7 Ecological Consequences of Parasite Invasions

David W. Thieltges[1,2]* and M. Anouk Goedknegt[3]
[1]Royal Netherlands Institute for Sea Research (NIOZ), Den Burg, the Netherlands; [2]Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, the Netherlands; [3]Rijkswaterstaat Noord Nederland, Leeuwarden, the Netherlands

Abstract
Invasions of pathogens and parasites can have far-reaching ecological consequences in their recipient ecosystems. In this chapter, we provide a conceptual overview of the various mechanisms underlying these ecological consequences, which we illustrate using examples from the literature. We first describe the different ways invasive parasites can interact with hosts and parasites in invaded ecosystems and then discuss the direct effects of invasive parasites on native and invasive hosts. Following this, we explore the indirect effects of invasive parasites on other species via altering species interactions and identify knock-on effects on the invaded communities and ecosystems. Finally, we highlight that parasite invasions can also affect native parasites, and we identify knowledge gaps and areas for future research.

7.1 Introduction

Biological invasions of free-living species are known to lead to a wide array of ecological consequences for native biodiversity such as altering species interactions and affecting ecosystem functioning (Elton, 1958; Vitousek *et al.*, 1996; Mack *et al.*, 2000; Simberloff *et al.*, 2013). It is increasingly recognized that invasions of pathogens and parasites can also have far-reaching ecological effects in their recipient ecosystems (Daszak *et al.*, 2000; Crowl *et al.*, 2008; Hatcher *et al.*, 2012a; Dunn and Hatcher, 2015; Goedknegt *et al.*, 2016). These either result from direct effects of invasive parasites on native and invasive hosts, as well as on native parasites, or from indirect effects on the surrounding communities that result from initial direct effects. Parasites encompass a large diversity of taxa and life histories, often divided into two major groups: (i) microparasites (often also categorized as pathogens) such as viruses, bacteria and protozoa; and (ii) macroparasites such as helminths and arthropods (Schmid-Hempel, 2011). From an ecological perspective, parasitism is a species interaction (like predation and competition) where one species (the parasite) benefits from the interaction, while the other (the host) suffers (Combes, 2001; Begon *et al.*, 2006). Although by definition parasites exert negative effects on their hosts, not all parasites are disease-causing pathogens in a veterinary sense (i.e. unwanted organismal malfunctioning). In this chapter, we provide a conceptual overview of the various mechanisms and ecological consequences of

*Corresponding author: David.Thieltges@nioz.nl

© CAB International 2023. *Parasites and Biological Invasions* (eds J. Bojko *et al.*)
DOI: 10.1079/9781789248135.0007

how invasive parasites affect hosts and other parasites in invaded ecosystems, which we illustrate using examples from the literature. It is not our intention to provide a comprehensive review of the existing literature, instead we aim to give a synopsis of the key mechanisms underlying the ecological consequences of parasite invasions.

7.2 Interactions of Invasive Parasites in Invaded Ecosystems

There are several ways invasive parasites can interact with hosts and parasites in invaded ecosystems. First, when a parasite species invades an ecosystem, either without (Fig. 7.1a) or with its original host (Fig. 7.1b), it can spill over to native hosts and use them as novel hosts in the invaded ecosystem (parasite spillover; Daszak *et al.*, 2000; Power and Mitchell, 2004; Prenter *et al.*, 2004; Kelly *et al.*, 2009). Due to the naivety of native hosts to the novel parasites, these new infections can lead to particularly strong disease outbreaks and emerging diseases in native hosts (Daszak *et al.*, 2000). Alternatively, in cases where a parasite species invades a new ecosystem together with its invasive host (parasite co-introduction; Lymbery *et al.*, 2014; Fig. 7.1b–e), the invasive parasite can remain solely in its invasive host without spilling over to the native hosts (Fig. 7.1c). It can also happen that invasive hosts become infected by native parasite species from the invaded ecosystem ('parasite acquisition'; Kelly *et al.*, 2009; Poulin *et al.*, 2011; Telfer and Bown, 2012; Fig. 7.1d) and serve as a reservoir from which native parasites can reinfect native hosts ('parasite spillback'; Kelly *et al.*, 2009). Finally, invasive parasites can not only interact with native hosts but also with native parasites after parasite spillover into native hosts infected with native parasites (Fig. 7.1e) or when a native parasite species infects invasive hosts in the invaded ecosystem ('parasite acquisition'; Fig. 7.1d).

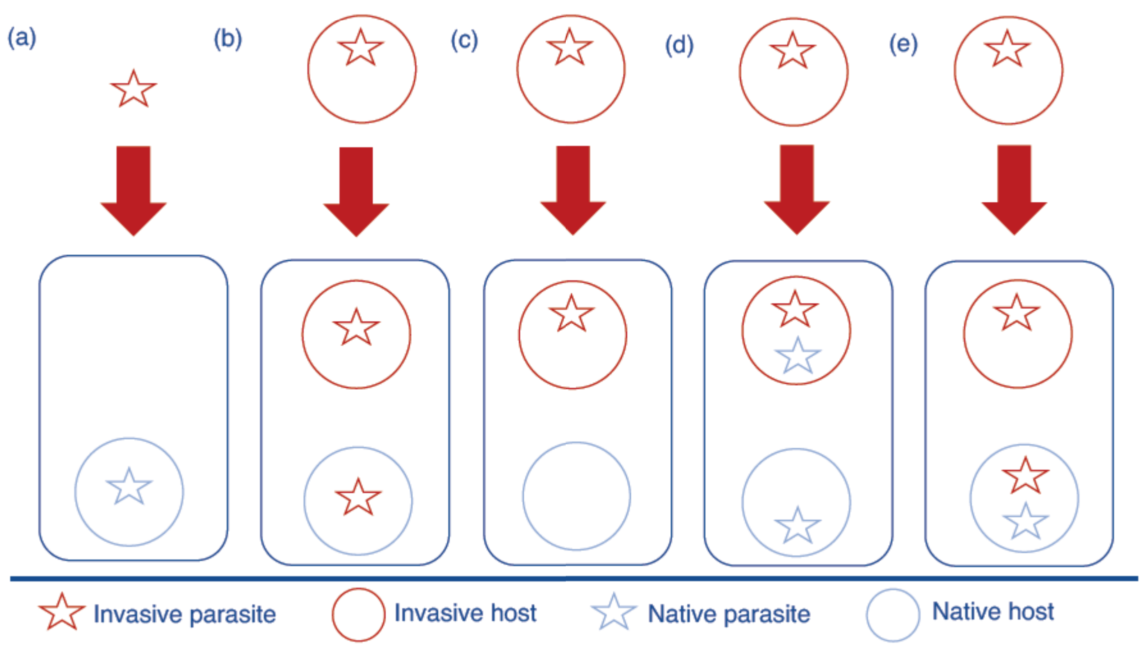

Fig. 7.1. Five ways of how invasive parasites can interact with hosts and parasites in invaded ecosystems. A parasite species can invade a system (a) without or (b) with its original host and spill over to native hosts, potentially causing emerging diseases and altering interactions of infected hosts with other species. In some cases (c) parasites co-introduced with invasive hosts do not spill over to native hosts and thus only affect invasive hosts in the invaded ecosystem. It is also possible that (d) invasive hosts become infected by native parasite species ('parasite acquisition') and serve as a reservoir to reinfect native hosts ('parasite spillback'). Interactions between invasive and native parasites can occur either (e) in native hosts after spillover or (d) in invasive hosts if invasive hosts acquire native parasites.

In the following sections, we discuss the ecological consequences of these novel interactions in the course of parasite invasions. We will do so by focusing on four different types of effects at different organizational levels (Fig. 7.2). We first discuss the direct effects of invasive parasites on hosts (section 7.3; Fig. 7.2a). Then we describe how these direct effects on infected hosts can indirectly affect their interactions with other hosts in the surrounding communities (section 7.4; Fig. 7.2b). Following this, we highlight how direct and indirect effects of invasive parasites can also have repercussions at the community and ecosystem levels (section 7.5; Fig. 7.2c). Finally, we discuss how invasive parasites can affect disease dynamics by interacting with native parasites (or hyperparasites) in invaded ecosystems (section 7.6; Fig. 7.2d). We close this chapter with thoughts on current knowledge gaps and future research needs (section 7.7).

7.3 Direct Effects on Native and Invasive Hosts

As all parasites energetically rely on their hosts for their own survival and reproduction, parasite infections frequently come with a cost for the host (Combes, 2001; Poulin, 2011). These costs can range from more subtle sublethal effects of infections such as a loss in body condition, tissue damage or reduction in growth, to more dramatic fitness effects such as loss in fertility or even mortality of the host (Combes, 2001; Poulin, 2011). In general, the costs of parasitic infections depend on traits of both the host and the parasite (Fig. 7.3). For example, more infective and more virulent parasites will cause a greater reduction in host fitness, but hosts can counteract this by preventing infections (by investing in host resistance) or by limiting the damaging effects of infections (host tolerance; Råberg *et al*., 2009). However, resistance and tolerance are costly and may lead to trade-offs between maintaining immune defences and reproductive output: for example this could result in short-lived hosts that die young but reproduce prolifically (Råberg *et al*., 2009; Martin *et al*., 2011). The arms race between traits of hosts (resistance, tolerance) and parasites (virulence, infectivity) is continuously evolving during the coevolutionary history of a parasite–host relationship (Fig. 7.3). The older the coevolutionary relationship, the more likely the host is co-adapted and able to defend itself against a specific parasite. However, in the case of invasive parasites entering new ecosystems, naive native hosts lack this co-evolved resistance

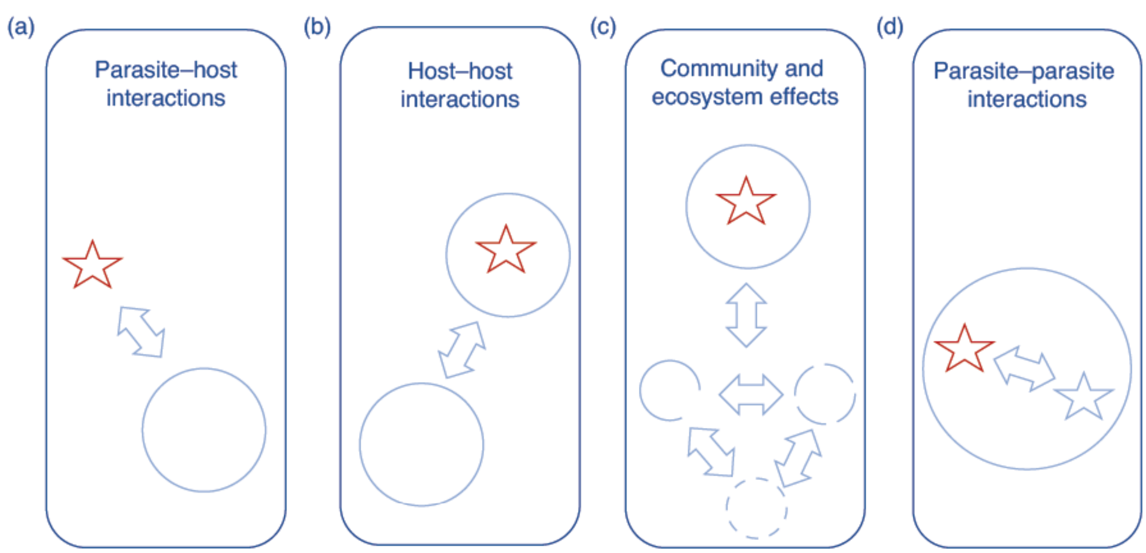

Fig. 7.2. Ecological consequences of novel interactions in the course of parasite invasions at different organizational levels: (a) direct effects on individual hosts via parasite–host interactions; (b) indirect effects on interactions between infected and non-infected hosts; (c) direct and indirect effects at the community and ecosystem levels; and (d) interactions with native parasites in invaded ecosystems.

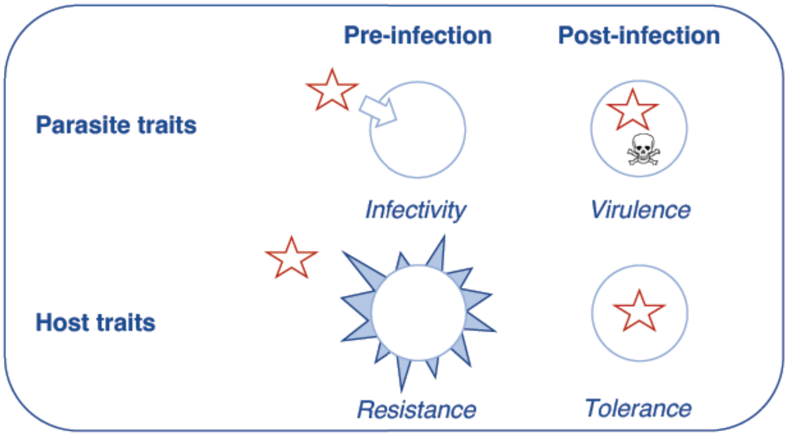

Fig. 7.3. Parasite and host traits that determine the outcome and costs of infections and that continuously evolve in the cause of the co-evolutionary arms race between parasites and hosts. Adapted from Goedknegt, 2017.

or tolerance (Blakeslee *et al.*, 2021). As a consequence, these native hosts may more easily become infected, leading to severe pathogenic effects and emerging diseases in some native hosts (Daszak *et al.*, 2000; Mastitsky *et al.*, 2010; Fassbinder-Orth *et al.*, 2013).

This 'naive host theory' has been confirmed by observations from the wild in a variety of ecosystems. Parasite spillover events after the co-introduction of invasive parasites with their hosts (Fig. 7.1b) are well known causes of serious emerging diseases and mass mortality events in terrestrial, freshwater and marine ecosystems (reviewed in Harvell *et al.*, 1999; Strauss *et al.*, 2012; Lymbery *et al.*, 2014; Goedknegt *et al.*, 2016). For example, in the 1930s and 1970s, mass mortalities of native bastard sturgeons in the Aral Sea were caused by an invasive monogenean parasite that was co-introduced with starry sturgeons originating from the Caspian Sea (Bauer *et al.*, 2002). Furthermore, in the UK, populations of native white-clawed crayfish are threatened with extinction after the oomycete *Aphanomyces astaci*, which causes crayfish plague that is lethal to the native crayfish, was co-introduced in the 1970s with red signal crayfish (*Pacifastacus leniusculus*) that are immune to the plague (Holdich, 2003; Jussila *et al.*, 2015). Besides such strong effects of parasite spillover events in the form of mass mortalities and local extinction of native hosts, there are also many examples of parasite invasions with more subtle direct effects on the fitness of native hosts, such as: (i) host castration of native crabs by a rhizocephalan barnacle (Farrapeira *et al.*, 2008); (ii) growth reductions in a marine gastropod by a polychaete (Culver and Kuris, 2004); or (iii) reduction in condition of mussels by a parasitic copepod (Goedknegt *et al.*, 2018).

In contrast to parasite spillover effects on native hosts, much less is known about the direct effects of invasive parasites on their invasive host species, in particular in cases where parasite co-introductions did not lead to a spillover event but where invasive parasites remain in invasive hosts (Fig. 7.1c). Such co-introduced parasites may offset the competitive advantages that invasive hosts often gain from leaving their parasites behind in the process of the invasion (enemy release hypothesis; Torchin *et al.*, 2003; Colautti *et al.*, 2004; Blakeslee *et al.*, 2013; Goedknegt *et al.*, 2016). Parasite co-introductions without spillover are probably a common phenomenon as a literature review of 98 cases of co-introductions revealed that 22% of the co-introduced parasites did not (yet) spill over to native hosts and only remained infecting the invasive host (Lymbery *et al.*, 2014). Such co-introduction without host-switching to native populations have been found, for example, in lungworms in cane toads in Australia (Pizzatto *et al.*, 2012), the oyster herpes virus in Pacific oysters in the Netherlands (Engelsma, 2010), and pumpkinseed fish in the Danube River Basin in Central Europe (Ondračková *et al.*, 2011). Any negative impacts on reproduction and survival because of infection by their invasive parasite may translate into reduced population growth of invasive hosts in the invasive range. Furthermore, co-introduced parasites may make small initial invasive host populations more vulnerable to stochastic events, which can ultimately affect their chances for successful establishment and spread (Blackburn and Ewen, 2017).

7.4 Indirect Effects on Species Interactions

Besides causing direct impacts on the fitness and survival of native and invasive hosts, invasive parasites can also have indirect effects on other species via altering species interactions. In general, indirect effects occur when one species is interacting with a second species and thereby the interaction of a third species is altered (Wootton, 1994; Abrams, 1995; Dunn *et al.*, 2012). Invasive parasites can affect the interaction between two species (e.g. in competitive or consumer–resource interactions) via density-mediated indirect effects (DMIEs) or via trait-mediated indirect effects (TMIEs). In DMIEs, invasive parasites affect the survival or reproduction of a host species, leading to direct changes in host abundance that indirectly affect the abundance of a third species (Wootton, 1994; Abrams, 1995; Hatcher *et al.*, 2006; Dunn *et al.*, 2012). In TMIEs, invasive parasites induce changes in the behaviour, morphology, life history or physiology of a host species that have an indirect effect on a third species (Abrams, 1995; Werner and Peacor, 2003; Hatcher *et al.*, 2006; Dunn *et al.*, 2012). Both types of indirect effects can play a role when invasive parasites infect a competitor in competitive interactions (Fig. 7.4a), or a resource (Fig. 7.4b) or consumer (Fig. 7.4c) in consumer–resource interactions.

Competitive interactions can be altered by DMIEs when an invasive parasite negatively affects the survival or reproduction of one host but not the other, thereby altering the outcome of competition (Hatcher *et al.*, 2006; Dunn *et al.*, 2012; Fig. 7.4a). This type of parasite-mediated competition can lead to two potential outcomes, depending on which competitor is most negatively affected by the parasite: (i) when the superior competitor is affected most, both competitors are likely to coexist; or (ii) when the inferior competitor is most adversely affected, it is likely to be outcompeted and displaced by the stronger competitor. The second scenario can be observed in two case studies from the UK which both also represent important conservation

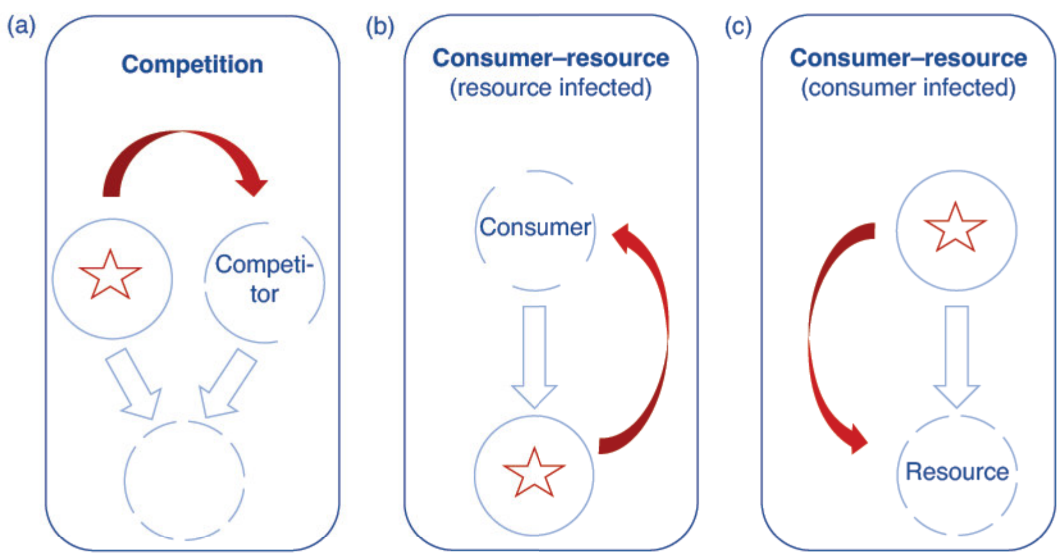

Fig. 7.4. Indirect effects (red arrows) of invasive parasites (red asterisks) on species interactions in invaded ecosystems. These effects result from direct effects of invasive species on (a) competitors, (b) resources, or (c) consumers, either in the form of a change in numbers (density-mediated) or a change in traits (trait-mediated) of the infected hosts. These changes in turn alter competitive or consumer–resource interactions of the infected hosts with their competitors, consumers or resources.

issues – the grey squirrel and the common pheasant invasions. Both species were introduced from North America to the UK, are superior competitors and act as reservoirs for invasive parasites, including a poxvirus (squirrel) and a nematode (pheasant), which are only highly virulent in native species – the red squirrel and the grey partridge, respectively (Tompkins *et al.*, 2000, 2003). In both cases, these infections led to strong DMIEs in the form of sharp declines in native red squirrel and grey partridge populations in the UK (Tompkins *et al.*, 2000, 2003).

Invasive parasites can also influence competitive interactions via TMIEs. In this type of parasite-mediated competition, the parasite does not cause differences in mortality or reproduction between two competitors but affects the competitive ability of infected hosts via changes in host behaviour or other traits. Because of their intimate relationship with their hosts, parasites can influence a variety of traits, including growth rates, morphology and behavioural responses (Hatcher *et al.*, 2006; Dunn *et al.*, 2012). For example, invasive plants are known to increase their competitive ability through root-borne parasites, which can have negative impacts on native competitors. For instance, some invasive weeds and grasses are known to carry parasites in their root systems that reduce growth rates and seed viability in native competitors (Malmstrom *et al.*, 2005; Mangla and Callaway, 2008; Beckstead *et al.*, 2010).

Consumer–resource interactions can be affected by invasive parasites through indirect effects, for example when invasive parasites infect species that are resources of a consumer (herbivores and predators; Fig. 7.4b). In this scenario, both the consumer and the parasite share the same resource, resulting in a combined impact via DMIEs on the resource (Dunn *et al.*, 2012). For example, when an invasive parasite causes mortality in a prey species, this species can no longer serve as a resource for the consumer. This was the case when introduced viral diseases severely decimated populations of European rabbits in Spain. Due to the population declines of rabbits, they were not available anymore as a resource for the Iberian lynx and Iberian imperial eagle, which could be problematic for these two large predators because of their inability to switch to alternative prey (Ferrer and Negro, 2004). This type of DMIE induced by invasive parasites has even led to the extinction of prey species in the past. For instance, when an invasive fungus (*Cryphonectria parasitica*) caused chestnut blight in the American chestnut, and this became an epidemic, the native tree species almost became extinct, which possibly resulted in the complete extinction of several butterfly species that depended on the trees (Opler, 1978; Freinkel, 2009).

Similarly, invasive parasites that affect resources can also lead to TMIEs when infections of the resource alter the likelihood of infected hosts being consumed, for example making them more susceptible to predation by consumers (Hatcher *et al.*, 2015). An example for these types of TMIEs is the invasion of a parasitic barnacle that infects native panopeid mud crabs in North America. Infections with the invasive parasite lead to alterations in the behavioural traits of crabs, such as activity levels and hiding behaviour, which make the crabs more susceptible to predation by their predators (Brothers and Blakeslee, 2021). For parasites that need trophic transmission to complete their complex life cycle, this type of indirect effect can be adaptive when they modify their hosts' behaviour or other traits in such a way that this increases consumption by the next hosts in their life cycle (reviewed in Lefèvre *et al.*, 2008). However, this is not the case in the parasitic barnacles discussed above as they are directly transmitted (Brothers and Blakeslee, 2021).

Indirect effects can also occur when consumers are infected by invasive parasites (Fig. 7.4c), which cause declines in the consumer population density. Such a decline in consumer density can result in indirect effects on the consumer's resources through reduced consumption which in turn can lead to an increase in resource population sizes. For instance, these DMIEs have been observed when an invasive virus infected wolves in North America, resulting in large reductions in the wolf population, which in turn had a positive effect on moose, the prey of wolves (Wilmers *et al.*, 2006). Regarding herbivores, there can be similar indirect effects. When the population of rabbits declined in the UK as the result of infection by an invasive virus, this resulted in a rise in the oak population (Dobson and Crawley, 1994).

TMIEs of invasive parasites infecting consumers can also occur, for example when parasites alter the feeding behaviour or consumption rates of consumers, which can then lead to an indirect effect on the resource. For instance, in the USA, native crabs infected with an invasive rhizocephalan barnacle need more time for handling their mussel prey, resulting in an eightfold decrease in maximum consumption rates (Toscano *et al.*, 2014).

7.5 Effects on Communities and Ecosystems

The direct (section 7.3) and indirect (section 7.4) effects of invasive parasites can scale up to the community and ecosystem levels, similar to what is known for parasites in general (Hatcher *et al.*, 2012b; Preston *et al.*, 2016; Fischhoff *et al.*, 2020; Paseka *et al.*, 2020). This can happen either in a direct way, when infections have negative effects on traits or survival of hosts with important ecosystem functions, for example resulting in a decrease of biomass production in dominant species (Fig. 7.5a). Alternatively, invasive parasites can indirectly affect communities and ecosystems via changes in density or traits that alter species interactions (see section 7.4), which in turn modifies the functional role of infected hosts and changes in community composition, ecosystem function and services (Fig. 7.5b).

Invasive fungal pathogens that infect trees causing Dutch elm disease, chestnut blight, white pine blister rust disease and beech bark disease are prime examples of the direct effects of invasive parasites on important ecosystem functions such as biomass production by primary producers (Anderson *et al.*, 2004; Loo, 2009). The usually high virulence of these pathogens leads to significant mortality of infected trees and thus lowers primary production which also causes effects on ecosystem services such as high economic losses in forestry (Anderson *et al.*, 2004; Loo, 2009; Lovett *et al.*, 2016). The mortality of specific tree species, in turn, can trigger a range of knock-on effects at the community and ecosystem levels. For example, the loss of dominant tree species will open niches for other plant species and will result in changes in the local plant community composition (Woods and Shanks, 1959; McCormick and Platt, 1980; Castello *et al.*, 1995; Elliott and Swank, 2008). In addition, the loss of specific tree species can also result in strong effects on local consumers such as insects, birds and mammals through the loss of habitat and food resources (Osborne, 1985; Faison and Houston, 2004; Monahan and Koenig, 2006; Loo, 2009). The combination

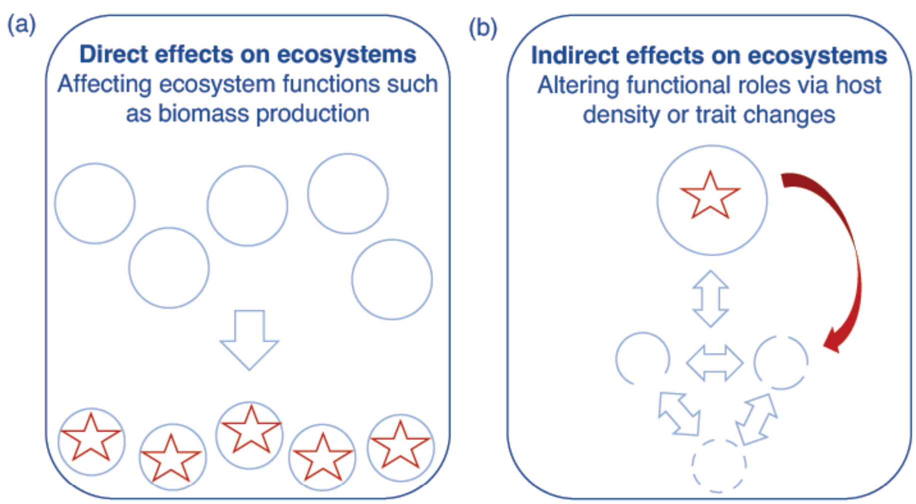

Fig. 7.5. Invasive parasites (red asterisks) can have effects at the community and ecosystem levels either by: (a) directly affecting hosts with important ecosystem functions (e.g. reducing growth of infected hosts and thus lowering biomass production); or (b) indirectly by changing the density or traits of hosts that affect the interactions of infected hosts with other species within the community, which alters the functional role of hosts in ecosystems.

of direct and indirect effects of invasive fungal pathogens on trees can thus have far-reaching effects on community structure and ecosystem functions and services.

Similar complex knock-on effects of invasive parasites are known when consumers are affected in invaded food webs. For example, crayfish plague, which is caused by a fungus (as mentioned earlier in section 7.3), has been introduced to Europe with invasive crayfish from North America (Alderman, 1996). While infections in the invasive crayfish are asymptomatic, mortality is very high in native crayfish species (Alderman, 1996). This results in the removal of an important predator from freshwater systems which in turn relaxes predation pressure on its resources and leads to increases in invertebrate densities and macrophyte biomass (Abrahamsson, 1966; Matthews and Reynolds, 1992). Such cascading effects can also occur when grazers are affected by invasive parasites. Arguably the most prominent example for ecosystem-wide effects of parasites is the introduction of the rinderpest virus which was introduced to Africa with domestic livestock around 1890 (Dobson and Hudson, 1986; Thomas *et al.*, 2005). The virus spread very rapidly and spilled over to native wildebeest and buffalo. The resulting decline in grazers led to increased primary production, diverse changes in the plant community structure and a reduction in top predator populations in the ecosystem (Dobson and Hudson, 1986; McNaughton, 1992; Thomas *et al.*, 2005). When vaccination of livestock led to an eradication of the virus in the late 1960s, ungulate populations recovered and the resulting increased grazing pressure reduced tree densities, with repercussions for ecosystem production and carbon storage (Holdo *et al.*, 2009).

Besides these unintended introductions, other examples for ecosystem-wide effects of invasive parasites come from the use of pathogens as a biocontrol measure. To control exploding invasive rabbit populations, which affected native plants and caused high losses in agriculture in Australia and the UK, a highly pathogenic virus was introduced in both countries in the 1950s, with diverse knock-on effects on the native ecosystems (Sumption and Flowerdew, 1985; Dobson and Crawley, 1994). Due to the strong mortality in rabbits, the virus led to a reduced grazing pressure which in turn allowed trees to regrow in former grasslands, resulting in profound changes in the plant community structure and productivity (Sumption and Flowerdew, 1985).

7.6 Effects on Native Parasites

Invasive parasites can not only affect native hosts in invaded ecosystems, but they can also have consequences for native parasites (Fig. 7.1d, e). One way that this can happen is via within-host interactions of invasive and native parasites, either in a direct way, when parasites compete for host resources or space inside hosts (Fig. 7.6a), or in an indirect way, when parasite infections modulate immune responses of infected hosts (TMIE; Fig. 7.6b). Both processes are well known from parasite co-infections in general (Cox, 2001; Pedersen and Fenton, 2007; Graham, 2008; Telfer and Bown, 2012; Rynkiewicz *et al.*, 2015). Another way for invasive parasites to affect native parasites is via their effects on the density of hosts which in turn can affect the population size of native parasites (DMIE; Fig. 7.6c; Telfer and Bown, 2012). While these different mechanisms can affect the population dynamics of native parasites, the outcome of parasite–parasite interactions will also affect hosts, either by decreasing or by increasing the fitness consequences of co-infections compared with single species infections (Bordes and Morand, 2011; Tompkins *et al.*, 2011; Telfer and Bown, 2012; Alizon *et al.*, 2013).

Although invasive parasites have strong potential to affect native parasites via within-host interactions, there are only a few empirical examples. The exact underlying mechanisms and ultimate outcomes of these interactions seem often more difficult to unravel. For example, experimental results on the effects of invasive sudden oak death fungal infections on native sympatric congeneric fungal pathogens, indicate that the invasive parasite is a stronger competitor (Kozanitas *et al.*, 2017; Fig. 7.6a). However, empirical data suggest that the outcome of the competition between the invasive and native fungal pathogens depends on the environmental conditions, with possible coexistence during drought periods (Kozanitas

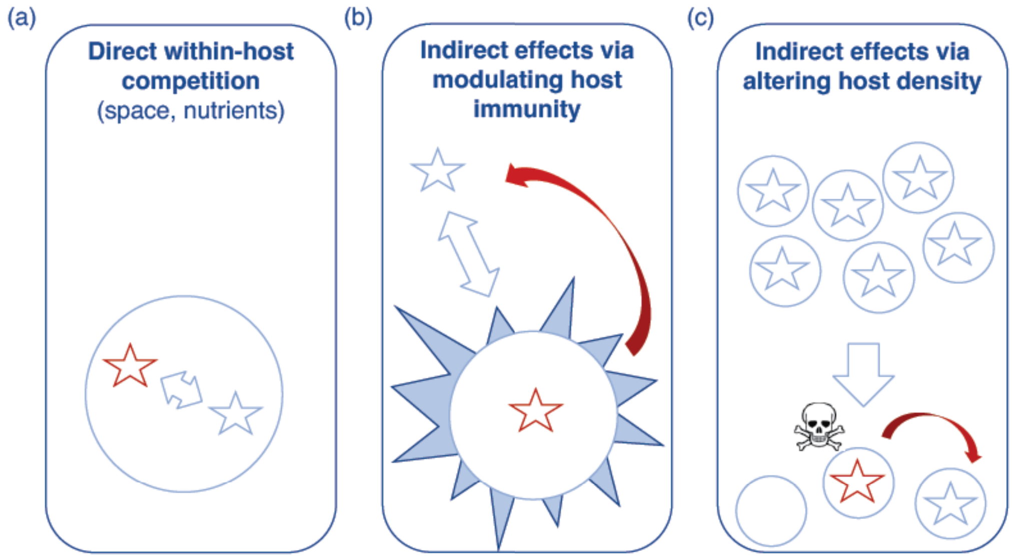

Fig. 7.6. Invasive parasites (red asterisks) can affect native parasites in invaded ecosystems through: (a) direct within-host competition; (b) immune system modulation of infected hosts (trait-mediated indirect effects, TMIE); or (c) by altering the density of hosts (density-mediated indirect effects, DMIE).

et al., 2017). Negative correlations between invasive and native parasite infections have also been observed in African buffalo populations. Infections with bacterial bovine tuberculosis, which was originally introduced to South Africa with cattle from Europe, are negatively correlated with native intestinal nematode infections, suggesting strong within-host competition (Michel *et al.*, 2006; Jolles *et al.*, 2008). However, the underlying mechanisms are probably a complex combination of cross-reactive immune responses, with weaker T-helper type one immune responses (against tuberculosis) and stronger T-helper type two responses (against helminths) in buffalo with higher resistance to worms and increased mortality of co-infected hosts compared with uninfected hosts or hosts with single infections (Jolles *et al.*, 2008; Ezenwa *et al.*, 2010; Fig. 7.6b). Differential immune responses to macro- and microparasite infections are probably also involved in within-host interactions between an invasive intestinal copepod and virulent bacteria in marine mussels (Demann and Wegner, 2018). Infections with the invasive copepod led to increased secondary infections with bacterial pathogens and elevated mortality, probably mediated by modulated cellular immune responses due to the copepod infections which lead to failure in clearing secondary infections by pathogenic bacteria (Demann and Wegner, 2018; Feis *et al.*, 2018). These examples show that within-host interactions of invasive and native parasites can also have strong repercussions for native hosts in invaded ecosystems.

There is little research to date on the effects of invasive parasites on native parasites via their effects on the density of hosts (Fig. 7.6c). However, such effects are inevitable given that epidemiological models predict that any changes in (susceptible) host density will affect population size of parasites by altering contact rates between parasites and hosts (Holt *et al.*, 2003; Dobson, 2004; Rudolf and Antonovics, 2005). For parasites with density-dependent transmission, these models also indicate that there are threshold host densities for parasite establishment and persistence (McCallum *et al.*, 2001; Begon *et al.*, 2002). Hence, the many direct and indirect effects of invasive parasites on their hosts described above will also have the potential to alter the population sizes and dynamics of native parasites. Interestingly, the negative effects of invasive parasites on their hosts can also backfire to the invasive parasites themselves as they rely on hosts for their persistence. For example, an outbreak of crayfish plague in native crayfish in Ireland led to rapid local population declines of the native crayfish, but the invasive parasite then became locally extinct because the original host, the invasive signal crayfish, was not present locally (Reynolds, 1988).

7.7 Knowledge Gaps and Future Research

Although the principal mechanisms behind the ecological consequences of parasite invasions are well understood, as outlined above, the number of studies detailing effects of parasite invasions on native biota is still limited. One of the reasons for this paucity of studies relates to our generally limited knowledge on the presence of invasive parasites in ecosystems. Co-introductions of parasites with invasive species are probably common (Lymbery *et al.*, 2014), despite invaders often leaving parasite species behind during the translocation process, as suggested by the enemy release hypothesis (Torchin *et al.*, 2003; Colautti *et al.*, 2004). However, many parasite invasions probably go unnoticed as the parasite faunas of most invasive host species are not known. Increasing the efforts to screen invasive species for potentially co-introduced parasites will thus be a first important step in identifying the ecological consequences of parasite invasions. Besides the classic methods of dissection and histology, molecular methods such as metabarcoding, genomics and environmental DNA (eDNA) are now promising additional approaches to identify invasive parasites in ecosystems (Bass *et al.*, 2015; Burge *et al.*, 2016; Tobias *et al.*, 2021; Chapter 2, this volume).

Also, for known invasive parasites, increasing research efforts are needed to identify their effects on native biota. Given the complexity of the potential consequences of parasite invasions for native ecosystems at different organizational levels, this is a challenging task. While mass mortalities in the wake of parasite invasions are relatively easy to link to the invasion, many of the more subtle and indirect effects of parasite invasions will easily go unnoticed. Experimental approaches have been proven to be powerful tools to unravel the direct and indirect ecological effects of parasites in general and ecological and epidemiological modelling approaches can be complementary tools to identify population-level consequences of parasite infections (Hatcher and Dunn, 2011; Wilson *et al.*, 2019). Applying such multi-pronged approaches to study parasite invasions will not only help increase our understanding of the ecological consequences of parasite invasions but will also have relevance for managing disease outbreaks in wildlife or farmed populations that have strong conservation or economic impacts.

Finally, with the numbers of studies on the ecological consequences of parasite invasions increasing, comparative and meta-analytical approaches will become possible. These will not only be powerful tools to reveal general patterns of the effects of parasite invasions, but they will also allow exploration into whether the ecological consequences of parasite invasions differ qualitatively or quantitatively from the effects of native parasites. In some cases, invasive parasites may exert similar sized effects compared to native parasites while in other cases their effects may generally be greater. For example, in the case of parasite spillover events, invasive parasites may show a generally higher virulence compared with native parasites. However, more studies on the various ecological consequences of invasive parasites are needed before larger synthesis approaches become feasible. We hope that this chapter will contribute to guiding future research efforts in this regard.

7.8 Conclusions

This chapter highlights the diversity of ecological consequences of parasite invasions in their recipient ecosystems. These consequences not only include direct effects of invasive parasites on hosts and other parasites in invaded ecosystems, but they can also encompass indirect effects on other species via altering species interactions and knock-on effects on the invaded communities and ecosystems. Currently, we have only a limited understanding of the generality and magnitude of the various effects of invasive parasites and future research efforts should be directed to identify potentially co-introduced parasites and to experimentally investigate their ecological consequences.

References

Abrahamsson, S.A.A. (1966) Dynamics of an isolated population of the crayfish Astacus astacus Linné. *Oikos* 17, 96–107. DOI: 10.2307/3564784.

Abrams, P.A. (1995) Implications of dynamically variable traits for identifying, classifying and measuring direct and indirect effects in ecological communities. *The American Naturalist* 146, 112–134. DOI: 10.1086/285789.

Alderman, D.J. (1996) Geographical spread of bacterial and fungal diseases of crustaceans. *Revue Scientifique et Technique* 15(2), 603–632. DOI: 10.20506/rst.15.2.943.

Alizon, S., de Roode, J.C. and Michalakis, Y. (2013) Multiple infections and the evolution of virulence. *Ecology Letters* 16, 556–567. DOI: 10.1111/ele.12076.

Anderson, P.K., Cunningham, A.A., Patel, N.K., Morales, F.J., Epstein, P.R. *et al*. (2004) Emerging infectious diseases of plants: pathogen pollution, climate change and agrotechnology drivers. *Trends in Ecology & Evolution* 19, 535–544. DOI: 10.1016/j.tree.2004.07.021.

Bass, D.W., Stentiford, G.D., Littlewood, D.T.J. and Hartikainen, H. (2015) Diverse applications of environmental DNA methods in parasitology. *Trends in Parasitology* 31(10), 499–513. DOI: 10.1016/j.pt.2015.06.013.

Bauer, O.N., Pugachev, O.N. and Voronin, V.N. (2002) Study of parasites and diseases of sturgeons in Russia: a review. *Journal of Applied Ichthyology* 18, 420–429. DOI: 10.1046/j.1439-0426.2002.00422.x.

Beckstead, J., Meyer, S.E., Connolly, B.M., Huck, M.B. and Street, L.E. (2010) Cheatgrass facilitates spillover of a seed bank pathogen onto native grass species. *Journal of Ecology* 98, 168–177. DOI: 10.1111/j.1365-2745.2009.01599.x.

Begon, M., Bennett, M., Bowers, R.G., French, N.P., Hazel, S.M. *et al*. (2002) A clarification of transmission terms in host-microparasite models: numbers, densities and areas. *Epidemiology and Infection* 129(1), 147–153. DOI: 10.1017/s0950268802007148.

Begon, M., Townsend, C.R. and Harper, J.L. (2006) *Ecology: From Individuals to Ecosystems*. Blackwell Science, Cambridge, Massachusetts.

Blackburn, T.M. and Ewen, J.G. (2017) Parasites as drivers and passengers of human-mediated biological invasions. *EcoHealth* 14, S61–S73. DOI: 10.1007/s10393-015-1092-6.

Blakeslee, A.M., Pochtar, D.L., Fowler, A.E., Moore, C.S., Lee, T.S. *et al*. (2021) Invasion of the body snatchers: the role of parasite introduction in host distribution and response to salinity in invaded estuaries. *Proceedings of the Royal Society B. Biological Sciences* 288(1953), 20210703. DOI: 10.1098/rspb.2021.0703.

Blakeslee, A.M.H., Fowler, A.E. and Keogh, C.L. (2013) Marine invasions and parasite escape: updates and new perspectives. *Advances in Marine Biology* 66, 87–169. DOI: 10.1016/B978-0-12-408096-6.00002-X.

Bordes, F. and Morand, S. (2011) The impact of multiple infections on wild animal hosts: a review. *Infection Ecology & Epidemiology* 1, 7346. DOI: 10.3402/iee.v1i0.7346.

Brothers, C.A. and Blakeslee, A.M. (2021) Alien vs predator play hide and seek: how habitat complexity alters parasite mediated host survival. *Journal of Experimental Marine Biology and Ecology* 535, 151488. DOI: 10.1016/j.jembe.2020.151488.

Burge, C.A., Friedman, C.S., Getchell, R., House, M., Lafferty, K.D. *et al*. (2016) Complementary approaches to diagnosing marine diseases: a union of the modern and the classic. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 371, 20150207. DOI: 10.1098/rstb.2015.0207.

Castello, J.D., Leopold, D.J. and Smallidge, P.J. (1995) Pathogens, patterns, and processes in forest ecosystems. *BioScience* 45, 16–24. DOI: 10.2307/1312531.

Colautti, R.I., Ricciardi, A., Grigorovich, I.A. and MacIsaac, H.J. (2004) Is invasion success explained by the enemy release hypothesis? *Ecology Letters* 7, 721–733. DOI: 10.1111/j.1461-0248.2004.00616.x.

Combes, C. (2001) *Parasitism: The Ecology and Evolution of Intimate Interactions*. The University of Chicago Press, Chicago, Illinois.

Cox, F.E. (2001) Concomitant infections, parasites and immune responses. *Parasitology* 122, S23–S38. DOI: 10.1017/s003118200001698x.

Crowl, T.A., Crist, T.O., Parmenter, R.R., Belovsky, G. and Lugo, A.E. (2008) The spread of invasive species and infectious disease as drivers of ecosystem change. *Frontiers in Ecology and the Environment* 6, 234–246. DOI: 10.1890/070151.

Culver, C.M. and Kuris, A.M. (2004) Susceptibility of California gastropods to an introduced South African sabellid polychaete, *Terebrasabella heterouncinata*. *Invertebrate Biology* 123, 316–323. DOI: 10.1111/j.1744-7410.2004.tb00165.x.

Daszak, P., Cunningham, A.A. and Hyatt, A.D. (2000) Emerging infectious diseases of wildlife--threats to biodiversity and human health. *Science*287, 443–449. DOI: 10.1126/science.287.5452.443.

Demann, F. and Wegner, K.M. (2018) Infection by invasive parasites increases susceptibility of native hosts to secondary infection via modulation of cellular immunity. *The Journal of Animal Ecology* 88, 427–438. DOI: 10.1111/1365-2656.12939.

Dobson, A. (2004) Population dynamics of pathogens with multiple host species. *The American Naturalist* 164 Suppl 5, S64–78. DOI: 10.1086/424681.

Dobson, A.P. and Hudson, P.J. (1986) Parasites, disease and the structure of ecological communities. *Trends in Ecology & Evolution* 1(1), 11–15. DOI: 10.1016/0169-5347(86)90060-1.

Dobson, A.P. and Crawley, M. (1994) Pathogens and the structure of plant communities. *Trends in Ecology & Evolution* 9(10), 393–398. DOI: 10.1016/0169-5347(94)90062-0.

Dunn, A.M. and Hatcher, M.J. (2015) Parasites and biological invasions: parallels, interactions, and control. *Trends in Parasitology* 31(5), 189–199. DOI: 10.1016/j.pt.2014.12.003.

Dunn, A.M., Torchin, M.E., Hatcher, M.J., Kotanen, P.M., Blumenthal, D.M. *et al*. (2012) Invasions and infections: indirect effects of parasites in invasions. *Functional Ecology* 26(6), 1262–1274.

Elliott, K.J. and Swank, W.T. (2008) Long-term changes in forest composition and diversity following early logging (1919–1923) and the decline of American chestnut (*Castanea dentata*). *Plant Ecology* 197, 155–172. DOI: 10.1007/s11258-007-9352-3.

Elton, C.S. (1958) *The Ecology of Invasions*. Methuen, London.

Engelsma, M.Y. (2010) "*Verslag monitoring oester herpesvirus 2010. Resultaten van onderzoek naar de aanwezigheid van oester herpesvirus in Japanse oesters van het Grevelingenmeer en de Oosterschelde.*" CVI-Report. Lelystad,The Netherlands.

Ezenwa, V.O., Etienne, R.S., Luikart, G., Beja-Pereira, A. and Jolles, A.E. (2010) Hidden consequences of living in a wormy world: nematode-induced immune suppression facilitates tuberculosis invasion in African buffalo. *The American Naturalist* 176, 613–624. DOI: 10.1086/656496.

Faison, E.K. and Houston, D.R. (2004) Black bear foraging in response to beech bark disease in eastern Vermont. *Northeastern Naturalist* 11, 387–394. DOI: 10.1656/1092-6194(2004)011[0387:BBFIRT]2.0.CO;2.

Farrapeira, C.M.R., Marrocos de melo, A.V. and Barbosa, D.F. (2008) Introduction of *Loxothylacus panopaei* (Cirripedia: Rhizocephala), a marine non-indigenous parasitic castrator in estuarine area of recife, pernumbaco, Brazil. *Biociências* 16, 157–159.

Fassbinder-Orth, C.A., Barak, V.A. and Brown, C.R. (2013) Immune responses of a native and an invasive bird to buggy creek virus (Togaviridae: alphavirus) and its arthropod vector, the swallow bug (*Oeciacus vicarius*). *PloS One* 8, e58045. DOI: 10.1371/journal.pone.0058045.

Feis, M.E., John, U., Lokmer, A., Luttikhuizen, P.C. and Wegner, K.M. (2018) Dual transcriptomics reveals co-evolutionary mechanisms of intestinal parasite infections in blue mussels *Mytilus edulis*. *Molecular Ecology* 27, 1505–1519. DOI: 10.1111/mec.14541.

Ferrer, M. and Negro, J.J. (2004) The near extinction of two large European predators: super specialists pay a price. *Conservation Biology* 18(2), 344–349. DOI: 10.1111/j.1523-1739.2004.00096.x.

Fischhoff, I.R., Huang, T., Hamilton, S.K., Han, B.A., LaDeau, S.L. *et al*. (2020) Parasite and pathogen effects on ecosystem processes: a quantitative review. *Ecosphere* 11(5), e03057. DOI: 10.1002/ecs2.3057.

Freinkel, S. (2009) *American Chestnut: The Life, Death, and Rebirth of a Perfect Tree*. University of California Press, Berkeley, California.

Goedknegt, M.A., Feis, M.E., Wegner, K.M., Luttikhuizen, P.C., Buschbaum, C. *et al*. (2016) Parasites and marine invasions: ecological and evolutionary perspectives. *Journal of Sea Research* 113, 11–27. DOI: 10.1016/j.seares.2015.12.003.

Goedknegt, M.A. (2017) Pacific oysters and parasites: species invasions and their impact on parasite–host interactions. PhD thesis, VU University Amsterdam, the Netherlands.

Goedknegt, M.A., Bedolfe, S., Drent, J., van der Meer, J. and Thieltges, D.W. (2018) Impact of the invasive parasitic copepod *Mytilicola orientalis* on native blue mussels *Mytilus edulis* in the western European Wadden Sea. *Marine Biology Research* 14(5), 497–507. DOI: 10.1080/17451000.2018.1442579.

Graham, A.L. (2008) Ecological rules governing helminth-microparasite coinfection. *Proceedings of the National Academy of Sciences of the United States of America* 105, 566–570. DOI: 10.1073/pnas.0707221105.
Harvell, C.D., Kim, K., Burkholder, J.M., Colwell, R.R., Epstein, P.R. *et al*. (1999) Emerging marine diseases--climate links and anthropogenic factors. *Science* 285, 1504–1510. DOI: 10.1126/science.285.5433.1505.
Hatcher, M.J. and Dunn, A.M. (2011) *Parasites in Ecological Communities: From Interactions to Ecosystems*. Cambridge University Press, Cambridge, UK. DOI: 10.1017/CBO9780511987359.
Hatcher, M.J., Dick, J.T.A. and Dunn, A.M. (2006) How parasites affect interactions between competitors and predators. *Ecology Letters* 9(11), 1253–1271. DOI: 10.1111/j.1461-0248.2006.00964.x.
Hatcher, M.J., Dick, J.T.A. and Dunn, A.M. (2012a) Disease emergence and invasions. *Functional Ecology* 26(6), 1275–1287. DOI: 10.1111/j.1365-2435.2012.02031.x.
Hatcher, M.J., Dick, J.T.A. and Dunn, A.M. (2012b) Diverse effects of parasites in ecosystems: linking interdependent processes. *Frontiers in Ecology and the Environment* 10(4), 186–194. DOI: 10.1890/110016.
Hatcher, M.J., Dick, J.T.A., Paterson, R.A., Alexander, M.E., Bunke, M. *et al*. (2015) Trait-mediated effects of parasites on invader-native interactions. In: Mehlhorn, H. (ed.) *Host Manipulations by Parasites and Viruses. Parasitology Research Monographs*, Vol. 7. Springer, Cham, Switzerland, pp. 29–47. DOI: 10.1007/978-3-319-22936-2.
Holdich, D.M. (2003) *Ecology of the white-clawed Crayfish*. In: *Conserving Natura 2000 Rivers Ecology Series*. English Nature, Peterborough, UK.
Holdo, R.M., Sinclair, A.R., Dobson, A.P., Metzger, K.L., Bolker, B.M. *et al*. (2009) A disease-mediated trophic cascade in the serengeti and its implications for ecosystem C. *PLoS Biology* 7, e1000210. DOI: 10.1371/journal.pbio.1000210.
Holt, R.D., Dobson, A.P., Begon, M., Bowers, R.G. and Schauber, E.M. (2003) Parasite establishment in host communities. *Ecology Letters* 6(9), 837–842. DOI: 10.1046/j.1461-0248.2003.00501.x.
Jolles, A.E., Ezenwa, V.O., Etienne, R.S., Turner, W.C. and Olff, H. (2008) Interactions between macroparasites and microparasites drive infection patterns in free-ranging African buffalo. *Ecology* 89, 2239–2250. DOI: 10.1890/07-0995.1.
Jussila, J., Vrezec, A., Makkonen, J., Kortet, R. and Kokko, H. (2015) Invasive crayfish and their invasive diseases in Europe with the focus on the virulence evolution of the crayfish plague. In: Canning-Clode, J. (ed.) *Biological Invasions in Changing Ecosystems: Vectors, Ecological Impacts, Management and Predictions*. De Gruyter Open, Berlin, pp. 183–211. DOI: 10.1515/9783110438666.
Kelly, D.W., Paterson, R.A., Townsend, C.R., Poulin, R. and Tompkins, D.M. (2009) Parasite spillback: a neglected concept in invasion ecology? *Ecology* 90, 2047–2056. DOI: 10.1890/08-1085.1.
Kozanitas, M., Osmundson, T.W., Linzer, R. and Garbelotto, M. (2017) Interspecific interactions between the sudden oak death pathogen *Phytophthora ramorum* and two sympatric *Phytophthora* species in varying ecological conditions. *Fungal Ecology* 28, 86–96. DOI: 10.1016/j.funeco.2017.04.006.
Lefèvre, T., Roche, B., Poulin, R., Hurd, H., Renaud, F. *et al*. (2008) Exploiting host compensatory responses: the "must" of manipulation? *Trends in Parasitology* 24, 435–439. DOI: 10.1016/j.pt.2008.06.006.
Loo, J.A. (2009) Ecological impacts of non-indigenous invasive fungi as forest pathogens. *Biological Invasions* 11, 81–96. DOI: 10.1007/s10530-008-9321-3.
Lovett, G.M., Weiss, M., Liebhold, A.M., Holmes, T.P., Leung, B. *et al*. (2016) Nonnative forest insects and pathogens in the United States: impacts and policy options. *Ecological Applications* 26, 1437–1455. DOI: 10.1890/15-1176.
Lymbery, A.J., Morine, M., Kanani, H.G., Beatty, S.J. and Morgan, D.L. (2014) Co-invaders: the effects of alien parasites on native hosts. *International Journal for Parasitology. Parasites and Wildlife* 3, 171–177. DOI: 10.1016/j.ijppaw.2014.04.002.
Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. *et al*. (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10, 689–710. DOI: 10.1890/1051-0761(2000)010[0689:BICEGC]2.0.CO;2.
Malmstrom, C.M., Hughes, C.C., Newton, L.A. and Stoner, C.J. (2005) Virus infection in remnant native bunchgrasses from invaded California grasslands. *The New Phytologist* 168, 217–230. DOI: 10.1111/j.1469-8137.2005.01479.x.
Mangla, S. and Callaway, R.M. (2008) Exotic invasive plant accumulates native soil pathogens which inhibit native plants. *Journal of Ecology* 96, 58–67.

Martin, L.B., Hawley, D.M. and Ardia, D.R. (2011) An introduction to ecological immunology. *Functional Ecology* 25(1), 4. DOI: 10.1111/j.1365-2435.2010.01820.x.

Mastitsky, S.E., Karatayev, A.Y., Burlakova, L.E. and Molloy, D.P. (2010) Parasites of exotic species in invaded areas: does lower diversity mean lower epizootic impact? *Diversity and Distributions* 16, 798–803. DOI: 10.1111/j.1472-4642.2010.00693.x.

Matthews, M. and Reynolds, J.D. (1992) Ecological impact of crayfish plague in Ireland. *Hydrobiologia* 234, 1–6. DOI: 10.1007/BF00010773.

McCallum, H.I., Barlow, N. and Hone, J. (2001) How should pathogen transmission be modelled? *Trends in Ecology & Evolution* 16, 295–300. DOI: 10.1016/s0169-5347(01)02144-9.

McCormick, J.F. and Platt, R.B. (1980) Recovery of an appalachian forest following the chestnut blight or Catherine Keever – you were right! *American Midland Naturalist* 104, 264–273. DOI: 10.2307/2424865.

McNaughton, S.J. (1992) The propagation of disturbance in savannas through food webs. *Journal of Vegetation Science* 3, 301–314. DOI: 10.2307/3235755.

Michel, A.L., Bengis, R.G., Keet, D.F., Hofmeyr, M., Klerk, L.M. *et al*. (2006) Wildlife tuberculosis in South African conservation areas: implications and challenges. *Veterinary Microbiology* 112, 91–100. DOI: 10.1016/j.vetmic.2005.11.035.

Monahan, W.B. and Koenig, W.D. (2006) Estimating the potential effects of sudden oak death on oak-dependent birds. *Biological Conservation* 127, 146–157. DOI: 10.1016/j.biocon.2005.08.005.

Ondračková, M., Dávidová, M., Přikrylová, I. and Pečínková, M. (2011) Monogenean parasites of introduced pumpkinseed *Lepomis gibbosus* (Centrarchidae) in the Danube River Basin. *Journal of Helminthology* 85, 435–441. DOI: 10.1017/S0022149X10000805.

Opler, P.A. (1978) Insects of American chestnut: possible importance and conservation concern. In: McDonald, J. (ed.), *The American Chestnut Symposium*, West Virginia University Press, pp. 83–85.

Osborne, P. (1985) Some effects of Dutch elm disease on the birds of a Dorset dairy farm. *The Journal of Applied Ecology* 22, 681–691. DOI: 10.2307/2403221.

Paseka, R.E., White, L.A., Van de Waal, D.B., Strauss, A.T., González, A.L. *et al*. (2020) Disease-mediated ecosystem services: pathogens, plants, and people. *Trends in Ecology & Evolution* 35, 731–743. DOI: 10.1016/j.tree.2020.04.003.

Pedersen, A.B. and Fenton, A. (2007) Emphasizing the ecology in parasite community ecology. *Trends in Ecology & Evolution* 22, 133–139. DOI: 10.1016/j.tree.2006.11.005.

Pizzatto, L., Kelehear, C., Dubey, S., Barton, D. and Shine, R. (2012) Host-parasite relationships during a biologic invasion: 75 years postinvasion, cane toads and sympatric Australian frogs retain separate lungworm faunas. *Journal of Wildlife Diseases* 48, 951–961. DOI: 10.7589/2012-02-050.

Poulin, R. (2011) *Evolutionary Ecology of Parasites*. Princeton University Press, Princeton, New Jersey.

Poulin, R., Paterson, R.A., Townsend, C.R., Tompkins, D.M. and Kelly, D.W. (2011) Biological invasions and the dynamics of endemic diseases in freshwater ecosystems. *Freshwater Biology* 56, 676–688. DOI: 10.1111/j.1365-2427.2010.02425.x.

Power, A.G. and Mitchell, C.E. (2004) Pathogen spillover in disease epidemics. *The American Naturalist* 164, 79–89. DOI: 10.1086/424610.

Prenter, J., Macneil, C., Dick, J.T.A. and Dunn, A.M. (2004) Roles of parasites in animal invasions. *Trends in Ecology & Evolution* 19, 385–390. DOI: 10.1016/j.tree.2004.05.002.

Preston, D.L., Mischler, J.A., Townsend, A.R. and Johnson, P.T.J. (2016) Disease ecology meets ecosystem science. *Ecosystems* 19, 737–748. DOI: 10.1007/s10021-016-9965-2.

Råberg, L., Graham, A.L. and Read, A.F. (2009) Decomposing health: tolerance and resistance to parasites in animals. *Philosophical Transactions of the Royal Society B* 364, 37–49. DOI: 10.1098/rstb.2008.0184.

Reynolds, J.D. (1988) Crayfish extinctions and crayfish plague in central Ireland. *Biological Conservation* 45, 279–285. DOI: 10.1016/0006-3207(88)90059-6.

Rudolf, V.H.W. and Antonovics, J. (2005) Species coexistence and pathogens with frequency-dependent transmission. *The American Naturalist* 166, 112–118. DOI: 10.1086/430674.

Rynkiewicz, E.C., Pedersen, A.B. and Fenton, A. (2015) An ecosystem approach to understanding and managing within-host parasite community dynamics. *Trends in Parasitology* 31, 212–221. DOI: 10.1016/j.pt.2015.02.005.

Schmid-Hempel, P. (2011) *Evolutionary Parasitology: the Integrated Study of Infections, Immunology, Ecology, and Genetics*. Oxford University Press, Oxford, UK.

Simberloff, D., Martin, J., Genovesi, P., Maris, V., Wardle, D.A. *et al*. (2013) Impacts of biological invasions: what's what and the way forward. *Trends in Ecology & Evolution* 25, 58–66. DOI: 10.1016/j.tree.2012.07.013.

Strauss, A., White, A., Boots, M. and Perkins, S. (2012) Invading with biological weapons: the importance of disease-mediated invasions. *Functional Ecology* 26, 1249–1261. DOI: 10.1111/1365-2435.12011.

Sumption, K.J. and Flowerdew, J.R. (1985) The ecological effects of the decline in Rabbits (*Oryctolagus cuniculus* L.) due to myxomatosis. *Mammal Review* 15, 151–186. DOI: 10.1111/j.1365-2907.1985.tb00396.x.

Telfer, S. and Bown, K. (2012) The effects of invasion on parasite dynamics and communities. *Functional Ecology* 26, 1288–1299. DOI: 10.1111/j.1365-2435.2012.02049.x.

Thomas, F., Bonsall, M.B. and Dobson, A.P. (2005) Parasitism, biodiversity, and conservation. In: Thomas, F., Renaud, F. and Guegan, J.F. (eds) *Parasitism and Ecosystems*. Oxford University Press, Oxford, UK, pp. 124–139. DOI: 10.1093/acprof:oso/9780198529873.001.0001.

Tobias, Z.J.C., Fowler, A.E., Blakeslee, A.M.H., Darling, J.A., Torchin, M.E. *et al*. (2021) Invasion history shapes host transcriptomic response to a body-snatching parasite. *Molecular Ecology* 30, 4321–4337. DOI: 10.1111/mec.16038.

Tompkins, D.M., Greenman, J.V., Robertson, P.A. and Hudson, P.J. (2000) The role of shared parasites in the exclusion of wildlife hosts: Heterakis gallinarum in the ring-necked pheasant and the grey partridge. *The Journal of Animal Ecology* 69, 829–840. DOI: 10.1046/j.1365-2656.2000.00439.x.

Tompkins, D.M., White, A.R. and Boots, M. (2003) Ecological replacement of native red squirrels by invasive greys driven by disease. *Ecology Letters* 6, 189–196. DOI: 10.1046/j.1461-0248.2003.00417.x.

Tompkins, D.M., Dunn, A.M., Smith, M.J. and Telfer, S. (2011) Wildlife diseases: from individuals to ecosystems. *The Journal of Animal Ecology* 80, 19–38. DOI: 10.1111/j.1365-2656.2010.01742.x.

Torchin, M.E., Lafferty, K.D., Dobson, A.P., McKenzie, V.J. and Kuris, A.M. (2003) Introduced species and their missing parasites. *Nature* 421, 628–630. DOI: 10.1038/nature01346.

Toscano, B.J., Newsome, B. and Griffen, B.D. (2014) Parasite modification of predator functional response. *Oecologia* 175, 345–352. DOI: 10.1007/s00442-014-2905-y.

Vitousek, P., D'Antonio, C., Loope, L.L. and Westbrooks, R. (1996) Biological invasions as global environmental change. *The American Scientist* 84, 468–478.

Werner, E.E. and Peacor, S.D. (2003) A review of trait-mediated indirect interactions in ecological communities. *Ecology* 84, 1083–1100. DOI: 10.1890/0012-9658(2003)084[1083:AROTII]2.0.CO;2.

Wilmers, C.C., Post, E., Peterson, R.O. and Vucetich, J.A. (2006) Predator disease out-break modulates top-down, bottom-up and climatic effects on herbivore population dynamics. *Ecology Letters* 9(4), 383–389. DOI: 10.1111/j.1461-0248.2006.00890.x.

Wilson, K., Fenton, A. and Tompkins, D. (eds) (2019) *Wildlife Disease Ecology: Linking Theory to Data and Application*. Cambridge University Press, Cambridge, UK. DOI: 10.1017/9781316479964.

Woods, F.W. and Shanks, R.E. (1959) Natural replacement of chestnut by other species in the great smoky mountains national park. *Ecology* 40, 349–361. DOI: 10.2307/1929751.

Wootton, J.T. (1994) The nature and consequences of indirect effects in ecological communities. *Annual Review of Ecology and Systematics* 25, 443–466. DOI: 10.1146/annurev.es.25.110194.002303.