


Review

The Future of Complementarity:
Disentangling Causes from Consequences

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Evidence suggests that biodiversity supports ecosystem functioning. Yet, the mechanisms driving this relationship remain unclear. Complementarity is one common explanation for these positive biodiversity–ecosystem functioning relationships. Yet, complementarity is often indirectly quantified as overperformance in mixture relative to monoculture (e.g., ‘complementarity effect’). This overperformance is then attributed to the intuitive idea of complementarity or, more specifically, to species resource partitioning. Locally, however, several unassociated causes may drive this overperformance. Here, we differentiate complementarity into three types of species differences that may cause enhanced ecosystem functioning in more diverse ecosystems: (i) resource partitioning, (ii) abiotic facilitation, and (iii) biotic feedbacks. We argue that disentangling these three causes is crucial for predicting the response of ecosystems to future biodiversity loss.

The Confusion over Complementarity

Global biodiversity is declining at unprecedented rates [1,2]. Yet, biodiversity is crucial for maintaining **ecosystem functioning** (see [Glossary](#)) and the ability of ecosystems to deliver goods and services (reviewed by [3,4]). Complementarity is often invoked to explain this enhanced ecosystem functioning in diverse plant communities [5,6]. The intuitive idea behind this concept is that plant species are complementary if they fit together like puzzle pieces. Each species (puzzle piece) adds, at least partially, to total community functioning.

Yet, complementarity is currently used as both a cause of enhanced ecosystem functioning in diverse communities and a consequence of some community process ([Figure 1](#)) [7]. For example, in biodiversity–ecosystem functioning research, it is common to calculate measures of overproduction such as the ‘**complementarity effect**’. These measures of overproduction are statistical measures that demonstrate whether the performance of plant species mixtures exceeds their expected performance based on the monocultures of their component species [8]. These measures ([Figure 1](#), right side) answer the question: do mixtures perform better than monocultures? The complementarity effect and other measures of overproduction of mixtures document the consequence (i.e., enhanced ecosystem functioning) but not the underlying mechanistic cause [7]. Yet, these measures of overproduction in mixture are often interpreted as evidence for complementarity in the colloquial sense as a cause or more specifically for **resource partitioning**. In a review of 137 studies that calculated a complementarity effect (see [Table 1](#) for search terms and methods), we found that 63% of studies conflated the complementarity effect (consequence) with complementarity (cause) already in the abstracts

Highlights

Complementarity is currently used as both a cause for enhanced ecosystem functioning and a consequence of some community process.

Using complementarity as a cause and a consequence makes it difficult to disentangle individual causes such as resource partitioning, abiotic facilitation, and biotic feedbacks.

There is strong evidence that resource partitioning, abiotic facilitation, and biotic feedbacks occur in grassland systems but there is little evidence that explicitly ties them to the consequence of enhanced ecosystem functioning.

Interactions between resource partitioning, abiotic facilitation, and biotic feedbacks may make the biodiversity–ecosystem functioning relationship stronger.

Ecological gradients such as stress, enemies, and resources may allow us to disentangle the contributions of resource partitioning, abiotic facilitation, and biotic feedbacks to enhanced ecosystem functioning.

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of the papers. Often, this interpretation is further misconstrued as evidence that species partition **resources** (e.g., [3,6,7,9]). Indeed, 30% of studies that conflated complementarity with the complementarity effect explicitly interpreted the complementarity effect as evidence that species partitioned resources in the abstract. This use of complementarity obscures the contribution of other causes that are not linked with the colloquial definition of complementarity and overemphasizes the contribution of resource partitioning to enhanced ecosystem functioning in more diverse mixtures.

In fact, several causes drive overproduction in mixture, including resource partitioning, **abiotic facilitation**, and **biotic feedbacks** (Figure 1, left side) [8,10]. Here, we formally integrate these three sets of species differences into complementarity. We review the evidence that these causes may drive enhanced ecosystem functioning in more diverse mixtures. Further, we argue that disentangling the causes of complementarity helps us to predict how ecosystems will respond to future biodiversity loss.

A Revised View of Complementarity: From Cause to Consequence

We define complementarity as differences between species, functional groups, or genotypes that may (but need not) enhance ecosystem functioning. For simplicity, we refer throughout to 'species' but other taxonomic levels may be equally relevant. In keeping with this definition, species in any given community can differ from one another in three ways: (i) species differ in the resources that they use (resource partitioning); (ii) species differ in their ability to alter their environment to benefit other species (abiotic facilitation); (iii) species differ in their biotic interactions with other trophic levels (biotic feedbacks). Species in any given community can differ in more than one of these ways. These differences form our preconditions for local plant diversity to enhance ecosystem functioning. Furthermore, these differences only enhance ecosystem functioning if, on average, they increase the performance of mixtures relative to the performance of monocultures (Box 1). Below, we review the current research on resource partitioning, abiotic facilitation, and biotic feedbacks, and the evidence that they enhance ecosystem functioning in plant communities (Table 1). We also discuss classic examples which may be the result of several of these causes combined, such as nitrogen fixation by legumes (Box 2).

Resource Partitioning

Resource partitioning occurs when species use different portions of the available resource pool (cause). The result of resource partitioning is that the existing resource pool is more completely used in higher-diversity communities compared with monocultures (consequence, Figure 2A, yellow line). In plant communities, resource partitioning happens across space (e.g., rooting depth [11]), time (e.g., phenology of nutrient uptake [12]), chemical form [i.e., nitrate (NO_3^-), ammonium (NH_4^+), and organic nitrogen (N)] [13], or all of these combined [14].

Spatial Partitioning

Quantifying spatial resource partitioning between plants generally relies on two approaches: (i) documenting space filling above- or belowground, or (ii) measuring resource uptake from different areas within the canopy or the rooting zone. Several studies demonstrate that plants more fully utilize vertical aboveground space with increasing diversity [15–20]. Belowground, this **pattern** is less clear. Indeed, several studies [21,22] found that plants allocate belowground biomass to deeper layers with increasing diversity. Yet others [23–26] found that plants are more likely to aggregate biomass in the topsoil with increasing diversity. Belowground, isotope tracers may provide better evidence of spatial resource partitioning than root distribution [25,27–29]. However, like studies of belowground biomass allocation, resource tracer

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studies show mixed [12,25] and largely nonsignificant [25,27,28] evidence for spatial resource partitioning of common soil resources in space.

Temporal Partitioning

Communities composed of groups of plants with distinct phenology often have enhanced ecosystem functioning relative to communities composed of species with similar phenology (e.g., if early- and late-season species are present). For example, Kahmen *et al.* [12] found that the uptake of nitrogen by different plant species varied across time (indicating the potential for resource partitioning), but that this variation was not associated with increased total N uptake. Alternatively, Jesch *et al.* [28] found no evidence that plant species partition water, nitrogen, or potassium across the growing season (also demonstrated by [14,30]).

Chemical Form

Ashton *et al.* [13] found strong evidence that grassland species partitioned forms of nitrogen when in **competition** with a dominant species that took up the most available chemical form of nitrogen. von Felten *et al.* [25] also found evidence that species partitioned different forms of nitrogen (cause). However, increased partitioning of nitrogen forms was not associated with enhanced ecosystem functioning (consequence).

Overall, even when there is some evidence that species differ in their spatial or temporal use of resources [21,25], studies often fail to correlate this evidence of resource partitioning (cause) with enhanced ecosystem functioning (consequence [21,22]). Thus, these studies provide only limited support for the role of resource partitioning in complementarity; evidence tying the cause to the consequence of enhanced ecosystem functioning in grasslands is limited (but see [21,22] where evidence of spatial resource partitioning is linked to enhanced ecosystem functioning in mixture).

Abiotic Facilitation

Abiotic facilitation occurs when a plant species benefits another plant species via changes to the abiotic properties of the environment, such as its microclimate, soil chemical properties, or soil physical properties (reviewed by [31–33] for arid environments, and [34] for agricultural systems). Abiotic facilitation may cause enhanced ecosystem functioning when species receive a benefit from being in high-diversity systems relative to low-diversity systems (Figure 2B, blue line). Here, we limit abiotic facilitation to plant–plant interactions. Thus, we exclude nitrogen fixation (and similar cases) from this category, because non-plant interaction partners mediate both the nitrogen fixation and the transfer of this nitrogen to other members of the community (for the role of nitrogen fixation in biodiversity–ecosystem functioning see Box 2). There are two nonmutually exclusive ways in which plants likely facilitate each other: (i) plants may enrich the resource pool for neighboring plants, or (ii) plants may mediate physical **stress**.

Resource Enrichment

Some plants make resources, which were previously unavailable, available to the community. We call this abiotic facilitation via resource enrichment. Abiotic facilitation via resource enrichment differs from resource partitioning in that specific plant traits enlarge the resource pool for the whole plant community. It is in contrast to resource partitioning, where different plant species together use the available resource pool more completely.

For example, some plant species exude enzymes or organic acids that promote mineral weathering and thereby enlarge the existing resource pool of plant-available soil nutrients (cause). Other members of the plant community may benefit from this increased availability of nutrients as well [34–36]. Another example where plants may enrich the local environment is

Glossary

Abiotic facilitation: occurs when an increase in the abundance of one species increases the relative performance of a different species via changes to the abiotic environment.

Biotic feedbacks: here narrowly defined as the amplifying (positive feedback) or dampening (negative feedback) effect on the performance of a plant species or community caused by another trophic level in response to changes in plant diversity.

Competition: occurs when an increase in the performance of one species decreases the performance of a different species.

Complementarity effect: the performance of mixtures relative to the performance of the component monocultures [8].

Density dependence: a process that increases in strength when a species becomes more abundant in a given area. For example, negative density dependent effects occur when the relative performance of a species is reduced with increasing abundance.

Ecological gradient: a gradient across which a specific environmental factor or ecological context varies (e.g., a gradient of abiotic stress, a gradient of pathogen specificity).

Ecosystem functioning: sizes of pools of materials or energy (pools of carbon, nitrogen, or biomass) and rates of processes (fluxes of materials or energy among pools). High or low values are not inherently good or bad [5].

Net response: the combined effect of two or more complementarity causes (does not refer to the statistical 'net biodiversity effect' used by the additive partitioning method).

Pattern: a set of circumstances created by a process (i.e., the effect in a cause–effect relationship).

Resources: limiting factors that decrease in availability as the total abundance of species in a community increases (e.g., nitrogen [79]).

Resource complementarity: the theory that posits that the addition of species to a community increases average relative performance of

through hydraulic lift. Plants with deep roots may draw water up from a depth where it was previously inaccessible [37]. These species then make the water available to plants with shallow roots. Hydraulic lift occurs in both woody [38] and herbaceous [39] communities (cause), but this has not yet been connected to enhanced growth of shallow-rooted neighbors in biodiversity–ecosystem functioning experiments in grasslands [40] (consequence).

Physical Stress Buffering

Plants may provide a barrier against physical stress for other members of their community. For example, Steudel *et al.* [41] found that high temperatures were better buffered in high-diversity communities. Plant species may ameliorate the microclimate for other members of their community by physically mediating wind, heat, or photoinhibition [32]. Milcu *et al.* [42] demonstrated that this was likely in higher-diversity systems that had proportionally lower evaporation and sensible heat flux (see also [43] for natural grasslands).

Overall, plants can enrich local resource availability and provide a buffer to physical stress simultaneously across diversity gradients [32,44]. However, evidence to date does not directly relate these effects to enhanced ecosystem functioning with higher diversity in grassland plant species (consequence, but see [45] for nonvascular plant species).

Biotic Feedbacks from Other Trophic Levels

Increasing plant diversity may alter the strength of interactions between plants and other trophic levels (reviewed by [46]). We refer to these interactions as biotic feedbacks from other trophic levels. Biotic feedbacks from other trophic levels may enhance ecosystem functioning in two ways. (i) Species differ in their enemies (consumers/herbivores, pests, and pathogens). The negative interactions between plant and enemy may create strong conspecific negative **density dependence**. This negative density dependence leads to reduced plant performance

species because each species specializes on different resources and thus the whole community more thoroughly utilizes the available resources [77].

Resource partitioning:

multidimensional measure of the share of the total resource pool that a species uses [82,83] (roughly synonymous to a resource niche). The fundamental resource partition is the species' resource partition when growing alone (similar to the fundamental resource niche); the realized resource partition is the species' resource partition when growing with other species (similar to the realized resource niche).

Resource partitioning: occurs when species use different portions of the available resource pool (cause). The result of resource partitioning is that the existing resource pool is more completely used in higher-diversity communities compared with monocultures.

Stress: limiting factors that are abundance independent (e.g., temperature [79]).

Complementarity causes

Complementarity consequences



Trends in Ecology & Evolution

Figure 1. Looking Inside the Black Box of Complementarity. We found that in the biodiversity–ecosystem functioning literature, uses for the term complementarity generally fall into two categories: complementarity causes (see left), and complementarity consequences (see right) of the coupling between diversity and ecosystem functioning. On the left, we list potential causes that, historically, are credited with driving complementarity. On the right, we list consequences that have historically been derived from species being complementary in some fashion. Some studies use complementarity as both a cause and a consequence. When complementarity is used by itself, which is common, it is often unclear whether the intended definition falls under a specific usage (on either the causes or consequences side) or rather as the center portrays. We believe that the multitude of uses of complementarity on both sides of this model and in the center, without explicitly stating which perspective is taken, often leads to misinterpretation and confusion in communicating.

Table 1. Quantifying Complementarity Uses and Complementarity Causes in the Biodiversity Ecosystem Functioning Literature^a

Search number	Cause	Search terms	Number of studies
1		Literature citing Loreau and Hector 2001 Nature AND ecosystem function*	400
2	Resource partitioning	('resource complementarity' OR 'resource partitioning' OR 'niche partitioning' OR 'niche differentiation') AND biodiversity AND ecosystem function* AND plant* AND complementarity	71
3	Abiotic facilitation	('facilitation' OR 'stress amelioration') AND biodiversity AND ecosystem function* AND plant* AND complementarity	57
4	Biotic feedbacks	('plant–soil feedback' OR 'mutualist' OR 'rhizobia' OR 'pathogen' OR 'enemies' OR 'herbivore') AND biodiversity AND ecosystem function* AND plant* AND complementarity	43
2 AND 3	Resource partitioning and abiotic facilitation		14
2 AND 4	Resource partitioning and biotic feedbacks		10
3 AND 4	Abiotic facilitation and biotic feedbacks		3
2 AND 3 AND 4	All three inclusive		2

^aIn order to quantify the use of the term complementarity in the biodiversity–ecosystem functioning literature, we performed a Web of Science search of study topics using the search terms: literature citing Loreau and Hector 2001 Nature AND ecosystem function* (* indicates Web of Science search function that allows Web of Science to search for terms including function in addition to function itself, e.g., functioning or functions). This search returned 400 results as of August 2018. We read the abstracts of these 400 studies and determined which ones calculated a 'complementarity effect' *sensu* Loreau and Hector [8] or Fox [101] (137 studies). We then determined which of these 137 studies explicitly used complementarity in the colloquial sense as a mechanism driving the complementarity effect in the abstract alone (86 studies). We also determined which of these studies further conflated the 'complementarity effect' with what we refer to as resource partitioning (25 out of 86 studies, 'resource use complementarity', 'resource partitioning', 'niche complementarity', or 'niche differentiation') in the abstract alone. In order to quantify the prevalence of each of our complementarity causes in the biodiversity–ecosystem functioning literature, we performed a number of Web of Science searches of study topics. As of August 2018, resource partitioning was more prevalent in the biodiversity–ecosystem functioning literature than both abiotic facilitation and biotic feedbacks. Similarly, abiotic facilitation was more commonly invoked than biotic feedbacks. Only two studies met all of our search criteria simultaneously.

at low diversity relative to high diversity (Figure 2A, pink line, [47]). (ii) Species differ in their mutualists; these mutualists may also benefit other species (positive biotic feedbacks, Figure 2B, blue line). If the benefit of mutualists increases with increasing diversity (cause), then ecosystem functioning increases with diversity (consequence, reviewed in [46]).

Negative Biotic Feedbacks

Plant species differ in both above- and belowground enemies (cause). When enemies are sufficiently species-specific, plants are suppressed when they occur among members of their own species in a negative density-dependent manner [48,49]. This monoculture suppression means that ecosystem functioning of diverse communities is enhanced relative to these poorly performing monocultures (consequence). Several studies now demonstrate that enemies in grassland ecosystems can be species-specific and that their damage decreases with increasing diversity (reviewed in [50,51]). Belowground, plant–soil feedback experiments (reviewed in [52,53]) often find that negative feedback from soil enemies (cause) through negative density dependence contributes to enhanced ecosystem functioning (consequence) [54–56]. For example, Hendriks *et al.* [57] found that soil inoculated with species-specific soil biota caused monocultures to underperform relative to mixtures. Seabloom *et al.* [58] found that removing aboveground enemies (cause) increased overall biomass production by a constant proportion across a biodiversity gradient, leading to a greater increase in aboveground biomass production in higher-diversity communities (consequence).

Positive Biotic Feedbacks

If the positive effect of other non-plant species increases with increasing diversity, positive biotic feedbacks between plants and other species (including their mutualists) may also enhance

Box 1. Abundance, Plasticity, and Biodiversity–Ecosystem Functioning Relationships

We define enhanced ecosystem functioning as the increase in the community performance of mixtures relative to monoculture. Plant populations may have altered performance in mixture relative to monoculture in two general ways: (i) via plastic changes to their individual performance (e.g., through growing larger or having deeper roots); or (ii) via changed numbers of individuals that perform at the same level (i.e., changed abundance) [86,87] (Figure I).

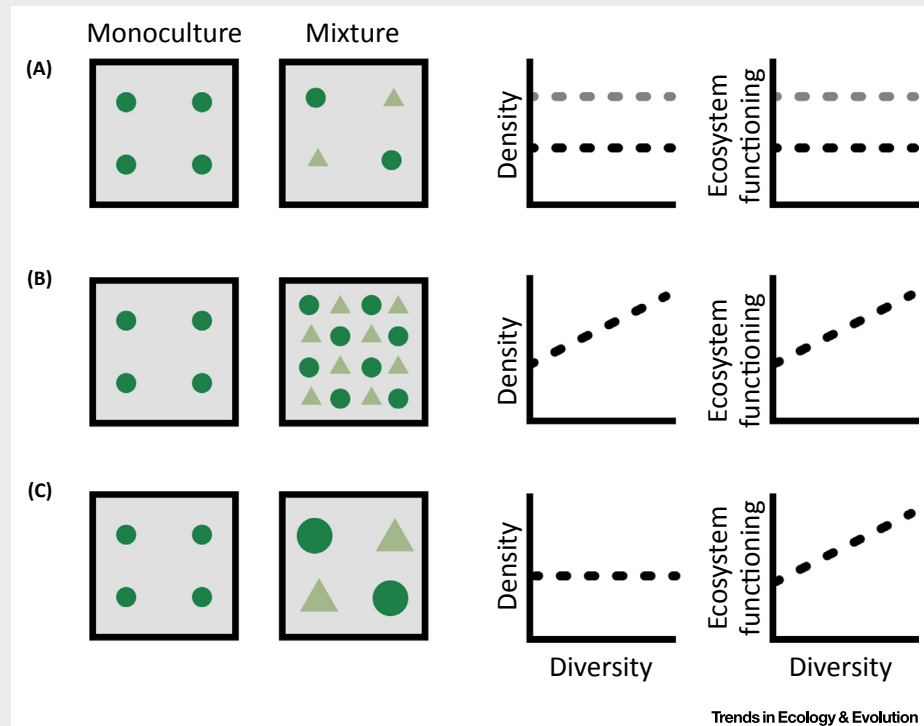


Figure I. Illustration of How Changes to Density and Performance Both Together and Alone Can Drive Enhanced Ecosystem Functioning in More Diverse Mixtures. If the abundance or individual performance relative to monoculture does not change, then ecosystem functioning is not enhanced relative to monocultures. (A), The black line represents a community with low abundance/small size, while the grey line represents high abundance/large size). Alternatively, if the abundance of individuals increases (B), individuals perform better (C), or both in mixture, then the ecosystem functioning of mixtures will increase relative to average monocultures. It should be noted that only scenario C or the combination of C and B are the result of plastic responses on the part of the plant to being in mixture. Yet, enhanced ecosystem functioning can be achieved by scenario B as well.

ecosystem functioning (reviewed belowground in [46,53], above and belowground in [59]). However, few studies have linked non-resource related mutualists to ecosystem functioning. We include these resource related mutualists, such as mycorrhizae and rhizobia, in the overlap between resource partitioning, abiotic facilitation, and biotic feedbacks (Box 2). However, aboveground, Ebeling *et al.* [60] demonstrated that pollinator communities increased in diversity with increasing plant diversity and that this increased the stability of plant flowering.

Overall, there is strong evidence that the release of negative biotic feedbacks with increasing plant diversity (cause) enhances ecosystem functioning (consequence) [55]. However, there is little evidence that positive biotic feedbacks enhance ecosystem functioning alone (but see Box 2).

The Future of Complementarity

Many studies report the presence of resource partitioning, abiotic facilitation, or biotic feedbacks. Yet, few quantify the contribution of these causes to enhanced ecosystem functioning

Box 2. Nitrogen Fixation, Mycorrhizal Colonization, and Root Interaction Partners

Plant roots harbor a diverse community of mutualists and interaction partners that influence the capacity of plants to take up resources and transfer those resources to their neighbors. We consider many of these interactions, including nitrogen fixation and increased nutrient availability from colonization by mycorrhiza, to be positive biotic feedbacks from a member of a different trophic level. These positive biotic feedbacks, however, result in both the ability of a species to potentially partition resources (one species specializes on nitrogen fixation while another must forage to find nitrogen) and the ability to confer resources to the surrounding community. The presence of nitrogen-fixing plants increases the overall availability of nitrogen [88–90]. Furthermore, there is significant evidence that legumes provide a generally positive effect on the biodiversity–ecosystem function relationship [91]. This nitrogen fixation also enables facilitation, and the proportion of N derived from legumes relative to non-legume sources increases with increasing plant diversity [90,92].

Similarly, mycorrhizae enable plants to take up additional resources. Thus, if resource partitioning occurs it may be enabled by mycorrhizal colonization. Alternatively, mycorrhizae may also transfer nitrogen that has been fixed by rhizobia to plants that do not harbor rhizobia, thus enabling facilitation [46]. There is limited evidence that a higher diversity of mycorrhizal fungi may increase plant productivity [93,94]. Additionally, Walder *et al.* [95] suggest that plant communities that harbor different mycorrhiza perform better in mixture. However, Schnitzer *et al.* [55] found that removing the beneficial portion of soil fungi from a diversity experiment had negligible effects on the relationship between biodiversity and productivity.

In addition to crucial mutualists, plants also harbor a diverse community of nonmutualist soil biota in and around their roots. There is strong evidence that plants increase soil microbial activity [81]. Furthermore, plant diversity alters decomposition [96–99]. These alterations to the soil community positively influence many ecosystem functions, including soil carbon storage [81]. Further, this impact on the soil community also influences resource availability and thereby provides a feedback on the plant community via resource partitioning and/or abiotic facilitation [100] (Figure 1).



Figure 1. Illustration of a Legume. Root nodules containing nitrogen-fixing rhizobia are highlighted in red.

(but see [21,22,25,28]). Quantifying how each of these causes individually contributes to ecosystem functioning may allow us to better predict the consequences of biodiversity loss in three ways. First, the consequences of biodiversity loss for ecosystem functioning may differ between these causes. Second, the relative importance of these causes likely changes with ecological context. Third, biodiversity may be more important for ecosystem functioning when several causes combine (Figure 2).

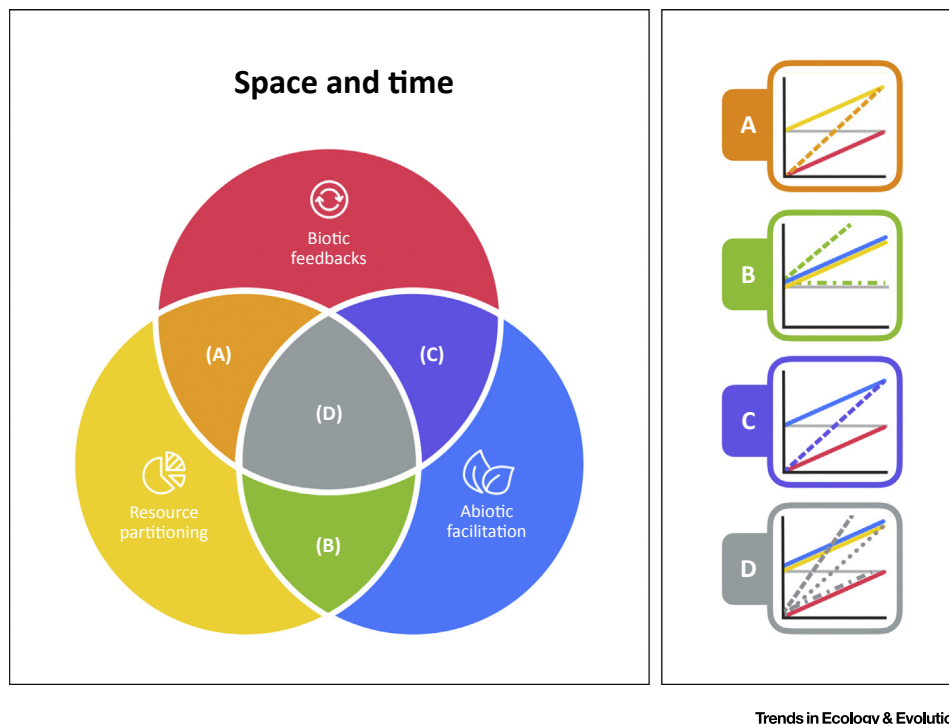


Figure 2. Proposed Framework for ‘Complementarity’ in the Biodiversity–Ecosystem Functioning Literature with Predictions for Enhanced Ecosystem Functioning. Resource partitioning (yellow), biotic feedbacks (red), and abiotic facilitation (blue) can each lead to enhanced ecosystem functioning. In many ecosystems, these three will occur at the same time. Thus, enhanced ecosystem functioning, when it occurs, is the net response of these different causes in this system. Here, we assume that when two or more processes are present, they are roughly the same magnitude. Inlaid plots (A–D) are our predictions for each complementarity cause and their combined effects on any generic ecosystem function (consequence, y-axis) with increasing diversity (x-axis). These predictions are general predictions for the slope and the intercept relative to the average ecosystem functioning over time (grey midline) when biodiversity enhances ecosystem functioning. These three causes can enhance ecosystem functioning via reduced performance in monoculture, via enhanced performance in mixture, or both, as indicated here by the intercept. That is, if the intercept is below the midline it indicates that performance is reduced in monoculture. The slope describes the strength of the increase in functioning. We do not intend to predict the magnitude of the differences between the intercepts of different causes. Furthermore, we depict these relationships as linear for simplicity, though they take a variety of forms depending on the function measured. Finally, we combine positive feedbacks and abiotic facilitation via nutrient addition for the purposes of these plots.

If enemies are species-specific then negative biotic feedbacks reduce performance of species in monoculture (A, C, and D, pink lines [57]). In contrast, resource partitioning (A, B, and D, yellow lines [25]) and abiotic facilitation via resource addition or positive feedback from biota (B, C, and D, blue lines [32,84]) will enhance ecosystem functioning when diversity is high.

We expect that when negative biotic feedbacks and resource partitioning act simultaneously, the slope of the biodiversity–ecosystem functioning relationship will increase as enemies suppress functioning in monoculture and resource partitioning enhances functioning in mixture (A, orange line; see [58] for general increase in biodiversity–ecosystem functioning relationship with multiple potential causes likely).

We expect that resource partitioning and abiotic facilitation both enhance function at high diversity if they occur for different limiting resources. Thus, the slope of the biodiversity–ecosystem functioning relationship may increase (B, dashed green line) relative to either process alone (B, blue or yellow line). Alternatively, if both resource partitioning and abiotic facilitation via nutrient addition or positive feedback from biota occur simultaneously for the same limiting resource and in the same amount, then that resource is no longer limiting and only abiotic facilitation or positive feedback will enhance ecosystem function (C, blue line [85]). Alternatively, if the resource that plants are able to partition and provide is nonlimiting, we expect a nonsignificant relationship between ecosystem functioning and biodiversity (C, green dashed-dotted line [85]).

Resource limitation is also an important concern for predicting the net result of combining resource partitioning, biotic feedback, and abiotic facilitation (D). Resource partitioning and abiotic facilitation both will enhance function at high diversity when they occur for different resources. Negative biotic feedback will suppress monoculture function [55]. We predict that this combination will increase the slope of the biodiversity–ecosystem functioning relationship (D, dashed grey line). Similarly, abiotic facilitation may enhance ecosystem functioning at high diversity while biotic feedback suppresses monoculture function (D, dotted line). If resource partitioning and abiotic facilitation both occur for the same limiting resource, then the net result is likely the same as the result for biotic feedback and abiotic facilitation combined (D, dotted line). Alternatively, if the resource that plants can partition and provide via abiotic facilitation is nonlimiting, then only the signal of biotic feedbacks may be present (D, dashed-dotted line).

We expect that the slope of the biodiversity–ecosystem functioning relationship increases for many interactions between processes relative to a single process alone. That is, each species likely adds more to ecosystem functioning when causes that reduce monoculture performance (such as negative feedback from species-specific enemies) and causes that enhance mixture performance (such as resource partitioning) occur together.

The Ecological Consequences of Understanding Underlying Causes

If resource partitioning between species enhances ecosystem functioning, then species loss may have no effect on overall ecosystem functioning or may decline proportionally to the contribution of the species lost. That is, the amount of functioning lost is the contribution of the species lost to functioning. This change in ecosystem functioning likely depends on the ability of the other species in a community to compensate for the functioning of the species lost via adjustments to their **resource partition** via plasticity [61]. For example, if species partition resources by depth, and the deepest rooting species goes extinct, another species may compensate for the lost species by growing deeper roots and the community overall resource uptake will stay the same [62]. If the remaining species are unable to compensate for the lost species, then the lost species' ecosystem functioning contribution is lost [61].

Alternatively, if abiotic facilitation between species enhances ecosystem functioning, then the loss of facilitators may disproportionately decrease ecosystem functioning. That is, if a facilitator is lost, their contribution to ecosystem functioning is lost, as is the amount that other species overperform because of their presence. Under extreme circumstances, if the whole community depends on a single facilitator, then the community may collapse [61]. In less extreme cases, the extinction of a facilitator reduces the abundance and performance of other species because they were dependent upon the resources or stress amelioration provided by the facilitator [61]. Even in this less extreme case, over several generations, facilitator loss can accelerate species loss in addition to reducing ecosystem functioning.

If feedbacks from biotic interaction partners enhance ecosystem functioning, then the loss of individual plant species depends on the type of interaction and whether the interaction is lost or only the species [63]. For example, if the species lost contributes a species-specific enemy, then the loss to ecosystem functioning will likely equal the contribution of the species lost. Alternatively, removing the enemies may increase overall ecosystem functioning, especially in terms of total biomass production [58]. If a system loses a species-specific herbivore, total biomass production may increase as species are released from herbivore pressure [58,64]. However, this increase in productivity may be accompanied by plant species loss. Less competitive species may be outcompeted by species that are now released from enemy pressure. This competition accelerates species loss even while dominant species maintain productivity [65]. Alternatively, if the plant species that is lost contributes an important mutualist, the species' contribution is lost, as is the amount that the population overperformed as a result of the species [63,66]. For example, if a legume that provides nitrogen to the surrounding plants via its rhizobia is lost, the contribution of the legume is lost, as is the amount that ecosystem functioning was increased due to the rhizobia's contribution to the local resource pool (Box 2).

Ecological Context Matters

Resource partitioning, abiotic facilitation, and biotic feedbacks are likely most relevant in different ecological contexts. These differences in relevance may contribute to variation in biodiversity–ecosystem functioning relationships across landscapes and between ecosystems. In a meta-analysis of forest and grassland biodiversity experiments, Guerrero-Ramírez *et al.* [67] found that forests and grasslands had variable biodiversity–productivity relationships that depended on environmental factors. In one grassland, reduced monoculture performance over time drove biodiversity–productivity relationships, suggesting that abiotic facilitation via stress amelioration or negative biotic feedbacks caused enhanced ecosystem functioning. In six other grasslands, increased mixture performance over time drove biodiversity–productivity relationships, suggesting that abiotic facilitation via resource enrichment, positive biotic feedbacks, or resource partitioning caused enhanced ecosystem functioning. Further, soil

characteristics such as soil organic carbon content, soil pH, sand and clay content, soil bulk density, cation exchange capacity, and volumetric water content at wilting point explained over 40% of these differences between sites. This context dependence suggests that not all causes are equally likely in all ecological contexts (see also [68]). In particular, three **ecological gradients** may influence the likelihood and relative importance of these different causes: resource availability, abiotic stress, and enemy abundance/specificity.

Resource availability may change plant community reliance on abiotic facilitation via resource addition and resource partitioning. When resources are severely limiting, abiotic facilitation via resource addition is likely to enhance ecosystem functioning. Without resource limitation, plants are unlikely to profit from the enhanced resource availability from abiotic facilitation via resource addition with increasing diversity. Further, unless plants are not in competition for resources, resource partitioning is likely to be more beneficial when resources are limiting [69].

Abiotic stress likely magnifies the contribution of abiotic facilitation via stress amelioration to enhanced ecosystem functioning [44,70,71]. The stress-gradient hypothesis suggests that as environments become more stressful, abiotic facilitation via stress amelioration becomes more important. In the biodiversity–ecosystem functioning context, this increased reliance on abiotic facilitation via stress amelioration means that high-diversity communities will suffer less in stressful conditions. There is some evidence that species can ameliorate the abiotic stress of flooding [72], heavy-metal contamination [73], and drought [45]. Under less stressful conditions, resource partitioning may contribute more than abiotic facilitation to enhanced ecosystem functioning. Similarly, positive feedback from biotic interaction partners is likely to be more beneficial under resource limitation and stress.

An enemy abundance/specificity gradient will likely amplify the contribution of negative biotic feedbacks to biodiversity–ecosystem functioning relationships. Plant–soil feedback experiments and aboveground enemy removals elucidate a strong and consistent contribution of enemies to enhanced ecosystem functioning [55–58]. A gradient of enemy types (specialist to generalist) or enemy abundance is likely to similarly provide evidence that species-specific enemies reduce monoculture performance. This gradient may be particularly relevant across latitude where changes in the strength and abundance of biotic interactions may contribute to latitudinal gradients in diversity [74]. This continental gradient in enemies may alter biodiversity–ecosystem functioning relationships across continental scales [75,76].

When Causes Combine to Enhance Ecosystem Functioning

When biodiversity enhances ecosystem functioning, it need not occur via any one mechanism alone. Rather, it may be more realistic to assume that resource partitioning, abiotic facilitation, and biotic feedbacks occur simultaneously in many systems. As a consequence, ecosystem functioning represents the **net response** of the ecosystem to combinations of these causes, and the individual effects of the causes are masked. Several studies now implicate multiple causes simultaneously. For example, Seabloom *et al.* [58] experimentally removed insects, foliar fungi, and soil fungi from plots at Cedar Creek Ecosystem Science Reserve. The biodiversity–productivity relationship changed as a result of this removal but was still present. This result implies that enemies are not the only cause of enhanced ecosystem functioning at this site. Similarly, Guerrero-Ramírez *et al.* [67] found that both enhanced functioning in mixture and reduced functioning in monoculture over time drove biodiversity–productivity relationships simultaneously at three grassland sites. This pattern again suggests that several causes are responsible. We hypothesize that when any cause that reduces the average performance of species in monoculture combines with any cause that increases their average performance in

mixture, the slope of the biodiversity–ecosystem functioning relationship will increase (Figure 2). This increase in slope means that diversity may be proportionally more important for ecosystem functioning under these circumstances.

Concluding Remarks and Future Perspectives

For plant communities, complementarity is one of the most commonly invoked drivers behind enhanced ecosystem functioning with increasing biodiversity. Yet, its current usage obscures the individual contributions of resource partitioning, biotic feedbacks, and abiotic facilitation to enhanced ecosystem functioning. The extent to which these different causes contribute to enhanced ecosystem functioning in higher-diversity systems is unclear. Disentangling these components is essential to predicting biodiversity–ecosystem functioning relationships across ecological contexts and under predicted accelerating species loss.

We suggest that there are several avenues by which biodiversity ecosystem functioning research should begin to disentangle these components (see Outstanding Questions). First, improved theoretical work that incorporates more than one cause of enhanced ecosystem functioning simultaneously will help to refine predictions for how these different causes may interact. Theoretical work on biodiversity–ecosystem functioning relationships has focused primarily on complementarity causes in isolation (e.g., [55,77,78]). Theoretical models that incorporate multiple complementarity causes simultaneously are necessary to refine predictions for how the different causes of complementarity may interact.

Second, we suggest that combining ecological gradients across resources, stress, and enemies will enhance differences between resource partitioning, abiotic facilitation, and biotic feedbacks and allow them to be more easily quantified (after [79]). For example, monocultures may perform more poorly than mixtures due to negative feedback from species-specific pests and pathogens (biotic feedback) or because other species mediate environmental stress (abiotic facilitation). Along a diversity gradient without species-specific enemies (enemy gradient) under stress (stress gradient) but with ample resources (resource availability gradient), if plants perform more poorly in monoculture than in mixture the most likely driver is abiotic facilitation via stress amelioration. Experimental work that utilizes these gradients will help to elucidate how these three sets of species differences interact to enhance ecosystem functioning across ecological contexts.

Finally, further synthesis work from long-term grassland biodiversity experiments may also contribute to a better understanding of the causes of complementarity. Many biodiversity–ecosystem functioning (BEF) experiments have now been established for over a decade. These long-term datasets provide particular power to determine whether monocultures are declining or mixtures are performing better (e.g., [67]). Further, these long-term datasets span natural climatic and resource gradients (e.g., [3,80]). Long-term data from these experiments of measures like leaf area index [81], resource uptake [28], or soil porosity [72] combined with the natural climatic variation inherent in time series data may be particularly useful. For example, during a drought, if monocultures perform more poorly than the mean performance over time, and this effect is linked to a lower leaf area index in these monocultures, then abiotic facilitation via stress amelioration likely enhances ecosystem functioning under these circumstances.

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Outstanding Questions

To what extent do resource partitioning, abiotic facilitation, and biotic feedbacks depend on abiotic conditions?

How strong must individual causes be in order to enhance ecosystem functioning?

Are the interactive effects of two or more causes on ecosystem functioning additive or synergistic?

How will climate change affect the causes of complementarity and via them ecosystem functioning?

How do changes in community composition rather than species loss affect resource partitioning, abiotic facilitation, and biotic feedbacks and thereby ecosystem functioning?

Are resource partitioning, abiotic facilitation, and biotic feedbacks relevant with increasing spatial scale?

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