INVASIONS AND INFECTIONS
Indirect effects of parasites in invasions

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Summary

1. Introduced species disrupt native communities and biodiversity worldwide. Parasitic infections (and at times, their absence) are thought to be a key component in the success and impact of biological invasions by plants and animals. They can facilitate or limit invasions, and positively or negatively impact native species.

2. Parasites have not only direct effects on their hosts, but also indirect effects on the species with which their hosts interact. Indirect effects include density-mediated effects (resulting from parasite-induced reduction in host reproduction and survival) as well as trait-mediated indirect effects (resulting from parasite-induced changes in host phenotype, behaviour or life history). These effects are not mutually exclusive but often interact.

3. The importance of these indirect interactions for invasion success, and the extent to which these effects ramify throughout communities and influence ecosystems undergoing biological invasion provide the focus of our review. Examples from the animal and plant literature illustrate the importance of parasites in mediating both competitive and consumer–resource interactions between native and invasive species.

4. Parasites are involved in indirect interactions at all trophic levels. Furthermore, the indirect effects of parasitic infection are important at a range of biological scales from within a host to the whole ecosystem in determining invasion success and impact.

5. To understand the importance of parasitic infection in invasion success and in the outcomes for invaded communities requires an interdisciplinary approach by ecologists and parasitologists, across animal and plant systems. Future research should develop a framework integrating community ecology, evolution and immunology to better understand and manage the spread of invasive species and their diseases.

Key-words: biological invasion, density-mediated indirect effect, indirect effect, parasitic infection, trait-mediated indirect effect

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Introduction

Biological invasions represent a global problem resulting in changes in community structure and biodiversity, with introduced species disrupting native communities via both direct and indirect effects (White, Wilson & Clarke 2006). There is a burgeoning interest in the role of parasites in invasion success and impact (Tompkins *et al.* 2011). Much research has focused on the direct impact that parasites have on biological invasion and on parasites that are themselves invasive (Hatcher, Dick & Dunn 2012a). Yet, the role of parasites in invasions may extend well beyond such direct effects. As parasites are involved in interactions at all trophic levels (Kuris *et al.* 2008; Hatcher & Dunn 2011), including those within individual hosts (Lello *et al.* 2004), indirect effects on species other than their hosts may be expected (Fig. 1). Interactions within an invaded community can be mediated by parasites through several processes: invaders may benefit from parasite loss, introduce novel parasites into resident communities and/or acquire new parasites themselves from those communities (Dunn 2009). Parasites may indirectly affect both competitive and

consumer–resource interactions, and ultimately, these influences may propagate through trophic levels within communities. Because of these hidden but potentially dramatic roles, parasites are likely to be important components in ecosystems (Thomas, Renaud & Guégan 2005; Hatcher, Dick & Dunn 2012b). Hence to understand the causes and implications of invasions, it is important to consider not only the direct effects of parasites, but also the indirect effects of parasites on native and invasive species. Throughout this article, we use the term parasite to refer broadly to disease-causing infectious agents including pathogens, parasites and parasitoids.

Indirect effects can influence community dynamics in at least two ways (Fig. 2). The interaction between two species (A and B) may be affected by a third species (C) either through the effects of C on the survival or reproduction of species A (a density-mediated indirect effect; Fig. 2a), or through induced changes in the behaviour, morphology, life history or physiology of A (a trait-mediated indirect effect; Fig. 2b–d).

The potential for trait changes to cause a variety of indirect effects has been long recognized (e.g. Abrams 1995; Werner & Peacor 2003), but their relevance to a broad range of community processes and patterns is only now being established (Raffel, Martin & Rohr 2008; Ohgushi, Schmitz & Holt in press). Parasitic infection may be a rich source of trait-mediated indirect effects, because, by virtue of their intimate association with the host, parasites can influence a variety of traits including growth rates, morphology, competitive behaviours and antipredator behaviours (Moore 2002; Hatcher, Dick & Dunn 2006; Table S1 in supporting information). By causing per capita changes in host resource utilization or likelihood of the host being consumed, parasites can induce positive or negative indirect effects on other species at the same (Fig. 2b,c) or different (Fig. 2d) trophic levels in the community.

The net fitness effects of parasites on individual hosts result from the direct effects of infection on host fitness (which are always negative) combined with the consequences of indirect effects on other species (which may be positive or negative). Further, the interaction networks of communities and ecosystems (including both food web and non-trophic interactions) will dictate how these effects are propagated among trophic levels and component species (Fig. 2; Table S1). From an evolutionary perspective, an introduced species generally perturbs a coevolved system and creates a novel suite of interactions. This transition from highly evolved interactions to novel ones may occur on an ecological time-scale, bringing together new host–parasite associations. Here, we explore the indirect ecological effects of parasites from the context of invaded communities, including parasite communities within an individual host, and examine the extent to which these effects ramify through the invaded communities. We first consider effects that propagate horizontally within the same trophic level (potential competitors) and then turn to those that propagate vertically between trophic levels (consumer–resource
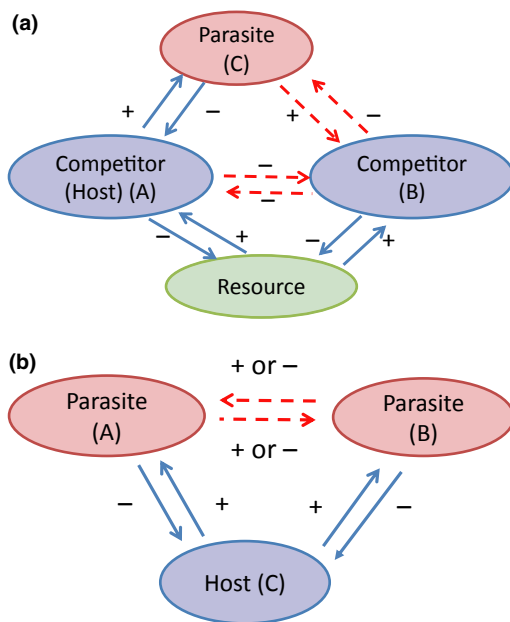
Fig. 1. Examples of indirect interactions and infection. (a) Parasite-mediated effects in competition and (b) host-mediated effects on coinfection. Direct interactions between species are shown by solid lines and indirect interactions by dashed lines; the sign of the interaction (+/−) shows whether fitness gain or loss accrues in the direction of the arrow. (a) A parasite can have a positive indirect effect on a nonhost that competes with the host for resources, by reducing the host's population density (a density-mediated indirect effect) or by reducing its competitive ability, for example by reducing its growth or foraging rates (a trait-mediated indirect effect). (b) Hosts can mediate positive or negative indirect interactions between parasites by virtue of shared immune/defence pathways and competition for the host as a resource; for instance, infection with parasite 1 may enhance or reduce susceptibility to infection by parasite 2; the effects may (or may not) be symmetric.
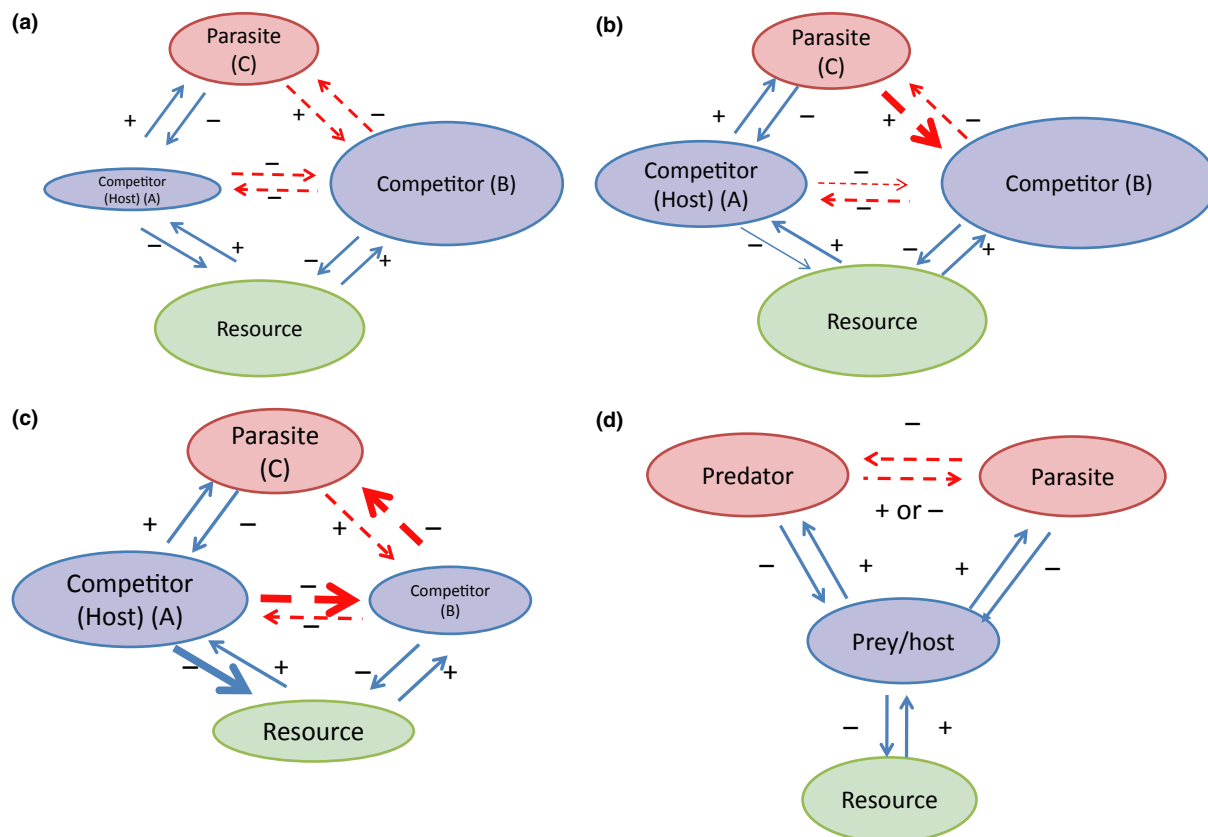
Fig. 2. Density- and trait-mediated indirect effects on competition. The size of the ovals depicts the immediate impact of the interaction on population density. Changes in arrow thickness indicate trait-mediated effects. Signs on arrows as in Fig. 1. (a) Density-mediated indirect effects on competition. The parasite causes mortality of the host (competitor/host A). As a result, competitor A consumes less resource, releasing B from competition. (b) Trait-mediated indirect effects on competition. The parasite causes no direct mortality of the host, so there is no immediate change in population density of host/competitor A. However, trait-mediated effects of the parasite lead to reduced per capita consumption by the host and hence reduce competition on B. The trait-mediated effects of the parasite are of the same sign as density-mediated effects and hence lead to similar patterns. (c) Trait-mediated indirect effects on competition. Here, the parasite increases the per capita impact of host A on the resource and hence its competitive impact on B. Hence, the sign of indirect effects between parasite and competitor B will be determined by the balance of density- and trait-mediated effects. (d) Indirect effects of parasite on predator–prey interactions. The parasite may decrease prey available to the predator through host (prey) mortality (a density-mediated effect) or may increase the vulnerability of the host (prey) to predation (a trait-mediated effect).

interactions), examining these interactions in the context of key invasion processes: enemy release, biotic resistance, parasite-mediated competition, apparent competition and consumer–resource interactions. We then consider host-mediated indirect effects on interactions between parasites within individual hosts with respect to immune responses and resource supply. We conclude by proposing future directions for this growing area of invasion biology.

Indirect effects of parasites on potential competitors

Parasites can theoretically induce indirect interactions in ecological communities at the same trophic level via effects on competing species (parasite-mediated competition Bowers & Turner 1997; Greenman & Hudson 1999) or by inducing competition-like indirect interactions between species that would not otherwise interact at all (apparent competition; Holt 1977; Holt & Pickering 1985). These general theoretical papers demonstrate that the indirect

effects of parasites can exert powerful forces on community composition, facilitating coexistence or promoting exclusion. In the context of biological invasions, indirect effects may also result from the absence of parasites in the introduced species (enemy release; Torchin *et al.* 2003) or, conversely, from the presence of parasites native to the novel habitat that can infect the introduced species (biotic resistance; Levine, Adler & Yelenik 2004). We discuss these processes below with reference to plant and animal systems. It should be noted that most of the theoretical insight in this area is concerned with density-mediated indirect effects; fewer models have considered trait-mediated effects although there is ample empirical evidence of their likely importance, making it a promising direction for future research.

ENEMY RELEASE AND BIOTIC RESISTANCE

The enemy release hypothesis posits that introduced species escape their natural enemies, including parasites

(Torchin, Lafferty & Kuris 2002; Torchin *et al.* 2003; Mitchell & Power 2003). Enemy release may lead to an absolute improvement in performance relative to that in the native range and may also result in an increased (relative) competitive advantage against native species that harbour their own parasites. Following enemy release, a reallocation of resources from defence against parasites to other traits can potentially enhance invaders' performance (the evolution of increased competitive ability hypothesis; Blossey & Notzold 1995). While studies suggest that populations of introduced plants (Mitchell & Power 2003) and animals (Torchin *et al.* 2003) are generally less parasitized compared to populations in their native range and that negative feedback from soil organisms also tends to be reduced or reversed in a plant's invaded range (Inderjit & van der Putten 2010), fewer studies examine the effect of this release on an invader's demographical performance. For instance, while invasive North American plants have escaped many of their floral and foliar parasites in Europe, some evidence suggests that this has not contributed substantially to their geographical spread (van Kleunen & Fischer 2009). These issues are more fully reviewed elsewhere (Torchin & Mitchell 2004; Inderjit & Putten 2010), and the challenge remains in translating parasite release into demographical release of the invader. Some insight can be gained from theoretical work. For example, Drake (2003) demonstrates that as the probability of escape from parasites will depend on the size of the founder population, successful establishment for introduced species will be the result of a trade-off over founder population size (with larger initial populations potentially avoiding Allee effects or genetic bottlenecks, but more likely to harbour parasites). Ecological genetics may provide the tools to allow us to investigate the role of multiple infections in enemy release (Roy & Lawson Handley 2012) and may also provide insight into founder population demographics.

The reverse of enemy release occurs when native species harbour parasites that can also infect introduced species, a form of biotic resistance (Levine, Adler & Yelenik 2004). If introduced species are more severely affected by native parasites, this may increase the native species' (relative) competitive advantage against the invader. For example, attempts to introduce eastern white pine, *Pinus strobus*, into Europe have failed because of attacks by the native blister rust *Cronartium ribicola*, which is sustained by more tolerant indigenous European pine hosts (Harper 1977). In animal systems too, some invasions may fail because of native parasites that reduce the fitness of the invader and prevent its establishment (Ricklefs 2010). However, failed invasions are often missed, and so this plausible process is not well-studied.

PARASITE-MEDIATED COMPETITION

Parasites may affect competitive dynamics between native and introduced animals and plants (Alexander & Holt 1998) through density and trait effects (Hatcher, Dick & Dunn 2006). General theoretical models of parasite-mediated competition have provided insight into the role of shared parasites in shaping communities of competing species (Yan 1996; Bowers & Turner 1997; Greenman & Hudson 1999). Both shared and specialist (infecting a single host species) parasites can influence community composition.

In these models, parasites are predicted to enhance the range of conditions leading to coexistence if, for example, superior competitors are more heavily impacted by the parasite. But parasites could also speed the rate of replacement if inferior competitors are more adversely affected. In the case of shared parasitism, parasite spillover and spillback between host populations is key to understanding population dynamic outcomes. The terms spillover and spillback describe transmission of a parasite from a reservoir host species; in spillover, the reservoir host is the original host, and in spillback, a novel host species acts as the reservoir for parasite transmission (Daszak, Cunningham & Hyatt 2000; Hatcher, Dick & Dunn 2012b). Biological invasions lead to novel opportunities for cross-species transmission, and spillover and spillback are anticipated to be common processes (Kelly *et al.* 2009).

Parasites that are co-introduced with the host always have a direct cost to the invader, but may also have indirect benefits to the invader if native competitors in the new range are more susceptible or are more adversely affected by the introduced parasite. Such parasites can be seen as novel weapons used by the invader against the native competitor (Price *et al.* 1986), analogous to the novel biochemical weapons that have been proposed to facilitate the success of invasive plants (e.g. Callaway & Ridenour 2004). For example, in the UK, the invasive grey squirrel *Sciurus carolinensis* was found to replace the native competitor, the red squirrel *S. vulgaris*. Spillover of a pox virus from the grey squirrel causes high mortality in the native species, speeding up its replacement by the invader (Tompkins, White & Boots 2003; Strauss, White & Boots 2012). There are a number of other empirical examples of parasite-mediated competition in invaded systems (Table S1). For example, spread of the invasive Asian cyprinid fish *Pseudorasbora parva* throughout Europe is facilitated by a co-introduced intracellular eukaryotic parasite that causes mortality of the native competitor cyprinid *Leucaspius delineatus* (Gozlan *et al.* 2005).

Native parasites can also mediate competition between native and introduced hosts. For example, in vineyards in the Central Valley of California, the introduced variegated leafhopper *Erythroneura variabilis* is excluding the native grape leafhopper *E. elegantula*. The two species compete, but interspecific competition and intraspecific competition are equivalent in strength (Settle & Wilson 1990). The reason the invasion proceeds is that the invader acts as a spillback reservoir, sustaining a native parasitoid *Anagrus epos*, but the parasitoid preferentially attacks the native host. This tilts the competitive balance towards the invader and facilitates its invasion (Settle & Wilson 1990). While

parasites can alter competitive interactions between host species, conversely competitive interactions can alter the impact of parasites on hosts. Species in an invaded community may, for instance, suffer greater exposure to parasites because of competition. For example, competition from invasive trout *Salmo trutta* in New Zealand has displaced native *Galaxias* fish into poor-quality refuges of low flow and higher temperature, which may increase exposure to trematode parasites (Poulin *et al.* 2011).

In the aforementioned examples, parasites influenced competition between native and invasive species by causing differential mortality of one competitor, that is, via density-mediated indirect effects (See Table S1, Fig. 2a). Parasites can also alter the outcome of competition through trait-mediated effects, which ultimately alter the competitive abilities of infected hosts (Fig. 2b,c). For example, the Mediterranean marine mussel *Mytilus galloprovincialis* was introduced to South Africa where it competes with the native mussel *Perna perna*. Two native trematode species infect the native mussel, but not the invader. These parasites have sublethal effects; one reduces host growth, while the second causes castration, reduced adductor muscle strength and water loss during low tide. Hence, these parasites have both density- and trait-mediated effects on their host that combine to reduce the ability of the native mussel to compete for space with the invader, and ultimately, parasitism may contribute to the invasion success of the Mediterranean mussel (Calvo-Ugarteburu & McQuaid 1998). Such alterations in individual growth rates because of parasitism are likely to influence competitive outcomes in animals wherever body size influences relative competitive abilities. Similarly, the outcome of competition between native (*Solenopsis geminata*) and invasive (*S. invicta*) ants in North America is modified by the native phorid fly *Pseudacteon browni* (Morrison 1999). Phorid flies are parasitoids of ants that develop in the head capsule, leading to decapitation. When phorid flies were present, the native ant adopted defensive behaviours resulting in a 50% decline in foraging rates and hence reduced competitive abilities against the invasive ant. This type of indirect effect has been exploited for biological control of invasive *S. invicta*. Phorid flies (*Pseudacteon tricuspis*) from *S. invicta*'s native range have been introduced to North America, where they induce defensive behaviour of the invasive species and thus reduce its ability to compete with the native ant *Forelius mccooki* (Mehdiabadi, Kawazoe & Gilbert 2004).

Parasites associated with invaders can also reduce the competitive ability of natives, facilitating invasion. For instance, the nearly complete replacement of native grasses in much of California with invasive annual grasses has been facilitated by barley yellow dwarf viruses (Malmstrom *et al.* 2005; Borer *et al.* 2007). These parasites cause both density- and trait-mediated effects and suppress native perennial bunchgrasses more severely than invaders, reducing growth rates of natives and thereby diminishing their ability to competitively exclude the invaders. Other classes of parasites may have similar effects. Root-borne parasites of invasive plants may indirectly enhance their competitive ability through negative impacts on native competitors. For instance, *Fusarium semitectum* accumulating on the roots of the invasive weed *Chromolaena odorata* reduced growth of native plants (Mangla, Inderjit & Callaway 2008). Likewise, spillover of a fungal seed pathogen (*Pyrenophora semeniperda*) from the invasive grass *Bromus tectorum* in western North America may reduce seed viability of native competitors (Beckstead *et al.* 2010).

Not all fungal infections are consistently pathogenic, and whether or not mycorrhizae and other symbionts are mutualists or parasites can be influenced by the resource state of their host (Hochberg *et al.* 2000). Both endophytes (Schardl, Leuchtmann & Spienng 2004) and arbuscular mycorrhizae (Pringle *et al.* 2009) range along a continuum from antagonistic to mutualistic interactions, but are typically beneficial in some host species, potentially increasing the ability of invasive hosts to outcompete native plants by improving resistance to herbivores and parasites, improving nutrient uptake and water conservation, and other effects. For example, a field experiment with the invasive grass *Lolium arundinaceum* found that endophyte-infected grasses were much more successful at suppressing growth and establishment of native trees (Rudgers *et al.* 2007). Similarly, mycorrhizae enhanced the ability of the invasive *Centaurea maculosa* to outcompete the native grass *Festuca idahoensis* (Marler, Zabinski & Callaway 1999). Conversely, invaders that interfere with natives' mutualists may gain a competitive advantage. An example is the nonmycorrhizal species, Garlic Mustard (*Alliaria petiolata*), which produces root exudates that inhibit mycorrhizae of native plants in North America (Stinson *et al.* 2006), potentially contributing both to its invasiveness and to its impacts on forest communities.

APPARENT COMPETITION

In the context of parasitism, apparent competition is predicted to occur when two species that do not otherwise interact both host the same parasite species (Holt & Pickering 1985). As both host species are a resource for the parasite, population density increases in either host lead to reductions in the other, via the (density-mediated) negative effects of the parasite. Hence, each host species acts as a reservoir for parasite transmission to the other species. Apparent competition can theoretically lead to the elimination of one host (Holt 1977), indirectly coupling the dynamics of host species with different habitat or resource requirements (Alexander & Holt 1998). For instance, infection with barley yellow dwarf viruses alters the composition of experimental annual grass communities (composed of species invasive in the US). Controlled experiments found no evidence for direct competition between the grasses, with the results consistent with apparent competition mediated by barley yellow dwarf viruses and its aphid

vectors, shared across grass species (Power & Mitchell 2004). Similarly, apparent competition between animal hosts may be mediated by parasites. Declines in the native UK grey partridge *Perdix perdix* have been attributed to apparent competition with managed pheasants *Phasianus colchicus*, mediated by the nematode *Heterakis gallinarum*. Although there may also be some interspecific competition between the birds, models predicted that the parasite cannot be maintained in partridge populations but will be maintained in pheasant populations with spillover leading to eventual partridge extirpation (Tompkins *et al.* 2000).

Spillover of parasites from invasive species may also be mediated by environmental factors. For example, chytridiomycosis (caused by the fungus *Batrachochytrium dendrobatidis*), which is contributing to global amphibian declines, has been spread by introduced amphibians including the American bullfrog *Rana catesbeiana* that is asymptomatic and acts as a reservoir. Disease spread and impacts can also be exacerbated by transport, temperature and precipitation (Lips *et al.* 2008). The importance of environmental factors in mediating trait effects is an area that demands further investigation.

Indirect effects of parasites in consumer–resource interactions

Consumer–resource interactions may be influenced by parasites through density-mediated and trait-mediated indirect effects, and general theoretical models have shown that parasites can have a diverse range of effects in these systems. These can be characterized by which species is parasitized: we can distinguish parasites of the resource species, parasites of consumers, and parasites shared by both resource and consumer species. This latter case covers systems involving trophic transmission (where predator and prey are host to successive developmental stages of the parasite) and cases of intraguild predation (where a parasite is shared between predator and prey that occurs within the same feeding guild). Examples of each of these interaction scenarios in the context of biological invasions are discussed below. Expected impacts of parasitism are highly contingent on the type of interaction under consideration, but can be broadly mapped on to predictions for basic consumer–resource theory (Hatcher & Dunn 2011). For instance, parasites of resource species may compete with predators/herbivores, so models of this class of interactions bear similarity to models of interspecific competition, whereas parasites of predators may exert top-down control on predator populations, resulting in systems akin to linear food chains. As with competition models discussed above, most theoretical models have concentrated on the density-mediated indirect effects of parasitism, although some models of parasites of prey incorporate trait-mediated effects, in particular allowing for increased vulnerability to predation of infected individuals (e.g. Hudson, Dobson & Newborn 1992; Hethcote *et al.* 2004; Fig. 2d).

PARASITES OF RESOURCE ORGANISMS

Where plants are attacked by both parasites and herbivores, the net effect on the invaded community depends on the extent to which herbivores and parasites compete exploitatively (density-mediated effects), adjusting for any facilitative or inhibitory (trait) effects of the consumers on each other. Similarly, predator–prey interactions may be mediated by parasite-induced mortality of the prey (a density-mediated effect; Fig. 2d) and through parasite-induced reduction in predator escape/avoidance abilities (a trait-mediated effect; Fig. 2d). Parasites and predators can at times compete exploitatively for shared resources resulting in combined regulatory impact via their density-mediated effects on the host/prey. For instance, times-series analysis of northern forest populations in the USA suggests that the invasive gypsy moth *Lymantria dispar* is regulated at lower densities by generalist predators, but when predators become satiated and moth populations reach higher densities, regulation by a baculovirus dominates (Dwyer, Dushoff & Yee 2004). Other nonlethal effects of parasitism, such as acquired immunity to infection, alter predicted predation–parasitism dynamics. For instance, predators, by disproportionately removing infected prey, may help maintain populations at lower levels of infection (the healthy herds hypothesis; Packer *et al.* 2003). However, if prey acquire immunity on recovery from infection and are regulated by strong density dependence, the inverse relationship may hold (Roy & Holt 2008). The role of such complex interactions in invasion scenarios has yet to be elucidated; existing theory, moreover, focuses on how predation influences equilibrial prevalence of infections, and it would be valuable to examine non-equilibrium dynamics, which are relevant to invasions.

Parasites of resources can have indirect effects that propagate up through the trophic levels. For example, outbreaks of the invasive myxomatosis virus and rabbit haemorrhagic disease virus in Spain led to European rabbit (*Oryctolagus cuniculus*) mortality, and the consequent reduction in the abundance of rabbits led to the decline of populations of two endangered predators, the Iberian Lynx (*Lynx pardinus*) and the imperial eagle (*Aquila adalberti*) (Ferrer & Negro 2004). Here, the lynx, eagle and viruses all competed for a shared resource, the rabbit. Similarly, density-dependent effects of parasites on plants can propagate through the trophic levels. For example, several lepidopteran species that specialized on American chestnut (*Castanea dentata*) became extinct when the epidemic of the invasive fungus, chestnut blight (*Cryphonectria parasitica*), led to the near extinction of their host (Dunn 2005). This is a classic example of exploitative competition and also demonstrates how parasites can elicit powerful density-mediated indirect effects.

The indirect effects of parasites on both competitive and consumer–resource interactions can be further complicated by the bottom-up effects of resources (for the host) on parasitism. Smith (2007) reviews evidence from a wide range

of plant and animal systems that changes in resource supply to hosts can have a profound impact on infectious disease dynamics. One possibility is that resource enrichment may 'feed' the pathogen. Nitrogen fertilization for instance can increase the severity of onion blight (caused by *Xanthomonas axonopodis*). An alternative possibility is that increased resource supply can improve the defensive capabilities of the host. Fertilizing with nitrogen or phosphate, for example, substantially reduces infection rates in take-all, a root disease of cereals and grasses caused by the fungal pathogen *Gaeumannomyces graminis*. In an invasion context, nitrogen fertilization in a tallgrass prairie increased fungal infection in the native grass *Andropogon gerardii*, but not its invasive congener *A. bladhii*, thereby accentuating enemy release (Han *et al.* 2008). Similarly, among 243 European plant species, those adapted to resource-rich environments hosted the most leaf pathogens in their native European range and escaped the most leaf pathogens upon introduction to the United States, suggesting that resource effects on host–parasite interactions can be common and can change with introduction (Blumenthal *et al.* 2009). Such bottom-up effects of resources are likely to be important in determining the strength of many direct and indirect effects of parasites. Many invasions, after all, occur in disturbed, anthropogenic landscapes, where successional processes often lead to a flush of resources.

Parasites and predators may also interact via trait-mediated indirect effects, and this can lead to facilitation rather than competition. For instance, in coastal New England, predation by the invasive green crab (*Carcinus maenas*) has selected for shell thickening in co-occurring native whelks. However, a native spionid polychaete worm *Polydora spp.* has trait-mediated indirect effects on this interaction. By weakening the structural integrity of the shell of infected whelks, this worm increases whelk vulnerability to predation, making larger individuals susceptible to predation by the invasive crab (Fisher 2010). Hence, the worm broadens the size range of prey resources that the introduced crab utilizes, magnifying both the ecological impact of the crab and success in its novel range. The importance of such synergistic interactions between parasitism and predation has been noted for other systems, but its importance in biological invasion warrants further study.

Similarly, parasites of plants may mediate attack by herbivores. For example, invasion of the dipteran *Chymomyza amoena* has been facilitated by seed-boring insect parasites that damage the fruit of a number of broad-leaved tree species hosts, allowing the dipteran to oviposit on the structurally modified fruit (Band, Bachli & Band 2005). Swope & Parker (2010) observed both synergy and interference between two enemies used in the biocontrol of the invasive yellow starthistle (*Centaurea solstitialis*): the recently introduced fungus *Puccinia jaceae f.s. solstitialis* and a seed-feeding weevil *Eustenopus villosus*. Infection by the fungus increased the impact of bud feeding by the adult weevils, but reduced the impact of seed feeding by larval weevils by influencing either plant quality or defence. Conversely, invasive herbivores can exacerbate the effects of parasites on plant hosts, both by serving as a vector, transmitting plant parasites, and by causing mechanical damage to plants (a trait-mediated effect), such that infection is increased. Reflecting this complexity, invaded communities exhibit a variety of consumer interactions, ranging from additive, through facilitative and even synergistic. For example, the ongoing population decline of American beech (*Fagus grandifolia*) caused by invasive beech bark disease (*Neonectria* spp) is exacerbated by the invasive scale insect *Cryptococcus fagisuga* that attacks the tree, creating injuries that facilitate fungal infection (Kenis *et al.* 2009). Similarly, the invasive fungal agents of Dutch elm disease *Ophiostoma ulmi* and *O. novo-ulmi*, which destroyed over half the native elm (*Ulmus americana*) trees in North America, are transmitted principally by the burrowing activity of the invasive European elm bark beetle (*Scolytus multistriatus*) (Kenis *et al.* 2009). Such facilitation of parasites by herbivores can be utilized in biocontrol. For example, two common parasitic fungal species, *Rhizoctonia solani* and *Fusarium oxysporum,* have only minor effects on the invasive spurge *Euphorbia esula* when applied in the absence of a herbivore, but lead to substantial mortality when applied in combination with flea beetles (*Aphthona* spp.) that facilitate fungal infection by damaging the plant roots (Caesar 2003).

PARASITES OF CONSUMERS

Parasites of predators (or herbivores) effectively act as top predators, in which case the parasite can potentially limit the predator/herbivore population density releasing the prey/plant population from consumption in a variant of a classic trophic cascade (Table S1). For instance, the massive decline in abundance of rabbits (*Oryctolagus cuniculus*, themselves introduced by the Normans) in Britain following the introduction of myxoma virus for biocontrol in the 1950s resulted in a wave of regeneration by oaks (*Quercus robur*) (Dobson & Crawley 1994). These cascading effects can be broad reaching and long lived. For instance, the accidental introduction of canine parvovirus to wolves (*Canis lupus*) on Isle Royale, USA, has resulted in a long-standing reduction in the wolf population, substantially reducing the regulatory impact of wolves on moose (*Alces alces*) (Wilmers *et al.* 2006). This shift in the regulation of moose from top-down (predator) to bottom-up (resource) is likely in turn to have influenced plant communities. Parasite removal can have similar long-lasting effects; vaccination of cattle for the invasive viral disease rinderpest in the 1960s halted spillover of the disease from cattle into wildebeest (*Connochaetes taurinus*), allowing the Serengeti wildebeest population to increase. This initiated a trophic cascade as the increased grazing of wildebeest resulted in the reduction in fuel loads (grass), ultimately leading to a decline in fire and an increase in tree cover (Holdo *et al.* 2009).

If parasites of herbivores result in decreased plant damage, natural selection may favour reduced investment in plant defensive traits if this results in a concomitant increase in plant fitness and demographical growth. For example, furanocoumarin produced by the invasive parsnip (*Pastinaca sativa*) deters against herbivory by the parsnip moth (*Depressaria sativa*). Widespread infection of *D. sativa* by a parasitoid, *Copidosoma sosares,* suppresses selection for such sophisticated and energetically costly chemical defences (Ode *et al.* 2004) and may therefore increase the reproductive rate and invasion ability of the parsnip; such hypotheses need further testing.

Trait-mediated indirect effects of parasites may also influence the impact of predators on their prey (Fig. 2b–d). Both increased and decreased foraging rates have been documented for infected consumers (Table S1). For example, in Ireland, replacement of the native amphipod *Gammarus duebeni celticus* by the invasive predator *Gammarus pulex* has led to reduced freshwater macroinvertebrate diversity and biomass (Kelly *et al.* 2006). Surprisingly, *G. pulex* that were infected by a native acanthocephalan parasite *Echinorhynchus truttae* consumed 30% more prey than did uninfected individuals, reflecting the metabolic demands and manipulative effect of the parasite (infected individuals were more active). Hence, the parasite may increase the impact of this invasive predator both on its prey and on its competitors (Dick *et al.* 2010). Similarly, in North America, the invasive Asian mud snail *Batillaria attramentaria* is out-competing the native California horn snail *Cerithidea californica* (Byers 2000). The invasive mud snail has been co-introduced with its trematode *Cercaria batillariae*, which induces castration, gigantism and shifts resource use of snails in the native range (Miura *et al.* 2006). This parasite is likely to alter the impact of the invader both on its resources and on the native competitors where it is introduced (Torchin, Byers & Huspeni 2005).

Alternatively, parasites may decrease the resource intake of their hosts (Fig. 2d, Table S1). For example, the predatory strength of the native white-clawed crayfish (*Austropotamobius pallipes*) is reduced by 30% in individuals infected with porcelain disease (caused by the microsporidia *Thelohania contejeani*), reducing both its impact on its invertebrate prey, and its ability to compete with the larger invasive signal crayfish (*Pacifastacus leniusculus*; Haddaway *et al.* 2012). Similarly, feeding rates of the invasive intertidal snail *Littorina littorea* are reduced by 40% in individuals infected by co-introduced trematode *Cryptocotyle lingua*. In New England, where the snail is the dominant intertidal herbivore, the per cent cover of edible algae was higher and the algal community composition was different in experimental enclosures with infected snails than in enclosures with uninfected snails (Wood *et al.* 2007). As noted above, changes in the resource state of hosts can influence parasite survival and reproduction, so impacts on resource intake rates can have secondary effects on parasite population dynamics.

PARASITES OF THE RESOURCE AND CONSUMER

In the context of predator–prey interactions, trait-mediated indirect effects (Fig. 2b–d) are frequently found when trophically transmitted parasites manipulate the behaviour of their intermediate host making it more susceptible to predation by the definitive host (Moore 2002). For example, the invasive American brine shrimp *Artemia franciscana* has acquired cestode parasites from native congener shrimps *A. parthenogenetica* and *A. salina* in its new Mediterranean range. However, while these parasites cause reversed phototaxis and colour change in native brine shrimps, this parasite manipulation (which increases likelihood of predation by bird definitive hosts) does not occur in the invader (Georgiev *et al.* 2007). As well as modifying predator–prey outcomes, this differential behavioural modification of native and invasive shrimps is likely to decrease competition between them by both reducing the abundance of the native species and by causing spatial segregation of the two species. Hence, by modifying both predatory and competitive interactions, the parasite may contribute to the rapid invasion. Similarly, in France, a native acanthocephalan parasite *Pomphorhynchus laevis* increases the vulnerability of the native amphipod host *Gammarus pulex* to fish predation but does not manipulate the behaviour of the invasive amphipod *G. roeseli* (Tain, Perrot-Minnot & Cezilly 2007). The net effects of parasitic manipulators on the predator may be positive, negative or neutral, depending on the balance of how parasites influence prey availability and resource acquisition vs. the impact of the direct effect of the trophically acquired infection on the predator (Lafferty 1992). Likewise, the net effect of predation on the population of the manipulative parasite will depend on the relative frequency of those acts of consumption that lead to trophic transfer of the parasite, compared to those where the parasite and its host are eaten by a nonhost predator, resulting in mortality for both the parasite and host.

Further invasion scenarios involving parasites of both consumer and resource species come from studies of intraguild predation, a predator–prey relationship where both parties also potentially compete for resources (Polis, Myers & Holt 1989). Intraguild predation combines aspects of consumer–resource and competitive interactions and frequently occurs in invaded communities; in many cases, intraguild predators and prey are closely related species, vulnerable to the same parasites. Many invasive species are strong intraguild predators, and invasive species that both compete with and eat native species are a serious threat to the long-term persistence of native populations (Hall 2011). Theory shows that parasites can substantially alter population dynamic outcomes for intraguild predation, in some cases enabling native persistence, but in others hastening its demise (Hatcher, Dick & Dunn 2008). The importance of parasites in intraguild predation is illustrated in an aquatic invasion in Ireland. Competition and intraguild predation occur between the native amphipod *Gammarus duebeni celticus* and three invasive amphipods.

The microsporidian parasite *Pleistophora mulleri* is specific to the native amphipod. It has no direct effect on host survival, but may facilitate invasions as a result of trait-mediated indirect effects. The parasite causes reduced motility, and parasitized individuals showed a reduced ability to predate the smaller invading species and were more vulnerable to intraguild predation by the dominant invader *G. pulex* (MacNeil *et al.* 2003a). A second parasite, the acanthocephalan *Echinorhynchus truttae*, also modifies intraguild predation, in this case reducing the impact of the invasive *G. pulex* on native species. Parasitized *G. pulex* show reduced intraguild predation of the native *G. duebeni celticus*, which may slow the displacement of the native species (MacNeil *et al.* 2003b). The importance of intraguild predation in invasions and biological control has become increasingly apparent (Hall 2011; Hatcher & Dunn 2011) and promises to be an area of fruitful research.

Host-mediated parasite–parasite interactions

The majority of indirect effects demonstrated in invasion ecology occur at the level of host populations and communities. Increasingly, it is recognized, however, that parasites can interact within individual hosts. Individual hosts are typically infected by multiple parasite species (termed coinfection) that are subject to complex indirect and direct interactions with each other and the host, paralleling those found in free-living communities (e.g. Lello *et al.* 2004). A new infection within an individual host is analogous to the establishment phase of an introduced species within a community, and we suggest that coinfection–host interactions generate a range of indirect effects comparable to those in invasion ecology.

Parasites infecting the same individual can interact both through density-mediated effects, such as competition for resources and space, and through trait-mediated indirect effects via the host's immune response (Lello *et al.* 2004; Graham 2008), leading to changes in host physiology, parasite transmission and virulence evolution. Host-mediated interactions are not limited to vertebrates; plants also have induced defences in some ways analogous to processes in vertebrate immune responses. Interactions between parasites (or herbivores) of individual plants are channelled through plant biochemical and metabolic defence pathways; broadly, attack by wound-inducing herbivores and parasites stimulate the jasmonic acid (JA) pathway, whereas biotrophic pathogens or piercing and sucking insects (e.g. aphids) stimulate salicylic acid (SA) production. These, and other, chemical cascades initiate changes in plant growth, resource allocation, gene expression and secondary metabolite production, mitigating the current attack and perhaps protecting the plant against a broad spectrum of microbes and future infection, a phenomenon termed 'systemic-acquired resistance'; analogous resistance to herbivores is termed 'induced resistance' (Stout, Thaler & Thomma 2006).

The crosstalk generated between parasites may initiate either top-down or bottom-up effects, depending on both the host's immune status/defence pathway and the composition of the parasite community. Predicting the impact of immune-mediated interspecific interactions on within-host parasite dynamics is not trivial and suffers from the same complexities as do interactions in other communities; community ecology modules can provide a mechanistic framework for understanding immune-mediated parasite interactions (Fenton & Perkins 2010). Dynamic models of such interactions in effect view host–parasite systems as metapopulations, where each individual host is a patch that can contain a multiplicity of interacting parasites, and the patches are coupled by dispersal and colonization (i.e. parasite transmission). The outcome of defence-mediated interactions is often a function of the dichotomous response of certain immune pathways and biasing of immunity towards specific pathways after priming. For example, vertebrates typically mount a T-helper type 1 (Th1) response against microparasites (e.g. viruses and bacteria) and Th2 responses against macroparasites (e.g. helminths and ectoparasites). These two responses are often antagonistic, leading to a trade-off in allocation of host resources, with indirect effects on the parasite community (Sears *et al.* 2011).

Allocation trade-offs between different defensive pathways in plants can also lead to crosstalk, analogous with the Th1-Th2 pathway of vertebrate immunity, with stimulation of one pathway inhibiting another. Immune crosstalk has been shown to generate variation in parasite establishment, growth and virulence. For instance, infection of T cells and macrophages by HIV directly impairs host immunocompetence; as a result, hosts suffer increased virulence from a wide range of other parasites such as TB, malaria and *Toxoplasma gondii* as observed in both humans and wildlife (Ezenwa *et al.* 2010). As another example, the cabbage moth *Mamestra brassicae* harbours a persistent asymptomatic infection of baculovirus that is only triggered into a lethal overt state by coinfection with a second, different species of baculovirus (Burden *et al.* 2003). Coinfection thus may synergize to cause increased host mortality, such that the coinfected individuals are removed from the infectious population (Marshall *et al.* 1999; Lass *et al.* in press). Alternatively, coinfection may increase the infectious output of an individual, such as during the 2003 Severe Acute Respiratory Syndrome (SARS) epidemic where a 'vital few' individuals were responsible for the majority of infections, the 'super-spreaders'. Putatively, the super-spreaders were not only those individuals with high contact rates (Hatcher, Dick & Dunn 2012b), but those that were shedding large amounts of virus because of an altered immune status arising from coinfection with other respiratory bacterial infections (Bassetti, Bischoff & Sheretz 2005).

Plant hosts also mediate interactions between parasites/herbivores and their consumers via the production of volatile or defensive compounds, potentially resulting in defensive crosstalk. For instance, maize (*Zea mays*) coinfected

with Western corn rootworm (*Diabrotica virgifera*) and the cotton leafworm (*Spodoptera littoralis*) released less root volatiles than singly infected plants, attracting fewer specialist parasites (the parasitoid *Cotesia marginiventris* and the nematode *Heterorhabditis megidis*; Rasmann & Turlings 2007). Alternatively, downstream overlap in the chemical cascades or trait modifications can result in defence stimulation by one class of parasites being effective against a different class (this effect was found in about one-third of experimental studies; a similar proportion to those where negative crosstalk was observed; Stout, Thaler & Thomma 2006). For instance, insect herbivores and fungal pathogens often may interact through alterations in host nutritional quality or defence (Hatcher 1995). As another example, in the tomato system, *Pseudomonas syringae* infection induces jasmonic and salicylic acids and protease inhibitors, reducing the growth rate of larvae of the invasive beet armyworm *Spodoptera exigua*, while infection with tobacco mosaic virus induces only salicylate, resulting in increased growth of *S. exigua* but reduced colonization by other herbivores (aphids) (Thaler, Agrawal & Halitschke 2010). Similar negative crosstalk is observed in parasites of vertebrates, but here, outcomes of the interactions are broadly predictable. For example, a meta-analysis of studies where vertebrates were coinfected with helminths and microparasites found negative crosstalk, such that coinfection reduced microparasite density when helminths and microparasite were directly competing for resources, for example host red blood cells (Graham 2008). Negative resource-based interactions can also occur: again in the tomato system, cultivated tomato infected with the parasitic plant dodder *Cuscuta pentagona* is less resistant to invasive beet armyworm attack; however, dodder-infected plants are of lower nutritional quality, resulting in reduced growth rates for armyworm caterpillars on coinfected plants (Runyon, Mescher & de Moraes 2008). Such host-mediated indirect interactions are very common in plants (Ohgushi *et al.* in press), and while few studies have explicitly considered their importance for invasions, many have used non-native or weedy plants as model species; we posit that further consideration of such effects in the context of biological invasions will be illuminating. Similar host-mediated interactions occur in vertebrates, where helminth-induced suppression of elements of host immunity (specifically the cytokine interferon-gamma) leads to increased microparasite density (Graham 2008), suggesting that microparasite population growth will be most explosive because of immune-mediated indirect effects.

The general literature on evolution of virulence suggests that coinfection can select for higher virulence (May & Nowak 1995). However, coinfection with different parasite species could also potentially select for shifts in parasite traits that enhance within-host competitive abilities (e.g. de Roode *et al.* 2005). These indirect effects of coinfection have broad-ranging implications for the use of pathogens as biocontrol agents and in parasite-specific disease control (e.g. vaccination). Given the regulating indirect effects of parasites upon one another via host immunity, careful consideration must be given when considering the treatment of a specific parasite. As such, there is merit in trying to elucidate the outcome of coinfections.

Finally, invasive hosts may themselves exhibit adaptive immunological phenotypes that indirectly make them more competitive against native conspecifics. Encounters with novel parasites may induce overly vigorous inflammatory responses, which can lead to severe or even mortal immunopathology (e.g. cytokine storm; Sears *et al.* 2011). Lee & Klasing (2004) suggest that successful invaders should dampen Th1 inflammatory responses, as compared to native hosts, although the field requires further empirical testing to ascertain consistent patterns (see also White & Perkins 2012).

Conclusions and future directions

The potential for parasites to mediate indirect effects has been recognized for some time (Price *et al.* 1986). Such effects are not only widespread but may be strong, as shown here with particular regard to biological invasions. Furthermore, the discrimination between two major types of indirect interaction (density and trait mediated; Abrams 1995) has allowed a greater appreciation of the diverse roles that parasites can play in structuring ecological communities. We demonstrate that both density-mediated and trait-mediated indirect effects of parasites may be important in influencing invasion success as well as the impact on the invaded community.

Biological invasions represent a global challenge, affecting biodiversity, community structure and ecosystem processes across a range of ecosystems. Such invasions bring together novel species combinations, giving scope for many novel interactions. We show here that parasites can be pivotal components of this interaction structure, producing important and varied indirect effects, shaping native–invader interactions in diverse taxa and ecosystems, at all trophic levels.

Several questions remain concerning the indirect effects of parasitism. We have shown here that effects propagate both within and between trophic levels, and further analysis may reveal differences in the patterns generated by such horizontal or vertical propagation within communities. Empirical research in this area needs to proceed in concert with theoretical approaches, for both community-level (Oghushi *et al.* in press) and within-host (Holt & Dobson 2006) processes. Understanding these patterns is important for community ecology generally and would aid risk assessment for biological invasion and control. Indirect effects of, or on control agents underlie several important issues in biocontrol including biological subsidy, multiple enemy approaches and nontarget effects (Hatcher & Dunn 2011). Our overview has focused on the interplay of parasites and interspecific interactions at a local scale. Yet, community structure often reflects processes playing out at larger spatial scales in meta-communities (Holyoak, Lei-

bold & Holt 2005) comprised of communities coupled by dispersal. Parasites can potentially modify traits that influence dispersal rates and thus mechanisms for coexistence such as colonization-competition trade-offs. This is a largely unexplored dimension of parasite ecology, but one that may be particularly pertinent to invasions.

Interactions between parasites and invaders also have the potential to result in unexpected and fascinating outcomes for humans. For example, the protozoan parasite *Toxoplasma gondii* manipulates the predator avoidance behaviour of its intermediate mammal hosts to enhance trophic transmission to its definitive host, one of the most successful mammalian invaders, the cat (*Felis catus*). Domestication of cats exposes humans to *T. gondii* and a provocative hypothesis is that human personalities can also be altered by this parasite, influencing culture in heavily infected regions (Lafferty 2006). This may be the ultimate trait-mediated indirect effect in human societies, highlighting the need for more research and a better understanding of indirect effects of infection in invaded communities.

To further our understanding of such complex interactions requires crosstalk between ecologists and parasitologists, animal and plant biologists, theoreticians and empirical researchers, and agricultural and conservation practitioners. The scientific and practical pay-off of such collaborations seems likely to be large. The complex nature of indirect interactions may have significant implications for biological invasions (White, Wilson & Clarke 2006), while examples of ecologically significant parasites continue to mount. It seems important not to simply amass examples of the influence of parasites in invasions, but also to gauge the importance of these effects in invasion outcomes more objectively (e.g. Byers & Goldwasser 2001). As the examples in this synthesis indicate, evidence is accumulating that subtle yet important interactions between invaders and parasites may be more the rule than the exception. In some cases (viral diseases of grasses and squirrels, for instance), these impacts may be very strong, yet may require careful observation and study to convincingly demonstrate. The challenge now is to tease apart the relative importance of direct and indirect effects of parasites, and of density and trait effects in determining the fates and impacts of introduced species. Future research should further develop a framework integrating community ecology, evolution and immunology to better understand and manage the spread of invasive species and their diseases in an increasingly connected and changing world.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Examples of direct and indirect effects of parasites in biological invasions.

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