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Evidence for constraint on species coexistence in vegetation of the Park Grass experiment

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Abstract

Repeated patterns, of a type that would be expected to result from limitations to species coexistence (i.e. 'assembly rules') were sought in the Park Grass experiment. This classical grassland experiment was sampled in two years, using replicated biomass samples. Variance in a number of measures was examined, and compared to the variance expected under appropriate null models, the latter based on assumptions of no interactions between species. In each case, an assembly rule would result in low variance. Examining variance in species richness between quadrats within a treatment, there was no indication of constraint on species co-occurrences; variance in richness was actually greater than expected under the null model, attributable to environmental variation or perhaps positive interactions between species. However, there was control on biomass, evidenced by variance in total biomass (i.e. over all species) within a treatment being significantly lower than expected under the null model. There was no indication of community structure based on guilds (i.e. functional types). Although there was in 1991 some, non-significant, indication of a constant proportion of species from the legume guild, there was no sign of such an effect in 1992. Searches for intrinsic guilds failed to converge. There was no indication at all of constancy in the proportional representation of guilds by biomass. Thus, there is good evidence for competitive control on plant growth, but none for control of species occurrences. There is no convincing evidence for guild structure in this community at the scale sampled. Possible conflict is discussed between the existence of evidence for temporal stability but the absence of evidence for spatial uniformity. It is concluded that most of the mechanisms proposed for temporal stability will not necessarily lead to control on spatial variation. For many mechanisms, this would depend on the spatial scale examined.

Introduction

Vegetation description has been a feature of ecology for a century, but in spite of increased knowledge of processes at the population level (Silvertown & Lovett Doust 1993), very little is known of the effects of these processes at the whole-community level. Recently, methods have been devised for investigating plant community structure, seeking the patterns that would be expected from current theories on population processes.

The aim of these methods has been to find regularities in the observed patterns of species occurrences and abundances, which could be the result of limitations to coexistence. This approach eschews examination of patterns that are likely to be due to differences in species composition between different environments, on the grounds that such effects are already well documented and accepted. Instead, it looks for patterns that are likely to result from competitive exclusion between species:

- both effects due to the elimination of species from certain mixtures (richness rules), and restrictions

on the amount of each species that can be present (biomass rules),

- processes that operate at the level of the whole community (species richness and total biomass), and those that operate at the level of the guild (e.g. guild proportionality).

Particularly interesting are regularities – tendencies for a feature of the community to remain rather constant across different patches of the community. These are assembly rules – generalised restrictions on species presence or abundance that are based on the presence or abundance of one or several other species, or types of species (not simply the response of individual species to the environment): Wilson & Whittaker (1995). Because of scepticism about the existence of such rules, as well as normal scientific rigour, it is vital to compare such patterns with those expected under null models, i.e. models in which there is no interaction between species (Wilson 1991). We examine four possible types of rule. Two examine species presence/absence:

1. *Variance in species richness*: A limit to species coexistence, caused by a limited number of niches, would result in a lower variance in species richness between quadrats than expected under a null model (Wilson et al. 1987; Wilson & Sykes 1988).
2. *Guild proportionality*: If limitation to species coexistence were guild-based, the proportion of species from different guilds (i.e. functional types) should be relatively constant, again in comparison with a null model. I.e. competitive exclusion within guilds should be manifest through neighbour relationships assuming homogeneity of the physical environment (cf. Cody 1986). Wilson (1989) made such a test using synusial guilds. Later, the same technique was applied to morphological guilds (Wilson & Roxburgh 1994; Wilson & Watkins 1994; Wilson & Gitay 1995a).

Beyond the presence and absence of species, it is possible that there might be assembly rules for the abundance of each species. We investigate two types of abundance rule:

1. *Biomass constancy*: Competition between species could result in a lower variance of total-quadrat-biomass than expected under a null model. The appropriate null model would be one in which the non-zero biomasses of a species were assigned at random (Wilson & Gitay 1995a, b).
2. *Guild biomass proportionality*: The logical fourth possibility, not previously examined, is that the proportion of biomass from each guild might show

a lower variance than under the biomass-constancy null model.

A particular interest in assembly rules is that because they limit the ways that species can coexist, they can be the basis of uniformity in time and space – mechanisms for temporal stability, and for spatial constancy.

A restriction in testing most community-structure theory is that it is intended to apply only to communities that are at equilibrium. None of the effects would be expected to be seen in communities still recovering from disturbance (Armesto & Pickett 1985); the same processes will occur, but they will not have time to produce patterns that are clear enough to be identified. Very rarely is it possible to state that any community is at equilibrium, because evidence is not available. However the Park Grass experiment, established at Rothamsted Experimental Station (UK) in 1856, has subplots which have received constant management for many years. There are biomass records from the experiment that allow us to judge whether the community is stable. This evidence shows that on most subplots there has been little long-term trend this century (Silvertown 1987). Biomass data on a species basis, recently obtained from replicated quadrats within subplots of the Park Grass experiment, enable the above four tests for community structure to be made, to seek evidence for the restrictions on species coexistence in a range of communities close to equilibrium.

Methods

The Park Grass experiment comprises a number of fertiliser treatments, applied to a pasture under hay management. The experiment was started in 1856, but there have been changes of treatment on some subplots since then. In 1991 and 1992, 89 subplots were sampled, including all the currently managed subplots and their liming subtreatments. (One of these subplots was omitted from analyses because all the quadrats contained only one species.) Each treatment subplot was sampled by six randomly-placed quadrats (a total of 534 quadrats), each 0.5 m × 0.25 m (0.125 m²). The above-ground biomass of all species in the standing crop above the ground surface) was determined in June each year.

Four analyses were used:

1. *Variance in species richness*: Index RV_r (the observed variance in quadrat richness divided by the null-model variance: Wilson et al. 1992) was

calculated from the variation between the six replicate quadrats of any treatment subplot (and the within-subplot variance summed over all subplots; see below). The analysis is based on a null model with species frequencies fixed at those observed, but with occurrences assigned to the six quadrats, independently for each species, at random within this constraint. If interactions between species were limiting local coexistence, i.e. with local species saturation, RV_r would (in the absence of complicating factors) be < 1.0 . If the species did not interact, RV_r would (again, in the absence of complicating factors) be 1.0.

2. *Guild proportionality*: Variation in the proportions of presences from each guild was tested by index RV_{gp} (the observed variance in guild proportions divided by the null-model variance: Wilson 1989). The null model has both species frequencies and quadrat richnesses fixed at those observed; the species are assigned to quadrats at random within these constraints (Wilson 1987), especially with no limitation on the ability of guild members to co-occur. If interactions between species were limiting the proportions of species from a guild, such that a species was less likely to enter a local community when the proportion of species from that guild was high, or such that if it did enter a member of the same guild was more likely to disappear locally, RV_{gp} would (in the absence of complicating factors) be < 1.0 . If the species did not interact, RV_{gp} would (again, in the absence of complicating factors) be 1.0.

3. *Biomass constancy* (variance in total biomass per quadrat): measured by index RV_b (the observed variance in total biomass per quadrat divided by the null-model variance: Wilson & Gitay 1995a). The null model takes the observed pattern of species occurrences as fixed: for each species (independently) it allocates the observed biomasses of that species at random to quadrats where the species was present (Wilson & Gitay 1995a). If interactions between species were limiting local coexistence, so that when one species was more abundant locally another (or others) was (were) likely to be less abundant, i.e. with local biomass saturation, RV_b would (in the absence of complicating factors) be < 1.0 . If the species did not interact, RV_b would (again, in the absence of complicating factors) be 1.0.

4. *Guild biomass proportionality*: Constancy in guild biomass proportions was measured by index RV_{gbp} . The same null model was used as for biomass constancy. For any guild, the biomass proportion, gbp , of guild g for a quadrat is:

$$gbp = \frac{\text{total biomass of species from guild } g \text{ in the quadrat}}{\text{total biomass of all species in the quadrat}}$$

The index used was:

$$RV_{gbp} = \frac{V_{obs}}{V_{exp}}$$

where

V_{obs} = observed variance (over the quadrats) in gbp

V_{exp} = the variance in gbp expected under the null model, estimated as the mean over the randomisations.

If interactions between species were limiting the proportions of species from a guild, such that a species was more likely to be abundant in a local community when the local proportion of biomass from that guild was otherwise low, RV_{gbp} would (in the absence of complicating factors) be < 1.0 . If the species did not interact, RV_{gbp} would (again, in the absence of complicating factors) be 1.0.

Thus, all four indices, RV_r , RV_{gp} , RV_b , RV_{gbp} , are the ratio of the observed variance over quadrats to that expected under the corresponding null model. Values of 1.0 give no indication of departure from the null model, and values < 1.0 indicate lesser variance in that attribute, i.e. a constraint on species coexistence – evidence for an assembly rule.

For all analyses, within-treatment variances were summed over all treatments, thus excluding between-treatment variation from the calculations. This was done for the observed data, and separately for each randomisation. Examination of joint within-treatment variation also gave considerable power to the tests. In conventional ‘degrees of freedom’ terms, there would be five d.f. within each treatment, giving in general over the 88 subplots $5 \times 88 = 440$ d.f.

For all analyses, a variance value was calculated from each of the 2000 randomisations. The mean of these values gave the value expected under the null model, and the proportion of randomisations giving a value equal to or more extreme than that observed gave the significance, expressed as a two-tailed test.

For Guild proportionality and Guild biomass proportionality analyses, species were split into three

guilds, determined a priori as the guild classification traditionally used in the experiment (Thurston 1969; Silvertown 1987):

Graminoid

Legume

Forb (excluding legumes, described as 'forb' for convenience).

The importance of the graminoid/forb distinction was demonstrated objectively by Wilson & Roxburgh (1994) and Wilson & Whittaker (1995). The separation of legumes from other forbs is based on the difference in nitrogen resources – atmospheric fixation for the legumes. The three guilds represent groups that respond differently to the fertilisers that have been applied in the experiment (Silvertown 1987). When a particular guild was absent from a subplot, the subplot was omitted from guild analyses. Following Wilson & Roxburgh (1994), we also searched for intrinsic guilds, by their method. This comprises a heuristic search for the guild classification that minimises RV_{gp} , i.e. that maximises indication of community structure, as seen in the tendency of species within a guild to exclude each other. Following them, we avoided circularity in this search by seeking intrinsic guilds on a random subset of half of the data (the Optimisation subset), and testing the resulting classification on the remaining data (the Test subset).

In some treatments of the experiment, application of ammonium sulphate has caused the soil to become acid (down to pH 3.5). This has led to low species richness and in extreme cases to low productivity. In case community structure was different in these treatments, we performed additional analyses omitting these treatments, and other with only these treatments.

Results

Variance in richness

There was no sign of a deficit of variance (i.e. of lower variance in quadrat richness than expected under the null model, low RV_r). Thus there was no evidence for species' excluding each other. On the contrary, there was a highly significant tendency for quadrats to be more variable in species richness than expected (i.e. $RV_r > 1.0$; Table 1). The deviation of RV_r from the null-model expectation was notably constant between years (RV_r of 1.440 and 1.444 respectively). Very similar results were obtained omitting the acid treatments, i.e. those where the soil pH has been reduced to 4.0 or less.

Guild proportionality

There was no evidence that there was, across a treatment, a constant proportion of species occurrences from the Graminoid and Forb guilds (Table 1). Variance in the proportion of species from the Legume guild in 1991 was lower than expected under the null model, but not significantly. In the 1992 data there was no sign at all of such an effect. It is clear from the very small departures from the null model that in most cases there would have been no significance even had more replication been possible.

Searches for intrinsic guilds gave no indication of guild structure. Although a low RV_{gp} (down to 0.480) could be obtained for the Optimisation subset, in no case did the resulting guild classification show significance on the Test subset. In case this was due to having only three quadrats per treatment once a random subset had been chosen, an alternative approach was tried. This comprised searching for an optimum guild classification using all the data for one year (e.g. 1991), and using the other year (e.g. 1992) to test the classification. In no case did this method show significant guild proportionality in the test year.

Biomass constancy

There was strong evidence of biomass constancy. That is, RV_b was considerably less than 1.0, indicating much lower biomass variation than expected if the biomass-es were allocated at random (Table 1). Results were similar if the acid treatments were excluded.

Guild biomass proportionality

Guild biomass proportionality analysis showed very small deviation from the null model for both years and for all guilds, clearly non-significant (Table 1). Again, the departures from the null model are so small that the lack of significance cannot have been because the test was not powerful enough.

Discussion

Generality of rules

Although the acid subplots are very different from the neutral/alkaline subplots in species composition, species diversity, species richness, yield range, and richness:yield relations (Dodd et al. 1994), there was very little evidence of difference in any aspect of community structure investigated here. The analysis on just

Table 1. Aspects of community structure in treatment subplots of the Park Grass experiment. 80 non-acid subplots, 8 acid subplots. ns = $P > 0.1$ (P values between 0.1 and 0.05 are shown for information, but are not interpreted as being significant). — = test impossible.

Aspect of community structure	index	year	all subplots		non-acid subplots		acid subplots	
			index value	P	index value	P	index value	P
Variance in richness	RV_r	1991	1.440	<0.001	1.436	<0.000	1.305	ns
		1992	1.444	<0.001	1.457	<0.000	0.761	ns
Guild proportionality	RV_{gp}							
Graminoid guild		1991	0.982	ns	0.996	ns	0.788	ns
		1992	0.992	ns	0.984	ns	1.022	ns
Legume guild		1991	0.882	0.069	0.882	0.068	—	
		1992	0.996	ns	0.996	ns	—	
Forb guild		1991	0.916	ns	0.927	ns	0.788	ns
		1992	1.016	ns	1.014	ns	1.022	ns
Biomass constancy	RV_b	1991	0.648	<0.000	0.643	<0.000	0.762	0.093
		1992	0.742	<0.000	0.736	<0.000	0.856	ns
Guild biomass proportionality	RV_{gbp}							
Graminoid guild		1991	1.035		1.033	ns	0.976	ns
		1992	1.044	ns	1.047	ns	0.928	ns
Legume guild		1991	0.938	ns	0.938	ns	—	
		1992	0.951	ns	0.952	ns	—	
Forb guild		1991	1.014	ns	1.012	ns	0.976	ns
		1992	0.986	ns	0.989	ns	0.928	ns

the acid treatments was based on only eight treatments (those with $\text{pH} < 4.0$). However, the biomass constancy results are in the same direction as for treatments with $\text{pH} > 4.0$. Even the direction of the difference between years was the same. For variance in richness, RV_r for the acid treatments was 1.305 in 1991, again comparable with the non-acid treatments, though the 1992 figure was different at 0.761. There was very little evidence of guild-based assembly rules in either type. Apparently, the same processes, and lack of processes, occur in subplots with very different species composition.

Control of species richness

Analysis of within-treatment variance in whole-community biomass (biomass constancy: RV_b) demonstrated that the biomass of each species that occurs in a treatment is constrained to give a relatively constant total, i.e. more constant than expected under the null model (Table 1). Clearly, the most likely explanation is that there is strong competition for resources, so that co-occurring species limit the growth of each other

(Wilson & Gitay 1995b). We make this conclusion in spite of assertions that competition cannot be detected from co-occurrence data (Abramsky et al. 1986; Hastings 1987).

However, there is no such control on species occurrences. In fact, there was more variation in species richness than expected at random (Table 1). In interpreting variance in richness lower than expected under the null model, all possible explanations have to be taken into account (Wilson 1995a, b). Similarly, several explanations have to be considered for a higher variance (Bycroft et al. 1993). These are:

1. 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). Such variation in species pools could be due to the individualistic effects of keystone species. For example, when *Lathyrus pratensis* L. occurs, it often has high cover, scram-

Table 2. Mechanisms of coexistence proposed (Wilson 1990), and their likely effects on temporal and spatial variation.

Mechanism	Resulting temporal variation	Resulting spatial variation	
		theoretical	likely at 0.125 m ² scale
1 Niche diversification			
a Vertical ^a	low	low	low
b. Spatial ^b	low	scale-dependent	low or high, depending on scale
c. Temporal	low ^c	no effect	no effect
2 Pest Pressure	low	scale-dependent	low or high, depending on scale
3 Equal chance ^d	no effect ^e	no effect ^e	no effect ^e
4 Gradual climate change	low	no effect	no effect
5 Intermediate-timescale disturbance	low	scale-dependent	low or high, depending on scale
6 Life history ^f differences	low	scale-dependent	low or high, depending on scale
7 Initial patch ^g composition	no effect ^h	no effect ^h	no effect ^h
8 Spatial mass effect	low	high	high
9 Circular competitive networks	low	low or high	low (probably)
10 Cyclic succession ⁱ	low	scale-dependent	low or high, depending on scale
11 Aggregation	low	high	high
12 Stabilising coevolution	no effect ^j	no effect ^j	no effect ^j

^a I.e. stratification

^b I.e. micro-habitat differentiation; environmental heterogeneity

^c Temporal niche differentiation: e.g. differentiation between different parts of the hay management cycle, could permit coexistence on a timescale of years

^d In a sense the null hypothesis. This mechanism is related to the 'lottery' model of Sale (1977)

^e This is in effect the null hypothesis, therefore by definition variability would be equal to that under the null hypothesis

^f The model of Skellam (1951), with one (annual) species being a better competitor, and the other more efficient at reproduction/dispersal

^g A suggestion of Levin (1974), based on stochastic occupancy of transient patches, and the unlikely situation of greater between- than within-species interference

^h This mechanism is probably unrealistic for plant communities

ⁱ Differing from Hypothesis 9 (Circular Competitive networks) in that: (a) whole communities are involved, not individuals of particular species, (b) the cycle between species is caused by their effects on the environment, and (c) as few as two phases may be involved

^j Aarssen's concept of mutually ever-increasing competitive ability between two species seems idealistic. Indeed, Aarssen himself seems to have replaced this concept with one based on circular competitive networks (Aarssen 1989)

bling over other species, and often suppressing them.

2. Heterogeneity in patch history, e.g. in disturbance and dispersal, giving an effect similar to the Water-hole effect (Zobel et al., 1993). Whilst this is a possibility, the long history of uniform treatment on the Park Grass subplots makes this less likely than in most communities.

3. That some species, by mutualistic interactions, facilitate species richness (Aguiar et al. 1992; Brown 1992; Ryser 1993; Bycroft et al. 1993).

Guilds

The analyses presented here gave no evidence for assembly rules based on guilds. Of course, a finding of significant guild proportionality or guild biomass proportionality would have to be considered against possi-

ble explanations other than an assembly rule, but here no such significant effects were found, so the question does not arise. Some have suggested that guilds are important for plant communities (Keddy 1990). Other have speculated as to what the guild structure would be, if guilds existed (Leishman & Westoby 1992). There have been very few tests against null models to see whether guild membership actually affects the ability of species to co-occur. Wilson (1989) found little evidence for guild structure in 10×10 m quadrats in a forest. We have found none for 0.125 m^2 quadrats in grassland. Wilson & Watkins (1994) did find evidence for guild-based assembly rules at the scale of $c. 1 \times 1$ cm in lawns, Wilson & Roxburgh (1994) at the scale of a point, also in a lawn, and Wilson et al. (1995) in 2 m diameter quadrats in a forest. The negative results of the guild analyses here cannot be explained as due to an inappropriate guild classification, because intrinsic guild searches failed to find stronger structure.

It is clear that in some plant communities guild-based assembly rules are operative; in other communities guilds seem to have no role in limiting species coexistence at the scale examined.

Stability

Silvertown (1987) suggested from temporal comparisons that the Park Grass vegetation was stable: there was no overall change in guild proportions through time, in spite of constant weather perturbations (Silvertown et al. 1994). This implies there is some process, internal to the community, that is stabilising it, i.e. returning species composition to an equilibrium when it departs. If there be such control on species composition through time, the same mechanism might work across space, stabilising variation from point to point within a treatment. The particular feature that Silvertown (1987) noted was low variation in the biomass proportions of the three guilds; this was one of the criteria used in the spatial variation analyses here, and there was no evidence for any control on guild proportions.

The evidence formally required to demonstrate temporal stability is return to the original state following disturbance. Silvertown argued that year-to-year variation in species composition caused by weather represented a natural perturbation experiment. The absence of a long-term trend in species composition on those subplots with constant management (and without acidification) supports this interpretation, and suggests that some density-dependent mechanism is stabilising

the species mixture, though the data are not adequate for a formal test against a null model of a random walk in species composition.

This raises a possible contradiction, that there is evidence for control of temporal variability, but none for control of spatial variability. However, the coexistence mechanisms producing low temporal variability may not all operate spatially, at least at the scale of our sampling (0.125 m^2). Wilson (1990) reviewed proposed mechanisms of temporal coexistence (Table 2). Most of these mechanisms lead to low temporal variation, which is indeed the reason they were proposed. Applied to the present results, three mechanisms can be excluded, one (3: Equal chance) as being the null model and therefore no explanation of departure from the null model, and two (7 and 12) as being unlikely to operate, at least in plant communities. Of the other nine mechanisms, two (8 and 11) would lead to high spatial variation, and four or five (1b, 2, 5, 6, 10) to either low or high variation, depending on the scale examined (here 0.125 m^2) in relation to the scale on which the process operates. We conclude that it is quite possible that the vegetation is temporally stable, yet spatially unstable in the sense of varying from one point to another within a treatment. More evidence would be required before these possibilities could be resolved.

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