

The potential impacts of invasions on native symbionts

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Abstract

Symbionts, including parasites, pathogens, and mutualists, can play important roles in determining whether or not invasions by host species will be successful. Loss of enemies from the native habitat, such as parasites and pathogens, can allow for higher invader fitness in the invaded habitat. The presence of mutualists (e.g., pollinators, seed dispersers, mycorrhizae, and rhizobial bacteria) in the invaded habitat can facilitate invasion success. Although there has been a great deal of research focusing on how invading hosts may benefit from enemy losses or mutualist gains, far less attention has focused on how native symbiont populations and communities respond to invasion by non-indigenous hosts and symbionts. In this paper, we present a conceptual framework examining how symbionts such as parasites, pathogens, commensals, and mutualists can influence invader success and whether these native symbionts will benefit or decline during invasion. The first major factor in this framework is the competence of the invading host relative to the native hosts. Low- or non-competent hosts that support few if any native symbionts could cause declines in native symbiont taxa. Competent invading hosts could potentially support native parasites, pathogens, commensals, and mutualists, especially if there is a closely related or similar host in the invaded range. These symbionts could inhibit or facilitate invasion or have no discernible effect on the invading host. An understanding of how native symbionts interact with competent versus non-competent invading hosts as well as various invading symbionts is critical to our understanding of invasion success, its consequences for invaded communities and how native symbionts in these communities will fare in the face of invasion.

KEYWORDS

commensalism, dilution effect, host competence, mutualism, parasitism, symbiont acquisition

INTRODUCTION

Biotic invasions are dramatically affecting biological diversity worldwide (Mack et al., 2000). Two of the dominant

perspectives on why invasions by non-indigenous species are successful are the enemy release hypothesis (ERH) and the mutualist facilitation hypothesis (MFH). The ERH posits that non-indigenous species are able to successfully

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invade new habitats because they left their normal pathogens and parasites behind in their native habitats and are colonized by few if any parasites and pathogens in the invaded habitat (Colautti et al., 2004; Keane & Crawley, 2002; Mitchell et al., 2006; Mitchell & Power, 2003). This reduction in natural enemies gives these invading species a competitive advantage in the invaded habitat and promotes successful naturalization and spread. Conversely, it has been well documented that many non-indigenous plant hosts colonize new habitats filled with potential mutualists, many of which can facilitate their invasions (Richardson et al., 2000; Traveset & Richardson, 2014). Absence of particular mutualists in the invaded habitat can prevent the establishment and spread of some invaders (Nuñez et al., 2009; Richardson et al., 2000). These potential mutualists include various pollinators, seed dispersers as well as bacterial and fungal symbionts that can influence fitness of the invading plant in the new habitat (Nuñez et al., 2009; Richardson et al., 2000; Traveset & Richardson, 2014). The contrasting perspectives of the ERH and the MFH are not entirely contradictory. Leaving negative symbionts behind and acquiring novel, facilitating symbionts in the invaded habitat are both mechanisms that can lead to a successful invasion.

Despite the different emphases of these two perspectives, both the ERH and the MFH focus on how either the loss or the acquisition of symbionts in the invaded habitat affects demographic properties of the invading host species, including their ability to successfully compete with resident species (Mitchell et al., 2006). Interactions with native symbionts are often critical in determining invasion success and the impacts on native host diversity (Nuñez et al., 2009; Richardson et al., 2000; Traveset & Richardson, 2014). Although the effects of symbionts (good and bad) on invading hosts are frequently investigated, the effects of the invading hosts on the populations and communities of native symbionts have received far less attention despite the potentially strong impacts invaders could have on this component of native biodiversity. These impacts are potentially commonplace, but because of a lack of research attention, these effects can, for the most part, only be only surmised as logical extensions of current knowledge. Native symbionts could lose a viable host if their native host is outcompeted by an invader. They could also be extirpated by invading symbionts, either through direct mechanisms (e.g., being outcompeted or preyed upon by invading symbionts) or indirectly through their native host being extirpated by a competitively superior invading host. Alternatively, native symbionts may benefit from the invasion of a competent host that is either more abundant than their native host or can support higher symbiont densities per host individual.

As invading hosts become established in the invaded habitat, they can establish new symbioses with native symbionts (Aslan et al., 2015; Hokkanen & Pimentel, 1989; Mitchell et al., 2006; Richardson et al., 2000). These new associations could be critical to determining whether an invasion is to be successful and may dictate an invader's rate of spread. They could also influence the habitats the invader ultimately occupies. Parasites and pathogens in the invaded habitat may colonize and negatively affect non-indigenous host populations. This perspective is supported by the fact that pathogens that have not coevolved with a host frequently cause declines, and sometimes extirpation, of these host populations. Introduced diseases such as Dutch elm disease and chestnut blight have devastated common tree species in North America. Chytrid disease is having similar effects on amphibian communities (Dunn & Hatcher, 2015). Although the presence of parasites and pathogens could explain unsuccessful invasions, the lack of mutualistic symbionts may also influence invasion success. Various introduced pine species in the southern hemisphere failed to spread due to the lack of the appropriate mycorrhizal symbionts. Pines became successfully established and spread only after the co-invasion of their appropriate mycorrhizal symbionts (Nuñez et al., 2009; Richardson et al., 2000). Therefore, both the absence of symbionts with negative impacts and those with positive impacts can prevent successful invasions from occurring (Keane & Crawley, 2002; Mitchell et al., 2006; Richardson et al., 2000). Symbiont acquisition is therefore a key aspect of invasions for both invading hosts and native symbiont communities.

Another critical issue for native symbionts is whether or not an invading host can regulate symbiont colonization and impact. Most studies have focused on plant hosts that appear to have limited abilities to control and regulate populations of colonizing symbionts but there are some exceptions. Some plants can regulate pollinator visits or abundance of larval pollinators. This regulation has been documented in some specialized plant–pollinator systems (Pellmyr & Huth, 1994; Wang et al., 2014). In more generalized plant–pollinator systems, such regulation either does not occur or is understudied. Similarly, some host plants may sanction underperforming rhizobium symbionts (Kiers & Densison, 2008) or mycorrhizal fungi (Bever et al., 2009), although within these symbioses, plant species vary widely in their imposition of such sanctions (Grman, 2012). Therefore, many non-indigenous plant hosts may offer major opportunities for exploitation by some native symbionts. This outcome seems especially likely if the invading host encounters closely related native hosts and their symbionts in the invaded habitat.

Animal hosts pose a different set of hurdles for colonizing symbionts, ranging from avoiding grooming

behaviors by the host (or conspecifics of the host, e.g., primates) to more sophisticated immune system responses (Jones & Dangl, 2006; Keesing et al., 2006; Owen et al., 2009; Randolph, 1979; Spoel & Dong, 2012). Keesing et al. (2009) found that opossums, which have recently expanded their range into New England, are efficient groomers and can significantly reduce their tick burden compared with co-occurring, native hosts. Similarly, crayfish are adept at removing ectosymbiotic worms by grooming with their smaller walking legs (Farrell et al., 2014; Skelton et al., 2014; Thomas et al., 2016). The invading crayfish *Faxonius cristavarius* grooms more aggressively than native crayfish and can suppress native worm abundance and diversity in streams (Bell, 2018; Creed et al., 2022; Farrell et al., 2014). Furthermore, animal hosts can develop immunity to ectoparasites such as ticks and fleas, reducing ectoparasite fitness and the severity of the attack (Owen et al., 2009). Animal hosts may also engage in cleaning symbioses in which cleaning symbionts could suppress abundances of other symbionts (Brown et al., 2002, 2012; Creed & Brown, 2018; Grutter, 1999). There may even be selective transport of particular symbionts in some phoretic associations such as those involving boring beetles and *Ambrosiella* fungi. Invading beetles are more likely to acquire new symbionts from native beetles that farm closely related *Ambrosiella* fungi than those that farm more distantly related species (Li et al., 2019; Skelton et al., 2019). Therefore, looking at how invading animal hosts may influence native symbiont abundance and diversity in the invaded habitat is clearly deserving of further attention.

Our goal in this paper is to incorporate both host and symbiont characteristics into a comprehensive conceptual framework of host invasion and symbiont acquisition during the initial stages of an invasion. Our framework takes a two-tiered approach, examining whether non-indigenous hosts are competent hosts for native symbionts, as well as the potential impact of the symbionts on competent hosts once they are acquired. We also assess how the relative competence of invasive hosts compared with native hosts could influence the outcome of the invasion for native symbionts. We evaluate all possible effects of symbionts on their hosts, not just positive or negative impacts, as well as how the symbiont populations and communities may respond to the invasion of a new host. Finally, we evaluate how invading symbionts might influence native symbiont populations and communities. This symbiont-focused perspective is complementary to the host-focused perspective that currently dominates invasion ecology (Colautti et al., 2004; Keane & Crawley, 2002; Mitchell et al., 2006; Richardson et al., 2000).

SYMBIONT ACQUISITION BY INVADING HOSTS

Host competence

Our first consideration is whether or not the invading host is a competent host for native symbionts. In parasitology, competence is defined as the ability of a host to transmit new parasites to another host or a vector (Barron et al., 2015). However, competence comprises various elements including the likelihood of a host being exposed to a parasite, the susceptibility of the host to the parasite, the ability of the host to support the parasite and, ultimately, its ability to transmit the parasite (Barron et al., 2015; Stewart Merrill & Johnson, 2020). Furthermore, hosts may be adept at removing parasites once they have colonized (Keesing et al., 2009; Farrell et al., 2014). All of these elements apply to the population dynamics of any type of symbiont (parasites, pathogens, commensals, and mutualists), so we apply the concept of competence to hosts of all symbiont types.

Host competence is the first bifurcation point in our conceptual framework of symbiont acquisition. If a host is competent then it could be colonized by native symbionts. If it is non-competent, then it could be a sink for native symbionts leading to declines in native symbiont abundance and diversity. The latter scenario is the non-competent invading host concept in Figure 1. This mechanism of impact has been documented in parasitic symbionts and recently in symbioses involving mutualists (Table 1).

We recognize that the binary classification of invading hosts as either competent or non-competent in Figure 1 oversimplifies the situation. Clearly, other levels of host competence are possible (Figure 2). The competence of the invading host relative to the native host will determine the outcome of the invasion on native symbionts. For example, invading plant species may be chemically defended against symbionts. The effectiveness of chemical defenses could be highest if the native symbionts are taxonomically similar to symbionts in the native range of the invading host and therefore more susceptible to these defenses. For invading animal hosts, they may have behavioral mechanisms, e.g., grooming, that prevent native symbionts from becoming established. Invading hosts may more actively groom than native hosts and reduce native ectosymbiont abundance (Farrell et al., 2014; Keesing et al., 2009). Differences in general immunological defenses could also contribute to these differences in competence between native and invading hosts (Owen et al., 2009; Randolph, 1979). Synergism between behavioral responses and immunological defenses could further suppress native symbiont abundance (Farrell et al., 2014). Invading hosts that have a significantly lower competence than native hosts could have negative effects

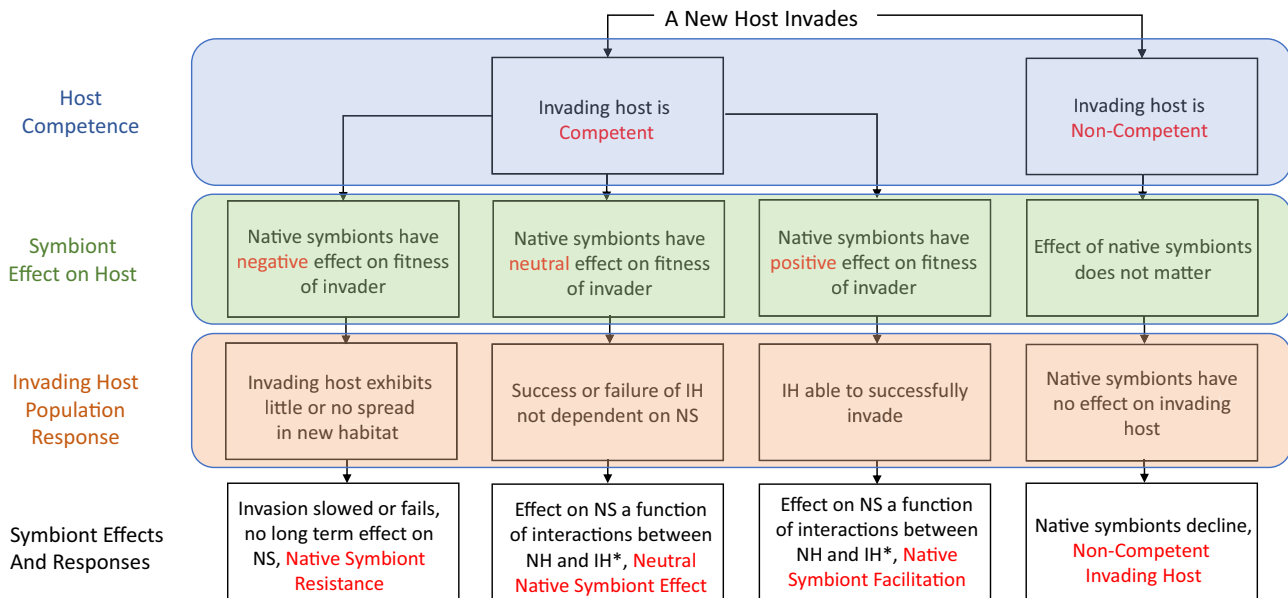


FIGURE 1 A conceptual framework outlining the responses of native symbionts to invasion of a community of native hosts by an invading host. The first bifurcation in the framework is whether the invading host is competent or not for native symbionts. If the invading host is a non-competent one for native symbionts (non-competent invading host) when native symbionts colonize it they will be removed or killed. In this scenario, the invading host is a sink for native symbionts and, over time, native symbiont abundance and diversity in a community are predicted to decline. If the invading host is a competent host for native symbionts then one of three scenarios is possible. If the native symbionts are parasites or pathogens then they are predicted to have negative effects on the invading host (native symbiont resistance). This could result in a failed invasion if the symbiont effect on the invading host is strong or naturalization of the invading host may occur but with limited spread. If the native symbionts have a positive effect on the invading host then they are predicted to increase abundance and facilitate spread of the invading host (native symbiont facilitation). Finally, if the native symbionts are commensals and have no net positive or negative effect on the invading host then they are not predicted to have any effect on colonization and spread of the invading host (neutral native symbiont effect). Abbreviations: IH, Invading host; NH, Native host; NS, native symbionts

on native symbionts if they support low densities of native symbionts. This scenario could result in many fewer dispersing symbionts being produced by these hosts with the result that symbiont populations decline. Symbionts that exhibit strong reproductive Allee effects could exhibit little or no reproduction on such hosts with the result that few if any new symbionts are produced that can disperse to new hosts (Creed & Brown, 2018). Therefore, low-competence hosts could have negative effects on some symbiont populations comparable with effects of non-competent hosts.

When the relative competence of the introduced host is similar to that of the native host it is likely that there will be no significant impact on symbiont populations if the native host is replaced by the invading species. If the invader and native host co-occur then symbiont populations could potentially increase (please refer to Type of native symbiont section below for further discussion). If the competence of the invading host is greater than the native host then this could result in larger symbiont populations. For parasitic symbionts or pathogens this mechanism could lead to disease amplification (Huang et al., 2016) that could actually be harmful for native hosts if they are being

colonized by more parasites than they were previously. If introduced hosts can tolerate higher densities of native parasites or pathogens then this could represent be an indirect mechanism by which invaders displace native hosts. Invading hosts with a higher competence than native hosts should be beneficial for native symbionts that are commensals or mutualists as they will have more hosts to colonize and from which more symbionts can disperse.

Type of native symbiont

An important distinction between our model and both the ERH and MFH is that not all native symbionts are enemies, nor are they all mutualists. Invaded habitats can contain parasitic and pathogenic symbionts as well as numerous taxa that are possible mutualists and commensals. By considering all possible interaction types, a range of responses by native symbionts is possible when non-indigenous hosts invade a novel habitat.

If an invading host is competent for either parasitic or pathogenic native symbionts then the outcome could be either reduced rates of spread by the invading host or

TABLE 1 Selected examples of the different responses exhibited by native symbionts in response to the presence of invading hosts and invading hosts to native symbionts

Mechanism	Native host (NH)	Invading host (IH)	Native symbiont (NS)	Impact of/on IH	Reference
Non-competent invading host	Mussels	Oysters, snails	Trematode	Parasite reduction in NH	Thieltges et al. (2009)
	Crayfish	Crayfish	Branchiobdellidans	Ectosymbiont reduction on NH	Creed et al. (2022)
	Snail	Snail	Trematode	Parasite reduction on NH	Kopp and Jokela (2007)
Native symbiont facilitation	Grass	Perennial shrub	Mycorrhizae	Native mycorrhizae increases competitive ability of IH	Carey et al. (2004)
	Plants	Plant	Insect pollinators	Native pollinators facilitated pollen transport of IH	Lopezaraiza-Mikel et al. (2007)
	Plants	Plant	Rhizobial bacteria	Native rhizobial bacteria facilitate nitrogen uptake by IH	Rodríguez-Echeverría et al. (2009)
Neutral native symbiont effect	Mussel	Mussel	Aquatic invertebrates	Increase in hosts for native commensals	Cichy et al. (2016)
	Mollusks	Mussels	Chironomid larvae	Increase in hosts for native commensals	Ricciardi (1994)
	Beetle	Beetle	Fungi	Increase in hosts for native commensals	Rassati et al. (2019)
Native symbiont resistance	Plants	Grass	Rust fungi	Native fungus attacked IH, reducing impact of IH on NH	Stricker et al. (2016), Warren and Bradford (2021)
	Plant	Plant	Weevil	Specialist herbivore of NH switched to IH, spends most of life history on IH, and has reduced IH abundance	Creed and Sheldon (1995)

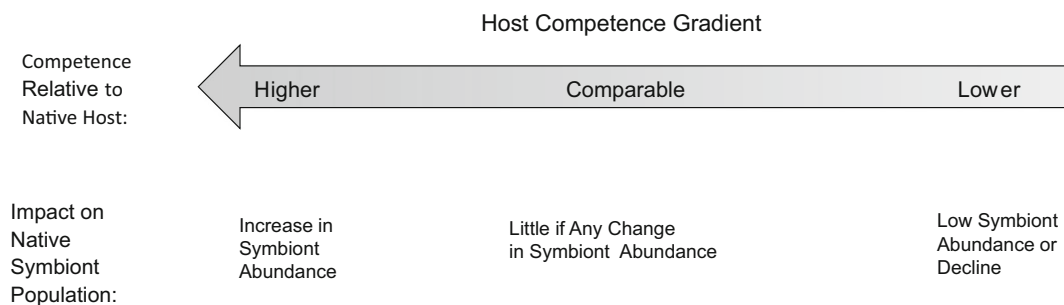


FIGURE 2 Competence of invading hosts relative to native hosts and consequences for native symbionts. Low-competence invading hosts should support and transmit few if any symbionts to new hosts. The impact of these hosts could be similar to non-competent hosts. Invading hosts that are similar in their level of competence to native hosts should support native symbionts. Invading hosts that have a higher level of competence relative to native hosts should support higher densities of symbionts that would result in symbiont amplification

even complete failure of the invasion in some cases. This outcome will be predicated upon the strength of the effect of native symbionts on the invading host. Native parasites and pathogens that have weak to moderate effects on the fitness of the invading host could potentially slow its rate of spread. Alternatively, these symbionts could limit its spread to regions where the

symbiont effect is weakest. For example, if climatic factors limit symbiont abundance or impact in some regions, then the invading host could persist in these areas. If, conversely, the invading host suffers dramatic reductions in fitness in the presence of these symbionts, then the invasion could fail completely. This outcome would be a form of biotic resistance, and this symbiont

resistance could be an important aspect of native biodiversity. This would be an example of native symbiont resistance (Figure 1).

Native symbiont resistance could be an important explanation for why so few invasions are successful (Simberloff & Gibbons, 2004; Williamson & Fitter, 1996). It could also be a difficult mechanism to detect if invaders are eliminated by native symbionts before they are noticed. In situations in which it has taken longer for native symbionts to colonize invading hosts effects have been detected (Table 1). Furthermore, Mitchell and Power (2003) found that non-indigenous host plants that acquired more pathogen species were less likely to be invasive.

In the native symbiont resistance scenario, native symbionts may exhibit increased abundance or diversity in the short term as they expand onto the non-indigenous host. In the long term, however, if the native symbionts exclude the invading host, we predict no long-term change in native symbiont abundance or diversity as long as native host abundance does not change. Conversely, if the invasive host can persist in the face of these deleterious symbionts then this persistence could result in a long-term increase in the abundance of the native symbionts as they would now have additional hosts.

If the native symbionts are engaged in a mutualism with one or more native host species and they can engage in a similar mutualism with a competent, invading host species, then these symbionts could facilitate the success and spread of invading host species (native symbiont facilitation; Figure 1). This outcome is similar to the MFH, but here we consider it from the symbiont's perspective. The long-term impacts on native symbiont communities in this case would depend on the interactions between the native and invading hosts. Native symbiont abundance and diversity could either increase, remain the same, or decline depending on the resulting abundance of potential hosts. If the native and invading hosts can coexist then it is likely that there will be an increase in the abundance and diversity of the native symbionts. If the invading host is a superior competitor, and there is one-to-one replacement of the native host by the invading host, then the expectation is that there would be no net change in native symbiont abundance or diversity. A third alternative is that the invading host eliminates the native host through competition or apparent competition and, ultimately, is less abundant than the native host. In this case, there would be a long-term decline in abundance and diversity of native symbionts relative to pre-invasion conditions.

There are some examples of native symbiont facilitation, and all involve plants. Some invading plants can interact with native fungi and bacteria that can facilitate the establishment and spread of invading hosts in the invaded

habitat (Richardson et al., 2000; Traveset & Richardson, 2014). Pollination is another important facilitative effect that native symbiont species can have on non-indigenous hosts (Richardson et al., 2000, Traveset & Richardson, 2014; Table 1). We are currently unaware of any examples involving animal hosts.

If the native symbionts are commensals and can successfully colonize and become established on a competent, invading host, there should be no net effect on the fitness of the invading host. Therefore, the success or failure of the invasion is not dependent on the impact of the native symbionts. This is the neutral native symbiont effect (Figure 1). With respect to the long-term effects on symbiont populations and communities the predicted outcomes are similar to those for native symbiont facilitation, i.e., the effects are a function of how many competent hosts are present in the community after the invasion occurs (Figure 1 and Table 1).

One scenario not considered in these models is the idea that the invader is not colonized by native symbionts. This scenario could also influence the success of an invasion event. For example, plant species that were engaged in an obligate mutualism with a specific species (e.g., pollinator, mycorrhizae, rhizobium) in their native habitat may become established but not spread in the invaded habitat. Furthermore, coevolution with particular symbionts in their home range may make establishing a mutualism with a similar species in their new range difficult or impossible. Zenni and Nuñez (2013) refer to this as “mutualism release.” Examples of this include the limited spread of certain introduced tree species in Patagonia as needed mycorrhizal species were absent (Nuñez et al., 2009). Similarly, lack of appropriate rhizobial strains may limit colonization success of legumes (Rodríguez-Echeverría, 2010). Some non-indigenous fig species became established in Florida but did not spread until their specific pollinators were introduced (Nadel et al., 1992; Ramirez & Montero, 1988). Lack of needed mutualists should not preclude colonization of invading hosts by symbionts with negative or neutral effects; symbionts with negative impacts may contribute to the failure of an invader to become established.

We should note that all of the above outcomes preclude any negative interactions among the native symbionts (e.g., Thomas et al., 2016). If there is intraguild predation or competition among native symbionts then these interactions could influence long-term trends in native symbiont abundance and diversity independent of host diversity and abundance. Interestingly, if invading hosts are colonized largely by native symbiont taxa that incur negative fitness outcomes from interactions with other native symbionts on their native host, then colonization of an invading host could benefit these

competitively subordinate symbiont taxa over the long term, especially if the competitively dominant symbiont is disproportionately removed by the invasive host. Essentially, an invading host could become a refuge for these competitively inferior native symbionts.

IMPACTS OF INVADING SYMBIONTS

In the conceptual framework described above in the section on *Host competence*, we evaluated the response of native symbionts to non-competent, non-indigenous hosts as well as those that vary in competence relative to native hosts. However, not only hosts invade communities but symbionts as well, frequently arriving on an invading host. Some non-indigenous symbionts may be introduced separately from their hosts such as mycorrhizae introduced in soil or by wind dispersal (Richardson et al., 2000). Native symbionts could also be affected by these invasions of non-indigenous symbionts by direct and indirect effects.

Direct effects

Direct competition between native and invading symbionts for hosts or host-associated resources undoubtedly occurs in many systems. If invading symbionts are better competitors for either hosts or the resources associated with the host then they could reduce the abundance of or displace native symbionts. Invading symbionts may also exclude native symbionts by some form of interference competition. It is also possible that invading symbionts could consume native symbionts (intraguild predation) again causing reductions or displacement of the native symbiont species. Examples of direct effects of non-indigenous symbionts on native symbionts include the replacement of native mycorrhizae by introduced mycorrhizal species from Australia in Portugal (Rodríguez-Echeverría, 2010).

Indirect effects

The most likely indirect effect of an invasive symbiont on a native symbiont is by the impact of the invading symbiont on the host of the native symbiont. If the invading symbiont causes declines or even the extirpation of native hosts then this outcome will have effects on native symbionts dependent on that native host, or group of native hosts, if they are unable to utilize an invading host (Figure 3a). If no alternative host is available for the invading symbiont, this scenario could also result in a

self-annihilating system for the invading symbiont. If there is co-invasion by an invading host and symbiont, then this scenario could also cause the extirpation of the native host and symbionts, but the invading symbiont could persist on the invading host (Figure 3b).

Co-introduction or the subsequent introduction of particular symbionts may greatly enhance the negative effects of invading hosts on the invaded community, a host-symbiont example of an invasional meltdown (Simberloff & Von Holle, 1999). An example of this type of invasional meltdown is the introduction of North American crayfish into Europe along with their associated, symbiotic water mold (*Aphanomyces astaci*), commonly referred to as crayfish plague (Holdich et al., 2009). North American crayfish carry crayfish plague but are not typically killed by it, whereas European crayfish are susceptible to severe pathology from the fungus. This plague decimated native crayfish

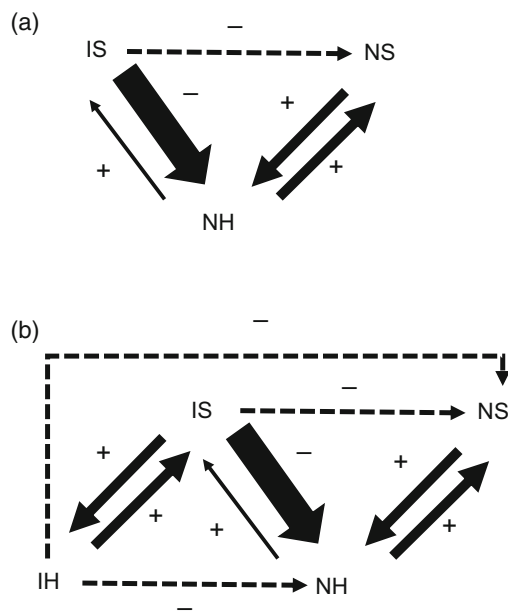


FIGURE 3 Direct and indirect effects of an invading symbiont (IS) on a symbiosis between a native host (NH) and a native symbiont (NS). (a) In this scenario the invading symbiont causes a decline or the extirpation of the native host (direct effect). This leads to the decline or extirpation of the native symbiont that was dependent on the native host (indirect effect). If there are no alternative hosts for the invading symbiont then it will also go extinct. (b) Direct and indirect effects of co-invasion by an invading symbiont and invading host (IH). As in panel (a), the invading symbiont can cause the decline or extirpation of the native host and, indirectly, the decline or extirpation of the native symbiont. There is the added negative indirect effect of the invading host on the native host by its association with the invading symbiont. There is also an indirect, negative effect of the invading host on the native symbiont. In this scenario, both the invading host and symbiont could persist. Direct effects are solid arrows; indirect effects are dashed arrows. Width of arrow indicates strength of proposed effect

species in Europe that removed the major competitors for non-indigenous crayfish, probably facilitating their spread across the continent (Holdich et al., 2009). Had native crayfish not been susceptible to the plague, it is possible that the spread of introduced crayfish hosts would have been considerably slower in Europe or only occurred in isolated areas with reduced abundances of native crayfish. Ultimately, the rate of spread would have been a function of the relative competitive abilities of the native and introduced crayfish species and the relative vulnerability of the two hosts to native predators. Any symbiont taxa obligately associated with the native European crayfish that could not colonize the invading North American crayfish would have been eliminated from those systems (Figure 3b).

Co-invasion or the subsequent invasion of habitats by mycorrhizae was critical to the spread of non-indigenous plants in various habitats including pines in the southern hemisphere, *Eucalyptus* in the Northern hemisphere and *Acacia* in Portugal (Nuñez et al., 2009; Richardson et al., 2000; Rodríguez-Echeverría, 2010). Many non-indigenous plant species had limited impacts until their mutualistic symbionts were also introduced. Examples include pines spreading after pine-associated mycorrhizae were introduced, figs spreading in Florida after their pollinators were introduced, and legumes spreading after needed rhizobia were introduced (Zenni & Nuñez, 2013). If native hosts suffer in the face of competition with invading hosts and their co-invading symbionts, then this scenario could lead to a decline in native symbiont abundance and diversity if these species are unable to use the non-indigenous host or are excluded from it by the invading symbionts.

DISCUSSION

There are multiple scenarios that can occur during an invasion with respect to symbiont loss and acquisition. Invading species can leave behind natural enemies that greatly enhances their probability of successfully invading and spreading in the new environment (Colautti et al., 2004; Dunn & Hatcher, 2015; Keane & Crawley, 2002). These same invading species can develop novel mutualisms with symbionts in the invaded habitats or invaders can spread once similar symbionts from their endemic habitats invade (Aslan et al., 2015; Nuñez et al., 2009; Richardson et al., 2000; Traveset & Richardson, 2014). Interactions with symbionts, native or co-invading, can influence interactions among invading and native host taxa (Mitchell et al., 2006). In general, researchers studying these scenarios have focused on the effects or responses of the invading or native host taxa. Here we have focused primarily on how populations and communities of native symbionts, groups that are often

overlooked, respond to invasions of both new hosts and new symbionts.

The first factor critical to native symbionts is whether or not an invading host is a competent host for native symbionts, i.e., will the invading host have potential positive or negative impacts on symbiont fitness? Given that most of the studies examining symbiont effects, exotic or native, have focused on plant hosts, this idea may have been largely understudied because plant hosts may have more limited abilities to regulate symbionts than animal hosts (but please refer to Bever et al., 2009; Kiers & Densison, 2008). Symbiont regulation has been demonstrated in some obligate plant-pollinator mutualisms (Pellmyr & Huth, 1994; Wang et al., 2014). However, given various morphological (e.g., trichomes) and physiological properties (e.g., release of resins) of plants, as well as the ability of some plant hosts to sanction symbionts (Bever et al., 2009; Kiers & Densison, 2008), there is potential for some symbiont regulation by some plant hosts. For example, can plants other than those engaged in obligate mutualisms spontaneously abort plant tissues overrun with parasites or mutualists? This question could be a fruitful avenue of potential research and provide additional evidence for explaining failed invasions (Nuñez et al., 2009) and perhaps the development of novel symbioses (Aslan et al., 2015). Understanding the relative competence of potential invasive hosts could be as important as determining host specificity in biological control programs if we want to minimize impacts of invasion on communities of native symbionts.

If a non-competent host invades a community of competent, native hosts then there is potential for a dilution effect that could have significant consequences for native symbiont populations and communities (Creed et al., 2022; Kopp & Jokela, 2007; Thieltges et al., 2009). If native symbionts frequently encounter these non-competent hosts when dispersing from one host to another, then there is an increased probability that these symbionts will be lost from the community. This outcome is particularly likely if the introduced, non-competent host is aggressive with respect to grooming or has a strong immune system. Over time, symbiont abundance and diversity on native hosts is predicted to decline as the non-competent host will function as a sink for native symbionts. Dilution effects are considered positive effects of increased host diversity with respect to parasite and disease transmission and could result in the decline of native parasites and pathogens (Johnson et al., 2013; Keesing et al., 2006; Kopp & Jokela, 2007; Thieltges et al., 2009). However, host dilution will also lead to declines in both mutualist and commensal symbionts. If these native mutualists are engaged in positive interactions with native hosts then the loss of these symbionts could reduce the fitness of many native hosts. A dilution effect involving a non-competent, invading crayfish host is

causing declines in the abundance and diversity of native symbionts (mutualists and commensals) in communities of stream crayfish in eastern North America (Bell, 2018; Creed et al., 2022).

As we stated above, host competence is more complex than a simple binary proposition of invading hosts being competent or not (Figure 2). There may, in fact, be a gradient in potential competence of invading hosts. Hosts may be able to groom some symbionts but not others. For example, crayfish can effectively remove crayfish worms but their grooming does not appear to be effective against other symbionts such as ostracods and stalked protozoa (Robert P. Creed, *personal observation*). The probability of acquiring new symbionts may also depend on phylogenetic relatedness to the hosts' typical symbionts (Skelton et al., 2019). Similarly, host immune systems may be effective defenses against some species and not others. This mechanism could lead to changes in symbiont community structure on hosts. Determining the degree of host competence could also be an interesting avenue of research as the consequences for native symbionts will depend on both symbiont acquisition by competent hosts and subsequent interactions among native and introduced symbionts if exotic symbionts co-invade a habitat or colonize an exotic host following an introduction. This symbiont colonization could be part of the process leading to the development of novel mutualisms as well as other novel symbiotic relationships (Aslan et al., 2015; Hokkanen & Pimentel, 1989). For example, novel parasitisms may arise when native parasites colonize non-indigenous species (Callaway et al., 2004; Klironomos, 2002).

Another interesting area of potential research is evaluating the differences between animal and plant hosts with respect to symbiont acquisition. Current evidence suggests that animals, with grooming behaviors as well as more sophisticated immune responses, are more likely to be non-competent hosts than plants. Evaluation of different types of animal hosts (vertebrate vs. invertebrate; fish vs. amphibians, etc.) could be useful in estimating the impacts of different types of animal hosts on native and invading symbionts. Host specificity could limit development of new symbioses between plants and new symbionts in novel habitats (e.g., specific plant–pollinator mutualisms, specific associations with particular fungi or bacteria; Nadel et al., 1992; Nuñez et al., 2009; Ramirez & Montero, 1988; Richardson et al., 2000).

Although the emphasis in the literature has been on the formation of novel mutualisms between non-indigenous hosts and native symbionts (Aslan et al., 2015; Richardson et al., 2000; Traveset & Richardson, 2014), the scope of this research needs to include novel commensalisms. The addition of new hosts

to a habitat could have important fitness consequences for commensal symbionts (Table 1). These associations may also develop more readily than novel mutualisms (Aslan et al., 2015) meaning that they could be far more common and potentially easier to study. In fact, novel commensalisms may be an early step in the process of forming novel mutualisms. The formation of these new associations, whether parasitic, commensalistic, or mutualistic, could also be the first steps in the speciation process for some of these symbionts, especially if they engage in assortative mating on their hosts.

Native symbionts may indirectly influence invasion success if they can influence the ability of their native hosts to persist in the face of interactions with invading hosts. Native symbionts may increase the competitive ability of their native hosts and increase the odds that they can outcompete invading species. Craig et al. (2011) found that a native grass with its native fungal symbiont was able to outcompete invading Japanese stiltgrass (*Microstegium*). Native North American crayfish engage in a mutualism with some species of crayfish worm (Brown et al., 2012; Thomas et al., 2016). Given that these crayfish worms can improve the growth and reduce mortality of their native hosts, it is likely that host competitive ability is enhanced when these ectosymbionts are present. This positive interaction may allow them to persist in the presence of invading crayfish hosts. Loss of these symbionts due to the invasion of a low- or non-competent host may therefore lead to a shift in the competitive relationships of native and introduced hosts that could result in the slow decline in the abundance of the native crayfish (Bell, 2018; Creed et al., 2022). Loss or declines in symbiont abundance on their native hosts could be an important mechanism by which invasions ultimately succeed. Similarly, invading symbionts extirpating native symbionts is another indirect mechanism by which invasions may succeed even if there is no short-term change in native host abundance.

One interesting issue not discussed here is the idea that native parasites and pathogens may have less of a negative effect on successful invaders than on native host species (Callaway et al., 2004; Klironomos, 2002). Non-indigenous species acquire native symbionts that have a negative impact, but the impact is less than that exerted on native host species. This scenario can lead to increased growth and spread of the introduced host species relative to native hosts (Callaway et al., 2004; Klironomos, 2002). Although the outcome is comparable with native symbiont facilitation it arises from a different mechanism, the lessening of negative impacts of parasites and pathogens. From the symbiont perspective, this outcome may be beneficial if the new host is more abundant than the native host.

The success or failure of invading hosts and symbionts and their impacts on native hosts and symbionts will undoubtedly be influenced by the abiotic environment. Environmental filtering may prevent invading hosts and symbionts from colonizing a habitat and disrupting native host–symbiont systems (Krasnov et al., 2015). Alternatively, if native hosts and symbionts occur across a range of environmental conditions (e.g., ranges in temperature, humidity etc.) then context dependence in the effects of invading hosts and symbionts may occur. Strong effects of invaders may be observed in one part of the range of a native host whereas little or no effect may be observed under other environmental conditions in other parts of its range.

Many symbioses have strong effects on community structure and ecosystem function. If native host–symbiont systems are disrupted by a non-competent invading host then these impacts could be altered considerably. The invading crayfish *Faxonius cristavarius* is causing declines in the abundance and diversity of native crayfish worms (Bell, 2018; Creed et al., 2022). Some of these worms can modulate the effect of their native crayfish hosts on community structure and sediment deposition (Creed et al., 2021). Loss of these worms could result in diminished effects of the native hosts on coexisting taxa. If the invading host does not compensate for the activities of the native host then there could be long-term changes in these communities.

The ideas presented here provide a conceptual framework for understanding how invading hosts and symbionts can alter populations and communities of native symbionts. They also provide a framework for understanding how native symbionts can influence invading hosts. These frameworks extend ideas such as the ERH and the mutual facilitation hypothesis while also evaluating explicitly how native symbionts are affected. Native symbionts, especially mutualists and commensals, are often an overlooked element of native biodiversity. We advocate the study of these native host–symbiont systems and how they may respond to invasion as well as how they may prevent it.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

REFERENCES

- Aslan, C. E., B. A. Sikes, and K. B. Gedan. 2015. “Research on Mutualisms between Native and Non-native Partners Can Contribute Critical Ecological Insights.” *NeoBiota* 26: 39–54. DOI: [10.3897/neobiota.26.8837](https://doi.org/10.3897/neobiota.26.8837)
- Barron, D. G., S. S. Gervasi, J. N. Pruitt, and L. B. Martin. 2015. “Behavioral Competence: How Host Behaviors Can Interact to Influence Parasite Transmission Risk.” *Current Opinion in Behavioral Sciences* 6: 35–40. DOI: [10.1016/j.cobeha.2015.08.002](https://doi.org/10.1016/j.cobeha.2015.08.002)
- Bell, S.S. 2018. “Impacts of Invasion on Symbiotic Systems.” MS Thesis. Blacksburg, VA: Virginia Tech.
- Bever, J. D., S. C. Richardson, B. M. Lawrence, J. Holmes, and M. Watson. 2009. “Preferential Allocation to Beneficial Symbiont with Spatial Structure Maintains Mycorrhizal Mutualism.” *Ecology Letters* 12: 13–21. DOI: [10.1111/j.1461-0248.2008.01254.x](https://doi.org/10.1111/j.1461-0248.2008.01254.x)
- Brown, B. L., R. P. Creed, and W. E. Dobson. 2002. “Branchiobdellid Annelids and their Crayfish Hosts: Are they Engaged in a Cleaning Symbiosis?” *Oecologia* 132: 250–5. DOI: [10.1007/s00442-022-0961-1](https://doi.org/10.1007/s00442-022-0961-1)
- Brown, B. L., R. P. Creed, J. Skelton, M. A. Rollins, and K. J. Farrell. 2012. “The Fine Line between Mutualism and Parasitism: Complex Effects in a Cleaning Symbiosis Demonstrated by Multiple Field Experiments.” *Oecologia* 170: 199–207. <https://doi.org/10.1007/s00442-012-2280-5>.
- Callaway, R. M., G. C. Thelan, A. Rodriguez, and W. E. Holben. 2004. “Soil Biota and Exotic Plant Invasion.” *Nature* 427: 731–3. DOI: [10.1038/nature02322](https://doi.org/10.1038/nature02322)
- Carey, E. V., M. J. Marler, and R. M. Callaway. 2004. “Mycorrhizae Transfer Carbon from a Native Grass to an Invasive Weed: Evidence from Stable Isotopes and Physiology.” *Plant Ecology* 172: 133–41. DOI: [10.1023/B:VEGE.0000026031.14086.f1](https://doi.org/10.1023/B:VEGE.0000026031.14086.f1)
- Cichy, A., M. Urbanska, A. Marszewska, W. Andrzejewski, and E. Zbikowska. 2016. “The Invasive Chinese Pond Mussel *Sinanodonta woodiana* (Lea, 1834) as a Host for Native Symbionts in European Waters.” *Journal of Limnology* 75: 288–96. DOI: [10.4081/jlimnol.2016.1334](https://doi.org/10.4081/jlimnol.2016.1334)
- Colautti, R. I., A. Ricciardi, I. A. Grigorovich, and H. J. MacIsaac. 2004. “Is Invasion Success Explained by the Enemy Release Hypothesis?” *Ecology Letters* 7: 721–33. DOI: [10.1111/j.1461-0248.2004.00616.x](https://doi.org/10.1111/j.1461-0248.2004.00616.x)
- Craig, S., S. Kannadan, S. L. Flory, E. K. Siefert, K. D. Whitney, and J. A. Rudgers. 2011. “Potential for Endophyte Symbiosis to Increase Resistance of the Native Grass *Poa alsodes* to Invasion by the Non-native Grass *Microstegium vimineum*.” *Symbiosis* 53: 17–28. DOI: [10.1007/s13199-010-0102-2](https://doi.org/10.1007/s13199-010-0102-2)
- Creed, R. P., and B. L. Brown. 2018. “Multiple Mechanisms Can Stabilize a Freshwater Mutualism.” *Freshwater Science* 37: 760–8. DOI: [10.1086/700560](https://doi.org/10.1086/700560)
- Creed, R. P., G. L. Bailey, J. Skelton, and B. L. Brown. 2022. “The Dilution Effect in a Freshwater Mutualism: Impacts of Introduced Host Species on Native Symbionts.” *River Research and Applications*: 1–9. <https://doi.org/10.1002/rra.3940>.
- Creed, R. P., and S. P. Sheldon. 1995. “Weevils and Watermilfoil: Did a North American Herbivore Cause the Decline of an Exotic Plant?” *Ecological Applications* 5: 1113–21. DOI: [10.2307/2269358](https://doi.org/10.2307/2269358)
- Creed, R. P., J. Skelton, K. J. Farrell, and B. L. Brown. 2021. “Strong Effects of a Mutualism on Freshwater Community Structure.” *Ecology* 102(2): e03225. DOI: [10.1002/ecy.3225](https://doi.org/10.1002/ecy.3225)

- Dunn, A. M., and M. J. Hatcher. 2015. "Parasites and Biological Invasions: Parallels, Interactions, and Control." *Trends in Parasitology* 31: 189–99. DOI: [10.1016/j.pt.2014.12.003](https://doi.org/10.1016/j.pt.2014.12.003)
- Farrell, K. J., R. P. Creed, and B. L. Brown. 2014. "Preventing Over-exploitation in a Mutualism: Partner Regulation in the Crayfish–Branchiobdellid Symbiosis." *Oecologia* 174: 501–10. DOI: [10.1007/s00442-013-2780-y](https://doi.org/10.1007/s00442-013-2780-y)
- Grman, E. 2012. "Plant Species Differ in their Ability to Reduce Allocation to Non-beneficial Arbuscular Mycorrhizal Fungi." *Ecology* 93: 711–8. DOI: [10.1890/11-1358.1](https://doi.org/10.1890/11-1358.1)
- Grutter, A. S. 1999. "Cleaner Fish Really Do Clean." *Nature* 398: 672–3. DOI: [10.1038/19443](https://doi.org/10.1038/19443)
- Hokkanen, H. M. T., and D. Pimentel. 1989. "New Associations in Biological Control: Theory and Practice." *Canadian Entomologist* 121: 829–40. DOI: [10.4039/Ent121829-10](https://doi.org/10.4039/Ent121829-10)
- Holdich, D. M., J. D. Reynolds, C. Souty-Grosset, and P. J. Sibley. 2009. "A Review of the Ever Increasing Threat to European Crayfish from Non-indigenous Crayfish Species." *Knowledge and Management of Aquatic Ecosystems* 394-395: article 11. DOI: [10.1051/kmae/2009025](https://doi.org/10.1051/kmae/2009025)
- Huang, Z. Y. X., F. Van Langevelde, A. Estrada-Pena, G. Suzan, and W. F. De Boer. 2016. "The Diversity-disease Relationship: Evidence for and Criticisms of the Dilution Effect." *Parasitology* 143: 1075–86.
- Johnson, P. T. J., D. L. Preston, J. T. Hoverman, and K. L. D. Richgels. 2013. "Biodiversity Decreases Disease through Predictable Changes in Host Community Competence." *Nature* 494: 230–3. DOI: [10.1038/nature11883](https://doi.org/10.1038/nature11883)
- Jones, J. D. G., and J. L. Dangl. 2006. "The Plant Immune System." *Nature* 444: 323–9. DOI: [10.1038/nature05286](https://doi.org/10.1038/nature05286)
- Keane, R. M., and M. J. Crawley. 2002. "Exotic Plant Invasions and the Enemy Release Hypothesis." *Trends in Ecology and Evolution* 17: 164–70. [https://doi.org/10.1016/S0169-5347\(02\)02499-0](https://doi.org/10.1016/S0169-5347(02)02499-0).
- Keesing, F., R. D. Holt, and R. S. Ostfeld. 2006. "Effects of Species Diversity on Disease Risk." *Ecology Letters* 9: 485–98. DOI: [10.1111/j.1461-0248.2006.00885.x](https://doi.org/10.1111/j.1461-0248.2006.00885.x)
- Keesing, F., J. Brunner, S. Duerr, M. Killilea, K. LoGiudice, K. Schmidt, H. Vuong, and R. S. Ostfeld. 2009. "Hosts as Ecological Traps for the Vector of Lyme Disease." *The Proceedings of the Royal Society B: Biological Sciences* 276: 3911–9. <https://doi.org/10.1098/rspb.2009.1159>
- Kiers, E. T., and R. F. Densison. 2008. "Sanctions, Cooperation, and the Stability of Plant-Rhizosphere Mutualisms." *Annual Review of Ecology, Evolution, and Systematics* 39: 215–36. DOI: [10.1146/annurev.ecolsys.39.110707.173423](https://doi.org/10.1146/annurev.ecolsys.39.110707.173423)
- Klironomos, J. N. 2002. "Feedback with Soil Biota Contributes to Plant Rarity and Invasiveness in Communities." *Nature* 417: 67–70. DOI: [10.1038/417067a](https://doi.org/10.1038/417067a)
- Kopp, K., and J. Jokela. 2007. "Resistant Invaders Can Convey Benefits to Native Species." *Oikos* 116: 295–301. DOI: [10.1111/j.2006.0030-1299.15290.x](https://doi.org/10.1111/j.2006.0030-1299.15290.x)
- Krasnov, B. R., G. I. Shenbrot, I. S. Khokhlova, M. Stanko, S. Morand, and D. Mouillot. 2015. "Assembly Rules of Ectoparasite Communities across Scales: Combining Patterns of Abiotic Factors, Host Composition, Geographic Space, Phylogeny and Traits." *Ecography* 38: 184–97. DOI: [10.1111/ecog.00915](https://doi.org/10.1111/ecog.00915)
- Li, Y., Y. Y. Ruan, E. L. Stanley, J. Skelton, and J. Hulcr. 2019. "Plasticity of Mycangia in *Xylosandrus* Ambrosia Beetles." *Insect Science* 26: 732–42. <https://doi.org/10.1111/1744-7917.12590>
- Lopezaraiza-Mikel, M. E., R. B. Hayes, M. R. Whalley, and J. Memmott. 2007. "The Impact of an Alien Plant on a Native Plant-Pollinator Network: An Experimental Approach." *Ecology Letters* 10: 539–50. DOI: [10.1111/j.1461-0248.2007.01055.x](https://doi.org/10.1111/j.1461-0248.2007.01055.x)
- Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. "Biotic Invasions: Causes, Epidemiology, Global Consequences and Control." *Ecological Applications* 10: 689–710. [https://doi.org/10.1890/1051-0761\(2000\)010\[0689:BICEGC\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2000)010[0689:BICEGC]2.0.CO;2)
- Mitchell, C. E., A. A. Agrawal, J. D. Bever, G. S. Gilbert, R. A. Huffbauer, J. N. Klironomos, J. L. Maron, et al. 2006. "Biotic Interactions and Plant Invasions." *Ecology Letters* 9: 726–40. DOI: [10.1111/j.1461-0248.2006.00908.x](https://doi.org/10.1111/j.1461-0248.2006.00908.x)
- Mitchell, C. E., and A. G. Power. 2003. "Release of Invasive Plants from Fungal and Viral Pathogens." *Nature* 421: 625–7. DOI: [10.1038/nature01317](https://doi.org/10.1038/nature01317)
- Nadel, H., J. H. Frank, and R. J. Knight. 1992. "Escapees and Accomplices: The Naturalization of Exotic *Ficus* and their Associated Faunas in Florida." *Florida Entomologist* 75: 29–38. DOI: [10.2307/3495478](https://doi.org/10.2307/3495478)
- Núñez, M. A., T. R. Horton, and D. Simberloff. 2009. "Lack of Belowground Mutualisms Hinders Pinaceae Invasions." *Ecology* 90: 2352–9. DOI: [10.1890/08-2139.1](https://doi.org/10.1890/08-2139.1)
- Owen, J. P., M. E. Delany, C. J. Cardona, A. A. Bickford, and B. A. Mullens. 2009. "Host Inflammatory Response Governs Fitness in an Avian Ectoparasite, the Northern Fowl Mite (*Ornithonyssus sylviarum*)." *International Journal for Parasitology* 39: 789–99. DOI: [10.1016/j.ijpara.2008.12.008](https://doi.org/10.1016/j.ijpara.2008.12.008)
- Pellmyr, O., and C. J. Huth. 1994. "Evolutionary Stability of Mutualism between Yuccas and Yucca Moths." *Nature* 372: 257–60. DOI: [10.1038/372257a0](https://doi.org/10.1038/372257a0)
- Ramirez, W., and J. Montero. 1988. "*Ficus Microcarpa* L., *F. Benjamina* L., and Other Species Introduced into the New World, their Pollinators (Agaonidae) and Other Fig Wasps." *Revista de Biología Tropical* 36: 441–6.
- Randolph, S. E. 1979. "Population Regulation in Ticks: The Role of Acquired Resistance in Natural and Unnatural Hosts." *Parasitology* 79: 141–56. DOI: [10.1017/S00331182000052033](https://doi.org/10.1017/S00331182000052033)
- Rassati, D., L. Marini, and A. Malacrino. 2019. "Acquisition of Fungi from the Environment Modifies Ambrosia Beetle Mycobiome during Invasion." *PeerJ* 7: e8103. DOI: [10.7717/peerj.8103](https://doi.org/10.7717/peerj.8103)
- Ricciardi, A. 1994. "Occurrence of Chironomid Larvae (*Paratanytarsus* Sp.) as Commensals of Dreissenid Mussels (*Dreissena polymorpha* and *D. bugensis*)." *Canadian Journal of Zoology* 72: 1159–62. <https://doi.org/10.1139/z94-155>
- Richardson, D. M., N. Allsopp, C. M. D'Antonio, S. J. Milton, and M. Rejmanek. 2000. "Plant Invasions – The Role of Mutualisms." *Biological Reviews* 75: 65–93. DOI: [10.1017/S0006323199005435](https://doi.org/10.1017/S0006323199005435)
- Rodríguez-Echeverría, S. 2010. "Rhizobial Hitchhikers from Down under: Invasional Meltdown in a Plant-Bacteria Mutualism?" *Journal of Biogeography* 37: 1611–22. DOI: [10.1111/j.1365-2699.2010.02284.x](https://doi.org/10.1111/j.1365-2699.2010.02284.x)
- Rodríguez-Echeverría, S., J. A. Crisotomo, C. Nabais, and H. Freitas. 2009. "Belowground Mutualists and the Invasive Ability of *Acacia Longifolia* in Coastal Dunes of Portugal." *Biological Invasions* 11: 651–61.
- Simberloff, D., and L. Gibbons. 2004. "Now you See them, Now you don't! – Population Crashes of Established Introduced

- Species.” *Biological Invasions* 6: 161–72. DOI: [10.1023/B:BINV.0000022133.49752.46](https://doi.org/10.1023/B:BINV.0000022133.49752.46)
- Simberloff, D., and B. Von Holle. 1999. “Positive Interactions of Non-indigenous Species: Invasional Meltdown?” *Biological Invasions* 1: 21–32. DOI: [10.1023/A:1010086329619](https://doi.org/10.1023/A:1010086329619)
- Skelton, J., R. P. Creed, and B. L. Brown. 2014. “Ontogenetic Shift in Host Tolerance Controls Initiation of a Cleaning Symbiosis.” *Oikos* 123: 677–86. <https://doi.org/10.1111/j.1600-0706.2013.00963.x>.
- Skelton, J., A. J. Johnson, M. A. Jusino, C. C. Bateman, Y. Li, and J. Hulcr. 2019. “A Selective Fungal Transport Organ (Mycangium) Maintains Coarse Phylogenetic Congruence between Fungus-Farming Ambrosia Beetles and their Symbionts.” *Proceedings of the Royal Society B* 286(1894): 20182127. DOI: [10.1098/rspb.2018.2127](https://doi.org/10.1098/rspb.2018.2127)
- Spoel, S. H., and X. Dong. 2012. “How Do Plants Achieve Immunity? Defense without Specialized Immune Cells.” *Nature Reviews: Immunology* 12: 89–100. DOI: [10.1038/nri3141](https://doi.org/10.1038/nri3141)
- Stewart Merrill, T. E., and P. T. J. Johnson. 2020. “Towards a Mechanistic Understanding of Competence: A Missing Link in Diversity-Disease Research.” *Parasitology* 147: 1159–70. DOI: [10.1017/s0031182020000943](https://doi.org/10.1017/s0031182020000943)
- Stricker, K. B., P. F. Harmon, E. M. Goss, K. Clay, and S. L. Flory. 2016. “Emergence and Accumulation of Novel Pathogens Suppress an Invasive Species.” *Ecology Letters* 19: 469–77. DOI: [10.1111/ele.12583](https://doi.org/10.1111/ele.12583)
- Thieltges, D. W., K. Reise, K. Prinz, and K. T. Jensen. 2009. “Invaders Interfere with Native Parasite–Host Interactions.” *Biological Invasions* 11: 1421–9. DOI: [10.1007/s10530-008-9350-y](https://doi.org/10.1007/s10530-008-9350-y)
- Thomas, M. J., R. P. Creed, J. Skelton, and B. L. Brown. 2016. “Ontogenetic Shifts in a Freshwater Cleaning Symbiosis: Consequences for the Host and Symbionts.” *Ecology* 97: 1507–17. DOI: [10.1890/15-1443.1](https://doi.org/10.1890/15-1443.1)
- Traveset, A., and D. M. Richardson. 2014. “Mutualistic Interactions and Biological Invasions.” *Annual Review of Ecology, Evolution and Systematics* 45: 89–113. DOI: [10.1146/annurev-ecolsys-120213-091857](https://doi.org/10.1146/annurev-ecolsys-120213-091857)
- Wang, R.-W., D. W. Dunn, and B. F. Sun. 2014. “Discriminative Host Sanctions in a Fig-Wasp Mutualism.” *Ecology* 95: 1384–93. <https://doi.org/10.1890/13-0749.1>.
- Warren, R. J., and M. A. Bradford. 2021. “Non-native *Microstegium vimineum* Populations Collapse with Fungal Leaf Spot Disease Outbreak.” *Plant Ecology* 222: 107–17. DOI: [10.1007/s11258-020-01091-4](https://doi.org/10.1007/s11258-020-01091-4)
- Williamson, M., and A. Fitter. 1996. “The Varying Success of Invaders.” *Ecology* 77: 1661–6. DOI: [10.2307/2265769](https://doi.org/10.2307/2265769)
- Zenni, R. D., and M. A. Nuñez. 2013. “The Elephant in the Room: The Role of Failed Invasions in Understanding Invasion Biology.” *Oikos* 122: 801–15. DOI: [10.1111/j.16000706.2012.00254.x](https://doi.org/10.1111/j.16000706.2012.00254.x)

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