

# A world without parasites: exploring the hidden ecology of infection

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Parasites have historically been considered a scourge, deserving of annihilation. Although parasite eradications rank among humanity's greatest achievements, new research is shedding light on the collateral effects of parasite loss. Here, we explore a "world without parasites": a thought experiment for illuminating the ecological roles that parasites play in ecosystems. While there is robust evidence for the effects of parasites on host individuals (eg affecting host vital rates), this exercise highlights how little we know about the influence of parasites on communities and ecosystems (eg altering energy flow through food webs). We present hypotheses for novel, interesting, and general effects of parasites. These hypotheses are largely untested, and should be considered a springboard for future research. While many uncertainties exist, the available evidence suggests that a world without parasites would be very different from the world we know, with effects extending from host individuals to populations, communities, and even ecosystems.

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What would happen if all parasites disappeared? This intriguing thought experiment, recently posed in BBC Earth's "Strange & Beautiful" series (Jones 2015), is a useful exercise for considering the ecological roles of parasites in ecosystems. So far, humanity has managed to drive only one of its parasites to extinction: *Variola*, the viral genus that causes smallpox (Panel 1). Until it was eradicated in 1980 through global-scale public health efforts, naturally occurring smallpox was one of the most dominant drivers of mortality in recorded history, killing 500 million people in the 20th century alone (Koplow 2003). By many metrics, the elimination of viruses, bacteria, protozoa, and parasitic arthropods and worms (here, collectively referred to as "parasites") would contribute to

reduced rates of human mortality, less disability, improvements in quality of life (Murray *et al.* 2012), and even reduced poverty (Bonds *et al.* 2010). The disappearance of parasites would also substantially benefit livestock production (Perry and Randolph 1999) and wildlife conservation (Daszak *et al.* 2000), particularly in developing countries.

But while the eradication of disease agents is critically important for ensuring human well-being, parasites often play important yet underappreciated roles in nature. Every ecosystem on Earth contains parasites; indeed, virtually every metazoan hosts at least one parasite species (Poulin and Morand 2000). Parasites represent ~40% of described species (Dobson *et al.* 2008) and are at least twice as rich in species as their vertebrate hosts (Poulin and Morand 2004). Considering only viruses in the ocean, a projected  $\sim 4 \times 10^{30}$  species exist, with the standing stock of carbon in viral biomass estimated at ~200 megatons (Suttle 2005). Despite this ubiquity and abundance, the diversity of parasites is poorly known (Poulin and Morand 2000) and our understanding of parasites' ecological influence remains rudimentary (Gomez *et al.* 2012; Hatcher *et al.* 2012).

Here, we explore a "world without parasites" as a vehicle for identifying the ecological changes that accompany the elimination or loss of infectious organisms. The elimination of all parasites is improbable and perhaps impossible, but as Holt (2010) noted, "it can be illuminating to ponder all kinds of implausible and radical scenarios, in effect bracketing the real world with visions of possible worlds". We limit our discussion to parasites of animals, focusing on empirical and theoretical research on parasites' influence at several levels of ecological organization (individual, population, community, and ecosystem), posing hypotheses for general mechanisms by which parasites may be ecologically influential, and identifying attributes of parasites, hosts, and ecosystems that may

## In a nutshell:

- Since antiquity, humans have tried to eliminate their own parasites and those of their domesticated animals; what would happen if they succeeded?
- We explore the ecology of a "world without parasites" as a way to understand the roles of parasites in ecosystems
- What functions would be lost in a world without parasites? Might there be unexpected ecological or epidemiological outcomes?
- This exercise highlights major knowledge gaps about the ecological roles of parasites
- We close by presenting hypotheses for novel, interesting, and general effects of parasites, positing that a world without parasites might be one with very different free-living communities

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### Panel 1. Controlling, eliminating, and eradicating parasites

Humans have been attempting to manage the transmission of parasites for hundreds and possibly thousands of years. For example, variolation – an early vaccination technique by which recipients were intentionally exposed to scabs, fluids, or clothing of smallpox patients, usually those who had lived through a mild form of the disease – was practiced in India as early as the 16th century (Plotkin and Plotkin 2008). Efforts to manage parasite transmission have met with varying levels of success. Studying the outcomes of such attempts may offer opportunities for understanding the ecological roles that parasites play in ecosystems.

#### Definitions

Here, we adopt the following terminology, after Dowdle (1999):

- **Eradication:** worldwide incidence of infection is reduced to zero
- **Elimination:** incidence of infection is reduced to zero in a defined geographic area, but transmission continues in other parts of the world
- **Control:** prevalence of a parasite is reduced to a level that is locally acceptable

#### Parasites of humans

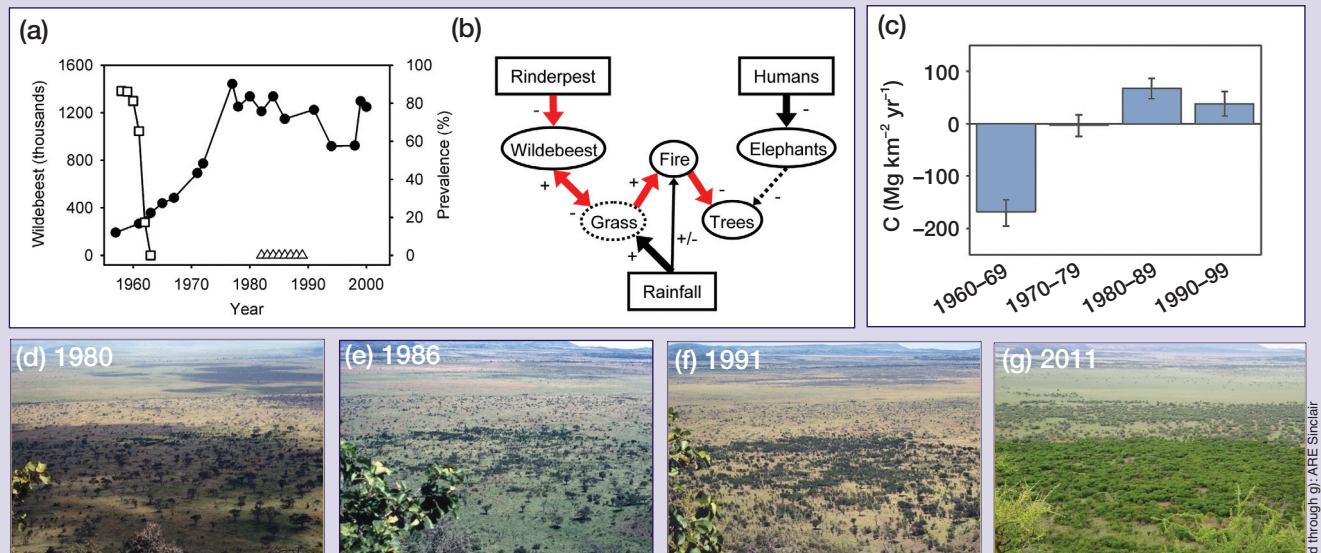
Although humanity has succeeded in eradicating only one human parasite – the smallpox virus (*Variola* spp) – countless attempts to control other parasites have been made, some highly successful (Center for Global Development 2004). International efforts to eradicate polio (Aylward and Tangermann 2011) and guinea worm (Al-Awadi et al. 2014) are nearing completion. Numerous other diseases – including lymphatic filariasis, onchocerciasis, Chagas disease, and leprosy – have been the focus of international efforts. These are considered by the World Health Organization (WHO) to be potentially “eradicable” (Dowdle 1999), and for many of these diseases, elimination has been achieved in some regions (Center for Global Development

2004). According to the WHO, a key feature of “eradicable” diseases is their specificity to the human species; it would be much more difficult to eradicate a parasite species that could “bide its time” in a reservoir host or as spores or eggs in the environment (Center for Global Development 2004).

Although strides have been made toward eradication, elimination, and control of many human parasites, there have also been many failures. Malaria – the disease responsible for more deaths over the course of human history than any other (Garnham 1966) – has been intensively targeted for eradication since 1955, with only local or regional progress toward elimination (Alonso et al. 2011), despite substantial investments (\$630 million invested in malaria research and development funding in 2011 alone; Moran et al. 2013). These failures are largely due to the evolution of resistance to pesticides among mosquitoes and anti-malarial drugs among *Plasmodium* parasites (Alonso et al. 2011). The *Schistosoma* spp, causative agents of schistosomiasis, have proved similarly recalcitrant to control (Chitsulo et al. 2000). Despite many national-level control programs (Rollinson et al. 2013), schistosomiasis remains very prevalent – it currently infects about 240 million people, mostly in sub-Saharan Africa (WHO 2013).

#### Parasites of non-human animals

Substantial efforts have also been invested in eradicating or eliminating the parasites of non-human animals, including domestic animals and wildlife. To date, the only animal disease to be (purposefully) globally eradicated is rinderpest. When the success of this eradication effort was announced in 2011, it was only the second intentional eradication to have been achieved in human history – after smallpox (Roeder et al. 2013). Native to Central Asia, rinderpest was introduced into Africa in 1887 with Indian cattle (Scott 1998). The morbillivirus devastated populations of cattle, buffalo, antelope, giraffe, wildebeest, and warthogs throughout the African continent (Dobson et al. 2011). Long-



**Figure 1.** African wildebeest (*Connochaetes taurinus*) were decimated by rinderpest in an 1889 outbreak and remained at low abundance for decades. When rinderpest eradication efforts were initiated in the 1960s, wildebeest abundance increased dramatically (a). Because wildebeest grazing reduces biomass of flammable grasses, thereby reducing fire frequency and increasing woody plant abundance, the return of wildebeest increased the abundance of trees (b), increasing savanna carbon sequestration (c). These changes have been very evident in the Serengeti ([d] through [g]). In (a), circles indicate wildebeest population size, whereas squares and triangles indicate prevalence of rinderpest before and after eradication, respectively. In (b), solid and dashed lines indicate direct and indirect effects, respectively; the plus and minus signs indicate direction of effects. In (c), columns show means with 95% confidence intervals (error bars). Panels (a) through (c) were adapted from Dobson et al. (2011), adapted from Holdo et al. (2009).

**Panel 1. – continued**

term monitoring of wildlife in and around Serengeti National Park revealed the ecological outcomes of this eradication: in the absence of rinderpest-induced mortality, herbivore abundance increased several times over, triggering increases in the abundance of their predators (lions and hyenas), reductions in the frequency of fire (due to more efficient grazing and less unconsumed, flammable grass), a shift of grassland ecosystems to *Acacia*-dominated woodland and bush, and a shift of the Serengeti from a source of atmospheric carbon to a sink (Figure 1; Holdo *et al.* 2009; Dobson *et al.* 2011). These considerable ecological changes were among the first demonstrations of the important role that parasites can play.

Although the example of rinderpest on the African continent is one familiar to ecologists, the disease was not native to Africa and its eradication was therefore akin to ecological restoration. Back in its indigenous Indian range, rinderpest's ecological role – and the ecological effects of its removal – were poorly documented. India was declared rinderpest-free in 2004 (Global Rinderpest Eradication Program 2011) and the last recorded instance of rinderpest in South Asia occurred in 2000 (Roeder *et al.* 2013). Eradication has undoubtedly benefited the subcontinent: the economic benefit–cost ratio for rinderpest eradication in India has been estimated at >60, primarily because livestock can now be freely exported (Roeder *et al.* 2013). Prior to its eradication, the disease also affected wild mammals in the region, including threatened gaur (*Bos gaurus*; Ashokkumar *et al.* 2012) and Asiatic wild buffalo (*Bubalus bubalis*; Choudhury 1994). Whether any regional ecological impacts have resulted is unknown.

An additional animal disease has been globally eradicated, although this came not as the result of a purposeful campaign, but as an unintended consequence of conservation. In a last-ditch effort to rescue the California condor (*Gymnogyps californianus*) from extinction, the surviving few birds were removed from the wild into captivity and de-loused with pesticides. This act eradicated the condor louse (*Colpocephalum californici*), a species that has been found on no other bird host and is presumed to be extinct (Dunn 2009), although its host has since rebounded. Whether there have been any ecological impacts of the louse's extinction is also unknown.

**Why consider the ecological outcomes of parasite eradication?**

Eradication efforts – which can be costly – usually target only those parasites of major public health, economic, or conservation concern (Stringer and Linklater 2014). Each successful eradication effort outlined above was an unmitigated triumph for humankind – in our opinion, no ecological argument can overshadow the benefit of, for example, ridding humanity of the scourge of smallpox. Nonetheless, we believe it is worth considering the ecological functions that are lost when parasites are eliminated from an ecosystem, particularly parasites of ecologically influential wildlife species. Here, we identify several priority research areas:

- (1) *Identify opportunities to experimentally assess the ecological role of parasites:* Exclusion experiments – those in which a taxon is excluded from an area and ecological effects of this exclusion are quantified – have driven tremendous progress in ecology (Lubchenco and Real 1991). Parasite eliminations can serve as “natural experiments” that reveal the functional roles of parasites in ecosystems, providing critical information that would otherwise be difficult to obtain. Indeed, some of the most informative studies of parasites' ecological roles to date have used control programs as “natural experiments” (eg Holdo *et al.* 2009) or have experimentally manipulated the presence of parasites (eg Hudson *et al.* 1998).
- (2) *Anticipate unintended consequences of parasite eradication:* Collateral ecological impacts can arise from the eradication or elimination of an animal parasite. For example, the eradication of rinderpest and subsequent cessation of vaccination may have led to recent upticks in the prevalence of another ungulate morbillivirus in Africa, peste des petits ruminants (Libeau *et al.* 2011). The potential for such unintended consequences should be assessed in a risk–benefit analysis before attempts at parasite control are made (Stringer and Linklater 2014).
- (3) *Identify opportunities to reap economic and conservation benefit from parasite eradication:* Conversely, parasite eradication or elimination may have important economic and conservation benefits. An accurate assessment of potential benefits is also a key component of risk–benefit analyses (Stringer and Linklater 2014).

predict a strong ecological influence of parasites (Panel 2, see p 433–434). We focus on ecological effects of parasites, but evolutionary effects are also likely to be important (Holt 2010; Stringer and Linklater 2014). We emphasize those cases where parasites' effects are likely to be consistent across contexts, excluding impacts of parasites that are likely to be highly context-specific. The studies reviewed below suggest that the influence of parasites, though frequently hidden, can be substantial.

**■ Individuals and populations**

The fitness effects of parasites on host individuals, although negative by definition (Combes 2001), vary strongly among species. A parasite may reduce its host's growth, prevent it from reproducing, or change its behavior. Parasites may even have positive collateral effects on a host (eg by competing with other, more virulent parasites within the same host [Panel 2, see p 433–434]). When individual-level effects accrue, parasites may also influence host populations in a variety of ways.

**Parasites influence host immunity**

A growing body of research illustrates the ecological importance of within-host interactions among parasites, as well as interactions between parasites and the host's immune system. Although co-infections would be impossible in a world without parasites, we address interactions among co-infecting parasites in Panel 2 (see p 433–434). Even without co-infecting species, the absence of parasites can drive unexpected outcomes in host health, through effects on host immune function. Some chronic illnesses of humans – including allergies and autoimmune diseases – have been linked to a lack of exposure to parasites, particularly worms (the “hygiene hypothesis”; Okada *et al.* 2010). Paradoxically, parasites may have net positive fitness benefits for hosts if the immunologic consequence of parasite absence takes a sufficiently high toll on host fitness (Holt 2010; Stringer and Linklater 2014). In the absence of parasites, hosts should shed costly – and useless – immune defenses. But nature abhors a vacuum. Hosts that initially lost their





K. Lafferty / US Geological Survey

**Figure 2.** An isopod parasite (*Anilocra laticaudata*) attached to the cheek of its fish host, a coney (*Cephalopholis fulva*), in the Bahamas.

immunity would later be susceptible to re-infection by newly evolved parasites (Stringer and Linklater 2014; Jones 2015).

### Parasites affect the dynamics of host populations

Many parasites affect the rate of host population growth and total population size. Indeed, there are numerous examples demonstrating regulation of wild host populations by parasites, including both “micro-parasites” and “macro-parasites”, whose fitness effects on hosts are independent and dependent, respectively, on the number of initial infecting transmissive stages (Lafferty and Kuris 2002). For instance, crustacean parasites such as isopods and copepods (Figure 2) can reduce growth, reproduction, and survivorship of coral reef fishes, resulting in population-level regulation of hosts (Forrester and Finley 2006). In British heathland ecosystems, experimental application of anti-helminthic drugs (which clear red grouse of infections with the parasitic nematode *Trichostrongylus tenuis*) dampened the boom-and-bust cycles that characterize the population dynamics of infected grouse (Hudson *et al.* 1998). But parasites need not kill their hosts to exert regulatory effects on host populations; many parasites castrate their hosts (eg the bacterium *Pasteuria ramosa* in *Daphnia* spp; Ebert *et al.* 2004), thereby regulating host populations (Decaestecker *et al.* 2005). Removal of such influential parasites may lead to loss of regulation of host populations and an increase in host abundance (Panel 2, see p 433–434).

## ■ Communities

### Parasites alter the composition of ecological communities

The effects of parasites vary among host species, and this can lead to community-level effects (Panel 2, see p 433–434). Many examples, most accumulated over the

past several years, demonstrate that parasites can alter the composition of communities through demographic (density-mediated) or morphological/physiological/behavioral (trait-mediated) indirect effects. Because these effects have been reviewed elsewhere (eg Gomez *et al.* 2012; Hatcher *et al.* 2012), we give only a few illustrative examples here. In a classic case of a density-mediated indirect effect of parasites and of parasite-mediated apparent competition (an interaction that looks like competition between two species but is actually caused by a third factor; Stringer and Linklater 2014), the invasive gray squirrel (*Sciurus carolinensis*) was able to replace the native red squirrel (*Sciurus vulgaris*) throughout the UK because the invader brought with it a parapoxvirus. Only

the native red squirrel experienced substantial parasite-induced mortality, allowing gray squirrels to expand into the niche vacated by the natives (Tompkins *et al.* 2003). Parasites may also have trait-mediated indirect effects. In the rocky intertidal zone of New England, periwinkle snails (*Littorina littorea*) infected with a trematode parasite eat less algae than do uninfected snails, probably due to infection-related changes in the digestive system; as a result, edible macroalgal species are more abundant in the presence of infected snails than in the presence of uninfected snails, with implications for the other intertidal species that use this macroalgae as habitat and food (Wood *et al.* 2007). Finally, parasites may affect interactions among free-living species (Holt 2010; Mordecai 2011; Stringer and Linklater 2014); for example, the presence of larval trematodes increases intertidal diversity on New Zealand mud flats by changing interactions between host bivalves and the organisms that depend on bivalve shells for habitat (Mouritsen and Poulin 2005). Whether by effects on host density or traits, or on species interactions among hosts, the composition of free-living communities can be radically reshaped by parasites.

In addition to affecting the composition of communities, parasites may also affect variability in composition (ie food web stability), but whether the presence of parasites generally increases or decreases such variability is controversial and may be context-dependent (Lafferty *et al.* 2008; McQuaid and Britton 2015). Parasites could increase stability in community composition by regulating host populations (Anderson and May 1978), contributing “weak links in long loops” (Neutel *et al.* 2002), or by producing apparent competition (Dobson 2004). Alternatively, parasites could decrease stability by increasing the length of food chains (Williams and Martinez 2004), overwhelming stable predator–prey links with unstable parasite–host links (Otto *et al.* 2007), or merely by contributing additional species to total community richness (Chen *et al.* 2011). While the presence of parasites is generally thought to decrease the robustness of food webs (ie the likelihood of secondary extinc-

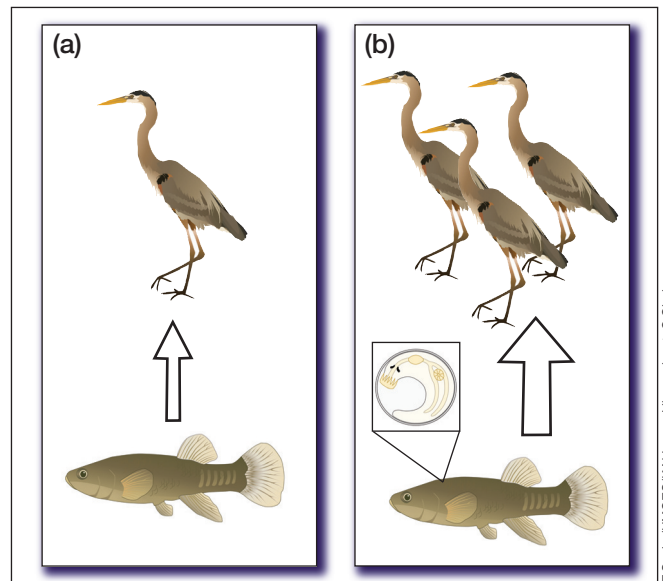
tions occurring after a primary species loss), this is primarily because parasites themselves are prone to secondary extinctions (Chen *et al.* 2011; McQuaid and Britton 2015). Whether there is a general role for parasites as a stabilizing force in free-living food webs remains an open question.

As suggested in the example of gray squirrels, parasites may mediate the ability of non-native species to invade a community (Tompkins *et al.* 2003). According to the “enemy release hypothesis”, when a species is introduced into a region to which it is not native, it experiences weaker population regulation by natural enemies (eg parasites, predators) than it would in its native range (Prenter *et al.* 2004). Indeed, host species of various taxa are infected by twice as many parasites in their native ranges than in their invaded ranges (Torchin *et al.* 2003). If parasites disappeared, native and invasive species might be placed on equal footing – that is, release from parasitic enemies would benefit both native and invasive species. Alternatively, if the parasites of invasive hosts facilitate invasion by infecting native hosts (the “biological weapons hypothesis”, as in the case of the gray squirrel; Tompkins *et al.* 2003), parasite loss might result in a disadvantage to invasive species and reduced rates of invasion. Native parasites also have the potential to slow the progress of invaders (the “biotic resistance hypothesis”; Torchin *et al.* 2002; Panel 2, see p 433–434); for instance, European settlers were repelled from large swaths of land in southern and central Africa by trypanosomiasis, so that patterns of early European settlement mostly matched areas that were trypanosomiasis-free (Ford 1971; Beinart and Coates 1995). Thus, whether the loss of parasites will increase or decrease invasibility of an ecosystem ultimately depends on the relative fitness effects of invasive parasites on native and invasive hosts, the propensity of native parasites to infect invasive hosts, and other factors.

### Parasites alter trophic interactions and predation rates

In a world without parasites, energy should become available to free-living consumers that would otherwise have been siphoned away by parasitic consumers (Holt 2010; Jones 2015); this follows from the expectation that the loss of parasites should ameliorate individual-level fitness effects associated with parasitism (eg make prey larger) and release some free-living species from regulation (eg make prey more numerous). But parasites can also influence host individuals through sublethal effects, which affect their quality and availability as prey (Holt 2010). Whether elimination of a parasite species will increase or decrease energy flow to consumers/predators will therefore depend on the balance between the regulatory and individual-level effects of the parasite.

We suggest that the ability of parasites to manipulate host behavior facilitates a substantial amount of energy flow from lower to upper trophic levels (Figure 3; Panel 2, see p 433–434; Haderler and Freedman 1989; Kuris *et al.*



**Figure 3.** In many second intermediate hosts (hosts of the second larval stage) of trematode parasites – like the California killifish (*Fundulus parvipinnis*) – the parasite induces behavioral changes to facilitate transmission to the final host (in this example, bird predators). (a) In the absence of parasites, fish display evasive and camouflaging behavior that minimizes the likelihood of bird predation. (b) When trematode metacercariae (larval stage) infect killifish, the fish perform behaviors that make them conspicuous to bird predators, effectively increasing the availability of fish resources to birds (Lafferty and Morris 1996). In this way, parasites may provide a “subsidy” to predators. Such behavioral manipulations are common across the diversity of parasite life.

2008). Host manipulation is a common strategy by which parasites alter their host’s phenotype to increase their own fitness, usually by inducing or exaggerating host traits that favor parasite transmission or dispersal (Dobson 1988; Poulin 2010). Adaptations for host manipulation have been documented in hundreds of parasite species across the tree of life – including platyhelminths, acanthocephalans, nematodes, nematomorphs, arthropods, protozoa, fungi, bacteria, and viruses (Hughes *et al.* 2012) – and have evolved at least 20 separate times (Poulin 2010). Some manipulations increase the likelihood of parasite transmission from prey to predator (trophic transmission) by inducing changes in the prey host’s phenotype that make it more susceptible to predation (Figure 3). Other parasites induce behaviors that facilitate transmission among conspecifics; for example, in infected vertebrates, rabies can increase aggression, promoting transmission of the virus via bite wounds (Klein 2003). Parasites may also cause their hosts to move from habitat preferred by the host to habitat suitable for the parasite as, for example, in nematomorph parasites that induce a “water drive” in their cricket hosts, causing the crickets to drown themselves in streams, where the nematomorph emerges to complete its aquatic life stage (Figure 4; Hanelt *et al.* 2005). Our understand-





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**Figure 4.** Many parasites are capable of manipulating the behavior of their hosts. Nematomorphs (also sometimes called Gordian or horsehair worms) induce a “water drive” in their cricket host, causing the host to drown itself in puddles, ponds, or streams, where the parasite can wriggle free and proceed with the aquatic stage of its life cycle. In this way, nematomorphs drive across-ecosystem subsidies that have strong effects on the recipient ecosystem (Sato et al. 2011).

ing of the ecological effects of manipulation is still limited (Weinersmith and Faulkes 2014), possibly because manipulations are diverse and can have varying, context-dependent ecological effects. The net influence of parasite loss on consumer populations will depend on the balance between loss of regulation on prey populations versus loss of manipulated prey individuals; but because many taxa in many ecosystems engage in host manipulation for trophic transmission, we predict that a world without parasites could be a world with fewer predators (Panel 2, see p 433–434).

## ■ Ecosystems

### *Parasites alter the cycling of energy and nutrients*

The ways in which parasites affect the cycling of energy and nutrients are only beginning to receive research attention (Preston et al. in review), but because parasites can represent a large proportion of total biomass in some ecosystems (Kuris et al. 2008; Preston et al. 2013) and can directly alter rates of host nutrient excretion (eg Bernot 2013), their influence on such cycles could be substantial. Behavior-manipulating parasites, in particular, may have strong effects on these cycles; we discussed above the influence of manipulation on the abundance of predatory species (which can be thought of as the “nodes”, architecture, or topology of a food web), but parasites can also affect the movement of energy and nutrients through food webs (Kuris et al. 2008). For instance, by inducing behaviors in intermediate hosts that increase their sus-

ceptibility to predation, parasites may intensify trophic interactions and strengthen predator–prey linkages (see above; Lefevre et al. 2009). Parasites may also alter the rates of other important ecosystem processes, such as grazing (eg rinderpest; Panel 1; Sinclair et al. 2008), decomposition (eg nematomorphs; Sato et al. 2011), and bioturbation (eg trematodes; Mouritsen and Haun 2008), as well as carbon sequestration and cycling of other nutrients (eg marine viruses; Panel 2, see p 433–434; Danovaro et al. 2011). Whether energy flow to upper trophic levels is strengthened or weakened by parasite removal will depend on the relative influence of manipulative versus host-population regulating parasites.

### *Parasites alter across-ecosystem subsidies*

In many cases, parasites’ manipulation of their hosts to move from habitat preferred by the host to habitat suitable for the parasite can result in a transfer of energy and nutrients from one ecosystem to another. To demonstrate this effect, Sato et al. (2011) showed that parasite-driven energy subsidies from terrestrial ecosystems in Japan (where crickets were experimentally added to stream reaches at rates equivalent to the rate at which nematomorph-infected crickets enter stream habitats) are sufficient to set off a trophic cascade. In this cascade, fish predators switch to feeding on crickets, releasing their usual prey – benthic invertebrates – from predation pressure, and thereby decreasing biomass of benthic algae and increasing the leaf breakdown rate. Thus, in the absence of parasites, we may observe weakening of across-ecosystem subsidies (eg nematomorph-infected crickets will no longer cross the boundary between terrestrial and aquatic ecosystems), but the extent of the contribution of manipulation or other parasite-mediated processes to across-ecosystem subsidies remains unknown.

## ■ Conclusions

A world without parasites is impossible to achieve, and can be approximated only in specific circumstances (eg zoo enclosures, aquaria, and intensive agriculture), which – despite strenuous effort – are often still hotbeds of infection (eg hospitals). Even if parasites did somehow all disappear, other species would evolve to occupy the newly vacant niches (Lloyd-Smith 2013). Despite its improbability, imagining such a world can help expose the otherwise hidden ecological roles of parasites. These roles are hidden because the ecosystem of a parasite (ie inside the host) is often nested within the ecosystems that ecologists

are accustomed to considering (eg forests, grasslands, coral reefs). A better understanding of how parasites contribute to the communities and ecosystems in which they are embedded is a critical need as we consider how to make the world “less wormy” (Loker 2013).

The hypotheses outlined here (Panel 2, see p 433–434) posit several general effects of parasites on ecosystems, including on host community structure and energy flow. Parasites may be small and inconspicuous relative to their hosts, but data collected so far suggest that they are far from unimportant. We must begin to consider their influence within ecosystems, particularly when planning disease management interventions or conservation efforts.

There are some cases in which elimination of a parasite species is both possible and highly desirable. In these instances, potential benefits to human health and well-being trump any other considerations. However, many of the contemporary disease challenges faced by society and imperiled wildlife involve more complex chains of transmission – frequently including multiple host species, multiple parasite species, reservoirs, or resilient environmental resting stages. As a result, eradication will often be impossible, and “ecological surprises” associated with control efforts will probably appear with greater frequency. For example, without an appreciation for the antagonistic relationship between worms and protozoa living in the human intestine (Panel 2, see p 433–434; Martin *et al.* 2013), a well-intentioned de-worming campaign could make people very sick. We do not argue that human parasites should be conserved, but rather we urge the importance of understanding the ecology of a parasite before attempting to control it. As Jones (2015) wrote, “Surprisingly, a world without parasites might not be a nicer one”. Thoughtful planning will prevent the loss of ecologically important parasites and the processes they facilitate, as we progress slowly toward a parasite-free world.

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## Panel 2. Hypotheses for general roles of parasites in ecosystems

Here, we present some general, novel, and interesting hypotheses regarding the roles of parasites in ecosystems. These address broad questions: which ecological processes are most likely to change as the result of parasite removal? Under what conditions will parasite effects be strongest? Which parasite effects might be general across ecosystems? For each hypothesis, we sketch a brief explanation or example, and define conditions under which we expect the hypothesis might hold. These hypotheses await testing.

### Individual level

#### **Elimination of one parasite species might lead to increased abundance of other parasite species**

*Explanation:* Most free-living organisms – including humans – host numerous species of symbionts, including viruses, bacteria, fungi, worms, and arthropods. These symbionts can interact with one another directly (eg through predation or interference competition) or indirectly (eg via immunity-mediated apparent competition; Stringer and Linklater 2014). Not all of the symbionts that live on and in humans are parasitic, but even those that are may still confer a net benefit if they deter other, more deleterious pathogens (Costello et al. 2012).

*Example:* Anti-helminthic treatment increases risk of *Giardia* infection in humans, and anti-protozoal treatment increases the risk of hookworm infection – probably the result of competitive inhibition (competition between parasites) or cross-immunity (susceptibility of one parasite to the immune response provoked by the other) between worms and protozoans (Martin et al. 2013).

#### *Conditions:*

- When there are parasites in the system that are ecologically similar to the parasite targeted for eradication (and therefore likely to engage in intra-host competition)
- When there are parasites in the system that are closely related to the parasite targeted for eradication (and are therefore likely to be affected by the same component of host immunity), but are unaffected by the eradication effort (eg Libeau et al. 2011)
- When parasite interactions (direct or indirect) are an important determinant of parasite community composition (ie when intra-host interactions matter), as may be true for highly abundant parasites, those with strong cross-reactive immunity, or when priority effects are strong

#### **Removal of one parasite species might lead to reduced abundance of another parasite species**

*Example:* Infection with the parasitic worms that cause human urinary schistosomiasis (*Schistosoma haematobium*) increases the risk of contracting HIV for women in sub-Saharan Africa (Rollinson 2009). Elimination of schistosomiasis through distribution of anti-helminthic drugs has been suggested as an approach for controlling the African HIV epidemic (Hotez et al. 2009).

#### *Conditions:*

- When the parasite removed depresses the efficacy of host immune defenses
- When the parasites in question are less likely to compete (eg are ecologically or phylogenetically distinct) or trigger different branches of the host's immune defenses (eg Ezenwa et al. 2010)
- When host immune function is an important regulator of parasite abundance or transmission potential

### Population level

#### **Removal of “keystone” parasite species or groups will influence host populations**

*Explanation:* “Keystone” species have strong trophic links to many other species, and extirpating them can have important effects on food webs. Great theoretical progress has been made in predicting the result of a species' extinction. This work demonstrates that – for free-living taxa – outcomes of extinction are variable from species to species, with many weak interactors and a few “keystone” species (Wootton and Emmerson 2005). Do parasites follow the same pattern? If so, can we predict which parasitic species are likely to be “keystones”?

*Example:* In some salt marsh ecosystems of western North America, trematode biomass exceeds that of any other parasite group (Kuris et al. 2008). Standing trematode biomass and trematode production of infective stages (cercariae) each exceed the biomass of top predators (Kuris et al. 2008). Therefore, the influence of trematodes on energy flow in these ecosystems is probably substantial.

*Conditions:* Ecologically influential (“keystone”) parasites should tend to be:

- Those that infect ecologically influential (“keystone”) hosts
- Those that commandeer a substantial proportion of host biomass (eg parasitic castrators, Kuris et al. 2008; behavior manipulators, Sato et al. 2011)
- Those that can behaviorally manipulate their hosts, because these parasites might affect energy flow by strengthening predator–prey links (eg trophically transmitted trematode metacercariae in killifish; Lafferty and Morris 1996) or causing the host to move into a novel habitat (eg nematomorphs that induce “water drive” in cricket hosts; Sato et al. 2011)

#### **Removal of a parasite species might lead to loss of regulation of the host population**

*Example:* Hudson et al. (1998) administered anti-helminthic drugs to red grouse and observed a dampening of the population's boom-and-bust cycles.

#### *Conditions:*

- When parasites are highly host-specific
- When parasites are pathogenic
- When ecosystems are stable and where abiotic factors (eg drought, desiccation, fire, wave action) do not limit host populations
- When hosts are high trophic-level species, and the likelihood of control by predators is therefore lower

### Community level

#### **Removal of a parasite species may alter community composition**

*Examples:* Parasites have variable effects on communities: for instance, they can either increase (eg Thomas et al. 1995; Mouritsen and Poulin 2005) or decrease (eg Tompkins et al. 2003) coexistence and community-level species diversity.

*Conditions:* While there may be few general ways in which parasites change community composition, we predict that the conditions that favor a strong effect of parasites on community com-

**Panel 2. – continued**

position include:

- When hosts are abundant and/or ecologically influential
- When hosts vary in their tolerance to parasitic infection
- When parasites are highly host-specific, and the magnitude of parasite impacts is therefore highly divergent among species in the free-living assemblage
- When parasites are highly pathogenic
- When ecosystems are stable and where abiotic factors (eg drought, desiccation, fire, wave action) do not limit host populations
- When the host community is strongly influenced by inter-specific interactions rather than other forces (eg dispersal, stochastic effects)

**Removal of a parasite species may change a community's invasibility**

The removal of parasites might make communities more difficult to invade (because release from parasitic enemies puts natives and invasives on “equal footing” or removes the “biological weapons” that might otherwise facilitate invasion) or easier to invade (because removal of parasites removes the “biotic resistance” of native communities).

Possible tests:

- Experimentally assembled parasite-rich and parasite-free communities
- Comparing the number or proportion of invasive species across habitats that naturally vary in the number of parasites they support
- Experimentally manipulating the number of parasite species or individuals (eg using anti-helminthic drugs) in a habitat experiencing an ongoing or progressive invasion
- Identifying the cause of failure in intentional introductions

**Removal of parasite species that regulate populations may increase predation rates**

*Explanation:* Parasites drain the resources of their hosts. In the absence of parasites, this energy can be exploited by other natural enemies, including predators.

*Example:* Before its eradication, rinderpest devastated populations of cattle, buffalo, antelope, giraffe, wildebeest, and warthogs throughout the African continent (Dobson *et al.* 2011). After Africa became rinderpest-free, the abundance of lions and hyenas increased, probably due to increased availability of prey (Figure 1; Holdo *et al.* 2009; Dobson *et al.* 2011).

Conditions:

- When parasites strongly regulate the host/prey species and removal of parasites releases this regulation
- When the host/prey species is abundant and ecologically influential

**Removal of manipulative parasite species may reduce predation rates**

*Explanation:* Manipulations of host behavior or morphology that increase susceptibility of an intermediate host to a downstream host are among the most common manipulations known and – in many cases – the behavioral manipulation is accompanied by an increase in the lipid and glycogen content of the intermediate host (Lefevre *et al.* 2009). By making prey easier to catch and more valuable as food resources, manipulative parasites may

functionally increase predation rates and, by extension, the amount of resources accessible to predators.

Conditions:

- When manipulation drives a large change from host's uninfected state
- When parasites are abundant and manipulation is common among prey individuals
- When the host is abundant or ecologically influential

**Ecosystem level**

**Removal of regulating parasite species may increase flow of energy to higher trophic levels**

*Explanation:* Parasites drain the resources of their hosts. In the absence of parasites, this energy can be exploited by other natural enemies, including predators, with additional downstream effects on energy flow.

Conditions:

- When parasites strongly regulate the host/prey populations and removal of parasites releases this regulation
- When the host/prey species is abundant and ecologically influential

**Removal of manipulative parasite species may reduce flow of energy to higher trophic levels**

*Explanation:* We hypothesize that manipulative parasites are responsible for subsidizing populations of predators, shunting energy that would otherwise fail to flow to higher trophic levels; this is accomplished through host behavioral manipulation to improve the odds of trophic transmission. If the loss of predator fitness due to parasitic infection does not outweigh this gain, this could represent a subsidy that lifts resource constraints on predators (Lafferty *et al.* 2000). Therefore, a world without manipulative parasites may also be a world with fewer predators (Figure 3). Given the commonness of behavioral manipulations that facilitate trophic transmission, this could be a general effect across ecosystems.

Conditions:

- When manipulation drives a large change from host's uninfected state
- When parasites are abundant and manipulation is common among prey individuals
- When host is abundant or ecologically influential
- When parasite has high biomass / secondary production

**Removal of a parasite species may alter across-ecosystem subsidies**

*Explanation:* Some parasites induce their hosts to move from habitat preferred by the host to habitat suitable for the parasite (eg Hanelt *et al.* 2005), increasing the exchange of energy and materials (in the form of host and parasite biomass) across ecosystems. Others may reduce host movement by sapping host resources, by suppressing overall activity levels, or by reducing the abundance of a host that otherwise might traverse ecosystem boundaries (eg Dobson *et al.* 2011). Is there any consistency in the effect of parasites on across-ecosystem processes? We anticipate that these will be extremely context-dependent effects.

See WebReferences for all references in Panel 2