Biol Invasions
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Biological invasions in forest ecosystems

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Abstract Forests play critical roles in global ecosystem processes and provide numerous services to society. But forests are increasingly affected by a variety of human influences, especially those resulting from biological invasions. Species invading forests include woody and herbaceous plants, many animal species including mammals and invertebrates, as well as a variety of microorganisms such as fungi, oomycetes, bacteria and viruses. These species have diverse ecological roles including primary producers, herbivores, predators, animal pathogens, plant pathogens, decomposers, pollinators and other mutualists. Although most non-native species have negligible effects on forests, a few have profound and often cascading impacts. These impacts include alteration of tree species composition, changes in forest succession, declines in biological diversity, and alteration of nutrient, carbon and water cycles. Many of these result from competition with native species but also trophic

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influences that may result in major changes in food web structure. Naturally regenerating forests around the world have been substantially altered by invading species but planted forests also are at risk. Non-native tree species are widely planted in many parts of the world for production of wood and fibre, and are chosen because of their frequently exceptional growth in their new environment. This greater growth is due, in part, to escape from herbivores and pathogens that exist in their native ranges. Over time, some pest species can "catch-up" with their hosts, leading to subsequent declines in forest productivity. Other impacts result when native herbivores or pathogens adapt to exotic trees or when novel associations form between pathogens and vectors. Additionally, planted non-native trees are sometimes invasive and can have substantial adverse effects on adjacent natural areas. Management of invasions in forests includes prevention of arrival, eradication of nascent populations, biological control, selection for resistance in host trees, and the use of cultural practices (silviculture and restoration) to minimize invader impacts. In the future, the worlds' forests are likely to be subject to increasing numbers of invasions, and effective management will require greater international cooperation and interdisciplinary integration.

Keywords Producer · Herbivore · Predator · Decomposer · Resistance · Enemy release

Introduction

A millennium ago, forests covered ca. 44% of the world's land area but ongoing deforestation has reduced this to ca. 30% (Goldewijk 2001; MacDicken et al. 2015). Nevertheless, forests remain a predominant natural land cover and are crucial in many ways. They represent an important reservoir of biological diversity, harboring the majority of the Earth's terrestrial species [CBD (Convention on Biological Diversity) 2016]. They also play key roles in global nutrient, water and C cycles; for example, forests are responsible for 75% of the world's primary production and comprise one of the Earth's largest C sink (Pan et al. 2011). Further, forests provide a multitude of important ecosystem goods and services. These include non-market services such as the provisioning of clean water and sequestration of C to mitigate climate change, as well as a variety of market resources, including fiber, fuel and food (McKinley et al. 2011). More than 200 million people in the world's poorest countries rely directly on forests for energy, shelter, and their livelihoods [CBD (Convention on Biological Diversity) 2010].

Natural disturbance plays an important role in forest dynamics worldwide (Barnes et al. 1997). The evolution of forest tree species has occurred in the presence of a variety of recurrent disturbance processes such as fire, storms, flooding, geotectonic activity and pest (insect and pathogen) outbreaks. With increases in human populations worldwide, forests have also been affected by a variety of novel anthropogenic disturbances. These include direct impacts of forest clearing as well as indirect effects of air pollution, N deposition, climate change, loss of top predators that control herbivore densities and invasions by non-native species. Together, these are considered elements of "global change" and they occur in addition to natural disturbances. The extent to which each of these factors have altered forest ecosystems varies considerably among world regions. In many regions, forest invasions by non-native species are acting collectively as a "megadisturbance" that is fundamentally changing the composition and ecological properties of forests (Millar and Stephenson 2015).

Forests have been increasingly invaded by non-native organisms representing nearly every taxon. Invading species include both woody and herbaceous plants, animals including mammals, other vertebrates, arthropods and nematodes, as well as a variety of microorganisms such as fungi, oomycetes, bacteria, archaea and viruses (see examples in Fig. 1). Though comprehensive lists of non-indigenous forest species are not available for many countries, some patterns are evident from available records (Table 1). First, insects tend to be the most species-rich group of invaders, which reflects the exceptional diversity of insects worldwide. Second, the proportions of mammals invading forests versus other habitats are greater than those of insects and plants; this likely reflects the fact that most mammals were introduced intentionally, and forest-dwelling species were often selected. Finally, while plant invasions are common world wide, the proportion of plant invasions in forests is relatively small compared to other habitats, most notably grasslands and agriculture lands (Essl et al. 2012). Invading species act in a variety of ecological

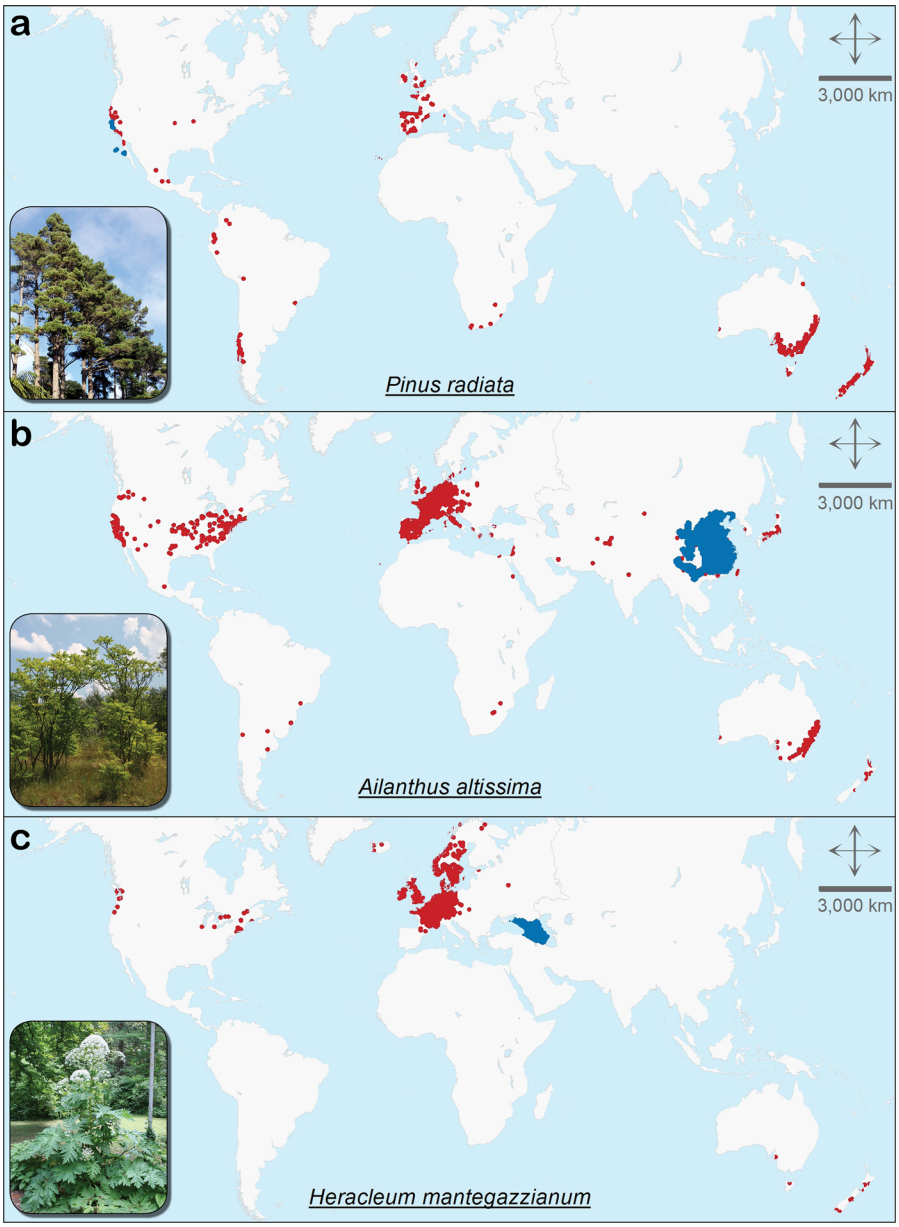

Fig. 1 World distributions of selected non-native species in forests. See Online Resource 2 for sources of data used in drawing range maps and for photo credits. **a** Despite having a very localized native distribution the tree species, *Pinus radiata* is widely distributed around the world, though mostly in sites where it has been planted in commercial forests, **b** the Asian tree species *Ailanthus altissima* is highly invasive, having colonized most of the world's temperature regions, **c** giant hogweed, *Heracleum mantegazzianum*, is native to the Cuacusus Mountain region but is invasive through much of the world, **d** the wild pig, *Sus scrofa*, was widely introduced to forests globally for purposes of game hunting but are now widely invasive, **e** the *Eucalyptus* snout beetle, *Gonipterus scutellatus* sensu lato, is native to Australia but has been accidentally introduced to most regions where host *Eucalyptus* spp. are planted for commercial forestry, **f** Dothistroma needle blight is caused by the fungal pathogens *D. pini* and *D. septosporum*; they are believed to be native to parts of the Northern Hemisphere though their native range is uncertain and is therefore not shown here

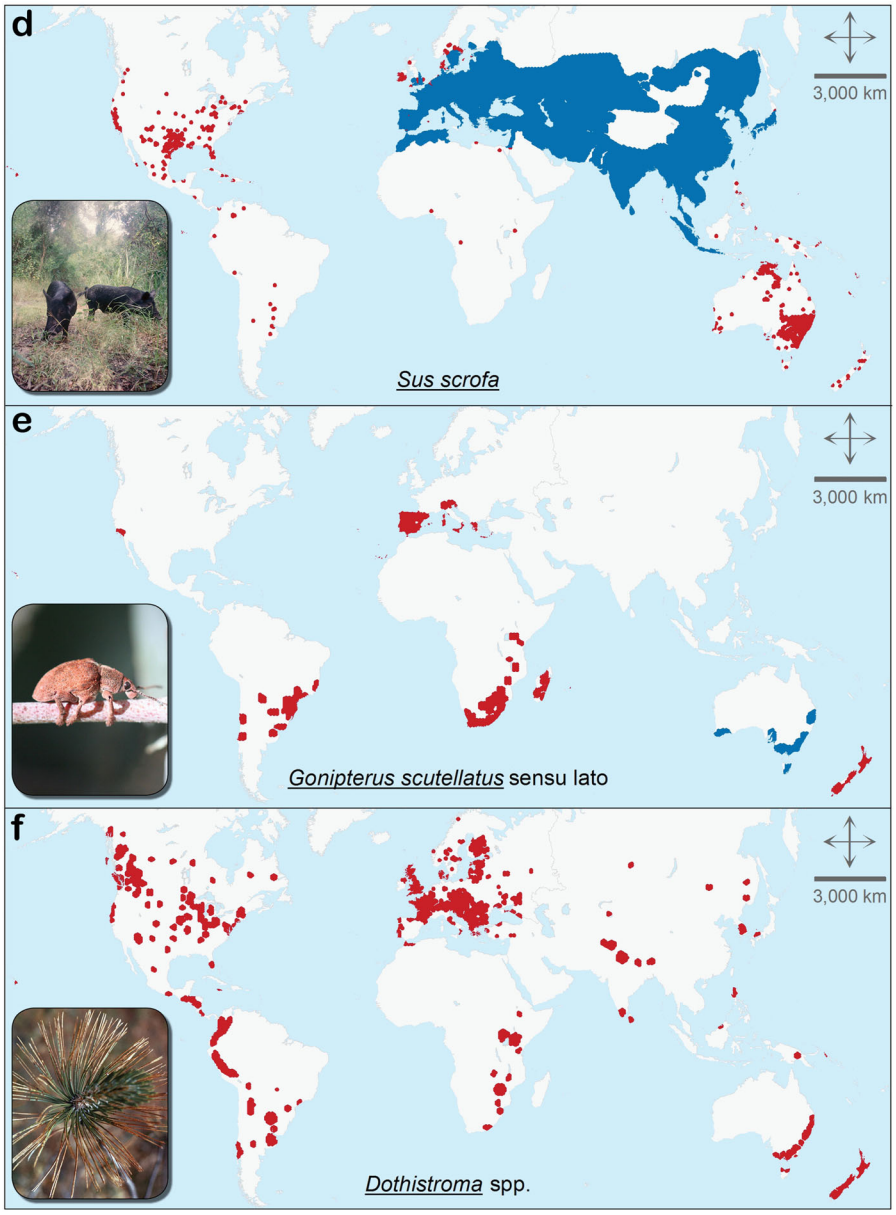

Fig. 1 continued

roles in forests including as primary producers, herbivores, predators, animal pathogens, plant pathogens, pollinators, decomposers, and mutualists. While most non-native species have negligible ecological effects, the establishment of certain species can drastically alter endemic ecological processes and thereby substantially alter forest community composition and food web structure, often resulting in a variety of cascading effects.

Unfortunately, invasions by this diverse array of species in forests may be more difficult to detect than invasions in other ecosystems. Because of the characteristically long life cycles of trees, most forests are subjected to relatively little direct management or monitoring compared to other land-uses such as agriculture and horticulture. Forests that are remote from human intervention may have fewer opportunities for being invaded. However, even the most

Table 1 Examples of the number of non-native species of various higher-level taxa occurring in forests in different parts of the world

Taxon	Criteria and selection of species	Region	Number of non-native species in forests (and % of total number of naturalised non-native species)	Total number of naturalised non-native species in this taxon (in any habitat, forest or non-forest)
Mammals	Non-native species occurring in forests	Japan	13 (76.5%)	17
Mammals	Non-native species occurring in forests	New Zealand	27 (84.3%)	32
Vascular plants	Non-native invasive species (including subspecies and varieties) occurring in deciduous forest	Eastern USA	129 (4.9%)	2629
Vascular plants	Non-native invasive species (including subspecies and varieties) occurring in deciduous forest	Eastern Asia (Russian Far East, China, North Korea, South Korea)	63 (4.9%)	1293
Vascular plants	Non-native species invading the understorey of undisturbed native forest	New Zealand	19 (1.1%)	1780
Vascular plants	Non-native species occurring in the understorey of exotic pine plantation forest (non-exhaustive)	New Zealand	70 (3.9%)	1780
Vascular plants	Non-native species occurring in woodland and forest	Europe	668 (31.5%)	3749
Insects	Non-native species feeding on forest trees	USA	455 (12.9%)	3540
Insects	Non-native species feeding on woody plants	Canada	416 (25.2%)	1654
Insects	Non-native species feeding on woody plants	Europe	416 (28.4%)	1466
Insects	Non-native insects feeding on trees	New Zealand	272 (18.1%)	1500
Plant pathogens	Non-native invasive species of pathogens of woody plants	Europe	27 (69.2%)	39
Plant pathogens	Non-native invasive species of pathogens of forest trees	USA	16	Unknown
Birds	Non-native species occurring in native or exotic forest or on forest margins	New Zealand	22 (61.1%)	36
Birds	Non-native species occurring in woodland and forest	Europe	25 (32.5%)	77
Reptiles and amphibians	Non-native species occurring in woodland and forest	Europe	34 (61.8%)	55

See Online Resource 1 for complete table with references

intensively managed forest plantations may not be directly monitored for non-native invasive species over periods of several decades, meaning that invasions can remain undetected over decadal time scales (Von Holle et al. 2003).

Species invasions have the capacity to alter the stability and productivity of forest ecosystems that provide critical resources for human wellbeing, as well as forest biodiversity globally. Here we present a current perspective on the phenomenon of biological invasions in forests. First we provide background information covering the wide array of the taxonomic composition of invading species. Next we contrast invasions in natural versus planted forests, the latter of which comprise an increasing proportion of the world's forest (Brockerhoff et al. 2013). Finally we describe various approaches to managing invasions in forests and discuss future prospects. We do not consider native species range expansions resulting from climate and land use change, because while these are becoming increasingly prevalent in forests (Hanewinkel et al. 2013), their causes and consequences have many differences from those of exotic species invasions.

Ecological roles of invading species

Invasions by primary producers

Though undisturbed closed canopy forests are widely assumed to be more resistant to plant invasions than are earlier-successional habitats (Crawley 1987; Von Holle et al. 2003), the prevalence of invasive plant species in forested ecosystems is increasing at an alarming rate worldwide (Martin et al. 2009). A wide variety of types of invasive plants are establishing in forests. These include herbaceous invaders (Wavrek et al. 2017), some of which form dense monospecific layers in forest understories and preclude recruitment of trees and other plants (Royo and Carson 2006). There are also numerous invasive woody plants that are increasingly present in forests worldwide (Webster et al. 2006). Some of these may dominate forest understories, while other woody invasive species are trees that may eventually dominate forest overstories, outcompeting native species.

Multiple factors and mechanisms have been proposed to explain the success and dominance by invasive plants. Their exceptional growth and reproduction in new habitats could be due to escape from herbivores and pathogens that limit their success in their native range (Keane and Crawley 2002; Engelkes et al. 2008) and effects of mammalian herbivores that create disturbances or other conditions that favor invaders (Vavra et al. 2007; Knight et al. 2009; Kalisz et al. 2014). But for many species, invasiveness may be explained by various functional traits (Elton 1958; Drenovsky et al. 2012), such as greater efficiency of resource capture and use (Funk and Vitousek 2007), sexual or asexual reproductive ability in the absence of mates or pollinators (Baker 1965), phenotypic plasticity (Davidson et al. 2011), efficient dispersal mechanisms and production of allelochemicals or 'novel weapons' that inhibit growth of competing plant species (Callaway and Ridenour 2004). Yet, in reality, no single factor explains most plant invasions in forests. Indeed, multiple mechanisms were repeatedly found to be responsible for the invasion success of a single species. This result was noted in a literature review of exotic trees (Lamarque et al. 2011) and a review of understory herbs (Wavrek et al. 2017). These contradictory explanations likely result from different mechanisms varying in the scales at which they operate (Fridley et al. 2007), and from genetic variation and phenotypic heterogeneity among source populations of invaders and their subsequent evolution in the introduced range (Prentis et al. 2008).

Some non-native plants in forests in Europe are considered archaeophytes (i.e., 'ancient' plant invasions prior to 1500) that were largely introduced unintentionally (Essl et al. 2012). However, most plant invasions are attributed to intentional importations of species, either for ornamental plantings (e.g., Dehnen-Schmutz et al. 2007) or for use in agriculture or forestry (Schulz and Gray 2013). While plantings of most species of non-native species have remained confined to limited areas, a small subset has become highly invasive, spreading across large regions and impacting natural and modified forest communities. Mechanisms of local spread vary among species; most spread via natural means such as dispersal of seeds by wind or by birds, though in some cases humans facilitate spread by moving plants from nurseries as stock or seeds (Dehnen-Schmutz et al. 2007). In managed forests, the incidence of non-native plants tends to be much greater following overstory harvest operations, which may facilitate their establishment (Brothers and Spingarn 1992). Similarly, dominance

by invasive plants may be much greater at forest edges, along roads and railways or in agricultural clearings as a consequence of greater disturbance (Mortensen et al. 2009).

One of the dominant impacts of invading plants in forests is the exclusion of native plant species via either direct or indirect competition for resources such as water, nutrients and light. While instances of total extinction of native plant species caused by invasions are rare (Gurevitch and Padilla 2004), there are many situations in which the composition of native forests has been dramatically altered by plant invaders. Local loss of native plant species from communities due to plant invasions is challenging to assess, but the effects of invaders on local plant populations can be strong (Downey and Richardson 2016). Elimination or reduction of native plants can result in a plethora of cascading influences on many members of the forest community. For example, plant invasions may adversely affect the biodiversity of invertebrate and vertebrate species that utilize native plants as host resources (Gandhi and Herms 2010) if invaders cause a loss of habitat heterogeneity (sensu Tews et al. 2004). Likewise, allelopathic forest invaders can disrupt important nutritional mutualisms with soil microbes (e.g., beneficial arbuscular mycorrhizal fungi (AMF), ectomycorrhizal fungi (EMF) and N-fixing nodulating bacteria) upon which most native herbaceous and woody plant species rely (Hale and Kalisz 2012). Allelochemical disruption of these nutritional mutualisms destabilizes native plant physiology and fitness (Hale et al. 2016; Portales-Reyes et al. 2015) and can ultimately drive vital rate declines (Brouwer et al. 2015).

Plant invasions can also result in a multitude of negative impacts on ecosystem processes and services (Vilà and Hulme 2017). Nitrogen fixing plants feature disproportionately in invasive floras. A classic example is the invasion of the nitrogen-fixing shrub *Morella faya*, which can replace the endemic tree *Metrosideros polymorpha* in nitrogen-limited dominated forests of Hawaii and cause substantial increases of soil and total ecosystem nitrogen (Vitousek and Walker 1989). Some invasive plants can transform ecosystem properties by producing litter that is either more or less favorable for decomposition than litter from native species (Wardle and Peltzer 2017). In other cases, ecosystem effects may result from alteration of ecosystem disturbance regimes. For example, invasions of tropical savannas of northern Australia by Gamba grass, *Andropogon gayanus*, increases fuel loads, consequently elevating fire intensity (Burrows et al. 2002). Survival of large trees is substantially diminished in more intense fires and the invasion consequently reduces live-tree C stocks and the potential for future C sequestration.

Invasions by detritivores and decomposers

Although most decomposers are not particularly charismatic and have therefore not been studied as much as other invaders, invasions of forests by decomposers have been numerous and can be ecologically significant. Important forest decomposers include invertebrates such as ants, millipedes, isopods, beetles, and earthworms, as well as a range of microorganisms. A large variety of non-native organisms colonize dead trees and play important roles in their decomposition. Among these are various ambrosia beetles and other woodboring species, which over the last two centuries have been accidentally moved among continents in wood and wood packaging material (Brockerhoff et al. 2006). In many regions, non-native ambrosia beetles outnumber native species (Reed and Muzika 2010) but almost nothing is known about what, if any, effect their presence has on decomposition rates or other ecosystem processes.

Non-native decomposer organisms play key ecological roles in the litter and soil layers in many forested regions around the world. Although there are few studies exploring the ecological impacts of non-native decomposer microorganisms (Van der Putten et al. 2007) and most decomposer invertebrate groups (Bardgett and Wardle 2010), a large literature has emerged over the past two decades on the impacts of invasive earthworm species in many parts of the world. For example, many species of earthworms have invaded regions of North America that have lacked a native earthworm fauna since the most recent glaciation. Invading earthworm populations are known to alter microbial and microarthropod communities in soil, cause loss of soil organic matter and nutrient capital, and increase rates of forest nutrient cycling (Frelich et al. 2006; Paudel et al. 2016). By altering soil conditions, invading earthworms are capable of altering the relative dominance of various tree species seedlings, which may cause large shifts in forest composition over time (Bohlen et al. 2004).

Invasions by herbivores

Both mammalian and invertebrate herbivores play key roles in forest ecosystems. As consumers, they can regulate primary production and influence nutrient cycling by mobilizing nutrients contained in tree tissues, returning them to soil and, at least partially, to the atmosphere (Mattson and Addy 1975; Wardle and Peltzer 2017). They can also serve as important drivers of forest succession and rapidly drive the replacement of those plant species that they consume by other, and often functionally very different, plant species. For example, in some regions tree-killing bark beetles may convert conifer-dominated stands into broad-leaf forests (Edburg et al. 2012), while large mammalian herbivores can convert broad-leaved forests into coniferous forests (Wardle and Bardgett 2004).

In certain forest regions, introduced mammals may reach exceptionally high numbers and exert strong ecological effects (Nuñez et al. 2010). Typically these effects occur through consumption. For example, brushtail possums, deer and goats were intentionally introduced to New Zealand (which lacks native browsing mammals) over 100 years ago. These herbivores have thrived, feeding on the foliage of native plant species with which they have no prior evolutionary contact. In stands where they are abundant, preferential feeding on certain host species results in large shifts in species composition and subsequent changes in belowground biota, soil fertility and carbon storage (Wardle et al. 2001; Bellingham et al. 2016). Similarly, in Patagonia, Argentina, exotic deer are promoting invasion by non-native trees (mainly Pinaceae) by preferentially consuming native vegetation that lacks evolved defenses (Nuñez et al. 2008; Relva et al. 2010). However, invasive mammals can also transform ecosystems through non-consumptive effects by introducing novel disturbances. For example, in the southern tip of South America, beaver were intentionally introduced for purposes of fur production but are now abundant. These animals fell overstory trees throughout extensive areas and thereby impact tree age distributions and also eliminate riparian forests via flooding (Jaksic et al. 2002).

Non-native insect herbivores are numerous, and given their economic impacts, there is more information on this group than for other taxa. Although there are notable impacts in many areas, their effects can be region-specific. For example, in North America there are more species of damaging forest insects established in the eastern half of the continent than in the west; this may reflect differences both in historical propagule pressure (i.e., a longer history of trade in the east) but also differences in invasibility (eastern forests host a greater diversity of tree genera that provides more opportunities for herbivore invasions) (Liebhold et al. 2013). Most herbivorous insects specialize on plants at the genus or family level. This may explain not only why regions with more tree diversity receive more invasions but also why more species may invade from regions with forests comprised of more taxonomically similar species (Mattson et al. 2007).

Damage caused by introduced insect herbivores largely reflects the feeding habits of these organisms. Seed- and flower-feeding insects reduce reproductive outputs of host trees. High densities of other insects, such as sap-, foliage- and root-feeding insect species lead to a general loss of host tree vigor. Bark and wood-boring insects can cause tree die-back and ultimately tree death. A few species of introduced insect herbivores have caused massive levels of tree mortality resulting in a variety of direct and indirect ecological effects.

In some cases, the tendency of insect herbivores to reach high population levels leading to extensive mortality of hosts may be related to escape from control by natural enemies (Hajek et al. 2016; Kenis et al. 2017a). The explosive nature of several introduced forest insect herbivores can also be a consequence of a lack of host resistance. For example, in its native range in East Asia, the emerald ash borer, *Agrilus planipennis*, feeds on the phloem of dying ash trees (*Fraxinus* spp.) and is typically not abundant. However, in contrast to Asian host trees, N. American ash trees lack resistance to colonization by this insect which enables it to successfully establish, reproduce and ultimately kill healthy trees (Herms and McCullough 2014). As this insect spreads through N. America, it is eliminating the majority of ash species as overstory components in that continent.

Vast tree mortality caused by insect invasions can substantially alter the composition of forests across large regions (e.g., Morin and Liebhold 2015). Perhaps not surprisingly, massive defoliation or tree mortality caused by insect herbivore invasions can have substantial effects on forest ecosystem processes that are both short- and long-term (Lovett et al. 2006; Gandhi

and Herms 2010). For example, Flower et al. (2013) predict that the loss of N. American ash as a result of emerald ash borer invasion is likely to result in the loss of 2.5% of total above ground carbon across the 48 conterminous states of the USA, though it can be anticipated that much of that loss will eventually be compensated by increased growth in other tree species already present. The long-term impacts of these massive mortality events vary among forest types; in some cases invasions can cause dramatic changes in C and N stocks (Crowley et al. 2016).

Invasions by pathogens

A wide variety of microorganisms function as tree pathogens in forest ecosystems. The best-represented group of these pathogens is the fungi although oomycetes (i.e., fungus-like eukaryotes, particularly those in the genus *Phytophthora*) are increasingly emerging as some of the most damaging non-native tree pathogens (Santini et al. 2013; Ghelardini et al. 2017; Wingfield et al. 2017a). While fewer examples of non-native bacteria and viruses are known invasives in forest and other woody ecosystems, these have been less-well studied and should not be overlooked. Many consequences of invasions by tree pathogens resemble those caused by forest herbivores. Like insects, several tree pathogen invasions have induced massive tree die-offs. Among the best-known examples is chestnut blight caused by *Cryphonectria parasitica*, now known to be native to Asia. This pathogen was accidentally introduced into Europe and North America where its impact first became obvious in the early 1900s (Paillet 2002). Within a relatively short period, the pathogen spread in its introduced range, killing the vast majority of susceptible chestnut trees in forests.

Host trees may have evolved resistance to pathogens in a manner similar to evolution of resistance to insect herbivores (Rausher 2001). Further, when pathogens are moved to new regions, they also often encounter hosts that lack resistance and may therefore display extreme virulence. However a common trait of tree pathogens is that several strains of a single species can exist, sometimes in sympatry, and these strains may exhibit considerable variation in pathogenicity. In many systems, various pathogen strains have moved around the world with successive invasions by distinct strains, resulting in new waves of tree mortality. Also, pathogen species may occasionally hybridize and this can result in greater levels of aggressiveness. This phenomenon is well illustrated for Dutch elm disease where two distinct pathogen species, *Ophiostoma ulmi* and *O. novo-ulmi* are involved (Brasier 2001). The initial invasion in Europe and North America was caused by *O. ulmi* but a new wave of disease emerged due to the accidental introduction of *O. novo-ulmi* into North America and subsequently into Europe. *O. novo-ulmi*, which has introgressed with and largely replaced *O. ulm*i, is now the dominant pathogen in North America and Europe, and it continues to kill large numbers of trees. There are also two distinct strains of *O. novo-ulmi* (the North American and Eurasian strains) and their respective distributions might be expected to influence the Dutch elm disease pandemic in the future (Brasier 2001).

Another common characteristic of tree pathogens is that they often exist in mutualistic associations with insects, which they depend on for dispersal or access to tree tissue (Wingfield et al. 2016, 2017b). Invasion by tree pathogens may result not only in novel associations of pathogens with host trees, but also with mutualistic insect species. Dutch elm disease provides a classic example of a symbiotic relationship between an insect and fungal pathogen that leads to a devastating tree disease. In this case, the pathogens involved are believed to be native to Asia but were introduced into Europe and North America with infected elm timber. Native and non-native scolytine beetles infested this timber and transmitted the pathogens to highly susceptible naïve European and North American elms. Transmission of this pathogen occurs when adult beetles feed in the twig-crotches of healthy elms and infected elms become a host resource for larvae of these same scolytines. Pine wilt disease is another important example of a tree disease that arises from a symbiosis between a pathogen and an insect, but in this case the pathogen is a nematode (*Bursaphelenchus xylophilus*) that is vectored by pine-infesting cerambycid beetles. In this system, the pathogen is native to North America and has been introduced into Japan, Korea, China and Portugal where it has become associated with native cerambycid beetles. When adults of these insects feed on foliage of highly susceptible and naïve Asian and European pines, the nematodes enter the trees and cause rapid death, thereby providing a host resource for the cerambycids (Suzuki 2002).

In addition to such tree disease epidemics caused by pathogens in symbioses with insects, there are new and emerging examples of tree diseases where insects are involved as vectors of fungi but where these relationships are casual. Important examples are found for the pathogenic fungi *Ceratocystis* spp. that are commonly vectored by sap-feeding beetles in the family Nitidulidae. These fungal pathogens produce fruity aromas that are attractive to the insects that carry them to freshly made tree wounds where serious canker and wilt diseases result (Wingfield et al. 2017b). Emerging diseases caused by these fungi include canker stain disease of *Platanus orientalis* in Europe caused by *Ceratocystis platani* (Tsopelas et al. 2017), wilt of plantation grown *Acacia* spp. in Asia and Africa caused by *Ceratocystis manginecans* and *C. albifundus* (Wingfield et al. 2017b) and a new and emerging *Ceratocystis* disease of Ohia (Mortenson et al. 2016) in Hawaii.

Tree diseases resulting from invasions are notoriously difficult to diagnose and resultant epidemics may develop for many years before they the causal agents are recognized or understood. In many cases they emerge unexpectedly in a manner that could not have been predicted in advance (Ploetz et al. 2013). The difficulty of predicting damaging disease invasions is due, in part, to the complexity of disease systems such that it is difficult to differentiate between primary as opposed to secondary organisms. Pathogens are also difficult to work with, not only because they are small, but also because the global flora of fungi and other microorganisms is largely undescribed (Crous et al. 2016). Thus, there are many cases where the causal agent of a disease or the origin of a pathogen can remain unknown or uncertain for long periods of time. And in many cases, when the cause of a new tree disease is determined, the causal agent is commonly an undescribed species and its native range may be unknown. A contemporary example is the 'laurel wilt' disease that is devastating native Lauraceae in the southeastern USA. The disease was first reported in the area in 2008 (Fraedrich et al. 2008) and was associated with the non-native ambrosia beetle *Xyleborus glabratus*; the causal ambrosia fungus *Raffaelea lauricola* was described as a new species in that same year (Harrington et al. 2008). It was only some years later that the *R. lauricola* was discovered in Asia where it is apparently native (Harrington et al. 2011). Another example is provided by Dothistroma needle blight which has a global distribution (Fig. 1f); though the disease is known to be caused by two distinct fungal species *Dothistroma pini* and *D. septosporum*, there is considerable uncertainty about their respective native ranges (Drenkhan et al. 2016).

Invasions by predators

Many different types of introduced predators exist in forest regions around the world. These include a variety of mammal species, which are particularly significant in island habitats where predator communities may otherwise be lacking. For example, numerous forested island ecosystems worldwide have been severely affected by accidental introductions of rats and mice.

Non-native invertebrate predators are also common element of forest assemblages. Notably, thousands of insect predator and parasitoid species have been introduced for the purpose of biological control of insect herbivores and plants globally (Kenis et al. 2017a). Though the vast majority of biocontrol releases have not affected non-target species, early efforts were made with little regard for such collateral effects and some had adverse consequences. While most countries now regulate biocontrol introductions and require testing for the susceptibility of native species as hosts, early releases included some parasitoids and predators that had wide host ranges and in a few cases adversely affected native hosts (Hajek et al. 2016). Not all invertebrate predators are introduced intentionally, and there are many species of insect parasitoids that are believed to have been introduced accidentally with their hosts.

Around the world, there are many examples of ant and wasp invasions, several of which have had profound ecological impacts (Holway et al. 2002; Beggs et al. 2011). For example, in New Zealand, the invasive European wasp *Vespula vulgaris* reaches extremely high abundances in *Nothofagus* forests through consumption of honeydew produced by native scale insects. As a consequence, this wasp severely reduces a wide range of aboveground and belowground invertebrates through predation (Beggs 2001), in turn impacting soil carbon and nutrient dynamics (Wardle et al. 2010). Another example involves the yellow crazy ant (*Anoplolepis gracilipes*) greatly promoting seedling recruitment and impairing leaf litter decomposition through predation of the

herbivorous native land crab *Geracoidea natalis* (Green et al. 2008).

Due to the hierarchical nature of forest food webs, many predators are strongly connected with other species and their presence can have dramatic cascading effects both on other organisms and on the ecosystem processes that they drive (Wardle and Peltzer 2017). For example, Fukami et al. (2006) compared forest ecosystems in several forested oceanic islands in northern New Zealand, some of which were invaded by rats and others which were uninvaded. They found that predation by rats on the eggs and chicks of seabirds greatly reduced nesting seabird densities, which thwarted nutrient transfers from the ocean to the land. This has reduced soil fertility considerably, with cascading effects on both aboveground and belowground invertebrate food webs, decomposer processes, and plant nutrition and growth. Invasive mammalian predators have also caused the decline and local or total extinction of several naïve forest bird species in New Zealand (Innes et al. 2010) and on numerous oceanic islands (Blackburn et al. 2004). Although several non-native bird species visit flowers and fruit of New Zealand's forest plants, they usually play only a minor role as pollinators and seed dispersers and do not represent effective substitutes for native bird species (Kelly et al. 2006). In Guam, the invasive brown treesnake has caused the extinction of most native forest bird species and more than half of Guam's native lizards and bats. This has had cascading effects including increased damage from insect pests and loss of pollination and seed dispersal services for forest trees and shrubs (Mortensen et al. 2008).

Invasions by mutualists

Mutualists play key roles in the functioning of forest ecosystems, and their invasions can severely modify ecosystem processes and properties. For example, invasions of pollinators, seed dispersers, mycorrhizal fungi and nitrogen-fixing bacteria can alter competitive interactions among forest trees and thereby drastically transform forest composition (Richardson et al. 2000). Although the adverse effects of mutualist invasions may be less obvious in comparison to the impacts of invading pathogens or predators, they can be equally problematic.

Invasions by soil microorganisms, including mycorrhizal fungi and nitrogen-fixing bacteria, can profoundly alter interactions among plant species. Evidence suggests that the competitive success of many non-native plant species is dependent on the invasion of non-native mutualists. The term "co-invasion" describes the phenomena where two non-native species form a mutualistic relationship that facilitates invasions by each species or exacerbates their impact (Nuñez and Dickie 2014). For example, successful invasion by several Pinaceae trees species is dependent on the presence ectomycorrhizal fungi that are not native to invaded regions (Dickie et al. 2010; Hayward et al. 2015). Invasion of N-fixing bacteria or arbuscular fungi can have more subtle effects given their apparent lower level of host specificity. There is little evidence that the lack of co-evolved arbuscular mycorrhizal fungi or N-fixing bacteria can totally prevent establishment of non-native plant species, but different fungi or bacteria species can increase the growth of these plants and therefore promote their spread (Rodriguez-Echeverria et al. 2012; Koziol and Bever 2017).

Invasions by nonnative seed disperses and pollinators can also have severe impacts. These species can disrupt interactions of plants with native co-evolved seed disperses and pollinators (Traveset and Richardson 2006). Pollinator invasions can fundamentally alter the architecture of plant–pollinator food webs (Aizen et al. 2008). Invading pollinators can also act as vectors of introduced pathogens affecting native pollinator abundance, as is the case with bumblebees in Patagonian forests (Arbetman et al. 2013). Invasive seed dispersers can also profoundly affect forest communities; for example, introduction of an ineffective dispersal agent (e.g., one that deposits seeds in sites that are unsuitable for germination) can have adverse impacts on populations of plant species occurring in areas with sparsely scattered resource patches. (Traveset and Richardson 2006).

Invasions in forested natural areas

While virtually all forests have been influenced by some sort of human influence such as cutting, elevated nitrogen deposition or climate change, it is nevertheless useful to contrast planted forests versus forests that regenerate without direct human intervention.

Natural forests are typically (though not exclusively) more diverse than planted and intensively managed forests. There has been much debate whether greater plant diversity makes forests more resistant to invasions. The answer may not be simple and may vary among different taxa and trophic levels of invasive species.

Beginning with Elton (1958), many authors have reported that greater native plant diversity imparts greater resistance to invasions by non-native plants (Iannone et al. 2016). The rationale supporting this conclusion is that fewer niches are available for invaders in more diverse communities, and this has been supported by several observational and experimental studies, especially those focusing at smaller spatial scales (e.g., Kennedy et al. 2002). However, field based observational studies have also provided evidence that non-native plant species may be more numerous in communities with a higher native species richness (Stohlgren et al. 2003). These apparently contradictory conclusions, described as the "Invasion Paradox", have partly been reconciled by the conclusion that native–exotic–species richness relationships are driven by multiple ecological factors that vary in their importance at different spatial scales (Fridley et al. 2007). There is a multitude of processes that govern native and exotic species richness at the local scale, including niche partitioning, competitive exclusion, stochastic mortality and immigration, top-down control (e.g., effects of herbivores and higher trophic levels), disturbance and nonequilibrium conditions and physiological trade-offs (Fridley et al. 2007). At larger spatial scales it is likely that environmental heterogeneity, which promotes native species richness, is responsible for providing more niches and opportunities for the establishment of non-native species (Fridley et al. 2007). Consequently, invasions may be more common in naturally species-rich ecosystems, but reduction of local species richness (e.g., as a result of management or disturbance) may promote invasions. Furthermore, recent evidence suggests that native–exotic richness relationships may not be linear but hump-shaped such that the effects of native species richness on reducing forest invasibility by non-native species only become apparent in very rich regions (Nunez-Mir et al. 2017).

Biotic resistance to herbivores is inherently different from forest resistance to plant invasions. While direct competition for space and resources are considered key factors limiting growth of plant populations, they are generally not as important for regulating herbivore population dynamics. For herbivores, the key requirement for establishment is the presence of a host. Consequently, a diverse plant community increases the probability that a herbivore may find a suitable host and thus establish. However, limited information documenting such a phenomenon exists in forests because forest tree diversity may be confounded with propagule pressure and other factors that promote establishment of invading species (Liebhold et al. 2013). Also, at small spatial scales such as that of individual stands, elevated forest tree diversity may delay invasive herbivore establishment because any particular tree species has a lower density when there are more tree species present, and there may be a greater density of effective natural enemies of the herbivore (Jactel et al. 2006; Rigot et al. 2014).

There is also ample evidence that initial invasions of forests may facilitate invasions by other species. For example, in China invasion of forests understories by the aster *Ageratina adenophora* alters soil chemistry and microflora, creating conditions that favor other invasive species over native species (Niu et al. 2007). Introduced herbivores (e.g., deer and pigs) may alter forest conditions and facilitate plant invasions (Relva et al. 2010). Insect herbivores, such as the hemlock woolly adelgid, *Adelges tsugae*, may reduce light interception by the forest canopy and thereby create conditions that promote plant invasions (Eschtruth et al. 2006).

In addition to resistance to invasions, forest tree diversity may affect susceptibility of forests to invasion impacts. For example, the presence of additional tree species may provide greater capacity for forests to compensate for the elimination of focal species by pest invasions. Evidence from some systems indicates that spread and population growth of invading insects may be lower in more diverse mixed stands due to enhanced predation and a potential host tree dilution effect (Jactel et al. 2006). Detailed analyses indicate the importance of plant phylogenetic diversity over simple species richness in reducing herbivore invasion because herbivores are less likely to utilize more distantly related host plants (Bertheau et al. 2010).

Natural forests provide a multitude of valued ecosystem services and many of these can be strongly affected by invasions (Vilà and Hulme 2017). For example, invasions by a variety of different types of

organisms may affect forest carbon sequestration, both positively and negatively (Peltzer et al. 2010). Additionally, invasions can directly or indirectly alter forest wildlife which are often valued game species. For example, beech bark disease and chestnut blight have resulted in dramatic declines in the availability of hard mast in eastern N. America and this has resulted in poorer conditions for certain wildlife species (Loo 2009). Many natural forests provide a source of food such as wildlife, berries, mushrooms, honey and nuts, and thereby affect the livelihood of residents. In Europe, chestnut production, both in orchards and forests, has been devastated by two Asian invasive organisms, i.e., the chestnut blight pathogen *C. parasitica* and the chestnut gall wasp *Dryocosmus kuriphilus* (Kenis et al. 2017b).

Invasions in planted forests

Historically, most timber and other forest products were sourced from managed natural forests. But in recent decades, the role of intensively managed planted forests in meeting the world's demand for such products has been growing. Currently, planted forests account for only about 7% of the world's forests but ca. 70% of wood produced for industrial use (Carle and Holmgren 2008), and the area of planted forest is estimated to increase by twofold or more by the end of the century (Brockerhoff et al. 2013). The majority of these forests are medium- to short-rotation plantations of non-native *Pinus*, *Eucalyptus* and *Acacia* in the southern hemisphere and plantations of mostly native species in several northern hemisphere countries (e.g., China, USA, Russia) (Payn et al. 2015).

Some of the exceptional growth of non-native trees can be attributed to escape from herbivores and pathogens (Wingfield et al. 2015). However, such high growth rates are often dependent upon the presence of microbial symbionts (notably mycorrhizal fungi and N fixing symbionts) that are also translocated from the native range of these trees (Dickie et al. 2010; Nuñez and Dickie 2014). When these microbial symbionts are not present in the area where the trees are planted, the trees can fail to establish or have low growth rate (Mikola 1970; Nuñez et al. 2009). High productivity in plantations of exotic trees can often only be maintained via continued exclusion or management of herbivores and pathogens (Wingfield et al. 2015). But many such plantations are increasingly affected by insect pests and pathogens that are accidentally moved around the world, potentially threatening the world's supply of wood (Hurley et al. 2016). Managing risk in planted forests in the face of potentially catastrophic invasions may be complex. Mixtures of genotypes or species within individual stands could potentially reduce the risk of losses, but management may be easier and yields in unaffected forests may be greater in pure stands (Roberds and Bishir 1997). However, planted forests could also be diversified by planting a variety of species in a mosaic of single-species stands, which should reduce the risk of catastrophic pest impacts while allowing more efficient silviculture and management.

Another phenomenon observed in non-native tree plantations is that over time, native insects and pathogens can sometimes expand their host ranges to also utilize exotic trees (Wingfield et al. 2010; Paine et al. 2011; Branco et al. 2015). In some cases, such organisms may be pre-adapted to new hosts, but in others, the switch may correspond to a genetic change via selection. In either case, there is often a substantial time lag between when the non-native hosts are first planted and when native insects may start damaging them.

In addition to impacts on plantations of non-native trees, the establishment of new host pest/pathogen associations in these plantations can pose serious threats to host tree species in their native ranges. A dramatic recent example is that of myrtle rust caused by the fungal pathogen *Puccinia psidii*. The pathogen is native to South and Central America where it has a wide host range on native Myrtaceae. A genotype of the pathogen, now referred to as the 'pandemic' strain, has apparently moved out of this area to cause serious disease problems on Myrtaceae in other parts of the world including the native range of *Eucalyptus* in Australia (Graca et al. 2013) but a different strain has been found in South Africa (Roux et al. 2016). Interestingly, neither the pandemic strain that has yet to be discovered in its native range nor the South African genotype of *P. psidii* have been found in Brazil where myrtle rust is well-known, including on the widely planted non-native *Eucalyptus*. However, to our knowledge there is no evidence that eucalyptus plantations have facilitated invasions by *P. psidii*. Despite this, it is logical that large areas of exotic trees

that are established in plantations can facilitate their colonization by native herbivores and plant pathogens, resulting in large populations that may subsequently invade elsewhere (Garnas et al. 2016). Indeed, there are numerous serious pathogens, notably those in the Cryphonectriaceae, emerging in plantation-grown *Eucalyptus* outside the native range of these trees (Hurley et al. 2016; Burgess and Wingfield 2017). Despite this potential risk of plantations facilitating invasions, most evidence for this is still incomplete so it may be too early to generalize about this phenomenon.

There is often an initial period of exceptional growth in plantations of non-native tree species before they are subjected to damage from either exotic herbivores/pathogens that have invaded from their native range or native herbivores/pathogens that have switched to non-native trees. This period is typically followed by a phase of ever-increasing problems with insects and diseases (Wingfield et al. 2015; Burgess and Wingfield 2017). Sometimes these problems can be mitigated via biological control or breeding resistance, but in a few cases, plantations of exotic trees need to be abandoned because of insurmountable pest problems. For example, invasion by the green spruce aphid, *Elatobium abietinum*, caused extensive defoliation and growth loss, ultimately leading to the abandonment of the planting of non-native *Picea sitchensis* in commercial plantations in southern Iceland (Halldórsson et al. 2003). Similarly, extensive planting of *Acacia mangium* in southeast Asia has been severely curtailed due to a wilt disease caused by *C. manginecans* (Tarigan et al. 2011), and the pitch canker pathogen *Fusarium circinatum* has severely damaged plantations of *Pinus radiata* in various parts of the world (Wingfield et al. 2008).

Another serious problem associated with non-native plantation tree species is the tendency for them to become invasive in their own right (Richardson and Rejmánek 2011; Nuñez et al. 2017). Once established over larger areas, these invading populations are often difficult to control or eliminate. There is considerable variation among both sites and tree species in the extent to which planted exotic species become invasive in nearby areas, but the problem is well-documented in those parts of the world where planting of *Pinus*, *Eucalyptus* and *Acacia* is widespread. However, there is also emerging evidence that with time, invasive insect pests and pathogens are "catching up" with the invasive trees and that over longer periods, these invasions could arguably be tempered (Crous et al. 2017), though in some areas this may happen too late to prevent serious impacts (Policelli et al. 2017).

Non-native mutualistic organisms such as root-associated fungi and bacteria are often intentionally introduced together with commercial plantings of exotic trees, but they may over time become associated with surrounding native plants (Nuñez and Dickie 2014). These mutualists can themselves become invasive or interact with additional invasive species, creating novel complex interactions (Wandrag et al. 2013; Wood et al. 2015; Zenni et al. 2017).

Managing invasions in forests

Biological invasions are a problem in virtually all forests worldwide and are likely to become progressively more serious in the future. For example, Aukema et al. (2010) estimate that new non-native tree-feeding forest insects are establishing in the USA at a rate of 2.5 species per year. In many forest areas, invasive plants are becoming increasingly dominant, as disturbance following successive forest harvests have promoted their presence. Thus, there is an ever-increasing need to improve approaches to managing the problem.

Perhaps the most important approach to managing the invasion problem is to prevent future arrivals by identifying and managing pathways. While good progress has been made in identifying pathways for forest invaders, much work is still needed on managing these pathways. For example, introductions of forest insects have primarily occurred via imported live plants or with wood, especially wood packaging material (Kiritani and Yamamura 2003; Brockerhoff et al. 2006; Liebhold et al. 2012). Over time, governments have recognized the dangers associated with plant imports and have implemented regulations that limit accidental imports of plant pests (MacLeod et al. 2010). Similarly, the International Plant Pest Convention (IPPC) has agreed to implement mandatory phytosanitary treatment of wood packing from 2003 (ISPM-15), which has at least partially reduced the incidence of insects associated with this pathway (Haack et al. 2014; Leung et al. 2014). While phytosanitary management of these two pathways

has reduced pest entry somewhat (Liebhold et al. 2012; Haack et al. 2014; Leung et al. 2014), neither pathway is effectively "closed", and potentially damaging plant pests continue to circulate globally. Though the IPPC has made good progress in harmonizing quarantine measures among countries, considerable variation still exists, especially for regulation of plant imports (Eschen et al. 2015).

Because the extraordinary growth of exotic tree species in planted forests can be attributed in part to enemy release, implementation of a strong plant quarantine program may be particularly important for countries that implement plantation forestry on a large scale. While plantation forests provide considerable economic opportunities for many countries with developing economies, those countries may not have the resources to implement a strong plant quarantine program (Nuñez and Pauchard 2010). Also, the likelihood of invasions taking place in one country may be strongly affected by quarantine programs in other countries; lack of effective quarantine may allow countries to act as "bridgeheads" in which establishments lead to further invasions elsewhere (Garnas et al. 2016). Recognizing this dilemma, Wingfield et al. (2015) suggested the need for greater international cooperation in plant quarantine together with the application of available and novel technologies to maintain the productivity of planted forests.

Given that quarantine efforts are unlikely to be completely successful at excluding all potentially damaging invasive organisms, other measures are needed to prevent establishment of these species. Coupling surveillance for newly established potentially damaging populations with eradication provides a second level of prevention. Unfortunately, this strategy is not equally effective for all species. Some organisms are very difficult to detect at low levels and this may limit the practicality of surveillance and eradication (Liebhold et al. 2016). When species are difficult to detect, invading populations may not be found until they have grown to a level where eradication may no longer be possible. Nevertheless, there has been substantial progress in developing better surveillance and eradication technologies and this has resulted in steady increases in the numbers of successful eradication programs worldwide (Keitt et al. 2011; Tobin et al. 2014).

Once species are established and eradication is no longer practical, there may be a benefit in containing the spread of invading species. Though such approaches are not common, there can be considerable benefit in even slowing a species' spread so that the timing of eventual impacts is delayed. In the USA, nearly $12 million US dollars are spent annually to slow the spread of the gypsy moth by deploying a grid of pheromone traps in a ca. 100 km wide band along the advancing front (Sharov et al. 2002). These traps are used to locate new populations which are then treated (mostly by using mating disruption) and the program has succeeded in reducing spread by over 50%.

Once species are established, there are several mitigation approaches that can be particularly effective for managing invading species in forests. Kenis et al. (2017a) report that 3387 species of insect predators have been introduced for control of insect pests of woody plants worldwide and that ca. 10% of these have led to the successful control of target species; partial control has been achieved for an additional fraction. While a minority of introductions have resulted in successful control, such successes can have dramatic benefits and justify the practice of biological control. Moreover, Kenis et al. (2017a) report that biological control introductions are on average more frequently successful when targeting insect pests of trees than species feeding on herbaceous plants, suggesting that biological control is a particularly beneficial practice in forest ecosystems.

In addition to classical biological control, there are also a few examples of the use of inundative releases of biological control agents for control of invading species in forests. For example, in many parts of the world (Australia, Africa and South America) the entomopathogenic nematode *Deladenus siridicola* is propagated and periodically released for control of the tree-killing wood wasp *Sirex noctilio* (Slippers et al. 2015). The bacterial pesticide *Bacillus thuringiensis* has virtually replaced the use of chemical insecticides for control of foliage-feeding forest insects worldwide, even though this agent is not highly specific in its effects and can adversely affect native Lepidoptera (Hajek et al. 2008).

In planted forests, managers have control over the genetics of planted trees and this offers options for managing invasive pests via resistance management (Wingfield et al. 2015; Sniezko and Koch 2017). The two dominant ecological processes responsible for the invasive behavior of forest herbivores and pathogens

are enemy release and lack of host resistance. Classical biological control obviously has potential when enemy release dominates, but in many cases invading herbivores and pathogens encounter "naïve" host trees that lack resistance due to lack of previous evolutionary contact and co-evolution. This situation appears to be particularly common for invading species that are intimately associated with their hosts, including many tree pathogens and some insect groups such as bark and woodboring insects (Villari et al. 2016). For such species, there is potential for using tree breeding to develop resistant hosts. Tree breeding programs exploit naturally occurring variation in traits conferring resistance to pests and pathogens through four different approaches: classical selection, hybrid backcrossing, cisgenesis, and transgenesis (Telford et al. 2015).

Restoration of forest ecosystems, such as by deploying resistant tree strains, is another important component of managing invasions in forests (Muzika 2017). Forest activities for managing invasions may include such practices as mixed plantings to promote biotic resistance to invasions and damage (Jactel and Brockerhoff 2007), the use of fire to limit plant invasions (Dodson and Fiedler 2006), and silvilcultural practices (e.g., thinning) that may increase the vigor and resistance to attack of individual trees or their ability to survive damage such as defoliation (Gottschalk 1993). Following control of invasives, forest manipulations may be necessary to restore forest ecosystems to their previous state and resumption of provisioning of ecosystem services. For example, in arid regions of the southwestern USA, biological control of salt ceder, *Tamarix* spp., has necessitated the restoration of riparian cottonwood–willow forests to maintain habitat for endangered populations of the willow flycatcher, *Empidonax traillii* (Dudley and Bean 2012).

Ultimately, the selection of strategies for managing invasions necessitate comparison of their costs with their benefits (Epanchin-Niell 2017). Given the diverse nature of the effects of forest herbivore invasions on ecosystem services (Boyd et al. 2013), estimation of the economic impacts of these invasions is challenging. Analyses to date indicate that greatest economic impacts of invasive species in forests are due to the loss of nonmarket values (Holmes et al. 2009). For example, a recent analysis estimated that invasions by bark and woodboring insects in the USA cause about $1.7 billion in local government expenditure (mostly for removal of dead trees in urban areas) annually but only $130 million on lost timber revenue (Aukema et al. 2011).

Outlook for the future

In all likelihood, impacts on forest ecosystems from invasions of most taxa are likely to continue to increase. While there are now regulations in place in most parts of the world that limit releases of non-native mammals and plants, many species that are already established are becoming more abundant due to their domestic spread and disturbances that promotes their dominance (Bradley et al. 2012). Progress has been made in controlling pathways by which forest insects and pathogens arrive, but arrivals with both live plants and wood nevertheless continue (Liebhold et al. 2012; Haack et al. 2014). Reductions in propagule pressure due to implementation of phytosanitary measures may be offset by continued increases in trade volumes to produce a near constant rate of species establishments in the future (Liebhold et al. 2017). Given the impossibility of preventing arrivals entirely, additional effort may be warranted to prevent establishment of potentially damaging new species via surveillance and eradication. However, the identification of candidate species via risk analysis is challenging (Liebhold et al. 2016). This is especially true for microbial tree pathogens where the majority of new invasions have been caused by pathogens that are unknown in their native ranges and that could not have been predicted in advance of their first appearance (Ploetz et al. 2013).

We live in a world where humans engineer species ranges to our benefit. Classical biological control is an example both of such engineering and of where regulation of introductions has been used successfully to prevent adverse impacts (Hajek et al. 2016; Kenis et al. 2017a). Plantation forestry using non-native trees is an example of how enemy release has been exploited to meet global demands for wood and fiber. But, like biological control, such forest practices can have adverse impacts, notably through the spread of non-native trees that then become invasive outside of the plantation. The regulation of biological control potentially serves as a good model for how the adverse ecological impacts of plantation forestry can be

reduced; limits on where and which alien tree species may be planted could curtail impacts while still allowing plantations in most regions (Nuñez et al. 2017). Clearly, there are tradeoffs between the adverse impacts of tree invasions associated with wood production in exotic tree plantations and the ecological impacts of extraction of comparable amounts of fiber from less productive forests. Quantification of these tradeoffs would be useful for the development of policies regulating plantation forestry.

Though plantations of exotic trees are particularly prone to devastation resulting from non-native herbivore or tree pathogen establishment, history has shown that natural forests have also been severely impacted. In many cases, there may be few practical options for managing invasive species, and this highlights the importance of biosecurity efforts both at and beyond borders. Given that establishment of non-native species in one part of the world is often followed by their spread into other parts of the world, effective biosecurity efforts require international cooperation; this may be an area that governments can work on together in the future. Better international cooperation is also needed on research on biological invasions in forests since most of our knowledge about invasions (including that described in this review) comes from economically developed countries (Hurley et al. 2017).

Finally, there are a large number of non-native species already established in forests around the world (Table 1). Improvement of post-border approaches for management of invading species will likely to continue to increase in importance. Technological developments have improved our ability to find new incursions and eradicate species of a variety of taxa before they become established (Keitt et al. 2011; Liebhold et al. 2016). Resistance breeding and biological control also both offer great potential for mitigating the impacts of a variety of invasive organisms. Perhaps most challenging is the search for silvicultural methods for moderating the impacts of invasions as well as devising effective approaches to restoring forest ecosystems that have been degraded by historical invasions.

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