Preface: Mechanistic links between biodiversity and ecosystem functioning

Biodiversity–ecosystem functioning (BEF) research is currently one of the most vibrant research areas in Ecology, as ecosystem functioning is critical for human well-being, and the time available to make decisions for preserving global biodiversity is short. Since the first experiments in the early 1990s, BEF research has evolved, as the knowledge gained has inspired new questions, ideas, and approaches. By combining case studies, data syntheses, reviews, and perspectives papers, this special issue on the *Mechanisms underlying the relationship between biodiversity and ecosystem functioning* provides an overview of the key achievements, current research frontiers, and future perspectives in BEF research, with a strong focus on terrestrial, mostly grassland, ecosystems. Moreover, this special issue is mostly based on research in the framework of the Jena Experiment, a large-scale and long-term grassland BEF experiment. Since its establishment in 2002, the Jena Experiment has focused on grassland biodiversity effects on multitrophic interactions and carbon and nutrient cycling and has utilized trait-based approaches to understand the mechanisms underlying BEF relationships. At the same time, researchers of the Jena Experiment have synthesized data and information from other experiments and natural ecosystems—this plethora of approaches is reflected by the diversity of chapters of this special issue. The first chapter provides a short history of the key advances and future challenges of BEF research. The subsequent chapters fall into two broad categories: Chapters 2–6 cover case studies, reviews, and syntheses that explore different mechanisms underlying BEF relationships; and Chapters 7–10 review current BEF knowledge to provide recommendations for future research. Together, this special issue represents a synthesis of the *status quo* in terrestrial BEF research as well as stimulating perspectives of the most pressing challenges and important future research directions in this field.

In Chapter 1, Eisenhauer et al. (2019a) review the key achievements of hundreds of experiments that have manipulated biodiversity as an independent variable and present a multitrophic, eco-evolutionary perspective on future biodiversity–ecosystem functioning research. The authors summarize the history of research that inspired BEF experiments. For instance, one important step was to appreciate that biodiversity is not only a dependent variable of the environmental context, but that biodiversity itself is

important for the functioning of ecosystems. Based on the extensive scientific debate, the design and focus of BEF experiments changed over time, and the authors explain how this field of research became more integrative in terms of scientific disciplines. As a result, in addition to a general exploration of BEF relationships, the underlying mechanisms came into focus. A whole-ecosystem perspective allowed an exploration of the implications of BEF relationships for ecosystem services, contributing to the establishment of and discussions in The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES, 2018). In this chapter, Eisenhauer and colleagues argue that a multitrophic and eco-evolutionary perspective of biotic interactions, in random- and non-random biodiversity change scenarios, will be key to further advances in the field. They discuss how multitrophic interactions and their eco-evolutionary underpinnings will help to understand the context dependency of BEF relationships and to scale up BEF to management-relevant spatial scales across ecosystem boundaries, potentially allowing implementation of this knowledge for ecosystem management, society, and policy.

In order to better understand BEF relationships, the key role of plants needs to be explored, such as competition for above- and belowground resources. In Chapter 2, Barry et al. (2019b) present the results of a case study that explores plant species richness effects on above- and belowground plant productivity in the Trait-Based Experiment (Ebeling et al., 2014) in the Jena Experiment (Roscher et al., 2004). Specifically, the authors explore potential relationships between above- and belowground overyielding at the community and species level. Barry et al. (2019b) find support for positive correlations between above- and belowground overyielding at the community level and at the species level for 8 out of 13 investigated species. Notably, plants tended to invest more in overyielding aboveground than belowground, which leads to the conclusion that aboveground competition (i.e. for light) might be stronger than for belowground resources like nutrients. Moreover, these results indicate that the competitive environment changes along the plant diversity gradient, which may lead to differential biomass allocation into plant organs and potentially different selection pressures (Tilman and Snell-Rood, 2014; Zuppinger-Dingley et al., 2014). Related changes in plant traits over time might contribute to increasing biodiversity effects in long-term experiments (Eisenhauer et al., 2019a, Chapter 1; Tilman and Snell-Rood, 2014).

Another mechanism underlying positive BEF relationships may be that high-diversity plant communities have a higher capacity to adapt to

environmental changes through shifts in dominance structure and community composition. In Chapter 3, Vogel et al. (2019b) synthesized data from five long-term biodiversity experiments in grassland. These experiments manipulated different drivers of environmental change related to stress (e.g. drought) and nutrient availability (e.g. nitrogen addition). Vogel et al. (2019b, Chapter 3) used species-specific plant traits to calculate functional diversity and determined the phylogenetic diversity of the plant communities. Overall, high-diversity plant communities indeed showed a greater capacity to shift in functional trait space over time, supporting the notion that they are more flexible at adapting to different environments (Isbell et al., 2017) and maintaining high and stable levels of ecosystem functioning (Isbell et al., 2015).

Empirical evidence suggests that short-term variation of plant productivity between seasons is important for understanding the stability of ecosystem functions (Wagg et al., 2017), and that studying the fine temporal-scale dynamics of ecosystem processes might provide additional insights into species interactions and biodiversity effects. In Chapter 4, Guimarães-Steinicke et al. (2019) used terrestrial laser scanning to study the effects of different plant diversity facets on an approximated measure of plant growth every 2 weeks across two growing seasons in the Trait-Based Experiment (Ebeling et al., 2014). Terrestrial laser scanning was found to be an appropriate method to quantify plant growth in a nondestructive way. Moreover, they report that different diversity facets varied in their explanatory power for plant productivity across the seasons, with functional identity being of higher importance after disturbance (e.g. mowing) and functional dispersion being of higher significance when competition for light was high (e.g., close to peak biomass). These results indicate that in order to understand how plant interactions contribute to BEF relationships, the temporal dynamics of interactions and activity patterns need to be explored in detail, as the functions of plant interactions can range between facilitation and competition depending on the environmental context, such as along the plant diversity gradient (Wright et al., 2017).

In the same experiment, Beugnon et al. (2019) report in Chapter 5 the community responses of soil animals to variations in plant species richness, functional diversity, and the community-weighted means of different plant traits related to spatial and temporal resource use (Ebeling et al., 2014). While significant plant diversity effects on soil organisms have been reported before (e.g., Eisenhauer et al., 2013; Scherber et al., 2010), the underlying mechanisms are not well understood, and exploring the role

of plant traits may be a promising approach to gain better insight (Eisenhauer and Powell, 2017; Laliberté, 2016). Beugnon et al. (2019, Chapter 5) classified different groups of soil fauna by considering their body size (meso- and macrofauna) and feeding strategy (prey [i.e. mostly detritivores and herbivores] and predators). Plant traits had a higher predictive power than plant species richness in explaining variation in soil animal abundances and diversity. However, the significance of different traits varied across the soil animal groups, contributing further evidence to the working hypothesis that different plant diversity facets are key to driving consumer communities (Schuldt et al., 2019), ecosystem processes (Guimarães-Steinicke et al., 2019, Chapter 4), and their stability (Craven et al., 2018).

In Chapter 6, Lange et al. (2019) summarized recent findings for the effects of plant diversity on nutrient, carbon, and water cycles in the Jena Experiment. In line with previous studies (e.g. Fornara and Tilman, 2008; Lange et al., 2015), carbon and nitrogen stocks accumulated over the course of the experiment, and this increase was more pronounced at higher than at lower plant diversity. However, they observed the opposite temporal trend for nitrogen and phosphorous concentrations in soil solution, an effect that they relate to the constant removal of plant biomass from the experimental plots during harvest. Moreover, Lange et al. (2019, Chapter 6) discuss the important role of soil microbial communities in soil nutrient dynamics, which may primarily be driven by rhizodeposition (Lange et al., 2015). This effect of root-derived inputs was found to be more pronounced at high plant diversity, with effects also reaching down to deeper soil layers. The authors conclude that tightening interactions between plants and soil microbes over time may not only be important for altered nutrient cycling and stocks along the plant diversity gradient but also influence other ecosystem functions, such as plant productivity.

Soil feedback effects on plant productivity will be studied in the new ΔBEF Experiment, which is introduced by Vogel et al. (2019a) in Chapter 7. This experiment was inspired by observations of a strengthening biodiversity effect on ecosystem functioning over time (e.g., Guerrero-Ramírez et al., 2017; Reich et al., 2012). Vogel et al. (2019a, Chapter 7) present the rationale and design of the experiment to explore soil history effects on ecosystem functioning and to separate plant diversity-induced gradual changes in abiotic and abiotic conditions from environmental effects. This will be achieved by comparing soil treatments, with and without plant community-specific history, to the long-term plots of the Jena

Experiment, set up in 2002 (Roscher et al., 2004). The first results show significant differences among the experimental treatments for different ecosystem functions like plant productivity and soil nematodes. Differences in soil conditions and communities are likely to have even stronger feedback effects on multiple ecosystem functions in the future (Lange et al., 2019, Chapter 6). However, the authors note that future studies should also comanipulate plant and soil history in order to investigate any potential interactions.

In Chapter 8, Barry et al. (2019a) present a unifying framework based on ecological first principles of resources, and abiotic and biotic conditions. The authors review the ways in which ecosystem functioning may be linked to coexistence in plant communities and the implications for BEF relationships. They explore population-level effects of resources and abiotic and biotic conditions on fecundity, growth, and survival of plants, and how the ecological first principles influence trade-offs among fecundity, growth, and survival, which in turn affect plant coexistence and ecosystem functioning. This combination of theory and empirical results exemplifies how complementary theories from otherwise unconnected research fields can be brought together to study the reciprocal relationships between different coexistence processes and ecosystem functioning. While a simple mapping of biological processes that promote coexistence to those generating BEF relationships might not be feasible (Turnbull et al., 2016), coexistence theory can help understanding the context dependency of BEF relationships (Eisenhauer et al., 2019a, Chapter 1) and developing working hypotheses for future experiments.

In Chapter 9, Hines et al. (2019) use a keyword co-occurrence analysis to study the past three decades of BEF research. They document the rapid growth of the field and define four core research domains that have emerged over time. Notably, the authors also identify elements that connect associated research domains, such as the integrative domain of food web research that link BEF experiments to science policy. Given the important role of plant–consumer interactions in multiple ecosystem functions and that many consumer species at higher trophic levels of food webs may be particularly sensitive to environmental change (Eisenhauer et al., 2019a, Chapter 1; Hines et al., 2015), there is concern that plant–consumer interactions will suffer from biodiversity declines (Dirzo et al., 2014; Eisenhauer et al., 2019a). That multitrophic biodiversity research integrates different BEF research domains suggests that food web research must have a high research priority in the future.

Despite these now obvious links between multitrophic biodiversity and ecosystem functioning and the recent establishment of IPBES, knowledge from BEF research has, to date, had little influence on policy and the management of 'real-world' ecosystems in agriculture and managed grasslands (Eisenhauer et al., 2019a, Chapter 1). In Chapter 10, Manning et al. (2019) try to bridge this gap by classifying BEF research into three clusters by considering the level of human control over species composition and the spatial scale of the BEF studies. They suggest how the research of each cluster can inform particular fields of ecosystem management, discuss the barriers to and challenges of knowledge transfer, and present means to overcome these challenges. Notably, 1:1 comparisons between BEF experiments and real-world ecosystems can be misleading (Wardle, 2016), but important mechanisms have been identified that play a role in real-world ecosystems and that have advanced our understanding of ecosystem responses to species gains and losses (Eisenhauer et al., 2016; Isbell et al., 2017). Manning et al. (2019, Chapter 10) recommend an intensification of transdisciplinary research that considers the social–ecological context of the ecosystems in order to address challenges of sustainable land use. They conclude that the social and economic value of biodiversity for ecosystem services needs to be recognized and communicated to land managers and policy makers. The clustering approach may be a first critical step towards operationalizing BEF insights for ecosystem management, society, and policy (Eisenhauer et al., 2019a, Chapter 1).

Taken together, the chapters of this special issue show that there is no one single mechanism that can explain all BEF relationships, but that multiple, nonmutually exclusive mechanisms are likely to link the multitrophic biodiversity of ecosystems to the multiple functions provided by ecosystems (Fig. 1; e.g. Eisenhauer et al., 2019a, Chapter 1; Hines et al., 2019, Chapter 9). The field has moved away from a purely plant-centred perspective that mainly focused on resource use complementarity and competition. The list of potential BEF mechanisms presented here is not supposed to be comprehensive. Yet, the chapters of this special issue suggest that in addition to studying competitive interactions (Barry et al., 2019b, Chapter 2) and the consequences for and feedback effects of plant coexistence (Barry et al., 2019a, Chapter 8), changes in soil abiotic (Lange et al., 2019, Chapter 6) and biotic conditions (Eisenhauer et al., 2019a, Chapter 1; Vogel et al., 2019a, Chapter 7), multitrophic interactions in complex food webs (Eisenhauer et al., 2019a, Chapter 1; Hines et al., 2019, Chapter 9), and changes in plant traits and their composition (Beugnon et al., 2019, Chapter 5; Vogel et al., 2019b, Chapter 3) are likely to contribute to different biodiversity facets driving the functioning of

Fig. 1 Schematic illustration of researchers with different expertise exploring several nonmutually exclusive mechanisms underlying BEF relationships (as indicated by the multiple ends of the Gordian knot). Depicted are broad categories of mechanisms, including mutualism of plants with multitrophic interaction partners above and below the ground (top left), above- and belowground complementarity in habitat space use (bottom left), the role of plant pathogens (top right), and plant community-induced changes in nutrient dynamics (bottom right). Apart from testing the different hypotheses presented in this special issue, a future challenge will be to integrate the respective mechanisms in order to understand in which contexts they may prevail. Ultimately, by addressing and integrating these different hypotheses, i.e., cutting the Gordian knot, BEF research will become a predictive science.

ecosystems (Beugnon et al., 2019, Chapter 5; Guimarães-Steinicke et al., 2019, Chapter 4) (Fig. 1). Accordingly, complementary future research directions are proposed to develop a more comprehensive understanding of the mechanisms underlying BEF relationships across environmental contexts as well as spatial and temporal scales. Ultimately, such knowledge will be integral to information for land managers and policy makers about implications of BEF research for the sustainable management of ecosystems (Eisenhauer et al., 2019a, Chapter 1; Manning et al., 2019, Chapter 10).

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