16

PATHOGENS AND PESTS IN NORTH AMERICAN FOREST ECOSYSTEMS

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Introduction

Trees are usually thought of as the organisms that define forests because of their overriding biomass. Trees, however, account for only a small part of the biodiversity of forests. Microbes and invertebrates are much larger contributors to biodiversity. Collectively, they also perform a variety of functions that are critical to the continuous functioning of forest ecosystems. Bacteria, fungi and invertebrates are key players in the development and fertility of forest soils. Living trees are hosts to and form a range of associations with a wide variety of endophytic microbes. Sexual reproduction of trees is greatly aided by insect pollinators. Once trees die, a succession of wood boring invertebrates, bacteria, and decay fungi allows for the recycling of the lignocellulosic complex, and in so doing, forms the widely recognized complexity of biodiversity associated with the world's forests.

Living trees are also impacted by a variety of disease-causing microbial pathogens and by invertebrates (often referred to as pests) that feed on organs or tissues, either aerial or below ground. Depending on the combination of host, pathogen/pest and environmental conditions, the outcome may vary from no observable effect to decreased growth to tree death. The effect of pathogens and pests may be observable at different scales, from individuals to species, from communities to forest stands. Losses caused by pathogens and pests range from the conspicuous to the spectacular, from short-term catastrophic tree mortality to long-term successional changes in forest ecosystems. Although this may look counterintuitive to forest managers, pathogens and pests are important drivers of forest composition, succession and evolution through disturbance. They contribute to stand structure, availability of deadwood, and creation of suitable habitat for plants and wildlife. Consequently, the older utilitarian concept of healthy forests characterized by low tree mortality and an absence of forest diseases and pests has gradually given way to an ecosystem-based concept, one that recognizes that disease and pests are natural components of healthy forests, and in fact define them (Kolb *et al.*, 1994; Castello *et al*, 1995; Ostry and Laflamme, 2009). Today, the diversity of these biological communities, often formally termed biodiversity, is quantified and converted to indices that measure forest health.

Unfortunately, pathogens and invertebrate pests may also jeopardize the resilience of forest ecosystems. This phenomenon is becoming increasingly apparent with the intensification of

management and anthropogenic activities that disturb natural ecosystems. Forestry practices, such as silviculture, management and harvesting, all have a direct effect on the structure and function of forest ecosystems. Indirect anthropogenic effects are also a cause for concern, particularly in the case of invasive pathogens, pests and weeds. When these diverse communities are disrupted and replaced with simpler, more uniform complexes, the forest ecosystem is destabilized and its resilience compromised. Already, a combination of direct and indirect factors has pushed some forest ecosystems over the tipping point, after keystone tree species were destroyed or cascading effects were set in motion (Kenis *et al.*, 2009).

In this chapter, we discuss how pathogens and pests shape the structure and functions of forest ecosystems. We address this issue both in the 'traditional' context in which natural forests are interacting with native pathogens and insect pests with which they have co-evolved, as well as in the current context of intensive forest management and plantation-based forestry, biological invasions, and climate change.

Biological features of pathogens and pests

Prior to discussing the effect of pathogens and pests, it is important to recall some of the salient features of these organisms. This is also a good opportunity to introduce terminology used in the forest health disciplines to readers who may not be familiar with this field.

Pathogens are biotic agents that cause disease. They include viroids, viruses, bacteria, phytoplasmas, fungi, nematodes and parasitic plants. With the exception of nematodes, invertebrates are not considered pathogens. Disease refers to any malfunctioning of host cells or tissues that result from continuous irritation by a pathogen or environmental factor and lead to the development of symptoms (Agrios, 2005). Fungi figure prominently among the most successful pathogens of plants and are responsible for epidemics that have decimated natural populations of several tree species during the last centuries. Dutch elm disease, chestnut blight, beech bark disease, white pine blister rust, and maple decline are examples of diseases that are well documented.

Deleterious herbivores, often referred to more generically as 'pests', are the other major group of biotic agents that can have negative impacts on forest ecosystems. A pest refers to any animal that interferes with the survival and successful development or reproduction of trees. Invertebrate pests include insects, acari (mites), molluscs (slugs/snails), as well as exotic annelids (earthworms). Well-recognized vertebrate pests, especially in plantations, include rodents (mice, rabbits, squirrels, porcupines), ungulates (deer, moose) and infrequently, depending on the context, birds (sapsuckers, cormorants). Most commonly, pests are restricted to specific stages of tree growth, with some attacking only young seedlings, others only early successional stages or mature closed canopies, while some are found only on older, declining trees (Coulson and Witter, 1984). Invertebrate pests are usually specialized and classified, according to the part of the tree they feed on or the type of localized damage they inflict, as leaf feeders, tip and shoot feeders, xylem and phloem feeders, root feeders or seed and cone feeders.

Pests are typically mobile and locate their hosts primarily through chemotaxis (i.e. smell, taste, etc.), initially orienting to the optimal habitat (habitat location), and then refining their search to susceptible targets within that area (host location). Most invertebrates rely on specific chemical cues (kairomones) emitted from their host plants and can recognize healthy or stressed trees from considerable distances, in some cases kilometers. Some species use other cues such as sound for drought-responsive scolytid beetles (Mattson and Haack, 1987) and recently burned areas for fire-responsive species such as cerambycids (long-horned beetles) (McCullough, 1998).

Unlike invertebrates, pathogens that attack aerial parts of plants are unable to actually 'locate' their host. Instead, they are dispersed passively by wind, rain splash, running water, or by biological vectors. Many pathogenic fungi produce very large quantities of spores (through asexual reproduction, sexual reproduction, or both) that are released in the air when environmental conditions are favorable, e.g. under high moisture conditions. The vast majority of spores land on host plants that are not suitable for infection and colonization. When spores land on a suitable host species, two outcomes are possible: either the pathogen is able to establish itself in the host plant (compatible interaction) or it fails to do so (incompatible interaction). Success or failure is determined by a combination of genetically-controlled internal plant and microbe factors and is mediated by external, environmentally-controlled factors.

Pathogens rely heavily on free water movement and air currents for dispersal, and usually produce sporulating structures directly on the surface of infected plants. Pathogens that are dispersed by biological vectors, however, may produce their sporulating structures inside host tissues. For example, ophiostomatoid fungi produce their sporulating structures in wood galleries made by bark beetles. Masses of fungal spores found in these structures are often coated with mucilage, thus promoting their adherence to insects that exit the galleries on their way to colonizing new host trees. Other fungal species emit volatiles that attract insects, and sometimes vertebrates. Some interactions between fungi and vectors are highly specific. For example, female southern pine beetles (*Dendroctonus frontalis*) carry the mutualistic fungi *Ceratocystiopsis ranaculosus* and *Entomocorticium* sp. in specialized structures known as mycangia. These fungi are inoculated by the insect into the inner bark and phloem of host trees, and their development in galleries has been associated with increased fitness of developing larvae of *D. frontalis*. Mycangial associates of *D. frontalis* also includes actinomycetes that selectively inhibit the sapstaining fungus *Ophiostoma minus*, which is transported phoretically by the insect and has an antagonistic effect on the development of beetle larvae (Scott *et al.* 2008). Another group of wood colonizing insects, ambrosia beetles, also have highly specific interactions with fungi and are, in fact, considered to actively grow and maintain fungus gardens (Biedermann *et al.* 2013).

Pathogens use various means to penetrate and invade host plant tissues. Specialized structures called appressoria enable some fungal pathogens to physically penetrate host tissue. Furthermore, several pathogens secrete lytic enzymes that weaken host tissues or components thereof, and toxins that allow them to kill host tissue ahead of their progression. Additional weapons in the arsenal of pathogens include molecules that may block the production of defense molecules by plants, or detoxify such molecules if they are produced. Some pathogens also secrete homologs of plant growth hormones, which allow them to alter the physiology of their host (Agrios, 2005).

Fungal pathogens are subdivided in three broad classes based on how they interact with their host. Necrotrophs kill tissues as they grow through them and complete their life cycle (including reproduction) on dead tissue. Several species of canker-causing agents fall in this category. Biotrophs need host tissue to remain alive for completion of their life cycle. They are often host-specific and include aggressive pathogens that cause stem rusts and leaf rusts. While the host must remain alive for the pathogen to complete its life cycle, diseases caused by biotrophs are nevertheless highly destructive. The third class of pathogens, termed hemibiotrophs, exhibit an intermediate lifestyle characterized by an initial growth phase in living host tissue, followed by a reproductive phase on dead tissue.

Typically, pests are localized to either the dead or living parts of the tree; the former would include saproxylic species such as most wood boring long-horned or buprestid beetles and carpenter ants, ~~and~~ while the latter would include the majority of invertebrate species that attack the phloem, photosynthetic or meristematic tissues of trees (i.e. leaf-feeding caterpillars,

leafminers, shoot and phloem feeders, gallformers, seed and root feeders) as well as vertebrate animals such as ungulates, rodents and sapsuckers (Coulson and Witter, 1984). Pests can kill trees quickly in a year or less by breaking the vascular transport of the tree (phloem feeders), or more slowly through repeated removal of photosynthetic parts that limit overall tree growth and nutrient storage (e.g. leaf feeders causing defoliation).

Pests play an important role in the death spiral of trees and can act as the primary or secondary agents in this process. Agents that create physical openings for pathogens to invade living trees (e.g. beech bark scale, elm and other scolytid bark beetles) act indirectly while those who play an obligatory role in the pathogen's lifecycle include leaf viruses and phytoplasmas introduced into the tree through the sucking mouthparts of insects such as aphids and scales (Weintraub and Beanland, 2006).

Pests usually display a preference for feeding on a specific part of the tree, with invertebrates often being solely dependent on this localization for their complete life cycle. Defoliators are the most common guild, and include all pests that feed on living leaf or needle tissues. They can be external feeders such as caterpillars (lepidopteran, coleopteran and hymenopteran immatures), adult beetles, vertebrates such as ungulates and rodents, and usually consume the photosynthetic material of the tree. Many invertebrates such as leafminers and gallformers also feed internally on these leaf tissues and are recognized by their characteristic feeding patterns (blotch leafminer, serpentine leafminer, etc.); all have chewing mouthparts and mechanically destroy plant tissue, as do vertebrate pests.

Tip and shoot feeding pests rarely cause whole tree mortality. Their impact changes the form and growth of the tree, and may cause serious timber defects in plantation forests. Under natural growing conditions, species such as balsam fir adelgid and white pine weevil cause weakened trees to be out-competed by their neighbors, thus altering stand succession. Root-feeding pests spend the majority of their time underground and can lead to overall tree decline (in some cases tree mortality). Their impact in natural forest dynamics is unknown but is thought to be similar to that in managed plantations, albeit at a lower frequency (Coulson and Witter, 1984).

Trunk-feeding pests that attack phloem or vascular tissues of the tree are usually considered the most damaging of all feeding guilds, leading quickly to whole tree mortality if the trunk or main branches become completely girdled by feeding. Aggressive *Dendroctonus* bark beetle species such as the mountain pine beetle (*D. ponderosae*) and southern pine beetle (*D. frontalis*) are two well-known pests that have caused major stand and landscape-level mortality. Recent research shows that they, along with widespread defoliators such as the spruce and jack pine budworms, are linked to stand breakup and increased fire probability under natural conditions (McCullough, 1998). In all cases, these pests are considered nature's 'silviculturalists', as they remove slow-growing, declining trees and stands to allow for vigorous understory succession.

Pests that feed on the reproductive parts of trees (flowers, seeds and cones) can almost completely deplete a tree's annual reproductive potential, with often over 90 percent of a crop lost (Coulson and Witter, 1984). In most cases, this is of minor ecological consequence as trees either overproduce reproductive structures or vary their annual output through masting (e.g. family Fagaceae). In so doing, they ensure that pests are unable to track this unpredictable, yet highly valuable food resource every year.

Ecological effect of pathogens and pests on forest ecosystems

Natural pathogen and invertebrate-host interactions that have co-evolved tend to be at equilibrium (Dinoor and Eshed, 1984). However, this does not imply that the equilibrium

persists at all times or over the entire host range. For example, pests that damage or kill individual trees contribute to gap formations in the stand dynamics of temperate forests, while those impacting large forested areas are often precursors of fire and stand replacement. Natural forest stands can be strongly impacted by insect defoliators, such as spruce budworm (*Choristoneura fumiferana*) and jack pine budworm (*C. pinus pinus*) in coniferous forests and forest tent caterpillar (*Malacosoma disstria*) and gypsy moth (*Lymantria dispar*) in hardwood stands. In most cases, trees do not die immediately from defoliation but instead become weakened and susceptible to attack by other agents (Coulson and Witter, 1984). Whole tree or stand mortality occurs if this is repeated over time. Although these epidemics may be spectacular, they do not compromise forest ecosystems as they are often the disturbance factor needed to transition a mature forest canopy into a new cycle of succession. Studies show an increasing number of native pest species that interact with forest systems on such large scales, causing extensive, periodic landscape-level stand mortality and subsequent forest renewal. For example, dendroecological evidence suggests that the larch sawfly (*Pristiphora erichsonii*), an endemic defoliator causing extensive tree mortality, has been a major driver in larch dynamics in eastern North America (Jardon *et al.*, 1994).

Epidemics caused by introduced pathogens and/or invertebrates may alter significantly the composition of forest ecosystems, impact ecosystem services, and eventually lead to ecosystem meltdown. Chestnut blight, caused by the fungus *Cryphonectria parasitica*, almost eradicated American chestnut (*Castanea dentata*) within the few decades after the pathogen was accidentally introduced from Asia to the United States. The impact of the disease has been especially visible in northeastern USA, where chestnuts accounted for more than 20 percent of the canopy in some areas. The widespread death of these trees allowed other deciduous tree species, such as pignut hickory (*Carya glabra*), red maple (*Acer rubrum*), and sugar maple (*A. saccharum*), to colonize those areas (McCormick and Platt, 1980). A similar shift in forest composition has occurred following the past century of invasion (from Europe) by gypsy moth in oak–dominated forests across eastern North America, with a significant loss of the oak complement (Davidson *et al.*, 1999); concomitant with this change has been responses at multiple trophic levels in native faunal communities. Such widespread forest restructuring is also being repeated with the loss of ash following the introduction from Asia of the emerald ash borer (*Agrilus planipennis*) into North America.

Diseases, pests, and fire are often investigated separately by pathologists, entomologists and fire specialists, respectively. Many important forest and tree health issues, however, result from associations between at least two disturbance agents. For example, the pandemics of Dutch elm disease (DED) that have devastated native elm populations in Europe and North America resulted from the acquisition of the exotic fungal pathogens *Ophiostoma ulmi* and *O. novo-ulmi* by elm bark beetles, specifically the native elm bark beetle (*Hylurgopinus rufipes*) and the smaller European elm bark beetle (*Scolytus multistriatus*). In fact, in the absence of the DED fungi, elm bark beetles can hardly be considered as pests, since they cause very little, if any, damage to elm trees. DED illustrates how otherwise benign invertebrates become pests once they serve as vectors for aggressive pathogens.

Diseases of trees may result from successions of attacks by different disturbance agents. This is the case for beech bark disease which occurs when the bark of trees that have been attacked and damaged by the beech scale insect, *Cryptococcus fagisuga*, is colonized by spores of the fungi *N. ditissima* or *N. coccinea*. While beech have developed a degree of tolerance to the fungus, especially while young and actively growing, the disease has intensified with the arrival of beech bark scale, which feeds by puncturing the bark with sucking mouthparts, allowing the pathogen to enter the vascular system of the tree (Houston, 1994). This has led to widespread beech mortality where the two disturbance agents co-occur.

There are also several cases where insect attacks follow initial attack by pathogens. For example, trees that have been weakened by root pathogens, such as *Armillaria mellea* and *Heterobasidion annosum*, are highly attractive to secondary insects. Stress compounds emitted by weakened trees are the main cues used by all saproxylic beetles to locate potential hosts for colonization. The larger pine shoot beetle, *Tomicus piniperda*, is one recent North American example of the impact of sequential stress factors, where the combination of poor site conditions, root pathogens and beetle attack on both the shoots and trunks of trees lead to rapid stand mortality (Paine *et al.*, 1997). Some authors have hypothesized that pathogens that rely on arthropods for dissemination may manipulate their host in order to make it more attractive to vectors. An interesting case was presented by McLeod *et al.* (2005) who suggested the DED pathogens modify the biochemistry of their host in order to make it more attractive to elm bark beetles through the release of volatile terpenes acting as aggregation pheromones.

A final example of complex interaction is provided by forest declines which have been proposed to result from interactions among successive predisposing, inciting and contributing factors (reviewed in Manion, 2003). Predisposing factors are usually abiotic and long-term acting. They alter the ability of trees to withstand or respond to pathogens or pests. Inciting factors can be abiotic or biotic and are characterized by high intensity and short duration. They further weaken the trees and usually result in dieback. These trees may not survive the effect of contributing factors such as canker fungi, decay fungi or wood boring insects. Central to the concepts proposed by Manion (2003) is the notion that some forest declines are part of natural cycling of populations and are not expected to result in the death of ecosystems. Thus, forest declines might, in fact, act as a stabilizing selection agent, whereby competitive dominant trees are selectively killed, whereas stress-tolerant dominant individuals survive and gain the opportunity to contribute to the gene pool.

Effect of changing environments on pathogens and pests

Traditional forest management

So far, we have focused on the impact of pathogens and pests on forest ecosystems. We will now address how shifts in the environment, either natural or anthropogenic in nature, affect biotic disturbance agents.

The indirect role of abiotic factors in predisposing trees to attack by pathogens and invertebrate pests has already been noted. Environmental factors can also directly affect populations of pathogens and pests. For instance, populations of fungal leaf pathogens fluctuate widely according to climatic conditions. Under conditions of higher moisture, large populations may arise swiftly through rapid and repeated cycles of asexual reproduction. In addition, the impact of fires in reducing inoculum of parasitic dwarf mistletoes (*Arceuthobium* spp.) in coniferous forests of interior western North America is well documented (Parker *et al.* 2006). Likewise, high-intensity wildfires may lower populations of pathogens and arthropods that inhabit forest soils, litter and coarse woody debris (Parker *et al.* 2006).

Silvicultural practices may increase tree mortality incited by both pathogens and pests. In many localities in the northern hemisphere, hardwood or mixed stands have been converted into conifer plantations. After a few years of growth, high levels of mortality are sometimes observed in these plantations. Pronos and Patton (1978) reported that mortality caused by the root pathogen *Armillaria mellea* in young red pine plantations in Wisconsin was more noticeable in plantations established on sites that had previously supported oak (*Quercus rubra* and *Q. alba*). *Armillaria mellea* was present on the roots of living oaks, on which it grew as an epiphyte,

without being able to invade the cambial area and cause diseases. However, oaks that were herbicide-killed when the pine plantations were established were heavily colonized by the fungus and became reservoirs for further attacks on red pine saplings. Due to its ability to produce large and long-lived underground rhizomorphs, as well as its capacity to grow saprophytically on dead trees and coarse woody debris, *A. mellea* can persist for decades on suitable sites. In particular, the presence of large stumps provides the fungus with a food base that it may exploit for decades.

Another example of silvicultural prescriptions that may lead to unforeseen changes in tree growth, form and structure has been reported when young conifer stands were thinned very early in stand establishment, thereby promoting the survival of the white pine weevil (*Pissodes strobi*). This major shoot and tip pest kills the tree leader and reduces tree height growth by one to three years. Open, sunny microhabitat conditions favor overwintering survival of adult weevils in the ground and promote larval feeding and development in the leaders. When tree densities are reduced and stands opened up early, weevil populations thrive and attack the remaining tree leaders, and do not decline again until the stand canopy closes (Paine *et al.*, 1997).

Inadequate logging practices may also promote the spread of pathogens within forest stands. Annosus root and butt rot of coniferous species is caused by the basidiomycete fungus *Heterobasidion annosum* which is an efficient colonizer of fresh wounds (Hodges, 1969). Although the disease can be expected in unmanaged forest stands, its occurrence in managed stands can increase dramatically if thinning operations are carried out during periods when high concentrations of *H. annosum* spores are present in the air. Freshly cut stumps will rapidly be colonized by the fungus, which will later move to adjacent, living trees through root contacts. Mycelium of *H. annosum* will then infect and kill the roots of newly infected trees. As a result, several new infection centers around stumps may be created and expand radially over ensuing years. Similarly, high rates of tree damage, or failure to remove infested material during logging, may result in outbreaks of pest species that can build up in high enough populations to kill healthy living trees in adjacent areas.

In many parts of the world, industrial forestry and the need to protect human dwellings have resulted in aggressive suppression of wildfires. This has led to significant alterations of the landscape, including changes in tree species composition, distribution patterns, and increases in stand density. These changes have, in turn, altered the balance between fire, pathogens and invertebrate pests. According to Teale and Castello (2011), the rapid expansion of fusiform rust of pines in the southeastern United States in the twentieth century is, in part, due to fire suppression. The latter favored the expansion of slash pine (*Pinus elliottii*) and loblolly pine (*P. taeda*), both more sensitive to fire and fusiform rust than longleaf pine (*P. palustris*). Fire suppression also stimulated the regeneration of oak, which is the alternate host required by the fusiform rust fungus (*Cronartium quercuum* f. sp. *fusiforme*) to complete its life cycle, thus allowing pathogen populations to expand.

Fire suppression has also been associated with a suite of diseases and pests in forests of western North America (Parker *et al.*, 2006). Root pathogens and bark beetles appear to have been the main beneficiaries from this situation. The massive outbreak of mountain pine beetle (*Dendroctonus ponderosae*) during the past decade is another example of secondary pest outbreaks thought to be due, at least partially, to fire suppression. Although many factors are involved, including warmer winters and drier summers, one of the main drivers is thought to be overmature, declining pine that would have been removed by natural wildfire. Large contiguous stands on the landscape under fire suppression become susceptible to lightning strikes and fuel ignition (Parker *et al.*, 2006). This is also true in eastern North America where mature conifer stands maintained under fire suppression lead to increased susceptibility to spruce budworm (Blais, 1983).

Modern forestry also relies increasingly on plantations. The deployment of monospecific, even-aged plantations poses phytosanitary risks, as it may promote outbreaks that would not otherwise be observed in natural stands characterized by a broader diversity and heterogeneous age structure. For example, the epidemic of *Gremmeniella* canker that started in several US states and Canadian provinces in the 1970s was in good part fueled by the establishment of red pine (*Pinus resinosa*) plantations. The epidemic was worsened by the fact that several tree nurseries that supplied red pine seedlings were unknowingly exporting contaminated, yet asymptomatic material. This led to a rapid expansion of the disease zone, before proper quarantine measures were put in place to restrict movement of red pine seedlings (Warren *et al.*, 2011). Similarly, the recent outbreak of emerald ash borer (*Agrilus planipennis*) has been fueled in part by the over abundance of susceptible ash cultivars in eastern North America (Aukema *et al.*, 2010). All urban areas in this region have been planting their parks, streets and new suburbs with nursery stock of green ash (*Fraxinus pennsylvanica)* grafted from clonal material that is highly susceptible to this recently introduced pest. This has allowed emerald ash borer populations to establish rapidly and expand spectacularly throughout the region.

Monospecific plantations are not necessarily composed of genetically uniform material. In fact, it is a recommended practice to deploy a variety a genotypes, to minimize the risk that an entire plantation is destroyed by a given pathogen or pest. This strategy has been used for decades in Europe for managing poplar leaf rust caused by *Melampsora larici-populina*. Epidemiological studies of European populations of *M. larici-populina* have shown that this pathogen was evolving rapidly in response to the deployment of new varieties of poplars that carried specific resistance genes that had been selected for by breeders (Xhaard *et al.*, 2011). Thus, over the years, increasingly complex races of the pathogen that had acquired the genes necessary to overcome poplar resistance genes were recovered. This observation confirms observations that had been made earlier in agricultural systems, where strong selection pressure for crop resistance is a major driver of pathogen and pest rapid evolution (Stukenbrock and McDonald, 2008).

The introduction of exotic tree species may have unexpected consequences on pathogens and pests, as shown by the rise of *Septoria* canker in North America. Poplar breeding programs initiated in the mid-1900s in the USA and Canada relied extensively on interspecific crosses among native and exotic poplars. Although breeders had selected material with high resistance against the known diseases of aspens and poplars, entire plantations were decimated by a new canker disease. Investigations revealed that it was caused by a native fungus (*Mycosphaerella populorum*) responsible for a relatively benign leaf spot disease on native poplars (Feau *et al.*, 2010). Although resistance to *Septoria* canker has been successfully integrated into poplar breeding programs, this episode is a potent reminder of the genetic and behavioral plasticity of pathogens and pests. In the case of pests, resistance breeding has been pursued for effective management, however, in most cases, this tactic is still in its infancy. Recent research using molecular tools to identify hybridized lodgepole and jack pine under attack by mountain pine beetle suggests that tree resistance may have some promise (Cullingham *et al.*, 2011); however, tree lifespans and the specialized attack patterns of pests are likely to limit the success of this strategy in the long run.

Invasive species

Early cases of introduced pathogens and pests led to legislation and quarantine measures aimed at preventing the intercontinental spread of these agents. Unfortunately, the efficiency of these measures has been in good part diminished by the explosion in international trade and

movements of people during the last decades. As a result, new invasive pathogens and pests are being encountered annually in various countries (Aukema *et al.*, 2010; Boyd *et al.*, 2013). The introduction of novel pathogens and pests into new geographic areas threatens the integrity of global forest ecosystems. In many cases, we have seen epidemic outbreaks of exotic pathogens and pests on native tree species, to the detriment and sometimes extinction of the latter. In others, both deliberate and accidental introductions have led to major concerns over potential invasion meltdown of native ecosystems, those already threatened by shrinkage, intensified management and urbanization.

Some of our most significant introduced pathogens and pests have resulted in large-scale and costly management programs, including chestnut blight, DED, gypsy moth, many species of conifer sawflies, and now hemlock woolly adelgid, emerald ash borer and the Asian long-horned beetle. Hundreds of exotic forest species are currently regulated in Canada and the USA based on their potential to cause economic loss. Pimentel *et al.* (2005) reported about 50,000 foreign species in the USA causing losses of up to $120 billion per year, with 42 percent of endangered or threatened species at risk primarily due to these invaders. Lovett *et al.* (2006) provide an overview assessing the potential ecological impact of both groups in North American forests based on mode of action, host specificity, virulence, importance of host, uniqueness of host and phytosociology of host. Without question, this is the single most important factor affecting the future ecological integrity of North American forests.

Although the impact of exotic invasive pests on the landscape can be dramatic, affected tree species may recover if they exhibit genetic diversity for traits such as tolerance and/or resistance to invaders. Since resistant individuals occur at very low frequency, tree species that include large populations stand a better chance of surviving than those in low numbers. Butternut (*Juglans cinerea*) is one example of tree species put at risk of extinction due to a single pathogen, *Ophiognomonia clavigignenti-juglandacearum*, believed to have been introduced into North America during the twentieth century (Woeste *et al.*, 2009). Although the geographic range of butternut is large, encompassing most of temperate eastern North America, it is not an abundant species. The fate of butternut is further impacted by loss of habitat due to anthropic activities and 'genetic invasion' due to hybridization with exotic congeners (*J. ailantifolia* and *J. regia*). Interestingly, since these interspecific hybrids usually are highly resistant to butternut canker, controlled interspecific crosses followed by introgression of resistance through backcrosses have been proposed as a strategy against the disease. A similar path had been chosen to save American chestnut from possible extinction caused by the fungus *C. parasitica* (Anagnostakis, 2012). In the case of butternut, however, the observation of disease resistance within nature has led researchers to advocate resistant germplasm from single-tree intraspecific selection and breeding, rather than developing interspecific hybrids (Michler *et al.*, 2006).

Dramatic ecosystem changes may occur as a result of pathogen or pest introductions. For example, whitebark pine (*Pinus albicaulis*), considered a keystone species in subalpine ecosystems of western North America, is under threat across its range as a result of white pine blister rust (caused by the introduced pathogen *Cronartium ribicola*), attacks by mountain pine beetle, fire exclusion and climate change. Cascade effects from the potential loss of whitebark pine have been predicted to include provision of high-energy food for wildlife, nurse trees for other species in open terrain, and retention of snowpack (Smith *et al.*, 2013). Broad scale ecosystem concerns have also been expressed with respect to other invasive insect species, such as the hemlock woolly adelgid. Although at different spatial and temporal scales, Kizlinski *et al.* (2002) showed profound changes in stand structure, composition, and ecosystem function in forests dominated by hemlock following invasion by the adelgid.

Similarly, the slow advance of native and introduced earthworm populations has shown significant ecological impacts on forests in northeastern North America. The non-selective feeding, characteristic mucus channels, and soil compaction activities of these newly-arrived annelids have been linked to shifts in soil communities, away from native mycorrhizae in favor of bacterial and microbial communities (Hendrix, 2006). As species co-evolved with native forest flora are disrupted and fungi lost from the forest floor, small mammal communities shift from fungal-based voles to omnivorous deer mice, which have been linked to higher tick populations and the spread of human lyme disease in forest stands of eastern North America. These cascading effects are complex and the true impact of such ecological changes on long-term forest vegetation and succession in native forests remains poorly known.

A single invasive species may alter the landscape over a large area without necessarily inducing ecosystem meltdown, as in the case of chestnut blight. However, some areas have suffered regular invasions by different invasive species, which may eventually negatively affect the resilience of forests. This is clearly the case in many urban forests in North America that were first hit by chestnut blight, and then DED in the twentieth century. In many of these cities and towns, street chestnuts were replaced with elm and then with ash (*Fraxinus* spp.) or Norway maple (*Acer platanoides*). Ash is now being decimated by the emerald ash borer, an invasive beetle in North America, while maple is the prime target of the Asian long-horned beetle (*Anoplophora glabripennis*), a new species that attacks over ten species of trees and may never be eradicated from North America (Dodds and Orwig, 2011).

Climate change

Several decades ago, plant pathologists began to speculate that climate change might influence the fate of tree–pathogen/pest interactions at the landscape level (Coakley *et al.*, 1999). Evidence is now accumulating that this is happening in various regions of the world (Sturrock, 2012). For instance, shifts to warmer and wetter climate have been associated with outbreaks of *Diplodia* shoot blight of pines in France (Fabre *et al.*, 2011) and *Dothistroma* needle blight in western North America (Welsh *et al.*, 2014). This result is not surprising, given that such environmental conditions are known to promote the expansion of plant pathogen populations.

Similar insights have been gleaned by those making predictions about the future impact of climate change on invasive pests in forest systems. Most models point to increasing tree mortality under rising temperatures, however, the complexity of the models and high degree of uncertainty means that no specific predictions can be made (Dukes *et al.*, 2009). General consensus is that the increasing variability and extremes in weather patterns will favor some pest species and not others. The mobility and short generation times of most pests relative to their hosts means that even though they can disperse and adapt quickly in the short term, shifts in temperature and moisture will have significant effects on survival and reproduction in the long run, especially along range edges where intensive selection pressure occurs. Ultimately, the success of highly specific invertebrate pests will be heavily dependent on the ability of their host itself to survive the effects of rapidly changing, extreme weather patterns.

Conclusion

Forest insects and pathogens are the most pervasive and important agents of disturbance in North American forests, affecting an area almost 50 times larger than fire and with an economic impact nearly five times as great (Aukema *et al.*, 2010). Disturbances caused by pathogens and pests are a constant challenge to forest managers but are nevertheless a vital driver of forest

composition, succession and evolution. In light of these complex ecological processes and natural disturbances, our response to pest and pathogen challenges must be cautious. We need to develop a strong understanding of these processes, our human footprint on them, and the large temporal and spatial scales on which they operate, especially in the remaining intact forests. We must avoid focusing on specific isolated pathogen and pest problems, and instead, respond strategically with integrative thinking that supports the development of broad forest resilience.

Many factors are converging that will constrain our ability to retain healthy, resilient forests. Increasing intensification of forest practices for timber production and land use changes that result in deforestation for agricultural and urban development will dramatically restrict most tree species. This, combined with the rapidly expanding introduction of invasive alien species to most of the world's forests, will exacerbate the effect of pathogens and pests. On top of this is the large unknown of climate change, a new factor that will have major implications for pathogen–insect interactions in our forests. We must be cautious in believing we can predict, let alone manage, the outcome of disturbances under these complex scenarios.

If we are to successfully retain ecological balance in our forests, our response must become more considered than simply removing every individual (the naturally resistant along with the susceptible) when faced with a pathogen or pest problem. The concept of a healthy forest requires thinking about gene pools and species interactions at the population level in order to achieve successful adaptation under a changing environment. This means working with forest systems to avoid ecological tipping points and supporting natural biodiversity that enables a return to natural states. Moving forward, we need to aim for ecosystem resilience in our forests, where forest health is defined not by the lack of specific pests or pathogens, but by the complex ecological interactions and functioning of diverse forest organisms and communities.

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