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STATISTICAL ANALYSIS OF SPATIAL PATTERN IN PLANT COMMUNITIES

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Abstract. A direct way of spatial series analysis is presented to analyze spatial pattern of multispecies communities. A test of randomness is proposed based on the average number of species per plots and its variance in a series of increasing plot sizes. Complete spatial randomness (CSR) is used as a neutral or null hypothesis model. The statistical inference presented in the paper nothwistanding this test procedure should be viewed as a heuristic tool for characterizing the constraints on pattern manifested by deviations from the null model at different scales of vegetation. The usefulness of the method is demonstrated in a study of the regeneration pattern in a beech forest (*Melico-Fagetum silvaticae*) after clear-cutting. This suggests four characteristic plot sizes for describing the vegetation. The *maximum area*, that is the plot size at which vegetation heterogeneity is maximal, is 1.3 m by 1.3 m. The *comparative area*, where variation is reduced, is 2 m by 2 m. The *discriminatory area*, where the average number of species for the actual and the random community is significantly different, is 4 m by 4 m. The *spurious area*, which is an upper limit of the relevant plot sizes for the studied community, is 8.5 m by 8.5 m.

Introduction

There is a long history of pattern analysis in vegetation (Blackman 1935, Clapham 1936, Greig-Smith 1952, Kershaw 1957, Greig-Smith 1983, Podani 1984, 1992) and interest is increasing in spatial patterns and processes with biology (Diggle 1983) and geology (Cressie 1991, Matheron 1962-1963) leading the way. Fractal geometry has brought into focus the relevance of pattern in other areas of science and mathematics as well (Mandelbrot 1982, Falconer 1985).

The importance of patchiness on community level was recognized very early in botany; as seen from accounts in Godwin and Conway (1939) and Watt (1925, 1937). Watt (1947) suggested that plant communities are composed of a mosaic pattern of patches which are dynamically related to each other. It is incredibly time-consuming, however, to study multispecies spatial patterns quantitatively because it needs much sampling, usually with different plot sizes and sometimes, tedious calculations. It should be stressed that before the widespread availability of computers, the calculations even for a species-poor community would have presented a formidable task. Even with present day computational power, it is all too easy to consume inordinate amounts of computer time. Erdei and Tóthmérész (1993) reported numerical estimates for this. Probably the computational difficulty was a main reason that the "golden age" of pattern analysis was based on the study of one-species patterns or at most two taken simultaneously (Greig-Smith 1983, Kershaw 1973). Variance has long recognized importance in statistics, and in ecology going back as far as the works of Fisher (Fisher 1925, Fisher *et al.* 1943). In this paper, I am interested in the spatial pattern of multispecies communities. My approach is based on the comparison of counts of individuals and the variance of counts in a series of different sized plots to a neutral or null model. I demonstrate the usefulness of the procedures analysing the spatial pattern of a shrub community on a clear-cut area in beech forest (*Melico-Fagetum).*

There are many developmental constraints on the evolution of vegetation analogous on the constraint of the evolution of a populations (Maynard Smith *et al.* 1985, Bartha 1992, Czárán and Bartha 1992). The methods presented here are useful to explore where the constraints act and how they act before the next step aiming the study of the actual generating mechanisms and models of the processes.

Methods

Sample site and sampling methods

This study is related to the "REJTEK PROJECT" research program which is focused on secondary successional changes after clear-cutting of a beech forest developing on shallow soil derived from limestone in Northern Hungary (Jakucs 1987). The area, which is 500-550 m above sea level, was covered by an approximately 100-200 year old zonal submontane beech forest *(Melico-Fagetum silvaticae)*. In January of 1981 part of this forest was clear-cut. In August of 1988 the shrub individuals were mapped in a 15 m by 15 m plot. A total of 2026 individuals of 15 species were recorded.

Spatial series analysis

I analyzed the spatial pattern using a series of different sized plots (Podani [1992] proposed to refer to this method as *space series analysis*). For each plot size I placed n plots randomly in the site and calculated the average number of the species, aver(S), and the variance of the number of species, var(S):

$$\text{aver}\,(S) = \bar{S} = \sum_{i=1}^{n} S(i)/n \tag{1}$$

$$\text{var}\,(S) = \sum_{i=1}^{n} (S(i) - \bar{S})^2/(n-1) \tag{2}$$

In these S(i) is the number of species in the plot i. I plotted aver(S) and var(S) against the logarithm of plot size. My plot sizes ranged from 0.35 m by 0.35 m until 12 m by 12 m. I have used 20, 50, 100, 1000 and 10000 random plots on a digitized map for each plot size. In this paper I mainly concentrate on the results based on 50 plots because 50 plots were the smallest sample size which produced clear results. Largest sample sizes were used to check whether the results are not artefacts but I preferred to use as small sample size as possible because the plots were not independent using too large sample size. The importance of spatial analyses with a series of increasing plot size was recognized and emphasized very early by Juhász-Nagy (1967, 1976), but his method was different than mine. I calculate the statistics describing the spatial structure of the vegetation directly from the frequency data of the plant individuals of the plots. This method might be mentioned as *direct spatial series analysis*. According to the methods developed by Juhász-Nagy, the number of plots having different species list are counted first and after that the statistics describing the spatial structure of the vegetation are calculated from this derived data set. Therefore, it might be mentioned as an *indirect spatial series analysis*.

Null hypothesis model and confidence intervals

It is natural to use as a null hypothesis or null model the hypothesis of *Complete Spatial Randomness* (CSR). CSR is frequently used in ecology and elsewhere to the formulation of hypotheses concerning the pattern and its genesis (Diggle 1983, Ripley 1981). The CSR hypothesis can be stated as follows: Given the occurrence of m individuals in a finite region A, the location of those individuals are a random sample of size m from the uniform distribution on A. An alternative but equivalent characterization of CSR is based on that the number of individuals in any finite region follows a Poisson distribution with mean λA, where A is the area of the region and λ is the intensity or mean number of individuals per unit area (Diggle 1983). CSR is synonymous with a homogeneous Poisson point process (Cressie 1991). A large number of various statistics for testing CSR were developed; a comprehensive presentation and discussion of these can be found in the book of Upton and Fingleton (1985). These tests are developed for univariate point processes, when the distribution of only one species is studied. I have studied multispecies communities, therefore these methods are not applicable here. In statistics these processes are usually mentioned as *multidimensional point processes*. Instead of this I prefer to say *multispecies point process* because, using the previous terminology, it is not straightforward that the individuals of one species are located in a multidimensional space or the individuals of a multispecies community in a two-dimensional space. Multispecies point patterns can be constructed by extending univariate models. The simplest such models compound independent components. In many respects, the role of independence here is analogous to the role of CSR in the univariate case (Cressie 1991). In ecology, one of the most intriguing tasks is to explore positive and negative spatial dependence between the individuals of the species.

Spatial statistics derived from the null model and their confidence intervals

The expected number of species, E(Sm) in a random sample of m individuals drawn from a large collection containing N individuals and S species is

$$E(S_m) = S - \sum_{i=1}^{S} (1-p_i)^m \tag{3}$$

where S is the total number of species in the community and p_i is the relative frequency of the i-th species (Engen 1978). For fixed m, the contribution of each species to $E(S_m)$ is the probability that it will appear among m individuals drawn at random from the collection. The variance of the number of species, var(S), can be derived as well (Heck *et al.* 1975):

$$\begin{aligned} \text{var}(S_m) = & \sum_{i=1}^{S} (1-p_i)^m \,[1-(1-p_i)^m] + \\ & + 2\sum_{i=1}^{S} \sum_{j=i+1}^{S} [(1-p_i-p_j)^m - (1-p_i)^m(1-p_j)^m] \end{aligned} \tag{4}$$

The details of the calculation are given in Harris (1959).

Analysing spatial pattern we are usually working with plot size instead of number of individuals. Since the expected number of individuals in an area is proportional to the size of the area we can calculate m as

$$m = N\,\frac{\text{plot size}}{\text{total area}} \tag{5}$$

where N is the total number of individuals in the total area.

A diagnostic procedure for detecting deviations from the null model is to compare (in a graphical form or using statistical test) the curve of the average species number of the actual community to the curve produced by the null model in a spatial series plotting the confidence levels as well. When the distributions of species are aggregated then the average number of species in the plots is less than the expected number of species under CSR, while in the case of a regular distribution it is higher. When the studied multispecies community is composed of species-rich and species-poor patches then the variance of the number of species is higher than under CSR. In the case of regular pattern it is less than under CSR.

Suppose that we have observations from independent and identically distributed normal distributions with unknown mean and variance. The minimum-variance unbiased estimator of the mean is (2) and of the variance is (3). An inference on S is straightforward. A two-sided $t_{\alpha[n-1]}$ confidence interval of probability 1-α for the mean is

$$\left(\bar{S}-t_{\alpha[n-1]}\sqrt{\frac{\mathrm{var}(s)}{n}},\ \bar{S}+t_{\alpha[n-1]}\sqrt{\frac{\mathrm{var}(s)}{n}}\right) \qquad (6)$$

where $t_{\alpha[n-1]}$ is the t-distribution with n-1 degrees of freedom.

Confidence limits for the variance of the number of species in a spatial series analysis can be provided in the following way:

$$\left(\frac{(n-1)\ \mathrm{var}(S)}{\chi^2_{(\alpha/2)\,[n-1]}},\ \frac{(n-1)\ \mathrm{var}(S)}{\chi^2_{(1-\alpha/2)\,[n-1]}}\right) \qquad (7)$$

where the two quotients will enclose the value of the variance with a probability of 1-α; $\chi^2_{(\alpha/2)[n-1]}$ is the chi-square distribution with n-1 degrees of freedom (Sokal and Rohlf 1981).

Results

There were 15 shrub species present in the study site; the total number of mapped individuals was 2026. The Shannon diversity of the community was 1.41 (natural logarithm used). The dominance structure of the community is shown by Figure 1. There are 5 species which were represented only with 1 individual (singles) and three more species were rare (3, 5 and 14 individuals). "Rare" means here simply that the number of individuals of the species was less than 1% of the total number of individuals in the community. The dominant species were the following: *Fraxinus excelsior* (1127 individuals), *Carpinus betulus* (339 individuals), *Acer pseudoplatanus* (231 individuals), and *Fagus silvatica* (145 individuals).

The actual curve of the average number of species for the community is different from the curve produced by the CSR (Figure 2). The difference is not significant in statistical sense for plot sizes less than 1.5 m by 1.5 m. For plot sizes ranging from 1.5 m by 1.5 m to 4 m by 4 m the average number of species is significantly different from the null model; the 95% confidence levels, however, are very close to each other. The average number of species is more significantly different for the plot size of 4 m by 4 m to 7 m by 7 m. The average number of species was less than the expected under CSR suggesting the presence of aggregation. For the plot size of higher than 8.5 m by 8.5 m the average number of species is higher than for the null model.

The average number of species is 4 for the plot size of 1.5 m by 1.5 m, just the same as the number of dominant species. For the plot size of 4 m by 4 m the average number of species is close to 7, which is the number of the dominant plus subdominant species in the community suggesting that the stronger deviation from the CSR for higher plot size due to the rare species.

The variance of the average number of species is strikingly different for the actual pattern and for the CSR (Figure 3). The variance is much higher for the actual community suggesting that the community is a mosaic of different patches; some of them are species-rich while the others are relatively species-poor. The variance of the species number is significantly higher for the actual community than for the null model in the case of small plot sizes approximately up to 2 m by 2 m. They are relatively, yet not significantly, different for the 2 m by 2 m to 7 m by 7 m plot size range.

The maximum variability is at 1.36 m by 1.36 m, suggesting that the shrub community is more patchy on a small scale than on a large one, and the differences are the most pronounced using approximately 1.36 m by 1.36 m plots. Using large sample size I can make more precise estimation: the characteristic plot size for the variance is 1.3 m by 1.3 m (Figure 4). For plot sizes larger than 7 m by 7 m the variance decreases rather much and above 8.5 m by 8.5 m it is less than the variance of CSR.

The previous results were based on the community without species that were represented only by one individual

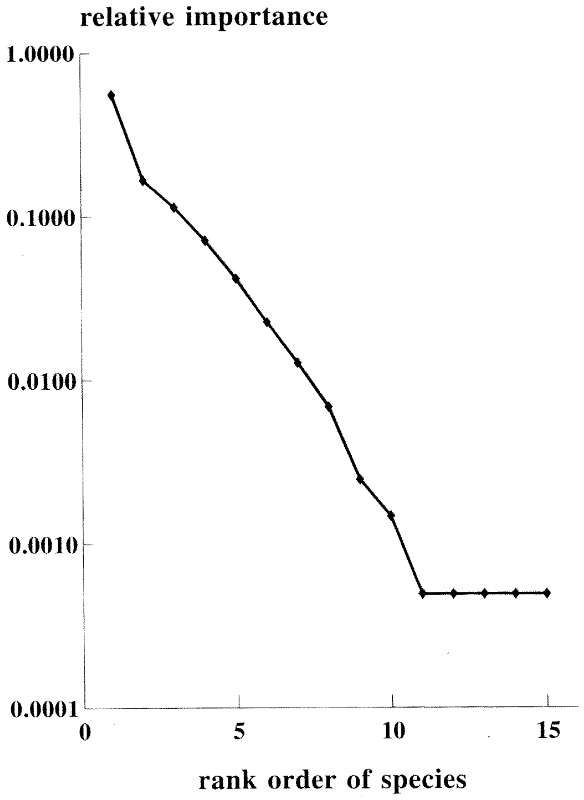

Figure 1. Dominance-diversity curve of the community. The first species is highly dominant (1127 individuals). There are five species which were represented by 1 individual. Three other species were rare (3, 5 and 14 individuals).

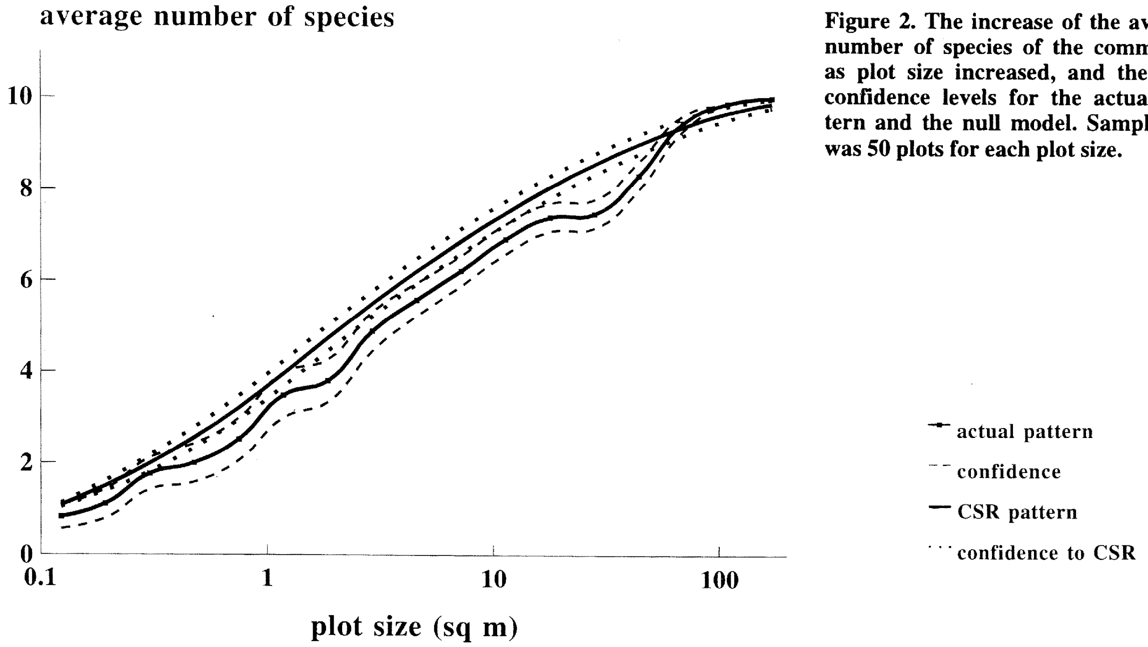

Figure 2. The increase of the average number of species of the community as plot size increased, and the 95% confidence levels for the actual pattern and the null model. Sample size was 50 plots for each plot size.

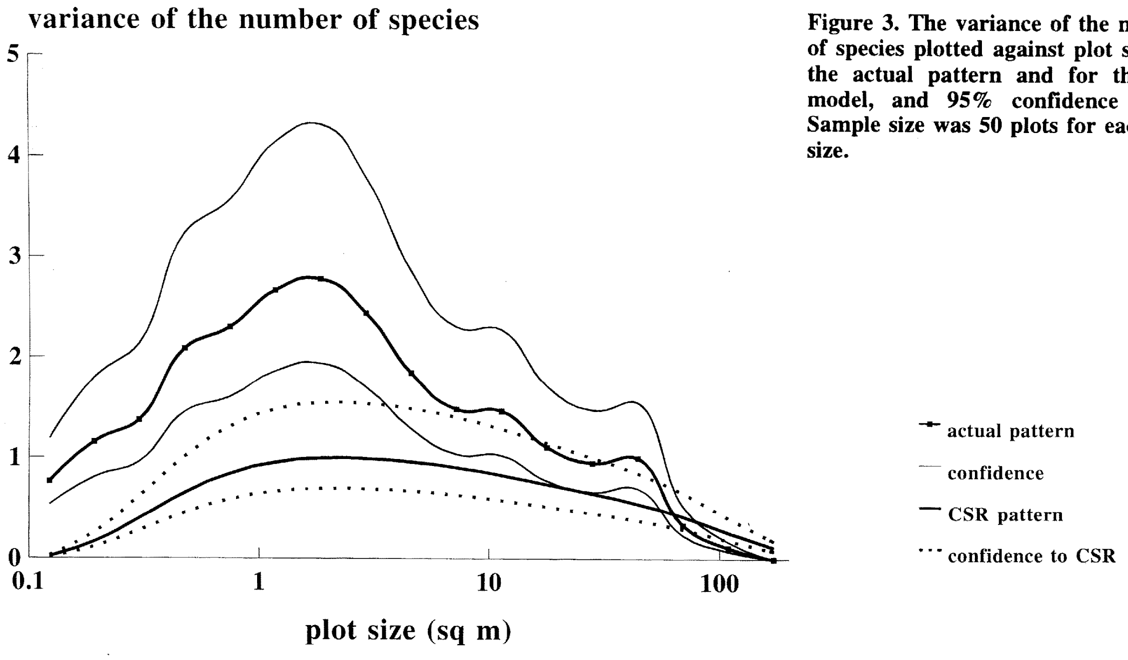

Figure 3. The variance of the number of species plotted against plot size for the actual pattern and for the null model, and 95% confidence levels. Sample size was 50 plots for each plot size.

on the total area. I have checked the effect of these species and the result is partly presented in Figure 4. In the case of the total community for the CSR pattern the peak produced by the community without singles disappears and another peak has emerged at an extremely large plot size. It is approximately 10.5 m by 10.5 m. The actual pattern for the total community produced two other local peaks beyond the peak which was not observable for the community without singles. The absolute value of these peaks is lower than that of the first one.

Discussion

Historical notes and alternative interpretations

The curve defined by (3) is frequently mentioned in botany and zoology as species-area curve; more exactly that is a species-area curve of a "random" or unstructured community. There is a long history of the study of the relationship of the number of species found in an area and the size of the area. Arrhenius (1921) studying species-area relationship

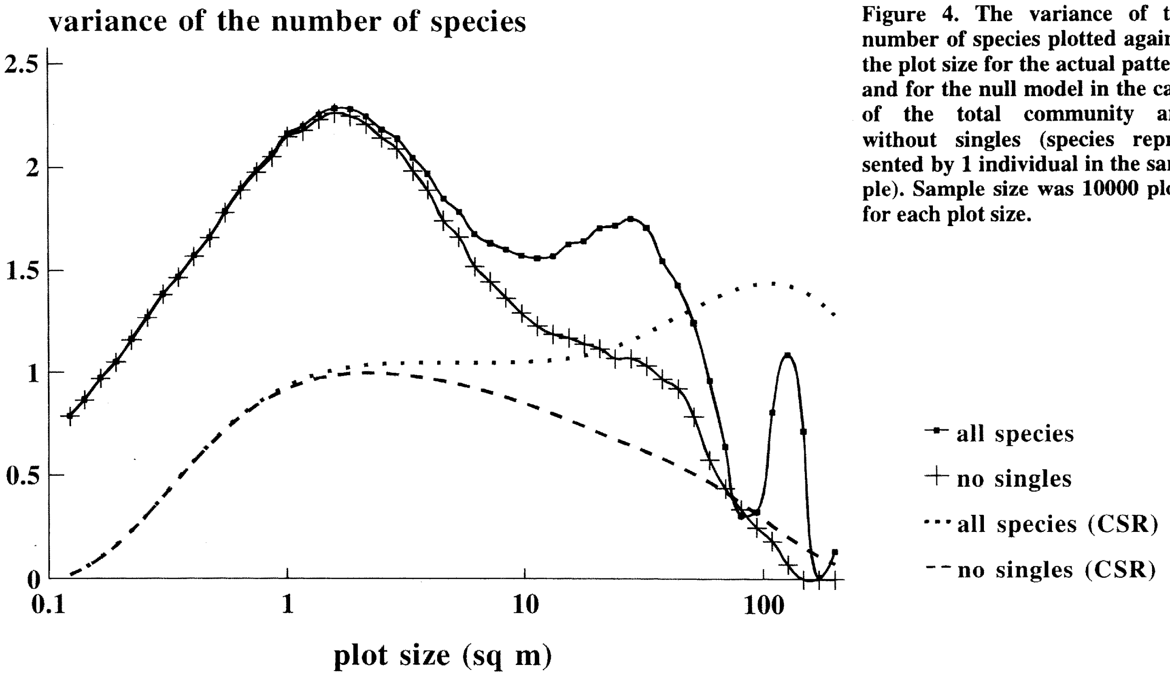

Figure 4. The variance of the number of species plotted against the plot size for the actual pattern and for the null model in the case of the total community and without singles (species represented by 1 individual in the sample). Sample size was 10000 plots for each plot size.

found that log(S) was approximately proportional to log(area). Gleason proposed a slightly different model; according to that S is approximately proportional to log(area) (see also Kilburn 1963, 1966). Engen (1978) demonstrated that both of these relationships can be derived from a more general model.

S_m is frequently used in a different context as a measure of diversity. In that case, it is mentioned as the species richness of the community. Many ecologists consider species richness as by far the most important aspect of a community's diversity and the best and simplest measure of it. Hurlbert (1971) proposed to use (3) to measure species richness as an improvement on Saunders' (1968) rarefaction method. In a statistical sense this is a very favourable measure of species richness because the unbiased minimum variance estimation of it is known (Smith and Grassle 1977). Thus $E(S_m)$ is widely used in ecology as a measure of species richness (Fager 1972, Peet 1974, Siegel and Germain 1982, and Raup 1975). In fact, this is a one-parametric family of diversity indices and it can be used for diversity ordering of communities (Patil and Taillie 1979, Tóthmérész 1993).

Recently, Solow and Smith (1991) proposed to use (3) in a somewhat similar context as I use it in this paper. They compared the estimated species-area curve with its distribution under a complete random distribution of individuals. Their method, however, is based on quadrat samples of one particular size and on just the presence or absence of the species in the quadrats to test departure from randomity.

Critical plot sizes

Regarding the studied pattern, we find it interesting to mention characteristic plot sizes that may be important to analyze the vegetation. The first one is the so-called *characteristic area* or *maximum area.* Juhász-Nagy (1967) proposed to use this terminology for the plot size where the studied statistics takes its maximum in an indirect spatial analysis. It also can be used in the case of direct spatial analysis when the studied characteristic has a maximum (i.e. in the case of variance in this paper). Comparing different stands of the same type community it is advised to use a plot size where the variance of the number of species is not too high, i.e. the number of species does not change much from plot to plot. Again, we prefer as small plot size as possible. This plot size might be mentioned as *comparative area.*

Another important characteristic plot size is where the number of species are different for the actual and CSR pattern. There are many plot sizes to fulfil this condition, however, and I prefer the smallest one. Because I would like to discriminate between the compared patterns, I refer to this as a *discriminatory area.*

In increasing plot size, there is a critical level, above that the result must be spurious because the plots are almost identical. We can find that level easily, checking the curve of the average number of species for the actual pattern and for the CSR pattern. The rather high similarity of sample plots appears like a regular occurrence of the individuals of the species and thus produce an increase of the average number of species of the plots. At the plot size of 8.5 m by 8.5 m, or a little less than that, the curve of the actual pattern cross the curve of the CSR pattern. It means that the actual pattern is more regular than that of a random pattern. This may be produced by the rather high correlation between the plots i.e., they are almost identical with respect to their species composition. This is also supported by the variance. After the plot size of 6 m by 6 m, the variance starts to decrease very rapidly and after 8 m by 8 m it is extremely low. This plot size might be mentioned as *spurious area*. The appearance of the regularity for small or medium plot size, of course, may indicate a real regularity in the pattern of the community. This is not the case here.

This fact brings a new application of the "average number of species" curve. It can be used to detect a critical plot size. There is no reason to use higher plot size to analyze the community than that because it produces only artifacts. In the case of the studied pattern this limit is approximately one-third of the total area. Bartha (1992) found the same limit analysing spatial pattern of weed assemblages using the methods of indirect spatial analysis developed by Juhász-Nagy (1967).

For the studied community this plot size was very characteristic. Almost independently of the number of sampled plots it appeared at the same plot size. Usually 20 plots or less was enough to recognize the appearance of the false regularity.

The characteristic or maximum area is 1.3 m by 1.3 m for the studied community. That plot size is in a good agreement with common sense and usually used to study small-scale variation of communities. The comparative area is 2 m by 2 m, while the discriminatory area is approximately 4 m by 4 m. There is an important contribution of the subdominant and rare species here, thus the large plot size is well justified.

The effect of rare species

The role and/or effect of rare species is a crucial problem of the botanical data sets (Goff 1975, Orlóci and Mukkattu 1973, Webb *et al.* 1967, Wildi and Orlóci 1967). The extremely rare species usually do not provide any meaningful information to the analysis. Sometimes they produce rather serious false result (Tóthmérész and Erdei 1992). From a biological point of view the picture is not so clear, such as in environmental conservation where frequently the rare, endangered species are the most important. I tried to retain as many species in the analysis as possible. I have no intention to give a detailed analysis of rareness, but it is evident from the result that the elimination of those species which were represented by 1 individual on the total area was advantageous.

The maximum or characteristic area for the community (including the singles) in the case of CSR was higher than 10 m by 10 m. That plot size may be realistic from the point of view of a study concentrating on the rare species but it is certainly unreasonably large for a standard botanical and/or ecological study. In the case of the actual pattern the maximum or characteristic area does not change by the elimination of the singles; the two other peaks are shorter than the first one.

The relatively strong departure from the random alternative in the case of the average number of species for larger plot sizes is certainly due to the effect of (relatively) rare species (Figure 2). This plot size is high enough to let the rare species produce recognizable impact on the average number of species per plots. Their behaviour is frequently quite irregular, but a few individuals cannot always produce pattern, just increase the risk of spurious results.

Sample size and other problems

The numbers of individuals falling in a plot are integer valued random variables. As long as the plots do not overlap, we assume that these random variables are statistically independent. In practice this assumption is satisfied only approximately. When the plot size is large and the number of plots is also high, this assumption is evidently violated. From the point of view of the statistical analyses of the data that is certainly a serious problem. Exceeding a critical level, it can produce totally false results. The analyses of real data sets, however, shows that when the plot size is not higher than a critical level it is better to use large sample size (or at least medium) instead of a small one because it gives a better estimation of the statistics in a spatial series analysis. It produces a smoother curve which is less subjected to random sampling errors, thus the interpretability of the result improves. This is not the case when we are plotting confidence levels or making statistical inferences. In these cases a moderate sample size is preferred where the variables are more or less independent.

In this study I have used 20, 50, 1000 and 10000 sample plots for each plot size. A mere 20 plots were not sufficient to characterize pattern. Only the spurious area was recognizable. The curves of the statistics in the spatial series analyses were too wobbly to interpret clearly. Results based on 50 samples are presented in this paper. The outcome did not improve much for 100 plots, thus I opted to use the 50 plot sample which is not unrealistically large. The sample based on 1000 plots produced much more smooth curves yet not as smooth as the samples of 10000 plots which I present in Figure 4.

Further perspectives

There are many possibilities. One of the most intriguing is to understand clearly the effect of rare species and to characterize their contribution to the spatial characteristics of the community. This might be achieved in a way as Tóthmérész and Erdei (1992) did in a simulation study of direct and indirect spatial series analysis. The effect of rare species appeared many times during the analysis of the spatial pattern of the shrub communities and sometimes in rather surprising ways. For example, some of the results suggest the appearance of the false regularity for large plot sizes in the case of the average number of species, and as for rare species increased the spurious area decreased. Sometimes the effect of the rare species is present even in a less obvious way, which certainly deserves studies by computer simulation and field data. It is, of course, important to characterize the contribution of the dominant and subdominant species to spatial series statistics.

It is a real challenge to involve more sophisticated statistics in the analyses. The first to be mentioned are the diversity statistics (He and Orlóci 1993, Izsák and Papp 1994). I can mention three separate reasons for this. (i) Diversity is one of the most frequently used statistics to characterize communities therefore they must be used in spatial series analysis as well. (ii) Diversity is closely related to the number of species. exp(H) is a measure of the effective number of species, where H is the Shannon diversity. This is the number of species that would be found in a hypothetical community of perfect evenness having the same H as the community whose diversity is to be measured. The same is true for $1/\Sigma p_i^2$, which is related to the Simpson diversity (where p_i is the relative frequency of the i-th species). For an even community, where all the species are equally represented, the number of species is identical with the effective number of species. The effective number of species decreases with the increase of the species unevenness or dominance. In this way diversity can be regarded as a generalization of the average number of species statistics. (iii) Diversity is a measure of spread for categorial variables, just as the variance for continuous variables. This might be another motivation to use it.

Indeed, the Shannon and Simpson diversities and the number of species are also related to each other in another way which brings us an even more sophisticated statistics to use in spatial series analysis. All of these are in the one parametric diversity index family of Rényi included as a special case (Tóthmérész 1993). There is a scale parameter for these diversity index families; for a small value of the scale parameter the diversity is sensitive to the rare species and for a large value of the scale parameter it is sensitive to the dominants. Thus, as an additional benefit, changing the scale parameter of the index families we can control the influence of the rare, subdominant and dominant species in spatial series analysis. Here we have another tool to study the effect of rareness. There is no straightforward and simple way of deriving the standard deviations of these statistics. However, it is necessary if we would like to make statistical inference or to calculate confidence levels.

It is well-known from the literature of robust statistics that the variance is an extremely sensitive statistics to the effect of outliers (Huber 1981). Therefore, it would be wise to use a more sophisticated robust statistics to characterize the heterogeneity of vegetation instead of the variance, especially in the case of small sample size. Certainly the biweight midvariance is a preferred choice because its asymptotic breakdown point is greater than zero and it has the highest triefficiency of all measures of scale examined by Lax (1985).

Finally I have to mention a less intensivesly tudied aspect of spatial series analysis. When high number of different sized plots is used to analyze the pattern, the increase of plot size from step to step is small, than the produced curve is very wobbly for small and medium sized plots and even for large plot size as well. It is oscillating more heavily than expected. Tóthmérész and Erdei (1992) reported this phenomenon as a special feature of the direct spatial analysis without any further comments. Their experience was based on simulated point patterns. I also observed this phenomenon for real data sets. I think it must be related to the discontinuity of the pattern for the small scale. In geostatistics a somewhat similar effect is known as "*nugget effect*". This refers to the discontinuity of the variogram at the origin (Cressie 1991, Matheron 1962-1963). The correct modelling of small scale and micro scale variation is reported to be crucial in the case of variogram (Laslett *et al.* 1987). This effect is not well-understood for the spatial series analysis and needs further analyses.

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