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Parasitism and the biodiversity-functioning relationship

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Abstract*:* 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 research. Parasites might increase or decrease ecosystem functioning by reducing host abundance. Parasites could also increase trait diversity by suppressing dominant species or increasing within-host trait diversity. These different mechanisms by which parasites might affect ecosystem function pose challenges in predicting their net effects. Given the ubiquity of parasites, we propose that parasite-host interactions should be incorporated into the biodiversity-ecosystem functioning framework.

Keywords: ecosystem functioning; functional trait diversity; parasites; phenotypic diversity

Incorporating parasitism into the biodiversity and ecosystem functioning framework

How might biodiversity, ecosystem functioning, and the relationship between biodiversity and ecosystem functioning respond to parasitism? Parasites are ubiquitous organisms with the potential to regulate and limit host abundance [1] and the ecosystem processes that such hosts influence [2]. For instance, Preston et al. [2] reviewed how parasites might reduce herbivore abundance [3,4], or alter plant productivity and edibility [5]. Similarly, Lafferty and Kuris [6] considered how manipulative parasites could help predators control herbivores like moose, create new habitat (e.g. stranding infected cockles) [7] and generate food subsidies to trout by inducing suicide in crickets [8]. A parasite's effect on ecosystem function arises primarily from its effects on that host. Most clearly, parasites can reduce ecosystem functioning by impacting host species that play key roles in ecosystem services. For example, honey-bee colony collapse can in part be explained by the increase in parasite infection in bee hives exposed to fungicides, which lower bee resistance to the microsporidian (fungal) parasite *Nosema ceranae* [9]. Bee population decline has strong negative consequences for plant pollination and crop production, which are important ecosystem functions and services. In another case, ungulate population regulation by rinderpest increased fire events and decreased tree biomass, with negative effects on carbon storage [10]. Parasite impacts on host-derived functions are likely pervasive, although compensation by competing species may mitigate the effects of host suppression at the ecosystem level. In this regard, the impact of parasites is not different from that of other biological pressures, as any factor altering the activity or abundance of functionally important species should also affect ecosystem function.

Besides altering ecosystem functioning through direct effects on host abundance, parasites could also affect ecosystem functioning through their effects on biodiversity. Biodiversity and ecosystem functioning (BD-EF) research postulates that effects of diversity on ecosystem functioning depend on the types and relative abundances of species functional traits present in a community [11,12], and on how interactions among species influence trait expression [13]. For example, animal communities comprising multiple contrasting feeding methods can process more basal resources resulting in more efficient nutrient and energy transfer to higher trophic levels [14]. Plant biomass production [15,16], nutrient and energy cycling [17], and nutrient uptake from freshwaters [18], are often more efficient with increasing biodiversity, especially if functional trait diversity increases simultaneously [19].

Mechanisms that can drive diversity effects on functioning include selection effects [20], facilitation [21,22], and niche differentiation [23], which are often linked to positive diversity effects. Parasites might be instrumental for an additional mechanism resulting in positive net diversity effects. Under some circumstances, like host-specific diseases transmitted by generalist vectors, communities with low diversity could support more disease transmission than those with high diversity [24,25] though the generality of this has been questioned [26,27]. As diseases tend to decrease productivity, a positive BD-EF relationship could be explained by reduced disease transmission in high-diversity communities [28,29] (Fig. 1a). Although a diversity-induced disease dilution could explain some diversity effects on ecosystem functioning, the BD-EF literature largely ignores the effect of parasites in BD-EF relationships.

The BD-EF field has also neglected parasites by focusing on interactions occurring within trophic levels, especially among primary producers [11] and consumers [21], with some exceptions [14,30]. Less considered, and our focus here, has been that, by increasing community diversity or modifying trait identity and modulating trait diversity within a host species, parasites could increase ecosystem functioning, precisely the opposite effect we predict for host suppression.

Parasite effects on trait distribution and diversity

Parasites can affect biodiversity [31] and alter community structure [1,32-34] by reducing host abundance, affecting species richness, altering community evenness, and facilitating or limiting species invasions [35,36]. The parasite effect could in turn affect functional trait distribution within communities. In general, communities dominated by a few traits are expected to be associated with less efficient ecosystem functioning, whereas communities with more evenly distributed traits are associated with enhanced functioning [37,38]. 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 enhance ecosystem functioning (Fig. 1b). Diversity will decline if dominant species are tolerant to a parasite that spills over to intolerant competitors [39]. On the other hand, by reducing host abundance, parasites might alleviate competition [35] and thus favor otherwise rare functional traits. 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 superior species' performances) [31], which is consistent with the Janzen-Connell hypothesis for tree diversity in tropical forests [40,41]. In any given system, there are likely to be several parasite species, some promoting competitive exclusion, others promoting coexistence, and others having little effect.

Positive and negative interactions are possible between host and parasite diversity. Higher host diversity increases opportunities for host-specific parasites, particularly those with complex life cycles [42,43]. Higher parasite diversity might have further knock-on consequences for functional trait diversity in the community, and for ecosystem functioning (Fig. 1c). On the other hand, if higher host diversity results in lower host densities, high host diversity could dilute parasite prevalence [44,45]. Such interactions between host and parasite diversity could generate unpredictable feedbacks that might alter ecosystem functioning. Furthermore, interactions among parasites within a host [46] might further change the outcome of BD-EF relationships. Clearly, the complex interactions and feedbacks between parasites and biodiversity cast uncertainty on how parasites will affect ecosystem functioning.

Parasite effects on trait composition

Parasites alter host physiology, morphology, fecundity, and behaviour. 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 (Fig. 2). Parasite effects on functioning arising from changes in trait composition are often termed trait-mediated indirect effects. Below we indicate three mechanisms by which parasites might affect trait composition with potential consequences to biodiversity and thus to BD-EF relationships.

1. 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 *Batillaria cumingi*, whose individuals infected by the trematode *Cercaria batillariae* can be 20 to 30% longer than uninfected ones [47]. 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 [48-50]. Allometric scaling between metabolic rates and body size will lead small-bodied populations to have higher bulk resource processing rates than large-bodied populations [51] 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 [52].

2. 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 seen as important, given the strong enrichment of these elements in consumers relative to the lower concentrations in the environment [53]. A stoichiometric imbalance between chemical elements in consumers and their diet can reduce growth, survival rates, and increase resource consumption [54], with implications for ecosystem functioning.

Parasites require essential nutrients for their own growth and reproduction. However, parasites are not always in stoichiometric balance with their hosts [55]. Energy and nutrient sequestration by parasites can induce strong nutrient limitation in the host [56,57], affecting host growth and survival rates [57,58]. Moreover, parasite-induced effects could be further enhanced if the host already has a diet deficient in certain nutrients [59]. By causing or even enhancing nutrient deficiency, parasites will affect host consumption rates or even alter host consumption preferences [60] 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 increases its survival when infected by a virus [61], and snails infected with trematodes excrete a higher N:P ratio compared with uninfected snails [62]. Overall, parasite-induced nutrient imbalances between the host and its diet are expected to affect the rates by which the host consumes or excretes different resource types, which can affect ecosystem functioning [63].

3. Behaviour

Many parasites affect host behaviour [64]. Manipulative parasites can impair vertebrate host response to predators and shift invertebrate host microhabitat use [65]. Parasites that manipulate top predators or foundation species can alter ecosystem functioning through trait-mediated effects [6]. 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 [8]. Such trait-mediated indirect effects due to behavioural alterations are known for insects [8], crustaceans [66], molluscs [67], reptiles [68], fish [69], and mammals [70], and could increase host intraspecific functional diversity [67].

Parasites can also affect host feeding behaviour and preferences. Infected *Littorina littorea* snails eat less algal biomass than the uninfected conspecifics [33], increasing algal biomass accrual, and the detritus-feeder isopod *Caecidotea communis* eats less leaf litter when infected by *Acanthocephalus tahlequahensis* [66]. Sometimes, these parasite-induced alterations are so large that parasitized hosts function like a separate species. For example, the Asian mud snail *B. cumingi* grows larger and moves deeper when infected by the trematode *C. batillariae* [47]. Instead of competing with uninfected snails, infected snails exploit a novel algal resource, effectively akin to adding a new species to a community.

Parasites as potential resource supply to maintain diversity

Although most parasites negatively impact host nutrition, some free-living infective stages are edible food resources for non-host species. For instance, small fish may feast on trematode cercariae [71]. 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 few suitable primary producers for food [5]. Because such parasites are common in aquatic systems, edible parasites could drive important ecosystem processes when they convert inedible resources into food for consumers.

Research directions on the role of parasitism for ecosystem functioning

Despite the various mechanisms by which parasites might affect ecosystem functioning [2], parasites have seldom been considered as promoting ecosystem functioning through their effects on trait diversity. Parasites increase within-host trait diversity by altering host phenotypes, including host morphology, behaviour 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 BD-EF relationships through disease-dilution mechanisms in diverse communities if disease transmission depends on 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.

Parasites might represent 40% of all known metazoan species [72], with helminth parasites alone estimated to have 50% more species than there are vertebrate hosts [73,74]. The ubiquity of parasitism becomes overwhelming if parasitic viruses, bacteria, fungi, and protozoa are considered as well. Thus, researchers have a highly diverse set of organisms and parasite-host interaction types to address their questions on how biodiversity is related to functioning. Ignoring these numbers and the many effects parasites have on community diversity will only be detrimental to understanding how and when biodiversity affects ecosystem functioning.

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Figure 1. (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, as communities with more evenly distributed traits might compensate better for the loss of other important traits. (c) High parasite diversity might enhance functioning by increasing functional trait diversity, if the parasite-modified traits are positive to functioning. However, high host diversity can also dilute parasite prevalence in the community, reducing the parasite effects on functional diversity. The net outcome of parasite-dilution due to high host diversity will depend on the effect that parasites have on their hosts and on functioning (see (a)).

Figure 2. (a) Parasitism can affect an individual's phenotype, as indicated by . This parasite-induced functional trait can be similar to other common traits 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 functioning 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 functioning will depend on whether the novel trait has a positive or negative effect in the ecosystem. (b) Parasites can also alter interspecific diversity, adding or eliminating important traits from the community. Parasites might contribute to species coexistence or to species invasion by reducing the fitness of some dominant species. However, as for within-host diversity, the extent that diversity promotion increases ecosystem function depends on whether other species can compensate for supressed dominant species.

Glossary box:

Biodiversity: Refers to 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 a 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 by generalist vectors, which might reduce the disease load on key species underpinning ecosystem processes, resulting in enhanced ecosystem functioning overall.

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 consumers and primary producers, which is affected by species interactions and nutrient availability.

Facilitation: Occurs when the activities of one species enhance the activities of a second species.

Functional 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, behavioural, or ecological.

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.