Ecological Monographs, 83(4), 2013, pp. 441–470

Consequences of climate change for biotic disturbances in North American forests

AARON S. WEED,[1,3] MATTHEW P. AYRES,[1] AND JEFFREY A. HICKE[2]

[1]*Department of Biological Sciences, Dartmouth College, Hanover, New Hampshire 03755 USA*
[2]*Department of Geography, University of Idaho, Moscow, Idaho 83844 USA*

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. 2012*a*). 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

Manuscript received 25 January 2013; accepted 31 January 2013. Corresponding Editor: T. P. Young.

[3] E-mail: aaron.s.weed@dartmouth.edu

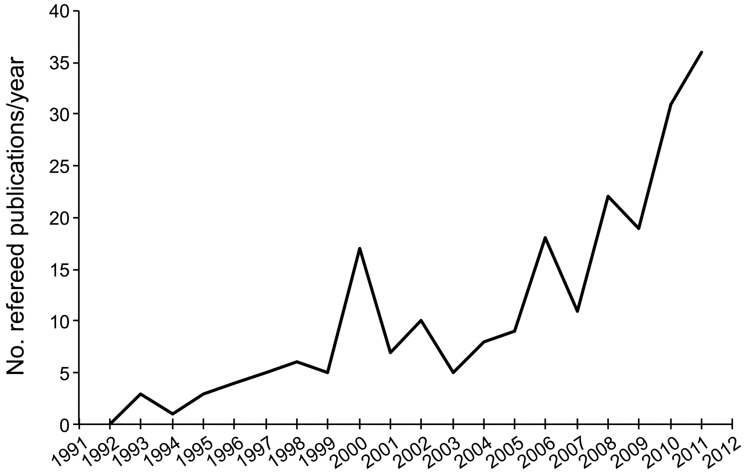

FIG. 1. Annual number of refereed articles published worldwide on forest biotic disturbances that address the role of climate as a driver of disturbance. The search criteria were: (climate OR temperature) AND forest AND (insect OR pathogen OR disease). Search results were refined further into the subject 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 CO_2 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 Lerdau 2004, Lindroth 2010). In

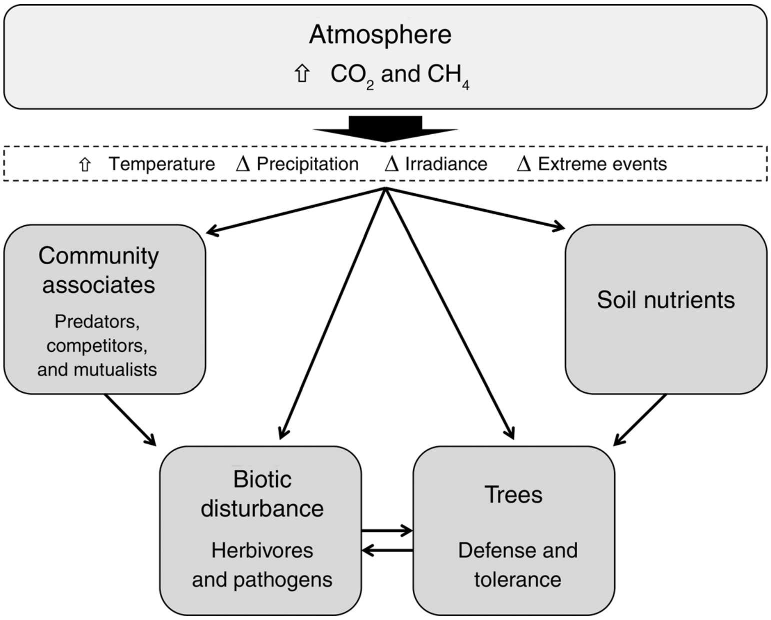

FIG. 2. A schematic of the general pathways by which atmospheric changes associated with increasing greenhouse gases can influence forest disturbance from insects and diseases.

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), Friedenberg et 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. (2010*b*)
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 (Negron 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

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[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 commonly 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 1995*a*, but see Reynolds et al. 2007), drought stress of host trees (Williams and Liebhold 1995*b*, 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.

			References	
Cases	Herbivore	Hosts	General references	Studies related to climate†
Defoliation by gypsy moths and tussock moths	*Lymantria dispar*,‡ *Orgyia* spp.	*Quercus* 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	*Acleris* spp., *Choristoneura fumiferana*, *C. occidentalis*, *C. pinus*	*Abies* spp., *Pseudotsuga* spp., *Picea* spp., *Pinus* 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 (1984*a*, *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),§ Rauchfuss et al. (2009; P,T)§
Defoliation by gracillariid leaf miners	*Micrurapteryx salicifoliella*, *Phyllocnistis populiella*	*Populus tremuloides*. *Salix* spp.	Condrashoff (1964), Furniss et al. (2001), Wagner et al. (2008), Morton and Pereya (2011)	Wagner et al. (2012; T)
Defoliation by loopers	*Enypia griseata*, *Lambdina*, *Nepytia* spp.	*Abies* spp., *Pseudotsuga* spp., *Picea* spp., *Pinus* spp., *Thuja* 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)	Rochefort et al. (2011; T), Delisle et al. (2012; T)
Defoliation by tent caterpillars	*Malacosoma* spp.	*Prunus* spp., *Populus* spp., *Betula* spp., *Nyssa* 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	*Anoplophora glabripennis*‡	*Acer* spp, *Ulmus* spp., *Populus* 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	*Agrilus anxius*, *A. auroguttatus*, and *A. planipennis*‡	*Betula* spp., *Quercus* spp., and *Fraxinus* spp., respectively	Balch and Prebble (1940), Cappaert et al. (2005), Kovacs et al. (2010, 2011*b*), 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	*Dendroctonus pseudotsugae*	*Pseudotsuga menziesii*	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	References: Studies related to climate†
Infestations by mountain pine beetle	*Dendroctonus ponderosae*	*Pinus* 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	*Ips* spp.	*Pinus* 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	*Dendroctonus frontalis*	*Pinus* 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),§ Friedenberg et 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	*Elatobium abietinum*‡	*Picea* spp.	Parry (1969), Day (1984), Lynch (2004)	Powell (1974; T), Powell and Parry (1976; T),§ Day et al. (2010; T)§
Infestations by spruce beetle	*Dendroctonus rufipennis*	*Picea* 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	*Dendroctonus brevicomis*	*Pinus* spp., chiefly *P. ponderosa*	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	*Pissodes strobi*	*Pinus* spp., *Picea* spp.	Bellocq and Smith (1995), Lavallee et al. (1996), Woods et al. (2010), Ostry et al. (2010)	Sullivan (1961; T)
Infestations by woolly adelgids	*Adelges piceae*,‡ *A. tsugae*‡	*Abies fraseri*, *A. balsamea*, *Tsuga* 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 (CO_2), 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.

			References	
Cases	Pathogen/ parasite	Hosts	General references	Studies related to climate†
Alder canker	*Valsa melanodiscus*	*Alnus* 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. (2010*a*; T)
Annosum root rot	*Heterobasidion annosum*	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)
Anthracnose leaf disease	*Discula destructiva*, *Glomerella cingulata*, *Colletotrichum gloeosporioides*, others	*Quercus* spp., *Fraxinus* spp., *Platanus* spp., *Cornus* spp.	Britton (1993), Dudt and Shure (1993), Stanosz (1993), McEwan et al. (2000), Holzmueller et al. (2006)	Britton et al. (1997; P), Chakraborty et al. (2000; CO_2)
Armillaria root rot	*Armillaria* spp.	Broadleaved trees and conifers, e.g., *Acer* spp., *Quercus* spp., *Picea* 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	*Neonectria* spp. (and associated scale insects *Cryptococcus fagisuga*‡ and *Xylococculus betulae*)	*Fagus grandifolia*	Shigo (1972), Houston (1998), Busby and Cantham (2011), Garnas et al. (2011*a*)	Dukes et al. (2009), Garnas et al. (2011*b*; P,T),§ Kasson and Livingston (2012; P,T)§
Butternut canker	*Sirococcus clavigignenti-juglandacearuma*‡	*Juglans cinerea*	Harrison et al. (1998), Fleming et al. (2000), Broders et al. (2001, 2012), Clark et al. (2008)	
Chestnut blight	*Cryphonectria parasitica*‡	*Castanea dentata*	McKeen (1995), Taylor et al. (1998)	
Dothistroma needle blight	*Dothistroma septosporum and D. pini*	Many conifers, *Pinus* 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	*Ophiostoma novoulmi*‡ (and associated bark beetles *Hylurgopinus rufipes* and *Scolytus multistriatus*‡)	*Ulmus* spp.	Holmes (1980), Fleming et al. (2000)	Sutherland et al. (1997; T),§ Boland et al. (2004)
Dwarf mistletoe	*Arceuthobium* spp.	*Pinus* spp., *Tsuga* spp.	Bennetts et al. (1996), Synder et al. (1996), Kipfmueller and Baker (1998)	Brandt et al. (2004; T), Stanton (2007; P,T), Cullings and Hanely (2010), Barrett et al. (2012; P,T)§
Fusiform rust	*Cronartium quercuum*	*Pinus* spp., chiefly southern pine	Walkinshaw and Barnett (1995), Doudrick et al. (1996), Nelson et al. (1996)	Runion et al. (2010; CO_2)
Laurel wilt	*Raffaelea lauricola*‡ (and associated bark beetle *Xyleborus glabratus*‡)	Lauraceae	Fraedrich et al. (2008), Harrington et al. (2011)	Koch and Smith (2008; T)
Oak wilt disease	*Ceratocystis fagacearum*	*Quercus* 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	*Phytophthora cinnamomi*‡	*Quercus* spp., *Castanea* spp., *Abies* 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	*Gibberella circinata* (anamorph *Fusarium circinatum*)	*Pinus* 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†
Procera, black stain, and other *Leptographium* root diseases	*Leptographium* spp.	Many conifers, e.g., *Pinus* spp	Harrington and Cobb (1983), Klepzig et al. (1996), Jacobi et al. (2008)	
Scleroderris canker	*Gremmeniella abietina*‡ (= *Sclerroderris lagerbergii* and *Ascocalyx abietina*)(anamorph *Brunchorstia pinea*)	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	*Populus tremuloides*	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, 2010*b*; P,T),§ Michaelian et al. (2011; P),§ Hanna and Kulakowski (2012; P)§
Sudden oak death	*Phytophthora ramorum*‡	*Quercus* spp., *Lithocarpus* spp.	Monahan and Koenig (2006), Dodd et al. (2008), Vaclavik et al. (2010), Kovacs et al. (2011*a*, *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	*Phaeocryptopus gaeumannii*	*Pseudotsuga menziesii*	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	*Geosmithia morbida* (and associated bark beetle *Pityophthorous juglandis*)	*Juglans* spp.	Cranshaw (2011), Grant et al. (2011), Hadziabdic et al. (2011), Kolarik et al. (2011), Seybold et al. (2012)	
White pine blister rust	*Cronartium ribicola*‡	Five-needle pines, e.g., *Pinus strobus*, *P. albicaulis*	Hunt and Meagher (1989), Keane et al. (1990), Kinloch (2003), Six and Adams (2007), Loo (2009), Field et al. (2012)	Van Arsdel (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 (CO_2), 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. 2011*b*).

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

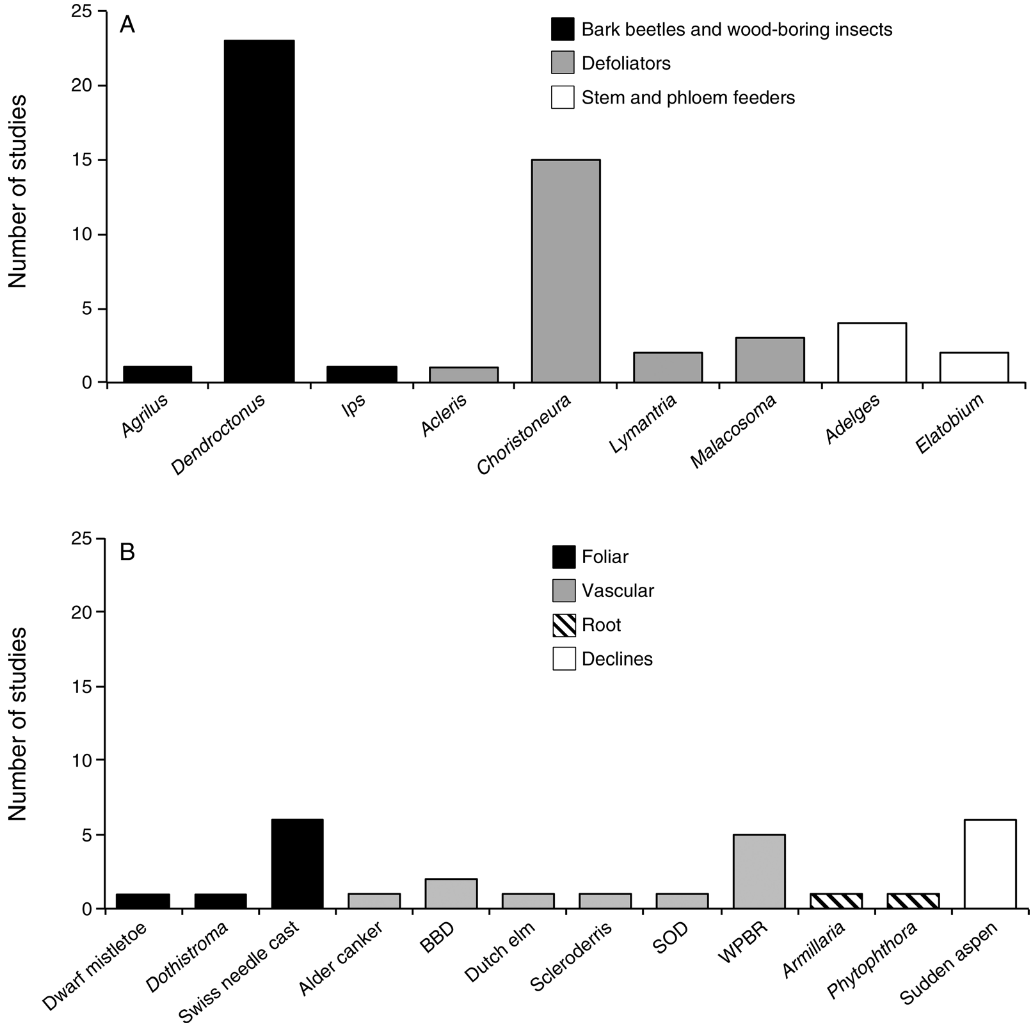

FIG. 3. (A) Frequency of studies evaluating the role of climate on forest disturbance from 1950 to 2012 (grouped by insect genera within feeding guild). (B) Frequency of studies evaluating the role of climate on forest disturbance by pathogens and declines from 1970 to 2012. Abbreviations are: BBD, beech 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]

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 Pinaleño 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

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

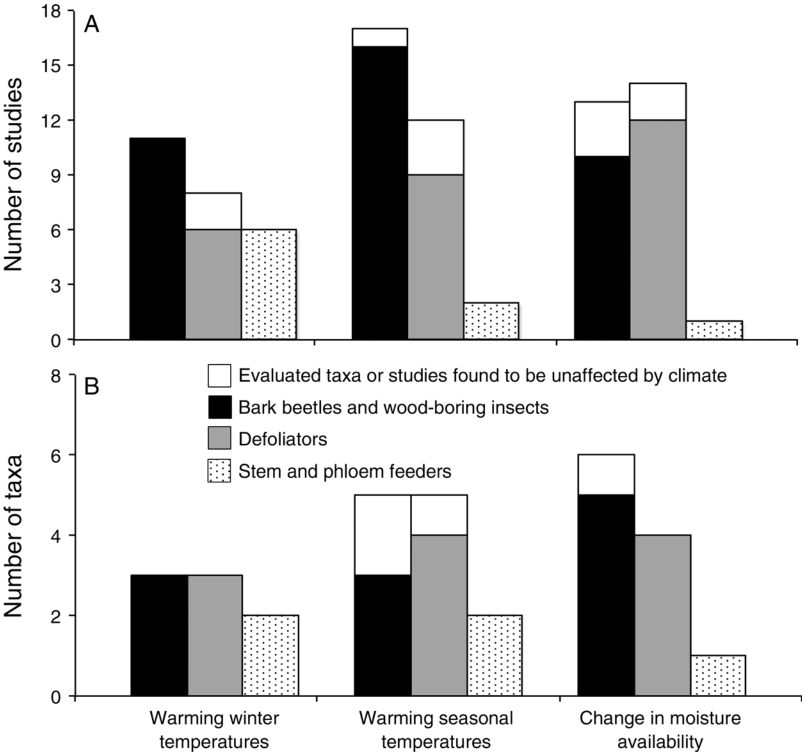

FIG. 4. (A) Frequency of studies evaluating the role of climate on forest disturbance among insect feeding guilds, and (B) frequency of taxa from these studies whose demography and population dynamics are demonstrably sensitive to climate.

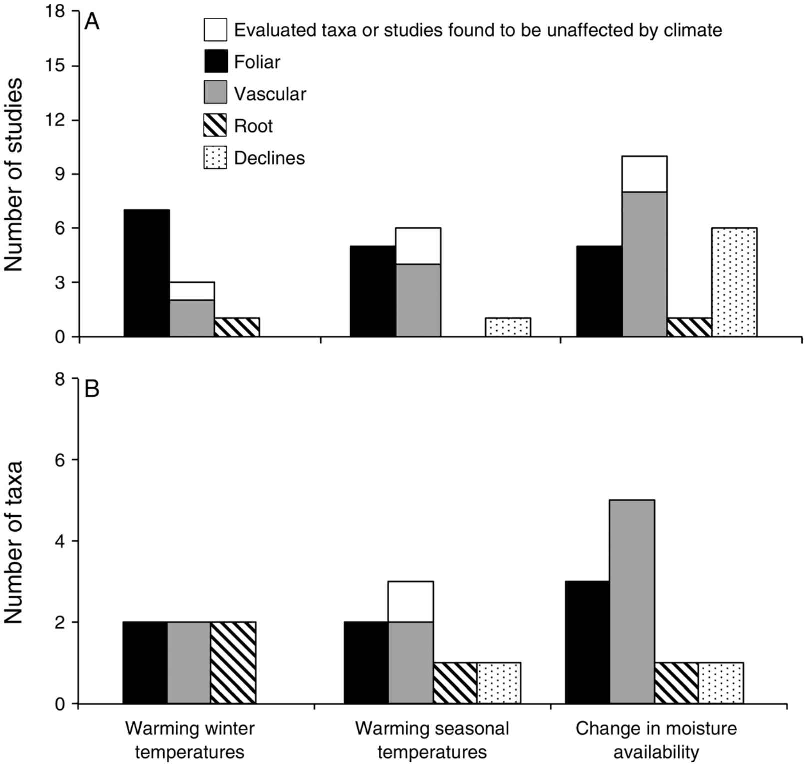

FIG. 5. (A) Frequency of studies evaluating the role of climate on forest disturbance by pathogens and declines, and (B) frequency of taxa from these studies whose demography and population dynamics are demonstrably sensitive to climate.

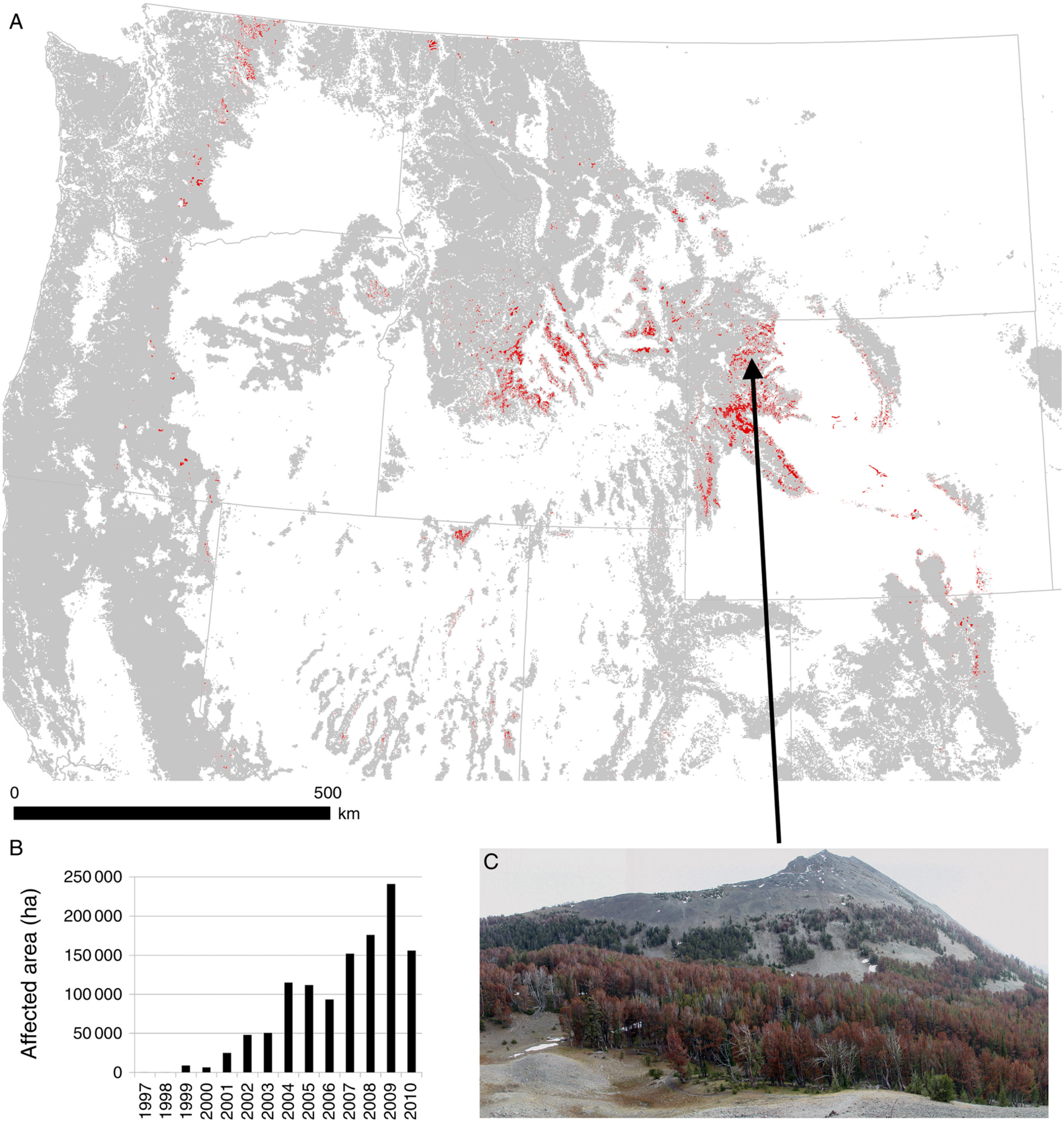

FIG. 6. (A) Area affected (red) by mortality in stands of *Pinus albicaulis* (whitebark), *P. flexilis* (limber), and *P. aristata* (bristlecone) pines in 1997–2010 as detected by aerial surveys conducted by the USDA Forest Service in the western United States. Affected areas include a mix of dead and 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

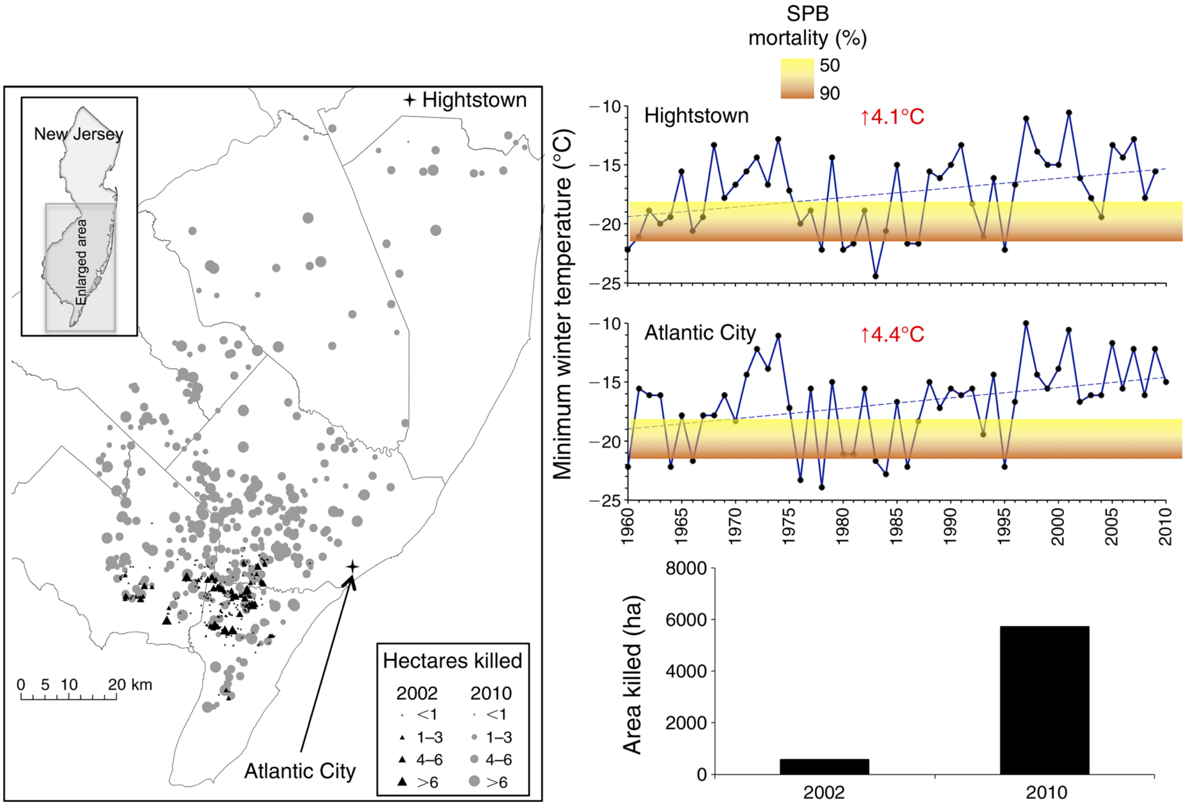

FIG. 7. The most cold-tolerant life stages of southern pine beetles (*Dendroctonus frontalis* Zimmermann [SPB]) die when winter air temperatures drop below about −18°C. A subcontinental pattern of warmer winters has eliminated a climatic barrier to occupancy of the New Jersey Pinelands (USA) by the beetle 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°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 experienced 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. 2011*a*). 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, streamflow 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

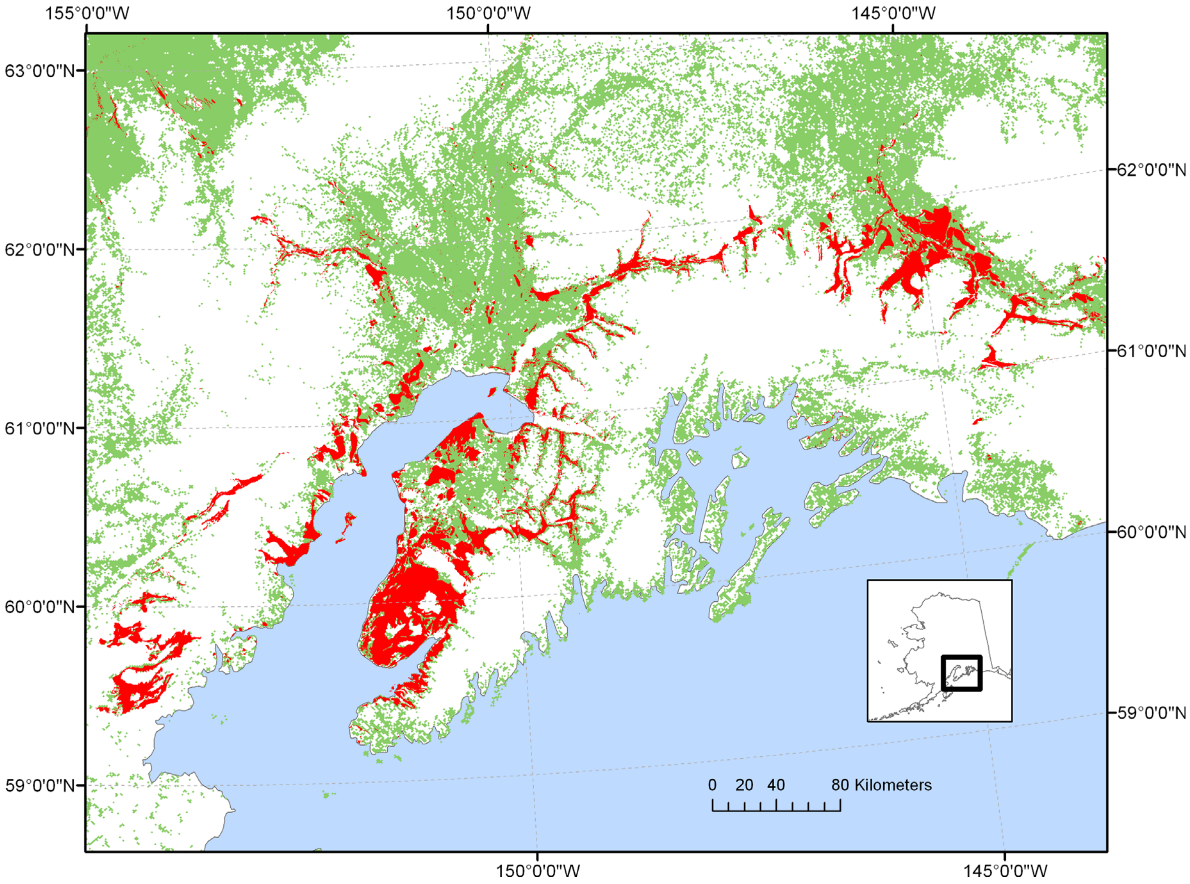

Fig. 8. Cumulative area of spruce (*Picea* spp.) affected (red) by the spruce beetle, *Dendroctonus rufipennis*, from 1989 to 2010 on Kenai Peninsula, Alaska (USA), documented during aerial surveys conducted by the USDA Forest Service. Green shading indicates all spruce forest types (data source: USFS 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. 2012*a*). Temperate forests are important carbon sinks for human CO_2 emissions (Schimel et al. 2001), and recurrent forest disturbances counteract climate change mitigation strategies (Hicke et al. 2012*a*). 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. 2012*a*).

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 CO_2 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 Unites 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 CO_2 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.

ACKNOWLEDGMENTS

This document was conceived as a part of the third National Climate Assessment evaluating the effects of climatic change on forest ecosystems and forest resources in the United States. We thank T. Holmes, K. Klepzig, M. Lombardero, A. Lynch, J. Lundquist, and S. McDermott for sharing their knowledge. We are also grateful for the comments from anonymous reviewers. Support was provided by NRI/AFRI 2009-65104-05731 and a cooperative agreement with the Southern Research Station, USDA Forest Service, as well as the USFS Western Wildland Environmental Threat Assessment Center and the USGS Western Mountain Initiative.

LITERATURE CITED

Abbott, B., B. Stennes, and G. Cornelis van Kooten. 2009. Mountain pine beetle, global markets, and the British Columbia forest economy. Canadian Journal of Forest Research 39:1313–1321.

Adams, H. D., M. Guardiola-Claramonte, G. A. Barron-Gafford, J. C. Villegas, D. D. Breshears, C. B. Zou, P. A. Troch, and T. E. Huxman. 2009. Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. Proceedings of the National Academy of Sciences USA 106:7063–7066.

Adams, H. D., A. K. Macalady, D. D. Breshears, C. D. Allen, N. L. Stephenson, S. R. Saleska, T. E. Huxman, and N. G. McDowell. 2010. Climate-induced tree mortality: Earth system consequences. EOS, Transactions of the American Geophysical Union 91:153.

Akers, R. C., and D. G. Nielsen. 1984. Predicting *Agrilus anxius* Gory (Coleoptera: Buprestidae) adult emergence by heat unit accumulation. Journal of Economic Entomology 77:1459–1463.

Allen, C. D., et al. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259:660–684.

Allen, J., S. Wesser, C. Markon, and K. Winterberger. 2006. Stand and landscape level effects of a major outbreak of spruce beetles on forest vegetation in the Copper River Basin, Alaska. Forest Ecology and Management 227:257–266.

Amman, G. D. 1968. Effects of temperature and humidity on development and hatching of eggs of *Adelges piceae*. Annals of the Entomological Society of America 61:1606–1611.

Anderegg, W. R. L., J. A. Berry, D. D. Smith, J. S. Sperry, L. D. L. Anderegg, and C. B. Field. 2012. The roles of hydraulic and carbon stress in a widespread climate-induced forest die-off. Proceedings of the National Academy of Sciences USA 109:233–237.

Anderson, K. J., A. P. Allen, J. F. Gillooly, and J. H. Brown. 2006. Temperature-dependence of biomass accumulation rates during secondary succession. Ecology Letters 9:673–682.

Anonymous. 1665. Some observations of swarms of strange insects, and the mischiefs done by them. Philosophical Transactions 1:137–138.

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[6] http://foresthealth.fs.usda.gov/portal

Appel, D. N. 1995. The oak wilt enigma: perspectives from the Texas epidemic. Annual Review of Phytopathology 33:103–118.

Aukema, B. H., A. L. Carroll, Y. Zheng, J. Zhu, K. F. Raffa, R. Dan Moore, K. Stahl, and S. W. Taylor. 2008. Movement of outbreak populations of mountain pine beetle: influences of spatiotemporal patterns and climate. Ecography 31:348–358.

Aukema, J. E., et al. 2011. Economic impacts of non-native forest insects in the continental United States. PLoS ONE 6:e24587.

Ayres, M. P. 1993. Plant defense, herbivory, and climate change. Pages 75–94 *in* P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, editors. Biotic interactions and global change. Sinauer Associates, Sunderland, Massachusetts, USA.

Ayres, M. P., and M. J. Lombardero. 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. Science of the Total Environment 262:263–286.

Balch, R. E., and J. S. Prebble. 1940. The bronze birch borer and its relation to the dying of birch in New Brunswick forests. Forestry Chronicle 16:179–201.

Bale, J. S. 2002. Insects and low temperatures: from molecular biology to distributions and abundance. Philosophical Transactions of the Royal Society of London B 357:849–862.

Bale, J. S., and S. A. L. Hayward. 2010. Insect overwintering in a changing climate. Journal of Experimental Biology 213:980–994.

Barrett, T. M., G. Latta, P. E. Hennon, B. N. I. Eskelson, and H. Temesgen. 2012. Host–parasite distributions under changing climate: *Tsuga heterophylla* and *Arceuthobium tsugense* in Alaska. Canadian Journal of Forest Research 42:642–656.

Bellocq, M. I., and S. M. Smith. 1995. Influence of reforestation technique, slash, competing vegetation, and duff depth on the overwintering mortality of *Pissodes strobi* (Coleoptera: Curculionidae), the white pine weevil. Forest Ecology and Management 78:1–10.

Bennetts, R. E., G. C. White, F. G. Hawksworth, and S. E. Severs. 1996. The influence of dwarf mistletoe on bird communities in Colorado ponderosa pine forests. Ecological Applications 6:899–909.

Benson, D. M. 1982. Cold inactivation of *Phytophthora cinnamomi*. Phytopathology 72:560–563.

Bentz, B. J., J. A. Logan, and G. D. Amman. 1991. Temperature-dependent development of the mountain pine beetle (Coleoptera: Scolytidae) and simulation of its phenology. Canadian Entomologist 123:1083–1094.

Bentz, B., et al. 2009. Bark beetle outbreaks in western North America: Causes and consequences. University of Utah Press, Salt Lake City, Utah, USA.

Bentz, B. J., J. Régnière, C. J. Fettig, E. M. Hansen, J. L. Hayes, J. A. Hicke, R. G. Kelsey, J. F. Negrón, and S. J. Seybold. 2010. Climate change and bark beetles of the western United States and Canada: Direct and indirect effects. BioScience 60:602–613.

Berg, E. E., J. D. Henry, C. L. Fastie, A. D. De Volder, and S. M. Matsuoka. 2006. Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: Relationship to summer temperatures and regional differences in disturbance regimes. Forest Ecology and Management 227:219–232.

Berggren, A., C. Bjorkman, H. Bylund, and M. P. Ayres. 2009. The distribution and abundance of animal populations in a climate of uncertainty. Oikos 118:1121–1126.

Bergot, M., E. Cloppet, V. Pérarnaud, M. Déqué, B. Marçais, and M. L. Desprez-Loustau. 2004. Simulation of potential range expansion of oak disease caused by *Phytophthora cinnamomi* under climate change. Global Change Biology 10:1539–1552.

Berryman, A. A. 1986. On the dynamics of blackheaded budworm populations. Canadian Entomologist 118:775–779.

Bethlahmy, N. 1974. More streamflow after a bark beetle epidemic. Journal of Hydrology 23:185–189.

Bidart-Bouzat, M. G., and D. J. Kliebenstein. 2008. Differential levels of insect herbivory in the field associated with genotypic variation in glucosinolates in *Arabidopsis thaliana*. Journal of Chemical Ecology 34:1026–1037.

Bjørnstad, O. N., C. Robinet, and A. M. Liebhold. 2010. Geographic variation in North American gypsy moth cycles: subharmonics, generalist predators, and spatial coupling. Ecology 91:106–118.

Blais, J. R. 1981. Effects of late spring frosts in 1980 on spruce budworm and its host trees in the Laurentian Park region of Quebec. Canadian Forestry Service Research Notes 1:16–17.

Boisvenue, C., and S. W. Running. 2006. Impacts of climate change on natural forest productivity: evidence since the middle of the 20th century. Global Change Biology 12:862–882.

Boland, G., M. Melzer, A. Hopkin, V. Higgins, and A. Nassuth. 2004. Climate change and plant diseases in Ontario. Canadian Journal of Plant Pathology 26:335–350.

Bonan, G. B. 2008. Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. Science 320:1444–1449.

Bonnot, T. W., J. J. Millspaugh, and M. A. Rumble. 2009. Multi-scale nest-site selection by black-backed woodpeckers in outbreaks of mountain pine beetles. Forest Ecology and Management 259:220–228.

Boon, S. 2011. Snow accumulation following forest disturbance. Ecohydrology 5:279–285.

Bradshaw, R. E. 2004. Dothistroma (red-band) needle blight of pines and the dothistromin toxin: a review. Forest Pathology 34:163–185.

Bradshaw, W. E., and C. M. Holzapfel. 2010. Insects at not so low temperature: Climate change in the temperate zone and its biotic consequences. Pages 242–275 *in* D. L. Denlinger and R. E. Lee, editors. Low temperature biology of insects. Cambridge University Press, Cambridge, UK.

Brandt, J., Y. Hiratsuka, and D. Pluth. 2004. Extreme cold temperatures and survival of overwintering and germinated *Arceuthobium americanum* seeds. Canadian Journal of Forest Research 34:174–183.

Brasier, C. M. 1996. *Phytophthora cinnamomi* and oak decline in southern Europe. Environmental constraints including climate change. Annals of Forest Science 53:347–358.

Breshears, D. D., et al. 2005. Regional vegetation die-off in response to global-change-type drought. Proceedings of the National Academy of Sciences USA 102:15144–15148.

Breshears, D. D., O. B. Myers, C. W. Meyer, F. J. Barnes, C. B. Zou, C. D. Allen, N. G. McDowell, and W. T. Pockman. 2009. Tree die-off in response to global change-type drought: mortality insights from a decade of plant water potential measurements. Frontiers in Ecology and the Environment 7:185–189.

Britton, K. O. 1993. Anthracnose infection of dogwood seedlings exposed to natural inoculum in western North Carolina. Plant Disease 77:34–37.

Britton, K. O., P. Berrang, and E. Mavity. 1997. Soil effects mediate interaction of dogwood anthracnose and acidic precipitation. Pages 635–646 *in* R. A. Mickler and S. Fox, editors. The productivity and sustainability of southern forest ecosystems in a changing environment. Springer-Verlag, New York, New York, USA.

Broders, K., L. Barbison, and G. Boland. 2001. Population structure of *Ophiognomonia clavigignenti-juglandacearum* reveals multiple introductions of the butternut canker fungus into North America. Phytopathology 101:S20.

Broders, K. D., A. Boraks, A. M. Sanchez, and G. J. Boland. 2012. Population structure of the butternut canker fungus, *Ophiognomonia clavigignenti-juglandacearum*, in North American forests. Ecology and Evolution 2:2114–2127.

Brunelle, A., G. E. Rehfeldt, B. Bentz, and A. S. Munson. 2008. Holocene records of *Dendroctonus* bark beetles in high elevation pine forests of Idaho and Montana, USA. Forest Ecology and Management 255:836–846.

Busby, P. E., and C. D. Canham. 2011. An exotic insect and pathogen disease complex reduces aboveground tree biomass in temperate forests of eastern North America. Canadian Journal of Forest Research 41:401–411.

Butin, E., A. H. Porter, and J. Elkinton. 2005. Adaptation during biological invasions and the case of *Adelges tsugae*. Evolutionary Ecology Research 7:887–900.

Butt, C., D. Quiring, C. Hébert, J. Delisle, R. Berthiaume, É. Bauce, and L. Royer. 2010. Influence of balsam fir (*Abies balsamea*) budburst phenology on hemlock looper (*Lambdina fiscellaria*). Entomologia Experimentalis et Applicata 134:220–226.

Campbell, E. M., R. I. Alfaro, and B. Hawkes. 2007. Spatial distribution of mountain pine beetle outbreaks in relation to climate and stand characteristics: a dendroecological analysis. Journal of Integrative Plant Biology 49:168–178.

Campbell, E. M., and J. A. Antos. 2000. Distribution and severity of white pine blister rust and mountain pine beetle on whitebark pine in British Columbia. Canadian Journal of Forest Research 30:1051–1059.

Campbell, I. M. 1989. Does climate affect host-plant quality? Annual variation in the quality of balsam fir as food for spruce budworm. Oecologia 81:341–344.

Campbell, R., D. J. Smith, and A. Arsenault. 2006. Multi-century history of western spruce budworm outbreaks in interior Douglas-fir forests near Kamloops, British Columbia. Canadian Journal of Forest Research 36:1758–1769.

Candau, J. N., and R. A. Fleming. 2005. Landscape-scale spatial distribution of spruce budworm defoliation in relation to bioclimatic conditions. Canadian Journal of Forest Research 35:2218–2232.

Candau, J. N., and R. A. Fleming. 2011. Forecasting the response of spruce budworm defoliation to climate change in Ontario. Canadian Journal of Forest Research 41:1948–1960.

Cappaert, D., D. McCullough, T. Poland, and N. W. Siegert. 2005. Emerald ash borer in North America: a research and regulatory challenge. American Entomologist 51:152–165.

Cavey, J. F., E. R. Hoebeke, S. Passoa, and S. W. Lingafelter. 1998. A new exotic threat to North American hardwood forests: an Asian longhorned beetle, *Anoplophora glabripennis* Motschulsky (Coleoptera: Cerambycidae): I. Larval description and diagnosis. Entomological Society of Washington 100:373–381.

Chakraborty, S., I. B. Pangga, J. Lupton, L. Hart, P. M. Room, and D. Yates. 2000. Production and dispersal of *Colletotrichum gloeosporioides* spores on *Stylosanthes scabra* under elevated CO_2. Environmental Pollution 108:381–387.

Chan-McLeod, A. C. A. 2006. A review and synthesis of the effects of unsalvaged mountain-pine-beetle-attacked stands on wildlife and implications for forest management. BC Journal of Ecosystems and Management 7:119–132.

Chapman, T. B., T. T. Veblen, and T. Schoennagel. 2012. Spatiotemporal patterns of mountain pine beetle activity in the southern Rocky Mountains. Ecology 93:2175–2185.

Charbonneau, D., F. Lorenzetti, F. Doyon, and Y. Mauffette. 2012. The influence of stand and landscape characteristics on forest tent caterpillar (*Malacosoma disstria*) defoliation dynamics: the case of the 1999–2002 outbreak in northwestern Quebec. Canadian Journal of Forest Research 42:1827–1836.

Chen, P. Y., C. Welsh, and A. Hamann. 2010. Geographic variation in growth response of Douglas-fir to interannual climate variability and projected climate change. Global Change Biology 16:3374–3385.

Clark, K. L., N. Skowronski, and J. Hom. 2010. Invasive insects impact forest carbon dynamics. Global Change Biology 16:88–101.

Clark, S. L., S. L. Brosi, S. E. Schlarbaum, and H. D. Grissino-Mayer. 2008. Dendrochronology of two butternut (*Juglans cinerea*) populations in the southeastern United States. Forest Ecology and Management 255:1772–1780.

Clinton, B. D., L. R. Boring, and W. T. Swank. 1993. Canopy gap characteristics and drought influences in oak forests of the Coweeta Basin. Ecology 74:1551–1558.

Clow, D. W., C. Rhoades, J. Briggs, M. Caldwell, and W. M. Lewis. 2011. Responses of soil and water chemistry to mountain pine beetle induced tree mortality in Grand County, Colorado, USA. Applied Geochemistry 26:S174–S178.

Coakley, S., H. Scherm, and S. Chakraborty. 1999. Climate change and plant disease management. Annual Review of Phytopathology 37:399–426.

Coleman, T. W., N. E. Grulke, M. Daly, C. Godinez, S. L. Schilling, P. J. Riggan, and S. J. Seybold. 2011. Coast live oak, *Quercus agrifolia*, susceptibility and response to goldspotted oak borer, *Agrilus auroguttatus*, injury in southern California. Forest Ecology and Management 261:1852–1865.

Coleman, T. W., and S. J. Seybold. 2011. Collection history and comparison of the interactions of the Goldspotted Oak Borer, *Agrilus auroguttatus* Schaeffer (Coleoptera: Buprestidae), with host oaks in southern California and southeastern Arizona, U.S.A. Coleopterists Bulletin 65:93–108.

Collins, B. J., C. C. Rhoades, R. M. Hubbard, and M. A. Battaglia. 2011. Tree regeneration and future stand development after bark beetle infestation and harvesting in Colorado lodgepole pine stands. Forest Ecology and Management 261:2168–2175.

Condrashoff, S. F. 1964. Bionomics of the aspen leaf miner, *Phyllocnistis populiella* Cham. (Lepidoptera: Gracillariidae). Canadian Entomologist 96:857–874.

Cranshaw, W. 2011. Recently recognized range extensions of the walnut twig beetle, *Pityophthorus juglandis* Blackman (Coleoptera: Curculionidae: Scolytinae), in the western United States. Coleopterists Bulletin 65:48–49.

Crosthwaite, J. C., S. Sobek, D. B. Lyons, M. A. Bernards, and B. J. Sinclair. 2011. The overwintering physiology of the emerald ash borer, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae). Journal of Insect Physiology 57:166–173.

Cudmore, T. J., N. Bjorklund, A. L. Carroll, and B. S. Lindgren. 2010. Climate change and range expansion of an aggressive bark beetle: evidence of higher beetle reproduction in naive host tree populations. Journal of Applied Ecology 47:1036–1043.

Cullings, K., and J. Hanely. 2010. Dwarf mistletoe effects on soil basidiomycete community structure, soil fungal functional diversity, and soil enzyme function: Implications for climate change. Soil Biology and Biochemistry 42:1976–1981.

Cushman, J. H., and R. K. Meentemeyer. 2008. Multi-scale patterns of human activity and the incidence of an exotic forest pathogen. Journal of Ecology 96:766–776.

Dale, V. H., et al. 2001. Climate change and forest disturbances. BioScience 51:723–734.

Daniel, C. J., and J. H. Myers. 1995. Climate and outbreaks of the forest tent caterpillar. Ecography 18:353–362.

Davis, F. W., M. Borchert, R. K. Meentemeyer, A. Flint, and D. M. Rizzo. 2010. Pre-impact forest composition and ongoing tree mortality associated with sudden oak death in the Big Sur region; California. Forest Ecology and Management 259:2342–2354.

Day, K. 1984. The growth and decline of a population of the spruce aphid *Elatobium abietinum* during a three year study, and the changing pattern of fecundity, recruitment and alary polymorphism in a Northern Ireland forest. Oecologia 64:118–124.

Day, K. R., M. P. Ayres, R. Harrington, and N. A. C. Kidd. 2010. Interannual dynamics of aerial and arboreal green spruce aphid populations. Population Ecology 52:317–327.

Delisle, J., L. Royer, M. Bernier-Cardou, and A. Labrecque. 2012. Impact of increasing temperatures and exposure duration on egg hatch in the hemlock looper, *Lambdina fiscellaria*. Entomologia Experimentalis et Applicata 144:231–243.

DeRose, R., and J. Long. 2007. Disturbance, structure, and composition: Spruce beetle and Engelmann spruce forests on the Markagunt Plateau, Utah. Forest Ecology and Management 244:16–23.

DeRose, R. J., and J. N. Long. 2012. Factors influencing the spatial and temporal dynamics of Engelmann spruce mortality during a spruce beetle outbreak on the Markagunt Plateau, Utah. Forest Science 58:1–14.

Desprez-Loustau, M.-L., B. Marcais, L.-M. Nageleisen, D. Piou, and A. Vannini. 2006. Interactive effects of drought and pathogens in forest trees. Annals of Forest Science 63:597–612.

Deutsch, C. A., J. J. Tewksbury, R. B. Huey, K. S. Sheldon, C. K. Ghalambor, D. C. Haak, and P. R. Martin. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. Proceedings of the National Academy of Sciences USA 105:6668–6672.

Dodd, R. S., D. Huberli, W. Mayer, T. Y. Harnik, Z. Afzal-Rafii, and M. Garbelotto. 2008. Evidence for the role of synchronicity between host phenology and pathogen activity in the distribution of sudden oak death canker disease. New Phytologist 179:505–514.

Dodds, K. J., S. L. Garman, and D. W. Ross. 2006. Landscape analyses of Douglas-fir beetle populations in northern Idaho. Forest Ecology and Management 231:119–130.

Dodds, K. J., and D. A. Orwig. 2011. An invasive urban forest pest invades natural environments: Asian longhorned beetle in northeastern U.S. hardwood forests. Canadian Journal of Forest Research 41:1729–1742.

Donaubauer, E. 1972. Environmental factors influencing outbreak of *Scleroderris lagerbergii* Gremmen. Forest Pathology 2:21–25.

Doudrick, R. L., R. C. Schmidtling, and C. D. Nelson. 1996. Host relationships of fusiform rust disease: I. Infection and pycnial production on slash pine and nearby tropical relatives. Silvae Genetica 45:142–149.

Drever, M. C., J. R. Goheen, and K. Martin. 2009. Species–energy theory, pulsed resources, and regulation of avian richness during a mountain pine beetle outbreak. Ecology 90:1095–1105.

Dudt, J. F., and D. J. Shure. 1993. The effect of anthracnose (*Discula destructiva*) infection on plant-herbivore interactions in dogwood (*Cornus florida*). Oecologia 96:108–113.

Duehl, A. J., F. H. Koch, and F. P. Hain. 2011. Southern pine beetle regional outbreaks modeled on landscape, climate and infestation history. Forest Ecology and Management 261:473–479.

Dukes, J. S., et al. 2009. Responses of insect pests, pathogens, and invasive plant species to climate change in the forests of northeastern North America: What can we predict? Canadian Journal of Forest Research 39:231–248.

Dunlap, J. M. 2012. Variability in and environmental correlates to white pine blister rust incidence in five California white pine species. Northwest Science 86:248–263.

Dvorak, M., L. Jankovsky, and K. Drapela. 2012. *Dothistroma septosporum*: spore production and weather conditions. Forest Systems 21:323–328.

Dwyer, G., J. Dushoff, and S. H. Yee. 2004. The combined effects of pathogens and predators on insect outbreaks. Nature 430:341–345.

Dyer, E. D. A. 1969. Influence of temperature inversion on development of spruce beetle *Dendroctonus obseus* (Mannerheim) (Coleptera: Scolytidae). Journal of the Entomological Society of British Columbia 66:41–45.

Edburg, S. L., J. A. Hicke, and P. D. Brooks. 2012. Cascading impacts of bark beetle-caused tree mortality on coupled biogeophysical and biogeochemical processes. Frontiers in Ecology and the Environment 10:416–424.

Edburg, S. L., J. A. Hicke, and D. M. Lawrence. 2011. Simulating coupled carbon and nitrogen dynamics following mountain pine beetle outbreaks in the western United States. Journal of Geophysical Research 116:G04033.

Edmonds, R. L., J. K. Agee, and R. I. Gara. 2000. Forest health and protection. McGraw Hill, Boston, Massachusetts, USA.

Edwards, D. K. 1964. Activity rhythms of Lepidopterous defoliators: ii. *Halisidota argentata* Pack. (Arctiidae), and *Nepytia phantasmaria* Stkr. (Geometridae). Canadian Journal of Zoology 42:939–958.

Edworthy, A. B., M. C. Drever, and K. Martin. 2011. Woodpeckers increase in abundance but maintain fecundity in response to an outbreak of mountain pine bark beetles. Forest Ecology and Management 261:203–210.

Ellison, A., M. Bank, B. Clinton, E. Colburn, K. Elliott, C. Ford, D. Foster, B. Kloeppel, J. Knoepp, and G. Lovett. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment 3:479–486.

Entry, J. A., K. J. Cromack, R. G. Kelsey, and N. E. Martin. 1991. Response of Douglas-fir to infection by *Armillaria ostoyae* after thinning or thinning plus fertilization. Phytopathology 81:682–688.

Evangelista, P. H., S. Kumar, T. J. Stohlgren, and N. E. Young. 2011. Assessing forest vulnerability and the potential distribution of pine beetles under current and future climate scenarios in the Interior West of the US. Forest Ecology and Management 262:307–316.

Evans, A., and T. G. Gregoire. 2007. A geographically variable model of hemlock woolly adelgid spread. Biological Invasions 9:369–382.

Evans, L. M., R. W. Hofstetter, M. P. Ayres, and K. D. Klepzig. 2011. Temperature alters the relative abundance and population growth rates of species within the *Dendroctonus frontalis* (Coleoptera: Curculionidae) community. Environmental Entomology 40:824–834.

Fauria, M. M., and E. A. Johnson. 2009. Large-scale climatic patterns and area affected by mountain pine beetle in British Columbia, Canada. Journal of Geophysical Research 114:G01012.

Field, S. G., A. W. Schoettle, J. G. Klutsch, S. J. Tavener, and M. F. Antolin. 2012. Demographic projection of high-elevation white pines infected with white pine blister rust: a nonlinear disease model. Ecological Applications 22:166–183.

Fitzgerald, T. D., S. Miller, and M. Smith. 2012. Thermal properties of the tent of early instar colonies of the eastern tent caterpillar, *Malacosoma americanum* (Lepidoptera: Lasiocampidae). Journal of Thermal Biology 37:615–624.

Fitzpatrick, M. C., E. L. Preisser, A. Porter, J. Elkinton, and A. M. Ellison. 2012. Modeling range dynamics in heterogeneous landscapes: invasion of the hemlock woolly adelgid in eastern North America. Ecological Applications 22:472–486.

Fleming, R. A. 1996. A mechanistic perspective of possible influences of climate change on defoliating insects in North America's boreal forests. Silva Fennica 30:281–294.

Fleming, R. A., and J. N. Candau. 1998. Influences of climatic change on some ecological processes of an insect outbreak system in Canada's boreal forests and the implications for biodiversity. Environmental Monitoring and Assessment 49:235–249.

Fleming, R. A., and W. J. A. Volney. 1995. Effects of climate change on insect defoliator population processes in Canada's boreal forest: Some plausible scenarios. Water, Air, and Soil Pollution 82:445–454.

Flint, C. 2006. Community perspectives on spruce beetle impacts on the Kenai Peninsula, Alaska. Forest Ecology and Management 227:207–218.

Flower, C. E., K. S. Knight, and M. A. Gonzalez-Meler. 2012. Impacts of the emerald ash borer (*Agrilus planipennis* Fairmaire) induced ash (*Fraxinus* spp.) mortality on forest carbon cycling and successional dynamics in the eastern United States. Biological Invasions 15:931–944.

Foley, J. A., et al. 2005. Global consequences of land use. Science 309:570–574.

Fraedrich, S. W., T. C. Harrington, R. J. Rabaglia, M. D. Ulyshen, A. E. Mayfield, III, J. L. Hanula, J. M. Eickwort, and D. R. Miller. 2008. A fungal symbiont of the redbay ambrosia beetle causes a lethal wilt in redbay and other lauraceae in the southeastern United States. Plant Disease 92:215–224.

Frid, L., and J. H. Myers. 2002. Thermal ecology of western tent caterpillars *Malacosoma californicum pluviale* and infection by nucleopolyhedrovirus. Ecological Entomology 27:665–673.

Friedenberg, N. A., J. A. Powell, and M. P. Ayres. 2007. Synchrony's double edge: transient dynamics and the Allee effect in stage structured populations. Ecology Letters 10:564–573.

Friedenberg, N. A., S. Sarkar, N. Kouchoukos, R. F. Billings, and M. P. Ayres. 2008. Temperature extremes, density dependence, and southern pine beetle (Coleoptera: Curculionidae) population dynamics in east Texas. Environmental Entomology 37:650–659.

Furniss, M. M., E. H. Holsten, M. J. Foote, and M. Bertram. 2001. Biology of a willow leafblotch miner, *Micrurapteryx salicifoliella*, (Lepidoptera: Gracillariidae) in Alaska. Environmental Entomology 30:736–741.

Gadgil, P. D. 1974. Effect of temperature and leaf wetness period on infection of *Pinus radiata* by *Dothistroma pini*. New Zealand Journal of Forestry Science 4:495–501.

Gadgil, P. D. 1977. Duration of leaf wetness periods and infection of *Pinus radiata* by *Dothistroma pini*. New Zealand Journal of Forestry Science 7:83–90.

Ganey, J. L., and S. C. Vojta. 2011. Tree mortality in drought-stressed mixed-conifer and ponderosa pine forests, Arizona, USA. Forest Ecology and Management 261:162–168.

Ganley, R. J., M. S. Watt, L. Manning, and E. Iturritxa. 2009. A global climatic risk assessment of pitch canker disease. Canadian Journal of Forest Research 39:2246–2256.

Garnas, J. R., M. P. Ayres, A. M. Liebhold, and C. Evans. 2011*a*. Subcontinental impacts of an invasive tree disease on forest structure and dynamics. Journal of Ecology 99:532–541.

Garnas, J. R., D. R. Houston, M. P. Ayres, and C. Evans. 2011*b*. Disease ontogeny overshadows effects of climate and species interactions on population dynamics in a nonnative forest disease complex. Ecography 35:412–421.

Gaylord, M. L., T. E. Kolb, K. F. Wallin, and M. R. Wagner. 2007. Seasonal dynamics of tree growth, physiology, and resin defenses in a northern Arizona Ponderosa pine forest. Canadian Journal of Forest Research 37:1173–1183.

Gaylord, M., K. Williams, R. Hofstetter, J. McMillin, T. Degomez, and M. Wagner. 2008. Influence of temperature on spring flight initiation for southwestern Ponderosa pine bark beetles (Coleoptera: Curculionidae, Scolytinae). Environmental Entomology 37:57–69.

Gillooly, J. F., E. L. Charnov, G. B. West, V. M. Savage, and J. H. Brown. 2002. Effects of size and temperature on developmental time. Nature 417:70–73.

Glück, P., J. Raynor, O. Berghall, S. Braatz, C. Robledo, and A. Wreford. 2009. Governance and policies for adaptation. Pages 187–210 *in* R. Seppälä, A. Buck, and P. Katila, editors. Adaptation of forests and people to climate change: a global assessment report. International Union of Forest Research Organizations, Helsinki, Finland.

Gordon, T. R., A. J. Storer, and D. Okamoto. 1996. Population structure of the pitch canker pathogen, *Fusarium subglutinans* f. sp. *pini*, in California. Mycological Research 100:850–854.

Gordon, T. R., K. R. Wikler, S. L. Clark, D. Okamoto, A. J. Storer, and P. Bonello. 1998. Resistance to pitch canker disease caused by *Fusarium subglutinans* f. sp. *pini*, in Monterey pine (*Pinus radiata*). Plant Pathology 47:706–711.

Grant, J. F., M. T. Windham, W. G. Haun, G. J. Wiggins, and P. L. Lambdin. 2011. Initial assessment of thousand cankers disease on black walnut, *Juglans nigra*, in Eastern Tennessee. Forests 2:741–748.

Gray, D. R. 2008. The relationship between climate and outbreak characteristics of the spruce budworm in eastern Canada. Climatic Change 87:361–383.

Greenbank, D. O. 1956. The role of climate and dispersal in the initiation of outbreaks of the spruce budworm in New Brunswick: I. The role of climate. Canadian Journal of Zoology 34:453–476.

Greenbank, D. O. 1963. Climate and the spruce budworm. Memoirs of the Entomological Society of Canada 95:174–180.

Greenwood, D. L., and P. J. Weisberg. 2008. Density-dependent tree mortality in pinyon-juniper woodlands. Forest Ecology and Management 255:2129–2137.

Griffin, G. J., D. Reaver, C. K. Osborne, and M. M. Yancey. 2009. Root recovery rates for *Phytophthora cinnamomi* and rate of symptom development from root rot on *Abies fraseri* trees over 7 years. Forest Pathology 39:15–27.

Grulke, N. E. 2011. The nexus of host and pathogen phenology: understanding the disease triangle with climate change. New Phytologist 189:8–11.

Hadley, J. L., P. S. Kuzeja, M. J. Daley, N. G. Phillips, T. Mulcahy, and S. Singh. 2008. Water use and carbon exchange of red oak- and eastern hemlock-dominated forests in the northeastern USA: implications for ecosystem-level effects of hemlock woolly adelgid. Tree Physiology 28:615–627.

Hadley, K. S., and T. T. Veblen. 1993. Stand response to western spruce budworm and Douglas-fir bark beetle outbreaks, Colorado Front Range. Canadian Journal of Forest Research 23:479–491.

Hadziabdic, D., P. A. Wadl, L. M. Vito, S. L. Boggess, B. E. Scheffler, M. T. Windham, and R. N. Trigiano. 2011. Development and characterization of sixteen microsatellite loci for *Geosmithia morbida*, the causal agent of thousand canker disease in black walnut (*Juglans nigra*). Conservation Genetics Resources 4:287–289.

Haight, R. G., F. R. Homans, T. Horie, S. V. Mehta, D. J. Smith, and R. C. Venette. 2011. Assessing the cost of an invasive forest pathogen: a case study with oak wilt. Environmental Management 47:506–517.

Hale, B. K., D. A. Herms, R. C. Hansen, T. P. Clausen, and D. Arnold. 2005. Effects of drought stress and nutrient availability on dry matter allocation, phenolic glycosides, and rapid induced resistance of poplar to two lymantriid defoliators. Journal of Chemical Ecology 31:2601–2620.

Hamelin, R. C., G. B. Ouellette, and L. Bernier. 1993. Identification of *Gremmeniella abietina* races with random amplified polymorphic DNA markers. Applied and Environmental Microbiology 59:1752–1755.

Hanna, P., and D. Kulakowski. 2012. The influences of climate on aspen dieback. Forest Ecology and Management 274:91–98.

Hansen, E. M., and B. J. Bentz. 2003. Comparison of reproductive capacity among univoltine, semivoltine, and re-emerged parent spruce beetles (Coleoptera: Scolytidae). Canadian Entomologist 135:697–712.

Hansen, E. M., B. J. Bentz, J. A. Powell, D. R. Gray, and J. C. Vandygriff. 2011. Prepupal diapause and instar IV developmental rates of the spruce beetle, *Dendroctonus rufipennis* (Coleoptera: Curculionidae, Scolytinae). Journal of Insect Physiology 57:1347–1357.

Hansen, E. M., B. J. Bentz, and D. L. Turner. 2001. Temperature-based model for predicting univoltine brood proportions in spruce beetle (Coleoptera: Scolytidae). Canadian Entomologist 133:827–841.

Hansen, M. C., S. V. Stehman, and P. V. Potapov. 2010. Quantification of global gross forest cover loss. Proceedings of the National Academy of Sciences USA 107:8650–8655.

Hansen, E., J. Stone, B. Capitano, P. Rosso, W. Sutton, L. Winton, A. Kanaskie, and M. McWilliams. 2000. Incidence and impact of Swiss needle cast in forest plantations of Douglas-fir in coastal Oregon. Plant Disease 84:773–778.

Hardham, A. R. 2005. *Phytophthora cinnamomi*. Molecular Plant Pathology 6:589–604.

Harrington, T. C., and F. W. J. Cobb. 1983. Pathogenicity of *Leptographium* and *Verticicladiella* spp. isolated from roots of western North American conifers. Phytopathology 73:596–599.

Harrington, T. C., H. Y. Yun, S. S. Lu, H. Goto, D. N. Aghayeva, and S. W. Fraedrich. 2011. Isolations from the redbay ambrosia beetle, *Xyleborus glabratus*, confirm that the laurel wilt pathogen, *Raffaelea lauricola*, originated in Asia. Mycologia 103:1028–1036.

Harrison, K. J., J. E. A. Hurley, and M. E. Ostry. 1998. First report of butternut canker caused by *Sirococcus clavigignenti-juglandacearum* in New Brunswick, Canada. Plant Disease 82:1282.

Harvell, C. D., C. E. Mitchell, J. R. Ward, S. Altizer, A. P. Dobson, R. S. Ostfeld, and M. D. Samuel. 2002. Climate warming and disease risks for terrestrial and marine biota. Science 296:2158–2162.

Hebertson, E. G., and M. J. Jenkins. 2008. Climate factors associated with historic spruce beetle (Coleoptera: Curculionidae) outbreaks in Utah and Colorado. Environmental Entomology 37:281–292.

Herms, D. A., and W. J. Mattson. 1992. The dilemma of plants: to grow or defend. Quarterly Review of Biology 67:283–335.

Hicke, J. A., et al. 2012*a*. Effects of biotic disturbances on forest carbon cycling in the United States and Canada. Global Change Biology 18:7–34.

Hicke, J. A., M. C. Johnson, J. L. Hayes, and H. K. Preisler. 2012*b*. Effects of bark beetle-caused tree mortality on wildfire. Forest Ecology and Management 271:81–90.

Hicke, J. A., J. A. Logan, J. Powell, and D. S. Ojima. 2006. Changing temperatures influence suitability for modeled mountain pine beetle (*Dendroctonus ponderosae*) outbreaks in the western United States. Journal of Geophysical Research-Biogeosciences 111:G02019.

Hofstetter, R. W., T. D. Dempsey, K. D. Klepzig, and M. P. Ayres. 2007. Temperature-dependent effects on mutualistic, antagonistic, and commensalistic interactions among insects, fungi and mites. Community Ecology 8:47–56.

Hogg, E. H. 2008. Impacts of a regional drought on the productivity, dieback, and biomass of western Canadian aspen forests. Canadian Journal of Forest Research 38:1373–1384.

Hogg, E., J. Brandt, and B. Kochtubajda. 2002. Growth and dieback of Aspen forests in northwestern Alberta, Canada, in relation to climate and insects. Canadian Journal of Forest Research 32:823–832.

Hogg, E. H. T., J. P. Brandt, and B. Kochtubajda. 2005. Factors affecting interannual variation in growth of western Canadian aspen forests during 1951–2000. Canadian Journal of Forest Research 35:610–622.

Hogg, E., and A. Schwarz. 1999. Tree-ring analysis of declining aspen stands in west-central Saskatchewan. Naturual Resources Canada, Canadian Forest Service, Northern Foresty Centre, Edmonton, Alberta, Canada.

Holmes, F. W. 1980. Bark beetles, *Ceratocystis ulmi*, and Dutch elm disease. Academic Press, New York, New York, USA.

Holmes, T. P., A. M. Liebhold, K. F. Kovacs, and B. Von Holle. 2010. A spatial-dynamic value transfer model of economic losses from a biological invasion. Ecological Economics 70:86–95.

Holsten, E. H., R. A. Werner, and R. L. Develice. 1995. Effects of a spruce beetle (Coleoptera: Scolytidae) outbreak and fire on Lutz spruce in Alaska. Environmental Entomology 24:1539–1547.

Holton, M. K., R. L. Lindroth, and E. V. Nordheim. 2003. Foliar quality influences tree-herbivore-parasitoid interactions: effects of elevated CO_2, O_3, and plant genotype. Oecologia 137:233–244.

Holzmueller, E., S. Jose, M. Jenkins, A. Camp, and A. Long. 2006. Dogwood anthracnose in eastern hardwood forests: what is known and what can be done? Journal of Forestry 104:21–26.

Hood, I. A. 1982. *Phaeocryptopus gaeumannii* on *Pseudotsuga menziesii* in southern British Columbia. New Zealand Journal of Forestry Science 12:415–424.

Houston, D. R., and J. E. Kuntz. 1960. The effects of temperature and moisture on oak wilt development. Phytopathology 50:640.

Huang, C.-Y., and W. R. L. Anderegg. 2012. Large drought-induced aboveground live biomass losses in southern Rocky Mountain aspen forests. Global Change Biology 18:1016–1027.

Huey, R. B., M. R. Kearney, A. Krockenberger, J. A. M. Holtum, M. Jess, and S. E. Williams. 2012. Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. Philosophical Transactions of the Royal Society B 367:1665–1679.

Hunt, R. S., and M. D. Meagher. 1989. Incidence of blister rust on resistant white pine *Pinus monticola* and *Pinus strobus* in coastal British Columbia plantations Canada. Canadian Journal of Plant Pathology 11:419–423.

Inman, A. 2005. Temperature as a potential barrier for the spread of pitch canker. Phytopathology 95:S46.

Inman, A. R., S. C. Kirkpatrick, T. R. Gordon, and A. V. Shaw. 2008. Limiting effects of low temperature on growth and spore germination in *Gibberella circinata*, the cause of pitch canker in pine species. Plant Disease 92:542–545.

Iqbal, J., D. A. MacLean, and J. A. Kershaw, Jr. 2011. Impacts of hemlock looper defoliation on growth and survival of balsam fir, black spruce and white birch in Newfoundland, Canada. Forest Ecology and Management 261:1106–1114.

Ives, W. G. H. 1973. Heat units and outbreaks of the forest tent caterpillar, *Malacosoma disstria* (Lepidoptera: Lasiocampidae). Canadian Entomologist 105:529–543.

Jacobi, W. R., S. Zeglen, and J. D. Beale. 2008. Black stain root disease progression in coastal Douglas-fir in British Columbia. Canadian Journal of Plant Pathology 30:339–344.

Jenkins, M. J., E. Hebertson, W. Page, and C. A. Jorgensen. 2008. Bark beetles, fuels, fires and implications for forest management in the Intermountain West. Forest Ecology and Management 254:16–34.

Jepsen, J. U., L. Kapari, S. B. Hagen, T. Schott, O. P. L. Vindstad, A. C. Nilssen, and R. A. Ims. 2011. Rapid northwards expansion of a forest insect pest attributed to spring phenology matching with sub-arctic birch. Global Change Biology 17:2071–2083.

Jewett, J. T., R. L. Lawrence, L. A. Marshall, P. E. Gessler, S. L. Powell, and S. L. Savage. 2011. Spatiotemporal relationships between climate and whitebark pine mortality in the Greater Yellowstone Ecosystem. Forest Science 57:320–335.

Jones, C. G., R. S. Ostfeld, M. P. Richard, E. M. Schauber, and J. O. Wolff. 1998. Chain reactions linking acorns to gypsy moth outbreaks and Lyme disease risk. Science 279:1023–1026.

Jones, E. A., D. D. Reed, G. D. Mroz, H. O. Liechty, and P. J. Cattelino. 1993. Climate stress as a precursor to forest decline paper birch in Northern Michigan 1985–1990. Canadian Journal of Forest Research 23:229–233.

Juzwik, J., D. Appel, and W. MacDonald. 2011. Challenges and successes in managing oak wilt in the United States. Plant Disease 95:888–900.

Juzwik, J., T. C. Harrington, W. L. MacDonald, and D. N. Appel. 2008. The origin of *Ceratocystis fagacearum*, the oak wilt fungus. Annual Review of Phytopathology 46:13–26.

Kasson, M. T., and W. H. Livingston. 2012. Relationships among beech bark disease, climate, radial growth response and mortality of American beech in northern Maine, USA. Forest Pathology 42:199–212.

Keane, R. E., S. F. Arno, J. K. Brown, and D. F. Tomback. 1990. Modelling stand dynamics in whitebark pine *Pinus albicaulis* forests. Ecological Modelling 51:73–96.

Keen, F. P., and R. L. Furniss. 1937. Effects of subzero temperatures on populations of western pine beetle *Dendroctonus brevicomis* Lee. Journal of Economic Entomology 30:482–504.

Keena, M. A. 2006. Effects of temperature on *Anoplophora glabripennis* (Coleoptera: Cerambycidae) adult survival, reproduction, and egg hatch. Environmental Entomology 35:912–921.

Keena, M. A., and P. M. Moore. 2010. Effects of temperature on *Anoplophora glabripennis* (Coleoptera: Cerambycidae) larvae and pupae. Environmental Entomology 39:1323–1335.

Kimberley, M. O., I. A. Hood, and R. L. Knowles. 2011. Impact of Swiss needle-cast on growth of Douglas-fir. Phytopathology 101:583–593.

Kingsolver, J. G., H. A. Woods, L. B. Buckley, K. A. Potter, H. J. MacLean, and J. K. Higgins. 2011. Complex life cycles and the responses of insects to climate change. Integrative and Comparative Biology 51:719–732.

Kinloch, B. B. 2003. White pine blister rust in North America: past and prognosis. Phytopathology 93:1044–1047.

Kipfmueller, K. F., and W. L. Baker. 1998. Fires and dwarf mistletoe in a Rocky Mountain lodgepole pine ecosystem. Forest Ecology and Management 108:77–84.

Klapwijk, M. J., M. P. Ayres, A. Battisti, and S. Larsson. 2012. Assessing the impact of climate change on outbreak potential. Pages 429–450 *in* P. Barbosa, D. K. Letourneau, and A. A. Agrawal, editors. Insect outbreaks revisited. Academic Press, New York, New York, USA.

Klein, W. H., and M. W. Minnoch. 1971. On the occurrence and biology of *Nepytia freemani* (Lepidoptera: Geometridae) in Utah. Canadian Entomologist 103:119–124.

Klepzig, K. D., J. Flores-Otero, R. W. Hofstetter, and M. P. Ayres. 2004. Effects of available water on growth and competition of southern pine beetle associated fungi. Mycological Research 108:183–188.

Klepzig, K. D., E. L. Kruger, E. B. Smalley, and K. F. Raffa. 1995. Effects of biotic and abiotic stress on induced accumulation of terpenes and phenolics in red pines inoculated with bark beetle-vectored fungus. Journal of Chemical Ecology 21:601–626.

Klepzig, K. D., E. B. Smalley, and K. F. Raffa. 1996. Interactions of ecologically similar saprogenic fungi with healthy and abiotically stressed conifers. Forest Ecology and Management 86:163–169.

Knoepp, J. D., J. M. Vose, B. D. Clinton, and M. D. Hunter. 2011. Hemlock infestation and mortality: impacts on nutrient pools and cycling in Appalachian forests. Soil Science Society of America Journal 75:1935–1945.

Koch, F. H., and W. D. Smith. 2008. Spatio-temporal analysis of *Xyleborus glabratus* (Coleoptera: Curculionidae: Scolytinae) invasion in eastern U.S. forests. Environmental Entomology 37:442–452.

Kolarik, M., E. Freeland, C. Utley, and N. Tisserat. 2011. *Geosmithia morbida* sp. nov., a new phytopathogenic species living in symbiosis with the walnut twig beetle (*Pityophthorus juglandis*) on Juglans in USA. Mycologia 103:325–332.

Kovacs, K., R. Haight, D. McCullough, R. Mercader, N. Siegert, and A. M. Liebhold. 2010. Cost of potential emerald ash borer damage in US communities, 2009–2019. Ecological Economics 69:569–578.

Kovacs, K., T. P. Holmes, J. E. Englin, and J. Alexander. 2011*a*. The dynamic response of housing values to a forest invasive disease: evidence from a sudden oak death infestation. Environmental and Resource Economics 49:445–471.

Kovacs, K. F., R. J. Mercader, R. G. Haight, N. W. Siegert, D. G. McCullough, and A. M. Liebhold. 2011*b*. The influence of satellite populations of emerald ash borer on projected economic costs in U.S. communities, 2010–2020. Journal of Environmental Management 92:2170–2181.

Kovacs, K., T. Vaclavik, R. G. Haight, A. Pang, N. J. Cunniffe, C. A. Gilligan, and R. K. Meentemeyer. 2011*c*. Predicting the economic costs and property value losses attributed to sudden oak death damage in California (2010–2020). Journal of Environmental Management 92:1292–1302.

Krauss, C. 2005. Canada warns that tariffs on lumber could imperil U.S. access to oil. New York Times, 12 October, 2005.

Kulakowski, D., and D. Jarvis. 2011. The influence of mountain pine beetle outbreaks and drought on severe wildfires in northwestern Colorado and southern Wyoming: a look at the past century. Forest Ecology and Management 262:1686–1696.

Kurz, W. A., C. C. Dymond, G. Stinson, G. J. Rampley, E. T. Neilson, A. L. Carroll, T. Ebata, and L. Safranyik. 2008. Mountain pine beetle and forest carbon feedback to climate change. Nature 452:987–990.

Laflamme, G. 2005. Impact of scleroderris canker, American race, on seeded *Pinus banksiana*. Phytopathology 95(Supplement):S170.

La Porta, N., P. Capretti, I. Thomsen, R. Kasanen, A. Hietala, and K. Von Weissenberg. 2008. Forest pathogens with higher damage potential due to climate change in Europe. Canadian Journal of Plant Pathology 30:177–195.

Latta, G., H. Temesgen, D. Adams, and T. Barrett. 2010. Analysis of potential impacts of climate change on forests of the United States Pacific Northwest. Forest Ecology and Management 259:720–729.

Lavallee, R., L. Archambault, and J. Morissette. 1996. Influence of drainage and edge vegetation on levels of attack and biological performance of the white pine weevil. Forest Ecology and Management 82:133–144.

Lester, J. D., and J. T. Irwin. 2012. Metabolism and cold tolerance of overwintering adult mountain pine beetles (*Dendroctonus ponderosae*): Evidence of facultative diapause? Journal of Insect Physiology 58:808–815.

Leuschner, W. A., J. A. Young, and F. W. Ravlin. 1996. Potential benefits of slowing the gypsy moth's spread. Southern Journal of Applied Forestry 20:65–73.

Lewis, R. 1981. Interior tree temperatures favor *Ceratocystis fagacearum* survival during summer in Texas. Phytopathology 71:236.

Lewis, R. 1985. Temperature tolerance and survival of *Ceratocystis fagacearum* in Texas. Plant Disease 69:443–444.

Liebhold, A. M., P. Berck, N. A. Williams, and D. L. Wood. 1986. Estimating and valuing western pine beetle *Dendroctonus brevicomis* impacts. Forest Science 32:325–338.

Lindroth, R. L. 2010. Impacts of elevated atmospheric CO2 and O_3 on forests: phytochemistry, trophic interactions, and ecosystem dynamics. Journal of Chemical Ecology 36:2–21.

Lindroth, R. L., K. K. Kinney, and C. L. Platz. 1993. Responses of deciduous trees to elevated atmospheric carbon dioxide: productivity, phytochemistry, and insect performance. Ecology 74:763–777.

Lindroth, R. L., S. Roth, E. L. Kruger, J. C. Volin, and P. A. Koss. 1997. CO_2-mediated changes in aspen chemistry:

effects on gypsy moth performance and susceptibility to virus. Global Change Biology 3:279–289.

Lindroth, R. L., S. A. Wood, and B. J. Kooper. 2002. Response of quaking aspen genotypes to enriched CO_2: foliar chemistry and tussock moth performance. Agricultural and Forest Entomology 4:315–323.

Lines, E. R., D. A. Coomes, and D. W. Purves. 2010. Influences of forest structure, climate and species composition on tree mortality across the Eastern US. PLoS ONE 5:e13212.

Littell, J. S., E. E. Oneil, D. McKenzie, J. A. Hicke, J. A. Lutz, R. A. Norheim, and M. M. Elsner. 2010. Forest ecosystems, disturbance, and climatic change in Washington State, USA. Climatic Change 102:129–158.

Logan, J. A., and B. J. Bentz. 1999. Model analysis of mountain pine beetle (Coleoptera: Scolytidae) seasonality. Environmental Entomology 28:924–934.

Logan, J. A., W. W. Macfarlane, and L. Willcox. 2010. Whitebark pine vulnerability to climate-driven mountain pine beetle disturbance in the Greater Yellowstone Ecosystem. Ecological Applications 20:895–902.

Logan, J. A., and J. A. Powell. 2001. Ghost forests, global warming and the mountain pine beetle (Coleoptera: Scolytidae). American Entomologist 47:160–173.

Logan, J. A., and J. A. Powell. 2009. Ecological consequences of climate change altered forest insect disturbance regimes. Pages 98–109 *in* F. H. Wagner, editor. Climate change in western North America: evidence and environmental effects. University of Utah Press, Salt Lake City, Utah, USA.

Lombardero, M. J., and M. P. Ayres. 2011. Factors influencing bark beetle outbreaks after forest fires on the Iberian Peninsula. Environmental Entomology 40:1007–1018.

Lombardero, M. J., M. P. Ayres, B. D. Ayres, and J. D. Reeve. 2000. Cold tolerance of four species of bark beetle (Coleoptera: Scolytidae) in North America. Environmental Entomology 29:421–432.

Lombardero, M. J., M. P. Ayres, R. W. Hofstetter, J. C. Moser, and K. D. Klepzig. 2003. Strong indirect interactions of *Tarsonemus mites* (Acarina: Tarsonemidae) and *Dendroctonus frontalis* (Coleoptera: Scolytidae). Oikos 102:243–252.

Loo, J. 2009. Ecological impacts of non-indigenous invasive fungi as forest pathogens. Biological Invasions 11:81–96.

Lovett, G. M., M. A. Arthur, K. C. Weathers, and J. M. Griffin. 2010. Long-term changes in forest carbon and nitrogen cycling caused by an introduced pest/pathogen complex. Ecosystems 13:1188–1200.

Lovett, G., C. Canham, M. Arthur, K. Weathers, and R. Fitzhugh. 2006. Forest ecosystem responses to exotic pests and pathogens in eastern North America. BioScience 56:395–405.

Lovett, G. M., L. M. Christenson, P. M. Groffman, C. G. Jones, J. E. Hart, and M. J. Mitchell. 2002. Insect defoliation and nitrogen cycling in forests. BioScience 52:335–341.

Lovett, G. M., K. C. Weathers, M. A. Arthur, and J. C. Schultz. 2004. Nitrogen cycling in a northern hardwood forest: do species matter? Biogeochemistry 67:289–308.

Lucuik, G. S. 1984. Effect of climatic factors on post-diapause emergence and survival of spruce budworm larvae (Lepidoptera: Tortricidae). Canadian Entomologist 116:1077–1083.

Luyssaert, S., E. D. Schulze, A. Borner, A. Knohl, D. Hessenmoller, B. E. Law, P. Ciais, and J. Grace. 2008. Old-growth forests as global carbon sinks. Nature 455:213–215.

Lynch, A. 2004. Fate and characteristics of *Picea* damaged by *Elatobium abietinum* (Walker) (Homoptera: Aphididae) in the White Mountains of Arizona. Western North American Naturalist 64:7–17.

MacLean, D. A., and P. Ebert. 1999. The impact of hemlock looper (*Lambdina fiscellaria fiscellaria* (Guen.)) on balsam fir and spruce in New Brunswick, Canada. Forest Ecology and Management 120:77–87.

Magnani, F., et al. 2007. The human footprint in the carbon cycle of temperate and boreal forests. Nature 447:848–850.

Manter, D. K., P. W. Reeser, and J. K. Stone. 2005. A climate-based model for predicting geographic variation in Swiss needle cast severity in the Oregon coast range. Phytopathology 95:1256–1265.

Marçais, B., F. Dupuis, and M. L. Desprez-Loustau. 1996. Modelling the influence of winter frosts on the development of the stem canker of red oak, caused by *Phytophthora cinnamomi*. Annals of Forest Science 53:369–382.

Marchetti, S. B., J. J. Worrall, and T. Eager. 2011. Secondary insects and diseases contribute to sudden aspen decline in southwestern Colorado, USA. Canadian Journal of Forest Research 41:2315–2325.

Marini, L., M. P. Ayres, A. Battisti, and M. Faccoli. 2012. Climate affects severity and altitudinal distribution of outbreaks in an eruptive bark beetle. Climatic Change 115:327–341.

Marosy, M., R. F. Patton, and C. D. Upper. 1989. A conductive day concept to explain the effect of low temperature on the development of Scleroderris shoot blight. Phytopathology 79:1293–1301.

Mason, R. R. 1996. Dynamic behavior of Douglas-fir tussock moth populations in the Pacific Northwest. Forest Science 42:182–191.

McClure, M. S. 1989. Importance of weather to the distribution and abundance of introduced adelgid and scale insects. Agricultural and Forest Meteorology 47:291–302.

McClure, M. 1991. Density-dependent feedback and population cycles in *Adelges tsugae* (Homoptera: Adelgidae) on *Tsuga canadensis*. Environmental Entomology 20:258–264.

McClure, M., E. Cannell, and E. Despland. 2011. Thermal ecology and behaviour of the nomadic social forager *Malacosoma disstria*. Physiological Entomology 36:120–127.

McDonald, B., A., B. K. Bellamy, J. Zhan, and D. N. Appel. 1998. The effect of an oak wilt epidemic on the genetic structure of a Texas live oak population. Canadian Journal of Botany 76:1900–1907.

McDowell, N. G., D. J. Beerling, D. D. Breshears, R. A. Fisher, K. F. Raffa, and M. Stitt. 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. Trends in Ecology and Evolution 26:523–532.

McEwan, R., R. Muller, M. Arthur, and H. Housman. 2000. Temporal and ecological patterns of flowering dogwood mortality in the mixed mesophytic forest of eastern Kentucky. Journal of the Torrey Botanical Society 127:221–229.

McKeen, C. D. 1995. Chestnut blight in Ontario: past and present status. Canadian Journal of Plant Pathology 17:295–304.

McMahon, S. M., G. G. Parker, and D. R. Miller. 2010. Evidence for a recent increase in forest growth. Proceedings of the National Academy of Sciences USA 107:3611–3615.

McNamee, P. J. 1979. A process model for eastern blackheaded budworm (Lepidoptera: Tortricidae). Canadian Entomologist 111:55–66.

McNulty, S. G., P. L. J. Lorio, M. P. Ayres, and J. D. Reeve. 1997. Predictions of southern pine beetle populations under historic and projected climate using a forest ecosystem model. Pages 617–634 *in* R. A. Mickler and S. Fox, editors. The productivity and sustainability of southern forest ecosystems in a changing environment. Springer-Verlag, New York, New York, USA.

Meadows, J. S., and J. D. Hodges. 1996. Biotic agents of stress in the south. Pages 244–280 *in* S. Fox and R. A. Mickler, editors. Ecological studies analysis and synthesis. Volume 118. Impact of air pollutants on southern pine forests. Springer-Verlag, New York, New York, USA.

Michaelian, M., E. H. Hogg, R. J. Hall, and E. Arsenault. 2011. Massive mortality of aspen following severe drought along the southern edge of the Canadian boreal forest. Global Change Biology 17:2084–2094.

Millar, C. I., R. D. Westfall, D. L. Delany, M. J. Bokach, A. L. Flint, and L. E. Flint. 2012. Forest mortality in high-elevation whitebark pine (*Pinus albicaulis*) forests of eastern California, USA; influence of environmental context, bark beetles, climatic water deficit, and warming. Canadian Journal of Forest Research 42:749–765.

Miller, D. R., T. K. Mo, and W. E. Wallner. 1989. Influence of climate on gypsy moth defoliation in southern New England. Environmental Entomology 18:646–650.

Miller, J. M. 1931. High and low lethal temperatures for the western pine beetle. Journal of Agricultural Research 43:303–321.

Mitchell, R., and P. E. Buffam. 2001. Patterns of long-term balsam woolly adelgid infestations and effects in Oregon and Washington. Western Journal of Applied Forestry 16:121–126.

Mitchell, R. G., and H. K. Preisler. 1998. Fall rate of lodgepole pine killed by mountain pine beetle in central Oregon. Western Journal of Applied Forestry 13:23–26.

Mitton, J. B., and S. M. Ferrenberg. 2012. Mountain pine beetle develops an unprecedented summer generation in response to climate warming. American Naturalist 179:E163–E171.

Monahan, W. B., and W. D. Koenig. 2006. Estimating the potential effects of sudden oak death on oak-dependent birds. Biological Conservation 127:146–157.

Morehouse, K., T. Johns, J. Kaye, and M. Kaye. 2008. Carbon and nitrogen cycling immediately following bark beetle outbreaks in southwestern ponderosa pine forests. Forest Ecology and Management 255:2698–2708.

Morton, M. L., and M. E. Pereya. 2011. Mining patterns of the aspen leaf miner, *Phyllocnistis populiella*, on its host plant, *Populus tremuloides*. Western North American Naturalist 71:33–37.

Moser, J. C., B. A. Fitzgibbon, and K. D. Klepzig. 2005. The Mexican pine beetle, *Dendroctonus mexicanus*: First record in the United States and co-occurrence with the southern pine beetle *Dendroctonus frontalis* (Coleoptera: Scolytidae or Curculionidae: Scolytidae). Entomological News 116:235–243.

Munroe, E. 1963. A new species of *Nepytia* (Lepidoptera: Geometridae), of economic importance to Douglas fir in British Columbia. Canadian Entomologist 95:407–413.

Mwangi, L. M., D. Lin, and M. Hubbes. 1990. Chemical factors in *Pinus strobus* inhibitory to *Armillaria ostoyae*. Forest Pathology 20:8–14.

Myers, J. H. 2000. Population fluctuations of the western tent caterpillar in southwestern British Columbia. Population Ecology 42:231–241.

Nair, V. M. G. 1996. Oak wilt: an internationally dangerous tree disease. Pages 181–198 *in* S. P. Raychaudhuri and K. Maramorosch, editors. Forest trees and palms: Diseases and control. Oxford and IBH Publishing, Chicago, Illinois, USA.

Negron, J. F. 1998. Probability of infestation and extent of mortality associated with the Douglas-fir beetle in the Colorado Front Range. Forest Ecology and Management 107:71–85.

Negron, J., J. A. Anhold, and A. Munson. 2001. Within-stand spatial distribution of tree mortality caused by the Douglas-fir beetle (Coleoptera: Scolytidae). Environmental Entomology 30:215–224.

Negron, J., J. McMillin, J. Anhold, and D. Coulson. 2009. Bark beetle-caused mortality in a drought-affected ponderosa pine landscape in Arizona, USA. Forest Ecology and Management 257:1353–1362.

Nelson, C. D., R. C. Schmidtling, and R. L. Doudrick. 1996. Host relationships of fusiform rust disease. II. Genetic variation and heritability in typical and South Florida varieties of slash pine. Silvae Genetica 45:149–153.

Nielsen, D. G., V. L. Muilenburg, and D. A. Herms. 2011. Interspecific variation in resistance of Asian, European, and North American birches (*Betula* spp.) to bronze birch borer (Coleoptera: Buprestidae). Environmental Entomology 40:648–653.

O'Halloran, T. L., et al. 2012. Radiative forcing of natural forest disturbances. Global Change Biology 18:555–565.

Økland, B., A. M. Liebhold, O. N. Bjørnstad, N. Erbilgin, and P. Krokene. 2005. Are bark beetle outbreaks less synchronous than forest Lepidoptera outbreaks? Oecologia 146:365–372.

Orwig, D. A., R. C. Cobb, A. W. D'Amato, M. L. Kizlinski, and D. R. Foster. 2008. Multi-year ecosystem response to hemlock woolly adelgid infestation in southern New England forests. Canadian Journal of Forest Research 38:834–843.

Osier, T. L., and R. L. Lindroth. 2006. Genotype and environment determine allocation to and costs of resistance in quaking aspen. Oecologia 148:293–303.

Ostry, M. E., G. Laflamme, and S. A. Katovich. 2010. Silvicultural approaches for management of eastern white pine to minimize impacts of damaging agents. Forest Pathology 40:332–346.

Otvos, I. S., L. J. Clarke, and D. S. Durling. 1979. A history of recorded eastern hemlock looper outbreaks in Newfoundland. Information Report N-X-179. Canadian Forest Service, Newfoundland Forest Research Center, St. John's, Newfoundland, Canada.

Paradis, A., J. Elkinton, and K. Hayhoe. 2008. Role of winter temperature and climate change on the survival and future range expansion of the hemlock woolly adelgid (*Adelges tsugae*) in eastern North America. Mitigation and Adaptation Strategies for Global Change 13:541–554.

Parker, B. L., M. Skinner, S. Gouli, T. Ashikaga, and H. B. Teillon. 1998. Survival of hemlock woolly adelgid (Homoptera: Adelgidae) at low temperatures. Forest Science 44:414–420.

Parker, B. L., M. Skinner, S. Gouli, T. Ashikaga, and H. B. Teillon. 1999. Low lethal temperature for hemlock woolly adelgid (Homoptera: Adelgidae). Environmental Entomology 28:1085–1091.

Parker, T. J., K. M. Clancy, and R. L. Mathiasen. 2006. Interactions among fire, insects and pathogens in coniferous forests of the interior western United States and Canada. Agricultural and Forest Entomology 8:167–189.

Parkins, J. R., and N. A. MacKendrick. 2007. Assessing community vulnerability: A study of the mountain pine beetle outbreak in British Columbia, Canada. Global Environmental Change 17:460–471.

Parry, W. H. 1969. A study of the relationship between defoliation of Sitka spruce and population levels of *Elatobium abietinum* (Walker). Forestry 42:69–82.

Paulson, L. C. 1995. Monitoring and dynamics of a Douglas-fir beetle outbreak in Jasper National Park, Alberta. Journal of the Entomological Society of British Columbia 92:17–23.

Pearce, R. B. 1996. Antimicrobial defences in the wood of living trees. New Phytologist 132:203–233.

Peng, C., Z. Ma, X. Lei, Q. Zhu, H. Chen, W. Wang, S. Liu, W. Li, X. Fang, and X. Zhou. 2011. A drought-induced pervasive increase in tree mortality across Canada's boreal forests. Nature Climate Change 1:467–471.

Perkins, D. L., and T. W. Swetnam. 1996. A dendroecological assessment of whitebark pine in the Sawtooth-Salmon River region, Idaho. Canadian Journal of Forest Research 26:2123–2133.

Perrakis, D. D. B., and J. K. Agee. 2006. Seasonal fire effects on mixed-conifer forest structure and ponderosa pine resin properties. Canadian Journal of Forest Research 36:238–254.

Peterson, A. T., and R. Scachetti-Pereira. 2004. Potential geographic distribution of *Anoplophora glabripennis* (Coleoptera: Cerambycidae) in North America. American Midland Naturalist 151:170–178.

Pfister, S. E., S. Halik, and D. R. Bergdahl. 2000. Dothistroma needle blight, caused by *Dothistroma septospora*, of *Pinus* spp. in Vermont. Plant Disease 84:706–706.

Piao, S. L., et al. 2008. Net carbon dioxide losses of northern ecosystems in response to autumn warming. Nature 451:49–52.

Pilon, J. G., and J. R. Blais. 1961. Weather and outbreaks of the spruce budworm in the province of Quebec from 1939 to 1956. Canadian Entomologist 93:118–123.

Potts, D. F. 1984. Hydrologic impacts of a large-scale mountain pine beetle (*Dendroctonus ponderosae* Hopkins) epidemic. Water Resources Bulletin 20:373–377.

Powell, J. A., and B. J. Bentz. 2009. Connecting phenological predictions with population growth rates for mountain pine beetle, an outbreak insect. Landscape Ecology 24:657–672.

Powell, J. A., J. L. Jenkins, J. A. Logan, and B. J. Bentz. 2000. Seasonal temperature alone can synchronize life cycles. Bulletin of Mathematical Biology 62:977–998.

Powell, W. 1974. Supercooling and the low-temperature survival of the green spruce aphid *Elatobium abietinum*. Annals of Applied Biology 78:27–37.

Powell, W., and W. H. Parry. 1976. Effects of temperature on overwintering populations of the green spruce aphid *Elatobium abietinum*. Annals of Applied Biology 82:209–219.

Powers, J. S., P. Sollins, M. E. Harmon, and J. A. Jones. 1999. Plant-pest interactions in time and space: a Douglas-fir bark beetle outbreak as a case study. Landscape Ecology 14:105–120.

Preisler, H. K., J. Hicke, A. Ager, and J. L. Hayes. 2012. Climate and weather influences on spatial temporal patterns of mountain pine beetle populations in Washington and Oregon. Ecology 93:2421–2434.

Price, J. I., D. W. Mccollum, and R. P. Berrens. 2010. Insect infestation and residential property values: A hedonic analysis of the mountain pine beetle epidemic. Forest Policy and Economics 12:415–422.

Pugh, E., and E. Small. 2011. The impact of pine beetle infestation on snow accumulation and melt in the headwaters of the Colorado River. Ecohydrology 5:467–477.

Pye, J. M., T. P. Holmes, J. P. Prestemon, and D. N. Wear. 2011. Economic impacts of the southern pine beetle. Pages 213–222 *in* R. N. Coulson and K. D. Klepzig, editors. Southern pine beetle II. General Technical Report SRS-140. USDA Forest Service, Southern Research Station, Asheville, North Carolina, USA.

Rabenold, K. N., P. T. Fauth, B. W. Goodner, J. A. Sadowski, and P. G. Parker. 1998. Response of avian communities to disturbance by an exotic insect in spruce-fir forests of the southern Appalachians. Conservation Biology 12:177–189.

Raffa, K. F., B. H. Aukema, B. J. Bentz, A. L. Carroll, J. A. Hicke, M. G. Turner, and W. H. Romme. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics of bark beetle eruptions. BioScience 58:501–517.

Raffa, K. F., S. C. Krause, and P. B. Reich. 1998. Long-term effects of defoliation on red pine suitability insects feeding on diverse plant tissues. Ecology 79:2352–2364.

Randerson, J. T., et al. 2006. The impact of boreal forest fire on climate warming. Science 314:1130–1132.

Rauchfuss, J., S. S. Ziegler, J. H. Speer, and N. W. Siegert. 2009. Dendroecological analysis of spruce budworm outbreaks and their relation to climate near the prairie-forest border in northwestern Minnesota. Physical Geography 30:185–204.

Reeve, J. R., M. P. Ayres, and P. L. J. Lorio. 1995. Host suitability, predation, and bark beetle population dynamics. Pages 339–357 *in* N. Cappuccino and P. W. Price, editors. Population dynamics: New approaches and synthesis. Academic Press, San Diego, California, USA.

Régnière, J., and B. J. Bentz. 2007. Modeling cold tolerance in the mountain pine beetle, *Dendroctonus ponderosae*. Journal of Insect Physiology 53:559–572.

Régnière, J., and P. Duval. 1998. Overwintering mortality of spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae), populations under field conditions. Canadian Entomologist 130:13–26.

Rehfeldt, G. E., D. E. Ferguson, and N. L. Crookston. 2009. Aspen, climate, and sudden decline in western USA. Forest Ecology and Management 258:2353–2364.

Reichenbach, N. G., and G. R. Stairs. 1984*a*. Response of the western spruce budworm (Lepidoptera: Tortricidae) to temperature and humidity: developmental rates and survivorship. Environmental Entomology 13:611–618.

Reichenbach, N. G., and G. R. Stairs. 1984*b*. Response of the western spruce budworm, Choristoneura occidentalis (Lepidoptera: Tortricidae), to temperature: the stochastic nature of developmental rates and diapause termination. Environmental Entomology 13:1549–1556.

Rejmánek, M., J. D. Smith, and R. A. Goyer. 1987. Population dynamics of the forest tent caterpillar *Malacosoma disstria* in a water tupelo *Nyssa aquatica* forest a simulation model. Ecological Modelling 39:287–306.

Reynolds, L. V., M. P. Ayres, T. G. Siccama, and R. T. Holmes. 2007. Climatic effects on caterpillar fluctuations in northern hardwood forests. Canadian Journal of Forest Research 37:481–491.

Rindge, F. 1967. A new species of *Nepytia* from southern Rocky Mountains (Lepidoptera: Geometridae). Journal of the New York Entomological Society 75:74–76.

Rizzo, D. M., R. A. Blanchette, and G. May. 1995. Distribution of *Armillaria ostoyae* genets in a *Pinus resinosa-Pinus banksiana* forest. Canadian Journal of Botany 73:776–787.

Robin, C., G. Capron, and M. L. Desprez-Loustau. 2001. Root infection by *Phytophthora cinnamomi* in seedlings of three oak species. Plant Pathology 50:708–716.

Robinet, C., A. Liebhold, and D. R. Gray. 2007. Variation in developmental time affects mating success and Allee effects. Oikos 116:1227–1237.

Rochefort, S., R. Berthiaume, C. Hébert, M. Charest, and É. Bauce. 2011. Effect of temperature and host tree on cold hardiness of hemlock looper eggs along a latitudinal gradient. Journal of Insect Physiology 57:751–759.

Rodenhouse, N. L., L. M. Christenson, D. Parry, and L. E. Green. 2009. Climate change effects on native fauna of Northeastern forests. Canadian Journal of Forest Research 39:249–263.

Rohrs-Richey, J. K., C. P. H. Mulder, L. M. Winton, and G. Stanosz. 2011. Physiological performance of an Alaskan shrub (*Alnus fruticosa*) in response to disease (*Valsa melanodiscus*) and water stress. New Phytologist 189:295–307.

Roland, J. 1993. Large-scale forest fragmentation increases the duration of tent caterpillar outbreak. Oecologia 93:25–30.

Roland, J. 2005. Are the "seeds" of spatial variation in cyclic dynamics apparent in spatially-replicated short time-series? An example from the forest tent caterpillar. Annales Zoologici Fennici 42:397–407.

Roland, J., B. G. Mackey, and B. Cooke. 1998. Effects of climate and forest structure on duration of forest tent caterpillar outbreaks across central Ontario, Canada. Canadian Entomologist 130:703–714.

Ross, D. W., and H. Solheim. 1997. Pathogenicity to Douglas-fir of *Ophiostoma pseudotsugae* and *Leptographium abietinum*, fungi associated with the Douglas-fir beetle. Canadian Journal of Forest Research 27:39–43.

Rosso, P. H., and E. M. Hansen. 2003. Predicting Swiss needle cast disease distribution and severity in young Douglas-fir plantations in coastal Oregon. Phytopathology 93:790–798.

Rotenberg, E., and D. Yakir. 2010. Contribution of semi-arid forests to the climate system. Science 327:451–454.

Royama, T. 1984. Population dynamics of the spruce budworm, *Choristoneura fumiferana*. Ecological Monographs 54:429–462.

Ruess, R. W., J. M. McFarland, L. M. Trummer, and J. K. Rohrs-Richey. 2009. Disease-mediated declines in n-fixation inputs by *Alnus tenuifolia* to early-successional floodplains in interior and south-central Alaska. Ecosystems 12:489–502.

Runion, G. B., S. A. Prior, H. H. Rogers, and R. J. Mitchell. 2010. Effects of elevated atmospheric CO_2 on two southern forest diseases. New Forests 39:275–285.

Ryan, R. B. 1959. Termination of diapause in the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins (Coleoptera: Scolytidae), as an aid to continuous laboratory rearing. Canadian Entomologist 91:520–525.

Ryerson, D. E., T. W. Swetnam, and A. M. Lynch. 2003. A tree-ring reconstruction of western spruce budworm outbreaks in the San Juan Mountains, Colorado, USA. Canadian Journal of Forest Research 33:1010–1028.

Safranyik, L., and A. L. Carroll. 2006. The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. Pages 3–66 *in* L. Safranyik and W. R. Wilson, editors. The mountain pine beetle: a synthesis of biology, management, and impacts on lodgepole pine. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia, Canada.

Safranyik, L., A. L. Carroll, J. Regniere, D. W. Langor, W. G. Riel, T. L. Shore, B. Peter, B. J. Cooke, V. G. Nealis, and S. W. Taylor. 2010. Potential for range expansion of mountain pine beetle into the boreal forest of North America. Canadian Entomologist 142:415–442.

Safranyik, L., and D. A. Linton. 1998. Mortality of mountain pine beetle larvae, *Dendroctonus ponderosae* (Coleoptera: Scolytidae) in logs of lodgepole pine (*Pinus contorta* var. *latifolia*) at constant low temperatures. Journal of the Entomological Society of British Columbia 95:81–87.

Salzer, M. W., M. K. Hughes, A. G. Bunn, and K. F. Kipfmueller. 2009. Recent unprecedented tree-ring growth in bristlecone pine at the highest elevations and possible causes. Proceedings of the National Academy of Sciences USA 106:20348–20353.

Sambaraju, K. R., A. L. Carroll, J. Zhu, K. Stahl, R. D. Moore, and B. H. Aukema. 2011. Climate change could alter the distribution of mountain pine beetle outbreaks in western Canada. Ecography 35:211–223.

Schenk, J. A., and D. M. Benjamin. 1969. Notes on the biology of *Ips pini* in central Wisconsin jack pine forests. Annals of the Entomological Society of America 62:480–485.

Schimel, D. S., et al. 2001. Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems. Nature 414:169–172.

Schmid, J. M., and R. H. Frye. 1977. Spruce beetle in the Rockies. GTR RM-49. USDA Forest Service, Fort Collins, Colorado, USA.

Seppälä, R., A. Buck, and P. Katila. 2009. Adaptation of forests and people to climate change: a global assessment report. International Union of Forest Research Organizations, Helsinki.

Seybold, S. J., J. A. King, D. R. Harris, L. J. Nelson, S. M. Hamud, and Y. Chen. 2012. Diurnal flight response of the walnut twig beetle, *Pityophthorus juglandis* Blackman (Coleoptera: Scolytidae), to pheromone-baited traps in two northern California walnut habitats. Pan-Pacific Entomologist 88:231–247.

Shaw, D. C., G. M. Filip, A. Kanaskie, D. A. Maguire, and W. A. Littke. 2011. Managing an epidemic of swiss needle cast in the Douglas-fir region of Oregon: the role of the Swiss needle cast cooperative. Journal of Forestry 109:109–119.

Shaw, J. D., B. E. Steed, and L. T. Deblander. 2005. Forest inventory and analysis (FIA) annual inventory answers the question: what is happening to pinyon-juniper woodlands? Journal of Forestry 103:280–285.

Sheppard, S., and P. Picard. 2006. Visual-quality impacts of forest pest activity at the landscape level: A synthesis of published knowledge and research needs. Landscape and Urban Planning 77:321–342.

Sherriff, R. L., E. E. Berg, and A. E. Miller. 2011. Climate variability and spruce beetle (*Dendroctonus rufipennis*) outbreaks in south-central and southwest Alaska. Ecology 92:1459–1470.

Shigo, A. L. 1972. The beech bark disease today in the northeastern U.S. Journal of Forestry 70:286–289.

Shore, T. L., L. Safranyik, and J. P. Lemieux. 2000. Susceptibility of lodgepole pine stands to the mountain pine beetle: testing of a rating system. Canadian Journal of Forest Research 30:44–49.

Siegert, N. W., D. G. McCullough, R. C. Venette, A. E. Hajek, and J. A. Andresen. 2009. Assessing the climatic potential for epizootics of the gypsy moth fungal pathogen *Entomophaga maimaiga* in the north central United States. Canadian Journal of Forest Research 39:1958–1970.

Silver, G. T. 1960. The relation of weather to population trends of the black-headed budworm *Acleris variana* (Fern.) (Lepidoptera: Tortricidae). Canadian Entomologist 92:401–410.

Simard, M., W. Romme, J. Griffin, and M. Turner. 2011. Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Ecological Monographs 81:3–24.

Six, D. L., and J. Adams. 2007. White pine blister rust severity and selection of individual whitebark pine by the mountain pine beetle (Coleoptera: Curculionidae, Scolytinae). Journal of Entomological Science 42:345–353.

Six, D. L., and B. J. Bentz. 2007. Temperature determines symbiont abundance in a multipartite bark beetle-fungus ectosymbiosis. Microbial Ecology 54:112–118.

Smith, G. F., and N. S. Nicholas. 2000. Size- and age-class distributions of Fraser fir following balsam woolly adelgid infestation. Canadian Journal of Forest Research 30:948–957.

Smith, M. L., J. N. Bruhn, and J. B. Anderson. 1994. Relatedness and spatial distribution of *Armillaria* genets infecting red pine seedlings. Phytopathology 84:822–829.

Sobek, S., A. Rajamohan, D. Dillon, R. C. Cumming, and B. J. Sinclair. 2011. High temperature tolerance and thermal plasticity in emerald ash borer *Agrilus planipennis*. Agricultural and Forest Entomology 13:333–340.

Sobek-Swant, S., J. C. Crosthwaite, D. B. Lyons, and B. J. Sinclair. 2011. Could phenotypic plasticity limit an invasive species? Incomplete reversibility of mid-winter deacclimation in emerald ash borer. Biological Invasions 14:115–125.

Spaulding, H. L., and L. K. Rieske. 2011. A glimpse at future forests: predicting the effects of *Phytophthora ramorum* on oak forests of southern Appalachia. Biological Invasions 13:1367–1375.

Stadler, B., T. Muller, and D. Orwig. 2006. The ecology of energy and nutrient fluxes in hemlock forests invaded by hemlock woolly adelgid. Ecology 87:1792–1804.

Stahl, K., R. D. Moore, and I. G. McKendry. 2006. Climatology of winter cold spells in relation to mountain pine beetle mortality in British Columbia, Canada. Climate Research 32:13–23.

Stanosz, G. R. 1993. Symptoms, association, and pathogenicity of *Discula campestris*, a cause of sugar maple seedling anthracnose. Plant Disease 77:1022–1026.

Stanosz, G. R., and M. A. Guthmiller. 1995. Root rot of red pine caused by *Heterobasidion annosum* in Wisconsin. Plant Disease 79:859.

Stanosz, G. R., L. M. Trummer, J. K. Rohrs-Richey, D. R. Smith, G. C. Adams, and J. J. Worrall. 2011. Response of *Alnus tenuifolia* to inoculation with *Valsa melanodiscus*. Canadian Journal of Plant Pathology 33:202–209.

Stanton, S. 2007. Effects of dwarf mistletoe on climate response of mature Ponderosa pine trees. Tree-Ring Research 63:69–80.

Stevens, R., V. Carolin, and C. Stein. 1983. Lepidoptera associated with western spruce budworm in the Southwestern United States. Journal of the Lepidopterist's Society 37:129–139.

Stinson, G., et al. 2011. An inventory-based analysis of Canada's managed forest carbon dynamics, 1990 to 2008. Global Change Biology 17:2227–2244.

Stone, J. K., L. B. Coop, and D. K. Manter. 2008. Predicting effects of climate change on Swiss needle cast disease severity in Pacific Northwest forests. Canadian Journal of Plant Pathology 30:169–176.

Stone, J. K., I. A. Hood, M. S. Watt, and J. L. Kerrigan. 2007. Distribution of Swiss needle cast in New Zealand in relation to winter temperature. Australasian Plant Pathology 36:445–454.

Storer, A. J., T. R. Gordon, D. L. Wood, and P. Bonello. 1997. Current and future impacts of pitch canker disease of pines. Journal of Forestry 95:21–26.

Sturrock, R. N., S. J. Frankel, A. V. Brown, P. E. Hennon, J. T. Kliejunas, K. J. Lewis, J. J. Worrall, and A. J. Woods. 2011. Climate change and forest diseases. Plant Pathology 60:133–149.

Sullivan, C. R. 1961. The effect of weather and the physical attributes of white pine leaders on the behaviour and survival of the white pine weevil, *Pissodes strobi* Peck, in mixed stands. Canadian Entomologist 93:721–741.

Sutherland, M. L., S. Pearson, and C. M. Brasier. 1997. The influence of temperature and light on defoliation levels of elm by Dutch elm disease. Phytopathology 87:576–581.

Swetnam, T. W., and A. M. Lynch. 1993. Multicentury, regional-scale patterns of western spruce budworm outbreaks. Ecological Monographs 63:399–424.

Synder, M. A., B. Fineschi, Y. B. Linhart, and R. H. Smith. 1996. Multivariate discrimination of host use by dwarf mistletoe *Arceuthobium vaginatum* subsp. *cryptopodum*: inter- and intraspecific comparisons. Journal of Chemical Ecology 22:295–305.

Tainter, F. H. 1986. Growth, sporulation, and mucilage production by *Ceratocystis fagacearum* at high temperatures. Plant Disease 70:339–342.

Taylor, D. R., A. M. Jarosz, R. E. Lenski, and D. W. Fulbright. 1998. The acquisition of hypovirulence in host-pathogen systems with three trophic levels. American Naturalist 151:343–355.

Tchakerian, M. D., and R. N. Couslon. 2011. Ecological impacts of Southern pine beetle. Pages 223–234 *in* R. N. Coulson and K. D. Klepzig, editors. Southern pine beetle II. General Technical Report SRS-140. USDA Forest Service, Southern Research Station, Asheville, North Carolina, USA.

Thompson, I., B. Mackey, S. McNulty, and A. Mosseler. 2009. Forest resilience, biodiversity, and climate change. A synthesis of the biodiversity/resilience/stability relationship in forest ecosystems. Technical Series Number 43. Secretariat of the Convention on Biological Diversity, Montreal, Quebec, Canada.

Thomson, A. J., and R. Benton. 2007. A 90-year sea warming trend explains outbreak patterns of western spruce budworm on Vancouver Island. Forestry Chronicle 83:867–869.

Thomson, A. J., R. F. Shepherd, J. W. E. Harris, and R. H. Silversides. 1984. Relating weather to outbreaks of western spruce budworm, *Choristoneura occidentalis* (Lepidoptera, Tortricidae), in British Columbia. Canadian Entomologist 116:375–381.

Thomson, A. J., and D. M. Shrimpton. 1984. Weather associated with the start of mountain pine beetle outbreaks. Canadian Journal of Forest Research 14:255–258.

Throop, H., and M. Lerdau. 2004. Effects of nitrogen deposition on insect herbivory: Implications for community and ecosystem processes. Ecosystems 7:109–133.

Tran, J. K., T. Ylioja, R. F. Billings, J. Régnière, and M. P. Ayres. 2007. Impact of minimum winter temperatures on the population dynamics of *Dendroctonus frontalis*. Ecological Applications 17:882–899.

Trotter, R. T., and K. S. Shields. 2009. Variation in winter survival of the invasive hemlock woolly adelgid (Hemiptera: Adelgidae) across the eastern United States. Environmental Entomology 38:577–587.

Trummer, L. 2006. Alder canker. Page 52 *in* C. Snyder, editor. Forest health conditions in Alaska: 2005. Forest Health Protection: Report R10-PR-5. USDA Forest Service, Alaska Region, Anchorage, Alaska, USA.

Turchin, P., P. L. Lorio, A. D. Taylor, and R. F. Billings. 1991. Why do populations of southern pine beetles (Coleoptera, Scolytidae) fluctuate? Environmental Entomology 20:401–409.

Ungerer, M. J., M. P. Ayres, and M. J. Lombardero. 1999. Climate and the northern distribution limits of *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae). Journal of Biogeography 26:1133–1145.

USDA Forest Service. 2010. Major forest insect and disease conditions in the United States: 2009 update. FS-952. USDA Forest Service, Washington, D.C., USA.

Vaclavik, T., A. Kanaskie, E. M. Hansen, J. L. Ohmann, and R. K. Meentemeyer. 2010. Predicting potential and actual distribution of sudden oak death in Oregon: prioritizing landscape contexts for early detection and eradication of disease outbreaks. Forest Ecology and Management 260:1026–1035.

Van Arsdel, E. P. 1972. Environment in relation to white pine blister rust infection. Pages 479–493 *in* R. T. Bingham, R. Hoff, and G. I. McDonald, editors. Biology of rust resistance in forest trees: Proceedings of a NATO-IUFRO Advanced Study Institute: Biology of rust resistance in forest trees. Miscellaneous Publication 1221. USDA Forest Service, Washington, D.C., USA.

Veblen, T. T., K. S. Hadley, M. S. Reid, and A. J. Rebertus. 1991. The response of sub-alpine forests to spruce beetle outbreak in Colorado. Ecology 72:213–231.

Vega, J., E. Jimenez, D. Vega, L. Ortiz, and J. R. Perez. 2011. *Pinus pinaster* Ait. tree mortality following wildfire in Spain. Forest Ecology and Management 261:2232–2242.

Venette, R. C., and S. D. Cohen. 2006. Potential climatic suitability for establishment of *Phytophthora ramorum* within the contiguous United States. Forest Ecology and Management 231:18–26.

Venier, L., and A. Hopkin. 1998. A spatial, climate-determined risk rating for Scleroderris disease of pines in Ontario. Canadian Journal of Forest Research 28:1398–1404.

Volney, W. J. A., and R. A. Fleming. 2000. Climate change and impacts of boreal forest insects. Agriculture, Ecosystems and Environment 82:283–294.

Volney, W. J. A., and R. A. Fleming. 2007. Spruce budworm (*Choristoneura* spp.) biotype reactions to forest and climate characteristics. Global Change Biology 13:1630–1643.

Wagner, D., L. Defoliart, P. Doak, and J. Schneiderheinze. 2008. Impact of epidermal leaf mining by the aspen leaf miner (*Phyllocnistis populiella*) on the growth, physiology, and leaf longevity of quaking aspen. Oecologia 157:259–267.

Wagner, D., P. Doak, T. Sformo, P. M. Steiner, and B. Carlson. 2012. Overwintering physiology and microhabitat use of *Phyllocnistis populiella* (Lepidoptera: Gracillariidae) in interior Alaska. Environmental Entomology 41:180–187.

Walkinshaw, C. H., and J. P. Barnett. 1995. Tolerance of loblolly pines to fusiform rust. Southern Journal of Applied Forestry 19:60–64.

Wang, F. G., Y. J. Xu, and T. J. Dean. 2011. Projecting climate change effects on forest net primary productivity in subtropical Louisiana, USA. Ambio 40:506–520.

Wargo, P. M. 1996. Consequences of environmental stress on oak: Predisposition to pathogens. Annales des Sciences Forestieres 53:359–368.

Waring, K. M., D. M. Reboletti, L. A. Mork, C.-H. Huang, R. W. Hofstetter, A. M. Garcia, P. Z. Fule, and T. S. Davis. 2009. Modeling the impacts of two bark beetle species under a warming climate in the southwestern USA: Ecological and economic consequences. Environmental Management 44:824–835.

Watt, M., R. Ganley, D. Kriticos, and L. Manning. 2011. Dothistroma needle blight and pitch canker: the current and future potential distribution of two important diseases of *Pinus* species. Canadian Journal of Forest Research 41:412–424.

Watt, M. S., D. J. Kriticos, S. Alcaraz, A. V. Brown, and A. Leriche. 2009. The hosts and potential geographic range of *Dothistroma* needle blight. Forest Ecology and Management 257:1505–1519.

Watt, M. S., J. K. Stone, I. A. Hood, and D. J. Palmer. 2010. Predicting the severity of Swiss needle cast on Douglas-fir under current and future climate in New Zealand. Forest Ecology and Management 260:2232–2240.

Weber, J. D., W. J. A. Volney, and J. R. Spence. 1999. Intrinsic development rate of spruce budworm (Lepidoptera: Tortricidae) across a gradient of latitude. Environmental Entomology 28:224–232.

Wellington, W. G., J. J. Fettes, R. M. Belyea, and K. B. Turner. 1950. Physical and biological indicators of the development of outbreaks of the spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). Canadian Journal of Research 28d:308–331.

Welsh, C., K. Lewis, and A. Woods. 2009. The outbreak history of Dothistroma needle blight: an emerging forest disease in northwestern British Columbia, Canada. Canadian Journal of Forest Research 39:2505–2519.

Werner, R. A., E. H. Holsten, S. M. Matsuoka, and R. E. Burnside. 2006. Spruce beetles and forest ecosystems in south-central Alaska: a review of 30 years of research. Forest Ecology and Management 227:195–206.

White, M. A., T. N. Brown, and G. E. Host. 2002. Landscape analysis of risk factors for white pine blister rust in the Mixed Forest Province of Minnesota, U.S.A. Canadian Journal of Forest Research 32:1639–1650.

Williams, A. P., C. D. Allen, C. I. Millar, T. W. Swetnam, J. Michaelsen, C. J. Still, and S. W. Leavitt. 2010. Forest responses to increasing aridity and warmth in the southwestern United States. Proceedings of the National Academy of Sciences USA 107:21289–21294.

Williams, D. W., and A. M. Liebhold. 1995*a*. Forest defoliators and climatic change: Potential changes in spatial distribution of outbreaks of western spruce budworm (Lepidoptera: Tortricidae) and gypsy moth (Lepidoptera: Lymantriidae). Environmental Entomology 24:1–9.

Williams, D. W., and A. M. Liebhold. 1995*b*. Herbivorous insects and global change: potential changes in the spatial distribution of forest defoliator outbreaks. Journal of Biogeography 22:665–671.

Williams, D., and A. M. Liebhold. 2002. Climate change and the outbreak ranges of two North American bark beetles. Agricultural and Forest Entomology 4:87–99.

Wilson, G. G. 1974. The effects of temperature and ultraviolet radiation on the infection of *Choristoneura fumiferana* and *Malacosoma pluviale* by a microsporidan parasite, *Nosema* (*Perezia*) *fumiferanae* (Thom.). Canadian Journal of Zoology 52:59–63.

Wilson, J. S., E. S. Isaac, and R. I. Gara. 1998. Impacts of mountain pine beetle (*Dendroctonus ponderosae*) (Col., Scolytidae) infestation on future landscape susceptibility to the western spruce budworm (*Choristoneura occidentalis*) (Lep., Torticidae) in north central Washington. Journal of Applied Entomology 122:239–245.

Witzell, J., M. Berglund, and J. Ronnberg. 2011. Does temperature regime govern the establishment of *Heterobasidion annosum* in Scandinavia? International Journal of Biometeorology 55:275–284.

Woods, A., K. D. Coates, and A. Hamann. 2005. Is an unprecedented Dothistroma needle blight epidemic related to climate change? BioScience 55:761.

Woods, A. J., D. Heppner, H. H. Kope, J. Burleigh, and L. Maclauchlan. 2010. Forest health and climate change: A British Columbia perspective. Forestry Chronicle 86:412–422.

Worrall, J. J. 2009. Dieback and mortality of *Alnus* in the Southern Rocky Mountains, USA. Plant Disease 93:293–298.

Worrall, J. J., G. C. Adams, and S. C. Tharp. 2010*a*. Summer heat and an epidemic of cytospora canker of *Alnus*. Canadian Journal of Plant Pathology 32:376–386.

Worrall, J. J., L. Egeland, T. Eager, R. A. Mask, E. W. Johnson, P. A. Kemp, and W. D. Shepperd. 2008. Rapid mortality of *Populus tremuloides* in southwestern Colorado, USA. Forest Ecology and Management 255:686–696.

Worrall, J. J., S. B. Marchetti, L. Egeland, R. A. Mask, T. Eager, and B. Howell. 2010*b*. Effects and etiology of sudden aspen decline in southwestern Colorado, USA. Forest Ecology and Management 260:638–648.

Ylioja, T., D. H. Slone, and M. P. Ayres. 2005. Mismatch between herbivore behavior and demographics contributes to scale-dependence of host susceptibility in two pine species. Forest Science 51:522–531.

Zentmyer, G. A. 1980. *Phytophthora cinnamomi* and the diseases it causes. Monograph 10. American Phytopathological Society, St. Paul, Minnesota, USA.

Zentmyer, G. A., L. J. Klure, and E. C. Pond. 1979. The influence of temperature and nutrition on formation of sexual structures by *Phytophthora cinnamomi*. Mycologia 71:55–67.

Zhao, J., D. B. Mainwaring, D. A. Maguire, and A. Kanaskie. 2011. Regional and annual trends in Douglas-fir foliage retention: Correlations with climatic variables. Forest Ecology and Management 262:1872–1886.

SUPPLEMENTAL MATERIAL

Data Availability

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