wilson, 1989).

The null model takes as fixed both the observed frequency of each species and the observed richness of each quadrat, but assigns species to quadrats at random within these constraints, i.e., with no limitation on the ability of members of the same guild to co-occur.

Guild proportions were calculated for each guild in each quadrat:

proportion of guild g in quadrat q =

$$\frac{\text{number of species in quadrat } q \text{ that belong to guild } g}{\text{total number of species in quadrat } q}$$

For each guild separately, the observed between-quadrat variance in guild proportions was calculated. The expected variance was calculated as the mean of similar calculations from randomisations under the null model.

The observed and expected variances were compared for each guild with index RV_{gp} :

$$RV_{gp} = \frac{\text{observed variance in guild proportions}}{\text{variance in guild proportions expected under null model}}$$

Index RV_{gp} takes a value of 1.0 when the observed variance in guild proportions is equal to that expected under the null model, and < 1.0 when guild proportions are more constant than this, indicating the assembly rule of guild proportionality (Wilson, 1989). $RV_r > 1.0$ is most likely to be due to environmental variation.

Guild proportion analyses were performed only with juveniles excluded.

Site- and patch-models

In both types of analysis, two kinds of null model were used: site-model and patch-model. The observed richnesses and guild proportions are identical between site- and patch-models; what differs is the basis for predicting the composition of a ('target') quadrat in randomisations under the null model. In a site-model, those predictions are based on species frequencies over the whole dataset. In a patch-model, they are based on species frequencies in a patch of quadrats centred on the target quadrat, in the present case a linear patch of 7 quadrats (c.f. Watkins and Wilson, 1992); some loss of statistical power is compensated for by a much reduced sensitivity to environmental patchiness (Watkins and Wilson, 1992).

Results

Niche limitation

There was greater variance in quadrat richness than expected under the null model (i.e. $RV_r > 1.0$) in all analyses and at all quadrat sizes (Fig. 1). This was significant at all but one analysis (the exception

being at quadrat length 1, using a patch-model and excluding juveniles). For all types of analysis, RV_r showed a general tendency to increase with quadrat size. Relative variance in richness (RV_r) was consistently less when juveniles were excluded from the analysis. The site-model analyses gave consistently greater RV_r values than the patch-model analyses.

Regression of quadrat richness on the subjectively estimated cover of *Blechnum discolor* (with square root and arcsine transformation respectively) showed a significant ($P < 0.001$) tendency for species richness to be lower where *B. discolor* cover was higher, but this effect accounted for only 9.7% of the variance. Most of this effect was attributable to juveniles; when they were excluded from the calculation of richness the regression (still negative, and still significant) accounted for only 2.4% of the variation in richness.

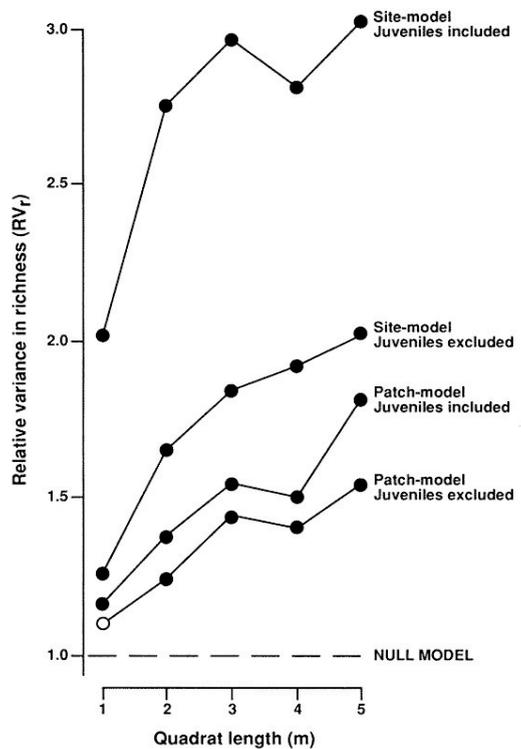


Figure 1: Niche limitation, as indicated by variance in quadrat richness compared to a null model, at five quadrat sizes. Open symbols indicate no significant difference from null model expectation; solid symbols indicate significance (i.e. $P < 0.05$).

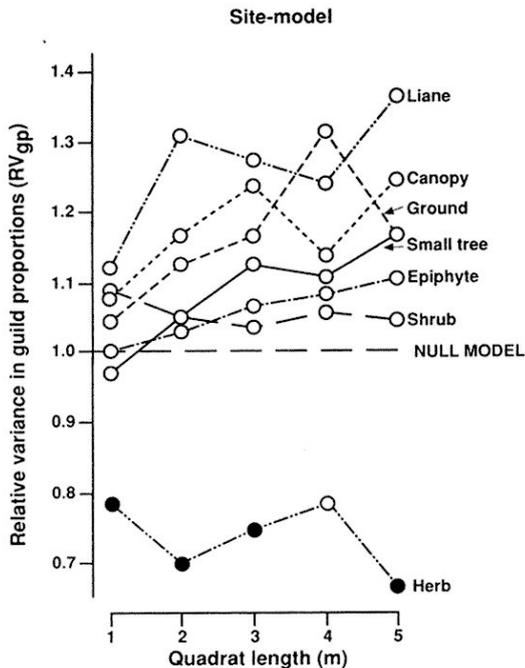


Figure 2: Guild proportionality, as indicated by variance in guild proportions compared to a null model, using a site-model, at five quadrat sizes. Symbols as in Fig. 1.

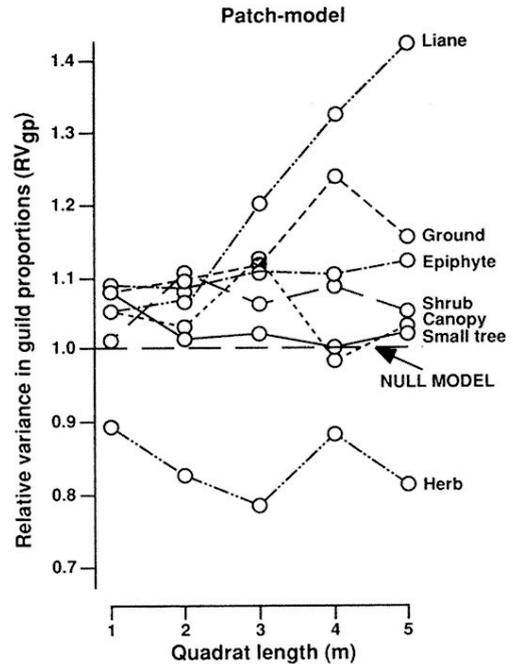


Figure 3: Guild proportionality, as indicated by variance in guild proportions compared to a null model, using a patch-model, at five quadrat sizes. Symbols as in Fig. 1.

Guild proportionality

Using site-model analyses (Fig. 2), the Herb guild gave an RV_{gp} (relative variance in guild proportions) considerably less than 1.0, significantly so for four of the five quadrat sizes, indicating that across quadrats the proportion of species that were herbs was relatively constant. The other guilds showed RV_{gp} values greater than 1.0, indicating a tendency for the proportion of species from those guilds to be more variable than expected on a random basis, but not significantly so in any individual case. However, it can be noted that at four of the quadrat sizes, RV_{gp} was greatest for the Liane guild.

Using patch-model analyses (Fig. 3), RV_{gp} was still less than 1.0 for the Herb guild, but not significantly so. For other guilds, RV_{gp} was again almost always greater than 1.0, but never significantly. Again, high RV_{gp} values for the Liane guild can be noted in the three larger quadrat sizes.

Discussion

There is no evidence, in this forest community, for niche limitation in terms of a low variance in the total complement of species in each quadrat (Fig. 1). Such low variance has been seen in herbaceous communities (Watkins and Wilson, 1992; Wilson *et al.*, 1992), and perhaps in the herbaceous layers in a forest (Zobel, Zobel and Peet, 1993). It has been found most clearly at small scales, down to the point scale of Wilson *et al.* (1992). However, no evidence has ever been found for such an assembly rule in the whole community of a forest. One explanation could be that an inappropriate sampling scale had been used. However, the present work shows no RV_{gp} value < 1.0 at any scale examined. We deliberately started from the smallest scale that seemed ecologically sensible: 1 x 1 m. Smaller scales would not be conceptually realistic in a forest, since extrapolation of the quadrat into the canopy would be meaningless. Using shoot

presence, it was common for more than one species from the same synusia to occur in a quadrat; nevertheless we regard a 1 x 1 m quadrat in forest as close to the equivalent of a point quadrat in grassland. We believe that at larger scales than 5 x 1 m environmental patchiness would predominate. The trend suggests that there would be no hope of finding such an assembly rule at larger scales. The trends therefore emphasise that plant community structure can be found only at a spatial scale that is small in relation to the size of the plants. This can be attributed to the short distances over which plant interactions occur (Wilson *et al.*, 1992), and the confounding effects of environmental variation at larger scales (Watkins and Wilson, 1992).

The reduction in RV_r using a patch-model suggests that the high RV_r under a site-model can partly be attributed to environmental patchiness, some patches being species-rich and some species-poor. The reduction in RV_r when juveniles were excluded indicates aggregation between juveniles and adults of other species, perhaps as a mutualism (Valiente-Banuet and Ezcurra, 1991; Carlsson and Callaghan, 1991; Vetaas, 1992). Only a small part of the high RV_r is attributable to the fern *Blechnum discolor*, even though the latter is absent from many quadrats, and casts considerable shade in others.

Variance in quadrat richness different from that expected under the null model can be caused by a number of factors. High variance in species richness (i.e. $RV_r > 1$) can be due to:

- H1. Heterogeneity in the current environment, when either: (a) the patches differ enough in environment for their species to be drawn from different pools, and those pools differ in size, or (b) species in all the patches are drawn from the same pool, but 'favourable' (or unfavourable) patches contain more species - the 'Waterhole effect' (Pielou, 1975; Wilson *et al.*, 1987),
- H2. Heterogeneity in patch history, e.g., in disturbance and dispersal, giving an effect similar to the Waterhole effect (Zobel *et al.*, 1993), or
- H3. Mutualism etc. between species, such that the presence of one species facilitates the presence of one or more others (Schluter, 1984).

High variance cannot give evidence of an assembly rule, because although mutualism-based rules could be envisaged which resulted in high variance, an explanation in terms of environmental heterogeneity would be very likely, and impossible to rule out.

Low variance in species richness (i.e. $RV_r < 1$) can also be caused by a variety of factors, primarily:

- L1. Heterogeneity in the current environment, if the sampling covers a wide environmental range, such that different pools of species are found in different environments, and if those pools of species are approximately equal in size (Watkins and Wilson, 1992),
- L2. Heterogeneity in patch history, e.g., in disturbance and dispersal, again with different and equal-sized pools of species in different patches (Zobel *et al.*, 1993),
- L3. Limitations to the number of individual plants or plant modules that can coexist in a quadrat (Watkins and Wilson, 1992; Wilson *et al.*, 1992), or
- L4. Limitations to the coexistence of species due to competitive exclusion - an assembly rule (Wilson *et al.*, 1987; Wilson 1991).

Thus, heterogeneity in the current environment (L1) can lead to low variance only when sampling covers a wider environmental range. The same situation applies to heterogeneity in patch history (L2). It was for this reason that we sampled, so far as possible, in a constant environment. A patch-model will remove most remaining environmental effects. Therefore, with careful choice of site and of analysis method, explanations of low variance L1 and L2 above can be effectively eliminated. The main interest is usually in obtaining evidence for the existence of assembly rules (L4). However, using species richness as the criterion, there remains the problem of effects via limitations on the packing of individuals into a small space (L3 above); there cannot be more species in a quadrat than there are individuals, so that it is not possible to be certain that assembly rules (L4) are the cause of the effect.

Analysis of guild proportions overcomes the complication of limitation to the packing of individuals (L3 above), because the number of species per quadrat is held the same in the randomised as in the observed. That is, low or high variance in quadrat richness for one reason or another is accepted, and only the representation of guilds within those constraints is examined. Again, the problem of limited species pools (points L1 and L2 above) can be minimised by selection of a uniform environment and the use of a patch-model.

The low variance of representation from the Herb guild therefore seems to represent an assembly rule. It confirms the very similar effect shown for the same guild in forest on Breaksea Island, in the high-rainfall south-west coast of Fiordland, New Zealand, an area only c. 75 km from our study area, but with higher rainfall (Wilson *et al.*, *in press*). The present work indicates

that the effect operates not only at one spatial scale. The effect could be taken as meaning that in any small area there is a fixed number of niches for herb species, and that this number is higher when the species richness of other guilds is greater, implying that upper-stratum species are determining the niche of the herb layer (Gleason, 1936). However, the reduction in the effect, and loss of significance, when a patch-model is used suggests that it may be partly due to environmental patchiness, with similar-sized pools of species adapted to different types of environmental patch. This is a type of assembly rule, but one determined by evolution and immigration as well as plant interactions, impossible to test formally using a single flora, and very difficult to test at all.

Although the high variance in representation from the Liane guild was not significant, it is compatible with previous reports. Wilson (1989), working in a gymnosperm-dominated forest in southern New Zealand, found significantly high variance in proportions of the Liane guild, and only in that guild. Wilson *et al.* (*in press*), on Breaksea Island, found significantly high variance in liane proportions in *Nothofagus*-broadleaved forest. The consistency of this effect across three areas of southern New Zealand suggests it is a general community feature in these forests. Liane richness can be related to host species (Campbell and Newbery, 1993) or soil nutrients (Balfour, 1993), but we suggest the most likely reason for the effect is patchiness of disturbance history, lianes invading gaps and edges (Putz, 1984; Caballe, 1984).

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