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FACILITATIVE MECHANISMS UNDERLYING THE EFFECTS OF BIODIVERSITY ON ECOSYSTEM FUNCTIONING

Guest Editorial

Biodiversity and ecosystem functioning: Have our experiments and indices been underestimating the role of facilitation?

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Abstract

1. After 25 years of biodiversity experiments, it is clear that higher biodiversity (B) plant communities are usually more productive and often have greater ecosystem functioning (EF) than lower diversity communities. However, the mechanisms underlying this positive biodiversity–ecosystem functioning (BEF) relationship are still poorly understood.
2. The vast majority of past work in BEF research has focused on the roles of mathematically partitioned complementarity and selection effects. While these mathematical approaches have provided insights into underlying mechanisms, they have focused strongly on competition and resource partitioning.
3. Importantly, mathematically partitioned complementarity effects include multiple facilitative mechanisms, including dilution of species-specific pathogens, positive changes in soil nutrient cycling, associational defence and microclimate amelioration.
4. *Synthesis*. This Special Feature takes an experimental and mechanistic approach to teasing out the facilitative mechanisms that underlie positive BEF relationships. As an example, we demonstrate diversity-driven changes in microclimate amelioration. Articles in this Special Feature explore photoinhibition, experimental manipulations of microclimate, lidar examinations of plant canopy effects and higher-order trophic interactions as facilitative mechanisms behind classic BEF processes. We emphasize the need for future BEF experiments to disentangle the facilitative mechanisms that are interlinked with niche complementarity to better understand the fundamental processes by which diversity regulates life on Earth.

KEYWORDS

complementarity, legumes, mechanism, microclimate, partition, pathogens, selection

1 | INTRODUCTION

Nearly 30 years ago, researchers gathered in Bayreuth, Germany to discuss the role of biodiversity (B) on ecosystem functioning (EF; Schulze & Mooney, 1994). These researchers were motivated by the mounting evidence that the ecosystem services upon which humans rely, such as carbon storage, resistance to environmental disturbance, pollination, nutrient cycling and agricultural yield, are affected by more than just abiotic conditions such as precipitation and temperature. They were interested in empirical evidence (Schulze & Mooney, 1994) indicating that some species, and perhaps biodiversity in general, might be fundamentally important for maintaining the health of our planet.

Since then, ecologists have established hundreds of experiments to explore the effects of biodiversity on ecosystem functioning (Grossman et al., 2019; Mulder et al., 2001; Naeem et al., 1994; O'Connor et al., 2016; Sun et al., 2017; Tilman & Downing, 1994; Tilman et al., 2006; Wilsey et al., 2013). The vast majority of this work has been done using random assemblages of species in grassland communities measuring annual net primary production (ANPP) or annual yield (Cardinale et al., 2011). The evidence from these experiments has been overwhelmingly consistent; when biodiversity is lost from a patch of land, some ecosystem functions are reduced (O'Connor et al., 2016). Most commonly, low diversity grasslands have been shown to yield less biomass than high diversity grasslands (Cardinale et al., 2011). While the effect of diversity on ecosystem function is remarkably consistent, the fundamental ecological mechanisms underlying this pattern remain poorly understood. Specifically, ecologists are still unravelling the intertwined processes that produce what has come to be known as 'the complementarity effect' (Barry et al., 2019).

In the early 2000s, critique of the randomized experimental biodiversity study design (e.g. Hector et al., 1999; Tilman et al., 2001) led to questions about whether the effects of biodiversity on productivity were the result of ecological interactions between species, or merely due to a higher probability of including productive species in the high diversity plots—the so-called probabilistic sampling effects (Huston, 1997). In response to this critique, Loreau and Hector (2001) proposed the mathematically tractable additive partition (Box 1). The additive partitioning method allowed for researchers to measure species-specific biomass in monoculture, compare this to species-specific biomass in mixture and determine whether species were growing better or worse with interspecific neighbours. When averaged across all species in a community, this is very powerful: one can conclude that there are ecological interactions occurring between species in higher diversity ecosystems that are not occurring in lower diversity ecosystems. Within the context of BEF research, this mathematical index came to be called 'the complementarity effect'.

Importantly, complementarity effects describe a great variety of direct and indirect ecological interactions between plants (resource partitioning, pathogen load, mycorrhizal interactions, ameliorated microclimate conditions, nutrient release, pollinator responses) that may result in individual species performing better when growing in mixture than in monoculture (Barry et al., 2019; Wright et al., 2017). More complete occupation of niches in polycultures and the alleviation of intense intraspecific competition (two related ideas) have been focal mechanisms in complementarity studies for decades, but recent analyses indicate that such 'resource partitioning' as a primary driver of BEFs is not well supported by the data (Barry et al., 2020; Jesch et al., 2018). Instead, interspecific facilitation may be more important than originally considered. The goal of this Special

BOX 1 Additive partitioning in biodiversity–ecosystem functioning literature.

One of the most common ways to explore the mechanisms underlying BEF relationships is by using the additive partitioning approach developed by Loreau and Hector (2001). This approach relies on two quantities: the biomass of each species growing in mixture and the expected biomass of each species growing in mixture based on their growth in monoculture. This approach assumes that the experimental design is a replacement series experimental design (discussed by Wagg et al., 2019). Briefly, a replacement series design is one in which each monoculture is sown with, say, 100 seeds of that species. In mixture, the community is still sown with 100 seeds, but this is subdivided equally among the species that are planted. For a 10-species mixture, there are thus only 10 seeds of each species. This design means that the expected biomass of each species in mixture is the monoculture biomass divided by the species richness of the mixture. The relative yield is then how much each species deviates from this expected biomass.

The LH approach 'partitions' the net effect of biodiversity (Figure 1a) into the selection effect and the complementarity effect. The selection effect describes the covariance between the monoculture biomass of each species and the biomass of each species growing in mixture. Conceptually, if the species that produces the most biomass in monoculture *also* produces the most biomass in mixture, then a positive selection effect occurs (Figure 1b). This could be because the most productive species is competitively superior, but it could also be due to other mechanisms (e.g. facilitation). Alternatively, a positive complementarity effect indicates that the majority of species produce more relative yield in mixture than they do in monoculture (Figure 1c, a full discussion of the Hector and Loreau partition is also discussed in Clark et al., 2019). Importantly, selection and complementarity effects do not map directly onto ecological mechanisms such as resource partitioning, facilitation via microclimate amelioration or pathogen suppression (reviewed by Barry et al., 2019).

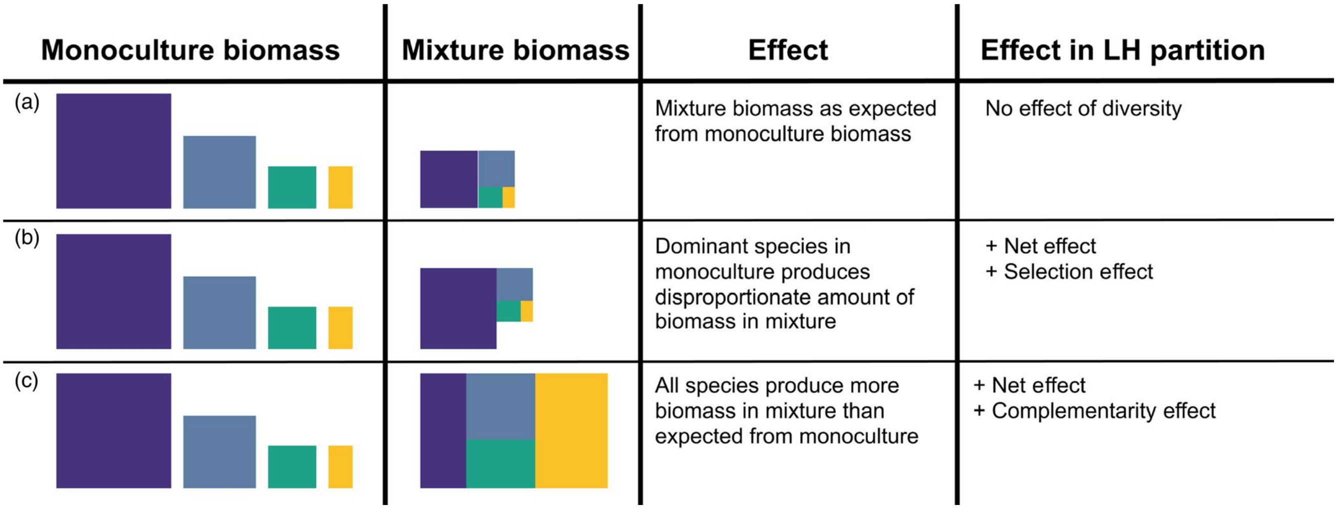

FIGURE 1 Visual depiction of the Loreau and Hector (2001) additive partitioning method. Each color represents a different species and the size of the box represents the amount of biomass produced by that species. All species are sown equally in a replacement series design. (a) Mixture biomass is predicted based on the performance of each species in monoculture. Because each species is planted at a lower density in mixture than in monoculture, it appears as if each species is growing less than expected. This is not the case. Each species is planted at ¼ the density in mixture and is producing exactly ¼ the biomass in mixture. (b) The dark blue species produces the most biomass in monoculture but also increases its relative yield in mixture. In this case, the LH partition will calculate a positive overall net effect of biodiversity and a positive selection effect. (c) Each species produces more in mixture than what is expected based on their performance in monoculture. The LH partition will calculate a positive net effect of diversity and a positive complementarity effect

Feature is to take a deeper look at facilitative mechanisms that underlie BEFs. These mechanisms may often be mathematically encompassed in the calculations of complementarity effects, but are different ecological processes. If facilitation is a key process in community diversity and ecosystem functioning, then communities may be fundamentally more interdependent and self-organized than we think.

1.1 | A brief history of facilitation in BEF research

Facilitation, as a major ecological process in community organization, has a long history. As early as the late 19th century, ecologists recognized the role of 'pioneer' species that ameliorated the environment after disturbance to make it habitable by other species (reviewed in Connell & Slatyer, 1977). And as early as 1910, Forrest Shreve noticed that young saguaro cacti were almost always found beneath woody plants (Shreve, 1910). This association was then studied intensively and was later coined the 'nurse plant syndrome' (Niering et al., 1963; Steenbergh & Lowe, 1969; Turner et al., 1966). These studies were contemporary with some of the earliest experiments on competition. In the early 1990s, Mark Bertness propelled facilitation into modern plant community ecology via experiments with salt marsh species along elevational gradients (Bertness & Shumway, 1993; Bertness, 1991; Bertness & Hacker, 1994; Bertness & Yeh, 1994). Bertness and Callaway (1994) proposed predictable relationships between the abiotic environment and the direction of plant interactions with the hypothesis that facilitation is more common in stressful environments (Bertness & Callaway, 1994). Since then beneficial or cooperative interactions have been experimentally reported through dozens of mechanisms and hundreds of studies (Callaway, 2007).

In the last 20 years, experimental work has identified clear cases where facilitation underlies positive BEF relationships. To our knowledge, the first study to use the randomized replacement series biodiversity study design (i.e. Wagg et al., 2019), and to find facilitation as a potential driver of BEF, was that by Johannes Knops et al., (1999) who built experimental communities that varied in diversity and then quantified disease severity on target plant species (Knops et al., 1999). All diseases that invaded were species-specific and for each of the four target plant species, foliar disease was highly negatively correlated with plant species richness. Not much later, Maria Caldeira et al., (2001) constructed plots with different numbers of herbaceous species in Portugal, and measured plant biomass and stable carbon isotope ratios (δ13C) in the leaves of five different species (Caldeira et al., 2001). Plot biomass increased with diversity, and four of the five target species had higher water-use efficiencies in polycultures than in monocultures. These higher water-use efficiencies were attributed to microclimate amelioration (though this explanation was observational and not tested experimentally, but see Kikvidze, 1996; Wright et al., 2015, and Aguirre et al. this issue). Importantly, facilitation was not shown via experimental manipulation to be the cause of the diversity–productivity relationship, instead facilitation occurred in the same plots in which diversity increased biomass.

Mulder et al. (2001) explicitly tested the stress gradient hypothesis (Bertness & Callaway, 1994) and BEF in moss communities (Bertness & Callaway, 1994; Mulder et al., 2001). They built communities of bryophytes from New Zealand and grew them in humid conditions for a year. Then, some replicates were kept in high humidity, but others were exposed to drought and much higher light. When humidity was high and light intensity low, there was no relationship between moss diversity and productivity. But, when bryophyte communities were exposed to drought and high light, total biomass increased with species richness. These authors reasoned that positive interactions in polycultures were due to greater architectural complexity, interruption of air flow, trapped boundary layer transpiration and consequent increases in humidity. More recently, Wright et al. (2021) demonstrated that drought-sensitive grassland species are protected from the negative impacts of drought when growing in higher diversity plant communities. They proposed microclimate amelioration as the probable cause of these patterns.

Other early BEF studies reported facilitation in high-diversity plots; Spehn et al. (2002) found that legumes increased nitrogen concentrations of neighbours in species-rich plots (Spehn et al., 2002). Lambers et al. (2004) demonstrated that legumes improved performance of nearly all non-legume neighbours in one of the oldest running plant biodiversity experiments in the world (Lambers et al., 2004). More recently, negative effects of soil pests and pathogens have been shown to be diluted in higher diversity plant communities (Hendriks et al., 2013). This type of higher-order interaction is more common in higher diversity mixtures and leads to improved performance of individual plants growing in polyculture (reviewed in Wright et al., 2017). These plant–soil feedbacks have been linked to BEF responses, suggesting that powerful indirect facilitation regulated by soil biota may be crucial for positive BEF responses. Maron et al. (2011) added soil fungicide to monocultures and polycultures of plant species from Montana grasslands and found the classic positive relationship between plant diversity and biomass only in those pots without fungicide (Maron et al., 2011). Fungicide, however, increased biomass by 141% in monocultures versus 33% in high diversity polycultures, indicating that high diversity strongly attenuated soil fungal pathogens. Instead of killing soil pathogens in the field, Schnitzer et al. (2011) added soil microbes to large outdoor pots containing different plant diversities (Schnitzer et al., 2011). These were treated with either un-manipulated field soil, gamma-irradiated field soil or pathogen-enriched soil. They found that low diversity communities were less productive because plants suffered far more from host-specific soil pathogens than in diverse communities. Since then a number of other studies have connected these kinds of soil biota-driven indirect facilitative effects to interspecific BEF (e.g. Bennett et al., 2017; Hendriks et al., 2013; Latz et al., 2012; Teste et al., 2017; Yang et al., 2015) and intraspecific BEF (Luo et al., 2016).

To our knowledge, the facilitation and BEF studies that have been undertaken thus far have fallen into three classes of mechanisms: species-specific pests and pathogens, nutrient enrichers, and microclimate amelioration. All have been variously and occasionally grouped into 'complementarity effects' as measured using the Loreau and Hector's (2001) mathematical partition. Niche complementarity may be related to some of these ecological interactions, or overwhelm them, but to fully understand how diversity affects ecosystem function, we should move beyond the mathematical calculation of complementarity effects and focus on experimental manipulations that can tease out the mechanisms within.

2 | A BRIEF EXAMPLE: BIODIVERSITY AND MICROCLIMATE AMELIORATION

For illustrative purposes, we explore one example of a facilitative *mechanistic* relationship between biodiversity and microclimate amelioration. Past work has shown that higher biodiversity plant communities are cooler and more humid than lower diversity plant communities. However, in experimental manipulations of biodiversity, higher diversity communities also have more biomass than lower diversity communities. Greater biomass and canopy cover surely contribute directly to a cooler and more humid microclimate. Thus, the question remains: is microclimate amelioration stronger in higher diversity communities or just in higher biomass communities? To answer this question, we re-analysed data from the Cedar Creek experiment in Central Minnesota (see Reich et al., 2001 for full details of this experiment). This experiment was established in 1997 and manipulated diversity of four herbaceous functional groups (C3 grasses, C4 grasses, forbs and legumes) at four levels of biodiversity (1, 4, 9 and 16 species). On average, biodiversity increased productivity (Reich et al. 2001, 2012), but there were cases where monocultures were highly productive and cases where higher diversity mixtures were less productive than these monocultures. With these plots, we compared temperature and humidity data that were measured during the 2011 and 2012 growing seasons using iButton dataloggers under plant canopies (Wright et al., 2014, 2015). From non-randomly selected examples of 1 and 9 species mixtures where biomass production followed the opposite trend to that observed on average, we compared the highest biomass monocultures (300–900 g/m^2) to only those 9-species mixtures that produced less biomass (150–300 g/m^2). We set biomass cut-offs between groups such that there were at least three replicates for each biodiversity level. Even when 9-species mixtures were restricted to those with much less biomass, they still increased humidity of the microclimate by 7% above the high-biomass monocultures (Figure 2). These low-biomass/high-diversity communities also reduced vapour pressure deficit at the leaf surface by 0.5 kPa. Importantly, the species with the greatest capacity to humidify the microclimate in monoculture (*Solidago* and *Petalostemum*) were not the most productive species, and were not present in the three most humid 9-species mixtures. This indicates that not only was this a diversity effect (not a biomass effect) but that the effect was driven by more than just probabilistic sampling. Higher diversity mixtures were not more humid because they were more likely to include the strong microclimate ameliorators. They were more humid due to emergent properties associated with diversity itself.

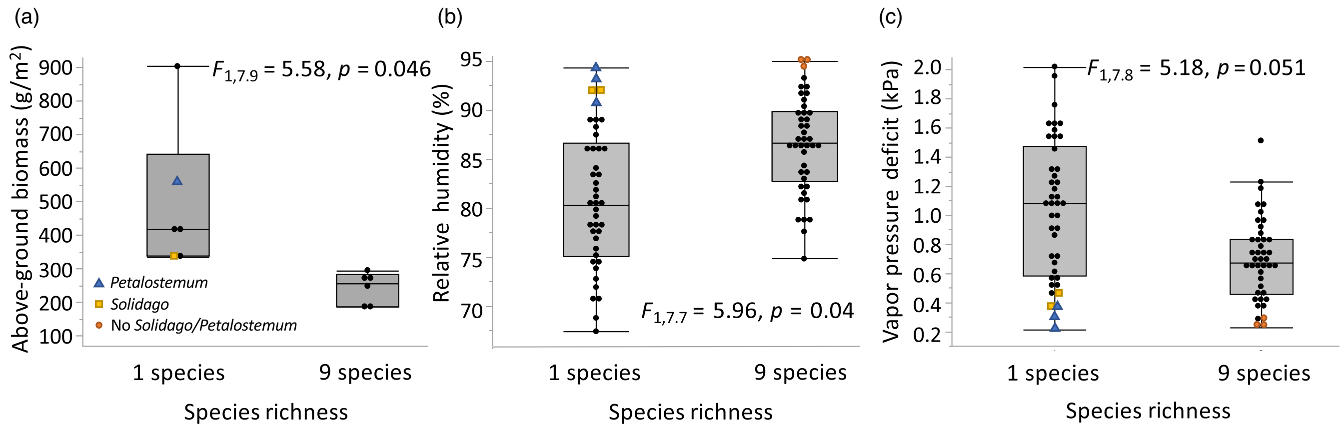

FIGURE 2 Biodiversity is uniquely related to microclimate amelioration. While biodiversity leads to increased productivity on average, we specifically chose plots from the Cedar Creek BioCON experiment where the higher diversity 9-species plots had less biomass than the monoculture plots (a). We then compared microclimate amelioration of this subset of plots. We found that the higher diversity, lower biomass plots were 7% more humid (b) and had a lower VPD (c) than the higher biomass but less diverse plots. We also found that the two species with the strongest effects on microclimate were Petalostemum (blue triangles) and Solidago (yellow squares). These two species were not the species with the most biomass. These species were also not included in the three higher diversity plots with the strongest microclimate amelioration

3 | PAPERS IN THIS SPECIAL FEATURE

For the purposes of this Special Feature, we take this mechanistic approach to facilitation in BEF research. The papers in this Special Feature are divided into two sections. In the first, the papers explore the facilitative mechanisms that underlie the effect that biodiversity has on productivity. For example, Kothari et al. (2021) isolate the suppressive effects of photoinhibition in monoculture to help explain biodiversity–productivity relationships in forested ecosystems. Guimarães-Steinicke et al. (2021) use hyperspectral data to examine how diversity and functional identity affect leaf surface temperatures in grasslands. They demonstrate that taller communities dominated by grasses are cooler than shorter stature communities. They also demonstrate that forb-dominated communities can be cooler, possibly due to stomatal conductance and evaporative cooling. Aguirre et al. (2021) manipulate microclimate conditions in low and high biodiversity California grasslands. The authors show that biodiversity can ameliorate the microclimate and lead to facilitation of *Poa secunda* when atmospheric conditions are dry. Conversely, biodiversity leads to increased competition for *P. secunda* when atmospheric conditions are humid. Brooker et al. (2021) use the facilitative mechanisms underlying positive BEF relationships to suggest areas for research in agricultural science. The authors explore how each of seven facilitative mechanisms could be used for crop breeding programmes and to design efficient intercropping and polyculture plantings.

In the second section, our authors explore whether higher diversity plant communities can drive increased rates of facilitation in real-world ecosystems. Lortie et al. (2021) examine how shrubs facilitate neighbours but facilitation is outweighed by interspecific competition in higher diversity ecosystems. Losapio et al. (2021) explore how understorey diversity interacts with shrub facilitators to increase ecosystem functioning. Ecosystem functioning is highest when understorey polycultures are associated with facilitators, in comparison to polycultures without facilitators. Cavieres et al. (2021) tackle the consequences of incorporating strong facilitators in communities as overall diversity increases, which, in turn, increases the chance of facilitating exotic species. And finally, Michalet et al. (2021) explore how the relationship between biodiversity and ecosystem functioning may shift along environmental stress gradients, and the mechanisms that explain a positive BEF shift as well. These studies demonstrate the richness of facilitative mechanisms underlying BEF and the need for a new integration of facilitation into BEF science: in terms of theory, application and science.

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AUTHORS' CONTRIBUTIONS

All co-authors contributed equally to conceptualizing the framework for the manuscript, A.J.W. wrote the first draft of the manuscript, A.J.W. analysed the data, K.E.B. produced the conceptual figure, A.J.W. and R.M.C. acted as guest editors for the associated Special

Feature, A.J.W., K.E.B., C.J.L. and R.M.C. contributed equally to revising subsequent drafts of the manuscript.

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DATA AVAILABILITY STATEMENT

Cedar Creek BioCON above-ground biomass data for the 2011 and 2012 growing seasons are freely available at https://www.cedarcreek.umn.edu/research/data.

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