ECOSYSTEMS

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Disease Ecology Meets Ecosystem Science

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ABSTRACT

Growing evidence indicates that parasites—when considered—can play influential roles in ecosystem structure and function, highlighting the need to integrate disease ecology and ecosystem science. To strengthen links between these traditionally disparate fields, we identified mechanisms through which parasites can affect ecosystems and used empirical literature searches to explore how commonly such mechanisms have been documented, the ecosystem properties affected, and the types of ecosystems in which they occur. Our results indicate that ecosystem-disease research has remained consistently rare, comprising less than 2% of disease ecology publications. Existing studies from terrestrial, freshwater, and marine systems, however, demonstrate that parasites can strongly affect (1) biogeochemical cycles of water, carbon, nutrients, and trace elements, (2) fluxes of biomass and energy, and (3) temporal ecosystem dynamics including disturbance, succession, and stability.

Mechanistically, most studies have demonstrated density-mediated indirect effects, rather than trait-mediated effects, or direct effects of parasites, although whether this is representative remains unclear. Looking forward, we highlight the importance of applying traits-based approaches to predict when parasites are most likely to exert ecosystem-level effects. Future research should include efforts to extend host–parasite studies across levels of ecological organization, large-scale manipulations to experimentally quantify ecosystem roles of parasites, and the integration of parasites and disease into models of ecosystem functioning.

Key words: parasite; pathogen; infection; host; ecosystem structure; ecosystem function; ecosystem dynamics; biogeochemistry; energy flow; stability.

INTRODUCTION

What is the most abundant organism in the earth's oceans? Many people might respond with fish, zooplankton, or perhaps bacteria. The answer, however, is viruses. Per liter of seawater, marine viruses can attain densities of 10^7 to 10^{10} and have been estimated to collectively contain as much carbon as approximately 75 million blue whales (Suttle 2005; Danovaro and others 2011). Through their controls on bacteria and phytoplankton populations, viruses play fundamental roles in con-

trolling cycles of carbon, nutrients, and trace elements (Suttle 2007). Despite their potential to alter biogeochemistry on the global scale, however, viruses are generally omitted from ecosystem function and earth system models. In part, this omission stems from the relatively recent recognition of their roles in marine ecosystems, but it is also representative of a broader pattern in which parasites are omitted from efforts to understand large-scale processes.

The fields of ecosystem science and disease ecology have traditionally experienced little overlap in their conceptual foci (Loreau and others 2005; Eviner and Likens 2008; Tompkins and others 2011). Ecosystem science seeks to understand the biotic and abiotic controls over the structure and functioning of ecosystems (Chapin and others 2011). Much research in this field aims to describe pools and fluxes of energy and matter, such as carbon, elemental nutrients, and biomass. Most

empirical and theoretical studies involve spatial scales ranging from a habitat patch to the biosphere. The nascent field of disease ecology, in contrast, focuses primarily on host–parasite interactions within individuals, populations, and more recently, communities (Collinge and Ray 2006). An empirical literature search reveals that less than 2% of disease ecology publications involve work at the ecosystem level (see Figure 1, ''The divide between disease ecology and ecosystem science''). Correspondingly, the disparate levels of biological organization studied in ecosystem—and disease ecology—coupled with the fact that parasites are typically small and inconspicuous, has resulted in relatively few efforts to incorporate parasitism and disease into our broader understanding of ecosystems. Host–parasite interactions are very rarely a focus of ecosystem ecology research (Figures 1, S1).

Despite their distinct foundations, recent movements seeking to integrate ecological research
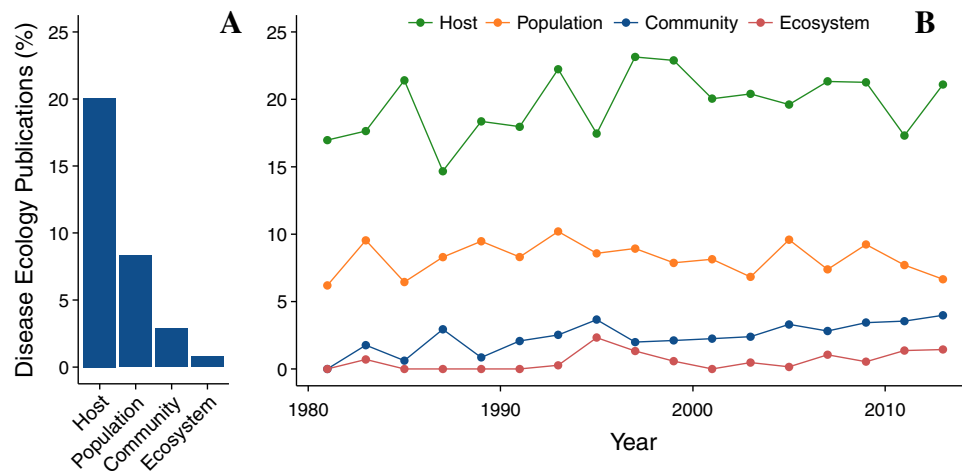

Figure 1. The divide between disease ecology and ecosystem science. To quantify the divide between disease ecology and ecosystem science, we conducted searches in the Web of Science database (1980–2013) to (1) determine the relative proportion of publications within disease ecology that focus on different levels of ecological organization (Figure 1) and (2) determine the relative proportion of publications within ecosystem science that focus on different types of ecological interactions (Figure S1) (see Supplemental Material for detailed search strings and analyses). In the first set of searches, we determined the percentage of disease ecology publications that included the title keywords 'host,' 'population,' 'community,' or 'ecosystem.' We found that the total number of disease ecology publications decreased sharply with increasing levels of ecological organization, such that the number of publications including the word 'ecosystem' remained less that 2% of the total (**A**). When correcting for changes in the total number of publications over time, we found that between 1980 and 2013, publications including the title keywords 'host' and 'population' remained at around 20 and 8% of the total, respectively (**B**). Publications with the keywords 'community' and 'ecosystem' increased significantly over the same time period ($p < 0.001$ and $p = 0.02$), although the totals only reached 4 and 2%, respectively (**B**; see Supplemental Material for details). In the second set of searches, we determined the percentage of ecosystem science publications that included the title keywords 'herbivory,' 'predation,' 'competition,' 'parasitism,' or 'mutualism' (Figure S1). Although these keywords for species interactions were all relatively rare in the titles of ecosystem science publications, 'parasitism' was two to fifteen times less common than 'herbivory,' 'predation,' or 'competition' (but more common than 'mutualism'). Taken together, these standardized literature searches indicate that research linking disease ecology and ecosystem science is uncommon, but increasing in prevalence.
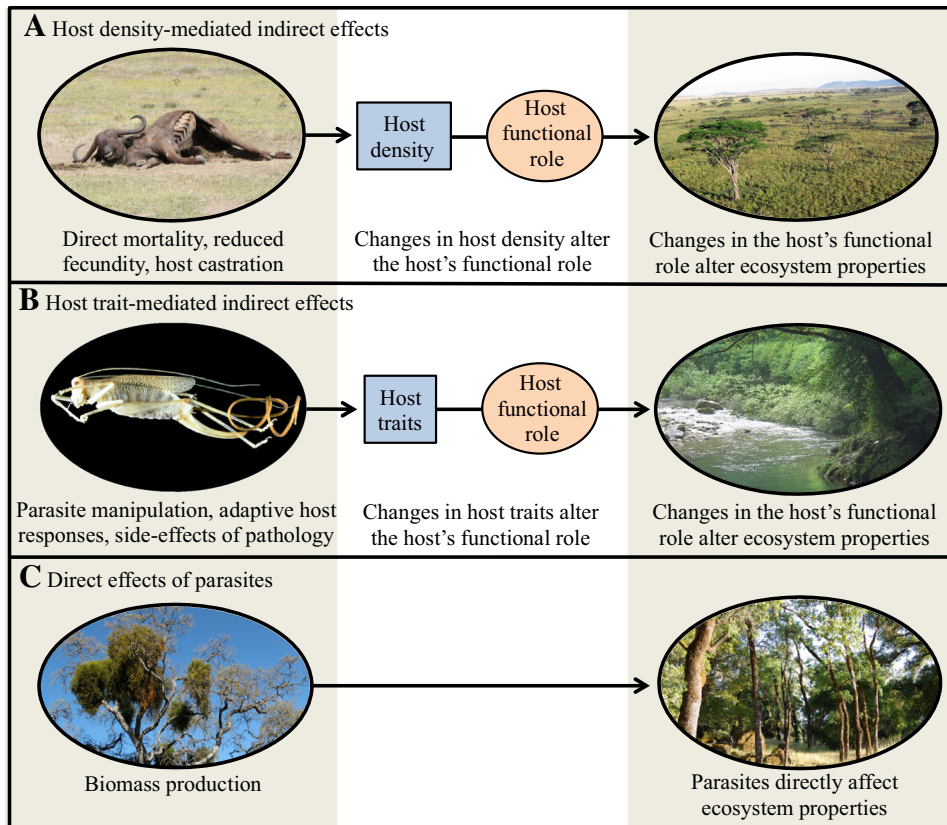
Figure 2. Mechanisms through which parasites can affect ecosystem properties. Density-mediated indirect effects (**A**), trait-mediated indirect effects (**B**), and direct effects of parasites (**C**). The examples shown include rinderpest virus in the African Serengeti, nematomorph worms in Japanese streams, and plant hemiparasites in Oak forests. Photos by N. Stolberg, D. Berkowitz, A. Schmidt-Rhaesa, and D. Preston.

across scales—from individuals to ecosystems—have set the stage for rapid developments in our understanding of how parasites can affect large-scale processes. The last two and a half decades have paid witness to a surge of research addressing how biodiversity affects the functioning of ecosystems (Hooper and others 2005; Balvanera and others 2006; Cardinale and others 2012). Concurrently, disease ecologists have increasingly recognized the potential for parasites to control community structure and shape the outcome of species interactions; the percentage of disease research that involves community ecology has increased approximately five-fold from 1980 to 2013 (Figure 1). A few compelling cases that helped bridge the gap between community composition and ecosystem properties—such as rinderpest virus restructuring the Serengeti (Dobson and Hudson 1986), chestnut blight transforming hardwood forests (McCormick and Platt 1980), and microbial pathogens of sea urchins driving coral reef dynamics (Lessios 1988)—alerted ecologists to the 'hidden' potential of parasites to influence whole ecosystems. Today, an increasing number of studies suggest that parasites can affect ecosystem structure and function in meaningful ways; yet to date, there have been few efforts to synthesize patterns in existing work, develop an underlying mechanistic framework, assess the generality of effects across ecosystems, or work toward a predictive capacity.

Here, we aim to broadly link disease ecology with core concepts in ecosystem science. We first consider potential mechanisms through which parasites can affect ecosystem structure and function, including density-mediated indirect effects, trait-mediated indirect effects, and direct effects of parasites (Figure 2). We then use an empirical literature review to explore the relative frequency with which such mechanisms have been documented, the ecosystem properties that they affect, the types of ecosystems in which they occur, and the approaches used to study them. We specifically review cases where parasites influence the foundational topics of ecosystem science, including (1) biogeochemical cycles, (2) ecosystem energy flow, and (3) temporal ecosystem dynamics. Building from these examples, we generate predictions about how traits of the ecosystem, the parasite, the host, and their interactions can facilitate ecosystem effects. Because parasites are unlikely to be equally important in all ecosystems, a goal of our review is to consider when parasites should be incorporated into ecosystem studies, and alternatively, when they can be safely ignored.

Lastly, we explore areas for future research that will strengthen the links between ecosystem science and disease ecology.

ECOSYSTEM ECOLOGY: A ROLE FOR PARASITES?

One conceptual approach used in biodiversity-ecosystem functioning research hinges on identifying species traits that result in a unique or disproportionately large role of organisms in ecosystem function (Hooper and others 2005; de Bello and others 2010). Organisms can play an important ecosystem role, even if they are uncommon, because they possess unique functional traits. Alternatively, some species may be important simply because they are extremely abundant in the ecosystem. The species that play disproportionate ecosystem roles, by virtue of their functional traits and/or their abundance, are sometimes termed 'dominant species,' 'foundation species,' 'keystone species,' or 'ecosystem engineers' (see Ellison and others 2005 for definitions). If these organisms cannot be replaced by other functionally similar species, their presence becomes influential in the overall functioning or characteristics of the ecosystem.

Extending the links between species' traits and their functional roles to host–parasite interactions provides a useful launching point from which to understand how and when parasites will influence ecosystems. Parasites, by definition, possess a specific suite of traits; all parasites live in or on a host species from which they gain resources for at least some portion of their life cycle (Price 1977; Lafferty and Kuris 2002). As a result, the most obvious way that parasites can influence ecosystems is through effects on their host. Such indirect effects of parasites can be broadly divided into two classes, which traditionally have been applied to predator–prey interactions: density-mediated effects and trait-mediated effects (Figure 2) (Werner and Peacor 2003; Preisser and others 2005). The regulation of host density can occur through direct host mortality or changes in host reproductive rates due to pathology or castration (Baudoin 1975; Anderson 1978; Scott and Dobson 1989). Trait-mediated effects can occur when parasites alter host traits due to parasite manipulation, adaptive host responses, or side effects of pathology (Poulin 2010). Whether or not parasites exert important indirect effects on ecosystems therefore depends largely on (1) the functional roles of their hosts within the ecosystem, and (2) the propensity of the parasite to change those roles by affecting host traits or host densities (Figure 2). Among existing empirical studies that quantify the roles of parasites in ecosystem structure and function (n = 39), the majority have involved indirect effects driven by changes in hosts (see Supplemental Material). Of these, 56% involved density-mediated effects and 31% involved trait-mediated effects (Figure S2).

In addition to indirect effects driven by changes in hosts, parasites can also exert direct effects on ecosystems, although such effects may be more difficult to detect (Figure 2). Traditionally, parasites were thought to have few direct effects on the ecosystem around them, yet several recent studies have revealed that parasites can play direct ecosystem roles through the production of biomass, which contributes to the movement of energy and matter through ecosystems (for example, Kuris and others 2008). Although more studies are needed to explore other direct pathways, these findings indicate that parasites can directly contribute to ecosystem processes, independent of effects driven by changes in their hosts. To date, such direct effects have been less commonly reported in the literature than indirect effects, comprising only 13% of the publications that quantify the effects of parasites on ecosystem structure and function (Figure S2). We note, however, that whether direct effects are truly less common or simply less commonly quantified is unclear. In the following sections, we will explore how these mechanisms—indirect effects due to changes in hosts, and direct effects of parasites themselves—can affect ecosystem properties, including biogeochemical cycles, fluxes of biomass and energy, and temporal ecosystem dynamics.

BIOGEOCHEMICAL CYCLES

Biogeochemical cycles are quantified in terms of the pools (standing stocks) and fluxes (transport between pools) of elements within ecosystems. Microbes, plants and animals can play fundamental roles in converting elements into biologically useable forms and in regulating pathways of cycling and pool sizes. As a result, parasites have the potential to exert controls on biogeochemical cycles through multiple mechanisms.

Perhaps the largest-scale effects of parasites on biogeochemistry involve viruses that cause mortality of heterotrophic bacteria and phytoplankton. Estimates of daily mortality rates vary widely, but can approach 40 to 50% of the host population in surface waters under typical environmental conditions and 100% during algae blooms (Fuhrman 1999; Suttle 2007). Because marine phytoplankton

account for as much as 40% of global primary production, and play a major role in the sequestration of carbon in the deep sea (del Giorgio and Duarte 2002), high rates of virus-induced plankton mortality will have profound consequences for global cycles of carbon and nutrients. Viral-induced cell lysis releases virus particles and host cellular contents into the water column through what has been termed the 'viral shunt' (Wilhelm and Suttle 1999). The specific fate and magnitude of such organic matter release remains uncertain; nutrient rich particles from proteins and nucleic acids are utilized by heterotrophs, leading to increased losses of carbon to the atmosphere via respiration and the assimilation of limiting elements (for example, iron) within the photic zone (Suttle 2007). The latter effect can lead to a positive feedback where limiting nutrients cycle through the base of the marine food web, rather than moving to higher trophic levels (Fuhrman 1999). Marine viruses even have potential to alter climate patterns and cloud formation when sulfur compounds are released during the lysis of phytoplankton cells (see Danovaro and others 2011 for a review).

In the terrestrial environment, hemiparasitic plants—plants that usurp nutrients and water from their host—have revealed the potential for parasites to accelerate nutrient cycling (Press and Phoenix 2005). In Swedish heathlands, the hemiparasite *Bartsia alpina* accelerates nutrient cycling and the growth of uninfected plants because its leaf tissue and litter are enriched in nitrogen and decompose more rapidly relative to other members of the local plant community (Quested and others 2002). Similar effects occur due to mistletoe hemiparasites (*Amyema miquelii*) in *Eucalyptus* trees in Australian forests (March and Watson 2010).

Herbivores in aquatic and terrestrial environments play important roles in recycling nutrients within an ecosystem through grazing and excretion, and these roles can be modified by parasites. This consumer-driven nutrient recycling can sometimes provide a far greater portion of the bioavailable nutrients to primary producers than the quantity supplied by external inputs (Elser and Urabe 1999). The functional roles of consumers as nutrient recyclers can be altered through changes in rates of host nutrient excretion per individual or through changes in host densities. For instance, freshwater snails infected with the trematode *Trichobilharzia physellae* excrete more nitrogen but less phosphorus than uninfected hosts (Bernot 2013). In many freshwater ecosystems, snails can exert strong controls on nutrient cycling and are the dominant grazers in terms of biomass, suggesting

that the individual-level effects of parasitism are likely to have consequences for nutrient cycling at the ecosystem scale (for example, Hall and others 2003).

Decomposition is another vital component of nutrient cycling and can be mediated by living organisms and their parasites (Gessner and others 2010). Within stream ecosystems, for example, isopods that consume leaf litter play significant roles in decomposition and their rates of litter consumption are decreased by infection with an acanthocephalan parasite (Hernandez and Sukhdeo 2008a). The magnitude of this effect varied across seasons, but approached a 47% reduction in the amount of detritus consumed when isopod densities where highest. Furthermore, some plant pathogens can affect the rates of decomposition directly because they are able to kill their host and subsequently feed on the dead plant material (for example, the fungal soil pathogens *Pythium* and *Phytophthora*) (Van der Putten and others 2001).

ECOSYSTEM ENERGETICS

Energy is a fundamental currency that connects organisms within an ecosystem. One method to estimate the importance of populations in energy flow is to measure their change in biomass over time (that is productivity). For parasites to directly contribute to energy flow they must therefore accumulate a large biomass or be exceptionally productive on the ecosystem scale. Indirect contributions to energy flow can occur when parasites alter host productivity or control pathways of energy flow by influencing the strength of trophic interactions.

Empirical studies suggest that parasites can exert direct controls on primary production that may rival the bottom-up controls induced by nutrient limitation and the top–down controls of herbivores. In a 3-year grassland experiment, for instance, the exclusion of foliar fungal pathogens led to a 31% increase in overall plant biomass (Mitchell 2003). This effect was driven by changes in root biomass, rather than aboveground biomass. Similarly, strong controls on grassland primary production have been observed as a result of belowground fungal pathogens (Maron and others 2011).

Parasites can also alter primary production when they induce trophic cascades by decreasing the densities of functionally important grazing species and release producers from top–down control. The intentional introduction of the highly pathogenic *Myxoma* virus into populations of non-native rabbits in England and Australia in the 1950s led to

cascading effects on producers (Sumption and Flowerdew 1985). In both countries, rabbits had devastating effects on native vegetation and agricultural crops. In England, the near eradication of rabbits after *Myxoma* introduction led to regeneration of oak trees within grasslands, and ultimately fundamental changes in productivity and ecosystem structure that remain evident today, 60 years later (Dobson and Crawley 1994).

Cascading effects of parasites on primary producers are not limited to the terrestrial environment. In freshwater streams in Michigan, USA, caddisflies (*Glossosoma nigrior*) play important roles controlling production of benthic periphyton. *Glossosoma* also experience periodic outbreaks of a lethal microsporidian (*Cougourdela* sp.) that exerts strong control on population densities. In a well-replicated survey design (six streams), microsporidian outbreaks, on average, caused a 25-fold decrease in the density of *Glossosoma* caddisflies and a subsequent increase in periphyton abundance that approached an order of magnitude at some sites (Kohler and Wiley 1997).

In addition to controlling rates of primary production, parasites can also directly contribute to secondary production. The first study to empirically estimate the ecosystem-level contributions of parasite to energy flow found that in three Pacific Coast estuaries, parasite biomass exceeded that of top bird predators and was comparable to the biomass of fishes and many invertebrate groups (Kuris and others 2008). Trematode worms with complex life cycles were prominent members of the parasite community from a biomass perspective. The annual production of free-swimming trematode larval stages that emerged from snail hosts was three to ten times greater than the winter bird biomass. Additional evidence from freshwater ecosystems suggests that these results are not unique. In three freshwater ponds in California, USA, the biomass of trematode parasites exceeded that of most aquatic invertebrate insect groups, including predatory dragonflies that often exert top–down effects that can structure fishless aquatic communities (Preston and others 2013). Furthermore, the estimated foliar fungal pathogen biomass in experimental grassland plots in Minnesota, USA (0.87 g m^{-2}) exceeded that of herbivorous insects (Mitchell 2003). Collectively, these results indicate that parasite production can directly contribute to the flow of energy through ecosystems in a previously overlooked way.

Although interaction strengths have yet to be widely quantified in food webs that include parasites, existing studies hint at the potential for parasites to play common roles in energy transfer via trophic interactions. Topological food webs from freshwater and marine ecosystems reveal that parasites are involved in a large number of trophic links within ecosystems. For example, parasites were involved in 78% of the links in a web from a Pacific Coast estuary (Lafferty and others 2006), 54% of the links in a web from the pelagic zone of a subarctic lake (Amundsen and others 2009), 45% of the links in a web from a freshwater pond (Preston and others 2014), and 29% of the links in a web from a freshwater stream (Hernandez and Sukhdeo 2008b). Within these webs, energy moves not only from hosts to parasites, but also from parasites to predators. Links from parasites to predators generally outnumber traditional host–parasite links (Thieltges and others 2013) and are most important to energy flow when parasites achieve a large biomass or when predators have evolved to feed exclusively on parasites (for example, cleaner fish on coral reefs) (Johnson and others 2010). Spores from fungal parasites of algae, for instance, provide a nutrient rich food source to zooplankton in freshwater lakes (Kagami and others 2007). When parasites do not achieve a significant biomass (for example, microparasites), however, such links likely contribute little to energy flow relative to the free-living host.

Although the previous examples have involved energy flow within an ecosystem, parasites can additionally affect linkages between ecosystems in the form of energetic subsidies. Parasites can either strengthen or weaken such links depending in part on how they influence the movement patterns or survival of their hosts in different environments. In one compelling example, horsehair worms (Nematomorpha) in Japan manipulate the behavior of their insect hosts, making them twenty times more likely to enter a stream than uninfected conspecifics. As a result, infected insect hosts contribute up to 60% of the yearly caloric intake for native trout within some streams (Sato and others 2011). Experimental results show that the parasite-driven subsidies can increase the biomass of benthic invertebrates by three-fold (through release from predation by fish), leading to cascading effects on periphyton biomass and rates of leaf decomposition (Sato and others 2012). In this example, parasite manipulation led to not only changes in energy flow across ecosystem boundaries, but also to fundamental alterations of aquatic ecosystem processes.

TEMPORAL ECOSYSTEM DYNAMICS

Ecosystems change over time due to long-term environmental trends, such as climate change, and

shorter-term events, such as fire or species introductions. Human alteration of the planet is fundamentally driving temporal ecosystem dynamics in new ways and parasites have potential to alter the type, frequency, and response of ecosystems to change.

Parasites and disease outbreaks can be thought of as disturbance events themselves or can alter the susceptibility of an ecosystem to other types of disturbance. Parasites that cause rapid host mortality to functionally important species over a wide geographic area are most likely to act as disturbance events (Castello and others 1995; Eviner and Likens 2008). Some of the most obvious examples come from non-native pathogens of trees that cause disturbances to forest ecosystems, including chestnut blight, white pine blister rust disease, Dutch elm disease, butternut canker, beech bark disease, and Port-Orford cedar root rot (Loo 2009; but see Holah and others 1997 and Worrall and others 2005 for examples with native pathogens). Widespread forest pathogens also have potential to alter the frequency and severity of other types of disturbance events, such as fires (Valachovic and others 2011; Metz and others 2013).

After a disturbance event, parasites can influence the process of succession, particularly when they mediate competition among colonizing species. In European sand dunes, for example, colonization and succession follows a predictable pattern in terms of plant community structure, in which a single clonal species generally dominates at one time. This pattern is mediated in large part by soil pathogens that are associated with successional species (Van der Putten and others 1993). The large literature on plant pathogens inducing negative feedbacks (for example, Janzen-Connell effects) provides extensive support for the ability of pathogens to mediate temporal processes of plant succession (for example, Petermann and others 2008).

Epizootics in animals can additionally act as direct disturbance events and can mediate succession in ecosystems. Perhaps the most highly cited example of parasites influencing ecosystem structure and function comes from the introduction and subsequent removal of rinderpest virus from African ungulates (reviewed in Dobson and Hudson 1986; Thomas and others 2005). Around 1890, the virus was introduced from domestic livestock and spread rapidly throughout the African continent, leading to sharp declines in wildebeest and buffalo populations, changes in vegetation structure, increases in primary production, and decreases in the numbers of top predators. These cascading effects were later reversed when the virus was eradicated in 1968 due to vaccinations of livestock. When ungulate populations recovered thereafter, there were strong declines in tree density that affected fire regimes and ecosystem carbon storage (Holdo and others 2009).

Parasites also have potential to influence ecosystem stability, although the direction of effects may depend on the type of stability in question. Although not yet quantified empirically, parasites are likely to participate in numerous weak interactions, which are thought to stabilize food webs (McCann and others 1998). In contrast, studies that consider robustness—the ability of species in a food web to persist after other species have gone extinct—suggest that the specialized life stages of parasites make food webs more susceptible to secondary extinctions (of parasites) and therefore might decrease stability (Dunn and others 2009; Rudolf and Lafferty 2011). Furthermore, parasites can contribute to ecosystem instability if they cause extinctions of their hosts directly (De Castro and Bolker 2005).

A final mechanism through which parasites can influence the stability of ecosystems is through their effects on transitions between alternative stable states. On Caribbean coral reefs, for example, parasites of a functionally important grazing species lowered ecosystem resilience by facilitating the switch from coral dominance to algae dominance. In the early 1980s, a combination of overfishing of herbivorous fish and a hurricane that reduced coral cover led to favorable conditions for algae dominance. At this time, the keystone grazers on the reef were sea urchins (*Diadema antillarum*), which play a critical role in facilitating the settlement of reef-building corals by removing macroalgae. When the functional role of urchins was removed due to a microbial epizootic, algae cover on some reefs increased from 1 to 95%, effectively leading to a transition between stable states (Lessios 1988). Phase shifts from urchin barrens to kelp forests have also been observed in temperature reefs as a result of urchin epizootics (Filbee-Dexter and Scheibling 2014).

FUTURE RESEARCH: WHEN CAN PARASITES BE IGNORED?

Despite a growing appreciation of their ecological significance, parasites are still omitted from the majority of ecosystem-level studies. Bridging this gap will require a better ability to predict when parasites should play important ecosystem roles

and new multidisciplinary approaches that allow scaling across different levels of organization (for example, from host physiology to ecosystem process). These advances should ultimately aim to determine when we can ignore parasites (at least from an ecosystem perspective), and conversely, when their roles must be quantified to gain a complete picture of ecosystem structure and function. Indeed, not all parasites will be important at the ecosystem level and not all ecosystems will be significantly affected by parasitism and disease. Clarifying these distinctions will require new observational studies, field experiments, and modeling approaches that span a diversity of host/parasite systems and ecosystems in which they are embedded.

A traits-based approach has proven useful in working toward a predictive capacity in many disciplines of ecology (McGill and others 2006; Webb and others 2010). Our review of the literature suggests that whether parasites exert important effects on ecosystems will depend on a combination of host and parasite traits, the dynamics of their interaction, and the characteristics of the ecosystem (Table S2). Parasites that infect host species with important functional roles that cannot easily be replaced by other community members will a priori have the greatest potential to alter ecosystem function. Therefore, the most important host traits are those that lead to important functional roles, and subsequently, the ability to maintain those functional roles after infection. Conversely, the most important parasite traits will be those that strongly alter the ability of the host to perform its functional role, both at the individual and population level (Table S2). One challenge to a traits-based approach, however, is that some traits cannot be clearly assigned to either the host or the parasite, but instead are characteristics of their interaction. For example, the degree of damage done to the host and the host mortality rate are predicted to influence the magnitude of changes to a host's functional role. Importantly, this outcome is dependent on both host traits (for example, resistance and tolerance) and parasite traits (for example, virulence). Such characteristics of the host–parasite interaction, such as infection prevalence and intensity, transmission rate, and host outcome may be most useful in predicting the magnitude and scale of ecosystem effects of parasites. Lastly, parasites that achieve a high ecosystem-level biomass are, thus far, the only types of parasites that can be predicted to exert direct effects on ecosystem properties (see Table S2). Future research should seek to identify which traits are most important in

predicting when and where parasites will exert ecosystem-level effects, and whether such traits should be assigned to hosts, parasites, or their interaction.

Integrating across scales with observational studies presents an additional promising approach to quantifying ecosystem roles of parasites. Disease ecologists frequently examine the effects of a parasite on one or several host species, often using controlled exposures in an artificial setting. Response variables in these experiments include host survival and host traits that can influence functional roles (for example, behavior, growth, fecundity, feeding rates). Scaling such studies to the ecosystem level requires integrating per-capita measurements from infected and uninfected individuals with observational field data which place that host's roles into the wider context of ecosystem function. This latter aim will generally require field data on host densities, infection prevalence, and intensity, and the relative role of the host in the ecosystem property of interest (for example, host nutrient excretion rates relative to other community members). As an example, to fully understand the effects of a honeybee pathogen on rates of ecosystem pollination, a researcher must determine (1) the per-capita effects of the pathogen on bee pollination, in terms of either survival probability, changes in traits, or both, (2) the host density, infection intensity, and prevalence of the pathogen in the ecosystem, and (3) the relative role in pollination of the host species relative to other organisms within the ecosystem. Most studies accomplish the first aim, and occasionally the second, but rarely the third, which requires interdisciplinary expertise. Whenever possible, replicating observational studies across ecosystems can be informative in reaching generalizations and revealing whether certain systems represent 'special cases' or widespread phenomena. This may be feasible by simply measuring a selected group of variables across several replicate ecosystems (for example, host density and infection prevalence).

Among the most promising and novel approaches, to understanding ecosystem roles of parasites involves large-scale field experiments that add or remove parasites from a system. Community ecology has a rich history of exclusion and addition experiments (for example, Paine 1966), yet such approaches are not commonly employed in disease ecology research (but see Hudson and others 1998; Tsao and others 2004; Pedersen and Antonovics 2013). Experiments of any kind were less common in our literature search results than observational studies (Figure S2). Parasite addition or exclusion

experiments will be particularly valuable in disentangling the ubiquitous ecological roles of endemic parasites, which are often overlooked relative to more obvious effects of non-native parasites on naïve host populations that result in dramatic epizootics (for example, rinderpest). Both introductions and removals of parasites present unique challenges; parasite introductions must be carefully designed to avoid unintended consequences for non-target organisms, whereas parasite removals are difficult to implement and replicate on the ecosystem scale. Similar experiments that involve the controlled introduction or removal of invasive species from an ecosystem may provide a useful framework (for example, Vredenburg 2004).

A final approach that will be useful in future work involves the integration of parasites and disease into models of ecosystem function. Dynamical models that are parameterized based on laboratory and field data can generalize and extend data from one or a few ecosystems and can allow simulating the effects of a parasite under multiple scenarios, such as variation in characteristics of the hosts, the parasites, and the ecosystem. This flexibility allows addressing the important question of which conditions facilitate the strongest ecosystem effects of parasites. For example, temperature, precipitation, or nutrient availability may drive infection rates or changes in host densities, and such context-dependency can be revealed most practically with modeling approaches. Furthermore, models that can incorporate changes in parasite traits, such as transmission mode, basic reproductive rate (R_0), or virulence, will be useful in revealing which characteristics are most useful in predicting when ecosystem effects will occur (Table S2).

Energy fluxes and biogeochemical cycles are two topics that are well suited to integrating parasites into traditional 'box and arrow' models of ecosystem function. Accomplishing this aim will require more precise estimates of the effects of parasites on pools and fluxes of energy and matter over large spatial scales. Collecting such data has rarely been achieved. For instance, fungi of phytoplankton in freshwaters are known to exert strong controls on plankton populations, yet they are not generally considered in models of freshwater primary production, nutrient cycling, or carbon balance (Rasconi and others 2011). Such approaches are currently uncommon; within our literature search results (Figure S2), approaches that involved incorporating parasites into models were less common than observational studies and experiments, comprising just 5% of the total.

Ideally, a multi-faceted approach will be best at revealing the ecosystem roles of parasites. A combination of laboratory studies to evaluate per-capita impacts, field data to 'scale-up' results, controlled experiments to determine the magnitude of effects, and modeling approaches to generalize findings under different scenarios can provide the most compelling evidence for ecosystem effects of parasites and disease.

CONCLUSION

In 2005, Loreau and colleagues lamented that there had not been a single paper in the journal *Ecosystems* that included the words 'parasite,' 'parasitism,' or 'parasitoid' in its title, keywords or abstract (Loreau and others 2005). In the short time since, at least five papers that involve parasites and disease have been published in *Ecosystems* (Connelly and others 2008; Ruess and others 2009; Lovett and others 2010; Cobb and others 2012; Whiles and others 2012). Such progress demonstrates that parasites can influence ecosystem structure, biogeochemical cycles, energy flow, and temporal ecosystem dynamics; yet, how often they do so remains uncertain. Current rates of environmental change, including the emergence of novel diseases, the movement of species around the globe, and ongoing extinctions, further underscore the need to integrate parasites and disease into our understanding of ecosystems. Although research in this area is still in its infancy, the unification of disease ecology and ecosystem science promises to mutually benefit both fields by enhancing our understanding of how ecosystems function.

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