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Plant diversity effects on arthropods and arthropod-dependent ecosystem functions in a biodiversity experiment

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Abstract

Biodiversity-ecosystem function experiments test how species diversity influences fundamental ecosystem processes. Historically, arthropod driven functions, such as herbivory and pest-control, have been thought to be influenced by direct and indirect associations among species. Although a number of studies have evaluated how plant diversity affects arthropod communities and arthropod-mediated ecosystem processes, it remains unclear whether diversity effects on arthropods are sufficiently consistent over time such that observed responses can be adequately predicted by classical hypotheses based on associational effects. By combining existing results from a long-term grassland biodiversity experiment (Jena Experiment) with new analyses, we evaluate the consistency of consumer responses within and across taxonomic, trophic, and trait-based (i.e. vertical stratification) groupings, and we consider which changes in arthropod community composition are associated with changes in consumer-mediated ecosystem functions.

Overall, higher plant species richness supported more diverse and complex arthropod communities and this pattern was consistent across multiple years. Vegetation-associated arthropods responded more strongly to changes in plant species richness than ground-dwelling arthropods. Additionally, increases in plant species richness were associated with shifts in the species-abundance distributions for many, but not all taxa. For example, highly specialized consumers showed a decrease in dominance and an increase in the number of rare species with increasing plant species richness. Most ecosystem processes investigated responded to increases in plant species richness in the same way as the trophic group mediating the process, e.g. both herbivory and herbivore diversity increase with increasing plant species richness. In the Jena Experiment and other studies, inconsistencies between predictions based on classic hypotheses of associational effects and observed relationships between plant species richness and arthropod diversity likely reflect the influence of multi-trophic community dynamics and species functional trait distributions. Future research should focus on testing a broader array of mechanisms to unravel the biological processes underlying the biodiversity-ecosystem functioning relationships.

Keywords: Plant-consumer interactions; Invertebrates; Herbivores; Carnivores; Pollinators; herbivory; Seed predation; Parasitism

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Introduction

Over the past several decades, we have come to realize that species are being lost, gained, and redistributed at a rate that is faster than expected (Barnosky et al., 2011; Ceballos et al., 2015). This trend has caused scientists to conduct experiments focused on understanding the question "Does biodiversity 'matter' for ecosystems?" Specifically, the last 30 years have seen a strong increase in the number of experiments investigating the effects of biodiversity on various aspects of ecosystem functioning (Balvanera et al., 2006; Tilman, Isbell, & Cowles, 2014). Because plants fix carbon from the atmosphere and ultimately determine the amount of carbon entering an ecosystem, and because plant communities are easier to handle, the manipulation of the producer level provided an obvious starting point for experiments testing the relationship between biodiversity and ecosystem functioning (BEF) (but see Naeem, Thompson, Lawler, Lawton, & Woodfin, 1994). The ultimate aim is to consider how multitrophic interactions are influencing multiple ecosystem functions (Hines et al., 2015).

Arthropods are a dominant component of biodiversity in terrestrial ecosystems, driving important ecosystem processes such as pollination, herbivory or pest-control, and affecting nutrient cycling in direct and indirect ways (reviewed in Yang & Gratton, 2014). For example, herbivorous insects can directly reduce standing biomass of plants through consumption of plant tissue. Alternatively, by consuming seeds, herbivores can indirectly influence plant community composition by reducing the success of seed-limited plant species without directly damaging plants (Maron & Simms, 1997). Herbivores also influence ecosystem processes by increasing nutrient leaching from foliage, influencing nutrient availability by excretion, transmitting plant pathogens, and changing plant resource allocation (Finke, 2012; Yang & Gratton, 2014). At higher trophic levels, carnivores and omnivores can control herbivore communities by regulating their density and composition. Given the strong influence of consumers on ecosystem functioning, a key focus in ecological research has been to evaluate the role of consumers as a response to, and also a cause of, BEF relationships.

Several classic hypotheses describe how increasing plant diversity should affect consumer communities and thereby ecosystem functions that they drive (Table 1, left column). The hypotheses can be broadly categorized as "Associational effects" hypotheses (reviewed in Barbosa et al., 2009; Underwood, Inouye, & Hambäck, 2014). However, these hypotheses are not mutually exclusive and often focus on populations of focal species rather than the entire community or on ecosystem processes. Therefore, considering them together provides somewhat conflicting predictions, leaving uncertainty as to whether consumer effects on ecosystem processes should be strengthened or diluted in more diverse ecosystems (Table 1, middle column). Associational effects can be negative (Associational susceptibility) or positive (Associational resistance) for any given species (Barbosa et al., 2009), and can influence plants, consumers, and feedback between the two. We structure our review according to the classical hypotheses previously proposed (Table 1, left column). Since the development of these hypotheses, researchers have provided mixed empirical support (Table 1, middle column). Variation among results may be due to system-specific differences, biases imposed by short-term experiments that report responses of a narrow subset of the community, or an overemphasis on the response of consumer species richness as opposed to more detailed consideration of consumer community composition.

Here we use a case study approach to address some of those biases and evaluate a more comprehensive representation of the effects of plant diversity on arthropod communities and arthropod-mediated ecosystem processes. The Jena Experiment is a long-term (15 years) grassland biodiversity experiment, where the response of arthropods and arthropod-mediated processes to the manipulation of plant species richness have been measured (Table 1, right column). Using data from this experimental platform helps to evaluate questions about the relationship between plant diversity and arthropod communities for several reasons. First, an experimental manipulation of plant species richness in a replicated design allows for tests of plant diversity effects per se, which are not confounded by concomitant changes in environmental conditions. Second, due to the long-term character of the experiment, consistent patterns can be derived from observations in multiple years or seasons. Observations in single years or seasons could differ from consistent patterns, due to high inter- or intra-annual variation. The long time since the establishment of the experimental platform in 2002 has given arthropods enough time to colonize plots, making the plant diversity gradient well suited for examining shifts in arthropod communities and ecosystem processes (Eisenhauer et al., 2011). Third, arthropod communities in the Jena Experiment have been identified to high taxonomic resolution (mainly species level), allowing us to evaluate the influence of plant diversity on measures of community composition, such as evenness, dominance or rarity of species within communities, as well as functional composition of the community (based on species traits).

In this paper, we build on published studies from the Jena Experiment (Weisser et al., 2017) and new analyses to evaluate (1) how arthropod communities respond to changes in plant diversity, and (2) if those changes affect arthropod-mediated ecosystem processes. The ecosystem processes that we consider include herbivory, predation, seed dispersal, seed predation, and parasitism. We report the results of new analyses that synthesize consumer data over multiple years for the first time, and extend previously reported measures of arthropod community structure (diversity, species composition, species interactions) to include species abundance distributions. We evaluate the species and ecosystem functioning responses observed in the Jena Experiment in the context of

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