Climate Change and Bark Beetles of the Western United States and Canada: Direct and Indirect Effects

BARBARA J. BENTZ, JACQUES RÉGNIÈRE, CHRISTOPHER J. FETTIG, E. MATTHEW HANSEN, JANE L. HAYES, JEFFREY A. HICKE, RICK G. KELSEY, JOSE F. NEGRÓN, AND STEVEN J. SEYBOLD

Climatic changes are predicted to significantly affect the frequency and severity of disturbances that shape forest ecosystems. We provide a synthesis of climate change effects on native bark beetles, important mortality agents of conifers in western North America. Because of differences in temperature-dependent life-history strategies, including cold-induced mortality and developmental timing, responses to warming will differ among and within bark beetle species. The success of bark beetle populations will also be influenced indirectly by the effects of climate on community associates and host-tree vigor, although little information is available to quantify these relationships. We used available population models and climate forecasts to explore the responses of two eruptive bark beetle species. Based on projected warming, increases in thermal regimes conducive to population success are predicted for Dendroctonus rufipennis *(Kirby) and* Dendroctonus ponderosae *Hopkins, although there is considerable spatial and temporal variability. These predictions from population models suggest a movement of temperature suitability to higher latitudes and elevations and identify regions with a high potential for bark beetle outbreaks and associated tree mortality in the coming century.*

Keywords: cold tolerance, mountain pine beetle, seasonality, spruce beetle, temperature

During the 21st century, mean annual global temperature is expected to increase between 1.8 and 4.0 degrees Celsius (°C) as a result of growing atmospheric greenhouse gas concentrations created by human activities. Across North America, the rise in temperatures is projected to exceed global mean increases, particularly at high latitudes and elevations, and more frequent extreme weather events are expected (IPCC 2007). Associated changes in precipitation patterns may result in earlier and longer dry seasons across the western United States, with a greater frequency and duration of droughts (Seager et al. 2007). These changes in climatic conditions over the next century will significantly affect the condition, composition, distribution, and productivity of multiple ecosystems (Easterling et al. 2000).

Coniferous forests, which provide essential ecosystem services and host a vast array of plant and animal species, are expected to be significantly affected by shifts in temperature, precipitation, and atmospheric greenhouse gas concentrations (McNulty and Aber 2001). By the end of the century, about 48% of the western US landscape is predicted to experience climate profiles with no contemporary analog to the current coniferous vegetation (Rehfeldt et al. 2006). Population irruptions of phytophagous insects—disturbance events important to forest ecosystem functioning—are also directly sensitive to

climate change components (Dale et al. 2001). Although there are many possible avenues for atmospheric changes to influence phytophagous insect outbreaks, because of the direct link between insect population success and seasonal temperature (Danks 1987), outbreaks are predicted to be affected dramatically by global warming (Bale et al. 2002). Rapid genetic adaptation of insects to seasonal changes in temperature has already been documented (Balanyá et al. 2006, Bradshaw and Holzapfel 2006), and range expansion has occurred in many cases as species move into new niches created by increasing temperature (Battista et al. 2006, Nealis and Peter 2009).

Native bark beetles (Coleoptera: Curculionidae, Scolytinae), which evolved within the coniferous forest ecosystems of western North America, are key agents of change in these systems. Beetle outbreaks raise tree mortality rates and can result in subsequent replacement by other tree species and plant associations (Veblen et al. 1991). In recent decades, billions of coniferous trees across millions of hectares have been killed by native bark beetles in forests ranging from Mexico to Alaska, and several of the current outbreaks are among the largest and most severe in recorded history (Bentz et al. 2009). Although gaps exist in our understanding of the processes, it is clear that mechanisms contributing to widespread bark beetle outbreaks are complex and

include density-independent factors, in addition to spatial and temporal dependencies at multiple scales (Aukema et al. 2008, Raffa et al. 2008). Large areas of suitable host trees of susceptible vigor, age, and density are required for an outbreak to develop (Fettig et al. 2007). Because bark beetle population survival and growth are highly sensitive to thermal conditions, and water stress can influence host-tree vigor, outbreaks have been correlated with shifts in temperature (Powell and Logan 2005) and precipitation (Berg et al. 2006). However, a comprehensive synthesis of the direct and indirect effects of climate change on the population dynamics of bark beetles is lacking.

In this article we assess and synthesize the state of knowledge regarding effects of climate change on bark beetles that cause extensive conifer mortality in the western United States and Canada (table 1). We discuss potential direct and indirect impacts of climate change on multiple aspects of host trees, and bark beetle community ecology and population dynamics. We present two case studies to illustrate the potential impacts of global warming on the population outbreak dynamics of eruptive bark beetles.

Direct effects of climate change on bark beetles

Of the hundreds of native bark beetle species in the western United States and Canada, few species (< 1%) attack and reproduce in live trees. Frequently referred to as aggressive bark beetles, these species can kill healthy trees and have the capacity to cause landscape-scale tree mortality (table 1). Host selection and colonization behavior by bark beetles are complex processes that involve both long- and short-range behavioral components (Graves et al. 2008) with multiple thresholds and rapid feedback (Raffa et al. 2008). Bark beetle adults have sophisticated chemoreceptors and behaviors that allow them to recognize host tree species in addition to the potential defensive capacity of the host. Once a host is selected, colonization requires overcoming constitutive and inducible tree defenses, which include anatomical, physical, and chemical components (Franceschi et al. 2005). These defenses are overcome only when a critical minimum number of beetles are recruited to the host tree. This number varies with changes in host vigor, and therefore will be affected indirectly as host trees respond to a changing climate (see below). In most cases, recruitment is facilitated by aggregation pheromones that attract other colonizing adults (Raffa 2001). Following aggregation and subsequent mating, adults lay eggs in the phloem, and larvae excavate feeding tunnels in this tissue or in the outer bark, depending on the beetle species—a process that eventually results in the mortality of the host tree. Mature adult beetles of the next generation tunnel outward through the bark and initiate flight in search of a new host tree.

Synchronous adult emergence and life-cycle timing, critical strategies used by many bark beetle species to kill trees, are in large part dictated by several temperature-dependent physiological processes. Direct effects of climate change on bark beetle population dynamics will therefore occur predominantly through the influence of temperature on life-history strategies that (a) maintain adaptive developmental timing leading to synchronized population emergence and life-cycle timing, and (b) facilitate cold tolerance and avoidance of low-temperature-induced mortality.

Table 1. Bark beetle species that have the capacity to cause landscape-scale tree mortality in the western United States and Canada.

Common name	Scientific name	Major host species
Arizona fivespined ips	*Ips lecontei*	*Pinus ponderosa*, and others
California fivespined ips	*Ips paraconfusus*	*Pinus attenuata, Pinus contorta, Pinus coulteri, Pinus jeffreyi, Pinus lambertiana, P. ponderosa, Pinus radiata, Pinus torreyana*, and others
Douglas-fir beetle	*Dendroctonus pseudotsugae*	*Pseudotsuga menziesii*
Eastern larch beetle	*Dendroctonus simplex*	*Larix laricina*
Fir engraver	*Scolytus ventralis*	*Abies concolor, Abies grandis, Abies magnifica*
Jeffrey pine beetle	*Dendroctonus jeffreyi*	*P. jeffreyi*
Mountain pine beetle	*Dendroctonus ponderosae*	*Pinus albicaulis, Pinus aristata, Pinus balfouriana, P. contorta, Pinus flexilis, P. lambertiana, Pinus monticola, P. ponderosa*, and others
Northern spruce engraver	*Ips perturbatus*	*Picea engelmannii, Picea glauca, Picea × lutzii, Picea mariana, Picea sitchensis*
Pine engraver	*Ips pini*	*P. contorta, P. jeffreyi, P. ponderosa*, and others
Piñon ips	*Ips confusus*	*Pinus edulis, Pinus monophylla*
Roundheaded pine beetle	*Dendroctonus adjunctus*	*Pinus arizonica, Pinus engelmannii, P. flexilis, Pinus leiophylla, P. ponderosa, Pinus strobiformis*
Southern pine beetle	*Dendroctonus frontalis*	*Pinus engelmannii, P. leiophylla, P. ponderosa*
Spruce beetle	*Dendroctonus rufipennis*	*Picea engelmannii, Pi. glauca, Pi. sitchensis*
Western balsam bark beetle	*Dryocoetes confusus*	*Abies lasiocarpa*, and others
Western pine beetle	*Dendroctonus brevicomis*	*P. coulteri, P. ponderosa*

Developmental timing. The time required to complete a generation varies among bark beetle genera, species within a genus, populations within a species, and individuals within a population. Some species, such as the western pine beetle, *Dendroctonus brevicomis* LeConte, and the piñon ips, *Ips confusus* LeConte, produce more than one generation per year. Others, including the spruce beetle, *Dendroctonus rufipennis* [Kirby], and mountain pine beetle, *Dendroctonus ponderosae* Hopkins, require one, two, or even three years to produce a single generation, depending on the temperature profile at a particular locale within their large geographic ranges. Moreover, as a result of the evolution of narrow thermal windows that minimize excess physiological costs (Pörtner and Farrell 2008), the adaptation of life-cycle timing to a local climate can result in a genetically predetermined variability in temperature response across the range of a single bark beetle species (Bentz et al. 2001). Although little is known about specific temperature-dependent developmental processes of many bark beetle species, research suggests that at least two predominant strategies, diapause and direct temperature control, have evolved to maintain appropriate life-cycle timing. Each strategy may be differentially affected by climate change.

Diapause is a dynamic, endocrine-mediated and environmentally driven dormancy that occurs at a specific life stage. Diapause not only offers a mechanism to keep insects synchronized with their environment and food availability but also provides tolerance to environmental extremes (Tauber et al. 1986). Although not all species have been investigated, diapause has been demonstrated or suggested to exist in five bark beetle species indigenous to western North America: (1) fir engraver, *Scolytus ventralis* LeConte (Scott and Berryman 1972); (2) spruce beetle (Hansen et al. 2001); (3) Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins (Ryan 1959); (4) eastern larch beetle, *Dendroctonus simplex* LeConte (Langor and Raske 1987); and (5) pine engraver, *Ips pini* (Say) (Birch 1974). The effect of climate change on these species will depend on the life stage in which diapause occurs. For example, high summer temperatures prevent facultative prepupal diapause of the spruce beetle, resulting in beetles that complete their life cycles in a single year, compared with two years when the diapause is invoked, potentially leading to exponential population growth (Hansen and Bentz 2003). Conversely, an obligatory adult diapause initiated by low temperatures, as in spruce beetles and Douglas-fir beetles, could be disrupted by higher minimum temperatures.

Direct temperature control also maintains appropriate seasonality in bark beetles (*sensu* Danks 1987). In the mountain pine beetle, for example, life stage–specific developmental thresholds aid in synchronizing adult emergence at appropriate times of the year (Powell and Logan 2005). Later life stages (e.g., fourth instar larvae) have higher temperature threshold requirements for development than earlier life stages. The higher temperature thresholds serve to synchronize individuals during autumn, as temperatures decrease, and also prevent development to the cold-intolerant pupal life stage (Logan and Bentz 1999). Temperature pattern

throughout a life cycle is therefore critical to appropriate seasonality, and predicted rises in temperature could affect both developmental thresholds and rates in multiple life stages. Additional fitness parameters potentially affected include higher adult longevity and prolonged adult emergence and flight. Warming trends have been associated with shifts in generation duration for populations of spruce beetle in Alaska, Utah, and Colorado (Hansen et al. 2001, Werner et al. 2006), and mountain pine beetle in high-elevation forests (Bentz and Schen-Langenheim 2007).

Little is known about developmental strategies of the many bark beetle species indigenous to the southwestern United States and Mexico. These species are significant because of their potential to move northward with climate change by following range expansion of current hosts or by adapting to novel hosts. The roundheaded pine beetle, *Dendroctonus adjunctus* Blandford, for example, colonizes pines from southern Utah and Colorado south into Guatemala, and its life-cycle timing differs depending on geographical location (Chansler 1967). Although it appears that the northern extent of this bark beetle species, and others restricted to the southwestern United States and Mexico, is currently limited by climate and not host-tree availability (Salinas-Moreno et al. 2004), information is lacking on temperature-dependent physiological aspects of its life history that may be range limiting. The polyphagy exhibited by the roundheaded pine beetle and other bark beetles currently found in Mexico suggests they may do well in pine species they would encounter in a northward range expansion, potentially invading niches vacated by beetle species whose population success is disrupted by climate change. Novel species assemblages could be created, as exemplified by recent documentation of the Mexican pine beetle, *Dendroctonus mexicanus* Hopkins, formerly thought to be limited to northern Mexico, and the southern pine beetle, *Dendroctonus frontalis* Zimmermann, attacking the same individual pine trees in the Chiricahua Mountains of Arizona. This incidence is potentially a result of an increase in climate suitability and the number of beetle generations per year (Waring et al. 2009).

Cold tolerance. In addition to climate controls on adaptive developmental timing, mortality from cold exposure is considered a key temperature-related factor in bark beetle population dynamics, although there are few data for most bark beetle species. Cold hardening is the dynamic acquisition of cold tolerance through biochemical and physiological processes, and is most often triggered by cold temperatures (Lee 1989). Similar to the adaptations in temperature-dependent developmental timing described above, cold tolerance will undoubtedly vary among genera and within populations of the same bark beetle species because of the temperature-dependent nature of cold hardening and the metabolic costs involved (Régnière and Bentz 2007). Spruce beetles and mountain pine beetles accumulate cryoprotectant compounds such as glycerol as temperatures decline during autumn (Miller and Werner 1987, Bentz and Mullins 1999).

Cold tolerance for these insects is therefore greatest during the winter months, and lowest during periods of glycerol synthesis and catabolism in autumn and spring, respectively, suggesting a direct correlation between increasing minimum temperatures associated with climate change and a reduction in cold-induced beetle mortality.

Indirect effects of climate change on bark beetles

Bark beetle population success will be influenced indirectly by the effects of climate on community associates, host-tree vigor, and host abundance.

Community associates. Upon colonizing a tree, bark beetles introduce an array of fungi, bacteria, nematodes, and mites that can significantly influence their fitness (Hofstetter et al. 2006, Cardoza et al. 2008). The relationship between bark beetle species and their associates is often described as symbiotic, as many bark beetles have evolved morphological adaptations to assist in the transport of specific associates, derive nutritional and defensive benefits from them, or both (Klepzig and Six 2004). For example, spruce beetles have specialized body structures to carry associated nematodes (Cardoza et al. 2008), and mountain pine beetles and western pine beetles have structures to transport symbiotic fungi (Klepzig and Six 2004). Developing mountain pine beetle larvae acquire vital nutrients not found in plant tissue by feeding on two fungi, *Grosmannia clavigera* and *Ophiostoma montium*, the hyphae of which spread throughout the phloem and sapwood following inoculation into the tree by attacking beetles. Although both fungi are important, evidence suggests that one species (*G. clavigera*) supports faster brood development, larger body size, and higher brood production than does the other (Bleiker and Six 2007). Each fungus possesses different thermal ranges for optimal growth (Rice et al. 2008), and seasonal temperature dictates which fungal species is ultimately vectored by dispersing beetles (Six and Bentz 2007). Because benefits to the mountain pine beetle are not the same for each fungal species, shifts in temperature and precipitation associated with climate change could indirectly affect mountain pine beetle population success through direct effects on fungal symbionts.

Other community associates and trophic interactions, including avian predators and insect parasitoids and predators (McCambridge and Knight 1972, Boone et al. 2008), undoubtedly will also be influenced by abiotic factors associated with climate change. The ecological roles and temperature dependencies of the majority of bark beetle community associates are not well understood, which hampers full comprehension of the consequences of climate change on bark beetle population dynamics.

Host-tree physiology. Climate change will influence bark beetle–host interactions in complex or nonlinear ways. Although plants tend to thrive in carbon-enriched atmospheres, mature wildland conifer species are not necessarily carbon limited and therefore may not express large growth increases in response to increased carbon dioxide (CO_2; Millard et al. 2007). However, when grown in the presence of elevated CO_2, plants accumulate carbon and the carbon-to-nitrogen ratio increases (Zvereva and Kozlov 2006), resulting in reduced nutrition (low nitrogen content) for insect herbivores (Mattson 1980). To compensate, insects consume more but grow more slowly, a trade-off with the potential to disrupt phenological synchrony important to bark beetle survival, in addition to prolonging exposure to mortality agents. The indirect negative effects of enhanced CO_2 on bark beetle growth and survival are, at least in part, outweighed by other climate-change-induced effects on host trees, including reduced defenses.

An important consequence of climate change is higher frequency and severity of droughts (Seager et al. 2007). In addition to directly affecting tree death through carbon starvation and cavitation of water columns within the xylem, climatic water stress can have profound effects on tree susceptibility to bark beetle attack. To avoid drought-induced hydraulic failure, plant stomates close to restrict transpiration. However, stomatal closing also limits carbon assimilation, which can result in carbon starvation (McDowell et al. 2008). Changes in carbon assimilation will also alter within-plant allocation of carbohydrates available for growth, defense, and tissue repair, affecting the production of constitutive or inducible chemical defenses (Herms and Mattson 1992) and thus a tree's ability to respond to bark beetle invasions. Hydraulic failure may be further amplified when water transport is interrupted by symbiotic fungi inoculated into trees during the bark beetle attack process (McDowell et al. 2008). Drought-induced alterations to tree defensive capacity ultimately reduce the threshold number of beetles necessary for a successful mass attack, thereby relaxing the constraints on critical thresholds that must be surpassed for bark beetle outbreaks to occur.

Although the mechanisms connecting drought stress to bark beetle outbreaks are not well understood in western North American ecosystems, it is clear that effects will vary regionally and by bark beetle–host species complex because of differences in critical feedbacks driving beetle population dynamics, as well as physiological differences among tree species. For example, the regional-scale piñon ips epidemic associated with severe drought in the southwestern United States (Breshears et al. 2005) ended as the supply of drought-stressed trees was exhausted. In contrast, although drought stress facilitated progression from an incipient to epidemic mountain pine beetle population in British Columbia, a significant correlation with precipitation was no longer found after the beetle population became self-amplifying (Raffa et al. 2008). In both cases, elevated temperatures, which directly influence bark beetle population success in ways described above, were associated with drought conditions that affected tree stress.

Host-tree distribution. The distribution of coniferous vegetation across western North America resulted from climatic shifts dating back millions of years (Brunsfeld et al. 2001), in

addition to more recent recolonization of deglaciated lands from multiple refugial populations (Godbout et al. 2008). In response to an approximately 2°C increase in temperature, significant changes in community composition occurred over the past several thousand years, including the formation of new communities, many of which no longer exist today (Shugart 2003). As tree species ranges shifted, so did the ranges of phytophagous insects such as bark beetles as they tracked environmental changes and followed host tree species (Seybold et al. 1995). These historical patterns foreshadow large modifications to current forest ecosystem dynamics as climate change accelerates.

In a rapidly changing environment, coniferous tree species will persist through migration or adaptation to new conditions, or they will go locally extinct. The fate of any individual species will depend on multiple factors, including phenotypic variation, fecundity, and biotic interactions (Aitken et al. 2008). On the basis of the best existing data for 130 tree species in North America and associated climate information, and assuming no limitations to individual tree growth, McKenney and colleagues (2007) predicted that the average range for a given tree species will decrease in size by 12% and will shift northward by 700 kilometers (km) during this century. Under a scenario in which survival occurs only in areas where anticipated climatic conditions overlap with current climatic conditions, niches for tree survival will decrease in size by 58% and shift north by 330 km. More specific to this synthesis, range predictions for several hosts of notable bark beetle species provide striking comparisons. Relative to contemporary distributions, by 2060 the range of Engelmann spruce, *Picea engelmanni* Parry ex Engelm., a principal host for spruce beetle, is projected to decrease by 47% within the contiguous western United States. During the same period, the areas inhabited by ponderosa pine, *Pinus ponderosa* Laws., and Douglas-fir, *Pseudotsuga menziesii* Franco, hosts of several bark beetle species, are projected to increase by 11% and 7%, respectively (Rehfeldt et al. 2006). If we assume that current tree distributions are driven by nonclimatic biotic factors such as bark beetles in addition to climate, models used to forecast specific tree distributions may already include an inherent measure of the influence of bark beetles on tree species distributions.

Case studies

Despite uncertainties, changes in temperature predicted by general circulation models can be an important basis for estimating biological response to changing conditions (Millar et al. 2007). When used in conjunction with quantitative models that are based on a mechanistic understanding of biological responses to temperature, results can provide insight into ecosystem responses to climate change. We explore the potential effects of changing climate on bark beetle outbreak dynamics using two case studies: (1) spruce beetle and (2) mountain pine beetle. We chose these species for analysis because mechanistic models for predicting temperature effects on population success have been developed.

Because models incorporating the direct effects of climatic changes on conifers and their subsequent response to bark beetle attacks are not currently available, our quantitative assessments are based solely on bark beetle population success. Our assessment assumes no change in current tree distributions, and that thermal conditions conducive to bark beetle population success result in increased levels of tree mortality, although we do not explicitly model the impacts to forests.

Weather data and bark beetle model projections. Simulated past and future climates (1961–2100) were obtained from the Canadian Regional Climate Model (CRCM) version 4.2.0 runs ADJ and ADL (Music and Caya 2007). We used the Intergovernmental Panel on Climate Change A2 emissions scenario, which results in relatively high projected warming in 2100 among all scenarios (IPCC 2007), but which has been realistic thus far given emissions estimates in the last 20 years (Raupach et al. 2007). The simulations provided a 201 × 193 gridded database of daily maximum and minimum air temperatures and precipitation over North America with a horizontal resolution of 45 km (true at 60°N). From these data, 30-year normals were computed for each decade in the interval between 1961 and 2100, and the "delta" method (differences between modeled decadal normals and the reference period 1961–1990) was used to generate unbiased decadal sets of 30-year normals into the future. Observed (1961–1990) and predicted (2001–2030, 2071–2100) normals were used to generate stochastic daily minimum and maximum temperatures (Régnière and St-Amant 2007) for input to the spruce beetle and mountain pine beetle models.

The spruce beetle and mountain pine beetle models (described below) are driven by hourly temperature (interpolated between the minimum and maximum temperatures on successive days) and were integrated with weather and topography using BioSIM (*http://cfs.nrcan.gc.ca/factsheets/biosim*). We ran models for 25,000 simulation points across North America, north of Mexico, with an emphasis on mountainous and forested areas. Elevations were obtained from digital elevation models (DEM) at 30-as resolution (*http://eros.usgs. gov/products/elevation/gtopo30/gtopo30.html*). Because weather inputs are stochastic and responses are nonlinear, we replicated each model run 30 times, each with a stochastically different one-year temperature time series for each simulation point and normals period. We averaged model output over replicates. From these averaged outputs, maps were generated by universal kriging, with elevation provided by the input DEM as external drift variable (Hudson and Wackernagel 1994). Probability values were linearized by logistic transformation before interpolation and before the maps were back transformed. Maps depict a continuous measure of bark beetle population success (as defined by each insect model) for the three climate periods. Model output was masked using polygons that estimate the 20th-century locations of spruce (for spruce beetle) and pine (for mountain pine beetle) habitat in the United States and Canada (Little 1971).

Spruce beetle. The spruce beetle is distributed in spruce forests throughout western North America, across the boreal forest of Canada, and into the northeastern United States. Extensive spruce beetle outbreaks have occurred throughout the contiguous western United States, Alaska, and western Canada during the past decade, affecting more than 3 million hectares (ha) of forest (USDA Forest Service, Forest Health Protection, and Natural Resources Canada, Canadian Forest Service). In Alaska alone, the spruce beetle affected approximately 2 million ha during a prolonged outbreak in the 1980s and 1990s (Werner et al. 2006). High summer temperatures are correlated with a rising proportion of beetles that complete a generation in a single year rather than in two years, contributing significantly to population growth (Hansen and Bentz 2003) and to greater levels of spruce-beetle-caused tree mortality (Berg et al. 2006). To examine the direct effects of higher temperature on spruce beetle population success and growth, we used an empirical model that predicts spruce beetle life-cycle duration as a function of hourly air temperature (Hansen et al. 2001). A higher probability of one-year beetles translates to a higher probability of a population outbreak.

Spruce beetle model results. Model predictions suggest that during the historical period 1961–1990, the majority of spruce forests in Alaska, and those at high elevations in the contiguous western United States and northern latitudes of Canada, would have a moderate to low probability of spruce beetle populations developing in a single year (figure 1a, 1d). In the period 2001–2030 and again from 2071 to 2100, we would expect substantial increases in spruce forest area with high probability of spruce beetle offspring produced annually rather than semiannually (figure 1b, 1c, 1e, 1f). By the end of the century, the change in temperatures across the boreal forests of central Canada may cause markedly higher probability of spruce beetle outbreak potential, based on developmental timing alone. A model for predicting the cold tolerance of this insect is not available. In addition to favorable weather, large expanses of mature spruce forest are required for a widespread outbreak. Therefore, although spruce beetle outbreak potential will be enhanced by higher temperatures throughout the century, reductions in the range of Engelmann spruce in the western United States, also as a result of climate change (Rehfeldt et al. 2006), could cause an overall reduction in long-term spruce beetle impacts in that region.
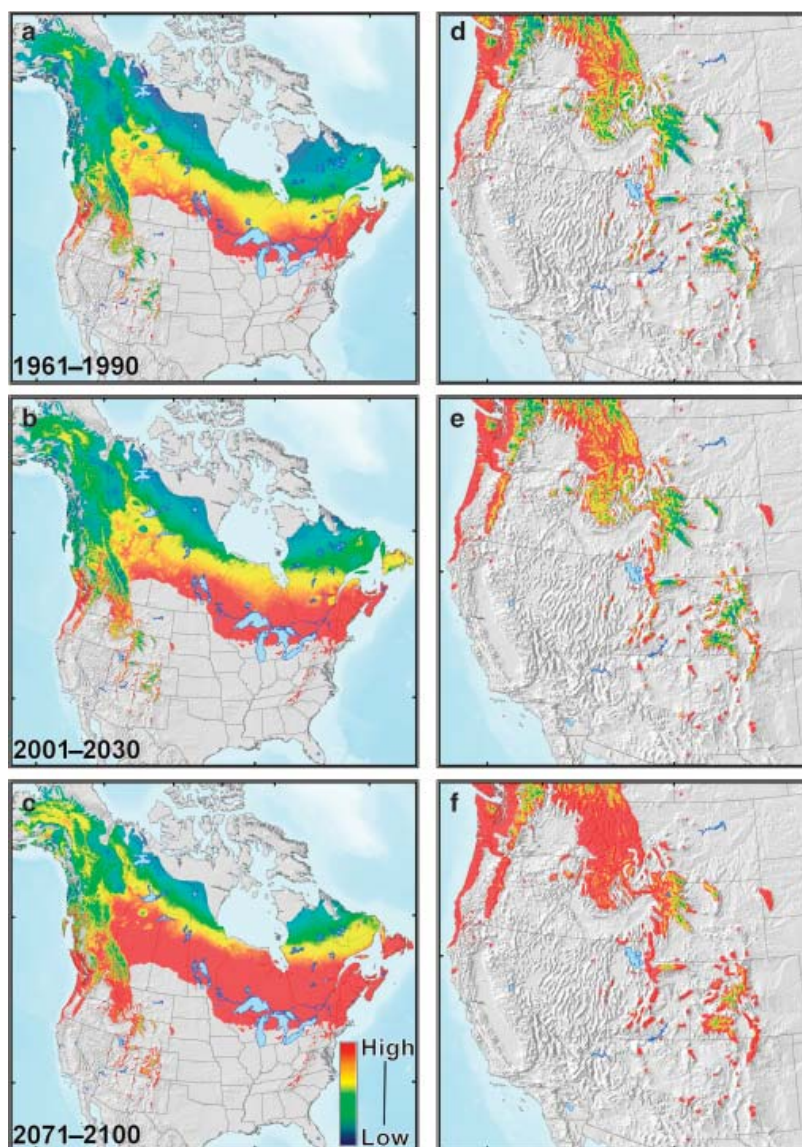

Figure 1. Predicted probability of spruce beetle offspring developing in a single year in spruce forests across the range of this insect in North America during three climate normals periods: (a) 1961–1990, (b) 2001–2030, and (c) 2071–2100, and only in the western United States in (d) 1961–1990, (e) 2001–2030, and (f) 2071–2100. Higher probability of one-year life-cycle duration translates to higher probability of population outbreak and increased levels of spruce-beetle-caused tree mortality. Model results are shown only for areas estimated to be 20th-century spruce habitat (from Little 1971).

Mountain pine beetle. The mountain pine beetle ranges throughout southern British Columbia, portions of eastern Alberta, and most of the western United States. The geographic distribution of the beetle generally reflects the range of its primary hosts (table 1), although the range of lodgepole pine extends further to the north and ponderosa and other pine species further to the south than where mountain pine beetles are currently found. In the past decade, widespread mountain pine beetle outbreaks in British Columbia and

the northern and central US Rocky Mountains have been severe and long lasting, affecting more than 25 million ha (USDA Forest Service, Forest Health Protection, and Natural Resources Canada, Canadian Forest Service). Population outbreaks are also occurring in areas outside the recorded historical range, including lodgepole pine forests in central British Columbia and lodgepole pine and jack pine hybrids, *P. banksiana* Lamb., in western Alberta (Nealis and Peter 2009). Significant tree mortality caused by mountain pine beetles, relative to historical records, has also recently occurred in high-elevation pine forests across the western United States (Gibson et al. 2008). We analyzed the influence of future temperature patterns on mountain pine beetle population success within its current range in the western United States and Canada using models describing the insect's seasonality and tolerance to cold. Because pine hosts extend beyond the current mountain pine beetle range, and because the beetle is a known polyphage, we also provide projections of the potential for expansion into pine forests of northern, central, and eastern Canada and the eastern United States.

The seasonality model used here was described by Logan and Bentz (1999), analyzed by Powell and Logan (2005), and used by Hicke and colleagues (2006). In addition to predicting the probability of beetles developing in a single year, as described above for the spruce beetle, a constraint on the timing of adult emergence is included in the model to further describe the adaptive nature of a particular temperature regime to the mass attack process and subsequent population survival. In the model, if annual adult emergence occurs before 1 June or after 30 September for three or more consecutive years, that temperature time series is considered maladaptive. A higher number of years (out of the 30-model-run replicates for each stochastically different one-year temperature time series) that were not part of a maladaptive series translates to a higher probability of mountain pine beetle success, and hence a higher risk of associated tree mortality. We also used the cold tolerance model developed by Régnière and Bentz (2007) to predict the probability of annual survival given a one-year temperature regime. This model describes the dynamic temperature-dependent process of polyhydric alcohol

accumulation and loss influencing mountain pine beetle supercooling capacity. We ran the model on the same series of 30-year weather data for each simulation point and set of climatic normals, and we calculated the location average probability of survival. A higher probability of low-temperature survival translates to a higher probability of mountain pine beetle population success.
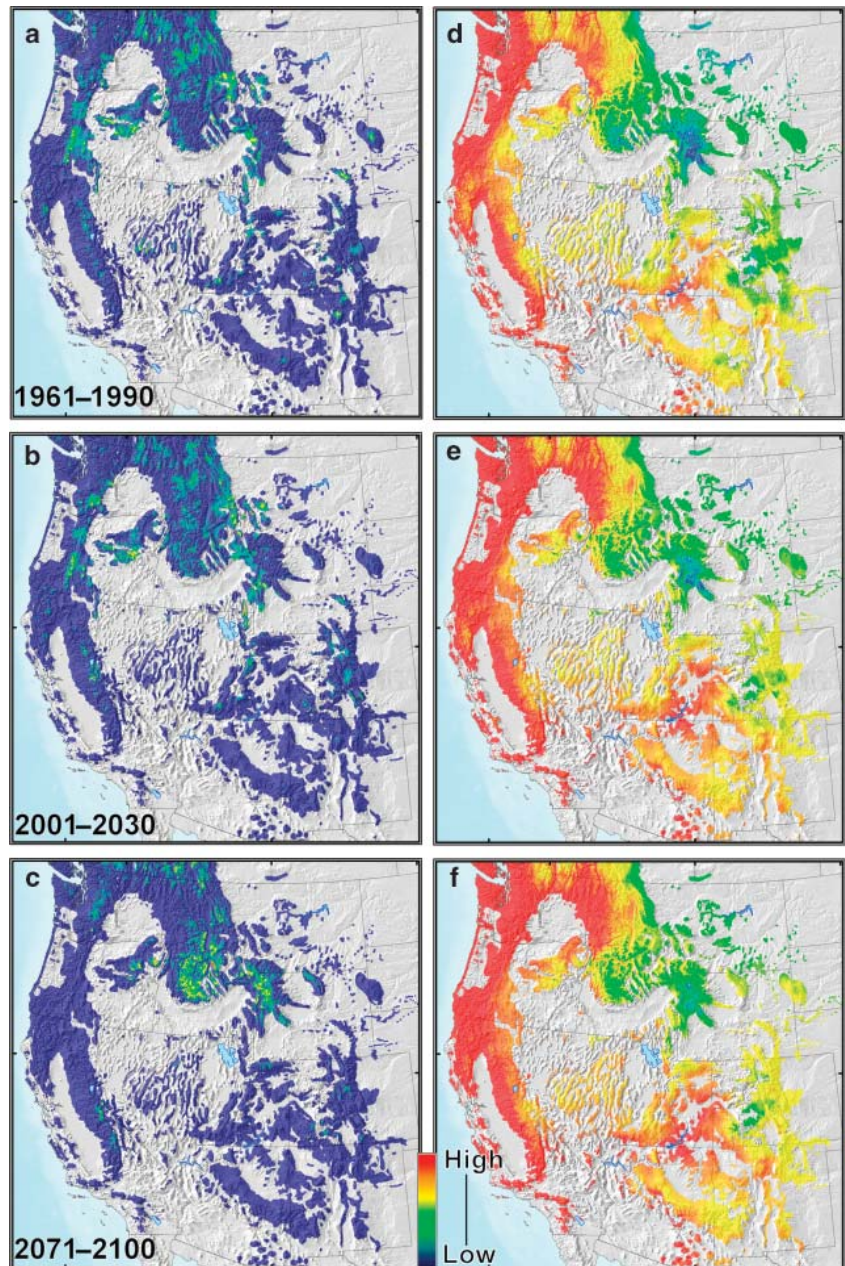

Figure 2. Predicted probability of mountain pine beetle adaptive seasonality (a–c) and cold survival (d–f) in pine forests of the western United States during three climate normals periods: (a) and (d) 1961–1990; (b) and (e) 2001–2030; and (c) and (f) 2071–2100. High probability of adaptive seasonality and cold survival suggests increased population success and increased levels of mountain pine beetle-caused tree mortality. Model results are only shown for areas estimated to be 20th-century pine habitat (from Little 1971).

Mountain pine beetle model results. Temperature data from the historical period 1961–1990 show that the majority of the area within the current range of the mountain pine beetle had low predicted probability of adaptive seasonality, although scattered areas throughout the area had moderately high probability (figures 2a, 3a). During this same period, low temperature survival would have been high in coastal regions and other low-elevation forests across the current range, although quite low in high-elevation areas of the United States and Canadian Rocky Mountains (figures 2d, 3d). As temperatures rise throughout this century, the area suitable for both adaptive seasonality and low-temperature survival is predicted to grow, although results are highly spatially variable (figures 2b, 2e, 3b, 3e). Notably, both models predict greater probability of population success in portions of the current range that have experienced significant increases in tree mortality caused by mountain pine beetles during the past decade, including high-elevation forests of the western United States and Canadian Rocky Mountains, and lodgepole pine forests in central British Columbia, Colorado, and central Idaho. We note that this insect's flexibility in life-history strategies appears greater than previously anticipated (Bentz and Schen-Langenheim 2007), and our working definition of adaptive seasonality and associated rules that drive the seasonality model may be too restrictive. Moreover, observed genetic variability in response to temperature (Bentz et al. 2001) is not currently incorporated, and the development model used for this analysis was derived using data from populations in northern Utah and central Idaho. Predictions for mountain pine beetle in the southwestern United States, in particular, may differ as new developmental parameters are incorporated. An updated modeling framework that addresses these concerns is being developed.

Our modeling results provide some insight into concerns expressed about the potential for mountain pine beetle range expansion across the boreal pine forests of central Canada and into pine forests of central and eastern United States. The potential for adaptive seasonality in central Canada decreases dramatically from the historical period to the end of this century, with high probability of population success restricted to northern provinces (figure 3a, 3b, 3c). Given assumptions of

the seasonality model, these results suggest that substantial warming would disrupt the emergence timing and generation duration required for population success. Across pine habitats in the central and eastern United States, adaptive seasonality remains low throughout the century. An increase in low-temperature survival is predicted for spatially isolated areas in Canada, including west-central Alberta, where mountain pine beetle has recently been found attacking lodgepole/jack pine hybrids (Nealis and Peter 2009). By the end of
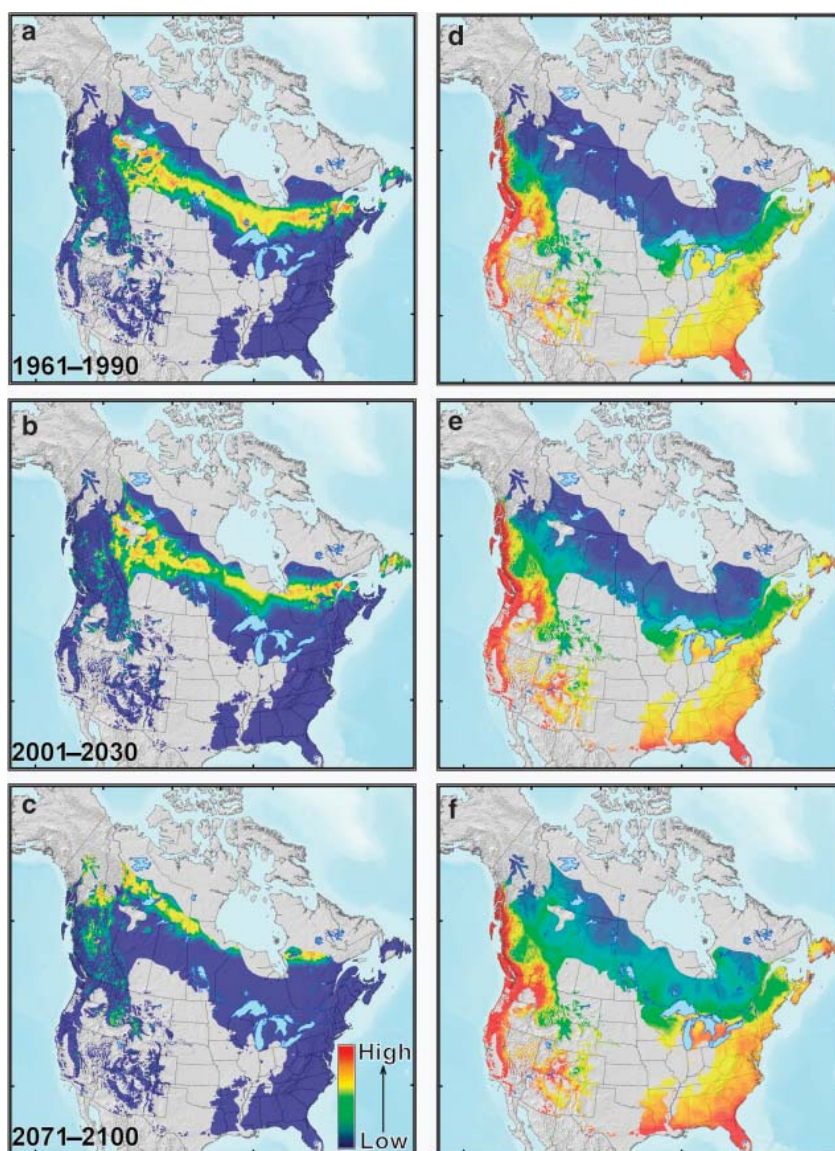

Figure 3. Predicted probability of mountain pine beetle adaptive seasonality (a–c) and cold survival (d–f) across the range of pine species in the United States and Canada during three climate normals periods: (a) and (d) 1961–1990; (b) and (e) 2001–2030; and (c) and (f) 2071–2100. Mountain pine beetle outbreak populations are currently restricted to pine forests in the western United States, central British Columbia and west-central Alberta. Based solely on the modeled response of mountain pine beetle to temperature, results suggest that by the end of this century probability of range expansion across Canada and into central and eastern US forests will be low to moderate.

Figure 4. Mountain pine beetle–killed whitebark pine on the Bridger Teton National Forest, Wyoming. The photograph was taken on 13 July 2009 and shows trees attacked and killed over several years. Following mountain pine beetle attack, tree foliage turns yellow, orange, then red over a one- to two-year period. Eventually the needles drop to the forest floor, leaving a grey canopy. Photograph: Courtesy of Wally Macfarlane.

the century, cold-survival probability substantially increases across Canada, although in areas key to mountain pine beetle migration in central Canada, the probability for low-temperature survival remains low. Our model results suggest that without adaptation to increasing temperature, the probability of mountain pine beetle range expansion across jack pine forests and into eastern US pine forests will remain low to moderate throughout this century (figure 3c, 3f).

Conclusions

Bark beetle response to climate change can be characterized by a high degree of complexity and uncertainty, as populations are influenced directly by shifts in temperature and indirectly through climatic effects on community associates and host trees. Because changes in climate will not be uniformly distributed across years, and not all temperature-dependent processes will be equally affected, a mechanistic understanding is imperative for making predictions of direct effects of climate change on future population trends. On the basis of temperature projections from the CRCM and mechanistic models developed for spruce beetle and mountain pine beetle, we expect positive changes in thermal regimes conducive to population success of both species throughout this century. Significant temporal and spatial variability in thermal suitability is predicted, however, emphasizing the complexity in both the thermal habitat and temperature-based physiological processes of these insects. Temperature profiles that promote cold-temperature survival may not also result in appropriate

developmental timing, and vice versa. Although detailed information on temperature-dependent physiological processes is not available for the majority of bark beetle species in the southwestern United States and Mexico, many of these species are currently limited by climate rather than host availability, suggesting a high potential for range expansion northward. Developmental life-history strategies have evolved to maintain appropriate seasonality, and higher temperatures may not always translate into population growth or range expansion without adaptation to rapidly changing environmental conditions, a phenomenon documented in several insect species (Bradshaw and Holzapfel 2006). Because the extreme difference in generation times between bark beetles and their coniferous hosts dictates a faster relative rate of adaptation for beetles, this is a critical missing component in our predictions. Models that incorporate genetic variability in bark beetle temperature-dependent parameters are also needed.

Despite uncertainty in forecasts of future climate parameters that have been downscaled to a forest landscape, predictions of trends in bark beetle population success as a function of the direct effects of temperature will be instrumental in development and application of strategies for management of future forests. There is clearly a need, however, for a better understanding and more refined models that integrate indirect effects of climate change on host trees with bark beetle population success, as well as interactions among bark beetle outbreaks and other forest disturbances. For example, drought and other

processes can homogenize host-tree species age, structure, and vigor, thereby indirectly contributing to landscape-wide, bark-beetle-caused tree mortality (McDowell et al. 2008). More frequent extreme weather events will also likely provide abundant resources for some bark beetle species creating the potential to trigger localized outbreaks (Gandhi et al. 2007). Fire, an important forest disturbance that is directly influenced by climate change (Wester-ling et al. 2006), can reduce the resistance of surviving trees to bark beetle attack. Furthermore, climate-change-induced shifts in bark beetle outbreak frequency and intensity may indirectly affect patterns and severity of wildfire, although the relationships are poorly understood, highly complex, and temporally and spatially dynamic (Jenkins et al. 2008).

Bark beetles are inextricably linked to their host trees, and will undoubtedly influence the formation of new western North American coniferous forests as predicted broad-scale tree migrations occur this century. At the retreating and expanding margins of tree distributions, bark beetles may play a significant role in colonizing and killing stressed individuals as trees and their progeny strive to adapt to a changing environment. Current tree distributions may have been significantly influenced by bark beetles preferentially colonizing trees in environmentally compromised positions at the range margins, and future tree distributions will most likely be affected similarly by these agents of mortality.

Rapid and broad-scale tree mortality events, such as those that have recently occurred across western North America, can have long-term impacts on ecosystem structure and community dynamics, with feedbacks that further influence climate and land use (Kurz et al. 2008, McDowell et al. 2008). Bark beetle outbreaks driven by climate change may also result in trajectories beyond the historical resilience boundaries of some forest ecosystems, causing irreversible ecosystem regime shifts. The recent loss of entire stands of long-lived, high-elevation whitebark pine, *Pinus albicaulis* Engelm., as a result of the mountain pine beetle (figure 4) underscores the need for greater understanding of climate change effects on complex interactions important to ecosystem resiliency and stability. Characterizing thresholds for systems beyond which changes are irreversible will be an important component of forest management in a changing climate.

Acknowledgments

References cited

Aitken SN, Yeaman S, Holliday JA, Wang T, Curtis-McLane S. 2008. Adaptation, migration or extirpation: Climate change outcomes for tree populations. Evolutionary Applications 1: 95–111.

Aukema BH, Carroll AL, Zheng Y, Zhu J, Raffa KF, Moore RD, Stahl K, Taylor SW. 2008. Movement of outbreak populations of mountain pine beetle: Influences of spatiotemporal patterns and climate. Ecography 31: 348–358.

Balanyá J, Oller JM, Huey RB, Gilchrist GW, Serra L. 2006. Global genetic change tracks global climate warming in *Drosophila subobscura*. Science 313: 1773–1775.

Bale JS, et al. 2002. Herbivory in global climate change research: Direct effects of rising temperature on insect herbivores. Global Change Biology 8: 1–16.

Battistia A, Stastny M, Buffo E, Larsson S. 2006. A rapid altitudinal range expansion in the pine processionary moth produced by the 2003 climatic anomaly. Global Change Biology 12: 662–671.

Bentz BJ, Mullins DE. 1999. Ecology of mountain pine beetle cold hardening in the Intermountain West. Environmental Entomology 28: 577–587.

Bentz BJ, Schen-Langenheim G. 2007. The mountain pine beetle and whitebark pine waltz: Has the music changed? Proceedings of the Conference Whitebark Pine: A Pacific Coast Perspective. (17 June 2010; *www.fs.fed.us/r6/nr/fid/wbpine/papers/2007-wbp-impacts-bentz.pdf*)

Bentz BJ, Logan JA, Vandygriff JC. 2001. Latitudinal variation in *Dendroctonus ponderosae* (Coleoptera: Scolytidae) development time and adult size. Canadian Entomologist 133: 375–387.

Bentz BJ, et al. 2009. Bark Beetle Outbreaks in Western North America: Causes and Consequences. University of Utah Press.

Berg EE, Henry JD, Fastie CL, De Volder AD, Matsuoka SM. 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.

Birch MC. 1974. Seasonal variation in pheromone-associated behavior and physiology of *Ips pini*. Annals of the Entomological Society of America 67: 58–60.

Bleiker KP, Six DL. 2007. Dietary benefits of fungal associates to an eruptive herbivore: Potential implications of multiple associates on host population dynamics. Environmental Entomology 36: 1384–1396.

Boone CK, Six DL, Zheng Y, Raffa KF. 2008. Parasitoids and dipteran predators exploit volatiles from microbial symbionts to locate bark beetles. Environmental Entomology 37: 150–161.

Bradshaw WE, Holzapfel CM. 2006. Evolutionary response to rapid climate change. Science 312: 1477–1478.

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

Brunsfeld SJ, Sullivan J, Soltis DE, Soltis PS. 2001. Comparative phylogeography of northwestern North America: A synthesis. Pages 319–339 in Silvertown J, Antonovics J, eds. Integrating Ecology and Evolution in a Spatial Context. Blackwell.

Cardoza YJ, Moser JC, Klepzig KD, Raffa KF. 2008. Multipartite symbioses among fungi, mites, nematodes, and the spruce beetle, *Dendroctonus rufipennis*. Environmental Entomology 37: 956–963.

Chansler JF. 1967. Biology and life history of *Dendroctonus adjunctus* (Coleoptera: Scolytidae). Annals of the Entomological Society America 60: 760–767.

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

Danks HV. 1987. Insect dormancy: An ecological perspective. Monograph Series no. 1. Biological Survey of Canada (Terrestrial Arthropods).

Easterling DR, Meehl GA, Parmesan C, Changnon SA, Karl TR, Mearns LO. 2000. Climate extremes: Observations, modeling, and impacts. Science 289: 2068–2074.

Fettig CJ, Klepzig KD, Billings RF, Munson AS, Nebeker TE, Negrón JF, Nowak JT. 2007. The effectiveness of vegetation management practices

for prevention and control of bark beetle infestations in coniferous forests of the western and southern United States. Forest Ecology and Management 238: 24–53.

Franceschi VR, Krokene P, Christiansen E, Krekling T. 2005. Anatomical and chemical defenses of conifer bark against bark beetles and other pests. New Phytologist 167: 353–376.

Gandhi KJK, Gilmore DW, Katovich SA, Mattson WJ, Spence JR, Seybold SJ. 2007. Physical effects of weather events on the abundance and diversity of insects in North American forests. Environmental Reviews 15: 113–152.

Gibson K, Skov K, Kegley S, Jorgensen C, Smith S, Witcosky J. 2008. Mountain Pine Beetle Impacts in High-Elevation Five-Needle Pines: Current Trends and Challenges. US Department of Agriculture Forest Service, Northern Region, Missoula, Montana. R1-08-020.

Godbout J, Fazekas A, Newton CH, Yeh FC. 2008. Glacial vicariance in the Pacific Northwest: Evidence from a lodgepole pine mitochondrial DNA minisatellite for multiple genetically distinct and widely separated refugia. Molecular Ecology 17: 2463–2475.

Graves AD, Holsten EH, Ascerno ME, Zogas K, Hard JS, Huber DPW, Blanchette R, Seybold SJ. 2008. Protection of spruce from colonization by the bark beetle, *Ips perturbatus*, in Alaska. Forest Ecology and Management 256: 1825–1839.

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

Hansen EM, Bentz BJ, Turner DL. 2001. Temperature-based model for predicting univoltine brood proportions in spruce beetle (Coleoptera: Scolytidae). Canadian Entomologist 133: 827–841.

Herms DA, Mattson WJ. 1992. The dilemma of plants: To grow or defend. Quarterly Review of Biology 67: 283–335.

Hicke JA, Logan JA, Powell J, Ojima DS. 2006. Changing temperatures influence suitability for modeled mountain pine beetle outbreaks in the western United States. Journal of Geophysical Research 11: GO2019. doi:10.1029/2005JG000101

Hofstetter RW, Cronin JT, Klepzig KD, Moser JC, Ayres MP. 2006. Antagonisms, mutualisms and commensalisms affect outbreak dynamics of the southern pine beetle. Oecologia 147: 679–691.

Hudson G, Wackernagel H. 1994. Mapping temperature using kriging with external drift: Theory and an example from Scotland. International Journal of Climatology 14: 77–91.

[IPCC] Intergovernmental Panel on Climate Change. 2007. Climate Change 2007: The Scientific Basis. Cambridge University Press.

Jenkins MJ, Hebertson EG, Page W, Jorgersen CA. 2008. Bark beetles, fuels, fire and implications for forest management in the Intermountain West. Forest Ecology and Management 254: 16–34.

Klepzig KD, Six DL. 2004. Bark beetle fungal symbiosis: Context dependency in complex interactions. Symbiosis 37: 189–206.

Kurz WA, Dymond CC, Stinson G, Rampley GJ, Neilson ET, Carroll AL, Ebata T, Safranyik L. 2008. Mountain pine beetle and forest carbon feedback to climate change. Nature 452: 987–990.

Langor DW, Raske AG. 1987. Reproduction and development of the eastern larch beetle, *Dendroctonus simplex*, in Newfoundland. Canadian Entomologist 119: 985–992.

Lee RE. 1989. Insect cold-hardiness: To freeze or not to freeze. BioScience 39: 308–313.

Little EL Jr. 1971. Atlas of United States Trees, vol. 1: Conifers and Important Hardwoods. US Department of Agriculture Miscellaneous Publication 1146.

Logan JA, Bentz BJ. 1999. Model analysis of mountain pine beetle (Coleoptera: Scolytidae) seasonality. Environmental Entomology 28: 924–934.

Mattson WJ Jr. 1980. Herbivory in relation to plant nitrogen content. Annual Review of Ecology and Systematics 11: 119–161.

McCambridge WF, Knight FB. 1972. Factors affecting spruce beetles during a small outbreak. Ecology 53: 830–839.

McDowell N, et al. 2008. Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? New Phytologist 178: 719–739.

McKenney DW, Pedlar JH, Lawrence K, Campbell K, Hutchinson MF. 2007. Potential impacts of climate change on the distribution of North American trees. BioScience 57: 939–948.

McNulty SG, Aber JD. 2001. US national climate change assessment on forest ecosystems: An introduction. BioScience 51: 720–722.

Millar CI, Stephenson NL, Stephens SL. 2007. Climate change and forests of the future: Managing in the face of uncertainty. Ecological Applications 17: 2145–2151.

Millard P, Sommerkorn M, Grelet GA. 2007. Environmental change and carbon limitation in trees: A biochemical, ecophysiological and ecosystem appraisal. New Phytologist 175: 11–28.

Miller LK, Werner RA. 1987. Cold-hardiness of adult and larval spruce beetles *Dendroctonus rufipennis* (Kirby) in interior Alaska. Canadian Journal of Zoology 65: 2927–2930.

Music B, Caya D. 2007. Evaluation of the hydrological cycle over the Mississippi River basin as simulated by the Canadian Regional Climate Model (CRCM). Journal of Hydrometeorology 8: 969–988.

Nealis V, Peter B. 2009. Risk Assessment of the Threat of Mountain Pine Beetle to Canada's Boreal and Eastern Pine Forests. Natural Resources Canada, Canadian Forest Service. Information Report BC-X-417.

Pörtner HO, Farrell AP. 2008. Physiology and climate change. Science 322: 690–692.

Powell JA, Logan JA. 2005. Insect seasonality: Circle map analysis of temperature-driven life cycles. Theoretical Population Biology 67: 161–179.

Raffa KF. 2001. Mixed messages across multiple trophic levels: The ecology of bark beetle chemical communication systems. Chemoecology 11: 49–65.

Raffa KF, Aukema BH, Bentz BJ, Carroll AL, Hicke JA, Turner MG, Romme WH. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: Dynamics of biome-wide bark beetle eruptions. BioScience 58: 501–517.

Raupach MR, Marland G, Ciais P, Le Quéré C, Canadell JG, Klepper G, Field CB. 2007. Global and regional drivers of accelerating CO_2 emissions. Proceedings of the National Academy of Sciences 104: 10288–10293.

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

Régnière J, St-Amant R. 2007. Stochastic simulation of daily air temperature and precipitation from monthly normals in North America north of Mexico. International Journal of Biometeorology 51: 415–430.

Rehfeldt GE, Crookston NL, Warwell MV, Evans JS. 2006. Empirical analyses of plant-climate relationships for the western United States. International Journal of Plant Science 167: 1123–1150.

Rice AV, Thormann MN, Langor DW. 2008. Mountain pine beetle-associated blue-stain fungi are differentially adapted to boreal temperatures. Forest Pathology 38: 113–123.

Ryan RB. 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.

Salinas-Moreno Y, Mendoza MG, Barrios MA, Cisneros R, Macías-Sámano J, Zúñiga G. 2004. Areography of the genus *Dendroctonus* (Coleoptera: Curculionidae: Scolytinae) in Mexico. Journal of Biogeography 31: 1163–1177.

Scott BA, Berryman AA. 1972. Larval diapause in *Scolytus ventralis*. Journal of the Entomological Society of British Columbia 69: 50–53.

Seager R, et al. 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. Science 316: 1181–1184.

Seybold SJ, Ohtsuka T, Wood DL, Kubo I. 1995. The enantiomeric composition of ipsdienol: A chemotaxonomic character for North American populations of *Ips* spp. in the *pini* subgeneric group (Coleoptera: Scolytidae). Journal of Chemical Ecology 21: 995–1016.

Shugart HH. 2003. A Theory of Forest Dynamics: The Ecological Implications of Forest Succession Models. Springer.

Six DL, Bentz BJ. 2007. Temperature determines symbiont abundance in a multipartite bark beetle-fungus ectosymbiosis. Microbial Ecology 54: 112–118.
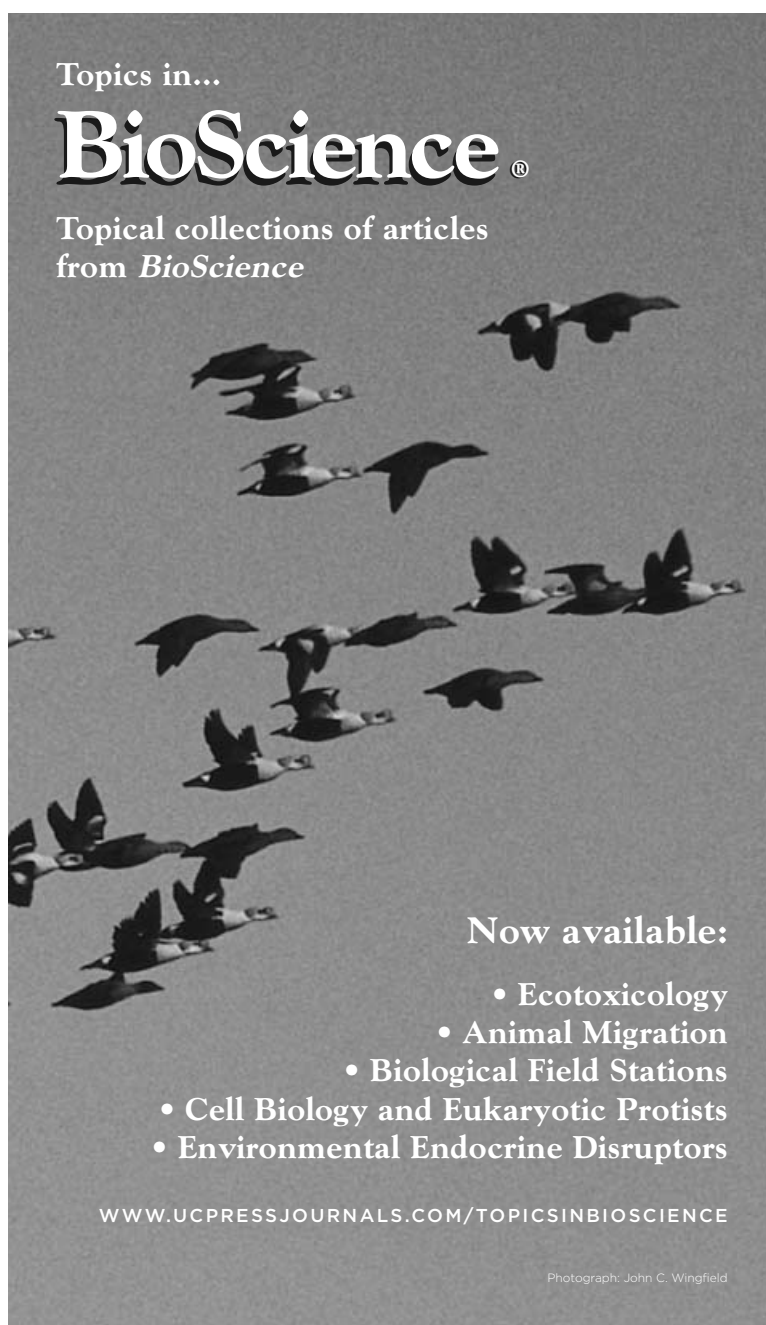
Tauber MJ, Tauber CA, Masaki S. 1986. Seasonal Adaptations of Insects. Oxford University Press.

Veblen TT, Hadley KS, Reid MS, Rebertus AJ. 1991. The response of subalpine forests to spruce beetle outbreak in Colorado. Ecology 72: 213–231.

Waring KM, Reboletti DM, Mork LA, Huang C, Hofstetter RW, Garcia AM, Fulé PZ, Davis TS. 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.

Werner RA, Holsten EH, Matsuoka SM, Burnside RE. 2006. Spruce beetles and forest ecosystems in south-central Alaska: A review of 30 years of research. Forest Ecology and Management 227: 195–206.

Westerling AL, Hidalgo HG, Cayan DR, Swetnam TW. 2006. Warming and earlier spring increase western US forest wildfire activity. Science 313: 940–943.

Zvereva EL, Kozlov MV. 2006. Consequences of simultaneous elevation of carbon dioxide and temperature for plant-herbivore interactions: A metaanalysis. Global Change Biology 12: 27–41.

Barbara J. Bentz (bbentz@fs.fed.us) and E. Matthew Hansen are with the US Department of Agriculture (USDA) Forest Service, Rocky Mountain Research Station, in Logan, Utah. Jacques Régnière is with the Canadian Forest Service in Quebec, Canada. Christopher J. Fettig and Steven J. Seybold are with the USDA Forest Service, Pacific Southwest Research Station, in Davis, California. Jane L. Hayes is with the USDA Forest Service, Pacific Northwest Research Station, in La Grande, Oregon. Jeffrey A. Hicke is with the Department of Geography at the University of Idaho, Moscow. Rick G. Kelsey is with the USDA Forest Service, Pacific Northwest Research Station, in Corvallis, Oregon. Jose F. Negrón is with the USDA Forest Service, Rocky Mountain Research Station, in Fort Collins, Colorado.