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SMALL-SCALE DISTRIBUTION OF SPECIES RICHNESS IN A GRASSLAND (BÍLÉ KARPATY MTS., CZECH REPUBLIC)

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Abstract: Variation in the number of species was studied in a subthermophilous grassland at a scale of 0.05 × 0.05 m during a 5-year period. The observed variance of species richness (VSR) was compared with a null model based on random distribution of species over a set of squares. It was found that distribution of species richness had more values than expected around the mean and less values at the "shoulders". Both tails fell within the predicted limits. Application of the procedures removing spatial dependence (random shifts, rotation/reflection method by Palmer & van der Maarel 1995) and environmental heterogeneity (patch model by Watkins & Wilson 1992) did not change the observed pattern.

Using simulations in which the number of clumps and clumping intensity were manipulated it was found that the effect of the clumped spatial pattern on VSR results in a wide range of variances. Both variance excess and variance deficit were found more frequently than expected under the null model.

To test the effect of the limitation to the number of individuals per square a null model was developed which included the observed number of plant shoots per square, the observed distribution of the number of shoots belonging to individual species per square and the observed spatial distribution of the shoots. The observed VSR was still lower than that produced by the null model. Therefore, it is concluded that at a scale of 0.05 × 0.05 m plant species combine in a non-random way in the studied grassland. It is suggested that the shape of left and right "shoulders" of the species richness distribution may be caused by different factors, such as positive and negative covariance between species, respectively. Their simultaneous impact can generate the observed pattern in species richness.

INTRODUCTION

The complexity of biotic communities makes utilisation of field experiments complicated. Therefore, descriptive and comparative approaches still play a significant role in community ecology. In addition, the structure of natural communities has been studied using comparisons with simulated species assemblages (Harvey et al. 1983). If a difference between the random and the observed patterns is found, then one investigates for possible mechanisms. Owing to the simplicity of this approach, and difficulties with manipulation in natural communities (Wilson 1995b, Aarssen & Epp 1990), inferring mechanisms from the observed pattern is quite frequent in community ecology (Greig-Smith 1983, Jongman et al. 1987).

One of the recently developed methods used for detecting community structure utilises the variance of species richness (VSR) (Schluter 1984, Palmer 1987, Wilson et al. 1987). In this approach the observed VSR is compared with the expected one, calculated for randomly distributed species with fixed frequencies.

Forum: Assembly rules, niche limitation and data on pattern

The approach has recently been discussed by Lepš (1995) and Wilson (1995b). They suggested that the null model is not correct because "competition of individuals (genets) for space" (Lepš 1995) and limitation to the number of plant modules (Bycroft et al. 1993, Wilson 1995b) decrease the expected VSR. It has been argued (Watkins & Wilson 1992) that if the number of individuals is usually > 1 the results are not affected. However, Palmer & van der Maarel (1995) showed that the problem persists unless the number of individuals per area is much higher than the species pool. I agree both with Lepš (1995) and Wilson (1995b) that there is, theoretically, a limit to the number of individuals and modules which can fit into a plot. However, it is still unclear whether the above-mentioned limitation plays a role in real plant communities. Based on computer simulations Bartha et al. (1995b) suggested that clumping of plants results in a high variance in species richness. Using a different method Palmer & van der Maarel (1995) found that clumping may result in variance both lower and higher than expected.

I tested the effects of spatial pattern of plant individuals and limitation to the number of shoots using real data. For this study I selected a homogeneous species-rich grassland because it has been suggested that the chance to find the variance deficit is highest in this type of community (Wilson et al. 1987, Bartha et al. 1995b). Most studies dealing with the VSR at small scales have used data from a single observation or a single season (but see Wilson et al. 1992). Here I utilise 5 years of data from a fixed plot to assess the year-to-year changes.

MATERIAL AND METHODS

The sample plot was established in the National Reserve of Čertoryje in South Moravia, Czech Republic (48°54' N, 17°25' E), in a subthermophilous meadow dominated by *Bromus erectus* and *Carex montana*. The area is not fertilized and is mown regularly at the end of June. A detailed description of flora, vegetation and soils can be found in Tlusták (1975), Jongepierová et al. (1994) and Klimeš et al. (1995).

A permanent quadrat (1.5 × 1.5 m) was established on the selected plot in June 1991. The quadrat was divided into 900 squares, 0.0025 m^2 each, by a cord. In these squares rooted vascular plants were recorded during the second week of June, from 1991 to 1995, usually 1 to 3 weeks before the meadow was cut. From 1993 to 1995 I also recorded the number of individuals, defined as shoots.

The observed VSR was compared with the expected one calculated for the same number of species, randomly distributed over the set of squares, with fixed frequencies (e.g. Wilson et al. 1987). I calculated 2000 randomizations for 2-tailed tests. The differences were interpreted as significant when $P < 0.05$. The results were expressed as a relative deficit or excess of the VSR (RV[%] = 100 * observed VSR / expected VSR). The 900 squares were merged to 225 (i.e. 4 neighbouring squares merged to form a quadrat), 100, 36 and 25 squares for evaluation of the effect of different scales on RV.

Due to the spatial arrangement of squares in the grid, nearby samples are more similar, on average, than distant samples (Palmer 1987, Palmer & van der Maarel 1995). Therefore, the probability of Type I error is inflated unless spatial dependence is corrected. I used two methods suggested by Palmer & van der Maarel (1995) to remove the effect of spatial dependence. The rotation/reflection method is the only method keeping the original spatial pattern exactly. There are eight possible permutations of the grid data for each species. As the number of potential permutations increases exponentially with the number of species (8^{n-1}, where n is number of species) and the number of species in the studied grassland ranged between 57 and 69 during the five-year period of observations, there was a sufficient number of potential permutations. The other method suggested by Palmer & van der Maarel (1995) uses random shifts. Each species is shifted a random number of squares along a grid and squares beyond the edge of the grid are wrapped back on to the opposite edge. This method slightly modifies spatial distribution of the species.

If a community consists of several species pools restricted to large patches of different environments, a variance deficit is expected. This effect can be removed using a patch model by Watkins & Wilson (1992). The probability of a species occurring in a square is not equal to overall frequency of that species; it is calculated from a patch consisting of a target square and several neighbouring squares. I used two sizes of quadrat patches - 5 and 9 squares.

I estimated the effect of the spatial distribution of plants on RV using computer simulations. Individuals were distributed in clumps of different sizes and numbers. The clumped distribution was achieved using the following procedure: clump centres and individual plants were randomly placed on the plot. Then, each plant was assigned to its nearest centre. The new position of the plants was recalculated using two-dimensional normal distribution of individuals within a clump with a given standard deviation. To avoid an edge effect, the plot was enlarged to 2.4 × 2.4 m, the target quadrat (1.5 × 1.5 m) was placed in the centre of the plot and the observed numbers of individuals was multiplied by 2.56. The number of clumps was calculated as $N_i/(5.12 * \exp(1.0986*C))$ where N_i is the number of individuals of the i-th species and C is a constant ranging between 1 (many clumps) and 5 (few clumps). The minimum number of clumps was 1 by definition. The clumped distributions were calculated for standard deviation (s. d.) = 0.5, 4.5, 6.5 and 8.5 cm. One hundred simulations were calculated for each combination of input values.

I used two null models to test limitation of the number of shoots. In these models I fixed the number of shoots per square. In the first model individual shoots were assigned to species randomly, as in Palmer & van der Maarel (1995). In the second model, individuals were assigned to species according to the observed species frequency calculated for individual numbers of shoots per square and the observed degree of clumping was respected. The number of shoots per square was taken randomly from the observed distributions of the number of shoots per square. This distribution was calculated for individual species.

I used the random number generator developed by Marsaglia et al. (1990).

RESULTS

The total number of species recorded in the 900 squares (2.25 m^2) ranged between 57 and 69 from 1991 to 1995 (Tab. 1). The mean number of species in each 0.0025 m^2 square ranged between 2.91 and 3.56 with a minimum of 0 and maximum of 8 species (Tab. 1). The total number of individuals recorded in the 900 squares varied between 7553 and 8535 from 1993 to 1995 (Tab. 2). The mean number of individuals in each 0.0025 m^2 square ranged between 8.39 and 9.48 with a minimum of 0 and maximum of 95 individuals (Tab. 2).

Both the expected and the observed distribution of species richness calculated for 0.0025 m^2 squares were positively skewed (Tab. 1, Fig. 1). The observed distribution had more values than expected around the mean and fewer values at the "shoulders" (Fig. 1). However, both

Table 1. Distribution characteristics for the number of species in 0.0025 m^2 squares. All values of skewness are significant at $P < 0.001$.

Year	1991	1992	1993	1994	1995
Average	3.33	2.91	2.99	3.11	3.56
Minimum	0	0	0	0	0
Maximum	8	7	8	7	8
Variance	1.61	1.61	1.68	1.66	1.81
Skewness	0.246	0.295	0.330	0.264	0.245
Total	57	60	61	65	69

Table 2. Distribution characteristics for number of individuals in 0.0025 m^2 squares (n = 900). All values of skewness are significant at $P < 0.001$.

Year	1993	1994	1995
Average	8.56	8.39	9.48
Minimum	0	0	0
Maximum	57	95	56
Variance	36.9	38.2	35.8
Skewness	2.528	4.613	2.188
Total	7701	7553	8535

Table 3. Variance of species richness indicated by index RV from 1991 to 1995 for five different square sizes. * - $P < 0.05$. Negative values indicate variance deficit, positive values variance excess.

Square size [m^2]	1991	1992	1993	1994	1995
0.0025	-30.9*	-25.4*	-20.0*	-27.5*	-26.0*
0.01	3.5	-2.7	1.1	-14.5	-9.2
0.0225	7.9	6.7	37.2*	-6.0	8.1
0.0625	-12.8	-11.2	35.4	27.4	-7.3
0.09	28.7	-0.6	35.2	56.5*	36.8

tails fell in the predicted range. This pattern was consistent over the five years. The observed VSR was much lower than the expected one calculated from the random models. The two models removing spatial dependence shifted the distribution of the expected values towards lower values. The two patch models were even more effective. However, the observed values of VSR were still much lower than expected. The pattern was the same in all five years (see Fig. 2 for years 1994 and 1995).

If four neighbouring squares were merged, the distribution of the number of species fell in the 95% limit in all four years except for negligible differences for single values in three years. No difference between the observed and expected distributions was found at larger scales (not shown). Variance deficit (VD) was found in all five years at the smallest spatial scale (0.0025 m^2) (Tab. 3). VD was never found at larger scales. Variance excess (VE) was found twice above a plot size of 5 × 5 cm. Because of its irregular occurrence I will not consider it further.

Simulations, using a clumped spatial pattern, resulted in both VD and VE more frequently than expected. This effect was small for dense clumps and increased for clumps occupying larger areas. However, there was little difference between the results for s.d. = 4.5, 6.5 (not shown) and 8.5. The proportion of simulations giving significant results increased with the number of clumps (Fig. 3).

The first null model which was developed to test the effect of limitation to the number of shoots per square utilised a random assigment of shoots to species. It predicted both a high mean number of species per square and a high VSR (Fig. 4A). The other model, which included the observed frequency of species calculated for individual number of shoots per square and clumped pattern of shoots, produced a distribution with the expected mean number of species per square. However, the observed VD in species richness was significant (Fig. 4B).

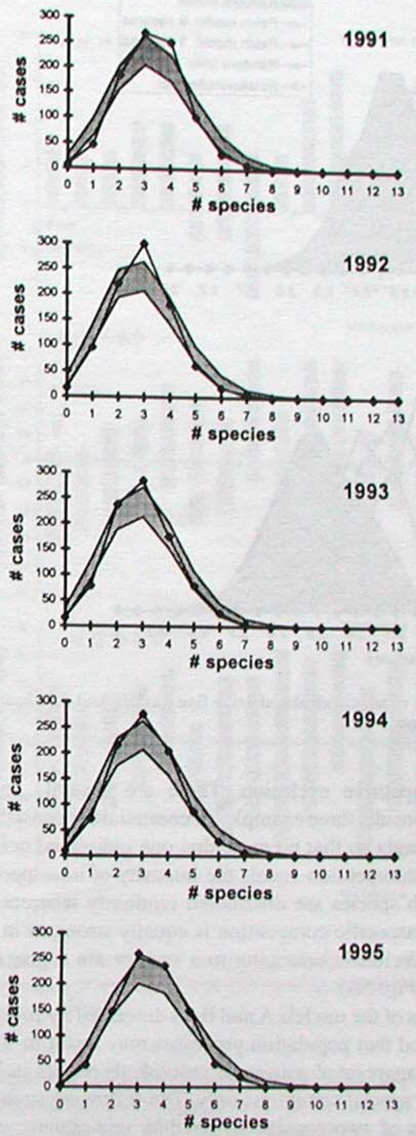

Fig. 1. Species richness distribution for 900 squares 0.0025 m^2 in size, from 1991 to 1995. The shaded area delimits 95% confidence intervals, full lines with diamonds denote observed distribution.

DISCUSSION

Using real data I showed that the distribution of the number of species in the squares has more values than expected around the mean and less values at the "shoulders". Clumped spatial distribution did not result in consistent effects even if the clumps were very distinct: both VE and VD were obtained more frequently than expected under the null model when numerous small clumps were formed (see Palmer & van der Maarel 1995, Fig. 4, for similar results).

The truncated distribution of species richness, predicted by Lepš (1995) for plant communities in which the number of individuals per square is limited, may be found if the number of individuals per square is much higher than the number of species in the species pool and individuals are randomly assigned to species. In this case, however, limitation to the number of individuals per square is rather weak (Palmer & van der Maarel 1995).

Heterogeneity in space or time results in VE in most cases. There are, however, other possible explanations of this effect (Schluter 1984). VD is a more interesting phenomenon. Bycroft et al. (1993) and Wilson (1995a) listed four explanations for it: (1) heterogeneity in space if the patches are colonised by different approximately equal-sized species pools, (2) heterogeneity in time, (3) limitations to the number of coexisting individual plant modules and

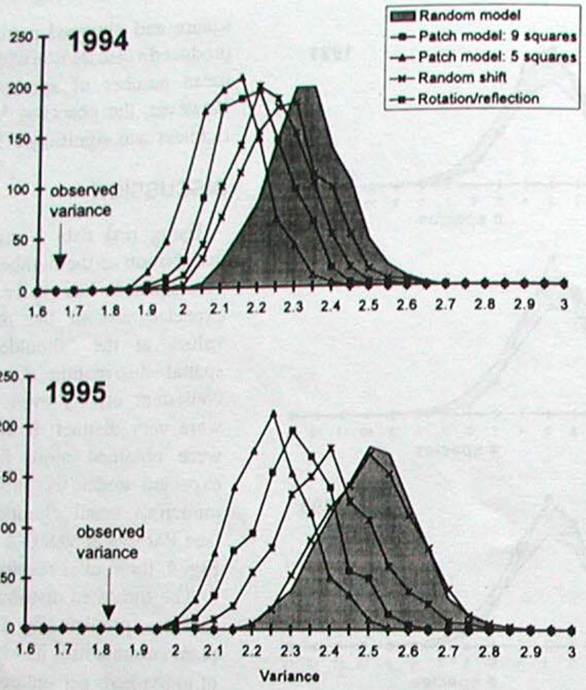

Fig. 2. Distribution of the expected variance of species richness calculated using five models, and the observed values of variance of species richness in 1994 and 1995.

(4) limitations to coexistence due to competitive exclusion. There are several more mechanisms which may result in VD. Let us consider three examples of communities consisting of two species. (1) The species compete strongly so that no more that one individual occurs in a square and the intensity of intraspecific competition equals the intensity of interspecific competition. In this case individuals of both species are distributed randomly whereas all individuals are segregated (Fig. 5A). (2) Intraspecific competition is equally strong as in (1) and interspecific competition is missing. Individuals belonging to a species are segregated and all individuals together are aggregated (Fig. 5B).

These two examples are simplified versions of the models A and B, as described by Bartha et al. (1995b). Using simulations they showed that population processes may result in VD.

Bartha et al. (1995b) suggested that an aggregated pattern of individuals results in VE. It seems that VD may also result, but under special conditions only. The following example (3) shows this: Let us consider individuals of two species larger than one square; each individual occupies four squares. VD is obtained if there is the same intensity of intra- and interspecific competition which does not permit coexistence of any two individuals in a square. Distribution of individuals belonging to a species is aggregated, distribution of all individuals is segregated and patches are distributed randomly (Fig. 5C). Then VD is observed. Note that a community consisting of clonal plants may resemble this example.

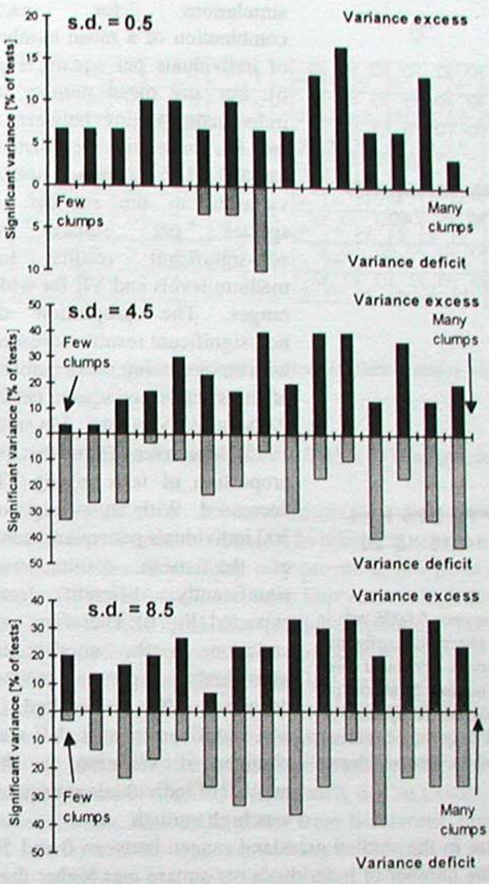

Fig. 3. The effect of the number of clumps and intensity of clumping on proportion of tests [%] showing significant variance of species richness.

The three above-mentioned examples are straightforward. However, segregated distribution of plants of individual species, as well as of all plants in a community, has been observed rarely in the field (Greig-Smith 1983). Plants in the studied grasslands are not distributed randomly or even regularly, except for a few rare species; nearly all species, including annuals, are clumped (Klimeš, in prep.). Year-to-year changes in position of plant individuals are remarkable in most species (Herben et al. 1993, van der Maarel & Sykes 1993). Still, the distribution of species richness at smallest scale is very stable with more values than expected around the mean and less values at the "shoulders" over the whole five-year period in the studied grassland.

Palmer & van der Maarel (1995) and Wilson (1995b) suggested that limitation of the number of individuals is a serious problem even if squares have a high number of individuals. Using a simple model in which the number of individuals per square was fixed, Palmer & van der Maarel (1995) assigned individuals randomly to species. They found that VD is often observed if the number of individuals per square is of the same order of magnitude, or less, than the size of the species pool (Palmer & van der Maarel 1995). This result persists even if some variation in the number of individuals per square is permitted (Palmer & van der Maarel 1995: 206). To test this prediction, I used the same model as Palmer & van der Maarel (1995) but I calculated the VSR for 69 species distributed over 900 squares. The number of individuals per square was taken randomly from a uniform distribution with a given mean and a fixed range. I calculated 100 simulations for each combination of a mean number of individuals per square (Fig. 6). For any mean number of individuals ranging between 5 and 80, there was a consistent trend of VD for a small range of variation in the number of species per square to non-significant results for medium levels and VE for wide ranges. The proportion of non-significant results increased with an increasing mean number of individuals per square (as in Palmer & van der Maarel 1995). Moreover, I found that the proportion of tests giving VE decreased. With an average of 300 individuals per square, none of the mean results was significantly different from expected (Fig. 6). Therefore, any variation in the number of individuals per quadrat decreased VD or resulted in non-significant results. VE was obtained if variation in the number of individuals per square was high enough.

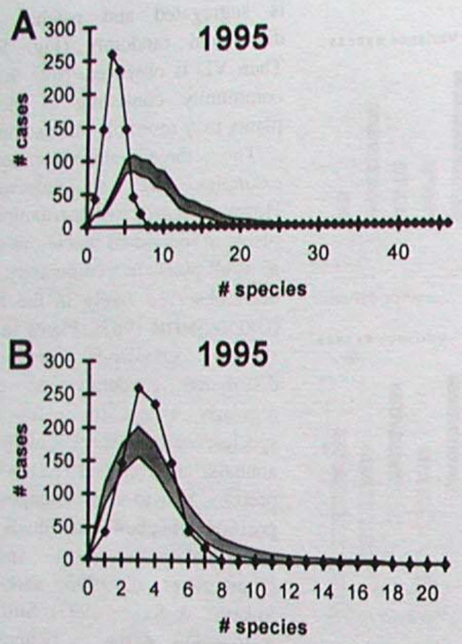

Fig. 4. Species richness distribution for 900 squares 0.0025 m^2 in size, in 1995. Full lines with diamonds denote observed distribution. The shaded area delimits 95% confidence intervals calculated using following null models in which the observed number of shoots per square was fixed and individuals were assigned to species A) randomly; B) respecting the observed species frequency calculated for individual numbers of shoots per square and the observed degree of clumping.

The number of individuals per square in the studied grassland ranged between 0 and 56 in 1995 and the observed variance of the number of individuals per square was higher than the expected one calculated from random distribution of individuals among squares (Fig. 7). This means that the limitation of the number of individuals per square was overcompensated by clumping pattern.

The random assignment of individuals to species is undoubtedly an unrealistic assumption. In reality the individuals found in a great number in a square are usually small-sized and those found individually are often bigger. However, this does not indicate limitation of the number of coexisting individuals in this case, but limitation of above-ground biomass or leaf area.

The null model in which the observed frequency of species and clumping of individuals in squares was taken into consideration produced much higher variation in species richness than observed in the field (Fig. 4B). This model seems to be quite realistic because only rules describing combination of species are allowed to vary. The results of the simulation given in

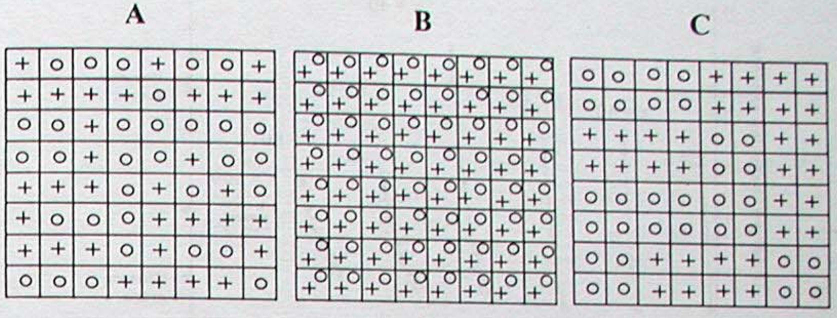

Fig. 5. Three examples of spatial pattern of plants causing variance deficit in species richness. Crosses and circles denote two different species.

Fig. 4B indicate that at a scale of 0.05 × 0.05 m species combine non-randomly in the studied community.

There could be several mechanisms, operating simultaneously, responsible for the observed distribution of species richness. In relatively severe environments, such as subthermophilous grasslands, positive effects may prevail at low plant densities whereas negative effects (e.g. competitive exclusion) are more important at high densities. It is thus reasonable to consider the left and right "shoulders" of the distribution of species richness separately. The steep left slope of the distribution may be caused by adversity of the abiotic environment, which prevents establishment of seedlings in the late spring and in summer due to high temperatures and the drying out of soil profiles on south-facing slopes. Seedling establishment is often more successful on places with a moderately dense vegetation than on completely open places (Ryser 1990, 1993). Similar positive relationships between plants in severe environments are well known but neglected (Bertness & Callaway 1994). Neighbours may ameliorate the microclimate, hide other plants from herbivores, improve nutrient conditions, etc. (Hunter & Aarssen 1988). The explanation of the pattern at the right "shoulder" of the distribution may involve several mechanisms. Lepš (1995) suggested that "competition of individuals for space causes limits to the number of individuals per sampling unit". There is a difference between competition for space and for traditional resources, such as light and nutrients (Rabotnov 1992). However, both are often used in the latter sense (Lepš 1995, Lepš, pers. comm.). Competition for space has been demonstrated belowground (McConnaughay & Bazzaz 1991). Similar results for aboveground are missing in herb assemblages. As no more than about 0.3-1.0% of available aboveground space is utilised in plant communities (Utkin et al. 1969, Klimeš, unpubl.), competition for space is hardly crucial in plant communities (Rabotnov 1992). Instead, nutrients and light are usually the most important limiting resources in grasslands (Grace & Tilman 1990, Caldwell & Pearcy 1994). Therefore, the values of leaf area and above-ground biomass are likely to be more limited in squares than the number of individuals.

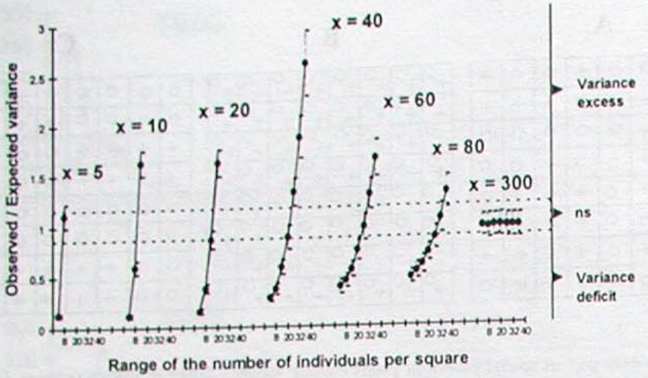

Fig. 6. The effect of the number of individuals per square on the variance ratio in simulations. The number of individuals per square was taken randomly from uniform distributions with a given range of values. Mean value of the number of individuals per square equalled to *x*. The individuals were randomly assigned to species. Species pool consisted of 69 species. The error bars indicate mean ± 3*standard deviation.

The hypothesis of niche limitation (Wilson et al. 1987) considers competitive effects in biotic communities. However, positive relationships between plants are also important in some grasslands (Bertness & Callaway 1994). They may result in "niche facilitation" at medium plant densities (Ryser 1990, 1993) and therefore affect the distribution of plant richness. The density-dependent variation in the intensity of positive and negative relationships between plants may easily generate any distribution of species richness observed so far. The role of niche limitation may also be important in some plant communities (Bartha et al. 1995b).

Using snapshot data and calculation of RV, the main factor determining distribution of species richness can probably be identified if its effect is strong. However, in the field, we find more complicated situations in most cases. I agree with Lepš (1995), Goldberg (1995) and Palmer & van der Maarel (1995) that an experimental approach is then needed.

The results based on the data collected during a five-year period in species-rich grasslands should be generalised very carefully. The studied plant assemblage is specific in several traits determining or affecting spatial pattern in the site, such as environmental heterogeneity (including the effects of the plants themselves), intensity of competition aboveground/belowground, size of the species pool, abundance of plants belonging to individual species, etc. My conclusion is that in the studied grassland VD at the scale of 5 × 5 cm is not caused by limitation of the number of individuals or, at least, this mechanism does not explain the observed pattern completely.

Finally, I would point out that I fully agree with Lepš (1995) that the observed pattern "might be roughly suggestive ... at best" and with Wilson (1995b) that several alternative hypotheses should be tested, if possible. However, these arguments are not new (Cale et al. 1989). Similar reasoning can be found also in the long-lasting discussion about mechanisms involved in plant succession. There are numerous examples showing how the observed pattern can be explained in very different ways - Clements 1916, McIntosh 1981, Pickett & McDonnell 1989. I do not think that anybody seriously suggests that inferring mechanisms from the observed pattern is the only possible and the most efficient way to understand Nature even if some of us are using this approach (e.g. Bartha et al. 1995a, Lepš & Štursa 1989, Wilson et al. 1992, Klimeš et al. 1995).

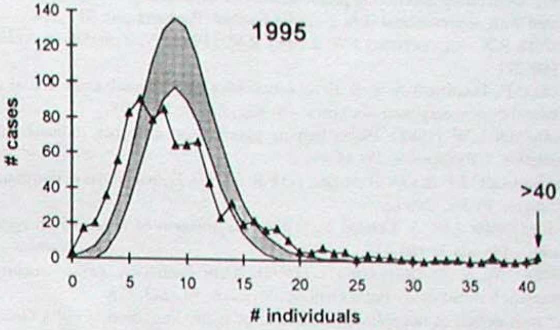

Fig. 7. Distribution of the number of individuals in 900 squares placed in a grid on a grassland in 1995. The shaded area delimits 95% confidence area calculated from 2000 simulations in which 8535 individuals were randomly assigned to the 69 observed species, the full line with triangles denotes observed distribution.

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REFERENCES

Aarssen L.W. & Epp G.A. (1990): Neighbor manipulations in natural vegetation: a review. - J. Veg. Sci. 1: 13-30.

Bartha S., Collins S.L., Glenn S.M. & Kertész M. (1995a): Fine-scale spatial organization of tallgrass prairie vegetation along a topographic gradient. - Folia Geobot. Phytotax. 30: 169-184.

Bartha S., Czárán T. & Oborny B. (1995b): Spatial constraints masking community assembly rules: a simulation study. - Folia Geobot. Phytotax. 30: 471-482.

Bertness M.D. & Callaway R. (1994): Positive interactions in communities. - Trends Ecol. Evol. 9: 191-193.

Bycroft C.M., Nicolasou N., Smith B. & Wilson B. (1993): Community structure (niche limitation and guild proportionality) in relation to the effect of spatial scale, in a *Nothofagus* forest sampled with a circular transect. - New Zealand J. Ecol. 17: 59-65.

Caldwell M.M. & Pearcy R.W. (1994) [eds.]: Exploitation of environmental heterogeneity by plants. - Academic Press, San Diego.

Cale W.G., Henebry M. & Yeakley J.A. (1989): Inferring process from pattern in natural communities. - BioScience 39: 600-605.

Clements F.E. (1916): Plant succession: an analysis of the development of vegetation. - Carnegie Inst., Washington, Publ. No. 242.

Grace J.B. & Tilman D. (1990) [eds]: Perspectives on plant competition. - Academic Press, San Diego.

Greig-Smith P. (1983): Quantitative plant ecology. Ed. 3. - University of California Press, Berkeley.

Goldberg D. (1995): Generating and testing predictions about community structure: which theory is relevant and can it be tested with observational data ? - Folia Geobot. Phytotax. 30: 511-518.

Harvey P.H., Colwell R.K., Silvertown J.W. & May R.M. (1983): Null models in ecology. - Annual Rev. Ecol. Syst. 14: 189-211.

Herben T., Krahulec F., Hadincová V. & Kovářová M. (1993): Small-scale spatial dynamics of plant species in a grassland community over six years. - J. Veg. Sci. 4: 171-178.

Hunter A.F. & Aarssen L.W. (1988): Plants helping plants: New evidence indicates that beneficence is important in vegetation. - BioScience 38: 34-40.

Jongman R.H., ter Braak C.J.F. & van Tongeren O.F.R. (1987): Data analysis in community and landscape ecology. - Wageningen, Pudoc, 299 pp.

Jongepierová I., Jongepier J.W. & Klimeš L. (1994): Restoration of species-rich meadows in the Bílé Karpaty Mountains. - Příroda 1: 185-189.

Klimeš L., Jongepier J.W. & Jongepierová I. (1995). Niche limitation, guild structure and small-scale dynamics in species-rich meadows. - Folia Geobot. Phytotax. 30: 243-253.

Lepš J. (1995): Variance deficit is not reliable evidence for niche limitation. - Folia Geobot. Phytotax. 30: 455-459.

Lepš J. & Štursa J. (1989): Species-area curve, life history strategies, and succession: a field test of relationships. - Vegetatio 83: 249-257.

Marsaglia G., Narasimhan B. & Zaman A. (1990): A random number generator for PC's. - Comp. Physics Comm. 60: 345-349.

McConnaughay K.D.M. & Bazzaz F.A. (1991): Is physical space a soil resource? - Ecology 72: 94-103.

McIntosh R.P. (1981). Succession and ecological theory. - In: West D.C., Shugart H.H. & Botkin D.B. [eds.]: Forest succession: Concepts and applications. - Springer-Verlag, New York, pp. 10-23.

Palmer M.W. (1987): Variability in species richness within Minnesota oldfields: a use of the variance test. - Vegetatio 70: 61-64.

Palmer M.W. & van der Maarel E. (1995): Variance in species richness, species association and niche limitation. - Oikos 73: 203-213.

Pickett S.T.A. & McDonnell M.J. (1989): Changing perspectives in community dynamics: a theory of successional forces. - Trends Ecol. Evol. 4: 241-245.

Rabotnov T.A. (1992): Javljaetsja li ob"em fizičeskoj sredy resursom dlja rastenij? (Is physical space a resource for plants?). - Bjull. Moskovsk. Obšč. Isp. Prir., Otd. Biol. 97(5): 81-82.

Ryser P. (1990): Influence of gaps and neighbouring plants on seedling establishment in limestone grasslands. - Veröff. Geobot. Inst. ETH, Stiftung Rübel, Zürich, 104.

Ryser P. (1993): Influences of neighbouring plants on seedling establishment in limestone grassland. - J. Veg. Sci. 4: 195-202.

Schluter D. (1984): A variance test for detecting species associations, with some example applications. - Ecology 65: 998-1005.

Tlusták V. (1975): Syntaxonomický přehled travinných společenstev Bílých Karpat (Syntaxonomical survey of grasslands in the Bílé Karpaty Mountains). - Preslia 47: 129-144.

Utkin A.I., Byastrov L.G., Dylis N.V. & Solntseva O.N. (1969): Vertikal'no-frakcionnoe raspredelenie fitomassy i principy vydelenija biogeogorizontov v lesnych biogeocenozah (Vertical-fractional distribution of biomass and principles of recognition of biogeohorizons in forest biocenoses). - Bjull. Moskovsk. Obšč. Isp. Prir., Otd. Biol. 74(1): 85-100.

van der Maarel E. & Sykes M.T. (1993): Small-scale plant species turnover in a limestone grassland: the carousel model and some comments on the niche concept. - J. Veget. Sci. 4: 179-188.

Watkins A.J. & Wilson J.B. (1992): Fine-scale community structure of lawns. - J. Ecol. 80: 15-24.

Wilson J.B. (1995a): Variance in species richness, niche limitation, and vindication of patch models. - Oikos 73: 277-279.

Wilson J.B. (1995b): Testing for community structure: a Bayesian approach. - Folia Geobot. Phytotax. 30: 461-469.

Wilson J.B., Gitay H. & Agnew A.D.Q. (1987): Does niche limitation exist? - Funct. Ecol. 1: 391-397.

Wilson J.B., Roxburgh S.H. & Watkins A.J. (1992): Limitation to plant species coexistence at a point: a study in a New Zealand lawn. - J. Veg. Sci. 3:711-714.