

Diverse effects of parasites in ecosystems: linking interdependent processes

Melanie J Hatcher^{1,2*}, Jaimie TA Dick³, and Alison M Dunn²

Community ecologists generally recognize the importance of species – such as pollinators – that have clear positive effects within ecosystems. However, parasites – usually regarded in terms of their detrimental effects on the individuals they infect – can also have positive impacts on other species in the community. We now recognize that parasites influence species coexistence and extirpation by altering competition, predation, and herbivory, and that these effects can, in turn, influence ecosystem properties. Parasites and pathogens act as ecosystem engineers, alter energy budgets and nutrient cycling, and influence biodiversity. Equally, because ecosystem properties – such as biodiversity – affect parasite populations, there is the potential for feedback between parasitism and ecosystem states. Using examples from animal and plant systems, we examine this potential bidirectional interdependence and challenge the conventional wisdom that parasites have only negative or inconsequential impacts on ecological communities.

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Say the word “parasite” and most people think of the negative impacts on the health of individuals unlucky enough to be infected. This is not surprising, given that stealing resources from a host lies at the heart of the various definitions of parasitism. However, parasites can have both positive and negative effects on populations of non-host species, with consequences that ripple throughout ecological communities (Thomas *et al.* 2005; Hatcher and Dunn 2011). Indeed, because of their potential influence on ecosystem functioning and resilience, it has even been proposed that a diversity of parasites can be a sign of ecosystem health (Hudson *et al.* 2006). Here, we review the effects of parasites on ecological communities as well as the influence of community structure on the spread of parasites. We use the term “parasite” to include macroparasites such as helminths, fleas, and parasitic plants; microparasites such as

protists, viruses, bacteria, and fungi; and parasitoids.

The potential for parasites to influence community structure can be seen in relatively simple, three-species interactions, which show the positive and negative effects of parasites on non-host species (Figure 1). For example, parasites shared by two species can cause apparent competition, even if the hosts do not interact directly (Holt and Pickering 1985). This can lead to species exclusion, as one host acts as a reservoir of disease for the other (Figure 1a). Alternatively, parasites can enhance the coexistence of two species, by ameliorating the deleterious effects of one host on another. Parasites can play this keystone role when a dominant competitor (Figure 1b) or consumer (Figure 1c) is more strongly regulated by the parasite (Hatcher *et al.* 2006, 2008).

Parasites mediate interactions between hosts at all trophic levels, modifying competitive and consumer–resource interactions. These indirect effects of parasitism may be population-density mediated. There is also increasing realization regarding the importance of parasite-induced changes in host behavior (termed trait-mediated, indirect interactions; Werner and Peacor 1993), and such keystone effects may also influence community structure (Hatcher and Dunn 2011). For instance, parasites may mediate biological invasions, such as one in the UK in which a key processor of basal resources (the crustacean *Gammarus duebeni celticus*) is challenged by invasive species (*Gammarus pulex*, *Gammarus tigrinus*) that differ in their functional roles (Figure 2; MacNeil *et al.* 2003a; Dick *et al.* 2010). This is one of many recently documented systems in which parasites appear to play an important structuring role. Here, we review this developing field, which is challenging the conventional wisdom that parasites only have either negative or inconsequential impacts on ecological communities. We discuss how parasites influence food-web structure and stability, and their effects on ecosystem function

In a nutshell:

- Parasites can have positive effects on other species within communities, despite the negative impacts on their hosts
- Parasites affect the complexity of food webs and can influence how community composition responds to local species extinctions
- Parasites also contribute to ecosystem energy budgets and can alter the physical and chemical properties of ecosystems
- Understanding the complex relationship between host and parasite diversity is important for conservation management and public health

¹School of Biological Sciences, University of Bristol, Bristol, UK (*mel.hatcher@bristol.ac.uk); ²Institute of Integrative and Comparative Biology, University of Leeds, Leeds, UK; ³School of Biology and Biochemistry, Medical Biology Centre, The Queen's University of Belfast, Belfast, Northern Ireland, UK



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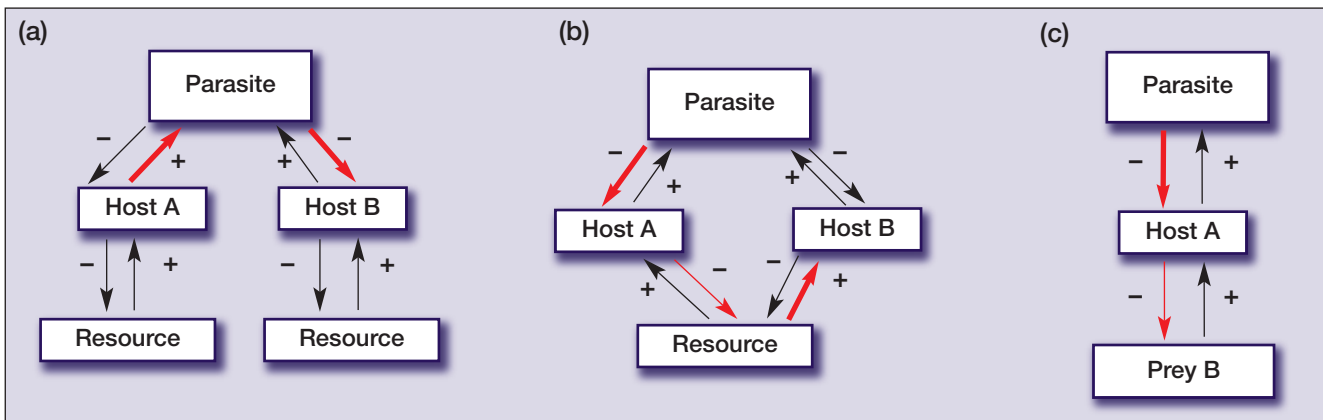


Figure 1. Keystone effects of parasitism. Arrows depict positive (+) and negative (–) direct effects (the numerical effects on population density resulting from the impact of a consumer or resource species); arrow thickness indicates strength of interaction; red arrows indicate key interactions, leading to the following patterns: (a) apparent competition: higher densities of host species A support higher parasite population densities, which have a greater detrimental effect on host species B: thus, A acts as a reservoir of infection to B. (b) Parasite-mediated coexistence: regulation of a superior competitor A by a parasite enables B, less harmed by the parasite, to persist. (c) Parasite-mediated trophic cascade: regulation of herbivore (or predator) A by a parasite induces a top-down trophic cascade, releasing the immediately lower trophic level B from herbivory or predation pressure.

(for instance, by altering nutrient cycling or by engineering the physical characteristics of ecosystems). We then examine how parasites might influence biodiversity, and how biodiversity could affect parasite populations. Further research is required to establish how common these diverse effects of parasites on ecosystems (and of ecosystems on parasites) are, but the results are likely to have important implications for parasite and ecosystem management in a variety of conservation and public health settings.

■ Food-web studies: putting the parasites back

The potential importance of parasites in ecosystems is becoming clear from studies of food webs that include parasites as part of an ecological community (Table 1). Food webs describe ecological communities as a network of trophic relationships; despite their long history of use, prior to the beginning of the 21st century, few of these networks included parasites. This is surprising; although parasites are often inconspicuous and may be missed in ecological studies, parasitism is regarded by many as the most common consumer strategy of all (Lafferty *et al.* 2008). However, we now know that, despite their generally small size, the impact of parasites on ecological networks can be considerable. The well-studied food webs of estuarine communities and herbivorous insects can contain just as many parasites as free-living species; parasites therefore increase web complexity by increasing species richness and food-chain length.

Parasites enhance food-web connectivity

More recent studies indicate that parasites can influence other structural properties in ecological networks (Figure 3). Not only do parasites interact with their hosts, they

also interact with their hosts' prey, predators, and other parasites. In addition, many parasites can infect multiple host species, some as more or less generalist consumers, others as specialists on different host species at different stages of their life cycles. In a groundbreaking study, Lafferty *et al.* (2006) used network analysis to examine a food web involving parasites, based on over 20 years of data collected from the Carpinteria Salt Marsh in California. Including parasites almost doubled connectivity (the proportion of possible links realized) and quadrupled nestedness (a measure of web structure; well-nested webs have a strong core of generalist species that interact with each other; specialists interact with subsets of these). When properly accounted for, over 78% of all links in the food web involved parasites, with parasite–predator links (which had been missing from earlier studies) dramatically enhancing food-web connectivity. It is unclear whether this study is representative of the effects of parasites in other ecosystems; however, other lake and river systems show similar (albeit less dramatic) effects (Table 1).

Parasites and the stability of ecological networks

Ecological communities are regarded as stable if they possess three properties: population dynamic stability (rapidly reaching and returning to equilibrium, or with only mild fluctuations); robustness to secondary extinction (if one species is removed, few others go extinct as a result); and resilience (if the community is perturbed, it quickly returns to its former state). Network studies suggest that the properties we might expect to be associated with parasitism will generally increase stability (reviewed in Poulin 2010). One reason for this is that interactions between hosts and parasites are often weak (compared to, for instance, predatory interactions), as effects on indi-

Figure 2. Simplified food web for the native and invasive *Gammarus* system. In Northern Ireland, UK, the native amphipod *Gammarus duebeni celticus* is challenged by three non-native invasive species. Parasites modify competition and intra-guild predation (predation between species that potentially compete) between natives and invaders, as well as increasing the predatory impact of the invasive *Gammarus pulex* (Dunn 2009; Dick *et al.* 2010). Arrows show energy flow. All five Crustacea are detritivores, with four also predating smaller invertebrates. The three *Gammarus* species are arranged in an intraguild predation hierarchy (N: native *G. duebeni celticus*; I1: invader *G. pulex*; I2: invader *G. tigrinus*); they also compete for smaller invertebrate prey. Parasites (shaded boxes) influence interactions at all trophic levels. Infection of the native amphipod with *Pleistophora mulleri* (a microsporidian) reduces predation by the native *G. duebeni celticus* on *Asellus aquaticus* and weakens its impact as an intraguild predator on the invading *G. tigrinus*, facilitating continued native–invader coexistence in the field (MacNeil *et al.* 2003a). Infection of the invasive *G. pulex* by the acanthocephalan parasite *Echinorhynchus truttae* increases its vulnerability to predation by fish (the next host for *E. truttae*) but also increases the predatory impact of *G. pulex* on smaller invertebrates, likely facilitating the competitive exclusion of the native *G. duebeni celticus* by this invader (Dick *et al.* 2010). Moving up the trophic levels, native and invasive amphipods are also predated by the white-clawed crayfish (*Austropotamobius pallipes*). Outbreaks of crayfish plague (*Aphanomyces astaci*) can reduce crayfish densities, thereby reducing predation pressure on amphipods, while the microsporidian *Thelohania contejeani* reduces the ability of the crayfish to catch its amphipod prey (Hatcher and Dunn 2011).

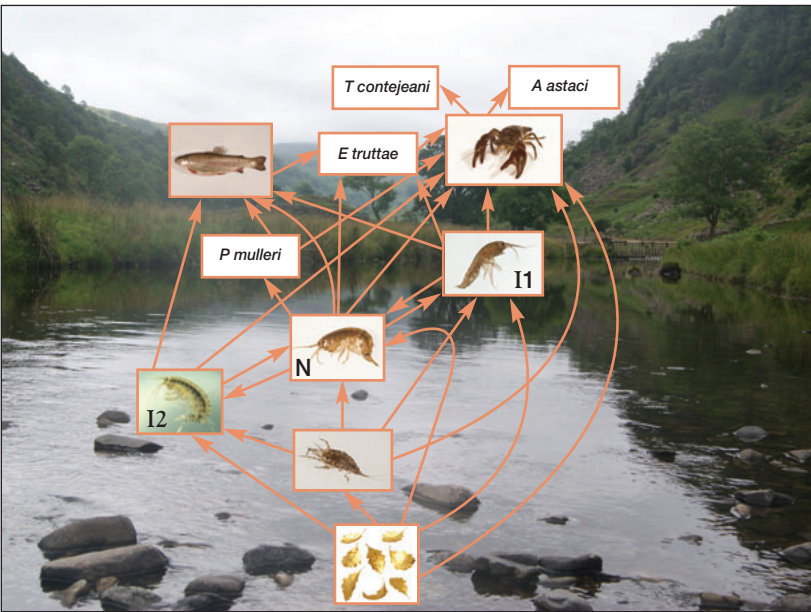


Table 1. Food-web studies including parasites				
Community	# of free-living species	# of parasites	Effects of including parasites	Reference
Ythan Estuary, Scotland	94	41	*Chain length increased; linkage density and connectivity increased or decreased slightly; % omnivory increased	Huxham <i>et al.</i> (1995)
Loch Leven Estuary, Scotland	22	30	Chain length increased; linkage density slightly increased; % omnivory increased	Huxham <i>et al.</i> (1995)
Scotch broom (<i>Cytisus scoparium</i>), Silwood Park, England	85	69	Predators, parasitoids, and pathogens contribute to connectivity, but predators (the most generalist) have greatest impact	Memmott <i>et al.</i> (2000)
Company Bay intertidal mudflat, New Zealand	67	9	*Greatly increased food-chain length; linkage density increased slightly; connectivity reduced slightly	Thompson <i>et al.</i> (2005)
Muskingum Brook, Pinelands, New Jersey	28	10	*Increased linkage density, decreased nestedness; slight increase in connectivity	Hernandez and Sukhdeo (2008a)
Carpinteria Salt Marsh, California	87	47	Strongly increased linkage density, nestedness (439%), and connectivity (93%), when all logically possible parasite links included; Muskingum, Company Bay, and Ythan, when re-examined, showed similar patterns	Lafferty <i>et al.</i> (2006)
Takvtan Lake pelagic zone, Norway	37	13	Increased food-chain length, linkage density, connectivity, and omnivory; more connected host species supported more trophically transmitted parasite species	Amundsen <i>et al.</i> (2009)
Notes: Inclusion of parasites inevitably increases species richness and average food-chain length. Original analyses of other food-web metrics produced conflicting results, but some studies (marked with an asterisk), when re-examined to take into account missing data on parasite–non-host links, showed consistent patterns: inclusion of parasites increases linkage density and connectivity. Re-analyses (see Lafferty <i>et al.</i> 2006) were based on the methods used for Carpinteria Salt Marsh, where the effects of parasitism on web metrics were strongest.				

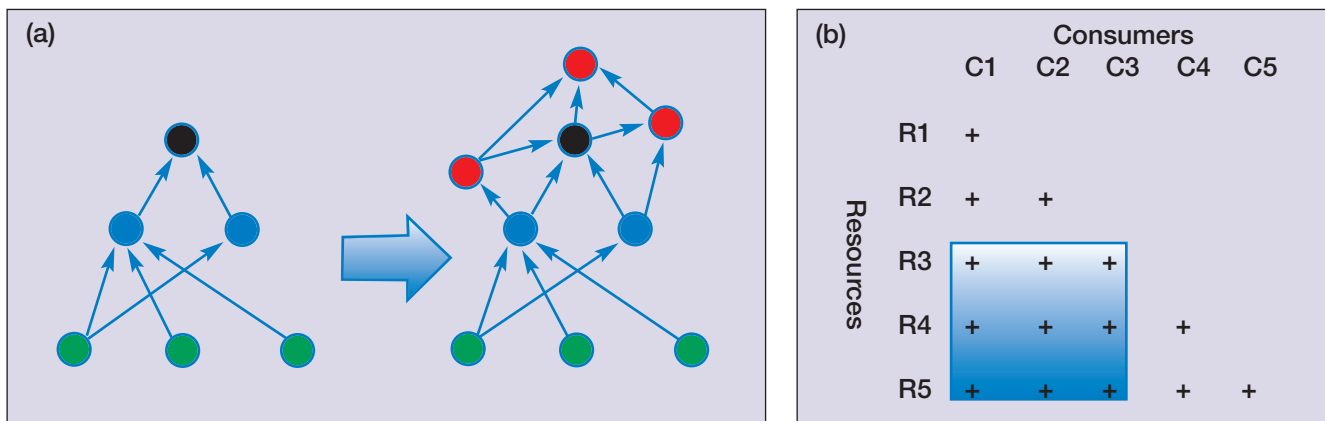


Figure 3. Effects of parasites on network structure. (a) Connectivity measures the proportion of possible trophic links that are realized in the food web. Adding parasites to the web can boost connectivity substantially if all the realized links (parasite–parasite, parasite–predator, and host–parasite links) are included. In this example, including parasites (in red) more than doubles the number of links in a simple network, even though parasite species number only half those of free-living species (basal resource species: green; herbivores: blue; predators: black). Provided these interactions are generally weak, increased connectivity increases community resilience by increasing dynamic stability. (b) Nestedness describes how consumer–resource links are organized in a network. Well-nested communities have a core of strongly interacting species (shaded) around which other, less connected species associate, so generalist consumers use strongly and weakly connected resources, and specialists tend to consume the dominant, well-connected resource species. Well-nested webs tend to be less vulnerable to secondary extinction, and food webs involving parasites tend to be strongly nested.

vidual hosts are usually sublethal (Hatcher *et al.* 2006; Hatcher and Dunn 2011). The addition of many such weak interactions offsets the destabilizing effects of fewer strong interactions, enhancing the community's dynamic stability. Hence, at the ecosystem level, we might predict that parasites may counteract the strong feedback relationships between predators and prey, enhancing resilience and robustness to secondary extinction. However, this concept has yet to be put to direct empirical testing, and there is evidence that parasites may cause – or may themselves be more vulnerable to – secondary extinction, counteracting any stabilizing effect (de Castro and Bolker 2005; Lafferty and Kuris 2009). Nevertheless, recent food-web analyses attest to the importance of parasites in food-web topology. For instance, the non-random distribution of parasites within food webs suggests that parasites exploit – and alter – food-web topology. Trophically transmitted parasites (parasites that infect both predators and their prey and are transmitted when the definitive host preys upon an infected intermediate host) are more likely to exploit highly connected host species and are more often generalists that exploit many host species (Chen *et al.* 2008; Amundsen *et al.* 2009).

■ Parasites as ecosystem engineers

Parasites can alter the physical properties of ecosystems through direct effects on the environment, or by influencing their hosts; as such, they can be regarded as ecosystem engineers. In New Zealand, the cockle (*Austrovenus stutchburyi*) plays a role in sediment bioturbation (releasing nutrients and exposing algae to light). This effect is reduced by trematodes of the *Curtuteria australis* species complex, which induce surfacing behavior,

exposing the cockles to predation by their definitive oystercatcher (*Haematopus ostralegus finschi*) host. This parasitic manipulation of cockle behavior increases surface hard structure and decreases sediment disturbance with community-wide effects. Here, therefore, parasitism has a positive effect on the diversity and abundance of benthic invertebrates and a negative effect on primary production (Mouritsen and Poulin 2010).

Parasitic plants also influence the chemical and physical structure of communities through their effects on water relations and host growth. Witchweed (*Striga hermonthica*, a major parasite of cereal crops) can increase transpiration rates among host plants, leading to a reduction in leaf temperature of up to 7°C and thereby potentially affecting surrounding soil-water and nutrient relations (Phoenix and Press 2005). Many mistletoes engineer the physical structure of the environment (Figure 4). Dwarf mistletoes (*Arceuthobium* spp) induce the growth of dense, twiggy masses (witches' brooms), which are used by birds and mammals for concealment, shelter, or nesting. Mistletoe is now recognized in wildlife conservation policy for iconic species such as the northern spotted owl (*Strix occidentalis caurina*), and for biodiversity in general (Aukema 2003). However, the use of dwarf mistletoe in conservation requires careful management, as severe infestation results in substantial economic losses and increases the likelihood of dangerous forest crown fires (Mathiasen *et al.* 2008).

■ Parasites and energy budgets

Parasites themselves can contribute substantially to the energy budget of ecosystems (Johnson *et al.* 2010). They may be consumed incidentally when an infected host is

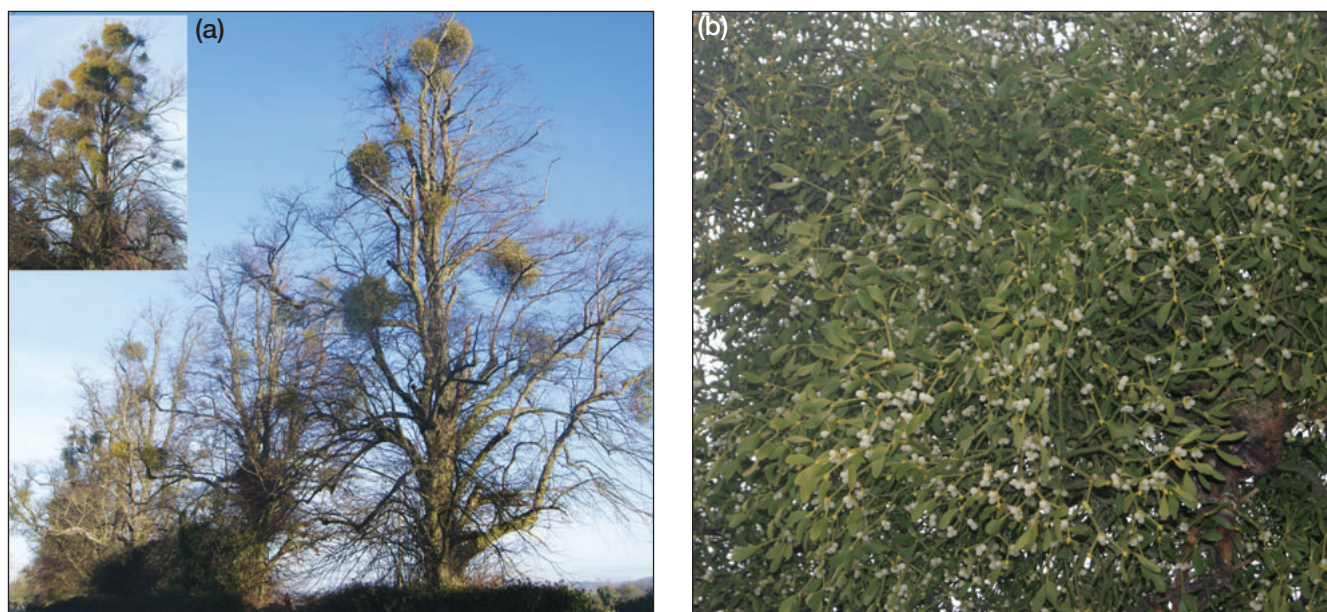


Figure 4. Mistletoe in winter. The European mistletoe – *Viscum album*, once common in the UK on apple trees in traditional orchards – can also use a broad range of other tree species as hosts (here, lime *Tilia cordata*). This hemiparasite produces dense clumps of leafy shoots throughout the year, providing food and shelter for a variety of insects and birds. Its spatially clumped distribution ([a] and inset), the result of uneven seed dispersal by birds feeding on the abundant white berries (b), can lead to locally high biomass of this parasitic plant in parts of Europe and the US. Although evergreen, mistletoes frequently drop their leaves, releasing nutrients that were previously locked away in the long-lived host tree. Many insects feed on mistletoe, including at least five specialist insect herbivores in the UK, with a greater diversity in its core range in continental Europe.

eaten, or they may be actively preyed upon (for example, the exploitation of external parasites during grooming behavior). In Carpinteria Salt Marsh, parasitic trematodes have a biomass equal to that of birds, fish, burrowing shrimp, and worms combined (Kuris *et al.* 2008). Trematodes in the California horn snail *Cerithidea californica* – the dominant invertebrate grazer in this ecosystem – represent, on average, 22% of the soft-tissue weight of infected snails, denoting a sizeable resource for predators. In addition, annual production of the free-living stages produced by these trematodes can be three times the standing stock biomass of the parasitic stage and up to ten times the standing stock biomass of birds, the top predators in this system. Many of these free-living stages fail to reach the next host but become food for planktivorous species. Similarly, many parasitic plants produce abundant berries and seeds that provide food for both vertebrates and invertebrates (Figure 4; Aukema 2003). The tropical mistletoes (Loranthaceae spp) have evolved in close association with particular bird species; many have elaborate flower-opening mechanisms and offer large quantities of sugar-rich nectar in exchange for pollination services (Mathiasen *et al.* 2008).

Trophically transmitted parasites often change their host's behavior, increasing their chances of being eaten (reviewed in Lefevre *et al.* 2008); this will also influence energy budgets in food webs. For example, trematode (*Euhaplorchis californiensis*)-induced changes in killifish (*Fundulus parvipinnis*) behavior make the host more conspicuous to predators, resulting in a 30-fold increase in pre-

dation by the definitive bird host (Lafferty and Morris 1996). Manipulation of host behavior can affect energy flow both to and from the infected host. For example, *G. duebeni celticus* (Figure 2; a freshwater amphipod) infected by the acanthocephalan *Echinorhynchus truttae* are more active than uninfected individuals and, rather than seeking shade, they move toward light, where they are an easier target for trout predators – the definitive host for this parasite (MacNeil *et al.* 2003b). Such altered behavior will increase energy flow to predators; in addition, these more active, infected individuals had a 30% higher rate of predation on smaller prey (Dick *et al.* 2010).

Some parasitic plants alter energy flow patterns within ecosystems via their effects on nutrient cycling. Plant parasites are often short-lived or have high rates of tissue turnover, whereas their hosts, often long-lived trees, sequester resources for long periods, where they are difficult to obtain by most consumers and scavengers. In eucalypt forests in Australia, trees infected with box mistletoe (*Amyema miquelii*) contribute nearly twice as much litter biomass as uninfected trees, enhancing understory plant biomass (March and Watson 2007). Rattles (*Rhinanthus* spp) and velvetbells (*Bartsia* spp) also enhance nitrogen cycling, by releasing nutrients that may enable colonization by other plants in low-productivity environments (Qusted 2008). In contrast, parasites can also reduce rates of energy flow; for instance, processing of detritus – the basal energy resource in a freshwater stream – by the isopod *Caecidotea communis* was reduced by more than 40% as a result of infection by the acantho-

cephalan parasite *Acanthocephalus tahlequahensis* (Hernandez and Sukhdeo 2008b).

A recent study has provided quantitative evidence that parasitic manipulation can alter energy flow within and between ecosystems. The nematomorph parasite *Gordionus* spp causes its terrestrial cricket hosts to jump into water, where the free-living stage of the worm exits the host and swims away to seek a mate. This provides novel opportunities for predation of these terrestrial insects by fish, a subsidy amounting to 60% of the annual energy intake of Japanese trout (*Salvelinus leucomaenis japonicus*; Sato *et al.* 2011).

■ Parasites and biodiversity

The relationship between parasitism and biodiversity is complex (Hatcher and Dunn 2011). Although parasites themselves are a substantial element of biodiversity, they may be more vulnerable to extinction than are free-living species, an important consideration for conservation policy (Dobson *et al.* 2008). Specialist parasites are particularly vulnerable to secondary extinction following the demise of their host; for instance, the California horn snail (*C. californica*), host to at least 17 specialist trematodes, is under threat of replacement by the invasive Japanese mudsnail or Japanese false cerith (*Batillaria attramentaria*), host to only one trematode (Lafferty and Kuris 2009). Epidemiological models predict that many parasites require a threshold host population size, below which the parasite will inevitably become extinct. Thresholds for establishment depend on transmission and virulence characteristics and can be quite high; for instance, measles and other modern “crowd” diseases were unknown before the Agricultural Revolution, when human populations reached critical numbers.

Parasites as bioindicators

In some systems, it may be easier to monitor parasites than hosts; hence, parasites might be used as indicators of ecosystem state. Helminths, for example, accumulate heavy metals at higher rates than their hosts, and may therefore have a role as pollution sentinels or chemical buffers for ecosystems (Dobson *et al.* 2008). For specialist parasites, the more host species that are present in a community, the more parasite species should also be present; consequently, these parasites could be used as biodiversity indicators. For instance, parasitoid diversity is correlated with that of arthropods in Irish farmland, so the former might be used as bioindicators of the effects of farming practices (Anderson *et al.* 2011). Huspeni and Lafferty (2004) used the trematode parasites of the snail *C. californica* to assess the success of a salt-marsh restoration project in boosting avian (the final host) biodiversity and found that trematode abundance and species richness increased as a result of restoration efforts. Research into parasites as biological indicators is still in its infancy;

these patterns will not necessarily be repeated across all ecosystems, and parasites may respond to environmental change at different rates than their hosts.

Biodiversity affects parasites

The relationship between biodiversity and the prevalence of generalist parasites is complicated and depends on many factors, including the relative frequency of species that can amplify and transmit the parasite effectively (known as competent hosts) and the transmission mode of the parasites (Keesing *et al.* 2010). Parasite establishment is predicted to be enhanced with increasing biodiversity if transmission success is strictly host-density dependent (Dobson 2004). However, if parasite transmission depends on host frequency, parasite prevalence will be determined by the relative frequency of competent hosts, which may increase, decrease, or be unrelated to biodiversity. In some disease systems, more diverse communities contain a higher frequency of less competent hosts, to some extent buffering the more sensitive species against infection (reviewed in Keesing *et al.* 2010). Such “dilution effects” of biodiversity can be caused by several different processes, including transmission mode, reduction of host density in more diverse communities, and “wasted bites” of vectors on non-competent hosts. A growing list of examples show evidence that reduced biodiversity is associated with increased disease risk, including Lyme disease, West Nile virus, hantavirus, and foliar fungal pathogens (reviewed in Keesing *et al.* 2010). For highly virulent parasites that regulate host populations, variation in the relationship between diversity and transmission might, under some circumstances, set up alternative patterns of feedback between parasitism and biodiversity (Figure 5). Moreover, some of the life-history characteristics that improve species’ resilience to ecosystem change (eg high reproductive output, low immune investment) may also make these species competent hosts (Keesing *et al.* 2010); such a relationship would perpetuate feedback between biodiversity and parasitism. However, the dilution effect is not directly related to biodiversity; it depends on whether biodiversity increases the relative abundance of non-competent hosts. The literature commonly conflates these issues, giving the mistaken impression that biodiversity per se decreases infectious disease.

Parasites affect biodiversity

Parasites can enhance biodiversity when a dominant consumer or competitor is the more vulnerable host (Figure 1). Diversity, spatial heterogeneity, and succession in a wide range of plant communities are maintained in part by specialist soil-borne pathogens; these processes may even underlie global patterns in diversity (Kulmatiski *et al.* 2008). Some parasitic plants, such as yellow rattle (*Rhinanthus minor*), can enhance plant species richness in

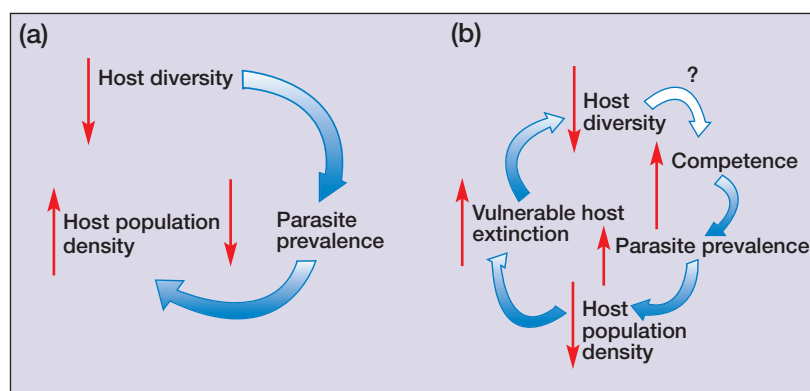


Figure 5. A conceptual model of biodiversity–disease relationships for parasites of multiple host species. (a) If parasite transmission is density dependent (where success depends on the product of infectious and susceptible host densities), lowering host biodiversity reduces transmission and lowers parasite prevalence. In this case, the most vulnerable host species may increase in population density (if the parasite regulates host numbers), and parasitism will not feed back on host diversity. (b) If transmission is frequency dependent (it depends only on the density of infectious hosts or their vectors), a reduction in host diversity can potentially increase total parasite transmission and prevalence in the community. This process is contingent upon reduced host diversity resulting in a higher frequency of competent hosts, a relationship found in some ecosystems but not necessarily predicted in general (white arrow). The most vulnerable host population would then decline with increasing parasite prevalence, making it more vulnerable to extinction. This could potentially set up a cycle of positive feedback, with successive extinctions of more vulnerable hosts. This latter scenario is more likely to occur when (1) transmission is frequency dependent, both within and between species; (2) the parasite regulates host population density and is highly deleterious to some species but is widely transmitted by others, allowing the required relationship between host diversity and community competence (white arrow) to occur.

meadowlands, and this parasite has been piloted as a tool for grassland restoration in the UK (Pywell *et al.* 2004). Parasites can also influence biodiversity by inducing trophic cascades; effects can propagate to varying degrees through food webs and can be found in a range of ecosystems. For instance, reductions in the rabbit populations of Europe, following the introduction of myxomatosis, led to conversion of grassland to scrub and woodland in parts of southern England (Dobson and Crawley 1994), and also underlie the endangerment of two specialist predators, the Iberian lynx (*Lynx pardinus*) and the Spanish imperial eagle (*Aquila adalberti*; Ferrer and Negro 2004). The introduction of rinderpest to Africa in the 1890s caused wildebeest (*Connochaetes* spp) and African buffalo (*Syncerus caffer*) population crashes and influenced plant community structure in parts of East Africa; its eradication in the 1960s led to equally strong effects on several herbivore species and their predators and has caused a shift in the ecosystem regime, making the modern Serengeti a net carbon sink (Holdo *et al.* 2009). Endophyte infection of grasses is associated with reduced herbivory, while lab and field experiments have demonstrated effects on population densities and species richness among aphids and their parasitoids (Omacini *et al.* 2001), predatory spiders, and

detritivores (Finkes *et al.* 2006), as well as influencing mammalian herbivore and plant community composition (Rudgers *et al.* 2007). Generalist pathogens are more likely to cause species extirpation if a reservoir host is present at a suitable density. For instance, rabies and canine distemper are regarded as extinction threats to the Ethiopian wolf (*Canis simensis*) and African wild dog (*Lycaon pictus*); feral dog populations, which have increased in recent years, act as reservoirs for these pathogens (Haydon *et al.* 2006). An increase in the number of feral dogs in parts of South Africa has been attributed to the effects of HIV, with increased mortality leading to the dissolution of human family units and the subsequent abandonment of domestic dogs (Nel and Rupprecht 2007). This additional cascade effect illustrates another route whereby parasites can interact with each other to drive extinction risk.

■ Introduction of parasites and extinction risk

The introduction of novel parasites or their vectors is regarded as a major factor in the decline or extinction of many birds, amphibians, and reptiles (eg Plowright *et al.* 2008). For instance, extinction or endangerment of unique Galapagos avian and reptilian fauna is a distinct possibility if

West Nile virus were accidentally imported to the archipelago; the ability of native mosquito species to act as vectors for this virus further raises the risks (Eastwood *et al.* 2011). This scenario may, however, be the exception rather than the rule, as disease has been cited as a causative factor in only a few cases among the International Union for Conservation of Nature's red-listed species (<4% of extinctions and <8% of critical endangerments; Smith *et al.* 2006). However, the same survey shows that disease is implicated as an additional factor, operating in concert with other ecological drivers more frequently than would be expected by chance. Populations that are declining as a result of other factors (eg habitat loss, invasive species) may be more prone to disease-induced extinction risk (de Castro and Bolker 2005; Tompkins *et al.* 2011).

Parasites (introduced or native) can influence native–invasive interactions in several ways (Dunn 2009; Tompkins *et al.* 2011). In the UK, the invasive gray squirrel (*Sciurus carolinensis*) is a reservoir for squirrel pox virus, and this disease (which is usually fatal to the native red squirrel *Sciurus vulgaris*, but largely benign in grays) has caused a 25-fold increase in the speed of invasion by grays in England, where the virus is present (Rushton *et*

al. 2006). Non-native invaders may also act as reservoirs for the spillback of native parasites, amplifying their incidence in the more vulnerable native species (Kelly *et al.* 2009). For example, the invasive crayfish *Pacifastacus leniusculus* is an asymptomatic host to both the introduced fungus *Aphanomyces astaci* (crayfish plague) and the native microsporidian *Thelohania contejeani*, both of which are lethal to the endangered native white-clawed crayfish *Austropotamobius pallipes* (Dunn 2009; Dunn *et al.* 2009). Parasites can also facilitate biological invasions and the extirpation of native species by modifying competitive and predatory interactions between natives and invaders, as illustrated in Figure 2. As well as acting as reservoirs for native and introduced parasites, some invaders may benefit from enemy release; loss of parasites during invasion may in turn enhance the competitive and predatory impact of an invader. For example, two meta-analyses of native and invasive animals and plants both revealed a higher-than-average parasite diversity in native populations (Torchin *et al.* 2003; Mitchell and Power 2003).

■ Conclusions

The role of parasites in community ecology is often oversimplified or underappreciated. Parasites may not always have a negative impact; indeed, they can be associated with processes or characteristics that are often regarded as “positive” attributes for ecosystems, such as enhancement of biodiversity and network stability. We have discussed examples of how parasites can increase or decrease biodiversity, and affect ecosystem function by altering nutrient cycling and engineering the physical structure of ecosystems, but more focused research is needed to ascertain the generality of such patterns. Ideally, we need to predict the conditions under which parasites are important in influencing community patterns and ecosystem processes. For instance, under what circumstances do parasites generally increase biodiversity, and when do they reduce it? Are the dramatic effects of parasites on salt-marsh food-web structure and their contribution to energy budgets common to other types of ecosystems? Are parasites other than parasitic plants responsible for enhanced rates of nutrient cycling, and can similar effects be quantified in a range of ecosystems? In addition, we need to know what aspects of biological communities influence parasites (their establishment, prevalence, and diversity), because interdependence between biodiversity and parasitism could potentially drive species extinctions and/or parasite emergence. The effects of parasites on ecosystems, and of ecosystems on parasites, are the result of a complex array of interactions between parasites, hosts, and non-hosts. Because biodiversity (and other ecosystem properties) and parasitism may potentially feed back on each other, we cannot fully understand the effects of one without the other. Understanding the bidirectional interaction of parasites with ecosystems is therefore of broad importance,

and could contribute valuable information for decision making in a variety of conservation, animal, and public health settings.

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