

# Ecological impacts of non-indigenous invasive fungi as forest pathogens

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**Abstract** Non-indigenous pathogenic fungi increasingly threaten North American tree species. Ecosystems may be fundamentally changed when abundant tree species are functionally eliminated, as occurred with American chestnut (*Castanea dentata* (Marsh.) Borkh.). Conversely, changes may be more subtle but still significant and long lasting when populations are lost, or all trees in the larger size classes are killed. Proposed approaches for characterizing the magnitude of ecological impacts use characteristics of both the non-indigenous pathogen and the host species. Impacts are most significant when highly successful invading pathogens attack foundation species, setting in motion a long-lasting cascade of effects on the host and associated species. Such impacts have generally not been well documented at the ecosystem level. Several North American forest tree species have been functionally eliminated or severely reduced by non-indigenous pathogens. Historical invasions, such as that of chestnut blight (*Cryphonectria parasitica* (Murr.) Bar), caused very significant ecological impacts that will never be completely understood because of lack of quantitative data. Beech bark disease, caused by a combination of an introduced scale insect

(*Cryptococcus fagisuga* Lindinger) and a fungus (*Neonectria faginata* (Lohman et al.) Castl. & Rossman), is still advancing and provides opportunities for studying ecosystem-level impacts when a major tree species is removed or markedly reduced in abundance from the overstorey. Butternut canker, caused by the fungus, *Sirococcus clavigignenti-juglandacearum* N.B. Nair, Kostichka & Kuntz, has spread throughout the host range, endangering species' survival. Other non-indigenous invasive fungi such as *Cronartium ribicola* J.C. Fisch and *Phytophthora lateralis* Tucker & Milbrath continue to move into new populations, causing high mortality and associated restructuring of these ecosystems. Global trade and environmental change trends will ensure new challenges by non-indigenous fungal pathogens, presenting an urgent need for improved understanding of long-term impacts across ecological systems.

**Keywords** Beech bark disease · Butternut canker · Chestnut blight · Dutch elm disease · Ecological impacts · Invasive fungi · Non-indigenous species · Pathogen · Port-Orford cedar root rot · White pine blister rust

## Introduction

Non-indigenous invasive species constitute one of the greatest global threats to native biodiversity in North America, second only to habitat loss (McNeely 2005;

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Novacek and Cleland 2001; Enserink 1999; Walker and Steffen 1997; Desprez-Loustau et al. 2007). Pimentel et al. (2000) noted that about 400 of the 958 species listed in the US as threatened or endangered are threatened, at least in part, because of non-indigenous invasive species. Vitousek et al. (1996) suggested that biological invasions constitute a significant component of global environmental change. Among the thousands of non-indigenous species that have invaded North America since European colonization, insect pests and pathogens pose the greatest threat to forest ecosystems (Lovett et al. 2006). Vitousek et al. (1996, 1997) claimed that the greatest perturbations to forest ecosystems in the twentieth century resulted from waves of introduced pests and pathogens, and they suggested that non-native species will continue to be the greatest threat to diversity of eastern North American hardwood forests in the future. These introductions have greatly reduced the frequency and relative dominance of at least seven eastern North American native tree species (Orwig 2002; Liebhold et al. 1995). More than 20 non-indigenous species of pathogens attack forest trees in the US (Pimentel et al. 2000). Many of them also occur in Canada.

Non-indigenous fungal pathogens are often highly destructive to species that are closely related to the pathogens' host species, which are relatively unaffected in the native range of the fungus, presumably due to host-pathogen co-adaptation (Parker and Gilbert 2004). White pine blister rust (*Cronartium ribicola* J.C. Fisch.) is an example of a pathogen that has devastating impacts on five-needle pines (*Pinus* spp.) in North America, but in Asia where the fungus and pine species coevolved, the impact is much less and the native Asian pine species have developed a relatively high level of resistance (Kinloch and Dupper 2002). Similarly, chestnut blight (*Cryphonectria parasitica* (Murr.) Bar) is very destructive to American chestnut (*Castanea dentata* (Marsh.) Borkh.), but Japanese chestnut (*C. crenata* Sieb. et Zucc.) and some Chinese chestnut (*C. mollissima* Blume) trees are relatively resistant to the disease (Anagnostakis 2001). Although it has been proposed that selection should favor less aggressive strains of non-indigenous pathogens over time, there is little or no empirical evidence of this occurring (Jarosz and Davelos 1995; Parker and Gilbert 2004; Brasier and Buck 2001).

Examples of non-indigenous invaders that have changed ecosystem function and the fundamental nature of ecosystems are numerous (Mack et al. 2000). However, the magnitude of impacts of particular historical invasions remains unclear, even when the influence of an invader led to the virtual loss of a native species (Parker et al. 1999). This is in part because the ecological importance of the native species prior to the invasion was generally not quantified. The extent and ecological impacts of introduced fungi are unclear because of the lack of baseline information on fungal communities (Desprez-Loustau et al. 2007). Although introduced pathogenic fungi have received much more attention than non-parasitic fungal species, knowledge of impacts at the community or ecosystem level remains incomplete.

Loss of foundation or keystone species is an extreme example of a change in the fundamental nature of an ecosystem. Ellison et al. (2005) identified several foundation species, including trees, that have been or are currently in the process of being effectively removed from forest ecosystems as a result of non-indigenous fungal invasions. They defined foundation species as those that are locally abundant and regionally common, usually occupying low trophic levels, and stabilizing fundamental ecosystem processes such as productivity and water levels. They noted that, in many ecosystems, a single foundation species controls ecosystem dynamics and modulates processes. In forest ecosystems, trees are usually foundation species because they define the structure and microclimate (Ellison et al. 2005). Loss of such species has serious and long-term impacts on energy and nutrient fluxes, hydrology, food webs, and biodiversity.

A successful non-indigenous invasive species becomes part of a pre-existing complex ecosystem and may influence native species in unpredictable ways, whereas native species have concurrent effects on them, often ultimately stabilizing them. Castello et al. (1995) asserted that pathogens, whether native or not, regulate and are regulated by patterns and processes in forest ecosystems. They noted that the magnitude of pathogenic species' impacts on forest ecosystems is often not recognized. Many non-indigenous pests and pathogens do not become serious problems. For example, a sclerotinia pathogen, *Gremmeniella abietina* (Lagerb.) Morelet, introduced from Europe caused alarm in northeastern

North America, but outside of plantations, it never became a serious pest (Liebhold et al. 1995; Laflamme et al. 1998). Non-indigenous pathogens are affected by other drivers of global change, often in ways that increase their invasive potential, because of the destabilizing effect of changing climate and pollution, and the greater vulnerability of simplified ecosystems in general (Liebhold et al. 1995; Vitousek et al. 1996; Walker and Steffen 1997; Mack et al. 2000; Anderson et al. 2004; Harvell et al. 2002).

In this article, I review approaches for understanding ecological effects of non-indigenous fungal pathogens and the documented impacts of such species on the different levels of ecological organization from genes to ecosystems. Examples are described throughout the article and several case studies are discussed in greater detail to illustrate types of ecological impacts.

### Approaches for characterizing ecological impacts of non-indigenous species

The ecological effects of non-indigenous pathogenic invaders may be limited in time and space, affecting only the host species. Alternatively, there may be additional indirect effects on a large number of non-host species, which may extend over multiple generations. The direct and indirect impacts are greatest when one or more foundation or keystone species are lost from ecosystems, resulting in cascading effects (Ellison et al. 2005). Conversely, the impacts of a non-indigenous pathogen may be small in terms of overall ecosystem integrity, even when host mortality results and when the effect is long term (Parker et al. 1999). Such is the case when an invader influences directly only one species, which is a relatively minor constituent of the ecosystems it inhabits. Short-term impacts include defoliation, seed crop failures, and temporary shifts in energy flows within ecosystems; long-term impacts include widespread host mortality and reduction in frequency, with subsequent replacement by other species (Lovett et al. 2006). Non-indigenous invasive fungi provide examples for each of these types of ecological effects.

Long-term impacts of non-indigenous pathogens involve a change in ecosystem state such as shifting species composition and altering successional pathways with consequent changes in ecosystem processes.

Chestnut blight provides a dramatic example of long-term impacts, including direct and indirect effects on species. The direct effect is the effective removal of the tree species itself and the consequent shift in tree species composition. Smock and MacGregor (1988) provided an example of long-term indirect impacts. They examined the potential for lower leaf shredder activity by aquatic invertebrates in streams, as a result of a compositional shift from chestnut to oak (*Quercus* spp.), and concluded that such long-term indirect effects on non-host species were likely.

Parker et al. (1999) discussed the need for a consistent and quantitative approach to assessing impacts of non-indigenous invasive species. They used three measures to describe the level of impact of such species: the range, abundance, and per capita or per biomass effect of the invader. They suggested a multiplicative relationship between the three to describe the impact severity of an introduced species on the host ecosystem. Range and abundance of both the pathogen and the host influence the degree or gravity of ecological impacts at the ecosystem level. Characteristics of both the invasive species and the host were considered in a more comprehensive approach, proposed by Lovett et al. (2006). They identified sets of characteristics of the invader and the host tree by which to quantify ecological impacts. Characteristics of the pathogen or pest include mode of action, host specificity, and virulence. Those of the host are importance (dominance), uniqueness, and phytosociology (species' associates and successional status).

Three modes of action of pathogens are exemplified by the prevalent symptoms: defoliation, root rot, and stem cankers. Ecological effects of introduced pathogens causing root rot, *Phytophthora lateralis* Tucker & Milbrath, for example, and stem cankers, such as *Sirococcus clavignenti-juglandacearum* N.B. Nair, Kostichka & Kuntz, the causal agent of butternut canker, tend to be more severe than of those causing defoliation. Host specificity is often high for forest tree pathogens. For example, pathogens causing beech bark disease (*Neonectria faginata* (Lohman et al.) Castl. & Rossman [previously *Nectria coccinea* var. *faginata*]), butternut canker (*Sirococcus clavignenti-juglandacearum*), Dutch elm disease (*Ophiostoma ulmi* (Buisman) Nannf. and *O. novo-ulmi* Brasier) and chestnut blight, each have devastating impacts, and are restricted in North America to a single tree species or a low number of native species (Ehrlich 1934; Ostry

1995; Ostry and Kastovich 1997; Schlarbaum et al. 1997; McKeen 1995). In each of these cases, virulence is high with widespread mortality, but the range and abundance of the pathogen is limited by the range and abundance of the host species. American beech (*Fagus grandifolia* Ehrh.) and American chestnut were both very abundant within the species' ranges, but both are limited to temperate hardwood forests of eastern North America. Butternut (*Juglans cinerea* L.) has a similar range but much lower natural abundance within its native range, whereas elm species (*Ulmus* spp.) are more broadly distributed but occurred with relatively lower frequency than the first two, even before the introduction of Dutch elm disease.

In contrast, white pine blister rust results in widespread mortality of all of the Hapoxylon (five-needled) pines (Liebhold et al. 1995), and a relatively new, not yet widespread pathogen, *Phytophthora ramorum* S. Werres, A.W.A.W. de Cock & W.A. Man, is lethal for Fagaceae species (*Quercus* spp. in the red oak group and *Lithocarpus densiflora* (Hook. & Arn.) Rehd.). It also causes damage ranging from shoot dieback to leaf blights on up to 100 other North American species, including Ericaceous shrubs and commercially important conifers (Goheen et al. 2006). Both of these introduced pathogens have had or potentially will have devastating impacts throughout North America.

Ellison et al. (2005) used the concept of foundation species to describe the consequences of non-indigenous invaders. Dominant and co-dominant trees are "foundation species," as their architectural, functional, and physiological characteristics define forest structure and alter microclimates, and their biomass and chemical makeup contribute greatly to ecosystem processes (Jones et al. 1997). High mortality of a widespread, abundant foundation species has a much greater ecological effect than the same mortality rate for a less common species (Lovett et al. 2006). However, if the less common species has a unique role, providing ecosystem services that are not provided by other species in the ecosystem, the impact is disproportionately greater (Parker et al. 1999).

### How do alien invasive pathogens affect forest ecosystems?

Impacts of non-indigenous invaders are expected to be greatest when the invading species performs a new

ecological function in the invaded ecosystem (Parker et al. 1999). A new ecological function, although apparently minor, may result in a cascade effect. For example, the introduced beech scale, *Cryptococcus fagisuga* Lindinger does not apparently cause tree mortality or even significant damage alone, but it predisposes American beech trees for attack by the fungus *Neonectria faginata* (Houston 2005), which in turn kills or seriously debilitates the tree, resulting in a cascade of ecological effects.

Crooks (2002) discussed the concept of invaders as "exotic engineers," and invaders with greatest impact are those that directly modify ecosystems and have cascading effects. These cascading effects may include altering system-level flows and availability or quality of nutrients, food, and physical resources (living space, water, heat, light). "Ecosystem engineers" create, modify, and maintain habitats, changing the availability of resources used by other taxa (Jones et al. 1994). Little attention has been paid to date to the control of physical resources through modification of habitats by non-indigenous invasive species, particularly fungi, but invasive pathogens, such as the causal agent of chestnut blight, are clearly ecosystem engineers by this definition. Non-indigenous species are often considered to reduce biodiversity (Vitousek et al. 1996; Altizer et al. 2003). For example, McNeely (2005) stated that increasing global domination by a relatively few invasive species threatens to create a more homogeneous world rather than one characterized by great biodiversity and local distinctiveness, thus affecting the capacity of ecosystems to adapt to changing conditions. Crooks (2002) pointed out, however, that exotic ecosystem engineers may not always simplify ecosystems. Those that increase habitat complexity increase species richness whereas those that reduce the complexity reduce the species richness. Engineering impacts are often greatest when the modified resource flows are used by many other species or when there is an effect on abiotic factors, such as soil or hydrology (Jones et al. 1994). Pathogen-induced changes in leaf litter composition or rooting depth have such effects.

The impacts on host species of invaders, such as non-indigenous fungi, as ecosystem engineers may be measured at five levels (Parker et al. 1999): (1) individuals, including demographic factors such as growth and survival; (2) genetic effects; (3)

population dynamics effects; (4) community effects including species richness, diversity, and trophic structure; and (5) effects on ecosystem processes, such as nutrient cycling and primary productivity. In examining effects of non-indigenous fungi in forest ecosystems, research has been focused mainly on impacts on host species, and sometimes on the cascading effects on other species that depend on the host, but little attention has been paid to the effects on native fungal species (Desprez-Loustau et al. 2007). Effects of pathogens that cause serious damage have been studied and can be categorized in various ways. However, there are undoubtedly many invasive fungal species that are unknown because their impacts are small, at least with respect to their effects on trees. In some cases, native fungal species are adversely affected as a result of competition by a new aggressive pathogen that may effectively exclude the host species as a resource for more benign co-adapted fungal associates. Alternatively, native pathogens and saprophytes may benefit from mortality (of a tree or tree part) caused by non-indigenous species.

Effects on host species, at the individual level, are obvious for many non-indigenous pathogenic fungi, for example individual tree mortality, or reduced growth or reproduction rates. Genetic effects are less obvious, little studied (Parker et al. 1999), but no less real. The selection pressure imposed by non-indigenous pathogens may result in changed gene frequencies and, in the case of high mortality, loss of genetic diversity in the host species (Altizer et al. 2003). This may have long-term evolutionary effects, reducing the capacity of the host species to respond to other environmental changes over time. When a pathogen eliminates populations of a host species, gene flow is disrupted and genetic diversity of remaining populations is gradually lost over subsequent generations. Genetic effects may be exacerbated by human activities, if healthy trees are selected over diseased ones for harvesting.

The third level named by Parker et al. (1999), changes in population dynamics, is a common outcome of invasion by non-indigenous pathogens. Most commonly, this is observed as changes in local abundance of host species, which in turn affect population sizes. There may be more subtle changes at the population level as well. Population level changes occur, for example, when few trees survive

to reach reproductive maturity and most regenerating individuals are of root sprout origin. Under such conditions, the oldest age classes are lost and population structure may tend toward groups of clones rather than mixtures of less closely related individuals. This is observed in beech stands in northeastern North America where beech bark disease has caused heavy damage (Ostrowsky and McCormack 1986).

Vitousek (1990) described three ways by which an invasive species may alter communities or ecosystems: by differing substantially from native species in their resource use; by changing the trophic structure of the invaded ecosystem; and by changing disturbance frequency and/or intensity. Although his work focused on animal and plant invasions, pathogens may be categorized using the same principles. For example, resource use by a non-indigenous fungal species such as *C. parasitica* differs from that of the native fungi associated with chestnut, in its aggressiveness, effectively eliminating its host in a short period of time. Trophic structure is changed through indirect means, through the cascading effects of the loss of a major food source for other species. When high-quality hard-mast sources are removed from an area, or are substantially diminished, as has occurred in areas where the native ranges of chestnut, beech, and butternut overlap, top trophic level species such as black bear (*Ursus americanus* Pallas) and marten (*Martes americana* Turton) may be affected (Jakubas et al. 2005). Another community-level change, as a result of impacts of invasive pathogens, is associated with the loss of canopy species in forest ecosystems, which may in turn result in greater or lower species diversity. The loss of chestnut from forest canopies in large areas of eastern North America resulted in increased tree species diversity because several species filled the niche abandoned by chestnut (Castello et al. 1995).

Alteration of disturbance frequency and intensity is the most obvious ecosystem-level impact of non-indigenous fungal invaders that cause widespread mortality. Widespread mortality of a dominant or co-dominant species constitutes a severe disturbance to forest ecosystems. Dieback and mortality of conifer species in fire-prone areas contribute to the fuel load, indirectly affecting a second disturbance agent by increasing and intensifying the fire cycle (Castello et al. 1995). Despite the availability of severity



evaluation frameworks such as this one, even when the impacts can be deduced to be extreme, for example when an ecologically important tree species is eliminated from ecosystems over a very broad area, the actual impact to the ecosystem has rarely been quantified and long-term implications are still debated.

Dukes and Mooney (2004) noted that ecological impacts of alien species include large-scale effects, such as altering geomorphology, fire regime, hydrology, microclimate, atmospheric composition, nutrient cycling, and productivity. Plant pathogens that attack dominant forest trees can, at least temporarily, reduce the system's productivity and live biomass. Thus, it is useful to categorize the ecosystem-level effects of non-indigenous pathogens in terms of their impacts on foundation species. Introduction of invasive pathogens is resulting in decline of foundation tree species throughout the world.

### **Case studies: non-indigenous fungi-mediated loss or reduction of foundation tree species and associated effects**

During the past 120 years, at least seven significant new fungal diseases have had serious impacts on native tree species of importance in North America forests. Six of these are summarized in Table 1. Several non-indigenous species attack more than one tree species. In Canada, a country with only about 140 tree species, at least one-tenth of the native tree species are subject to serious damage and mortality caused by non-indigenous pathogens

#### **Chestnut blight**

American chestnut was once a dominant or co-dominant canopy tree over much of eastern North America (Russell 1987). It occurred on a variety of sites, usually on well-drained moist sandy soils (Waldron 2003), often in association with oak species (Ellison et al. 2005). It was a prolific nut producer and provided an important source of wildlife mast (Waldron 2003).

Chestnut blight was introduced from Asia in the late 1800s and was first observed in the US in 1904 (Bramble 1934). The fungus was thought to have arrived on nursery stock (McKeen 1995;

Anagnostakis 2001), and had a rapid and devastating impact on eastern hardwood forests. In 30 years it had killed most of the mature native chestnut in the middle Atlantic and New England States (Bramble 1934). Nelson (1955) found that the basal area of chestnut had declined from 41% to less than 1% in the previous 18 years in western North Carolina. When American chestnut was effectively extirpated by the fungal pathogen within a few decades of the fungus' appearance (Mack et al. 2000), a variety of mostly hardwood species replaced it. McKeen (1995) called the loss of the chestnut "the greatest single catastrophe in the annals of forest history." Two decades after its appearance in New York, the disease had spread into southern Ontario and had caused similar destruction there (McKeen 1995).

Nutrient cycling has been altered by chestnut blight because chestnut wood is slower to decay than any of the other hardwoods, such as oak species, that were associated with it (Ellison et al. 2005). Chestnut leaves decay more rapidly, however, and have higher nutritional value than oak. Woods and Shanks (1959) reported that in the Great Smoky Mountains National Park, 41% of all replacements of chestnut were oak species. They found that pure stands of hemlock (*Tsuga canadensis* (L.) Carr.) replaced chestnut in some areas, thereby changing the ecology of such sites significantly. Nelson (1955) reported that tulip-tree (*Liriodendron tulipifera* L.) was the most frequent replacement species in western North Carolina. A study of the effect of naturalized chestnut at a site 600 km from the species' natural distribution revealed that on sandy loam soils, total soil carbon and nitrogen, and net mineralization and nitrification rates were 10–17% higher under chestnut canopies than under mixed hardwood canopies (Rhoades 2006). These results indicate that nutrient status of soils may have declined as a result of the loss of chestnut from eastern hardwood forests.

Ecological impacts of chestnut blight are numerous, but mostly not quantified. The loss of the high-quality food source associated with effective extirpation of chestnut, undoubtedly influenced wildlife populations. Diamond (2000) estimated a 34% reduction in hard-mast output after chestnut blight killed mature chestnut trees, seriously decreasing the carrying capacity for some wildlife species. Smock and MacGregor (1988) looked at the impact on water courses of the replacement of chestnut by other

**Table 1** Examples of non-indigenous fungal pathogens and their ecological impacts in forest ecosystems

Pathogen name and mode of action	North American host(s)	Impact on host species	Ecological impact: dominance, successional status, uniqueness
Chestnut blight ( <i>Cryphonectria parasitica</i> ) Girdles stem	American chestnut ( <i>Castanea dentata</i> )	Very high mortality Highly virulent and aggressive pathogen effectively eliminates species Stem cankers kill trees of all ages	Very high: devastation and conversion of 25% of eastern hardwood forest Loss of dominant mid-successional tree species with unique ecosystem services Loss of wildlife food source
White pine blister rust ( <i>Cronartium ribicola</i> ) Girdles stem	Five-needle pine species ( <i>Pinus</i> spp.)	High mortality Highly virulent, moderately to highly aggressive pathogen reduces or destroys populations Stem cankers (rust) kill trees of all ages	High: conversion of pine forest; very high in montane regions Reduction or loss of dominant early to late-successional species; very broad geographic area Loss of crucial food source for Clark's nutcracker, grizzly bear
Dutch elm disease ( <i>Ophiostoma ulmi</i> and <i>O. novo-ulmi</i> ) Vascular wilt, kills branches	Elm species ( <i>Ulmus</i> spp.)	High mortality Highly virulent, variably aggressive pathogens eliminates large trees Crown death kills trees after age of reproductive maturity	Medium: loss of large trees, localized ecological importance Reduction of scattered dominant mid-successional species over very large geographic area Loss of food source and habitat for some bird species
Butternut canker ( <i>Sirococcus clavignenti-juglandacearum</i> ) Girdles stem	Butternut ( <i>Juglans cinerea</i> )	Very high mortality Highly virulent and aggressive pathogen effectively eliminates species Stem cankers kill trees of all ages	Medium: effective loss of species; localized ecological importance Loss of early successional sub-dominant species with scattered occurrence in eastern hardwood forests Loss of food source for birds and mammals
Beech bark disease ( <i>Neonectria faginata</i> )* Girdles stem	American beech ( <i>Fagus grandifolia</i> )	High initial mortality; severe damage in aftermath forest Highly virulent, moderately aggressive pathogen kills trees after age of reproductive maturity Stem cankers	Medium: conversion to short-lived, short-stature, defective trees Loss of dominant, late-successional species in eastern hardwood forest Reduction of important food source for birds and mammals
Port-Orford cedar root rot ( <i>Phytophthora lateralis</i> ) Root rot	Port-Orford cedar ( <i>Chamaecyparis lawsoniana</i> )	High mortality Highly virulent and aggressive pathogen Root rot kills trees of all ages	Medium: severe reduction of species with unique ecological role; localized ecological importance Loss of dominant, late-successional tree species in specialized habitat Loss of nutrient source

\*Until recently, known as *Nectria coccinea* var. *faginata*; thought to be introduced. Origin of the pathogen is now in question, but the disease develops only in the presence of an introduced insect

species, in terms of processing rates and nutritional quality of chestnut leaves, and impacts on shredding macro-invertebrates. The forest that replaced chestnut has a greater diversity of tree species, so local biodiversity may have increased as a result of the disease (Castello et al. 1995), but the functional

loss of a species with such ecological dominance undoubtedly influenced species diversity at a variety of trophic levels, including mast-dependent birds and mammals and their associated predators, parasites, and pathogens, as well as soil micro flora and fauna.

A gradual resurgence of chestnut has been observed in Ontario, and is thought to be the result of very low ambient levels of the fungal pathogen (McKeen 1995). The fungal population crashed as the great majority of its host trees died, allowing more trees to escape infection now, but likely *C. parasitica* will experience resurgence as well if chestnut recovers to a significant degree.

### Beech bark disease

American beech was also a dominant or co-dominant canopy tree in temperate hardwood forests of eastern North America, and still maintains dominance beyond the area infected by beech bark disease. Although it can form pure stands, it is usually found in mixtures with species such as sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britt.), and red spruce (*Picea rubens* Sarg.) and attains best growth on well-drained alluvial soils, but occurs over a wide range of site conditions (Tubbs and Houston 1990). In the northern part of its range, beech is the only common nut-producing tree and the species provides an important source of mast for a variety of birds and mammals.

Beech bark disease is caused by the combined effects of a non-indigenous scale insect, *Cryptococcus fagisuga* and one of two bark-killing fungal species. Although the disease is often initiated by the native species, *Neonectria galligena* Bres., *N. faginata* usually becomes more prevalent soon after the disease has established. *N. faginata* may or may not have been introduced (Castlebury et al. 2006; Houston 2005). It behaves as a non-indigenous species, because it becomes a problem only in association with the non-indigenous beech scale. The insect was introduced to Halifax, Nova Scotia, more than 110 years ago, and there have probably been one or more subsequent introductions in north-eastern US (Houston 2005). Three phases of the disease represent different ecosystem states (Shigo 1972). The “advancing front” is the term for the movement and rapid build up of insect populations in newly invaded beech stands. Ecosystem change is minimal in this phase, but the stage is set for a cascade of effects initiated by high-density infestation by the scale insect, predisposing the trees for the fungal infection that follows, often resulting in 50–85% mortality of large trees within 10 years at the

“killing front” (Houston et al. 1979; Houston 1994; Witter et al. 2005). The third phase, called the “aftermath zone,” consists in large part of small trees mainly of root sprout origin, that over time are attacked repeatedly by endemic levels of beech scale and *Neonectria* fungus. Thickets of often distorted and defective beech stems of low vigor may result (Shigo 1972; Houston 1975).

Ecological impacts of beech bark disease are sequential, beginning with the loss of a dominant species from the canopy at the killing front. The disease is most severe in nearly pure stands of mature beech. Immediate ecological impacts are associated with a dramatic shift in forest structure (Storer et al. 2005) resulting from the concurrent loss of canopy trees and a proliferation of root suckers from dead and dying trees (Fahey 1998), an increase in coarse woody debris as dead trees fall (Paipak et al. 2005), and the loss of hard-mast source for wildlife (Storer et al. 2005). Black bear dependence on hard mast and beech nuts, in particular, in areas where beech dominates among nut tree species, has been studied by several researchers (Faison and Houston 2004). Jakubas et al. (2005) reported that 80% of female bears at a study site in Maine reproduced following good nut crops whereas only 20% reproduced following years of poor nut crops.

As the aftermath forest develops from root suckers and seedlings, where causal agents of the beech bark disease are present at endemic levels, a shift in species succession is observed in some cases. For example, DiGregorio et al. (1999) found that sugar maple is stimulated by as much as 30% in the understory due to the thinned canopy. Beech leaves have higher lignin concentration and break down more slowly than sugar maple and yellow birch leaves (Lovett et al. 2006). Replacement of beech by maple results in reduced forest-floor mass, increased nitrification, increased leaching of nitrate into stream water, and decreased retention of atmospherically deposited nitrogen, because soil organic matter formed from maple has a higher propensity for nitrification than that of beech (Lovett and Rueth 1999; Lovett et al. 2006). In other cases, there is a gradual shift to a greater proportion of hemlock and yellow birch in the overstorey (Papaik et al. 2005). A shift to hemlock probably will result in the opposite effect from that of a shift to maple, with increased forest-floor mass, and less nitrogen loss (Lovett et al. 2006).



Beech thickets may persist, however, constituting a high proportion of stand composition with little change in frequency of tree species, and nut production may rebound even to previous levels (McNulty and Masters 2005), but the trees usually do not attain dominance in the crown canopy and are easily broken, rendering the nut crop less available for black bear than in healthy stands. The main ecological effect in such stands is related to a shift in forest structure and age-class distribution.

Papaik et al. (2005) found that in NY, diseased beech was almost twice as likely to experience stem break, than uprooting in severe windstorms. Stem break frequency was a function of disease severity. In the southeastern US, beech in intermediate size classes have high resistance to stem break, until affected by beech bark disease. Overall coarse woody debris increased two- to four-fold in stands affected by the disease. Even without severe windstorms, results reported by Papaik et al. (2005) show that the effect of beech bark disease on beech stands is to make them more disturbance prone, with a higher rate of canopy tree turnover and gap formation. Krasny and Whitmore (1992) examined gap formation in northern hardwood forest and reported that beech had a disproportionate importance in relation to its abundance in affected stands, with almost all gap formation being gradual rather than sudden. They found a two-fold difference between proportion of gap-maker trees that were beech and the frequency of the species in the stands. The implications of gradual gap formation are not well studied, but probably understorey shifts are less dramatic in stands with gradual rather than sudden gap formation.

Long-term effects of beech bark disease on northeastern North American forest ecosystems are likely to be substantial, but the full implications are yet to be understood as the disease is still in progress. For example, it is unknown whether aftermath-zone forests will be stable over time, or if subsequent outbreaks will occur, resulting in periodic elevated mortality. Some of the diseased but relatively vigorous trees in the aftermath-zone may attain large size and canopy dominance, or they may be destroyed in windstorms because of a greater tendency to stem breakage. Continued evaluation of ecosystem change and beech development in aftermath-zone forests is thus important. The

modeling approach proposed by Le Guerrier et al. (2003) may prove useful in identifying and understanding long-term impacts.

Genetic resistance of beech to beech bark disease has been reported, but this resistance is indirect through resistance to the beech scale (Houston 2005; Koch and Carey 2005; Ramirez et al. 2007). Research is underway on a number of fronts to understand the mechanism and mode of inheritance of the resistance, to develop a somatic embryogenesis protocol, and to identify molecular markers.

#### Butternut canker

Butternut is another eastern North American, mast-producing, temperate hardwood species that has been devastated by an invasive pathogen. The species has best growth in riparian areas, and rich upland forests, though it also grows on dry outwash sands and gravels (Farrar 1995; Waldron 2003). The loss of the species is less significant ecologically than the loss of chestnut or beech as it rarely grows as a pure stand or a dominant canopy species, and is usually associated with a variety of other temperate hardwoods including mast-producing species such as oaks (Ostry and Pijut 2000). Butternuts are highly nutritious and are eaten by mice, squirrels, deer, other wildlife species, and humans (Waldron 2003). In areas without other high-quality wildlife mast sources, the species provides an important ecological service (Ostry et al. 1994).

The species has been in decline for most of the past century, and was first reported to be in trouble in the US in 1923 (USDA Forest Service 1979). Widespread mortality in Wisconsin was first attributed to the fungus, *Melanconis juglandis* (Ellis & Everh.) Graves var. *caryae* Wehmeyer. However, in 1967, a previously unknown fungus, *Sirococcus clavigignenti-juglandacearum* was found to be the causal agent for butternut canker (Renlund 1971). The role and taxonomy of *S. clavigignenti-juglandacearum* was not fully understood until after extensive research and determination that the fungus merited description as a new taxon in 1979 (Nair et al. 1979). The origin of the species is not known but it is thought likely to be non-indigenous in North America because of its sudden appearance, its aggressiveness, and the lack of genetic variability (Furnier et al. 1999).

By the early 1990s, infected butternut had been found throughout most of the species range (Ostry 1995). In Canada, the first report of this species was in Quebec in 1990 (Innes and Rainville 1996), then in Ontario in 1991 (Davis et al. 1992), and finally in New Brunswick in 1997 (Harrison et al. 1998). New Brunswick may have the last uninfected populations, but recent work there indicated that the disease is continuing to spread (Hopkins et al. 2001; Harrison et al. 2005). Butternut was listed as endangered on Canada's Schedule 1 (list of wildlife species at risk), in July 2005 under the federal Species at Risk Act. In the US it is listed as a "species of Federal Concern" by the Fish and Wildlife Service (Schlarbaum et al. 1997).

Butternut canker is reminiscent of chestnut blight, in that it occurs on trees of all ages and on all sites. Infection can occur through buds, leaf scars, and wounds (Ostry 1995) and spores may be spread by rain splash, birds, insects, or on seeds (Innes 1998). The fungus usually starts on small branches and twigs in the crown, although it may also be observed on the trunk and near the root collar. The pathogen is very aggressive and has spread rapidly since it was first detected in 1967 (Ostry 1998). Although it has been found on black walnut (*Juglans nigra* L.), infection has been limited (Ostry 1997; Ostry and Kastovich 1997).

Trees are killed when multiple cankers girdle the stem or when much of the crown has been killed by branch-girdling cankers. Sprouts may develop but are also infected and are usually killed within a few years. In Wisconsin, Ostry and Woeste (1994) reported that in a span of 15 years, butternut declined by 58%, and by 84% in Michigan. In the US, the Forest Service estimated that in 1995, 77% of the butternut had been killed in the southeast (Schlarbaum et al. 1997), whereas in Canada mortality has been estimated to be 80% in Ontario (Fleguel 1996). Many of the surviving trees are already infected, so mortality will likely rise with time. There are few sprouts from dying trees and those that occur succumb to the disease. Seed production is reduced by crown dieback after infection, and the seedlings that are produced, are commonly infected as well. Genetic resistance may be present at very low frequency in natural populations (Ostry and Woeste 2004), but populations are being lost rapidly with their repositories of unique genetic variability (Schlarbaum et al. 1997).

## White pine blister rust

Five-needle (Hapoxylon) pines include economically important white pine species in eastern and western North America, as well as several species with smaller ranges and lower economic importance, but having high ecological value. The white pine group extends into Mexico with large populations of economically and ecologically important species such as *Pinus ayacuahuite* Shaw and *P. strobiformis* Engelm. Five-needle pines inhabit a variety of sites, from moist, relatively rich, well-drained soil in eastern and western river valleys, to high-elevation windswept sites with poor shallow soil (Farrar 1995). Their prolific seed crops provide an important source of food for many wildlife species.

All five-needle pines are susceptible to an introduced fungal stem rust, known as white pine blister rust (Kinloch 2003), which is thought to have been first brought to North America from Europe in the 1890s (Spaulding 1922; Liebhold et al. 1995). It arrived in western North America on a shipment of eastern white pine seedlings, grown in France, in 1910 (Allen and Humble 2002). The fungus has a complex life cycle involving five spore stages and an obligate alternate host in the genera *Ribes*, *Pedicularis* and *Castilleja* (Liebhold et al. 1995; McDonald et al. 2006). Blister rust rapidly girdles and kills shoots or stems of young trees. In an infected area, seedlings and saplings are destroyed and many mature trees die. The disease spreads unevenly, becoming established where conditions are appropriate, and eliminating or seriously reducing populations, resulting in the creation of metapopulation patterns (Kinloch 2003). The degree to which the artificial imposition of metapopulation structure affects genetic and other ecological processes has not been evaluated.

Whitebark pine (*Pinus albicaulis* Engelm.), a foundation species, is native to high elevations of the US and southern Canadian Rockies. It has an important role in hydrology and its loss results in increased flashiness of streams and altered dynamics of wildlife populations (Ellison et al. 2005). Whitebark pine populations are being destroyed by a combination of factors, most importantly, white pine blister rust. Less than one tree in 10,000 is rust resistant according to Vitousek et al. (1996) and mortality is occurring throughout the species' range.

The demise of whitebark pine over large areas of its native range is likely to have catastrophic impacts on a number of dependent species. Grizzly bear (*Ursus arctos* L.) depends on the large, highly nutritious seed produced by whitebark pine, and the loss of the tree species hinders bear recovery in the western US (Kendall 1995). The highly coevolved relationship between whitebark pine and Clark's nutcracker (*Nucifraga columbiana* Wilson) (Lanner 1999) has given the species a unique ecological role, and its occurrence as pure stands at or near the tree line ensures high ecological importance. Clark's nutcracker feeds on the seed, tearing apart closed cones to do so. The cones do not open if left alone. Many of the seeds harvested by the bird are cached for winter, just under the surface of the soil and all regeneration of whitebark pine is thought to result from the cached seed (Hutchins and Lanner 1982). Because of the nutcracker's high dependence on whitebark pine seed, as populations of the tree species drop when they succumb to rust infection, bird populations are also expected to decline.

Limber pine (*Pinus flexilis* James) occupies similar but usually not overlapping environments as whitebark pine. It also has a mutual dependency on Clark's nutcracker (Lanner 1999), and is also declining rapidly because of white pine blister rust. Limber pine cones open readily, dropping seed, but the only means of dispersion aside from gravity is by birds or animals. The species has a classic metapopulation distribution with populations periodically eliminated by fire and re-established by Clark's nutcracker planting and forgetting seed caches, up to 22 km from the source tree (Vander Wall and Balda 1977; Tomback and Kramer 1980).

Langor (2007) reported that mortality due to the introduced blister rust increased dramatically between 1996 and 2004 to approximately 50% in two areas of Alberta. He noted that the low regeneration rate in heavily infected stands means that mortality exceeds recruitment, leading to general decline of the species in its Canadian range. Loss of limber pine will have significant effects on their montane habitat as the species is adapted to harsh conditions where it is often the only tree species providing cover and food for wildlife as well as modulating hydrology. The seeds are large and nutritious, and are an important source of food for black and grizzly bears (Langor 2007).

Eastern and western white pine (*Pinus strobus* L. and *P. monticola* Dougl.) are both foundation species in their respective ranges and populations are being lost to the introduced pathogen. According to LaFlamme and Hofacker (2001), white pine populations dropped dramatically in many areas; in Minnesota, old-growth white pine covered 3,500,000 acres in 1837, but dropped to less than 60,000 acres by 1990, in part due to blister rust. From 1917 to 1970, there was a 60% reduction in white pine in Quebec. In western US, up to 95% of original western white pine stands have been killed or damaged (Liebhold et al. 1995). Areas in both eastern and western North America that formerly produced prime white pine timber are no longer managed for white pine because of the pathogen. Genetically based resistance has been found with low frequency in both eastern and western white pine and breeding programs have met with some success (Liebhold et al. 1995; Sniezko 2006).

Sugar pine (*Pinus lambertiana* Dougl.) is also very susceptible to the pathogen. Sugar pine trees attain the largest size among all pine species in the world. In addition to the effects on forest structure and the ongoing mortality of the species, Millar et al. (1996) predicted that the impact on the genetic diversity of sugar pine would be highly significant within the next 50–60 years. According to Liebhold et al. (1995), only approximately 5% of the original stands of sugar pine remain undamaged. Damage often involves top death and loss of branches resulting in a shorter and thinner canopy.

Recently, the first report of a natural blister rust infection on Rocky Mountain bristlecone pine (*Pinus aristata* Engelm.) served as a reminder that the pathogen continues to advance and threaten additional species (Blodgett and Sullivan 2004).

#### Dutch elm disease

Six elm species are native to eastern North America, and are found on a variety of soils from well-drained to periodically inundated, usually mixed with other temperate hardwood species such as maple, basswood (*Tilia americana* L.), and butternut (Farrar 1995). The best known of these species is white or American elm (*Ulmus americana* L.), which has one of the largest natural ranges of any North American tree (Gibbs 1978). Even before the introduction of Dutch

elm disease, it was seldom found in pure stands; common associates are red and silver maple (*Acer rubrum* L., *A. saccharinum* L.), black and green ash (*Fraxinus nigra* Marsh., *F. pennsylvanica* Marsh.), balsam poplar (*Populus balsamifera* L.), various oak species, birch species (*Betula* spp.) and other species of elm (Bey 1990). White elm has been planted extensively in rural as well as urban settings (Hubbes 1999). The prolific seed production by healthy elm trees gives the species an important ecological role because the seed is consumed by many species of birds and small mammals. The branches provide important nesting sites and deer and rabbits browse on twigs and buds (Waldron 2003).

White elm leaf litter decomposes more rapidly than that of maple and oak associates. The leaves have relatively high contents of potassium and calcium. White elm is considered to be a “soil-improving” species because of the combination of rapid leaf decomposition and the release of desirable nutrients during leaf processing (Bey 1990).

Dutch elm disease has eliminated large elm trees throughout much of North America (Farrar 1995). In many populations, the disease has continued at epidemic levels until almost all trees have died (Gibbs 1978). The disease is caused by two fungal strains, a non-aggressive strain, *Ophiostoma ulmi*, and an aggressive strain, *O. novo-ulmi* (Sinclair and Lyon 2005). The non-aggressive strain was first introduced from Europe to the US in the late 1920s. It had made a dramatic appearance in Europe a few years earlier (Gibbs 1978). The aggressive strain appeared in North America in the 1940s and was carried to Great Britain and western Europe in the late 1960s, where it had a devastating impact on mature elm trees (Gibbs 1978). In eastern North America, as in western Europe, the more aggressive species, *O. novo-ulmi* has out-competed *O. ulmi* and now dominates the pathosystem (Houston 1985). *O. ulmi*, no longer is found in Great Britain.

When trees are infected, they may die in a single year or decline for several years before succumbing (Sinclair and Lyon 2005). The overt signs of wilting leaves are an indicator of internal symptoms which shut down the vascular system. The disease depends on one or more species of bark beetles for transmission of fungal spores from dead or diseased trees to healthy host trees (Gibbs and Wainhouse 1986; Gibbs 1978; Sinclair and Lyons 2005). As for beech bark

disease which is caused by the interaction of a native species and one or more non-indigenous ones, Dutch elm disease provides an example of an interaction between native and non-indigenous species (Allen and Humble 2002); in this case, an indigenous insect and non-indigenous fungus. The native elm bark beetle, *Hylurgopinus rufipes* Eichhoff, is the usual vector in Canada and the northern US, and the introduced European elm beetle (*Scolytus multistriatus* Marsh.) is also a common vector. A new potential vector introduced from Asia, *Scolytus schevyrewi* Semenov, has been identified in Colorado, where it behaves very similarly to the European elm beetle. It was recently detected in Canada, in both Alberta and Ontario, but is not yet established (G. Pohl pers. comm.).

Most large elm trees have been eliminated from the North American landscape but not before producing seed. In many areas, young elm trees survive long enough to reproduce before being infected and killed by the pathogen, thus the tree size and age structure in ecosystems where elm was and sometimes continues to be a major component, have been altered significantly (Castello et al. 1995), but the species is not in danger of being extirpated in any part of its range (Bey 1990). In addition to loss of a food source for wildlife as a result of reduced seed production, and increased levels of coarse woody debris in streams, ecological effects of elm mortality include increased shrub density in canopy gaps as well as local shifts in tree species composition (Castello et al. 1995), and decreased availability of nesting sites for birds (Osbourne 1985).

The existence of large, healthy, reproductively mature elm trees in the wild indicates the possibility of genetic resistance (Hubbes 1999; Loo et al. 2007), and four cultivars have been developed that have moderate resistance to the disease (Sinclair and Lyon 2005).

#### Port-Orford cedar root rot

Port-Orford cedar (*Chamaecyparis lawsoniana* (A. Murr.) Parl.) is an example of a less well-known foundation species found in a relatively small area of southwestern Oregon and northwestern California. Its small native range means that, on a North American scale, the species is insignificant, but locally, the species has high ecological importance in ecosystems

where it dominates or co-dominates the forest canopy (Ellison et al. 2005). Litter under this species has higher calcium content than that of associated species, and it is known as a soil improver (Zobel 1990). The species is highly shade tolerant and frequently grows in riparian zones stabilizing soil and stream banks (Hansen et al. 2000).

The species is threatened throughout its range by *Phytophthora lateralis*, a root pathogen, believed to have been introduced at least 80 years ago (Murray and Hansen 1997; Hanson et al. 2000). It spread through infected nursery seedlings and causes high mortality (Hansen et al. 2000). Loss of Port-Orford cedar will have locally serious impacts because it is often the only tree species in riparian zones with ultramafic soils (Hansen et al. 2000, Ellison et al. 2005). It recycles calcium to surface soils, provides shade, stabilizes streamside soil, and its rot-resistant wood provides habitat structure long after trees die.

Hansen et al. (2000) noted that although the tree species is not in danger of extinction, its frequency especially along stream banks and in sensitive habitats has dramatically declined with potentially serious ecological consequences. As well, the size and age structure has changed with large old trees now replaced by smaller, younger ones. Snieszko (2006) offers hope for the species in his description of the feasibility of breeding for resistance. An active breeding program has resulted in substantial improvement in survival level.

## Conclusion

Non-indigenous invasive pathogens have caused large-magnitude changes in forest structure, food webs, nutrient cycling, and tree species composition in many areas of North America. Global trade in combination with climate change is almost certain to present new challenges. Despite many excellent studies on effects of the pathogens on their host species, in most cases little is known about the impacts on associated species. Information required for predicting long-term ecological effects is generally lacking.

Many questions remain to be addressed to gain an understanding of the full ecological impacts of non-indigenous invasive species and of non-indigenous pathogens in particular. Parker et al. (1999) pointed out that in most cases it is not known whether impacts

on native populations are strongly correlated with impacts on ecosystem functions. In order to develop predictive models for long-term impacts, studies are needed that will integrate effects at multiple scales and multiple levels of organization.

Among the research themes identified by Mack et al. (2000) two are crucial to generate a better understanding of ecosystem-level impacts: the effects on food webs and associated cascading impacts, and effects of sequential losses of tree species on nutrient-cycling dynamics. The current difficulty in defining impacts of past invasions points to the importance of collecting and maintaining broadly based ecosystem baseline information before invasions occur.

As Ellison et al. (2005) and Novacek and Cleland (2001) advised, the best insurance to counter the loss of foundation species is to maintain very large natural reserves of intact forests and adopt practices that preserve ecosystem integrity in managed forests. Genetic resistance to invasive pathogens occurs at low frequencies in natural populations of several of the host species. Maintaining large, relatively natural populations of all native tree species will allow natural selection to operate with sufficient intensity to ensure different mechanisms and levels of resistance and tolerance can develop over time, without catastrophic losses of genetic diversity.

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