

## Can underlying mechanisms be deduced from observed patterns?

Jan Lepš

*Department of Biomathematics, Biological Research Centre, Branišovská 31, CS-370 05 České Budějovice, Czechoslovakia.*

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**Abstract.** The aim of this paper is to evaluate attempts to estimate underlying mechanisms from observed patterns. The following cases are discussed:

1. The spatial pattern of a single population and interactions among individuals.
2. The spatial arrangement of two populations (statistical 'interspecific associations') and interactions between populations.
3. Analysing the distribution of population abundances and comparison with a neutral model to detect interspecific interactions. The neutral model of Caswell (1976) will be taken as an example.
4. Use of species-area relationship to distinguish between founder-controlled and dominance-controlled communities (Lepš and Štursa 1989).
5. Combining spatial pattern with supplementary information about particular individuals (their vitality, size, etc.).

It is concluded that evidence obtained from manipulative experiments is usually stronger than that deduced from observed patterns. Nevertheless, the analysis of patterns is necessary for suggesting proper hypotheses to be tested. The more appropriate auxiliary variables are included in the analysis of pattern, the more are the results suggestive of underlying mechanisms.

### Introduction

Attempts to estimate the underlying mechanisms from observed patterns are numerous. Opinions about the reliability of these estimates differ considerably. In classic works and textbooks of quantitative ecology (Greig-Smith 1952, Kershaw 1974), the spatial pattern of a population (measured as the intensity of clumping) or the frequency of statistically significant "interspecific associations" have been considered to be measures of biological organization. For example, Kershaw (1974, p. 57, repeated in Kershaw and Looney 1985) writes: "Interactions between species or individuals of the same species can be conveniently measured by means of a  $\chi^2$ -test or by an analysis of the 'pattern' of species distribution

respectively." In contrast, Shipley and Keddy (1987) clearly state that: "Hypotheses of pattern should be tested using inferential statistics. Hypotheses of mechanisms should be tested by experimental manipulations, making sure not to equate correlation with causation." This statement is well supported in their paper and it is clear that the evidence obtained from manipulative experiments is much more reliable than that based on observed patterns. Unfortunately, manipulative experiments are not always feasible or practicable. They may be extremely expensive or time-consuming. The aim of this paper is to critically examine the possibilities for estimating underlying mechanisms by studying patterns, with special attention paid to spatial patterns. The aim of this paper is neither to review the particular methods of pattern description nor to evaluate their statistical validity. The paper focuses on the interpretation of results. Thus methods of description will be accepted (usually from authoritative textbooks) without any discussion. The following cases will be discussed in detail:

1. The spatial pattern of a single population and interactions among individuals.
2. The spatial arrangement of two populations (statistical "interspecific associations") and interactions among populations.
3. Analysing the distribution of population abundances and comparison with a neutral model to detect interspecific interactions. The neutral model of Caswell (1976) will be taken as an example.
4. Use of species-area relationship to distinguish between founder-controlled and dominance-controlled communities (Lepš and Štursa 1989).
5. Combining spatial pattern with supplementary information about particular individuals (their vitality, size, etc.).

The mechanisms may be deduced either by comparing a single observed state with a state generated (predicted) by a neutral model (i.e. a model in which interactions we intend to demonstrate are not included), or from differences between two or more states in a time sequence.

### **Spatial pattern of a single population**

There are several ways to describe spatial pattern of a species (see e.g. Kershaw 1974, Pielou 1977, Ripley 1987). As a neutral model, the "random pattern" is considered, where individuals are distributed randomly and independently. There are many ways to compare this neutral model with the observed distribution of individuals. Generally, the approaches fall into two basic groups: so called distance methods, based on measurements of distances between individuals, and methods based on counts in quadrats. Theoretically developed, but seldom used is the analysis of two-phase mosaic (Pielou 1977).

Pattern is described by its scale and intensity (size of the departure from randomness). In the aggregated pattern, the probability of finding an individual is increased by the presence of another individual. As a result, an aggregated pattern has been considered as an indicator of positive interactions among individuals and regular (uniform) pattern as an indicator of negative interactions. However, there are many causes of clumping (most of which are reviewed in Kershaw 1974); the most important are environmental heterogeneity, type of dispersal, and competition with other species (sometimes called environmental, morphological, sociological pattern). On the other hand, the tendency toward regularity

may be almost entirely ascribed to competition among neighbouring individuals. The influences of particular factors act on various scales and often cancel one another. The pattern of each population is influenced by historical events (for example, the factors influencing the establishment of an individual might have no influence on an adult; the distribution of anemochorous seed is influenced by microrelief formation). Consequently, the resulting intensity of spatial pattern is influenced by many different factors and it may hardly be considered as a measure of a single one. The causes of aggregation are statistically indistinguishable (Ripley 1987). For example, as shown by the simulation study by Lepš and Kindlmann (1987), a nearly random spatial pattern may result from selfthinning of an initially aggregated population due to strong competition between neighbouring individuals.

Different factors express their effect on different scales. For example, it is often found that individuals are evenly distributed on a small scale (due to competition among neighbours) and aggregated on larger scales (due to environmental heterogeneity). Consequently, pattern analysis that considers various scales is much more informative and suggests much more about underlying mechanisms, particularly when it is accompanied by analysis of environmental factors (Kershaw 1961). It should be noted that the classic distance methods (Hopkins and Skellam 1954, Clark and Evans 1954) mix together the influence of pattern on various scales, with small scale phenomena given highest weight. This is caused by measuring only distance to the nearest neighbour. Recently, methods have been developed (Ripley 1987) using distances to all other individuals in the population; in these, various scales may be considered. However, they are practicable mainly for analysis of digitized maps.

Whereas the interpretation of "snapshot" analysis of pattern is difficult, much more may be said from repeated observations. In particular, changes toward regularity may be considered as a good indicator of negative interactions between neighbouring individuals (usually competition, see Lepš and Kindlmann 1987). Increase in clumping suggests positive interaction (Vacek and Lepš 1987). However, even in this case, it is a suggestion only — some other factors may play a role, such as changes in sensitivity to environmental factors with individual age, or uncontrolled changes in environmental factors.

### Interspecific associations

As in the case of single species pattern, there are two groups of methods for determination of "interspecific associations". The first group is based on presence or counts of individuals in a set of plots (usually quadrats). The second is based on comparison of the relative position of individuals of species or on their distances (testing for segregation according to Pielou 1977).

We shall consider the determination of interspecific associations on the basis of presence-absence data (described in textbooks of quantitative ecology, e.g. Kershaw 1974). However, very similar reasoning may be applied to assessment based on quantitative data. In this case, the presence of the two species is noted in a set of (usually randomly placed) quadrats and the number of common occurrences is compared with that expected under the hypothesis of independence of the two species. The significance of departure is tested using a  $2 \times 2$  contingency table by a  $\chi^2$ -test. A significant result of the test is labelled as a

positive or negative interspecific association. Usually, all the species are recorded and the procedure is repeated for all possible pairs of species or for species with frequencies higher than a certain threshold. The percentage of significant results has been considered to be a measure of community organization (Greig-Smith 1952). There are several problems with this procedure: first, there are problems of a statistical nature — the repeated test for all pairs of species leads to multiple inference from a single data set and increased probability of type I error. Analysis of multiway contingency tables requires a very high number of sampling units when the number of species exceeds four. Limited information on prevalence of positive or negative associations may be obtained from species counts in sampling units (Barton and David 1959). Within a single pair, the strength of test varies with frequencies of particular species and is particularly low when the frequency is too high or too low. Consequently, the percentage of species pairs exhibiting a significant association is considerably affected by the heterogeneity of the plot and by the distribution of species frequencies. Pielou (1969) has shown the possibility of detecting "random association" as a sampling artefact. However, more important difficulties appear with interpretation. Whereas the direct trophic relationships (like those of parasitic plants and their hosts) are usually studied by other methods, the association is usually considered to be active when one species modifies the environment in a way supporting (positive association) or suppressing (negative association) the other species. The passive association is caused by concordant (positive association) or discordant (negative association) response to some third factor. The third factor is usually interpreted as an environmental factor, but it may well be the rest of the community; two species may be found to exhibit a positive association simply because their mutual competitive relation is weaker than that with other plants. For example, in the steppe grasslands, the spring therophytes are usually found in common in gaps between tussocks of perennial grasses. Conflicting interpretations of interspecific association are possible (according to what we consider to be a cause and what we consider to be a consequence): (1) The (active) negative association is a consequence of competition between species - consequently the species pairs exhibiting the negative association are those with the strongest competitive relations. (2) The (passive) positive association is a consequence of concordant response to an environmental factor; the species exhibiting the positive association have the most similar niche and so they are the strongest competitors.

There is no way to distinguish the causes of associations from the  $2 \times 2$  table. The omission of the  $d$ -field (e.g. Fager 1957) is unjustified (see Pielou 1977). Similarly, the  $2 \times 2$  table does not provide information on the mutual influence of the two species (i.e. which species is influencing and which is the influenced one). All the two-sided indices (e.g. Ipatov *et al.* 1974) show that the more influential species is the more frequent one — Fig. 1 provides a simple counterexample.

It has been shown that interspecific associations change with the size of the plot of the sampling unit (Kershaw 1974). For example, two species may exhibit negative association on a small scale due to competitive exclusion and positive association on a larger scale due to concordant response to some environmental factor. So the common pattern analysis of the two species (Kershaw 1961) shows the mutual spatial relationship better and is more suggestive about their causes than any observation on a single scale. Even more suggestive

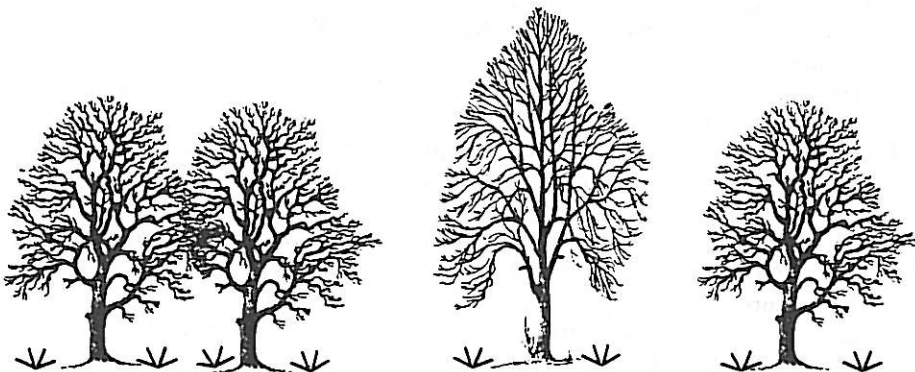


Fig. 1. A simple example, where a herbaceous plant depends on two species of tree. The herbaceous plant has greater frequency than either of the two trees and consequently, any two-sided index shows that the trees depend on the herb.

results are obtained when underlying environmental factors are included in the analysis.

In conclusion, analysis of interspecific associations describes the spatial relationships of populations and, in many cases, is suggestive about their causes. The percentage of interspecific associations (or some similar index) may be regarded as a measure of spatial heterogeneity or spatial diversity (a measure of departure from random independent dispersion), but by no means as a measure of functional organisation. Hence it is unjustified to deduce the validity of the individualistic community concept from the minimum interspecific associations found in climax communities (as in Greig-Smith 1952, or Kershaw and Looney 1985). Similarly, attempts to estimate the community matrix (or other dynamic parameters of multipopulation models) on the basis of "interspecific associations" are unsound. Similar conclusions were drawn by Hastings (1987).

The methods based on distances between individuals are described by Pielou (1966) for many species (the pattern diversity) and by Pielou (1974, p. 227) or Ripley (1987) for two species. The approach is based on the composition of nearest neighbour pairs or groups or on the distribution of monospecific and mixed pairs of individuals. As shown in the above mentioned papers, the segregation is influenced by both the initial pattern of studied species and the interactions among individuals (both inter- and intraspecific). However, some conclusions about mechanisms may be suggested when a time-sequence of observations is available. In the above mentioned case, a decrease in segregation (increase in the pattern diversity) in the course of self-thinning suggests the influence of intraspecific competition.

## Distribution of species abundances and analysis of neutral models

Attempts to determine the degree of biological organization (the strength of biological interactions) from a single "relevé" (i.e. abundances of all species present on a site) are among the most ambitious projects in community ecology. The usual procedure compares the observed state with that predicted by a neutral model; that of Caswell (1976) is probably the most popular (see references in Lamshead and Platt 1988). In this case, the observed diversity is compared with that predicted by the neutral model. However, the analysis given in this paper will show that a single relevé does not contain sufficient information to do this. Here I will first develop general arguments about neutral models and then will focus on the model of Caswell (1976). The model III adapted from the neutral allele model of Ewens (1972) which is used in most calculations will be discussed.

The procedure should be performed in two steps: first, the neutral model may be rejected and second, if so, the departure from the neutral model is interpreted as a measure of biological organization. It seems meaningless to test the neutral model in communities where there are direct trophic links, because the "no interaction" assumption may be rejected *a priori*. The interpretation of the size of departure from predicted diversity as a measure of biological organization is problematic, too. For example, the selective and non-selective grazing may have contradictory effects on diversity and as a final result, they may negate each other.

In each neutral model, two assumptions are included — (1) there are no interactions among populations and (2) there are no differences among population responses to the environment (i.e. there are no differences among carrying capacities of the environment for particular species). Consequently, the differences in population abundances are purely a matter of chance. The second assumption is not always explicitly stated, but is always included. (Note that in the original genetic model of Ewens, both the corresponding assumptions are feasible: the allele is selectively neutral, if it changes neither an individual's competitive ability nor its response to environment.) The rejection of the neutral model means that either one of the assumptions is not valid. There is no *a priori* reason to conclude that the first assumption is violated. The relevé does not contain any information which would enable one to reject the assumption that species abundances are determined solely by the environment (i.e. that abundance of each species corresponds to its carrying capacity); in other words, that the species would attain the same abundance if grown in the site alone. A habitat usually provides a (physiological) optimum for some species, whereas it is only suboptimal or marginal for others.

Competition proceeds on the "individual with individual" level; similarly, the model of Caswell (1976) is based on individuals (i.e. on the random exchange of individuals regardless of species). Hence, the model does not describe a community without interactions among individuals, but one where the intraspecific and interspecific interactions (among individuals) are the same for all species. (The hypothesis that there are no interactions among individuals of a population may be rejected *a priori*). This interpretation follows immediately from the analogy with the original genetic model - individuals differing in a locus do compete, but in the same way as individuals with the same allele. Similar points have been made by Ugland and Gray (1983), who state that fixed community size means competition. The response of Caswell (1983) did not reject their points. He states that



"Since Models II and III assume a fixed number of individuals, and Model I does not, nothing in the conclusions can possibly be an artifact of this fixed community size." The reliance on equivalence of the three models is unsound. If several models, some of which include interspecific interactions, give similar predictions of distribution of species abundances or of diversity, then the prediction may not be used as a yard-stick for detection of interactions.

In conclusion, the distribution of species abundances and their comparison with neutral model predictions is able neither to detect nor to measure the biological interaction within a community. The interpretation of departures is ambiguous.

On the other hand, it has been found that certain types of distribution (e.g. broken-stick, logarithmic, lognormal, see Whittaker 1975) are typical of certain types of communities or of certain successional stages, and may be suggestive in some cases, particularly when used on a comparative basis. But the mechanisms leading to a particular distribution may differ considerably; for example, Cohen (1968) has shown that the distribution predicted by the broken stick model may result also from other underlying models, and consequently this distribution may not be regarded as evidence for any of them.

Diversity also has been used to measure community stability. The first attempt was by MacArthur (1955). However, no unique relationship between diversity (or distribution of species abundances) and stability was found (Pimm 1986), and so it is unjustified to measure stability by community diversity. Particularly misleading is an approach when no operational definition of stability is provided and diversity (with other structural parameters) is used to quantify this fuzzy concept, as was attempted e.g. by Ružicka *et al.* (1983).

### Species-area relationship and the type of competitive interactions

Yodzis (1978) distinguished two types of communities of sedentary organisms with regard to the type of competitive network — founder-controlled and dominance-controlled. Roughly speaking, in founder-controlled communities, the species occupying a gap first (the founder) remains there, whereas in a dominance-controlled community it may be outcompeted by another species. It is clear that founder and dominance control are the two extreme points of a continuum. Based on a set of simulation experiments with a reaction-dispersal model, Yodzis predicted differences between the species-area relationships of the two types of communities. When considering the relationship  $S = c.A^z$ , where  $S$  is the number of species,  $A$  is area and  $c$  and  $z$  are parameters, the value of the  $z$ -parameter should be higher in founder-controlled communities. The species-area relationship on the within-community scale (not influenced by habitat heterogeneity) is considered.

Lepš and Štursa (1989) examined species-area relationships of two sets of communities and found that the relationship, particularly the parameter  $z$ , changes in a predictable way in the course of succession and on an environmental gradient. The changes may be partially accounted for by the distinction between founder-controlled and dominance-controlled communities (Yodzis 1978). According to the model of Yodzis (1978), this distinction is caused by differences in niche differentiation between species. Could the form of the species-area relationship thus be used to estimate the underlying competitive relationships and even the degree of niche differentiation?

The species-area relationship is influenced also by other factors, namely by the available species pool. The species pool may be limited by dispersal constraints, or by constraints superimposed by the physical environment (not all the species propagules which are present are able to grow in a given environment). These constraints usually cause a decrease in the  $z$ -value in the species-area relationship. It seems that the high value of  $z$  (in our case about 0.3 and higher) may be taken as very suggestive of founder-control, whereas low values may have several causes. To get a better idea, the information should be combined with information on life histories of species present. In contrast, the relationship between the degree of niche differentiation and founder/dominance-control has not been tested experimentally and the use of species-area relationship for estimating extent of niche differentiation would be unsound.

### **Combining spatial pattern with supplementary information about particular individuals**

Pielou (1974, p.252) described a method for detection and crude measurement of competition using spatial pattern. The method involved correlating the distance from a tree to its nearest neighbour with the sum of their circumferences (both variables were transformed to logarithms). A positive correlation was considered to be a sign of competition. In a multispecies stand, the correlations of single species and mixed species pairs may be compared. Similar reasoning was used by Vacek and Lepš (1987) to compare changes in the degree of defoliation caused by air pollution stress with distance to the nearest neighbour. In some cases, the evidence for "ecological sheltering" was found. Malik *et al.* (1976) compared the spatial pattern of individuals of *Atriplex vesicaria* of various sizes (ages) and found that the young ones are more clumped, which is the indication for competition among neighbours. Ishizuka (1984) used the comparison of the spatial pattern of centres of crowns with the pattern of stems in various layers for the study of processes influencing crown distribution.

These methods seem to be the most promising ones, particularly when a time series of observations is used. For example, the total size of two neighbours is influenced not only by their competition. The size of the yearly increment adjusted to the total tree size may be a better indicator of competition. (Tree ring analysis may provide useful information.) Generally, analyses that include a greater degree of appropriate information about individuals will give more constructive results.

### **Pattern recognition and experimentation**

As noted by Tillman (1988), the central goal of ecology is to understand the causes of the patterns we observe in the natural world. However, to do this, the patterns have to be sufficiently described. It is obvious that properly designed experiments provide much stronger inference about underlying mechanisms than observed patterns themselves. Experiments are usually done to test some hypothesis about underlying mechanisms. For a test to be strong enough, the hypothesis must be stated as precisely as possible. Moreover, experimental tests, particularly those carried out in the field, are laborious and time-consuming and have many limitations (see Diamond 1986). As noted by Haila (1988), science is not advanced through planning rigorous tests of patently unrealistic hypotheses. The analysis



of pattern is essential for suggesting hypotheses that are both testable and interesting. It is necessary to search for repeatable patterns, for similarities from habitat to habitat. It is impracticable to carry out experiments in all these habitats. The strength of evidence based on these observed patterns differs among particular cases; reliable evidence is obtained when it is known beforehand that some pattern is correlated with some independently (experimentally) measured dynamic characteristics. Weak evidence is usually obtained from comparison of an observed pattern with a pattern generated by a neutral model; all the neutral models we examined are patently unrealistic and/or are very sensitive to factors other than the mechanisms that the models are designed to detect. The use of the size of departure from the pattern predicted by a neutral model is also problematic — particularly when the effects of various mechanisms on the resulting pattern negate one another. The danger of misinterpretation increases when some characteristic of the observed pattern is used as a direct estimate of some dynamic parameter of underlying mechanisms, particularly when the estimated parameter is undefined or poorly defined (as with a measure of biotic organization, stability, etc.). Sometimes, the conclusiveness differs even with the direction of the departure. For example, whereas a clumped spatial pattern is very common in nature and itself says nothing about possible causes, a uniform pattern is relatively rare and is highly suggestive of competition among neighbouring individuals.

It should be stressed that, whereas the departure may be suggestive of a particular mechanism, the agreement with neutral model prediction provides extremely weak (if any) evidence for absence of a mechanism. For example, neither random nor clumped patterns indicate that neighbouring individuals do not compete.

More meaningful evidence may be obtained from a time sequence of observations. In some cases, comparison between sites may also be useful. When the spatial and temporal comparisons are combined, the evidence may be very suggestive (e.g. when we compare the development of spatial pattern of two populations differing in initial density). Such comparisons may be considered to be "natural experiments"; however, in comparison with manipulative experiments, they lack the advantage of experimental design. In the above example, the differences in initial density may be caused by an uncontrolled factor.

Very compelling evidence is obtained when the information about spatial pattern is combined with additional information, particularly when such a combined observation is carried out in a time sequence.

It is obvious that pattern analysis serves mainly to suggest hypotheses about underlying mechanisms, which can be tested through manipulative experiments. Nevertheless, the distinction between uses of pattern analysis and manipulative experiments is not absolute. Depending on the spatial and temporal scales of the problem, manipulative experiments are considerably limited. Reliance on natural experiments is often unavoidable (Diamond 1986). The relative representation of the two approaches depends on the "maturity" of research in a certain area (Loehle 1987). Experimental studies are implemented after plausible hypotheses have been suggested by observed repeatable patterns.

It may be concluded that mechanisms can be suggested on the basis of observed patterns, but they cannot be tested. In no case does the size of the departure of observed pattern from randomness (from the prediction of neutral model) allow for measuring the intensity of biological interactions. The limited interpretability of observed patterns does

not deny the general usefulness of pattern analysis.

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