

Impacts of invasive biota in forest ecosystems in an aboveground–belowground context

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Abstract Forest ecosystems world-wide are being subjected to invasion by organisms representing all domains of life. Here we use a combined aboveground–belowground approach to provide a conceptual framework for assessing how forests respond to biological invasions. We first address mechanisms by which invasive plants and aboveground and belowground consumers impact on forests, and highlight that although we have a growing understanding of the determinants of the effects of invasive plants, for invasive consumers we have yet to move from a series of iconic case studies to the development of general principles. We also address the effects of invasive biota in the context of the drivers of invasion, co-invasion and invasional meltdown, the issue of simultaneous species gains and losses, and forest restoration and recovery post-invasion. We then highlight areas that would benefit from further

work, particularly regarding underlying mechanisms, determinants of context-dependency of invader effects, and linkages between causes and consequences of invasion. In concluding, we emphasize that biological invaders have the potential for large-scale and long-term impacts on forest processes, and consideration of these impacts in an aboveground–belowground context will enable better prediction of future responses of forests to invaders and their management as well as of restoration efforts.

Keywords Belowground biota · Ecological processes · Ecosystem impacts · Multitrophic interactions · Plant–soil feedbacks · Soil microbial communities

Introduction

Human activities are causing major shifts in the community composition of many biological communities worldwide. This is due in a large part to humans causing increasing homogenization of the Earth's biota by transporting species and introducing them outside of their natural ranges and across biogeographic barriers. While most species introduced to new regions do not establish viable populations, a proportion of these do, and of those that become established in their new location, a small subset become highly invasive in their new environment (Thompson et al. 1995; Richardson and Pyšek 2012).

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These invasive species can reach a high level of dominance within their trophic level in their new community, and can exert powerful effects on ecosystem processes and properties in their new environment. As such, there are a growing number of examples worldwide where the functioning of forested ecosystems has been radically transformed by invasive plants, invertebrate and vertebrate herbivores and predators, and microorganisms (Ehrenfeld 2010; Wardle et al. 2011; Simberloff et al. 2013).

All terrestrial ecosystems, including forests, consist of plants, and aboveground and belowground consumers. Aboveground consumers include pathogens, and herbivores and their predators. Belowground consumers include both organisms that interact directly with plant roots (pathogens, root herbivores, mycorrhizal fungi, symbiotic bacteria) and indirectly with plants (i.e., saprophytic bacteria and fungi that

mineralize nutrients and maintain plant nutrition) as well as their predators. The interaction between plants and aboveground and belowground consumers is critical for driving ecosystem functioning both aboveground and belowground (Hooper et al. 2000; Wardle 2002; Eisenhauer 2012). It is well recognized that within trophic groups, species differ in their effects on other organisms and ecosystem processes as a consequence of their fundamental attributes or traits. Thus, when a community is invaded by a species that differs greatly from trophically equivalent species already present, this has the potential to greatly alter the interactions between the various aboveground and belowground components, and ultimately the functioning of the ecosystem (Fig. 1).

The purpose of this review is to consider the mechanisms by which invasive organisms may influence ecosystem functioning within an aboveground-

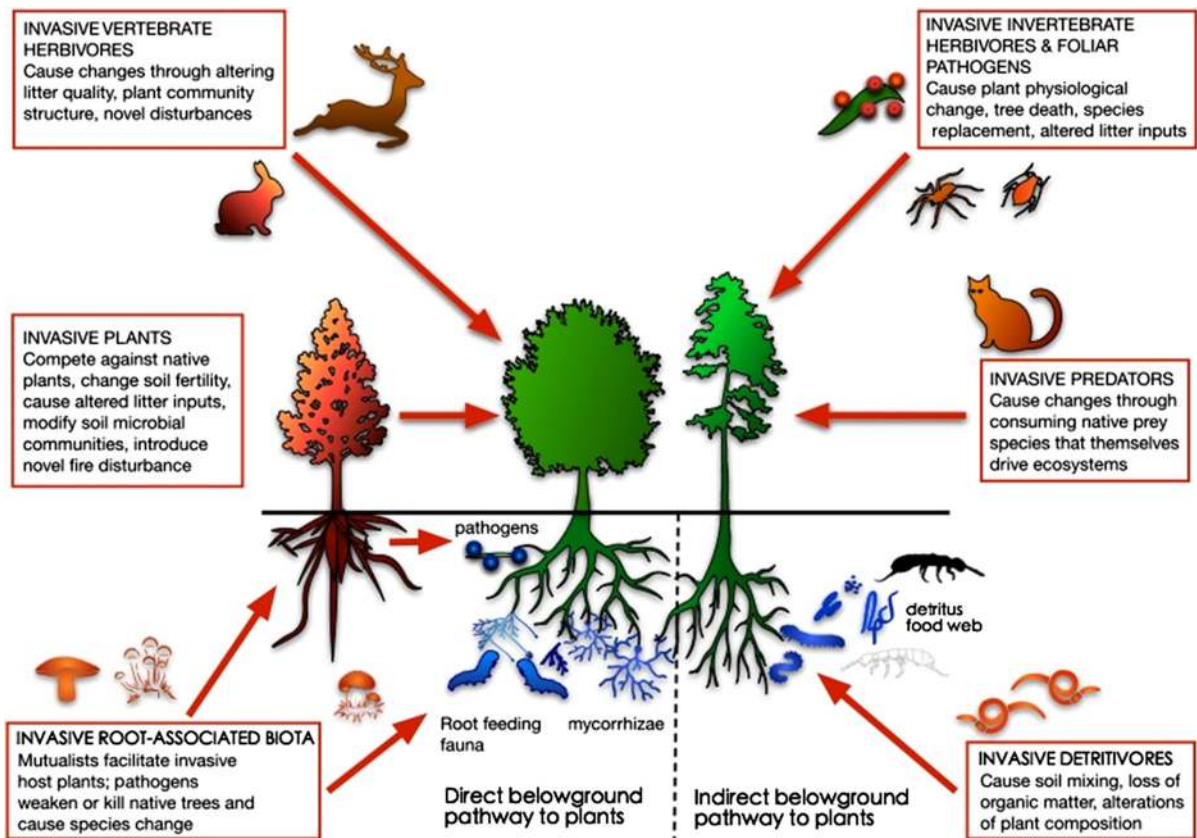


Fig. 1 Aboveground and belowground biota are linked in forest ecosystems both by direct pathways (i.e., through soil organisms that interact directly with plant roots) and by indirect pathways (i.e., through decomposer organisms that mineralize nutrients required for plant nutrition and growth) (Wardle et al.

2004); these linkages collectively drive ecosystem functioning. These linkages are disrupted by both aboveground and belowground invasive organisms, representing all major trophic groupings, and through a wide variety of mechanisms

belowground context (Fig. 1), and with explicit reference to forested ecosystems. There have now been many studies exploring how invasive plant species may affect processes, particularly pertaining to fluxes of carbon and nutrients (see syntheses by Ehrenfeld 2003; Peltzer et al. 2010; Vilà et al. 2011, Pyšek et al. 2012), and a smaller though rapidly growing number on ecosystem effects of invasive consumers (Bardgett and Wardle 2010; Wardle et al. 2011). Our purpose is not to exhaustively review the extensive literature and examples on this topic, but rather to provide a conceptual assessment of the mechanisms by which forested ecosystems may be impacted by biological invasions. In doing this, we will first address the means by which invasive plants, and aboveground and belowground consumers, impact on forest ecosystem processes. We will then consider these effects in relation to the role of determinants of invasion, the issue of species gains and losses in ecosystems, and

ecosystem restoration, and highlight what we see as major gaps in understanding and productive avenues for further work. In doing this we aim to highlight general principles regarding when and how invasive biota may impact on the functioning of forest ecosystems.

Invasive plants

For invasive plant species to exert effects on ecosystem processes requires not only that they reach a high relative biomass, but also that they have traits that differ from those of the native species already present, and that those traits that differ are important in driving ecosystem processes (Wardle et al. 2011) (Fig. 2). Comparative studies of sets of invasive and native species (including woody species and in forests) have shown that traits of the two sets can differ due to

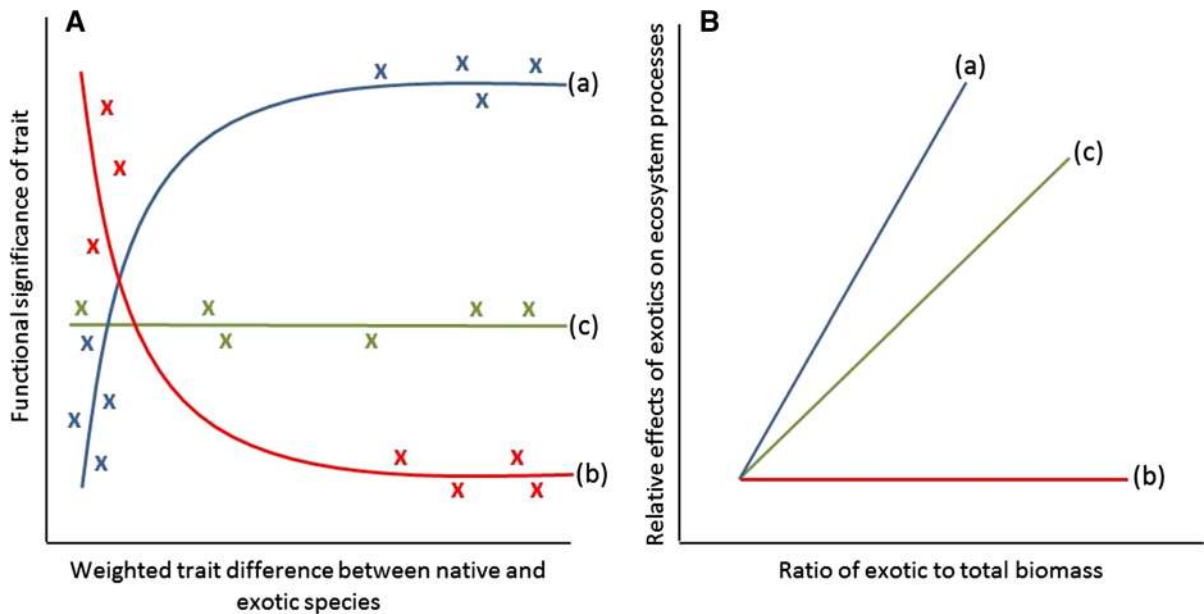


Fig. 2 Role of species traits in determining how gains of exotic species within trophic levels may affect ecosystem processes. **A** Different relationships at the whole community level between the functional significance of traits for ecosystem processes and (standardized) biomass-weighted differences in trait values between native and exotic species, with each cross representing a different trait. (a) Situations in which those traits that differ between invasive and native species are the functionally most important, such as when N-fixing plants invade ecosystems lacking N fixers (Vitousek and Walker 1989) or beavers invade ecosystems lacking functionally equivalent herbivores (Anderson et al. 2009). (b) Cases where traits that drive ecosystem

processes are different than traits that differ between invasive and native species, such as for decomposition of litter from native and invasive species on New Zealand floodplains (Kurokawa et al. 2010). (c) A situation that is intermediate between (a) and (b). The ecosystem effect of invasive species is also determined by whether they occupy a high proportion of community biomass within their trophic level, and **B** shows the effects of invaders on ecosystem processes as a function of their contribution to community biomass for the scenarios for each of (a)–(c), assuming that the relationship between relative invader biomass and its effects on processes is linear; other relationships are possible. Reproduced from Wardle et al. (2011)

invasive species having attributes associated with greater resource acquisition, e.g., higher specific leaf area, foliar nitrogen photosynthetic rate and relative growth rate (Funk and Vitousek 2007; Liao et al. 2008; Peltzer et al. 2016). However, on a global scale, these differences are not large (Ordonez et al. 2010), and are influenced to some extent by nitrogen-fixing plants, which feature disproportionately in invasive floras, often having acquisitive traits. Further, even when functional traits do differ between invasive and native species, these traits can be different to those that actually drive ecosystem processes. For example, Kurokawa et al. (2010) found for woody plant species on a river plain in New Zealand that those traits which differed between co-occurring native and invasive species were not the same as those that regulated litter decomposition, and Jo et al. (2016) found the same outcome for North American forest species. Other comparative and synthetic studies have also shown comparatively weak overall differences between invasive and native plant species, although overall positive effects on soil microbial activity and nitrogen availability (Liao et al. 2008; Godoy et al. 2010; Vilà et al. 2011; Pyšek et al. 2012).

The relatively weak and inconsistent overall effect of invasive plants on many ecosystem properties as shown in synthetic studies could emerge either because invasive organisms are comparatively unimportant (Davis et al. 2011) or because there is high context-dependency in the effects of invaders with both strong positive and negative effects being common. The latter is most likely, at least in forested ecosystems. There are several examples of strong positive effects of invasive plants on belowground processes. For example, invasion by plants that are capable of symbiotic nitrogen fixation into woody ecosystems that lack such plants leads to substantially greater inputs of nitrogen to the ecosystem and enhanced soil fertility, with consequences for both the decomposer and producer subsystems. This has been shown both through classical studies on invasion by *Morella faya* in forest understory in Hawaii (Vitousek and Walker 1989), and for invasions by *Acacia* species in South Africa and elsewhere (Yelenik et al. 2004; Richardson and Rejmanek 2011). Further, invasive plants that have much higher litter quality than native species can greatly enhance densities of decomposer organisms and processes, and rates of nutrient supply from the soil, as has been shown for invasion of *Tradescantia*

fluminensis into forest understories in New Zealand (Standish et al. 2004). Conversely negative belowground effects of invasive plants are also common, and a recent meta-analysis showed a weak overall negative effect of invasive plants on soil detritivores in forests (McCary et al. 2016). As such, members of the Northern Hemisphere Pinaceae, which are invasive in many Southern Hemisphere ecosystems (Fig. 3a), often produce poorer and more heavily defended litter than that produced by the native species present. For example, invasive *Pinus contorta* in New Zealand greatly impairs soil detritivores relative to native *Nothofagus* species (Dehlin et al. 2008).

While the above examples show links between invasive plants and soil biota via indirect pathways, invasive plants also interact with soil biota via the direct pathway (Klironomos 2002; Wardle et al. 2004; Fig. 1). As such, invasive plants often not only escape soil pathogens that may keep them in check in their native range, but can also enter novel mutualistic relationships with soil biota in their new range (Reinhart and Callaway 2006; Nuñez and Dickie 2014). Invasive plants often experience more positive or less negative interactions with soil biota in their new range, and there are a modest but growing number of examples from forested ecosystems. For example, Reinhart et al. (2003) showed that while *Prunus serotina* in its native North American range promoted soil biota that adversely affected its growth, it promoted soil biota that benefited it in its invasive range in north-east Europe, through a positive feedback. Further, Gundale et al. (2014) found that *Pinus contorta* underwent negative feedbacks with soil biota when grown in soil from its native range in Canada, but positive feedbacks when grown in soil from its introduced range in Sweden. Invasive species may impact soil biota in such a way as to affect not only their own performance but also that of native vegetation in their new habitats; a meta-analysis by Meisner et al. (2014) revealed that native species in forests were overall adversely affected by prior soil conditioning by invasive species. Similarly, invasive plants can indirectly affect mutualisms of native forest plant species, for example through disruption of mycorrhizal associations by root exudates (Brouwer et al. 2015; Hale et al. 2016). These examples suggest that direct interactions and feedbacks between invasive plants and soil biota can contribute to the success of invaders in their new habitat, and to the effects that



Fig. 3 Examples of ecosystem transformations by invasive organisms from a range of trophic positions, each of which has introduced novel traits to the ecosystem. **a** Invasion of the Brazilian cerrado (*left*) by *Pinus eliotii* and elimination of the native flora (*right*). **b** Effect of invasive fallow deer (*Dama dama*) in northern New Zealand; on the *left* of the fence the deer have access while on the *right* they are excluded. **c** Tree dieback caused by the balsam woolly adelgid (*Adelges piceae*), Great Smoky Mountains, USA. **d** Felling of *Nothofagus antarctica* forest in southern Chile following invasion by North American

beavers (*Castor canadensis*). **e** Loss of understory vegetation and litter by native nesting seabirds (*left*) is reduced when seabird eggs and chicks are subject to predation by invasive *Rattus rattus* (*right*). **f** Understory vegetation in *Acer saccharum* forest (*left*) is severely impaired when the burrowing earthworm *Lumbricus terrestris* invades (*right*). Photo credits: **a** R. Callaway, **b** D. Wardle, **c** R. Billings, Texas A&M Forest Service, bugwood.org, **d** A. Valenzuela, **e** D. Wardle (*left*), T. Fukami (*R*), **f** P. Ojanen

they may exert on forest vegetation composition and ultimately ecosystem properties.

In addition to affecting linkages between above-ground and belowground organisms and processes, invasive plants can also modify ecosystems through altering abiotic processes, like hydrology and disturbance regime (Levine et al. 2003). In forested ecosystems, these effects are most obvious in relation to fire. As such, in many regions in North and South America, and in Hawaii and Australia, invasion of flammable grasses into woody ecosystems greatly increases fire load, leading to enhanced fire frequency

and intensity (D'Antonio and Vitousek 1992; Brooks et al. 2004). This can in turn lead to a grass-fire cycle and ultimately conversion of woody ecosystems to grassland that may be difficult or impossible to reverse (D'Antonio et al. 2011). Given that fire exerts a wide range of effects on the belowground subsystem (Certini 2005) it is expected that an increased fire regime caused by invasive grasses should have large effects on soil biota, fertility, and nutrient supply for plants, although this has seldom been explored. However, Mack et al. (2001) found that uninvaded forest in Hawai'i supported greater amounts of

biological nitrogen fixation (and thus nitrogen inputs), lower nitrogen mineralization and enhanced plant nitrogen uptake than did forest that had been converted grassland following grass invasion and associated fire, leading to a more leaky nitrogen cycle. These effects were driven primarily by the loss of native species and their leaf litter inputs caused by the grass invasion.

Invasive aboveground consumers

Aboveground invasive consumers include herbivorous mammals and invertebrates, pathogens, and predators. Their ecological effects are especially apparent when they have escaped their natural enemies and when dominant species in the host community are not well adapted to the invader. As such, vertebrate herbivores such as deer and goats have invaded forests in many parts of the world, where they can cause important effects on both the aboveground and belowground subsystems through altering forest community composition (Wardle and Bardgett 2004). For example, several species of deer, and domestic goats (*Capra aegagrus*), were introduced to New Zealand (which lacks native browsing mammals) between the 1770s and 1920s. These mammals generally remove plant species with relatively large palatable leaves that produce fast decomposing litter, causing their replacement of less palatable plant species with slow decomposing litter, leading to large changes in the functional composition of the vegetation (Fig. 3b; Wardle et al. 2002; Forsyth et al. 2015). Long term deer exclusion studies throughout New Zealand showed that these aboveground effects of deer were manifested belowground, with strong but context-dependent effects on soil nutrients, microbes and nematodes (i.e., positive effects in some locations, negative in others) (Wardle et al. 2001). However, the effects of deer on larger-bodied soil biota were consistently strongly negative, likely due to physical disturbance or treading. Studies on tree seedlings in New Zealand revealed that growth of plants was less when planted in soils from plots where deer had been present versus from where they had been excluded, but that this was primarily due to deer changing soil physical properties (through trampling and reducing soil bulk density) rather than altering the soil biota (Kardol et al. 2014). This indicates that invasive browsers can affect plant growth through multiple

indirect pathways belowground, for example by altering soil abiotic properties or by changes to the soil biota (Fig. 1).

Invasive vertebrate herbivores can also influence forest ecosystems through non-consumptive means, notably when they introduce a novel type of disturbance to the ecosystem that is not provided by native biota; these effects can be considerably greater than consumptive effects. As an extreme example, North American beavers (*Castor canadensis*) have been deliberately introduced to *Nothofagus* forests of southern South America, where they have felled extensive areas of riparian forest (Fig. 3d). This leads to conversion of forest to herbaceous meadows and greatly altered landscape hydrology (Anderson et al. 2009, 2014); the belowground consequences of this change have not explicitly been explored, but they are likely to be substantial. As another example, pigs (*Sus scrofa*) have been introduced to forested areas in many areas outside of their natural range, such as South America, Hawaii and New Zealand, and their foraging for belowground resources can cause considerable soil turnover and belowground disturbance. This can lead to substantial reductions in standing vegetation, but variable effects on the belowground decomposer subsystem (Vtorov 1993; Barrios-Garcia et al. 2014; Parkes et al. 2015), which appears to be driven by environmental context and that may only become apparent in the longer term.

Outbreaks of aboveground invasive herbivorous invertebrates and fungal pathogens can cause significant forest disturbance through defoliation and death of host tree species, and there are many examples particularly in temperate regions (Kenis et al. 2009; Loo 2009; Morin and Liebhold 2015). These invaders can cause large changes in tree species composition, with potentially major ecosystem consequences (Fig. 3c). For example, loss from North American forests of American chestnut (*Castanea dentata*) caused by invasive chestnut blight (*Cryphonectria parasitica*) or of hemlock (*Tsuga* spp) by the hemlock woolly adelgid (*Adelges tsugae*), has led to replacement by other tree species that produce higher quality residues and are therefore likely to promote decomposer activity and nutrient cycling (Ellison et al. 2005; Lovett et al. 2006; Finzi et al. 2014). Invertebrate and fungal pathogen outbreaks also have the potential to modify forest ecosystem processes even when they exert major but sublethal effects. For example,

defoliation of oak (*Quercus* spp.) in North America caused by outbreaks of the invasive gypsy moth (*Lymantria dispar*) results in a large pulse of nutrients to the soil in the form of frass, dead caterpillars and unconsumed fallen foliage, which can in turn be utilized by soil microbes and transformed to organic matter (Lovett and Ruesink 1995). Sublethal effects of invertebrate and pathogen outbreaks also lead to physiological changes in host plants that alter their inputs to the soil (Cobb and Rizzo 2016), which may impair associated soil biota (Vendettuoli et al. 2015) and alter nutrient cycling rates (Rubino et al. 2015). Whether and how the effects of invasive herbivorous invertebrates and pathogens on the belowground subsystem feedback aboveground remains unexplored, but such feedbacks may be important in perpetuating their impacts over the longer term.

Invasive predators can also alter both aboveground and belowground organisms and processes, particularly when they impact on native prey species that are themselves ecosystem drivers. In forested ecosystems there are examples for both vertebrate and invertebrate predators. With regard to vertebrates, native seabirds are major ecosystem drivers on forested islands and coastal communities of New Zealand, by transporting nutrients from the ocean to the land and through extensive burrowing during nesting (Fukami et al. 2006; Orwin et al. 2016). Many of these communities have been invaded by rat species (*Rattus* spp) which, when present, predate upon seabird eggs and chicks and severely reduce their densities and thus their ecosystem effects (Fig. 3e). The net consequence of rat invasion is large reductions in soil nutrient levels, soil microfauna and macrofauna, plant nutrient supply and uptake, and litter decomposability (Fukami et al. 2006; Towns et al. 2009; Wardle et al. 2009). Further, studies on tree seedlings reveal that plants grown on soils from invaded islands grow less well than on soils from uninvaded islands, but that this is due to effects of rats reducing soil nutrient levels rather than reducing soil biota (Wardle et al. 2012). With regard to invertebrate predators, various ant species have invaded a range of forested ecosystems worldwide, although few studies have quantified their effects on ecosystem processes. In forested ecosystems on Christmas Island in the Indian Ocean, the red land crab (*Geracoidea natalis*) is the main consumer of seeds and seedlings, and also breaks down leaf litter. Invasion of this island by the yellow crazy ant

(*Anoplolepis gracilipes*), which serves as a major predator of this crab, eliminates its ecological role, and this leads to increased seedling recruitment and impaired litter decomposition (O'Dowd et al. 2003; Green et al. 2008). These examples illustrate that major effects of invasive aboveground consumers in forest ecosystems are often driven by multiple indirect pathways involving belowground processes (Fig. 1).

Invasive belowground consumers

The belowground biota consists of microorganisms (fungi and prokaryotes) and invertebrates. Invasive soil microorganisms can affect ecosystems through functioning as saprophytes, mutualists or pathogens, at least when they introduce novel attributes to the ecosystem (van der Putten et al. 2007). Little is known about invasion by saprophytic microbes, and were invasions by these microbes to occur, they would likely remain undetected given that most saprophytes have not been characterized at the species level (van der Putten et al. 2007). Moreover, even if invasion by saprophytes occurred, it is unlikely that they would possess sufficiently novel attributes relative to native saprophytes for them to exert an important effect (Bardgett and Wardle 2010). With regard to mutualists, while some invasive ectomycorrhizal fungal species form associations with native tree species in their new range, notably *Amanita phalloides* and *Amanita muscaria* (Pringle and Vellinga 2006), their impact on vegetation, or on the belowground subsystem, remains little understood. Indeed, impacts of invasive mycorrhizal fungi are best known in terms of their co-invasion with invasive host tree species, as we discuss later. However, there are several reported cases of invasive pathogenic soil-borne fungi causing widespread death of native tree species, for example *Phytophthora cinnamom* in Australia (Peters and Weste 1997) and *Phytophthora ramorum* in California (Venette and Cohen 2006). Such examples highlight instances where invasive pathogens have novel means of attack that the natural vegetation is ill-equipped to resist. There have been few instances where the long-term ecosystem impacts of these types of invasions have been considered in an aboveground-belowground context, but these impacts are likely to be substantial.

Human activity has introduced a range of belowground invertebrates to new ecosystems, and there are

several examples of invasion of forested ecosystems by larger bodied soil organisms such as millipedes, isopods, beetles, dipterans and earthworms (Bardgett and Wardle 2010). However, the effects of invasion by these invertebrates on community and ecosystems aboveground or belowground has been explored in few studies (Cameron et al. 2016), with the exception of invasive earthworms which have been subjected to substantial research effort over the past two decades (reviewed by Bohlen et al. 2004; Hendrix et al. 2008). For example, burrowing earthworms have been introduced to many North American forests that lack a native earthworm fauna (due to their elimination by Pleistocene glaciations), and thereby introduce a novel disturbance that has wide-ranging ecological impacts (Fig. 3f; Hendrix et al. 2008). Belowground effects include homogenization of soil physical structure, stimulation of soil microbial activity and greater mineralization of nutrients, and loss of organic matter (Bohlen et al. 2004). Aboveground, effects can include short term enhancement of plant nutrition and growth (Scheu and Parkinson 1994), but adverse longer term biogeochemical effects and impaired recruitment of forest tree species resulting from the loss of organic matter (Frelich et al. 2006; Eisenhauer et al. 2009; Paudel et al. 2016). However, earthworm invasion of natural forests is comparatively recent, and we still have limited knowledge of how this will impact on forest dynamics and ecosystem functioning over the longer term.

Role of determinants of invasion: context and co-invasion

As discussed this far, there are many examples of invasive biota exerting important aboveground and belowground effects in forest ecosystems around the world via a number of mechanisms. However, an understanding of how invasive organisms affect ecosystems requires explicit consideration of the extent to which ecosystems allow or resist invasion in the first place, because if the organisms are unable to invade and reach high abundance then they will be unable to exert large impacts. Ecosystems differ greatly in the extent to which they can be invaded, and this issue has been explored primarily for plant communities. Several studies have explored how plant invasion can vary across ecosystems due to the level of

biotic resistance exerted by the resident community (e.g., its competitiveness, diversity and herbivore load) (Levine et al. 2004; Pyšek et al. 2012), and edaphic site characteristics such as soil fertility and disturbance regime (Davis et al. 2000). It stands to reason that those communities which are most likely to be impacted by invaders are those that are least resistant to invasion, although this link has seldom been made. Further, even when communities are invaded, the magnitude of the effect of the invader may be driven by environmental conditions and thus vary across ecosystems, although this has received little attention. Although the same dominant plant species can exert contrasting effects on ecological processes among different ecosystems that vary in edaphic properties (Wardle and Zackrisson 2005), our understanding of how the impacts of a given abundant invasive species may be influenced by environmental context remains very limited. However, work on invasive vertebrates has revealed that the impacts of introduced deer in New Zealand forests varies strongly among forest types (Wardle et al. 2001), driven strongly by both differences in native species vegetation composition and soil fertility (Forsyth et al. 2015).

Organisms often do not invade in isolation, and invasion by one organism can be dependent on co-invasion by other organisms. For example, ingress of invasive plant species into forests may be facilitated by invasions of animals that initiate novel disturbances, such as beavers (Anderson et al. 2009), earthworms (Eisenhauer et al. 2012) and pigs (Barrios-Garcia et al. 2014). Moreover, different invaders can have positive effects on one another, leading to 'invasional meltdown' (Simberloff and von Holle 1999). For example, invasive woody plants may be dependent on co-invasion by invasion of their mutualists such as nitrogen fixing bacteria or ectomycorrhizal fungi (Nuñez and Dickie 2014; Traveset and Richardson 2014). Recent studies have also shown that invasive mammals can in turn facilitate the dispersal of invasive ectomycorrhizal fungal species required for the successful establishment of invasive tree species, in both Argentina (Nuñez et al. 2013) and New Zealand (Wood et al. 2015). Such studies provide evidence the effect of invasive organisms on ecosystem properties can be dependent on, or exacerbated by, co-invasion by other organisms, although this has been explicitly addressed in few studies. However, it has been shown that co-invasion by earthworms enhances

the effect that the invasive nitrogen fixing shrub *Morella faya* has on nitrogen accretion and cycling in a Hawaiian forest, by enhancing burial of nitrogen-rich litter (Aplet 1990). As another example, invasion of forest by yellow crazy ants as described above occurs in tandem with invasive honeydew-producing scale insects with which they form a mutualism (O'Dowd et al. 2003). This mutualism enables the ant to impact forest regeneration and litter decomposition as a consequence of their consumption of red land crabs, and the scale insect to cause forest dieback through producing sooty molds.

Simultaneous gains and losses of species

The gain of species in local communities through invasion is an opposing process to the loss of species due to local extirpation. However the ecosystem-level consequences of these two processes have usually been conducted entirely separately from each other and via different approaches (Wardle et al. 2011). The impacts of species gains has been primarily addressed at the species level through assessing what happens when a new species invades an ecosystem, as we have discussed this far. In contrast, the effects of species losses on ecosystem processes has been explored mostly through community-level studies that assess relationships between biodiversity and ecosystem functioning (Cardinale et al. 2012), often to the exclusion of other approaches (Wardle 2016). It stands to reason that, as gains and losses of species are occurring simultaneously, understanding how forests are responding to human-induced species changes requires joint consideration of the effects of both species gains and losses as well as the net effect of both processes (Rodriguez-Cabal et al. 2013). Disentangling the ecosystem effects of species gains and losses is non-trivial. As such, despite claims that studies which experimentally vary species richness to inform on what is happening in the Earth's ecosystems as a result of extinctions (Hooper et al. 2012; Tilman et al. 2012), at local scales species richness is often increasing because gains of species through invasion often exceed species losses (Vellend et al. 2013; Dornelas et al. 2014), except for ecosystems subjected to intensive land use or resource exploitation (Gerstner et al. 2014; Newbold et al. 2015).

An improved understanding of how human-induced species changes affect the aboveground and belowground components of ecosystems requires that we compare how species that are gained through invasion impact on the ecosystem relative to those that are lost through local extinction (Wardle et al. 2011). There have been few explicit tests of this in forested ecosystems, but Mascaro et al. (2012) addressed this issue for lowland Hawaiian rainforest. Here, a functional trait approach was used to show that invaded forests had greater aboveground biomass, productivity, nutrient turnover and carbon storage, which was due to functional differences of invasive species in the forest from both resident native species and native species that had gone extinct. Further, with regard to animals, in New Zealand forests the primary native megaherbivores (moa birds) were hunted to extinction by the first human settlers around 700 years ago, and subsequent settlers have introduced mammalian megaherbivores over the past 250 years, many of which (notably goats and various deer species) have become invasive. Although these invaders feed on many of the same resources as did the moa, their impact on forest ecosystem processes both above and below ground are likely to be much greater, in part because of the relatively high population densities achieved (McGlone and Clarkson 1993), but also because their foot structure means that they exert greater physical disturbance in the uppermost soil layer (Duncan and Holdaway 1989; Wardle et al. 2001). Other examples include those in which predatory invasive animals cause local extinction of other animals that themselves drive ecosystem processes (Bellard et al. 2016), such as we discuss above for effects of invasive rats on burrowing seabirds, or of yellow crazy ants on land crabs.

Implications for restoration

Restoration of invaded communities requires an understanding of the ecological impacts of the invaders both aboveground and belowground, as well as the persistence of invader legacy effects following their removal (Fig. 4; Kardol and Wardle 2010). As such, restoration of invaded communities frequently requires not only a reduction or removal of the invader itself, but additional interventions to reduce or remove its legacy. In forested systems, legacy effects of

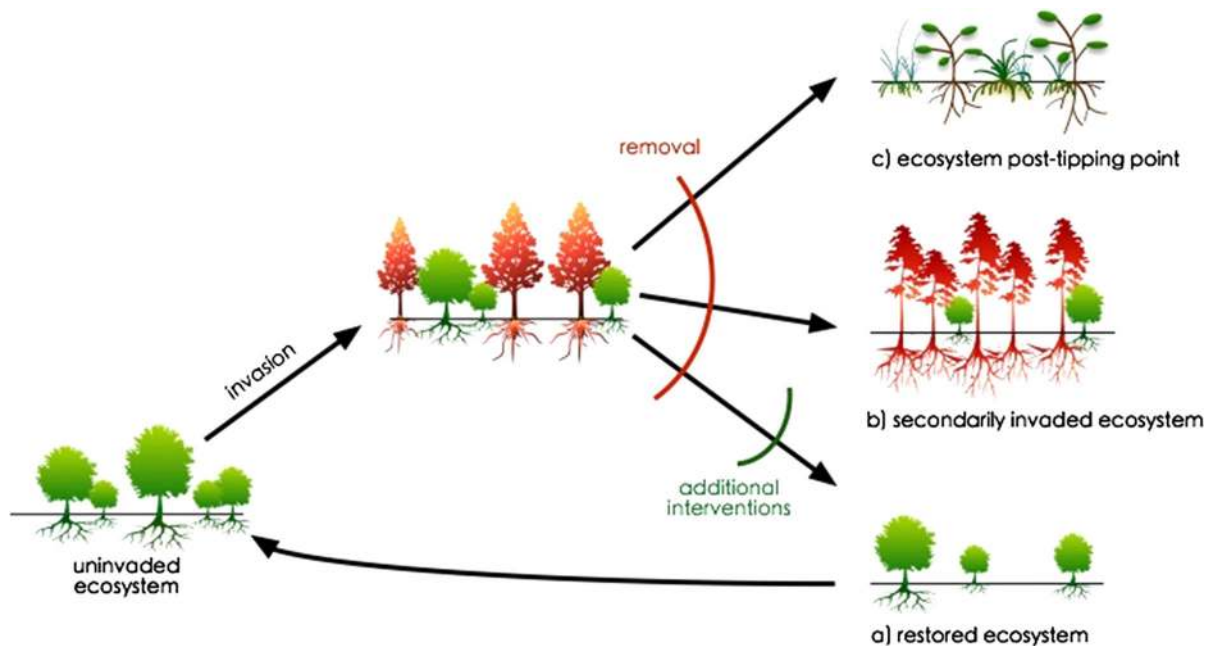


Fig. 4 Three possible trajectories of change in forest ecosystems that may occur following removal or loss of an invasive species. These trajectories are: (a) return to the original native community. This may require additional interventions such as reintroduction of lost native species or mutualists of native species, or modification of habitat conditions to make them more suitable for native species establishment. (b) Persistence of the legacy of the removed invader through secondary invasion

invasive plants can persist for several years post-removal especially when the invader differs greatly from that of native species, as shown for example for invasive nitrogen fixing trees such as *Acacia longifolia* (Marchante et al. 2009), and for biogeochemical disruption by invasive *Pinus contorta* (Dickie et al. 2014). Active interventions to reduce legacies of invasive plants post-removal can potentially be achieved by reconstructing aboveground and belowground communities that are characteristic of the ecosystem prior to invasion, for example by reintroducing native mutualists of native plant species during replanting, although this has seldom been done (Wolfe and Klironomos 2005). More recently, functional traits have been used to guide restoration (Laughlin 2014). For example, in Hawaiian forests, functional traits have been used to guide selection of plant species, including exotic non-invasive species, that have characteristics that are comparable to those of the resident native species (Cordell et al. 2016). Other interventions that have been attempted during

by other invasive species. (c) Movement of the ecosystem past a tipping point that prevents the ecosystem reverting back to its pre-invasion state and that differs fundamentally both from the originally uninvaded and invaded ecosystems. Note that although invasive plants are depicted here, exactly the same set of principles also applies to invasive aboveground and belowground consumers whenever they transform ecosystems. See main text for further discussion

restoration in grasslands have involved addition of carbon to reduce soil fertility and create an environment less suitable for invasive plants, thus minimizing their ecosystem impacts (Corbin and D'Antonio 2004). However, this has had variable success, and in a forest setting is probably only tractable over small areas.

Much effort has been invested in reducing or eradicating vertebrate invaders worldwide, including in many forested ecosystems. However, even post-eradication, legacy effects of the invader can persist, especially when removal of the invader is followed by secondary invasion by other invasive species (Pearson et al. 2016), or when the invader has transformed the ecosystem's disturbance regime or has removed organisms in lower trophic levels that themselves drive ecosystem processes. As an example of the latter, invasion by rats described above greatly transforms coastal and island forests in New Zealand through predation on nesting seabirds which themselves serve as ecosystem drivers (Fukami et al. 2006).

Extirpation of rats on several islands has failed to restore aboveground and belowground ecosystem properties, because restoration requires not only the loss of rats but also reintroduction of lost seabird populations (Mulder et al. 2009). In the absence of seabirds, islands with rats removed are therefore likely to enter a different ecosystem state both to invaded islands and to islands that have never been invaded. Restoration of ecosystems invaded by invertebrate or microbial consumers is especially problematic or intractable, because of obvious problems in removing these organisms. However, even here, explicit consideration of aboveground-belowground linkages can assist. For example, given that in North American forests invasive earthworms and invasive plants are positively associated, the removal of exotic plants can also lead to a reduction in invasive earthworms (Madritch and Lindroth 2009).

Conclusions and the way forward

An aboveground-belowground perspective on invasive biota is essential for understanding the causes and consequences of invader impacts in forested ecosystems, because belowground legacies can be persistent, and because of the key role of aboveground and belowground biota in driving many ecological processes and ecosystem functions. However, several unresolved issues remain with regard to explaining the wide variation in impacts of invasive biota in forests. Based on what we know and what we have discussed this far, we identify some important but unresolved issues that represent productive avenues for future research as follows:

1. Invader impacts on community and ecosystem properties are often indirect, and frequently involve multiple taxa and trophic levels. As such, invasive species can have unforeseen but important effects on other trophic levels and the diversity of taxa within those trophic levels (Carvalho et al. 2010; Schirmel et al. 2016). The consequences of these effects for forest ecosystem functioning are little understood especially in the longer term, but lend themselves to empirical evaluation.
2. Biological invasions (i.e., species gains) often coincide with species losses through local extirpation, and although those processes are most often considered separately, their net effect, along with the development of novel associations such as co-invasion (Dickie et al. 2010), ultimately drives changes in community structure (Sax and Gaines 2008; Wardle et al. 2011). As such, the net effects of biological invaders need to be understood in the context of both species gains and losses in communities, and their overall consequences for ecological processes or functions.
3. The magnitude of ecosystem impacts by invasive species can be driven by differences in the timing and magnitude of their effects, not just through introducing novel or distinct processes *per se*. An example of this involves the seasonal differences in resource uptake and litter loss by non-native forest understory species compared to native species (Fridley 2012; Jo et al. 2015). Thus, determination of functional novelty and impact should be expanded to include the asynchrony of their impacts relative to those of the resident community.
4. Biological invasions both cause and are driven by a range of environmental factors such as disturbance regimes and soil fertility (Davis et al. 2000; MacDougall and Turkington 2005; Moles et al. 2012), however most studies of invader impacts do not include explicit consideration of the factors that promote invasions themselves. These factors could be disentangled through more explicit consideration of invader effects in combination with factors that promote or reduce invasions. Restoration or adaptive management of biological invasions lends itself particularly well to resolving this issue especially if coupled with theory on sequence or priority effects (Fukami 2015; Stuble and Souza 2016).
5. An unresolved issue is whether and how invader effects and thus impacts vary predictably among ecosystems. Recent studies demonstrate that variation among populations or rapid phenotypic or evolutionary change of invaders can occur (e.g., Zenni et al. 2014; Chown et al. 2015), suggesting that impacts should vary across both time and space due to changes in the invasive species themselves. Both comparative and experimental approaches could be used to evaluate and predict such variation in invader effects across

ecosystems, and whether impacts are likely to amplify or dampen over time (Yelenik and D'Antonio 2013).

6. Other drivers of global change act as large-scale factors that can interact with biological invasions to determine current and future impacts in communities. However the role of global change drivers in mediating the impacts of biological invasions has been seldom considered (Tylianakis et al. 2008). Because the interactions between biological invaders and other drivers of global change are large-scale and long-term, this is likely to become an issue of increasing importance in the future.
7. While a considerable body of literature has focused on identifying the characteristics that determine which plant species are most likely to be invasive and to have the largest effects when they do invade, we know considerably less for consumer organisms. Despite a growing number of examples of major transformations of ecosystems by invasive consumers, we have yet to move from a series of iconic case studies to the formation of general principles about how and when invasive consumer species might exert such effects.
8. A long-term perspective for invader impacts is needed, particularly in forested ecosystems. Although rapid declines in forest species can be caused by invasive pathogens, impacts by other groups of invaders involve alteration of individual plant performance or the regeneration niche of species, and the community and ecosystem level consequences of this may not become apparent for decades or longer for long-lived tree species. As invasion proceeds from early to later stages, the focus should shift from resolving the effects of individual invasive species to a broader consideration of their longer term ecosystem effects.

Invasive biota in forest ecosystems comprises a diverse range of taxa representing all domains of life, and that can have potential impacts ranging from the trivial to the profound. We highlight that consideration of invader impacts on both above and belowground processes is essential for understanding this variability. Forest ecosystems are particularly well suited to generating broad principles and an improved understanding of invader impacts, because the imprint of

different invaders on long-lived tree species can often be observed directly, even if the mechanisms involved can include multiple direct and indirect effects via belowground biota and soils. Moreover, better understanding of both the causes and consequences of such invasions is essential for reliably predicting large-scale and long-term changes in many forest systems. The challenge is now to better integrate an improved understanding of the causes and consequences of invaders with longer-term forest ecosystem processes. Biological invaders have the potential for both large-scale and long-term impacts on forest ecosystem processes, and as such, should receive increased attention not only for research on invasions themselves, but also to predict future responses of forest ecosystems to invaders and their management as well as of restoration efforts.

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