

Review

The Overlooked Role of Facilitation in Biodiversity Experiments

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Past research has demonstrated that decreased biodiversity often reduces ecosystem productivity, but variation in the shape of biodiversity–ecosystem function (BEF) relationships begets the need for a deeper mechanistic understanding of what drives these patterns. While mechanisms involving competition are often invoked, the role of facilitation is overlooked, or lumped within several less explicitly defined processes (e.g., complementarity effects). Here, we explore recent advances in understanding how facilitation affects BEF relationships and identify three categories of facilitative mechanisms that can drive variation in those relationships. Species interactions underlying BEF relationships are complex, but the framework we present provides a step toward understanding this complexity and predicting how facilitation contributes to the ecosystem role of biodiversity in a rapidly changing environment.

BEF Experiments and the Consequences of Biodiversity Loss

Current and projected rates of global species loss emphasize the need to more precisely understand how biodiversity promotes ecosystem function in different types of ecosystem [1]. Over the past 20 years, ecologists have tackled this need via controlled experimental manipulations of the richness of species, genotypes, and functional groups. These BEF experiments have been used to assess the role of biodiversity in many different ecological contexts [2]. We now know that, when species diversity decreases, ecosystem responses, such as net primary productivity (NPP), stability of NPP, and resistance to species invasion, often also decrease.

More recently, work has focused on understanding BEF relationships across systems and scales at a mechanistic level [3,4]. This research has primarily examined the roles of so-called niche complementarity and **selection effects** (see Glossary) to explain BEF relationships [5–7]. Niche complementarity is usually examined as the way in which coexisting species differ in their resource needs and acquisition strategies. Greater overall species diversity leads to increased occupation of niche space (up until some point of saturation), more comprehensive resource use, and increased community-level biomass production (but see [8,9] for examples of other mechanisms that are explored within the calculation of ‘complementarity effects’ as defined by [5]). By contrast, selection effects can occur when higher-diversity communities are more productive than lower-diversity communities due to the increased probability of including a particularly productive species that dominates in a mixture [7,10].

Despite the commonly reported positive effect of species diversity on ecosystem functioning, there is a great range in the magnitude and shape of the BEF relationship that is not easily explained by **resource complementarity** or selection effects [11–13]. In several cases,

Trends

Understanding the functional role of biodiversity in an ecosystem is an essential component of predicting the consequences of biodiversity loss. Experimental studies have consistently shown that the loss of biodiversity can lead to a loss in ecosystem functioning (BEF relationships).

Our ability to predict the consequences of biodiversity loss in understudied ecosystems, and in a global change context, requires a deeper mechanistic understanding of BEF relationships.

Here, we highlight three categories of facilitation that can be important drivers of BEF relationships: indirect biotic interactions due to pathogens and mutualists; abiotic interactions due to nutrient enrichment; and abiotic interactions due to microclimate amelioration.

We demonstrate how increased environmental severity, abundance of specialist pathogens, and biological nitrogen fixation rates likely drive increased facilitation and, thus, the strength of the BEF relationship, across ecosystems.

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facilitation has been suggested as a mechanism that drives variation in BEF relationships [14–19]. Here, we propose that a better understanding of these facilitative mechanisms can help explain variation in the shape and magnitude of BEF relationships in different ecological contexts [20,21]. We develop a conceptual framework for how different types of facilitative mechanism affect BEF relationships. This framework should also help us to predict how biodiversity could influence ecosystem functioning in systems where it may be impractical to establish large-scale BEF experiments.

Community and Species-Specific Mechanisms Responsible for BEF

BEF research has often used the terms ‘niche complementarity’ and ‘overyielding’ interchangeably [22–25]. To reduce confusion, we suggest distinguishing between community overyielding and **species-specific overyielding**. Here, we restrict our discussion to the mechanistic underpinnings of species-specific overyielding [26]. As such, species-specific overyielding is the case where a species grows more in mixture than it does in monoculture, after accounting for differences in proportion of seed planted [27]. Using this definition, there are at least three groups of facilitative mechanism that can explain species-specific overyielding in BEF experiments: (i) indirect **biotic facilitation**; (ii) **abiotic facilitation** via nutrient enrichment; and (iii) abiotic facilitation via microclimate amelioration. Past work focused strongly on the role of resource partitioning (stronger intraspecific than interspecific competition or interference competition) for driving species-specific overyielding and, thus, we direct the reader to that work for a more comprehensive discussion of these processes and their role in driving BEF relationships [9,13,28].

Indirect Biotic Facilitation

When species grow in dense conspecific clusters or in conspecific soils, species-specific pathogen loads can increase, which can lead to the decreased success of conspecifics [29]. In the context of BEF experiments, negative density dependence due to species-specific pathogens is a clear demonstration of facilitation that could explain species-specific overyielding [29], and the BEF relationship in general [14,29–31]. Specifically, diversity can confer a facilitative effect by diluting the effects of pathogens in higher diversity communities (Figure 1A). In addition, higher diversity communities will accumulate a greater diversity of specialist pathogens, driving the absolute abundance of any individual specialist pathogens to lower levels, thereby potentially resulting in plant species overyielding in mixtures [29].

Indirect biotic facilitation in BEF experiments can also occur via positive effects of belowground mycorrhizal fungi and rhizobacteria [31,32]. Wagg *et al.* [33] proposed that higher diversity plant communities may be better at harboring more diverse AMF communities. These higher diversity AMF communities might then help expand the total niche space utilized by the plant community. This could lead to increased performance of individual species (species-specific overyielding) in higher diversity mixtures. However, empirical support for this proposed mechanism is still lacking.

Indirect biotic facilitation can also be the result of indirect competitive interactions in higher diversity systems [34]. When more than two species interact in a plant community, there is the potential for complex indirect interaction networks. For example, species *a* might limit species *b*. If species *b* is usually a strong competitor and limits the success of species *c*, we might see an indirect positive interaction between species *a* and species *c*. In the context of BEF experiments, this should theoretically be more likely with increasing species diversity (because the probability of indirect interactions increases with an increasing number of species), although the probability of negative interactions could also increase with an increasing number of species. These complex interaction networks can also be amplified by the higher diversity soil biota found in higher diversity plant communities [35].

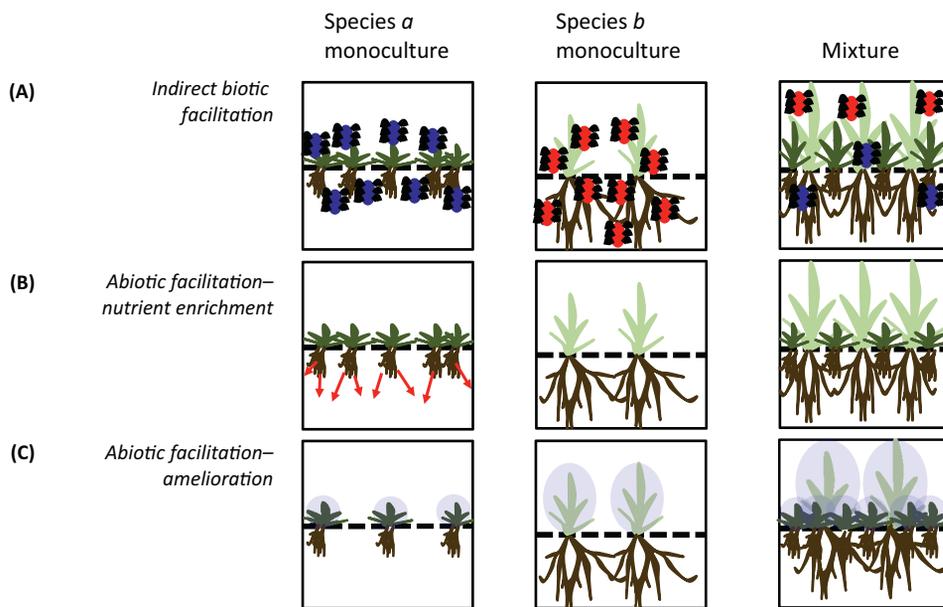
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Figure 1. Facilitative Mechanisms that Explain Species-Specific Overyielding in Biodiversity–Ecosystem Function (BEF) Experiments. There are at least three facilitative mechanisms that can explain species-specific overyielding. First, indirect biotic facilitation can occur via diversity effects on species-specific pathogen loads (A), or through indirect competitive interactions increasing the productivity of a species growing in mixture. Here, all pathogens (fungal, bacterial, viral, etc.) are indicated with a drawing of an insect. When a single plant species grows alone in monoculture, it can accumulate species-specific pathogens over time. When these same species grow together in mixture, the species-specific pathogen load is reduced, and plants can grow more due to overall release from pathogenic attack. Second, facilitation of neighbors can result from abiotic effects on nutrient availability. In particular, the legume–rhizobia symbiosis can directly increase nitrogen availability for neighboring plants (B). In (B) if species *a* is leguminous, it can have a positive effect on the growth of species *b* due to nitrogen inputs into the soil. Third, facilitation can be mediated through abiotic effects on microclimate conditions. For example, if species *a* is sensitive to irradiance or high temperatures, the microclimate effect provided by species *b* can improve the performance of species *a* in mixture of those species (C).

Abiotic Facilitation: Nutrient Enrichment

By far the most well-discussed form of facilitation in the BEF literature is the direct positive effects that certain species (e.g., legumes) can have on neighbors due to species effects on nutrient availability [36–39]. Importantly, legumes likely contribute to both competitive and facilitative interactions. Legumes can increase resource partitioning when they uniquely have direct access to atmospheric nitrogen, a source of nitrogen that is otherwise not accessible to the plant community (e.g., [40]). However, here we focus on instances where nitrogen inputs facilitated by legumes increase resource availability for nonlegume neighbors (Figure 1B) a clear indication of interspecific facilitation. We extend the well-documented positive effects that legumes have on nitrogen availability and cascading consequences for nonlegume neighbors [18,36,41] to include several other species interactions that may be common and that should result in similar predictions for species-specific overyielding.

Biological nitrogen fixation is a widespread phenomenon that occurs in diverse hosts (e.g., legumes, feather mosses, and woody actinorhizal species) and symbiont taxa (e.g., *Rhizobia*, *Frankia*, and cyanobacteria) [37]. Past BEF experiments have shown that nonleguminous plants can overyield by up to twofold when growing in the presence of legumes [18,42,43]. Similarly, actinorhizal species (e.g., *Alnus* spp.) can have positive effects on overyielding of neighbors via nitrogen fixation with *Frankia* [44]. Feather mosses in boreal ecosystems can also positively

Glossary

Abiotic facilitation: facilitation that is mediated through changes in the abiotic environment (e.g., vapor pressure deficit, soil porosity, soil moisture, or nutrient enrichment).

Biotic facilitation: facilitation that results from the activity of a higher order trophic interaction (e.g., bacterial, rhizobial, or arbuscular mycorrhizal fungal communities).

Facilitation: occurs when an increase in the density of species *b* increases the performance of species *a*.

Resource complementarity: occurs when species have unique and complementary resource requirements that can allow some species to stably coexist; these groups of species can be more productive and capture available resources more comprehensively than any species in monoculture.

Selection effects: occurs when higher diversity mixtures have a higher statistical probability of including particularly productive species. When those species that are more productive in monoculture are also better competitors in mixture, higher diversity communities can be more productive than lower diversity communities.

Species-specific overyielding: the case where an individual species grows more in mixture than it does in monoculture, after accounting for differences in the proportion of seed planted. For example, corn seed in monoculture might be planted at 100%, while corn seed in a two-species mixture might be planted at 50%. If corn grows 100 g per unit area in monoculture, but greater than 50 g per unit area in a two-species mixture, this is considered species-specific overyielding.

affect neighbors via nitrogen fixation with the cyanobacteria that they host [38]. Both legumes (e.g., *Lupinus*) and nonlegumes (e.g., *Buddleja davidii*) can also have positive effects on neighbors via enhanced phosphorus mobilization (due to the production of phosphate-mobilizing root exudates), which enhances the growth of neighboring species [39,45,46]. These mechanisms should all theoretically increase species-specificoveryielding through facilitation and increase the strength of the BEF relationship.

Abiotic Facilitation: Microclimate Amelioration

Neighboring plants can also benefit each other through amelioration of adverse microclimatic conditions. Plants growing in severe climates are often more limited by physiological strain than by competition with neighbors [47]. In these instances, physiological strain and microclimate amelioration in higher diversity communities can increaseoveryielding and affect the shape of the BEF relationship.

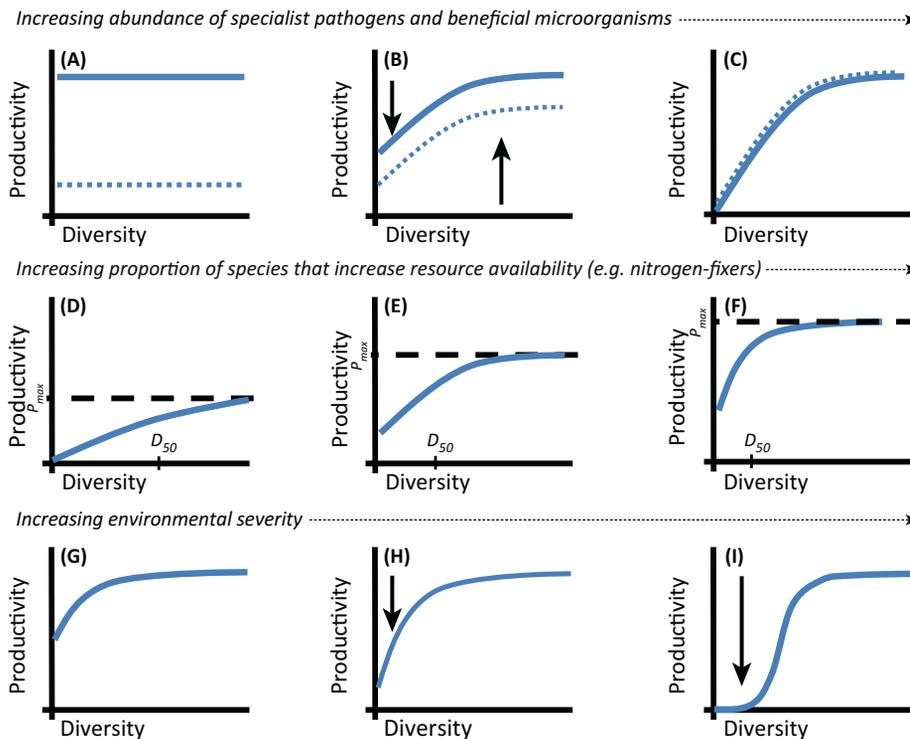
Research using BEF experiments has demonstrated the importance of microclimatic amelioration in higher diversity plant communities (Figure 1C). In ecosystems that experience periodic drought stress, increased aboveground biomass in higher diversity experimental plots increases shade, which, in turn, reduces surface drying and increases surface soil moisture [48]. Furthermore, increased shade decreases temperature, increases relative humidity, and decreases vapor pressure deficit around the leaves, particularly on unusually hot and dry days [48]. While this effect is likely partially driven by aboveground biomass effects on shade, it may also be related to a type of sampling effect. Higher diversity communities are more likely to include species that have greater drought tolerance and that can maintain higher stomatal conductance during drought. These species are likely to facilitate others via the cooling effects of evapotranspiration. A strong microclimatic amelioration effect on hot, dry days can lead to reduced water stress for neighboring plants that are less drought tolerant [15,48,49]. While potential temperature amelioration effects in Arctic or alpine systems have yet to be shown in the context of biodiversity experiments, they are likely to operate in similar ways (e.g., the buffering of low temperature extremes in higher diversity or higher biomass communities [50]).

Implications for BEF Relationships

Understanding the underlying mechanisms behind BEF relationships will allow us to extend our knowledge of BEF patterns to untested systems. Below, we discuss each of the three types of facilitation in detail, together with conceptual predictions about how these might alter BEF relationships in different types of ecosystem.

Indirect Biotic Facilitation across Systems

We predict that indirect biotic facilitation (Figure 2A–C) should increase with increasing specialist pathogen load and increasing abundance of species-specific mutualistic associations (although for opposite reasons). Specialist pathogen load can vary with latitude [51], although the directionality of this response is debated [52,53]; it can also shift with elevation [54] and with different agricultural practices [55]. High specialist pathogen loads should drive most species to perform poorly in monoculture. At higher levels of diversity, dilution effects should universally decrease pathogen pressures and all species shouldoveryield. Conversely, beneficial microorganism diversity should increase niche space available for stable species coexistence [32]. A low diversity of beneficial microorganisms would lead to reduced diversity of niche space, resulting in low overall species coexistence, and experimental additions of species should not result in large increases in productivity. As the diversity of beneficial microorganisms increases, higher diversity plant communities should be increasingly capable of stable coexistence, which should lead to increased productivity and a steeper BEF relationship (Figure 2A).



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Figure 2. Illustration of Potential Diversity–Productivity Curves [i.e., Biodiversity–Ecosystem Function (BEF)] across Ecosystems. The figure demonstrates how plant diversity (or species richness) on the X-axis can affect productivity (or biomass production) on the Y-axis. (A–C) demonstrate that an increasing abundance of specialist pathogens (solid line) or beneficial microorganisms (dotted line) could increase the strength of the BEF. These biotic facilitative interactions drive stronger BEF relationships for two different reasons. The solid line shows that, as specialist pathogen load increases, monocultures become more suppressed. This is consistent with the findings of Hendriks et al. [29], that monoculture suppression occurred in the presence of pathogens but not when pathogens were absent. Conversely, the broken line shows that, as specialist beneficial microorganisms increase, niche space can theoretically increase [33], and productivity of mixtures might be enhanced. (D–F) demonstrate that an increasing proportion of nitrogen-fixers (or other nutrient-enhancing species) can also increase the magnitude of the BEF relationship (abiotic facilitation via nutrients). More nitrogen-fixers can increase the total size of the nitrogen pool and increase the maximum potential productivity (P_{max}) of the system. A greater proportion of nitrogen-fixers would also increase the probability of including a nitrogen-fixer at lower diversity and, therefore, increase the slope of the BEF [e.g., smaller D_{50} in (F)]. These predictions follow patterns observed due to experimental nutrient enrichments in a recent meta-analysis [60]. (G–I) demonstrate how increasing environmental severity can increase the strength of the BEF, consistent with the stress gradient hypothesis (abiotic facilitation via microclimate). When environmental severity is low, diversity–productivity curves likely saturate as a function of niche space (in line with most past BEF experimental evidence [2]). As environmental severity increases, average monoculture productivity should be suppressed because an increasingly large number of species cannot survive in monoculture (i.e., classic nurse plant effects in deserts [47]). As diversity increases, there should be a higher likelihood of including a particularly well-adapted nurse plant species that ameliorates the environment for other species and makes it possible for them to persist (sampling effects). The cumulative effects of higher species richness on microclimate can also improve microclimatic conditions and enhance species-specific overyielding at higher levels of diversity (e.g., [49]). In the special case where environmental severity reduces the overall resource pool, P_{max} could also decrease with increasing environmental severity (not shown here).

Abiotic Facilitation via Nutrient Enrichment across Systems

When there is a greater abundance of plant species that serve as nutrient enrichers in the species pool, there will be greater abiotic facilitation via nutrient enrichment, which should also increase the strength and slope of the BEF relationship (Figure 2B). This is because these nutrient enrichers should increase the size of the available resource pool, leading to greater maximum productivity of the system (P_{max} in Figure 2B) [56]. Increased abundance of legumes

and other nutrient enrichers in an ecosystem should also increase the probability of adding a nutrient enricher through sampling effects. As the proportion of nitrogen-fixers in the species pool increases, the probability of a low-diversity system including nitrogen-fixers should also increase and, thus, the slope and half-saturation constant of the saturation curve should increase (D_{50} in Figure 2B). Thus, systems that do not have a high proportion of nitrogen-fixers in their species pools can demonstrate weaker BEF relationships than those that do.

Abiotic Facilitation via Microclimate Amelioration across Systems

How environmental severity gradients shape BEF relationships has been explored explicitly in a handful of experiments involving bryophytes or algae, and among ecosystems that vary in disturbance regimes [57]. The results from those experiments have been idiosyncratic. Mulder *et al.* [20] found that bryophyte richness had more positive effects on productivity when bryophytes were subjected to drought, because bryophytes reduced desiccation by increasing microclimatic humidity. Steudel *et al.* [21] found that heat and salinity stress had stronger suppressive effects for lower diversity communities, because species growing in monoculture are more vulnerable to temperature and salinity extremes.

We hypothesize that the effects of direct abiotic facilitation should increase with increasing environmental severity, in line with the stress gradient hypothesis (Figure 2G–I). Furthermore, results from BEF experiments suggest that the shape of the BEF relationship changes with environmental stress. In relatively severe climates where facilitation is theoretically important, many species are likely to grow poorly in monoculture (Figure 2I). However, when more species are present, the effect of diversity on microclimate should be strong enough to reduce physiological strain and promote the growth of sensitive species (e.g., [48]). At this level of microclimate amelioration, there might be an inflection point whereby most species overyield due to either incremental whole-community habitat amelioration (e.g., [49]), or an increased probability of including key facilitator species [58]. In more benign environmental conditions, competitive interactions and niche complementarity might be more important than facilitation and, therefore, the BEF might follow a similar saturating relationship, but with less monoculture suppression due to environmental severity (Figure 2G).

Concluding Remarks and Future Directions

The past 20 years of BEF research have illuminated our understanding of the role of biodiversity in ecosystems worldwide, but many types of ecological system remain poorly tested [2]. Here, we have outlined the mechanisms responsible for these relationships and the overlooked importance of three types of facilitation that can drive these patterns (Figure 1). We have also introduced a conceptual framework for how and why these three types of facilitation can drive changes in the shape of the BEF relationship across different types of system (Figure 2). This framework can be used to predict how biodiversity might affect ecosystem functioning in systems that have been studied less intensively in the past (see Outstanding Questions).

Beyond this, there is a need for future work to focus on how facilitative mechanisms can affect BEF relationships for ecosystem functions other than biomass production. In particular, the relationships between facilitation and decomposition, elemental fluxes, and ecosystem stability are likely to be complex. For example, while indirect biotic facilitation might improve the productivity of higher diversity mixtures, the increased interaction complexity resulting from this facilitation might decrease ecosystem stability, depending on the interaction strength in particular [59].

Finally, understanding the mechanisms that drive BEF relationships will be essential to predicting how biodiversity will be affected by global change phenomena. Global change factors will likely independently affect both competitive and facilitative interactions: drought might, for

Outstanding Questions

What is the relative importance of facilitative interactions versus competitive interactions in driving species-specific overyielding and BEF relationships?

What are the mechanisms by which facilitative interactions contribute to biodiversity–productivity relationships in severe environments (e.g., arid, nutrient depleted, or cold) and how does this affect species redundancy? How might this be important for biodiversity conservation in severe environments?

How strongly is the role of facilitation in biodiversity–productivity relationships driven by indirect biotic interactions? Would BEF relationships be weaker in the absence of certain groups of biota, such as mutualists or pathogens?

How strongly do nonlegume nutrient enrichers drive biodiversity–productivity relationships in different ecosystems?

How do facilitative interactions contribute to ecosystem resistance and resilience in a global change context? How does facilitation help buffer higher diversity communities against the most negative effects of climate change?

Do facilitative interactions affect decomposition rates, elemental fluxes, and ecosystem stability in contrasting ways depending on biodiversity context? In particular, are there instances where facilitation improves productivity in higher diversity communities while decreasing some other ecosystem functions (e.g., decomposition)?

example, increase competition for water, but aridity might simultaneously increase the importance of facilitation. While these underlying species interactions are complex, our framework presents a first step toward teasing out this complexity.

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