Roles of parasites in animal invasions

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Biological invasions are global threats to biodiversity and parasites might play a role in determining invasion outcomes. Transmission of parasites from invading to native species can occur, aiding the invasion process, whilst the 'release' of invaders from parasites can also facilitate invasions. Parasites might also have indirect effects on the outcomes of invasions by mediating a range of competitive and predatory interactions among native and invading species. Although pathogen outbreaks can cause catastrophic species loss with knock-on effects for community structure, it is less clear what impact persistent, sub-lethal parasitism has on native-invader interactions and community structure. Here, we show that the influence of parasitism on the outcomes of animal invasions is more subtle and wide ranging than has been previously realized.

Biological invasions are global phenomena that threaten terrestrial, marine and freshwater biodiversity [1–4]. In particular, invasions are leading to BIOTIC HOMOGENIZATION (see Glossary), with widespread ecological and evolutionary implications [4,5]. In spite of such realization, the rate of invasions resulting from anthropogenic activities is increasing [6,7]. Indeed, we are now facing INVASIONAL MELTDOWN [7–9]. Therefore, we must identify mechanisms underpinning the invasion process if we are to understand the determinants of invasion success, and be able to predict the outcomes of ongoing and potential invasions. PARASITES are pervasive in biological communities and are implicated as being key in an increasing number of biological invasions [10–13]. A review of the roles of parasites in invasions is therefore timely, and here we focus on their influence on the success or failure of invasive species when encountering native species and associated communities. However, there are still gaps in our understanding of the linkage between parasites and invasions, particularly of the impacts of parasites at broader community scales.

Parasitism of natives and invaders

There are several causes and consequences of differences in parasitism between invaders and natives, including factors associated with the transmission of parasites between hosts and with the translocation of parasites with invaders.

Parasite transmission from invaders to natives

Parasites have detrimental effects on the survival and

Glossary

Allee effects: low density populations, and those with skewed sex ratios, might decline because individuals have lower reproductive rates (e.g. because mating encounters are rare) [34].

Apparent competition: indirect interaction leading to negative effects of one species on another, mediated through a shared natural enemy, such as predators and parasites. For example, parasite-mediated apparent competition might occur when (i) the parasite differentially affects one competitor, reducing its population growth rate and abundance and hence competitive impact on another species or (ii) one host species acts as a reservoir for the parasite, increasing the impact of the parasite on the second host species [35,36].

Biotic homogenization: increasing replacement of native species by generalist invaders, altering global biodiversity [5].

Cryptic virulence: the parasite does not affect host fitness in single-species populations, but virulence becomes apparent when the host interacts with another species.

Density dependence: mortality rates in a population might increase, and/or birth or growth rates decrease, as the density of the population increases.

Enemy release hypothesis: invading organisms might lose parasites (and other enemies) during invasion [24]. The 'release' from the constraints of natural enemies might enable populations of invading organisms to increase at a higher rate than in the presence of these natural enemies. This, in turn, can lead to a competitive advantage for the invaders over the natives.

Horizontal transmission: occurs between hosts of the same or different generations, commonly through ingestion of the parasite, venereal transmission or direct invasion through an outer layer of covering tissue.

Intraguild predation (IGP): predation between species using the same resources in a similar way [52]. Such mutual predators are not necessarily taxonomically related, but often are. Thus, a propensity for cannibalism is often associated with species engaging in IGP.

Invasional meltdown: the invasional meltdown model [8] suggests that frequent species introductions generate an increasing threat to biological communities. It proposes that ecosystems become more easily invaded as the cumulative number of species introductions increases, and that facilitative (rather than antagonistic) interspecific interactions can exacerbate the success and impact of invaders.

Parasites: organisms living on or in another organism, deriving substances from the host organism, without benefit to the host. Here, we use a broad definition of parasite [64] including parasitoids and other pathogens (disease-causing organisms) producing damage.

Parasitoid: an animal parasitic for only one stage of its life history and free-living at other stages.

Resource competition: competition between species for the use of shared resources such as food and space, where superior competitors utilize or consume resources making them unavailable to inferior competitors.

Sex-ratio-distorting parasites: vertically transmitted parasites are usually only transmitted to offspring by the mother (transovarial transmission), because small sperm size precludes parasite transmission. Several strategies of reproductive manipulation have evolved that enhance the relative frequency of the transmitting sex [65]. For example, feminizing parasites convert genetic males to phenotypic females, thus increasing their opportunities for transmission to new hosts.

Transmission routes: how a parasite is passed between hosts.

Vertical transmission: when parasites are passed from generation to generation of hosts via the host ova (transovarial transmission). Because vertically transmitted parasites rely on host reproduction for their own transmission to new hosts, they are frequently associated with low virulence. Some parasites have a direct life cycle involving only one host species. Others have indirect life cycles involving horizontal transmission between two or more host species, the final host species (where sexual reproduction of the parasite occurs) and one or more intermediate host species.

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fecundity of individuals and can regulate host population dynamics [14–17]. Classically, parasites have been recognized as being important in invasions when naïve host populations are infected by a new parasite transported with introduced hosts. For example, the Aral Sea sturgeon *Acipenser nudiventris* was decimated by a monogenean gill fluke *Nitzschia sturionis* carried by the introduced Caspian Sea sturgeon *Huso huso* [18]; the native European crayfish *Austropotamobius pallipes* has been driven locally extinct as a result of transmission of crayfish plague *Aphanomyces astaci* from the introduced North American crayfish *Pascifastacus leniusculus* [19]; and there are many other examples of introduced pathogens decimating naïve host populations [20–23].

Parasite loss during translocation

The ENEMY RELEASE HYPOTHESIS proposes that invaders lose their (co-evolved) parasites in the process of invasion, leading to higher demographic success of invaders [24,25], which might give them a competitive advantage over natives [26]. Empirical support for this hypothesis comes from observations across a range of taxa, which confirm that invader populations harbour significantly fewer parasites than do native populations [12,24,25]. Although potential mechanisms leading to such patterns are regularly proposed, such as the low probability of parasitized hosts being translocated and the potential for loss of parasites during such movements [24], there is still little empirical discrimination among mechanisms of parasite loss. This is important because, for example, if an invader lacks parasites as a result of low population density, and its parasites can arrive and establish in subsequent invasion waves, the invader will eventually suffer reduced demographic success. However, if the lack of parasites is due to the consistent mortality of parasitized hosts and/or their parasites during translocation, the parasite cannot arrive and have such an effect. Experimental tests of parasite and host tolerances of environmental features of the translocation route, such as ballast water, would begin to address this issue.

Furthermore, depending on the mechanism of parasite loss in the invading species, there are different consequences for the invasion process. The demographic release from parasites might be manifest at any one of the three different phases of invasion: introduction, establishment and demographic spread [2,27]. Each of these phases would require separate theoretical and empirical examination because, in one published model, parasite release appears unlikely to affect the chance of an invader becoming established but might affect the spread of an invader [27]. Also, accumulation of parasites over time in invader populations will influence invasion success [25]. Studies of invasive plants have demonstrated this effect [25], however, the impact of parasite accumulation on invasive animals requires further investigation.

Parasite transmission from natives to invaders

Protection from the effects of parasites might occur in invaders as a result of a lack of TRANSMISSION ROUTES [12,24]. In addition, parasites of native counterparts are often host specific and unable to spread to invaders [10,28].

However, new host–parasite associations can occur, as illustrated by infection of the invading snail *Potamopyrgus antipodarum* by the native trematode *Sanguinicola* sp. [29]. Therefore, investigation of the likelihood of transmission between natives and invaders is crucial to our understanding of invasion success. For example, a recent study showed that, whereas the microsporidian parasite *Pleistophora mulleri* is transmitted via cannibalism between conspecifics of the native amphipod *Gammarus duebeni celticus*, ingestion of parasitized tissue by three invading amphipod species did not lead to their becoming infected [13,30]. However, these native and invading amphipods share acanthocephalan (spiny-headed worm) parasites *Echinorhynchus truttae* and *Polymorphus minutus*, which are transmitted to common final hosts [31]. Because parasitism altered interspecies interactions in this multi-species invasion scenario, determination of transmission routes helped to clarify the success and failure of invaders. However, there remains a paucity of information about behavioural, ecological, immunological and physical barriers that might cause parasite transmission to fail among natives and invaders.

Impacts of host and parasite characteristics on invasion success

Whether parasites survive the translocation process might depend on their mode of transmission. VERTICALLY TRANSMITTED parasites are more likely to be successfully introduced with their invading hosts than are parasites that rely on HORIZONTAL TRANSMISSION. Vertical transmission is often associated with low parasite virulence, thus increasing the likelihood of both the parasite and the host surviving the invasion process. In addition, vertical transmission to new hosts is not dependent on host density. A recent study found that the vertically transmitted microsporidian *Fibrillanosema crangonictidae* had been introduced to Europe along with its North American amphipod host *Crangonyx pseudogracilis* [32]. This is significant, because host SEX-RATIO DISTORTION by this parasite might also facilitate host (and parasite) invasion and establishment [32]: female-biased sex ratios might lead to higher rates of host population increase [33]. Although DENSITY-DEPENDENT and ALLEE EFFECTS [34] might be expected to limit such population growth (because males are relatively rare), males of this species are precocious, promiscuous and not limited in mate search time as occurs in mate-guarding species [32]. However, further testing is required of the demographic effects of sex-ratio distortion during the different stages of invasion.

In addition, there are other traits of both parasite and host that might determine whether invader host and parasite linkages are established. For instance, in parasites with complex life cycles, such as acanthocephalans, all the intermediate hosts must co-occur with the final host [24,31]. Types of host species that feature in recurrent invasion waves as opposed to single events might be more prone to parasitism, because, once an invader population density has increased, more individuals arriving infected with parasites might result in increased transmission efficiency [24]. The black rat *Rattus rattus* has featured in

repeated introductions worldwide and 38% of its native parasites have been recovered from introduced populations [24]. However, we lack comparable data for other invaders that would enable the elucidation of broad patterns of host and parasite traits that are associated with repeated invasions and accumulation of parasites.

Parasite-mediated competition

Parasites and predators have also been implicated historically in the more indirect mediation of interspecies interactions, primarily through shared natural enemies resulting in APPARENT COMPETITION ([35−37], Table 1). Clearly, therefore, where invader and native hosts differ in prevalence and types of parasitism, there is a role for parasites in determining invader success or failure. Indeed, we must realize that interspecific interactions other than competition, such as predation, might also be mediated by parasites.

In a classic laboratory experiment, the sporozoan parasite *Adelina tribolii* was shown to reverse the outcome of competition between two species of flour beetles *Tribolium confusum* and *T. castaneum* [20,38]. Furthermore, a field study [39] suggested a role for the malaria parasite *Plasmodium azurophilum* in reducing the competitive superiority of the *Anolis* lizard *A. gingivinus* over the smaller *A. wattsi*. Such parasite-mediated competition is increasingly recognized as a contributing factor in determining invasion success. For example, in the invasion by the variegated leafhopper *Erythoneura variabilis* (a hemipteran) of vineyards in the USA and the replacement of the native grape leafhopper *E. elegantula* [10], direct interspecific competition was not crucial. However, the decline in the native leafhopper was attributed to the differential effects of the shared hymenopteran PARASITOID *Anagrus epos*. Establishment of the invader contributed to an increased parasitoid population and led to high rates of infection in the native leafhopper.

More recently, there is support [40,41] for the suggestion that invasion by the grey squirrel *Sciurus carolinensis* and the concomitant decline of the native red *S. vulgaris* in the UK is the result of apparent competition mediated through a parapox virus, for which the asymptomatic invader acts as a reservoir for the disease that is usually fatal in the native. Similarly, transmission of the caecal nematode *Heterakis gallinarum* from introduced pheasants *Phasianus colchicus* to wild grey partridge *Perdix perdix* has been implicated in the decline in partridge populations also in the UK [42,43]. Introduced pheasants are largely unaffected by the infection but, as in the previous example, act as a reservoir for the parasite and, without the presence of the invading host, the parasite cannot be maintained in the wild partridge population. This has important implications for future risk assessments of accidental and deliberate wildlife introductions, and the management and conservation of native species.

However, such a complex and intangible force as apparent competition might be attractive as an explanation but difficult to demonstrate conclusively (see also [36]). For example, the cestode parasite *Cylindrotaenia* sp. was implicated in the competitive replacement of the native gecko *Lepidodactylus lugubris* by the invader gecko

Hemidactylus frenatus on Pacific islands. Infestation levels were higher in natives on islands where they were found in sympatry with invaders [44]. However, subsequent experimental studies found no evidence that this parasite played a role in the replacement of *L. lugubris*, leaving RESOURCE COMPETITION as the most likely explanation [45]. However, controlled laboratory experiments with the ichneumonid parasitic wasp *Venturia canescens* and two of its moth hosts *Plodia interpunctella* and *Ephestia kuehniella* successfully separated the effects of resource competition from apparent competition [46]. This demonstrates the need for detailed empirical examination of each putative case of apparent competition.

Parasite mediation of predation: natives and invaders sharing predators

Where invasive and native hosts differ in susceptibility to parasitism and/or in their responses to particular parasites, this might render them differentially vulnerable to shared predators ([11,47], Table 1). Of particular interest are indirectly transmitted parasites that manipulate the behaviour of their intermediate hosts to facilitate transmission to their final host [48]. For example, many species of acanthocephalan induce enhanced activity levels and photophilic ('light loving') behaviour in their intermediate arthropod hosts (e.g. amphipods), rendering them more vulnerable to predation by the final vertebrate fish and bird hosts [48]. Recent studies suggest that such parasites skew the vulnerability of native and invading amphipods to fish predation, thereby influencing the invasion process [47,49]. However, this proposed parasite-mediated predation requires further critical evaluation. Explicit tests are required to examine whether fish prey differentially on native versus invading amphipod species and how parasites influence such predation. Furthermore, because the acanthocephalan *Pomphorhynchus laevis* exists in genetically and morphologically distinct forms, which differ in their manipulative capacities towards host behaviour [50], future work should test for variation in the manipulative effects of different strains of the same parasite on native versus invader.

Parasite mediation of predation: natives and invaders at the same trophic level

It has been argued that potential of transmission of debilitating parasites by ingestion of infected material should select against cannibalism [51] and might also select against INTRAGUILD PREDATION (IGP), where the species are often closely related [30,52]. However, both cannibalism and IGP are common in nature [52]. A recent study showed that a native amphipod *G. d. celticus* varies widely in the prevalence and burden of the microsporidian parasite *Pleistophora mulleri*, whereas none of three invasive amphipod species were infected [13]. The parasite had no detectable direct effect on host fitness, but parasitized hosts were more vulnerable to predation by a larger invading species and showed a reduced capacity to prey on a smaller invading species. Thus, *P. mulleri* exhibited CRYPTIC VIRULENCE, altering mutual predation patterns among native and invaders. The challenge is to understand how the parasite alters the physiology and

Table 1. Mediation of competition and predation by parasites in animal invasions

Parasite/ Parasitoid	Host; nature of parasitism	Effect	Outcome	Interaction/ Comment	Refs
Ascogregarina taiwaiwanensis (Sporozoa)	Mosquito; gut parasite	Survival of native mosquito *Ocherltatus triseriatus* reduced when reared with unparasitized larvae of invader, *Aedes albopictus*, but survival increased when invader larvae are parasitized	Escape from parasites favours range expansion in invader	Mediation of competition – enemy release	[26]
Pleistophora mulleri (Microspora)	*Gammarus duebeni celticus*; parasite necrotizes abdominal musculature of native but does not infect three species of invading amphipods (*G. pulex, G. tigrinus* and *Crangonyx pseudogracilis*)	Cryptic virulence, effect on survivorship only apparent when native and invaders interact; parasitized natives showed reduced ability to prey upon smaller invaders and suffered increased predation by large invaders	Two invaders favoured (*G. tigrinus* and *G. pulex*); one neutral (*C. pseudogracilis*)	Mediation of intraguild predation	[13]
Cylindrotaenia sp. (Cestoda)	Gecko (*Lepidodactylus lugubris, Hemidactylus frenatus*); gut tapeworm	Cestode levels higher in native *L. lugubris* on Pacific islands when in sympatry with invading *H. frenatus*	Neutral (although implicated in competitive replacement of natives by invaders, no effect evident)	Apparent competition – but rejected	[44,45]
Heterakis gallinarum (Nematoda)	Wild grey partridge *Perdix perdix* and pheasant *Phasianus colchicus*; caecal damage in host birds, infective egg stage might also act as carrier of the pathogenic protozoan *Histomonas meleagridis*	Spread of parasites from released pheasant *P. colchicus* results in decline of wild grey partridge *P. perdix* populations	Invader favoured	Apparent competition – parasite-mediated competition	[42,43]
Echinorhynchus truttae (Acanthocephala)	*Gammarus duebeni celticus*; increases activity level and alters microdistribution	Makes parasitized natives more vulnerable to shared fish predators than are unparasitized natives and invaders	Invader might be favoured; empirical test required	Mediation of shared predation	[66]
Pomphorhynchus laevis (Acanthocephala)	*Gammarus pulex*; behavioural manipulation (photophilic) of native but not invading *G. roseli* (remains photophobic), also O_2 consumption lowered, haemocyanin concentrations increased	Increases the exposure to predation in the native species	Invader might be favoured; empirical test required	Mediation of shared predation	[47]
Anagrus epos (Hymenoptera: Mymaridae)	Native grape leafhopper *Erythoneura elegantula*; egg parasite – also invading variegated leafhopper *Erythoneura variabilis* in Californian vineyards	Reduced susceptibility of invader to egg parasitism, owing to differences in egg-laying behaviour; produces rapid decline in native populations	Invader favoured	Apparent competition	[10]
Dinocampus coccinellae (Hymenoptera: Braconidae)	Ladybird beetle (Coccinellidae); endoparasitoid; lays eggs and larvae exits host to pupate	Invader is reservoir (egg source), adult natives are more susceptible to parasitism than are invaders	Invader favoured	Apparent competition	[11]
Pseudacteon solenopsidis (Diptera: Phoridae)	Insect parasitoid of ants; flies lay eggs in head case of larvae	Lack of specific pathogens and parasites (e.g. phorid flies) for invasive *Selenopsis* fire ants might remove controls on activity and population density, and shift competitive balance between ant species at food sites	Invader favoured	Apparent competition – enemy release	[67,68]
Parapoxvirus	Squirrel; parapoxvirus carried by invading grey squirrels *Sciurus carolinensis* infects native reds *S. vulgaris*	Invader is reservoir host (unaffected); native suffers high and rapid mortality when exposed	Invader favoured	Apparent competition	[40,41]

behaviour of hosts to manifest such drastic alterations in both susceptibility and ability to engage in IGP. Parasites can alter host physiology, for example, redistributing lipid and glycogen stores [53] and this might manifest as behavioural changes during invader–native interactions. Indeed, intraspecific aggressive behaviour in animals is constrained by physiological factors, such as anaerobic capacity and metabolic reserves [54,55]. Thus, studies of interspecies differences in physiological responses to parasitism, coupled with correlating such responses with behavioural activity, should prove a fruitful area for research into parasite mediation of interspecific interactions and the determination of invasion success or failure.

Wider implications of parasitism for community structure

There is increasing consensus, therefore, that parasites can mediate the outcome of interspecific interactions, such as competition and predation, and that this might determine the outcome of invader–native interactions. Thus, many examples of two-host, one-parasite scenarios are now explicable in terms of which host 'wins'. In invasion scenarios, the facilitation of the invasion process through parasites might lead to a species replacement, with the new resident having profoundly different impacts on the wider community compared with the native. For example, freshwater community structure is radically altered when the invasive amphipod *G. pulex* replaces the native *G. d. celticus* [56]. Many studies, however, have used two-host, one-parasite systems to suggest, by extrapolation, that parasites structure biological communities or assemblages [46,57]. However, very few studies have examined the role of parasites at the community level [58] and still fewer involve invasions. Of the ten examples claiming parasite-mediated apparent competition (Table 1), plus 20 additional examples of enemy-(predator)mediated apparent competition available from [57], only two [13,21] involved the examination of more than a species pair and a single parasite. MacNeil *et al.* [13] examined interactions in multiple species pairs of amphipods parasitized by the microsporidian *P. mulleri*, whilst Kohler and Wiley [21] describe the community implications of the complete loss of a key species, the caddisfly *Glossosoma nigrior*, through a catastrophic outbreak of the microsporidian parasite *Cougourdella* sp. There are many other examples of pathogens that produce outbreaks and total loss of species with profound knock-on effects for larger communities, such as mass mortalities of marine taxa caused by emerging diseases [23], cascading effects of disease [59] and species introductions having dramatic unforeseen effects at higher tropic levels [60,61].

The predominant pressure exerted by parasites on communities, however, might not be as a result of catastrophic outbreaks, but of less virulent, persistent and sublethal infections. Hosts might, as a result, harbour a variety of parasites. It would seem timely, therefore, to investigate the role of less virulent parasites in determining community metrics, such as species diversity and richness. Community-level effects are expected because parasites affect the predatory and competitive capabilities of invaders and natives (as seen in amphipod assemblages [13]). Parasites

also have more subtle and complex effects. For example, acanthocephalan infection of *G. pulex* causes reduced predatory activity and also switching in size classes of prey taken [62]. Such sub-lethal effects might have knock-on community-wide effects [62]. Parasites might, therefore, not only drive community differences by facilitating invasions and species replacements, but also mediate diverse interspecific interactions at the broader community level. However, a significant lag is expected in the effects of invasive species on higher trophic levels becoming evident compared with their effect at lower trophic levels [21]. It is thus essential that studies of the community- and ecosystem-level consequences of parasites in invasions are conducted on spatially and temporally large scales (smaller scale experiments tend to underestimate the impact of parasite-induced reductions [21]), such that more covert influences of parasites can be determined [63] and a clearer understanding of the mechanisms structuring these invaded communities can be developed. This will need to involve experimental manipulations of parasites in the field (see also [58]). This is a difficult and perhaps ethically sensitive undertaking, but with potentially high rewards for our understanding of the links among parasites, invaders and community structure.

Concluding remarks

Parasites have wider ranging impacts on community interactions during animal invasions than was previously acknowledged. Future research should thus focus on the impacts of parasitism on broader community scales than has been previously attempted. The global scale of animal invasions necessitates the identification of general patterns of host and parasite characteristics associated with invasion success. Empirical testing of fundamental processes linked to parasitism, thought to facilitate invasion, is also necessary. Only with these results can we fully appreciate the multitude roles of parasites in animal invasions.

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