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Are there assembly rules for plant species abundance? An investigation in relation to soil resources and successional trends

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Summary

1 The distribution of relative abundances between the species of a plant community has been remarkably little analysed. We examine differences in relative abundance distribution (RAD) between different soil fertility levels, and trends through time in the development of a community, using data from three grassland experiments: Monks Wood grassland restoration, Park Grass long-term fertilizer trial and Compton grassland restoration.

2 Comparing plots with different fertilizer treatments, the evenness of plant species abundance was higher where phosphorus had been applied; other effects of soil fertility on evenness were inconsistent. There were no consistent effects of soil fertility on the relative fit of the Geometric, General Log-normal and Zipf–Mandelbrot models of RAD, contrary to previous theories. However, the Broken Stick model fitted relatively better, though still poorly in absolute terms, in plots with high species richness and where phosphorus had been applied. Parameter γ of the General Log-normal distribution was higher in the high-nitrogen and species-poor plots, disproving the theory that γ should be constant. Parameter β of the Zipf–Mandelbrot model was higher in more species-rich and in high-phosphorus plots, a result not predicted in the literature. The variation in γ and β seems to be largely a reflection of the variation in evenness and in species dominance. The consistency in species dominance across space (rank consistency) was higher in plots with phosphorus addition. It is concluded that resource availability had little effect on which model of community assembly fitted. However, under high phosphorus conditions the community was more spatially consistent, and there was less dominance.

3 Through time, the evenness of species abundances increased, consistently between two separate experiments. Examining the shape of the abundance distribution at a more detailed level, there were no time trends in which relative abundance model fitted best, except that the fit of the Broken Stick model became less poor. However, the shape of the General Log-normal and Zipf–Mandelbrot curves, as seen in indices γ and β, respectively, changed through time, consistently between two separate experiments, supporting the implication from increased evenness of increasing niche diversification. Rank consistency increased in the early years of succession, then decreased, supporting the Three-phase succession model of Gitay & Wilson (1995), in which a middle 'building' phase has higher rank consistency than the preceding 'pioneer' phase or the succeeding 'mature' phase.

Keywords: abundance, assembly rules, community structure, dominance/diversity, evenness, grassland, rank consistency, succession, vegetation restoration

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Introduction

One of the most obvious features of a biological community is the pattern of relative abundances among the species. Is there one dominant species? Are there many species of about equal abundance? Is there a long tail of increasingly minor species? These questions offer the opportunity to find repeated patterns among communities, which might lead to generalizations about community structure that are independent of species composition. Ideally, the questions offer tests of the mechanisms by which communities are assembled (Wilson 1991b; Tokeshi 1993).

However, there have been rather few attempts to investigate such questions (Tokeshi 1993). We examine two factors that have been suggested to affect the abundance pattern:

1 Resource availability: Tilman (1982) suggested that abundance patterns would vary with resource availability. He used the example of variation in soil nutrient status in the Park Grass Experiment at Rothamsted Experimental Station (Thurston 1969), but made no analyses to demonstrate the effects. We examine these questions in the Park Grass experiment itself, and also in an experiment at the Compton Experimental Station.
2 Temporal trends: It has often been suggested that abundance patterns will change through succession (e.g. MacArthur 1960; Gray 1987). However, this question has never been examined by using genuine successional data. We do so using the Compton experiment, and also an experiment at the Monks Wood Experimental Station. (Most plots of the Park Grass experiment seem to be at equilibrium, be it a plagioclimax, and the Park Grass data are therefore not included in examination of temporal trends.)

The special value of the three experiments is that resource availability was manipulated experimentally, actual succession was recorded through time on the same plots, and all three experiments were recorded using biomass as the measure of abundance.

Assembly rules are restrictions on species presence or abundance that are based on the presence or abundance of one or several particular other species, or types of species (not simply the response of individual species to the environment) (Diamond 1975; Wilson & Gitay 1995). Most assembly rules so far proposed have been based on the presence/absence of species (Drake 1990; Wilson 1991b), but more meaningful rules may be possible taking into account species abundance (Rahel 1990). We examine three facets of abundance patterns:

1 evenness,
2 relative abundance distribution (RAD), and
3 rank consistency.

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EVENNESS

The simplest feature to extract from the abundance pattern is evenness, a measure of how similar are the abundances of different species (Pielou 1977; Bulla 1994). A low value of evenness indicates that one or a few species are highly dominant, whilst others are present in very small amounts. A high value of evenness indicates that all the species in the community have rather similar abundance.

Evenness can be an index of community structure, able to find general patterns among communities that differ in species composition (Bulla 1994). For example, it has been suggested that strong current competition leads to unevenness (Cotgreave & Harvey 1994), an argument similar to the one that Grime (1979) used to support the humped-back model of species richness (Oksanen 1996; Wilson *et al.*, in press).

RELATIVE ABUNDANCE DISTRIBUTION (RAD)

Several models have been proposed to explain RADs. Ideally, the degree of fit of actual communities to curves obtained from such models enables discrimination between different theories of how communities are assembled (Pielou 1975; Wilson 1991a). For example, a model in which species use a fixed proportion of the remaining resources, in order of their competitive ability, leads to the Geometric model; random division of the resource spectrum into niches leads to either the Broken stick or the General Log-normal model (Watkins & Wilson 1994).

The RAD also summarizes, in a way that does not depend on the identity of the species, the structure of a community, enabling a theory-free search for general patterns (Pielou 1975; Tokeshi 1993). Very few tests have been made of these models, apparently because appropriate methods have only recently become available (Wilson 1991a; Watkins & Wilson 1994).

RANK CONSISTENCY

Whatever the RAD of a community, the question arises (Pielou 1975) as to whether the pattern is determined by:

1 evolutionary factors: i.e. the intrinsic properties of the species, which may partly reflect the effects of previous competition – the 'ghosts of competition past' (Connell 1980), giving 'dominance-controlled communities' (Yodzis 1978); or
2 ecological factors, i.e. processes of invasion and competition that operate in the establishment and maintenance of the community (Morris 1994), giving 'founder controlled communities' (Yodzis 1978).

Watkins & Wilson (1994) pointed out that calculation of rank consistency could be used to distinguish between these possibilities. If evolutionary factors are predominant, the same ranking of species will be obtained in all quadrats, and rank consistency will be high, as Grubb *et al.* (1982) suggested was the norm for plant communities. If ecological processes dominate, rank consistency could be lower.

Sites

MONKS WOOD EXPERIMENT

The experiment was established in 1978, to investigate techniques for establishing amenity grassland. It is on a site at Monks Wood Experimental Station, Abbots Ripton, Huntingdonshire, UK, open except for hedges on two sides. The soil is heavy clay.

Four 5-m × 2-m plots are being considered, each surrounded by a 1 m buffer of *Phleum pratense*. The plots were cultivated in spring 1978 to remove all vegetation, and then left to natural colonization (no seed was sown). There was natural seed dispersal not only from the general area but also from nearby plots establishing from various wild-flower–grass mixtures (Wells 1995). The plots were cut annually in mid-August, as in agricultural/conservation hay management. Floristic composition was estimated in dry weight herbage samples in 1979–82, 1984–6, 1988–9 and 1991, from 1 to 4 replicate 40 cm × 40 cm quadrats.

In total, 24 forbs and 10 grasses were recorded in the plots. *Trifolium repens* was particularly abundant in the first year. From 1979 to 1981 it was gradually replaced by *Agrostis stolonifera* and *Holcus lanatus*. *Lotus corniculatus* also increased up to 1981–82, after which it declined as *Alopecurus pratensis* increased. By 1991 the latter three grasses comprised 76.9% of the herbage.

PARK GRASS EXPERIMENT

The classical Park Grass experiment, at Rothamsted Experimental Station, Hertfordshire, UK, comprises a number of fertilizer treatments, applied to a pasture under hay management (Thurston 1969; Tilman *et al.* 1994). The experiment originated in 1856, but there have been changes of treatment on most plots since then. In 1991 and 1992, 89 plots (in some publications termed 'subplots') were sampled (Wilson *et al.* 1996), including all the currently managed plots and their liming subtreatments, but six of the plots were omitted from analyses, because species richness was too low for the RAD to be meaningfully examined. Each plot was sampled in June by six randomly placed quadrats, each 0.5 m × 0.25 m (0.125 m^2), determining the above-ground biomass of all species in the standing crop (> 2.5 cm above the ground surface).

The plots were treated as individual units in multiple regression of the variate of interest on nitrogen application (0, 1 or 2), phosphorus application (0 or 1), potassium application (0 or 1), soil pH, species richness per quadrat, and dry weight yield. Species richness and yield were included in the regressions to guard against the possibility of indirect effects via these factors (cf. Dodd *et al.* 1994). This set of independent factors is referred to as 'soil/vegetation factors'. We then used a step-down procedure to eliminate ineffective predictors, guarding against the problem of spurious significance (Flack & Chang 1987) by interpreting such regressions only when the overall regression was significant. To examine consistency in results between 1991 and 1992, regression equations calculated from the data of each year were tested also on data from the other year, representing a further guard against spurious results from the step-down procedure.

COMPTON EXPERIMENT

A succession experiment, to investigate the practicalities of creating species-rich grasslands, was set up in July 1987 at the Compton Experimental Station of Wolverhampton University, in the UK Midlands. In the treatments being considered, the previous vegetation was removed by glyphosate herbicide, after which the plots were cultivated and harrowed. Hay from a species-rich meadow (similar to community MG5 of Rodwell 1992) was strewn over the ground. There were two treatments, – nitrogen and + nitrogen, in 3-m × 3-m plots, with three replicates in a randomized block design. Nitrogen was applied in the first year only, at 150 kg N ha^{-1}, in the form of ammonium sulphate. Each year, hay was cut in July; in 1988, 1989, 1991, 1993 and 1994 the hay from the central 2 m × 2 m of each plot was sorted into species and dry weighted.

In the early years of the experiment the dominant species on both – nitrogen and + nitrogen plots were *Holcus lanatus* and *Leucanthemum vulgare*. By 1993–94 these had been replaced by *Festuca rubra* and *Plantago lanceolata*.

Analysis methods

EVENNESS

Evenness was calculated by the index E' of Camargo (1993). Let: S = the number of species in the sample; x_s = the abundance of the sth species

$$p_s = x_s / \sum_{t=1}^{S} x_t$$

then:

$$E' = 1 - \sum_{s1=1}^{S} \sum_{s2=s1+1}^{S} \mathrm{abs}(p_{s1} - p_{s2}) / S$$

This index is independent of species richness, unlike many evenness indices (Smith & Wilson, in press).

Evenness was calculated for each quadrat (Monks Wood and Park Grass) or plot (Compton). For the Monks Wood and Park Grass data, differences in evenness between plots were first tested against between-quadrat variation by analysis of variance; then the plot means were used to examine variation with time (Monks Wood) or soil/vegetation factors (Park Grass) by regression. For the Compton data, differences in evenness between treatments were tested against replicate-plot differences by analysis of variance.

RELATIVE ABUNDANCE DISTRIBUTION (RAD)

RAD models were fitted, all by the method of Wilson (1991a) which maximizes the fit (i.e. minimizes the sum of squares deviance) between log of the observed species biomass values and the log of model predictions, on a ranked-abundance plot (e.g. Fig. 1). The following models were examined:

Broken Stick (MacArthur 1957). This is a model of simultaneous random division of resource space into species' niches. The result is a curve with a few abundant species, several with similar intermediate abundance, and a tail of minor species (Fig. 1a)

Geometric (Motomura 1947; Whittaker 1972). This can be seen as the species each taking a constant proportion of the remaining resources, in order of their competitive dominance (Whittaker's 'Niche preemption' interpretation). The result (Fig. 1b) is a geometrically decreasing sequence of abundances (i.e. a linear decrease on a log abundance scale).

General Log-normal (Preston 1948). Sugihara's (1980) ecological interpretation of the General Log-normal was sequential random division of resource space into niches. The result is a curve similar to the Broken Stick one, but more highly parameterized and therefore more flexible in shape (Fig. 1c). We analyse separately the Preston/May parameter γ (Wilson 1991a), which indicates the shape of the General Log-normal fit, and the degree of conformity to Preston's (1962) 'Canonical' hypothesis.

Zipf–Mandelbrot (Frontier 1985). Under this model of community structure, the entry of a species into a community is dependent on prior changes (as in the 'facilitation' model of succession). An additional parameter β represents the degree of niche diversification. The result (Fig. 1d) is a few very abundant species, with many minor species of comparable abundance.

These models constitute all the realistic models available for continuous (biomass) data (Wilson 1991a).

Differences between treatments in the fit of the above models (i.e. sums of squares of the logs of discrepancies between the observed and model-predicted values) were expressed relative to zero for the best-fitting model by subtracting the deviance for that model from all deviances for that site. These deviances were then analysed by analysis of variance and regression as for evenness. Wilson (1991a) discussed the basis for such an analysis, and demonstrated that the requirements for an analysis of variance were met.

As with evenness, for Park Grass and Monks Wood differences between plots were first tested against quadrat differences, before taking plot means.

RANK CONSISTENCY

For each site (see below), a table was formed of:

m replicates × the n species found at that site.

The value in each cell of this table was the abundance (i.e. biomass) rank of the species in the replicate, from 1 for the most abundant to N for the least abundant. From this we calculated C_r, an index of consistency

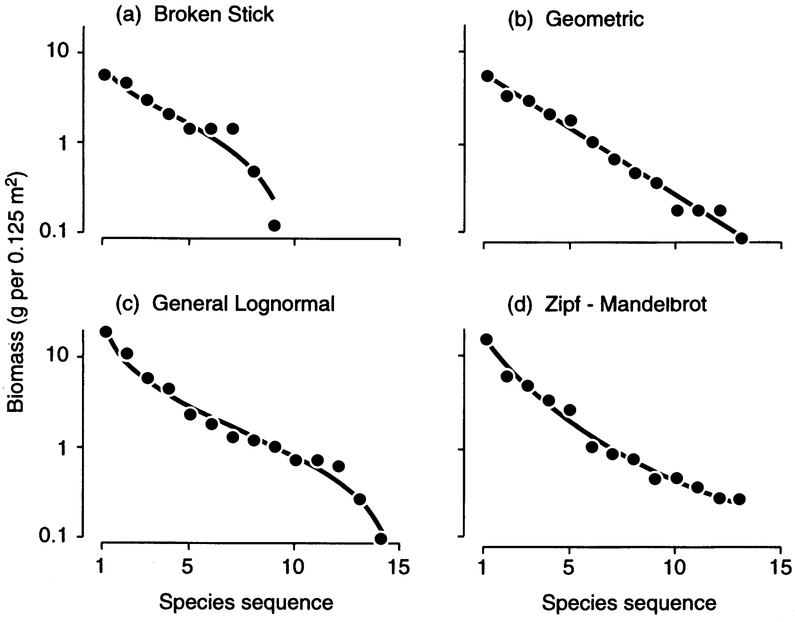

Fig. 1 Examples of fits of the four models to abundance distributions (expressed as ranked-abundance plots) in quadrats of the Park Grass experiment. (a) Plot 9.1a (NPK application, pH 5.7) in 1991, fitting the Broken Stick model; (b) Plot 4.1a (P application, pH 6.5) in 1992, fitting the Geometric model; (c) Plot 16b (NPK application, pH 6.8) in 1992, fitting the General Log-normal model; (d) Plot 17b (N application, pH 6.8) in 1992, fitting the Zipf–Mandelbrot model.

of ranks introduced by Watkins & Wilson (1994). This index has the values:

+ 1 when the ranks are identical between replicate quadrats,
0 when the ranks are as would be expected, on average, at random, and
− 1 when the ranks are as different as they could be.

As in Watkins & Wilson (1994), the significance of the departure of C_r from the null-model value of zero was tested by a randomization test, using 2000 randomizations and a two-tailed test, but significance was generally high, and is not reported; the existence of consistency greater than random is unsurprising, and has already been documented for plant communities (Grubb *et al.* 1982).

For the Park Grass experiment the 'site' in rank consistency calculations (see above) was the treatment plot. For Monks Wood the site was the treatment × replicate plot. For these two sites, the 'replicates' were the within-plot replicates, thus examining within-plot spatial consistency. For Compton the 'site' was the treatment, and the 'replicates' were the plot replicates, therefore the year–nitrogen interaction was used for error in analysis of variance.

Results

THE EFFECT OF RESOURCE AVAILABILITY ON EVENNESS

Park Grass experiment

In 1991, overall mean evenness (by index E') was 0.361; in 1992 it was 0.378. Evenness differed significantly between soil fertility treatments. A regression of plot evenness on all soil/vegetation factors was significant both years (P in 1991 $= 0.0022$, in 1992 $= 0.0037$), explaining 23% and 22%, respectively, of the variance.

The 1991 formula was simplified by step-down regression to one which indicated greater evenness in plots with phosphorus addition and in plots with low yield (P for the two-factor regression $= 0.0001$, explaining 20% of the variance in E'). The effect of soil phosphorus status alone explained 15% of the variation in evenness ($P = 0.0004$). In 1992, the step-down formula indicated greater evenness in plots with phosphorus addition and in plots with lower species richness ($P = 0.0003$, explaining 18% of the variance). Soil phosphorus alone explained 12% of the variation (P for the difference $= 0.0015$).

Compton experiment

There was no indication that evenness differed between nitrogen treatments. In plots without nitrogen application, the mean of index E' was 0.27; with nitrogen application mean E' was 0.26 ($P = 0.68$).

THE EFFECT OF RESOURCE AVAILABILITY ON RAD

Park Grass experiment

The relative fit of all models (Broken Stick, Geometric, General Log-normal and Zipf–Mandelbrot) and parameters (γ from the General Log-normal fit and β from the Zipf–Mandelbrot fit) differed significantly between soil fertility treatment plots, except for General Log-normal in 1991 (Table 1).

The relative fit of the Broken Stick model was closer in plots with phosphorus application and in those with higher species richness (Table 2). This effect was highly significant in both years, it was in the same direction in both years, and the contribution of species richness was greater than that of phosphorus in both years (Table 2). However, very rarely did Broken Stick provide the best fit of the four models (Table 3). (Fig. 1a gives one of the rare examples of a best fit to the Broken Stick model.)

In 1992, the fit of the Geometric model (relative to other models) was closer in plots with phosphorus applied, no potassium addition and high pH ($P < 0.001$, explaining 39% of the variance in fit

Table 1 Tests of the differences in relative abundance distribution between plots of the Park Grass and of the Monks Wood experiments, using analysis of variance against the within-plot variation. $F =$ the variance ratio (d.f. for Park Grass $= 82$, 390; for Monks Wood $= 39$, 84), $P =$ probability (i.e. significance)

			Relative abundance distribution, model or parameter					
Experiment/ year		Evenness index E′	Broken Stick	Geometric	General Log-normal	γ	Zipf-Mandel-brot	β
Monks Wood	F	2.46	1.91	1.12	0.95	4.99	1.26	2.26
	P	0.0003	0.0071	0.33	0.56	<0.0001	0.19	0.0010
Park Grass1991	F	3.22	2.34	1.52	1.21	6.47	1.55	6.26
	P	<0.0001	<0.0001	0.0048	0.12	<0.0001	0.0036	<0.0001
Park Grass1992	F	3.08	1.99	2.09	1.78	8.83	1.34	3.84
	P	<0.0001	<0.0001	<0.0001	<0.0002	<0.0001	<0.035	<0.0001

Table 2 Park Grass experiment, relative abundance distribution: multiple regression of the relative fit against environmental and vegetation factors, in an overall regression (*i.e.* with all independent variates used) and in a step-down reduced regression. The environmental factors listed are those remaining as significant in the step-down regression, with the sign of the relation, and the percentage of variation explained. Rich = species richness. − or + indicates the direction of the relation, i.e. + indicates an improved fit at higher levels of the factor

	Broken Stick	Geometric	General log-normal	γ	Zipf–Mandelbrot	β
Model for 1991 data fitted to 1991 data						
Overall regression (% explained)	26***	3	10	64***	15*	69***
Step-down regression (% explained)	23***	n/a‡	n/a‡	62***	13**	67***
Step-down regression (factors remaining)	Rich + 71 P + 29	none	none	Rich + 70 N − 15 P + 15	K − 60 Rich − 40	Rich − 90 N + 5 P − 5
Model for 1991 data fitted to 1992 data						
Step-down regression (% explained)	as 1991†	n/a‡	n/a‡	57***	13**	62***
Model for 1992 data fitted to 1992 data						
Overall regression (% explained)	18*	39***	26***	61***	29***	65***
Step-down regression (% explained)	14**	34***	19***	56***	25***	63***
Step-down regression (factors remaining)	Rich + 55 P + 45	P + 76 K − 11 pH + 13	P + 100	Rich + 91 N − 9	P − 33 Rich + 30 Yield − 37	Rich − 3 pH − 65 P − 32
Model for 1992 data fitted to 1991 data						
Step-down regression (% explained)	as 1992†	1	0	56***	9	67***

$^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

†The step-down formulae for the two years include the same independent variates, therefore the regression model was the same.

‡Not applicable: because the overall regression was not significant, no step-down procedure was performed.

across the plots: Table 2). (Fig. 1b gives an example of a Geometric fit.) However, in 1991 these factors explained a negligible proportion of the variance. In both years, Geometric was the best-fitting of the four models for just over a quarter of the quadrats (Table 3).

General Log-normal was the best-fitting model in 1992 for about half the quadrats (Table 3), and the fit was significantly better in plots with phosphorus application (Table 2). In 1991, it was the best fit in only a quarter of the quadrats, and there was no correlation with any soil/vegetation factor. (Fig. 1c gives an example of a General Log-normal fit.) The Preston–May parameter γ (Wilson 1991a) varied significantly between treatments. About 60% of the variance in γ could be explained by the soil/vegetation factors, with γ higher in species-poor sites, independently of this higher in high-nitrogen treatments, and (in 1991) in low-phosphorus plots. The resulting regression formulae for the two years were quite similar, and either fitted well the data from the other year (Table 2).

Zipf–Mandelbrot provided the best fit to the plant community of almost half the quadrats in 1992, but only a quarter in 1991 (Table 3; e.g. Fig. 1d). There was a significant relation between soil/vegetation factors and the goodness of fit of the Zipf–Mandelbrot model in both 1991 and 1992, but it was attributable largely to different factors (potassium in 1991; phosphorus and yield in 1992), and for the factor that was in common (species richness), the effect was in the opposite direction in the two years (Table 2). The 1991 step-down formula, which retained potassium and species richness, was significant when tested on the 1992 data, but the 1992 formula was not significant when tested on the 1991 data (Table 2). How-

Table 3 The frequencies of best-fits to four models of relative abundance in the three experiments analysed: best fits as a percentage of total fits for the site

	Model			
	Broken Stick	Geometric	General Log-normal	Zipf–Mandelbrot
Monks Wood	1	29	43	27
Park Grass				
1991	2	28	46	24
1992	2	28	22	48
Compton	0	58	42	0

ever, the type of Zipf–Mandelbrot fit did vary significantly and consistently between plots, in that β was higher in more species-rich and phosphorus-added plots, with additional effects of nitrogen in 1991 and of pH in 1992 (which is no real conflict: because of the acidification effect of some of the nitrogen fertilizers, the nitrogen and pH conditions are far from independent). Both regression formulae for β fitted almost equally well in the other year.

There was, for all models, consistency in fits between years, seen in a tendency towards a positive correlation between the goodness of fit of a particular model in 1991 and that for the same plot in 1992 (Table 4), but this was significant only for the Broken Stick and Geometric models. The values of γ and of β were also correlated between years.

Compton experiment

There was no significant effect of nitrogen application on the relative fit of any of the four models, or on γ or β.

THE EFFECT OF RESOURCE AVAILABILITY ON RANK CONSISTENCY

Park Grass experiment

In both years, rank consistency (C_r) was related to the soil/vegetation factors (for the overall regression in 1991, $P < 0.0001$, $R^2 = 38\%$; in 1992, $P = 0.0003$, $R^2 = 29\%$). The 1991 regression simplified to one predicting greater rank consistency in plots with phosphorus added, potassium not added, and with high yield ($P < 0.0001$, $R^2 = 34\%$). Of the 34% explained, the contribution of phosphorus application was 19%. In 1992, the step-down procedure indicated that almost all of the explicable variation in C_r was due to phosphorus application ($P < 0.0001$; $R^2 = 27\%$). Mean C_r was 0.847 in 1992 in plots where no phosphorus had been applied, and 0.897 where it had (although the difference in values are small, rank consistency normally varies within a narrow range).

Table 4 Park grass experiment, relative abundance: correlation across plots of deviance from models (Broken Stick, Geometric and General Log-normal and Zipf–Mandelbrot) and of parameters values (γ and β) in 1991 compared with those for the same plots in 1992

Model/ parameter	Correlation between 1991 and 1992	
	r	*P*
Broken Stick	+ 0.60	< 0.000001
Geometric	+ 0.24	0.029
General log-normal	+ 0.20	0.076
γ	+ 0.61	< 0.000001
Zipf–Mandelbrot	+ 0.13	0.25
β	+ 0.68	< 0.000001

Compton experiment

There was no consistent difference in rank consistency between the two nitrogen treatments ($P = 0.33$).

TEMPORAL TRENDS IN EVENNESS

Monks Wood experiment

Evenness (as measured by index E') increased linearly with the age of the community (P for differences between year < 0.0001, 74% of the differences between years were attributable to the linear component; Fig. 2a). Quadratic and cubic components of the time trend were not significant.

Compton experiment

Evenness (E') varied between years ($P = 0.0030$), with the only significant component being a linear increase in E' (Fig. 2b; $P = 0.0013$). There was no difference in time trend between the two nitrogen treatments (P for the year–nitrogen interaction = 0.96).

TEMPORAL TRENDS IN RAD

Monks Wood experiment

The plots differed significantly in the relative fit of the Broken Stick model ($P = 0.0057$), but not of the Geometric, General Log-normal or Zipf–Mandelbrot models.

The relative fit of the Broken Stick model varied significantly between years ($P < 0.0001$). This was mainly due to a linear increase in fit with time (explaining 72% of the year-to-year variation, curvature being nonsignificant). This yearly trend was consistent across spatial blocks (i.e. there was no significance for the blocks effect or the block-year interaction). However, Broken Stick was hardly ever the best-fitting model (Table 3). The relative fit of the Geometric, General Log-normal, and Zipf–Mandelbrot models did not differ significantly through succession (or between blocks), the general pattern being for General Log-normal to fit almost half the quadrats, and Geometric and Zipf–Mandelbrot the others about equally (Table 3). However, values of General Log-normal parameter γ decreased linearly through succession (P for the differences between years < 0.0001; P for the linear component = 0.0002; there was no significant quadratic or cubic curvature). The change reflected a decrease in the slope of the abundance/rank plot (example fits are shown in Fig. 3). However, the yearly trend differed between blocks (P for the year–block interaction = 0.0013). β varied between years ($P < 0.0001$), but in this case the time course was more complicated, with quadratic

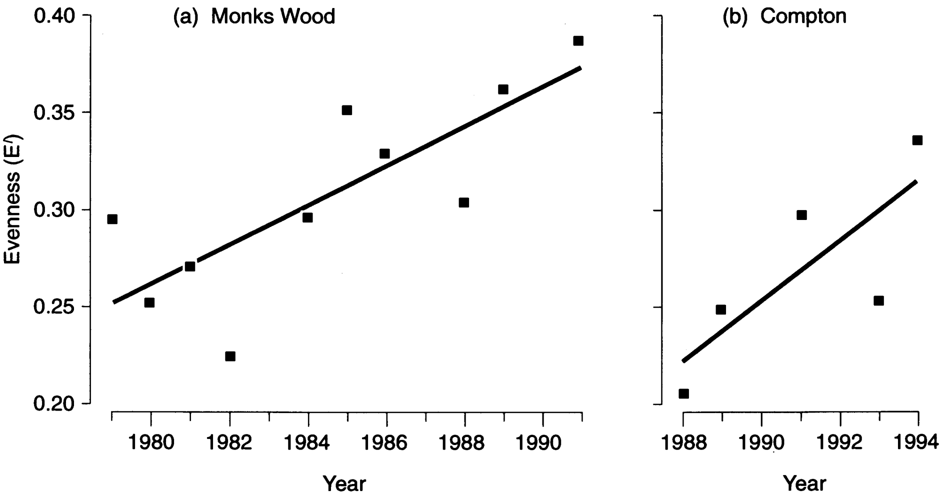

Fig. 2 Successional trends in evenness (measured by index E'), with a best-fit linear regression line: (a) Monks Wood experiment; (b) Compton experiment.

and cubic components significant, superimposed on an upward trend.

Compton experiment

Unlike the Monks Wood experiment, the relative fit of the Broken Stick model did not differ between years. However, the fit of the Geometric model was different in different years ($P = 0.0073$). There was no overall change through the experiment (P for linear effect $= 0.28$), rather, there was an increase in fit, followed by a decrease (P for quadratic effect $= 0.0017$). There was no change with time in the relative fits of the General Log-normal or Zipf–Mandelbrot models.

However, although the degree of General Log-normal fit did not change, the shape of the fit did, since parameter γ showed a linear decrease ($P = 0.0001$), as it did in the Monks Wood experiment.

Similarly, though the fit of Zipf–Mandelbrot did not change, parameter β increased with time, as in the Monks Wood experiment, again with a decrease later, after 1991 (P for linear component $= 0.011$, for quadratic component $= 0.0022$). This reflected a lower slope to the abundance/rank curve (example fits are shown in Fig. 4).

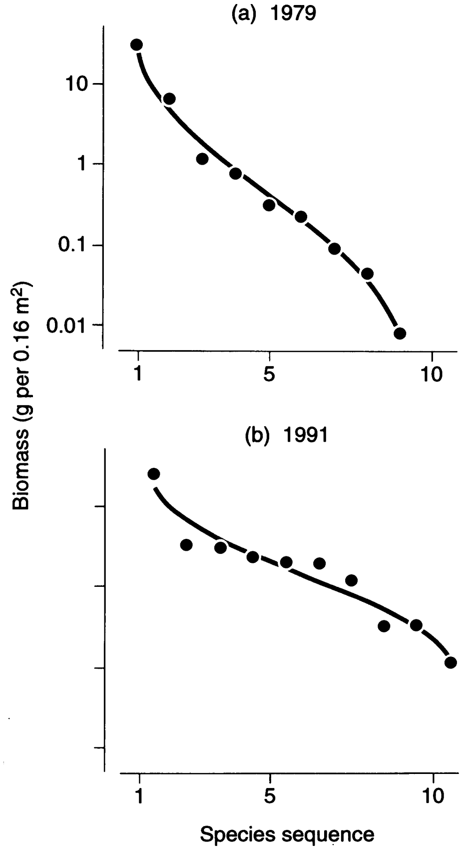

Fig. 3 Ranked-abundance plots for two Monks Wood quadrats which fitted the General Log-normal model well, with the curve for that model: (a) 1979, block 1, replicate 2, for which the fitted value of γ was high (1.76); (b) 1991, block 2, replicate 2, for which the fitted value of γ was low (0.91).

TEMPORAL TRENDS IN RANK CONSISTENCY

Monks Wood experiment

Rank consistency at Monks Wood increased until 1984, then decreased again (P for the quadratic component $= 0.019$; Fig. 5a). By the definition of index C_r there should be no effect on it of the number of replicates over which it is calculated, and regression confirmed this (P for the partial slope $= 0.50$).

Compton experiment

There was no significant difference in rank consistency between years, not surprisingly in view of the weak test (since no replication was available for C_r, the nitrogen–year interaction had to be used for the error). However, it can be noted that the trend, meaned over both nitrogen treatments (Fig. 5b) was similar to the trend at Monks Wood (Fig. 5a).

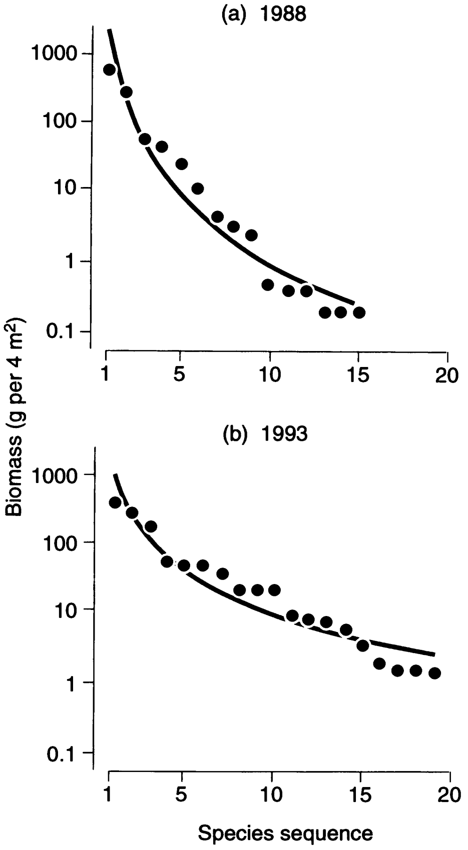

Fig. 4 Ranked-abundance plots for two Compton quadrats which fitted the Zipf–Mandelbrot model well, with the curve for that model: (a) 1988, + N, replicate 1, for which the fitted value of β was low (5.9); (b) 1993, – N, replicate 3, for which the fitted value of β was high (19.0).

Discussion

PHOSPHATE, EVENNESS AND RANK CONSISTENCY

In both years, evenness was higher in those Park Grass plots to which phosphorus had been applied, with a corresponding increase in the relative fit of the Broken Stick model. Rank consistency was also higher. According to the model of Grime (1979), the application of a nutrient such as phosphorus, which increased the standing crop, should increase 'competition' and hence allow some species to dominate, resulting in a lower evenness. This did not happen in the Park Grass experiment, where evenness increased. However, since species richness was lower in plots where phosphorus had been applied, the increase in evenness could be seen as a loss of niches for the minor species. Competition for light tends to amplify any random initial advantage (Wilson 1988), so rank consistency should have been lower in P-applied plots, but in fact it was higher. No effects on evenness or rank consistency were seen between different nitrogen or potassium treatments. This suggests the effects are due to the specific effect of phosphorus, perhaps due to the particular species that responded to phosphorus in the Park Grass experiment.

MODELS OF RELATIVE ABUNDANCE DISTRIBUTION (RAD)

Overall fit

The Log-normal distribution has been described as almost ubiquitous for communities at stable equilibrium (May 1975; Hughes 1986; Gray 1987), and the Zipf–Mandelbrot as rarely fitting over the whole range of abundances in a community (Frontier 1985). Neither suggestion is supported here. The generalizations were not based on any rigorous comparison of the models with real data.

More highly parameterized models are likely to fit more readily, but several of the trends are seen in spite of this tendency, for example the more frequent fit in the Compton experiment to the Geometric model

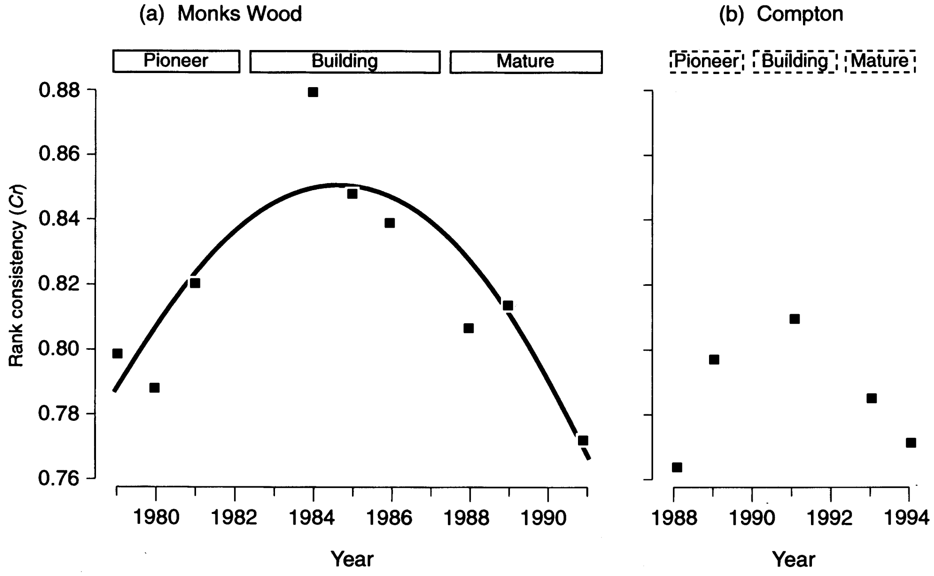

Fig. 5 Successional trends in rank consistency, as measured by index C_r, with a best-fit regression line: (a) Monks Wood experiment; (b) Compton experiment (the trend is nonsignificant).

than to the more highly parameterized Zipf–Mandelbrot model (Table 3).

Species richness

The Geometric model has been said to fit especially when species richness is low (Whittaker 1965; Whittaker 1972; Pielou 1975; Gray 1987), and General Log-normal distribution when it is high (Whittaker 1965; Hughes 1986). There was no indication of either trend at Park Grass. There was a consistent tendency for the Broken Stick model to fit relatively better in plots with more species, a trend not predicted in the literature.

Resource availability

The Geometric model has been suggested to fit especially in stressful environments (Whittaker 1965, 1972), but there was no significant relation of the Geometric fit to soil conditions at Park Grass in 1991, and in 1992 Geometric fitted relatively better in sites with *higher* phosphorus status and with *less* acidic soil, i.e. *less* stress. A similar discrepancy between years at Park Grass was seen for the ability of soil phosphorus status to predict where the General Log-normal model would fit. Although it was possible to predict on which plots the Zipf–Mandelbrot model would fit at Park Grass in both years, the soil/vegetation factors involved were quite different between the two years.

Succession

The RAD model applying to a community has been seen as dependent on successional age (MacArthur 1960; Gray 1987). Indeed, the relative fit of the Broken Stick model did increase through succession in the Monks Wood experiment. However, when the Broken Stick fails to fit, this is often because it predicts greater evenness than actually exists (Wilson 1993). Thus, the increased fit (or, rather, the decrease in poor fit) may be a reflection of the increase in evenness. No other model showed a trend with successional time. In both experiments, General Log-normal parameter γ decreased with successional time, and in both there was an overall increase in Zipf–Mandelbrot parameter β. In both cases this seems to be a reflection, and a confirmation, the increase in evenness.

Conclusions on RADs

There were highly significant differences in the fit of different RAD models between the treatments of the Park Grass experiment and between the plots of the Monks Wood experiment. It is difficult to explain this away as a statistical artefact since the overall regression was significant in six out of eight model/year cases, a proportion significantly greater than the 5% of $P < 0.05$ significance values expected by chance ($P < 0.0001$, by binomial test).

Evenness, one aspect of the RAD, was clearly related to phosphorus status at Park Grass and to successional age at Monks Wood and Compton. These differences in evenness are reflected in changes in the fit of the Broken Stick model, and in parameters γ and β. According to previous interpretations, this should be seen as an increase in niche diversification.

Beyond evenness, there is very little predictability as to which RAD model will fit in which circumstances. Watkins & Wilson (1994), comparing 12 plant communities, were not able to find correlations between which RAD model fitted best and any community characteristic they considered. They suggested that clear trends might emerge if it were possible to compare a larger number of communities. Here we have compared seven times as many communities, using several predictor variates, and there are still no clear patterns. This points towards a conclusion that communities are individualistic in structure. The structure depends on the characteristics of the particular species that happen to be members of the community which occurs under that combination of soil factors (Watkins & Wilson 1994). The RAD must vary through each year, due to the differences in phenology between species. It is therefore not surprising that, with differences in weather and hence in phenology between years, there should be differences between years in RAD, as found here in the Park Grass results.

MODELS OF SUCCESSION

Temporal trends in evenness

Previous literature has been ambiguous on the trend in evenness through succession. Odum (1969) suggested, without evidence, that evenness would increase during succession. Symonides (1985), comparing oldfields of different ages, found a trend for evenness to *decrease*. Nicholson & Monk (1974), in a similar study, found a tendency for evenness to increase during the herbaceous phase. Shafi & Yarranton (1973), comparing forest areas previously burnt at a range of times, and Long (1977), comparing forest stands of different ages, found no trends in evenness with time. However, these studies compared different plots, which were estimated to be of different successional age. They also used indirect measures of species abundance. The experiments at Monks Wood and Compton seem to provide the first evidence from direct biomass measurement of actual succession recorded from the same plots. The results from both experiments agree with Odum's expectation of an increase in evenness through succession. This trend is reflected in the increased relative fit through time of the Broken Stick model, in the decrease in γ, and in the increase in β in both experiments (Fig. 4). The consistency between the Monks Wood and Compton experiments gives considerable confidence in the conclusion.

It should be noted that in both experiments the succession is secondary, and both concern British grassland. The conflicting results of Symonides (1985), Shafi & Yarranton (1973) and Long (1977) may be due to their using an indirect estimate of abundance, or to the error involved in sampling different plots and assuming they form a time sequence, or they may indicate that the pattern found in British grassland cannot be extrapolated to other types of vegetation.

The 'Competitive-sorting' model and the 'Gradient-in-time' model

Peet (1992) identified two current models of succession: the 'Gradient-in-time model', and the 'Competitive-sorting model'. Under the Gradient-in-time model, the environment changes through succession, and species composition changes in response. This implies that the degree of control of species composition by microenvironmental variation remains constant, and therefore the predictability of species composition should remain constant, *i.e.* rank consistency (here index C_r) should not change with successional time. The changes found in rank consistency found (Fig. 5) therefore disprove the Gradient-in-time model for these particular successions, noting that both are secondary successions, towards a mowing plagioclimax, and were followed for only 7 and 13 years, respectively. Nor, since competition for light would be expected to increase dominance and hence decrease evenness (Wilson 1988), does the increase in evenness in both experiments readily agree with the alternative Competitive-sorting model.

The Three-phase model

Gitay & Wilson (1995) synthesized the Competitive-sorting model with the Greig-Smith (1952) model, giving the 'Three-phase' model of succession, reusing terms coined by Watt (1947) for the three phases. In the first, 'Pioneer', phase, the theory suggests there is small-scale heterogeneity due to dispersal limitation (reduced in the Compton experiment here, because of the hay inoculum), chance and low competition, resulting in unpredictable species composition. Ecological processes predominate over evolutionary ones, in the terms of Pielou (1975). This should result in low rank consistency (C_r), as we found (Fig. 5).

In the second 'Building' phase, the spread of many species has reduced the initial effect of dispersal, and increased competition has forced out poorer competitors, resulting in more predictable community composition, i.e. higher C_r, again as we found. In the terms of Pielou (1975), evolutionary forces begin to predominate – the composition of the community is determined by the innate characteristics of the species. The increased compositional predictability and the loss of weak competitors are both compatible with the increase in evenness observed (Fig. 2). These trends are seen over the variation in species composition expected for such communities (Grubb *et al.* 1982), and seen in the experiment (Wells 1995).

In the third 'Mature' phase, the Three-phase theory suggests that interference between species leads to competitive exclusion between species, and greater differentiation between microhabitats. This would lead to lower C_r, again as seen in our results (Fig. 5), and to the continued increase in evenness (Fig. 2). The results therefore give strong support to the Gitay–Wilson 'Three-phase' model of succession.

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