REVIEW / SYNTHÈSE

Responses of insect pests, pathogens, and invasive plant species to climate change in the forests of northeastern North America: What can we predict?[1]

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Abstract: Climate models project that by 2100, the northeastern US and eastern Canada will warm by approximately 3–5 °C, with increased winter precipitation. These changes will affect trees directly and also indirectly through effects on "nuisance" species, such as insect pests, pathogens, and invasive plants. We review how basic ecological principles can be used to predict nuisance species' responses to climate change and how this is likely to impact northeastern forests. We then examine in detail the potential responses of two pest species (hemlock woolly adelgid (*Adelges tsugae* Annand) and forest tent caterpillar (*Malacosoma disstria* Hubner)), two pathogens (armillaria root rot (*Armillaria* spp.) and beech bark disease (*Cryptococcus fagisuga* Lind. + *Neonectria* spp.)), and two invasive plant species (glossy buckthorn (*Frangula alnus* Mill.) and oriental bittersweet (*Celastrus orbiculatus* Thunb.)). Several of these species are likely to have stronger or more widespread effects on forest composition and structure under the projected climate. However, uncertainty pervades our predictions because we lack adequate data on the species and because some species depend on complex, incompletely understood, unstable relationships. While targeted research will increase our confidence in making predictions, some un-

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certainty will always persist. Therefore, we encourage policies that allow for this uncertainty by considering a wide range of possible scenarios.

Résumé : Les modèles climatiques prévoient des températures 3–5 °C plus élevées et des précipitations hivernales plus abondantes vers 2100 dans le nord-est des États-Unis et l'est du Canada. Ces changements affecteront les arbres directement et indirectement via leurs effets sur des espèces nuisibles telles que les insectes ravageurs, les agents pathogènes et les plantes invasives. Nous passons en revue la façon dont les principes écologiques peuvent être utilisés pour prédire la réaction des espèces nuisibles aux changements climatiques et la façon dont cela pourrait affecter les forêts du nord-est. Nous étudions ensuite en détail les réactions potentielles de deux insectes ravageurs : le puceron lanigère de la pruche (*Adelges tsugae* Annand) et la livrée des forêts (*Malacosoma disstria* Hubner), deux agents pathogènes : le pourridié agaric (*Armillaria* spp.) et la maladie corticale du hêtre (*Cryptococcus fagisuga* Lind. + *Neonectria* spp.) et deux espèces de plantes invasives : le nerprun bourdaine (*Frangula alnus* Mill.) et la célastre asiatique (*Celastrus orbiculatus* Thunb.). Plusieurs de ces espèces auront probablement des effets plus prononcés ou plus étendus sur la composition et la structure de la forêt dans les conditions climatiques anticipées. Cependant, nos prédictions demeurent incertaines à cause du manque de données adéquates sur ces espèces et parce que certaines espèces dépendent de relations complexes, peu connues et instables. La recherche orientée nous permettra de faire des prédictions avec une plus grande confiance, mais il restera toujours une certaine incertitude. Par conséquent, nous encourageons les politiques qui tiennent compte de cette incertitude en considérant une vaste gamme de scénarios potentiels.

[Traduit par la Rédaction]

Introduction

In northeastern North America, forests host a variety of native and introduced insect pests, invasive plant species, and pathogens (which we collectively term "nuisance species") that currently affect forest structure and function. While these species differ widely in their natural history and ecological relationships, they share an ability to thrive in the current climate and context of these forests. This paper explores how the ranges and impacts of these nuisance species may respond to the ongoing changes in the region's climate.

Native and nonnative insect pest species (e.g., Table 1) possess a great capacity to alter habitat and modify ecological processes in northeastern forests, often leading to extensive ecological and economic damage (Liebhold et al. 1995; Fleming and Candau 1998). Pest outbreaks damage foliage and reduce tree vitality and can result in widespread tree mortality (Volney and Fleming 2000; Stadler et al. 2005).

Native and nonnative forest pathogens (e.g., Table 2) also have strong influences on forest structure, species composition, and ecosystem function (Fig. 1). The widespread and transformative effects of nonnative pathogens are well documented (e.g., Castello et al. 1995; Liebhold et al. 1995). Working in conjunction with other disturbance agents (i.e., wind and defoliating insects), native pathogens can also produce widespread forest decline and mortality that facilitates the recycling of stored nutrients and provide habitat for wildlife and microorganisms (Hansen 1999).

Northeastern forests also are increasingly affected by invasive plant species (e.g., Table 3). A suite of fruit-bearing shrubs and vines has extensively modified forest understories, particularly in young, overbrowsed, or physically disturbed forests. These species form dense thickets, effectively eliminating tree regeneration (Brudvig and Evans 2006) and reducing native understory shrub and herb diversity (e.g., Hunter and Mattice 2002; Miller and Gorchov 2004).

Climate affects the distributions and ecological dynamics of nuisance species and, therefore, influences their economic, aesthetic, and ecological impacts on northeastern for-

ests. Climate also affects pathogens and insect pests through its influence on their host species (i.e., through changes in a host's distribution, population dynamics, nutrition, and defense compounds) and through effects on other predators, pathogens, and mutualists. Further, all types of nuisance species respond to continually evolving patterns of land use, the changing spatial mosaic of forest versus nonforest, local management practices, and anthropogenic movements of species (e.g., Parker and Gilbert 2004). These factors complicate attempts to predict future impacts.

Since 1970, temperatures across the northeastern US have warmed 0.25 °C per decade. This warming has been accompanied by a wide range of biological changes, suggesting that the region's biota are already responding to climate change (Hayhoe et al. 2006). Simulations using global-scale climate models have generally underestimated the magnitude of observed trends in the Northeast, implying that regional processes may have enhanced warming trends and that global-scale models do not capture these processes (Hayhoe et al. 2006). Using observed regional climate relationships to adjust the output of nine global-scale climate models, Hayhoe et al. (2006) developed projections for the future climate of northeastern North America. Results suggest that by 2070–2099, the Northeast will see increases in average annual surface temperature of 2.9–5.3 °C relative to 1961–1990. This warming would lengthen the growing season by 4–6 weeks. As the mean temperature increases, the distribution of daily temperatures is also projected to shift toward the warmer end of the spectrum, increasing the frequency of days that fall above high-temperature thresholds and decreasing the frequency of days that fall below cold-temperature thresholds (DeGaetano and Allen 2002). Winter precipitation is projected to increase by 10%–15%, consistent with recent observed trends. Overall summer precipitation is projected to change little or decrease; however, it is likely that variability in the timing of rain events will lead to an increased frequency of midterm and severe drought.

In general, it is thought that "warmer is better" for nuisance species. In the absence of water stress, warmer tem-

Table 1. Forest insect pests that have caused or threaten to cause significant tree decline in northeastern North America.

Pest*	Principal hosts	Date introduced
Asian longhorn beetle[H] (*Anoplophora glabripennnis*)	*Acer*, *Betula*, *Populus*, *Ulmus* spp.	1996
Balsam woolly adelgid[C] (*Adelgis piceae*)	*Abies balsamea*, *Abies fraseri*	1900
Bark beetles[C] (*Ips* spp.)	Conifer species	Native
Basswood thrips[C] (*Thrips calcaratus*)	*Tilia americana*	1925
Bronze birch borer[C] (*Agrilus anxius*)	*Betula papyrifera*	Native
Elm spanworm[N] (*Ennomos subsignaria*)	*Ulmus*, *Quercus*, *Acer*, *Fagus*, *Fraxinus*, and other hardwoods	Native
Elongate hemlock scale[C] (*Fiorinia externa*)	*Tsuga* spp.	1908
Emerald ash borer[N] (*Agrilus planipennis*)	*Fraxinus* spp.	2002
Fall cankerworm[C] (*Alsophila pometaria*)	*Fraxinus*, *Tilia*, *Fagus*, and other hardwoods	Native
Forest tent caterpillar[C] (*Malacosoma disstria*)	*Acer*, *Populus*, *Quercus*, and other hardwoods	Native
Gypsy moth[C] (*Lymantria dispar*)	*Quercus* and other hardwoods	1869
Hemlock looper[C] (*Lambdina fiscellaria*)	*Tsuga*, *Abies*	Native
Hemlock woolly adelgid[C] (*Adelgis tsugae*)	*Tsuga canadensis*, *Tsuga caroliniana*	1950s
Introduced pine sawfly[C] (*Diprion similes*)	*Pinus* spp.	1914
Jack pine budworm[C] (*Choristoneura pinus*)	*Pinus* spp., especially *Pinus banksiana*	Native
Maple borer[C] (*Glycobius speciosus*)	*Acer* spp.	Native
Maple leafcutter[C] (*Paraclemensia acerifoliella*)	*Acer saccharum*, *Acer rubrum*, *Betula* spp.	Native
Red oak borer[N] (*Enaphalodes rufulus*)	*Quercus rubra*	Native
Saddled prominent[C] (*Heterocampa guttivitta*)	*Acer* spp. and other hardwoods	Native
Sirex woodwasp[N] (*Sirex noctilio*)	*Pinus* spp., *Abies*, *Larix*, *Picea*, *Pseudotsuga*	2004
Spruce budworm[C] (*Choristoneura fumiferana*)	*Picea*, *Abies*	Native
Two lined chestnut borer[C] (*Agrilus bilineatus*)	*Quercus* spp.	Native
Winter moth[C] (*Opherophtera brumata*)	*Quercus*, *Acer*, *Tilia*, *Ulmus*, and other hardwoods	1940s

*Superscripts indicate whether pests pose current (C), nascent (N), or hypothetical (H) risks based on current distribution and (or) potential responses to climate change. List is ordered alphabetically and is nonexhaustive.

Table 2. Forest pathogens that have caused or threaten to cause significant tree decline in northeastern North America.

Pathogen*	Principal hosts	Date introduced
Armillaria root rot[C] (*Armillaria* spp.)	Hardwoods/conifers	Native
Ash yellows[H] (*Candidatus* Phytoplasma)	*Fraxinus* spp.	Native
Bacterial leaf scorch[N] (*Xylella fastidiosa*)	Many hardwoods (maple, elm, oak, and sycamore; mulberry)	1986
Beech bark disease[C] (*Neonectria* spp.)	*Fagus grandifolia*	1890s
Black knot disease[C] (*Apiosporina morbosa*)	*Prunus* spp.	Native
Butternut canker[C] (*Sirococcus clavigignenti-juglanda-cearum*)	*Juglans cinerea*	1967
Chestnut blight[C] (*Cryphonectria parasitica*)	*Castanea dentata*	1904
Coral spot canker[H] (*Nectria cinnabarina*)	Hardwoods	Native
Dogwood anthracnose[C] (*Discula destructiva*)	*Cornus florida*	1978
Dutch elm disease[C] (*Ophiostoma ulmi/nova-ulmi*)	*Ulmus* spp.	1933
Hypoxylon canker[C] (*Hypoxylon* spp.)	Hardwoods (esp. aspen and other *Populus*)	Native
Nectria canker (*Neonectria galligena*)	Hardwoods (esp. *Betula* spp. and *Juglans nigra*)	Native
Oak wilt[H] (*Ceratocystis fagacearum*)	*Quercus* spp.	Native
Red trunk rot[H] (*Phellinus pini*)	Conifers	Native
Sclerroderis canker[H] (*Scleroderris lagerbergii*)	Conifers	Early 1960s (if nonnative)
Sudden oak death[H] (*Phytophthora ramorum*)	*Quercus* spp.	1990s
White pine blister rust[C] (*Cronartium ribicola*)	*Pinus strobus*	Early 1900s
White trunk rot[H] (*Phellinus igniarius*, *Phellinus laevigatus*, and *Phellinus tremulae*)	Hardwoods (esp. aspen, beech, birch, and maple)	Native

*Superscripts indicate whether pathogens pose current (C), nascent (N), or hypothetical (H) risks based on current distribution and (or) potential responses to climate change. List is ordered alphabetically and is nonexhaustive.

Fig. 1. Conceptual diagram showing how climate can affect ecosystem structure and function directly and indirectly via insect pests.
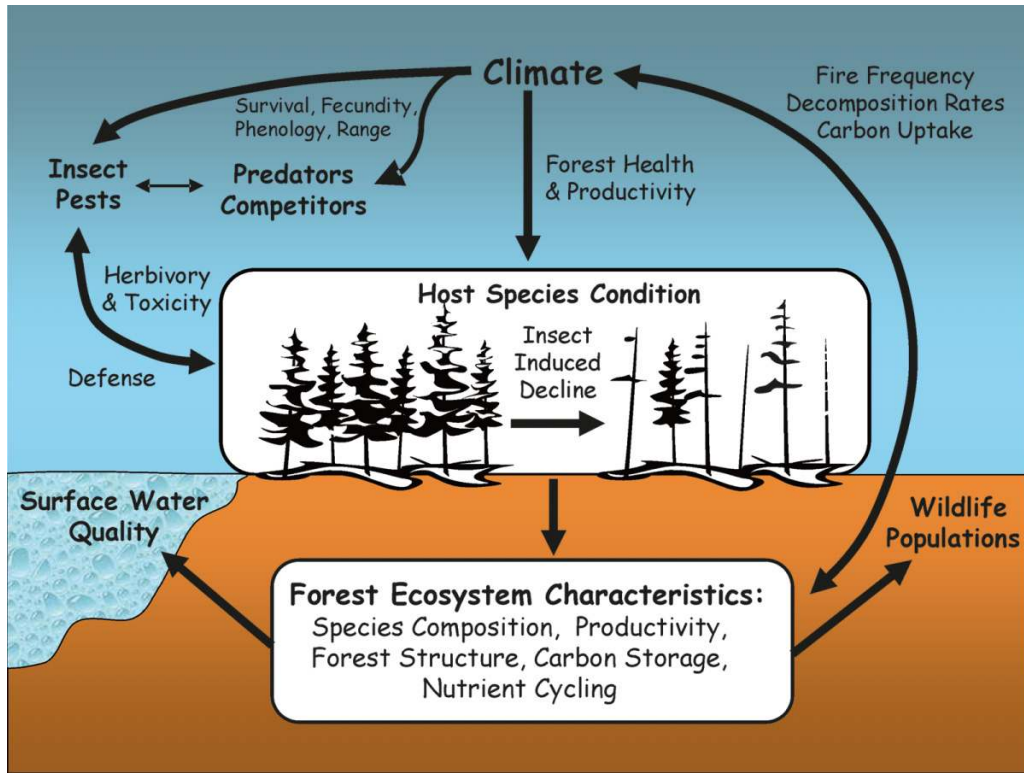

Table 3. Some invasive plant species in northeastern North America and their impacts.

| Invasive plant species*	Impacts; date introduced to US[†], date naturalized	References
Japanese barberry (*Berberis thunbergii*)	Alters soil chemistry and microbial dynamics, reduces native plant recruitment; 1875, 1910	Ehrenfeld 1997; Ehrenfeld et al. 2001
Oriental bittersweet (*Celastrus orbiculata*)	Associated with declines in native congener abundance, vine chokes native saplings and trees; 1860, 1916	Steward et al. 2003
Glossy buckthorn (*Frangula alnus*)	Suppresses native tree saplings, may delay succession in gaps; <1800, ∼1900	Fagan and Peart 2004
Common buckthorn (*Rhamnus cathartica*)	Reduces native plant diversity, alters forest soil properties, increases native bird nest predation; <1800, ∼1900	Schmidt and Whelan 1999; Knight and Reich 2005; Heneghan et al. 2006
Norway maple (*Acer platanoides*)	Alters decomposition and microbe dynamics, alters native macroinvertebrate community, reduces native plant abundance; 1756	Hobbie et al. 2006; Reinhart and VandeVoort 2006; Reinhart et al. 2006
Garlic mustard (*Alliaria petiolata*)	Disrupts native mycorrhizae mutualisms, reduces performance and diversity of native plants, reduces native butterfly populations; 1868	Porter 1994; Meekins and McCarthy 2002; Stinson et al. 2006
Japanese stilt grass (*Microstegium vimineum*)	May outcompete native grasses, alters soil microbial structure; 1919, reached New England by 1980s	Ehrenfeld et al. 2001; Leicht et al. 2005

*All species currently cause problems in some forests of northeastern North America.

[†]Invasive plant introduction dates taken from IPANE (http://nbii-nin.ciesin.columbia.edu/ipane/index.htm); single dates indicate introduction only.

peratures increase metabolism, reproductive rates, and survival. However, predicting how climate change will affect regional nuisance species is a complex task because of the uncertainties in climate models and the complex interactions, feedbacks, and cascading impacts inherent in all ecosystems. Here, we discuss how projected future climates might affect insect pests, pathogens, and invasive plant species in the forests of northeastern North America based on general ecological principles. We then examine possible responses of six key species, to probe our current ability to make predictions. Finally, we discuss the complexities and uncertainty inherent in such an exercise.

Fig. 2. Mean minimum annual temperatures (i.e., coldest temperature of the year) for the northeastern United States in 1961–1990 (top panel) and for 2081–2100 (middle panel), based on projected climate changes in northeastern North America using nine atmosphere–ocean general circulation models (AOGCMs; bottom panel; courtesy of K. Hayhoe and J. Van Dorn). Historical values are based on results from the PRISM climate mapping system (http://www.ocs.orst.edu/prism/). Projected values in the bottom panel are averages for each location across the nine AOGCM simulations based on the A2 IPCC emission scenario. See Hayhoe et al. 2006 for details of methods used to derive data in bottom panel.
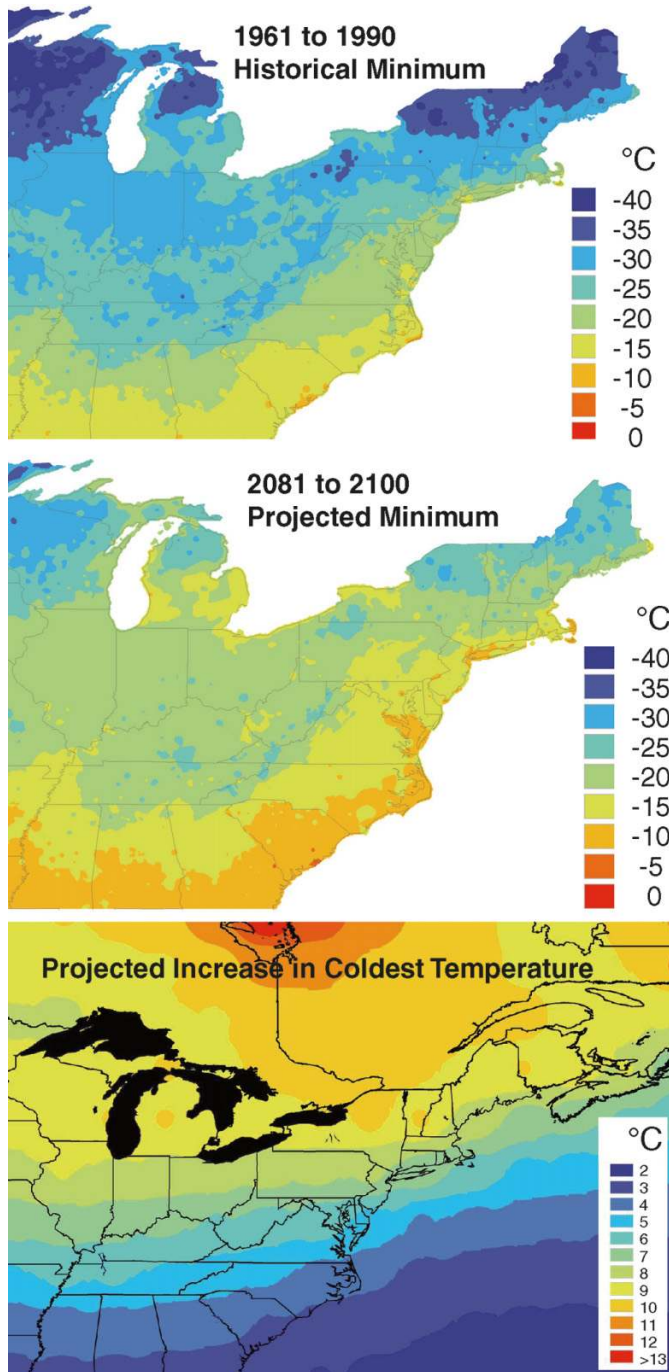
Ecological principles

Insect pests

Insect physiology is highly sensitive to temperature, with metabolic rate tending to about double with an increase of 10 °C (Gillooly et al. 2001; Clarke and Fraser 2004). Thus, climatic warming tends to accelerate insect consumption, development, and movements, which can influence (and likely amplify) population dynamics via affects on fecundity, survival, generation time, and dispersal (Bale et al. 2002). Indeed, the fossil record indicates higher herbivory during geological epochs that are relatively warm (Currano et al. 2008). The timing of life history stages (phenology) of many insect species has already been demonstrably advanced by warming temperatures (Harrington et al. 2001; Logan et al. 2003), and there are growing examples of insect distributions extending northward (Parmesan 2006). Advances in phenology and poleward extensions of distributions are not necessarily problematic, but there are increased risks of consequential pestilence in ecosystems where insect herbivores are more diverse and more metabolically active as a result of climate warming. Accordingly, there are reports of growing damage from some forest pests at the poleward and (or) alpine limits of their historical occurrences (e.g., Jepsen et al. 2008; Lima et al. 2008). It is challenging to rigorously attribute causation, but with the development and validation of process-based models, sometimes in combination with transplant experiments, it now seems very probable that climate warming has contributed to recent epidemics of, for example, mountain pine beetle (*Dendroctonus ponderosae*) in British Columbia (Regniere and Bentz 2007; Raffa et al. 2008), and the processionary moth (*Thaumetopoea pityocampa*) in Europe (Battisti et al. 2005, 2006). In addition to increasing insect metabolism during the growing season, climatic warming also reduces the risk to insect populations of winter mortality from extreme cold (Ayres and Lombardero 2000; Bale et al. 2002).

The nature and frequency of extreme climate events (minimum winter temperatures, drought severity and duration, etc.) have been difficult for climate modelers to predict, but there is progress. Climate projections using the approach of Hayhoe et al. (2006) suggest that in northeastern North America the coldest annual temperature will increase between 2.6 and 15.1 °C by 2081–2100, relative to 1961–1990, with the largest increases at the highest latitudes (Fig. 2). Such increases in extreme temperatures will likely expand the northern ranges for many insect pests. Already, extreme minimum temperatures have increased by 3.3 °C in the southeastern US between 1960 and 2004. Over that same time period, outbreaks of southern pine beetle (*Dendroctonus frontalis*) have extended northward by ∼200 km, matching the predictions of physiologically based models of cold tolerance for this species (Trân et al. 2007).

Climate change may also affect pest populations through impacts on other organisms within the community. For instance, it is well known that climate can affect concentrations of secondary metabolites and nutrients in plants, with consequences for herbivores (Ayres 1993; Ayres and Lombardero 2000). Also, climate can affect natural enemies of insect pests (Burnett 1949) and ecologically important symbionts (Lombardero et al. 2003; Six and Bentz 2007). Currently, we

have less basis for predicting the magnitude or even the direction of these indirect effects compared with the more direct effects of climatic warming on insects.

Although the literature tends to emphasize climate-induced increases in pestilence, it is logical that climate change will also reduce insect pestilence in some systems. For example, the many insects that overwinter in forest litter may face higher mortality rates because of decreased snow depth (Ayres and Lombardero 2000). More generally, it is possible that pestilence will tend to decrease in the warmer edges of contemporary distributions, as predicted by the model of climatic envelopes (Williams and Liebhold 1995). However, it is possible that warmer is generally better for insects, even in climates that are already warm (Frazier et al. 2006). Empirical studies of these topics unfortunately remain rare.

Pathogens

As with insects, it is tempting to suggest that increasing temperatures will simply relax climatic limitations on forest pathogens and increase the pool of species that might produce consequential tree mortality (Scherm and vanBruggen 1994; Harvell et al. 2002). However, it remains difficult to forecast the responses of many plant pathogens to climate change (Coakley et al. 1999; Harvell et al. 2002). Many fungal pathogens can survive and infect within a wide range of temperatures (Pratt 1943; Agrios 2005), but the conditions that favor epidemic growth can be constrained to within a few degrees Celsius (Cooke and Whipps 1993; Lonsdale and Gibbs 1994). Less is known about viral or bacterial sensitivity to climate in forest systems, but infection and transmission rates have been reported to vary with temperature (Goodman et al. 1986; Coakley et al. 1999).

Direct effects of climate change on forest pathogens are likely to include (*i*) increased growth and reproduction; (*ii*) altered propagule dispersal, transmission rates, and infection phenology; and (*iii*) changes in overwinter survival. Indirect effects may include changes in (*i*) host nutrient status, resource allocation, and susceptibility to pathogen attack; (*ii*) distribution, life cycles, or phenology of insect associates or other vectors; (*iii*) the distribution of primary and alternate hosts; (*iv*) mismatches between adult tree location and optimal conditions, resulting in tree stress and increased disease susceptibility; and (*v*) the creation of novel community assemblages or mismatches between locally or regionally co-adapted genotypes that could enhance the potential for virulence.

In addition to temperature, patterns of precipitation and storm severity, nitrogen deposition, atmospheric ozone and CO_2 concentration, and UV-B radiation all can affect forest pathogens (Garrett et al. 2006). For example, increased precipitation will favor many forest pathogens by enhancing sporulation and dispersal by rain splash (Lonsdale and Gibbs 1994). Many rust fungi require moist surfaces to infect their hosts and will be favored by increased humidity (Vanarsdel et al. 1956). In contrast, tissue colonization by powdery mildew can be deterred by high moisture (Lonsdale and Gibbs 1994). Higher minimum winter temperatures or decreased frequency or intensity of extreme cold will favor overwintering survival (Coakley et al. 1999), but decreased snow cover may increase exposure to lower lethal temperatures (Ayres and Lombardero 2000). In a rare experimental manipulation,

disease incidence and plant damage were generally found to be higher in warmed plots having earlier snowmelt dates when compared with control plots, though the trend was reversed for some herbivores and pathogens (Roy et al. 2004).

Mechanical damage from storms, lightning, frost cracking, and snow loading provides infection opportunities for organisms otherwise limited in their ability to penetrate bark tissues (Shigo 1964). A future with more frequent and (or) severe winter storms would very likely benefit these organisms. Nitrogen deposition and increased CO_2 concentrations are likely to interact to alter plant growth rates and nutrient availability, and indirectly affect resource allocation to chemical or structural defense (Herms and Mattson 1992). Nutrient dynamics in the rhizosphere can impact saprophytic microbes and mycorrhizae in ways that influence root infection by pathogenic fungi (Chakraborty et al. 2000). Changes in atmospheric CO_2 may also affect pathogens, as the $O_2:CO_2$ ratio influences competitive interactions among fungi (Boddy 2000) and strain aggressiveness (Burdon et al. 2006).

Climate change is almost certain to be a strong driver of evolutionary change in plant and pathogen populations (Harvell et al. 2002). Short generation time among pathogens relative to tree hosts allows a faster genetic response (Hafner et al. 1994; Brasier 2001). In general, introduced pathogens undergoing sustained population growth while encountering novel hosts should exhibit greater potential for rapid evolutionary response to changing abiotic conditions than native pathogens (Brasier 1995). Additionally, rapid evolution via interspecific hybridization in several fungal pathogens has recently been established, and contact between historically isolated genotypes facilitated by climate-induced range shifts could promote such hybridization (Brasier 2001). By this mechanism, pathogens could adapt to changing environmental conditions even if genetic diversity is low.

Several reviews have emphasized the potential for climate change to disrupt forest structure and function via increased impacts from forest pathogens (Coakley et al. 1999; Burdon et al. 2006; Garrett et al. 2006). However, forests have long experienced a wide range of impacts from pathogens, and typically recover from these impacts. In many cases, pathogens promote enhanced diversity of the tree community (Packer and Clay 2000; Winder and Shamoun 2006). Although this review focuses on relatively direct consequences of climate change, the impacts of forest pathogens in the decades to come also will be strongly influenced by human actions.

Invasive plant species

Plants respond directly to many aspects of climate, including means (e.g., temperature, total precipitation), timing (e.g., frost-free period length, temperature regimes during critical life-history stages), and variability (magnitude and duration of climate extremes). Climate changes will also affect plants indirectly by altering ecosystem processes; plant responses often reflect the indirect effects of climate on soil nutrients and moisture as much as the direct effects on plant physiology itself (Shaver et al. 2000; Brooker and van der Wal 2003). Initially, plant responses to climate change will shift the competitive balance among species within a plant community. Warming will lead to range changes: some expansions, often at colder, northern population boundaries, and some retractions in response to warmer or drier climates.

Several lines of reasoning suggest that as a group, invasive plant species could disproportionately benefit from climate change, but these have not been directly tested. This can be attributed to invasive plant species' ability to "tolerate" new climates better than the average species. Some invasives demonstrate a potential for disproportionately rapid evolutionary change (Maron et al. 2004) and (or) high phenotypic plasticity (Schweitzer and Larson 1999). Several studies suggest that invasive plant species tend to have broad environmental tolerances (Goodwin et al. 1999; Qian and Ricklefs 2006). All of these properties could allow them to maintain or even increase their fitness relative to other species in a changing climate.

In addition, invasive plants might be better than average at "keeping up" with climate change. Many invasive species have traits that facilitate long-range dispersal (Pitelka et al. 1997; Dukes and Mooney 1999); we expect these species to rapidly establish populations in areas with newly suitable climates. There, they might initially compete with species that are less well adapted to the new climate.

Traits that facilitate rapid range shifts do not necessarily lead to straightforward predictions of success under climate change. If invasive plants migrate more rapidly than introduced biocontrol agents or native pests and pathogens, then invasive species will sometimes benefit from escaping these enemies (Sax and Brown 2000). Alternatively, if the phenological responses of plants differ from those of pollinators and dispersers, mutualistic relationships will sometimes weaken, which could suppress migration of some introduced plant species (Parker 1997). However, one would expect that obligate mutualisms are less likely to limit ranges of invasive species than native species, based on the invasives' proven abilities to expand their populations in new regions.

Invasive plants will respond to elevated CO_2 at the same time that they respond to climate change, and these responses may sometimes interact. For example, Ziska (2003) showed that a group of highly invasive weedy species responded strongly to increasing CO_2 concentrations, possibly explaining their increased prevalence during the past century. However, Alberto et al. (1996) showed that the competitiveness of *Echinocloa glabrescens*, an important agricultural weed, decreased under elevated CO_2, but this effect diminished under warmer temperature regimes. The direct effects of climate and CO_2 on a given invasive species will also be modified by the climate and CO_2 responses of competitors and mutualists (Dukes and Mooney 1999).

Changes in climate and atmospheric composition will sometimes alter plant leaf chemistry (Dury et al. 1998; Mohan et al. 2006; but see Fajer et al. 1992), with consequences for both herbivore–plant interactions and interactions among native and introduced plant species. However, these complex responses are not well-enough understood to apply to invasive species as a category.

From ecological principles alone, we have described several reasons to suspect that climate change will increase the prevalence of invasive plant species. However, this reasoning is virtually untested. By thoroughly examining the cases of individual species, we can better understand the degree to which we are capable of predicting changes in the forests of northeastern North America.

Case studies

To examine the likely responses of nuisance species to climate change and to illustrate the data available from which to make such predictions, we have chosen six species for case studies. These species are chosen to represent a sample of the important nuisance species present; they are not necessarily the most damaging species. For instance, because they have a well-developed literature of their own, we omit detailed consideration of the spruce budworm (Volney and Fleming 2000; Gray 2008) and the gypsy moth (Logan et al. 2003; Robinet et al. 2007). The six case studies include two pests: the exotic *Adelges tsugae* Annand (hemlock woolly adelgid) and the native *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae) (forest tent caterpillar), both common insect stressors in northeastern North American forests. We examine Armillaria root rot (primarily *Armillaria* ostovae) and beech bark disease (*Cryptococcus fagisuga* + *Neonectria* spp.) as examples of common diseases influencing the structure and function of the region's forests. Finally, we consider two of the more noxious invasive plant species in northeastern forests: *Frangula alnus* Mill. (glossy buckthorn), a shrub species, and *Celastrus orbiculatus* Thunb. (oriental bittersweet), a woody vine.

Hemlock woolly adelgid

The recent unimpeded infestation of hemlock woolly adelgid (HWA; *Adelges tsugae*) across the northeastern US provides an unusual and important opportunity to examine how climate may limit a pest as it expands into the range of its new host. HWA, an introduced aphid-like insect from Japan that attacks and kills eastern hemlock (*Tsuga canadensis*), is generating widespread mortality and initiating intensive hemlock logging from North Carolina to New Hampshire. Continued infestation threatens to produce a range-wide decline or elimination of this ecologically, culturally, and economically important species (Orwig and Foster 1998; Orwig et al. 2002).

Laboratory studies have shown that HWA is sensitive to cold temperatures and that HWA populations exhibit reduced survival at increasingly lower temperatures (Parker et al. 1998). HWA survival dropped significantly at temperatures below –25 °C, a small percentage survived exposure to –30 °C, and none survived below –35 °C (Parker et al. 1999; Skinner et al. 2003). Interestingly, HWA cold hardiness depends on geographic location and time of year; the organisms gradually lose their ability to tolerate cold as the winter progresses (Skinner et al. 2003).

Several field studies have provided data that corroborate these laboratory results. McClure and Cheah (2002) reported high (>90%) HWA mortality at sites across northern Connecticut following temperatures below –20 °C during the winter of 2000. In addition, in a study examining 36 sites across the northeastern US, HWA mortality was positively correlated with degrees of latitude and the minimum temperatures recorded per site (Shields and Cheah 2005).

Currently, HWA is distributed among hemlocks growing in areas where minimum winter temperatures stay above –28.8 °C (Skinner et al. 2003). Paradis et al. (2008) suggest that a mean winter temperature of –5 °C is required to prevent HWA populations from expanding and

Fig. 3. The current distribution of eastern hemlock (*Tsuga canadensis*; hatched areas) in the northeastern United States, superimposed on maps of current and projected minimum temperature thresholds for hemlock woolly adelgid survival (red, grey, and black areas). The current distribution of HWA in the US is limited to locations where minimum winter temperatures stay above –28.8 °C (white areas; Skinner et al. 2003). Based on recent climate projections (Fig. 2; Hayhoe et al. 2006), the area of hemlock protected by this extreme cold could be significantly reduced by 2070 (red areas). If HWA adapts to extreme cold (see text), hemlock may be limited to small pockets in the extreme northern portions of Maine, Vermont, New Hampshire, New York, and Wisconsin where temperatures drop below –35 °C (black areas).
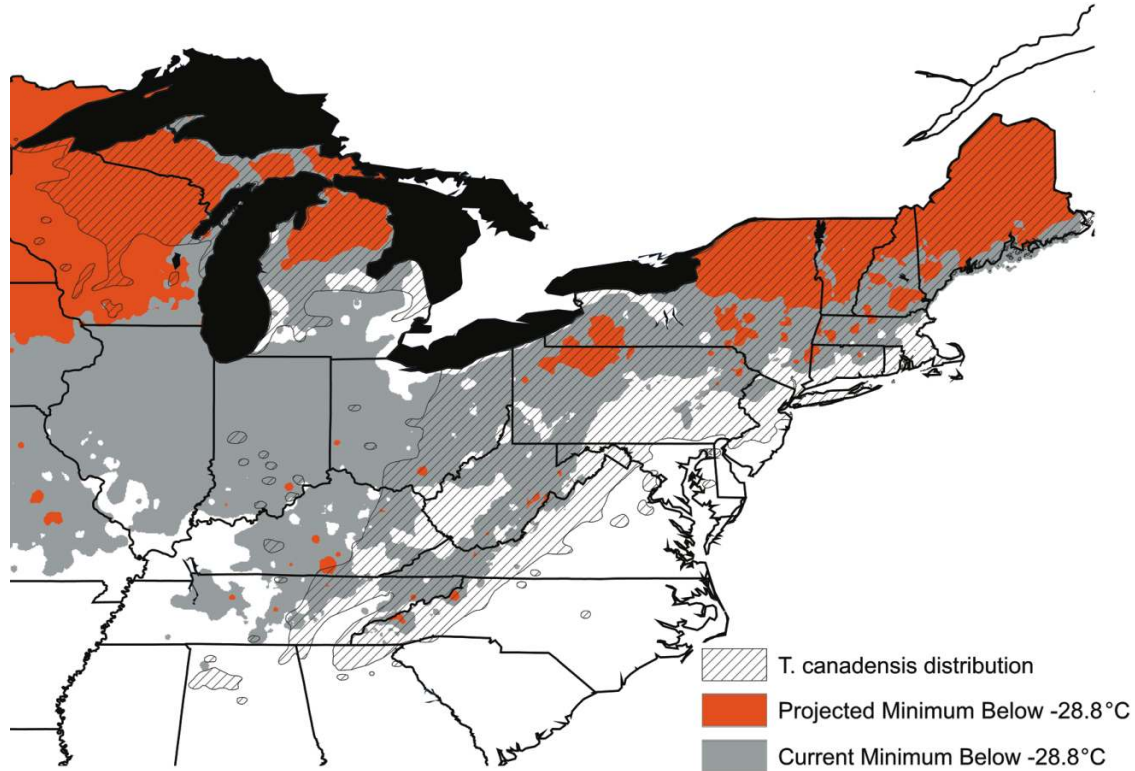
spreading. The northerly spread and ultimate range of HWA may therefore be controlled by the severity, duration, and timing of minimum winter temperatures (McClure and Cheah 2002).

Based on the most recent climate projections (Fig. 2), warming would reduce the range of hemlock protected by extreme cold to the northernmost edge of hemlock's current distribution in the US (Fig. 3). The problems for hemlock may be worse than climate models would imply; recent evidence that suggests that HWA may have the ability to develop greater cold tolerance at the northern extent of its range (Butin et al. 2005).

In addition to relaxing range constraints, milder winters may lead to increased survival and fecundity and may result in higher HWA population levels, which have been associated with a more rapid decline of infested hemlocks (Pontius et al. 2002, 2006).

If warming occurs in the future as predicted (Hayhoe et al. 2006), particularly during the months of December, January, and February, HWA may spread unimpeded throughout the range of hemlock distribution in North America. The potential impacts of widespread hemlock mortality include changes in forest composition, structure, nutrient cycling, surface water quality, and populations of associated wildlife (e.g., Jenkins et al. 1999; Kizlinski et al. 2002; Tingley et al. 2002; Ross et al. 2003).

Forest tent caterpillar

The forest tent caterpillar (FTC; *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae)) is one of the most widespread insects in North America. Its range extends over 30° of latitude, from the Gulf of Mexico to northern Canada, and from the Pacific to the Atlantic Ocean (Stehr and Cook 1968). FTC feed on a taxonomically diverse array of broadleaf trees. These classic early season defoliators overwinter as pharate larvae inside eggs laid in aggregate near the buds of preferred hosts (mainly species of *Quercus*, *Acer*, and *Populus*). Outbreaks generally last 3–4 years, and the repeated defoliation can generate substantial tree mortality over large areas (Horsley et al. 2002). The factors promoting outbreaks are still poorly understood (Cooke and Roland 2000), although climatic mechanisms such as favorable warm temperatures during larval development (Ives 1973) and phenological synchrony with the leaf out of host trees (Parry et al. 1998) are likely candidates. Population collapse is often attributed to high rates of parasitism (Parry 1995) or viral epizootics (Myers 1993), although evidence indicates that harsh winter temperatures also can be responsible (Witter 1979).

Climate change projections indicating warmer winter temperatures (Hayhoe et al. 2006) might suggest increased overwinter survival of pharate FTC larvae. However, the cold tolerance varies seasonally in response to temperature; a se-

quence of warm days can decrease egg glycerol content, thereby decreasing cold tolerance (Hanec 1966). Accordingly, egg mortality increased dramatically in an Alberta outbreak following a winter that experienced sudden transitions between extreme warm and extreme cold (Cooke and Roland 2003). If average winter temperatures are tending to become warmer, then occasional bouts of extreme cold could become an increased source of mortality for FTC (especially in the early spring) and could tend to prevent or shorten periods of FTC outbreaks. This scenario is consistent with predictions of increased variance in climatic extremes (Overpeck 1996; Karl and Trenberth 2003). Other climate models predict fewer freezing events in late winter and early spring (Hayhoe et al. 2006), which would decrease FTC egg mortality.

Synchrony between larval emergence and host plant budbreak is important for survival and growth performance of both FTC (Parry et al. 1998; Jones and Despland 2006) and scores of other early season lepidopteran defoliators (Hunter and Elkinton 2000; Klemola et al. 2003). For early spring feeding insects, optimal growth depends on access to young foliage, since nitrogen and water content decrease and leaf toughness and secondary metabolite content increases as the leaves mature (Mattson and Scriber 1987). Larvae that emerge too early starve, and those that emerge too late show decreased growth rates, longer larval stages (including additional stadia), and lower pupal masses, indicating reduced female fecundity (Parry et al. 1998; Jones and Despland 2006). Climate warming is already showing discernible effects on the phenology of first leaf dates (Schwartz et al. 2006). While many lepidopteran herbivores show a high ability to adjust their egg hatch to the timing of leaf out despite substantial interannual variation in host plant phenology (Buse and Good 1996; Tikkanen et al. 2006), the population dynamics of other lepidopteran defoliators are more sensitive to phenological asynchrony (Hunter and Elkinton 2000; Visser and Holleman 2001; Bale et al. 2002). If FTC and host trees respond differently to thermal cues terminating winter diapause, climate change could result in fewer FTC outbreaks.

However, insect metabolism and development, like leaf maturation, tend to accelerate with increasing temperature. If leaf maturation is less responsive to temperature than insect development rate, larval FTC will be able to complete more of their development while feeding on nutritious immature foliage (Ayres 1993). Other things being equal, this would tend to increase the population growth potential of FTC and increase the severity, frequency, or duration of outbreaks.

Analysis of FTC outbreaks in Ontario indicated that the thermal sum in the early part of the growing season is an important determinant of outbreak duration (Roland et al. 1998). This mechanism might contribute to a general tendency for increased abundance of a forest caterpillar community in years that follow longer, warmer summers. However, years with increased caterpillar abundance in the Hubbard Brook Experimental Forest (New Hampshire, USA) have not resulted in insect outbreaks or a discernable effect on primary productivity over the 22 years that caterpillar abundance has been monitored there (Reynolds et al. 2007). From the perspective of neotropical migrant birds, the effect of warmer temperatures on forest caterpillars is demonstrably positive: increased caterpillar abundance benefits fledglings and increases recruitment of new breeders in avian populations (Sillett et al. 2000; Nagy and Holmes 2005).

Armillaria root rot

Armillaria is a common root and butt rot pathogen that inhabits an array of forest types throughout the northeastern US and eastern Canada (Harrington and Rizzo 1993; McLaughlin 2001). In eastern deciduous forests, *Armillaria* largely behaves as a secondary pathogen, killing only weakened or stressed hosts (Wargo and Shaw 1985). Insect defoliations, drought, and air pollution are just a few of these predisposing stresses. As a forager of weakened trees, *Armillaria* serves an important ecological role in forests by aiding in structural diversification, creating habitat for wildlife and microbes, and recycling nutrients (Hansen and Goheen 2000; Worrall et al. 2005).

Because endemic pathogens like *Armillaria* are already well established across the Northeast, the effects of climate change on further dispersal are of minor interest. What is of particular concern, however, is how *Armillaria* will respond to heightened levels of stress that forest trees will experience because of higher annual temperatures and more frequent and severe drought conditions predicted during summer months (Aber et al. 2001; Hayhoe et al. 2006). Furthermore, if insect defoliations become more frequent and severe, *Armillaria* will likely benefit, exacerbating tree mortality at the individual species or forest-wide levels (Ayres and Lombardero 2000). By causing mobilization of root carbohydrates, defoliation stimulates growth and penetration of host tissues by *Armillaria* (Wargo 1972). However, stress-induced compounds in roots may accelerate the oxidation of phenols, the primary chemical defense against *Armillaria* (Fox 2000).

Armillaria has been previously associated with mortality of sugar maple affected by drought, insect defoliations, and nutrient deficiencies (Bauce and Allen 1992; Horsley et al. 2002); with oak species stressed by drought and gypsy moths (Clinton et al. 1993; Burrill et al. 1999); with an increased mortality in jack pine damaged by jack pine budworm (Mallett and Volney 1990); and with an increased incidence of beech infected by beech bark disease (Wargo 1983).

As climate change increases stress levels for trees, *Armillaria* will take advantage throughout every forest type in northeastern North America. Higher annual temperatures, especially during winter months in this region, will allow wood decay pathogens like *Armillaria* to function for a greater fraction of the year (Harvell et al. 2002). This could allow for increased growth of rhizomorphs, additional spore production and dispersal, and a greater buildup of nutrient reserves from inocula, such as stumps and downed logs. Higher summer temperatures coupled with more frequent and severe drought conditions may allow *Armillaria* to behave more aggressively in colonizing live hosts, especially in forests where additional stress agents such as defoliating insects are present.

Beech bark disease

Beech bark disease (BBD) in North America is a decline complex of American beech (*Fagus grandifolia* Ehrh.) that arises from interactions between an introduced scale insect (*Cryptococcus fagisuga* Lind.) and an ascomycete fungi of

the genus *Neonectria* (Lohman et al.). The native scale insect *Xylococculus betulae* (Perg.) can also be important to the system, particularly in forests where the disease agents are endemic, as feeding by these insects predisposes bark tissue to colonization by *C. fagisuga*. The association between the fungus and the scale insects seems to be synergistic, in that *Neonectria* gains access to phloem resources by exploiting the feeding wounds and activity of scale insects. Similarly, bole cankering in response to *Neonectria* infection modifies bark structure in a way that provides microhabitat refugia that protect scale populations from stemflow and extreme temperatures (Shigo 1964; Houston et al. 1979). Although the insects and fungi appear to mutually benefit one another, the interactions have also been described as weakly to moderately antagonistic (e.g., competition for phloem resources within a tree (Shigo 1964)). This is probably a case of conditional interactions (Bronstein 1994), where species interactions can change character, depending upon the environmental conditions and the spatiotemporal scale of consideration.

There appears to be a direct connection between climate and scale insect populations. In northern latitudes, scale insects appear to be limited by low winter temperature; minimum daily temperatures of −34 °C or below correlate with scale population dieback in analyses of abundance time series (Barter 1953; Houston and Valentine 1988). Historically, beech bark disease has been excluded from sites in northern Maine where populations are limited by harsh conditions even when interspersed among relatively mild years (Gove and Houston 1996). However, recent reports suggest that the disease has been spreading northward in recent years (Kasson 2006). In cold winter environments where periodic dieback is common, residual scale colonies are often able to persist at low levels below snowline on tree bases and root collars (Gove and Houston 1996). Decreases in persistence of snow could lead indirectly to local extirpation by reducing or eliminating these refugia. In addition, precipitation in autumn has been shown to negatively impact the mobile 1st instar crawler stage of the insect, limiting recruitment and dispersal as stemflow washes unprotected animals down the bole (Houston et al. 1979).

Far less is known about the direct effects of climate on fungal growth and reproduction within trees. The arrival of *Neonectria* in previously uninfected stands often trails the advance of the scale insect by up to a decade. To date, *Neonectria* appears to be limited geographically only by the current distribution of scale insects, suggesting that population expansion is not currently constrained by climate. In many stands, however, perithecium production appears to be highest during the winter. Some researchers have hypothesized that host dormancy limits the capacity of trees to actively wall off infection by producing callus tissue during winter months (Gove and Houston 1996). In this scenario, unless warmer winter temperatures allow trees to break dormancy and allocate resources to callus growth or defense, an increase in the number of winter days above freezing would be predicted to facilitate fungal infection (Lonsdale and Gibbs 1994).

Climate change could affect disease dynamics indirectly through changes in host resistance. Tree vigor is positively correlated with BBD infection (Gove and Houston 1996),

and the bark tissue of resistant trees tends to have lower nitrogen concentrations and higher phenolic content (Wargo 1988; Latty et al. 2003). Atmospheric nitrogen deposition and increases in atmospheric CO_2 should both tend to increase tree growth rate and perhaps therefore increase susceptibility to BBD. On the other hand, increases in CO_2 tend to decrease tissue nitrogen concentrations in leaves (Cotrufo et al. 1998). If the effect is similar on bark nitrogen concentration, this could decrease tree susceptibility to BBD. Increases in the frequency or severity of storms could also influence the longevity of infected trees, which are highly susceptible to windthrow (Papaik et al. 2005).

Finally, climate-induced changes in natural enemy populations could alter the epidemiology of BBD. There are two primary natural enemies in North America: the twice-stabbed ladybeetle (*Chilochorus stigma* Say) (Shigo 1964) and the fungus *Nematogonum ferrugineum* (*Gonatorrhodiella highlei*) (Houston 1983). Both are currently considered incidental to the beech bark disease dynamics, though the extent to which these populations will be favored or limited under future climate scenarios, and their potential importance in disease regulation is unknown.

In this system, one can envision many scenarios in which climate change affects community interactions with consequences for the epidemiology of BBD, but we are unable to assign probabilities to these scenarios. Anything that affects interactions between scale insects and fungi could be broadly consequential.

Glossy buckthorn

Glossy buckthorn (*Frangula alnus*) was introduced to North America from Eurasia around 1800. Its range now spans Tennessee in the southeast, Nova Scotia in the northeast, Manitoba to the northwest, and Idaho in the west (Converse 1984; Mehrhoff et al. 2003). In the eastern parts of its range, *F. alnus* colonizes a wide range of habitats and forms dense, monospecific stands that exclude native understory species (Converse 1984) and reduce canopy tree recruitment (Frappier et al. 2003*a*; Fagan and Peart 2004). Populations have the potential to delay gap filling in forests and favor shade-tolerant species in these gaps (Fagan and Peart 2004), to change ecosystem and community dynamics within the forest (Frappier et al. 2003*a*), and to reduce the quality of food available to birds (Mehrhoff et al. 2003). It has been suggested that *F. alnus* may also have economic impacts with detrimental effects on the native white pine (*Pinus strobus* L.) timber industry in North America (Fagan and Peart 2004).

The northern range limit of *F. alnus* may reflect cold tolerance and a time lag in the spread of the species (Howell and Blackwell 1977; Frappier et al. 2003*b*), but our ability to make predictions is limited by a lack of specific data describing cold hardiness. *Rhamnus cathartica* L., an invasive relative, shows cold hardiness to −24 °C and similar broad-scale northern range distributions throughout North America. Thus, warming might extend the potential northern and northwestern range boundaries of these species through the boreal forest and might improve their ability to compete with other species in these regions by relieving physiological limitations. However, extrapolations of climate responses across genera (or even species) are tenuous at best.

Data from European pollen studies suggest that following the Holocene ice age, *F. alnus* expanded its range northwards in Europe more quickly than other species in response to warming. The species' short generation times and high dispersal rates may have made this rapid expansion possible (Hampe and Bairlein 2000). At its southern range boundary in Europe, *F. alnus* may be limited by desiccation and (or) scarcity of pollinator resources (Hampe 2005). Because higher temperatures lead to ovule desiccation, lower seed production, and insufficient cold for seeds to break embryo dormancy, warming could decrease fecundity of *F. alnus* at the southern end of its range margins (Heit 1968). Consequently, it is tempting to speculate that the entire range of *F. alnus* will shift northwards in response to warming, rather than simply extending at the northern boundary. However, because environmental tolerances and responses are not known for this species, we cannot make a confident prediction.

Oriental bittersweet

Oriental bittersweet (*Celastrus orbiculatus*), a temperate vine native to southeastern Asia (Hou 1955), inhabits eastern North American forests from central Maine to Louisiana (Patterson 1974). It is considered a severe pest plant by forest managers in the southeastern US and in parts of the northeast (McNab and Meeker 1987; Dreyer 1994). *Celastrus orbiculatus* severely damages trees by girdling their trunks, breaking tree branches (Lutz 1943), shading young seedlings (McNab and Meeker 1987), and increasing tree susceptibility to ice damage (Siccama et al. 1976). It can overtop trees and may inhibit forest succession (Fike and Niering 1999). Like many other invasive vines, it is most abundant on forest edges. However, *C. orbiculatus* also survives in very low light conditions (Leicht and Silander 2006). The invasion of *C. orbiculatus* has been associated with a quasi-stable forest state in which dense vines substitute for the development of a mature canopy tree stratum (Fike and Niering 1999).

Celastrus orbiculatus produces abundant seed, which is dispersed over long distances by birds and can establish in a variety of habitat types (Patterson 1974). Throughout its range, this invasive liana outcompetes and sometimes hybridizes with its native forest congener, American bittersweet (*Celastrus scandens*) (Pooler et al. 2002). Under the light conditions typical of forest understory environments, *C. orbiculatus* increases its height 15 times faster than *C. scandens*.

Celastrus orbiculatus is abundant in southern New England, but many areas of northern New England and Canada are currently free of the species (Mehrhoff et al. 2003). Using Bayesian biogeographic models, Leicht (2005) predicted that *C. orbiculatus* has the potential to spread further throughout New England. Based purely on climate in its native range in Asia, some of the highest likelihoods of occurrence were in northern New England. These models suggested *C. orbiculatus* was most likely to occur in regions where minimum temperatures in the coldest month of the year were higher and where annual precipitation or precipitation in the driest months was greater (Leicht 2005). Therefore, this species might be more likely to invade a wider area in a climate with warmer minimum temperatures (Fig. 2) and more precipitation.

Using a rapid survey technique, McNab and Loftis (2002) modeled the probability of occurrence of *C. orbiculatus* in relation to the environment, competition dynamics, and disturbance history. They found that *C. orbiculatus* was significantly associated with increased wind disturbance, topographic variables indicative of mesic environments, scarification of the forest floor, past tree harvests, and gaps in the tree canopy. The species has broad habitat requirements (Patterson 1974) and highly plastic responses in growth (Ellsworth et al. 2004) and photosynthetic rate (Clement et al. 1991), all of which may enhance its success in a changing climate.

The available data on *C. orbiculatus* suggest that the vine is likely to benefit from warming and increased precipitation in northeastern North America. As with other species, more information on its current range and environmental tolerances would increase confidence in this prediction.

Uncertainty

Predicting how climate change will affect regional nuisance species is a complex task for a variety of reasons (Bradshaw and Holzapfel 2006; Parmesan 2006). Four types of uncertainty accompany any future projection. These are the uncertainties associated with internal ecosystem processes, with climate projections, with future human actions, and with those arising from a lack of data on the nuisance species themselves. The first three categories are difficult to avoid. Because many organisms and ecological processes disturb forests, the timing and location of disturbances are largely unpredictable. Climate change projections add uncertainty on two levels—scientific and sociological. Computer models differ in their structure and assumptions. While recent projections broadly agree that mean annual surface temperatures will increase, the amount of warming and the nature of accompanying precipitation change depends on the model. The factors driving both climate change and the transport of nuisance species around the landscape will depend on human actions, which are difficult to predict. Other human actions, such as land-use changes that drive habitat fragmentation, may interact with the effects of climate change. These interactions may alter communities, increase the abundance of invasive organisms and pests, and spur the declines of natives. The final category of uncertainty is the most easily addressed—uncertainty due to a lack of data. In many cases, our confidence in identifying likely responses would improve substantially if the ranges and (or) climatic tolerances of the species were better understood and if information were available about the species' basic ecological interactions.

Uncertainty can arise in even well-studied "model systems". The case of feedback-driven, periodically irruptive forest-defoliating insects (Cooke et al. 2007) illustrates how uncertainty could lead to counter-intuitive predictions. Because weather events inject randomness into insects' population dynamics, it is difficult to predict when a population oscillation will exceed a threshold for damage that defines "outbreak". In northern forest ecosystems, where insect outbreaks are thought to be temperature-limited, climate warming could reduce variability in annual survival rates, which in turn could reduce the frequency and duration of out-

Table 4. Predicted responses of six problematic species to climate change in forests of northeastern North America.

Species	Response to climate change*		Confidence in predictions	Uncertainty level†	
	Range	Impact in range		Species data	Ecosystem dynamics
Adelges tsugae (hemlock woolly adelgid)	+	0	High	Low	Low
Malacosoma disstria (forest tent caterpillar)	+/0	+/–	Medium	Low	Medium/high
Armillaria spp. (root rot)	0	+	Medium	Medium	Medium
Cryptococcus fagisuga + *Neonectria* spp. (beech bark disease)	+	+/–	Medium	Medium	Medium
Celastrus orbiculatus (oriental bittersweet)	+	0	Low	Medium	Medium
Frangula alnus (glossy buckthorn)	0	0	Low	High	Medium

*+, signifies increase in range of species or in impact of species on trees within its range; –, signifies decrease; 0, signifies no change.

†Categories indicate primary sources of uncertainty in predicting responses to climate change. "Species data" refers to uncertainty stemming from a lack of available data on the range and relevant traits of the nuisance species, such as environmental tolerances. "Ecosystem dynamics" refers to uncertainty stemming from a lack of understanding of how nuisance species interact with other species in the system, or how they respond to environmental variables that are not directly linked to climate, or from a lack of ability to predict how these interactions might be altered by climate change.

breaks. Note that this is the opposite of what is often predicted for areas that under today's climate, already experience frequent outbreaks. We do not necessarily expect climate warming to result in shorter, less frequent outbreaks. However, this scenario helps to illustrate that climate change could have a range of consequences in these forests.

Outbreaks of pests, pathogens, and invasive species, in turn, can initiate complex cascades of change throughout whole ecosystems. This has been well documented for invasive plant species; for example, invasions of purple loosestrife affect the growth and survival of American toad tadpoles (Maerz et al. 2005; Brown et al. 2006), and invasive shrubs increase predation on songbirds (Borgmann and Rodewald 2004). Cascading in the opposite direction, exotic rats and rabbits enhance the dispersal of the exotic plant (*Carpobrotus edulis*), which in turn enhances the population growth of the two animal invaders (Bourgeois et al. 2005). Uncertainties stemming from such cascades within food webs and facilitations across trophic levels add to the complexity of anticipating climate change effects on forest pests.

We will never predict climate responses of these systems with certainty. Nevertheless, we can assess the likelihood of possible outcomes and identify research that would maximize our confidence. At the same time, we can encourage acceptance of an inherently high degree of uncertainty, and encourage policies that make allowances for ignorance, imprecision, stochasticity, and surprise. Given the daunting challenge of modeling these complex systems' responses to climate change, we suggest this should be given serious thought.

Uncertainty is a common feature of environmental problems that require management decisions. Land managers already cope with many sources of uncertainty in managing species; some use quantitative estimates of uncertainty and risk to inform decision-making (Maguire 2004). This approach can serve as a model for developing approaches to managing pests, pathogens and invasive species in a warming world.

Conclusions

Insect pests, pathogens, and invasive plant species are among the primary agents of biotic disturbance in North American forests (Fike and Niering 1999, Logan et al. 2003). Predicting how their role in northeastern forest dynamics will

change with a changing climate is fraught with uncertainty. As illustrated above, two or three of the six studied species are likely to become more widespread or more abundant in northeastern North America under projected climate change (Table 4). For some of these species, the primary response will be a northward range expansion. HWA, for instance, is very likely to expand northward simply because its northern range boundary is cold-limited. *Celastrus orbiculatus* may have a similar restriction, although its tolerances are less well tested. Other nuisance species such as *F. alnus* and *Armillaria* are already widespread within the region, and their potential response is less clear. We have not presented any species likely to become less problematic across northeastern forests because of climate change, but we cannot rule out the possibility that such species exist.

Our inability to make confident predictions for five of the six nuisance species highlights a need for new research on several fronts.

- First, we should test whether some very general mechanisms might provide advantages to nuisance species. Few studies have addressed these, such as the relative mobility, rapid evolution, and phenotypic plasticity of nuisance species compared with others. There is also a need for research that evaluates general theoretical models of how the structure and function of northeastern forests will respond to the changes in biotic disturbance regimes that we anticipate.

- In addition, it would be useful to predict potential ranges of nonnative nuisance species in northeastern forests based on their ranges on their home continents, and to model possible range changes caused by climate change. While climate-matching models have been used to explore the potential effects of climate change on distributions of some invasive species (e.g., Richardson et al. 2000; Kriticos et al. 2003), these exercises have rarely been carried out for nuisance species in North America (but see Zavaleta and Royval 2002; Gray 2008; Paradis et al. 2008). Bioclimatic models can provide crude predictions for future ranges, but with important limitations (Araújo and Rahbek 2006). For instance, we have little information on how demographic processes and competitive interactions among species at the northern and southern range limits might interact with climate-driven range shifts.

Although targeted studies of this sort will be quite useful to managers, merely studying single-species responses to climate factors (e.g., changes in temperature, humidity, or soil moisture) is too slow and too limited to permit adequate understanding of the potential and unfolding responses of complex systems to climate change. There is an urgent need for whole-systems modeling of host–pathogen, host–pest, and invasive plants within an ecosystem context to anticipate the range of possible responses of these complex systems. However, such modeling demands a highly detailed understanding of the system.

Regardless of how nuisance species respond to the changing climate, these responses will have potentially significant economic, aesthetic, and ecological consequences for forest ecosystems (Ayres and Reams 1997; Ayres and Lombardero 2000). Our ability to predict these responses will never be precise, but targeted research in the near term could lead to more quantitative and geographically relevant projections. We recommend that policymakers and land managers prepare for continued high levels of uncertainty and take actions that have clear benefits under a wide range of possible future scenarios.

Acknowledgements

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