BIODIVERSITY AND ECOSYSTEM FUNCTIONING: EXPERIMENTAL SYSTEMS

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Keywords: Biodiversity experiments, ecosystem functioning, additive partitioning of biodiversity effects, diversity and stability.

Contents

Summary

Experimental studies of the relationship between biodiversity and ecosystem functioning have taken two main approaches: the experimental removal of species from real communities and the construction of model communities to form gradients of diversity. The fundamental difficulty in designing biodiversity experiments is the large number of possible species combinations that make simple, unambiguous fully-factorial designs impossible with all but the smallest species pools. Nevertheless, experimental and analytical methods have developed to include the replication of both diversity and composition, multi-site experiments and the simulation of non-random extinction scenarios. Methods that calculate deviations from expected null values and that employ covariance approaches have also been developed and these can distinguish between some of the underlying mechanism. Experiments that omit key functional groups can demonstrate that biodiversity effects occur in their absence but approaches that can identify how much different species contribute to the overall relationship between biodiversity and ecosystem processes remain a challenge for future experimental design.

1. Biodiversity experiments

Research on biodiversity and ecosystem functioning attempts to identify the effects of biodiversity on ecosystem processes. To identify causal relationships most researchers have employed biodiversity experiments. A biodiversity experiment typically manipulates one or more aspects of the diversity of model ecosystems while attempting to hold other factors as constant as possible. There are two main ways to manipulate biodiversity. The most common approach is to construct 'synthesized' communities by combining species. Examples of model communities include microorganisms in laboratory culture, aquatic animals in artificial ponds or streams, forest plantations or, most commonly, field plots of grassland plants. An alternative approach is the removal experiment: species are removed from natural communities, most commonly by weeding plant species from field plots (Wardle *et al* 1999, Diaz *et al* 2003). Both approaches have strengths and disadvantages (see *Biodiversity and Ecosystem Functioning: Basic Principles*).

2. Experiment and observation

An important factor contributing to the 'biodiversity debate' is a failure to clearly distinguish biodiversity experiments from observational studies of the correlation between diversity and productivity (see *Biodiversity and Ecosystem Functioning: Basic Principles*). The approaches differ in several important ways. Biodiversity experiments typically examine the effects of biodiversity at the local scale - typically the scale of the interactions of the organisms involved - while observational studies examine the correlation between diversity and productivity across larger scales from regional to global (Ricklefs & Schluter 1993; Grace, 1999; Mittelbach *et al* 2001). Well-conducted biodiversity experiments also isolate the causal effect as biodiversity, although identifying which aspect of biodiversity is effective has proved surprisingly difficult. In contrast, identifying causal links from the analysis of observational studies can be more difficult due to potential additional environmental variables that can be confounded with diversity. Observational studies traditionally place productivity on the X-axis of the bivariate plot as the explanatory (independent) variable while biodiversity experiments plot the relationship the other way around in trying to examine biotic feedback: can local diversity itself influence productivity (see *Biodiversity and Ecosystem Functioning: Basic Principles*, Figure 8)?

3. Experimental design and analysis

At first sight, biodiversity experiments appear straight-forward: assemble experimental communities with different numbers and types of species and measure the ecosystem processes of interest. However, biodiversity is not a simple variable to manipulate. An immediate problem is the diversity of most systems. Even when concentrating on a single trophic level - as most experiments to date have done - the number of possible experimental communities soon exceeds what is logistically possible when more than a hand full of species is examined. This means that fully-factorial designs are only possible when examining very low levels of diversity. One way around this is to combine species into a small number of functional groups. At higher levels of diversity a subset of communities must be chosen - either at random or using some non-random criteria. Many experiments have attempted to simultaneously manipulate species and functional groups but a fully factorial approach is again not possible because at low diversity the number of species can never be less than the number of functional groups, while at the opposite end the species diversity of functionally poor treatments is limited to the most speciose functional group; The fully factorial matrix of species richness versus functional groups inevitably looses two corners. The analysis of biodiversity experiments therefore often involves complex general linear models in which it is not possible to uniquely partition the variance due to collinearity between explanatory variables that are correlated. The design and analysis of biodiversity experiments is comprehensively reviewed in Schmid *et al* (2002).

4. Interpretation and mechanism

The interpretation of biodiversity experiments is complicated by the existence of two classes of underlying mechanism. Selection effects (Loreau & Hector 2001) occur when communities become dominated by particular species. When dominant species occur more frequently in high diversity—a sampling effect (Huston 1997; Tilman 1997)—then the traits of these dominant species may drive ecosystem functioning. Alternatively, complementary or positive interactions may allow diverse systems to utilise more resources or to suffer lower levels of pests and diseases. These mechanisms can be quantified with the additive partitioning method.

4.1. Additive partitioning of biodiversity effects

The additive partitioning method (Loreau & Hector 2001) defines a net effect of biodiversity which is the difference between the observed yield of a mixture and that of the average monoculture yield. This net effect is then partitioned into two additive components: the selection and complementarity effects. The selection effect is the standard statistical measure of covariance applied to the relationship between yield in monoculture and the change in relative yield in mixture. Selection effects will be positive when species with higher-than-average yield dominate communities and negative when species with lower-than-average yield dominate. The complementarity effect uses relative yields to ask whether increases in the abundance of some species exactly cancel with declines in others. When this is the case resource partitioning is a zero-sum game with some species taking more of a fixed total pool of resources and others taking less. Positive complementarity effects occur when decreases in the abundance of some species do not compensate for the increases in the abundance of other species, and could result from facilitation, resource partitioning or decreased impact of natural enemies in more diverse communities. The additive partitioning method has revealed widespread complementarity contributing to most published results. However, unanticipated negative selection effects have emerged as a widespread result. One consequence is that complementarity effects are often masked by the negative selection.

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Biographical Sketch

Andy Hector did his BSc. in Environmental Sciences at the University of Sheffield, UK (1991) before completing a PhD on insect-plant interactions at Imperial College London (1995). He then took up a post-doc at the NERC Centre for Population Biology as scientific co-ordinator of the EC-funded BIODEPTH Project. The BIODEPTH project was winner of the Earth Science section for the European Commission Descartes Award of 2001. Andy stayed on at the CPB first as a Post-Doctoral Research Fellow and later with a Royal Society University Research Fellowship. He is currently Assistant Professor (with tenure-track), at the Institute of Enviromental Sciences, University of Zürich. From 1998 to 2005 he published 35 articles in international peer-reviewed journals and books. His research interests focus on community ecology, biodiversity, and ecosystem functioning and services, with study organisms ranging from annual plants to tropical forest trees. Andy is a member of *The Faculty of 1000* for biodiversity and community ecology and co-chair, with Economist Erwin Bulte, of *ecoSERVICES,* the core project of *DIVERSITAS* that examines the effects of biodiversity change on ecosystem functioning and services.