The Role of Symbiotic Microbes in Insect Invasions

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Abstract

The number of insect species transported to non-native regions is increasing, and, once established, these invasive insects have serious impacts on the environment and regional economies. Recent research highlights several cases of insect invasions facilitated by symbiotic microbes. Symbioses impact biological invasions, but few reviews have addressed the role of symbiotic microbes in insect invasions. Focusing on the insect–microbial symbiosis, we show the importance of microbial symbionts in determining the pest status of insects at insect–microbial levels, insect–plant–microbial levels, and other multispecific levels. Drawing on examples from different ecosystems, we review the key mechanisms and principles whereby facultative/mutualistic microbes affect insect invasions and coevolve with the invasive insects. We propose a conceptual framework for assessing the role of symbiotic microbes in insect invasions that promises improved risk analyses, spread and impact modeling, and management of invasive insects.

1. INTRODUCTION

1.1. Insect Invasions

Propagule pressure: a composite measure of the number of individuals of species released into a region to which they are not native

Invasive: a non-native organism that spreads into the environment and causes damage to the environment, human economy, and/or human health

Symbiosis: two or more organisms living together in close association

Mutualism: reciprocally positive interactions between pairs of species

A growing number of insects are transported to non-native regions and become invasive, and these invasive insects are impacting both the environment and local or regional economies (Holway et al. 2002, Goulson 2003, Snyder & Evans 2006). They also exert evolutionary pressures (Mooney & Cleland 2001, Lee 2002, Suarez & Tsutsui 2008) and can alter even geomorphic processes (Fei et al. 2014) and the fundamental structure and function of ecosystems (Ehrenfeld 2010). Attempts to explain why some insects become successful pests have tended to focus on population ecology (Sakai et al. 2001, Liebhold & Tobin 2008), propagule pressure (Simberloff 2009), dispersal abilities, adaptability, and the evolutionary history of the invaders as well as the invaded ecosystems (Mack et al. 2000, Lee 2002, Shea & Chesson 2002). A few experimental studies have also illustrated the reason from the following perspectives. For example, loss of intraspecific aggression was used to explain the invasion success of an invasive social insect, the Argentine ant (*Linepithema humile*), in the United States (Holway et al. 1998). Asymmetric mating interactions may have driven widespread invasion of an invasive whitefly, *Bemisia tabaci*, in China (Liu et al. 2007). Purging deleterious alleles was shown to enable the evolution of a worldwide invasive ladybird beetle (*Harmonia axyridis*), maintaining high fitness even when inbred (Facon et al. 2011). Recent research highlighted several cases of insect invasions that were facilitated by microbes (Himler et al. 2011, Lu et al. 2011, Frago et al. 2012, Vilcinskas et al. 2013, Zhao et al. 2013). The number of such cases is increasing, and it is becoming clear that the role of microbes in facilitating insect invasions is likely much more important than researchers, industries, and regulators have previously believed.

1.2. Symbiotic Interactions and Biological Invasions

Symbiosis is extremely important for the structure and function of ecosystems. Among the different types of symbioses (mutualistic, commensal, and antagonistic), mutualism is ubiquitous in all types of ecosystems and plays essential roles in organization and performance of communities (Boucher et al. 1982, Bronstein 2009). Symbioses, especially mutualisms, enhance invasions of many alien species. In turn, invasions disrupt native symbioses, leading to population declines, reduced biodiversity, and altered ecosystem functioning (Richardson et al. 2000, Traveset & Richardson 2014).

Symbioses can be important at all stages of the introduction–naturalization–invasion continuum for plants and at all phases of a plant's life cycle (Richardson & Pyšek 2012, Traveset & Richardson 2014). During the establishment phase, a plant can benefit from symbiotic interactions with fungi and/or bacteria (Richardson et al. 2000, Pringle et al. 2009, Shah et al. 2009). Plant–mycorrhizal symbioses are ubiquitous interactions involving the plants and soil fungi of most terrestrial ecosystems (Pringle et al. 2009). Both the interactions of legumes and Proteobacteria (e.g., *Bradyrhizobium* spp. and *Rhizobium* spp.) and the interactions of actinorhizal plants and actinomycetes (e.g., *Frankia* spp.), which fix atmospheric nitrogen at approximately the same efficiency, are implicated in the invasive spread of alien plants (Richardson et al. 2000). The mechanisms by which mycorrhizal fungi and/or nitrogen-fixing bacteria facilitate plant invasion include the alteration of nutrient uptake, competitive dynamics, successional changes, and multitrophic interactions to the advantage of the alien species and the detriment of native species (Richardson et al. 2000, Rodríguez-Echeverría et al. 2012, Morrien & van der Putten 2013, Ndlovu et al. 2013, Traveset & Richardson 2014).

Although several symbioses involving insects, such as ant–Hemiptera, plant–insect pollinators, and plant–insect seed dispersers, have contributed to the success of insect invasions (Wilder et al. 2011, Traveset et al. 2013), this phenomenon has received relatively little attention (Traveset & Richardson 2014). Recently, such examples are becoming increasingly important. The red imported fire ant (*Solenopsis invicta*) ranks as one of the world's most destructive invasive species because of its ability to affect human health (Jemal & Hugh-Jones 1993) and to disrupt natural and agricultural systems (Tschinkel 2006). This introduced species benefits from the food-for-protection symbioses with honeydew-producing Hemiptera and other carbohydrate-producing organisms (Wilder et al. 2011). Invasive ants and plants can benefit one another through seed dispersal (Prior et al. 2015), and at least 15% of the introduced insects in the Galápagos archipelago visit native flowers for pollen and nectar (Traveset et al. 2013), suggesting that their invasion success is probably related to the generalized symbiotic interactions they establish with plants (Traveset & Richardson 2014).

1.3. The Aim of This Review

Focusing on one of the most pervasive and influential symbioses—insect–microbial symbiosis—we aim to integrate issues relating to the symbiotic interactions between insects and their symbiotic microbes into considerations of ecological and evolutionary principles in insect invasions. First, we show the high probability that microbial symbionts would enhance pest invasions through illustration of the microbial symbionts in pest status of insects at insect–microbial, insect–plant–microbial, and other multispecies levels. Next, we describe how symbiotic microbes impact pest invasions. We provide examples of facultative/mutualistic microbes and insect invasions, and we synthesize complex symbiotic relationships ranging from antagonism to mutualism with diverse functions of microbes in insect invasions. Finally, we develop a coevolution model of invasive insects and associated microbes and propose a conceptual framework for the role of symbiotic microbes in insect invasions. This framework for evaluating symbiotic microbes in pest invasions holds promise in the future for improving risk analyses, spread and impact modeling, and management of invasive pests. Our review, therefore, should interest a wide array of scientists and policy makers, including ecologists, entomologists, microbiologists, invasion biologists, phytosanitary regulators, and border protection agencies. Although the roles of population ecology (Sakai et al. 2001, Liebhold & Tobin 2008) and propagule pressure (Simberloff 2009) in insect invasions have been reviewed, to our knowledge, this is the first review of the role of symbiotic microbes in insect invasions.

2. IMPORTANCE OF MICROBIAL SYMBIONTS IN INSECTS

Symbiotic microbes colonize insects on the insect exoskeleton, in the insect gut, and within insect cells (Douglas 2015). Although the insect exoskeleton is recognized as an important physical barrier protecting insect cells and tissues from the external environment and pathogens (Vallet-Gely et al. 2008), it is also a substrate for the development of various symbiotic microbes. In particular, the mycangia of insects such as beetles and wasps are essential culture vessels that protect microbial symbionts against abiotic factors and contamination by other microorganisms (Paine et al. 1997, Slippers et al. 2015). The insect gut poses multiple challenges for symbiotic microbes ingested along with the food, but insects benefit from its colonization by symbiotic microbes; these benefits include increased availability of nutrients, protection from pathogens, and production of pheromone components (Dillon et al. 2000, 2005; Dillon & Dillon 2004; Douglas 2015; Xu et al. 2015). Intracellular microorganisms restricted to cells such as bacteriocytes (also

Mycangia: cuticular structures that carry fungal propagules and mycelia

Bacteriocytes (also called mycetocytes): specialized adipocytes that harbor mutualistic bacteria in some insect groups called mycetocytes) are widespread in certain insect groups (Douglas 1989, 2015; Braendle et al. 2003). In this section, we show the importance of symbiotic microbes in insects and the high probability that microbial symbionts could enhance insect invasions at insect–microbial, insect–plant–microbial, and other multispecific levels.

Essential amino acids: amino acids that cannot be synthesized de novo by organisms and therefore must be supplied in their diets

Embryonic male-killing: death of male hosts during embryogenesis

Larval male-killing: death of male hosts during larval instars

Feminization: conversion of hosts that would develop as males to female development

Parthenogenesis induction: induction of asexual daughter development

Cytoplasmic incompatibility: sterility of crosses between infected males and females that are either uninfected or infected with a different strain of symbiont

2.1. Insect–Microbial Interactions

Many studies have focused on the nutritional contributions of symbiotic microbes in insects (Douglas 1989, 2009, 2015; Dillon & Dillon 2004). Plant tissues are generally low in essential amino acids, nitrogen, vitamins, and sterols, but in some cases symbiotic microbes can synthesize these compounds for insects (Cruden & Markovetz 1987; Douglas 1989, 2015; Feldhaar et al. 2007; Sabree et al. 2009). The role of symbiotic microbes in providing essential amino acids and nitrogen recycling has been demonstrated in aphids (Douglas et al. 2001), ants (Feldhaar et al. 2007), planthoppers (Sasaki et al. 1996), termites (Potrikus & Breznak 1981), and cockroaches (Sabree et al. 2009). Although the black bean aphid (*Aphis fabae*) can synthesize essential amino acids de novo, they lose this capability when *Buchnera* bacteria are eliminated by antibiotic treatment (Douglas et al. 2001). Genomic analysis and metabolic reconstruction of the *Blattabacterium* genome from the cockroach (*Periplaneta americana*) indicate that the microbial symbiont can produce all of the essential amino acids for the insect host (Sabree et al. 2009). Persuasive evidence for nitrogen fixation by symbiotic microbes has been obtained for termites (Ohkuma et al. 1999), ants (Russell et al. 2009), and bark beetles (Morales-Jiménez et al. 2009). Future work should focus on the quantitative contribution of this capability to the nitrogen economy of the insects (Douglas 2015).

Early studies focused on analysis of insects' dietary requirements to explore the contribution of symbiotic microbes to the vitamin requirements of insects (Douglas 1989). Recent work on genome sequences of endocellular obligate symbionts of insects shows that the symbiotic microbes retain genes involved in the biosyntheses of vitamin metabolites, apparently essential for host insect nutrition (Akman et al. 2002, McCutcheon & Moran 2007). Sterol analyses of anobiid beetles and planthoppers suggest that these insects derive their sterols from yeast symbionts (Douglas 2015).

To enhance their transmission, symbiotic microbes have evolved mechanisms, including embryonic male-killing, larval male-killing, feminization, parthenogenesis induction, and cytoplasmic incompatibility, to manipulate their hosts on a large scale (Stouthamer et al. 1999, Engelstädter & Hurst 2009). Maternally inherited factors that kill male progeny have since been recorded in more than 20 species of insects belonging to several orders, such as Diptera, Lepidoptera, Coleoptera, Hemiptera, and Hymenoptera (Hurst et al. 1997, Engelstädter & Hurst 2009). In live-bearing hosts, females typically produce more embryos than are brought to term, and maternal resource reallocation from dead male embryos to female siblings provides a physiological mechanism that could increase the number of daughters born to infected females, thereby promoting male-killing endosymbiont spread (Zeh & Zeh 2006). In cases of larval male-killing, the parasite benefits from maternal transmission where possible, but infectious transmission where not (Nakanishi et al. 2008).

The adaptive benefit of feminization and the induction of parthenogenesis is more obvious, as there is the conversion of host sex (Engelstädter & Hurst 2009). Feminizing symbionts, bacteria, and protists alter their insect hosts' normal pattern of sex determination and convert individuals from a male developmental pathway to female development (Stouthamer et al. 1999, Hiroki et al. 2002, Negri et al. 2006). The induction of parthenogenesis, a form of asexual reproduction in which females produce eggs that develop without fertilization, seems almost a perfect manipulation of the insect host's reproduction in favor of that of the cytoplasmically inherited symbiont (Bourtzis & O'Neill 1998). The most common effect that *Wolbachia* bacteria can have on arthropod host reproduction is cytoplasmic incompatibility (Stouthamer et al. 1999). The cytoplastic incompatibility phenotype results in the removal of uninfected lineages (Engelstädter & Hurst 2009).

2.2. Insect–Plant–Microbial Interactions

Plants are largely composed of indigestible structural compounds, such as cellulose and lignin, that contain a diversity of toxic chemicals and thus are unpromising food for insects. Insects have evolved many strategies to feed on plants, including associations with symbiotic microbes (Pieterse & Dicke 2007, Frago et al. 2012). Symbiotic microbes contribute to the degradation of plant cell wall material and detoxification of plant material in insects (Calderón-Cortés et al. 2012, Douglas 2015). Hindgut symbiotic bacteria can significantly digest plant cell walls in higher termites (Warnecke et al. 2007), and cellulysis by hindgut bacteria has also been reported in some Orthoptera, Coleoptera, and Diptera species (Calderón-Cortés et al. 2012). Calderón-Cortés et al. (2012) have suggested that insects with fermentation chambers or projecting papillae in their hindguts can maintain permanent microbial populations that can contribute to plant cell wall digestion.

Most described instances of detoxification in insects are mediated by capabilities encoded by the insect genome, including cytochrome P450 mono-oxygenases, glutathione *S*-transferases, and esterases. Symbiotic microbes have, however, been implicated in detoxification processes in ants and beetles (Adams et al. 2013, De Fine Licht et al. 2013). The fungal symbiont of attine ants produces a laccase enzyme, which mediates the detoxification of plant material brought to the nest by the worker ants (De Fine Licht et al. 2013). Species of *Pseudomonas*, *Rahnella*, and other gut symbiotic bacteria that have the genetic capacity to degrade terpenes also facilitate the capacity of the mountain pine beetle (*Dendroctonus ponderosae*) to use terpene-rich trees (Adams et al. 2013).

An increasing number of examples show symbiotic microbes benefiting their host insects by manipulating plant physiology. One of the better-known examples is the fungi associated with bark and ambrosia beetles. In some cases, these fungi appear to assist their adult hosts in overcoming tree defense mechanisms and to make wood digestible for their larval hosts (Paine et al. 1997, Sun et al. 2013). In turn, *Dendroctonus* conifer bark beetles strongly influence the community composition of their symbiotic yeasts (Rivera et al. 2009). Endosymbiotic bacteria have a similar, though less well understood, role (Frago et al. 2012). Barr et al. (2010) showed that the activation of defense-related genes in maize was higher when fed on by *Wolbachia*-free Western corn rootworms (*Diabrotica virgifera virgifera*). Similarly, high concentrations of a bacterial endosymbiont in the tomato psyllid correlate with reduced expression of tomato defensive pathways (Casteel et al. 2012).

2.3. Multispecific Interactions

Insect symbionts are known to protect their insect hosts against pathogens and carnivores by multiple mechanisms, including competition for nutrients or space, production of toxins, and activation of the insect's immune system (Frago et al. 2012, Douglas 2015). These phenomena have been most intensively studied in pea aphids. One secondary symbiont, *Hamiltonella defensa*, confers pea aphid resistance to parasitoids (Oliver et al. 2003, 2005), whereas another, *Regiella insecticola*, provides protection against a fungal pathogen (Scarborough et al. 2005). An endosymbiont in the genus *Rickettsiella* is also likely to protect pea aphids from higher trophic levels, because it affects aphid color, a phenotype known to influence the rate at which insects are preyed upon or parasitized (Tsuchida et al. 2010).

Antimicrobial compounds are of particular importance to insects because they suppress opportunistic fungal or bacterial infections. Antibiotic-producing *Streptomyces* spp. improved the survival of solitary digger wasp European beewolf (*Philanthus triangulum*) (Kaltenpoth et al. 2005).

Similarly, toxins and polyketides have been implicated in the *Pseudomonas*-mediated protection of *Paederus* rove beetles against predators (Piel 2002) and in a putative protection of *Profftella armatura*, localized in the bacteriocytes of the Asian citrus psyllid (*Diaphorina citri*) (Nakabachi et al. 2013).

Facultative microbial symbionts: the microbial symbionts and insects that can, but do not have to, live with the other organism

Multiple infections of symbionts in the same insect host are prevalent and can subsequently lead to complex community interactions, but whether individual members of such communities are truly mutualistic and whether they increase fitness of the host remain to be clarified. Leaf-cutting attine ants and their fungal mutualist are dependent upon each other for survival (Currie et al. 2003). It has additionally been suggested that a *Streptomyces* sp. bacterial symbiont protects the fungal symbiont by suppressing the non-Lepiotaceae fungi and, in turn, aids the survival of its ant host (Oh et al. 2009). However, other research suggests that the bacterial community in the fungal garden is not specific enough to fit the model of coevolved mutualism (Mueller 2012). A similar protection of a fungal mutualist by a *Streptomyces* sp. has been suggested for the Southern pine beetle *Dendroctonus frontalis* (Scott et al. 2008), but subsequent research showed that these bacteria are rather nonspecific and infrequent (Hulcr et al. 2010, 2012; Six 2013). Therefore, whereas the possible existence of tripartite defensive mutualisms is exciting, decisive tests of their specificity and contribution to the insect fitness are yet to be conducted.

3. ECOLOGICAL AND EVOLUTIONARY PRINCIPLES IN SYMBIOTIC MICROBES AND INSECT INVASIONS

3.1. Facultative Microbial Symbionts and Insect Invasions

In some cases, the insect–microbe associations are facultative, and the presence of a particular symbiont is what turns a non-native insect into an invasive one. Other cases involve switches of facultative symbionts or the evolution of new symbiont functions. Facultative microbial symbionts have symbiotic relationships with their hosts in both native and introduced ranges, but distinct genotypes shaped by altered host plants and environments in introduced ranges can enhance insect invasions. The invasive insect–facultative microbial symbiont system provides opportunities to study fidelity and specificity in insect–mutualist interactions. These systems may also offer the opportunity to use recent culture-independent techniques in the context of invasion ecology to increase efficient discovery of microbial diversity associated with insects.

A prominent example of facultative associations directing an invasion is the whitefly (*B. tabaci*) system. The insect species comprises several biotypes that differ strongly in invasiveness. Only a few biotypes are responsible for worldwide invasions, specifically biotypes Q and B, and these biotypes have specific associations with their microbial symbionts (Gueguen et al. 2010). The microbial community is largely transmitted maternally as expected; however, hybrids between the invasive B biotype and an indigenous biotype carrying *Arsenophonus* were found significantly less often than expected, suggesting either loss of this symbiont in viable hybrids or lower viability of hybrids carrying it. Associations of symbiotype and certain nuclear host alleles were found in hybrids, indicating genotype × genotype interactions between host and symbionts (Thierry et al. 2011). Thus, microbial symbionts could favor the spread of invasive whitefly lineages that they are associated with to benefit their own reproduction (Feldhaar 2011). For example, the sweet potato whitefly (*B. tabaci*), an invasive agricultural pest in the southwestern United States, produces more offspring, has higher rates of survival to adulthood, develops faster, and produces a higher proportion of daughters when infected by *Rickettsia* sp. near *bellii* (Himler et al. 2011). Similarly, the invasive B biotype whitefly is an invasive agricultural pest in southern China, and it increases its fecundity and longevity when feeding on plants infected with *Tobacco curly shoot virus* and *Tomato yellow leaf curl China virus* (Jiu et al. 2007).

Multispecific interactions have recently been shown in studies of facultative microbial symbionts and insect invasions. Invasion of the harlequin ladybird (*Harmonia axyridis*) throughout Europe has been facilitated by a microsporidium closely related to *Nosema thompsoni* that is harmless when infecting *H. axyridis* but is a lethal pathogen to native ladybird beetles (Vilcinskas et al. 2013). Another example, the pinewood nematode (*Bursaphelenchus xylophilus*), was accidentally introduced from Japan to China, where it is found in the host pines with other species, including its vector beetles, *Monochamus* spp. (Akbulut & Stamps 2012, Zhao et al. 2014). The nematode produces more offspring with a female-biased sex ratio and develops faster in the presence of *Sporothrix* sp. 1, an ophiostomatoid fungus native to China. Its presence also significantly increases the growth and survival rates of the vector *Monochamus alternatus* (Zhao et al. 2013). The nematode and its microbiome have also established a potentially symbiotic relationship with complementary pathways in xenobiotic degradation (Cheng et al. 2013).

Mutualistic microbial symbionts: these microbial symbionts and insects benefit each other and typically live with each other

3.2. Mutualistic Microbial Symbionts and Insect Invasions

In some of the most destructive invasions, the invader is not a single species but a mutualistic complex, and its invasion ecology cannot be understood without considering the interdependence of the obligate microbial symbionts and the extended phenotype conferred by mutualism. Examples of invasive insect–mutualistic microbial symbiont systems can offer a great depth of background knowledge, numerous collections spanning vast areas, and active global research communities working on the systems. These examples also offer the opportunity to manipulate experimental populations in the laboratory or the field to address questions such as the influence of genetic diversity and phenotypic plasticity on adaptability.

For example, the Sirex woodwasp (*Sirex noctilio*), an invasive wood-feeding wasp that threatens commercial and natural pine forests throughout the Southern Hemisphere, is associated with the fungal mutualist, *Amylostereum areolatum* (Talbot 1977, Slippers et al. 2015). Female *S. noctilio* drill 1–5 small holes in host pines, injecting phytotoxic venom and the arthrospores of *A. areolatum*, and deposit eggs into some of the holes (Talbot 1977). *A. areolatum* is a pathogen of pine, and its pathogenicity is linked to its wood-degrading ability; it decomposes wood by degrading cellulose, hemicellulose, and lignin in the host pines (Martínez et al. 2005). Together, the fungus and venom act to kill the pines. Subsequent wood decay caused by the fungus provides *S. noctilio* larvae with an environment suitable for development (Talbot 1977). In turn, the fungus relies on emerging adult females that collect oidia produced in the insect galleries in their mycangia for dispersal and inoculation into new pines.

In the *Sirex–Amylostereum* system, chemical information derived from the fungal symbiont comprises reliable and detectable host-locating and ovipositing cues that are used by *Ibalia* parasitoids (Martínez et al. 2006). Fungal volatiles also elicit increased parasitoid activities and provide information on relative densities of host insects available for parasitism (Martínez et al. 2006). Despite the above-mentioned research efforts, details of the fungal volatiles that influence host-finding and mating behavior of the Sirex woodwasp remain obscure, and this field still presents exciting opportunities.

3.3. Complex Symbiotic Relationships Range from Antagonism to Mutualism with Diverse Functions of Microbes in Insect Invasions

More recent studies suggest that insect–microbial interactions are variable and range from antagonistic to mutualistic. Mutualistic and antagonistic associations are drivers of ecological function and coevolutionary interactions during the process of insect invasions. Symbiotic microbes such as bacteria and fungi are found together in myriad environments associated with invasive insects, in which associated species interact through diverse mechanisms. Invasive insect–mutualistic–antagonistic microbe systems provide opportunities to study the diverse direct and indirect interactions inevitably embedded in community-level interactions of varying degrees of complexity. These systems also offer the opportunity to study cross-kingdom interactions in the context of a multitrophic-level community.

In the early 1980s, the red turpentine beetle (RTB) (*Dendroctonus valens*), a North American bark beetle of minor importance in its native region, was accidentally introduced into China, where it has killed more than 10 million healthy Chinese pines (*Pinus tabuliformis*) (Sun et al. 2013). A comparative study of fungal associates of RTB in its native and introduced regions was performed to elucidate the possible role of symbiotic fungi in the beetle's behavioral shift in the introduced region (Lu et al. 2009, Taerum et al. 2013). The symbiotic relationship between RTB and its phoretic fungi, *Leptographium* spp., especially the two most commonly isolated strains of *Leptographium procerum* in China, is probably mutualistic because the fungi can benefit from these symbioses by being translocated to new host trees, and RTBs benefit from the activity of fungi to help overcome tree defenses (Lu et al. 2010) (**Figure 1**). RTB carries several genotypes of *L. procerum*, and its invasion into China has been facilitated by novel genotypes of the fungus that appear to be restricted to China. These genotypes are more pathogenic to Chinese host pines than other genotypes, and they also induce the tree to release higher amounts of the host attractant for the invasive beetle (Lu et al. 2011). In addition, gut-associated bacteria can convert *cis*-verbenol to verbenone, a multifunctional pheromone of RTB, suggesting microbial involvement in RTB pheromone production (Xu et al. 2015) (**Figure 1**).

Ophiostomatoid fungi also have antagonistic relationships with the RTB and challenge its invasion in China. In laboratory experiments, sugar-mediated antagonistic effects are caused by three beetle-associated fungal isolates (*Ophiostoma minus*, *Leptographium sinoprocerum*, and *L. procerum*) on development (body weight change) of RTB larvae (Wang et al. 2013). More importantly, high levels of naringenin induced in host pines by three Chinese resident fungal isolates (*Hyalorhinocladiella pinicola*, *Leptographium truncatum*, and *L. sinoprocerum*) seriously suppress RTB and its fungal mutualist, *L. procerum*. RTB gallery microbiota, such as bacteria and yeasts (Lou et al. 2014), however, have strong naringenin-biodegrading activities, lowering the strength of pine phenolic resistance toward the invasive beetle–fungus complex. Moreover, pinitol, the main carbohydrate of Chinese pines, enhances the growth of several microbial strains, consequently increasing its biodegradation of naringenin, the decrease of which appears to benefit the beetle. Although these interactions include non-coevolved participants and cannot be thought of as adaptive, they nevertheless contribute to the success of the invasive insect (Cheng 2015) (**Figure 1**). The diterpene resin acid that is rapidly induced by three Chinese resident fungal isolates (*H. pinicola*, *L. truncatum*, and *L. sinoprocerum*) more significantly suppresses the sympatric fungi than it does *L. procerum*. In addition, the antagonistic effects of the three Chinese resident fungi on *L. procerum* are drastically reduced under induced rosin defense. These findings imply that pine oleoresin defenses (turpentine and rosin) might have been exploited by the exotic fungus *L. procerum*, which may explain the success of the fungus and, by extension, its vector RTB in China (Cheng et al. 2015) (**Figure 1**). Another laboratory study also demonstrated RTB-associated microorganisms capable of α-pinene degradation in vitro and their tolerance to high levels of α-pinene, suggesting that the microorganisms may help both microorganisms and the RTB overcome host α-pinene defense (Xu et al. 2016) (**Figure 1**). Whereas the terpenoid-degrading features of subcortical microbiota are probably universally beneficial to bark beetles (Adams et al. 2013), in this case they support a specific invasive species that occupied a previously vacant bark beetle niche.

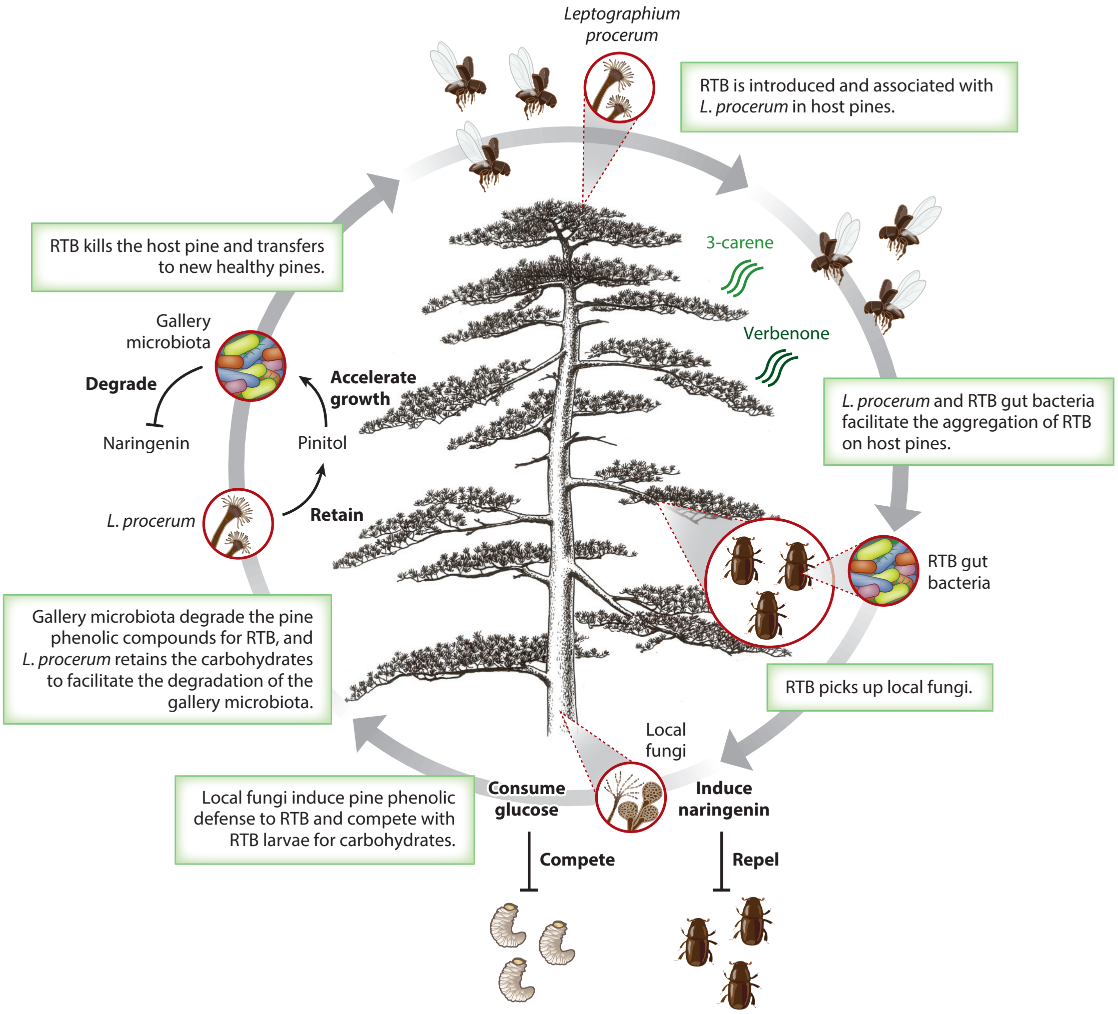


Figure 1

The role of symbiotic microbes in red turpentine beetle (RTB) invasion.

3.4. Coevolution of Microbial Symbionts and Invasive Insects

The term coevolution is typically used for long-term reciprocal interactions between two or more organisms that result in heritable changes in the participants' genotypes and phenotypes. Microbial symbiosis has played a fundamental role in the evolution of eukaryotes (Henry et al. 2015). Such a process normally requires an evolutionary timescale of thousands or millions of years, whereas human-mediated invasions discussed in this review occur on an ecological timescale of no more than several hundred years. Yet, some invasions can be best understood as evolutionary phenomena, as they either occur as a result of two-species interactions or are key mechanisms in two-organism invasions. In this section, we discuss three examples of insect–microbe invasions in which coevolution played a major role.

Contemporary forestry provides many examples of pests whose native niches are weakened host plants or trees that became pests of living, healthy trees in non-native regions (Hulcr & Dunn 2011). Why the ecological shift? The period shortly after tree death presents residual host defenses, which many insect–microbe symbionts overcome by the joint action of mechanical damage and weak pathogenicity. One example is the previously mentioned horntail woodwasp *S. noctilio* and its basidiomycete fungal mutualist, *A. areolatum* (Talbot 1977). In their native habitats across Eurasia, female wasps search for weakened or freshly dead pine trees, into which they lay eggs, the fungal symbiont inoculum, and a cocktail of toxins and digestive enzymes. In their native Eurasia, healthy pines are rarely attacked and generally can defend themselves. Yet in several recently invaded regions where intense plantation forestry is practiced, namely South America, Australia, and South Africa, this symbiotic pair has turned into a critical threat to forestry. The original evolution toward exploiting stressed tree tissue almost certainly occurred in the native Eurasia, but the two species enjoy much greater fitness in the non-native habitats in the Southern Hemisphere, where their populations are now much greater on pines planted in unnatural conditions.

A formerly harmless insect can become an ecological and economic threat if it acquires a new pathogenic symbiont that enables it to exploit previously unavailable plant hosts. An example is the recent development of the laurel wilt epidemics in the southeastern United States. Laurel wilt is an acute disease of Lauraceae, including bays and avocados, caused by an ambrosia fungus, *Raffaelea lauricola*, that is vectored by its redbay ambrosia beetle mutualist, *Xyleborus glabratus* (Fraedrich et al. 2008, Kendra et al. 2013). Trees in the native Asia appear to tolerate or resist this pathogenic fungus, whereas naive trees in the newly invaded North America die within weeks of being infected. The symbiotic ambrosial pathogen *R. lauricola* is not entirely specific to its original vector, *X. glabratus* (Kostovcik et al. 2015). The fungus is relatively promiscuous within the ambrosia beetle tribe Xyleborini and is now vectored by several other beetle species, both native and non-native, in the southeastern United States, and those new symbiotic associations appear to be driving the current avocado die-off in southern Florida even in the absence of the original beetle vector (Carrillo et al. 2014). This scenario is close to what has been termed invasional meltdown (Simberloff & Von Holle 1999), but it is not a result of a random encounter of unrelated invaders. It is a result of symbiont switching between closely related vectors: a coevolutionary phenomenon.

Evolution by natural selection is unlikely to have facilitated many cases of establishment and spread of new phenotypes in human-mediated invasions, given their short history. Instead, changes in genome that produce new instantaneous phenotypes are more likely to be fixed and spread within an observable period. An example of such rapid changes may be introgression between species with complementary features, which may give rise to superior hybrids. Dutch elm disease is caused by several pathogenic *Ophiostoma* spp. and bark beetles in the genus *Scolytus*. The disease spread in several waves through Europe and North America during the twentieth century and ravaged populations of elm trees throughout both continents. Interestingly, the fungal pathogens have gone through instances of apparent sudden increase in virulence and virus resistance, both facilitated by introgression through hybrids (Et-Touil et al. 1999). As in the cases above, the historical coevolution between the insect vector and the fungal pathogen determined the tolerance for multispecies symbiosis, but unique to this case, the recent encounter of new partners facilitated gene exchange leading to an increase in fitness for both partners. That is a bona fide coevolutionary scenario.

4. CONCEPTUAL FRAMEWORK FOR THE ROLE OF SYMBIOTIC MICROBES IN INSECT INVASIONS

The benefit of symbiotic microbes such as fungi, bacteria, and viruses to insect invasion success has been shown in studies in the Americas, Europe, Australia, and China (**Table 1**). Given their

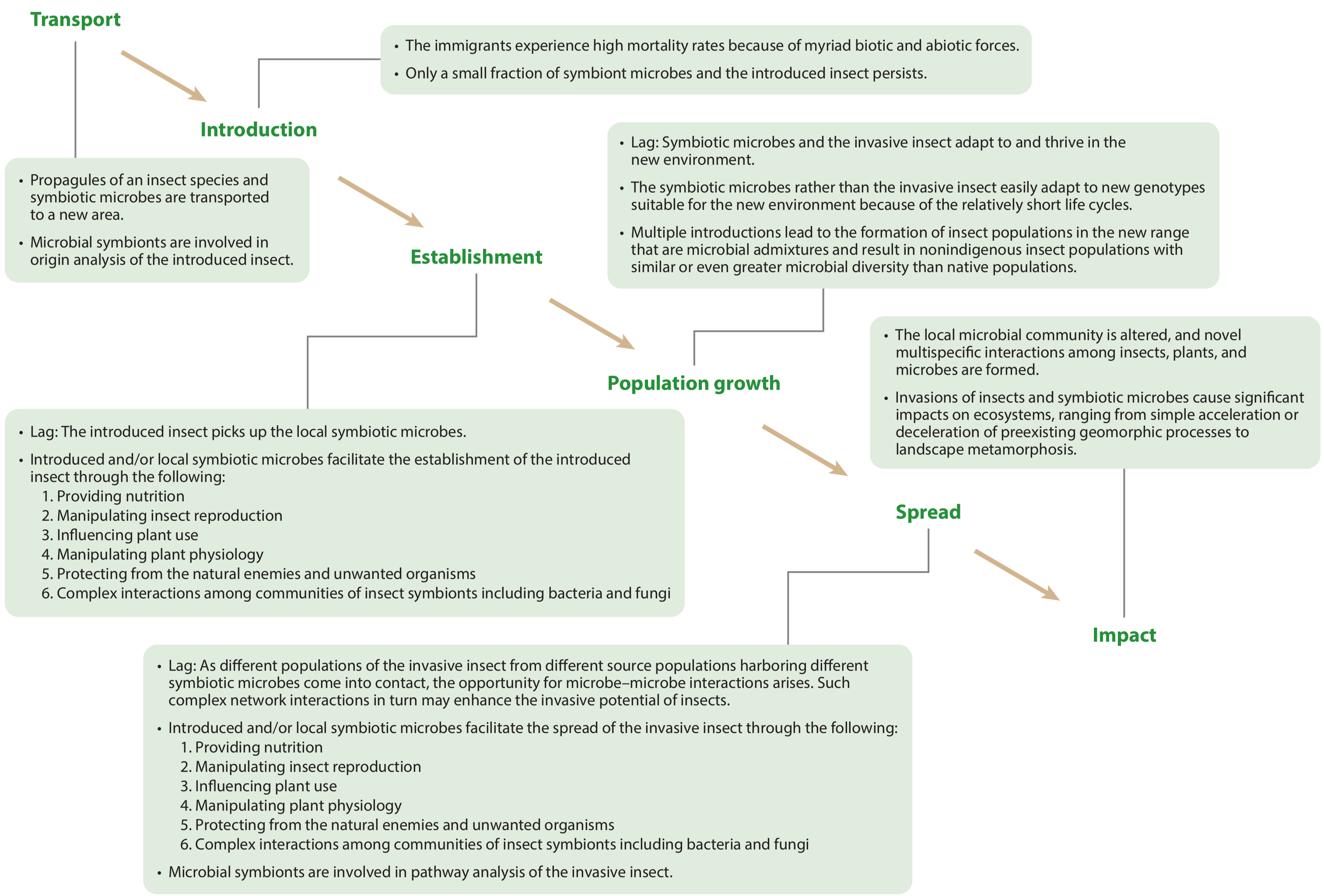
Table 1 Cases demonstrating the role of symbiotic microbes in pest invasions

Invasive pest	Introduced ranges	Symbiotic microbes	Functions	References
Bemisia tabaci	United States	*Rickettsia* sp. near *bellii*	Fitness benefits	Himler et al. 2011
B. tabaci	China	*Tobacco curly shoot virus* and *Tomato yellow leaf curl China virus*	Fitness benefits	Jiu et al. 2007
Bursaphelenchus xylophilus	China	*Sporothrix* sp. 1	Fitness benefits	Zhao et al. 2013, 2014
Dendroctonus valens	China	*Leptographium procerum*	Inducing host pines to produce 3-carene, an attractant of the beetle	Lu et al. 2010, 2011; Sun et al. 2013
Harmonia axyridis	Europe	Microsporidia closely related to *Nosema thompsoni*	Suppressing native competitors	Vilcinskas et al. 2013
Sirex noctilio	Australia, New Zealand, South Africa, North America, and South America	*Streptomyces*, γ-Proteobacteria, and *Amylostereum areolatum*	Nutrient acquisition	Talbot 1977, Adams et al. 2011
Xyleborus glabratus	United States	*Raffaelea lauricola*	Host tree pathogen and nutrition provision	Fraedrich et al. 2008

global importance, we therefore propose a general conceptual model for the role of symbiotic microbes in the insect invasion process (**Figure 2**). The insect invasion process can be viewed as a series of steps initiated when a sample of propagules of a species (eggs, larvae, etc.) and their symbiotic microbes is collected in the native range and transported to a new area (Desprez-Loustau et al. 2007, Grarock et al. 2013). These immigrants probably experience high mortality rates after colonizing their new territory because of a myriad of biotic and abiotic forces. Thus, only a small fraction of the insect species and their symbiotic microbes are successfully transported and brought to a new range to establish and persist (Mack et al. 2000). Such insect species and their symbiotic microbes are said to be naturalized, and most remain permanently within this category. There may be a lag period before an introduced insect species becomes established and is able to maintain a self-replicating wild population and have a close relationship with the local symbiotic microbes. After a lag period, a few naturalized insect species with the aid of introduced and/or local symbiotic microbes become so fecund, vigorous, and wide-ranging that they can cause ecological and economic damage in the new range and are termed invasive (Mack et al. 2000, Sakai et al. 2001, Grarock et al. 2013).

Insect invasions often exhibit a lag period before population growth (**Figure 2**). This period can last decades or even centuries for some insect species because of the time it takes for the insect species and their symbiotic microbes to adapt to and thrive in the new environment (Mack et al. 2000, Gurevitch et al. 2011). Small population sizes often occur with the establishment of nonindigenous insect species and their symbiotic microbes in their new range, and small populations are prone to alterations or reductions of genetic diversity through founder effects and genetic bottlenecks. Reduced genetic diversity may limit the evolutionary potential of nonindigenous populations in their new range (i.e., limit their capacity to evolve). Owing to their relatively shorter life cycles, the symbiotic microbes may adapt more readily than the invasive insects to the new environments. Propagule pressure is now recognized as one of the key factors influencing the establishment of nonindigenous insect species and the ultimate success or failure of an insect invasion (Kolar &

Naturalized: a non-native organism that spreads into the environment and whose reproduction is sufficient to maintain its population



- Propagules of an insect species and symbiotic microbes are transported to a new area.
- Microbial symbionts are involved in origin analysis of the introduced insect.

- The immigrants experience high mortality rates because of myriad biotic and abiotic forces.
- Only a small fraction of symbiont microbes and the introduced insect persists.

- Lag: The introduced insect picks up the local symbiotic microbes.
- Introduced and/or local symbiotic microbes facilitate the establishment of the introduced insect through the following:
  1. Providing nutrition
  2. Manipulating insect reproduction
  3. Influencing plant use
  4. Manipulating plant physiology
  5. Protecting from the natural enemies and unwanted organisms
  6. Complex interactions among communities of insect symbionts including bacteria and fungi

- Lag: Symbiotic microbes and the invasive insect adapt to and thrive in the new environment.
- The symbiotic microbes rather than the invasive insect easily adapt to new genotypes suitable for the new environment because of the relatively short life cycles.
- Multiple introductions lead to the formation of insect populations in the new range that are microbial admixtures and result in nonindigenous insect populations with similar or even greater microbial diversity than native populations.

- Lag: As different populations of the invasive insect from different source populations harboring different symbiotic microbes come into contact, the opportunity for microbe–microbe interactions arises. Such complex network interactions in turn may enhance the invasive potential of insects.
- Introduced and/or local symbiotic microbes facilitate the spread of the invasive insect through the following:
  1. Providing nutrition
  2. Manipulating insect reproduction
  3. Influencing plant use
  4. Manipulating plant physiology
  5. Protecting from the natural enemies and unwanted organisms
  6. Complex interactions among communities of insect symbionts including bacteria and fungi
- Microbial symbionts are involved in pathway analysis of the invasive insect.

- The local microbial community is altered, and novel multispecific interactions among insects, plants, and microbes are formed.
- Invasions of insects and symbiotic microbes cause significant impacts on ecosystems, ranging from simple acceleration or deceleration of preexisting geomorphic processes to landscape metamorphosis.

Figure 2

A general conceptual model for the role of symbiotic microbes in insect invasions.

Lodge 2001, Lockwood et al. 2005). With increasing propagule pressure, multiple founder events (i.e., multiple introductions) may originate from divergent native insect populations and lead to the formation of insect populations in the new range that are microbial admixtures (they combine the microbial diversity of several sources). Multiple introductions can result in nonindigenous insect populations with similar or even greater microbial diversity than native populations.

An invasion of insects and their symbiotic microbes may exhibit a lag period before spreading to new areas (**Figure 2**). In this period, different populations of an invasive insect from different source populations harboring different symbiotic microbes come into contact, and the opportunity for microbe–microbe interactions arises. Such complex network interactions in turn may enhance the invasive potential of insects. After the lag period, ranging from a brief period of time to decades (Larkin 2012), the spread of invasive insects facilitated by symbiotic microbes often continues until all suitable habitats are occupied. Microbial symbiont DNA, a high-resolution population genetic marker, is useful for studies of invasive insect spreading (Zhang et al. 2014). Although depicted as the final stage of the insect invasion process, impacts can occur throughout the entire insect invasion process (Simberloff 1997). The symbiotic microbes introduced by invasive insects may alter the local microbial community and form novel multispecific interactions among insects, plants, and microbes. After a period of such interactions, insect invasions facilitated by symbiotic microbes may cause significant impacts on ecosystems ranging from simple acceleration or deceleration of preexisting geomorphic processes to landscape metamorphosis (Fei et al. 2014). This framework for considering symbiotic microbes in pest invasions promises to improve risk analyses, advance spread and impact modeling, and optimize the management of invasive pests. Predictive invasion models should be expanded to address the number and function of potential microbial symbionts. Risk analyses need to consider potential microbial or fungal symbionts, particularly in cases in which microbial symbionts and pests may be introduced together or in which pests can acquire new symbionts.

5. OUTLOOK

Microbial symbionts have received limited attention in invasion ecology because of a lack of information about their ecology, biogeography, and biodiversity (Humble & Allen 2006, Desprez-Loustau et al. 2007). High-throughput DNA barcoding for tentative species identifications has been employed in the detection of new exotic species (deWaard et al. 2009). Likewise, recent culture-independent techniques allow increasingly efficient discovery of microbial diversity associated with plants and animals. Improved culturing techniques allow the study of biological features of suspect microbes, and our knowledge of the invasive insect vectors is growing. We argue that if we integrate current models of biological invasions with data sets on the role of symbiotic microbes and use high-throughput approaches to assay microbial and fungal symbionts across many taxa and regions, the role of symbiotic microbes in invasive insects will be much clearer.

Because ecological dominance of invasive species is often facilitated by microbial associates, invasion ecology and plant protection strategies should no longer focus only on the nominal invading species. More specific and efficient studies need to be done to discover how symbiotic microbes impact insect invasions. The very recent use of *Wolbachia* in Australia to curb dengue transmission in mosquitoes may be an effective strategy to help manage potential invasion in the future (Joubert et al. 2016). The more we understand the role of symbiotic microbes during insect invasions, the better we will be able to predict the ecological trajectories of future introductions. We advocate better connections among scientific fields, including ecology, microbiology, biogeography, biodiversity, and entomology, to exchange knowledge, cross-fertilize concepts, and advance our understanding and control of invasive insects.

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Erratum

LITERATURE CITED

Adams AS, Aylward FO, Adams SM, Erbilgin N, Aukema BH, et al. 2013. Mountain pine beetles colonizing historical and naïve host trees are associated with a bacterial community highly enriched in genes contributing to terpene metabolism. *Appl. Environ. Microbiol.* 79:3468–75

Adams AS, Jordan MS, Adams SM, Suen G, Goodwin LA, et al. 2011. Cellulose-degrading bacteria associated with the invasive woodwasp *Sirex noctilio*. *ISME J.* 5:1323–31

Akbulut S, Stamps WT. 2012. Insect vectors of the pinewood nematode: a review of the biology and ecology of *Monochamus* species. *For. Pathol.* 42:89–99

Akman L, Yamashita A, Watanabe H, Oshima K, Shiba T, et al. 2002. Genome sequence of the endocellular obligate symbiont of tsetse flies, *Wigglesworthia glossinidia*. *Nat. Genet.* 32:402–7

Barr KL, Hearne LB, Briesacher S, Clark TL, Davis GE. 2010. Microbial symbionts in insects influence down-regulation of defense genes in maize. *PLOS ONE* 5:e11339

Boucher DH, James S, Keeler KH. 1982. The ecology of mutualism. *Annu. Rev. Ecol. Syst.* 13:315–47

Bourtzis K, O'Neill S. 1998. *Wolbachia* infections and arthropod reproduction. *BioScience* 48:287–93

Braendle C, Miura T, Bickel R, Shingleton AW, Kambhampati S, et al. 2003. Developmental origin and evolution of bacteriocytes in the aphid–*Buchnera* symbiosis. *PLOS Biol.* 1:69–76

Bronstein JL. 2009. The evolution of facilitation and mutualism. *J. Ecol.* 97:1160–70

Calderón-Cortés N, Quesada M, Watanabe H, Cano-Camacho H, Oyama K. 2012. Endogenous plant cell wall digestion: a key mechanism in insect evolution. *Annu. Rev. Ecol. Evol. Syst.* 43:45–71

Carrillo D, Duncan RE, Ploetz JN, Campbell AF, Ploetz RC, et al. 2014. Lateral transfer of a phytopathogenic symbiont among native and exotic ambrosia beetles. *Plant Pathol.* 63:54–62

Casteel CL, Hansen AK, Walling LL, Paine TD. 2012. Manipulation of plant defense responses by the tomato psyllid (*Bactericera cockerelli*) and its associated endosymbiont *Candidatus* Liberibacter psyllaurous. *PLOS ONE* 7:e35191

Cheng C. 2015. *Ecological mediations of diverse microbial associates in a bark beetle* Dendroctonus valens *invasion in China*. PhD Dissertation, 130 pp., Institute of Zoology, Chinese Academy of Sciences, Beijing, China

Cheng C, Zhou F, Lu M, Sun JH. 2015. Inducible pine rosin defense mediates interactions between an invasive insect–fungal complex and newly acquired sympatric fungal associates. *Integr. Zool.* 10:453–64

Cheng X-Y, Tian X-L, Wang Y-S, Lin R-M, Mao Z-C, et al. 2013. Metagenomics analysis of the pinewood nematode microbiome reveals a symbiotic relationship critical for xenobiotics degradation. *Sci. Rep.* 3:1869

Cruden DL, Markovetz AJ. 1987. Microbial ecology of the cockroach gut. *Annu. Rev. Microbiol.* 41:617–43

Currie CR, Wong B, Stuart AE, Schultz TR, Rehner SA, et al. 2003. Ancient tripartite coevolution in the attine ant-microbe symbiosis. *Science* 299:386–88

De Fine Licht HH, Schiøtt M, Rogowska-Wrzesinska A, Nygaard S, Roepstorff P, et al. 2013. Laccase detoxification mediates the nutritional alliance between leaf-cutting ants and fungus-garden symbionts. *PNAS* 110:583–87

Desprez-Loustau M-L, Robin C, Buée M, Courtecuisse R, Garbaye J, et al. 2007. The fungal dimension of biological invasions. *Trends Ecol. Evol.* 22:472–80

Excellent summary of fungal dimension of biological invasions.

deWaard JR, Landry J-F, Schmidt BC, Derhousoff J, McLean JA, et al. 2009. In the dark in a large urban park: DNA barcodes illuminate cryptic and introduced moth species. *Biodivers. Conserv.* 18:3825–39

Dillon RJ, Dillon VM. 2004. The gut bacteria of insects: nonpathogenic interactions. *Annu. Rev. Entomol.* 49:71–92

Dillon RJ, Vennard CT, Buckling A, Charnley AK. 2005. Diversity of locust gut bacteria protects against pathogen invasion. *Ecol. Lett.* 8:1291–98

Dillon RJ, Vennard CT, Charnley AK. 2000. Pheromones: exploitation of gut bacteria in the locust. *Nature* 403:851

Douglas AE. 1989. Mycetocyte symbiosis in insects. *Biol. Rev.* 64:409–34

Douglas AE. 2009. The microbial dimension in insect nutritional ecology. *Funct. Ecol.* 23:38–47

Douglas AE. 2015. Multiorganismal insects: diversity and function of resident microorganisms. *Annu. Rev. Entomol.* 60:17–34

Douglas AE, Minto LB, Wilkinson TL. 2001. Quantifying nutrient production by the microbial symbionts in an aphid. *J. Exp. Biol.* 204:349–58

Ehrenfeld JG. 2010. Ecosystem consequences of biological invasions. *Annu. Rev. Ecol. Evol. Syst.* 41:59–80

Engelstädter J, Hurst GDD. 2009. The ecology and evolution of microbes that manipulate host reproduction. *Annu. Rev. Ecol. Evol. Syst.* 40:127–49

Et-Touil A, Brasier CM, Bernier L. 1999. Localization of a pathogenicity gene in *Ophiostoma novo-ulmi* and evidence that it may be introgressed from *O. ulmi*. *Mol. Plant-Microbe Interact.* 12:6–15

Facon B, Hufbauer RA, Tayeh A, Loiseau A, Lombaert E, et al. 2011. Inbreeding depression is purged in the invasive insect *Harmonia axyridis*. *Curr. Biol.* 21:424–27

Fei S, Phillips J, Shouse M. 2014. Biogeomorphic impacts of invasive species. *Annu. Rev. Ecol. Evol. Syst.* 45:69–87

Feldhaar H. 2011. Bacterial symbionts as mediators of ecologically important traits of insect hosts. *Ecol. Entomol.* 36:533–43

Feldhaar H, Straka J, Krischke M, Berthold K, Stoll S, et al. 2007. Nutritional upgrading for omnivorous carpenter ants by the endosymbiont *Blochmannia*. *BMC Biol.* 5:48

Fraedrich SW, Harrington TC, Rabaglia RJ, Ulyshen MD, Mayfield AE, et al. 2008. A fungal symbiont of the redbay ambrosia beetle causes a lethal wilt in redbay and other Lauraceae in the southeastern United States. *Plant Dis.* 92:215–24

Frago E, Dicke M, Godfray HCJ. 2012. Insect symbionts as hidden players in insect–plant interactions. *Trends Ecol. Evol.* 27:705–11

Goulson D. 2003. Effects of introduced bees on native ecosystems. *Annu. Rev. Ecol. Evol. Syst.* 34:1–26

Grarock K, Lindenmayer DB, Wood JT, Tidemann CR. 2013. Using invasion process theory to enhance the understanding and management of introduced species: a case study reconstructing the invasion sequence of the common myna (*Acridotheres tristis*). *J. Environ. Manag.* 129:398–409

Gueguen G, Vavre F, Gnankine O, Peterschmitt M, Charif D, et al. 2010. Endosymbiont metacommunities, mtDNA diversity and the evolution of the *Bemisia tabaci* (Hemiptera: Aleyrodidae) species complex. *Mol. Ecol.* 19:4365–78

Gurevitch J, Fox GA, Wardle GM, Inderjit, Taub D. 2011. Emergent insights from the synthesis of conceptual frameworks for biological invasions. *Ecol. Lett.* 14:407–18

Henry LM, Maiden MCJ, Ferrari J, Godfray HCJ. 2015. Insect life history and the evolution of bacterial mutualism. *Ecol. Lett.* 18:516–25

Himler AG, Adachi-Hagimori T, Bergen JE, Kozuch A, Kelly SE, et al. 2011. Rapid spread of a bacterial symbiont in an invasive whitefly is driven by fitness benefits and female bias. *Science* 332:254–65

A case study on the role of a bacterial symbiont in an invasive insect.

Hiroki M, Kato Y, Kamito T, Miura K. 2002. Feminization of genetic males by a symbiotic bacterium in a butterfly, *Eurema hecabe* (Lepidoptera: Pieridae). *Naturwissenschaften* 89:167–70

Holway DA, Lach L, Suarez AV, Tsutsui ND, Case TJ. 2002. The causes and consequences of ant invasions. *Annu. Rev. Ecol. Syst.* 33:181–233

Holway DA, Suarez AV, Case TJ. 1998. Loss of intraspecific aggression in the success of a widespread invasive social insect. *Science* 282:949–52

Hulcr J, Adams AS, Raffa K, Hofstetter RW, Klepzig KD, et al. 2010. Presence and diversity of *Streptomyces* in *Dendroctonus* and sympatric bark beetle galleries across North America. *Microb. Ecol.* 61:759–68

Hulcr J, Dunn RR. 2011. The sudden emergence of pathogenicity in insect–fungus symbioses threatens naive forest ecosystems. *Proc. R. Soc. B* 278:2866–73

Comprehensive summary of native and invasive insect–fungus symbioses in forestry ecosystems.

Hulcr J, Rountree NR, Diamond SE, Stelinski LL, Fierer N, et al. 2012. Mycangia of ambrosia beetles host communities of bacteria. *Microb. Ecol.* 64:784–93

Humble LM, Allen EA. 2006. Forest biosecurity: alien invasive species and vectored organisms. *Can. J. Plant Pathol.* 28:S256–59

Hurst GDD, Hammarton TC, Bandi C, Majerus TMO, Bertrand D, et al. 1997. The diversity of inherited parasites of insects: The male-killing agent of the ladybird beetle *Coleomegilla maculata* is a member of the Flavobacteria. *Genet. Res.* 70:1–6

Jemal A, Hugh-Jones M. 1993. A review of the red imported fire ant (*Solenopsis invicta* Buren) and its impacts on plant, animal and human health. *Prev. Vet. Med.* 17:19–32

Jiu M, Zhou X-P, Tong L, Xu J, Yang X, et al. 2007. Vector-virus mutualism accelerates population increase of an invasive whitefly. *PLOS ONE* 2:e182

Joubert DA, Walker T, Carrington LB, De Bruyne JT, Kien DHT, et al. 2016. Establishment of a *Wolbachia* superinfection in *Aedes aegypti* mosquitoes as a potential approach for future resistance management. *PLOS Pathog.* 12:e1005434

Kaltenpoth M, Gottler W, Herzner G, Strohm E. 2005. Symbiotic bacteria protect wasp larvae from fungal infestation. *Curr. Biol.* 15:475–79

Kendra PE, Montgomery WS, Niogret J, Epsky ND. 2013. An uncertain future for American Lauraceae: a lethal threat from redbay ambrosia beetle and laurel wilt disease. *Am. J. Plant Sci.* 4:727–38

Kolar C, Lodge DM. 2001. Progress in invasion biology: predicting invaders. *Trends Ecol. Evol.* 16:199–204

Kostovcik M, Bateman C, Klarik M, Stelinski L, Jordal B, Hulcr J. 2015. The ambrosia symbiosis is specific in some species and promiscuous in others: evidence from community pyrosequencing. *ISME J.* 9:126–38

Experimental evidence on ambrosia symbiosis from community pyrosequencing.

Larkin DJ. 2012. Lengths and correlates of lag phases in upper-Midwest plant invasions. *Biol. Invasions* 14:827–38

Lee CE. 2002. Evolutionary genetics of invasive species. *Trends Ecol. Evol.* 17:386–91

Liebhold AM, Tobin PC. 2008. Population ecology of insect invasions and their management. *Annu. Rev. Entomol.* 53:387–408

Liu S-S, De Barro PJ, Xu J, Luan J-B, Zang L-S, et al. 2007. Asymmetric mating interactions drive widespread invasion and displacement in a whitefly. *Science* 318:1769–72

Lockwood JL, Cassey P, Blackburn T. 2005. The role of propagule pressure in explaining species invasions. *Trends Ecol. Evol.* 20:223–28

Lou QZ, Lu M, Sun JH. 2014. Yeast diversity associated with invasive *Dendroctonus valens* killing *Pinus tabuliformis* in China using culturing and molecular methods. *Microb. Ecol.* 68:397–415

Lu M, Wingfield MJ, Gillette NE, Mori SR, Sun JH. 2010. Complex interactions among host pines and fungi vectored by an invasive bark beetle. *New Phytol.* 187:859–66

The first evidence of symbiotic invasion of a beetle–fungus complex.

Lu M, Wingfield MJ, Gillette NE, Sun JH. 2011. Do novel genotypes drive the success of an invasive bark beetle–fungus complex? Implications for potential reinvasion. *Ecology* 92:2013–19

The first study on novel fungal genotypes driving the invasion success of a beetle–fungus complex.

Lu M, Zhou XD, De Beer ZW, Wingfield MJ, Sun JH. 2009. Ophiostomatoid fungi associated with the invasive pine-infesting bark beetle, *Dendroctonus valens*, in China. *Fungal Divers.* 38:133–45

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, et al. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol. Appl.* 10:689–710

Martínez AS, Fernández-Arhex V, Corley JC. 2006. Chemical information from the fungus *Amylostereum areolatum* and host-foraging behavioural in the parasitoid *Ibalia leucospoides*. *Physiol. Entomol.* 31:336–40

Martínez ÁT, Speranza M, Ruiz-Dueñas FJ, Ferreira P, Camarero S, et al. 2005. Biodegradation of lignocellulosics: microbial, chemical, and enzymatic aspects of the fungal attack of lignin. *Int. Microbiol.* 8:195–204

McCutcheon JP, Moran NA. 2007. Parallel genomic evolution and metabolic interdependence in an ancient symbiosis. *PNAS* 104:19392–97

Mooney HA, Cleland EE. 2001. The evolutionary impact of invasive species. *PNAS* 98:5446–51

Morales-Jiménez J, Zúñiga G, Villa-Tanaca L, Hernández-Rodríguez C. 2009. Bacterial community and nitrogen fixation in the red turpentine beetle, *Dendroctonus valens* LeConte (Coleoptera: Curculionidae: Scolytinae). *Microb. Ecol.* 58:879–91

Morrien E, van der Putten WH. 2013. Soil microbial community structure of range-expanding plant species differs from co-occurring natives. *J. Ecol.* 101:1093–102

Mueller UG. 2012. Symbiont recruitment versus ant-symbiont co-evolution in the attine ant–microbe symbiosis. *Curr. Opin. Microbiol.* 15:269–77

Nakabachi A, Ueoka R, Oshima K, Teta R, Mangoni A, et al. 2013. Defensive bacterome symbiont with a drastically reduced genome. *Curr. Biol.* 23:1478–84

Nakanishi K, Hoshino M, Nakai M, Kunimi Y. 2008. Novel RNA sequences associated with late male killing in *Homona magnanima*. *Proc. R. Soc. B* 275:1249–54

Ndlovu J, Richardson DM, Wilson JRU, Le Roux JJ. 2013. Co-invasion of South African ecosystems by an Australian legume and its rhizobial symbionts. *J. Biogeogr.* 40:1240–51

Negri I, Pellecchia M, Mazzoglio PJ, Patetta A, Alma A. 2006. Feminizing *Wolbachia* in *Zyginidia pullula* (Insecta, Hemiptera), a leafhopper with an XX/XO sex-determination system. *Proc. R. Soc. B* 273:2409–22

Oh D-C, Poulsen M, Currie CR, Clardy J. 2009. Dentigerumycin: a bacterial mediator of an ant-fungus symbiosis. *Nat. Chem. Biol.* 5:391–93

Ohkuma M, Noda S, Kudo T. 1999. Phylogenetic diversity of nitrogen fixation genes in the symbiotic microbial community in the gut of diverse termites. *Appl. Environ. Microbiol.* 65:4926–34

Oliver KM, Moran NA, Hunter MS. 2005. Variation in resistance to parasitism in aphids is due to symbionts not host genotype. *PNAS* 102:12795–800

Oliver KM, Russell JA, Moran NA, Hunter MS. 2003. Facultative bacterial symbionts in aphids confer resistance to parasitic wasps. *PNAS* 100:1803–7

Paine TD, Raffa KF, Harrington TC. 1997. Interactions among Scolytid bark beetles, their associated fungi, and live host conifers. *Annu. Rev. Entomol.* 42:179–206

Piel J. 2002. A polyketide synthase-peptide synthetase gene cluster from an uncultured bacterial symbiont of *Paederus* beetles. *PNAS* 99:14002–7

Pieterse CMJ, Dicke M. 2007. Plant interactions with microbes and insects: from molecular mechanisms to ecology. *Trends Plant Sci.* 12:564–69

Potrikus CJ, Breznak JA. 1981. Gut bacteria recycle uric acid nitrogen in termites: a strategy for nutrient conservation. *PNAS* 78:4601–5

Pringle A, Bever JD, Gardes M, Parrent JL, Rillig MC, et al. 2009. Mycorrhizal symbioses and plant invasions. *Annu. Rev. Ecol. Evol. Syst.* 40:699–715

Prior KM, Robinson JM, Meadley Dunphy SA, Frederickson ME. 2015. Mutualism between co-introduced species facilitates invasion and alters plant community structure. *Proc. R. Soc. B* 282:20142846

Richardson DM, Allsopp N, D'Antonio CM, Milton SJ, Rejmánek M. 2000. Plant invasions: the role of mutualism. *Biol. Rev.* 75:65–93

Richardson DM, Pyšek P. 2012. Naturalization of introduced plants: ecological drivers of biogeographical patterns. *New Phytol.* 196:383–96

Rivera FN, González E, Gómez Z, López N, Hernández-Rodríguez C, et al. 2009. Gut-associated yeast in bark beetles of the genus *Dendroctonus* Erichson (Coleoptera: Curculionidae: Scolytinae). *Biol. J. Linn. Soc.* 98:325–42

Rodríguez-Echeverría S, Fajardo S, Ruiz-Díez B, Fernández-Pascual M. 2012. Differential effectiveness of novel and old legume–rhizobia mutualisms: implications for invasion by exotic legumes. *Oecologia* 170:253–61

Russell JA, Moreau CS, Goldman-Huertas B, Fujiwara M, Lohman DJ, et al. 2009. Bacterial gut symbionts are tightly linked with the evolution of herbivory in ants. *PNAS* 106:21236–41

Sabree ZL, Kambhampati S, Moran NA. 2009. Nitrogen recycling and nutritional provisioning by *Blattabacterium*, the cockroach endosymbiont. *PNAS* 106:19521–26

Sakai AK, Allendorf FW, Holt JS, Lodge DM, Molofsky J, et al. 2001. The population biology of invasive species. *Annu. Rev. Ecol. Syst.* 32:305–32

Sasaki T, Kawamura M, Ishikawa H. 1996. Nitrogen recycling in the brown planthopper, *Nilaparvata lugens*: involvement of yeast-like endosymbionts in uric acid metabolism. *J. Insect Physiol.* 42:125–29

Scarborough CL, Ferrari J, Godfray HCJ. 2005. Aphid protected from pathogen by endosymbiont. *Science* 310:1781

Scott JJ, Oh D-C, Yuceer MC, Klepzig KD, Clardy J, et al. 2008. Bacteria protection of beetle-fungus mutualism. *Science* 322:63

Shah MA, Reshi ZA, Khasa DP. 2009. Arbuscular mycorrhizas: drivers or passengers of alien plant invasion. *Bot. Rev.* 75:397–417

Shea K, Chesson P. 2002. Community ecology theory as a framework for biological invasions. *Trends Ecol. Evol.* 17:170–76

Simberloff D. 1997. Eradication. In *Stranger in Paradise: Impact and Management of Nonindigenous Species in Florida*, ed. D Simberloff, DC Schmitz, TC Brown, pp. 221–28. Washington, DC: Island

Simberloff D. 2009. The role of propagule pressure in biological invasions. *Annu. Rev. Ecol. Evol. Syst.* 40:81–102

Simberloff D, Von Holle B. 1999. Positive interactions of nonindigenous species: invasional meltdown? *Biol. Invasions* 1:21–32

Six DL. 2013. The bark beetle holobiont: why microbes matter. *J. Chem. Ecol.* 39:989–1002

Slippers B, Hurley BP, Wingfield MJ. 2015. *Sirex* woodwasp: a model for evolving management paradigms of invasive forest pests. *Annu. Rev. Entomol.* 60:601–19

Snyder WE, Evans EW. 2006. Ecological effects of invasive arthropod generalist predators. *Annu. Rev. Ecol. Evol. Syst.* 37:95–122

Stouthamer R, Breeuwer JAJ, Hurst GDD. 1999. *Wolbachia pipientis*: microbial manipulator of arthropod reproduction. *Annu. Rev. Microbiol.* 53:71–102

Suarez AV, Tsutsui ND. 2008. The evolutionary consequences of biological invasions. *Mol. Ecol.* 17:351–60

Sun JH, Lu M, Gillette NE, Wingfield MJ. 2013. Red turpentine beetle: Innocuous native becomes invasive tree killer in China. *Annu. Rev. Entomol.* 58:293–311

Taerum SJ, Duong TA, de Beer ZW, Gillette N, Sun JH, et al. 2013. Large shift in symbiont assemblage in the invasive red turpentine beetle. *PLOS ONE* 8:e78126

Talbot PHB. 1977. The *Sirex-Amylostereum-Pinus* association. *Annu. Rev. Phytopathol.* 15:41–54

Thierry M, Becker N, Hajri A, Reynaud B, Lett J-M, et al. 2011. Symbiont diversity and non-random hybridization among indigenous (Ms) and invasive (B) biotypes of *Bemisia tabaci*. *Mol. Ecol.* 20:2172–87

Traveset A, Heleno R, Chamorro S, Vargas P, McMullen CK, et al. 2013. Invaders of pollination networks in the Galapagos Islands: emergence of novel communities. *Proc. R. Soc. B* 280:1–9

Traveset A, Richardson DM. 2014. Mutualistic interactions and biological invasions. *Annu. Rev. Ecol. Evol. Syst.* 45:89–113

Tschinkel WR. 2006. *The Fire Ants*. Cambridge, MA: Harvard Univ. Press

Tsuchida T, Koga R, Horikawa M, Tsunoda T, Maoka T, et al. 2010. Symbiotic bacterium modifies aphid body color. *Science* 330:1102–4

Vallet-Gely I, Lemaitre B, Boccard F. 2008. Bacterial strategies to overcome insect defences. *Nat. Rev. Microbiol.* 6:302–13

Vilcinskas A, Stoecker K, Schmidtberg H, Röhrich CR, Vogel H. 2013. Invasive harlequin ladybird carries biological weapons against native competitors. *Science* 340:862–63

A case study on the role of a fungal symbiont in an invasive insect.

Xu L, Lou Q, Cheng C, Lu M, Sun JH. 2015. Gut-associated bacteria of *Dendroctonus valens* and their involvement in verbenone production. *Microb. Ecol.* 70:1012–23

Xu L, Lu M, Sun JH. 2016. Invasive bark beetle-associated microbes degrade a host defensive monoterpene. *Insect Sci.* 23:183–90

Wang B, Lu M, Cheng C, Salcedo C, Sun JH. 2013. Saccharide-mediated antagonistic effects of bark beetle fungal associates on larvae. *Biol. Lett.* 9:20120787

Warnecke F, Luginbühl P, Ivanova N, Ghassemian M, Richardson TH, et al. 2007. Metagenomic and functional analysis of hindgut microbial of a wood-feeding higher termite. *Nature* 450:560–69

Wilder SM, Holway DA, Suarez AV, LeBrun EG, Eubanks MD. 2011. Intercontinental differences in resource use reveal the importance of mutualisms in fire ant invasion. *PNAS* 108:20639–44

Zeh JA, Zeh DW. 2006. Male-killing *Wolbachia* in a live-bearing arthropod: brood abortion as a constraint on the spread of a selfish microbe. *J. Invertebr. Pathol.* 92:33–38

Zhang B, Edwards O, Kang L, Fuller S. 2014. A multi-genome analysis approach enables tracking of the invasive of a single Russian wheat aphid (*Diuraphis noxia*) clone throughout the New World. *Mol. Ecol.* 23:1940–51

Zhao L, Lu M, Niu H, Fang G, Zhang S, et al. 2013. A native fungal symbiont facilitates the prevalence and development of an invasive pathogen-native vector symbiosis. *Ecology* 94:2817–26

Zhao L, Mota M, Vieira P, Butcher RA, Sun JH. 2014. Interspecific communication between pinewood nematode, its insect vector, and associated microbes. *Trends Parasitol.* 30:299–308

The first evidence of the role of a microbial symbiont in the spread of invasive insects.

A comprehensive review of chemical communication between an invasive nematode, native vector beetle, and associated microbes.

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