SPECIAL FEATURE

Mechanistic explanations of community structure

Editors

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Contents

Mechanistic explanations of community structure: Introduction

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This special feature incorporates papers focusing on mechanistic explanations of patterns in community structure, all based on presentations from the Budweis symposium held in České Budějovice in 1997. This simple theme masks considerable controversy and confusion over what exactly constitutes a mechanistic explanation and how these patterns should be determined, as well as considerable variation in the types of patterns in community structure, that we, as vegetation scientists, seek to explain. In this special feature we view a mechanistic approach as a process of reduction in which patterns at one level are explained by phenomena at a lower hierarchical level. This is consistent with the typical mechanistic approach in community ecology, which involves explaining patterns in aspects of community structure in terms of processes occurring at the level of the individual organisms that make up that community (Schoener 1986; Tilman 1987). However, it is important to note that this focus on proximate ecological processes does not incorporate at least two other types of processes that contribute to the ecological patterns we observe. These are (1) evolutionary explanations (such as size of the species pool, coevolution of species, and the like) and (2) different types of constraints that are due to larger-scale structure of the environment (such as absence or presence of a particular bedrock type, or a particular migration barrier). Studying these processes requires a rather different set of questions and methodological approaches (see e.g. Zobel 1992, 1997); in fact, they constitute a rather separate field in themselves.

Nevertheless, even with this somewhat restrictive definition, what constitutes a mechanism may depend on the particular phenomenon (pattern) to be explained and can even be rather subjective. For example, when the phenomenon to be explained is positive or negative associations of different species, intraspecific competition among individuals (in the widest possible sense, including apparent competition) can be the underlying mechanism. However, when we take competition among neighboring individuals as the phenomenon to be explained, then the mechanisms might be, for example, direct shading (Lepš 1999), or increased abundance of specialized herbivores.

In ecology, there is an old tradition to deduce the mechanisms from observed patterns. This general approach is often subject to the criticism that the same pattern could arise from very different mechanisms and a correlation approach cannot distinguish among them (see references in Strong et al. 1984; Lepš 1995). For example, in this volume, Lepš (1999) shows a positive correlation between moss cover and seedling recruitment, which suggests some protective role of the moss layer. However, Kotorová & Lepš (1999) performed a moss removal experiment in the same system and showed that the moss layer actually suppressed seedling recruitment. Consequently, the positive correlation between moss layer and seedling recruitment is not a consequence of a direct causal relationship, but rather a concordant response of both variables to the external environment (to manipulations in this case). Other examples of the problems of interpreting correlational or pattern data abound.

Because of these problems, carefully designed manipulative experiments have come to be viewed as the *conditio sine qua non* of mechanistic approaches to ecology (Goldberg 1995; Varley 1957; Hairston 1989). However, experiments that directly test a proposed mechanism are not always feasible and excluding such questions from the realm of scientific investigation would be an extreme response; such a view would, for example, eliminate astronomy as a science. Below, we describe the approaches used by the authors of these papers, based both on whether experiments or observations are used and on how directly either of these test the role of particular mechanisms in explaining community patterns. Note that none of these approaches is mutually exclusive, in fact several authors use several of them.

The most straightforward approach to testing a mechanism underlying some phenomenon is to conduct an experiment in which the purported mechanism is

manipulated; treatments in which the mechanism is absent should also not show the phenomenon being investigated, while treatments in which the mechanism is present should show the phenomenon. For example, in this volume, Stampfli & Zeiter (1999) investigated why adding mowing to long-abandoned fields resulted in only a very slow rate of increase in species diversity. Their hypothesized mechanism was seed limitation – the species pool of these fields no longer included many species typical of regularly-mowed fields and so these species could not establish even when mowing was reintroduced. They conducted the conceptually simple experiment of adding seeds of many species and found that seed limitation could indeed explain their pattern of slow community response. Brewer & Rejmánek (1999) also used this very straightforward approach: the pattern they sought to explain was the spatial distribution of diaspores of tropical trees and they hypothesized that the mechanism was dispersal by rodents. They manipulated the ability of rodents to disperse seeds (by caging or not) and found that indeed rodents could account for the observed pattern. Both studies are also good examples of the hierarchical nature of definitions of patterns and mechanisms. Brewer & Rejmánek hypothesized that differential spatial distribution of diaspores is itself a mechanism that explains coexistence in species-rich tropical forest. In the Stampfli & Zeiter study, the slow recovery (due to seed limitation) is hypothesized to explain the particular distribution of species-rich and species-poor sites in the landscape.

A second, and probably much more common, approach towards testing mechanisms of community patterns is to test, often experimentally, whether the conditions hold that are necessary for the mechanism to work. For example, because most models predict that some kind of differentiation among species is necessary for long-term coexistence, a necessary first step in testing any particular model is testing whether differentiation among species in the predicted aspects of the niche actually exists. In this volume, Kotorová & Lepš (1999) studied a number of aspects of the regeneration niche (sensu Grubb 1977) in a species-rich wet meadow, using a combination of greenhouse and field experiments to quantify differences in germination and establishment responses of many of the common species. Testing the assumption that differentiation exists is a critical first step for any community, but the next step of actually testing whether these differences are responsible for coexistence is often much more difficult. At a more general level, the approach of testing conditions amounts to finding mechanisms that are *capable* of affecting or determining some pattern in the field. For any given pattern, there obviously may be more such mechanisms; the crucial question then is to decide which

of them really *operates* in the field. This action of any particular mechanism is constrained by a set of conditions in the field system; one has to make a set of assumptions on these conditions to conclude that the mechanism is indeed operating. This inference is often done by means of modelling, which can constitute a link between this approach and the deductive approaches described below.

A third group of approaches, with several subgroups, uses ecological theory (conceptual or mathematical) to predict particular patterns that should occur if a given mechanism does, or does not, operate and then compares predicted and observed patterns. This is essentially the deduction-from-patterns approach discussed above. The point to be made here is that the process of formulation of the hypothesis and deduction/modeling has to be fully explicit, and the critical assumptions during this process have to be clarified; otherwise the approach has little value. It may actually turn out that many of these assumptions can be supported by good evidence from the system studied or from elsewhere.

In perhaps the most straightforward type of observational approach, ecologists have investigated mechanisms by using formal mathematical models to predict a pattern based on some postulated mechanism and then checking to see whether the predicted pattern exists in nature. For example, in this volume, Braakhekke & Hooftman (1999) focus on what controls the number of coexisting plant species in a community. They postulate that an important mechanism of coexistence is differentiation among species in the required ratio of resources. If this mechanism is operating, their model predicts that diversity should be highest when resources are most balanced, i.e. the ratio of two resources is intermediate such that neither one is likely to be limiting to all species. Braakhekke & Hooftman (1999) then tested this resource balance hypothesis by comparing diversity among grasslands with different ratios of nitrogen, phosphorus, and potassium (but similar standing crops) and found results consistent with the prediction. There is a direct link between this approach and that of Kotorová & Lepš discussed above; both approaches contain a body of evidence (which may, as in Kotorová & Lepš, but need not be, obtained by experiments), but its use in particular is made possible by inference.

LeJeune & Tlidi (1999) also use this approach, to investigate a highly unusual spatial vegetation pattern. They show that linear stripes and spots of regularly-spaced vegetation can be found in aerial photographs in a variety of arid regions of the world. Unlike aggregated spatial patterns, which are widespread and can be explained by a number of different mechanisms (spatial heterogeneity in environment, dispersal, nursing, etc.), regular patterns are rarely found in nature and the only

feasible mechanism that has been proposed is competition (*sensu lato*) among neighboring individuals. LeJeune & Tlidi (1999) develop a mathematical model of competitive interactions that satisfactorily accounts for the specific kinds of regular patterns observed. In these two studies this approach is applied in a rather qualitative way, but it can be made fully quantitative, including quantitative comparison of predicted and observed patterns (Pacala et al. 1996).

Another example of an observational approach involves the use of null models, i.e. randomization of data done under the assumption that the mechanism of interest is *not* present. This approach can be viewed as an observational analogue of the direct experimental approach described above (Stampfli & Zeiter 1999, Brewer & Rejmánek 1999). In this approach, a null model is used to generate the null hypothesis pattern, as well as the direction and magnitude of deviation from the null model caused by the mechanism of interest. The observed pattern is then compared statistically to that predicted by the null model. Significant deviations of the observed pattern in the appropriate direction from that predicted by the null model are then interpreted as evidence that the mechanism absent in the null model is operating. For example, in this volume, Klimeš (1999) developed null models of the effect of spatial expansion by plants on patterns of species richness on a small spatial scale and found that models of purely random movement (cf. van der Maarel & Sykes 1997) did not adequately account for the observed patterns, while more complex models incorporating restricted movement could account for observed patterns. The null model approach has been highly controversial in community ecology (Strong et al. 1984; Wilson 1995; Lepš 1995; Goldberg 1995). In addition to the general problem of inferring process from pattern discussed above, to enable prediction, the null models often must be greatly simplified; unfortunately, there is no canonical way how to decide on the appropriate null model even if the hypothesis on the mechanism to be tested is made explicit. The critical issue in this is always to decide which part of the observed patterns should be made external (i.e. part of the null model not being tested). There are two opposing risks here: (1) the risk of a 'Narcissus effect', i.e. inadvertent incorporation of the community structure being tested into the null model; this leads to a situation similar to a high Type II error rate, see e.g. Armbruster 1995), and (2) the opposite risk of formulating a very nonspecific model which has a great likelihood to be rejected. Such a rejection would prove little, since in such a nonspecific model, the differences between predicted and observed patterns might be caused by many factors. The result of such a test is then critically dependent on the researcher's formulation of the null model.

A third type of observational approach uses ecological theory to predict either relationships among different traits of a group of taxa or between traits of taxa and habitats such that the taxa essentially become the individual data points in an analysis of pattern (Silvertown et al. 1997). In a qualitative example of this approach in this volume, Klimeš (1999) sought to explain variation in degree of mobility of species within a community in terms of their growth form and reproductive mode. In another example in this volume, Lepš (1999) experimentally manipulated fertilization in the field and found the typical result that diversity declined. One of the patterns he sought to explain, however, was not just this diversity decline, but *which* species declined, i.e., the variation among species in response to the experimental treatment. Lepš's proposed mechanism was variation in competitive ability for light among species but testing this directly for tens of species would be very difficult. Instead, he further assumed that plant height was positively correlated with competitive ability for light and tested quantitatively whether taller species were less likely to decline with fertilization. This correlative approach strongly supported the proposed mechanism. One important, although controversial, caution in using this comparative method for testing mechanisms is that because of phylogenetic branching patterns, individual species cannot necessarily be used as independent data points (Harvey & Pagel 1991; Silvertown & Dodd 1996; but see Westoby et al. 1995). This is because it may be that species share some trait of interest because of a common evolutionary history rather than because of a common set of adaptive solutions to ecological problems. Therefore, the species could also share other, unmeasured, traits, making it difficult to isolate the direct effects of the trait of interest.

Although well-designed experiments can provide compelling evidence that particular mechanisms are indeed operating to explain particular patterns, it is clear from the examples in this Special Feature that many mechanisms may be very difficult to test directly by experiments and that non-experimental approaches can nevertheless provide important insights into the mechanisms determining vegetation patterns. Their power is always greatly strengthened when the assumptions made in the reasoning are fully explicit, but this is, of course, true also for experimental approaches. In fact, there may well be a trade-off between the ecological relevance of mechanisms tested by experimental manipulations and the feasibility of carrying out relevant manipulations and ability to control relevant parameters (see also Diamond 1986). The experimental protocol for studying competition of two isolated species in homogeneous environment can be straightforward; however, the

relevance of such an experiment for mechanisms maintaining species diversity in species-rich natural communities is not clear. Similarly, it is possible to control environmental parameters in a growth chamber experiment studying competition of two species; however, it may well be that random fluctuations of environment (Kotorová & Lepš 1999) or the spatial context of the species (Klimeš 1999) is the most important factor maintaining the coexistence of the species in nature. In such a case, direct experimental testing is rarely possible; only a careful combination of observations, experiments (mainly of the 'second' type above) and modeling would reveal the really important factors. The papers in this special feature illustrate the basic building blocks of this broad approach. We believe the future of mechanistic approaches to understanding community patterns will require combining such building blocks, as well as more explicit comparisons among taxa and among communities to explore the generality of this understanding.

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