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Ecology of forest insect invasions

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Abstract Forests in virtually all regions of the world are being affected by invasions of non-native insects. We conducted an in-depth review of the traits of successful invasive forest insects and the ecological processes involved in insect invasions across the universal invasion phases (transport and arrival, establishment, spread and impacts). Most forest insect invasions are accidental consequences of international trade. The dominant invasion 'pathways' are live plant imports, shipment of solid wood packaging material, "hitchhiking" on inanimate objects, and intentional introductions of biological control agents. Invading insects exhibit a variety of life histories and include herbivores, detritivores, predators and parasitoids. Herbivores are considered the most damaging and include wood-borers, sap-feeders, foliage-feeders and seed eaters. Most non-native herbivorous forest insects apparently cause little noticeable damage but some species have profoundly altered the composition and ecological functioning of forests. In some cases, non-native herbivorous insects have virtually eliminated their hosts, resulting in major changes in forest composition and ecosystem processes. Invasive predators (e.g., wasps and ants) can have major effects on forest communities. Some parasitoids have caused the decline of native hosts. Key ecological factors during the successive invasion phases are illustrated. Escape from natural enemies explains some of the extreme impacts of forest herbivores but in other cases, severe impacts result from a lack of host defenses due to a lack of evolutionary exposure. Many aspects of forest insect invasions remain poorly understood including indirect impacts via apparent competition and facilitation of other invaders, which are often cryptic and not well studied.

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Introduction

Insects are by far the world's most species rich group of organisms with approximately 1 million described species (Brusca and Brusca 2003). It is estimated that there are perhaps another seven million species that remain undescribed (Groombridge and Jenkins 2002) and that insects represent more than 50% of all species on earth. Insects play important roles in food web interactions (as herbivores, saprophages, predators and parasites), ecosystem processes (such as pollination, energy flow, biogeochemical cycling, ecological succession), and eco-evolutionary processes (e.g., Price et al. 2011). Given their species richness and wide involvement in ecosystem processes, it is not surprising that insects are also prominent as invasive species both in terms of their number and their impacts (e.g., Kenis et al. 2009; Roques et al. 2009; Brockerhoff et al. 2010). Similar observations have been made for invasive insects specific to forests. In the USA alone, ca. 455 non-native insect species feeding on trees were recorded, with about 2.5 new species detections per year (Aukema et al. 2010) (Fig. 1). In Europe, more than 200 non-native insects inhabiting woodlands and forests are known (Roques et al. 2009) and approximately 400 species feeding on woody plants (Roques et al. 2016).

The most widely reported ecological impacts of invasive forest insects are those by herbivores damaging or killing trees. A well-documented example concerns the hemlock woolly adelgid, *Adelges tsugae*, a sap-feeder that was accidentally moved from Japan to N. America (Virginia) probably in 1911, first detected there in the 1950s and has since spread across most of the range of eastern hemlock, *Tsuga canadensis*, in the eastern USA (Havill and Montgomery 2008). It kills hemlock trees and this has led to a regional decline in the dominance of hemlock and reversal of successional trends in eastern N. American forests (Small et al. 2005; Morin and Liebhold 2015). The impacts of emerald ash borer, *Agrilus planipennis*, following its invasions of eastern N. America and western Russia, are even more spectacular, as it is causing massive mortality of ash trees, *Fraxinus* spp., and eliminating the majority of its host trees in the invaded areas of N. America (Straw et al. 2013; Herms and McCullough 2014; Morin et al. 2017). A range of indirect impacts of herbivores have been reported, including (i) changes in plant species composition
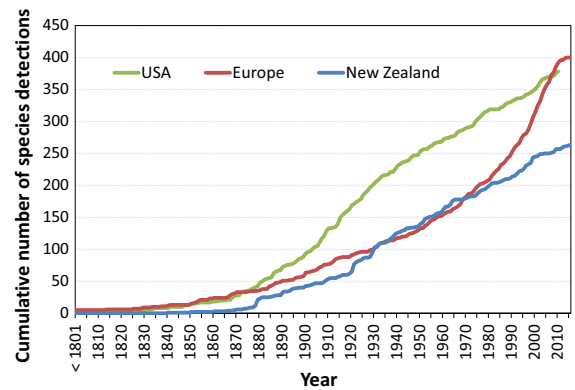

Fig. 1 Cumulative number of detections (i.e., new establishments) of non-native forest insect species over time in the USA, Europe, and New Zealand. Data shown are for non-native insects 'feeding on forest trees' in the USA and New Zealand) or 'feeding on woody plants' (Europe). Data for the USA (showing detections until 2010) are based on Aukema et al. (2010) and Yamanaka et al. (2015); data for Europe are according to Roques et al. (2016) and Alain Roques (pers. comm.); for New Zealand data see Suppl. Mat. 1

such as hemlock woolly adelgid causing an increase of trees and shrubs other than hemlock, including some invasive non-native species (Small et al. 2005), (ii) temporary or ongoing decline of forest fauna (e.g., Brooks 2001), and (iii) changes in forest ecosystem processes and the provision of ecosystem services (Stadler et al. 2005; Boyd et al. 2013). The economic impacts of invasive tree-feeding forest insects can be very substantial with annual costs in the USA of ca. $2.2 billion in local and federal government expenditures, $1.5 billion in lost residential property values, and $150 million in forest landowners' timber loss (Aukema et al. 2011).

Non-native saprophytic insects, as well as predators, parasitoids and parasites, are also numerous in forests around the world, but these are generally less well studied. Exceptions to this trend include invasive ants and wasps which have impacts on other fauna that are well documented (e.g., Gillespie and Reimer 1993; Beggs 2001; O'Dowd et al. 2003). In New Zealand, the invasive European wasp *Vespula vulgaris* is extremely abundant in *Nothofagus* forests where it preys on a wide range of invertebrates and may totally extirpate some species locally (Beggs 2001). In addition, *V. vulgaris* consumes large quantities of honeydew and it thereby competes with native invertebrates and birds for this important food source

(Beggs 2001). In some cases, invasive predators can have indirect effects on forest plant communities such as those following the invasion of Christmas Island by the yellow crazy ant, *Anoplolepis gracilipes* (O'Dowd et al. 2003). Invasive pollinators may reduce the rate of pollination of native plants; for example, the introduced bumblebee *Bombus terrestris* 'robs' nectar from New Zealand's kowhai trees by biting holes into its flowers without actually pollinating them (Donovan 1980).

Although there are thousands of invasive insects, these represent only a very small fraction of the world's insect species. These species have succeeded in overcoming multiple barriers along the successive universal phases of invasions that are transport and arrival, establishment in an invaded area, spread and impact (Liebhold and Tobin 2008; Blackburn et al. 2011). Invasive species are thought to possess certain traits that predispose them to becoming successful invaders. This has received much attention in plants; for example, invasive plants tend to be larger and 'more fit' than non-invasive plant species (van Kleunen et al. 2010). For insects these traits have not been examined comprehensively; however, the widespread occurrence of asexual reproduction such as parthenogenesis is thought to be a key factor explaining the apparent success of Hemiptera among invasive insects (Liebhold et al. 2016), although this group is also over-represented in invasion pathways (Liebhold et al. 2012), and it is uncertain which factor is the key driver.

Despite the ubiquity and major impacts of non-native forest insect invasions around the world, a review focusing specifically on this group is largely lacking. Here our objectives are to examine the relevant ecological processes that are involved in forest insect invasions and the traits of successful invasive species. We do this by considering the roles of various ecological processes across the universal phases of invasions (transport and arrival, establishment, spread and impacts). Most of the examples we cite are based on studies in North America, Europe and Australasia, even though numerous forest insect invasions have occurred elsewhere. This geographical bias is primarily a result of the more comprehensive literature on insect invasions from those regions (Kenis et al. 2009). Nevertheless, the general principles we discuss are largely applicable worldwide.

Ecology of transport and arrival

World trends of increasing international trade and globalization during the last two centuries have led to unprecedented movement of species around the world. While most insect invasions are accidental, some species, such as certain pollinators and biological control agents, have been introduced intentionally. As the mechanisms of transport and arrival differ considerably between accidental invasions and intentional introductions, we will consider these separately.

Accidental introduction pathways

Contrary to other taxa such as mammals, birds and plants, intentional introductions are not the main cause of non-native insect invasions. Most non-native insect species have been accidentally transported with imported goods or unintentionally carried by passengers. However, information on the pathways responsible for insect invasions is imperfect and based mainly on indirect information from (i) known or assumed relationships between non-native insects and certain products or pathways, (ii) border interception records obtained from inspections of imports by officials, and (iii) risk assessments for pests and pathways. Information on the identity and relative frequency of species arriving is inconsistent and varies among data sources. For example, many successful invaders have never been intercepted (e.g., Eschen et al. 2015a); however, such data are still very valuable and the best source of information on pathway risks (Brockerhoff et al. 2014; Caley et al. 2015).

Sap-feeding insects (such as aphids and thrips) and foliage-feeders (common among Lepidoptera and some families of Hymenoptera and Coleoptera) are especially common among non-native tree-feeding insects. For example, dominance by sap- and foliage-feedings insects was evident among the ca. 455 non-native forest insects established in the USA (Aukema et al. 2010). Most of these species probably arrived with live plants imported for planting (e.g., Liebhold et al. 2012) although more effective plant quarantine practices have been implemented in some countries (Eschen et al. 2015b; Liebhold and Griffin 2016). In Europe, live plant imports have also historically been the most common pathway that led to the establishments of non-native insects on woody plants (Roques 2010). The lesser budmoth (*Recurvaria nanella*) is one

such species that was probably introduced with live plants. Detected in 1776, it is the earliest known invasive forest insect in North America (Aukema et al. 2010).

Another important pathway of accidental movement of unwanted species is 'hitchhiking'—the inadvertent transport of organisms that are not associated with particular commodities, but instead are transported unintentionally as 'stowaways' with machinery, sea containers, vehicles, ships, etc. This pathway is well documented to be responsible for the historical introduction of European Carabidae (ground beetles) and many other species to N. America. The unidirectional export of goods from Newfoundland (in eastern North America) to Europe from the 1600s onwards required that sailing ships returning empty from Europe had to carry ballast such as soil and stones. But this material was often contaminated with soil-dwelling insects and these species initially established in locations where ballast was discarded (Lindroth 1957). This pathway became less important as the use of solid ballast ceded with the advent of steam ships in the late 1800s. However, the substantial growth in containerized trade since the 1950s continued to facilitate the transport of hitchhiker pests including those found on the outside of sea containers (Toy and Newfield 2010). One such example is provided by the painted apple moth, *Teia anartoides*, a forest defoliator native to Australia accidentally transported to Auckland, New Zealand, presumably as eggs deposited on the outside of a sea container. The species was considered to pose a risk to forests and successfully eradicated between 1999 and 2003 (Suckling et al. 2007).

Wood borers and phloem feeders (including bark beetles) are a prominent group of invasive forest insects (e.g., Brockerhoff et al. 2006, 2014; Roques et al. 2009). In the USA, the rate of new wood- and phloem-feeding insects has increased dramatically over the last 5 decades (Aukema et al. 2010). The increasing use of wood packaging materials along with imports of roundwood and sawn timber are responsible for the introduction of many such insects (e.g., Brockerhoff et al. 2006; Haack 2006; Liebhold et al. 2012). Most shipping containers hold cargo that comes with wood packaging materials, such as pallets and dunnage. These are typically made from low-value wood that may be infested with insects and other organisms. Prominent, high-impact species that are

thought to have been introduced via this pathway are Asian longhorned beetle, *Anoplophora glabripennis*, and emerald ash borer. Both of these species invaded parts of both North America and Europe where they are causing substantial tree mortality and economic damages (Haack et al. 2009; Straw et al. 2013; Herms and McCullough 2014). Another example of a high-impact invader that was probably introduced by this pathway is the redbay ambrosia beetle, *Xyleborus glabratus*, along with a pathogen, *Raffaelea lauricola*, which are responsible for widespread mortality of trees in the Lauraceae family in the southeastern USA (Hanula et al. 2008). The implementation of harmonized phytosanitary measures under 'ISPM 15' by the FAO International Plant Protection Convention has been effective in reducing infestation rates of wood packaging materials, but some insects continue to be accidentally transported in this high-volume pathway (Haack et al. 2014).

Unfortunately, increasing volumes of international trade across all pathways have historically counteracted the benefits of improved phytosanitary practices. For example, historical imports (inflation-corrected using the U.S. consumer price index) to the USA have grown more than 70-fold in the 100 years from 1908 to 2007 (U.S. Department of Commerce 1975; U.S. Census Bureau 2015). The net result has often been a growing, or at least steady, rate of invasions by forest insects in most parts of the world (Liebhold et al. 2017a) (Fig. 1). The effect of increasing trade is particularly apparent in observations from Europe (Roques 2010; Roques et al. 2016) (Fig. 1) where measures to mitigate pathway risks have traditionally been less rigorous than in many other countries (e.g., Eschen et al. 2015b). In the USA, detections have decreased or plateaued in recent decades, except for wood-borers and bark beetles (Aukema et al. 2010). In New Zealand, where biosecurity measures have long been given a high priority, the rate of annual detections of forest insects appears to decline somewhat (Fig. 1).

Arrivals of potential invaders vary among countries in terms of the number of species, their abundance, and their origins, largely reflecting trade patterns. However, there is no comprehensive direct information on this, as most arrivals go unnoticed. A small subset of arrivals is intercepted by officials inspecting imports, and some countries keep these records in databases. Such data provide a basis for analyses to determine biogeographic and temporal patterns regarding the

origins of arriving species and how these change as a result of changing trade patterns, for example (e.g., Brockerhoff et al. 2006; McCullough et al. 2006). These points are addressed in more detail below under 'establishment'.

Intentional introductions

Intentional introductions of forest insects primarily consist of predators and parasitoids released as biological control agents. Classical biological control involves the introduction of natural enemies from the native range of target invasive species with the aim of long-term self-sustaining control (Hajek et al. 2016; Kenis et al. 2017a). Worldwide more than 6000 introductions of parasitoids or predatory insects for classical biological control of pest insects have taken place, with slightly more than half of these targeting pests of woody plants (Cock et al. 2016; Kenis et al. 2017a). However, most of these target pests affect fruit trees and other non-forest woody plants rather than forests as such. Some 550 classical biological control introductions of about 270 different species specifically targeted ca. 75 pests in natural or planted forests (Kenis et al. 2017a). However, only about a third of the introductions are known to have led to successful establishments, and not all of the ca. 270 released species became established. Conversely, some species introduced for control of non-forest pests (not included in the totals above) have colonized forests (e.g., Munro and Henderson 2002).

A few insects introduced for biological control, especially those targeting insect hosts, have adversely affected populations of non-target species (Hajek et al. 2016; Kenis et al. 2017a). As a result, such introductions are now more regulated in many countries, and the species considered as biological control agents need to be studied carefully to determine their host specificity and the potential occurrence of non-target attack (Hajek et al. 2016). Consequently, fewer such biological control programs have been initiated in recent years, and the number of introductions of parasitoids and predators for biological control of insects of woody plants has dropped by more than 80% since its peak in the 1950s and 1960s (Kenis et al. 2017a).

A number of pollinators have been introduced intentionally to many countries, especially species of *Apis* and *Bombus*. However, their involvement with pollination systems in forests appears to be minor (e.g., Donovan 1980).

Ecology of establishment

Establishment of a non-native species is defined as 'growth of a population to sufficient levels such that natural extinction is highly unlikely' (Liebhold and Tobin 2008). Establishment is a key step in the invasion process, and much research has been undertaken to elucidate the many factors that determine why some species are highly successful invaders while others, despite ample opportunity to invade, often fail to establish. Likewise, there is substantial variation in the degree of invasion among habitats, ecosystems and regions, and many hypotheses have been explored to explain these patterns and to identify the responsible key factors. With many factors acting in concert, it is often difficult to determine their relative importance, especially because establishments are rarely observed directly, and our understanding is mainly based on indirect evidence.

Propagule pressure and the role of Allee effects

Though trends of increasing globalization have resulted in ever-increasing rates of arrival of non-native species, most arriving populations fail to establish (Liebhold and Tobin 2008). Records of insects intercepted at ports by inspectors document that rates of species arrival are vastly greater than rates of establishment (McCullough et al. 2006). Many species may fail to establish because they arrive in an unsuitable climate or in an environment lacking suitable hosts. Furthermore, most newly arrived populations are typically small and subject to extinction. Propagule pressure is probably the single most important determinant of species establishment and it often explains why some invading populations establish while others fail (Lockwood et al. 2005). The importance of propagule pressure is evidenced by historical records of both accidental introductions (e.g., Brockerhoff et al. 2014; Fig. 2) and intentional introductions (Hopper and Roush 1993), documenting that species arriving in greater numbers are more likely to establish. Temporal and spatial variation in propagule pressure therefore explains considerable historical (Aukema et al. 2010) and geographical

variation in rates of establishment of non-native forest insects (Liebhold et al. 2013).

High propagule pressure may result not only from high pathway volumes (e.g., elevated imports), but it may also be associated with high population levels in source regions. For example, Asian strains of the gypsy moth are observed as hitchhikers arriving in non-native regions during periods when outbreaks exist in source regions (Gray 2010). In many cases, invading insect species have established in non-native regions, become extremely abundant, and this greater abundance has facilitated secondary invasions elsewhere. This phenomenon, referred to as the "bridgehead effect", has facilitated the global spread of several forest insect species. For example, numerous Eucalyptus-feeding insect species have moved from continent to continent in a stepping stone fashion (Hurley et al. 2016).

Our knowledge of the population biology of low-density invading populations is extensively informed by the rich literature on the population ecology of rare species (i.e., conservation biology) (Liebhold and Tobin 2008). Low-density populations are strongly affected by random effects, which include both environmental stochasticity (e.g., yearly variation in effects of weather) as well as demographic stochasticity (random variation in birth and death rates) (Palamara et al. 2016). But for many species there may be specific population processes that cause decreasing per capita population growth with decreasing density,
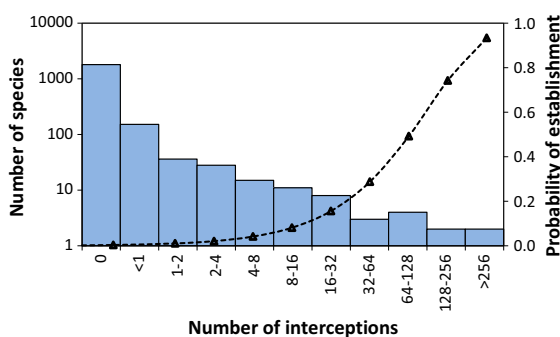
a phenomenon known as the Allee effect. When Allee effects are strong, there may exist a threshold below which low-density populations are driven toward extinction, and this may severely limit the potential for establishment when initial population sizes are low (Liebhold and Tobin 2008).

There are many mechanisms that may drive Allee dynamics. For sexually reproducing species, mate finding may be constrained at low densities (Tobin et al. 2009). In several insect groups, such as bark beetles (Scolytinae), large numbers of conspecifics must simultaneously colonize trees in order to overcome host resistance (Goodsman et al. 2016). For species that are subject to predation by generalist predators, there may be a predator satiation phenomenon such that survival from predator attack may decrease with decreasing densities (Bjørnstad et al. 2010). Perhaps the most common cause of Allee dynamics is mate-finding failure, a phenomenon that may limit reproduction in low-density populations of sexually reproducing species.

Life history traits

Certain life history traits are key determinants that make particular species more successful invaders than others. These traits can impact the strength of Allee effects and subsequently limit establishment probabilities for invading populations that arrive at low densities. For example, *Ips typographus* is a common bark beetle species in Europe and has been frequently intercepted arriving at ports in N. America, yet it has never successfully established outside its native range. This failure may be attributed to the existence of a strong Allee effect arising from the necessity of large numbers of individuals to successfully overcome host defenses (Liebhold and Tobin 2008).

The strength of Allee effects arising from mate finding failure is affected by species mating behaviors and breeding systems (Liebhold and Tobin 2008). For example, parthenogenesis (asexual reproduction) and sib-mating are likely to weaken Allee effects and favor establishment and invasiveness. Taxa where parthenogenesis is common are among the most successful invasive insects. In the Hemiptera, many species are well-known to reproduce parthenogenetically and this order is clearly over-represented among invaders (Kiritani and Yamamura 2003; Liebhold et al. 2016). The exceptional historical invasion success of the

Fig. 2 Frequency distribution of border interceptions of longhorned beetle species (primary y axis) and the relationship between the number of border interceptions (as a proxy of propagule pressure) and the probability of establishment (secondary y axis) over a 100-year period for any species in the corresponding interception class, predicted according to a Weibull establishment probability model. For details see Brockerhoff et al. (2014)

Hemiptera worldwide may be attributed in part to their frequent use of asexual reproduction, thereby avoiding Allee effects arising from mate-finding failure (Liebhold et al. 2016). In New Zealand, aphids are the most species-rich family of invasive insects with 110 species (Martin and Paynter 2014), and they are also the most species-rich family among invasive forest insects (Suppl. Mat. 1). Reproduction by parthenogenesis is very common among the 110 species of invasive aphids in New Zealand (Macfarlane et al. 2010). Parthenogenesis is also very common among invasive aphids in Hawaii and more common than among congenerics that are not invasive (Mondor et al. 2007). In the USA, aphids (Hemiptera: Aphidoidea) are also among the most species-rich groups of invasive forest tree-feeding insects (Aukema et al. 2010). An example of a particularly successful invasive aphid is *Essigella californica* (Monterey pine aphid). It is native to western North America and invaded France, Spain, Italy, Great Britain, Madeira, Tunisia, Australia, New Zealand, Brazil and Argentina (Théry et al. 2017).

Sib-mating (brother-sister mating) and other forms of inbreeding are also successful strategies to avoid mate-finding failure. Sib-mating is widespread among Curculionidae (weevils, including bark beetles) which are another particularly successful group of invaders (Gohli et al. 2016). In the USA, Curculionidae are the most species-rich group of invasive forest tree-feeding insects (Aukema et al. 2010), and they are the second-most species rich group in New Zealand (Martin and Paynter 2014; Suppl. Mat. 1). Inbreeding is particularly common among Scolytinae (bark and ambrosia beetles, especially the latter). Inbreeding Scolytinae are over-represented among invasive species in this family in Europe, North America and numerous small oceanic islands (Jordal et al. 2001; Gohli et al. 2016).

There are several other life history adaptations that favor (or disadvantage) establishment. Aggregation behavior of adults or larvae may be beneficial, for example, if aggregation reduces predation and thereby overcomes an Allee effect arising from predator satiation (Codella and Raffa 1995). Conversely, some aggregating species, such as tree-killing bark beetles in the genus *Dendroctonus*, aggregate to overcome host defenses, but this requires the presence of large numbers of individuals (Raffa and Berryman 1983) which can be an impediment to successful

establishment (Liebhold and Tobin 2008). The ability to disperse effectively may assist in finding suitable host plants; however, flightlessness and lack of dispersal can also be an advantage (South and Kenward 2001). For example, flightless individuals of gypsy moth may be at an advantage over flighted individuals because mating success is more likely when offspring stay relatively close to the location of the egg mass from which they originated (Robinet and Liebhold 2009). A lack of host specificity may be beneficial for invasion success because it increases the likelihood of encounter of suitable host plants, although generalists are likely to be faced by a wider range of competitors. Finally, species that can colonize areas affected by disturbance appear to be particularly successful invaders based partly on the observation that disturbed areas are more invaded than undisturbed natural areas (see below).

Variation in invasion success among taxa

In most world regions, sap-feeding insects (Hemiptera; e.g., aphids, thrips) and foliage-feeders (certain Lepidoptera, Hymenoptera and Coleoptera) tend to be over-represented in non-native insect assemblages compared to native species (Kiritani and Yamamura 2003; Aukema et al. 2010; Liebhold et al. 2016). Apart from possessing life history characteristics (see above) that predispose some sap-feeding and foliage-feeding insects to be successful colonizers, the apparent invasion success of such species is also due their common association with live plants traded internationally (Kiritani and Yamamura 2003; Liebhold et al. 2012). In the late nineteenth century and early twentieth century, international movement of live plants was largely unregulated and extensive plant imports during this period resulted in a large surge in establishments of sap- and foliage-feeders (Aukema et al. 2010; Liebhold and Griffin 2016). More recently, an increase in invasions of bark and wood-boring insects has been noticed, and in some countries, such insects are now over-represented in non-native insect assemblages compared to native insect assemblages (Liebhold et al. 2016). Wood, especially wood packaging material, is considered the primary invasion pathway (Brockerhoff et al. 2006), and the expansion of international trade and widespread use of containerized cargo which involved the extensive movement of wood packaging material is thought to be the

main reason for the increasing prominence of bark and wood-boring insects (Aukema et al. 2010).

Host specificity, biogeography, geographical variation in invasion frequency

A large proportion of tree-feeding insects are more or less host-specific, attacking only certain or all species within one genus ('monophagous' insects) or several genera within a single family ('oligophagous') (Jaenike 1990; Bertheau et al. 2010; Herms and McCullough 2014). A recent comprehensive assessment of diet breadth of more than 7500 species of insect herbivores concluded that approximately 75% were host specific (i.e., feeding on plants in no more than one plant family) (Forister et al. 2015). Host plant use and host range are strongly influenced by plant chemistry (especially secondary metabolites) and physical plant traits, but these are strongly driven by host phylogenetic relationships, which can also predict host suitability (Gilbert et al. 2012). For example, non-native oak species that are more closely related to the natural host plants of oak-feeding leaf-chewing insects are more likely to be attacked by those species (Pearse and Hipp 2009). Consequently, non-native insect herbivores pose a threat mainly to trees and forest plants that are closely related to their natural hosts in their native region. This can be confirmed by retrospectively examining the host use of successful invaders. For example, emerald ash borer attacks almost exclusively congeners of its natural host, *Fraxinus* species (Herms and McCullough 2014), and the red turpentine beetle, *Dendroctonus valens*, attacks local pines in its invaded range in China, congeners of its natural hosts in North America (Sun et al. 2013).

The distributions of particular plant genera and families are strongly linked to particular biogeographic regions. Since most forest insects are herbivores and host associations track plant phylogeny, patterns of insect invasions track biogeographical patterns of plants. Therefore, the most likely sources of damaging invasive insects are areas in related biogeographic regions. This was observed by Niemelä and Mattson (1996) who analyzed the origin of the almost 400 non-native insects feeding on trees and shrubs in North America known at that time. About 75% of those originated from Europe (note that Europe shares most native tree genera with North

America). In general, the dominant pattern in insect invasions in the Holarctic regions (the northern part of the northern hemisphere) is that most invasive species have originated from other parts of the Holarctic, since these regions share many of the same tree genera, thus increasing the possibility of herbivores finding hosts (Yamanaka et al. 2015). In contrast, there have been relatively few invasions of forest insects in the northern hemisphere originating from the southern hemisphere, because these regions share far fewer tree genera.

It has also been noted that there have been more invasions from Europe to N. America than in the opposite direction (Mattson et al. 2007); this pattern is hypothesized to be due to Pleistocene/Holocene glaciations that reduced European host tree diversity, creating fewer niches for invading species. Within North America, there have been a disproportionate number of invasions by forest insects in the northeastern portion of the continent. Liebhold et al. (2013) suggested that this pattern is the combined effect of historically higher propagule pressure in this region, along with greater diversity of tree species thus increasing the likelihood that European and Asian insect species may find a suitable host.

Temporal variation in origins of established invaders and depletion of species pools

It can be expected that temporal and geographic patterns of trade and changes in trading partners are reflected in the origins of invaders. For centuries, Europe had been the predominant trading partner with North America, which meant that European species had a disproportionately greater opportunity to be transported to North America and become established there. More recently, trade with Asian countries, especially in northeast Asia, has greatly increased. This is clearly reflected in the changing origins of bark and ambrosia beetles (Coleoptera: Scolytinae) established in the USA, which we have examined as an example. In the 1800s and until about 1940, European species were the dominant invaders in the USA; however, since then Asian species have become increasingly dominant (Fig. 3).

Centuries of historical movement and establishment of invading species may over time deplete the supply of species available for future invasions (Levine and D'Antonio 2003). It has been shown that

for the Scolytinae, there is a small number of abundant species in invasion pathways emanating from specific world regions, but many more less-common species (Brockerhoff et al. 2014; Liebhold et al. 2017a). Over time, invasions deplete the common species but with increasing import rates, it is possible for the less abundant species to also become established (Liebhold et al. 2017a). They predicted that despite the depletion of the species most common in pathways, increased imports will counter act the depletion trend, leading to near constant rates of future establishments.

Habitat characteristics driving invasibility

There are a number of characteristics of forest stands, regions and countries that affect their invasibility—i.e. their susceptibility for invasion. The availability of host plants or prey, or particular habitat characteristics required by an invader is a critical factor in establishment. Given the degree of host specificity of many forest insects and considering the limited distribution of many plant taxa (see above), it is easy to see why an individual species may only be able to successfully invade specific areas where its host plant is present. Historically, this was an even stronger factor than today because many plants are now planted outside their native range. The planting of non-native plant species as crop plants or ornamentals has generally increased opportunities for invasion. For example, across the temperate southern hemisphere, a large number of exotic trees, especially pines and eucalypts,

Fig. 3 Changes in origins of detections of establishments of bark and ambrosia beetles (Coleoptera: Scolytinae) in the USA since 1800. Note that Eurasian species are native to parts of both Europe and Asia, and their establishments could not be traced back to the particular region from which these Eurasian species originated. Based on Liebhold et al. (2017a)

are planted widely across the production landscape. These exotic trees have been colonized by many invasive insects from the native range of pines and eucalypts (Withers 2001; Brockerhoff et al. 2010; Wingfield et al. 2015; Hurley et al. 2016), whereas the phylogenetically more isolated native trees have remained largely unaffected by these or other non-native forest insects (Brockerhoff et al. 2010).

A lack of natural enemies such as predators, parasitoids, or insect pathogens may also facilitate establishment of invasive species. For example, maritime pine plantations in Corsica have been invaded by the invasive maritime pine bast scale, *Matsucoccus feytaudi*. Pure stands of maritime pine (*Pinus pinaster*) have very low numbers of specialized natural enemies of this scale insect, whereas mixed stands of maritime pine and the native Corsican pine (*Pinus nigra laricio*), as well as maritime pine stands close to Corsican pine stands, have a native predatory bug that preys on *Matsucoccus* scales (Jactel et al. 2006). As a result, *M. feytaudi* is less abundant in mixed stands of maritime pine and Corsican pine than in pure stands, and it is likely that the presence of the predator also reduces the rate of local establishment of the invading scale insect. The effects of natural enemies on forest insect populations is well documented from biological control projects (Kenis et al. 2017a), suggesting that natural enemies also affect establishment of invaders; however, to our knowledge, there are no specific studies on this concerning forest insects.

The presence of vacant ecological niches is widely considered an important driver of invasibility, evidenced by observations of numerous invasions of island ecosystems which typically have relatively limited native diversity. Elton (1958) noticed that oceanic islands, characterized by an impoverished flora and fauna, a shortage of competitors and an abundance of unoccupied niches, were particularly prone to invasions. Many of the cases cited by Elton (1958) concern forest insects. New Zealand is a typical example of a heavily invaded archipelago with a large invasive insect fauna of about 1500 species (with nearly 300 attacking forest trees), which is approximately the same size as the invasive insect fauna of all of Europe (Liebhold et al. 2017b), even though New Zealand's land area is only about 5% of the area of Europe. Forest insect food webs on islands are considered simpler, with comparatively fewer herbivores and especially fewer predator and parasitoid
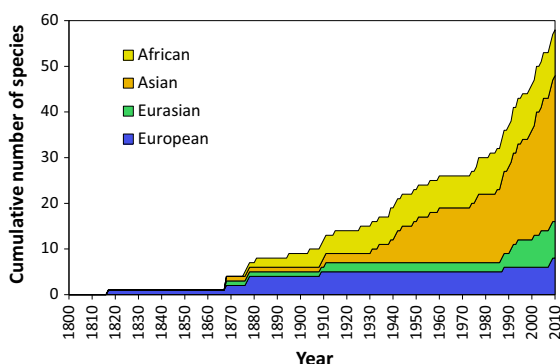
species because, according to theory, the relative richness of herbivores and higher trophic levels decreases as the available area decreases (e.g., Gravel et al. 2011). There appears to be a wide variety of empty niches in New Zealand's forest ecosystems, based on some case studies and a general review of invertebrate diversity (Macfarlane et al. 2010), although the evidence for forest insects appears to be mostly anecdotal. However, the availability of vacant niches is compounded by the large number of introduced tree species that are phylogenetically more or less distant from the native flora. Consequently, there are very few native forest insects feeding on introduced trees such as pines and eucalypts, but they are being colonized by a growing number of non-native invading insects (e.g., Withers 2001; Brockerhoff et al. 2010). The extraordinary abundance of invasive vespid wasps in New Zealand (Beggs 2001), especially in native "*Nothofagus*" forests, has probably also been facilitated by the lack of any native species in this niche (i.e., there are no native vespids in New Zealand). Islands are known to be among the regions most-invaded by vespids, with Hawaii having the most species (15) and New Zealand in third place (6 species) (Beggs et al. 2011).

Regarding the mechanisms that explain these patterns, the high number of invasions on islands ultimately can be related to the relatively low biodiversity of island ecosystems, compared with continental areas. It is thought that more diverse communities have (i) fewer unoccupied ecological niches, (ii) less resources available for potential invaders, and are (iii) generally more 'competitive', collectively leading to biotic resistance to invasion (e.g., Kennedy et al. 2002; Nunez-Mir et al. 2017). However, most theory regarding this topic is based on studies on plant invasions, and there is little evidence that it applies to forest insect invasions. The few studies on relationships between forest diversity and insect invasions provided apparently conflicting information. For example, Guyot et al. (2015) found that single-species stands of chestnut in Italy were more heavily attacked by an invading chestnut gall wasp than stands composed of more tree species. Although there was no direct evidence of effects on invasions per se, the observation suggests that tree diversity could reduce invasibility. By contrast, Liebhold et al. (2013) noticed that regions with a greater diversity of tree species have been invaded by more non-native

tree-feeding insects, which lends support to the vacant-niche theory (see above). However, these observations are not necessarily mutually exclusive because they may be expressions of different ecological processes operating at different spatial scales.

Disturbed habitats are thought to be particularly prone to invasion, although again this relationship has been mostly documented for plant invasions rather than insect invasions (Lozon and MacIsaac 1997). In the case of forests, disturbance can refer to any kind of human modification, forestry activities (including tree felling, site preparation, tree planting), windthrow, fire, climate change, etc. Disturbed habitats are likely to offer vacant niches, reduced competition and potentially a shortage of natural enemies. A study comparing native and non-native beetles along a disturbance gradient from native forest to old pine plantation, clear-felled pine plantation and grazed pasture found that the number of non-native beetle species and their proportion among all beetles increased consistently with increasing disturbance (Pawson et al. 2008) (Fig. 4). Documenting the impact of disturbance on invasibility is made difficult by the fact that disturbance intensity may frequently be confounded with high propagule pressure. Invasions may also precipitate further invasions, potentially causing 'invasional meltdown' (Gandhi and Herms 2010a).

Ecology of spread

Following initial establishment, most invasions proceed through the spread phase, as a species expands its ranges into suitable habitats. Spread is driven by population growth coupled with dispersal, so rates of spread are dependent on any factors promoting either growth or dispersal of populations (Liebhold and Tobin 2008). While most insects are capable of dispersal at some life stage, we know that the spread of forest insects is generally facilitated by anthropogenic dispersal. A dominant feature in the spread of most invading forest pest species is coupling of local dispersal with long distance dispersal to spread via "stratified dispersal", a dynamic whereby long distance dispersal founds isolated populations ahead of the invasion front, which then gradually expand and coalesce (Liebhold and Tobin 2008). While local dispersal typically occurs via insect adaptations for
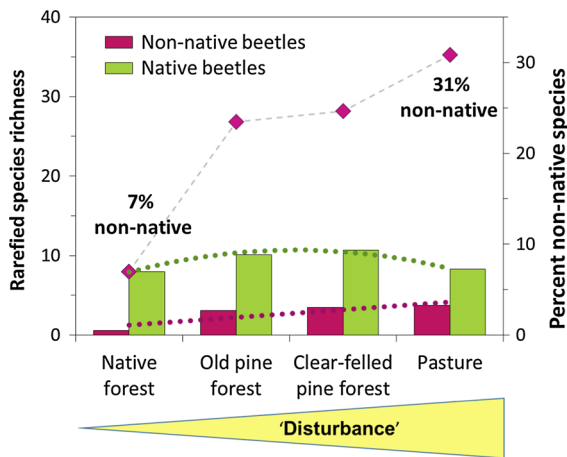
Fig. 4 Number of non-native beetle species (*left columns*, primary y axis) and their percentage of all beetles (*hatched line* and secondary y axis) along a gradient of habitat disturbance from undisturbed native forest to clear-felled pine plantation forest and cleared forest. Data are pitfall-trapped specimens of Carabidae, Scarabaeidae and Scolytinae (Curculionidae). Modified from Pawson et al. (2008)

dispersal, long range spread is typically mediated via anthropogenic dispersal. For forest insects, the long-distance dispersal mechanisms that most commonly are important are movement of wood (e.g., wood for home heating, camp fire wood or wood for manufacturing), movement with live nursery plants, and hitchhiking on inanimate objects. For example spread of the emerald ash borer and other wood-boring insects in N. America is facilitated by their accidental movement in firewood (Haack et al. 2010). Historical patterns of spread of the invasive leafminer *Cameraria ohridella* in Europe reflects patterns of human mobility due the accidental movement of overwintering pupae in soil (Gilbert et al. 2004).

It is not unusual for some species to exhibit lags between the time of initial establishment and the commencement of spread. These lags sometimes reflect poor population growth in areas of initial low habitat suitability. For example, the hemlock woolly adelgid, *A. tsugae*, was most likely introduced to eastern N. America in 1911 in Richmond, VA, a location well outside the range of its host *Tsuga* spp. (Havill and Montgomery 2008). Rapid spread of this organism did not commence until the 1970s, prior to which it had slowly been spreading through a region of low host density (Morin et al. 2009). In other species, such as the gypsy moth, *Lymantria dispar* (Liebhold

and Tobin 2006), and the emerald ash borer, *A. planipennis* (Siegert et al. 2014) lags result from the time required for newly founded populations to grow to greater densities such that they are noticed.

There may be considerable variation among species in their rates of spread, often reflecting differences in life history traits related to dispersal (Roques et al. 2016). In many forest insects, the quality of the local habitat may strongly influence local rates of spread. Specifically, the density of hosts may affect population growth rates, and this is reflected in a correlation between local spread rates and host tree density (Hudgins et al. 2017). Local habitat feature can also influence the strength of Allee effects and this can strongly influence geographical variation in rates of invasion spread (Tobin et al. 2007).

Ecology of impacts

Types of impacts

Invasive forest insects can have a wide range of impacts on forest and urban ecosystems, and these impacts have consequences for people and communities, including effects on several types of economic values.

Ecosystem impacts

The ecological effects of invasive insects were reviewed comprehensively by Kenis et al. (2009), and this covered numerous examples of forest insects. Most obvious and best known are the effects of herbivores feeding on trees. Severe cases of defoliation, such as those caused during outbreaks of gypsy moth, are highly visible and may have substantial effects on forest ecosystems as a result of tree mortality and reduced growth in host trees (oak species). Both impacts may shift competitive processes in favor of non-host tree species, leading to changes in the tree species composition of forests, and potentially affecting long-term successional patterns (Morin and Liebhold 2016). This can have subsequent indirect effects on other species associated with oaks, such as other herbivores and other species in wider food webs. For example, direct and indirect competition between gypsy moth and a native swallowtail butterfly, *Papilio canadensis*, a native herbivore of

oaks, has led to declines in populations of the native butterfly (Redman and Scriber 2000). Similar observations were made regarding the effects of hemlock woolly adelgid, a sap-feeding insect, which causes a more dramatic decline of its host tree, eastern hemlock (*T. canadensis*) (Small et al. 2005; Eschtruth et al. 2006). The rapid decline of ash species (*Fraxinus* spp.) resulting from the widespread mortality caused by emerald ash borer will also cause substantial changes in the community ecology and biodiversity of forests where ash was an important component (Herms and McCullough 2014).

Invasive forest insects can also have wider effects on ecosystem processes. Invasive species that cause defoliation or tree death can affect light penetration, transpiration, carbon sequestration and storage, water drainage, nitrogen and carbon flows to the soil and into waterways, changes in stream temperatures, and various other impacts (Stadler et al. 2005; Lovett et al. 2006; Kenis et al. 2009; Boyd et al. 2013). Furthermore, the loss of host trees can affect communities of other organisms that use these same species as hosts (Gandhi and Herms 2010b). The vast majority of non-native herbivorous forest insects are not known to have any visible ecological impact (Aukema et al. 2010); however, this may reflect, in part, the general lack of information about impacts. For example, non-native ambrosia beetles generally outnumber native species in many world regions (Reed and Muzika 2010), but almost nothing is known about what, if any, effect their presence has on decomposition rates or other ecosystem processes.

Socioeconomic and community impacts

Estimates of economic impacts from forest insect invasions are difficult to quantify and vary widely. Some types of costs and damages are relatively well known, such as expenditure for eradication campaigns. For example, Asian longhorned beetle eradications in several cities in North America and Europe between 1996 and 2008 exceeded $400 million USD, considering only expenses by state and federal agencies (Haack et al. 2009). A more comprehensive assessment of economic impacts of non-native forest insects damaging trees, across all species in the main guilds (borers, sap-feeders, foliage-feeders), was undertaken by Aukema et al. (2011). Their assessment also considered timber

losses to forest owners, local government expenditure, household expenditure, and losses in property value, whereby the latter amounted to considerably greater economic impacts than federal expenditure and timber losses. Collectively their estimate of damages exceeded 4 billion USD annually, even though impacts on values such as ecosystem services were not considered (Aukema et al. 2011). Impacts on such non-market values can indeed exceed impacts on wood and non-wood forest products (e.g., Kenis et al. 2017b). However, damages from the reduced provision of regulating services and cultural services (e.g., reduced human wellbeing) (Boyd et al. 2013) are difficult to capture in monetary terms and are often ignored in assessments. Some invasive forest insects can also have direct or indirect effects on human health. For example, urticating hairs shed by non-native processionary moths and tussock moths can cause dermatological reactions in residents or other individuals coming in contact with such insects.

Another complication with impact assessments and predictions relates to the inherent time lag between the time of establishment and when impacts occur. Even with a very high-impact invader such as emerald ash borer, more than 10 years passed between the actual establishment and when the presence of this species and its impacts were first noticed (Siegert et al. 2014). Lags result from a variety of causes, but in most species considerable time may pass between a species' initial arrival and the point at which newly founded populations have grown to densities such that they are noticed. This lag between arrival and establishment, as well as the magnitude and spatial extent of impacts, have important implications for the assessment of economic impacts (Epanchin-Niell and Liebhold 2015). Furthermore, impacts of particular invasive forest insects may not persist indefinitely. It has been noticed on a number of occasions that populations of invading non-native forest insects (after an initial lag) undergo a population explosion, which eventually collapses after several years (Simberloff and Gibbons 2004). These 'boom and bust' population dynamics have been described, for example, for the invasions of browntail moth, *Euproctis chrysorrhoea*, in N. America (Elkinton et al. 2006) and manuka blight scale, *Eriococcus orariensis*, in New Zealand (van Epenhuijsen et al. 2000), suggesting that the impacts of at least some invaders may be temporary. However, there are

many other examples of non-native species with long-lasting impacts, and this is probably the more common situation.

Interactions with other species

There are several direct and indirect mechanisms by which non-native forest insects can interact with native species as well as other invaders, some of which are poorly known. Genetic effects caused by hybridization between non-native and native species are relatively well-known from other taxa, but there is only limited information about this phenomenon involving forest insects (e.g., Havill et al. 2017). Facilitation is an indirect impact that involves a non-native species improving the likelihood of establishment of another invader, and its subsequent impacts, by providing missing resources, reducing competition or predation, or by providing an obligate mutualism. The role of mutualisms in facilitation has been demonstrated many times. An intriguing example concerns non-native fig wasps that are obligate pollinators of certain non-native fig trees. There are several cases of the establishment of specific pollinating fig wasps facilitating seed production, spread and invasion by cultivated non-native fig trees that previously did not produce seed and were not invasive (Richardson et al. 2000). Mutualisms between forest insects and tree pathogens have been crucial in several high-impact invasions. The invasion and spread of Dutch elm disease and its impact on elms, native and exotic, has depended on the presence of suitable vectors, and in most cases this involved the European smaller elm bark beetle, *Scolytus multistriatus*, which also invaded affected areas (outside Europe) (Webber 2000). Likewise, the invasion of the redbay ambrosia beetle, *X. glabratus*, facilitated the invasion and spread of the invasive pathogen, *Raffaelea* sp., that causes laurel wilt disease of lauraceous trees in parts of the USA (Hanula et al. 2008).

Species characteristics and mechanisms driving invasiveness and impacts

Not all non-native species are 'invasive' and cause impacts; in fact, it is widely recognized that the majority of non-native species have little or no 'impact'. According to the 'tens rule', only one in 10 established species becomes a 'pest'; and although this

is a somewhat simplistic generalization, it has been shown to be approximately true for non-native species of many different taxa (Williamson and Fitter 1996). An examination of the tens rule for forest tree-feeding insects in the USA confirms this, as 62 out of the total of 455 species (14%) on the list of Aukema et al. (2010) cause known impacts. Interestingly, taxonomic patterns of 'frequency of impact' differ from patterns of relative frequency of establishment. Although Hemiptera contribute the most species of established forest tree-feeding insects, the proportions of high-impact species are greater in Coleoptera and Hymenoptera (Fig. 5).

So what makes certain species more invasive and having more impacts than most others? Hufbauer and Torchin (2007) assessed a number of ecological hypotheses that have been proposed to explain the success of biological invaders. Based on the cases they studied (none involving forest insects), they suggest that novel weapons, enemy release, and (lack of) biotic resistance are characteristic of 'strong' invaders, whereas inherent superiority, preadaptation, disturbance, exploitation of empty niches, facilitation by mutualists, and the occurrence of invasional meltdown were less common factors among strong invaders. However, among high-impact invasive forest insects, this distinction of predictors appears to be less useful, and often several interacting factors appear to be
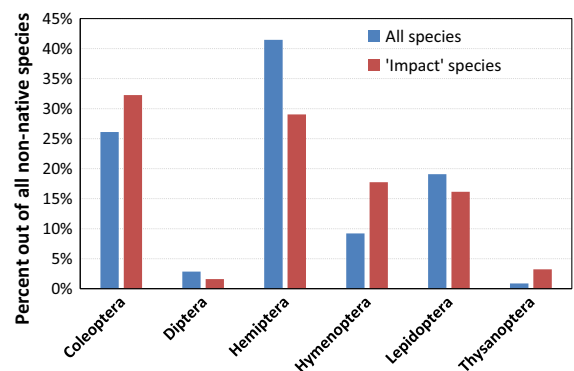

Fig. 5 Invasive insects causing 'impacts' (*right columns*) relative to all non-native forest tree-feeding insects (*left columns*) in the USA (based on Aukema et al. 2010). *Note*: the data shown represent 454 insect species (119 Coleoptera, 13 Diptera, 189 Hemiptera, 42 Hymenoptera, 87 Lepidoptera, and 4 Thysanoptera) of which 62 species were considered to cause 'impacts'. The differences in proportions between orders were significant ($P = 0.0159$) according to a Fisher's Exact test (procedure FREQ in SAS Version 9.3)

involved. Furthermore, some of the factors listed by Hufbauer and Torchin (2007) not only describe characteristics of the invading species but also characterize habitats that are more prone to be invaded. Below, we explore the species characteristics and mechanisms that are understood to be involved in high-impact forest insect invasions.

New associations and the lack of host resistance

Many of the impacts of forest insect invasions can be considered a consequence of novel species associations. Most examples include novel associations between insect herbivores and their host trees and the inability of "naïve hosts" to defend against herbivores to which they have had no prior evolutionary exposure, such as emerald ash borer and naïve species of *Fraxinus* (Herms and McCullough 2014). However, novel species associations also sometimes include new associations of insects with mutualistic micro-organisms. For example, much of the damage associated with the introduction of the N. American bark beetle *D. valens* to China is believed to be due to the novel association of this insect with ophiostomatoid fungi native to China (Sun et al. 2013).

Enemy release

Escape from natural enemies is widely considered a key driver in the success of non-native invasive species. The enemy release hypothesis posits that populations of non-native species are less constrained by natural enemies in their invaded range than in their native range and this results in population growth to higher levels (Colautti et al. 2004). Although this argument is compelling and has been well documented, most 'tests' of the hypothesis are based on invasions of plants and animal taxa other than insects. However, there are numerous examples of invasive tree-feeding insects that caused severe damage until they were controlled by the introduction of their natural enemies (i.e., parasitoids, predators, or pathogens) from their native range (Kenis et al. 2017a). A good example of this is the extensive defoliation of hardwood trees by winter moth, *Operophtera brumata*, that occurred in its invaded range in Nova Scotia prior to the introduction of two biological control agents which lowered the defoliator populations to sub-outbreak levels (Fig. 6; Embree 1965). An even

more impressive example of enemy release is the case of browntail moth, *E. chrysorrhoea*, a polyphagous defoliator of many hardwood tree species. Following its invasion of eastern N. America in the late 1800s, browntail moth eventually spread into most of New England and New Brunswick and parts of Nova Scotia (Elkinton et al. 2006); however, *Compsilura concinnata*, a tachinid parasitoid that was introduced in 1906 along with two other parasitoids, subsequently caused such high mortality that browntail moth nearly became extinct (Elkinton et al. 2006). This contrast in the population growth between the initial period of escape from natural enemies followed by the re-association with parasitoids from the native region demonstrates the regulatory strength of these agents.

Apparent competition and other indirect impacts

Beyond the more obvious direct impacts of invaders on their hosts and other organisms, indirect impacts may also occur but these are often overlooked and generally not well understood. Indirect competition between two insect species that feed on different plant species (and therefore do not compete for food or habitat resources) can affect each other's populations indirectly via shared natural enemies. This is known as 'apparent competition' and was demonstrated, for example, in communities of native leaf miners and their parasitoids in tropical forest in Belize (Morris et al. 2004). However, effects of non-native forest insects on native species via apparent competition are
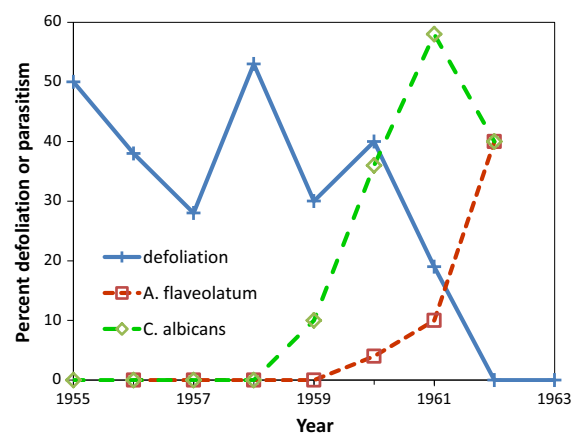

Fig. 6 Substantial decline in defoliation by winter moth following the release and re-association with two parasitoids (reproduced from Embree 1965)

rarely documented. The invasive horse-chestnut leaf-mining moth *C. ohridella* is very abundant across invaded areas in Europe, and a decline of populations of native leaf miners on other tree species near host horse-chestnuts was observed (Péré et al. 2010). This appeared to be consistent with impacts caused by apparent competition between *C. ohridella* and leaf miners; however, the role of indirect effects via shared parasitoids could not be confirmed (Péré et al. 2011). There are confirmed examples of apparent competition in agricultural ecosystems (e.g., Kaplan and Denno 2007), but more research is needed to assess the frequency and impacts of apparent competition associated with forest insect invasions.

Invasional meltdown, whereby one invader facilitates further invasions and impacts by other species, has been described in several instances. Perhaps the best-known and most dramatic case is the interaction and mutualism between the non-native yellow crazy ant, *A. gracilipes*, and a non-native sap-feeding scale insect on Christmas Island (O'Dowd et al. 2003). The honeydew produced by the scale insect provides an abundant food source that enabled an increase in the ant population, which then increased the ants' predation of a native land crab. The decline in the land crab substantially alters the forest understory which is normally more sparse due to the crab's feeding on seed and seedlings. Invasional meltdown may occur more often than is recognised (Gandhi and Herms 2010a). For example, non-native ambrosia beetles and ophiostomatoid fungi may facilitate each other's invasion and worsen the impacts (Wingfield et al. 2017). Non-native ambrosia beetles are often more abundant than native species, but apart from some high-profile species (Hanula et al. 2008; Ploetz et al. 2013), their interactions with fungal associates are not well known. The same is true for indirect effects of invasive forest insects on ecosystem processes. These may result in, for example, changes in light penetration through the canopy, water drainage, nitrogen and carbon flow (see above), and are likely to have indirect effects on other species.

Conclusions and challenges for the future

The phenomenon of biological invasions is increasingly dominating the field of forest entomology. Given the steady accumulation of non-native species establishments around the world, forest insect research increasingly focuses on these species, their biology, ecology, impacts and control. As mentioned earlier, most of the literature on invasive forest insects originates from N. America, Europe and Australasia but the phenomenon of insect invasions is ubiquitous around the world. As more remote and less connected regions begin to increasingly trade in global markets, we can anticipate more exchanges of species among world regions. Given this trend, there is an urgent need to better characterize forest insect assemblages from all world regions and the pathways that enable exchanges among species pools that were previously isolated.

There also continues to be a need to better understand the ecological and socio-economic impacts of invasive forest insects. The majority of non-native forest insects are believed to have no significant impact in their invaded habitat (e.g., Aukema et al. 2010). However, it is likely that many of these apparently benign species are having significant ecological impacts, but because they do not involve large numbers of dead trees, they remain undocumented or even unrecognized. This is especially true for saprophytic insects and pollinators in forests, which historically have received little attention. Likewise, indirect effects of invasive forest insects via apparent competition and facilitation of other invaders can be cryptic and are not well studied.

Worldwide, society is increasingly relying on plantation forests of non-native tree species to meet demands for wood and wood products. Much of the exceptional growth of non-native tree species can be attributed to the escape of these species from the insect herbivores that are indigenous in these trees' native ranges. The high productivity of these forests is thus dependent upon preventing these herbivores from invading and "catching up" with their hosts (Wingfield et al. 2015). An additional trend is the phenomenon by which native insect herbivores adapt to utilizing non-native hosts, and occasionally these can cause considerable damage (Berndt et al. 2004; Bertheau et al. 2010). These trends, along with the tendency of invading insects to form novel association with pathogenic fungi (Ploetz et al. 2013), point toward the need to predict the outcomes of novel host associations. The ability to better predict damaging invading species and novel species associations would strengthen the ability of society to protect forest

resources and ecosystems in the future. Finally, understanding factors contributing to biotic resistance to insect invasions is lacking, but this information would allow for the development of forest management practices that may reduce the frequency and impacts of invasions.

References

Aukema JE, McCullough DG, Von Holle B, Liebhold AM, Britton K, Frankel SJ (2010) Historical accumulation of non-indigenous forest pests in the continental US. Bioscience 60:886–897

Aukema JE, Leung B, Kovacs K, Chivers C, Britton KO, Englin J, Frankel SJ, Haight RG, Holmes TP, Liebhold AM, McCullough DG, Von Holle B (2011) Economic impacts of non-native forest insects in the continental United States. PLoS ONE 6:e24587

Beggs J (2001) The ecological consequences of social wasps (*Vespula* spp.) invading an ecosystem that has an abundant carbohydrate resource. Biol Conserv 99:17–28

Beggs JR, Brockerhoff EG, Corley JC, Kenis M, Masciocchi M, Muller F, Rome Q, Villemant C (2011) Ecological effects and management of invasive alien Vespidae. Biocontrol 56:505–526

Berndt L, Brockerhoff EG, Jactel H, Weiss T, Beaton J (2004) Biology and rearing of *Pseudocoremia suavis*, an endemic looper (Lepidoptera: Geometridae) with a history of outbreaks on exotic conifers. N Z Entomol 27:73–82

Bertheau C, Brockerhoff EG, Roux-Morabito G, Lieutier F, Jactel H (2010) Novel insect-tree associations resulting from accidental and intentional biological 'invasions': a meta-analysis of effects on insect fitness. Ecol Lett 13:506–515

Bjørnstad ON, Robinet C, Liebhold AM (2010) Geographic variation in North American gypsy moth cycles: subharmonics, generalist predators, and spatial coupling. Ecology 91:106–118

Blackburn TM, Pyšek P, Bacher S et al (2011) A proposed unified framework for biological invasions. Trends Ecol Evol 26:333–339

Boyd IL, Freer-Smith PH, Gilligan CA, Godfray HCJ (2013) The consequence of tree pests and diseases for ecosystem services. Science 342:1235773

Brockerhoff EG, Bain J, Kimberley M, Knížek M (2006) Interception frequency of exotic bark and ambrosia beetles (Coleoptera: Scolytinae) and relationship with establishment in New Zealand and worldwide. Can J For Res 36:289–298

Brockerhoff EG, Barratt BI, Beggs JR, Fagan LL, Malcolm K, Phillips CB, Vink CJ (2010) Impacts of exotic invertebrates on New Zealand's indigenous species and ecosystems. N Z J Ecol 34:158–174

Brockerhoff EG, Kimberley M, Liebhold AM, Haack RA, Cavey JF (2014) Predicting how altering propagule pressure changes establishment rates of biological invaders across species pools. Ecology 95:594–601

Brooks RT (2001) Effects of the removal of overstory hemlock from hemlock-dominated forests on eastern redback salamanders. For Ecol Manag 149:197–204

Brusca RC, Brusca GJ (2003) Invertebrates, 2nd edn. Sinauer Associates, Sunderland

Caley P, Ingram R, De Barro P (2015) Entry of exotic insects into Australia: does border interception count match incursion risk? Biol Invasions 17:1087–1094

Cock MJW, Murphy ST, Kairo MTK, Thompson E, Murphy RJ, Francis AW (2016) Trends in the classical biological control of insect pests by insects: an update of the BIOCAT database. Biocontrol 61:349–363

Codella SG, Raffa KF (1995) Contributions of female oviposition patterns and larval behavior to group defense in conifer sawflies (Hymenoptera: Diprionidae). Oecologia 103:24–33

Colautti RI, Ricciardi A, Grigorovich IA, MacIsaac HJ (2004) Is invasion success explained by the enemy release hypothesis? Ecol Lett 7:721–733

Donovan BJ (1980) Interactions between native and introduced bees in New Zealand. N Z J Ecol 3:104–116

Elkinton JS, Parry D, Boettner GH (2006) Implicating an introduced generalist parasitoid in the invasive browntail moth's enigmatic demise. Ecology 87:2664–2672

Elton C (1958) The ecology of invasions by animals and plants. Methuen, London

Embree DG (1965) The population dynamics of the winter moth in Nova Scotia, 1954–1962. Mem Entomol Soc Can 97(S46):5–57

Epanchin-Niell RS, Liebhold AM (2015) Benefits of invasion prevention: effect of time lags, spread rates, and damage persistence. Ecol Econ 116:146–153

Eschen R, Roques A, Santini A (2015a) Taxonomic dissimilarity in patterns of interception and establishment of alien arthropods, nematodes and pathogens affecting woody plants in Europe. Divers Distrib 21:36–45

Eschen R, Britton K, Brockerhoff E et al (2015b) International variation in phytosanitary legislation and regulations governing importation of plants for planting. Environ Sci Policy 51:228–237

Eschtruth AK, Cleavitt NL, Battles JJ, Evans RA, Fahey TJ (2006) Vegetation dynamics in declining eastern hemlock stands: 9 years of forest response to hemlock woolly adelgid infestation. Can J For Res 36:1435–1450

Forister ML, Novotny V, Panorska AK et al (2015) The global distribution of diet breadth in insect herbivores. Proc Natl Acad Sci USA 112:442–447

Gandhi KJ, Herms DA (2010a) Direct and indirect effects of alien insect herbivores on ecological processes and

interactions in forests of eastern North America. Biol Invasions 12:389–405

Gandhi KJ, Herms DA (2010b) North American arthropods at risk due to widespread *Fraxinus* mortality caused by the alien emerald ash borer. Biol Invasions 12:1839–1846

Gilbert M, Grégoire JC, Freise JF, Heitland W (2004) Long-distance dispersal and human population density allow the prediction of invasive patterns in the horse chestnut leaf-miner Cameraria ohridella. J Appl Anim Ecol 73:459–468

Gilbert GS, Magarey R, Suiter K, Webb CO (2012) Evolutionary tools for phytosanitary risk analysis: phylogenetic signal as a predictor of host range of plant pests and pathogens. Evol Appl 5:869–878

Gillespie RG, Reimer N (1993) The effect of alien predatory ants (Hymenoptera: Formicidae) on Hawaiian endemic spiders (Araneae: Tetragnathidae). Pac Sci 47:21–33

Gohli J, Selvarajah T, Kirkendall LR, Jordal BH (2016) Globally distributed *Xyleborus* species reveal recurrent intercontinental dispersal in a landscape of ancient worldwide distributions. BMC Evol Biol 16:37. doi:10.1186/s12862-016-0610-7

Goodsman DW, Koch D, Whitehouse C, Evenden ML, Cooke BJ, Lewis MA (2016) Aggregation and a strong Allee effect in a cooperative outbreak insect. Ecol Appl 26:2621–2634

Gravel D, Massol F, Canard E, Mouillot D, Mouquet N (2011) Trophic theory of island biogeography. Ecol Lett 14:1010–1016

Gray DR (2010) Hitchhikers on trade routes: a phenology model estimates the probabilities of gypsy moth introduction and establishment. Ecol Appl 20:2300–2309

Groombridge B, Jenkins MD (2002) World atlas of biodiversity. UNEP World Conservation Monitoring Centre, University of California Press, Berkeley

Guyot V, Castagneyrol B, Vialatte A, Deconchat M, Selvi F, Bussotti F, Jactel H (2015) Tree diversity limits the impact of an invasive forest pest. PLoS ONE 10:e0136469

Haack RA (2006) Exotic bark-and wood-boring Coleoptera in the United States: recent establishments and interceptions. Can J For Res 36:269–288

Haack RA, Hérard F, Sun J, Turgeon JJ (2009) Managing invasive populations of Asian longhorned beetle and citrus longhorned beetle: a worldwide perspective. Annu Rev Entomol 55:521–546

Haack RA, Petrice TR, Wiedenhoeft AC (2010) Incidence of bark-and wood-boring insects in firewood: a survey at Michigan's Mackinac Bridge. J Econ Entomol 103:1682–1692

Haack RA, Britton KO, Brockerhoff EG, Cavey JF, Garrett LJ, Kimberley M, Lowenstein F, Nuding A, Olson LJ, Turner J, Vasilaky KN (2014) Effectiveness of the international phytosanitary standard ISPM No. 15 on reducing wood borer infestation rates in wood packaging material entering the United States. PLoS ONE 9(5):e96611

Hajek AE, Hurley BP, Kenis M, Garnas JR, Bush SJ, Wingfield MJ, van Lenteren JC, Cock MJW (2016) Exotic biological control agents: a solution or contribution to arthropod invasions? Biol Invasions 18:953–969

Hanula JL, Mayfield AE, Fraedrich SW, Rabaglia RJ (2008) Biology and host associations of redbay ambrosia beetle (Coleoptera: Curculionidae: Scolytinae), exotic vector of

laurel wilt killing redbay trees in the southeastern United States. J Econ Entomol 101:1276–1286

Havill NP, Montgomery ME (2008) The role of arboreta in studying the evolution of host resistance to the hemlock woolly adelgid. Arnoldia 65:2–9

Havill NP, Elkinton J, Andersen JC, Hagen SB, Broadley HJ, Boettner GJ, Caccone A (2017) Asymmetric hybridization between non-native winter moth, *Operophtera brumata* (Lepidoptera: Geometridae), and native Bruce spanworm, *Operophtera bruceata*, in the Northeastern United States, assessed with novel microsatellites and SNPs. Bull Entomol Res 107:241–250

Herms DA, McCullough DG (2014) Emerald ash borer invasion of North America: history, biology, ecology, impacts, and management. Annu Rev Entomol 59:13–30

Hopper KR, Roush RT (1993) Mate finding, dispersal, number released, and the success of biological control introductions. Ecol Entomol 18:321–331

Hudgins EJ, Liebhold AM, Leung B (2017) Predicting the spread of all invasive forest pests in the United States. Ecol Lett. doi:10.1111/ele.12741

Hufbauer RA, Torchin ME (2007) Integrating ecological and evolutionary theory of biological invasions. In: Nentwig W (ed) Biological invasions. Ecological studies 193. Springer, Berlin, pp 79–99

Hurley BP, Garnas J, Wingfield MJ, Branco M, Richardson DM, Slippers B (2016) Increasing numbers and intercontinental spread of invasive insects on eucalypts. Biol Invasions 18:921–933

Jactel H, Menassieu P, Vetillard F, Gaulier A, Samalens JC, Brockerhoff EG (2006) Tree species diversity reduces the invasibility of maritime pine stands by the bast scale, *Matsucoccus feytaudi* (Homoptera: Margarodidae). Can J For Res 36:314–323

Jaenike J (1990) Host specialization in phytophagous insects. Annu Rev Ecol Syst 21:243–273

Jordal BH, Beaver RA, Kirkendall LR (2001) Breaking taboos in the tropics: incest promotes colonization by wood-boring beetles. Glob Ecol Biogeogr 10:345–357

Kaplan I, Denno RF (2007) Interspecific interactions in phytophagous insects revisited: a quantitative assessment of competition theory. Ecol Lett 10:977–994

Kenis M, Auger-Rozenberg M-A, Roques A, Timms L, Péré C, Cock MJW, Settele J, Augustin S, Lopez-Vaamonde C (2009) Ecological effects of invasive alien insects. Biol Invasions 11:21–45

Kenis M, Hurley BP, Hajek AE, Cock MJW (2017a) Classical biological control of insect pests of trees: facts and figures. Biol Invasions. doi:10.1007/s10530-017-1414-4

Kenis M, Roques A, Santini A, Liebhold A (2017b) Impact of non-native invertebrates and pathogens on market forest tree resources. In: Vilà M, Hulme PE (eds) Impact of biological invasions on ecosystem services. Springer, Cham, pp 103–117

Kennedy TA, Naeem S, Howe KM, Knops JM, Tilman D, Reich P (2002) Biodiversity as a barrier to ecological invasion. Nature 417:636–638

Kiritani K, Yamamura K (2003) Exotic insects and their pathways for invasion. In: Ruiz GM, Carlton JT (eds) Invasive species—vectors and management strategies. Island Press, Washington, pp 44–67

Levine JM, D'Antonio CM (2003) Forecasting biological invasions with increasing international trade. Conserv Biol 17:322–326

Liebhold AM, Griffin RL (2016) The legacy of Charles Marlatt and efforts to limit plant pest invasions. Am Entomol 62:218–227

Liebhold AM, Tobin PC (2006) Growth of newly established alien populations: comparison of North American gypsy moth colonies with invasion theory. Popul Ecol 48:253–262

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

Liebhold AM, Brockerhoff EG, Garrett LJ, Parke JL, Britton KO (2012) Live plant imports: the major pathway for forest insect and pathogen invasions of the US. Front Ecol Environ 10:135–143

Liebhold AM, McCullough DG, Blackburn LM, Frankel SJ, Von Holle B, Aukema JE (2013) A highly aggregated geographical distribution of forest pest invasions in the USA. Divers Distrib 19:1208–1216

Liebhold AM, Yamanaka T, Roques A, Augustin S, Chown SL, Brockerhoff EG, Pyšek P (2016) Global compositional variation among native and non-native regional insect assemblages emphasizes the importance of pathways. Biol Invasions 18:893–905

Liebhold AM, Brockerhoff EG, Kimberley M (2017a) Depletion of heterogeneous source species pools predicts future invasion rates. J Appl Ecol. doi:10.1111/1365-2664.12895

Liebhold AM, Brockerhoff EG, Kalisz S, Nuñez MA, Wardle DA, Wingfield MJ (2017b) Biological invasions in forest ecosystems. Biol Invasions. doi:10.1007/s10530-017-1458-5

Lindroth CH (1957) Faunal connections between Europe and North America. Wiley, New York

Lockwood JL, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species invasions. Trends Ecol Evol 20:223–228

Lovett GM, Canham CD, Arthur MA, Weathers KC, Fitzhugh RD (2006) Forest ecosystem responses to exotic pests and pathogens in eastern North America. Bioscience 56:395–405

Lozon JD, MacIsaac HJ (1997) Biological invasions: are they dependent on disturbance? Environ Rev 5:131–144

Macfarlane RP, Maddison PA, Andrew IG et al (2010) Phylum Arthropoda, subphylum Hexapoda: Protura, springtails, Diplura, and insects. In: Gordon DP (ed) New Zealand inventory of biodiversity, vol 2, Kingdom Animalia. Canterbury University Press, Christchurch, pp 233–467

Martin NA, Paynter Q (2014) Predicting risk from adventive herbivores to New Zealand indigenous plants. N Z Entomol 37:21–28

Mattson W, Vanhanen H, Veteli T, Sivonen S, Niemelä P (2007) Few immigrant phytophagous insects on woody plants in Europe: legacy of the European crucible? Biol Invasions 9:957–974

McCullough DG, Work TT, Cavey JF, Liebhold AM, Marshall D (2006) Interceptions of nonindigenous plant pests at US ports of entry and border crossings over a 17-year period. Biol Invasions 8:611–630

Mondor EB, Tremblay MN, Messing RH (2007) Morphological and ecological traits promoting aphid colonization of the Hawaiian Islands. Biol Invasions 9:87–100

Morin RS, Liebhold AM (2015) Invasions by two non-native insects alter regional forest species composition and successional trajectories. For Ecol Manag 341:67–74

Morin RS, Liebhold AM (2016) Invasive forest defoliator contributes to the impending downward trend of oak dominance in eastern North America. Forestry 89:284–289

Morin RS, Liebhold AM, Gottschalk KW (2009) Anisotropic spread of hemlock woolly adelgid in the eastern United States. Biol Invasions 11:2341–2350

Morin RS, Liebhold AM, Pugh SA, Crocker SJ (2017) Regional assessment of emerald ash borer, Agrilus planipennis, impacts in forests of the Eastern United States. Biol Invasions 19:703–711

Morris RJ, Lewis OT, Godfray HCJ (2004) Experimental evidence for apparent competition in a tropical forest food web. Nature 428:310–313

Munro VMW, Henderson IM (2002) Nontarget effect of entomophagous biocontrol: shared parasitism between native lepidopteran parasitoids and the biocontrol agent Trigonospila brevifacies (Diptera: Tachinidae) in forest habitats. Environ Entomol 31:388–396

Niemelä P, Mattson WJ (1996) Invasion of North American forests by European phytophagous insects. Bioscience 46:741–753

Nunez-Mir GC, Liebhold AM, Guo Q, Brockerhoff EG, Jo I, Ordonez K, Fei S (2017) Biotic resistance in forest ecosystems: facts, artifacts, and moving forward. Biol Invasions (this issue)

O'Dowd DJ, Green PT, Lake PS (2003) Invasion 'meltdown' on an oceanic island. Ecol Lett 6:812–817

Palamara GM, Carrara F, Smith MJ, Petchey OL (2016) The effects of demographic stochasticity and parameter uncertainty on predicting the establishment of introduced species. Ecol Evol 6:8440–8451

Pawson SM, Brockerhoff EG, Meenken ED, Didham RK (2008) Non-native plantation forests as alternative habitat for native forest beetles in a heavily modified landscape. Biodivers Conserv 17:1127–1148

Pearse IS, Hipp AL (2009) Phylogenetic and trait similarity to a native species predict herbivory on non-native oaks. Proc Natl Acad Sci USA 106:18097–18102

Péré C, Augustin S, Tomov R, Peng LH, Turlings TC, Kenis M (2010) Species richness and abundance of native leaf miners are affected by the presence of the invasive horse-chestnut leaf miner. Biol Invasions 12:1011–1021

Péré C, Bell R, Turlings TC, Kenis M (2011) Does the invasive horse-chestnut leaf mining moth, Cameraria ohridella, affect the native beech leaf mining weevil, Orchestes fagi, through apparent competition? Biodivers Conserv 20:3003–3016

Ploetz RC, Hulcr J, Wingfield MJ, de Beer ZW (2013) Destructive tree diseases associated with ambrosia and bark beetles: black swan events in tree pathology? Plant Dis 97:856–872

Price PW, Denno RF, Eubanks MD, Finke DL, Kaplan I (2011) Insect ecology: behavior, populations and communities. Cambridge University Press, New York

Raffa KF, Berryman AA (1983) The role of host plant resistance in the colonization behavior and ecology of bark beetles. Ecol Monogr 53:27–49

Redman AM, Scriber JM (2000) Competition between the gypsy moth, *Lymantria dispar*, and the northern tiger swallowtail, *Papilio canadensis*: interactions mediated by host plant chemistry, pathogens and parasitoids. Oecologia 125:218–228

Reed SE, Muzika RM (2010) The influence of forest stand and site characteristics on the composition of exotic dominated ambrosia beetle communities (Coleoptera: Curculionidae: Scolytinae). Environ Entomol 39:1482–1491

Richardson DM, Allsopp N, d'Antonio CM, Milton SJ, Rejmánek M (2000) Plant invasions—the role of mutualisms. Biol Rev 75:65–93

Robinet C, Liebhold AM (2009) Dispersal polymorphism in an invasive forest pest affects its ability to establish. Ecol Appl 19:1935–1943

Roques A (2010) Alien forest insects in a warmer world and a globalised economy: impacts of changes in trade, tourism and climate on forest biosecurity. N Z J For Sci 40:S77–S94

Roques A, Rabitsch W, Rasplus JY, Lopez-Vaamonde C, Nentwig W, Kenis M (2009) Alien terrestrial invertebrates of Europe. In: Nentwig W (ed) Handbook of alien species in Europe. Springer, Dordrecht, pp 63–79

Roques A, Auger-Rozenberg M-A, Blackburn TM, Garnas JR, Pyšek P, Rabitsch W, Richardson DM, Wingfield MJ, Liebhold AM, Duncan RP (2016) Temporal and interspecific variation in rates of spread for insect species invading Europe during the last 200 years. Biol Invasions 18:907–920

Siegert NW, McCullough DG, Liebhold AM, Telewski FW (2014) Dendrochronological reconstruction of the epicentre and early spread of emerald ash borer in North America. Divers Distrib 20:847–858

Simberloff D, Gibbons L (2004) Now you see them, now you don't!—population crashes of established introduced species. Biol Invasions 6:161–172

Small MJ, Small CJ, Dreyer GD (2005) Changes in a hemlock-dominated forest following woolly adelgid infestation in southern New England. J Torrey Bot Soc 132:458–470

South AB, Kenward RE (2001) Mate finding, dispersal distances and population growth in invading species: a spatially explicit model. Oikos 95:53–58

Stadler B, Müller T, Orwig D, Cobb R (2005) Hemlock woolly adelgid in New England forests: canopy impacts transforming ecosystem processes and landscapes. Ecosystems 8:233–247

Straw NA, Williams DT, Kulinich O, Gninenko YI (2013) Distribution, impact and rate of spread of emerald ash borer *Agrilus planipennis* (Coleoptera: Buprestidae) in the Moscow region of Russia. Forestry 86:515–522

Suckling DM, Barrington AM, Chhagan A, Stephens AEA, Burnip GM, Charles JG, Wee SL (2007) Eradication of the Australian painted apple moth *Teia anartoides* in New Zealand: trapping, inherited sterility, and male competitiveness. In: Vreysen MJB, Robinson AS, Hendrichs J (eds) Area-wide control of insect pests. Springer, Dordrecht, pp 603–615

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

Théry T, Brockerhoff EG, Carnegie AJ, Favret C et al (2017) EF-1α DNA sequences indicate multiple origins of introduced populations of *Essigella californica* (Hemiptera, Aphididae). J Econ Entomol 110:1269–1274

Tobin PC, Whitmire SL, Johnson DM, Bjørnstad ON, Liebhold AM (2007) Invasion speed is affected by geographical variation in the strength of Allee effects. Ecol Lett 10:36–43

Tobin PC, Robinet C, Johnson DM, Whitmire SL, Bjørnstad ON, Liebhold AM (2009) The role of Allee effects in gypsy moth, *Lymantria dispar* (L.), invasions. Popul Ecol 51:373–384

Toy SJ, Newfield MJ (2010) The accidental introduction of invasive animals as hitchhikers through inanimate pathways: a New Zealand perspective. Rev Sci Tech 29:123–133

US Department of Commerce (1975) Historical statistics of the United States, Colonial Times to 1970. U.S. Department of Commerce, Washington

US Census Bureau (2015) Foreign trade statistics. https://www.census.gov/foreign-trade/index.html. Accessed 1 Dec 2016

van Epenhuijsen KC, Henderson RC, Carpenter A, Burge GK (2000) The rise and fall of manuka blight scale: a review of the distribution of *Eriococcus orariensis* (Hemiptera: Eriococcidae) in New Zealand. N Z Entomol 23:67–70

van Kleunen M, Weber E, Fischer M (2010) A meta-analysis of trait differences between invasive and non-invasive plant species. Ecol Lett 13:235–245

Webber JF (2000) Insect vector behavior and the evolution of Dutch elm disease. In: Dunn CP (ed) The elms: breeding, conservation, and disease management. Kluwer Academic Publishers, Boston, pp 47–60

Williamson M, Fitter A (1996) The varying success of invaders. Ecology 77:1661–1666

Wingfield MJ, Brockerhoff EG, Wingfield BD, Slippers B (2015) Planted forest health: the need for a global strategy. Science 349:832–836

Wingfield MJ, Barnes I, de Beer ZW, Roux J, Wingfield BD, Taerum SJ (2017) Novel associations between ophiostomatoid fungi, insects and tree hosts: current status—future prospects. Biol Invasions. doi:10.1007/s10530-017-1468-3

Withers TM (2001) Colonization of eucalypts in New Zealand by Australian insects. Austral Ecol 26:467–476

Yamanaka T, Morimoto N, Nishida GM, Kiritani K, Moriya S, Liebhold AM (2015) Comparison of insect invasions in North America, Japan and their Islands. Biol Invasions 17:3049–3061