

## Time and space in the community structure of a species-rich limestone grassland

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**Abstract.** The community structure of a species-rich grassland was investigated at a small spatial scale (0.001 m<sup>2</sup>), to determine whether evidence suggesting assembly rules could be found in temporal or spatial variation in either species richness or guild proportions. The community was alvar limestone grassland on the island of Öland, Sweden. Three sites were sampled: two lightly grazed, the other recently ungrazed. Plots with and without fertilizer were compared.

Evidence was sought for restriction on the ability of species to co-occur within a limited spatial area. Restriction due to a limited number of niches available, 'niche limitation', could be manifest as lower variance in quadrat richness than expected under a null model (i.e.  $RV_r$ , the ratio of observed: expected variance in richness, would be < 1.0). In several cases,  $RV_r$  values were significantly < 1.0, even using a patch model to allow for possible spatial variation in the environment. Low  $RV_r$  values were found only at the smallest square quadrat size, 10 cm<sup>2</sup>. On Fertilized plots in the years immediately after application of fertilizer, low  $RV_r$  could not be demonstrated. Explanations of low  $RV_r$  other than niche limitation are considered, such as environmental heterogeneity (present and/or historical) and limitations to the co-occurrence of individual plant modules.

Assembly rules based on guild membership were sought by looking at the variance across quadrats in the proportions of species from morphological guilds. An assembly rule would be seen as relatively constant proportion, estimated via  $RV_{gp}$ , the ratio of observed:expected variances in guild proportions. Significant guild proportionality was found in some cases. There was no evidence of guild proportionality in the years after the application of fertilizer.

The significant effects in  $RV_r$  were more numerous than expected on a random basis, though not observed in every site in every year. Similar trends were seen in  $RV_{gp}$ . At the space/time scales examined, the species in a plant community may be constrained by assembly rules only intermittently, e.g. when resources are more limiting (Wiens 1977). Under this concept, when competition is relaxed, such as following fertilizer application, there is a temporary microhabitat 'waterhole' in which more species can coexist, and the assembly rules break down, at least temporarily whilst the species composition adjusts. There was some indication of a return to more deterministic community structure four years after fertilization commenced.

Variants of van der Maarel's Carousel model were tested. A Niche-limited Carousel Model (i.e. a model in which there is some limitation in the number of species that can occupy a microsite) would imply restricted variation in richness through time for a single quadrat (temporal  $RV_r$ ). Overall differences between years in species richness were demonstrated, and their effect removed; after this adjustment there was support for the Niche-limited Carousel Model. The extent of this limitation varied between sites. There were also consistent differences between quadrats in species richness. There was little evidence for constancy of guild proportions through time.

The site that showed the strongest community structure in time and space, least year-to-year variation in mean species richness, and least response to fertilizer perturbation, is that on the shallowest soil. Possibly the thin soil results in greater resource limitation, supporting suggestions that assembly rules are stronger when resources are more limited.

**Keywords:** Assembly rule; Guild; Negative feedback; Niche limitation; Perturbation; Species richness.

**Nomenclature:** Tutin et al. (1964-1980).

### Introduction

#### Assembly rules

Ecologists have repeatedly investigated plant community structure in search of generalized restrictions on species co-occurrence - assembly rules (Zobel & Zobel 1988; Drake 1990a; Wilson 1991; Wilson & Roxburgh 1994). We here follow Diamond's (1975) original concept of assembly rules, as generalized co-occurrence patterns, rather than Cole's (1983) concept of assembly rules as the possible processes leading to such patterns. Assembly rules have usually been sought by examining *spatial* patterns of co-occurrences (e.g. Wilson et al. 1987; Zobel et al. 1993; Wilson 1989), but rarely have temporal patterns been examined. Here, we examine co-occurrence over several years, to determine temporal consistency in community assembly. We also develop

methods to explicitly investigate temporal community structure (i.e. assembly rules governing a sequence of community states). We test whether community composition is consistent with the hypothesis that there are assembly rules. It is hard to find any test that unambiguously identifies assembly rules; rather we have to evaluate the evidence for and against possible explanations.

#### *Alvar grassland as a test community*

Communities and methods of analysis that provide evidence for assembly rules have proven difficult to find, perhaps because of factors such as environmental variation, site history, and the effect of individual species, that obscure the underlying rules. In this study, we seek assembly rules in species-rich alvar limestone grassland. There are two reasons why our study is special.

1. The community structure of species-rich vegetation is a crucial issue for mechanisms of coexistence (Shmida & Ellner 1984; Wilson 1990; Peet et al. 1990). If there are any restrictions on species packing, it seems likely that they will operate especially when species richness is higher. The species-rich alvar limestone grassland of southern Öland, which we examine, has small-scale species richness higher than any other documented vascular plant community at the scale of our study: 6.3 species per 10 cm<sup>2</sup>, 11.7 species per 100 cm<sup>2</sup>.

2. Previous work suggests that assembly rules can be demonstrated most clearly in plant communities at small spatial scales (Watkins & Wilson 1992; Wilson et al. 1992; Wilson & Watkins 1994), at least small-scale in relation to the size of the plants. Alvar vegetation is fine-grained (i.e. most variation is at a fine scale, it is relatively homogeneous at larger scales), and it was possible to sample it at a fine scale.

#### *Variance in richness*

An assembly rule could be based on a possible limitation to total species richness. Such a limitation would be predicted under the theory of 'niche limitation' - that there may be only a limited number of niches in a restricted area, so that there is a limit on how many species can locally coexist, even though that limit is not rigid (Elton 1953; Terborgh & Faaborg 1980; Wilson et al. 1987; Wiens 1989). For this concept, 'niche' does not need to be defined closely, because the basis of the concept is competitive exclusion.

We test this basic piece of ecological theory by examining the variance in richness across quadrats. The appropriate null model has the same number of occurrences of each species as in the observed data; however, these occurrences are allocated at random among the quadrats. Niche limitation, if it existed, would result in a lower variance in richness among the quadrats than

expected under the null model (Palmer 1987; Wilson et al. 1987). However, a low variance can arise from four causes (Bycroft et al. 1994):

1. Heterogeneity in the current environment: low variance in richness, compared to the null model, could result if the sampling covered a wide environmental range, with different pools of species with approximately equal size in different environments.

2. Heterogeneity in patch history: this would lead to low variance if there were different and equal-sized pools of species in patch types with different history.

3. Limitations to the number of individual plant modules (e.g. tillers, leaves) that can co-occur in a quadrat.

4. Limitations to the co-occurrence of species due to competitive exclusion - an assembly rule.

Techniques have been developed, such as patch models, to minimize the effect of causes '1' and '2'. When small quadrats are used, cause '3' always has to be considered as a possible explanation of low variance in richness. For this aspect, see van der Maarel et al. (1995).

In the past, such evidence for niche limitation has been sought spatially, by looking for relatively constant richness among quadrats. We also apply the technique to a temporal comparison, looking for relative constancy of species richness through the years within a single quadrat. In doing so, we introduce a refinement of the method, adjusting for any overall year effects.

#### *Guild proportionality*

Guild proportionality approaches the question of community structure by looking at the proportions of species from two or more guilds (Wilson 1989; Wilson & Watkins 1994), guilds being defined as groups of species that require similar resources. The concept which we test is that, by this definition of guilds, there will be more competition within a guild than between guilds. Competitive exclusion will, therefore, occur mainly between the species of one guild (Pianka 1980, 1988; Hawkins & MacMahon 1989; Fox & Brown 1993). The theory we are testing predicts that the relative representation of each guild would be rather constant, in particular more constant than in a null model (Wilson & Watkins 1994). Rather than suffer the difficulties of interpretation that are normal with field manipulation experiments (Wilson & Gitay 1995), we use the more indirect but non-interventionist approach of testing for the species-occurrence patterns that the theory predicts.

The appropriate null model takes as fixed both the observed quadrat richnesses and species frequencies, but assumes that species are assigned to quadrats at random within these constraints, especially with no limitation on the ability of guild members to co-occur (Wilson 1989; Wilson 1995a). We apply this approach across space, and within a quadrat across years.

## Methods

### *Treatments, sites and sampling*

We consider two treatments, Control and Full Fertilizer, with six replicates in a randomized block design, spread across three sites of alvar limestone grassland on the Swedish Baltic island of Öland. All sites were similar in original vegetation, important species being *Festuca ovina*, *Avenula pratensis*, *Filipendula vulgaris*, *Achillea millefolium* and *Galium verum*. The community was distinguished by Krahulec et al. (1986) as the *Veronica spicata*-*Avenula pratensis* association.

The Gettlinge site (56° 23' N, 16° 27' E) is lightly grazed by cattle and horses. The sward is short (5 - 10 cm) and dense. Soil depth is 20-30 cm. There are slight variations in topography. Block A was recorded 1985-93, Block B 1985-9, and Block C in 1985 and 1989. Mean species richness of the Control plots in 1985 - 1989 was 7.3 per 10 cm<sup>2</sup> and 13.3 per 100 cm<sup>2</sup>.

Kleva (56° 32' N, 16° 30' E) has not been grazed since 1980, and was only lightly grazed from some years before that. The vegetation is 15 - 30 cm tall, and the soil 20 - 40 cm deep. There was one block recorded each year 1985 - 1989, with an additional block recorded in 1985 and 1989. Mean species richness is 6.1 per 10 cm<sup>2</sup> square and 11.2 per 100 cm<sup>2</sup> square.

Skarpa Alby (56° 35' N, 16° 39' E) is lightly grazed by cattle. It is partly covered by open juniper scrub, but the 10- 15 cm tall grassland was sampled in open areas between shrubs. Soils are only 5 - 15 cm deep. Vegetation records were made 1985 - 1989. Mean species richness was 5.9 per 10 cm<sup>2</sup> and 12.5 per 100 cm<sup>2</sup>.

In each plot (i.e. block/treatment combination) there were 50 10-cm<sup>2</sup> square quadrats, arranged at 10-cm intervals along in two lines 1 m apart. These small quadrats were nested within contiguous 100 cm<sup>2</sup> square quadrats, which are used for some analyses. Only 20 of these larger quadrats were recorded in 1985, whereas all 50 were recorded in 1986 - 1989. 40 of the small and large quadrats were recorded for Gettlinge Block A in 1990-1993. The shoot presence of all vascular species was recorded each year in the latter half of June.

In the Fertilized treatment, complete fertilizer (N P K Mg Ca S Mn Mo Fe Cu Zn and B) was applied twice yearly in early May and the middle of June, starting in 1986 (Willems et al. 1993). Because the 'Fertilized' plots were first fertilized a week before recording in 1986, the 1985 and 1986 data from those plots are effectively replicates of the Control plots.

### *Analysis*

The ratio of observed to expected variance in species

richness was examined across quadrats (or years) ( $RV_r$  = relative variance in richness; Wilson et al. 1987; Wilson et al. 1992). The null model, taking as fixed the observed frequency of each species, gives  $RV_r = 1.0$ . Low variance, which is an indication of predictable community structure, is shown by  $RV_r < 1.0$ . (We see  $RV_r > 1.0$  as too ambiguous to interpret ecologically.)

Spatial analyses were performed using the original 'site model' of Wilson et al. (1987), and also using the 'linear patch model' of Bycroft et al. (1993). In each case, the null model is based on the observed species frequencies. In the site model these frequencies are calculated over all (usually 50) quadrats of a plot. In the linear patch model, the null model for each quadrat is based on frequencies in a patch of seven quadrats centred on the target quadrat (for appropriate procedure at ends of the sampled area, see Watkins & Wilson 1992).

Guild proportionality analysis uses the comparable index  $RV_{gp}$  (relative variance in guild proportions: Wilson 1989; Bycroft et al. 1993; Wilson & Watkins 1994). The null model takes as fixed both quadrat richness and species frequencies.  $RV_{gp}$  values of 1.0, and values  $< 1.0$ , are interpreted as for  $RV_r$ . The guild classification examined, delimited before any analyses were conducted, was morphological, contrasting graminoid and dicotyledonous species. In short grassland, an obvious functional difference between species is that between the narrow, upright leaves of graminoids and the broad, flat leaves of forbs (Wilson & Watkins 1994). Many ecologists have considered the morphology of the photosynthetic unit to be the key to the niche of plant species (Pianka 1988; Cody 1986; Barkman 1979). Wilson & Roxburgh (1994) produced independent evidence that these guilds can limit species coexistence in grasslands.

The alternative to using *a priori* guilds is to use 'intrinsic guilds', i.e. a guild classification based on the observed tendency in the data for species not to co-occur (Wilson & Roxburgh 1994). Searches for intrinsic guilds were performed by the method of Wilson & Roxburgh (1994). Following their method, the data being analyzed were divided at random into two subsets, the 'Optimization subset' for determining by heuristic search the guild classification that minimized  $RV_{gp}$ , and the 'Test subset' for testing the classification thus derived. This avoids the circularity of optimizing and testing a guild classification on the same data.

Both variance in richness and guild proportionality were examined within blocks (for spatial analysis) or quadrats (for temporal analyses); the overall analysis was performed by adding the within-block/quadrat variances. Annuals may not be limited by the same assembly rules as perennials, but occur in gaps in the structure (Grubb 1986). We therefore repeated most analyses with annuals and perennials separately.

All significance levels are for a two-tailed test, from 2000 randomizations.  $P$  values are interpreted as significant when  $<0.05$ , but are given in tables, for information, when  $<0.1$ .

## Results

### *Spatial variance in richness*

This approach examines the variance in species richness between the 10 cm<sup>2</sup> (or 100 cm<sup>2</sup>) quadrats within a plot. The null model took as fixed the species frequencies over the (usually) 50 quadrats in a plot, assigning them at random to those quadrats.

### *Control plots, 10 cm<sup>2</sup>, perennial species*

There was a general tendency for quadrat richness to be less variable than expected under the null model (i.e.  $RV_r < 1$ ), using either the site model (Table 1) or the more conservative patch model (Fig. 1). Out of 25 tests with the patch model,  $RV_r$  was less than 1.0 in 19. Whilst not all 19 were significant, such a proportion trending in one direction is itself a significant departure from expectation ( $P$  for 19/25 = 0.00091, i.e.  $<0.05$ ). Thus, there is significant indication of lower variation between quadrats in species richness than expected under the null model. The cases where this effect was significant tended to be those where there was sufficient replication for a powerful test, especially Gettlinge in 1985 and 1989. However, there were other sites in other years when there was no suggestion of a deficit of variance in richness,  $RV_r$  being ca. 1.0 or non-significantly greater.  $RV_r$  was uniformly low in 1985, and uniformly  $< 1.0$  in 1986, but in other cases sites responded differently in different years. There was a consistent trend (though with no significance, there being fewer replicates) for  $RV_r$  to decrease at Gettlinge from 1990 to 1993.

Since the patch model eliminates, or considerably reduces, the effect of spatial heterogeneity via limited species pools (Watkins & Wilson 1992), and since the effects seen using the site- and patch models are generally similar, it seems that the low variance in richness shown here was not an artefact of environmental heterogeneity, but was due to some limitation in the ability of species or individual plant modules to co-occur.

There is little obvious correspondence between the patterns in  $RV_r$  and yearly rainfall.

### *Annuals*

Using only annual species (Table 2),  $RV_r$  was usually close to the random-distribution value of 1.0, and never significantly different from it.

**Table 1.** Spatial variance in richness among perennial species in the Control plots, sampled with 10-cm<sup>2</sup> quadrats, analyzed with a site model.  $RV_r$  = Relative variance in richness (see text),  $P$  = probability under the null model (2-tailed test), n.s. =  $P > 0.1$  ( $P$  values between 0.1 and 0.05 are shown for information, but are not interpreted as being significant).

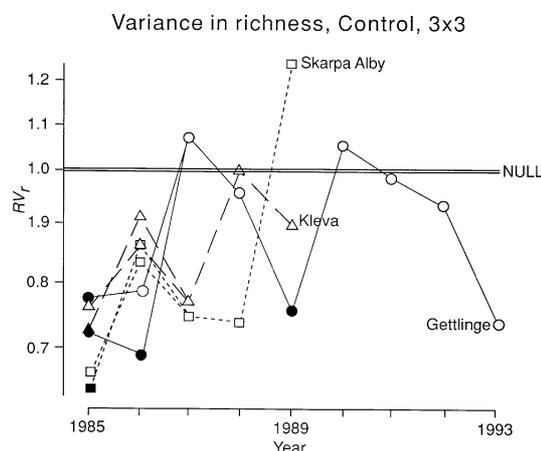
Year	Gettlinge		Kleva		Skarpa Alby	
	$RV_r$	$P$	$RV_r$	$P$	$RV_r$	$P$
1985	0.830	ns	0.752	0.066	0.556	0.009
1986	0.864	ns	1.005	ns	0.828	ns
1987	1.024	ns	0.978	ns	0.661	0.052
1988	1.030	ns	1.002	ns	0.684	0.095
1989	0.673	0.001	0.878	ns	1.102	ns
1990	1.007	ns				
1991	0.936	ns				
1992	0.960	ns				
1993	0.623	0.060				

### *Spatial scale*

In analyses performed at the spatial scale of 100 cm<sup>2</sup> (Fig. 2), all significant departures from the null model were with  $RV_r$  greater than 1.0, i.e. *more* variance in species richness than expected under the null model.

### *The effect of fertilizer application*

The 1985 - 1986 results from the Fertilized plots were similar to the Controls, as expected since there had been no opportunity for fertilizer application to have an effect. In 1987 - 1989,  $RV_r$  values in Fertilized plots were close to 1.0 (Fig. 3). The significantly low value seen in the Control for Gettlinge in 1989 is not seen at all in the Fertilized plots. Taking low  $RV_r$  values as indication of the degree of community structuring (Wilson et



**Fig. 1.** Spatial variance in richness of perennial species in the 10-cm<sup>2</sup> quadrats, Control plots, analyzed with a linear patch model. For index  $RV_r$ , a value  $< 1.0$  indicates lower variance than expected under the null model. Solid symbols indicate significant departure from the null model (i.e.  $P < 0.05$ ).

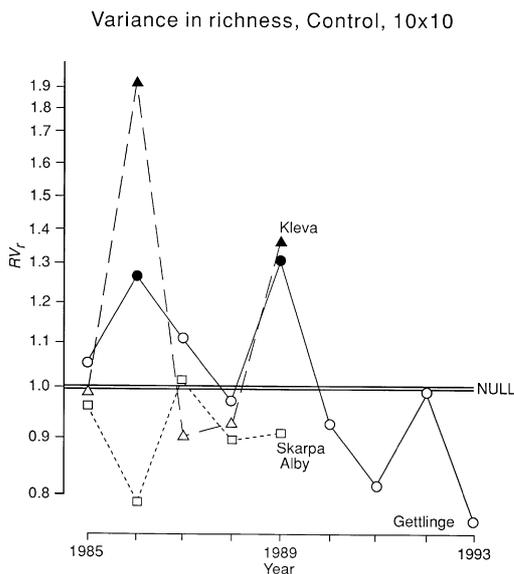
**Table 2.** Spatial variance in richness among annual species in the 10-cm<sup>2</sup> quadrats, Control plots, analyzed with a linear patch model. -- = no annual species were present. Other conventions as in Table 1.

Year	Gettlinge		Kleva		Skarpa Alby	
	$RV_r$	$P$	$RV_r$	$P$	$RV_r$	$P$
1985	1.067	ns	1.001	ns	1.092	ns
1986	1.032	ns	0.885	ns	1.015	ns
1987	1.023	ns	--	1.019	ns	
1988	0.942	ns	1.477	ns	1.009	ns
1989	1.075	ns	--	0.928	ns	
1990	0.730	ns				
1991	1.255	ns				
1992	1.039	ns				
1993	0.795	ns				

al. 1992), we hypothesize that the community had not had time to restructure itself after the change of nutrient status. The decrease in  $RV_r$  seen in the Controls at Gettlinge from 1990 to 1993 is seen in the Fertilized plots too, though again not significantly. Thus, by that time there is no evidence for the Fertilized plots being different from the Controls, though it is difficult to be sure because of the lower replication available then.

*Guild proportionality: Spatial*

Community structure can also be sought as constancy of guild proportions between quadrats, due to limitation in the ability of species from the same guild to



**Fig. 2.** Spatial variance in richness of perennial species in the Control plots, sampled with 100-cm<sup>2</sup> quadrats, analyzed with a patch model. Solid symbols indicate significant departure from the null model (i.e.  $P < 0.05$ ).

co-occur within 10-cm<sup>2</sup> square quadrats. The null model took as fixed the species frequencies and quadrat richnesses across the 50 replicates within a plot, but assumed species were assigned to quadrats at random within these constraints.

*Control plots*

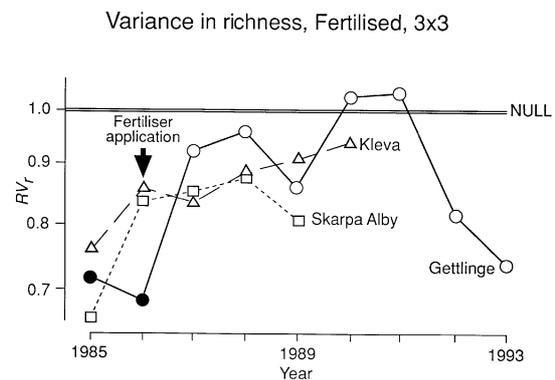
There were four cases of significant guild proportionality ( $RV_{gp} < 1.0$ ; Fig. 4), i.e. indication of relatively constant proportions of species from the two guilds. In the two cases where the data for such a result comprised two blocks (Gettlinge 1987 and Kleva 1989) the effect was seen in each block separately. In 1985, when the Fertilized plots were strict replicates of the Control plots because fertilizer had not yet been applied, the two replicate ‘treatments’ gave very similar results at each site. All this adds considerable confidence to the reality of the effect.

However, the significant values were scattered across years and sites, with 1985 and 1988 showing no effects.

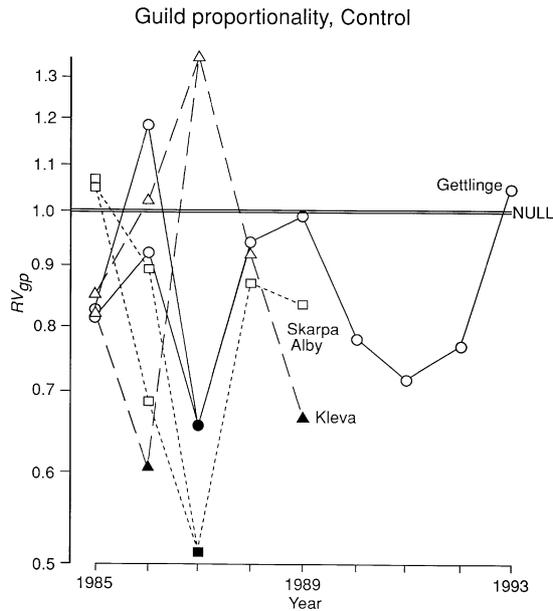
The search for intrinsic guilds (i.e. guilds based on the observed pattern of co-occurrences) produced none: searches of replicate optimization subsets (Wilson & Roxburgh 1994), each with a different random starting point, produced different ‘optimal’ classifications, none of which was significant when applied to the corresponding test subset (Wilson & Roxburgh 1994).

*Fertilized plots*

After fertilization (i.e. in 1987-1993),  $RV_{gp}$  values in Fertilized plots were generally greater than those in the Control plots, and, unlike the Control plots, in no case significantly  $< 1.0$  (Fig. 5). This is compatible with the conclusion for  $RV_r$ , that for the some years after fertilizer application the species had not regained equilibrium niche structure.



**Fig. 3.** Spatial variance in richness of perennial species in the Fertilized plots, sampled with 10-cm<sup>2</sup> quadrats, analyzed with a patch model. Solid symbols indicate significant departure from the null model (i.e.  $P < 0.05$ ).



**Fig. 4.** Spatial guild proportionality (graminoid v. forb guilds) in the 10-cm<sup>2</sup> quadrats, Control plots.  $RV_{gp} < 1.0$  indicates lower variance than expected under the null model. Solid symbols indicate significant departure from the null model (i.e.  $P < 0.05$ ).

#### Temporal variance in richness

The analysis of variance in richness that was applied above to spatial variation could also be applied to the five years (or nine years) data for a single 10-cm<sup>2</sup> quadrat, summed over the 50 or so quadrats. Here we test (as alternative hypothesis  $H_1$ ) a model that there is room in a microsite for only a certain number of species, though different species occupy those niches in different years. Again, alternative explanations have to be considered.

At Gettlinge, the test was performed for 50 sub-quadrats in each of two blocks, with the results summed over them. Overall, there was a significant excess of variance compared to null-model expectation (i.e.  $RV_r > 1$ ) (Table 3). This excess of variance can be attributed to some years having higher overall richness (Table 4). Including results for 1990-1993 for 40 quadrats did not qualitatively change the patterns.

The observed year-to-year variation in mean richness can itself be tested by comparing it with the variation in the randomizations above, the latter giving both the expected value of variance and a significance test. At all sites, there was significantly more variation in richness between years than expected under the null model (Table 5).

We adjusted for this overall year effect by calculating for each year an overall year effect [i.e. (yearly

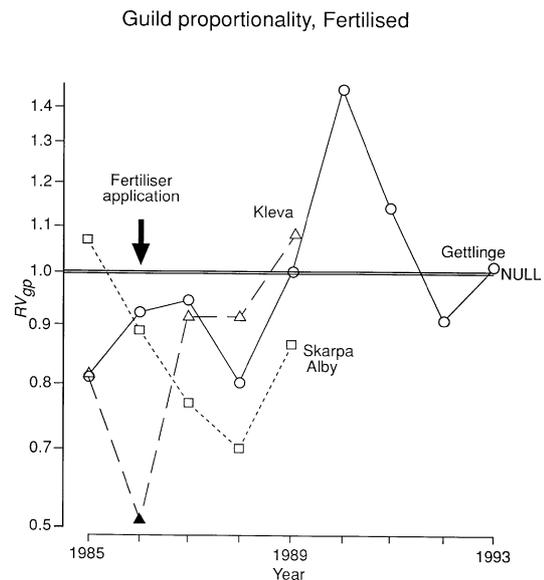
mean) - (mean over all years)], and subtracting the appropriate year effect from each quadrat/year richness value, both in the observed data (using year effects calculated from the observed data) and in the null-model randomizations (using year effects calculated afresh for each randomization). After making such adjustments,  $RV_r$  at Gettlinge (Table 3) was appreciably reduced, and no longer significantly  $> 1.0$ . This suggests that the significant excess of variance in the unadjusted analysis ( $RV_r = 1.295$  or  $1.656$ ) can be attributed to overall differences between years. At Kleva, a nonsignificant excess of variance (i.e.  $RV_r > 1$ ) before adjustment, changed to a significant deficit (i.e.  $RV_r < 1$ ) after adjustment. At Skarpa Alby, a nonsignificant deficit of variance changed after adjustment to a significant deficit of variance, indicating low temporal variance in richness.

The results analyzing perennials and annuals separately indicate that the effects are due to the perennial guild (Table 3).

#### A test for overcompensatory control

If there is control on species richness, as implied in the significantly low variance in richness demonstrated above, this implies negative-feedback control on species richness. Such control might be overcompensatory, leading to oscillation, such that quadrats that were species-rich one year tended to be species-poor another year.

An appropriate test statistic for this is to calculate for each quadrat the mean species richness over the five



**Fig. 5.** Spatial guild proportionality (graminoid vs. forb guilds) in the 10 cm<sup>2</sup> quadrats, Fertilised plots. Solid symbols indicate significant departure from the null model (i.e.  $P < 0.05$ ).

**Table 3.** Temporal variance in richness (all species) in the 10-cm<sup>2</sup> quadrats, Control plots. Conventions as in Table 1.

Yearly adjustment	Species	Years	Gettlinge		Kleva		Skarpa Alby	
			$RV_r$	$P$	$RV_r$	$P$	$RV_r$	$P$
None	All	1985-89	1.295	0.000	1.174	ns	0.922	ns
		1985-93	1.656	0.000				
Adjustment	All	1985-89	1.036	ns	0.786	0.018	0.785	0.017
		1985-93	1.100	ns				
Adjustment	Perennials	1985-89	1.018	ns	0.773	0.014	0.893	ns
		1985-93	0.926	ns				
Adjustment	Annuals	1985-89	1.073	ns	1.051	ns	1.042	ns
		1985-93	0.865	0.047				

years, and then calculate the variance in the mean richnesses across the 50 quadrats of a block. The null model would take as fixed the quadrat/year species richness values, and would keep them assigned to their own year of observation, but within each year the 50 values would be assigned at random to the 50 quadrats. That is, the null model assumes that there may be variation in richness from year-to-year as shown above, and within a year from quadrat-to-quadrat, but that there is no consistency between years in which quadrats have higher richness.

If there is some consistency (i.e. that some quadrats tend to be species-richer whatever the year, and others poorer), the observed variance in means-over-the-years will be greater than in the null model (i.e. the observed: expected ratio > 1). If there is negative species-richness feedback (i.e. overcompensatory control, so that if a quadrat is species-rich one year it tends to be species-poor in another), the observed variance will be lower than in the null model. In fact, the ratio is > 1 in all cases (Table 6), always with high significance. We conclude that there is no evidence of negative feedback between years. Rather, quadrats tend to be consistently species-rich or poor over years. Either the environment is more favourable (or unfavourable) in those microhabitats (perhaps related to soil depth), or there is mutualism, or shoot competition is reduced there (Newman 1973;

Wilson 1988), or the effect is simply due to the persistence of perennials. The latter explanation is supported by a lack of a consistency effect using only annuals (results not shown).

*Temporal guild proportionality*

It is possible that there is constancy between years not only in total richness but also in guild proportions. This suggests separate tests within each quadrat for such constancy over the five (or nine) years, summed as before over quadrats.

The result shows no significant constancy (i.e. no cases of  $RV_{gp}$  significantly < 1.0), though there is a trend in that direction for Gettlinge (Table 7).

**Discussion**

*Consistency and intermittency in community structure*

More significant departures of spatial variance in richness from null-model expectation were observed than the 5% of Type I errors expected at random (binomial  $P = 0.0030$ ). Taking into account that all are with  $RV_r < 1$ , the significance is even greater ( $P = 0.00011$ ). In the spatial guild proportionality test ( $RV_{gp}$ ) four of the 25 tests were significant ( $P = 0.068$ ), but all are with  $RV_{gp} < 1$ , giving  $P = 0.012$ . There is also consistency within and between many of the individual significant results (see above).

After 1985 with  $RV_r$  (Fig. 1), and in all years with  $RV_{gp}$  (Fig. 4), significant results are seen intermittently though time and space, and there is no correlation between spatial  $RV_r$  (Fig. 1) and  $RV_{gp}$  (Fig. 4). This suggests that, instead of assembly rules operating constantly, they operate in those years, and probably those seasons, when conditions allow competitive exclusion to occur. These would be the years when competition between species pushes the plants against the limits of species coexistence, and assembly rules operate.

**Table 4.** Yearly mean species richness (all species) in the Control plots sampled with 10-cm<sup>2</sup> quadrats.

Year	Gettlinge	Kleva	Skarpa Alby
1985	6.2	5.5	6.0
1986	6.5	5.6	4.9
1987	7.7	5.6	5.8
1988	8.4	7.3	6.3
1989	7.5	6.3	6.4
1990	6.1		
1991	7.5		
1992	4.8		
1993	4.5		

**Table 5.** Significance of between-year variation in overall richness (all species) in the 10-cm<sup>2</sup> quadrats, Control plots, as the ratio of observed variance in overall species richness (obs: Table 4) to that expected under the null model (exp), and the probability (*P*) of obs = exp under the null model (i.e. of departure of the ratio from 1.0).

Species	Parameter	Gettlinge		Kleva	Skarpa Alby
		1985-1989	1985-1992	1985-1989	1985-1989
Perennials	obs:exp variance	31.73	17.19	42.03	6.28
	<i>P</i>	0.000	0.000	0.000	0.000
Annuals	obs:exp variance	6.07	8.46	2.41	1.99
	<i>P</i>	0.000	0.000	0.092	ns

There is considerable evidence for year-to-year variation in plant communities (e.g. Figueroa & Davy 1991; Hobbs & Mooney 1991). Often the environmental control of this variation is very complex (Watt 1981; Tilman & Wedin 1991). The importance of competition might vary with resource availability (Kadmon & Shmida 1990). It would, therefore, be surprising if community structuring were visible continuously. Even if the rules themselves applied constantly, we would expect that often the community would be in disequilibrium between one assembly-rule state and another, with some species still arriving and some in the process of departing. The equilibrium patterns would therefore be visible only intermittently. This concept parallels the idea in animal ecology that community structure may be determined, not by continual constraints, but in occasional years when resources are limiting (Wiens 1977, 1989; Dunham 1980; Szaro 1986; Szaro & Balda 1986; Rogovin et al. 1992). An alternative explanation could be that particular combinations of species, which become established for historical reasons, compete with each other, whilst other combinations of species do not (J.A. Drake pers. comm.). It is clear that any niche limitation would give only a trend towards low variance in richness, which could be obscured by other factors; the actual result would be dependent on the characteristics of the particular species involved: what is a niche to one species could be part of a niche to another species, or two niches to yet other species.

Intermittent visibility of assembly rules may be part of the reason for previous failures to find such rules (e.g.

**Table 6.** Test for over-compensatory control of quadrat richness from year-to-year (all species; 10-cm<sup>2</sup> quadrats). Variance between quadrats in richness observed (obs) compared to that expected under the null model (exp).

Site/block	Years	obs:exp variance	<i>P</i>
Gettlinge A	1985-89	1.983	0.000
Gettlinge A	1985-93	2.432	0.000
Gettlinge B	1985-89	2.302	0.000
Kleva	1985-89	2.665	0.000
Skarpa Alby	1985-89	2.153	0.000

Wilson et al. 1987; Wilson 1989). In vegetation with a rapid turnover, such as the alvar grassland on Öland (Rusch & van der Maarel 1992; van der Maarel & Sykes 1993), the applicability of assembly rules may vary from year to year, but in communities such as forest it may vary on a scale of decades or maybe even centuries.

#### *Site differences in community structure*

Of the three study sites, Skarpa Alby showed the strongest, most consistent spatial community structure: (1) the lowest spatial  $RV_r$  values (Fig. 1), (2) typically lower  $RV_r$  values even at the 100-cm<sup>2</sup> scale (Fig. 2), and (3) the lowest spatial  $RV_{gp}$  (Fig. 4). Skarpa Alby also showed the lowest temporal variation: (1) the lowest year-to-year variation in overall species richness, compared to null-model expectation (Table 5), (2) low temporal  $RV_r$  (Table 3), and (3) little effect of fertilizer application on species composition (van der Maarel & Sykes unpubl. data).

Wilson et al. (in press) concluded that low temporal variation is not necessarily correlated with low spatial variation. However, Skarpa Alby is least variable in both. The explanation could be that with the shallower soil at Skarpa Alby, resources are more limiting, so there are more limits to species co-occurrence. Experiments would be useful in testing this speculation. Whatever the cause, the consistency of between-site differences supports the ecological reality of the results.

#### *Guild structure*

The significantly low  $RV_{gp}$  values for some sites in some years suggest that morphological guilds influence species composition in a fashion consistent with the

**Table 7.** Temporal Guild proportionality in the 10-cm<sup>2</sup> quadrats, Control plots. Conventions as in Table 1.

Site	Years	$RV_{gp}$	<i>P</i>
Gettlinge	1985-89	0.853	ns
	1985-93	0.785	0.094
Kleva	1985-89	0.829	ns
Skarpa Alby	1985-89	1.162	ns

existence of assembly rules, a hypothesis consistent with the results of Wilson & Roxburgh (1994) and Wilson & Watkins (1994). However, the effects are not strong. The weakness of guild structure is support for the Carousel model (van der Maarel & Sykes 1993; Sykes et al. 1994). We made guild-proportionality tests using only one guild classification. To have used more would have introduced the errors of multiple significance tests and *a posteriori* testing. A search using the method of Wilson & Roxburgh (1994) examined the possibility that there is an intrinsic guild classification, unrelated to our *a priori* graminoid vs. forb distinction. It failed to reveal any. This result provides additional evidence in support of the hypothesis that there is no strong guild structure in these grasslands.

The results of omitting annuals from the spatial  $RV_r$  analyses suggest that annuals are not involved in assembly rules, or at least not at the same scale as the perennials. This suggests the Matrix/Interstitial model of Grubb (1986), with the annuals being the Interstitial species. This differs from the Core-satellite model of Hanski (1982), in that the Grubb model assumes that the Matrix and Interstitial species are intrinsically different.

#### *Assembly rules after fertilizer application*

The evidence from the Fertilized plots, albeit negative, is that at least some of the community structure present in the undisturbed vegetation is lost in the three-four years after fertilizer application. This could be because at higher resource levels assembly rules do not apply, in which case the difference in community structure between treatments should continue. Alternatively, the loss of structure could be a temporary consequence of the temporary relaxation in competition resulting from the change in fertilizer level (Werner & Platt 1976; Christensen & Peet 1984). Assembly rules would be expected to reappear as species able to exploit the higher resource levels became predominant, and as the unpredictability caused by the species change-over decreased. The lower replication available during 1990-1993 does not enable a firm conclusion, but the trend is for the Fertilized plots to resemble the Control ones after 1989, suggesting the latter explanation.

#### *Interpretation of $RV_r$*

Environmental heterogeneity can lead to  $RV_r < 1.0$  if there are different species pools inhabiting the different environmental patches, and these pools happen to be approximately equal in size (Watkins & Wilson 1992; Bycroft et al. 1993). There are four reasons for rejecting this interpretation for the low  $RV_r$  values found here:

1. Within a block, the ecological range will be narrow. The evidence used by van der Maarel & Sykes (1993) for the Carousel model suggests that there is only

one pool of species at each site.

2. If the effect were due to environmental heterogeneity, the patch model should largely eliminate it. It does not.

3. If environmental heterogeneity were the cause, the effect would probably be evident equally at the 100 cm<sup>2</sup> scale, where greater heterogeneity is probable. In fact, it disappears or is reversed. This suggests the Waterhole effect (Pielou 1975; Wilson et al. 1987: higher or lower species richness in more 'favourable' sites) overwhelms any competitive exclusion that might occur at this scale.

4. The effect is shown also in the temporal analysis at Kleva and Skarpa Alby after yearly adjustment. With this approach, the same quadrat is being compared across time, so the effect of spatial environmental heterogeneity is excluded.

The significantly low  $RV_r$  supports the conclusion that there are real limitations to species co-occurrence in alvar grassland at the scale of 10 cm<sup>2</sup>.

It is possible that these restrictions are based on spatial limitations to the co-occurrence of individual plant modules - there cannot be more species than there are individuals (Watkins & Wilson 1992; Wilson et al. 1992; Bycroft et al. 1994). Thus, the lack of a deficit in richness variance at the 100 cm<sup>2</sup> scale could partly reflect the reduced limitations to the co-occurrence of modules at that scale. However, the small plant size, close intermingling and opportunity for vertical overlap in Öland limestone grassland, and the possibility for fractional plant representation in shoot-presence sampling, make this explanation less likely. Moreover, the demonstration of significant guild proportionality (i.e.  $RV_{gp} < 1$ ) argues against an explanation in terms of limitations to the co-occurrence of modules, since in that test the number of species per quadrat is held the same in the null model as observed. The possibility that the effects partly reflect limitations to the co-occurrence of individuals is considered in greater detail by van der Maarel et al. (1995).

Low values of  $RV_r$  are not the only possible result of community structure (Bycroft et al. 1994). High  $RV_r$  values could be caused by plant interactions such as mutualism via microclimatological and other effects - 'niche facilitation' rather than 'niche limitation' (Valiente Banuet & Ezcurra 1991; Carlsson & Callaghan 1991; Vetaas 1992; Bertness & Hacker 1994). However, such a process would be hard to demonstrate, because it would produce effects in the same direction as the Waterhole effect (i.e. the occurrence of higher or lower species richness in more 'favourable' sites: Wilson et al. 1987).

The community-structuring process we envisage is that species will continually invade a particular small

area, by seed immigration and by vegetative growth and spread. If a quadrat becomes empty because of plant death or disturbance, invasion will occur. Obviously, this invasion occurs rapidly in the alvar grassland on Öland, since in spite of disturbances caused by grazing practically no empty quadrats were found in sampling, and species-poor quadrats are rare (Fig. 6). As the quadrat fills, competition will increase, and further invasion will be slowed. When more species are present, those with lower competitive ability in the mixture will be eliminated, until a stable mixture is reached (Roughgarden 1983; Tregonning & Roberts 1979; Drake 1990b). Different species compositions of immigrants may produce different stable mixtures, or alternative stable states, which may differ in the number of species they contain (Case 1991; Law & Morton 1993). There will also be variation in species number because of quadrats where there has been recent disturbance and equilibrium composition has not been reached, or where there has been recent invasion and the local area is super-saturated with species (Roughgarden 1983; Drake 1990b; Case 1991). All these processes would probably lead to a bell-shaped distribution of richness, probably with a slight skewing to the right. Fig. 6. presents the actual distribution of species richness for two example sites that show significantly low  $RV_r$ . Both display exactly the pattern we expect: a shortage of low-richness quadrats because of ready colonization when competition is low, and a shortage of high-richness quadrats because of severe competition where many species have accumulated. Thus, our expectation of a narrow and basically symmetrical richness frequency distribution is borne out by our results.

In other cases, the distribution of quadrat species-richness values shows occasional quadrats with considerably more than the average richness. These may represent temporary escape from niche limitation in space, comparable to the temporary release from niche limita-

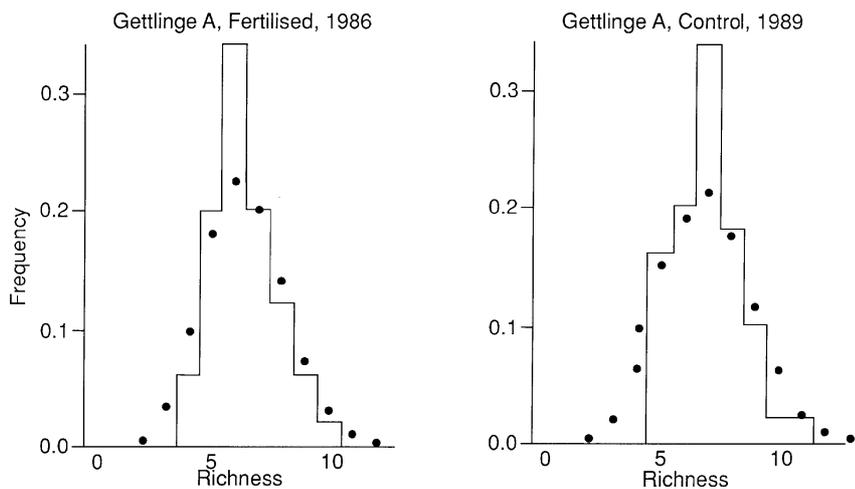
tion in time we are suggesting occurs when fertilizer is applied, though from our observations it is not possible to distinguish this from the Waterhole effect or niche facilitation. The shape of the richness distribution is considered further by van der Maarel et al. (1995).

#### The Carousel model

The Carousel model (van der Maarel & Sykes 1993; Sykes et al. 1994), developed using the same dataset as we use here, suggests that “in the course of time any microsite can be a niche for most of the species participating in the community”. It is essentially the same as the Lottery model (Sale 1977), the Ecological-equivalency concept (Shmida & Wilson 1985), and the Equal-chance hypothesis (Connell 1978; Wilson 1990). There are two basic ways in which the Carousel model can be understood, though van der Maarel & Sykes (1993) did not commit themselves either way:

1. Niche-limited Carousel: This version would assume that there is only a limited number of niches within a microsite. Each niche is occupied in a particular year by one species that is selected at random from the pool of species in the area. Two species cannot occupy a particular niche in a microsite at the same time, because of competitive exclusion. The Niche-limited Carousel model would tend to result in relatively constant richness, i.e.  $RV_r < 1.0$  (in the absence of confounding factors: Palmer & van der Maarel 1995; Wilson 1995b). This is the way other authors seem to have understood the Carousel model - e.g.: “on the island of Öland in the Baltic Sea [van der Maarel and Sykes] observed that while species richness was relatively constant over time, species composition was not”; Bengtsson et al. 1994).

2. Density-independent Carousel: Under this model, there is no limitation on the number of species, or at least none caused by competitive exclusion. Possible



**Fig. 6.** Distribution of species richness values among the 50 10-cm<sup>2</sup> quadrats in a block, in two example cases where  $RV_r$  is significantly less than 1.0 (Fig. 1).

reasons for such a lack of competitive exclusion could be that: (a) each species has its own niche, so that there is no competitive exclusion, or (b) competitive exclusion occurs too slowly to be effective. This explanation leaves open the question of why all species do not occur in all microsites in the area; presumably the answer would have to be in some density-independent factor(s). The Density-independent Carousel model would not give any tendency for  $RV_r$  to depart from the null-model value (though one cannot draw any conclusion from a lack of departure from the null model: Lepš 1995; Wilson 1995c).

The significant deficit of temporal variance in richness (i.e.  $RV_r < 1$ ) at Kleva and Skarpa Alby points towards the Niche-limited Carousel model for these limestone grasslands, but further work would be required to exclude alternative explanations.

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