# Individual-centered analysis of community pattern: some case studies

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**Keywords:** Florula diversity, Information theory, Likelihood, Plotless sampling, Plot sampling, Scale, Semidesert, Steppe, Variable-radius method, Vegetation.

**Abstract.** This paper evaluates multispecies plant pattern based on digitized field data to illustrate the utility of individual centered analysis formerly proposed by the authors. Three grassland communities were sampled for the present study; in each site the positions of all individuals were recorded within a rectangular tract of the community. These communities exemplify very different species patterns, in terms of of deviations from expected species combinations. A species-poor sand steppe stand shows a single spatial scale, whereas a richer version and a sagebush-bunchgrass community exhibit three. These scales result from the sensitivity of the measure to species density and, in particular, to the heterogeneity of individual patterns.

**Abbreviations:** CSR-complete spatial randomness, ICA-individual centered analysis, MCI-Mean compositional information, MNNA-multiple nearest neighbor analysis

#### Introduction

Studies of community pattern may be roughly divided into two categories, depending on the sampling strategy that provides the data. Plot sampling is the most common source of information; in this case the data express species performance (cover, presence/absence, biomass, abundance, etc.) in arbitrarily delineated, small portions of the study area. As a consequence of the fact that plots have to be defined in a spatial continuum, there are at least four different parameters that must be selected at the outset by the investigator: sampling unit size, shape, arrangement and number, which has enormous consequences as to the interpretability of results (cf. Kenkel, Juhász-Nagy & Podani 1989). Nevertheless, a vast proportion of our knowledge on plant communities relies upon information derived from plot sampling. The alternative strategy, plotless sampling (cf. Greig-Smith 1983), is free from many problems that make plot sampling

poorly defined so often. In this, neither quadrats nor other geometric shapes are used; instead, random points or random plants are located or selected and their immediate and farther neighbours are investigated. Some plotless sampling methods are free of all possible subjective choices: in an a priori selected area the positions of all plant individuals are recorded, and then each plant is surveyed for its neighbourhood (Dale, in this volume, gives an overview on such methods) or all plant-to-plant distances are determined. The neighbourhood analysis is typically chosen in multivariate situations, whereas all plant-toplant distances have been measured and displayed to evaluate single species pattern. An obvious disadvantage of many plotless sampling techniques is that complete enumeration is necessary by photographic or other means (Szőcs 1979), so that the size of the investigated area is usually much smaller than when sample plots are applied. In fact, in these cases the enumerated

study region itself represents a sampling unit taken from a larger section of the community.

Neighbourhood analysis considers scale dependence by definition: the change of some sampling parameter is an essence of the approach. This is obvious from the pioneering work of Williams et al. (1969), who proposed *multiple* nearest neighbor (MNNA). In this, each plant with its k nearest neighbors is considered as a sampling unit. The authors defined a series in which k is increased, this way implicitly enlarging sampling unit size. The imaginary circle thus drawn around plant individuals is of different size, however, in dense areas smaller than in sparsely populated parts of the study region. There is a largely plot-based family of methods, initiated and fully developed by Juhász-Nagy and his co-workers (Juhász-Nagy 1976, 1993, Juhász-Nagy & Podani 1983, Bartha 1992, to mention just a few references) in which the change of plot size is also an integral part. In this case, information theoretic functions are calculated based on the species list of each plot and they are illustrated in the function of plot size to detect scale of pattern (and potentially many more, as Bartha, Czárán & Podani, this volume, clearly demonstrate). It must be pointed out that Williams et al. (1969) in fact used pooled entropy for the point clumps they obtained for a given value of k, thus establishing an early and independent - but much later recognized relationship to Juhász-Nagy's approach. Podani & Czárán (1997) proposed a synthesis of MNNA and Juhász-Nagy's concepts, somewhat 'infected' by Ripley's (1977, 1981, 1987) widely used variable-radius method, originally proposed to evaluate single- or two-species point patterns only. This new strategy, individual centered analysis (ICA) is described briefly under the 'Method and materials' headline. Since the procedure has been demonstrated only on artificial and simulated data sets, we feel that some case studies are very badly needed to illustrate the utility of the approach based on actual field data. In this paper, we present the results of the analysis of three different communities and try to further evaluate the complexity and future perspectives of the method. Emphasis is placed upon the dependence of results of the method on species densities within the communities and on the spatial heterogeneity of plant pattern. Heterogeneity is understood here as in Diggle (1979) with a slight modification; species pattern which exhibits obvious variation in local density is deemed heterogeneous.

## Method and materials

Contrary to the usual structure of papers, let us start with introducing the method briefly and then continue with the description of the material, the actual point patterns to which the method was applied. More details, especially the mathematical and algorithmic features of the procedure are presented in Podani & Czárán (1997). The forthcoming discussion is entirely without mathematical formalism.

## Method: the main steps of ICA

- 1. The sampling design involves the determination of exact positions of all plants within a preferably rectangular study area. The coordinates and species identities are then entered to computer memory, and all subsequent work is accomplished by the hardware and software.
- 2. The density of each species is determined, thus allowing calculation of the probability that a given species occurs in a circular plot of a given radius, under the null hypothesis of complete spatial randomness (CSR, cf. Diggle 1979). In other words, the random reference is that the pattern of each species results from a two-dimensional Poisson point process, thus assuming independence (lack of association) among species.
- 3. Based on species probabilities, the likelihood that a given species combination (florula) appears in a circular plot of a given radius is obtained by simple multiplication. The higher this likelihood the lower our 'surprise' that the given florula actually appears what we get is mostly what we expect. On the other hand, if a florula with a low likelihood is found, something 'unexpected' happened as a result of the deviation from randomness.
- 4. The likelihood values pertaining to species combinations that we actually find around plant individuals are averaged to obtain the weighted mean compositional information, MCI. The expectation of this under CSR is derived from Shannon's entropy function and the departure of MCI from the expectation is calculated ( $\Delta$ MCI). A graph showing  $\Delta$ MCI as a function of plot radius is used to characterize multispecies pattern (Figure 6 shows, using an actual example, how the actual and expected values and their difference change over radius). The radius where the maximum deviation occurs is termed the characteristic radius,  $r_{char}$ , in this paper. This scale characterizes the pattern of the stand being evaluated. The contribution of each species to ΔMCI may also be illustrated to reveal differences and similarities of individual patterns.

The problem of whether or not to consider the center species in computing the expectation was discussed and examined in detail by Podani & Czárán (1997) using artificial patterns. It was found that analyses in

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Table 1. A summary of species and their abundances in the species rich sand steppe at Bugac (a) and the semidesert community from the Okanagan Valley, B. C. (b).

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		Density			Density	Heterogeneity
Species	Abundance	rank	Species	Abundance	rank	rank
1. Myosotis stricta	68	8	1. Poa sandbergii	273	2	2
2. Veronica arvensis	337	5	2. Erigeron pumilus	29	17	15
3. Erigeron canadensis	936	2	3. Lupinus sericeus	. 75	13	6
4. Tragus racemosus	842	3	4. Plantago patagonica	492	1	17
5. Arenaria serpyllifolia	32	12	5. Collomia linearis	148	8	4
6. Euphorbia cyparissias	714	4	6. Artemisia tripartita	259	5	1
7. Bromus sterilis	3	18	7. Madia exigua	337	3	9
8. Salsola kali	133	7	8. Antennaria rosea	205	6	7
9. Viola kitaibeliana	1474	1	9. Achillea millefolium	139	9	8
10. Koeleria glauca	44	10	10. Bromus tectorum	126	10	12
11. Linum hirsutum	77	9	11. Agropyron spicatum	166	7	3
12. Calamagrostis epigeios	311	6	12. Koeleria cristata	27	18	18
13. Senecio vernalis	7	17	13. Carex filifolia	426	2	2
14. Stipa borysthenica	19	15	14. Phlox longifolia	25	19	13
15. Colchicum arenaria	37	11	15. Stipa occidentalis	40	15	16
16. Poa bulbosa	21	13	16. Saxifraga integrifolia	31	16	19
17. Alkanna tinctoria	20	14	17. Polygonum majus	103	11	10
18. Crepis tectorum	11	16	18. Calochortus macrocarpu	ıs 5	21	21
			19. Zigadenus venenosus	1	22	22
			20. Erigeron corymbosus	96	12	11
			21. Festuca occidentalis	51	14	14
			22. Lithospermum ruderale	22	20	20
			23. Castilleja pallescens	1	23	23

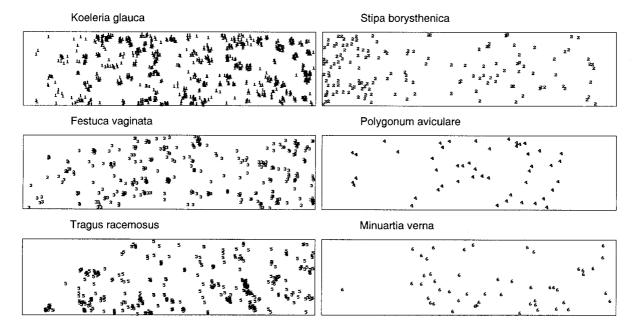


Figure 1. Plant pattern in the species-poor sand steppe community at Csévharaszt, Hungary (Map 1).

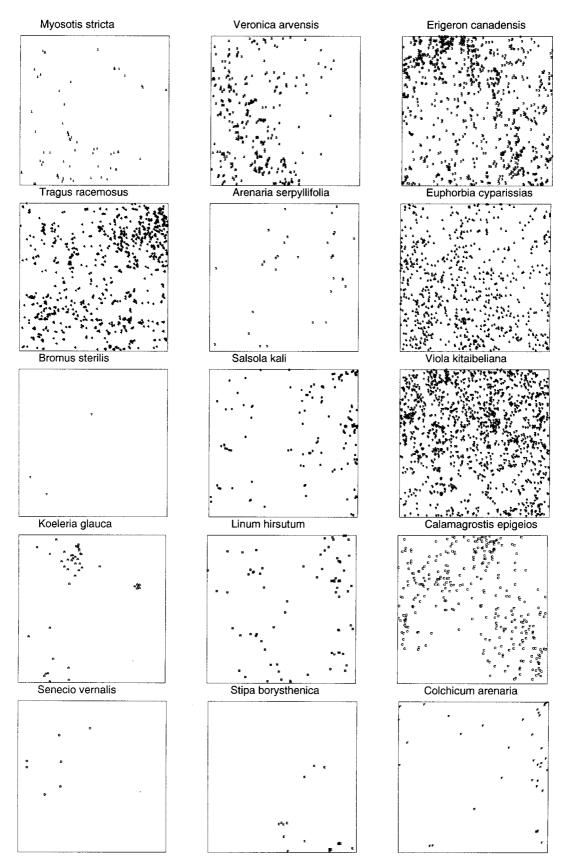
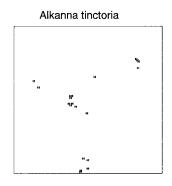
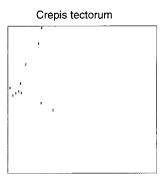


Figure 2 (continued on next page). Species patterns in the rich stand of a fescue sand steppe in Bugac, Hungary (Map 2).







'full' mode (considering the center species) and in the 'subcombination mode' (discarding the center species) produce similar results; the effect is manifested mostly at very small radii. (It will be shown also on the example of an actual data set, Map 1.) Therefore, for Maps 2-3 we decide to restrict ourselves to the full mode, which requires much less computing time. Furthermore, since sampling error is most influential at low scales, the 'early' sections of the curves can be safely neglected in the interpretations.

A further question is whether or not to examine the confidence intervals for the spatial statistics. Determination of confidence intervals is the most time-demanding part of the analysis. For a given pattern, a minimum of 19 random counterparts need to be simulated and then analyzed to obtain a reasonably good estimate of 95% confidence intervals for each value of the radius, i.e., a confidence envelope. In the present survey, the confidence envelope was determined only for one of the data sets, i.e., to the smallest one, because deviation from randomness is much more obvious in the other two cases.

## Study areas

Three community maps will be used to demonstrate the utility of ICA under different circumstances (number of species, abundance distributions and pattern heterogeneity). All come from grassland surveys and contain data for herbaceous species.

Map 1 was taken in a sand steppe community, usually dominated by fescue, at Csévharaszt, Kiskunság National Park, central Hungary (Szőcs 1979). The study region is of size 2 m by 10 m. The species and their frquencies in brackets are *Koeleria glauca* (755), *Stipa borysthenica* (147), *Festuca vaginata* (287), *Polygonum aviculare* (48), *Tragus racemosus* (324) and *Minuartia verna* (50). The total number of in-

dividuals is 1611. All species exhibit a more or less aggregated spatial distribution, which is most apparent for the commonest species (Fig. 1). There is only a slight heterogeneity of plant pattern, shown by the presence of empty parts, or lacuane, in the map of *Minuartia verna*, for example.

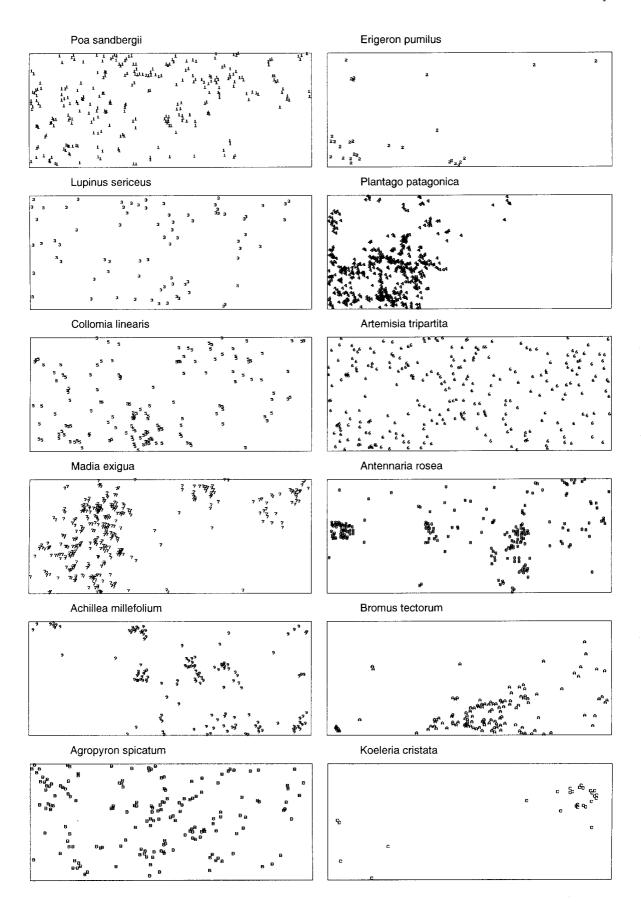
Map 2 is also derived from a sand-steppe, but from a different site. A 4 m by 4 m plot was selected by the authors in May 1996, in a relatively rich stand of the community near Bugac, Kiskunság National Park. The positions of all plants were recorded and then digitized to yield the point pattern map, shown in Fig. 2 separately for each species. The number of species is 18, the total number of individuals is 5086 (Table 1a). In this case, heterogeneity of pattern is conspicious for several species, while others exhibit a fair stationarity over the whole region.

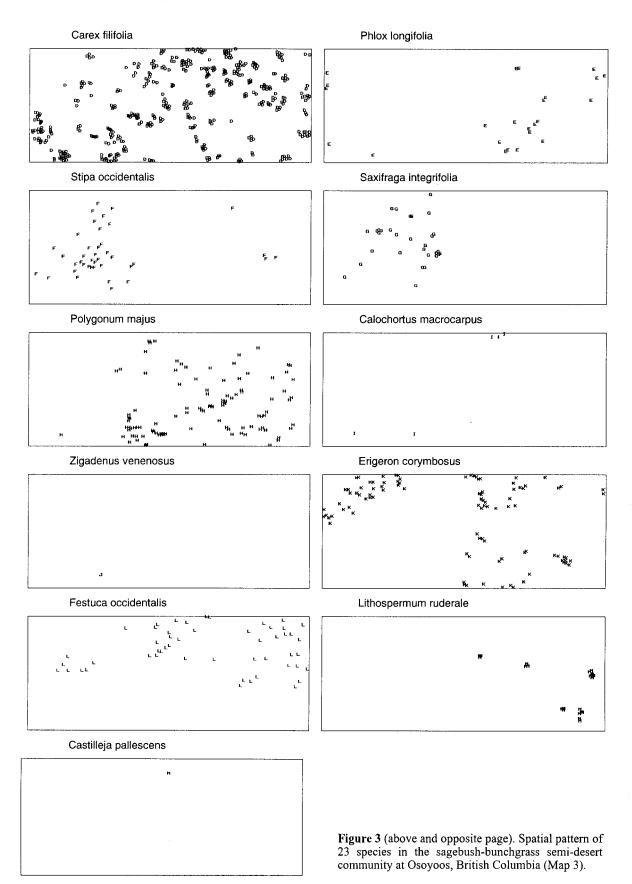
Map 3 was obtained by the first author in a sagebush/bunchgrass dominated semidesert grassland in the Okanagan Valley, British Columbia, Canada in June 1981, and was used extensively in computer-simulated sampling experiments using other techniques of pattern analysis (Podani 1984). The number of species is 23, the number of plants is 3077 (Table 1b). The study region is 2.5 m by 6.25 m. In this case, heterogeneity of pattern is striking again for a subset of species, because they occur in one side of the region (e.g., *Plantago patagonica* and *Festuca occidentalis*, see Fig. 3). Several species are scarce, represented by a few individuals or a singleton only.

#### Results

## Map 1: Species-poor sand-steppe pattern

Fig. 4a shows the change of  $\Delta$ MCI against the neighborhood radius for both the full and the subcombination modes. The diagram clearly demonstrates that, in





accordance with our findings on artificial patterns (Podani & Czárán 1997), the two modes differ mostly at very small scales. In the 'all species' mode, i.e., when the pattern of the center species is also influential, the highest negative deviation occurs at a larger

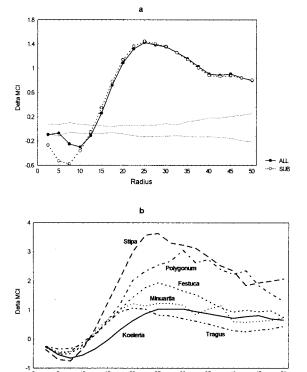
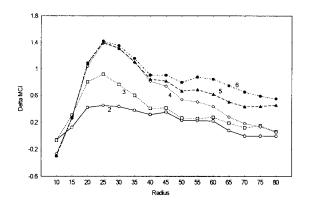


Figure 4. Individual-centered analysis of the sand steppe at Csévharaszt (Map 1). a: The change of  $\Delta$ MCI in the function of radius (cm) for the full and subcombination modes, plus the confidence envelope at p=0.05; b: species contributions to the full mode.

Radius



**Figure 5.** Abundance-ranked ICAs of the sand steppe community at Csévharaszt (Map 1). Numbers refer to the number of species considered in each analysis.

radius than in the subcombination mode, whereas the absolute deviations are smaller. As the radius increases, the difference between the two modes rapidly diminishes, while the position of the peak (the characteristic radius, now 25 cm) is unaffected. The shape of the curve is very similar to that of the artificially constructed clumped pattern (see Fig. 3a in Podani & Czárán 1997) with a less pronounced maximum and more moderate descent for large radii. This overall trend arises as the weighted average of species contributions (Fig. 4b). These curves are quite similar in appearance (the one for Minuartia is perhaps an exception); the maxima appear at a radius around 20-25 cm (for Polygonum, 30 cm), suggesting that the six species do not differ considerably in their individual scales of 'attracting' other species. Yet, there are some interpretable differences. For example, Stipa sabulosa has the highest deviation from randomness, suggesting that this is a 'central' species of the assemblage: at small radius it is the most repulsive whereas for larger areas it attracts the most surprising species combinations. The slowest rise and most flattened shape are resulted for Koeleria glauca, suggesting a random behavior in attracting the other species, which may be associated with the fact that this is the most abundant species of the community.

Most of both curves shown in Fig. 4a fall outside the p=0.05 confidence envelope, suggesting considerable departure from random species associations. Departure starts in the negative domain, and in the 'transitional zone', at around a radius of 12 cm, no deviation from randomness occurs. This means that if the community were sampled by circular plots of this radius only, the false conclusion that multispecies pattern is indistinguishable from the random version would be drawn. This underlines strongly the suggestion that multispecies pattern, just like single species patterns, can only be evaluated along with changes of scale, i.e., in a spatial series (Podani 1992).

Another possibility to evaluate the performance of ICA is to examine the effect of successive changes of species number on the curve of  $\Delta$ MCI. The six species were ranked according to their abundance (density), and ICA was performed consecutively using the first two, three, four, and five species, to allow comparison with the analysis that used all the six species. One expects, by judging the high overall similarity among the individual curves (Fig. 4b), that in this case stepwise inclusion of species based on density ranking would have relatively little effect upon the conclusions. The results, shown by the set of four curves in Fig. 5, confirm this expectation. (Note that in this case the range of radii examined is different from that shown in Fig.

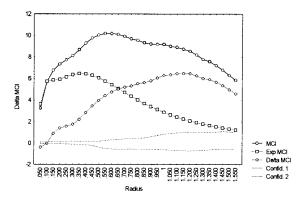


Figure 6. Individual-centered analysis of sand steppe data from Bugac (Map 2). This figure illustrates the relationship between actual and expected MCI values, and their difference, plus the confidence envelope for  $\Delta$ MCI at p=0.05. Radius is given in m.

4.) The curve for the pair of most common taxa (*Koeleria, Tragus*) is flattened (as are their individual curves in Figure 4b), with a less obvious maximum appearing at a radius of 25 cm (the same as for six species). When *Festuca vaginata* is added to form a triplet, the peak becomes more pronounced, while the addition of further species introduces negligible shape changes.

### Map 2: Species-rich sand-steppe pattern

For the rich sand steppe community at Bugac, the analysis is confined to the full mode plus the p=0.05 confidence envelope (Fig. 6). As seen, the peak appears at a very small radius (0.350 m) for the random expectation, the observed MCI provides the next peak (at 0.600 m) whereas their difference reaches its maximum at a much larger radius (1.15 m). For a radius lower than 0.1 m, a negative deviation from randomness is detected, as in other field and simulated patterns. Then, the function rapidly increases, and the maximum appears at a scale much larger than the characteristic radius found in the poorer version of the sand steppe. Individual species curves (not shown) are much more dissimilar than in the previous case, an obvious manifestation of heterogeneity and the large differences in density.

The idea that the increased maximum radius is caused by the increased number of species present immediately arises, and therefore the effect of species number included is analyzed in the same way as before. After ranking the species by abundance (Table 1a), ICA was performed considering the first 2, 3, 4,... 16, 17 species. The sequence of curves thus obtained (Fig. 7)

is completely different from the curves for species poor community: upon successive additions of new species to the analysis, the characteristic radius monotonically increases. The first significant change of shape appears after the fifth species is added. What is perhaps even more interesting is that after the first 10 most abundant species, a new peak starts to develop again in the graph; it reaches the height of the first peak at the 13th species (resulting in a slightly bimodal curve) to become the only one when the rarest species (15 to 18) are also considered. The detailed explanation of these trends, and other, less evident changes, is only possible if we consider the individual patterns step by step.

Looking at the mapped species patterns in Fig. 2, we find that the first 4 species in the rank order (Viola kitaibeliana, Erigeron canadensis, Tragus racemosus and Euphorbia cyparissias) are dispersed fairly evenly over the study region. For these species only, the situation is much the same as for all the six species from the species-poor sand steppe, i.e., there is no change in  $r_{char}$ , which is very small in this case (0.200). The first change of shape is caused when the fifth ranked species (Veronica arvensis) is also included. The flattening of the curve is a clear manifestation of the heterogeneous pattern of this species (Fig. 2, center map in first row). Since V. arvensis appears mostly on the left side of the map, and is much less abundant on the right side, it has practically no association with the first four, evenly dispersed species.

The next species in the rank order, Calamagrostis epigeios, is the rarest where V. arvensis is the most dense (lower left quarter, see Fig. 2), so that the association relationships for the first six species become further complicated. As an at least partial result of this, the flattened part of the curve develops into a peak (at r=0.400, so the radius is twice as much as in the previous steps). Inclusion of a further three species (Salsola kali, Linum hisutum and Myosotis stricta) causes a shift in the peak, in addition to the obvious increase of  $\Delta$ MCI. The latter three species agree in that they appear throughout the study region, but very unevenly.

The curve of  $\Delta$ MCI starts to become bimodal when the number of species considered rises to 10, by the addition of *Koeleria glauca*. This species is present in the form of a few aggregates and a few more individuals, scattered very unevenly in the area (left map in row 4 of Fig. 2). The peak remains subordinate with the next two species, so that the overall spatial scale of the community is still dominated by the common species. When some low-density species also appear in the analysis (species 13 in the rank order, namely, *Poa* 

bulbosa, represented by a single aggregate, and then species 14, Alkanna tinctoria, also aggregated and sparse) the two peaks attain approximately equal height. Inclusion of further rarities, since they are not dispersed randomly at all (Fig. 2), causes this newer peak to dominate. In this small portion of the sand steppe community, three spatial scales were thus identified, one pertaining to common species (0.20 m), shifting to the second peak (around 0.40 m) for lesser densities, and the third (1.15 m) reflecting the additional influence of less common and rare species.

# Map 3: Semidesert grassland pattern

In this case, the analysis that incorporates all species (23) also yields a relatively large characteristic radius (0.800 m, topmost curve in Fig. 8a). However, when the analysis follows the ranked abundance or densitybased strategy in the same manner as described above for the sand steppe, the pattern of change in the curves is remarkably different (Fig. 8a). The graph for the two most common species is very flattened, with a subtle maximum exactly at the same radius as for 23 species. In between the two extremes, there is an oscillation of the characteristic radius, but finally a single peak emerges from the flattening. This might suggest that the interpretation of this series of curves should be different from the series for Map 2. The explanation of this discrepancy becomes fairly simple when we look at the spatial pattern of the most common species in the community (Plantago patagonica, Fig. 3): the tiny individuals of this plant are confined to the left side of the study region. That is, the apparent heterogeneity of plant pattern manifests itself at the first step of the series in the density-ranked analysis, thus masking the additional effects of further, less abundant species.

In this case, therefore, the possibility of a different ranking strategy arises: instead of abundances, the species can be ranked according to their overall dispersion pattern in the area. The first in the order is the most common species that is evenly dispersed throughout, and so on, the sequence being closed by those that are confined with large numbers of individuals to a particular portion of the study region, i.e., ranking is performed from the most homogeneous to the most heterogeneous. Table 1b, right column, presents this rank order, determined on a visual basis only, which appears sufficient for the purposes of the present survey.

Stepwise analysis of plant pattern, based on heterogeneity ranking, provides the results of Fig. 8b. In this case, the pattern of change for the curves is more similar to the results for the species rich sand steppe (Fig. 7) than to the density-ranked analysis (Fig.

8a) for the very same community. The monotonous increase of characteristic radius over the number of species included is one feature that contributes to this similarity. In addition, for the first 8 species the radius is around 0.25-0.30 m, and from this point we can observe a development of a secondary peak, which dominates clearly for 15-16 species. This also bears some similarity with the set of curves on Fig. 7. Inclusion of the most heterogeneous species, particularly species 17 (*Plantago patagonica*) causes drastic changes, a third – and then final – peak starts to emerge at a radius of 0.80 m.

#### Discussion

Individual-centered analysis, implementing a plotless sampling strategy, provides a means of analyzing community level pattern with an essential difference from other strategies applied to the same purpose. While other methods use systematically or randomly arranged plots, in this case the spatial distribution of circles drawn around the plants agrees with the pattern of plant individuals themselves. That is, sampling is governed by plant pattern, a feature inherited from Ripley's (1977, 1981, 1987) variable-radius technique widely applied to analyzing univariate or bivariate point patterns in vegetation science (see Haase 1995, for review). As a result of this, highly populated areas are more intensively sampled than those with few individuals only: sampling intensity per unit area is proportional to plant density. The pattern/density dependence of sampling is certainly one explanation of the differences among results obtained for three community stands.

The two factors contributing to sampling intensity, abundance (density) and heterogeneity of spatial pattern of each species were investigated in the present study utilizing series of increasing numbers of species. In the species-poor version of the sand steppe at Csévharaszt (Map 1), the abundances are relatively high for four species, and all these occur in the whole study region. Two species have much fewer individuals, yet they also exhibit a fairly even dispersion. As a result, species curves are similar, and the community level graph shows the same changes as the curves obtained for the first two, three, four and then five most abundant species. In particular, the characteristic radius does not change along with this series of changes. Abundance differences, if associated with relatively homogeneous dispersion for all species, has therefore little influence upon the position of the maximum.

The picture becomes more complicated for the rich version of the sand steppe sampled at Bugac (Map 2).

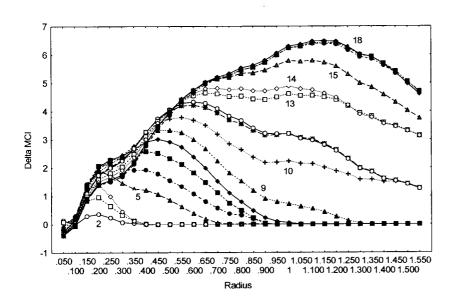


Figure 7. Abundance ranked ICA of the Bugac data (Map 2). Numbers refer to the number of species included. Radius is given in m.

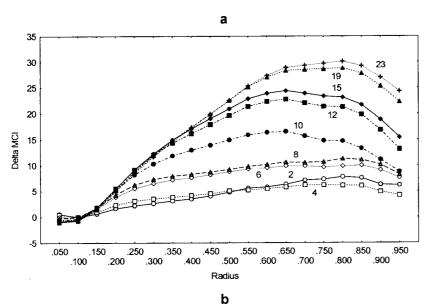
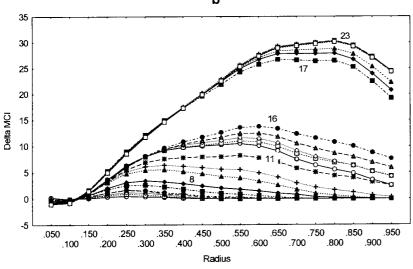


Figure 8. ICA results for the sagebush - bunchgrass community at Osoyoos (Map 3).

a. Abundance ranking, b. Species ranking according to the heterogeneity of spatial pattern. Radius is given in m.



The graph of  $\Delta$ MCI changes considerably when more species are included; the shifts in the position of the first peak and the emergence of two additional peaks indicate the presence of three different scales in the community. These changes are explained by obvious heterogeneities in the spatial pattern of some key species when they are added. Density-based ranking is of little help in revealing these different scales when there are very abundant species with strong spatial heterogeneity in their pattern, as exemplified by the sagebush-bunchgrass community mapped in British Columbia (Map 3). In this case, only two of the three scales are identified. On the other hand, if stepwise inclusion of species follows their spatial heterogeneity, three scales, the additional one pertaining to the most homogeneous species, are detected. Without examining single species patterns one by one, it is fairly obvious from the present survey that the scale of pattern is greatly influenced by heterogeneity. More precisely, the question whether all the species are dispersed fairly evenly or there are some species not appearing at all in a large portion of the study region appears crucial. To sum up, our impression is that ICA is more sensitive to plant heterogeneity than to abundance differences. Previous experience suggests that it is not so with plot sampling, which appears more substantially influenced by density relationships.

The examples clearly demonstrated that the analysis of multispecies point patterns is a much more complex subject than the evaluation of single species pattern ever can be. It is therefore not surprising that the literature of this subject is extremely poor (see Podani et al. 1993 and Podani & Czárán 1997, for reviews). The authors understand that evaluating the actual examples used in this paper, together with the artificial ones presented in Podani & Czárán (1997), may be considered only as an initial step towards a deeper analysis of the sensitivity of the method to different aspects of community pattern. Since each community was represented by a single study unit in this survey, the analyses should be extended to replicate sample regions to see how the conclusions can be generalized to the community level. In the future, attention must be directed towards other vegetation types, especially forests and communities of sessile animals. In this way, one could estimate how typical are the characteristics observed here and distinguish among types of multispecies patterns. The results presented in this paper suggest that a more meaningful joint evaluation of single species patterns and their assemblages is also in order.

**Acknowledgements:** The present survey was financially supported by the Hungarian National Research Fund (OTKA), grant no. T19364 (J. P.) and T19524 (T. C.).

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