Impacts of crustacean invasions on parasite dynamics in aquatic ecosystems: A plea for parasite-focused studies

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ABSTRACT

While there is considerable interest in, and good evidence for, the role that parasites play in biological invasions, the potential parallel effects of species introduction on parasite dynamics have clearly received less attention. Indeed, much effort has been focused on how parasites can facilitate or limit invasions, and positively or negatively impact native host species and recipient communities. Contrastingly, the potential consequences of biological invasions for the diversity and dynamics of both native and introduced parasites have been and are still mainly overlooked, although successful invasion by non-native host species may have large, contrasting and unpredictable effects on parasites. This review looks at the links between biological invasions and pathogens, and particularly at crustacean invasions in aquatic ecosystems and their potential effects on native and invasive parasites, and discusses what often remains unknown even from well-documented systems. Aquatic crustaceans are hosts to many parasites and are often invasive. Published studies show that crustacean invasion can have highly contrasting effects on parasite dynamics, even when invasive host and parasite species are phylogenetically close to their native counterparts. These effects seem to be dependent on multiple factors such as host suitability, parasite life-cycle or host-specific resistance to parasitic manipulation. Furthermore, introduced hosts can have drastically contrasting effects on parasite standing crop and transmission, two parameters that should be independently assessed before drawing any conclusion on the potential effects of novel hosts on parasites and the key processes influencing disease dynamics following biological invasions. I conclude by calling for greater recognition of biological invasions’ effects on parasite dynamics, more parasite-focused studies and suggest some potential ways to assess these effects.

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1. Introduction

Biological invasions are a global phenomenon resulting in profound changes in native communities (Simon and Townsend, 2003; White et al., 2006; Nalepa et al., 2009). Invasive species are among the main drivers of biodiversity decline, threatening both the environment and economy (Simberloff et al., 2013). Invasion rate and occurrence are constantly increasing due largely to global trade and travel (Dick and Platvoet, 2000; Keller et al., 2011). Invasive species may affect native species through direct competitive interactions or predation and indirectly through resource exploitation. The impact of invasive species can also extend beyond obvious effects of competition and predation on native species (Snyder and Evans, 2006). For example, pathogens can both influence and be affected by biological invasions. Native parasite communities and dynamics can be impacted by both introduced host and co-introduced parasite species (Telfer and Bown, 2012). However, our understanding of the effects of biological invasions and of the factors influencing invasive species impacts on parasites dynamics is still limited.

Interestingly, the role of pathogens in invasion success and impacts is widely recognized even though the number of studies focusing on pathogens compared to free-living organisms is proportionally small (Tompkins et al., 2011; Lowry et al., 2013). Parasites can play a key role in biological invasions, affecting species interactions and co-existence, and thus influencing the success of invasive species (Drake, 2003; Prenter et al., 2004; Hatcher et al., 2006; Dunn, 2009). Indeed, much focus has been put on how parasites may affect the outcome or impact of invasions through their potential effects on interactions among invasive and native host species (Dunn and Perkins, 2012; Dunn et al., 2012; Dunn and Hatcher, 2015). To put it simply, the effects of parasites in biological invasions have been extensively considered and studied while the consequences of biological invasions on parasite diversity and population dynamics have been and are still mainly ignored. It is widely accepted that parasites mediate invasions, but so too can biological invasions impact parasite communities, populations and dynamics (Telfer and Bown, 2012). For example, depending on the ability of a local, native parasite to survive and undergo transmission in a novel, invasive host species, this host can act as a sink or reservoir for native parasites, thus either decreasing or increasing their overall abundance (Gendron and Marcogliese, 2016). Successful invasion of an ecosystem by non-native host species can thus have contrasting, unpredictable effects on native parasites.

Invasive species are generally assumed to suffer less from infection by local pathogens than native hosts (Dunn and Dick, 1998; Torchin et al., 2002; Genner et al., 2008; Redón et al., 2015). Local parasites are not adapted to the new host immune system thus providing a competitive advantage to the invader over native hosts (Embledy Fromme and Dybdahl, 2006; Genner et al., 2008). For example, the fish acanthocephalan Pomphorhynchus laevis induces lower immuno-competence and imposes energetic costs only in its native amphipod host; invasive hosts become infected but are not affected like native hosts, thus supporting the idea of a maladaptation of native parasites to invasive hosts (Rigaud and Moret, 2003; Cornet et al., 2010). While there is now clear evidence for invading hosts often evading or being less affected by native parasites, studies focusing on the parasites themselves, whether native or introduced, are rare. Invasive host species can affect native host-parasite dynamics in two opposing ways. If an introduced species becomes a competent host to a native parasite, allowing survival and transmission, it may lead to an increase in parasite abundance and standing crop. If a native parasite is acquired by an invasive host that is unsuitable, preventing parasite survival or transmission, a decrease in parasite population may ensue (Telfer et al., 2005; Kopp and Jokela, 2007; Paterson et al., 2011; Lettoof et al., 2013). Interestingly, recent evidence also shows that pathogen dynamics in invasive host species may evolve over time as parasites adapt to the novel hosts, a parameter that has long been documented and accepted with respect to invasion by free-living species (Van Riel et al., 2003; Krakau et al., 2006; Gendron et al., 2012). The European green crab Carcinus maenas went from harbouring significantly fewer, immature native parasites compared to the native shore crab host (Hemigrapsus oregonensis) to being equally infected and affected as the native host in a matter of months (Torchin et al., 1996). Parasite dynamics following invasion by novel hosts may thus depend on time since invasion, and evolve over time; indeed, introduced species may accumulate native parasites (Guégan and Kennedy, 1993; Torchin and Lafferty, 2009). In this review I will first discuss the importance of and relation between biological invasions and pathogens in aquatic ecosystems. Secondly I will explore how parasites may affect biological invasion processes and vice-versa. Finally, I will present specifically the links between invasive crustaceans and parasite dynamics in aquatic ecosystems. I conclude by suggesting some ways to further our knowledge on this matter.

2. Biological invasions and parasites in aquatic ecosystems

Aquatic ecosystems are threatened by many factors such as urbanization, pollution, climate change and habitat alteration, but also largely by the introduction of non-native species (Gherardi, 2007). Fresh waters, in particular, are under constant threat from alien invasive species around the world (Gherardi et al., 2009; Strayer, 2010). Aquatic ecosystems have been rendered more susceptible to invasion by human activities such as the pet trade, live bait transport, shipping and ballast waters or construction of canals connecting once-isolated river basins (Arundell et al., 2015; Laverty et al., 2015). As a result, alien invasive species are considered to be the third most important threat to aquatic ecosystems (Sala et al., 2000). Macroinvertebrates in general and crustaceans in particular are highly successful aquatic invaders and often have substantial impacts on recipient ecosystems (Dumbauld et al., 2011; Hänfling et al., 2011; Blakeslee et al., 2015; Laverty et al., 2015; Ricciardi, 2015). Aquatic macroinvertebrates are important elements of freshwater ecosystems and also hosts to many parasites (Graber, 2017). In Europe, they represent around half of invasive freshwater species (Devlin et al., 2005; Karatayev et al., 2009; Hänfling et al., 2011). Ponto-Caspian crustaceans, for example, have largely colonized freshwater and brackish ecosystems in Europe and North America (Van den Brink et al., 1991; Ricciardi and Maclsaac, 2000). For amphipods alone, ten new species are now established in central and western Europe (Dick and Platvoet, 2000; Bij de Vaate et al., 2002). All of these are vehicles for a multitude of co-introduced parasites or potential novel hosts to local, native parasites in colonized ecosystems (Hatcher et al., 2015). Non-native free-living species may also alter native parasite dynamics and facilitate the establishment of independently arriving parasite species (Knudsen, 1995; Amundsen et al., 2013). However, changes in native or co-introduced parasite dynamics in areas colonized by novel hosts are mostly unknown and seldom documented unless they negatively affect native and/or invasive host species, thus influencing invasion patterns. Parasites can indeed alter the distribution and abundance of hosts, food-web structure, biomass and ecosystem integrity (Marcogliese and Cone, 1997; Marcogliese, 2005; Lafferty et al., 2006; Lagrue and Poulin, 2016). Changes in parasite dynamics following biological invasions are thus likely to have far-reaching effects on the whole ecosystem and vice-versa (Dumbauld et al., 2011; Amundsen et al.,...
the effects of native parasites on invasive host success have received much more attention than the opposite scenario.

3. Parasitism in aquatic crustaceans

Crustaceans are important components of aquatic ecosystems and hosts to a wide diversity of parasites (Hatcher et al., 2015; Grabner, 2017). Parasites can in turn alter the distribution and abundance of their hosts and significantly influence food-web structure, biomass and ecosystem integrity (Mangold and Cone, 1997; Lafferty et al., 2006; Kuris et al., 2008; Lagrue and Poulin, 2016). Parasites often influence the ecological relationships of free-living species and alter species diversity and coexistence (Mouritsen and Poulin, 2002; Hatcher et al., 2006). Potential changes in parasite or host communities through biological invasions may thus have in depth effects on aquatic ecosystem integrity but also parasite dynamics (Mastitsky et al., 2014).

Aquatic crustaceans are hosts to parasites with different life cycles (from single host and direct transmission to complex with trophic transmission) and with highly variable infection levels and pathological effects (Jackson et al., 1997; Wedekind et al., 2000; Stentiford et al., 2013); invasive crustaceans hosting high numbers of potentially harmful parasites (Mastitsky et al., 2014). For example, Cammarus spp. amphipods are hosts to intracellular microsporidians with direct vertical or horizontal transmission and a wide diversity of helminth parasites with complex life cycles such as acanthocephalans, trematodes, cestodes or nematodes (Grabner et al., 2015; Grabner, 2017). Prevalence (i.e. proportion of infected hosts) can vary widely among parasites infecting amphipod crustaceans, from very high (up to 100% in microsporidians) to relatively low for acanthocephalans for example (Kennedy, 2006; Grabner, 2017), and thus strongly influence the likelihood of pathogens being co-introduced with invasive crustacean hosts. Within crustaceans, some taxa are also more likely to be carriers of co-introduced pathogens or recipients of invasive parasites. Planktonic crustaceans in general and copepods in particular for instance are commonly introduced in new areas and hosts to a variety of pathogens including many species of potentially high impacts parasites such as the eel nematode Anguillicola crassus or Diphyllobothrium spp. cestodes (Milner and Mayer, 1982; Markogliese, 1995; Mastitsky et al., 2014). Furthermore, some of the most invasive aquatic crustaceans worldwide are hosts to a number of parasites, either co-invading with their original host or encountered in the colonized area. The European green crab, Carcinus maenas, is one of the most common invasive crustaceans worldwide and also one of the most intensively studied. It is host to a number of parasites occurring in varying intensities and prevalences (Torchin et al., 2001; Thielges et al., 2008). The cirriped Sacculina carmci, which forms conspicuous external brood sacks and castrates the crab host is well known but other parasites, mainly helminths with sea bird final hosts, are also extremely common, both in the native and invasive range of the crab host (Zetlmeisl et al., 2011; Blakeslee et al., 2015). However, native and introduced populations of parasites are hardly ever studied comparatively from an ecological or evolutionary perspective (Taraschewski, 2006).

Parasites can also have severe, but highly variable, pathogenic effects on their crustacean hosts such as increased mortality, castration, phenotypic alterations (Reinhard, 1956; Kuris and Lafferty, 1992; Kennedy, 2006; Lafferty and Kuris, 2009; Gehman and Byers, 2017). Crustacean pathogens can strongly influence host population dynamics, interspecific interactions and community structure (Mastitsky et al., 2014). In the Mediterranean, brine shrimps (Branchiopoda) are intermediate hosts to twelve species of cestode parasites using birds as definitive hosts (Vasileva et al., 2009). Larval cestodes have higher infection levels and pathogenic effects on native brine shrimps than on the invasive species Artemia franciscana (Redon et al., 2015). As a result, avian cestodes are likely to help A. franciscana outcompete native species. At the same time however, the invasive host may impact native parasite dynamics and eventually reduce its own parasite-mediated competitive advantage over native hosts. Overall, changes in parasite diversity in crustacean populations through introduction of new hosts and/or parasites can have large effects on both native and invasive hosts and parasites (Hatcher et al., 2015). Especially if shared parasites differentially infect and/or affect invasive and native hosts (Rode et al., 2013).

With the increasing recognition that parasites play important roles in ecosystem functioning and can influence species coexistence patterns, biological invasions, energy flow and community stability (Hudson et al., 2006; Hatcher et al., 2012a, b), the potential effects of biological invasions in parasite dynamics and infection levels in both native and introduced hosts now require further attention and specifically designed studies to assess their full extents. Novel pathogens continue to be co-introduced with invasive hosts and transfer to native species with potentially devastating consequences, yet the impact of parasitism on invasion of biological invasions remain poorly understood (Woolhouse et al., 2005; Peeler et al., 2011). Below I present the current state of knowledge and highlight areas of missing information about interactions between biological invasions and parasites with a particular focus on aquatic invertebrates and parasite dynamics.

4. Enemy release, dilution effects, spillover and spillback in aquatic invaders

Parasites may affect the establishment and spread of invasive host species in multiple ways. Stochastic effects and the small numbers of hosts present in the early stages of invasion often reduce the diversity of, and sometimes completely eliminate, parasites carried by invasive species (Blakeslee et al., 2012; Firmat et al., 2016). For example, the European green crab (Carcinus maenas), a notorious invader, has escaped more than two-thirds of its native parasite load when colonizing North America and its status as one of the most successful marine invasive species has partly been attributed to the loss of parasites (Zetlmeisl et al., 2011; Blakeslee et al., 2015). Depending on the pathogenic effects of parasites on the host, adverse conditions during invasion may also remove infected hosts, increasing the likelihood of parasite loss. Many other factors such as time since introduction, introduction vector or distance from native range may influence the likelihood of parasite loss. Other factors such as time since introduction, introduction vector or distance from native range may influence the likelihood of parasite loss. Many other factors such as time since introduction, introduction vector or distance from native range may influence the likelihood of parasite loss. Many other factors such as time since introduction, introduction vector or distance from native range may influence the likelihood of parasite loss. Many other factors such as time since introduction, introduction vector or distance from native range may influence the likelihood of parasite loss. Many other factors such as time since introduction, introduction vector or distance from native range may influence the likelihood of parasite loss. Many other factors such as time since introduction, introduction vector or distance from native range may influence the likelihood of parasite loss. Many other factors such as time since introduction, introduction vector or distance from native range may influence the likelihood of parasite loss. Many other factors such as time since introduction, introduction vector or distance from native range may influence the likelihood of parasite loss. Many other factors such as time since introduction, introduction vector or distance from native range may influence the likelihood of parasite loss. Many other factors such as time since introduction, introduction vector or distance from native range may influence the likelihood of parasite loss. Many other factors such as time since introduction, introduction vector or distance from native range may influence the likelihood of parasite loss. Many other factors such as time since introduction, introduction vector or distance from native range may influence the likelihood of parasite loss. Many other factors such as time since introduction, introduction vector or distance from native range may influence the likelihood of parasite loss. Many other factors such as time since introduction, introduction vector or distance from native range may influence the likelihood of parasite loss. Many other factors such as time since introduction, introduction vector or distance from native range may influence the likelihood of parasite loss. Many other factors such as time since introduction, introduction vector or distance from native range may influence the likelihood of parasite loss. Many other factors such as time since introduction, introduction vector or distance from native range may influence the likelihood of parasite loss. Many other factors such as time since introduction, introduction vector or distance from native range may influence the likelihood of parasite loss. Many other factors such as time since introduction, introduction vector or distance from native range may influence the likelihood of parasite loss. Many other factors such as time since introduction, introduction vector or distance from native range may influence the likelihood of parasite loss. Many other factors such as time since introduction, introduction vector or distance from native range may influence the likelihood of parasite loss.
As a result, parasite dynamics in invasive crustaceans do not always fit the enemy release hypothesis (Roy et al., 2011). For example, invasion of Great Britain by the amphipod Dikerogammarus villosus was accompanied by the loss of its microsporidian parasites despite multiple separate introductions (Arundell et al., 2015), but the invasive populations of the amphipod Crangonyx pseudogracilis show no sign of reduced parasite burden (Slothouber Gablearth et al., 2010).

Native parasites of the local fauna may also be less effective at infecting invading hosts (Ebert, 1994; Kaltz and Shykoff, 1998; Emblich Fromme and Dybdahl, 2006; Redon et al., 2015). Even if hosts are exonomically those parasites are often adapted to their local hosts and may not be able to infect or induce pathogenic effects in the invading host species (Cornet et al., 2010). For example, the invasive American brine shrimp (Artemia franciscana) have consistently lower cestode infection levels than its native counterpart, A. salina. Pathogenic effects of infection, especially host castration and manipulation, are much stronger in native than invasive brine shrimps (Redon et al., 2015). The same trend was observed between A. franciscana and another native brine shrimp species (A. parthenogenetica) infected with microsporidian parasites; the invader was four times less likely to be infected compared with native A. parthenogenetica (Rode et al., 2013). Native pathogens are thus often considered to influence competitive interactions between native and invasive hosts, favoring the invader and partly explaining its success (Georgiev et al., 2007; Sanchez et al., 2012). For example, the introduced amphipod Gammarus tigrinus is outcompeted by the native G. d. celticus in direct interactions but infection by native pathogens mitigates direct interactions and allows the smaller and less aggressive invader to coexist with the native species (MacNeil et al., 2003a). Failure of native pathogens to use invasive hosts may also decrease disease transmission among native hosts and negatively affect parasite population dynamics through dilution effects (Krakau et al., 2006; Hall et al., 2009; Kelly et al., 2009b; Osfeld and Keesing, 2012, Fig. 1B). Invasive hosts effectively become an infection sink for the native parasite (Paterson et al., 2011, 2013a). Overall, native and invasive hosts dramatically vary in their vulnerability to infection and suitability as transmission vectors and parasites in their host specificity, pathogenic effect, life cycles and transmission strategies (Redon et al., 2015). These combine to make predictions about the potential effects of parasites on novel host invasion success, as well as the effects of novel, invasive hosts on parasite dynamics extremely difficult.

Invasive species that acquire local, native parasites within their extended range may also act as reservoirs for parasite spillback to native hosts (Kelly et al., 2009a; Dunn et al., 2012, Fig. 1C). As shown above, biological invasions often expose parasites to new hosts in which local parasites are less successful (Cornet et al., 2010). However, in some cases, introduced host species are highly competent hosts for local, native parasites (Paterson et al., 2013b). This may have major effects on both the invasion success of these introduced host species and local parasite dynamics. For example, several microsporidian parasites of native amphipods appear capable of infecting D. villosus and spillback of these native parasites from the invasive species may lead to higher infection levels in native host species, thus increasing parasite prevalence and transmission rates (Wattier et al., 2007; Hatcher et al., 2012a). Invasive amphipods are also commonly infected by local acanthocephalan parasites and, although they often suffer lower levels of pathogenic effects and parasite-induced phenotypic changes than the local host species, they may act as a reservoir for these parasites (Lagre et al., 2007; Tain et al., 2007; Cornet et al., 2010). In rare cases native parasites may even be beneficial to their native hosts by reducing the invader’s impacts, mediating interspecific competition and allowing host co-existence (MacNeil et al., 2003b; MacNeil and Dick, 2011). However, invasive hosts may also be highly vulnerable to native pathogens and contain a significant proportion of the parasite standing crop but have a very limited influence on parasite population dynamics (Paterson et al., 2013b). The relative densities of native and introduced hosts and their respective suitability for parasites are further key components to consider when evaluating whether invasive host species affect native parasite dynamics.

Finally, parasites carried by invasive species may also spillover and infect native host species (Font and Tate, 1994; Strauss et al., 2012; Ishiko et al., 2013, Fig. 1D). The spread of invasive hosts may create new co-invasive parasites-native host combinations with potentially dramatic effects on native hosts naïve to the new parasites (Ishiko et al., 2013). Invasive crustaceans are important vectors of co-introduced microsporidian parasites, very common intracellular parasites in amphipods (Haine et al., 2007; Wattier et al., 2007; Bacela-Spychalska et al., 2012). For example, Dikerogammarus villosus, one of the most invasive freshwater species worldwide (Bi de Vaate et al., 2002; Bollache et al., 2004; Grabowski et al., 2007; Wattier et al., 2007), is the original host of Fig. 1. Hypothetical examples of enemy release (A), dilution effect (B), parasite spillback (C) and spillover (D) following introduction of a non-native host in a recipient ecosystem, illustrating the fundamental differences among the different processes. The thickness of the arrows represents transmission dynamics of the parasite and account for parasite loss during transmission. Enemy release (A) happens when the introduced species benefits from a reduction, or total loss as represented here, in parasitism as a result of invasion. This may in turn have drastic effects on invasion success and both native and invasive host abundances. Dilution effect (B) results from the failure of native parasites to use invasive hosts for successful reproduction and transmission. Native parasites may be unable to infect or be killed (as represented here) by the invasive host. Dilution may in turn decrease parasite transmission among native hosts and negatively affect parasite population dynamics. Parasite spillback (C) happens when invasive hosts acquire a native parasite that is already present in the native host population. Infected invasive hosts can then act as reservoirs of native parasites, potentially increasing infection levels in native hosts as represented here. Increased infection levels in the native host may in turn reduce native host abundance, compared to pre-invasion levels (not represented here). Parasite spillover (D) follows the co-introduction of non-native parasites with their invasive hosts and infection of native hosts by the introduced parasite. Infection of the native host can be maintained by the invasive host, which acts as a reservoir of infection, self-sustained if the parasite can reproduce in its novel host, or both as represented here. Infection of the native host by the introduced parasite can in turn influence host abundances, compared to pre-invasion levels. Note that in scenario D, the native host may or may not possess native parasites.
the microsporidian Cucumispora dikerogammaris (Wattier et al., 2007; Ovcharenko et al., 2010). Cucumispora dikerogammaris has spread out successfully with its host and has been detected in many invasive D. villosus populations all over Europe (Wattier et al., 2007). As a result, many native amphipod species have acquired the parasite along D. villosus’ invasion path (Bacela-Spychalska et al., 2012). However, the parasite’s epidemiology in these novel hosts compared to that in the original D. villosus host has never been documented to my knowledge. Generally, if native host species are more vulnerable to the parasite and/or suffer higher pathogenic effects, then parasite dynamics in these novel hosts may be drastically different to that observed in the original host species (Price et al., 1986; leshko et al., 2013).

5. Biological invasions, aquatic crustaceans and parasite dynamics

5.1. Introduced host and native parasites

Successful invaders may harbour fewer local parasites than native species in the same community (Roche et al., 2010; Redon et al., 2015). For example, when invasive, the amphipod Gammarus pulex has lower parasite diversity than the native G. duebeni celticus and lower burdens of the two shared parasite species (Dunn, 2009). In extreme cases, when introduced species exclude native host species, parasites specific to these native hosts will be excluded as well (Torchin et al., 2002). Nevertheless, introduced species may acquire native parasites, especially those transmitted through the food chain, and modify native host–parasite dynamics (Paterson et al., 2011; Poulin et al., 2011; Telfer and Bown, 2012; Reisinger and Lodge, 2016, Fig. 2). Invasive hosts acquire about five native parasite species on average, some becoming hosts to more than 16 (Torchin et al., 2003; Kelly et al., 2009b). The majority of invertebrates considered in studies assessing infection status of invasive species acquired some of the local parasites of colonized regions (Mastitsky et al., 2010; Redon et al., 2015). Invasive hosts can subsequently be affected by native parasites in unpredictable ways. For example, trematode parasites (Microphallus spp.) affect invasive crayfish (Orconectes rusticus) growth, behaviour and feeding, altering crayfish impacts on recipient lake communities (Reisinger and Lodge, 2016). However, the potential effects of invasive hosts on native parasite dynamics, transmission probabilities and standing crops are often unknown, most studies being host-focused.

The acanthocephalan Pomphorhynchus laevis uses a range of amphipod species as intermediate hosts (Kennedy, 2006). In France, many amphipod host communities are made of native Gammarus pulex/Gammarus fossarum and the invasive Gammarus roeseli (Chovet and Lécureuil, 1994; Bauer et al., 2000; Rigaud and Moret, 2003; Lagrue et al., 2007). Pomphorhynchus laevis is able to alter immune defences (Rigaud and Moret, 2003; Cornet et al., 2009) and various behavioural traits (Cézilly et al., 2000; Kaldonski et al., 2007) of the native G. pulex, thus favoring host exploitation and parasite transmission to the definitive fish hosts (Lagru et al., 2007). Behavioural and physiological alterations of the amphipod host are strongly related to parasite transmission dynamics; both have been shown to be more successful in native hosts than in the invasive G. roeseli (Rigaud and Moret, 2003; Moret et al., 2007; Tain et al., 2007). As a result, although both native and invasive amphipods are used by the parasite, native G. pulex/G. fossarum are more important to the parasite dynamics and can be considered a key host for P. laevis (Bauer and Rigaud, 2015). Key hosts are those contributing significantly more to the completion of the parasite life cycle (Streicker et al., 2013). In the context of biological invasions, whether the native host species consistently

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Unfortunately, the relative susceptibility of the invasive and
native host species to infection is rarely quantified. Yet this information is crucial to evaluate the relative importance of alternative hosts in native parasite dynamics. For example, if native amphipod hosts are more susceptible to infection by local acanthocephalans than the invasive *G. roeseli*, then both host susceptibility and manipulation maintain native host species as the main route for transmission and parasite dynamics. However, if the invasive *G. roeseli* proves more susceptible than native amphipod hosts but parasites are not transmitted due to the invader resisting manipulation, then parasite transmission and thus population dynamics should be negatively affected by the invasive host. The acanthocephalan *P. laevis* is indeed unable to manipulate *G. roeseli*; this host is thus inefficient at transmitting the parasite (Lagrue et al., 2007).

This could in turn impact parasite dynamics while increasing the standing crop of larval parasites in amphipod host populations (Hall et al., 2009; Johnson et al., 2009); the invasive *G. roeseli* accumulating most of the parasites that are seldom transmitted to definitive hosts (Lagrue et al., 2007; Bauer and Rigaud, 2015, Fig. 2A). Generally, *G. roeseli* is also less vulnerable to fish predation than native amphipods (Bollache et al., 2006; Kaldonski et al., 2008). Overall, fish parasites using *G. roeseli* as intermediate hosts have a lower probability of completing their life cycle and, in this case, the invasive host is a dead-end sink negatively affecting parasite dynamics.

However, such patterns are likely parasite-specific. Invasive *G. roeseli* hosts have been shown to be successfully manipulated by the native bird acanthocephalan, *Polymorphus minutus*, increasing predation by the appropriate definitive host and increasing transmission (Médoc et al., 2006). In this case, the invader has the potential to become the key host for *P. minutus* and influence parasite dynamics in a completely contrasting way to the fish acanthocephalan *P. laevis* (Fig. 2B). Contrastingly, the replacement on the native brine shrimp *Artemia salina* by a phylogenetically close American species (*A. franciscana*) may induce the co-extinction of some native bird cestode species using *A. salina* as intermediate hosts (Redón et al., 2015). Although *A. franciscana* has acquired a few novel parasites following its introduction, it is possible that some cestodes will not be able to infect this new host at all or at rates sufficient to ensure the survival of a viable population, according to the very low prevalences and the weaker manipulation observed in invasive hosts. However, quantitative estimations of parasite dynamics following native host replacement by the invasive *A. franciscana* are still required, as is often the case, to assess parasite population viability. Overall, quantitative effects of invasive hosts on native parasite dynamics and population size are difficult to predict and remain undocumented in most cases. Interactions between parasitism and biological invasions are usually considered in cases where invasive species share parasites with their native counterparts in the same community, whether increasing parasite prevalence and abundance or acting as a sink (Prenter et al., 2004; Kopp and Jokela, 2007; Paterson et al., 2011). However, in some cases, invasive host species may replace or create a whole new transmission pathway and may have positive effects on native parasites, in terms of population dynamics or distribution range (Emde et al., 2012; Reisinger and Lodge, 2016).

Finally, invasive species may also indirectly affect native parasites to which they are not actually hosts, by interfering with transmission pathways among hosts (Thieltges et al., 2008; Poulin et al., 2011). By altering the relative abundance of intermediate hosts needed in native parasite life cycles, particularly through predation, invasive species may negatively affect native parasite population dynamics (Poulin et al., 2011, Fig. 2C). For example, the invasive crayfish *Pacifastacus leniusculus* can decrease native parasite abundance through predation on benthic invertebrates, which act as transmission vectors of many parasites. Native fish hosts from crayfish-infested lakes have significantly fewer parasites transmitted from snails and benthic crustaceans than fish from areas free of *P. leniusculus* (Fig. 2C). In contrast, parasites transmitted to the same fish hosts from planktonic crustaceans, hosts not preyed upon by the benthic crayfish invader, remain unaffected (Pulkkinen et al., 2013). Indirect effects of invasive species on native parasites are here mediated via effects on native host populations and communities. Overall, effects of invasive host species on native parasites are thus likely to be complex and very rarely accounted for.

5.2. Introduced hosts and introduced parasites

Parasites have frequently been invoked as drivers of invasions, but have received less attention as invasion passengers (Blackburn and Ewen, 2016). Parasites can themselves be introduced and become invasive; most parasites are indeed disseminated by movements of infected hosts (Kennedy, 1993). Almost 80% of parasites known to have been co-introduced with invasive hosts were successful at infecting native hosts, regardless of their life cycle (direct or complex; Font and Tate, 1994; Ishiko et al., 2013; Lymbery et al., 2014, Fig. 3). Evidence also suggests that introduced parasites can alter local, recipient food webs qualitatively and quantitatively through shifts in trophic relationships within the web (Amundsen et al., 2013; Britton, 2013). These changes may in turn influence population dynamics of both introduced and native parasite species (Knudsen, 1995). For example, the microsporidian *Cucumispora dikerogammarii* infecting the invasive amphipod *Dikerogammarus villosus* has hitchhiked its way into most of Europe with its amphipod host and become a potential emerging disease into invaded areas (Ovcharenko et al., 2010). However, not all parasites are as likely to shift to or be as successful in new hosts (Prenter et al., 2004; Hatcher et al., 2012a). For successful establishment, maintenance and spread, invasive species must be able to survive and reproduce in new ecosystems and host communities (Miller and Ruiz, 2009). Introduced parasites thus need either their original hosts to establish and reproduce or to find alternative suitable hosts. The probability of either or both of these alternatives being met depends on traits relating to parasite life history (Blackburn and Ewen, 2016).

Parasites are generally more likely to transfer to native hosts phylogenetically close to their original host (Strauss et al., 2012). Introduced parasites may thus infect congenic native host species through spillover from their original, co-introduced host (Daszak et al., 2000). For parasites with complex life cycles such as acanthocephalans or trematodes, survival and establishment depends on the presence of a combination of multiple, phylogenetically distant suitable hosts (Blakeslee and Fowler, 2012). For example, trematodes are highly specific to their snail first intermediate hosts but are somewhat more flexible regarding second intermediate and definitive hosts (Graczyk, 1997). Availability of suitable native hosts to introduced parasites may strongly influence the presence or absence of such parasites. As a result, species with complex life cycles often retain one of their original, co-introduced hosts and use novel, native hosts to fill in the gaps and complete their life cycle (Taraschewski, 2006, Fig. 3A). In extreme cases, introduced parasites may even invade new host communities without the introduction of the original host(s) (Fig. 3C). The nematode parasite *Anguillicola crassus* is native to Japan where it infects the eel *Anguilla japonica* but is now found in the European eel *Anguilla anguilla* (Starkie, 2003; Norton et al., 2005). Introduction of *Anguillicola crassus* in Europe was partly through shipments of infected *A. japonica* but also, in some places, water containing only eggs of the parasite, not infected hosts (Kennedy and Fitch, 1990; Kirk, 2003). The life cycle was then completed through native
Both co-introduced and native hosts, 85% show that virulence was very few studies that looked at introduced parasite virulence on invasive host species and subsequently infect native hosts. Of the ally, invasive parasites are co-introduced with one of their original, exactly replaces the original de

life cycle. The situation represented here is the simplest one where the native predator in the original ecosystem (shown at the top left). (B) The parasite is again co-

tively affect native predators and change parasite dynamics compared to that observed parasite dynamics or host abundance. However, parasite invasion may in turn nega-

tion scenarios are possible with as many outcomes in terms of parasite dynamics.

is subsequently included in the recipient food web. The novel parasite may in turn lead to greater infection levels or pathogenic impacts tend to be documented and attract scientific attention but represent only part of the picture (Kennedy, 1993). Negative changes in parasite dynamics following invasion are seldom documented but represent perfect opportu-

ities to try and understand why some introduced parasite transfer are successful and other fail.

5.3. Native hosts and introduced parasites

Introduced host species often lose most of their parasites during invasion. However, the few co-introduced parasites that do stow-

away may spillover to native hosts with potentially considerable impacts on these naïve hosts (Mastitsky et al., 2014, Fig. 3). One well-known example is the directly transmitted oomycete patho-

gen Aphanomyces astaci causing crayfish plague. The oomycete was transmitted from invasive North American crayfish to native crayfish in large parts of Europe, resulting in a rapid spread of the disease followed by the decline of many populations of native crayfish (Holdich and Reeve, 1991; Holdich et al., 2009). In some cases, it was also followed by local extinction of the pathogen due to a subsequent lack of available hosts (Reynolds, 1988). Although the effects of crayfish plague on native crayfish host population dynamics have been extensively studied, the pathogen itself and its own dynamics have never been the focus of any studies. Similarly, the cestode Ligula intestinalis has been the focus of many studies for its pathological effects on fish hosts in both the native and invasive range of the parasite (Carter et al., 2005; Cowx et al., 2008; Hoole et al., 2010). Paraisite dynamics in fish hosts have been well-

studied too (Kennedy and Burrough, 1981; Kennedy et al., 2001). However, L. intestinalis has a three host life cycle also including a copepod crustacean (Dubinina, 1966). In areas where the parasite has been introduced, mostly with infected fish or bird hosts, the life cycle is completed using native copepod species but infection levels and potential effects on native copepod host populations have never been documented and/or compared to that observed in native copepods. In New Zealand, where the parasite was likely introduced by Australasian crested grebes (Podiceps cristatus australis) migrating from Australia, the copepod host has not even been identified yet (Weekes and Penlington, 1986; Lagrue et al., 2017).

Parasites introduced without their original hosts can also colonize novel hosts with the same dramatic consequences on native, novel hosts as Aphanomyces astaci on European crayfish species (see above). The eel nematode Anguillicola crassus has little effect in its original host Anguilla japonica but can have severe pathological impacts on the highly susceptible European eel A. anguilla within which it reaches higher parasite burdens than in A. japonica (Kirk, 2003). The parasites have been shown to have severe impacts on their novel eel host, both at the individual and population level; heavily infected eels showing increased mortality rates and being potentially unable to migrate and spawn (Kirk, 2003, Fig. 3C). Inv-

asion of the Asian isopod parasite Orthione griffensis in North America coincided with the collapse of populations of the native mud shrimp Upogebia pugettensis; infection by the introduced parasite caused severe reduction in fecundity in the naïve native host with potentially dramatic effects on the whole ecosystem (Dunbauld et al., 2011). Similarly, on the Atlantic coast of America, native mud crabs Eurypanopeus depressus are infected by the invasive barnacle parasite (Loxothylacus panopei) that castrates its host and renders it more prone to consumption by native predators (Gehman and Byers, 2017). The preferential consumption of native prey infected by introduced parasites by native predators may alter predator-prey dynamics and have in depth effects on the whole food chain and affect parasite infection levels and ultimately its ability to persist in this novel host (Gehman and Byers, 2017). The combined implications of higher host susceptibility to infection,
increased parasite burdens but also host mortality or lower fecundity on the population dynamics of the parasite itself are unclear, however.

Both the nematode *A. crassus* and cestode *L. intestinalis* use native copepod hosts for transmission to the next host but parasite dynamics in their novel, native crustacean hosts are unknown. Furthermore, introduced parasites may in turn impact their novel, native hosts and thus have complex cascading effects on recipient communities and native parasite dynamics (Médoc et al., 2017). Many known examples of introduced parasites are freshwater species, reflecting the vulnerability of aquatic ecosystems to invasion by new pathogens (Lymbery et al., 2014; Médoc et al., 2017). Well-documented examples of spillover of invasive parasites in native crustacean hosts are scant however, let alone quantitative assessment of parasite dynamics.

6. Conclusion

Aquatic ecosystems in general, and fresh waters in particular, are among the most invaded in the world and have been the focus of multiple studies contributing to our knowledge of the mechanisms influencing invasion success and the potential effects of introduced species (Ricciardi and MacIsaac, 2011). There is also increasing evidence that parasites play important roles in biological invasions. However, the impacts of biological invasion on parasite dynamics have clearly received less attention than the potential role of pathogens in invasion processes, especially in aquatic ecosystems even though freshwater parasites can be affected by introduced hosts (Taraschewski, 2006). For example, several studies have shown that invasive fish species can have drastic effects on local parasite communities and infection levels in native host species (Font and Tate, 1994; Dubois et al., 1996; Bergeron et al., 1997; Amundsen et al., 2013; Ieshko et al., 2013). However, studies focusing on the effects of biological invasions on aquatic parasite dynamics are still relatively rare (Blakeslee and Fowler, 2012). Furthermore, these studies most often focus on vertebrate definitive hosts of parasites, especially fish species as shown above (Poulin et al., 2011; Blakeslee and Fowler, 2012). Vertebrate species in general and crustaceans in particular are hosts to a multitude of parasites and are some of the most common invasive species in aquatic ecosystems (Hatcher et al., 2015). Yet, their potential effects on parasite dynamics following invasion of new ecosystems are very rarely accounted for. This partly comes from the logistical difficulties of such studies and the recurrent lack of reference points to which we can compare observed post-invasion patterns (Blakeslee and Fowler, 2012). Patterns of parasite communities and infection levels post-invasion can be extremely complex and give no information on changes in parasite dynamics specifically due to biological invasion (Grabner et al., 2015). An obvious way to assess biological invasion impacts on parasite dynamics would be to examine native disease dynamics in communities before and after invasion in natural settings (Telfer et al., 2005). When invasion fronts are known and identified, it should be possible to document parasite dynamics, along with host diversity and density, ahead of and behind the front of invasion. Alternatively, because aquatic systems, especially freshwater ecosystems, are patchy by nature, some invasive species are also patchily distributed, providing spatial replicates allowing a comparison of parasite population dynamics with and without invaders; see Dubois et al. (1996) and Bergeron et al. (1997) for excellent examples of study designs making great use of the patchy nature of freshwater systems and invasive fish species distributions. These studies highlight the complex and dramatic consequences of non-native fish introduction on parasite communities of both native and introduced fish host species in the field by using comparable lake ecosystems with and without introduced fish as geographical replicates. Unfortunately, these studies have been largely ignored and should be acknowledged for being some of the first to quantify the effects of invasive species on both native and co-introduced parasite communities. Observed field patterns should then be used in theoretical and empirical studies to try and elucidate key processes influencing disease dynamics following biological invasions (Telfer and Bown, 2012). There is a clear need for well-designed mesocosm and field experiments comparing parasite dynamics in the presence or absence of invasive crustaceans. Ideally and eventually, general predictions of how these commonly invasive taxa may influence disease dynamics may be drawn.

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