BIODIVERSITY AND ECOSYSTEM FUNCTIONING OF SELECTED TERRESTRIAL ECOSYSTEMS: GRASSLANDS

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Contents

Summary

Research regarding the relationship between biodiversity and ecosystem functioning is presently one of the most recognized fields in ecological research. Most of the studies addressing this relationship have been conducted in experimentally established grassland communities. The applicability of results achieved in these experiments to natural ecosystems has, however, been under debate.

In this chapter, evidence is summarized for the relationship between plant diversity and ecosystem functioning from natural and semi-natural grasslands. In particular, it addresses 1) diversity effects in grasslands where extrinsic factors co-vary with diversity, 2) effects of natural species loss scenarios on ecosystem functioning, and 3) the role of plant diversity and stability.

The relationship between plant diversity and ecosystem functioning in natural and semi-natural grasslands is complex. Studies in such grasslands indicate a large amount of functional redundancy among the plant species within these ecosystems, indicating that individual species effects in the system under study are important for ecosystem functioning.

However, when environmental variability is included in the analysis, there is evidence that species that are functionally redundant under stable environmental conditions become complementary if environmental conditions change. Thus, for natural grasslands, the insurance of ecosystem functions against environmental perturbations is an important property of biodiversity.

1. Introduction

In the last decade of the past century, the effect of biodiversity on various aspects of ecosystem function created enormous interest among ecologists. (Naeem, Loreau *et al.* 2002). As a consequence numerous experiments were established in aquatic and terrestrial microcosms, as well as in experimental plant communities, to asses the functional role of biodiversity for ecosystem functioning.

In general, these studies have detected a positive, asymptotic relationship between plant diversity and productivity (see *Biodiversity and Ecosystem Functioning: Basic Principles*). Of particular interest in biodiversity–ecosystem functioning research have been studies in experimental grasslands communities, where not only general patterns but also the functional mechanisms in the relationship between plant diversity and productivity have been tested (see *Biodiversity and Ecosystem Functioning: Experimental Systems*).

Grasslands are one of the most widely distributed vegetation types worldwide, covering roughly one-fifth of the global terrestrial surface, occurring in tropical and temperate latitudes and from near sea level to high mountain slopes. By definition, grasslands include regions where the dominant vegetative cover is herbaceous, such as natural steppes, prairies and savannahs as well as semi-natural managed rangelands and pastures. While grasslands are of vast importance for agriculture as rangelands and for fodder production, they also play a critical role in global biogeochemical cycles.

For instance, grasslands are estimated to hold between 10 and 30% of the global soil carbon (Scurlock and Hall 1998). In addition, grasslands are among the most biodiverse terrestrial ecosystems. Their high levels of diversity in combination with economic and agronomic wealth, as well as their important role in global biogeochemical cycles, has triggered much interest in the effects of reduced biodiversity for the functioning of these ecosystems. Consequently, the results from biodiversity-ecosystem function studies achieved in experimental grassland communities have been readily extrapolated to natural and semi-natural grasslands.

In a press release following the completion of the BIODEPTH project, one of the largest biodiversity-ecosystem functioning studies in experimetal grasslands in the last decade, the BIODEPTH team states that: “the results of the project [...] clearly show that plant communities grow better in species-rich teams, and that their productivity decreases when diversity declines”.

Furthermore, Schmid and Schläpfer (2000) have used the results of BIODEPTH to calculate the average annual financial cost of each species lost from a grassland as a result of reduced productivity. According to these calculations, each plant species lost from grasslands in Germany would result in reduced productivity at average costs of around 0.5 billion Euros annually.

Extrapolating the results from experimental grassland communities to natural or semi-natural grasslands has, however, been highly criticized by several authors in the scientific literature (Aarssen 1997; Grime 2002; Huston and McBride 2002). First, the authors argued that if results are to be extrapolated to established natural and semi-natural grasslands, not only plant diversity but also species composition of the respective communities needs to be considered in order to separate diversity effects from compositional effects on ecosystem functioning. For example, natural grasslands are composed of only a few species that are potentially dominant in a community and of many species that are potentially subdominant or are restricted to be rare in abundance.

Even in very diverse grasslands, most productivity is delivered by the few dominant species and the large body of subdominant and rare species does not contribute to ecosystem productivity, indicating that identity and not the mere number of species lost from an ecosystem is crucial for ecosystem functioning. Second, it has been criticized that species composition in experimental grassland communities is achieved by randomly drawing species from a species pool, while species loss in natural grassland is not random but directed.

Consequently, random species deletions as simulated in the experimental grassland studies do not mimic the directional loss of species and the resulting functional shifts observed in natural grasslands so that an extrapolation of results achieved in experimental grasslands can be misleading. Finally, critics argued that biodiversity in natural grasslands is not unidirectionally driving ecosystem functioning but is itself driven by extrinsic factors. Consequently, these feedback mechanisms need to be included in studies to fully understand the effect of biodiversity for ecosystem functioning in natural or semi-natural grasslands.

The wide criticism about the applicability of results achieved in experimental grassland studies has led advocates and critics of experimental biodiversity experiments to call for an expansion of experimental studies to natural and semi-natural grasslands to test whether: i) biodiversity effects can be measured in grasslands where extrinsic factors covary with biodiversity, i.e. move beyond unidirectional causality approaches, ii) to test more realistic species loss scenarios such as those observed in nature, and iii) expand studies to ecosystems with greater environmental heterogeneity and thus test the role of biodiversity and stability.

Studies that have directly tested the effect of plant diversity on ecosystem functioning in natural or semi-natural ecosystems are, however, scarce and only few examples exist in the scientific literature. In this chapter, the evidence is summarized for plant diversity and ecosystem functioning from natural or semi-natural grasslands, and the findings are linked to observations from experimental grassland.

2. Evidence from observational studies in natural and semi-natural grasslands

Traditionally, biodiversity in studies of natural ecosystems has been viewed as a response rather than a predictive variable and numerous studies have described changing diversity along various environmental gradients at very different geographic scales, ranging from individual ecosystems to the entire globe (Huston 1994). For ecosystems, and in particular for grasslands, plant diversity has been shown to peak at intermediate levels of productivity and to decrease at high or low productivity (Al-Mufti, Sydes *et al.* 1977; Grace 1999). This traditional view of biodiversity as a response variable, where high productivity results in low diversity, seems inconsistent with the recent experimental results, where diversity is treated as a predictive variable and drives productivity. A careful evaluation, however, reveals that both approaches are complementary rather than contradictory. While the traditional approach attempts to identify the spatial variation of diversity across environmental gradients, the experimental approach determines the consequences of species loss in a given system where all environmental factors remain constant.

A conceptual model introduced by Schmid (2002) combines the hump-shaped relationship from observational biodiversity studies with results from experimental studies where high diversity results in increased productivity. Schmid introduces site fertility as a third parameter in addition to productivity and diversity. The model assumes that productivity as well as diversity is ultimately driven by site fertility and that, given an intact species pool, species richness shows a hump-shaped relationship with productivity.

If the species pool at a given fertility level is, however, reduced as a result of extinction or experimental manipulation, diversity and eventually productivity will drop below the ideal hump-shaped line. Consequently, in Schmid's model diversity is treated as a response and a predictive variable at the same time and is regarded beyond unidirectional causality approaches thus, describing a more realistic scenario than experimental, unidirectional approaches.

Schmid's model was empirically tested by Kahmen *et al* (2005a) in semi-natural grasslands in central Germany, where environmental variables, plant species richness as well as plant species composition were determined in 78 semi-natural grassland sites and the direct and indirect effects of these variables on productivity determined in a single study. As suggested by Schmid's conceptual model, the effect of site fertility on diversity showed a hump-shaped relationship that resulted from an enveloping line around the outer data points (see Figure in *Biodiversity and Ecosystem Functioning: Basic Principles*).

In Schmid's model the data points below the ideal hump shaped line are suggested to result from sites where diversity is not saturated and thus, productivity has declined. However, Kahmen *et al* (2005a) found no evidence for plant diversity as predictor for productivity, independently of testing the effect of diversity directly or after statistically controlling for environmental variables. In contrast to diversity, community composition explained productivity very well in the investigated grasslands and was an even better predictor for productivity than environmental variables and management parameters.

Lacking evidence for a diversity effect on productivity in semi-natural grasslands seems to contradict Schmid's interpretation of scatter below the hump-shaped curve that is derived from experimental studies, where an asymptotic increase of biomass has been shown with increasing plant diversity (Hector, Schmid *et al* 1999; Tilman, Knops *et a.* 1997). The observed diversity effects on productivity in the experimental studies are, however, driven by very low species levels, which are not representative for natural or semi-natural grasslands. Tilman (2002) for example states that in his study only about five species might account for the observed biodiversity effects. In contrast, the lowest diversity level in semi-natural grasslands as studied by Kahmen *et al* (2005a) contained eight plant species (per 4 m^2). It therefore seems that plant diversity effects are strongest in ecosystems where diversity has dropped below a critical level such as in experimental grasslands, but that grasslands under natural and semi-natural conditions are above such critical diversity levels so that composition of a community and thus species identity is the most important biotic predictor of ecosystem functions in these grasslands.

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Biographical Sketch

Ansgar Kahmen was born in December 1974, in Karlsruhe (Germany). From 1994 to 2001 he studied

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Dr. Kahmen's scientific interest is in linking community ecology and plant ecophysiology. In his work, stable isotopes are an important tool to study the interface between plants and their environment. Specifically, he has conducted research on plant-nutrient-water relations in a hyper-arid environment in the Taklamakan Desert of north-western China and investigated plant population dynamics of understory herbs in old-growth Douglas fir forests in the Pacific Northwest, USA. In his PhD thesis he investigated different functional aspects of the biodiversity and ecosystem functioning relationship in semi-natural grasslands in central Germany.