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Is a healthy ecosystem one that is rich in parasites?

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Historically, the role of parasites in ecosystem functioning has been considered trivial because a cursory examination reveals that their relative biomass is low compared with that of other trophic groups. However there is increasing evidence that parasite-mediated effects could be significant: they shape host population dynamics, alter interspecific competition, influence energy flow and appear to be important drivers of biodiversity. Indeed they influence a range of ecosystem functions and have a major effect on the structure of some food webs. Here, we consider the bottom-up and top-down processes of how parasitism influences ecosystem functioning and show that there is evidence that parasites are important for biodiversity and production; thus, we consider a healthy system to be one that is rich in parasite species.

Introduction

In a classic paper 40 years ago, Robert Paine found that when he removed the predatory starfish *Pisaster ochraceus* from the rocks at Mukkaw Bay, Washington, *Mytilus californianus* mussels expanded their range downward, dramatically outcompeting many other sessile species for space [1]. This elegant experiment set the scene for examining how predators could shape community structure. Twenty years later, in the first issue of *TREE* [2], two of us explored how parasites differed from predators and examined how they shaped community structure as a result of their intimate association with their host. At that time, experimental data on host–pathogen interactions in the wild were limited, although reconstruction of data on rinderpest showed how the invasion of a pathogen could have repercussions throughout the whole community. When rinderpest invaded the wild ungulate community of the Serengeti in 1892, it reduced the abundance of several species and this altered interspecific competition, modified vegetation structure and changed fire regimes.

Research now ranges from detailed long-term studies of specific host–parasite systems through to attempts to quantify the diversity and biomass of parasite species in food webs. In many respects, it is not surprising how this field has taken off because, just as our article [2] was published, Cathy Toft wrote an important paper [3] showing that half of all biodiversity might comprise parasitic species. More recently, two texts published that examine aspects of how parasitism can shape community, and ecosystem, ecology [4,5]. The accumulating evidence indicates that, as parasite species diversity increases, ecosystem functioning improves. At first, this seems counterintuitive, given that parasites reduce host fitness and can threaten endangered species; alternatively, parasites can also be beneficial in the promotion of biodiversity. Here, we explore the role of parasites in communities and ecosystem functioning and address the question ‘Is a healthy ecosystem one that is rich in parasites?’ This begs the additional question ‘What is a healthy ecosystem?’ and this we address in Box 1. We follow the criteria laid down by Costanza and Mageau [6] that a healthy ecosystem is one that persists, maintains vigor, organization and resilience to change. We provide evidence to show that many of these features arise from both the bottom-up and top-down processes that are mediated by parasites. We argue that the past 20 years have seen a large increase in our understanding of the role that parasites have in community organization. We suspect that the next 20 years will see a sharp appreciation of the role they have in ecosystem processes.

Parasite processes and community consequences

There is now substantial evidence that parasites significantly reduce host fitness in the wild, interact with other population processes and shape community structure [7]. In the original article [2], we discussed the dynamics of red grouse *Lagopus lagopus scoticus* in relation to their infections with a gastrointestinal nematode and a vector-borne flavivirus that causes Louping ill. More detailed studies have since revealed how the parasites are embedded in a larger food web and how food quality, predation and competition [8] interact with the behavior of the birds [9] to generate a Pandora’s Box of nonlinear dynamics that reflect the large variation in cycle period and amplitude observed in the natural time series [10]. We now appreciate that, by starting from a simple understanding of interactions at the parasite–host and vector–host level, we can build up to an understanding of the broad-scale influences of parasites on community

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Box 1. What is a healthy ecosystem?

Health is a vague term that often conjures up images of 'human health', where we think of the disease-free status of the individual, a pristine condition without illness and with good prospects of continued survival. By contrast, the term 'ecosystem health' is focused on the functioning of a whole community; therefore the term must embrace the overall performance and persistence of the system. Thus, a healthy ecosystem is one that persists, maintains vigor (productivity), organization (biodiversity and predictability) and resilience (time to recovery) [6].

We often think of pristine ecosystems, such as the Serengeti, as being healthy because the species composition has persisted for at least 1000 years and, if perturbed, would no doubt lead to the loss of several charismatic species. Yet, if we examine the herbivores (e.g. wildebeest and zebra) or the carnivores (e.g. lions and hyenas), we would find that these animals harbor high levels of parasite prevalence and species richness, with most hosts infected with gastrointestinal nematodes, ticks and bacteria. Not only are the hosts heavily infected, but the parasites also link the different trophic levels (e.g. herbivore–carnivore) given that the tapeworm larvae inhabiting the muscles of the herbivores develop into adults in carnivores. These long chains of multispecies connections can stabilize the community structure in ways that increase resilience and that might help persistence [48]. Counting the parasitic species present can also double the species richness of the ecosystem [49].

The abiding image of a healthy ecosystem is therefore one in which the biodiversity of free-living organisms is shadowed by the parasites, where each host is a habitat patch to be colonized and exploited. This contrasts with recently disturbed or invaded systems, where parasitic diversity is often reduced. For example, when molluscs invade and replace native snails in coastal marshes, they disrupt the life cycle of many digenean trematodes, removing the hosts that are essential for the completion of a complex life cycle [50]. The absence of trematodes might lead to competition among prey species released from parasitism and be detrimental to piscivorous birds, as parasite-free fish might be harder to catch [51,52].

dynamics. At regional spatial scales, we also now appreciate how climatic conditions can synchronize the transmission of parasites across populations and that this process can bring populations into synchrony [11]. In this respect, the parasites not only provide organization and vigor in that they influence interspecific interactions, but also act to destabilize the dynamics so that when climatic conditions bring populations into synchrony, this destabilization can result in widespread outbreaks of disease, leading to increased extinction risk and reduced resilience.

Studies are now beginning to illustrate how parasite-mediated effects that act on individuals can also influence community structure and workings. For example, detailed studies of trematodes that infect the foot tissue of the *Austrovenus stutchburyi* cockle have shown that the parasites interfere with how the cockle uses its foot to move and burrow after it has been dislodged [12]. Experimental field studies show that these parasites have an indirect effect on the sediment disturbance, profoundly influencing the structure and functioning of the soft-bodied animal communities. This is because epifaunal organisms benefit from the increased surface structure, and the infauna are influenced by changes in the hydrodynamics that determine the particle composition in the upper sediment [13]. Interestingly, these consequences for community structure and function are a result of trait-mediated indirect effects of parasitism. Such effects can have a profound influence on ecosystem functioning because the parasites alter the rates of trophic energy flow and, simultaneously, parasite transmission [14].

Further evidence of the importance of parasites in shaping community structure comes from studies of invasive species, where two significant papers [15,16] have shown that invaders escape from their parasites in their native range (reviewed in [17]). Release from natural enemies could subsequently aid the performance of an invader. For example, detailed studies of the invasive green crab *Carcinus maenas* show that, when it invades a new habitat, it leaves behind part of its parasite community, grows larger and becomes more abundant [18]. In the case of invasive plants in the USA, there is a negative correlation between pathogen diversity and the number of States recording the plant as an invasive pest, suggesting that invasive species become pests when their parasites are absent [16]. In a sense, parasites are to invaders as kryptonite is to Superman: the advantage gained by their absence helps reveal the magnitude of their handicapping influence.

Generalist parasites, apparent competition and extinction

Generalist parasites that infect diverse host species can also have important and dramatic effects on community structure because parasite transmission between species and parasite-induced effects are invariably asymmetrical. Given that host species differ in their susceptibility and tolerance to parasites, one species might add more infective stages of the parasite to the shared pool of infective stages than does the other. Sensitive species are more likely to succumb to the pathogens that are maintained in abundance by tolerant species and this leads, ultimately, to local host extinction. Thus, apparent competition can act through parasitism when levels of infection depend primarily on the rate at which the parasites flow from a tolerant species to a sensitive species, rather than on the density of the sensitive species. Detailed studies of the shared parasite *Heterakis gallinarum* in pheasants and partridges show that the fitness of a single infective stage entering a pheasant is 100 times greater than a similar stage entering a partridge [19] because the parasite is more likely to establish, grow bigger and produce more infective stages in pheasants. Given that the partridges suffer reduced fitness from parasites, the presence of pheasants could increase infection in partridges and lead indirectly to their localized extirpation [19].

Parasite-induced competitive exclusion can occur when a rare spill-over event results in a serious epidemic. For example, an itinerant dog wandering into the home range of Ethiopian wolves *Canis simensis* in 2003 resulted in an outbreak of rabies that killed 38 wolves, ~10% of the global population [20]. Although extinction from parasitism alone appears rare, it is still a matter of concern, because parasitism can reduce numbers in a population to a size where there is an increased extinction risk from all the stochastic processes that affect small populations [21].

In reality, there are few documented cases of extinction by parasitism; for example, a microsporidian was found to have eliminated the last captive population of the land snail *Partula turgida* [22] even though the host had been wiped out in the wild as a consequence of the introduction of alien species. There is also evidence for the role of the introduced avian malaria in the disappearance of several species of Hawaiian birds but once again this has been exacerbated by the rooting behavior of feral pigs, which produces suitable breeding habitat for the mosquitoes [23]. Furthermore, more than 100 species of frog have gone extinct in the past ten years probably as a result of the interaction between climate change, anthropogenic factors and a chytrid fungal pathogen [24]; this gives cause for concern about how these factors might interact and influence the future of other species. In most cases where parasites are thought to have had a role in a species decline, the pathogen has spilled over from one host species into another species where there is little coevolutionary history, the wild animal equivalent of an emerging human disease. Such effects are not going to benefit ecosystem functioning but it is interesting to consider the duality of parasites in the ecosystem and the tension that the specialist species have in increasing and the generalist parasites have in reducing community organization.

Specialist parasites and biodiversity

Density-dependent transmission and host specificity can generate a causal link between parasitism and biodiversity. In the last section, we discussed the evidence that generalist parasites can reduce biodiversity through the process of apparent competition, but specialist parasites can act to increase biodiversity. The Janzen–Connell hypothesis [25,26] proposes that high biodiversity in rainforests occurs because strong levels of local frequency-dependent predation reduce the probability that plants of the same species will establish in the vicinity of a parent tree [27]. Although both Janzen and Connell individually proposed seed predators as the mechanism driving this effect, an increasing body of evidence suggests that specialized fungal pathogens produce a strong Janzen–Connell effect not only in tropical [28], but also in temperate forests [29] as well as other habitats [30]. This effect is analogous to the Red Queen Hypothesis, because parasites maintain species diversity within a guild similar to how parasites can select for genetic diversity within a population [31]. Thus, the growing evidence suggests that parasites have a major impact on ecosystem health through their impact on driving biodiversity and ecosystem organization.

Detailed studies by David Tilman and colleagues at Cedar Creek, USA have illustrated how reduced biodiversity can lead to reduced productivity [32]. Host-specific pathogens, such as some rust species, impact the productivity of grasslands by damaging photosynthetic ability and root production [33]. When species biodiversity falls but total plant abundance is held constant, specialist pathogens have a bigger effect because the higher host density of remaining species increases the transmission of the specialized rust between individuals [34]. In the wild, this effect would increase biodiversity by limiting the abundance of the most common species. Interestingly, the rust affects major ecosystem functioning and could help explain the findings of Tilman *et al.* [32] that low biodiversity reduces primary productivity. This evidence leads us to suppose that parasites have an important role in influencing ecosystem vigor, although the crucial next step would be to partition how much of this reduced productivity occurs through the effects of parasitism alone.

In addition to the effect of parasites on host diversity, parasite communities should reflect the hosts that are available to them. Given that many parasites are host specific, a community rich with hosts should also be one that is rich with parasites. For this reason, a diverse and abundant community of parasites might be reflective of a diverse and abundant community of hosts. Thus, we are left with the apparent quandary that a diverse and healthy ecosystem should also be one with many parasites [35]. This is a consequence of the ability of pathogens to diversify host communities and the dependence of parasite diversity on host diversity.

Parasites in food webs

David Marcogliese and others have made the cogent argument that one aspect of community ecology where parasites have been missing is food webs [36–38]. Given that food webs envelop most paradigms in community ecology, the lack of parasites in food webs could preclude their general consideration by community ecologists. Nevertheless, parasites are embedded in food webs and a food-web perspective helps indicate how disease might indirectly affect non-host species via trophic links. For instance, the Iberian lynx *Felis pardina* is currently at the edge of extinction because rabbit hemorrhagic disease virus has wiped out the rabbits on which it depends [39]. Parasites can also be affected by changes in food-web structure; for example, harvesting lobsters increases the abundance of their sea urchin prey, which, when abundant, are more likely to experience bacterial epidemics [40].

Although there is substantial information about the role of parasitoids in food webs [41], there are fewer data and fewer insights into to the role of parasites, and only recently have fairly complete lists of parasite species been added to empirical food webs. Some obvious effects of incorporating parasites include increases to species richness, chain length and the number of links [42]. More surprisingly, a recent food web of the Carpinteria Salt Marsh in California finds that parasites dramatically increase connectance and nestedness (Figure 1 [42]). Increases in connectance and nestedness should alter stability in food webs, suggesting that parasites have an important role in food web structure.

Parasites and ecosystems

In summary, parasites appear to have an important role in influencing vigor and organization within communities but what are the parasite-mediated effects that are important? Certainly their impact on reducing host fitness and modifying competitive and trophic interactions among species have profound effects on the abundance of

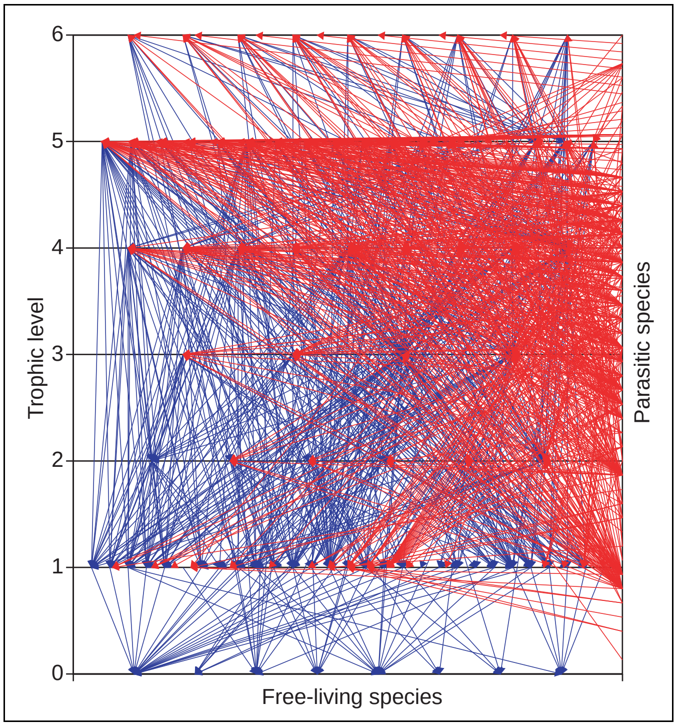

Figure 1. A food web of the Carpinteria salt marsh in California, USA. Each line connects a consumer species with a consumed species. Free-living species are distributed horizontally, where trophic level increases up the Y axis from basal (0) to top predator (6); parasitic species are ranged along the right vertical axis. Traditional predator–prey links are indicated by blue lines, whereas parasite–host links are indicated by red lines. The figure illustrates how parasites dramatically alter the topology of a good web. Reproduced with permission from [42].

different species and the strength of interactions between them and, therefore, the way that energy flows through the ecosystem. Pathogens are most likely to have ecosystem effects when they influence the behavior of the host [14,43], when they reduce the impact of herbivores [44] or make hosts more susceptible to predators [45,46]; these indirect effects coupled with the direct effects on abundance of hosts can have an important role in influencing how energy flows through communities. For example, pathogens of sea urchins can alter the state of temperate reefs by releasing kelps from grazing pressure [42]; similar pathogen–grazer–plant cascades occurred in the Serengeti following rinderpest, and in Australia following outbreaks of rabbit diseases.

Forty years ago, when Robert Paine carried out his classic starfish removal, few ecologists would have looked at the small and seemingly trivial parasites in his littoral zone community. Twenty years ago, when Dobson and Hudson published the first *TREE* article [2] on parasites, the data were poor and only a few parasite ecologists were undertaking field experiments. Since then, the field has blossomed and the role of parasites in host dynamics, community structure and ecosystems functioning is regaining the consideration that it had before the predation-minded 1970s and 1980s [4,5]. There is now increasing evidence that parasites can be a good proxy for estimating the health of an ecosystem (Box 2), not only because they integrate biodiversity over a period of time, but also because there is growing evidence that some parasites remove

Box 2. Parasites as measures of ecosystem health

Food-web dynamics affect parasites directly and indirectly when host abundance changes. The use of parasites as indicators of trophic complexity is gaining ground and even has commercial applications [53]. In some cases, it is easier to sample parasites than their hosts. In addition, the type of information provided by a parasite sample can be superior in the way in which it integrates space and time. For example, in estuaries, the abundance and diversity of birds is highly correlated with the abundance and diversity of trematodes in the snails that serve as the first intermediate host for these avian parasites [54]. Furthermore, whereas a bird survey provides a snapshot of bird presence, the trematodes provide a record of the community of birds that have visited a site during the life time of the snails sampled, and so provides an integral of past bird presence. In some cases, this can be information from several years.

Although the concentration of trematodes is low in degraded estuarine habitats, it can increase following habitat restorations that attract birds [52]. The ease of sampling trematodes in snails enables much larger spatial and temporal replication for appropriate statistical comparisons of restoration effectiveness (Figure I). Thus, there is increasing evidence that a healthy ecosystem is an infected ecosystem.

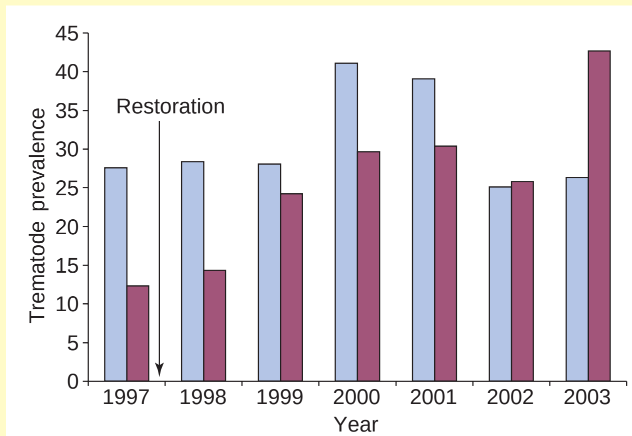

Figure I. Using parasites to evaluate restoration. Changes in the prevalence of larval trematodes that parasitize snails over time from two types of site: control sites (light-blue bars) and restored sites (maroon bars) showing that, following restoration, trematode prevalence increased to a level similar to that in the control sites. In this instance, trematodes were a good measure of restoration success. Reproduced, with permission, from [51].

environmental toxins when they are ingested by their hosts [47]. Box 2 suggests several ways in which workers could begin to measure the role of parasites in ecosystem health. Perhaps it is time for a young and enthusiastic ecologist to return to Makkaw Bay, record the abundance and distribution of the parasite biomass in the system, experimentally manipulate parasite species and predator species in a factorial experiment and then record the productivity, changes in organization and the resilience of the community, thus giving new insights into the role of different trophic interactions in ecosystem functioning.

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