

Forest Ecosystem Responses to Exotic Pests and Pathogens in Eastern North America

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The forests of eastern North America have been subjected to repeated introductions of exotic insect pests and pathogens over the last century, and several new pests are currently invading, or threatening to invade, the region. These pests and pathogens can have major short- and long-term impacts on forest ecosystem processes such as productivity, nutrient cycling, and support of consumer food webs. We identify six key features of the biology of exotic animal pests and the ecology of their hosts that are critical to predicting the general nature and severity of those impacts. Using three examples of introduced pests and pathogens in eastern forest ecosystems, we provide a conceptual framework for assessing potential ecosystem-scale effects.

Keywords: forest, pests, pathogens, nutrient cycling, invasive species

Exotic insect pests and pathogens pose the most serious current threat to the forests of eastern North America. The litany of pest and pathogen introductions is long; it includes well-known examples such as the chestnut blight (*Endothia parasitica*), which effectively eliminated adult American chestnut (*Castanea dentata*) trees from forests in which it had been a dominant species; Dutch elm disease (*Ophiostoma ulmi*), which has nearly eliminated a major riparian and shade tree species (*Ulmus americana*); gypsy moth (*Lymantria dispar*), which feeds preferentially on oaks (*Quercus* spp.) and is a major defoliator of eastern forests; and beech bark disease, which is causing a serious decline in American beech, one of the dominant species of northern hardwood forests (USDA Forest Service 1994). The list also includes some pests that are problematic but less well known, such as the balsam woolly adelgid (*Adelges piceae*), the hemlock woolly adelgid (*Adelges tsugae* Annand), and the dogwood anthracnose (*Discula destructiva*), and several that are threatening but not yet widespread, such as the emerald ash borer (*Agrilus planipennis* Fairmaire), *Phytophthora ramorum* (which causes the disease known as “sudden oak death”), and the Asian longhorned beetle (*Anoplophora glabripennis*; Campbell and Schlarbaum 2002). Although the biology of many of these pests and pathogens has been studied to the extent that researchers know (or are learning) their host preferences and life cycles (Doane and McManus 1981, Brasier 1991, MacDonald and Fulbright 1991, Houston 1994), the consequences of these introductions for forest community dynamics have received less attention, and their effects on forest ecosystem processes are just beginning to be understood. The purpose

of this paper is to provide a framework for understanding the ecosystem-level consequences of exotic pests and pathogens in eastern forests. We do this by identifying key features of the pest/pathogen–host system that permit general predictions about the impacts of new introductions. We illustrate this approach using three examples and discuss the potential impacts of emerging pests in the context of this framework. Our use of the term “exotic pests” refers to nonnative animals that damage trees. In the eastern United States, the primary animal pests are insects, but this analysis could also apply to other types of animal pests found elsewhere. We define an exotic pathogen as any nonnative organism that causes disease in trees.

Short- and long-term effects of exotic pests and pathogens

Exotic pests can produce both short- and long-term effects on forest ecosystems. The distinction between short-term and long-term effects is arbitrary, but for this paper we define short-term effects as those that occur on timescales of weeks to years after the attack of the pest or pathogen, and long-term effects as those that play out over decades or

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centuries. Short-term effects include the disturbances directly associated with the action of the pest or pathogen, which may cause tree defoliation, loss of vigor, or death. The ecosystem-level consequences may include temporary reduction in photosynthesis and productivity, increased circulation or leaching of nutrients, stimulation of decomposition, and change in microclimatic and light conditions in the forest (Webb et al. 1995, Jenkins et al. 1999, Lovett et al. 2002a).

Long-term effects are primarily mediated by changes in tree species composition and the consequent alterations of forest structure, productivity, nutrient uptake, and soil organic matter production and turnover (figure 1). Exotic pests and pathogens are more efficient than most abiotic disturbances (e.g., wind or fire) at producing long-term changes in species composition, because the pests and pathogens often target specific tree species and because, if they become established, they usually remain as permanent components of the ecosystem, continuously affecting the target species. Shifts in forest species composition ramify through the ecosystem in many ways because tree species have different, often unique, properties of nutrient and water uptake, growth rate, litter quality, soil organic matter production, and habitat and food quality for animals.

Features of the pest or pathogen. The occurrence and magnitude of these short- and long-term effects on forest ecosystem function depend in part on three key features of the pest or pathogen (table 1).

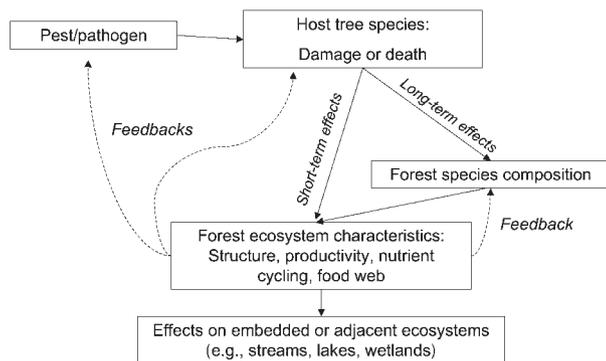


Figure 1. Pathways of impact of pests and pathogens on forest ecosystem processes. Ecosystem characteristics can be affected by the direct, short-term action of the pest or pathogen on the tree—for instance, defoliation or mortality. Longer-term effects are caused by pest-induced changes in forest species composition, which then produce changes in ecosystem processes. These ecosystem characteristics can feed back to affect the pests (e.g., increased nitrogen availability can increase the survival of phytophagous insects), the trees (e.g., increased light availability from tree death may improve the condition of the survivors), or the forest composition (e.g., increased light, water, and nutrients may change the relative competitiveness of different tree species).

Mode of action. How does the pest or pathogen attack the tree? For instance, the effects of a defoliating insect are substantially different from those of a pathogenic stem fungus.

Host specificity. Is the pest or pathogen specific to one tree species, or does it attack many different species in the forest? Does it affect particular size or age classes of the tree population?

Virulence. Does the pest or pathogen lead to widespread host mortality? Is the mortality rapid, or does the tree decline slowly over many years?

Features of the host tree. In addition to the features of the pest or pathogen, the short- and long-term effects on forest ecosystem function depend on three key features of its host.

Importance. Is the host tree a dominant in the forest, for example, in terms of basal area, litter production, or leaf area?

Uniqueness. Does the host have unique properties in the ecosystem, such as nitrogen fixation, production of large seed crops, quick regeneration after disturbance, or tolerance of unusual soil conditions?

Phytosociology. Does the host tend to grow in pure stands, or grow mixed with other trees that may not suffer from the attack? Where does the host appear in the successional dynamics of the forest? How effectively does the host regenerate after the adults are damaged or dead?

Given adequate knowledge of these six factors, ecologists can at least make rough predictions of the type and magnitude of the ecosystem-scale impacts of an exotic pest or pathogen. Specific predictions such as the magnitude of productivity loss or nitrogen leaching are highly site specific and require detailed understanding of particular ecosystems; however, knowledge is often unavailable. Some sites may even escape damage altogether, especially if the sites are isolated and the pest or pathogen has limited mobility. Nonetheless, pests and pathogens that become established usually spread throughout the range of susceptible hosts, and general predictions of the impacts are of value to forest scientists, managers, and policymakers to evaluate the seriousness of the threat and to plan management responses.

To illustrate the types of impacts caused by exotic pests and pathogens, we describe below three examples of introduced pests or pathogens that differ substantially in the six factors listed above (table 1).

Gypsy moth

The gypsy moth was introduced into North America at Medford, Massachusetts, around 1869 by Leopold Trouvelot, an amateur entomologist and entrepreneur who evaluated insects for their suitability as the basis of a silk-spinning industry in the United States (Liebhold et al. 1995). (Trouvelot went on to become a well-known astronomer of the time and eventually joined the staff of the Harvard Observatory; Liebhold et al. 1989.) Within a few years of its introduction, the gypsy moth became a serious problem in eastern Massachusetts, and in the last century it has spread west and south through the

Table 1. Key features regulating effects of exotic pests and pathogens on forest ecosystem processes, with examples from gypsy moth, hemlock woolly adelgid, and beech bark disease.

Key feature	Pest or pathogen		
	Gypsy moth	Hemlock woolly adelgid	Beech bark disease
Mode of action	Defoliator	Phloem feeder on twigs	Bark scale insect followed by bark-cankering fungus
Host specificity	Somewhat general, but prefers oak and aspen species	Very specific	Very specific
Virulence	Causes defoliation over many years; high mortality only in previously stressed trees and evergreens	Usually causes tree mortality within 4–5 years of establishment on a tree; little resistance	Causes tree mortality, usually slowly over 10 years or more; apparently some resistance in beech population
Importance of host	Oaks are a very important component of many eastern deciduous forests; aspens are an important successional species in the northern Midwest and West	Hemlock is often the most important conifer in northern hardwood forests and often dominant in specific landscape positions; its location proximal to streams may confer additional importance to downstream ecosystem effects	Beech has a broad range throughout eastern America and is a codominant in the northern hardwood forest
Uniqueness of host	Oaks are unique in their litter quality, nutrient cycling, and seed production; aspen have a unique seral role after fire and logging	Hemlock often creates coniferous “islands” in deciduous forests; casts deep shade; creates moist, organic-rich, acidic soil	Beech has unique litter quality and seed production among northern hardwoods
Phytosociology of host	Oaks as a genus often dominate in mixed forest stands in the eastern United States	Hemlock often grows in pure stands	Beech usually grows in and sometimes dominates mixed stands

Northeast, Mid-Atlantic, and North Central states (figure 2). Gypsy moth populations have been cyclical in the past, with severe and relatively synchronous outbreaks at roughly 10-year intervals. In the last decade, however, gypsy moth populations in many areas have been kept in check by pathogens (particularly the fungus *Entomophaga maimaiga*), and although the insect is continuing to spread (Tobin and Whitmire 2005), outbreaks may become less intense and less synchronous. Discerning such changes will require many years of data, because typically a decade elapses between peaks of the outbreak cycle.

The larvae of the gypsy moth (figure 2) are voracious folivores that show a preference for oak and aspen but, during outbreak phases, will consume almost anything green. Because this pest has presented a large problem for so long, it has been studied extensively and the knowledge has been quite well summarized (Doane and McManus 1981, Lovett et al. 2002a). Severe outbreaks of gypsy moth caterpillars can completely defoliate forest canopies. This defoliation has many short-term effects, including reduction of productivity, reduction of seed crops, increased light to the forest floor, reduced transpiration and consequently increased water drainage from the forest, and a pulse of nitrogen and labile carbon to the forest floor (Doane and McManus 1981, Lovett et al. 2002a, Kosola et al. 2004). The nitrogen pulse results from insect feces, dead caterpillars, unconsumed green foliage, and increased leaching of nitrogen from damaged foliage. Most of this nitrogen is subsequently immobilized by soil microorganisms (Lovett and Ruesink 1995) or incorporated into soil organic matter (Christenson et al. 2002), although some may be leached from the ecosystem in drainage water (Eshleman et al. 1998, Lovett et al. 2002a) or taken up by regrowing plants (Christenson et al. 2002, Frost and Hunter 2004, Russell et al. 2004). In forested watersheds of the Mid-Atlantic states that had

little nitrogen leaching beforehand, repeated gypsy moth defoliations in the early 1990s produced a dramatic rise in streamwater nitrate concentrations (Webb et al. 1995, Eshleman et al. 1998). Hardwood trees that are initially in good condition produce new leaves after a gypsy moth attack (which generally occurs in June and early July), and these trees can often withstand several years of defoliation without dying. However, stressed trees may die after a single defoliation event, and the initial wave of defoliation in an area may produce widespread mortality. In outbreak mode, gypsy moths also consume coniferous foliage, and these trees tend to be much less tolerant of defoliation and may die after a single attack.

When they are in high density, gypsy moths can be an important food for some birds and small mammals, and are involved in a complex web of interactions in oak forests that ramify up through the food chain (Ostfeld et al. 1996, Jones et al. 1998). The white-footed mouse (*Peromyscus leucopus*) feeds on the larvae and pupae of the gypsy moth and may regulate the insect's populations at low densities (Jones et al. 1998). Although some birds (such as cuckoos) follow gypsy moth outbreaks to feed on the caterpillars, defoliation can also result in an increase in nest predation (Thurber et al. 1994). One study in West Virginia indicated that several years of defoliation had little impact on most native bird species (Bell and Whitmore 1997a). In fact, this study indicated that pesticides applied to prevent gypsy moth attack had a greater effect on the bird populations than did the gypsy moths themselves (Bell and Whitmore 1997a). Further study indicated that eastern towhees (*Pipilo erythrophthalmus*) actually benefited from the opening of the canopy and the consequent increase in the understory and shrub vegetation (Bell and Whitmore 1997b). Acorn crops may be reduced for many years following gypsy moth outbreaks (McConnell 1988, Gottschalk

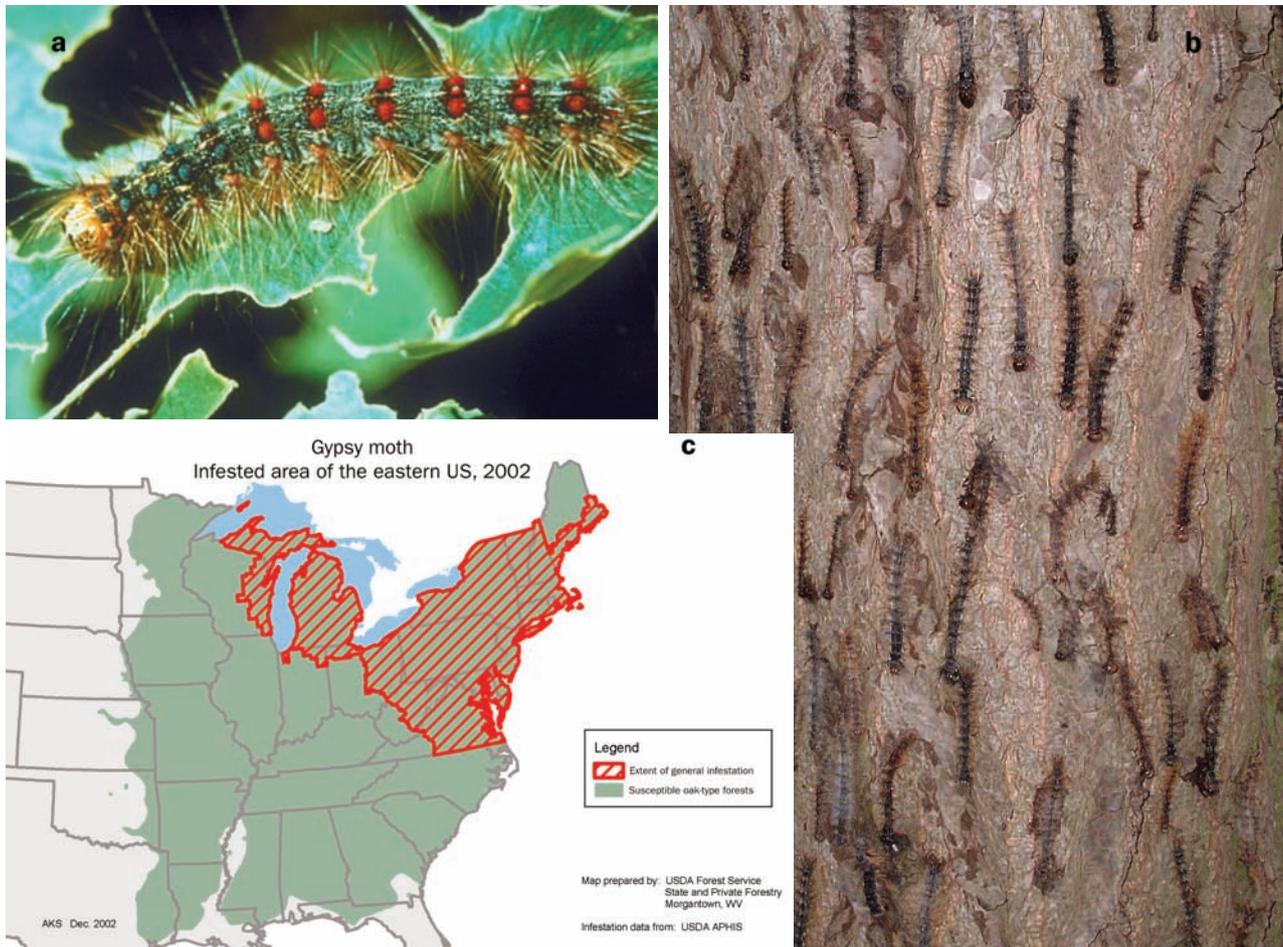


Figure 2. (a) Late-instar gypsy moth larva. Photograph: Minnesota Department of Natural Resources Archives, www.forestryimages.org. (b) Gypsy moth larvae on a tree trunk during an outbreak in the Catskill Mountains, New York, July 2005. Most of these larvae have died from fungal or viral diseases. Photograph: Lewis De Jaeger. (c) Range of general infestation of gypsy moth in the eastern United States as of 2002 (striped area) and approximate range of susceptible forests (green shaded area). The map is from the USDA Forest Service.

1990, Auchmoody et al. 1993). Because acorns are an important food source for small mammals, deer, bear, turkeys, and many other animals, gypsy moths are likely to have relatively long-lasting, indirect effects on many forest consumers.

Thus, the gypsy moth is a defoliator that, because it pulses to such high densities, can produce substantial short-term effects on forest production, hydrology, and nutrient (e.g., carbon and nitrogen) dynamics. However, because many trees survive the defoliations, and because in outbreak phase the gypsy moth is relatively nonspecific in its choice of hosts, we might expect its long-term consequences on forest species composition to be more subtle than those of a more specific and virulent pest (table 1). In fact, most studies of gypsy moth-induced compositional changes in forests report moderate declines in oak species abundance and variable effects on forest structure. In New England, Campbell and Sloan (1977) found that repeated gypsy moth defoliations in the early 20th century tended to reduce the forest understory (because the understory trees were more likely to die following

defoliation) and to decrease somewhat the proportion of oaks, a preferred food of the gypsy moth. In Pennsylvania, gypsy moth defoliation reduced oak abundance by killing many canopy oak trees and releasing subdominant red maples and sugar maples (Fajvan and Wood 1996). Similar releases of understory trees and shrubs occurred after gypsy moth-induced oak mortality in West Virginia and Michigan (Bell and Whitmore 1997b, Jedlicka et al. 2004). In mixed oak–conifer stands, gypsy moth attacks may actually favor the long-term dominance of the site by oaks because the conifers are much more likely to die from the defoliation than are the hardwood trees. For example, at the Institute of Ecosystem Studies in southeastern New York State, mixed oak forests in some areas had an understory dominated by eastern hemlock (*Tsuga canadensis*), a very shade-tolerant conifer that probably would have replaced the oaks in the canopy, given enough time. However, a severe gypsy moth defoliation in 1981 killed the understory hemlocks but left most of the oak overstory still alive, thus setting back succession in this forest.

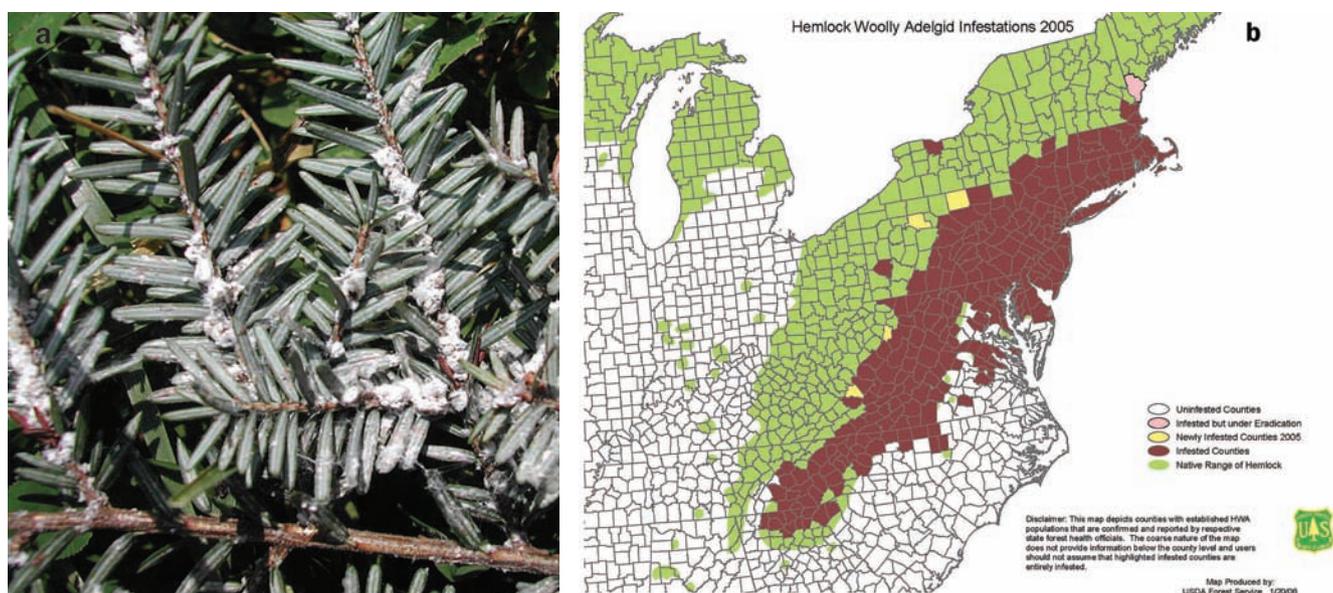


Figure 3. (a) White waxy covering of hemlock woolly adelgid on underside of hemlock twig. Photograph: Gary Lovett. (b) Map showing infestation of hemlock woolly adelgid in the eastern United States in 2004. Green area is native range of eastern hemlock. The map is from the USDA Forest Service.

Hemlock woolly adelgid

The hemlock woolly adelgid, an aphid-like pest of eastern hemlock and Carolina hemlock (*Tsuga caroliniana*), was probably introduced into Virginia in the 1950s on nursery stock (Cheah et al. 2004). It began to cause severe mortality of hemlocks in the Mid-Atlantic states and southern New England in the 1980s, and today it is continuing to spread throughout the range of eastern hemlock (figure 3). It feeds in the phloem of small hemlock twigs, and once the insect is established on a tree, populations can grow rapidly and usually result in tree death within 4–5 years (Young et al. 1995). It seems to be quite host specific, as it does not appear to attack other trees in the eastern forest, nor is it a major problem on western hemlock (*Tsuga heterophylla*) in the western United States. There appears to be little resistance in the eastern hemlock population, and it has been predicted that the pest will spread throughout the entire range of the tree (Cheah et al. 2004), causing a marked reduction in hemlock populations. In an ironic twist, one study documented an increase in hemlock abundance (before the arrival of the woolly adelgid) in some forests of the southern Appalachians where understory flowering dogwood (*Cornus florida*) populations had been devastated by a new fungal disease (the anthracnose fungus *D. destructiva*; Jenkins and White 2002). There have been attempts at biocontrol through introduction of several predators, most commonly an introduced beetle, *Sasajiscymnus tsugae* (previously *Pseudoscymnus tsugae*; Sasaji and McClure 1997). The effectiveness of all the putative biological control agents is still uncertain (Cheah et al. 2004).

Hemlock is a unique tree in the eastern hardwood forest. Slow growing, shade tolerant, and with dense canopies that cast deep shade, hemlock is a late successional species that will eventually dominate forests in which temperature and mois-

ture conditions are suitable (Canham et al. 1994). Hemlock litter is slow to decompose, and the soil under hemlocks tends to have low rates of nitrogen mineralization and nitrification (Finzi et al. 1998a, Lovett et al. 2004). In many areas hemlocks grow in nearly pure stands, and where hemlock dominates, the forest floor tends to be deep and acidic, and to receive very little light, minimizing the presence of understory plants and saplings (Rankin and Tramer 2002). Death of the trees opens up the canopy; increases light, moisture, and temperature at the forest floor; increases nitrogen mineralization and nitrification; and may increase nitrate leaching to groundwater or surface waters (Jenkins et al. 1999, Yorks et al. 2003). Jenkins and colleagues (1999) describe a cascade of potential ecosystem effects of this disturbance.

Because hemlock is one of the most common conifers in the northern hardwood forest, it has many features that may influence animal species. For instance, hemlocks often grow in moist stream banks where they shade the stream, and loss of the hemlock canopy is likely to increase stream temperature and algal growth and may increase bank erosion, all of which can affect fish, salamanders, and other animals in streams and riparian zones (Brooks 2001, Ellison et al. 2005). Hemlock stands are favored yarding areas for deer in winter, and hemlocks are the preferred habitat for many bird species in the hemlock–hardwood forest. For example, black-throated green warbler (*Dendroica virens*) populations declined precipitously in areas where hemlocks died from adelgid attack in Connecticut (Tingley et al. 2002).

There has been too little time since the introduction of the woolly adelgid to directly observe successional dynamics following hemlock mortality. In many areas of New England, black birch (*Betula lenta*) is the most common tree species regenerating in adelgid-killed hemlock stands (Jenkins et al.

1999), but this species is not shade tolerant and is likely to have only a relatively short tenure on those sites. A simulation study of a forest in Connecticut suggests that successional dynamics following hemlock mortality depend on the initial density of hemlock in a stand (Jenkins et al. 2000). In stands where hemlock is a dominant, its loss triggers secondary succession with an initial pulse of shade-intolerant species. In late successional stands where hemlock was a subordinate species co-occurring with other shade-tolerant species (primarily beech, *Fagus grandifolia*), the model predicted that loss of hemlock would trigger an increase in the abundance of the shade-tolerant competitors. In any case, whatever species replaces hemlock will probably not have its unique combination of evergreen foliage, long life, shade tolerance, and difficult-to-decompose litter, so the turnover in tree species will probably have a major long-term impact on the structure and functioning of the ecosystem.

In summary, the hemlock woolly adelgid is a virulent, host-specific pest attacking a unique species in the northern hardwood forest (table 1). As a result, it is likely to have large short-term and long-term impacts on areas where eastern hemlock is a significant part of the forest. This impact is mitigated somewhat on the regional scale because the areas where hemlock is dominant are restricted, both by the site requirements of the tree and in some areas by the history of intense harvesting of hemlock for tanbark in the 19th century (McIntosh 1962).

Beech bark disease

Beech bark disease, which is caused by the combination of the scale insect *Cryptococcus fagisuga* and pathogenic fungi of the genus *Neonectria*, has severely affected northern hardwood forests throughout the northeastern United States (Houston et al. 1979) and is currently spreading south and west. The disease was introduced into Nova Scotia around 1890 on nursery stock imported from Europe. Its current range extends as far south as North Carolina and as far west as Michigan (figure 4; Houston et al. 1979, Wainhouse and Gate 1988, Runkle 1990, Houston 1994). Attack by the scale insect permits infection by one of two fungal pathogens of the genus *Neonectria*: *N. galligena*, which is native, and *N. coccinea* var. *faginata*, which is probably introduced (Houston 1994). The fungal infection produces extensive cankering of the bark, which slows growth and usually kills the tree (Gavin and Peart 1993, Houston 1994). The disease causes the death of older beech trees slowly over 10 years or more, leading to “gradual gaps” in which the trees usually die standing (Krasny and Whitmore 1992, Gavin and Peart 1993).

The impact of the disease is not uniform across a landscape, even among stands of the same forest type, because of the variation in susceptibility of host trees and the poor dispersal of the scale insect (Houston et al. 1979, Twery and Patterson 1984). The severity of the disease is greatest in stands where beech is most dominant and where beech trees are larger in diameter (Griffin et al. 2003). In addition, the disease has been found to be more severe in trees with higher levels of bark ni-

trogen (Wargo 1988, Latty et al. 2003). In a recent vegetation survey in the Catskill Mountains of southeastern New York State, 19% of mature beech (> 30 centimeters in diameter at breast height) were classified as not substantially affected by the disease, even though signs of the disease were present on nearly all of the trees (Griffin et al. 2003). This figure probably includes some trees that are truly resistant to or tolerant of the disease, as well as some trees that will eventually succumb to it.

After the initial entry of the disease into a stand, mortality can reach 80%–90% of the mature beech stems (Wainhouse and Gate 1988), although this period of mortality may be protracted because of the slow progression of the disease. After this initial “killing phase,” forests enter an “aftermath phase” in which the stand dynamics reflect the reduced vigor and premature mortality of beech trees chronically infected with the disease (Houston 1994). The decline of trees affected by the disease is usually gradual, and filling of the vacated canopy space can proceed apace, either by lateral expansion of neighboring trees or by growth of saplings in the understory. The death of mature beeches is often followed by sprouting of multiple young stems from the roots, but the disease also infects these stems as they mature (Houston et al. 1979, Houston and Valentine 1988).

The course of vegetation change after the death of overstory beech trees appears to vary considerably from place to place. In the heart of its range in northeastern North America, beech usually grows in mixed stands along with codominants sugar maple, yellow birch, and eastern hemlock. In some areas where the disease is now endemic, beech has persisted as a smaller and deformed tree, and has even retained canopy dominance in some areas where it was previously dominant (Houston and Valentine 1988, Forrester et al. 2003). In these areas, the main effect of the beech bark disease is a shift in the size and age structure of the beech population, rather than a shift in the tree species composition. In other areas, the beech decline promotes the growth of competing species, such as hemlock (Twery and Patterson 1984, Runkle 1990) or sugar maple (DiGregorio et al. 1999, Griffin 2005). The stem defects produced by the disease may significantly increase the risk of windthrow of large beech stems (Papaik et al. 2005). An analysis using a simulation model suggests that this increase in susceptibility to disturbance would reduce the abundance of beech over the long term (i.e., several centuries), and that the resulting increase in coarse woody debris would favor the regeneration of two competing species—hemlock and yellow birch—with small seeds that take advantage of the favorable seedbed substrate formed by rotting logs (Papaik et al. 2005).

Beech is an important species in the northern hardwood forest for several reasons. First, it is very shade tolerant and long-lived, and dominates many stands in terms of basal area, density, and litter production. Second, the foliar litter produced by beech is high in lignin and slower to decompose than that of its principal hardwood codominants, yellow birch and sugar maple (Melillo et al. 1982). Litter quality influences



Figure 4. (a) Beech stem showing waxy covering of beech scale insect (white spots), fruiting bodies of *Neonectria* fungus (red spots), and bark cankers caused by the fungus. Photograph: Amanda Reddy. (b) Range of beech bark disease in eastern North America as of 2005. Pink areas are counties that have reported both the scale insect and the *Neonectria* fungus; dark blue areas have reported the scale insect but not yet the fungus; green area is the native range of American beech in this region. The map is from the USDA Forest Service.

the development of the forest floor and affects nutrient retention and cycling in the stands (Finzi et al. 1998a, 1998b, Lovett et al. 2004). Third, beech produces a large nut that is an important food source for many types of wildlife, including rodents, certain passerine birds, turkey, and bear (Faison and Houston 2004). In the central range of the northern hardwood forest, oaks are rare, and thus beech is the only species producing hard mast.

Despite the importance of beech, there has been relatively little study of the effects of beech bark disease on forest ecosystem processes. The slow deterioration of beech trees allows continuous reoccupation of their canopy and root space through growth of saplings and lateral encroachment by neighboring trees (Krasny and Whitmore 1992), which will tend to mitigate the short-term effects on forest productivity and nutrient cycling. However, longer-term changes in the forest ecosystem are likely to result from the changes in size structure and species composition produced by the disease (Griffin et al. 2003, Papaik et al. 2005). Shifts to either lower dominance or smaller size structure of beech will result in less beech nut production, and the consequences of this shift are likely to ramify through direct and indirect linkages throughout the food web. One potential direct effect is on bear populations, because bear are known to use beech nuts as an important food source before hibernation (Faison and Houston 2004). Indirect effects mediated through the food web have not been well studied in beech, but variation in acorn production in oak forests may provide a useful analogy. In many eastern oak forests, changes in acorn production control the populations of small mammals such as mice and chipmunks, and the variation in the abundance of these rodents affects not

only their predators (e.g., hawks, owls, foxes) but their alternate prey sources, such as insect larvae (including the gypsy moth) and the eggs of ground-nesting birds (Ostfeld et al. 1996, Jones et al. 1998, Schmidt 2003). Beech nuts may have a similar role in northern hardwood forests, and the reduction of beech nut production would be expected to substantially influence food web dynamics.

Shifts in species composition are also likely to affect forest nutrient cycling in this system. Replacement of beech by sugar maple would result in lower forest floor mass (Finzi et al. 1998a) and increased nitrification, increased leaching of nitrate into streamwater, and decreased retention of atmospherically deposited nitrogen because soil organic matter formed by sugar maple has a higher propensity for nitrification than that formed by beech (Lovett and Mitchell 2004). Replacement of beech by hemlock would most likely produce the opposite effects, with increased forest floor mass and decreased rates of nitrogen cycling and nitrogen loss (Finzi et al. 1998a, Lovett et al. 2004).

In summary, beech bark disease is a very host-specific, moderately lethal, and relatively slow-acting disease (table 1). The slow decline of the trees and the fact that beech usually grows in mixed stands may reduce the short-term effects of the disease on productivity and nutrient cycling, because competitive neighbors and saplings underneath beech canopies may have time to compensate for the reduced light and nutrient capture of the dying beech trees. Over the long term, however, the decline of beech is likely to have important consequences for carbon and nitrogen cycling and food web dynamics in northern hardwood forests because of the importance and uniqueness of beech in this ecosystem.

A look to the future

The three pests and pathogens described above will each have important short- or long-term effects, or both, on forest ecosystems in the eastern United States. The effects are specific to the pest/pathogen–host system, but with knowledge of six key features of the pest or pathogen and its host, we believe we can anticipate, in general terms, the nature and magnitude of the effects an introduced pest or pathogen will have on the forest ecosystem. These key attributes involve detailed knowledge of the biology of both the pest or pathogen and its host; we cannot overemphasize the importance of basic research in insect biology, phytopathology, and plant ecology for prediction of ecosystem-scale effects.

The six features vary continuously and independently, and we cannot detail all possible combinations. Suffice it to say that the most severe long-term impacts would be expected for a virulent, host-specific pest attacking a dominant and unique tree species that grows in nearly pure stands. This is a close approximation of the current situation with hemlock woolly adelgid (table 1), ameliorated somewhat by the fact, noted above, that in many areas hemlock is dominant only in a limited portion of the landscape. Each new pest or pathogen presents a unique situation, and the potential for ecosystem effects must be evaluated on the basis of knowledge of the pest or pathogen and its host, much as a doctor with a sick patient would offer a prognosis based on knowledge of the disease and the patient.

We believe that pests and diseases are likely to be the primary cause of species change in eastern forests in the next few decades. Forecasting the trajectory of those changes is nearly impossible, however, because we cannot predict with any certainty what new pests or pathogens will be established. We can at best hazard some informed guesses about pests and pathogens that are currently threatening eastern forests but are not yet widely established. These speculations are based on our knowledge, albeit still incomplete, of the six key features discussed above.

The emerald ash borer, a wood-boring beetle introduced from Asia, is currently affecting ash trees (*Fraxinus* spp.) in Michigan and Ontario. The range of the pest is apparently spreading despite quarantine and eradication efforts in both the United States and Canada. This insect appears to be a lethal, fast-acting pest specific to ash trees, and therefore could have serious short- and long-term effects in areas where ash is a dominant tree. This includes some areas of the northern hardwood forest type, some wetlands, and cities where ash has been widely planted as a street tree. Like sugar maple, white ash (*Fraxinus americana*) produces soil organic matter with a low carbon-to-nitrogen ratio and high nitrification rates (Finzi et al. 1998a, Venterea et al. 2003), so the loss of this species may have large effects on the carbon and nitrogen cycles of the affected areas. Over much of the northern hardwood forest, however, ash is a minor, though still important, component of the forest community, and its lower dominance (relative to beech, sugar maple, and birch) may mitigate the impacts of this pest on a regional scale.

The Asian longhorned beetle is another wood-boring beetle introduced from Asia, probably on wood packing material (Bartell and Nair 2004). North American populations of this insect have been discovered in New Jersey and near the cities of New York, Chicago, and Toronto; attempts at eradication are under way in all these areas. It has the capability of infesting a number of hardwood species, but seems to prefer maples (*Acer* spp.; USDA 2002). The lethality of this pest on North American host species is not yet clear. Because it may affect red maple and sugar maple, two of the most common tree species in northeastern North America, it has the potential to cause a major impact on forest community dynamics and ecosystem processes in that region.

Phytophthora ramorum, the pathogenic organism responsible for sudden oak death, has caused severe decline in some oak and tanoak species in the western United States, and has recently spread to the eastern United States through widespread shipments of contaminated nursery stock (Rizzo and Garbelotto 2003). In the western United States, it infects many different plant genera and causes a rapid decline and death in some oaks and tanoaks (Hansen et al. 2005). Though *P. ramorum* is not yet widespread in native forests of eastern North America, some important eastern oaks (such as northern red oak, *Quercus rubra*) are known to be susceptible (Brasier et al. 2002). This disease has the potential to cause major impacts to eastern forest ecosystems, because oak species are dominant in much of the eastern forest from southern New England southward, and they are a crucial source of mast for wildlife and thus have an important influence on the consumer food web in the forest (Ostfeld et al. 1996). In addition, some oaks have unique foliar and litter properties that affect carbon and nitrogen cycling, producing litter with low decomposition rates, and soils with low nitrification (Finzi et al. 1998a, Lovett et al. 2004), low nitrate leaching to surface waters (Lewis and Likens 2000, Lovett et al. 2002b), and high retention of atmospherically deposited nitrogen (Templer et al. 2005). A widespread outbreak of *P. ramorum* on one or more of the important eastern oak species (e.g., northern red oak) would be nearly a worst-case scenario: a virulent, host-specific pathogen acting on a dominant and unique host species.

In the eastern United States, species shifts due to exotic pests and pathogens may be the dominant force driving changes in ecosystem processes over the next few decades, perhaps even overwhelming other environmental changes occurring simultaneously. The unpredictability of new introductions and lack of knowledge about threatening, recently introduced pests and pathogens limits our ability to forecast the nature and scope of the change that is likely to come. Predictions of the impacts of other environmental changes, such as climate change and air pollution, must be considered against this rapidly changing and highly uncertain backdrop. Forecasting is made even more complex by the fact that many of the current environmental changes, including changes in climate and pollution by carbon dioxide, nitrogen, and ozone, alter the susceptibility of trees to pests and pathogens (Cole-

man and Jones 1988, Lindroth and Kinney 1998, Latty et al. 2003, Jones et al. 2004). Climate change can alter ranges of both pests and hosts (Simberloff 2000), and may change the timing of development of pests and the phenology of their hosts, possibly causing surprises such as the increased virulence of native pests (Woods et al. 2005).

Dealing with this challenge will require research progress on several fronts. First, basic biological knowledge of the insects, pathogens, and trees, sufficient to understand the six key features of the system as discussed above, is crucial to forecasting the effects of an introduction. Gathering this knowledge on newly introduced pests—for example, the ecology and life history of the pest in its home range, its virulence on its new hosts, its ability to spread, and its sensitivity to pesticides and predators—usually requires rapid initiation of a research program focused on the new threat. To predict the ecological impacts of the introduction, this knowledge of the pest must be coupled with basic ecological understanding of the host tree species and the ecosystem of which it is a part. Maintenance of the funding base that supports this research capacity in federal and state agencies, academia, and the private sector is a crucial challenge. Funds are often shifted to other priorities, and researchers are reassigned to other problems as soon as the “pest of the month” is no longer perceived to be a crisis.

In addition, better communication among the practitioners in the various disciplines involved—entomologists, pathologists, foresters, ecologists, and economists—would facilitate integrated research on the responses of forest ecosystems to these pests and pathogens. More advanced ecosystem models that incorporate the capacity to simulate forest compositional changes would allow better forecasting of the impacts of pests and pathogens and evaluation of their interaction with other environmental changes, such as air pollution and climate change.

Another clear research priority is integrated pest management, particularly with regard to biological control. Even with the best prevention and eradication efforts, some new pests and pathogens will become established, so the best hope for minimizing their impact will come from biological control. The record of success of biological control has been spotty at best, and it can pose grave risks if done poorly. Because the problems and failures stem from lack of knowledge, they are amenable to improvement by research. Providing the funding and building the capacity for that research in government agencies, academia, and the private sector is a clear national priority.

Ultimately, reducing the impacts of exotic pests and pathogens on eastern forests requires that we minimize new introductions through concerted national and international policy efforts aimed at eliminating the transfer of pests and diseases between countries (Campbell and Schlarbaum 2002, Chornesky et al. 2005). Agencies charged with inspecting imports and detecting new introductions must be cognizant of the importance of the task and have the resources necessary to accomplish it. Reducing the importation of pests and

pathogens will require improved standards for the trade of live plant material, wood products, and wood packing material, and some will undoubtedly view more stringent standards as running counter to the interests of free trade (Campbell 2001). In weighing these competing interests, policymakers should have a clear view of the economic, aesthetic, and ecological consequences of new introductions of pests and pathogens. Providing the necessary knowledge will require expanded and integrated research and improved communication between scientists and policymakers.

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