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Assessing the consequences of global change for forest disturbance from herbivores and pathogens

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Abstract

Herbivores and pathogens impact the species composition, ecosystem function, and socioeconomic value of forests. Herbivores and pathogens are an integral part of forests, but sometimes produce undesirable effects and a degradation of forest resources. In the United States, a few species of forest pests routinely have significant impacts on up to 20 million ha of forest with economic costs that probably exceed \$1 billion/year. Climatic change could alter patterns of disturbance from herbivores and pathogens through: (1) direct effects on the development and survival of herbivores and pathogens; (2) physiological changes in tree defenses; and (3) indirect effects from changes in the abundance of natural enemies (e.g. parasitoids of insect herbivores), mutualists (e.g. insect vectors of tree pathogens), and competitors. Because of their short life cycles, mobility, reproductive potential, and physiological sensitivity to temperature, even modest climate change will have rapid impacts on the distribution and abundance of many forest insects and pathogens. We identify 32 syndromes of biotic disturbance in North American forests that should be carefully evaluated for their responses to climate change: 15 insect herbivores, browsing mammals; 12 pathogens; 1 plant parasite; and 3 undiagnosed patterns of forest decline. It is probable that climatic effects on some herbivores and pathogens will impact on biodiversity, recreation, property value, forest industry, and even water quality. Some scenarios are beneficial (e.g. decreased snow cover may increase winter mortality of some insect pests), but many are detrimental (e.g. warming tends to accelerate insect development rate and facilitate range expansions of pests and climate change tends to produce a mismatch between mature trees and their environment, which can increase vulnerability to herbivores and pathogens). Changes in forest disturbance can produce feedback to climate through affects on water and carbon flux in forest ecosystems; one alarming scenario is that climate warming may increase insect outbreaks in boreal forests, which would tend to increase forest fires and exacerbate further climate warming by releasing carbon stores from boreal ecosystems. We suggest a list of research priorities that will allow us to refine these risk assessments and adopt forest management strategies that anticipate changes in biotic disturbance regimes and mitigate the ecological, social, and economic risks. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Climate change; Herbivory; Pathogens; Forest epidemiology; Risk assessment; Disturbance

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1. Introduction

There are numerous mechanisms by which climate change could influence forest disturbance by herbivores and pathogens. Changes in temperature and precipitation can exert strong direct effects on the survival, reproduction, dispersal and geographic distribution of herbivores and pathogens. Changes in temperature, precipitation, solar radiation, and atmospheric CO₂ concentrations can alter tree physiology in ways that influence resistance to herbivores and pathogens. Other potentially important indirect effects include: (1) impacts of climate change on competitors and natural enemies that presently restrict the abundance of potential pests and pathogens; and (2) interactions among direct effects of climate change and other human effects on forests such as fragmentation, pollution, fire frequency, and the introduction of exotic organisms. Presumably, many potential consequences of climate change will be buffered by the resilience of forest communities to natural climatic variation. However, it is likely that at least some of the plausible scenarios involving herbivores and pathogens will result in significant perturbations to the forests with lasting ecological and socioeconomic impacts. We face a considerable challenge in assessing and mitigating these risks.

The consequences of climatic perturbations to the forests will depend upon the perturbations and the ecosystem. Perturbations of high intensity but low frequency (e.g. fires, hurricanes, and bark beetle epidemics) can be described as disturbances (Huston, 1994). Perturbations of low intensity but high frequency (e.g. a trend towards warmer, drier summers or moderate sustained levels of herbivory and fungal infection) tend to exert continued low-level pressures on ecosystems that are sometimes referred to as 'stress' (Underwood, 1989; Winner, 1994; Milchunas and Lauenroth, 1995), although the effects are not necessarily undesirable (e.g. may sometimes include an increase in tree defenses, Lorio, 1993; or an increase in forest productivity, Teskey, 1997). Climate change could also produce perturbations of intermediate intensity and frequency, such as

changes in climatic extremes (e.g. occasional droughts, hard freezes, and hot spells) and mild epidemics of pests and pathogens. Populations, communities, and ecosystems may differ in their resistance to the effects of perturbations and their ability to recover (Cottingham and Carpenter, 1994; Carpenter et al., 1995; Larsen, 1995). Populations with an evolutionary history of environmental stability may be most affected by perturbations (Bazzaz, 1983; Wilson and Keddy, 1986; Miao and Bazzaz, 1990; Clark, 1991; Parker et al., 1993). Ecosystems with low species diversity may be most sensitive to climatic extremes (Tilman, 1996) and ecosystems with low productivity require the most time to recover from perturbations (Moore et al., 1993; Huston, 1994). Perturbations are a natural feature of most ecosystems and are not intrinsically deleterious (Lorimer, 1980; Glitzenstein et al., 1986; Frelich and Lorimer, 1991; Attiwill, 1994). For example, intermediate levels of disturbance may often maximize species diversity (Connell, 1978; Huston, 1979, 1994; Luken et al., 1992; Wilson, 1994). However, disturbances that are different or more extreme than those that have been historically experienced by an ecosystem can result in ecosystem degradation that is self-reinforcing and irreversible, even when the disturbance abates (Rapport and Whitford, 1999). Natural and anthropogenic perturbations are a dominant consideration in forest management because of the consequences for community composition, biodiversity, landscape structure, natural resources, ecosystem processes, and aesthetics (Turner, 1987; Dayton et al., 1992; Mladenoff et al., 1993; Robertson et al., 1993; Siitonen and Martikainen, 1994; Fleming, 1996).

2. Current impacts

To keep the scope of this review manageable, our assessment of current impacts of forest herbivores and pathogens is focused on the special case of North America. However, many of the patterns and processes are common to forests throughout the world.

Table 1
A partial listing of herbivores that are significant agents of biological disturbance in North American forests

Syndrome	Herbivore	Hosts	Selected references ^a
Defoliation by Douglas-fir tussock moth	<i>Orygia pseudotsugata</i>	<i>Abies</i> spp., <i>Pseudotsuga</i> spp.	Mason (1996)
Defoliation by gypsy moths	<i>Lymantria dispar</i> ^c	<i>Quercus</i> spp., many other broadleaved trees and conifers	Williams and Liebhold (1995), Leuschner et al. (1996) Jones et al. (1998)
Defoliation by jack pine budworm	<i>Choristoneura pinus</i>	<i>Pinus banksiana</i>	Fleming et al. (2000)
Defoliation by spruce budworm	<i>Choristoneura fumiferana</i> , <i>C. occidentalis</i>	<i>Abies</i> spp., <i>Pseudotsuga</i> spp., <i>Picea</i> spp.	Royama (1984), Campbell (1989), Fleming and Shoemaker (1992) Wickman et al. (1992)
Defoliation by tent caterpillars	<i>Malacosoma</i> spp.	<i>Prunus</i> spp., <i>Populus</i> spp., <i>Betula</i> spp., <i>Nyssa</i> spp., other broadleaved trees	Clancy et al. (1993), Fleming (1996) Fleming et al. (2000)
Infestations by Asian longhorned beetle ^b	<i>Anoplophora glabripennis</i> ^c	<i>Acer</i> spp., <i>Ulmus</i> spp., <i>Populus</i> spp.	Rejmanek et al. (1987), Myers (1992), Lindroth et al. (1993) Roland (1993) Fleming et al. (2000) Cavey et al. (1998)
Infestations by bronze birch borer	<i>Agrilus anxius</i>	<i>Betula</i> spp.	Balch and Prebble (1940), Jones et al. (1993)
Infestations by woolly adelgids	<i>Adelges piceae</i> ^c , <i>A. tsugae</i> ^c	<i>Abies fraseri</i> , <i>A. balsamea</i> , <i>Tsuga</i> spp.	McClure (1989, 1991), Rabenold et al. (1998)
Infestations by Douglas-fir beetle	<i>Dendroctonus pseudotsugae</i> ^c	<i>Pseudotsuga menziesii</i>	Hadley and Veblen (1993), Paulson (1995) Ross and Solheim (1997), Negron (1998)
Infestations by mountain pine beetle	<i>Dendroctonus ponderosae</i>	<i>Pinus</i> spp.	Raffa (1988), Anhold et al. (1996), Powell et al. (1996) Stone and Wolfe (1996), Shinneman and Baker (1997) White and Powell (1997)
Infestations by pine engraver beetles	<i>Ips</i> spp.	<i>Pinus</i> spp.	Logan et al. (1998), Wilson et al. (1998) Schenk and Benjamin (1969), Sartwell et al. (1971) Klepzig et al. (1996), Raffa et al. (1998)
Infestations by southern pine beetle	<i>Dendroctonus frontalis</i>	<i>Pinus</i> spp., chiefly southern pine	Reeve et al. (1995), Price et al. (1997) McNulty et al. (1997), Conner et al. (1998)
Infestations by spruce beetle	<i>Dendroctonus rufipennis</i>	<i>Picea</i> spp.	Veblen et al. (1991), Holsten et al. (1995) Reynold and Holsten (1996), Packee (1997)
Infestations by western pine beetle	<i>Dendroctonus brevicornis</i>	<i>Pinus</i> spp., chiefly <i>P. ponderosa</i>	Liebhold et al. (1986)
Infestations by white pine weevil	<i>Pissodes strobi</i>	<i>Pinus</i> spp., <i>Picea</i> spp.	Bellocc and Smith (1995), Lavallee et al. (1996) Alfaro et al. (1997)
Browsing by deer, elk, hares, and moose	<i>Odocoileus</i> spp., <i>Cervus canadensis</i> , <i>Alces alces</i>	Many broadleaved trees and some conifers	Ross et al. (1970), Pease et al. (1979), Gill (1992) Rossow et al. (1997), Pastor et al. (1998)

^a General references: Johnson and Lyon (1991), Rosenberger and Smith (1997), USDA (1998).

^b Asian longhorned beetle is a recent introduction whose impact is currently limited to New York City and Chicago, but which has potential for significant impacts in the future to temperate deciduous forests throughout North America.

^c Introduced species.

Table 2
A partial listing of pathogens and parasites that are significant agents of biological disturbance in North American forests

Syndrome	Pathogen/parasite	Hosts	Selected references ^a
Annosum root rot	<i>Heterobasidion annosum</i>	Most conifers. Some broadleaved trees.	Livingston et al. (1983), Kirby et al. (1990)
Anthracnose leaf disease	<i>Discula destructiva</i> , <i>Glomerella cingulata</i> , <i>Colletotrichum gloeosporioides</i> , others	<i>Quercus</i> spp., <i>Fraxinus</i> spp., <i>Platanus</i> spp., <i>Cornus</i> spp.	Schwacke and Hager (1992), Baker et al. (1993) LaFlamme and Blais (1995), Stanosz and Guthmiller (1995) Meadows and Hodges (1996) Pearce (1996)
Armillaria root rot	<i>Armillaria</i> spp.	Broadleaved trees and conifers, e.g., <i>Acer</i> spp., <i>Picea</i> spp.	Dudt and Shure (1993), Stanosz (1993), Colby et al. (1995) Zarnoch et al. (1995), Britton et al. (1997)
Beech bark disease	<i>Nectria</i> spp. (and associated scale insects <i>Cryptococcus fagisuga</i> ^b and <i>Xylococculus betulae</i>)	<i>Fagus grandifolia</i> <i>Fagus grandifolia</i>	James et al. (1984), Mallett and Volney (1990) Mwangi et al. (1990), Entry et al. (1991) Houston (1992), Smith et al. (1992), Clinton et al. (1993) Filip (1994), Smith et al. (1994)
Butternut canker	<i>Sirococcus clavigignenti-juglandacearum</i>	<i>Juglans cinerea</i>	Rizzo et al. (1995), Wargo (1996)
Cedar decline	??		Shigo (1976), Gavin and Peart (1993), Houston (1994, 1998) Fleming et al. (2000)
Chestnut blight	<i>Cryphonectria parasitica</i> ^b	<i>Chamaecyparis nootkatensis</i> <i>Castanea dentata</i>	Harrison et al. (1998), Katovich and Ostry (1998) Fleming et al. (2000)
Dutch elm disease	<i>Ophiostoma novoulmi</i> ^b (and associated bark beetles <i>Hylurgopinus rufipes</i> and <i>Scolytus multistriatus</i> ^b) <i>Arceuthobium</i> spp.	<i>Ulmus</i> spp. <i>Pinus</i> spp.	Shaw et al. (1985), Hennon et al. (1992) Koonin et al. (1991), Foster et al. (1992a), McKeen (1995) Abrams et al. (1997), Havar and Anagnostakis (1998) Ruffner and Abrams (1998) Taylor et al. (1998), Fleming et al. (2000) Holmes (1980), Hansen and Somme (1994) Johnsen et al. (1994), Canterbury and Blockstein (1997) Hughes and Cass (1997)
Dwarf mistletoe			Sutherland et al. (1997), Fleming et al. (2000) Nowak and McBride (1992), Seamans and Gutierrez (1995) Bennetts et al. (1996)
Fusiform rust	<i>Cronartium quercuum</i>	<i>Pinus</i> spp., chiefly southern pine	Synder et al. (1996), Kipfmüller and Baker (1998) Walkinshaw and Barnett (1995), Dieters et al. (1996) Nelson et al. (1996), Doudrick et al. (1996)
Maple decline	??	<i>Acer sacharum</i>	Wilcox et al. (1996), Pye et al. (1997) Allen et al. (1992), Daoust et al. (1992); Auclair et al. (1996) Cote and Ouimet (1996), Darveau et al. (1997) Martel and Mauffette (1997) Hutchinson et al. (1998)

Table 2 (Continued)

Syndrome	Pathogen/parasite	Hosts	Selected references ^a
Oak wilt disease	<i>Ceratocystis fagacearum</i>	<i>Quercus</i> spp.	Appel (1995), Nair (1996), McDonald et al. (1998)
Pitch canker	<i>Fusarium subglutinans</i> ^b	<i>Pinus</i> spp.	Hoover et al. (1996), Gordon et al. (1996), Storer et al. (1997) Storer et al. (1998), Gordon et al. (1998)
Procera and black stain root disease	<i>Leptographium</i> spp.	Many conifers, e.g., <i>Pinus</i> spp	Harrington and Cobb (1983), Highley and Tattar (1985) Raffa and Smalley (1988), Parmeter et al. (1989) Nevill and Alexander (1992a,b,c)
Spruce decline, fir decline	??	<i>Picea rubra</i> , <i>Abies fraseri</i>	Paine and Hanlon (1994), Klepzig et al. (1995) Klepzig et al. (1996), Nevill et al. (1995) Peart et al. (1992), Eagar and Adams (1992)
White pine blister rust	<i>Cronartium ribicola</i> ^b	Five-needle pines, e.g., <i>Pinus strobus</i> <i>P. albicaulis</i>	Nodvin et al. (1995), Battles and Fahey (1996) Fenn et al. (1998), Rabenold et al. (1998) Hunt and von Rudloff (1977), Hunt and Meagher (1989) Keane et al. (1990), Hamelin et al. (1995) Tomback et al. (1995), Baskin (1998) Fleming et al. (2000)

^a General references: Hepting (1971), Gibbs and Wainhouse (1986), Sinclair et al. (1987), Nebeker et al. (1995), Holmer and Stenlid (1996), USDA (1998).

^b Introduced species.

2.1. Current regional variation

Herbivores and pathogens exert strong impacts within every major forest type of North America (Tables 1 and 2). Bark beetles (Scolytidae) are among the largest source of natural disturbance in pine forests throughout the continent (Raffa, 1988; Price et al., 1997; Logan et al., 1998). Fungal root diseases, fusiform rust, and dwarf mistletoe can have further effects on pine forests (James et al., 1984; Filip, 1994; Nebeker et al., 1995; Walkinshaw and Barnett, 1995; Dieters et al., 1996; Klepzig et al., 1996; Meadows and Hodges, 1996; Synder et al., 1996; Kipfmüller and Baker, 1998). White pine blister impacts pine forests from New England to the west coast (Hunt and Meagher, 1989; Keane et al., 1990; Hamelin et al., 1995; Tomback et al., 1995; Baskin, 1998). Pitch canker disease is threatening endemic populations of pine trees in California (Storer et al., 1997), especially Monterey pine (*Pinus radiata*), which is probably the second most extensively planted tree species in the world after eucalyptus. The spruce budworm and spruce beetle are dominant sources of natural disturbance throughout the boreal forests (Royama, 1984; Vebler et al., 1991; Fleming and Shoemaker, 1992; Holsten et al., 1995; Fleming, 1996; Packee, 1997). The Douglas-fir tussock moth and western spruce budworm affect coniferous forests of the Pacific north-west (Wickman et al., 1992; Mason, 1996). There is currently a yellowheaded spruce sawfly outbreak in Newfoundland. Woolly adelgids (scale insects) have recently produced extensive mortality within alpine spruce/fir forests of the southern Appalachians and within Hemlock forests of the Atlantic states (McClure, 1989; Rabenold et al., 1998).

Within this century, the north-temperate deciduous forests of North America have been dramatically altered by forest tent caterpillars, gypsy moths, chestnut blight, Dutch elm disease, and beech bark disease (Foster et al., 1992a; Gavin and Peart, 1993; Johnson, 1994; McKeen, 1995; Leuschner et al., 1996; Abrams et al., 1997; Hughes and Cass, 1997; Ruffner and Abrams, 1998). Oak wilt threatens American oaks and is causing considerable damage in the midwest

(Appel, 1995; Nair et al., 1996). Butternut trees are decreasing dramatically because of butternut canker (Harrison et al., 1998; Katovich and Ostry, 1998). The bronze birch borer is a key determinant of the southern distribution limits of paper birch (Balch and Prebble, 1940; Jones et al., 1993). Browsing by deer, moose, elk, and hares have profound effects on species composition and forest structure throughout North America (Ross et al., 1970; Pease et al., 1979; Gill, 1992; Rossow et al., 1997; Pastor et al., 1998). Several dozen other species of herbivores and pathogens can also exert striking impacts on forests (Sinclair et al., 1987; Johnson and Lyon, 1991; Belsky and Blumenthal, 1997). The causes for dramatic patterns of maple decline in the Great Lakes states, red spruce decline in New England, and cedar decline in Alaska are still largely unknown and may be attributable to some undescribed process involving pathogens (Manion and Lachance, 1992).

2.2. Ecological importance

Any impacts of climate change on forest disturbance regimes can have far-reaching ecological consequences. Previous reviews all raise the specter of significant effects on forest biodiversity (Botkin and Nisbet, 1992; Franklin et al., 1992; Hartshorn, 1992; Murphy and Weiss, 1992; Devall and Parresol, 1997; Coley, 1998). Most tree species support a community of other organisms (e.g. breeding birds, specialist Lepidoptera, and many others) so the loss of any tree species, such as the virtual elimination of chestnut by chestnut blight, can reduce biodiversity. Most of the indirect consequences of disturbance from herbivores and pathogens must go unrecorded in the scientific literature. Nonetheless, there are many documented examples. Southern pine beetles eliminate nesting trees of the endangered red-cockade woodpecker (Conner et al., 1998). Woolly adelgids led to losses of endemic birds in the southern Appalachians (Canterbury and Blockstein, 1997). Dutch elm disease reduced nesting cavities for waterfowl in New Brunswick (Johnsen et al., 1994). Any disturbances that increase forest fragmentation can lower the reproductive success of

migrant birds (Robinson et al., 1995). Scale insects of pinyon pine have negative effects on mycorrhizal fungi (Gehring et al., 1997). White pine blister rust in the Rocky Mountains is threatening bear populations that depend upon seeds of white bark pine (Baskin, 1998). Forest decline of deciduous hardwoods in the Great Lakes region is associated with declining diversity of Lepidoptera (Martel and Mauffette, 1997). Herbivores and pathogens may also exert important effects on ecosystem processes such as carbon flux and nutrient cycling. Forest soil systems vary on a fine scale depending on tree species composition (Finzi et al., 1998a,b; Ferrari, 1999). So when herbivores and pathogens alter tree species composition they can also alter forest biogeochemistry. For example, mortality of hemlocks from the hemlock woolly adelgid is associated with increases in nitrogen mineralization rates, nitrogen turnover, and possibly nitrate leaching (Jenkins et al., 1999). In general, the potentially deleterious effects of climate change on forest disturbance from herbivores and pathogens tend to be underestimated in ecological risk assessments (Loehle and Leblanc, 1996).

Disturbance from herbivores and pathogens can also have beneficial effects. Moderate disturbance from bark beetle attacks can increase the diversity of understory plants (Stone and Wolfe, 1996). Forest disturbance associated with Dutch elm disease, drought, and windstorms conspicuously increased the abundance of three bird species, even while decreasing the abundance of two other bird species (Canterbury and Blockstein, 1997). Parasitism of pine by dwarf mistletoe provides nesting habitat for spotted owls (Seamans and Gutierrez, 1995) and can increase overall abundance and diversity of birds (Bennets et al., 1996). Maintenance of forest biodiversity may depend upon maintenance of natural disturbance regimes (Noss, 1991). Forests both sustain biodiversity and depend upon it. A single old-growth forest in Oregon contains at least 3400 species of arthropods, which collectively contribute to ecosystem function in ways that are just being elucidated (Lattin, 1993). Many species of arthropods and fungi that inhabit old growth forests exploit dead wood for their resource base

and habitat. Consequently, some time-honored practices to minimize pests and pathogens may actually have deleterious effects on forest communities. Thinning treatments in response to beech bark disease led to a decrease in the diversity of beneficial mycorrhizal fungi (Mihal, 1995). Similarly, modern ('efficient') logging practices that leave little wood within the forests can dramatically reduce arthropod diversity (Siitonen and Martikainen, 1994; Siitonen et al., 1996; Kaila et al., 1997; Martikainen et al., 1999).

2.3. *Economic impacts*

The economic costs of forest herbivores and pathogens are difficult to reduce to a single estimate because: (1) we only have estimates of lost market value for a fraction of economically important pest species in North America, perhaps 1 in 20; (2) we only have defensible estimates of non-market impacts for a few pests in a few locations; (3) we know of no estimates of opportunity costs — even though we can be quite certain that the US timber industry would be worth more each year if the eastern forests still contained chestnut trees, or if marketable white pine could be grown in the areas plagued with pine weevils; and (4) we cannot yet estimate the cost of increased risks of catastrophic impacts — even though we would probably be willing to pay for insurance against, for example, the extinction of native Monterrey pine from pitch canker, major forest fires following bark beetle outbreaks, or contamination of drinking water from the combination of atmospheric nitrogen deposition and forest pathogens.

Nonetheless, the economic costs that have been quantified are considerable. The value of timber and pulpwood lost to the southern pine beetle can reach \$237 million/year (Price et al., 1997). Losses to the western pine beetle can reach \$100/acre (Liebhold et al., 1986). The value of slowing the spread of gypsy moth defoliations has been estimated at > \$51 million/year (Leuschner et al., 1996). Losses of southern pine to fusiform rust are \$20–\$40 million/year (Pye et al., 1997). The timber value in 1912 of standing chestnut trees killed by chestnut blight in Pennsylvania,

West Virginia, and North Carolina alone was approximately \$82 million (USDA, 1991; in fact, chestnut blight virtually eliminated chestnut trees from forests throughout eastern North America). Approximately \$150 million has been spent in a largely futile effort to thwart white pine blister rust (Baskin, 1998). The total costs of herbivores and pathogens are much greater if we include the non-market impacts. For example, loss to residential property value from gypsy moths has been estimated at \$1175/acre; the value of a campground in the Pacific north-west drops by approximately \$1725 when 25 trees are killed by the Douglas-fir tussock moth; mountain pine beetle damage in the Targhee National Forest of Idaho costs approximately \$564 000/year in losses to consumer surplus and local expenditures; southern pine beetle damage near reservoirs of east Texas cost approximately \$1–\$4 million in recreation benefits; and residents of an 800 000 square mile area in the southern Appalachians were willing to pay \$11–\$36/household for protection of spruce-fir forests that are threatened by wooly adelgids (Rosenberger and Smith, 1997). The areal extent of significant impacts from forest herbivores and pathogens can exceed 20 000 000 ha in the United States alone (USDA, 1998).

2.4. *Impacts of human activity*

Human activities can intensify or mitigate forest disturbance from herbivores and pathogens. Nine of 31 syndromes in Tables 1 and 2 are associated with introduced species and there are hundreds more prospective pests that could show up in North American forests at any time (USDA, 1991; Niemelä and Mattson, 1996). Loss of genetic diversity in tree populations (e.g. from clonal propagation) increases the risks from pathogens (Steiner, 1998). Fire management is another important factor. Fires can promote outbreaks of pests and pathogens (Wood, 1982; Wingfield, 1983; Dixon et al., 1984; Gara et al., 1984; Geiszler et al., 1984; Thomas and Agee, 1986; Matlack et al., 1993; Ehnstrom et al., 1995) and pests and pathogens can increase the probability of fires (Geiszler et al., 1980; Wood, 1982; Raffa and

Berryman, 1987). In other situations, fires can reduce pest outbreaks and promote beneficial mycorrhizae (Hadley and Veblen, 1993; Mutch et al., 1993; Herr et al., 1994; Jurgensen et al., 1997; Kipfmüller and Baker, 1998). Herbivory can sometimes reduce the probability of fires (Belsky and Blumenthal, 1997). Fire suppression, in combination with insects and disease, can lead to the loss of keystone tree species (Keane et al., 1990; Tomback et al., 1995; Williams, 1998). Interactions between insects and fire can be a primary determinant of ecosystem structure and function (Showalter et al., 1981; Baker and Veblen, 1990). Anything that affects the species composition and age structure of tree communities can influence the epidemiology of forest pests (Menges and Loucks, 1984; Showalter and Turchin, 1993). Pest populations may commonly increase with increasing disturbance because disturbance tends to favor fast-growing plant species, which tend to be poorly defended against herbivores (Coley et al., 1985). Air pollution, atmospheric nitrogen deposition, and forest fragmentation are other human activities that can impact disturbance from herbivores and pathogens (Roland, 1993; Frankland et al., 1994; Klironomos and Allen, 1995; Nodvin et al., 1995; Jung and Blaschke, 1996; Kozlov et al., 1996; Meadows and Hodges, 1996; Britton et al., 1997; Redak et al., 1997; Erelli et al., 1998; Roth and Fahey, 1998).

2.5. *Feedback to climate from herbivores and pathogens*

Herbivores and pathogens can alter the species composition and size structure of forests, which can in turn affect ecosystem processes such as evapotranspiration, CO₂ flux, and heat transfer, thereby creating feedbacks to climate (Shukla et al., 1990; Aber and Federer, 1992; Kurz and Apps, 1994; Bonan et al., 1995; Starfield and Chapin, 1996; Otto and Upchurch, 1997). Effects of herbivores and pathogens on forest fires can create additional feedback to climate (Smith and Shugart, 1993; Kasischke et al., 1995).

3. Potential impacts of climate change

3.1. Direct effects on herbivores and pathogens

Climate, especially temperature, exerts strong direct effects on herbivores (Ayres, 1993). A 1931 review paper cited over 1000 scientific papers describing the effects of climate on insects (Uvarov, 1931). Thousands more papers have been published since then. At least in temperate and boreal forests, increases in summer temperatures will generally accelerate the development rate of insects (and other poikilotherms) and will commonly increase their reproductive potential (Sharpe and DeMichele, 1977; Asante et al., 1991; Porter et al., 1991). In Finland, species richness of macrolepidoptera increases from north to south by ≈ 93 species per increase in mean summer temperature of 1°C (Virtanen and Neuvonen, in press). The vast majority of forest insects have geographic distributions that are more limited

than that of their host plants, and have high mobility, so their distributions could change very rapidly in response to climatic amelioration (MacLean, 1983; Ayres and Scriber, 1994; Virtanen and Neuvonen, in press). Warmer winter temperatures frequently increase overwinter survival (Marcais et al., 1996; Virtanen et al., 1996, 1998). Even southerly distributed insects could benefit from increasing temperatures. For example, direct physiological measurements and published records of mortality in wild populations indicate that air temperatures of -16°C or less result in almost 100% mortality of the southern pine beetle (Ungerer et al., 1999). Such temperatures are common in the current northern range of the southern pine beetle ($\text{PLL} > 0.50$ in Fig. 1), which indicates that this species occurs as far north as possible given winter temperatures. For this and many other insect species, climatic warming may increase outbreaks in the northern and/or alpine regions of their current distribu-

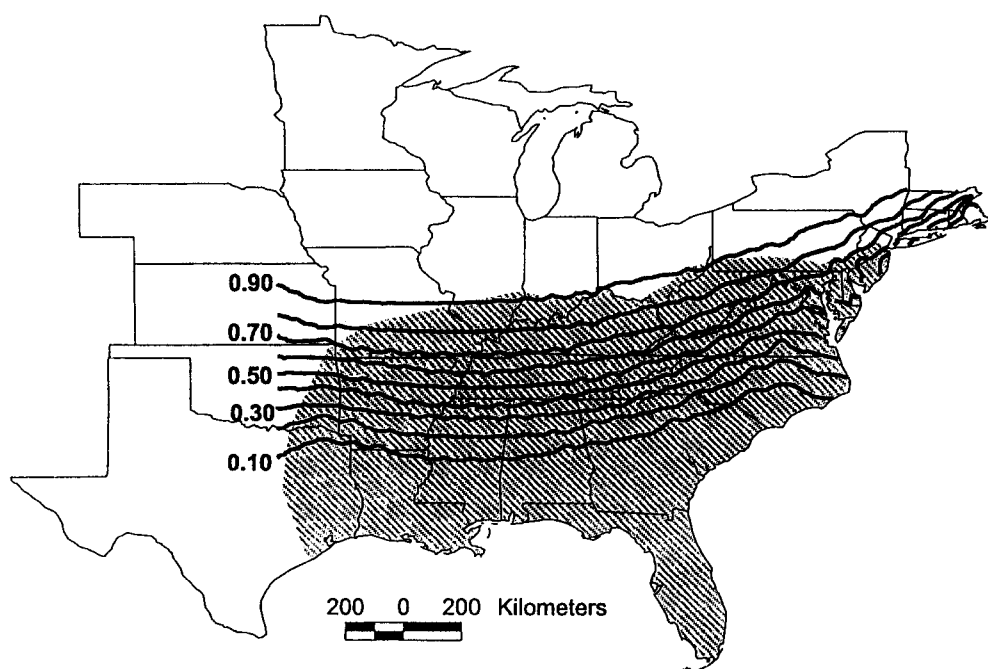


Fig. 1. Annual probability of reaching the lower lethal temperature for the southern pine beetle, *Dendroctonus frontalis* ($\approx -16^{\circ}\text{C}$ air temperature). Maximum recorded *D. frontalis* distribution is shown as the shaded area. The northern limits for economically meaningful outbreaks is ≈ 300 km farther south, where the annual probability of winter mortality is ≈ 0.5 . From Ungerer et al. (1999).

tions (Williams and Liebhold, 1995; Virtanen et al., 1996, 1998; Ungerer et al., 1999) and decrease outbreaks in the southern regions of distributions. Climatic warming may also facilitate the establishment of exotic species. Insect species that overwinter as eggs or adults may benefit the most from climatic amelioration (Virtanen and Neuvonen, in press).

Warmer winter temperatures will tend to decrease the food requirements of browsing mammals (homeotherms) such as deer, moose, and snowshoe hares (Moen, 1976), which could reduce their per capita impact on forest vegetation, but because their population size tends to be dictated by winter survival (Bartmann et al., 1992), populations would probably increase as a result of warmer winter temperatures, which would increase their collective impact on forests. Warmer winter temperatures and decreased snow depth could allow whitetail deer to extend their northern distributions farther into the boreal forests than they presently occur, which would increase the relative abundance of unpalatable tree species (Gill, 1992; Anderson and Katz, 1993; Abrams, 1998). Conversely, decreases in snow depth may decrease the overwinter survival for many forest insects that overwinter in the forest litter where they are insulated by snow cover from potentially lethal low temperatures.

Changes in temperature, precipitation, soil moisture, and relative humidity influence the sporulation and colonization success of some forest pathogens (Brasier, 1996; Lonsdale and Gibbs, 1996; Chakraborty, 1997; Houston, 1998) and tree-damaging storms can open wounds that allow entry of pathogens (Pearce, 1996; Irland, 1998). Additional effects could be produced by changes in thunderstorm activity because trees that are struck by lightning frequently act as foci for the initiation of bark beetle infestations (Flamm et al., 1993). In some cases, changes in climatic variability may be as important for forest organisms as changes in the average climate (Wigley, 1985; Hodkinson et al., 1998; Ruel and Ayres, 1999). Simulations with the southern pine beetle indicated that changes in the interannual variation in minimum annual temperatures could

influence beetle populations across > 200 km of latitude (Fig. 2).

3.2. Indirect effects through changes in plant resistance

In addition to the direct effects of climate change on herbivores and pathogens, other effects may result from climate-induced changes in tree physiology and tree defenses (Landsberg and Smith, 1992; Ayres, 1993; Coley, 1998). Changes in cloud cover, temperature, precipitation, soil nutrients, and CO₂ can all impact the primary and secondary chemistry of plant tissue, which influences nutritional suitability for herbivores. Physiologically-based plant allocation models offer a good foundation for predicting effects on constitutive plant chemistry (Herms and Mattson, 1992; Ayres, 1993): e.g. reduced irradiance or increased soil nutrients tend to reduce concentrations of secondary metabolites; increased CO₂ tends to reduce nitrogen content and sometimes increase secondary metabolite concentrations; and moderate water deficits tends to increase secondary metabolites while extreme water deficits decrease secondary metabolites. Temperature changes can influence the development rate of herbivores, and perhaps pathogens, relative to ephemeral tissue on which they depend (e.g. expanding leaves; Ayres, 1993). Understanding geographic patterns in tree defenses is essential for predicting geographic patterns in future disturbances from herbivores and pathogens, but most data come from relatively short-term manipulations of resource availability at a single site (e.g. Wilkens et al., 1997). It is possible that geographic patterns in tree defenses match the temporal responses of trees to short-term manipulations of resource availability, in which case we already have the basis for predicting geographic patterns in tree defenses. However, this hypothesis remains untested and other relationships are possible (Fig. 3). Depending upon the physiological acclimatization of trees, and the genetic variation among tree populations, forests that develop in regions of, for example, low precipitation or high mineral nutrients, may or may not have the

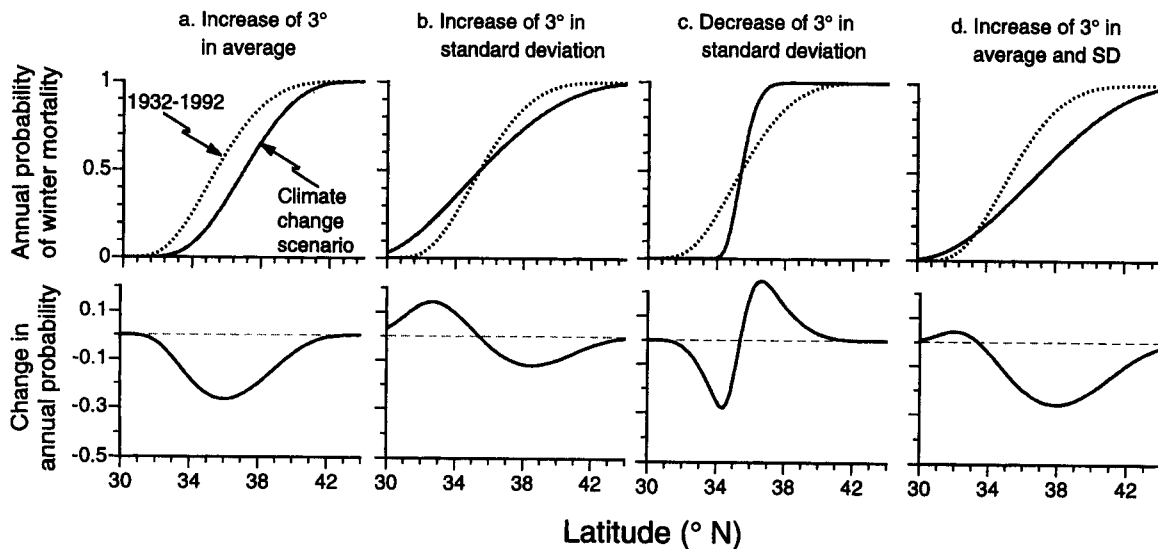


Fig. 2. Changes in the annual probability of reaching lower lethal temperatures (PLLT) for the southern pine beetle, *Dendroctonus frontalis* under four scenarios of climate change (a–d). Baseline function (dotted line in upper figure) was developed from 60 years of daily climate records at 33 sites. Bottom figure indicates the expected change in the annual probability of beetle mortality associated with each scenario. When the average minimum annual temperature was increased by 3°C (scenario a), the annual probability of winter mortality was generally decreased (by up to 0.27 at 36.0°N). If the standard deviation among minimum annual temperatures was increased by 3°C with the average held constant (scenario b), PLLT was increased by up to 0.14 (at 32.6°N) and decreased by up to 0.12 (at 38.6°N). When the standard deviation was decreased by 3°C (scenario c), PLLT decreased by 0.28 at 34.4°N and then increased by 0.25 at 36.6°N. When both the average and the standard deviation were increased by 3°C (scenario d), PLLT was decreased by up to 0.26 (at 38.0°N) and the effects occurred farther north and over a broader range of latitudes than the changes associated with an increase in the average alone (PLLT was markedly decreased over 465 km). Under this scenario, regular outbreaks could occur up to 170 km north of where they presently occur (to northern Missouri, Illinois, Indiana, Ohio, Pennsylvania, and New York) and outbreaks could sometimes occur as far north as the pine forests of Minnesota, Wisconsin, Michigan and New England. The standard deviation in minimum annual temperature varies by up to 2.5°C within the southeastern US, so a scenario of 3°C change does not seem unrealistic, but we know of no explicit predictions regarding possible changes in climatic variability. From Ungerer et al. (1999).

resistance to herbivores and pathogens that would be predicted from manipulations of water or nutrients.

Although there is abundant evidence that phenotypic changes in plant physiology can affect herbivores (reviewed in Herms and Mattson, 1992), comparable studies with pathogens are few and results are equivocal (Matson and Waring, 1984; Christiansen, 1992; Christiansen and Fjone, 1993; Kyto et al., 1996; Britton et al., 1997; Chakraborty et al., 1998). Plant defenses against pathogens, like defenses against herbivores, involve the synthesis of biologically active secondary metabolites (Julie and Daniel, 1995; Pearce, 1996), but plant pathology usually empha-

sizes genetic regulation of host–pathogen interactions rather than environmental effects (Smith, 1996; Glazebrook et al., 1997; Buell, 1998; but see Loomis and Adams, 1983). For aggressive pathogens such as Dutch elm disease and Chestnut blight, climatic effects on tree physiology are apparently trivial compared to the importance of tree genetics and pathogen dispersal. For other pathogens, such as *Annosum* root rot, *Armillaria* root rot, black stain root diseases, and anthracnose leaf disease, tree physiological condition may be quite important (see references in Table 2), and climate change may affect their epidemiology. However, it is difficult to predict how specific climate scenarios will influence tree resistance

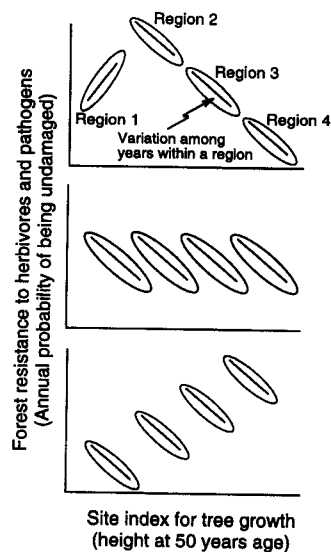


Fig. 3. Alternative hypotheses relating spatial and temporal patterns in the secondary metabolism of pine trees. UPPER: Spatial patterns could be driven by the same physiological principles as temporal patterns and follow the same patterns as have been demonstrated in experimental manipulations of water availability (e.g. Reeve et al., 1995) and mineral nutrients (e.g. Wilkens et al. 1997). This would imply that: (1) the effects of climatic variation on tree resistance will depend upon the magnitude of change and the initial conditions; and (2) we can expect similar effects of short-term climatic variation and directional climatic change. MIDDLE and LOWER: Spatial variation runs counter to short-term phenotypic responses of trees. The middle scenario would result if trees acclimatize (and/or adapt) to average resource availability (Bloom et al., 1985); this scenario predicts no geographic patterns in future pest outbreaks due to regional variation in climate. The lower scenario could result if forests that develop under different climates are quite different in the extent of crown closure and root competition; this scenario would indicate that the plant stress hypothesis (Larsson, 1989) accurately predicts variation in tree resistance at coarse geographic scales but not within-site responses to variation among years.

to pathogens. We need physiological models that can provide these predictions. The resource allocation models developed to understand plant-herbivore interactions (Ayres, 1993) provide a possible starting point, but may be unsatisfactory because plant defenses against pathogens tend to involve rapid inducible responses, while resistance against herbivores frequently depends upon constitutive defenses. Little is known about how environmental effects on tree physiology influ-

ence the inducible responses that are relevant to pathogens (i.e. signal recognition, generation of phytoalexins and reactive oxygen species, hypersensitive responses, callus growth, and systemic acquired resistance; Kobayashi et al., 1995; Doke et al., 1996; Hammond-Kosack et al., 1996; Mehdy et al., 1996; Bolwell and Wojtaszek, 1997; Greenberg, 1997; Kuc, 1997; Wojtaszek, 1997). However, some of the extensive agricultural literature must be relevant (e.g. evidence for the importance of temperature on hypersensitive responses; Valkonen, 1997; Moury et al., 1998; Tadege et al., 1998; Yang et al., 1999).

3.3. Indirect effects through other community interactions

Climate change could further impact the epidemiology of herbivores and pathogens through affects on other organisms within the community. This is particularly clear for the numerous disease syndromes that involve both insects and pathogens (Hatcher, 1995; Paine et al., 1997). For example, the distribution of Dutch elm disease could be influenced by climatic effects on the beetle that transports it (Hansen and Somme, 1994). The westward expansion of beech bark disease may have slowed because of some ecological constraint on the scale insects that are required by the pathogenic fungi to enter the tree (Houston, 1998). The spread of the pitch canker will depend in part upon the ecology of its insect vectors (Hoover et al., 1996; Storer et al., 1998).

Many of the herbivores in Table 1 are 'pests' because their population dynamics produce cyclical outbreaks. Population cycles generally result from biological interactions with other species, often natural enemies, that produce delayed density-dependence (Turchin and Taylor, 1992; Turchin et al., 1999). For example, population cycles of the southern pine beetle might be the result of delayed feedback from a specialized beetle predator (Reeve et al., 1995), or from a bluestain fungus that outcompetes other fungi that are fed upon by the beetle larvae (Lombardero et al., submitted). Population cycles of gypsy moths may result from interactions with mice that feed upon host plant acorns and prey

upon moth pupae (Jones et al., 1998) and/or nuclear polyhedral viruses that become more or less pathogenic to caterpillars depending upon inducible changes in oak leaf tannins (Foster et al., 1992b). For such systems, any direct or indirect effects of climate change on the species or processes that produce delayed density-dependence could make pest population dynamics more or less cyclical, with consequences for forest disturbance regimes. Identifying species interactions that produce population cycles is necessary to evaluate whether or not climate changes will alter the population dynamics. Understanding species interactions is also necessary to predict secondary ecological impacts of outbreaks. For example, the mice that interact with gypsy moths also happen to be hosts of the tick that carries the spirochaete bacteria that causes Lyme disease, so the epidemiology of Lyme disease in humans could be affected by anything that affects the population dynamics of gypsy moths (Jones et al., 1998).

Forest soil communities are also likely to sustain indirect effects from herbivores and pathogens. Herbivory and other environmental effects on trees can influence the extent and type of mycorrhizal infection in tree roots (Gehring and Whitham, 1994, 1995; Klironomos and Allen, 1995; Power and Ashmore, 1996; Gehring et al., 1997, 1998). This could beget additional disease because mycorrhizae compete with saprophytic fungi, some of which are opportunistic pathogens of living trees (Klironomos et al., 1996).

4. Research priorities

The following are suggested priorities for a research program to assess and mitigate the risks to forests of climatic effects on herbivores and pathogens. This research program should anticipate the possibility of important variation among regions in the magnitude and direction of future changes in forest disturbance, but at the same time strive to develop and test general theoretical models that have applicability beyond specific tree-pest interactions in specific regions.

- Identification of focal herbivores and pathogens that are likely to be key agents of forest disturbance in the next 50 years. Tables 1 and 2 are intended as a starting point for this task. This objective will be facilitated by:
 - the development and testing of general theoretical principles that predict the sensitivity of various epidemiological syndromes to environmental change; and
 - continue and expand integrated continental surveys of the abundance and impacts of forest herbivores and pathogens. These immensely valuable surveys have been compiled for some years by the US Forest Service and Canadian Forest Service (Evans et al., 1995; USDA, 1998). These qualitative surveys should be continued and expanded to include some efforts toward better quantification through the development of statistically rigorous field sampling protocols (e.g. Scott, 1998).
 - Improved understanding of the direct environmental effects of temperature and moisture on focal herbivores and pathogens. Ideally, conclusions should be expressed within a modeling framework that: (1) predicts regional patterns in abundance using historical climatic data and scenarios of projected climates; and (2) validates conclusions with geographical sampling programs.
 - Improved understanding of the effects of temperature, moisture, irradiance, CO₂, and mineral nutrient availability on tree secondary metabolism. Of these, temperature and moisture may require the most additional research (Ayres, 1993). Plant allocation theory already allows many reliable predictions of temporal variation in constitutive secondary metabolism, but research is needed to evaluate whether these models can also predict: (1) spatial variation in constitutive tree resistance (Fig. 3); and (2) spatial and temporal variation in inducible tree resistance (especially against pathogens).
 - Experimental studies of the effects of tree physiology on forest pathogens.
 - Descriptive and experimental studies of the epidemiology of focal herbivores and pathogens at the geographic margin of regions where they currently exert significant distur-

bance. One result should be an improved characterization of pathogen population dynamics to evaluate whether they tend to exhibit population cycles, as do many of the focal herbivores.

- Elucidation of the specific community interactions that produce delayed density-dependent feedback in focal herbivores and pathogens that exhibit population cycles.
- Improved understanding of interactions and feedback between forest fires and biological disturbance from herbivores and pathogens.
- Descriptive and experimental studies of the consequences of disturbance from herbivores and pathogens for forest structure and biodiversity. There is a need for general theoretical models that can predict consequences for different forest types of different classes of disturbance.
- Development of strategies for maintaining the genetic diversity of tree populations. This will be a critical determinant of future patterns in the epidemiology of forest pathogens.
- Refined predictions of future climatic patterns in precipitation, relative humidity, and climatic variance. This will be facilitated if biologists can specify the climatic parameters that are relevant to focal herbivores and pathogens (e.g. mid-summer precipitation or interannual variation in minimum annual air temperature; Figs. 1 and 2).
- Refined predictions of future patterns in mineralization rates and nutrient availability in forests. Nutrient availability has strong predictable effects on tree resistance to herbivores and pathogens, and nutrient availability is likely to change in many forests as a result of climate change, but for now we cannot even predict the direction of changes in nutrient availability.

5. Conclusions

An extensive body of scientific literature suggests many scenarios by which climate change could significantly alter patterns of disturbance

from forest herbivores and pathogens. It should be anticipated that some types of disturbances will increase overall, some will decrease overall, and others will shift in their geographic occurrence; in all these cases, there are potentially important ecological and socioeconomic consequences (Ayres and Reams, 1997). Strong deleterious impacts are possible for forestry economics, biodiversity, and landscape aesthetics. There could be feedback to climate from alterations of forest composition and resulting changes in ecosystem attributes such as water flux and carbon pools. Given the evidence already available, the gravity of potential consequences, and the likelihood that forest management practices will influence the outcome, it is prudent to treat these risks very seriously. The greatest challenge at present is to assess the full spectrum of scenarios, identify the biological systems and geographic regions that face the greatest risks, and evaluate how specific forest management practices can mitigate the risks. Satisfying the research objectives that are outlined here would go a long way towards meeting this challenge.

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