

Variation in species richness on small grassland quadrats: niche structure or small-scale plant mobility?

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Abstract. In this study we make clear that the significance of deviations from an expected variance in species richness as demonstrated in alvar grassland, is a function of spatial pattern at the scale richness was measured, i.e. 10 cm². If corrected for spatial dependence, more than half of the significant cases become nonsignificant. As regards cases of significant variance deficit, which has been interpreted as an indication of niche limitation, we suggest that there may be a simple physical limitation to the number of species on the scale of observation in the form of a low number of plant units which can find a place because of the modal plant size of the species involved. In most cases of significant variance deficit the modal size of the plant units involved was probably bigger than average.

Insofar as a significant variance deficit can be demonstrated, the resulting species richness distribution curve should be analyzed and we propose a skewness test, enabling us to differentiate between significantly left-skewed curves ('niche limitation'), significantly right-skewed curves ('niche facilitation') and symmetrical curves. We present results obtained with the *G*-test, a log-likelihood ratio goodness of fit test. Only few cases of significantly left-skewed curves and a majority of symmetrical curves were found.

Attempts to demonstrate guild proportionality in grasslands suffer from the heterogeneity of usually distinguished guilds, such as annuals vs. perennials or graminoids vs. dicotyledons.

We observe that niche limitation may occur in alvar grassland, but indications for niche facilitation are stronger. Finally, we conclude that deviations in species richness variance are interesting indications of community structure, but only of spatial structure. Niche structure resulting from assembly rules should be investigated through experiments.

Keywords: Alvar; Carousel model; Facilitation; Guild; Niche limitation; Öland; Spatial dependence.

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

Introduction

The related concepts of 'niche limitation', 'assembly rule' and 'community structure' have been discussed, and ways to demonstrate their existence in plant

communities have been advocated by J.B. Wilson in a series of stimulating papers (Wilson et al. 1987; Wilson & Sykes 1988; Watkins & Wilson 1992; Wilson et al. 1992). Wilson (1991, 1994) also linked these concepts to questions about existence of plant communities as integrated entities. The basic idea behind this approach is that species cannot be completely similar in their use of limited resources (e.g. Hutchinson 1959; MacArthur & Levins 1967; Schoener 1974) and that there must be an upper limit to the number of species that can coexist. Colwell (1979) and Putman & Wratten (1984) stated this in terms of niche structure, i.e. that there is an upper limit to the number of potential niches. This idea was formulated as niche limitation (Wilson et al. 1987) and subjected to a new test by counting species numbers on (small) quadrats while comparing the variance of the richness values with the variance expected under the null model of a random distribution of species over the subplots. The comparison is expressed in an index $RVr = \text{observed} / \text{expected variance}$ and deviations from the value 1 are tested for significance.

Wilson (1991) considered that showing a variance deficit could be a – badly needed – proof of an 'assembly' rule (Diamond 1975) governing a plant community. In terms of Noy-Meir & van der Maarel (1987) one could distinguish in this way between species co-occurrence and species coexistence, – or in terms of Kull & Zobel (1994) – between the stochastic and the functionally regulated community. Wilson et al. (1987) also paid some attention to the possibility that the index RVr can be > 1 , but stated that here the interpretation is more difficult because environmental heterogeneity would also lead to a variance surplus.

In discussions with J.B. Wilson it was suggested to apply this test to the extensive data set on species occurrences on very small plots available from a series of consecutive years in species-rich limestone grassland on the Great Alvar of the Swedish island of Öland (Rosén 1982; van der Maarel 1988), while considering (a) that a limitation in species richness would be more obvious in species-rich communities than in the mostly

species-poor communities investigated so far, (b) that it would be interesting to know whether richness variance deviations would show any pattern in time; and (c) that a space-time pattern of richness variance may be linked to the Carousel model (van der Maarel & Sykes 1993) dealing with the very high fine-scale species turnover demonstrated for this alvar grassland.

Results obtained by Wilson, presented in this issue (Wilson et al. 1995) show that a significant variance deficit on the smallest plot size included in the Öland material – 10 cm² – occurred in more cases than in earlier such studies. While studying these interesting results, and while fully accepting the possibility of niche limitation, we nevertheless doubted whether this evidence would be sufficient for the conclusion that community structure, in particular niche limitation, may occur. We decided to reconsider the approach for the Öland data in the light of the existing knowledge of pattern and process of the alvar grassland. While preparing the present paper we felt the need for a more general critical approach to the interpretation of richness variance and species associations, which has led to a companion paper (Palmer & van der Maarel 1995).

Richness terms instead of niche terms

As shown by van der Maarel & Sykes (1993) for the alvar grassland under study, year-to-year species turnover on small subplots is considerable. Most species occurring in the community move around and may sooner or later appear in virtually any small subplot (microsite). This makes the niche concept less useful: it is as if all species successively occurring in a small plot have the same niche, or rather the same microhabitat. Several species may share the same soil volume underneath a microsite and appear above-ground in different combinations in different years, for instance because of rapid fluctuations in local conditions; alternatively, high-speed facilitation occurs where species change their niche in favour of the next species. However, even if one would agree that the (regeneration) niches of the participating species are different, the differences are very subtle and certain different niches – as combinations of establishment factors – are realized only during very short periods of time. In this context the concept of niche limitation becomes less meaningful; hence, instead of niche limitation one may consider to speak of richness limitation, or, in case one wishes to take quantitative differences in occurrence into account – as for instance Zobel et al. (1993) did – of diversity limitation. Here, we will simply speak of richness limitation.

On the interpretation of values of $RVr < 1$

In the following, we will discuss variance in rich-

ness, where richness is the mean number of vascular plant species in multiple subplots of a small size in plots of a much larger size. When the observed variance is significantly lower than the expected one, the observed subplot richness frequency distribution is narrower than the expected one (see Fig. 6 in Watkins & Wilson 1992, Fig. 6 in Wilson et al. 1995, as well as our own Fig. 1). ‘Niche limitation’ would imply a deficit in subplots with relatively high species numbers. However, there may also be a deficit in subplots with relatively low species numbers (minimally zero). To contrast this with the first situation, one may speak of ‘niche (species) facilitation’, which we will explain below. Finally, both trends, limitation and facilitation, may occur simultaneously. In all cases, the deficit in subplots at either side of the frequency distribution will, out of necessity, be compensated by a surplus in subplots with medium species richness. The examples of richness frequency distribution figures in the Wilson papers mentioned above are examples of this third case. In order to differentiate between the various possibilities a skewness test should be applied to cases of significant variance deficit. In this way it would be possible to differentiate between ‘niche limitation’ (significantly left-skewed), ‘niche facilitation’ (significantly right-skewed) as well as the combination of both situations (no significant skewness).

On the interpretation of values of $RVr > 1$

The obvious explanation for RVr being > 1 is floristic heterogeneity, which is usually caused by environmental heterogeneity. This could imply the mixture of two or more different micro-environments, or the occurrence of favourable microsites – called the waterhole effect by Pielou (1975) after the concentration of animal species around waterholes in an arid environment; see also Wilson et al. (1987). The second special case is the occurrence of unfavourable, species-poor or even empty microsites. However, as indicated by van der Maarel & Sykes (1993 and unpublished), the alvar grassland is floristically homogeneous at the scale of the community, meaning that there is little variation in the floristic composition of samples of 0.25 m² and larger. If variance surplus occurs, the floristic homogeneity should be more directly tested by means of a similarity analysis, and also temporal patterns of richness should be investigated before explaining variance surplus in terms of heterogeneity. After eventual exclusion of spatial and temporal variance, a surplus could be approached as an expression of community structure.

On spatial dependence in the distribution of richness

From the direct determination of the expected richness variance, i.e. on the basis of species frequencies (Palmer 1987), it follows that if sets of subplots would

differ in their species frequency distribution they would also have different expected richness variances. The expected richness variance can be expressed in terms of the species frequencies as $\sum p_i(1 - p_i)$ where p_i is the probability of occurrence of species i . Hence, expected richness variance will be maximal if all species have a frequency of 50% – all p_i 's = 0.5 – and minimal if all species have frequencies either near to 0 or near to 1. The usual frequency distribution of species frequencies for larger plots, indicated as the reversed J-shape (Raunkiaer 1934, see also Williams 1964) approaches this opposite situation, with most species having a low frequency and few having a very high frequency. Williams (1964) provided evidence that frequency distributions based on very small quadrats tend to be more equal. Van der Maarel & Sykes (1993) showed that alvar grassland has a fairly large contribution of medium-frequent species in 100-cm² subplots. This means that the expected variance in richness in very small grassland subplots is relatively high, maybe higher than in other communities.

Another problem with the interpretation of deviations of richness variance from the null-model is the influence of the spatial dependence of subplots, i.e. subplots nearer to each other having a larger floristic similarity. This could be due to local concentrations of plants originating from a concentration of seeds, or from local vegetative spread, described as nucleation in a successional context. Zobel et al. (1993), in a successional context, specifically mention nucleation as a source of a deficit in richness variance. As was pointed out earlier in plant ecology (e.g. Malanson 1985; Palmer 1988; Palmer & van der Maarel 1995) on the basis of geostatistics (e.g. Cliff & Ord 1981), statistical tests, including variance tests, can be seriously affected by spatial dependence and corrections for this dependence should be made. Indeed, species in the alvar grassland community do occur in runs along the transects of subplots (van der Maarel & Sykes 1993) and may affect richness variance.

This paper aims at discussing some of the above-mentioned considerations, with special reference to Wilson et al. (1995) on the basis of an analysis of a large data set from alvar grassland on Öland: 32 plots with 20 - 50 subplots of both 10 and 100 cm², in 2 - 9 yr, a total of 304 cases.

Material and Methods

We used data from three different grassland sites on the vast limestone plateau known as Stora Alvaret (the Great Alvar), on the Baltic Island of Öland. On this plateau, at 30 m a.s.l., grassland assigned to the *Vero-*

nica spicata - *Avenula pratensis* association occurs on 10 - 50 cm deep, slightly acid to neutral brown soils developed in reworked glaciofluvial deposits on Ordovician limestone (Krahulec et al. 1986). Mean annual precipitation is only 430 mm; the growing period – May to September – is often subjected to low water availability and every 5 - 7 yr (most recently in 1992) the area is subjected to severe drought (Rosén 1982). Most of the alvar grassland has been grazed for hundreds, maybe thousands of years. Site G, at the Gettlinge alvar, the main study area (56° 23' N, 16° 27' E) is at present lightly grazed by cows and some horses; the vegetation is dense and short, ca. 5 - 10 cm tall. Site K is at Kleva (K; 56° 32' N, 16° 30' E) where there had been no grazing since 1980 and site S at Skarpa Alby (S; 56° 35' N, 16° 39' E) in an area of light cow grazing with a mosaic of grassland species and *Juniperus communis* shrubs.

At these sites fertilization experiments have been carried out in order to study the response of the grasslands in terms of species diversity and biomass; these experiments, including fertilization with (1) all usual macro- and micronutrients, (2) all without N, (3) all without P and (4) all without N and P, ran parallel to experiments in the Netherlands and the southeastern USA (see Peet et al. 1990). There are three series of plots on site G (G1, G2, G3), two on site K (which will be considered together because of their similarity) and one on site S. G1 represents the average situation regarding soil depth and water availability, G2 is on slightly moister, G3 is on shallower and much drier soil. Each series consists of five plots, which were laid out in 1985 (see Willems et al. 1993) – in 1986, an additional plot was laid out in sites G1 and G2 and irrigated from that year onwards. In each plot of 2.5 m × 1 m, the floristic composition (shoot presence) was determined in nested subplots of 10 cm² ($n = 50$), 100 cm² ($n = 20$; in some cases $n = 50$), 0.1 m² ($n = 10$) and 0.25 m² ($n = 10$). See Willems et al. (1993) or van der Maarel & Sykes (1993). The analysis was done yearly from 1985 to 1989 and in G1 from 1990-1993 as well.

As follows from Table 1, the vegetation in the five series of plots is floristically very similar, but some species are differential between the sites. Gettlinge 1 and 2 are rich in *Trifolium* species. *Helianthemum oelandicum* – which is found more abundantly on thinner and moister soils – occurs very frequently in G3 on relatively thin soil. Site S is differentiated by some indicators of open calcareous soil. The no-longer grazed site K is mainly characterized negatively by the reduced frequency of some species of open grassland.

For each series of subplots of 10 cm² and of 100 cm² in each year (2×152 cases) the following variables were determined:

Table 1. Vegetation characteristics of the plots. Values are frequency % over all 0.25-m² subplots 1985-1989. First species group: differentiating species; second group: highly frequent species; third group: less frequent in the Kleva site (no longer grazed). Bold: most frequent appearances. Not included: 46 species which do not reach a frequency of > 30 % in any of the sites and do not show a preference for one or two sites either. In relation to the question of guild structure, the following indications are added: a = annual; p = perennial; g = graminoid; d = dicot (see van der Maarel 1988). Total number of plots involved = 32; Nr. of plots × nr. of years 1985-1989 = 128; Nr. of 0.25-m² subplots × years = 1280.

Site/ plot series		G1	G2	G3	S	K
No. of plots		6	6	5	5	10
No. of plots × nr. of years 1985-1989		29	29	10	25	35
No. of 0.25-m ² subplots × years		290	290	100	250	350
<i>Trifolium striatum</i>	a d	20	8	3	1	0
<i>Bromus hordeaceus</i>	a g	42	43	21	-	2
<i>Trifolium repens</i>	p d	69	71	17	18	26
<i>Ranunculus bulbosus</i>	p d	75	89	14	28	33
<i>Trifolium campestre</i>	a d	56	76	23	26	10
<i>Euphrasia stricta</i>	a d	47	68	11	47	-
<i>Helianthemum oelandicum</i>	p d	53	73	97	34	28
<i>Antennaria dioica</i>	p d	25	50	54	41	4
<i>Pulsatilla pratensis</i>	p d	41	32	85	84	15
<i>Briza media</i>	p g	20	30	82	70	9
<i>Asperula tinctoria</i>	p d	31	24	77	68	77
<i>Phleum phleoides</i>	p g	-	-	-	82	70
<i>Oxytropis campestris</i>	p d	1	1	89	13	70
<i>Hieracium pilosella</i>	p d	8	9	36	52	9
<i>Sedum reflexum</i>	p d	-	0	1	52	1
<i>Prunella grandiflora</i>	p d	-	0	-	40	-
<i>Galium boreale</i>	p d	-	-	11	41	1
<i>Globularia vulgaris</i>	p d	-	1	-	23	-
<i>Polygala comosa</i>	p d	-	1	-	17	-
<i>Arabis hirsuta</i>	p d	1	0	2	14	29
<i>Stellaria graminea</i>	p d	1	2	-	4	23
<i>Agrostis vinealis</i>	p g	99	97	99	99	90
<i>Achillea millefolium</i>	p d	89	90	97	89	82
<i>Anthoxanthum odoratum</i>	p g	73	31	15	62	73
<i>Avenula pratensis</i>	p g	89	89	99	89	96
<i>Carex ericetorum</i>	p g	96	91	96	96	77
<i>Carex caryophylla</i>	p g	92	91	100	92	93
<i>Cerastium semidecandrum</i>	a d	71	79	73	60	48
<i>Festuca ovina</i>	p g	99	99	100	99	100
<i>Filipendula vulgaris</i>	p d	93	88	98	93	92
<i>Galium verum</i>	p d	71	67	82	81	92
<i>Helianthemum nummularium</i>	p d	90	91	100	91	91
<i>Plantago lanceolata</i>	p d	95	92	90	89	82
<i>Potentilla tabernaemontani</i>	p d	92	84	100	86	94
<i>Taraxacum spec.</i>	p d	14	52	24	69	88
<i>Thymus serpyllum</i>	p d	86	77	96	78	83
<i>Veronica spicata</i>	p d	33	81	60	48	86
<i>Anthyllis vulneraria</i>	p d	91	89	90	91	28
<i>Linum catharticum</i>	a d	89	89	47	71	11
<i>Lotus corniculatus</i>	p d	84	89	96	63	30
<i>Luzula campestris</i>	p g	80	71	77	66	38
<i>Sedum acre</i>	p d	32	63	46	33	6

- mean species frequency per series of subplots, F ;
- number of species per series of subplots, S ;
- mean richness, R , richness variance, VRO , and skewness of the richness frequency distribution;
- mean Jaccard similarity, J , between subplots and the standard deviation of this parameter, the Jaccard similarity following from:

$c/(a+b-c)$, where c is the number of species common to the two subplots under comparison, a the number of species in one plot, and b the number of species in the other subplot;

- mean Jaccard similarity, J_n , for pairs of nearest-neighbour subplots.

The observed values were compared with values expected under the null model of random species distribution over the subplots, i.e. no species interactions, by means of 2000 Monte Carlo permutations for each series of subplots. For each permutation, the species, with their observed frequencies, were randomly distributed over the subplots, the richness figures determined and the variance and skewness of these values calculated. The expected richness variance, VRE , is the mean of the permutation variances. The test statistic is $RVr = VRO / VRE$, and the significance level is given by the Monte Carlo permutations. The same applies to the observed and expected skewness. In addition to the variance test, the mean frequency distribution of the richness values was determined and a log-likelihood ratio goodness of fit test, the G -test, between the observed and expected distribution (again based on Monte Carlo permutations) was carried out (Zar 1984). Some of the above-mentioned parameters were compared between sites and between years, using a χ^2 -test.

For plots where data on contiguous subplots of 100 cm² or subplots of 10 cm² in contiguous larger subplots were available, two corrections for spatial dependence were applied (details in Palmer & van der Maarel 1995). In both corrections the species patterns are kept but the relative position of species towards each other is randomized: 1. With the rotation/reflection method, which functions optimally in a grid, species occurrence configurations are rotated and mirrored. 2. With the random shift method species patterns are shifted a random number of units along the grid or transect as well as subjected to the rotation/reflection method.

Results

Occurrence of deviations from the expected richness variance

The five series of plots do not show major differences. For both subplot sizes, site S has lower values for species frequency and average similarity, whereas series G1 and G2 have higher mean richness values (Table 2A); none of the parameters shows a trend in time (Table 2B).

Deviations from expected richness variance levels (at $P < 0.05$, not corrected for spatial dependence) occur quite frequently, particularly a variance surplus for the

Table 2. A. Number of cases (*N*), mean species frequency per subplot (*F*), mean Jaccard similarity (*J*), ratio between nearest neighbour subplot similarity and mean similarity J_n/J , mean species richness per series of subplots (R_t); mean species richness per subplot (*R*), mean richness variance (*RVO*) and mean expected richness variance (*RVE*), number of significant ($P < 0.05$) deviations from $RVR = 1$ (>, < and total), for five series of alvar plots on Öland, with subplots of 10 cm² and 100 cm², on the sites Gettlinge (G), Kleva (K) and Skarpa Alby (S) – the two blocks at Kleva combined. Figures are based on analyses from 1985-1989. **B.** Ibid., summarized for the sites.

A.												
	<i>N</i>	<i>F</i>	<i>J</i>	J_n/J	R_t	<i>R</i>	<i>RVO</i>	<i>RVE</i>	>	<	Tot	
10-cm ² subplots												
G1	29	0.27	0.36	1.22	27.2	7.2	2.59	3.16	1	13	14	
G2	29	0.25	0.34	1.24	29.0	7.2	3.01	3.64	2	6	8	
G3	10	0.22	0.30	1.30	27.5	6.1	2.91	3.35	0	4	4	
K	35	0.25	0.35	1.28	22.5	5.5	2.36	2.68	1	8	9	
S	25	0.20	0.29	1.34	30.1	5.7	2.40	3.40	0	11	11	
Total	128								4	42	46	
100-cm ² subplots												
G1	29	0.46	0.51	1.17	28.8	12.8	4.58	4.25	4	2	6	
G2	29	0.42	0.49	1.21	31.1	13.1	5.03	4.51	5	1	6	
G3	10	0.37	0.42	1.23	29.4	10.8	4.28	4.41	3	0	3	
K	35	0.39	0.46	1.23	24.4	9.5	3.98	3.55	6	2	8	
S	25	0.35	0.41	1.25	33.4	11.6	4.98	4.91	2	2	4	
Total	128								20	7	27	
B.												
	<i>N</i>	<i>F</i>	<i>J</i>	J_n/J	R_t	<i>R</i>	<i>RVO</i>	<i>RVE</i>	>	<	Tot	
10-cm ² subplots												
1985	30	0.23	0.33	1.27	27.0	6.1	2.46	3.22	0	13	13	
1986	22	0.23	0.35	1.25	26.5	5.9	2.46	3.00	0	6	6	
1987	22	0.24	0.34	1.28	27.8	6.6	2.89	3.39	1	5	6	
1988	22	0.26	0.36	1.30	28.2	7.2	3.45	3.51	3	6	9	
1989	22	0.25	0.35	1.27	25.6	6.3	2.60	3.20	0	12	12	
100-cm ² subplots												
1985	30	0.40	0.45	1.18	28.4	11.3	4.77	4.35	3	1	4	
1986	22	0.38	0.45	1.22	29.5	11.2	5.26	4.33	5	2	7	
1987	22	0.40	0.47	1.24	29.0	12.1	4.67	4.44	3	0	3	
1988	22	0.43	0.50	1.24	29.7	12.7	5.34	4.30	4	2	6	
1989	22	0.40	0.50	1.21	28.0	11.0	4.57	4.01	5	2	7	

100-cm² subplots, in 20 out of 118 cases (17%), and a variance deficit for the 10-cm² subplots, in 42 cases (36%). However, when corrected for spatial dependence, the number of significant deviations decreased considerably, i.e. to less than half, for variance deficit particularly with the reflection/rotation method, for variance surplus more with the random shift approach. Table 3 summarizes the results differentiated for the two directions of deviation. All cases which were significant at $P=0.001$ and most cases significant at $P=0.01$ before correction, remained so after correction for spatial dependence. Thus it seems reasonable to consider all cases, also when no correction for spatial dependence was possible at the significance level $P \leq 0.01$ before correction for spatial dependence (Table 4).

The cases of variance surplus are more or less equally distributed over the sites, while cases of variance deficit are more often found in Gettlinge 1 and Skarpa Alby. It would not be easy to relate a difference to an environmental factor. Regarding richness variance the fully fertilized and fully-minus N-fertilized plots, although generally showing a coarser structure after some years (Peet et al. 1990; Willems et al. 1993), did not differ significantly from the unfertilized ones, whereas the other fertilized plots were very similar to the control plots. The distribution of cases of variance deviance over the years is fairly equal (Table 5).

The coincidence in occurrences of variance deficit or surplus at either subplot size is weak (Table 6). In several cases a deficit at one subplot size coincides with a surplus at the other subplot size. The correlation between RVR values for 10 cm² and 100 cm² ($r = 0.38$; $n = 100$) is significant at $P < 0.001$, but this is entirely due to the occurrence of three very high values ($RVR > 2.30$ on 0.01 m²), two of which are also high on 10 cm². For the other cases ($n = 97$), $r = 0.13$ (N.S.). In this connection, the richness variance figures for the two next larger sizes, 0.10 m² and 0.25 m², were compared for the Gettlinge plots (1985-1993), i.e. 92 cases. The total number of significant deviations from $RVR=1$ ($P < 0.01$) was much less at the smaller subplot sizes: 6 (3 > and 3 <) for the 0.10-m² subplots and 8 (6 >> and 2 <<) for the 0.25-m² subplots, against 17 (15 > and 2 <) for the 100-cm² and 26 (4 > and 22 <) for the 10-cm² subplots. There was little coherence between the deviations for the different subplot sizes.

Since there are no big changes in species richness and species frequency over the years, one would expect that deviations in species richness variance are consistent, i.e. would occur more often in subsequent years than expected. This is hardly the case, as follows from Table 7 (note that we included cases up to $P = 0.10$ and $P = 0.05$ respectively to emphasize possible trends). Among the 20 plots with five years of observation, there are four plots with three or more cases of variance deficit ($P < 0.05$) in the 10-cm² subplots; in one plot (in Skarpa Alby) all five years had the same trend. On the other hand, there are also four plots with both variance deficit and surplus. Regarding the 100-cm² subplots, only two plots had three cases of variance surplus.

In conclusion, both upward and downward deviations from expected richness variance occur, i.e. in ca. 15% of all cases. However, the occurrence is capricious, both spatially and temporally. Richness itself does not show a temporal trend, but varies somewhat amongst the sites; however, this variation is not related to the variance ratio. In view of the large spatial mobility of species in alvar grassland (van der Maarel & Sykes 1993) we may consider two parameters of special inter-

Table 3. Comparison of observed richness variance values in 111 cases, 84 cases of 10-cm² subplots and 27 cases of 100-cm² subplots: not-corrected values for variance deficit compared with values corrected for spatial dependence with the reflection/rotation method; not-corrected values for variance surplus compared with values corrected for spatial dependence with the random shift method.

	Deficit			Corrected					Tot
	<i>P</i> ≤ 0.001	<i>P</i> ≤ 0.01	<i>P</i> ≤ 0.05	NS	NS	<i>P</i> ≤ 0.05	<i>P</i> ≤ 0.01	<i>P</i> ≤ 0.001	
Not corrected: Deficit									
<i>P</i> ≤ 0.001		3	1						4
<i>P</i> ≤ 0.01		2	2	2					6
<i>P</i> ≤ 0.05			2	6					8
NS			*3	48					51
Not corrected: Surplus									
NS					28				28
<i>P</i> ≤ 0.05					4				4
<i>P</i> ≤ 0.01					1	1			2
<i>P</i> ≤ 0.001					1	1	4	2	8
Total	0	5	8	56	34	2	4	2	111

* these cases were NS according to the random shift correction method.

est: the total number of species in the plot, *S*, and the average frequency of the species, *F*. A high subplot richness can be seen as the result of a high total number of species and a high mean frequency.

Comparison of the Variance Ratio test with the G-test

There are 34 cases of combined *G*-significance (*P* ≤ 0.05) and *VR*-significance (*P* ≤ 0.01) – 20 in the 100-cm² subplots and 14 in the 10-cm² subplots. These make up 76 % of all cases of *VR*-significance but only 44 % of all cases of *G*-significance (Table 8). There is a clear difference between the results for the two subplot sizes: the surplus deviations on the 100-cm² subplots (forming the majority) are all *G*-significant, whereas only 60 % of the deficit deviations on the 10-cm² subplots (forming the majority here) are *G*-significant. The coherence between the two tests, though significant according to a χ^2 -test, is not perfect. On inspection of several cases of

coherence and non-coherence, which is done by comparing the observed frequency distribution with the expected one, the following pattern emerges:

- The *G*-test tends to be significant if one or two richness classes are over-represented, because a strong excess gives a large contribution to the log-likelihood ratio. This usually concerns classes around the mean and involves a trend for *RVr* to be < 1. If at the same time some outliers to the right are found, meaning a trend for *RVr* to be > 1, the resulting *RVr* may be near to 1. As an example (Fig. 1a): plot G1-2 in 1989 (100-cm² subplots) had an *RVr* = 0.98, but the *G*-test is highly significant. The middle classes 12 and 14 are strongly over-represented while at the same time the outlier classes 19 and 21 have three and one representatives respectively – which makes this distribution significantly right-skewed. We have also found similar examples with significant left-skewness.
- If, on the other hand, we have a deficit in outlier

Table 4. Occurrence of significant (*P* ≤ 0.01) deviations from *RVr* = 1 for the five series Gettlinge (G1, G2, G3), Kleva (K) and Skarpa Alby (S) for all years. >₁₀ = *RVr* >> 1 in 10-cm² subplots; >₁₀₀ = *RVr* > 1 in 100-cm² subplots; <₁₀ = *RVr* < 1 in 10-cm² subplots; <₁₀₀ = *RVr* > 1 in 100-cm² subplots. *N* = number of cases. Percentage values relate to *N*. Fertilized = results for plots with full fertilization and full fertilization minus *N*. The last four columns compare the subtotals for >, < and NS cases. *c*² test of the difference between fertilized and unfertilized plots is non-significant.

	<i>N</i>	> ₁₀	%	> ₁₀₀	%	< ₁₀	%	< ₁₀₀	%	>	<	NS	%
G1	53	1	2	4	8	9	17	2	4	5	11	37	70
G2	29	2	7	2	7	4	14	0	0	4	4	21	72
G3	10	0	0	3	30	0	0	0	0	3	0	7	70
K	35	1	3	5	14	3	9	0	0	6	3	26	74
S	25	0	0	1	8	6	24	0	0	1	6	18	72
Total	152	4	3	15	10	22	14	2	1	19	24	109	72
Fertilized: NP, P	56	1	2	7	20	6	16	0	0	8	6	42	75
Other	96	3	3	8	8	16	17	4	4	11	20	65	68

Table 5. Occurrence of significant ($P \leq 0.01$) deviations from $RVr = 1$ for the years 1985-1989 for all series Gettlinge, Kleva and Skarpa Alby. $>_{10} = RVr > 1$ in 10-cm² subplots; $>_{100} = RVr > 1$ in 100-cm² subplots; $<_{10} = RVr < 1$ in 10-cm² subplots; $<_{100} = RVr < 1$ in 100-cm² subplots. N = number of cases. For each of the four types of deviation, the number of combinations with the type of deviation for the other subplot size is indicated. The last four columns compare the subtotals for $>$, $<$ and NS cases. c^2 test of the differences between years is non-significant.

N	$>_{10}$	$>_{100}$	$<_{10}$	$<_{100}$	$>$	$<$	NS	
1985	30	0	3	7	0	3	7	20
1986	22	0	3	4	1	3	5	14
1987	22	1	2	3	0	3	3	16
1988	22	3	3	2	0	6	2	14
1989	32	0	4	3	0	4	3	25
Total	128	4	15	19	1	19	20	89

Table 6. Coincidence of deviations from $RVr = 1$ ($P \leq 0.05$) on 10-cm² and 100-cm² subplots for the years 1985-1989.

	10-cm ² subplots				Tot.
	$<$	NS	$>$		
100-cm ² subplots	$<$	1	4	0	5
	$>$	7	12	2	21
	NS	30	61	11	102
Total		38	77	13	128

classes, while the excess in the middle classes is spread over several classes, the G -test is not significant but the Variance Ratio test is.

- The G -test tends to be significant, while the simulation test is not, if the two frequency distributions overlap but the representation of the middle classes of the observed distribution is irregular.

- Cases with an RVr value which, according to the simulation test, deviate significantly from 1 can almost always be interpreted in terms of significant skewness, in case of deviations greater than 1, or over-representation of the middle richness classes, in case of deviations below 1, which is the basis for an interpretation in terms of niche structure. In that sense the simulation test is appropriate.

- However, many cases with a nonsignificant deviation of RVr from 1, but a significant G -test, are equally interesting because they combine aspects of what could be interpreted as niche limitation with heterogeneity. The situation in plot G1-2 in 1989 (100-cm² subplots), already discussed and shown in Fig. 1a, exemplifies this combination: to the left there is a clear under-representation of classes 9 and 10: 'niche facilitation', to the right there are 'waterholes'. In the present study these hybrid cases have not been considered further.

Table 7. Number of times a significant deviation ($P < 0.10$) was followed by the same significant deviation in the following year ($>>$ and $<<$), no significant deviation (>0 and <0) or the opposite significant deviation ($><$ and $<>$). Int. = interruption, referring to a record in one year which is not followed by an analysis in the next year. ND = number of times no deviance was found. Observations for 1985/1986, 1986/1987, 1987/1988 and 1988/1989 are included.

Subplot	100 cm ²	10 cm ²
$>>$	6	0
>0	17	6
$><$	1	0
Interruption	8	0
$<<$	2	16
<0	6	25
$<>$	2	1
Interruption	3	14
ND	65	48
Total	110	110

Table 8. Relation between the results of the VR-test ($P < 0.01$) and the G -test ($P \leq 0.05$) for surplus and deficit deviations from expected richness variance in 100-cm² and 10-cm² subplots. $N = 152$. ** = $P \leq 0.01$; * = $0.01 < P \leq 0.10$; NS = Not significant.

	Significance VR- test				NS	Tot
	Surplus		Deficit			
	**	*	**	*		
100 cm ²						
G -test: $P \leq 0.05$	17	5	1	3	17	43
G -test: NS	0	13	1	9	86	109
Total	17	18	2	12	103	152
10 cm ²						
G -test: $P \leq 0.05$	3	2	13	11	6	35
G -test: NS	1	0	9	27	80	117
Total	4	2	22	38	86	152

Interpretation of a richness variance surplus

A surplus of richness variance, mostly found in 100-cm² subplots (Table 2) is usually a result of the occurrence of one or two outlier classes. Plot series G1-1 in 1986 is a typical example (Fig. 1b). The mean richness is 12.9 species/subplot and the RVr value is 2.05. Both tests suggest that the observed richness distribution is highly significantly differing from a null-model expectation. The high value is mainly built up by the occurrence of one subplot with 23 species (the highest individual score on 100 cm²) and an excess representation of the richness class 8. In other years this subplot had an average number of species. There were two other cases of significant variance surplus in this plot (one of the few plots with several such deviations), but the deviations in other years are caused by high species numbers

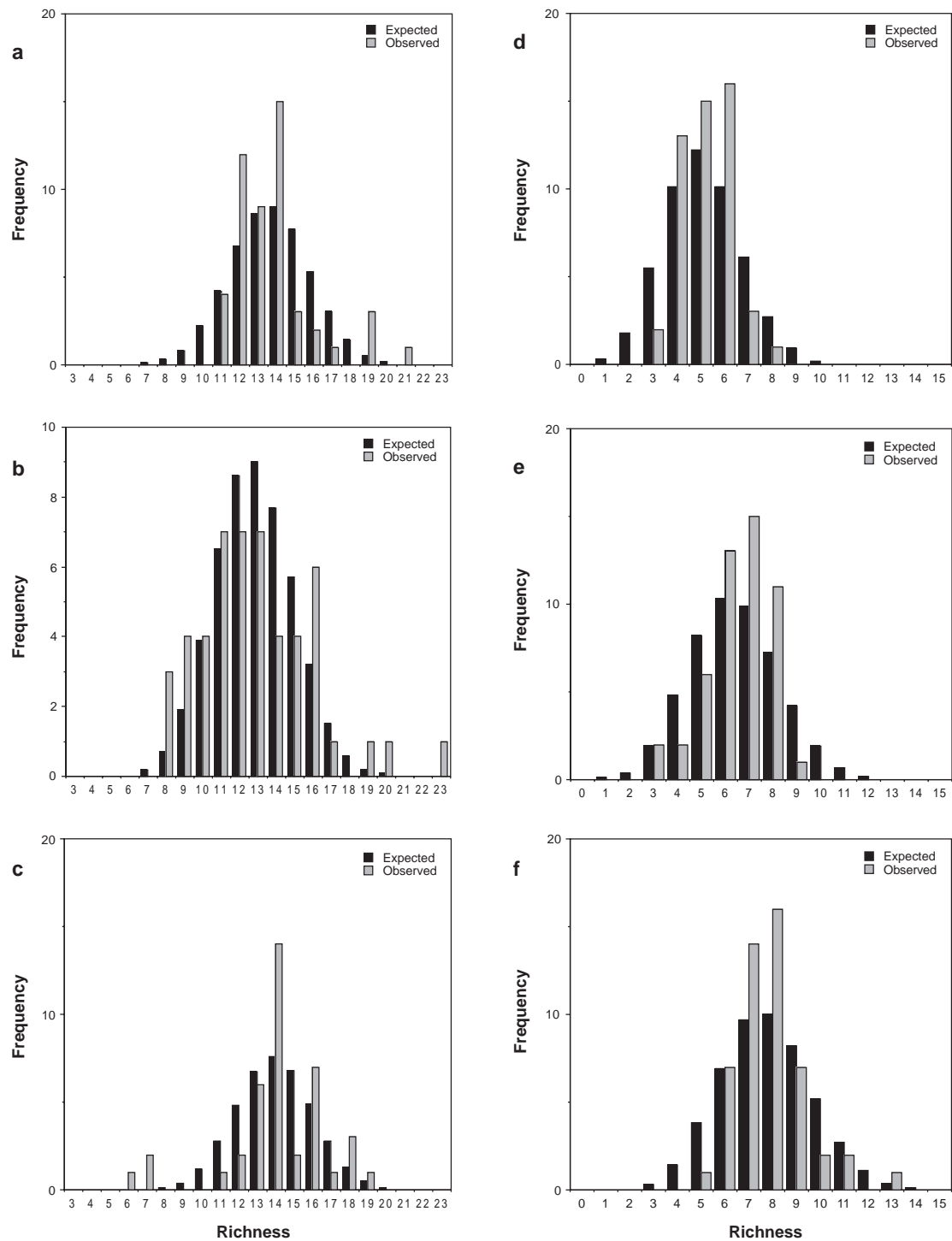


Fig. 1. Richness frequency distribution for six plots in alvar grassland (50 subplots) compared with the expected distribution. **a-c:** 100-cm² subplots; **d-f:** 10-cm² subplots. **a.** plot series G1-2 in 1989: $R = 13.7$; $RVr = 0.98$ (NS); G -test significant at $P = 0.001$; distribution significantly right-skewed ($P = 0.03$). **b.** Plot series G1-1 in 1986: $R = 12.9$; $RVr = 2.05$ ($P < 0.001$); G -test significant at $P = 0.005$; distribution significantly right-skewed ($P = 0.03$). Note the outlier class 23. **c.** plot series G1-2 in 1991: $R = 14.0$; $RVr = 1.68$ ($P < 0.001$); G -test significant at $P = 0.005$; distribution significantly left-skewed ($P = 0.001$). **d.** plot series K1-3 in 1987: $R = 5.2$; $RVr = 0.43$ ($P < 0.001$); G -test significant at $P = 0.005$; distribution not skewed. Classes 4 - 6 overrepresented. **e.** plot S1-5 in 1986: $R = 6.5$; $RVr = 0.50$ ($P < 0.001$); G -test significant at $P = 0.01$; distribution significantly left-skewed ($P < 0.001$). Classes 11 and 12 underrepresented. **f.** plot series G2-6 in 1989: $R = 7.8$; $RVr = 0.57$ ($P < 0.01$); G -test significant at $P = 0.025$; distribution significantly right-skewed ($P < 0.001$). Classes 4 and 5 underrepresented.

in other subplots than in 1986. Thus, if such subplots act as waterholes, their importance is ephemeral; they can be considered by-products of the shifting nature of the community.

Plot G1-2 in 1991 (Fig. 1c) shows the occurrence of the opposite of a waterhole, i.e. unfavourable microsites. Mean richness is higher than in the former case, the RVr value is lower, 1.68, but still highly significantly different from 1 ($P < 0.001$); the G -test is highly significant as well, at $P = 0.001$, the left-skewness is significant at $P = 0.03$. The main deviation from expected in terms of the G -test is the excess in the mean class 14, whereas the deviation from $RVr = 1$ is caused by occurrences in the outlier classes 6 and 7. On inspection, these low values occurred just once – compare also with Fig. 1a showing the same plot two years earlier.

A significant variance surplus can also follow from the occurrence of outliers at both sides of the distribution; so ‘favourable’ and ‘unfavourable’ microsites are both present.

There are cases of outliers at the species-poor side of the distribution curve causing a significant variance surplus, most of them on 10-cm² subplots, but the number of subplots with only 1 or 2 species is low in view of the presumed high frequency of gap formation (van der Maarel & Sykes 1993). There was one case of an empty subplot – in an otherwise not deviating plot – which appeared in one year but had become recolonized the year after. In this context it should be mentioned that deposition of cow dung is a frequent disturbance causing emptiness of microsites – from ca. 100 - 1000 cm², but during the period of analysis of the permanent plots newly occurring cow dung was immediately removed in order not to disturb the fertilization experiments.

In view of the lack of abiotic heterogeneity so far observed or deduced from the floristic similarity between subplots, we consider the occurrence of richness variance surplus to be a result of random fluctuations in species number per subplot caused by fluctuations in local immigration and extinction.

Interpretation of a richness variance deficit

A deficit of richness variance, mostly found in 10-cm² subplots (Table 2) is usually brought about by the over-representation of one to three middle classes in the richness frequency distribution. A typical example (Fig. 1d) is plot K1-3 in 1987 (10-cm² subplots) with a relatively low mean richness of 5.2 and a very low RVr of 0.43 (the lowest value in this analysis). The richness classes 4, 5 and 6 show an excess, and the classes to the left and right a deficit.

In the case of plot S1-5 in 1986 we have an example of ‘niche limitation’ (Fig. 1e) in that the higher classes 9

and 10 are under-represented. Plot G2-6 in 1989 on the other hand (Fig. 1f), suggests the existence of ‘niche facilitation’ with the lower classes 4 and 5 under-represented.

In summary, in most cases of richness variance surplus, occurring mostly on the 100-cm² subplots, the richness frequency distribution is right-skewed, whereas in most cases of variance deficit, occurring mostly on the 10-cm² subplots, the richness frequency distribution is symmetrical.

Discussion

Spatial dependence

The number of significant deviations from $RVr = 1$ is reduced by more than 50 % after correction for spatial dependence. Spatial dependence can also be indicated directly by comparing the average Jaccard similarity of nearest-neighbour subplots with the overall mean similarity in a plot. Indeed, the similarity between nearest neighbour subplots was systematically higher than the average subplot similarity, the highest deviation being found in the richest site, Skarpa Alby (Table 2). There are various explanations for spatial dependence, i.e. the occurrence of local patches of plant units of a species on a scale exceeding the distance between subplots. Of the three categories usually distinguished (Kershaw & Looney 1985): morphological, sociological and environmental pattern, microheterogeneity, particularly regarding soil depth, cannot be excluded, but in our measurements no clear patterns have been detected so far. More probably we are dealing with spatio-temporal effects of disturbance, particularly the dropping of cow dung; other disturbance mechanisms include local cattle trampling, ant activities and extreme summer drought in microsites on shallow soil. However, dung did not have any influence on the investigated plots because it was removed in order to avoid major heterogeneities during the experiments.

The results of the similarity measurements (Table 2) suggest the occurrence of morphological and sociological patterns as well, but these have not yet been investigated in detail, except for the association between seedlings of several species and existing adult individuals and structures built up by them (Rusch & Fernández-Palacios 1995).

Spatial and temporal patterns of variance deviation

There is neither a clear spatial nor a clear temporal trend in the deviations. Moreover, there is no relation between the situation on the 10-cm² and the 100-cm²

subplots. Upward deviations can directly be linked to the occurrence of outlier species numbers in one or two subplots, which is always a one-year phenomenon. It would be more realistic to suppose that the deviations are temporary and ephemeral results of local appearances and disappearances of species in small subplots, as indicated by the Carousel model (van der Maarel & Sykes 1993). According to Huber (1994 and in prep.), who has studied still smaller subplots, i.e. 4 cm², there is rapid turnover even within one season and patterns of richness variance would change even faster than we already assume.

Physical limitation to species richness

Another argument against interpretation of variance deficit as niche structure is the possibility of a physical (spatial) limit to the number of species on a very small plot. Our preliminary results from limestone grassland showed that variance deficit in 100-cm² subplots occurred much more rarely than in 10-cm² subplots. Wilson et al. (1995) did not find much evidence of variance deficit on larger subplots either. The most convincing evidence for variance deficit was found at the quadrat size of 1 cm² (Watkins & Wilson 1992) and in samples at a single point – i.e. along a pin (Wilson et al. 1992). This may have a trivial explanation in that there is an upper bound of species richness related to the low number of individuals (plant units) on very small subplots. This can be approached in the following way. For each plant species the plant unit size will follow a particular distribution with the modal size being very small for alvar grassland species. According to a rough estimation based on field experience, modal plant sizes (cm²) of 44 common species in the three alvar sites may be distributed as follows:

Plant size:	0.1	0.2	0.5	1	2	5	10
No. of species:	1	1	6	12	14	9	1

These sizes are very small indeed. Moreover, seedlings are not included in this estimation. In order to accommodate one plant unit of each of these 44 species, one would need 98.3 cm². Of course, in reality some species will occur with large numbers of units, in the case of the alvar grassland particularly *Festuca ovina*, with an estimated size of 0.1 cm². The average size (not weighted) of the plant units of these species is 2 cm². This would mean that on average five species would find room on an area of 10 cm² - assuming one unit per species. If we take into account the exclusion of species because of the abundance of a species such as *Festuca ovina*, but on the other hand add that some species may be present in different strata by plant parts from units rooting outside

the area and assume that one or two species may be represented by a seedling, one would arrive at an estimation of ca. 5 - 10 species per 10 cm². This is near to the actual average found in this study (Table 2). Thus, a possible limitation in the number of species on very small subplots can very well be a matter of space limitation. Palmer & van der Maarel (1995) elaborate on the relation between number of plant units and number of species, while emphasizing the upper bound of species richness determined by the limited number of units. In this connection we may remark that the Skarpa Alby plots, indeed showing a relatively high number of cases with variance deficit, also show some structural differences: the average species frequency is slightly lower and most of the differential species of this site (Table 1) are represented with plant units of a bigger size - rosettes or clumps - and the physical limitation by the small number of plant units mentioned above may be higher here.

Guild structure

We may also add some remarks on guilds here. Within guilds there may be more competition and hence niche limitation than between guilds, as assumed by Wilson & Watkins (1995) and Wilson et al. (1995). In their study of the alvar grassland, Wilson et al. (1995) distinguished a graminoid and a dicot guild. This distinction would separate species with narrow upright leaves from species with broad flat leaves. Apart from the occurrence of graminoids with a dicot stature, e.g. *Carex caryophylla*, and of dicots with a graminoid stature, e.g. *Asperula tinctoria*, the two groups are different as to their modal plant size: the graminoids in the alvar community are on average much smaller. Wilson et al. (1995) also treat the annuals separated from the perennials because the annuals would follow a different assembly rule. As van der Maarel & Sykes (1993) pointed out, the high small-scale species turnover in the alvar grassland implies that many ramets of most perennials behave like annuals, although there are differences in germination conditions (Rusch & van der Maarel 1992), and the genets of the annuals are generally smaller than the ramets of the perennials. In addition, Sykes et al. (1994) showed that the North American burnt savannas included in the joint project (Peet et al. 1990) have about the same small-scale turnover and accumulation rates as the Öland grasslands, but no annuals. Apparently, any division into guilds should refer to differences in size of individual ramets.

Effects of fertilization

We do not agree with the conclusion of Wilson et al. (1995) that the fertilized plots would show a different behaviour and some sort of response time. When all plots and both full fertilization and fertilization except for N are included (the two fertilizations giving a higher biomass) there is only some trend for a higher number of cases with variance surplus at the 100-cm² level, which may be connected to the generally coarser structure of the vegetation here. We also comment on the interpretation of the absence of guild proportionality in the fertilized plots, which would result from a disequilibrium in niche structure. What happened here was that (mainly annual) *Fabaceae* developed in patches of a size bigger than the subplots.

Richness limitation and facilitation

Our results with the *G*-test suggest that indications for species facilitation are stronger than those for richness limitation. Niche facilitation should be understood as a mechanism whereby certain matrix species would have to be established in a subplot immediately after a disturbance before certain other species would develop. The facilitation may consist of a more humid microclimate near the surface enabling seedlings to survive – we mention the study on the nurse function of shrubs by Valiente-Banuet et al. (1991) as just one example – or of dependence relations, such as the hemiparasitic *Euphrasia stricta* developing only if grass roots are available.

Wilson et al. (1995) recognize that species-poor subplots are rare. They explain this fact by assuming that empty subplots, which will occur every time a local gap arises, are rapidly filled through invasion. We agree (van der Maarel & Sykes 1993). The interesting point here, however, is that in many cases of niche limitation as deduced from variance deficit, the invasion goes faster than expected! Wilson et al. consider the possibility of facilitation but link this to a surplus of richness variance. This would imply that they did not adopt the original idea of facilitation as a mechanism in the colonization process after disturbance (Connell & Slatyer 1977).

Conclusions

Cases of a significant deficit in variance of species richness are few, do not show any pattern in space or time and can be explained by spatial dependence and by the small number of plant units involved. Apart from the theoretical problems mentioned, empirical evidence for

niche limitation is small, and that for niche facilitation larger. Cases of a significant surplus in variance can likewise be explained by spatial phenomena, namely the (random) concentrations of species in temporally favourable microsites, and their temporal absence under unfavourable conditions directly after a disturbance.

Thus, the field situation in limestone grassland provides little evidence for niche structure and hardly any evidence for niche limitation, whereas small-scale patterns of species occurrence and species mobility are obvious.

Niche (species) limitation as a plant community assembly rule may very well exist, and so may niche (species) facilitation, but these rules cannot be detected through the kind of spatial analysis described in this and related papers. We should explore statistical relations between frequency distributions, species associations and variance deficit, before using mechanistic explanations. Palmer & van der Maarel. (1995) have started with this exploration, following Palmer (1987) who applied the variance test for the occurrence of species interactions (Pielou 1972) to compare the variance of species richness values of plots of different sizes with the expected variance. As will be shown in the companion paper using simulated communities (Palmer & van der Maarel 1995), situations of real niche limitation may not find an expression in a variance deficit, and also situations of a variance deficit need not be linked to niche limitation. Variance deficit can even be the result of spatial heterogeneity, which is usually considered as a condition for variance surplus. However interesting the study of richness variation in the field may be, we have to approach the possibility of niche limitation, and of niche facilitation as well, in different ways, particularly by means of experiments.

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