A trait-based experimental approach to understand the mechanisms underlying biodiversity–ecosystem functioning relationships

Anne Ebeling[a,*], Sven Pompe[a,b], Jussi Baade[c], Nico Eisenhauer[a],
Helmut Hillebrand[d], Raphael Proulx[e], Christiane Roscher[f], Bernhard Schmid[g],
Christian Wirth[h], Wolfgang W. Weisser[a,b]

[a]*Institute of Ecology, University of Jena, Dornburger Straße 159, D-07743 Jena, Germany*
[b]*Terrestrial Ecology Research Group, Department of Ecology and Ecosystem Management, Center for Food and Life Sciences Weihenstephan, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, D-85350 Freising-Weihenstephan, Germany*
[c]*Department of Geography, University of Jena, Löbdergraben 32, D-07743 Jena, Germany*
[d]*Institute for Chemistry and Biology of the Marine Environment, Carl-von Ossietzky University, D-26111 Oldenburg, Germany*
[e]*Département des sciences de l'environnement, Université du Québec à Trois-Rivières, Trois-Rivières, QC G9A5H7, Canada*
[f]*Department for Community Ecology, Helmholtz Centre for Environmental Research – UFZ, Theodor-Lieser-Straße 4, D-06120 Halle, Germany*
[g]*Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstraße 190, CH-8057 Zurich, Switzerland*
[h]*Department for Systematic Botany and Functional Biodiversity, University of Leipzig, Johannesallee 21-23, D-04103 Leipzig, Germany*

Abstract

Plant functional characteristics may drive plant species richness effects on ecosystem processes. Consequently, the focus of biodiversity–ecosystem functioning (BEF) experiments has expanded from the manipulation of plant species richness to manipulating functional trait composition. Involving ecophysiological plant traits in the experimental design might allow for a better understanding of how species loss alters ecosystem processes. Here we provide the theoretical background, design and first results of the 'Trait-Based Biodiversity Experiment' (TBE), established in 2010 that directly manipulates the trait composition of experimental plant communities.

Analysis of six plant traits related to resource acquisition and use were analyzed using principal component analysis of 60 grassland species. The resulting two main axes describe gradients in functional similarity, and were used as the basis for designing plant communities with different functional and species diversity levels. Using such an approach allowed us to manipulate different levels of complementarity in spatial and temporal plant resource acquisition. In contrast to previous biodiversity experiments, the TBE is designed according to more realistic scenarios of non-random species loss along orthogonal

*Corresponding author. Tel.: +49 03641 949417; fax: +49 03641 949402.
E-mail address: anne.ebeling@uni-jena.de (A. Ebeling).

axes of species trait dissimilarities. This allows us to tease apart the relative importance of selection and complementarity effects on multiple ecosystem processes, and to mechanistically study the consequences of plant community simplification.

Zusammenfassung

Es wird angenommen, dass funktionelle Pflanzenmerkmale verantwortlich sind für beobachtete Effekte von Pflanzendiversität auf Ökosystemfunktionen, wodurch sich der Fokus der Biodiversitätsforschung von der Betrachtung der Effekte von Pflanzenartenzahlen hin zu der Betrachtung von Pflanzenmerkmalen in einer Gemeinschaft erweitert hat. Die Berücksichtigung von funktionellen Pflanzenmerkmalen hilft möglicherweise zu verstehen, wie der Verlust von Arten Ökosystemprozesse beeinflusst. Unseres Wissens wurde jedoch die funktionelle Ähnlichkeit verschiedener Pflanzenarten zueinander noch nie als Grundlage für ein Grasland-Biodiversitätsexperiment genutzt.

Wir präsentieren den theoretischen Hintergrund, das experimentelle Design und erste Ergebnisse eines sogenannten ‚Trait-Based Biodiversity Experiments' (TBE), welches 2010 im Rahmen des Jena Experimentes etabliert wurde und bei welchem direkt die funktionelle Diversität von Pflanzeneigenschaften manipuliert wurde.

Mithilfe einer Hauptkomponentenanalyse wurden sechs Pflanzenmerkmale von 60 Graslandarten analysiert, die bedeutend für Ressourcenaufnahme und -nutzung sind. Dabei bildeten die Pflanzenarten, die entlang zweier unabhängiger Achsen angeordnet waren, Gradienten in ihrer funktionellen Ähnlichkeit, die als Basis für das Design des TBE dienten. Auf neu angelegten Versuchsflächen etablierten wir Pflanzengemeinschaften mit unterschiedlicher Pflanzenartenzahl, die sich in ihrer räumlichen und zeitlichen funktionellen Komplementarität unterscheiden. Das neuartige Design des TBE erlaubt es uns in Zukunft den relativen Einfluss von Selektions- und Komplementaritätseffekten auf Ökosystemprozesse zu bestimmen und ermöglicht die mechanistische Erforschung der Konsequenzen von vereinfachten Lebensgemeinschaften.

Introduction

In the past decades an increasing number of studies has experimentally investigated the relationship between plant diversity and ecosystem functions such as plant productivity, carbon and nutrient cycling, and trophic interactions (Cardinale et al., 2011). Such biodiversity experiments assembled artificial plant communities with different levels of diversity to decouple the manipulated aspects (e.g., plant species richness) from environmental factors (e.g., site fertility), and to test for a causal relationship between biodiversity and ecosystem processes (Schmid & Hector, 2004). With the increasing recognition that plant species richness has a general positive effect on many ecosystem processes (Cardinale et al., 2012; Allan et al., 2013), new questions have arisen about the mechanisms underlying these relationships.

The first generation of biodiversity experiments manipulated plant productivity levels rather than plant species richness (Tilman, Wedin, & Knops, 1996; Huston, 1997), making it difficult to identify the drivers that could explain the observed positive relationship between species richness and productivity (Tilman et al., 1996; Huston, 1997). Subsequent experiments manipulated plant species richness directly and also found positive diversity–productivity relationships (Tilman, Lehman, & Thomson, 1997; Hector et al., 1999). A controversy arose whether these were caused through a selection effect, i.e. the increased probability of selecting a productive species in diverse mixtures when species are added in a fully randomized way, or a complementary effect, i.e. niche complementary (higher resource use efficiency in diverse communities or different pathogen niches) (Loreau & Hector, 2001). Later experiments directly tested for complementarity effects, e.g. by using large species pools and controlling species richness and functional group numbers (Roscher et al., 2004). Criticism on the artificially created plant communities of sown biodiversity experiments (Leps, 2004) led to alternative experimental approaches such as species removal experiments (e.g. Symstad & Tilman, 2001; Diaz, Symstad, Chapin, Wardle, & Huenneke, 2003; Urcelay et al., 2009) with their own limitations of confounding species richness and community density.

Most recently, the focus of biodiversity research has shifted toward manipulating functional (or phylogenetic) diversity directly (Cadotte, Albert, & Walker, 2013), because functional differences among plant species are assumed to be key in understanding diversity–ecosystem functioning relationships. Previous research has shown that the relationship between species richness and functional diversity is complex and context dependent (Cadotte, Carscadden, & Mirotchnick, 2011), and is likely to underlie both selection and complementarity effects (e.g. Tilman, 1999). In addition, it is increasingly accepted that functionally important aspects of biodiversity are better represented through measures of functional trait composition (Díaz & Cabido, 2001) than through traditional functional group assignments (e.g. legumes, forbs, grasses). In this context, functional traits are defined as