

Chapter 3

Trait-Mediated Effects of Parasites on Invader-Native Interactions

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3.1 Introduction

Most work on parasite-induced behavioural change in hosts focuses on the mechanisms underlying these changes and their direct consequences for parasite and host fitness (see other chapters in this volume). However, infected hosts do not exist in isolation; they form part of a community of organisms that interact through an array of trophic links. Here, we broaden the focus of parasite-modified behaviour to examine the indirect consequences of such behavioural changes for species that interact with the host, and explore how this may impact community structure. In particular, we review our work on crustacean host-parasite systems where we find that parasites affect a range of trophic interactions between invasive and native host species. We examine the potential significance of these parasite-induced behavioural effects in the biological invasion process.

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From a population perspective, we usually think of the direct effects of parasitism on the host – the morbidity and mortality induced by the parasite in hosts. However, recent theoretical and empirical research suggests that the indirect effects of parasitism may be equally important in structuring communities (Hudson et al. 2006; Hatcher and Dunn 2011). Indirect interactions occur when the impact of one species on another affects populations of a third species, with these interactions being density- or trait-mediated. Change in population density has been regarded as the main mechanism driving such indirect interactions. For example, the decline in the Iberian Lynx was an indirect result of parasite (myxamatosis & rabbit haemorrhagic disease) induced decline in its rabbit prey (Ferrer and Negro 2004). However, indirect interactions can also be caused by changes in behaviour, development or physiology; for example parasite (nematode) induced vulnerability to predation mediates population cycles in snowshoe hares (Murray et al. 1997). Such effects, known as trait-mediated indirect effects (Werner and Peacor 2003) can theoretically be as important as density-mediated effects for community structure and function (Abrams and Matsuda 1996) and are now considered an important driving factor in community ecology (Ohgushi et al. 2012).

Trait-mediated interactions may be especially relevant in parasite-host systems because parasites do not necessarily kill their hosts, at least not immediately, but frequently modify host behaviour or development (reviewed in Lefevre et al. 2009; Thomas et al. 2010 and chapters in this issue). Such trait changes may have no apparent deleterious effect on hosts measured in isolation. However, if these trait modifications reduce host fitness when interacting with other species, we can nevertheless regard them as aspects of virulence; we have referred to such characteristics as “cryptic virulence” (MacNiel et al. 2003c; Hatcher and Dunn 2011).

In our laboratories at The University of Leeds and Queen’s University Belfast, we are particularly interested in the roles played by parasites in biological invasions (Prenter et al. 2004; Dunn 2009; Hatcher and Dunn 2011; Dunn et al. 2012). Parasites (here we use the term to include macro- and microparasites and parasitoids) are an important consideration in biological invasions for a number of reasons (Fig. 3.1). Firstly, some invasions may succeed partly because the introduced species leaves behind its parasites (and their deleterious effects) in the native range (a mechanism known as enemy release; Mitchell and Power 2003; Torchin et al. 2003). In other cases, introduced species arrive with their parasites, but the parasites go on to infect populations of related host species in the recipient range (the phenomenon of spillover; Daszak et al. 2000), often with highly deleterious effects on the new host. Parasite spillback or dilution may also occur (from an invasions perspective, where native parasites in the invaders new invaded range cross into introduced hosts; Kelly et al. 2009). These can be considered as direct effects in that they influence host (novel or original) survival directly via presence (or absence) of the parasite. In addition, many parasites are themselves invasive, and the process of disease emergence shares many similarities with that of biological invasion (Hatcher et al. 2012a, b; Dunn and Hatcher 2015).

Furthermore, the importance of parasite-induced indirect effects in the process of biological invasion has now been recognized for a range of terrestrial

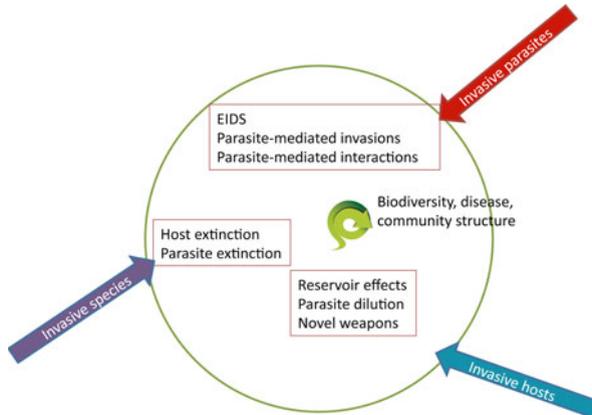


Fig. 3.1 Alternative ways in which invaders cause ecological novelty through their interactions with parasites. *Green circle*: native community. *Red arrow*: invasive parasites can drive changes in host abundance and extinction and can mediate native/invader interactions leading to changes in biodiversity and community structure. *Blue arrow*: invasive hosts can co-introduce parasites which may act as novel weapons; invasive species may also acquire endemic parasites resulting in parasite amplification or dilution. *Purple arrow*: extinctions and changes in community structure as a result of biological invasions can affect native parasite-host interactions. *Green spiral*: feedback between parasite prevalence and biodiversity (From Dunn and Hatcher 2015)

and aquatic, plant and animal systems (White et al. 2006; Dunn et al. 2012). Parasite-induced trait effects have been reported as important in ongoing biological invasions in diverse taxa and ecosystems, including wild oat (*Avena fatua*) in Californian grasslands, fire ants (*Solenopsis invicta*) in North America and amphipods in UK freshwaters (Dunn et al. 2012; Dunn and Hatcher 2015). Here, we review the importance of trait-mediated effects, with particular focus on the crustacean invasions studied in our laboratories in the UK. We use a community module-based approach (Holt 1997; Hatcher et al. 2006) to structure this review, allowing us to examine systematically the potential “targets” of indirect effects.

3.2 Crustacean Invasion Study Systems

Amphipod crustaceans are often keystone species in freshwater ecosystems. Through processing nutrients and providing prey for larger invertebrates and vertebrates, they provide important ecosystem services (MacNeil et al. 1997). They process the primary basal energy resource (leafy detritus) through shredding, with strong impacts on community structure. They also consume smaller invertebrate species in the food web, influencing macroinvertebrate species richness and diversity, and are key prey for commercial and recreational fish stocks, and for wildfowl. Furthermore, amphipod species differ in their propensity towards predation and

detritus processing, and thus from an ecosystem perspective, there is unlikely to be equality of functionality between invader and native. Therefore, the impact of parasitism on amphipod population dynamics or invasion outcomes could have profound ramifications for the diversity and structure of aquatic communities as well as having eco-economic costs.

3.2.1 Amphipod Invasion

In rivers and streams in Ireland, the native amphipod *Gammarus duebeni celticus* is being replaced by the European *Gammarus pulex*. In addition to influencing native amphipod populations, *G. pulex* invaded rivers also have lower macroinvertebrate abundance and diversity (Kelly et al. 2006). A further two species of non-native amphipods also co-occur; *Gammarus tigrinus* and *Crangonyx pseudoeogracilis*, despite being weaker competitors and being predated by the other invasive and native amphipods. In mainland Europe, the invasive *Dikerogammarus villosus* is a voracious predator of macroinvertebrates including native and other invasive amphipods (Dodd et al. 2014), with invaded regions showing a decrease in macroinvertebrate abundance and diversity (Rewicz et al. 2014).

Comparison of invasive and native amphipods reveal differences in detritivory, in predation on native invertebrates, as well as a hierarchy of competition and intraguild predation (i.e., predation of ecological guild members, that is, potential competitors; Polis et al. 1989) between these amphipods (Fig. 3.2).

Amphipods are host to a suite of parasites including viruses (Bojko et al. 2014; Arundell et al. 2015), microsporidia (Terry et al. 2003), trematodes (Arundell et al. 2015) and acanthocephala (MacNeil et al. 2003a), which modify competitive and trophic interactions of their hosts. There is correlative evidence that enemy release may be a factor in both *G. pulex* and *D. villosus* invasions. In Ireland, Dunn and Dick (1998) have shown that parasite diversity is higher in the native *G. duebeni celticus* than in the invading *G. pulex*. Five species of parasite were detected, of which three were shared but two, the microsporidian *Pleistophora mulleri* and the acanthocephalan *Polymorphus minutus*, were restricted to the native host. For two species (*Embata parasitica* and *Epistylus* sp.) that infected both native and invading species, parasite prevalence and burden was higher in native hosts. However, this pattern was not universal; prevalence of the acanthocephalan *Echinorhynchus truttae* was found to be higher in the invasive *G. pulex* (Dunn and Dick 1998; Hatcher and Dunn 2011). A recent study of newly invasive *D. villosus* populations in the UK provides evidence of enemy release from viral, metazoan and microsporidian parasites that are highly prevalent in the (invasive) continental range (Bojko et al. 2014; Arundell et al. 2015), although there is also evidence that parasite diversity has increased in the 5 years since this species has been reported in the UK (Bovey et al. unpublished).

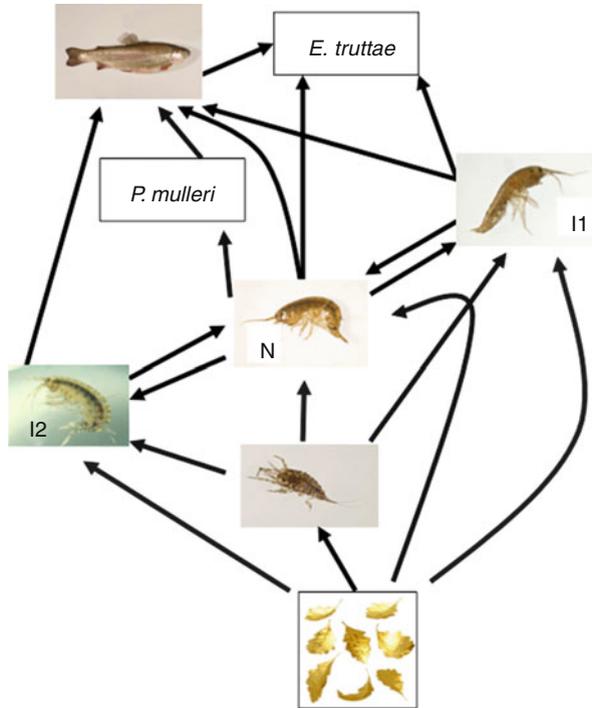


Fig. 3.2 Simplified food web depicting amphipod invader-native interactions in Ireland. The native *Gammarus duebeni celticus* (*N*) sits mid-way in an intraguild predation hierarchy between the invasives *G. pulex* (*I1*) and *G. tigrinus* (*I2*). Amphipods prey on smaller invertebrates (e.g. *Asellus aquaticus*, shown) and process leafy detritus. They are prey to salmoniid fish (e.g. *Salmo trutta*, shown). Two parasites modify gammarid interactions: *Pleistophora mulleri* infects *G. d. celticus*, and *Echinorhynchus truttae* infects *G. d. celticus* and *G. pulex* as intermediate hosts, utilizing salmoniid fish as the definitive host. Arrows depict direct trophic interactions; direction of arrow indicating direction of energy flow

3.2.2 Crayfish Invasions

In Europe, the decline of the native white-clawed crayfish (*Austropotamobius pal-lipes*) and its replacement by the North American signal crayfish (*Pacifastacus leniusculus*) is at least partly mediated by parasitism (Dunn 2009). The fungal parasite *Aphanomyces astaci* (which causes crayfish plague) was co-introduced with the signal crayfish (Holdich and Poeckl 2007), whilst an endemic microsporidian parasite *Thelohania contejeani* affects the endangered native species (Oidtmann et al. 1997).

3.3 Module Approach to Indirect Interactions

To examine how parasites influence invasion dynamics and impact, we need an understanding of the potential for indirect effects of parasitism on other species in the invaded community. Analysis of community modules helps to categorize all the potential indirect effects that may ramify from a focal host-parasite pairing (Fig. 3.3). Community modules (Holt 1997) are sets of three or more strongly

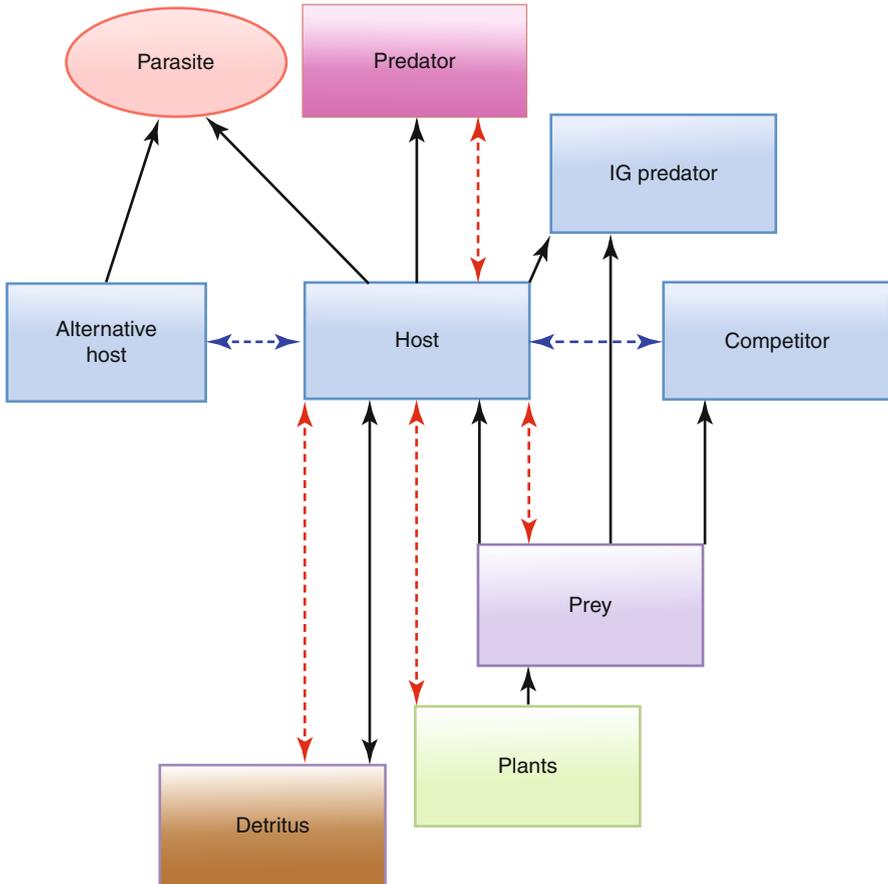


Fig. 3.3 Parasite-induced indirect interactions in community modules. Interaction links between a focal host (*blue, bold border*) and closely linked community members are shown. *Bold arrows* depict direct interactions between species; the direction of energy flow is indicated by the *arrow*. Crustacean amphipods are involved in many trophic interactions, as predators and prey, and as detritivores and processors of detritus, as well as being hosts to parasites. *Dashed arrows* depict sample indirect interactions with other species; the examples show where a parasite (*red*) may indirectly affect interactions between the host and other species by modifying host behaviour. Conceivably, interactions between any species pair may be modified; *red arrows* indicate vertical indirect interactions, *blue* show horizontal indirect interactions

interacting species, providing a bridge between simple single population or two-species dynamics and the inherent complexity of complete communities. Modules provide a basis for analysing indirect interactions mediated by a third species, and how interactions such as predation and parasitism themselves interact.

All the major trophic interactions in an ecosystem may be affected by parasitism (Hatcher and Dunn 2011). From the perspective of understanding invasions, we can distinguish between two relevant facets of module structure where parasites may have impact (Dunn et al. 2012):

Horizontal interactions between species on the same trophic level. These may include competitive interactions (which may be influenced by parasites in one or more host species at that level) or apparent competition and related interactions (for instance, where two species do not compete directly for resources, but are host to the same parasite species). Via their effects on competitive strength or apparent competition, parasites may therefore influence invasion rate/success, and coexistence/species replacement dynamics.

Vertical interactions between species at different trophic levels. These include consumptive predator-prey, herbivory and detritivory interactions. Such vertical interactions are relevant to understanding ecological impact in invasion biology, as some of the most devastating invasive species have been demonstrated as more voracious consumers than native counterparts (Dick et al. 2014). As we will review, parasites influence predation rates on or by their hosts, and therefore may strongly influence the strength of these interactions.

Here, we review evidence for each of these indirect interactions in the crustacean-parasite systems we study, along with a brief examination of evidence from other systems.

3.4 Trait Effects of Parasites on Trophic Interactions

3.4.1 Detritivory

In many aquatic ecosystems, leafy detritus provides the primary basal energy resource. Amphipods and isopods play an important role in processing this detritus, converting it from coarse to fine particulate organic matter that can be consumed by filter feeders and collector-gatherers (MacNeil et al. 1997). Parasitism has been shown to modify detritivore interactions in some of these systems. Infection by the acanthocephalan parasite *Acanthocephalus tahlequahensis* was found to cause a reduction in detritus processing by its isopod host, *Ceacidotea communis* in streams in North America (Hernandez and Sukhdeo 2008). This trait effect has community-wide ramifications, with parasites predicted to reduce detritus processing by up to 50 %, affecting energy transfer throughout the ecosystem. Biological invaders may have different rates of detritus processing than the native species that they replace. For example, leaf shredding function of the invasive *Dikergomarus villosus* was

lower than that of 3 native species MacNeil et al. (2011), and current work is exploring whether parasites can also influence detrital processing.

Trait-mediated effects can be both subtle and context-dependent. For example, larval *Drosophila melanogaster* compete with the fungus *Aspergillus niger* for dead organic matter; *D. melanogaster* larvae suppress fungal growth, whilst the fungus secretes toxins that inhibit the fly larvae. Infection with the parasitoid *Asobara tabida* reduces feeding by *D. melanogaster* larvae, and this influences its interaction with the fungus; this form of cryptic virulence leads to complex interactions between the competitors (Rohlf 2008).

3.4.2 Herbivory

Herbivory *per se* has not been studied in our crustacean systems. However, as herbivory is key to processing the basal energy resource in many ecosystems, it would be remiss not to discuss some key findings from other systems, especially as parasitism of herbivores is well documented as having profound effects on community structure. Disease outbreaks in vertebrate populations have led to some dramatic examples of cascading effects. For instance, myxomatosis and rinderpest have led to population declines of dominant grazers (rabbits *Oryctolagus cuniculus* and wildebeest, *Connochaetes taurinus*, respectively), with consequent effects on both plant and predator communities (reviewed in Hatcher and Dunn 2011). In these examples, parasitism has its impact via classical density-mediated effects (reduced host survival); however, recent work suggests that less obvious trait-mediated effects on host fitness may also have cascading effects in communities. For example, endophytes of grasses which reduce host palatability to herbivores can have knock-on effects for plant community composition and succession, and also appear to influence herbivore, detritivore and predator communities. Because these endophytes protect hosts from herbivory, infection with endophytes may underlie the invasive success of some grass species (Rudgers et al. 2007). The trematode *Cryptocotyle lingua* does not kill its intermediate host, the algal grazing periwinkle *Littorina littorea*, but damages the host digestive system. As a result, per capita algal grazing was reduced by 40 % in infected periwinkles, leading to a 65 % increase in algal cover, which is likely to influence the recruitment of other species that require a rocky surface for colonization (Wood et al. 2007).

3.4.3 Competition

Parasite-mediated effects on competition provide some of the most-cited cases of parasite impact on community structure. Parasite-induced density effects have long been recognized as having potential to drive community structure via their effects

on competitors (Elton 1958). Indeed, seedling mortality induced by specialist pathogens could be one of the chief drivers of plant biodiversity in tropical rainforests (Freckleton and Lewis 2006) and may explain aspects of global diversity patterns today (Kulmatiski et al. 2008). In contrast, multi-host parasites may reduce biodiversity, preventing coexistence or speeding the replacement of one host species by another. One well-documented case is that of squirrel poxvirus (SQPV) in the red squirrel *Sciurus vulgaris*, which is under threat of replacement by the grey squirrel *Sciurus carolinensis* in the UK (Tompkins et al. 2003). SQPV has a direct, strongly pathogenic effect on red squirrels (Tompkins et al. 2003) and can potentially be spread through multiple routes (Collins et al. 2014). In England, where the virus is present, decline in red squirrels is up to 25 times more rapid than in Scotland and Italy, where the virus is absent (Rushton et al. 2006).

However, trait-mediated competitive interactions are also known to affect both animal and plant invasions. For instance, plant pathogens can potentially influence plant community composition and grassland diversity via trait-mediated indirect effects on competition; Barley Yellow Dwarf Virus (BYDV) modifies competition between native perennial bunchgrasses and invasive annual grass species in the Californian plains. In field plot experiments, BYDV infection did not affect bunchgrass survivorship when grown alone, but halved survivorship of bunchgrass grown with invasive species (Malmstrom et al. 2006). This effect may facilitate the ecological replacement of bunchgrasses by invasive competitors (Borer et al. 2007). A further example of the power of parasite-induced trait effects concerns parasitic phorid flies. Phorids have surprising effects on their ant hosts, causing direct virulence effects in infected hosts, but indirectly exerting trait effects in *uninfected* hosts that exhibit parasite avoidance behaviour. These parasitoids develop in the head capsule of worker ants – leading to decapitation before the fly pupates and emerges as an adult. The presence of the phorid *Apocephalus* sp. induces refuge seeking behaviour in potential hosts, preventing defensive behaviour towards the competing ant species (Lebrun and Feener 2007). In the presence of phorid flies, an otherwise dominant species may be outcompeted by an inferior competitor. Interestingly, ant species that are dominant competitors experience higher levels of infection as host alarm and foraging trail pheromones are used by the parasitoid to detect hosts in which they will lay their eggs. Fear of parasitism may be more widespread than we appreciate: in the 2003 SARS pandemic, in addition to state-imposed contact control measures, there were notable decreases in social behaviour (such as restaurant usage and attendance of social events) as people attempted to reduce their risk of infection (Blendon et al. 2004).

In the Ireland *Gammarus* system, we suspect that trait effects of parasites may act via competition on the invasion process. For instance, parasite-induced changes in predation on shared invertebrate prey could release or exacerbate invader-native competition. However, intraguild predation is also key to invader-native interactions, thus it is difficult to tease apart the importance of competition versus predation (including intraguild predation between competing gammarids) in these community modules; these processes are discussed below.

3.4.4 Predation

Parasites can influence predation via trait effects in two ways; parasites of predators may alter the predatory behaviour of such hosts, whereas parasites of prey species can alter the likelihood of the host being consumed. Both scenarios are found in crustacean systems we study.

3.4.4.1 Predation by the Host on Lower Trophic Levels

In laboratory experiments, the microsporidian *P. mulleri* causes little direct mortality or reduction in fecundity to its host, the native *G. d. celticus*. However, this parasite leads to reduced predatory ability on smaller sympatric amphipods and isopods (MacNeil et al. 2003b; Fielding et al. 2005). The effects of a second parasite, the acanthocephalan *E. truttae*, on its host the invasive *G. pulex*, are more complex and depend on prey size and species (Dick et al. 2010; Paterson et al. 2015). Analyses of predator functional responses (the per capita prey consumption as a function of prey density; Holling 1966; Dick et al. 2014) reveal that, when provided with juvenile *A. aquaticus*, *E. truttae*-infected *G. pulex* exhibited a significantly higher functional response asymptote (i.e., exhibit higher predation rates) than uninfected individuals (Dick et al. 2010).

For both the invasive *G. pulex* and the native *G. d. celticus*, parasitism (with *E. truttae* and *P. mulleri* respectively) influenced foraging mostly through effects on prey handling time (Paterson et al. 2015). Whilst functional responses to some more mobile species (e.g. mayfly nymphs, *Baetis rhodani*) were lower for infected amphipods, predation was increased on the more sessile *Simulium* species. Furthermore, additional trait-mediated effects (the presence of higher-order fish predators) further modified foraging behaviour and the impact of parasites (Paterson et al. 2015). These findings, together with those for detritivory and cannibalism (see below), are strong indicators that parasites not only influence appetite, they influence prey choice and may induce trophic shifts in the host. This may be particularly relevant for our understanding of parasite impact in communities in general, as well as their role in invasion success and impact (Dick et al. 2014; Dunn and Hatcher 2015).

Parasitism also mediates interactions between invasive and native crayfish and their native prey (Dunn 2009). The invasive signal crayfish, *P. leniusculus*, which was introduced to Europe for aquaculture, is driving extirpation of native European crayfish including the endangered white clawed crayfish *A. pallipes*. Crayfish plague (caused by the fungus *Aphanomyces astaci*) is asymptomatic in the signal crayfish. However, the invader acts a reservoir for the parasite which causes mass mortality in the native species (Holdich and Poock 2007). In contrast, the microsporidian parasite *Thelohania contejeani* (Imhoff et al. 2011) mediates predation by the host through trait effects. *T. contejeani* causes porcelain disease, a chronic infection in the native crayfish, which suffer muscle damage and a reduction in their predatory abilities (Haddaway et al. 2012). Comparison of predatory functional

responses revealed that native crayfish had a lower prey intake rate than did the invasive species, reflecting a longer prey handling time. This difference is exacerbated by the parasite, which induced muscle damage leading to a reduced attack rate and increased prey handling time, contributing to a 30 % reduction in prey intake by parasitised native crayfish (Haddaway et al. 2012).

The effects of parasites on predator survival and/or behavior can have knock-on effects for prey species (Hatcher et al. 2006). In some cases, the effects can long outlive the duration of active infection in a population, and would be missed in contemporary experiments. For instance, an outbreak of canine parvovirus in grey wolves (*Canis lupus*) in the US National Park of Isle Royale 20 years ago precipitated a population crash from which the wolf population has never recovered (probably because the crash reduced genetic diversity in the wolf population). This density-mediated effect has shifted the balance of population regulation of the chief prey species (moose, *Alces alces*) away from predation and towards correlation with climatic factors (Wilmers et al. 2006). Whether trait-mediated effects can have such lasting impact has yet to be examined.

3.4.4.2 Predation on the Host by Higher Trophic Levels

In some cases, predators attack infected prey more frequently than healthy prey because parasitism weakens hosts making them easier to catch. This parasite-induced vulnerability to predation may determine population dynamics and community structure in some natural systems (Packer et al. 2003; Holt and Roy 2007). If infected prey provide an “easy” resource for predators to exploit, parasitism can enhance persistence of a predatory species (Hethcote et al. 2004). Alternatively, predators and parasites can interact to determine prey population persistence and dynamics. For instance, parasite-predator interactions can drive cyclic population dynamics in the snowshoe hare (*Lepus americanus*). Murray et al. (1997) found that hare populations prone to strong predation more than doubled their survival rates when treated with anthelmintics. Infection with nematode parasites had no other measurable effects on host fecundity or direct mortality, thus increased predation on infected hosts appears to be the sole cause of virulence in this system. Similarly, red grouse *Lagopus lagopus* killed by predators had significantly higher burdens of the caecal nematode *Trichostrongylus tenuis* and worm burden reflected the level of gamekeeper control of predators (Hudson et al. 1992).

Many of the behavioural changes described above represent “by products” of infection (Poulin 1995). Nonetheless, in the community context, their outcomes may be far from “boring” (Poulin 1995). Other changes in prey/host behavior may be adaptive, resulting from selection on the host to avoid infection, or selection on the parasite to enhance transmission. For example, parasites can influence predation via effects on the avoidance behavior of potential hosts. Tadpoles of the toad *Bufo americanus* exhibit an adaptive “fear” response of hyperactivity to chemical cues from cercariae of the trematode *Echinostoma trivolvis*, which reduce their chances of becoming infected (Rohr et al. 2009). This increased activity could potentially offset

adaptive predator avoidance strategies (predator presence elicits a decrease in activity) and lead to suboptimal foraging and developmental rates (Raffel et al. 2010).

Trophically transmitted parasites have indirect life cycles and are transmitted to the definitive host when it preys upon an infected intermediate host. Many species of acanthocephalan and trematode parasites have been found to manipulate the anti-predator behaviour of the intermediate host, thereby increasing its vulnerability to predation (Moore 2002; Lefevre et al. 2009). For example, the acanthocephalan parasites *E. truttae* and *P. minutus* both induced changes in activity and photophilic behaviour of their amphipod hosts: infected hosts show higher motility and are more photophilic than uninfected hosts (MacNeil et al. 2003a), enhancing transmission to the definitive fish and duck hosts. Although both the native and invasive species are used as intermediate hosts, *E. truttae* prevalence is higher in the invasive *G. pulex*, which could have ramifications for invasion dynamics as well as having the potential to increase parasite frequency in commercially important fish (Hatcher and Dunn 2011).

3.4.5 Intraguild Predation

Intraguild predation, that is, predation between potential competitor species, is widespread in ecological communities (Polis et al. 1989). For example, wolves compete with hyenas for prey, but also prey upon them, whilst invasive and native amphipods show mutual intraguild predation whilst perhaps also competing for other invertebrate prey. Intraguild predation is a special case wherein predation by and of focal host species need to be considered together. In the N. Ireland amphipod system, intraguild predation is key to understanding invasion and coexistence (Dick et al. 1993). The two species of parasite (the microsporidium *P. mulleri* and the acanthocephalan *E. truttae*.) have been shown to influence both the prey and predatory components of intraguild predation between these amphipods, with *P. mulleri* infecting the abdominal musculature in the native *G. d. celticus*, thus reducing host motility (MacNeil et al. 2003b). In field enclosure experiments, *P. mulleri* had no impact on *G. d. celticus* survival whether in single populations or in mixed species populations with the smaller *G. tigrinus*. However, infection of *G. d. celticus* resulted in increased survival of the smaller intraguild prey species; whilst *G. tigrinus* kept in mixed populations with *G. d. celticus* showed 90 % mortality over 2 weeks, this species was able to coexist with infected *G. d. celticus*. Laboratory experiments confirmed that coexistence was facilitated by a reduction in intraguild predation by infected *G. d. celticus* on *G. tigrinus* (Fig. 3.4). Similarly, infected *G. d. celticus* showed less intraguild predation of another smaller amphipod, *C. pseudogracilis*. In addition to modifying the intraguild predatory abilities of its host, *P. mulleri* infection also increased host vulnerability to becoming the intraguild prey of the larger invasive species *G. pulex*.

For *G. pulex*, infection by the acanthocephalan *E. truttae* not only modifies host predatory abilities on smaller invertebrate species, it also reduces predation on its intraguild prey, including the native *G. d. celticus* (MacNeil et al. 2003a). Field

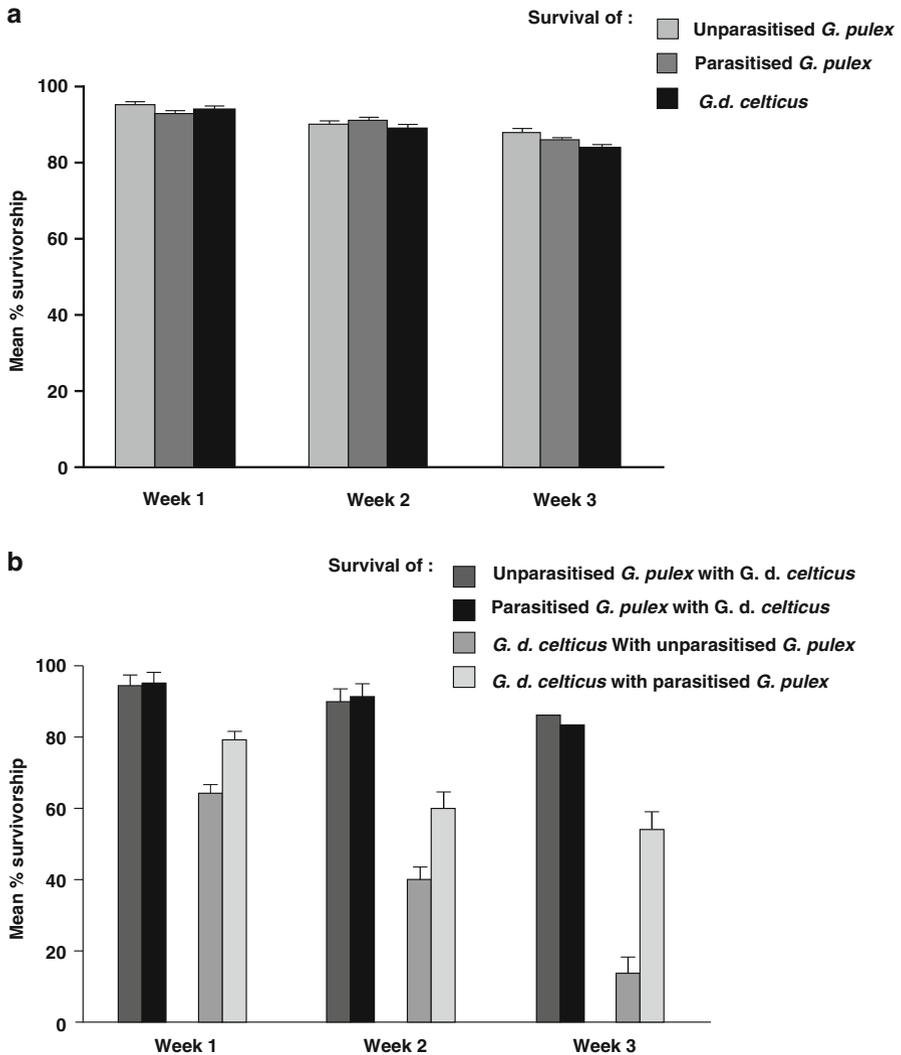


Fig. 3.4 Survival of the native species *Gammarus duebeni celticus* and of uninfected and *Echinorhynchus truttiae*-infected *Gammarus pulex* (invader) in (a) single and (b) mixed species enclosures. Parasitism did not direct affect survival of the host *Gammarus pulex* but enhanced survival of the native species (From MacNeil et al. 2003a)

enclosure experiments were used to assess the impact of parasitism on the native and invading hosts in single and mixed species populations. In single species populations, *E. truttiae* did not directly affect the survival of the native or the invader. In mixed species populations, the survival of *G. pulex* was again unaffected. However, parasitized *G. pulex* were less likely to attack the native species leading to higher survival of the native species (MacNeil et al. 2003a). This reduction in intraguild

predation can theoretically facilitate species coexistence, limiting spread of the invader (Hatcher et al. 2008, 2014).

Mathematical models of this process demonstrate that the trait-mediated effects of parasites on predation can act as a strong force on co-existence dynamics, equal to that generated by density effects (Hatcher et al. 2008, 2014). Intraguild predation is a curious population module because it is theoretically rather unstable, predicted in many cases to disintegrate to extinction of either the intraguild predator or prey. Whilst parasites with density (mortality) effects can promote coexistence of predators and prey (Hatcher et al. 2008), we have also found that parasites with trait effects can have an equally strong impact on coexistence (Hatcher et al. 2014). Indeed, parasites with zero classical virulence, but cryptic virulence in the form of altered vulnerability to or propensity for predation, can have as pronounced an impact as density in promoting or inhibiting coexistence (Fig. 3.5). Parasites can thus have strong ecological impacts, even if they have negligible classical virulence, underscoring the need to consider trait-mediated effects when predicting effects of parasites on community structure in general and biological invasions in particular.

3.4.6 *Cannibalism*

One further trophic interaction could be important in understanding the dynamics of these amphipod systems. Cannibalism is a frequent occurrence in many systems, being both stage- and sex-specific; adults frequently consume immature conspecifics, and adults at moult – in particular females that may be held in precopula – are also vulnerable to cannibalism (MacNeil et al. 2003c; Bunke et al. 2015). In *G. d. celticus*, infection with *P. mulleri* can cause increased vulnerability to cannibalism, which also leads to enhanced transmission of the parasite as it is transmitted directly *per os* (MacNeil et al. 2003b). Although more vulnerable to being cannibalized themselves, recent work has shown that infected individuals become more cannibalistic, eating twice as many conspecifics in laboratory experiments. This may reflect the metabolic demand of the parasite; infected individuals are less able to consume prey of different species, and it may be that smaller conspecifics are an easier food item to capture and handle (Bunke et al. 2015). Interestingly, choice experiments indicate that uninfected *G. d. celticus* preferentially cannibalise uninfected conspecifics (Bunke et al. 2015). The parasite is transmitted via cannibalism, thus it seems that this behavior is an adaptive mechanisms to avoid the risk of parasitic infection.

3.5 Conclusions

Our crustacean study system is one of few systems where the impact of parasites on a range of different community modules has been studied, and we have seen that trait-mediated indirect effects have the potential to ramify both horizontally and

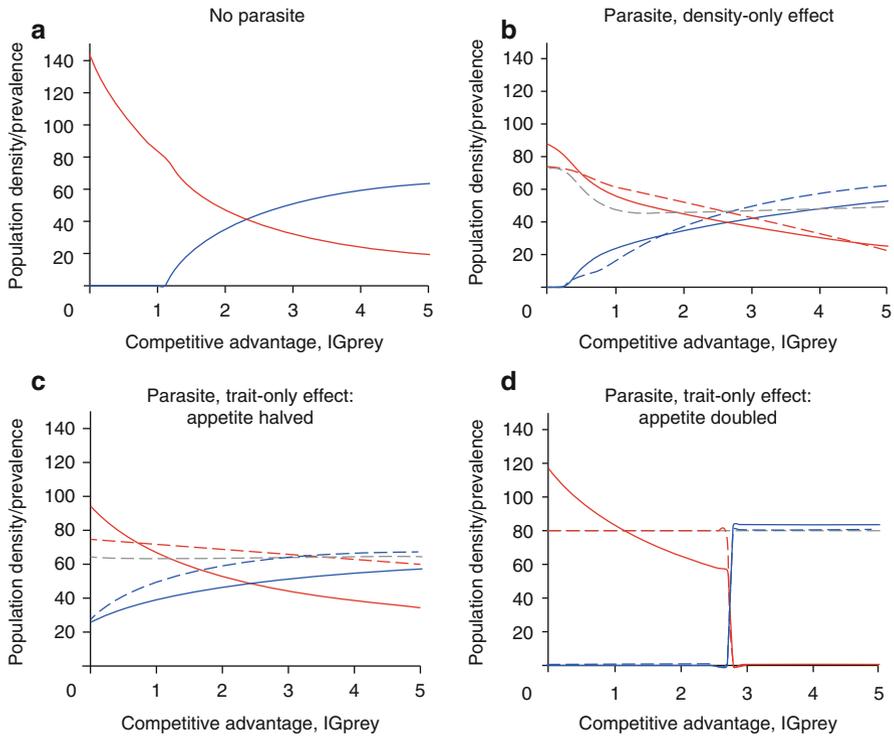


Fig. 3.5 Trait-mediated effects of parasitism on IGP systems. Equilibrium population densities (*solid lines*) and parasite prevalence (*dashed lines*) in the more predatory species (*intraguild predator*; *red*) and the weaker predator (*intraguild prey*, *blue*) plotted against the relative competitive advantage of the intraguild prey. **(a)** in the absence of parasitism, a strong intraguild predator excludes competitively weak intraguild prey; **(b)** virulent parasites (inducing 10 and 30 % mortality in the prey and predator respectively) enable coexistence of predator and prey over a broader parameter range; **(c)** parasites with no mortality effect but which reduce predatory ability strongly enhance coexistence whereas **(d)** parasites that increase predation strongly reduce coexistence (From Hatcher et al. 2014)

vertically in these modules. It is likely, therefore, that such effects underpin other systems. In particular, since parasites are known to have a wealth of effects on feeding behaviour and vulnerability to predation, it seems likely that they will strongly influence vertical trophic interactions. We have good evidence that, for a broad range of systems, invasion impact is related to the predatory propensity or resource consumption by the introduced species (Dick et al. 2014). Hence, parasites could potentially be important in modifying predation/consumption in a number of these systems, contributing to invasion success and impact. It is therefore important to study trait-mediated effects from the practical perspective of understanding and predicting invasion outcomes and also to understand the impact of parasites on biological invasion in particular and community ecology in general.

With the increasing realization that parasites are important components of ecosystems (Hudson et al. 2006; Lafferty et al. 2008), the potential importance of behavioural effects of parasites in a community context now deserves recognition (Lefevre et al. 2009). We have shown these community effects to be important both empirically and theoretically at the community module level (MacNeil et al. 2003c; Dick et al. 2010; Hatcher et al. 2014). Parasitologists and ecologists need to examine further the community and ecosystem-level consequences of trait-mediated effects and the cryptic virulence to which they lead. There is increasing recognition that parasites play important roles in ecosystem functioning, by influencing species coexistence patterns, biological invasions, energy flow and community stability (Hudson et al. 2006; Hatcher et al. 2012a, b). Underpinning all these ecosystem-level effects are the interactions between species in community modules. However, whilst we can demonstrate parasite-induced trait-mediated interactions at the level of modules, scaling up to the ecosystem level is a challenging proposition, both theoretically and empirically.

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