Basic and Applied Ecology

INVITED VIEWS IN BASIC AND APPLIED ECOLOGY

What do the biodiversity experiments tell us about consequences of plant species loss in the real world?

Jan Lepš*

Department of Botany, Faculty of Biological Sciences, University of South Bohemia, and Institute of Entomology, Czech Academy of Sciences, Na Zlaté stoce 1, CZ-370 05 České Budějovice, Czech Republic

Summary

Experiments where the diversity of species assemblage is manipulated are sometimes used to predict the consequences of species loss from real communities. However, their design corresponds to a random selection of the lost species. There are three main factors that limit species richness: harshness of the environment, competitive exclusion, and species pool limitation. Species loss is usually caused by increasing effects of these factors. In the first two cases, the species that are excluded are highly non-random subsets of the potential species set, and consequently, the predictions based on random selection of the lost species might be misleading. The data show that the least productive species are those being recently excluded from temperate grasslands and consequently, species loss is not connected with decline of productivity. The concurrent species loss in many communities, however, means also a reduction of the available diaspore pool on a landscape scale, and could result in increased species pool limitation in other communities.
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*Corresponding author. Tel.: +38-777-2374
  E-mail address: suspa@bf.jcu.cz (J. Lepš).

Introduction

The effect of biotic diversity on ecosystem functioning has long been one of the topics of ecological research (Pimm, 1984), with periods when the topic was intensively studied interchanged with periods of relative neglect. The present interest in this topic reflects the general concerns of species loss and resulting biodiversity decline. A large amount of experimental data has been accumulated (e.g. Kinzig, Pacala, & Tilman, 2002, Loreau, Naeem, & Inchausti, 2002, Wardle, 2002) and the data are often presented in support of the old idea that diversity begets ecosystem functioning. However, as noted by Kaiser (2000), the rift over biodiversity divides ecologists. The problem lies in the interpretation of the outcome of the experiments. What can we learn from them to predict consequences of species loss in real communities?

The contention is now fairly less sharp than it used to be in the year 2000. The paper published by Loreau, Naeem, Inchausti, Bengtsson, Grime et al. (2001) was an important and successful attempt to reach some agreement on this topic. Nevertheless, even reading this "consensus" paper, I sometimes feel that I would be able to assign individual members of the authors' team to individual paragraphs, according to their opinion. Many differences in opinion remain (compare the monographs of Kinzig et al., 2002 and Wardle, 2002) and the debate still continues.

Productivity is often used as the measure of "ecosystem functioning". I will demonstrate the problems using productivity as an example, but similar reasoning can be used for many other characteristics. There are two basic ways in which the relationship between diversity and ecosystem functioning can be studied (Schmid, 2002). In the first approach, we study a set of natural communities of different diversity, and then correlate their diversity with some measure of their functioning (e.g. productivity, nutrient uptake). In this case, we usually find some correlation, because ecosystem functioning and diversity are both affected by environmental conditions of the habitat (often habitat productivity), either directly, or indirectly through the prevailing species strategy (e.g. Lepš, Osbornová, & Rejmánek, 1982, Lepš, 2005). The correlation is sometimes negative, sometimes positive, depending mostly on whether the productivity of most of the investigated sites corresponds to the ascending or descending part of the "humped back" relationship between productivity and diversity (Al-Mufti, Sydes, Furness, Grime, & Band, 1977). Such relationships, however,

can hardly be interpreted as a causal effect of diversity on ecosystem functioning. Consequently, ecologists have started what I will call biodiversity experiments, where assemblages of plant species of varying diversity are created by sowing or planting. In these experiments, species diversity is considered as an independent variable, because it is manipulated and functioning (most often productivity) is measured as a response. The other possibility is to create depauperate communities by removing species from existing communities (Diaz, Symstad, Chapin, Wardle, & Huenneke, 2003). In most experiments, the species poor communities contain random subsets of species forming the species-rich communities. In this case, a positive effect of diversity on productivity is nearly always found. More precisely, the **average** productivity of assemblages (and usually other characteristics correlated with productivity or biomass) increases with the species richness. The fact that observational (between site) comparisons and experimental (within site) studies result in different relationships is not surprising; each of them studies a different phenomenon (Schmid, 2002). However, how do the results of biodiversity experiments relate to the real world? Does the positive diversity–functioning relationship predict anything about the consequences of species loss in the real world (as suggested by the title of the pioneering paper of Naeem, Thompson, Lawler, Lawton, & Woodfin (1994))? The answer is much more complicated.

Realism and generality of ecological experiments

Diamond (1986) in his seminal overview of ecological experiments coined two of their important characteristics: realism and generality. By realism is meant the existence of at least a single natural community to which the results of the experiment apply, while generality increases with the number of such communities in the real world. The problem of biodiversity experiments is the existence of highly unrealistic assemblages: in nature, species composition matches the environment, in biodiversity experiments, it does not. Some species combinations are extremely unlikely in nature. For example, assemblages of unproductive species in productive environments or assemblages formed solely of species that are usually subordinate in natural communities are usually not found in nature, but they are necessarily a part of the design of biodiversity experiments. Even worse,

the proportion of highly unrealistic assemblages increases with decreasing species number. (In my experimental meadow plots, low-productive species like *Carex pulicaris*, *Cerastium holosteoides*, or *Anthoxanthum odoratum* are regularly present, but never in the absence of dominant grasses and sedges. In a possible biodiversity experiment at this site, the proportion of unrealistic assemblages composed solely of those unproductive species would decrease with assemblage species richness.) Moreover, the effect of species life history is probably much more pronounced than the (possible) effect of species diversity. As noted by Aarssen (2001), it is more important which species are lost than how many of them are lost. All this reasoning is valid, when we compare **average** productivity of all assemblages of a given richness (note that the use of regression analysis, with each assemblage being an independent observation, is from this point of view equivalent to using averages). If we would be able to demonstrate that the more species rich assemblage is more productive than any of the assemblages consisting of a subset of its species (transgressive overyielding sensu Hector, Bazeley-White, Loreau, Otway, & Schmid, 2002), then we can predict that any species loss leads to decreased productivity. Unfortunately, this is usually not the case.

Factors limiting species richness

Three major factors limit species diversity in plant communities: 1. Adversity of the environment (low productivity or high disturbance), which limits establishment and species survival. 2. Competition in communities, preventing species establishment or leading to competitive exclusion. 3. Species pool limitation (species, which are potentially able to grow and survive in a community, are not present in a local species pool (Taylor, Aarssen, & Loehle, 1990)). Species poor communities that are limited by different factors would behave in very different ways. Plant communities on extremely unproductive sandy soils, on overfertilized meadows and on newly appearing islands could all be similarly species poor, but they will differ in the ecology of the constituent species and also in ecosystem functioning.

Similarly, we can note three main types of species loss from communities: 1. Increased adversity of the environment terminates species survival in a locality. As an example, species may be extinguished due to the effect of "acid rain", other toxic pollutants, or disturbance greater than the limits of species tolerance. 2. Species are excluded from a community by increased competition (or increased competition asymmetry), usually due to shifts in competition equilibria resulting from shifts in environmental conditions. Typical examples are eutrophication or decreased disturbance intensity, exemplified by management abandonment connected with present land use changes. 3. Many (sub)populations depend on a constant influx of diaspores from their surroundings (sink populations in a metapopulation, transient species according to Grime (1998)). Cessation of diaspore influx may lead to species extinction. Similarly, each population in a metapopulation has some probability of extinction. If the connectivity of the population network is decreased, the equilibrium between population extinction and establishment is lost and the richness in individual habitats will drop (Hanski, 1999). This case might be common in present fragmented and dynamic landscapes (but it is difficult to prove). Habitats are newly formed, and/or their properties are changed, and the lack of diaspores in the species pool may be an important limitation for their ecosystem dynamics.

Two questions arise immediately: can the consequences of different types of species loss be predicted from the results of biodiversity experiments? and how common are particular types of species loss in recent landscapes?

When species are lost because of increased harshness or competitive exclusion due to increased productivity or lack of disturbance, we can predict, based on species traits, which of them will be lost (e.g. Lepš, 1999). The loss is accompanied by shifts in both species life history spectra and the environment. Consequently, predictions can be misleading, when based on changes in the functioning of random subsets of species. Communities in fertilized meadows will be species poor, but never composed of unproductive species. Predictions based on species' life history will be more successful. The lessons learned from the comparative (between site) approach might be very useful here. Dispersal syndromes are only vaguely dependent on the established strategies (Grime, 2001). It thus seems that the design of biodiversity experiments corresponds most (but not completely) to species pool limitation.

There are undoubtedly other causes of species loss or mechanisms of species richness limitation, not mentioned earlier. One of them is the effect of other trophic levels. From the plant community perspective, a change in some of them (e.g. grazing pressure) could be considered as a change in disturbance regime, and their consequences predicted on the basis of life history or constituent

species. Others (e.g. mycorrhizal symbiosis, pathogens) are able to change the competitive equilibria, and/or the ability of species to survive. Their effect is often species specific (e.g. Dutch elm disease), and difficult to predict. The effect of human population could be considered as a special case of the effect of an organism from another trophic level. Humans have caused directly loss of species either by overexploitation or by deliberate extirpation. The reasons why humans do so are variable. Nevertheless, the species traits are usually known and the predictions based on them will be more successful than predictions based on change in species number. Extirpation of spruce from a monodominant (even natural) spruce forest in European mountains by clear-cutting leads to a decrease of productivity, despite the fact that the richness of vascular plants can increase considerably: the managed (grazed or mown) mountain meadows are usually more species rich than the original spruce forest.

Which species are lost from Central European grasslands?

Most experiments using synthetic communities have been carried out in temperate grasslands. In Central Europe (as well as in many other places in the world), field botanists have an intimate knowledge of the trends in plant species distribution, expressed formally in the categorization of endangered species in Red lists. Similarly, there is intimate knowledge of species' ecological demands, described in lists of species indicator values (e.g. Ellenberg, Weber, Düll, Wirth, Werner et al., 1992). The two pieces of information were put together to illustrate which species are being lost. The flora of the Czech Republic (Kubát, Hrouda, Chrtek, Kaplan, Kirschner et al., 2002) was used as an example of a temperate country. To conform to most biodiversity experiments, this demonstration was restricted to grasslands. Consequently, woody species were excluded. Then, two of the Ellenberg et al. (1992) indicator values—the indicator for light and nitrogen (L and N) were used. These values are available for most of the vascular plant species in Central Europe. Each species is characterized by a value on a scale from 1 to 9, with 1 meaning an ability to cope with extremely low resource levels, while species with a 9 value require extremely high levels of the resource. Plants with L values of 1 are extremely shade tolerant, while 9 indicates shade intolerant. Plants with N values of 1 are those of extremely

unproductive habitats, while high values indicate plants of highly productive habitats, which are usually very productive species. These values are considered reasonably reliable, and are generally treated as quantitative variables (e.g., their averages are calculated when needed, see Diekmann, 2003, ter Braak & Gremmen, 1987). Since the example was limited to grassland species, indicator values for light were used to exclude shade tolerant, i.e. forest, species (with light indicator value of 5 and smaller). On average, the most endangered species are those with the lowest N values (Fig. 1). Ellenberg (1985) noted a similar trend many years ago among all Central European species. His analysis also demonstrated that the relationship between a species' indicator value for N and its endangered status is the strongest among all of the examined indicator values. This is in good agreement with general field experience: species are lost because they are outcompeted in eutrophicated or abandoned grasslands. In this case, species loss can hardly cause a decrease in productivity (as predicted by biodiversity experiments), but is itself caused by an increase in productivity. Species are not lost at random, but according to their traits.

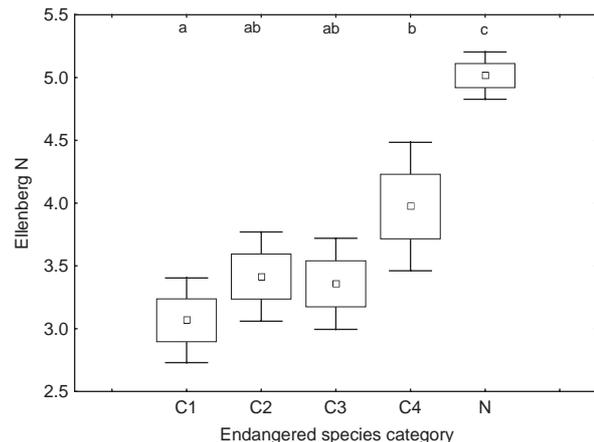When species are lost because of increased harshness of the environment (e.g. pollution), the

Figure 1. Average Ellenberg N values for various categories of endangered plant species in the flora of open habitats of the Czech Republic (details of species selection are in the text). The categories are (with the number of species from which the average is calculated). C1 (119)—critically endangered, C2 (118)—strongly endangered, C3 (128)—endangered, C4 (74)—potentially endangered, N (582)—not endangered. The differences between categories are highly significant (ANOVA, $P < 0.001$ means with the same letter do not differ, P[a posteriori SNK-test] > 0.05). The box is the standard error, whiskers the 95% confidence interval for the mean.

result can be even worse than predicted by biodiversity experiments. The trade-offs often cause resistance and growth rate to be negatively correlated. Consequently, in this case even loss of a very limited number of species (even of a single species) can have catastrophic consequences for ecosystem functioning. A typical example was forest dieback caused by "acid rain" in Central Europe. In most locations a single species, the spruce (*Picea abies*), was lost (and sometimes, even new species established in the understory, so that the species richness of vascular plants did not decrease at all), but the consequences for ecosystem functioning were tremendous. Again, the identity of species lost, and not the total richness, was the decisive factor.

If the community is species poor due to species pool limitation (lack of propagules in the landscape), the situation resembles more that in biodiversity experiments. Indeed, the more productive species might be more dispersal limited, so that the productivity decrease might be even worse than predicted by the biodiversity experiments.

The fact that biodiversity experiments reasonably predict the effect of species pool limitations, but not the effect of decreased diversity for other reasons, can be illustrated by the predictions of resistance to invasion. Naeem et al. (2000) have shown in a manipulative experiment that resistance to invasion decreases with species richness. In the real world, island communities are often less diverse than continental ones (apparently because of species pool limitation). They are less resistant to invasion, whereas continental species poor communities that are not limited by the species pool do not suffer from decreased resistance to invasions (Rejmánek, 1996).

Species pool limitation might be relatively common in present-day landscapes (Foster & Tilman, 2003). Direct species loss due to the lack of propagule influx is just one of many possible examples. Present day cultural landscapes are rather dynamic, with new habitats being created constantly. If many species able to colonize them had gone extinct in the whole landscape then the communities in the newly created habitats would be highly limited by the available species pool (Schmid, 2002). This might even apply to some conservation activities: Stampfli & Zeiter (1999) have shown that the attempt to restore species rich meadows, by the use of a proper management regime on neglected species poor meadows, is limited by the availability of diaspores on the site. As shown by a mathematical model (Loreau, Mouquet, & Gonzales, 2003), biodiversity can be considered as spatial insurance in heterogeneous landscapes.

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