Ecological Consequences of Pathogen and Insect Invasions

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Abstract The introduction and successful establishment of nonnative species poses a significant threat to the function and structure of native ecosystems and biodiversity. Forest ecosystems are especially threatened due to the worldwide importance of wood packaging material universally used in global trade, the importation of lumber and wood products, and the importation of live trees for planting. This collectively enables a number of invasion pathways that facilitate the introduction of forest insects and pathogens. Consequently, forest ecosystems worldwide are under threat from nonnative forest pest species, many of which pose little concern in their native habitats due to the checks and balances associated with natural enemies and host plant defensive responses. Unfortunately, the lack of concern for many species in their native habitats leads to a significant knowledge gap when such species are introduced into a new environment and begin to pose negative ecological consequences. In this review, I discuss variation in establishment success and ecological consequences exerted by nonnative forest insects and pathogens, define characteristics of high-impact species, and review recent research on the ecological consequences of these high-impact species in forest ecosystems. Although specific insect and pathogen examples are drawn from invasions in North American forest ecosystems, the concepts of habitat invasibility, species invasiveness, and the ecological consequences expressed by nonnative forest species are not unique to North America.

Keywords Biological invasions · Habitat invisibility · Forest ecosystem · Species invasiveness

Introduction

The introduction and establishment of species in new habitats has continuously occurred throughout the world's history and long before the arrival of humans and their immediate ancestors. Undoubtedly, some of these new species caused dramatic and cascading changes to native biodiversity and ecosystem function. The joining of the North and South American continents, for example, following the rise of the Isthmus of Panama during the Pliocene Epoch led to numerous interchanges of species along this newly formed land bridge [1]. This event certainly placed species with no prior evolutionary history into competition, which led to species extinctions and provided Alfred Russel Wallace with supporting evidence in his development of the concept of biogeography [2].

But while the interchange of species in the early stages of the Earth's history followed the formation of land bridges or other geological phenomenon that developed over millions of years, today's trends of global trade and travel have greatly facilitated the accidental hitchhiking of species on an unprecedented scale [3–5]. The world's busiest ports handle 10 million to more than 30 million 20-foot equivalent units of cargo each year [6]. Global forests are particularly challenged by trade pathways due to the widespread use of wood in packaging material such as crates, pallets, and dunnage, as well as the importation of wood, wood products, and live plants [7, 8, 9, 10, 11]. Consequently, there is a vast number of vehicles on which forest insects and pathogens can be accidentally transported and subsequently introduced into a new environment.

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Unfortunately, development of a broadly applicable paradigm useful to predict the invasiveness of a species has remained elusive, which is not terribly surprising given the tremendous variation in species life history traits and the unpredictable stochasticity associated with a species when it is introduced to a new habitat. Thus, this review will consider only broad conceptual hypotheses that have been proposed to explain variation in both rates of establishment and variation in the amount of ecological damage caused by nonnative species. I will then focus on the characteristics of high-impact nonnative forest insects and pathogens and review recent research on the ecological consequences of these high-impact species in forest ecosystems.

Variation in Rates of Establishment

Fortunately, most hitchhiking species are thought to fail to establish successfully when arriving to a new area [12, 13], and establishment is not a trivial obstacle [14, 15]. For example, to successfully establish in a new area, a species must be in a life stage that is conducive to surviving the voyage. It must also arrive under conditions favorable to its survival, such as arriving during the appropriate season given its phenological stage, as well as arriving in an area with a climate reasonably similar to its native range. The degree of habitat invasibility to which a new species arrives is also an important consideration. Habitats that are generally more likely to support successful establishment of an introduced species (e.g., high invasibility) are thought to be characterized by an availability of resources, higher levels of disturbance, and the lack of competitors and regulators [16–20]. For example, one hypothesis, the diversity-invasibility hypothesis, suggests that habitats with greater biodiversity are more resistant to invasion due to less available resources, and consequently less available niches, and a greater potential for a diverse natural enemy complex [21]. Because nonnative species tend to reduce native biodiversity, the continual establishment of nonnative species could initiate a cycle of reduced biodiversity followed by a consequent increase in habitat invasibility. However, many prior studies have observed a positive association between native and nonnative species richness, giving rise to a contradiction known as the invasion paradox [22].

Regardless of the drivers of habitat invasibility, an extremely important constraint, and perhaps the most critical constraint, to successful initial establishment is the sheer number of individuals that are actually transported and arrive in a new area alive. Several previous studies across taxa have highlighted the positive association between founder population size and rates of successful establishment [23–27]. Indeed, population size is an important component of the dynamics of any species and garners much attention from conservation biologists when managing low-density populations that are at risk

of extinction [28]. Inversely, nonnative species face similar challenges when attempting to establish and maintain a reproductively viable population when initiated at low densities [29]. Low-density populations can be subject to both demographic and environmental stochasticity, resulting in lower population growth rates [30]. The genetic architecture of the founder population can also influence establishment success [31]. Populations founded by fewer individuals generally have lower genetic diversity, which can produce a genetic bottleneck that could limit invasion success [32]. Finally, low-density populations can be subject to Allee effects (e.g., positive-density dependence [33–37]). The concept of Allee effects is based on the assertion that populations must comprise a minimum number of individuals to remain reproductively viable such that below this threshold populations are unable to replace themselves and instead are driven towards extinction [38]. Populations that are too small could challenge individuals to locate suitable mates, satiate natural enemies, or overcome host defensive responses [39, 28, 40, 41].

Unfortunately, despite these seemingly insurmountable challenges, some species do successfully establish in a new area upon their arrival, and some fraction of these species ultimately cause extensive ecological impacts when released into a novel habitat [12, 42, 43]. Moreover, in addition to the observation that not all introduced species cause disturbance when introduced into a new ecosystem, it is also important to note that many insects and pathogens posing severe ecological consequences in a novel environment are not regarded as pests in their native regions. To some extent, this is of major significance, as species not considered to be pests are not always studied as thoroughly as those that are pests. Consequently, when a new species is introduced to a new habitat and begins to pose ecological consequences, there is often a lack of information from the literature, such as research on its basic biology and ecology, host range, and appropriate control tactics, which could otherwise be useful in management efforts [44]. Although there is no rule that can be applied generally across taxa to estimate the potential for a specific nonnative species to detrimentally affect ecosystems, there are two concepts to consider: the enemy-release hypothesis and the defense-free space hypothesis.

Variation in Ecological Consequences

The enemy-release hypothesis describes the phenomenon in which a newly arrived species is free from the natural enemy complex that is present in its native habitat [45]. In the absence of such top-down enemies, important and potentially regulatory constraints are removed, thereby allowing for greater population growth through, for example, increased survivorship [46]. Insects in particular can be attacked by a number of generalist and specialist natural enemies in their native

environment, and such natural enemies are generally not introduced with their prey, although there are some exceptions, especially in the case of entomopathogens [47]. Historically, the enemy-release hypothesis has been cited as a primary mechanism through which an invading species becomes a particularly noxious one [48].

An example of the importance of natural enemies in providing invasive species control can be provided by the case of the brown-tail moth, *Euproctis chrysorrhoea*, invasion of the USA. Life stages of the brown-tail moth are believed to have been introduced from Europe on infested nursery stock in 1897 [49]. It quickly spread throughout the northeastern USA, where it caused severe defoliation to a number of host tree species [50]. However, following the importation of a natural enemy, the generalist parasitoid *Compsilura concinnata*, one of many such species introduced from Europe during biological control efforts spearheaded by the US Department of Agriculture to combat nonnative insect pests [51], populations dramatically declined. Nowadays, populations of *E. chrysorrhoea* are extremely restricted to dune habitats along Cape Cod where *C. concinnata* cannot persist [52]. Despite this example supporting the enemy-release hypothesis, this hypothesis provides only a partial explanation to the success of nonnative pests given that only a minority of established nonnative species cause severe ecological impacts in a novel environment, and the number of nonnative species posing little to no damage even in the absence of natural enemies [53].

The defense-free hypothesis can be considered as the bottom-up analog to the enemy-release hypothesis [54]. In a native environment, species generally evolve in close concert with that of their hosts, and insects and plant pathogens are no exception. Studies of plants and their interactions with herbivores and plant pathogens are extremely numerous, and many have collectively described the exciting chemical warfare between the two trophic levels (e.g., [55–57]). Plants produce constitutive, and when attacked, inducible chemical compounds that can reduce growth and digestion and induce mortality in the attacking herbivore [58, 59]. Natural enemies can also detect some defensive compounds and respond by attacking the plant-attacking herbivore [60]. This warfare is hardly one-sided, as insect herbivores and pathogens are capable of metabolically neutralizing the otherwise inimical effects of plant chemical compounds produced by their native host plants [61], or developing behavioral mechanisms, such as mass-attacks exhibited by some bark beetle species, to overwhelm the plant defensive capability [62]. However, these extremely intricate relationships between native plants, and their attacking pathogens and herbivores, do not always persist when insects and pathogens attack naïve host plants with which they have no prior evolutionary history [63, 64]. In such cases, plant defensive compounds are not always as effective as they would be against native insects and pathogens.

An example of the vulnerability of naïve host plants against attack by nonnative species can be found in congener species of *Agrilus*. One species, the bronze birch borer *Agrilus anxius*, is native to North America where it causes considerable mortality to nonnative birch [*Betula* spp.] species planted in North America, while native birch species are rarely killed [65]. Similarly, the emerald ash borer, *Agrilus planipennis*, which is native to Asia but was discovered in North America in 2002 [66], is causing extensive mortality to all species of North American ash [*Fraxinus* spp.], while ash species native to Asia are resistant [67]. The relationship between naïve host plants and nonnative species is certainly not limited to nonnative insects; indeed, one of the most dramatic changes to eastern forests in the USA followed the accidental importation of the fungus *Cryphonectria parasitica*, the causative agent of chestnut blight. This fungus is believed to have been imported from Asia through infested nursery stock in the early 1900s. By the 1940s, virtually all mature chestnuts, *Castanea dentata*, native to North America, which were once a dominant component of many eastern forests, were eliminated by this pathogen [68, 69••]. One current effort to restore chestnut to North America involves developing backcrossed blight-resistant chestnut trees using Chinese chestnut, *Castanea japonica* (a natural host of *C. parasitica*), as a genetic source of resistance [70].

High-Impact Nonnative Insects and Pathogens

Regardless of the mechanism(s) that otherwise would provide resistance against a nonnative species and its ability to disrupt ecological processes in a new environment, certain introduced species have caused major ecological consequences and dramatically altered and continue to alter the ecological landscape. Aukema et al. [43] estimated that between 1860 and 2006, ≈ 2.5 insects arrived and successfully established in the USA per year, but only ≈ 0.4 insects per year were considered to be high-impact pests. But what makes a particular nonnative species a “high impact” one? Although there are examples of species whose impacts include the potential loss of susceptible host tree species (i.e., *C. parasitica* and *C. dentata*, *A. planipennis* and North American *Fraxinus* spp.), ecological impact can often be a question of scale. For example, nonnative species attacking a spatially limited host, resulting in localized ecological disturbance, may not garner the attention of a more spatially widespread problem; yet, the localized consequences can still be profound, if merely on a smaller scale.

There are several characteristics of a high-impact nonnative species in forest ecosystems. First, such species tend to exhibit a high potential for population growth, and certainly a lack of top-down (e.g., effect of natural enemies) and/or bottom-up (e.g., effect of host plant chemistry) mechanisms plays a role in this population success. Second, the ecological

consequences they cause are ultimately significantly greater than the background level of disturbance. However, it is also important to note that during the initial stages of a forest insect or pathogen invasion, impacts are often initially limited and not readily apparent, which results in a latency period following arrival and establishment, and growth to sufficiently detectable damage levels [15]. Third, high-impact forest pest species often cause disturbance over a spatially widespread and/or contiguous area, which poses numerous consequences. For example, large areas exhibiting disturbance can overwhelm the budgetary and logistical abilities of regulatory agencies to suppress populations and thereby mitigate impacts [71]. Widespread disturbance caused by high-density populations of nonnative species can also dilute the control effects of natural enemies, as well as reduce the landscape's ability for buffering due to simultaneous disturbance [72, 73].

Ecological Consequences of High-Impact, Nonnative Insects and Pathogens

There have been two recent reviews that have addressed the ecological consequences of nonnative pathogenic fungi [69••] and nonnative insects [74••] in forest ecosystems. My goal is not to duplicate these efforts but to summarize them along with other recent advances in our knowledge of the ecological consequences of nonnative forest pests. A summary of some nonnative insect and pathogens affecting North American forests is presented in Table 1, and highlights the diversity in origin, presumed invasion pathway, and ecological damage among insect and pathogen invaders. Regardless of the causative species, the most visible consequence of high-impact nonnative forest pests is the direct effects to host trees, such as defoliation, die-back, branch failures potentially resulting in damage to household property, and tree death. There is tremendous variation in the amount of ecological impacts among nonnative forest pests, which can furthermore be expressed differently across forest types and climate zone. Some feeding guilds are generally more destructive given the nature of their attack. For example, wood and subcortical phloem feeders, such as *A. planipennis*, actively disrupt nutrient flow and, when extensive, can cause tree death either directly or indirectly by making the host more susceptible to attack by other organisms, including native species. Similarly, symbiotic interactions between the walnut twig beetle, *Pityophthorus juglandis*, which is native to North America, and the nonnative fungal pathogen *Geosmithia morbida* can also disrupt nutrient flow, leading to the disease known as thousand cankers disease. This disease was first detected in eastern North America in 2010 after being known in the western USA and has the potential to cause significant decline in eastern walnut [*Juglans* spp.] species [75]. In most cases, visual signs of tree decline due to nutrient flow disruption,

whether due to insect or pathogen, are not readily apparent. Rather, only after years of attack are signs of tree decline above human detectable thresholds. Indeed, a recent analysis of forest insect eradication programs highlighted the challenges in successfully eradicating insect pests whose initial signs of feedings are internal and not immediately visible [76].

In contrast, the direct damage to host trees by insect defoliators and leaf or needle pathogens is often more visually apparent; indeed, a denuded tree in summer is a hard sign to miss. However, the build-up to such defoliating populations or the presence of a high abundance of pathogenic activity is not always rapid, even in the absence of natural enemies and in the presence of naïve and suitable host trees. For example, following the introduction of the gypsy moth, *Lymantria dispar*, by E. Leopold Trouvelot at 27 Myrtle Street, Medford, Massachusetts, in 1879, it took over 10 years for larval population densities to be high enough and of sufficient nuisance to be detected by the neighbors residing at 29 Myrtle Street [77].

Regardless of the insect-feeding guild, the symbiotic interaction between an insect and a plant pathogen, or the independent effects of a plant pathogen, the ecological consequences of tree decline and/or death are profound. When such declines are present in the urban forest, the additional economic costs can be staggering. Tree death in the urban forest poses immediate safety and consequent liability concerns [78]. A recent study on the costs of oak wilt, caused by the pathogen *Ceratocystis fagacearum*, in the Minnesota urban forest showed that the bulk of costs due to this nonnative pathogen are associated with hazard tree removal on public and private lands [79]. Similar results were estimated for economic impacts of *A. planipennis* in Ohio [80]. Even in the case of a defoliator such as *L. dispar*, which is not a direct tree killer (as most defoliated trees will recover), hazard tree removal was estimated to represent approximately half of the costs associated with an outbreak in the urban forest [81].

Tree decline and death in the urban forest also can affect a number of other processes, including increased energy consumption in summer due to a lack of shading, decreased pollutant uptake and carbon emission sequestration, decreased property values, and increased consumer costs associated with dead tree removal on private lands [82]. Dead and dying trees, in any landscape, also provide a food source for ambrosia beetles. Although ambrosia beetles in general tend to attack already dead or dying host trees and thus have not historically been a major threat to live trees, some recently introduced species, such as *Xylosandrus germanus*, have shown an ability to attack stressed but otherwise healthy native trees [83]. Also, as with all ambrosia beetles, the nonnative red bay ambrosia beetle, *Xyleborus glabratus*, carries a symbiotic fungus that causes laurel wilt, and has been observed to be a cause of tree decline and death in several host trees species in the southeastern USA [84]. The accumulation of dead wood and down woody material through the action of nonnative forest pests

Table 1 Exemplar nonnative insect and pathogens affecting North American forests

Species	Introduced from	Year introduced	Likely introduction pathway	Susceptible host plants	Damage
Insect—gypsy moth, <i>Lymantria dispar</i>	Europe	1869	Imported life stages	>300 host trees, including oak, willow, and birch	Defoliator, periodically defoliating large forest areas; tree death could occur after repeated years of defoliation or through opportunistic organisms
Insect—emerald ash borer, <i>Agrilus planipennis</i>	Asia	At least by 2002	Solid wood packaging material	All North American ash species	Wood borer causing tree death; possible long-term consequences include the functional extinction of North American ash
Insect—hemlock woolly adelgid, <i>Adelges tsugae</i>	Japan	1950s	Infested nursery stock	Eastern and Carolina hemlock	Feed on ray parenchyma cells; causing extensive hemlock mortality in eastern forests
Pathogen—chestnut blight, <i>Cryphonectria parasitica</i>	Asia	Around 1900	Infested nursery stock	American chestnut	Girdles stem resulting in tree death. American chestnut mostly eliminated by 1940
Pathogen—beech bark disease, <i>Neonectria faginata</i>	Europe	1890	Infested nursery stock	American beech	Girdles stem resulting in tree death. Action involves the interaction between the pathogen and an insect, beech scale (<i>Cryptococcus fagisuga</i>)
Pathogen—Dutch elm disease, <i>Ophiostoma ulmi</i> , <i>O. novo-ulmi</i>	Europe	At least by 1928	Infected elm bark beetles residing in wood imports	Elm species	Vascular wilt disease causing death. Transmitted by nonnative and native elm bark beetles

could synergistically provide an additional food resource for nonnative ambrosia beetles, which are seemingly able to exploit healthier naïve host trees [85, 86]. Thus, this potentially compounds the threat of nonnative ambrosia beetles in novel habitats and especially to naïve host trees that could have less effective plant chemical defense response.

Although the costs associated with dead trees in traditional forested areas and wildlands may not include hazard tree removal, effects to native biodiversity can be considerably more severe. Urban forests certainly harbor a degree of native biodiversity, and recent attention given to the role of urban species in providing ecosystem services is surely warranted [87]. Undoubtedly, there are negative effects of nonnative forest pests to urban ecosystem services, and species that depend on urban trees affected by nonnative forest pests are directly and indirectly affected in similar ways as traditional forested areas. However, traditional forested areas and wildlands tend to represent a greater wealth of native biodiversity, and thus, the negative effects of nonnative forest pests, aside from a loss of host tree resources, can be dire.

One direct negative biological effect of nonnative forest pests is competition with native species for resources [74•, 69••]; these competitive interactions could also favor nonnative species when the defense-free space of naïve host trees is exploited. Furthermore, indirect effects may amplify negative impacts on native species; for example, native species associated with similar host trees of the gypsy moth suffered

increased rates of parasitism by generalist parasitoids in the presence of increased gypsy moth populations [88].

Management responses to nonnative forest pests could also directly and indirectly affect nontarget native species, despite the best intentions [89]. Management options for nonnative forest pests include the removal of host material as a means to provide a barrier zone around an infested area [90], thereby not only limiting population spread but also removing host material for native species. Another option is aerial applications of pesticides, such as formulations of the biopesticide *Bacillus thuringiensis kurstaki* (*Btk*) [71]. Although *Btk* is specific to Lepidoptera, there are reports of short-term effects to nontarget species with cascading effects to higher trophic levels, such as birds, that depend on caterpillars as a food source [74••]. Other pesticide applications, such as the broad spectrum diflubenzuron, can interfere with the synthesis of chitin during the molting process of all arthropods [91] and affect higher trophic levels [92]. However, it is important to consider the potential positive effects of management tactics as well as the potential negative effects to nontarget native species. For example, a recent study demonstrated that the direct effect of *L. dispar* defoliation had a much greater negative impact to nontarget species, and especially to Geometrids, than did applications of *Btk* deployed to mitigate outbreaking *L. dispar* populations [93].

In addition to the direct effects of nonnative forest pests on other organisms, for example through competition, or

indirectly through, for example, alterations in food web dynamics, forested areas disturbed by nonnative insects and pathogens also result in changes to ecosystem processes. Defoliation by nonnative forest pests can affect the biogeochemistry of terrestrial and aquatic communities [72, 94–96]. For example, large-scale defoliation by *L. dispar* significantly altered stream quality by altering water pH and increasing nitrate levels [97], with potential consequences to aquatic organisms. Invasions by nonnative forest pests can also result in considerable amounts of dead and down woody material, and areas of extensive tree mortality provide a fuel source for forest fires [98] that are becoming an increasing concern, especially at forest-urban interface. Forests containing trees killed by nonnative pests are often characterized by near-simultaneous mortality, which opens immediate and large-scale gaps. Such a large-scale disturbance event, especially when compressed over a smaller time scale, provides an opening for pioneer species, which nowadays more than likely includes nonnative plants that can both dominate the landscape as well as completely alter food web relationships that previously existed [99, 100].

Conclusions

Unfortunately, invasions by nonnative insects and pathogens will continue to affect forest ecosystems given our collective demand for worldwide goods that necessitates the current rate of imports and exports. Primary obstacles in stemming the tide of nonnative species introduction undoubtedly include the sheer quantity of trade imports, the lack of sufficient regulatory resources allocated to prevent their introduction at ports-of-entry, and the proverbial “known unknowns” associated with species introductions. In other words, the importance of global trade as a pathway for nonnative species introduction is undeniably understood [9•, 11, 8]; yet, it is nearly impossible to predict exactly what new species will be introduced at a given time and where it will appear. Moreover, a recent study suggested that 72 % of infestations on imported live plants evaded detection efforts by US plant inspectors at ports-of-entry [9•]. Even in New Zealand, a country considered to have one of the more robust biosecurity programs in the world, only approximately 10 % of consignments are examined by quarantine officers given the sheer number of imports [7]. Although regulatory emphasis on pests with a high-likelihood of introduction, given the timing and direction of global trade routes, is useful, it is challenging to envision any feasible mechanism to eliminate nonnative species introductions under current patterns of global trade. The unfortunate reality is the continual introduction of high-impact species, likely similar to the historical rate of 0.4 insects per year reported by Aukema et al. [43]. Efforts to synthesize our knowledge of the life history traits that facilitate a species to be an efficient invader,

and the habitat characteristic that enable species invasions, will continue to be in high demand to mitigate the inevitable ecological consequences of nonnative forest insects and pathogens.

Compliance with Ethics Guidelines

Conflict of Interest Statement Dr. Tobin has no conflicts of interests to declare.

Human and Animal Rights and Informed Consent This article contains no studies with human or animal subjects performed by the author.

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