

Consequences of climate change for biotic disturbances in North American forests

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Abstract. About one-third of North America is forested. These forests are of incalculable value to human society in terms of harvested resources and ecosystem services and are sensitive to disturbance regimes. Epidemics of forest insects and diseases are the dominant sources of disturbance to North American forests. Here we review current understanding of climatic effects on the abundance of forest insects and diseases in North America, and of the ecological and socioeconomic impacts of biotic disturbances. We identified 27 insects (6 nonindigenous) and 22 diseases (9 nonindigenous) that are notable agents of disturbance in North American forests. The distribution and abundance of forest insects and pathogens respond rapidly to climatic variation due to their physiological sensitivity to temperature, high mobility, short generation times, and high reproductive potential. Additionally, climate affects tree defenses, tree tolerance, and community interactions involving enemies, competitors, and mutualists of insects and diseases. Recent research affirms the importance of milder winters, warmer growing seasons, and changes in moisture availability to the occurrence of biotic disturbances. Predictions from the first U.S. National Climate Assessment of expansions in forest disturbances from climate change have been upheld, in some cases more rapidly and dramatically than expected. Clear examples are offered by recent epidemics of spruce beetles in Alaska, mountain pine beetle in high-elevation five-needle pine forests of the Rocky Mountains, and southern pine beetle in the New Jersey Pinelands. Pathogens are less studied with respect to climate, but some are facilitated by warmer and wetter summer conditions.

Changes in biotic disturbances have broad consequences for forest ecosystems and the services they provide to society. Climatic effects on forest insect and disease outbreaks may foster further changes in climate by influencing the exchange of carbon, water, and energy between forests and the atmosphere. Climate-induced changes in forest productivity and disturbance create opportunities as well as vulnerabilities (e.g., increases in productivity in many areas, and probably decreases in disturbance risks in some areas). There is a critical need to better understand and predict the interactions among climate, forest productivity, forest disturbance, and the socioeconomic relations between forests and people.

Key words: atmospheric drivers; bark beetles; defoliators; economic impact; ecosystem interactions; forest health management; greenhouses gases; outbreak; pathogens.

INTRODUCTION

All forests are products of their disturbance regimes. Biotic disturbances from outbreaks of insects and diseases are globally important agents of change in forest landscapes (Dale et al. 2001, Seppälä et al. 2009). Organisms that kill or damage trees play key roles in forest dynamics and composition, wildlife and biodiversity, and in biophysical and biogeochemical processes, including carbon sequestration and water cycling (Veblen et al. 1991, Adams et al. 2010, Boon 2011, Hicke et al. 2012a). However, changes in the location, severity, and form of biotic disturbance can alter forest ecosystems relative to historical norms and disrupt interactions between people and forests. This will be especially true if tree-killing insects and diseases

promote destabilizing positive feedbacks with other sources of forest disturbances (e.g., wildfires, drought, biological invasions, and human conversion of forested land to other uses; Jenkins et al. 2008, Adams et al. 2010, Simard et al. 2011). Understanding how these disturbances will change in the future as a result of various drivers, including climate change, is therefore critical for anticipating effects and adapting to them.

It is one of the oldest theories in ecology that climate affects insects and diseases (e.g., Anonymous 1665), and recognition of contemporary climate change has motivated a surge of scientific inquiry into climatic effects on the extent and severity of forest disturbances by insects and diseases (Fig. 1; reviewed by Ayres and Lombardero 2000, Volney and Fleming 2000, Dale et al. 2001, Boland et al. 2004, La Porta et al. 2008, Dukes et al. 2009, Sturrock et al. 2011, Klapwijk et al. 2012). Multiple reviews have been written describing the general effects of climatic variation on the physiology, distribution, and

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FIG. 1. Annual number of refereed articles published worldwide on forest biotic disturbances that address the role of climate as a driver of disturbance. The search criteria were: (climate OR temperature) AND forest AND (insect OR pathogen OR disease). Search results were refined further into the subject areas: environmental sciences and ecology (data source: Web of Knowledge, Thomson Reuters, Philadelphia, Pennsylvania, USA).

ecology of insects (or terrestrial poikilotherms in general; Bale 2002, Deutsch et al. 2008, Bale and Hayward 2010, Bentz et al. 2010, Bradshaw and Holzapfel 2010, Kingsolver et al. 2011, Huey et al. 2012, Klapwijk et al. 2012), as well as pathogens (Coakley et al. 1999, Harvell 2002, Desprez-Loustau et al. 2006, Sturrock et al. 2011). The reviews that focus specifically on climate change effects on biotic disturbances within forests typically either consider only one group of disturbance agents (Volney and Fleming 2000, Bentz et al. 2010, Sturrock et al. 2011, Klapwijk et al. 2012) or a limited geographical area (Boland et al. 2004, Dukes et al. 2009). The first National Climate Assessment in 2000 (published in Ayres and Lombardero 2000) considered climate change effects on insects and pathogens across the United States and projected changes in forest disturbance (sometimes increases), especially from insects because of their high physiological sensitivity to climate, short generation times, high mobility, and explosive reproductive potential. These projections have been upheld; in some cases, more rapidly and dramatically than anticipated a decade ago.

Here, we built upon the review from the first National Climate Assessment (Ayres and Lombardero 2000) by synthesizing the recent primary literature related to the effects of climate on the most important forest insects and diseases in North American forests. We evaluated the explicit role of climate on the occurrence of historical and recent outbreaks to identify the climate metrics that are most frequently associated with biotic disturbances. We highlight three case studies that provide clear examples of the effects of climate change on biotic disturbance agents. We discuss the socioeconomic and ecological consequences of these disturbances under climate change and identify key needs for improving forest health management in a changing climate.

CLIMATE AND BIOTIC DISTURBANCES OF FORESTS: GENERAL PRINCIPLES

Climate and atmospheric changes associated with increasing greenhouse gases can influence biotic disturbances of forests via three general mechanisms: (1) effects on the physiology of insects and pathogens that cause changes in their abundance and distribution, (2) effects on tree defenses and tolerance, and (3) effects on interactions between disturbance agents and their own enemies, competitors, and mutualists (Fig. 2, Table 1). Increasing temperatures can increase the risks of forest disturbance by reducing winter mortality of insects (e.g., Régnière and Bentz 2007, Tran et al. 2007, Paradis et al. 2008, Safranyik et al. 2010) and by increasing the development rate of insects and pathogens during the growing season (Gillooly et al. 2002, Harvell 2002, Bentz et al. 2010, Mitton and Ferrenberg 2012). Further effects via temperature changes can arise from changes in phenology of leaf maturation vs. insect feeding (Thomson and Benton 2007, Jepsen et al. 2011) or life cycle synchrony of bark beetles, which depend on mass attack to overwhelm tree defenses (Friedenberg et al. 2007, Bentz et al. 2010).

There is a broad set of atmospheric drivers that can affect tree defenses against, and tolerance to, herbivores and pathogens (Table 1; Ayres 1993, Bidart-Bouzat and Kliebenstein 2008, Lindroth 2010, Sturrock et al. 2011). Deficiencies of water or mineral nutrients and increases in CO₂ and input of inorganic N into the terrestrial N cycle can increase or decrease tree defenses, partly depending on the severity of the deficiency, the dominant biochemical pathways for secondary plant metabolism, and whether defenses are constitutive or inducible (Herms and Mattson 1992, Lombardero et al. 2000, Throop and Lerda 2004, Lindroth 2010). In

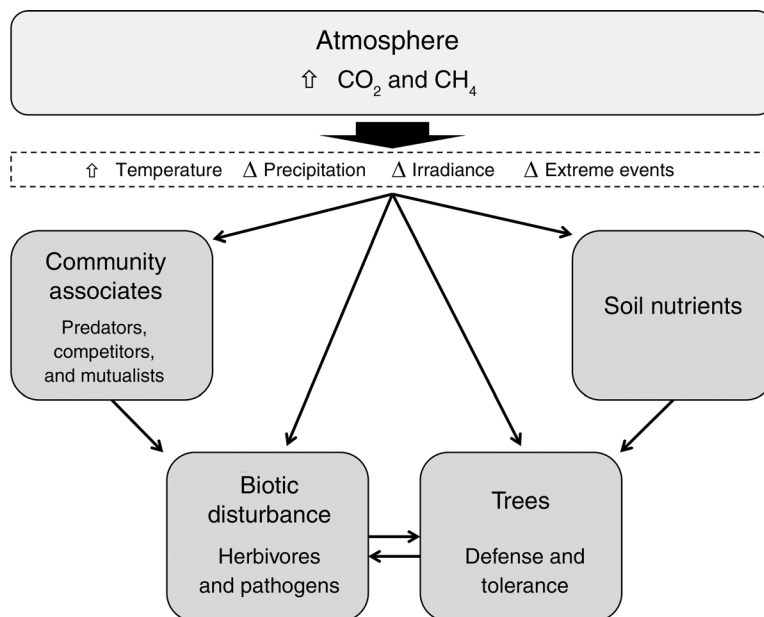


FIG. 2. A schematic of the general pathways by which atmospheric changes associated with increasing greenhouse gases can influence forest disturbance from insects and diseases.

addition, tree mortality from severe drought may permit an increase in bark beetles that then become abundant enough to successfully attack healthy trees (Shaw et al. 2005, Greenwood and Weisberg 2008, Raffa et al. 2008).

Population dynamics of forest insects respond to numerical interactions between herbivores and their enemies (Dwyer et al. 2004), and it should be expected that these interactions are sensitive to temperature

TABLE 1. Summary of biological and ecological processes affecting population dynamics of biotic disturbance agents that are mediated by climate.

Biological or ecological process and atmospheric driver	Outcome	Selected references
Developmental rate/population growth		
Temperature	change in abundance	Gillooly et al. (2002), Harvell et al. (2002), Powell and Bentz (2009)
Multi-trophic interactions		
Temperature	mutualisms	Six and Bentz (2007), Evans et al. (2011)
CO ₂ and temperature	natural enemies	Hodkinson (2005), Berggren et al. (2009), Lindroth (2010), Klapwijk et al. (2012)
Temperature	synchrony with host	Volney and Fleming (2007), Jepsen et al. (2011)
Seasonality		
Temperature	voltinism and synchrony of conspecific emergence	Powell et al. (2001), Hicke et al. (2006), Friedenberget al. (2007), Bentz et al. (2010)
Sporulation		
Precipitation	host infection	Hansen et al. (2000), Hardham (2005), Sturrock et al. (2011)
Host susceptibility		
CO ₂	tree defense	Chakraborty et al. (2000), Lindroth (2010), Sturrock et al. (2011)
N deposition	tree defense	Herms and Mattson (1992), Jones et al (2004), Throop and Lerdau (2004), Throop et al. (2004)
O ₃	tree defense	Jones et al (2004), Lindroth (2010)
Precipitation	tree defense	Breshears et al. (2005), Berg et al. (2006)
Temperature	tree defense	Berg et al. (2006), Worrall et al. (2010b)
Winter survival		
Temperature	geographical range shift	Harvell et al. (2002), Régnière and Bentz (2007), Tran et al. (2007), Paradis et al. (2008), Sturrock et al. (2011)

(Berggren et al. 2009, Klapwijk et al. 2012), but empirical studies are rare (Wilson 1974, Siegert et al. 2009). Similarly, for the many forest insects that involve mutualisms with fungi (e.g., *Dendroctonus* spp.), it is likely that outbreak dynamics will be sensitive to climatic effects on the mutualism, but studies are limited (Lombardero et al. 2003, Hofstetter et al. 2007, Six and Bentz 2007, Evans et al. 2011).

Effects of climate on forest insect and pathogen population dynamics

Despite our broad knowledge of climate effects on insect and pathogen demography, we still lack capacity to predict outbreaks under climate change. To address this knowledge gap we reviewed the primary literature to determine the most important climate metrics associated with historical outbreaks of the insects and pathogens presented in Tables 2 and 3. Our synthesis included studies that tested for: (1) spatial or temporal coincidence or correlation of outbreak/disease symptoms with climate event or trend (e.g., Greenbank 1963, Breshears et al. 2005, Barrett et al. 2012) and/or (2) concordance of population fluctuations with process-based models of physiologically explicit mechanisms linking climate and population dynamics (e.g., Tran et al. 2007, Powell and Bentz 2009). We identified 79 studies from 1950 to 2012 that satisfied the criteria; three of the 79 studies evaluated climate effects on more than one insect species and most (66% or 52) of the studies were focused on insects rather than pathogens. In each study we assessed the importance of up to three climate metrics that can have demonstrable effects on biotic agent demography and are projected to change from historical levels as a result of anthropogenic climate change: (1) winter temperatures, (2) growing-season temperatures, and (3) changes in moisture availability. Climate metrics were scored in each study as important when there was a significant statistical relationship between the metric and disturbance event (temporal or spatial) or when predictions from climate-driven mechanistic models coincided strongly with disturbance agent abundance.

Climate effects on outbreaks have been studied for 13 of the 27 insects listed in Table 2 and for 12 of the 22 pathogen/decline cases in Table 3. The majority of insect species that have been studied are native to North America (10 of 13 species) and skewed heavily towards bark beetles and defoliators within the genera *Dendroctonus* and *Choristoneura*, respectively (Fig. 3A). All three climate metrics that we evaluated have been reported to contribute to forest insect outbreaks, and a role for climate was identified in most studies and for all three feeding guilds that we recognized (Fig. 4A). Cold winter temperatures have been commonly associated with the termination of outbreaks or the location of northern distributional limits (Fig. 4B). Changes in growing-season temperatures and moisture availability can also affect outbreaks (Fig. 4B). Increased population growth was associated with warming year-round temperatures,

which affects voltinism and can synchronize cohort emergence (e.g., Friedenberg et al. 2007, 2008, Powell and Bentz 2009). Drought from warming summer temperatures and decreased precipitation facilitated insect outbreaks (Berg et al. 2006, Raffa et al. 2008).

Climate effects on disease and decline dynamics in forests are not as well studied as for insects (Figs. 3B, 5A); there is evidence that winter temperatures, growing-season temperatures, and moisture availability can be important (Fig. 5B). Both increased and decreased moisture availability influenced pathogens, whereas most insect outbreaks are associated with water deficits. Sudden aspen decline was associated with warm, dry conditions, whereas epidemics of foliar, vascular, and root pathogens (e.g., *Dothistroma* needle blight, Swiss needle cast, sudden oak death, and *Armillaria* root rot) were linked to warm summers and increasing precipitation (Fig. 5B). Mild winters influence disease incidence of Swiss needle cast by permitting mycelial growth in poleward regions (Manter et al. 2005, Zhao et al. 2011).

Bark beetles

The first National Climate Assessment identified bark beetles as a group of high-impact forest insects for which we should anticipate strong and relatively rapid responses to climate change (Ayres and Lombardero 2000). However, it underestimated the scale of impacts that would occur in the subsequent decade, particularly for bark beetles in the genus *Dendroctonus*. Mountain pine beetle (*D. ponderosae* Hopkins) is the most important disturbance agent of pines in the western United States, and is responsible for the largest recorded bark beetle epidemic, which continues now with major outbreaks ongoing from Colorado to British Columbia (see *Case Study 1. Mountain pine beetle . . .*, and Fig. 6). Southern pine beetle (*D. frontalis* Zimmermann) is the analogue in the highly productive pine forests of the southeastern United States (see *Case Study 2. Range expansion of . . .*, and Fig. 7). Spruce beetle (*D. rufipennis* Kirby) has recently killed trees across 1 Mha of forest in Alaska (Werner et al. 2006), with broad consequences for forest structure and function (see *Case Study 3. Spruce beetle . . .*, and Fig. 8; and see also the Special issue of Forest Ecology and Management 227(3), 2006). In the early 2000s, severe drought coupled with bark beetle outbreaks (primarily *Ips* spp.) killed trees of several conifer species in the Southwest (Negrón et al. 2009, Ganey and Vojta 2011) across 1.2 Mha (Breshears et al. 2005). Damage from bark beetles was prominent in arguments for the Healthy Forests Restoration Act of 2003 (*available online*),⁴ contributed to a North American Free Trade Agreement (NAFTA) softwood lumber dispute between the United States and Canada (Krauss 2005), and is a recognizable source of important changes

⁴ www.gpo.gov/fdsys/pkg/BILLS-108hr1904enr/pdf/BILLS-108hr1904enr.pdf

in carbon flux (see *Impacts of insect and disease outbreaks on landscapes and ecosystems*).

All of these bark beetles are native to North America, have population dynamics that are innately irruptive (from endogenous positive feedbacks), and have been exerting strong effects on American forests for millennia (Brunelle et al. 2008). However, it is now clear that the large extent and expanding distribution of recent outbreaks have been permitted or exacerbated by increasing temperatures during the last decades (Fig. 4; Logan and Powell 2001, Breshears et al. 2005, Berg et al. 2006, Raffa et al. 2008, Sherriff et al. 2011). Mountain and southern pine beetles are attacking hosts farther north and at higher elevations than historic norms (Safranyik and Carroll 2006, Tran et al. 2007, Logan et al. 2010). Greater impacts on forest ecosystems should be anticipated from these range expansions into areas with novel and naïve hosts (Cudmore et al. 2010). *Dendroctonus mexicanus* Hopkins, previously known only from Mexico, has been recently discovered in the southwestern United States (Moser et al. 2005). This is only one of several species of aggressive Mexican bark beetles that may expand into U.S. forests with continued warming trends (Bentz et al. 2010). We can anticipate that climate change will continue to reshape the patterns of bark beetle outbreaks in American forests, with outbreak tendencies increasing for some species in some regions and decreasing in others (Hicke et al. 2006, Bentz et al. 2010, Littell et al. 2010, Evangelista et al. 2011). Conversely, the unprecedented absence of southern pine beetle activity since the late 1990s in Louisiana and east Texas may be related to climatic warming (Friedenberg et al. 2008).

Defoliating insects

Five groups of defoliating insects comprise another notable class of biotic disturbances in American forests (Table 2). Current outbreaks of western spruce budworm (*Choristoneura occidentalis* Freeman) have already involved 1–2 Mha and are continuing (USDA Forest Service Aerial Detection Survey data; USDA Forest Service 2010). Eastern boreal forests have been similarly affected by many cycles of eastern spruce budworm (*C. fumiferana* [Clemens]) outbreaks (Candau and Fleming 2005). Other important defoliators include tussock moths, tent caterpillars, gypsy moths, and jack pine budworm (Table 2). Many of the most important defoliating insects are indigenous to American forests (gypsy moth being a notable exception) and have cyclical outbreak dynamics involving predators, parasitoids, and pathogens (Dwyer et al. 2004), but climatic effects on these predator–prey interactions remain largely unstudied (Fig. 4; Klapwijk et al. 2012). In general, it is less clear than with the bark beetles how climatic patterns influence the frequency, extent, and geographic distribution of defoliators in American forests. Our best examples come from studies of spruce budworm that indicate that historical outbreaks com-

monly followed a period of warm, dry summers every 30 to 40 years depending on stand maturity (Fig. 4; Greenbank 1963, Swetnam and Lynch 1993, Campbell et al. 2006). Predictions suggest that defoliation by the eastern spruce budworm, *C. fumiferana*, will expand north and develop different spatiotemporal patterns across forests in Ontario (Candau and Fleming 2011). Climatic effects are likely on overwinter survival (Ives 1973, Williams and Liebhold 1995a, but see Reynolds et al. 2007), drought stress of host trees (Williams and Liebhold 1995b, Ryerson et al. 2003, Campbell et al. 2006), and phenological synchronization of larval emergence and bud break (Thomson et al. 1984, Thomson and Benton 2007). Considerable uncertainty remains about future responses of defoliators to climate change (Dukes et al. 2009, Rodenhouse et al. 2009).

Plant diseases

We identified 22 taxa of plant diseases that are presently notable agents of disturbance in North American forests and candidates for consequential responses to climate change (Table 3). This list includes one case of disease-related decline (sudden aspen decline) where climatic variation and a complex of biotic agents (insects and/or microbes) have been associated with patterns of tree mortality (Edmonds et al. 2000, Marchetti et al. 2011, Anderegg et al. 2012). We excluded declines where the tree mortality was not evidently from biotic agents.

Climatic effects on diseases have been less studied than forest insects, but it can be expected that the severity of at least some of these diseases will be either directly affected by climatic influences on sporulation and infection and/or indirectly by changing tree susceptibility to infection (Sturrock et al. 2011). For diseases that involve associations with insects (e.g., beech bark disease, oak wilt, Dutch elm disease, black stain root diseases, laurel wilt, thousand cankers disease, and pitch canker), climatic effects on the animal associates (e.g., range expansion and population growth of insect vectors) may be important. Examples of diseases where there is some understanding of climatic effects include Swiss needle cast, which is caused by a foliar pathogen (*Phaeocryptopus gaeumannii*) and reduces growth rates of Douglas-fir in the Pacific Northwest. Projections of winter warming and higher spring precipitation suggest a likely increase in Swiss needle cast distribution and severity (Stone et al. 2008). The susceptibility of alder to a cankering disease is related to the phenology of the plant, the pathogen, and water availability (Grulke 2011, Rohrs-Richey et al. 2011). Substantial future mortality of aspen forests that are near the aridity limit for this species is expected to occur with continuing climate change due to sudden aspen decline (Rehfeldt et al. 2009). Outbreaks of some virulent invasive pathogens such as sudden oak death caused by *Phytophthora ramorum* are sensitive to climate

TABLE 2. Insects that are notable agents of biological disturbance in North American forests and therefore candidates for consequential changes to disturbance regimes as a result of climate change.

Cases	Herbivore	Hosts	References	
			General references	Studies related to climate†
Defoliation by gypsy moths and tussock moths	<i>Lymantria dispar</i> , [‡] <i>Orgyia</i> spp.	<i>Quercus</i> spp., many other broad-leaved trees and conifers	Leuschner et al. (1996), Mason (1996), Jones et al. (1998), Bjørnstad et al. (2010)	Miller et al. (1989; T),§ Williams and Liebhold (1995; P,T),§ Lindroth et al. (1997, 2002; CO ₂), Hale et al. (2005; P), Osier and Lindroth (2006; CO ₂), Robinet et al. (2007; T), Siegert et al. (2009; P,T)
Defoliation by budworms	<i>Acleris</i> spp., <i>Choristoneura fumiferana</i> , <i>C. occidentalis</i> , <i>C. pinus</i>	<i>Abies</i> spp., <i>Pseudotsuga</i> spp., <i>Picea</i> spp., <i>Pinus</i> spp.	McNamee (1979), Royama (1984), Berryman (1986), Campbell (1989), Fleming and Volney (1995), Fleming (1996), Fleming and Candau (1998), Fleming et al. (2000), Volney and Fleming (2000, 2007)	Wellington et al. (1950; P,T),§ Greenbank (1956, 1963; T),§ Silver (1960; P,T),§ Pilon and Blais (1961; P,T),§ Wilson (1974; T), Blais (1981; T),§ Lucuik (1984; P,T), Reichenbach and Stairs (1984a, b; T), Thomson et al. (1984; P,T),§ Swetnam and Lynch (1993; P,T),§ Williams and Liebhold (1995; P,T),§ Régnière and Duval (1998; T), Weber et al. (1999; T), Ryerson et al. (2003; P),§ Candau and Fleming (2005, 2011; P,T),§ Campbell et al. (2006; P,T),§ Thomson and Benton (2007; T),§ Gray (2008; P,T),§ Raichfuss et al. (2009; P,T),§
Defoliation by gracillariid leaf miners	<i>Micrurapteryx salicifoliella</i> , <i>Phyllocnistis populiella</i>	<i>Populus tremuloides</i> , <i>Salix</i> spp.	Condrashoff (1964), Furniss et al. (2001), Wagner et al. (2008), Morton and Pereya (2011)	Wagner et al. (2012; T)
Defoliation by loopers	<i>Enyptia griseata</i> , <i>Lambdina</i> , <i>Nepytia</i> spp.	<i>Abies</i> spp., <i>Pseudotsuga</i> spp., <i>Picea</i> spp., <i>Pinus</i> spp., <i>Thuja</i> spp.	Munroe (1963), Edwards (1964), Rindge (1967), Klein and Minnoch (1971), Otvos et al. (1979), Stevens et al. (1983), MacLean and Ebert (1999), Butt et al. (2010), Iqbal et al. (2011)	Rocheftort et al. (2011; T), Delisle et al. (2012; T)
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	Rejmánek et al. (1987), Roland (1993, 2005), Myers (2000), Volney and Fleming (2000), Charbonneau et al. (2012)	Ives (1973; T),§ Wilson (1974; T), Lindroth et al. (1993; CO ₂), Daniel and Myers (1995; T),§ Roland et al. (1998; T),§ Frid and Myers (2002; T), Holton et al. (2003; CO ₂), McClure et al. (2011; T), Fitzgerald et al. (2012; T)
Infestations by Asian longhorned beetle	<i>Anoplophora glabripennis</i> [‡]	<i>Acer</i> spp., <i>Ulmus</i> spp., <i>Populus</i> spp.	Cavey et al. (1998), Dodds and Orwig (2011)	Peterson and Scachetti-Pereira (2004; T), Keena (2006; T), Keena and Moore (2010; T)
Infestations by bronze birch, gold spotted oak, and emerald ash borers	<i>Agrilus anxius</i> , <i>A. auroguttatus</i> , and <i>A. planipennis</i> [‡]	<i>Betula</i> spp., <i>Quercus</i> spp., and <i>Fraxinus</i> spp., respectively	Balch and Prebble (1940), Cappaert et al. (2005), Kovacs et al. (2010, 2011b), Coleman and Seybold (2011), Coleman et al. (2011), Nielsen et al. (2011), Flower et al. (2012)	Akers and Nielsen (1984; T),§ Jones et al. (1993; P,T), Crosthwaite et al. (2011; T), Sobek et al. (2011; T), Sobek-Swant et al. 2011; T)
Infestations by Douglas-fir beetle	<i>Dendroctonus pseudotsugae</i>	<i>Pseudotsuga menziesii</i>	Hadley and Veblen (1993), Paulson (1995), Ross and Solheim (1997), Negron (1998), Negron et al. (2001), Dodds et al. (2006)	Ryan (1959; T), Powers et al. (1999; P),§

TABLE 2. Continued.

Cases	Herbivore	Hosts	References	
			General references	Studies related to climate†
Infestations by mountain pine beetle	<i>Dendroctonus ponderosae</i>	<i>Pinus</i> spp.	Wilson et al. (1998), Safranyik and Carroll (2006), Kurz et al. (2008), Logan and Powell (2009), Cudmore et al. (2010)	Thomson and Shrimpton (1984; P,T),§ Safranyik and Linton (1998; T), Bentz et al. (1991; T), Logan and Bentz (1999; T), Powell et al. (2000; T), Williams and Liebhold (2002; P, T),§ Stahl et al. (2006; T), Campbell et al. (2007; P,T), Régnière and Bentz (2007; T),§ Aukema et al. (2008; T),§ Raffa et al. (2008; P,T),§ Fauria and Johnson (2009; P,T),§ Powell and Bentz (2009; T),§ Bentz et al. (2010; P,T), Evangelista et al. (2011; T), Jewett et al. (2011; P,T), Sambaraju et al. (2011; T),§ Lester and Irwin (2012; T), Mitton and Ferrenberg (2012; T), Chapman et al. (2012; P,T),§ Preisler et al. (2012; P,T)§
Infestations by pine engraver beetles	<i>Ips</i> spp.	<i>Pinus</i> spp.	Schenk and Benjamin (1969), Klepzig et al. (1995), Raffa et al. (1998)	Lombardero et al. (2000; T), Breshears et al. (2005; P,T),§ Gaylord et al. (2008; T), Raffa et al. (2008; T),§ Evangelista et al. (2011; T)
Infestations by southern pine beetle	<i>Dendroctonus frontalis</i>	<i>Pinus</i> spp., chiefly southern pine	Reeve et al. (1995), McNulty et al. (1997), Klepzig et al. (2004), Økland et al. (2005)	Turchin et al. (1991; P,T),§ Ungerer et al. (1999; T), Lombardero et al. (2000; T), Williams and Liebhold (2002; P, T),§ Hofstetter et al. (2007; T), Tran et al. (2007; T),§ Friedenberget al. (2007, 2008; T),§ Gaylord et al. (2008; T), Waring et al. (2009; T),§ Duehl et al. (2011; P,T),§ Evans et al. (2011; T)
Infestations by spruce aphid	<i>Elatobium abietinum</i> ‡	<i>Picea</i> spp.	Parry (1969), Day (1984), Lynch (2004)	Powell (1974; T), Powell and Parry (1976; T),§ Day et al. (2010; T)§
Infestations by spruce beetle	<i>Dendroctonus rufipennis</i>	<i>Picea</i> spp.	Økland et al. (2005), Allen et al. (2006), DeRose and Long (2007)	Dyer (1969; T), Hansen et al. (2001; T), Berg et al. (2006; T),§ Hebertson and Jenkins (2008; P,T),§ Raffa et al. (2008; P),§ Bentz et al. (2010; T), Hansen et al. (2011; T), Sheriff et al. (2011; P,T),§ DeRose and Long (2012; T)§
Infestations by western pine beetle	<i>Dendroctonus brevicornis</i>	<i>Pinus</i> spp., chiefly <i>P. ponderosa</i>	Liebhold et al. (1986)	Miller (1931; T), Keen and Furniss (1937; T), Gaylord et al. (2008; T), Evangelista et al. (2011; T)
Infestations by white pine weevil	<i>Pissodes strobi</i>	<i>Pinus</i> spp., <i>Picea</i> spp.	Bellocq and Smith (1995), Lavallee et al. (1996), Woods et al. (2010), Ostry et al. (2010)	Sullivan (1961; T)
Infestations by woolly adelgids	<i>Adelges piceae</i> ,‡ <i>A. tsugae</i> ‡	<i>Abies fraseri</i> , <i>A. balsamea</i> , <i>Tsuga</i> spp.	McClure (1989, 1991), Rabenold et al. (1998), Smith and Nicholas (2000), Mitchell and Buffam (2001)	Amman (1968; T), Parker et al. (1998, 1999; T), Butin et al. (2005; T), Evans and Gregoire (2007; T),§ Paradis et al. (2008; T),§ Trotter and Shields (2009; T),§ Fitzpatrick et al. (2012; T)§

Note: The table is updated from Ayres and Lombardero (2000).

† Letters with references denote studies considering the effects of carbon dioxide (CO₂), precipitation (P), or temperature (T).

‡ Nonindigenous to North America.

§ Studies evaluating the link between winter temperatures, seasonal temperatures, and/or moisture availability on the occurrence and/or severity of biotic disturbances due to insects.

TABLE 3. Pathogens, parasites, and declines that are notable agents of disturbance in North American forests and therefore candidates for consequential changes to disturbance regimes as a result of climate change.

Cases	Pathogen/ parasite	Hosts	References	
			General references	Studies related to climate†
Alder canker	<i>Valsa melanodiscus</i>	<i>Alnus</i> spp.	Trummer (2006), Worrall (2009), Grulke (2011), Stanosz et al. (2011)	Ruess et al. (2009; T),§ Rohrs-Richey et al. (2011; P,T), Worrall et al. (2010a; T)
Annosum root rot	<i>Heterobasidion annosum</i>	Most conifers. Some broad-leaved trees.	Stanosz and Guthmiller (1995), Meadows and Hodges (1996), Pearce (1996)	Boland et al. (2004), Witzell et al. (2011; T)
Anthraxnose leaf disease	<i>Discula destructiva</i> , <i>Glomerella</i> <i>cingulata</i> , <i>Colletotrichum gloeosporioides</i> , others	<i>Quercus</i> spp., <i>Fraxinus</i> spp., <i>Platanus</i> spp., <i>Cornus</i> spp.	Britton (1993), Dudt and Shure (1993), Stanosz (1993), McEwan et al. (2000), Holzmüller et al. (2006)	Britton et al. (1997; P), Chakraborty et al. (2000; CO ₂)
Armillaria root rot	<i>Armillaria</i> spp.	Broadleaved trees and conifers, e.g., <i>Acer</i> spp., <i>Quercus</i> spp., <i>Picea</i> spp.	Mwangi et al. (1990), Entry et al. (1991), Smith et al. (1994), Rizzo et al. (1995), Wargo (1996)	Clinton et al. (1993; P),§ Dukes et al. (2009), Sturrock et al. (2011)
Beech bark disease	<i>Neonectria</i> spp. (and associated scale insects <i>Cryptococcus fagisuga</i> † and <i>Xylococcus betulae</i>)	<i>Fagus grandifolia</i>	Shigo (1972), Houston (1998), Busby and Canham (2011), Garnas et al. (2011a)	Dukes et al. (2009), Garnas et al. (2011b; P,T),§ Kasson and Livingston (2012; P,T)§
Butternut canker	<i>Sirococcus clavignenti-juglandacearuma</i> †	<i>Juglans cinerea</i>	Harrison et al. (1998), Fleming et al. (2000), Broders et al. (2001, 2012), Clark et al. (2008)	
Chestnut blight	<i>Cryphonectria parasitica</i> †	<i>Castanea dentata</i>	McKeen (1995), Taylor et al. (1998)	
Dothistroma needle blight	<i>Dothistroma septosporum</i> and <i>D. pini</i>	Many conifers, <i>Pinus</i> spp.	Pfister et al. (2000), Bradshaw (2004), Welsh et al. (2009)	Gadgil (1974, 1977; P,T), Woods et al. (2005; P,T),§ Watt et al. (2009, 2011; P,T), Sturrock et al. (2011), Dvorak et al. (2012; P,T)
Dutch elm disease	<i>Ophiostoma novoulmi</i> † (and associated bark beetles <i>Hylurgopinus rufipes</i> and <i>Scolytus multistriatus</i> †)	<i>Ulmus</i> spp.	Holmes (1980), Fleming et al. (2000)	Sutherland et al. (1997; T),§ Boland et al. (2004)
Dwarf mistletoe	<i>Arceuthobium</i> spp.	<i>Pinus</i> spp., <i>Tsuga</i> spp.	Bennetts et al. (1996), Synder et al. (1996), Kipfmüller and Baker (1998)	Brandt et al. (2004; T), Stanton (2007; P,T), Cullings and Hanely (2010), Barrett et al. (2012; P,T)§
Fusiform rust	<i>Cronartium quercuum</i>	<i>Pinus</i> spp., chiefly southern pine	Walkinshaw and Barnett (1995), Doudrick et al. (1996), Nelson et al. (1996)	Runion et al. (2010; CO ₂)
Laurel wilt	<i>Raffaelea lauricola</i> † (and associated bark beetle <i>Xyleborus glabratus</i> †)	Lauraceae	Fraedrich et al. (2008), Harrington et al. (2011)	Koch and Smith (2008; T)
Oak wilt disease	<i>Ceratocystis fagacearum</i>	<i>Quercus</i> spp.	Appel (1995), Nair (1996), McDonald et al. (1998), Juzwik et al. (2008, 2011), Haight et al. (2011)	Houston and Kuntz (1960; T), Lewis (1981, 1985; T), Tainter (1986; T), Boland et al. (2004)
Phytophthora root disease	<i>Phytophthora cinnamomi</i> †	<i>Quercus</i> spp., <i>Castanea</i> spp., <i>Abies</i> spp.	Zentmyer (1980), Brasier (1996), Robin et al. (2001), Hardham (2005), Griffin et al. (2009)	Zentmyer et al. (1979; T), Benson (1982; T), Marçais et al. (1996; T),§ Bergot et al. (2004; T)
Pitch canker	<i>Gibberella circinata</i> (anamorph <i>Fusarium circinatum</i>)	<i>Pinus</i> spp.	Gordon et al. (1996, 1998), Storer et al. (1997)	Inman (2005; T), Inman et al. (2008; T), Ganley et al. (2009; P,T), Runion et al. (2010; CO ₂), Watt et al. (2011; P,T)

TABLE 3. Continued.

Cases	Pathogen/ parasite	Hosts	References	
			General references	Studies related to climate†
Proceras, black stain, and other <i>Leptographium</i> root diseases	<i>Leptographium</i> spp.	Many conifers, e.g., <i>Pinus</i> spp	Harrington and Cobb (1983), Klepzig et al. (1996), Jacobi et al. (2008)	
Scleroderris canker	<i>Gremmeniella abietina</i> ‡ (= <i>Scleroderris lagerbergii</i> and <i>Ascovalyx abietina</i>)(anamorph <i>Brunchorstia pinea</i>)	Conifers	Hamelin et al. (1993), Laflamme (2005)	Donaubauer (1972), Marosy et al. (1989; T), Venier and Hopkin (1998; P,T),§ Coakley et al. (1999), Boland et al. (2004)
Sudden aspen decline	unknown	<i>Populus tremuloides</i>	Hogg and Schwarz (1999), Rehfeldt et al. (2009), Huang and Anderegg (2012)	Hogg et al. (2002, 2005),§ Hogg (2008; P,T),§ Worrall et al. (2008, 2010b; P,T),§ Michaelian et al. (2011; P),§ Hanna and Kulakowski (2012; P)§
Sudden oak death	<i>Phytophthora ramorum</i> ‡	<i>Quercus</i> spp., <i>Lithocarpus</i> spp.	Monahan and Koenig (2006), Dodd et al. (2008), Vaclavik et al. (2010), Kovacs et al. (2011a, c), Spaulding and Rieske (2011)	Venette and Cohen (2006; P,T), Cushman and Meentemeyer (2008; P,T),§ Davis et al. (2010; P,T)
Swiss needle cast	<i>Phaeocryptopus gaeumannii</i>	<i>Pseudotsuga menziesii</i>	Hood (1982), Hansen et al. (2000), Kimberley et al. (2011), Shaw et al. (2011)	Rosso and Hansen (2003; P,T),§ Manter et al. (2005; P,T),§ Stone et al. (2007, 2008; P,T),§ Watt et al. (2010; P,T),§ Zhao et al. (2011; P,T)§
Thousand cankers disease	<i>Geosmithia morbida</i> (and associated bark beetle <i>Pityophthorus juglandis</i>)	<i>Juglans</i> spp.	Cranshaw (2011), Grant et al. (2011), Hadziabdic et al. (2011), Kolarik et al. (2011), Seybold et al. (2012)	
White pine blister rust	<i>Cronartium ribicola</i> ‡	Five-needle pines, e.g., <i>Pinus strobus</i> , <i>P. albicaulis</i>	Hunt and Meagher (1989), Keane et al. (1990), Kinloch (2003), Six and Adams (2007), Loo (2009), Field et al. (2012)	Van Arsdell (1972; P,T),§ Campbell and Antos (2000; P,T),§ White et al. (2002; P,T),§ Sturrock et al. (2011), Millar et al. (2012; P,T),§ Dunlap (2012; P,T)§

Note: The table is updated from Ayres and Lombardero (2000).

† Letters with references denote studies considering the effects of carbon dioxide (CO₂), precipitation (P), or temperature (T).

‡ Nonindigenous to North America.

§ Studies evaluating the link between winter temperatures, seasonal temperatures, and/or moisture availability on the occurrence and/or severity of biotic disturbances due to pathogens, parasites, or declines.

(Sturrock et al. 2011), while others such as beech bark disease seem not to be (Garnas et al. 2011b).

Nonnative insects and pathogens

On a global scale, biological invasions by nonindigenous species may be at least as important as climate change as threats to the sustainability of forest ecosystems and the goods and services that they provide (Seppälä et al. 2009). This pattern is evident in the United States, where invasive insects and pathogens are becoming an increasingly important component of forest disturbance (see Tables 2 and 3). The United States spends billions of dollars annually to control and mitigate the impacts of invasive forest insects and pathogens (Dale et al. 2001, USDA Forest Service 2010). Of 27 taxa of insects and 22 disease agents highlighted in Tables 2 and

3, six and nine, respectively, are nonindigenous to North America. Gypsy moths, woolly adelgids, beech bark disease, chestnut blight, and Dutch elm disease are prominent among the long-established invasive species that have had broad and sometimes permanent effects on American forests (Ellison et al. 2005, Lovett et al. 2006). This list has grown in the last decade with the addition of emerald ash borer, sudden oak death, Dothistroma needle blight, laurel wilt, and Scleroderris canker (Tables 2 and 3). Climate warming, shifts in precipitation, and other alterations associated with climate change can alter forest vulnerability to at least some of these disturbance agents (Paradis et al. 2008, Sturrock et al. 2011). For example, the geographic range and incidence of Dothistroma needle blight, which reduces growth of many conifers by causing premature needle defoliation, may

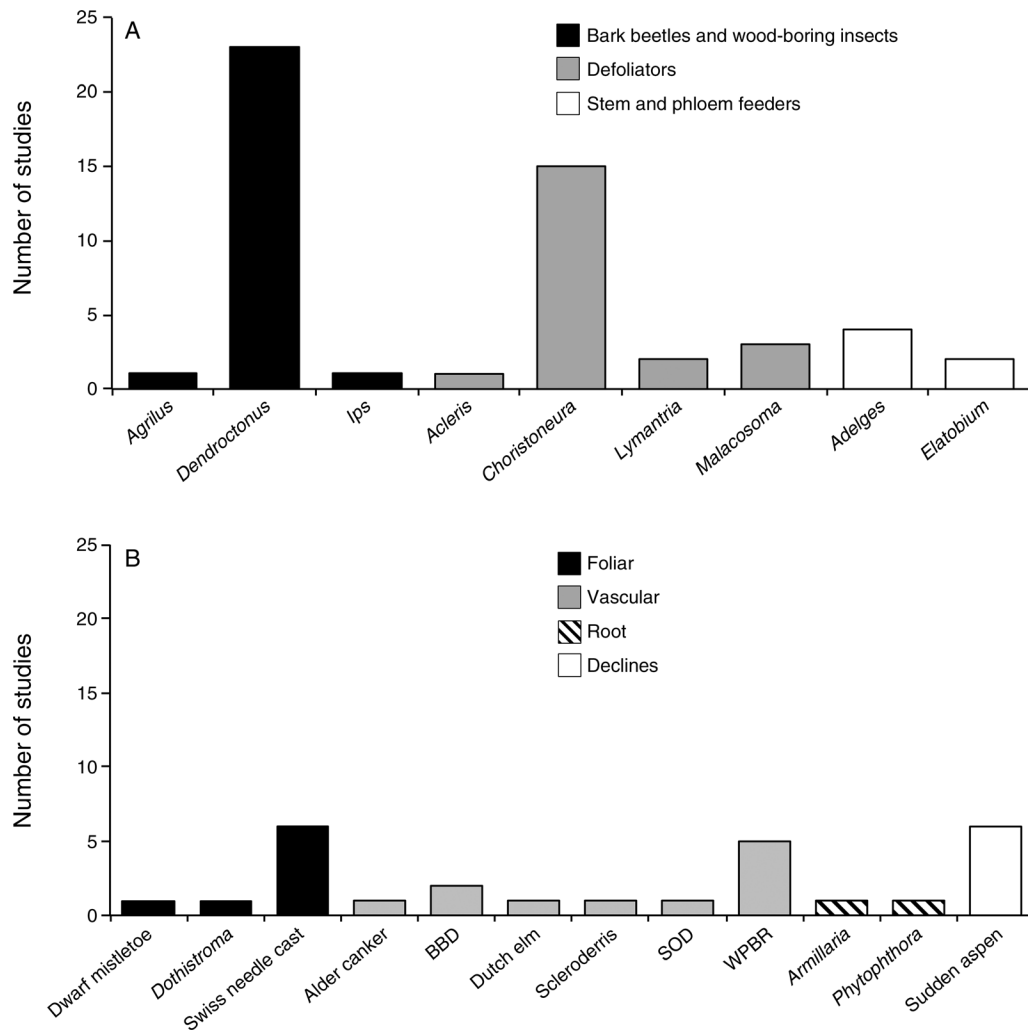


FIG. 3. (A) Frequency of studies evaluating the role of climate on forest disturbance from 1950 to 2012 (grouped by insect genera within feeding guild). (B) Frequency of studies evaluating the role of climate on forest disturbance by pathogens and declines from 1970 to 2012. Abbreviations are: BBD, beech bark disease; SOD, sudden oak death; and WPBR, white pine blister rust.

shift with changing precipitation patterns (Woods et al. 2010).

The underlying cause of biological invasions is propagule pressure from global transport, not climate change. However, climate change is strongly connected to management of risks from continuing invasions. Increasing temperatures are generally expanding the geographic zones where potential invasive species could survive and reproduce if they arrive, for example, at ports of entry on the Eastern Seaboard of North America and in the Great Lakes Waterway. The specter of global, climate-driven increases in invasion risks has prompted discussion of consequential changes in international trade restrictions to manage associated phytosanitation risks (World Trade Organization, Geneva, Switzerland; information available online).⁵

⁵ www.standardsfacility.org/en/TAClimateChange.htm

Emerging forest insects and pathogens

Outbreaks of lesser known forest insects have recently occurred in U.S. forests (Table 2). Aspen leaf miner, *Phyllocnistis populiella* Chambers, which reduces longevity of aspen leaves, has damaged 2.5 Mha of trembling aspen in Alaska since 1996 (Wagner et al. 2008). In two major river drainages in Alaska, hundreds of thousands of acres of willows (*Salix*) were damaged during two outbreaks of the leafblotch miner (*Micrurapteryx salicifoliella* [Chambers]) in the 1990s (Furniss et al. 2001). Further, defoliation of thousands of acres of spruce–fir forest by Janet’s looper (*Nepytia janetae* Rindge) in the White and Pinaleno mountain ranges in the southwestern United States appeared to weaken trees and increase their vulnerability to attack by opportunistic bark beetles (A. Lynch, personal communication). These are examples of native insects that were not previously known to display

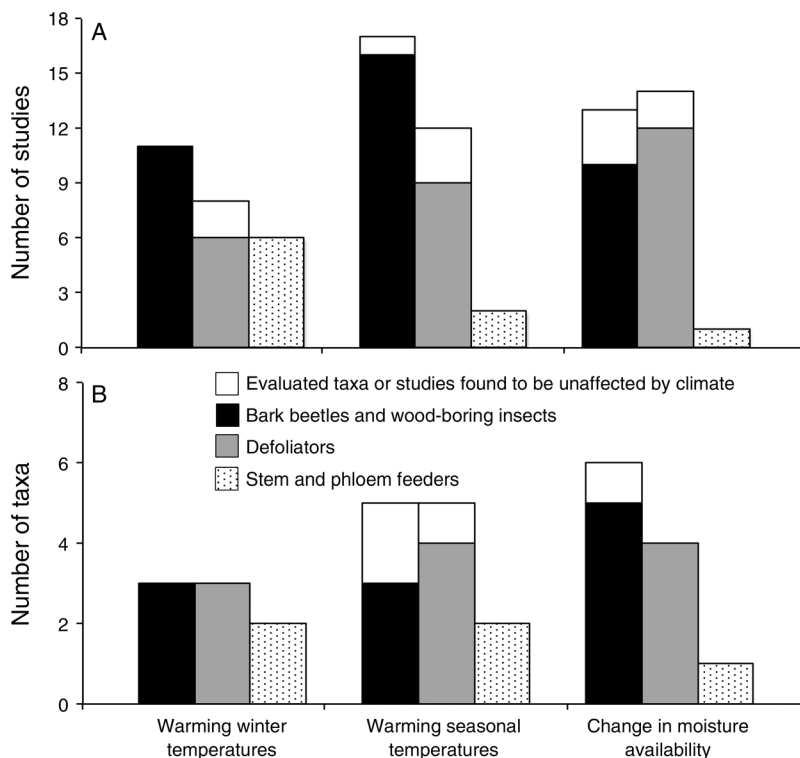


FIG. 4. (A) Frequency of studies evaluating the role of climate on forest disturbance among insect feeding guilds, and (B) frequency of taxa from these studies whose demography and population dynamics are demonstrably sensitive to climate.

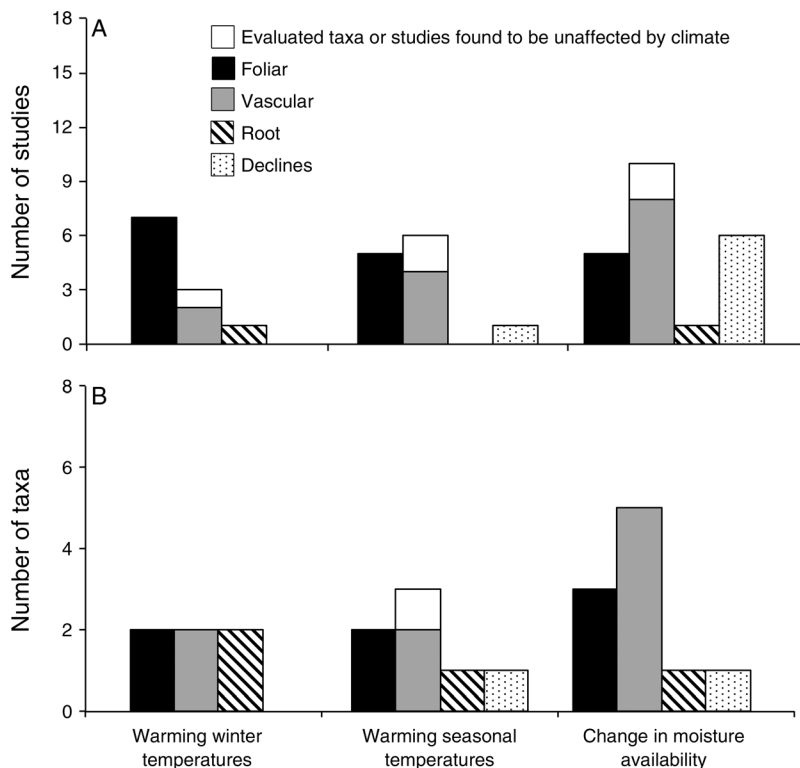


FIG. 5. (A) Frequency of studies evaluating the role of climate on forest disturbance by pathogens and declines, and (B) frequency of taxa from these studies whose demography and population dynamics are demonstrably sensitive to climate.

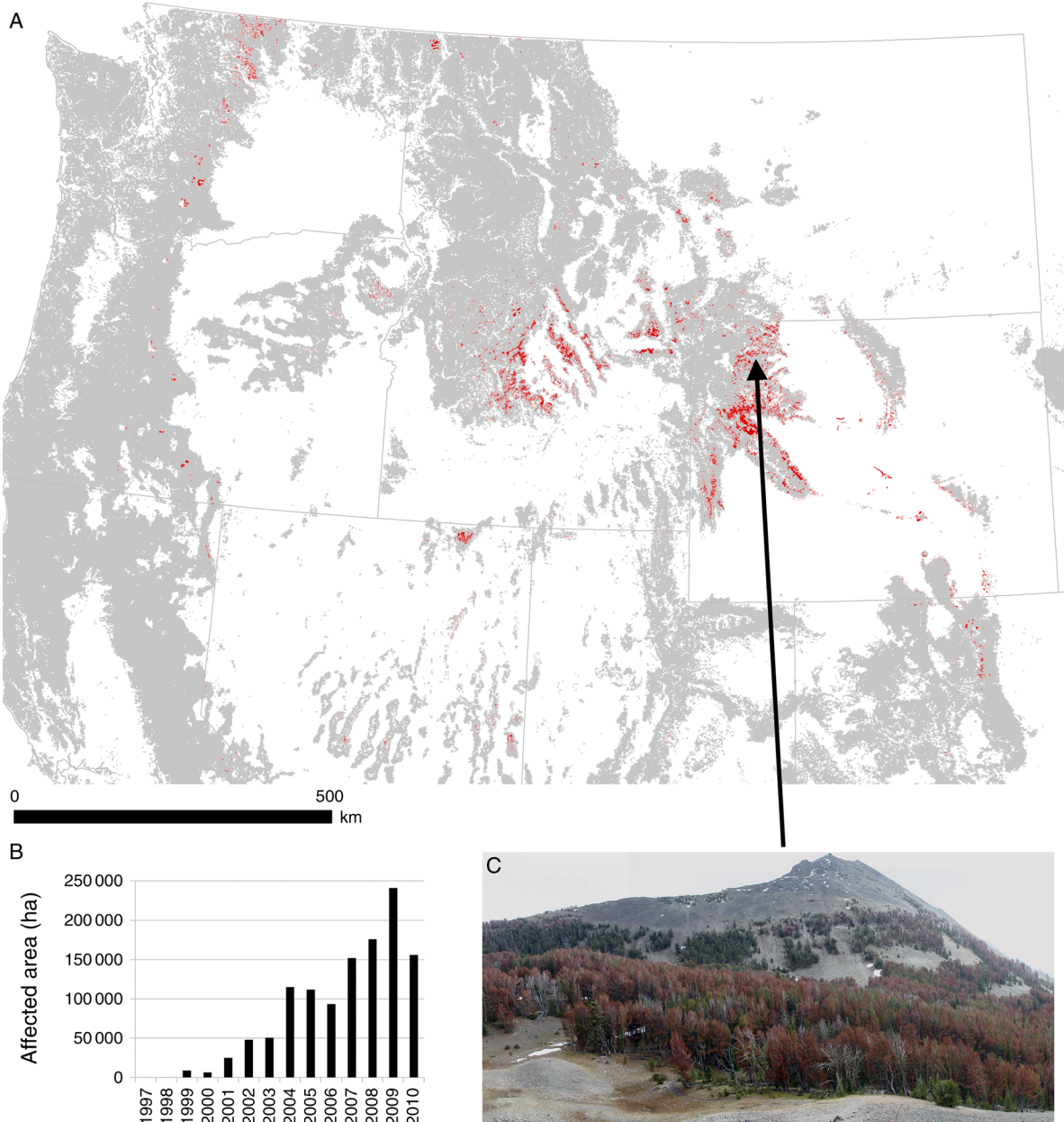


FIG. 6. (A) Area affected (red) by mortality in stands of *Pinus albicaulis* (whitebark), *P. flexilis* (limber), and *P. aristata* (bristlecone) pines in 1997–2010 as detected by aerial surveys conducted by the USDA Forest Service in the western United States. Affected areas include a mix of dead and live trees. Gray shading indicates locations of forest. (B) Affected area of five-needle pines. (C) The photo shows whitebark pine mortality in 2004 in Yellowstone National Park, USA. Credits: Polly Buotte, University of Idaho, Moscow, Idaho, USA (map); and Jeffrey Hicke (photo).

irruptive behavior or cause notable forest disturbances. Limited capacity to anticipate disturbances from previously innocuous native forest insects or pathogens in the face of climate change is a major concern to forest health and monitoring.

CASE STUDIES ILLUSTRATING RECENT CHANGES

Here we provide case studies of three insects whose recent outbreaks have been influenced by climate

change. These examples exhibit the strongest evidence linking climate change to biotic disturbance.

Case Study 1. Mountain pine beetle (*Dendroctonus ponderosae*) and five-needle pines

Five-needle pines, including whitebark (*Pinus albicaulis* Engelm.), limber (*P. flexilis* E. James), and bristlecone (*P. aristata* Engelm.) pines, play key roles in forest ecosystems of the western United States. As a result of

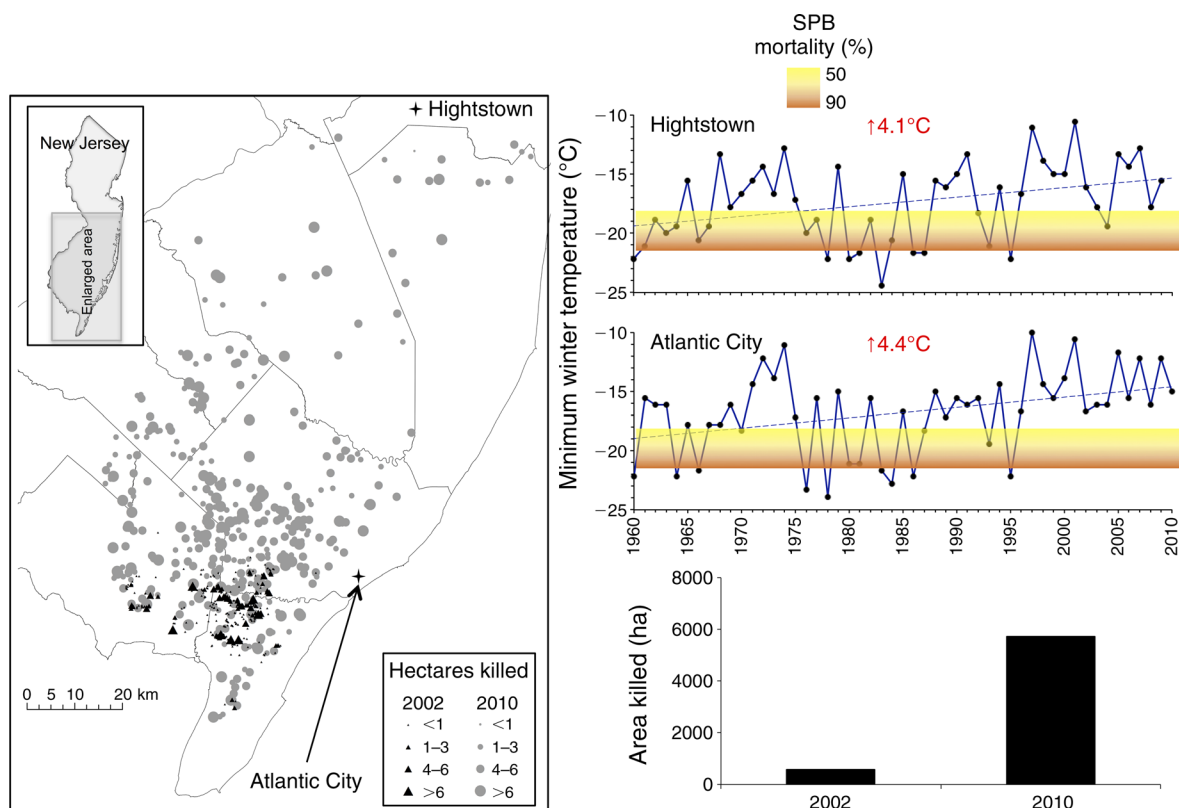


FIG. 7. The most cold-tolerant life stages of southern pine beetles (*Dendroctonus frontalis* Zimmermann [SPB]) die when winter air temperatures drop below about -18°C . A subcontinental pattern of warmer winters has eliminated a climatic barrier to occupancy of the New Jersey Pinelands (USA) by the beetle and permitted an epidemic that is presently growing and expanding northward. Yellow-red bars show southern pine beetle mortality (50–90%). Temperature data are from NOAA's National Climate Data Center (<http://www.ncdc.noaa.gov>).

recent warming trends, these conifers are being subjected to dramatic increases in mortality from mountain pine beetles. Aerial surveys indicated that 1 Mha of forest were affected by five-needle pine mortality during 1997–2010 (Fig. 6). Higher temperatures influence winter survival, development rate, and synchronization of attacks by beetles (Bentz et al. 2010, Logan et al. 2010) and drier conditions can influence susceptibility of host trees (Perkins and Swetnam 1996).

Similar epidemics occurred in the 1930s (Perkins and Swetnam 1996), but several differences exist between the pine mortality then and today. Most importantly, a cooler period followed the 1930s outbreaks (Logan and Powell 2001), but the current warming trend has persisted for several decades and is projected to continue (Hicke et al. 2006, Littell et al. 2010, Logan et al. 2010). Given the climate trajectory, the strong ties between temperature and beetle epidemics, and the extensive mortality that has already occurred in some areas such as the Greater Yellowstone Ecosystem, we can anticipate continuing losses of these forests and the ecosystem services that they provide (Logan et al. 2010). For example, the recent decision of the United States Court of Appeals to re-list grizzly bears as an endangered

species in the Greater Yellowstone area cited the expectation of increasing loss of food resources for bears due to climatic release of mountain pine beetle into whitebark pine forests (*Greater Yellowstone Coalition vs. Wyoming* 2011 case 09-36100 [ninth circuit], U.S. Court of Appeals).

Case Study 2. Range expansion of the southern pine beetle (*Dendroctonus frontalis*) into the New Jersey Pinelands

The southern pine beetle (Fig. 7) is the most destructive herbivore in the productive forests of the southeastern United States (Pye et al. 2011). The northern distribution limits of southern pine beetle are constrained by the occurrence of lethal winter temperatures (Ungerer et al. 1999). The first National Climate Assessment (Ayres and Lombardero 2000) projected an expansion of the northern distribution limits by about 175 km given a scenario in which minimum annual temperature increased by 3°C . In fact, minimum winter temperatures in the eastern United States have already increased by more than that ($>4^{\circ}\text{C}$ in the last 50 years in New Jersey; Fig. 7), which has permitted an epidemic of southern pine beetle in the New Jersey Pinelands about 200 km north of forests that have historically experi-

enced such epidemics (Tran et al. 2007). The New Jersey Pinelands is a National Reserve and international Biosphere Reserve. It is the largest forest on the Eastern Seaboard, is within 100 miles of 50 million people, and lies above the enormous Kirkwood-Cohansey aquifer that serves many of those people. Given the natural population dynamics of southern pine beetles and the continued absence of lethal winter temperatures, the Pinelands has entered a new phase where southern pine beetles will be influencing all aspects of forest ecology and management.

Case Study 3. Spruce beetle (Dendroctonus rufipennis) and western spruce (Picea spp.)

Spruce beetle attacks several species of spruce throughout the boreal forests of North America. Like many bark beetles, spruce beetles are affected by climate through multiple pathways (Schmid and Frye 1977, Werner et al. 2006, Hebertson and Jenkins 2008). Spruce beetles typically have a two-year life cycle, but may complete their life cycles in one year during warmer summers (Hansen et al. 2001, Hansen and Bentz 2003). Spruce is at greater risk from spruce beetle when beetles produce one generation per year (Hansen et al. 2011) and when warmer and drier conditions increase tree stress and susceptibility to spruce beetle attack (Berg et al. 2006, Hebertson and Jenkins 2008, DeRose and Long 2012).

Dendrochronological studies (tree-ring analysis) and historical reports indicate that many spruce beetle outbreaks have occurred in Alaska over the past 250 years and are commonly associated with warm, dry conditions (Berg et al. 2006, Sherriff et al. 2011). An epidemic of spruce beetle outbreaks in southern Alaska during the 1990s exceeded the extent of outbreaks during the previous 70 years (Fig. 8; Berg et al. 2006, Werner et al. 2006, Sherriff et al. 2011). Multiple years of very warm summers during the 1990s permitted higher beetle winter survival and production of univoltine broods, and stressed host trees that were of suitable age to support beetle outbreaks (Berg et al. 2006, Werner et al. 2006). The extensive tree mortality in the 1990s may foreshadow future outbreaks given the expectations of continued warming (Berg et al. 2006). Indeed, a model describing the influence of future climate change on life cycle duration of spruce beetles predicts enhanced probability of outbreaks throughout the range of spruce in North America (Bentz et al. 2010).

IMPACTS OF INSECT AND DISEASE OUTBREAKS
ON LANDSCAPES AND ECOSYSTEMS

Through their impacts on tree growth and mortality, insects and diseases have broad effects on landscapes and ecosystems, and some of these effects are changing due to climate change. By virtue of their host preferences, these disturbance agents typically alter tree species composition within stands and can change forest types (e.g., from conifers to hardwoods). In forests of

western North America, outbreaks of spruce and mountain pine beetles kill their respective hosts and shift stands toward subalpine fir (Veblen et al. 1991, Collins et al. 2011). Given the strong link between recent temperatures and epidemics by these beetles and the climate trajectory (Berg et al. 2006, Logan et al. 2010), we can anticipate similar impacts by these species to occur into the future. Forests of the southeastern United States infested by southern pine beetle have shifted towards landscapes with regenerating stands of younger trees (Ylioja et al. 2005, Tchakerian and Couslon 2011). Beech bark disease has almost eliminated large-diameter beech trees, dramatically shifting the age structure towards saplings (Garnas et al. 2011a). Mature elms (*Ulmus* spp.) have been similarly culled from American (and European) landscapes by Dutch elm disease (Holmes 1980). Nonnative chestnut blight and white pine blister rust have effectively eliminated their host tree species from large tracts of their historical ranges (McKeen 1995, Kinloch 2003, Lovett et al. 2006). Emerald ash borer, sudden oak death, butternut canker, and laurel wilt appear to now be in the early stages of greatly reducing their host populations (Tables 2 and 3).

Wildlife habitat and biodiversity are altered by forest insects and diseases, especially those that kill trees (Chan-McLeod 2006). Altered food supply, such as increases in insects and/or reductions in foliage, can affect multiple trophic levels (Chan-McLeod 2006, Drever et al. 2009). Other populations can be affected positively or negatively depending on the species, time since disturbance, surviving vegetation, ecosystem type, and spatial extent of outbreak (Chan-McLeod 2006). In the short term, the increase in standing dead trees (snags) creates favorable habitat for cavity nesting birds and mammals (Mitchell and Preisler 1998, Logan and Powell 2001, Bonnot et al. 2009, Edworthy et al. 2011). In the longer term, because tree mortality shifts forests toward younger stands of smaller trees, species that depend on mature forests will tend to lose habitat; this is made worse because mature forests have already been disproportionately diminished by human land use patterns (Ellison et al. 2005, Foley et al. 2005).

Elemental cycling and hydrologic processes are influenced by maturity and community composition of forest ecosystems and are therefore modified by biotic disturbances (Lovett et al. 2006). Reduced tree growth leads to reduced transpiration (Hadley et al. 2008) and increased soil moisture (Clow et al. 2011). Following outbreaks that cause widespread tree mortality, stream-flow increases, the annual hydrograph advances, and low flows increase (Bethlahmy 1974, Potts 1984). At the same time, snow accumulation increases and snowmelt is more rapid following needledrop because loss of canopy will decrease interception of snow by the canopy (leading to reduced sublimation and redistribution of snow) and increase solar radiation to the forest floor (Boon 2011, Pugh and Small 2011). Effects of biotic disturbance on nutrient cycling in forests are possible

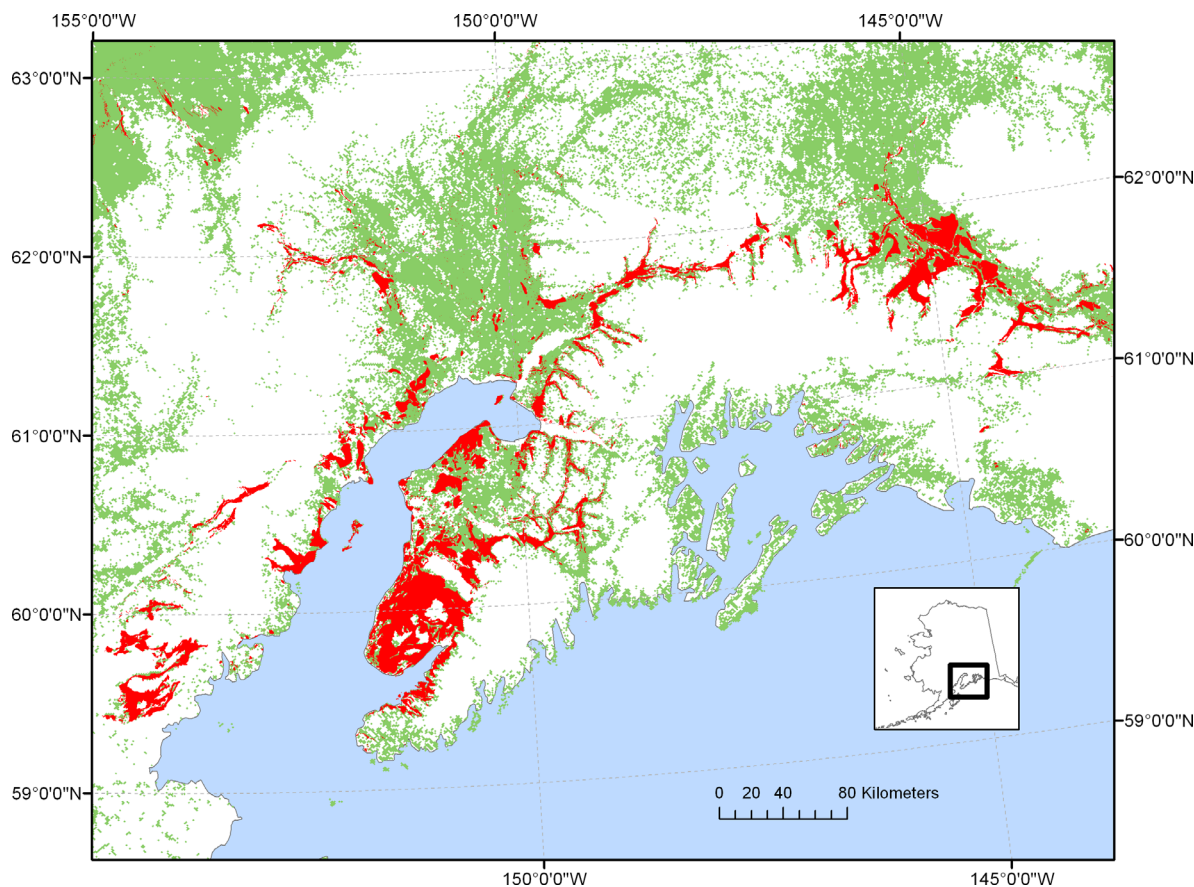


FIG. 8. Cumulative area of spruce (*Picea* spp.) affected (red) by the spruce beetle, *Dendroctonus rufipennis*, from 1989 to 2010 on Kenai Peninsula, Alaska (USA), documented during aerial surveys conducted by the USDA Forest Service. Green shading indicates all spruce forest types (data source: USFS FIA Library, Arlington, Virginia, USA; <http://fia.fs.fed.us/library/maps>).

anytime that species composition is changed because processes that affect N storage (i.e., sequestration in vegetative biomass or retention in soils) change during forest succession (Ellison et al. 2005, Lovett et al. 2006, Knoepp et al. 2011). Stand recovery and biogeochemical cycling following bark beetle attack affect and are affected by N availability (Edburg et al. 2011). Forests afflicted with beech bark disease have experienced an increase in litter decomposition, a decrease in soil C:N ratio, and an increase in extractable nitrate in the soil and nitrate in soil solution (Lovett et al. 2010). In hemlock stands infested with woolly adelgids, litter N increased and N mineralization accelerated even before tree mortality (Stadler et al. 2006, Orwig et al. 2008). Defoliation also tends to alter N pools and fluxes within forests (Lovett et al. 2002). Changes in nutrient cycling, and in particular N cycling, from biotic disturbances that stress or kill canopy trees can influence trajectories of forest dynamics with long-lasting effects on productivity, biodiversity, and elemental cycling (Lovett et al. 2004, Edburg et al. 2011). For example, bark beetles have immediate effects on N uptake by trees (Morehouse et al. 2008) and affect ecosystem-scale N cycling

during an outbreak. We can anticipate that outbreaks will commonly produce persistent changes in the feedbacks that connect biotic communities and elemental cycling (Edburg et al. 2012).

Growing evidence indicates that insect and disease outbreaks in forests can increase carbon efflux from forest ecosystems and therefore create a potential positive feedback to climate change (Kurz et al. 2008, Clark et al. 2010, Hicke et al. 2012a). Temperate forests are important carbon sinks for human CO₂ emissions (Schimel et al. 2001), and recurrent forest disturbances counteract climate change mitigation strategies (Hicke et al. 2012a). The net carbon flux (i.e., whether a forest stand is a carbon source or a sink) can be strongly negative (C source) immediately following a severe mortality event (Clark et al. 2010), and impacted regions can remain a carbon source for decades (Kurz et al. 2008, Stinson et al. 2011). However, the magnitude and duration of modifications to carbon fluxes vary greatly and depend on the type of damage, number of trees affected, response of the surviving vegetation, and time since attack (Hicke et al. 2012a).

Potential biogeophysical effects from stand-scale tree mortality include (1) increased surface albedo that governs absorption of solar radiation, (2) decreased transpiration that influences water cycling, and (3) decreased surface roughness that affects atmospheric drag (Bonan 2008). In spite of their importance as potential feedbacks to the atmospheric system (Randerson et al. 2006, Adams et al. 2010, Rotenberg and Yakir 2010), little is known about how these processes have been altered by insect and disease outbreaks. O'Halloran et al. (2012) estimated that the cooling associated with increased albedo exceeded the warming associated with increased atmospheric CO₂ in the first 14 years following beetle attack. Increases in surface albedo were especially pronounced in winter when mortality-induced needle loss exposed more of the highly reflective snow surface.

ECONOMIC IMPACTS

Forest damage from insects and pathogens has substantial socioeconomic costs (Dale et al. 2001) and analyses of the economic impacts of biotic disturbances have tended to focus on invasive forest insects (Aukema et al. 2011). The full valuation of impacts from biotic disturbances remains a challenge due to nonmarket costs and accounting for long-term losses (Holmes et al. 2010, Aukema et al. 2011, Kovacs et al. 2011*b, c*). For example, epidemics of the southern pine beetle frequently generate a surplus of timber and pulp that initially reduces timber prices, but over the longer term causes timber prices to increase because of a decrease in timber supply (Pye et al. 2011).

Valuation of forest resources is further complicated by the difficulty in quantifying nonmarket values such as ecosystem services (e.g., water regulation and supply, soil conservation, recreation, aesthetic values, biodiversity, and C sequestration; Holmes et al. 2010). Regions with dead and dying trees have reduced aesthetic value (Sheppard and Picard 2006), and there can be enhanced perceptions of wildfire risk and other infrastructure damage, and increased conflict regarding community responses and vulnerability (Flint 2006, Parkins and MacKendrick 2007). Hedonic modeling of impacts to property value offers a promising general tactic for valuation of nonmarketable forest costs where declines in housing prices in areas of outbreaks presumably reflect the collective decline in perceived quality of life (Holmes et al. 2010, Kovacs et al. 2010, Price et al. 2010).

Many estimates of direct costs of biotic disturbances are available. Killed trees represent a loss of income from timber production and can cause economic impacts in outbreak areas and beyond (Abbott et al. 2009). Even a simple accounting of direct losses to timber value from a single insect species can reveal costs that exceed \$1 billion (all dollars are shown in US\$) within 10 states over a period of 28 years (Pye et al. 2011). The costs to remove and replace trees across 25 states that were killed by the emerald ash borer exceed

\$10 billion (Kovacs et al. 2010, 2011*b*). Aukema et al. (2011) estimated that, in the United States, wood- and phloem-boring insects induce costs of about \$1.7 billion annually in local government expenditures and ~\$830 million in lost residential property values.

There are other socioeconomic costs that are generally unaccounted for because we lack the data and/or analytical tools to do so (Pye et al. 2011). These include opportunity costs. What is the cost of underinvestment in a forest region where climatic changes are reducing impacts from forest insects and diseases? We also lack capacity to estimate the cost of changing risks from changing patterns of forest disturbance. What would be the cost of insuring against the collapse of forest-based taxes that support local schools in North Carolina, disruptions of hydrology in the Kirkwood-Cohansey aquifer of the New Jersey Pinelands, or the lost revenues of resorts in Colorado with spoiled viewscapes?

INTERACTIONS WITH OTHER DISTURBANCE AGENTS

Fire and biotic disturbances interact in several ways. Fires can reduce stand susceptibility to insect attack (e.g., Shore et al. 2000) or increase populations of insects and pathogens by increasing a food resource (Parker et al. 2006). Insect-killed trees influence fuels and therefore fire behavior, which depends on the number of attacked trees within a stand and time since outbreak (Ayres and Lombardero 2000, Jenkins et al. 2008, Simard et al. 2011, Hicke et al. 2012*b*). It has been assumed that forest fires generally promote bark beetle outbreaks and vice versa (e.g., Holsten et al. 1995, Ayres and Lombardero 2000, Edmonds et al. 2000, Jenkins et al. 2008). However, new data indicate that (1) beetle outbreaks may not increase wildfire risks (Kulakowski and Jarvis 2011, Simard et al. 2011), (2) fire-induced increases in tree defenses may mitigate future bark beetle risks (Lombardero and Ayres 2011), and (3) fire-beetle interactions are frequently contingent on seasonal timing (Perrakis and Agee 2006, Vega et al. 2011).

Soil water deficits (droughts), which arise from reduced precipitation and/or increased temperatures, are becoming more common in some regions with climate change (Adams et al. 2009, Seppälä et al. 2009). Severe droughts can cause significant plant mortality by themselves (McDowell et al. 2011, Michaelian et al. 2011, Peng et al. 2011), but frequently act in concert with biotic agents. In the western United States and the Italian Alps, extreme drought stress appears to increase forest susceptibility to bark beetle epidemics and diseases (Raffa et al. 2008, Bentz et al. 2010, Williams et al. 2010, Sturrock et al. 2011, Marini et al. 2012). Historically, it has been thought that water limitations that reduce tree growth also reduce tree defenses, but now theory and data suggest that the opposite is often true (Herms and Mattson 1992, Reeve et al. 1995, Lombardero et al. 2000, Hale et al. 2005, Gaylord et al. 2007). The hypothesis that drought stress tends to increase constitutive plants defenses and decrease

Box 1. Summary of observed and anticipated effects of climate change on biotic forest disturbances and key areas to improve prediction, management, and mitigation of those impacts.

Key concepts

- 1) Epidemics of forest insects and diseases exceed other sources of disturbance to North American forests.
- 2) Insect populations are highly responsive to climate change due to their physiological sensitivity to temperature, high mobility, short generation times, and explosive reproductive potential. Pathogens and declines are also strongly influenced by climate change due to their sensitivity to temperature and moisture.
- 3) Previous predictions of expansions in biotic disturbances in forests as a result of climate change are being upheld even more rapidly and dramatically than expected. This is particularly evident with pine bark beetles.
- 4) Changes in biotic disturbance regimes have broad consequences for forest ecosystems and the services they provide to society.
- 5) Climatic effects on forest insect and disease outbreaks may beget further changes in climate by influencing the exchange of carbon, water, and energy between forests and the atmosphere.
- 6) Climate-induced changes in forest productivity and disturbance create opportunities as well as vulnerabilities (e.g., increases in productivity in many areas, and probably decreases in some disturbance risks in some areas).
- 7) There is a need to understand and predict the interactions among climate, forest productivity, forest disturbance, and the socioeconomic relations between forests and people.

inducible plant defenses may permit predictions of which herbivores and pathogens will be affected in which direction by drought stress.

IMPLICATIONS FOR FOREST MANAGEMENT

There is diverse support for general causal linkages between climate change and biotic forest disturbance in North America that matter for ecological processes and socioeconomics (Box 1). Geographic shifts in climate and disturbance place forests at risk even under the unrealistic scenario that there is no net increase in disturbance frequencies averaged across the broader region. Greater regional impacts are expected partly because the rate of tree mortality can greatly exceed the recruitment rate (Allen et al. 2010). Climate change increases the likelihood that forest stands will be exposed to a different and less suitable climate than that under which the current stands matured (e.g., Piao et al. 2008, Breshears et al. 2009), leading to more stands that are susceptible to insects and diseases (Bentz et al. 2009, Sturrock et al. 2011). These changes tend to reduce the extent of mature forests and can adversely affect ecosystem services provided to society. There is a broad need for increased capacity to predict future patterns of biotic disturbances and integrate this knowledge with forest ecosystem science and the socioeconomics of human land use.

Changing climates also introduce practical problems for forest management because they create geographic mismatches between disturbance types and management expertise. For example, suppression management of the southern pine beetle epidemic in New Jersey requires extrapolating knowledge that was developed in different forest types and is further complicated because there is

an administrative boundary of the USDA Forest Service that lies between the Northeast Region (Region 9) and Southeast Region (Region 8). The Southeast Region holds great institutional expertise in bark beetle management, whereas expertise in the Northeast Region lies in managing different forest health risks. Efficient coordination and technology transfer among regional forest resource managers is a step toward minimizing risks, shortening response times, and improving efficacy of management responses to forest disturbance as they continue to shift in the future.

From many perspectives, a key attribute of forested landscapes is the regional composition of forest stands of different maturity (Magnani et al. 2007, Kurz et al. 2008, Luyssaert et al. 2008, Thompson et al. 2009, Hansen et al. 2010, Latta et al. 2010). Climate warming and increases in CO₂ are tending to increase forest maturation rates in many regions of the United States and the rest of the world (Anderson et al. 2006, Boisvenue and Running 2006, Salzer et al. 2009, McMahon et al. 2010, Wang et al. 2011). Conversely, forest maturation rates are projected to decline in many ecosystems that are already arid (e.g., southwestern United States and intermountain regions; Boisvenue and Running 2006, Chen et al. 2010). The relative frequency of stands of different maturity reflects a dynamic balance between tree maturation rates and stand disturbance frequencies (Lines et al. 2010, Littell et al. 2010). Anticipating, mitigating, and adapting to continuing changes in biotic disturbance regimes calls for improved capacity to model forest maturation amidst insect and disease dynamics as a function of climate and land use. The development and refinement of these models is frequently data limited. There has been great

progress since the first National Climate Assessment in improving insect and disease monitoring and the dissemination of monitoring data to forest managers, scientists, and the public (e.g., see USDA Forest Service information *available online*).⁶ However, we still lack the technical ability to effectively monitor many of the disturbance agents listed in Tables 2 and 3, especially in forest types east of the Great Plains, where tree species diversity is high and species-specific impacts are difficult to detect by aerial detection or remote sensing.

Increases in forest productivity and/or decreases in biotic disturbance create opportunities for increases in the extent of forests and many of the services they provide (e.g., timber and pulpwood production, water regulation and supply, recreation, aesthetic values, and C sequestration), whereas the opposite patterns promote corresponding vulnerabilities. Public education, government policy, economic analysis, and informed decision-making on public land are among the tools for promoting opportunities provided in the first case and shielding against risks created in the second case (Glück et al. 2009). Without the efficient development and deployment of suitable new tactics for managing emerging biotic disturbances, we can anticipate that the extent of mature forests will decline even faster in regions of increasing insect and disease outbreaks because sensible land use decisions will disfavor future investments in forests. Without the development and transfer of suitable new knowledge, we should not anticipate that there will be compensatory land use responses in regions of decreasing biotic disturbance.

CONCLUSIONS

There are currently about 40 taxa of insects and diseases that are major sources of forest disturbance in North American forests. Some of these organisms are already responding to recent climatic trends with changes in their distribution and abundance that are altering forest disturbance regimes at regional and continental scales. We can anticipate continuing changes in the nature, extent, and spatial patterning of forest disturbances, with broad consequences for the ecology and socioeconomics of American forests. There are now process-based models that link climate to tree mortality by biotic disturbances and relate these disturbances to ecosystem properties. However, significant knowledge gaps remain regarding the influence of climate on biotic disturbance agents and the effects of forest disturbance on ecosystems (Box 1). The direct effects of climate on insect outbreaks are better understood compared to diseases. Indirect effects of climate on insects and disease (e.g., via changes in tree defenses or on interactions between insects and pathogens and their natural enemies) may be at least as important in determining the emerging new patterns of forest disturbance, but we generally lack mechanistic models that have been tested

against observations. As the frequency and geographic distributions of outbreaks shift, communication among regional forest resource managers will become increasingly important as will the development of general scientific theory to inform the management of situations for which there are no historical analogues. Perhaps the most valuable attainable goal in the short term is to further improve the collection, dissemination, and integration of data on biotic disturbance regimes and their consequences for interactions among forests, people, and climate.

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⁶ <http://foresthealth.fs.usda.gov/portal>

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SUPPLEMENTAL MATERIAL

Data Availability

Data associated with this paper have been deposited in Dryad: <http://dx.doi.org/10.5061/dryad.cq1r1>