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Opinion

Parasitism and the Biodiversity-Functioning Relationship

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Species interactions can influence ecosystem functioning by enhancing or suppressing the activities of species that drive ecosystem processes, or by causing changes in biodiversity. However, one important class of species interactions – parasitism – has been little considered in biodiversity and ecosystem functioning (BD-EF) research. Parasites might increase or decrease ecosystem processes by reducing host abundance. Parasites could also increase trait diversity by suppressing dominant species or by increasing within-host trait diversity. These different mechanisms by which parasites might affect ecosystem function pose challenges in predicting their net effects. Nonetheless, given the ubiquity of parasites, we propose that parasite–host interactions should be incorporated into the BD-EF framework.

Incorporating Parasitism into the BD-EF framework

How might **biodiversity** (see Glossary), **ecosystem functioning**, and the relationships between biodiversity and ecosystem functioning respond to parasitism? **Parasites** are ubiquitous organisms with the potential to regulate and limit host abundance [1] as well as the ecosystem processes that such hosts influence [2,3]. For instance, Preston *et al.* [2] reviewed how parasites might reduce herbivore abundance [4,5], and alter plant productivity and edibility [6]. Similarly, Lafferty and Kuris [7] considered how parasites that manipulate behavior could help predators to control herbivores such as moose, create a new habitat (e.g., by stranding infected cockles) [8], or generate food subsidies for trout by inducing suicide in crickets [9]. In another case, ungulate population regulation by rinderpest resulted in increased fire events and decreased tree biomass, with negative effects on carbon storage [10]. These examples indicate that the ecosystem-level effects of parasitism might arise from impacts on functionally significant hosts via trophic cascade pathways [11]. Parasite impacts on host-derived functions are likely pervasive, although compensation by competing species could mitigate the effects of host suppression at the ecosystem level. In this regard, parasites are no different from other biological pressures, given any factor altering the activity or abundance of functionally important species should also affect ecosystem function.

In addition to altering ecosystem functioning through direct effects on host abundance, parasites could also affect ecosystem functioning through their effects on biodiversity. BD-EF research postulates that effects of diversity on ecosystem functioning depend on the types and relative abundances of species functional traits that are present in a community [12,13] and on how interactions among species influence trait expression [14]. For example, diet diversity in animal communities results in more efficient nutrient and energy transfer to higher trophic levels [15]. Plant biomass production [16,17], nutrient and energy cycling [18], and nutrient uptake from freshwaters [19] are often more efficient with increasing biodiversity, especially if **functional trait diversity** also increases [20]. Parasites have the potential both to decrease or increase biodiversity. For example, parasites might decrease functional diversity by

Highlights

Biodiversity affects ecosystem functioning.

Biodiversity may decrease or increase parasitism.

Parasites impair individual hosts and affect their role in the ecosystem.

Parasitism, in common with competition, facilitation, and predation, could regulate BD-EF relationships.

Parasitism affects host phenotypes, including changes to host morphology, behavior, and physiology, which might increase intra- and interspecific functional diversity.

The effects of parasitism on host abundance and phenotypes, and on interactions between hosts and the remaining community, all have potential to alter community structure and BD-EF relationships.

Global change could facilitate the spread of invasive parasites, and alter the existing dynamics between parasites, communities, and ecosystems.

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eliminating certain traits or species, or by increasing trait similarity within the community. On the other hand, the effects of parasites on infected host phenotypes might increase functional diversity by generating novel traits or by decreasing trait similarity among species. The complex interactions and feedbacks between parasites and biodiversity complicate prediction of the outcomes for BD-EF relationships.

Mechanisms that can drive diversity effects on functioning include **selection effects** [21], **facilitation** [22,23], and niche differentiation (including **complementary resource use**) [24], which are often linked to positive diversity effects. Parasites might add an additional mechanism resulting in positive net diversity effects. In cases where host-specific diseases are transmitted by generalist vectors, communities with low diversity could support more disease transmission than those with high diversity [25,26], although the generality of this has been questioned [27,28]. Given that infectious diseases might decrease host productivity, reduced disease transmission in high-diversity communities could explain some positive BD-EF relationships [29,30] (Figure 1A). Similarly, if higher host diversity results in lower host densities, high host diversity could dilute the prevalence of host-specific parasites, particularly those with complex life cycles [31,32].

Parasitism has largely been neglected in BD-EF research [33], which has instead focused on interactions occurring within trophic levels, especially among primary producers [12] and consumers [13,22], with some exceptions [15,34]. Parasites might affect BD-EF relationships by altering community diversity or by modifying trait identity and increasing trait diversity even within a host species. Indeed, parasite-mediated increases in intra- or interspecific functional diversity could lead to increased resource consumption, which is precisely the opposite effect that would be expected for host suppression under parasite-induced trophic cascade effects [11]. Interactions among parasites within a host [35] might also change the outcome of BD-EF relationships. Clearly, there is a need to incorporate parasitism more explicitly into the BD-EF framework (Box 1).

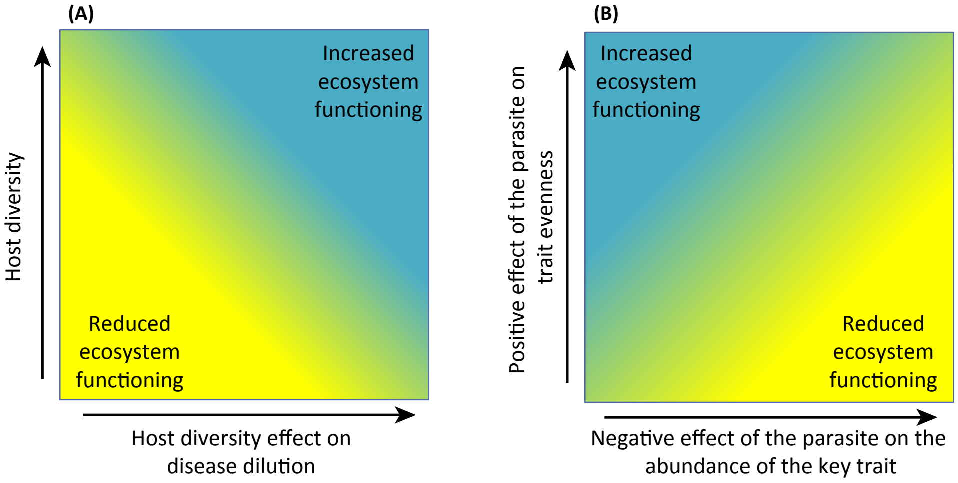

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Figure 1. Parasitism as a Mechanism Altering Biodiversity and Ecosystem Functioning (BD-EF) Relationships. (A) Parasitism could be a mechanism behind positive diversity effects on functioning if high host diversity dilutes diseases in the community. (B) Parasite effects on trait abundance can affect ecosystem functioning if the trait that is reduced is a key driver of ecosystem functioning. This effect will also depend on the distribution of traits in a community because communities with more evenly distributed traits might compensate better for the loss of other important traits.

Glossary

Biodiversity:	the diversity of species, traits, and genes, and even habitats, within and among ecosystems in a region.
Complementary resource use:	niche differentiation arising from differences in how taxa exploit a common resource, leading to more efficient use of that resource overall.
Disease-dilution effect:	a higher diversity of hosts has the potential to dilute the transmission of host-specific diseases.
Ecosystem functioning:	a set of ecological processes that arise from interactions among species and the environment. Examples of ecological processes underpinning ecosystem functioning include the cycling of nutrients assisted by detritivores or scavengers, and biomass accrual of consumer and primary producer communities, which are all regulated not only by the environment (e.g., nutrient availability) but also by the activities of multiple species, and interactions among them.
Facilitation:	occurs when the activities of one species enhance the activities of a second species.
Functional trait diversity:	an index summarizing the diversity of functional traits in a community.
Functional traits:	phenotypic characteristics which regulate the influences of species on ecosystem functioning. They are often morphological, physiological, behavioral, or ecological.
Parasite:	an organism that lives and feeds on a living host, often affecting its fitness and/or phenotype. Pathogens are here considered as a special case of microparasites.
Selection effects:	the increased likelihood that a more diverse community will include particular species that strongly regulate ecosystem process rates in their own right.
Trait-mediated effects:	the non-lethal effect of a predator or parasite on the attributes of the prey or host, which can affect population dynamics and species interactions without affecting species density.

Box 1. Estimating Relative Change in Ecosystem Functioning as a Result of Parasitism Effects on BD-EF Relationships

Although the potential for parasitism to regulate ecosystem functioning has been emphasized previously [33], there are currently no published assessments of how parasites might affect the outcome of BD-EF relationships. We combine here two independent studies that analyzed the effects of the same freshwater invertebrate detritivore species, *Gammarus fossarum*, on the same ecological process, leaf decomposition [15,85], to illustrate the potential effect of parasitism in altering BD-EF relationships.

In Jabiol *et al.* [15], leaf mass loss in a model freshwater food web was highest when the diversity of three trophic levels (fungal decomposers, invertebrate detritivores, and predatory fish, simulated using fish kairomones) was maximal. Specifically, single-detritivore species treatments had ~36% leaf-mass loss after 130 h of exposure at highest fungal diversity and fish presence. By comparison, three-detritivore species mixtures including *G. fossarum* had ~41% leaf-mass loss after the same period, a small but positive diversity effect attributable to complementarity among the detritivores. Similar three-detritivore treatments, but without fish presence, had ~35% leaf-mass loss, and the difference attributable to predator presence was statistically significant.

How might parasites affect this association? The acanthocephalan parasite *Pomphorhynchus tereticolli* can affect behavior and feeding rates in the *G. fossarum* [85]. Infected *G. fossarum* eat 30% less leaf mass (~0.43 compared to ~0.65 mg by mm of gammarid day^{-1} when uninfected) [85].

If this species was infected in the three-detritivore species treatments that included fish kairomones [15], leaf-mass loss would have been reduced by up to ~10% (assuming that the total *G. fossarum* effect on leaf-mass loss equals 1/3 in the three-species mixture). This reduction in consumption by *G. fossarum* could likely reduce leaf-mass loss from the original ~41% to ~37%, a result close to that observed when fish were not present in the three-detritivore species treatment and to the average single-species treatment (Figure I). Clearly, this cross-study assessment of relative change in BD-EF attributable to parasitism should be taken with care, given the different nature of the two studies, the multiple potential interaction outcomes among the three detritivore species if one of them is infected, and the potential variability in the response of gammarids to the parasite [85]. Nonetheless, this assessment demonstrates one of the many ways in which parasites could affect biodiversity functioning, and also how parasites could confound interpretations from biodiversity-functioning studies when their impacts are not accounted for. We are not suggesting the referenced study neglected parasitism; this parasite leaves a clear yellow-orange mark on the body of the amphipod that is difficult to miss [85]. However, parasites are harder to detect in most other species used in biodiversity-functioning studies.

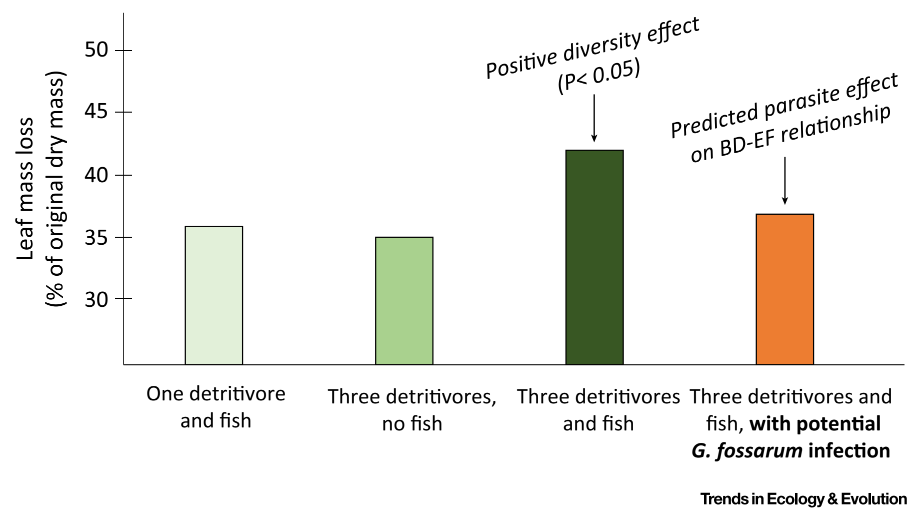

Figure I. Negative Parasite Effects on Leaf Consumption by the Detritivore *Gammarus fossarum* [85] Could Affect the Outcome of a Positive BD-EF Relationship [15]. Numbers on the three first columns (shades of green) are from [15] and are approximations from treatments under highest microbial diversity. The last column (orange) shows the predicted reduction in leaf-mass loss under parasite effect.

Parasite Effects on Community Structure, Species Diversity, and Trait Distribution

Parasites can affect biodiversity [36] and alter the taxonomic and functional structure of communities [1,37–39] by affecting host phenotype, reducing host abundance, and altering species richness and evenness. For example, the trematode *Cryptocotyle lingua* affects grazing by its snail host, which in turn increases ephemeral macroalgae dominance, altering the community structure of an intertidal macroalgal community [38]. Another trematode species predominantly infects cockle foot tissue, decreasing its ability to bury in the sediment. Infected cockles are more sessile, reducing their influence on sediment bioturbation and in turn increasing the abundance and richness of benthic invertebrates [40]. Parasites can also affect biodiversity by facilitating or limiting species invasions [41,42], as with the acanthocephalan *Pomphorhynchus laevis*, which infects both native and invasive amphipod species. However, although this parasite increases the vulnerability to predation of the native host species by inducing positive phototaxis, such an effect is not seen on the invading species [43]. Opposing effects of parasitism on native and invasive species are found in several aquatic and terrestrial species [44].

Diversity might also decline if dominant species are tolerant to a parasite that spills over to intolerant competitors [45]. On the other hand, by reducing host abundance, parasites might alleviate competition [41] and thus favor otherwise rare species. More specifically, parasites can promote coexistence by regulating relative abundance among competitors (density-dependent transmission that creates an advantage for rarity) or reducing fitness differences (e.g., penalizing the performance of superior species) [36], which is consistent with the Janzen–Connell hypothesis for tree diversity in tropical forests [46,47]. In any given system there are likely to be several parasite species, some promoting competitive exclusion, others promoting coexistence, and others having little effect.

The potential and documented effects of parasites on ecosystem functioning might be best understood by considering how their impacts on host phenotype and species composition alter functional trait distribution within communities. In general, communities dominated by a few traits are expected to be associated with lower processing rates, whereas communities with more evenly distributed traits are associated with higher processing rates [48,49]. Thus, declines in host population abundances following parasite infections might reduce important traits if no other similar species compensates for this loss. However, if parasites favor complementary traits within an assemblage, then, assuming no decrease in host abundance, parasites could increase some ecosystem processes through positive effects on trait distribution (Figure 1B).

Parasite Effects on Trait Composition

Parasites alter host physiology, morphology, fecundity, and behavior. For example, infected hosts might have different nutrient requirements or metabolic rates. Furthermore, parasites might alter host movement and habitat preferences. These effects add functional diversity to a community by (i) magnifying differences between host and non-host species, and (ii) generating differences between infected and uninfected individuals within a host species (Figure 2). Parasite effects on functioning that arise from changes in trait composition are often termed **trait-mediated** (indirect) **effects**. We indicate below three mechanisms by which parasites might affect trait composition with potential consequences for functional diversity and thus for BD-EF relationships.

Body Size and Metabolism

Parasites can alter host population size structure by affecting host growth rate and host body size. Although most parasites stunt growth, some parasites induce gigantism, as with the snail

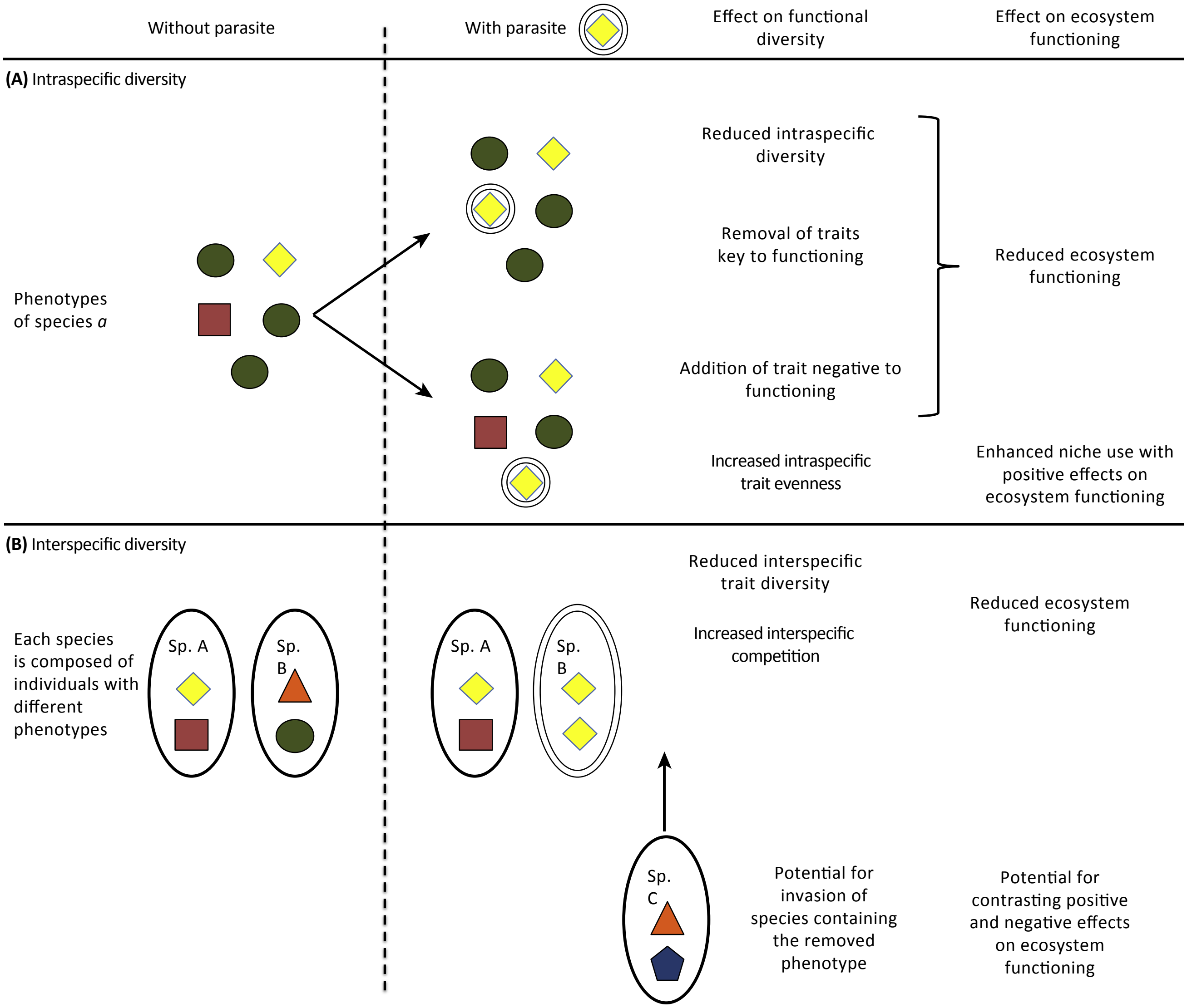

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Figure 2. Parasites May Alter Intra- and Interspecific Trait Diversity. (A) Parasitism can affect the phenotype of an individual, as indicated by ◈. This parasite-induced functional trait can be similar to other common traits that are already present in a population, in which case it might reduce intraspecific diversity. Parasitism can also have a negative effect on intraspecific diversity and on ecosystem processes by removing traits key to resource processing. If the parasite-modified trait is novel or rare, parasites can increase intraspecific diversity and trait evenness. The effect on ecosystem processes will depend on whether the novel trait has a positive or negative effect in the ecosystem. (B) Parasites can also alter interspecific diversity by adding or eliminating important traits from the community. Parasites might contribute to species (Sp.) coexistence or to species invasion by reducing the fitness of some dominant species. However, as for within-host diversity, the extent to which diversity promotion increases ecosystem processes depends on whether other species can compensate for a suppressed dominant species.

Batillaria cumingi, whose individuals infected by the trematode *Cercaria batillariae* can be 20–30% longer than uninfected individuals [50]. Effects on host body size are likely to have knock-on effects on important ecosystem processes involving the host species, including resource consumption and nutrient cycling. Body size can also drive ecosystem functioning and BD-EF relationships through its effect on metabolic rate [51–53]. Allometric scaling between metabolic rates and body size will lead small-bodied populations to have higher bulk resource processing rates than large-bodied populations [54] of the same total biomass. Parasites also respond to scaling properties; a gram of several small parasites will have a greater metabolic effect on an individual host than a gram of a few large parasites [55].

Nutrient and Other Resource Requirements

Most animals are homeostatic, meaning that they require nutrients in specific ratios that are seldom matched in their resources. Often the availability of carbon (C), nitrogen (N), and phosphorus (P) in specific ratios (N:P, C:N, and C:P) is considered to be important, given the strong enrichment of these elements in consumers relative to the lower concentrations in the environment [56]. A stoichiometric imbalance between chemical elements in consumers and their diet can reduce growth and survival rates, and increase resource consumption [57], with implications for ecosystem functioning [58].

Parasites require essential nutrients for their own growth and reproduction. However, parasites are not always in stoichiometric balance with their hosts [59]. Energy and nutrient sequestration by parasites can induce strong nutrient limitation in the host [60,61], affecting host growth and survival rates [61,62]. Moreover, parasite-induced effects could be further enhanced if the host already has a diet deficient in specific nutrients [63]. By causing or even enhancing nutrient deficiency, parasites will affect host consumption rates or even alter host consumption preferences [64] toward food sources containing the parasite-induced limiting nutrient. Hosts might also seek food items that contain particular nutrients or nutrient combinations that aid resistance to the parasite infection. The caterpillar *Spodoptera exempta* shows a preference for low C:P diets that increase its survival when infected by a virus [65], and snails infected with trematodes excrete a higher N:P ratio compared to uninfected snails [66].

Behavior

Many parasites affect host behavior [67]. Manipulative parasites can impair vertebrate host responses to predators and shift invertebrate host microhabitat use [68]. Parasites that manipulate top predators or foundation species can alter ecosystem functioning through trait-mediated effects [7]. For example, nematomorph worms manipulate terrestrial crickets to enter trout streams, which, in addition to providing food for trout, reduces predation pressure on aquatic insects, increases algal production, and decreases litter decomposition [9]. Such trait-mediated indirect effects due to behavioral alterations are known for insects [9], mollusks [40], crustaceans [69], reptiles [70], fish [71], and mammals [72], and could increase host intraspecific functional diversity [40].

Parasites can also affect host feeding behavior and preferences. Infected *Littorina littorea* snails eat less algal biomass than the uninfected conspecifics [38], thereby increasing algal biomass accrual, and the detritus-feeder isopod *Caecidotea communis* eats less leaf litter when infected by *Acanthocephalus tahlequahensis* [69]. Sometimes these parasite-induced alterations are so large that parasitized hosts function as a separate species. For example, the Asian mud snail *B. cumingi* grows larger and moves deeper when infected by the trematode *C. batillariae* [50]. Instead of competing with uninfected snails, infected snails exploit a novel algal resource, effectively akin to adding a new species to a community.

Parasites Can Directly Contribute to Productivity

Although most parasites negatively impact host nutrition, some free-living infective stages are edible food resources for non-host species. For instance, small fish will feast on trematode cercariae [73]. Similarly, during diatom blooms in lakes, zooplankton might have little to eat, but parasitic chytrids that kill inedible diatoms produce edible spores that can represent ~50% of the zooplankton diet, sustaining much secondary production despite the overall lack of suitable primary producers for food [6]. Because such parasites are common in aquatic systems, edible parasites could drive important ecosystem processes when they convert inedible resources into food for consumers. Hemiparasitic plants might also contribute to overall productivity by increasing nutrient availability in the soil, despite their potential negative effect on host biomass [74].

Parasitism and Biodiversity-Functioning Relationships under Global Change

Global change, including climate-driven changes and species introduction and extinction, have potential to affect BD-EF at regional and global scales [75]. In particular, invasive species often carry new parasites which can further affect the biodiversity of native organisms [42,76]. Parasites that cause disease epidemics might wipe out keystone or foundation species, transforming the structural configuration of habitats and landscapes, and strongly impacting ecosystem functioning and services [77–79]. Climate warming might further influence the host–parasite balance by increasing parasite development and survival rates (especially for invasive parasites), thus facilitating disease transmission or promoting host susceptibility [80]. Biodiversity loss might also favor increased transmission rates [81]. Accordingly, parasites could influence how global change alters BD-EF relationships. Indeed, the likely increasing prevalence of invasive parasites is an often overlooked component of global change, but one which poses a great ecological and economic threat, as well as substantial management challenges [78–81].

Research Directions on the Role of Parasitism for Ecosystem Functioning

Among the various mechanisms by which parasites might affect ecosystem functioning [2], parasites have seldom been considered as agents that modify ecosystem processes through their effects on trait diversity. Parasites increase within-host trait diversity by altering host phenotypes, including host morphology, behavior, and stoichiometry, and they can also increase trait diversity within a community by facilitating coexistence among competing species. These impacts on trait diversity or distribution could then alter the ecosystem processes they underpin. Finally, parasites could support positive BD-EF relationships through **disease-dilution effects** in diverse communities where disease transmission is strongly increased by higher relative encounter rates between hosts. Hence, BD-EF assessments should consider how parasites might modulate and modify diversity, and drive diversity effects on functioning, and here we hope to stimulate researchers to investigate these scenarios. Including parasites in BD-EF studies will require incorporation of the effect of parasitism on host trait expression into current measures of intraspecific diversity, in conjunction with standard diversity measures.

It is worth noting that parasites might represent 40% of all known metazoan species [82], and helminth parasites are alone estimated to comprise 50% more species than there are vertebrate hosts [83,84]. Parasite diversity becomes overwhelming if parasitic viruses, bacteria, fungi, and protozoa are also considered. It is unlikely that ecological processes are not influenced by parasites in one way or another. Thus, there is no shortage of processes or parasite species with which to study biodiversity functioning (see Outstanding Questions). Considering the many effects parasites might have on community diversity will improve our understanding of how and when biodiversity affects ecosystem functioning.

Outstanding Questions

When does parasitism increase or decrease community functional diversity?

When does community functional diversity increase or decrease parasitism?

What is the importance of parasitism relative to other species interactions (competition, predation, facilitation) in mediating the effects of biodiversity on ecosystem functioning?

What are the main mechanisms by which parasites can affect ecosystem functioning through changes in biodiversity?

Does parasitism increase ecosystem processes by increasing niche partitioning or niche complementarity?

Does parasitism reduce ecosystem processes by reducing host fitness?

Do positive effects of parasitism on functional diversity help to compensate for impacts on parasitized individuals?

Are there specific types of parasitism that show consistent positive or negative effects on BD-EF relationships?

Is the parasite effect on the diversity-functioning relationship dependent on the functional/trophic structure of the community?

How important are the effects of parasitism on the stability of food web structure and function relative to other types of trophic (e.g., omnivory, intraguild predation) and non-trophic (e.g., commensalism) interactions?

How do the effects of parasitism on BD-EF relationships vary with warming and other aspects of global change?

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