



10

Responses of Tree-killing Bark Beetles to a Changing Climate

Kenneth F. Raffa,^{1*} Brian H. Aukema,² Barbara J. Bentz,³ Allan L. Carroll,⁴ Jeffrey A. Hicke⁵ and Thomas E. Kolb⁶

¹*Department of Entomology, University of Wisconsin, Madison, Wisconsin, USA;* ²*Department of Entomology, University of Minnesota, St Paul, Minnesota, USA;* ³*USDA Forest Service, Rocky Mountain Research Station, Logan, Utah, USA;*

⁴*Department of Forest and Conservation Sciences, University of British Columbia, Vancouver, British Columbia, Canada;*

⁵*Department of Geography, University of Idaho, Moscow, Idaho, USA;* ⁶*School of Forestry, Northern Arizona University, Flagstaff, Arizona, USA*

Abstract

Bark beetles cause widespread tree mortality, so understanding how climate change will influence the distribution and magnitude of outbreaks by this group of herbivores is important. We first develop a framework of outbreak dynamics that emphasizes transitions from states dominated by negative feedback to those dominated by positive, density-dependent feedback. We then consider mechanisms by which temperature and precipitation changes can allow populations to breach critical thresholds, and the empirical data relating outbreaks to weather. Finally, we consider how anticipated climatic change, and relationships with new hosts and natural enemy guilds, may influence dynamics in new habitats. There is strong evidence that elevated temperature can increase overwintering survival and decrease generation times of bark beetles, although evolved traits can also constrain response to warming in some habitats. Moreover,

combinations of phenotypic plasticity, genotypic variation and physiological thresholds yield a broad range of conditions under which adults emerge synchronously, and thus can mass attack trees. There is likewise strong evidence that severe drought reduces tree defences against attack. Drought stress can occur through lower precipitation and/or higher temperatures that reduce soil moisture and/or raise vapour pressure deficit. We also delineate three categories of range modifications: increased and more persistent establishment in areas where trees experienced only intermittent exposure historically; establishment in areas dominated by host species but where local populations experienced little or no pressure historically; and movement into new areas containing susceptible species that have not been exposed previously. Each of these has been documented for bark beetles. Trees in areas that experienced minor or no exposure generally had lower defences than their more historically exposed counterparts. However, there can be lags in beetle

* Corresponding author; e-mail: raffa@entomology.wisc.edu

behavioural responses. In some cases, more heterogeneous forest structure, more abundant local predators and competitors and low host nutritional quality could potentially lessen risk in new habitats. Direct comparative studies are needed to evaluate outbreak potentials following range expansions driven by climate warming.

10.1 Introduction

Understanding how bark beetles respond to changing temperature and precipitation regimes can be particularly useful for several reasons. First, these insects inhabit both natural and managed ecosystems and exert both environmental costs and benefits. Second, bark beetles include several historically eruptive species that undergo natural outbreaks, thereby providing opportunities to evaluate both potential changes in historical outbreak dynamics and novel dynamics in new habitats. Third, their behaviours can exert positive feedbacks on population dynamics at organismal and stand levels that translate into non-linear dynamics at higher levels. This is particularly relevant to our understanding and projections of climate-driven tipping points. Fourth, these insects affect fundamental ecological processes and exert major influences on the landscapes in which they reside. Fifth, bark beetles have close symbiotic associations with fungi and bacteria, as well as strong antagonistic interactions with some microbes. Each of these microorganisms undergoes its own responses to temperature and moisture conditions, so understanding these systems can improve our ability to project how species complexes and communities will react to climate change. Sixth, several bark beetle species are already showing both altered outbreak dynamics within their historical ranges and expanded geographic and host ranges, in response to changing climate. This allows us to incorporate both mechanistic and empirical modelling approaches into future projections. Here, we integrate existing knowledge on bark beetles in North American conifer

forests with projected temperature and precipitation regimes, to assess how these systems may respond to climate change.

10.2 Ecology and Population Dynamics of Bark Beetles: The Template on which Responses to Anthropogenic Change Occur

10.2.1 Ecological roles and generalized life history of bark beetles

Bark beetles (Curculionidae: Scolytinae) contain a high diversity of life histories, host-plant associations, geographic ranges, ecological roles and symbiotic relationships. Most species cause little to no negative economic impacts, and provide environmental benefits such as nutrient cycling, gap formation and nutrition for wildlife. The overwhelming majority of species in native systems are associated with dead or dying trees, or dead tissues of live trees (Lindgren and Raffa, 2013). A much smaller proportion can sometimes kill trees. Populations of a small subset of tree-killing species intermittently rise to sufficiently high levels to both cause socio-economic losses and function as landscape-scale disturbance agents. The tree-killing and outbreaking species are almost entirely colonizers of the main stems of conifers, primarily in the genera *Dendroctonus*, *Ips* and *Scolytus*. We focus primarily on these groups in North American conifers.

Bark beetles spend most of their lives in host plants. Adults emerge from the trees in which they developed, fly, land in response to visual and olfactory stimuli, and use host chemical and tactile cues to determine whether to enter a tree or resume flight. They tunnel through the bark into the phloem and produce aggregation pheromones that attract both mates and additional members of the same sex. These pheromones are complex mixtures and are closely linked to tree physiology. Many species exploit host monoterpenes as precursors and/or synergists of their pheromones (Wood, 1982). Females construct galleries

along which they oviposit, and the larvae feed on phloem and fungi. The brood pupate, undergo a brief teneral adult stage and emerge as adults. Because bark beetles and their microbial associates develop in tissues critical to plant nutrient and water transport, successful development typically results in tree death. This has two important ramifications to their population dynamics. First, the mortality they cause has placed strong selective pressures on trees to evolve complex, multi-component defence systems. Second, the tree is usually an available resource for only one beetle generation, so each cohort must locate and colonize new trees. Generation times vary with species, latitude and weather, ranging from multiple generations per year in *Dendroctonus frontalis* Zimmermann to one generation every several years in *Dendroctonus ponderosae* Hopkins at its range limits. Within a given locale, and across latitudes, a single species can exhibit plasticity in temperature-dependent voltinism (Hansen *et al.*, 2001; Bentz *et al.*, 2011).

Bark beetles are closely associated with a broad range of microorganisms. Typically, one or two ophiostomatoid fungi are associated with each beetle species. Their roles vary among systems. Some fungi benefit larval nutrition (Bleiker and Six, 2007), others are antagonistic and some have context-dependent relationships (Klepzig *et al.*, 2009). Some fungi appear capable of killing trees or degrading host toxins (Lee *et al.*, 2006; Diguistini *et al.*, 2011; Hammerbacher *et al.*, 2013), but the extent to which they do so is under debate (Lieutier *et al.*, 2009; Six and Wingfield, 2011). The composition of fungal associates can vary with temperature (Six, 2003; Addison *et al.*, 2013), beetle population phase (Aukema *et al.*, 2005) and other factors. Bacteria (Brand *et al.*, 1975; Scott *et al.*, 2008; Morales-Jimenez *et al.*, 2012; Boone *et al.*, 2013) and yeasts (Davis and Hofstetter, 2011) may likewise contribute to nutritional exploitation of the substrate, reduction of chemical defences, protection from antagonists and possibly pheromone synthesis. Bacteria vary among bark beetle species, hosts and populations (Adams *et al.*, 2010, 2013a).

10.2.2 Population dynamics

Populations of tree-killing bark beetles undergo dramatic fluctuations. Within a given region, abundances remain low and relatively stable for lengthy periods, varying with minor changes in resource availability, weather and predisposing biotic agents. During these periods, beetles are limited to highly stressed trees, which pose relatively little resistance but are ephemeral in space and time, often provide relatively low nutritional value and are available to many competing species (Safarynik and Carroll, 2006). Under certain conditions, however, populations rise suddenly, spread over large areas and kill enormous numbers of previously healthy trees.

In systems with such bimodal behaviour, understanding how populations can transform from a state dominated by negative feedback to one of net positive feedback can suggest how changing climate may alter dynamics. Four major components are important for bark beetles (Fig. 10.1) (Raffa *et al.*, 2008). First, a stand must have the appropriate host species and age structure. Most tree-killing bark beetles are confined to one or sometimes two tree genera. Beetles are further limited to mature trees that are large enough to support broods within their phloem. Stands that have low species and age diversity, are dense and are old are more likely to experience outbreaks (Safarynik and Carroll, 2006).

Second, conifers are equipped with multi-component integrated defences that can resist attack by beetle-microbial complexes, but these are highly sensitive to environmental stress. Conifer defences include physical features such as bark toughness and resin flow (Raffa and Berryman, 1983; Kane and Kolb, 2010), histological defences such as autonecrosis and traumatic duct formation (Franceschi *et al.*, 2005; Schmidt *et al.*, 2011), and chemical defences such as monoterpenes, diterpene acids, phenylpropanoids and phenolics (Klepzig *et al.*, 1996; Kelsey *et al.*, 2001; Faccoli and Schlyter, 2007; Manning and Reid, 2013). These modalities are highly integrated. For example, resin acts as both a physical barrier and a matrix of

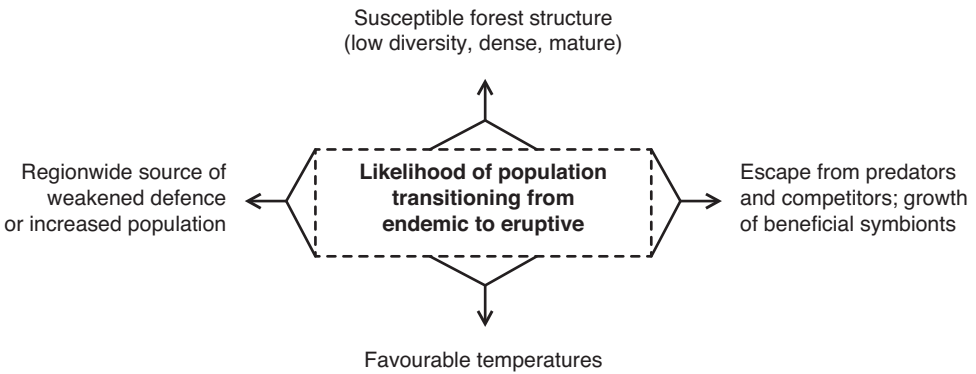


Fig. 10.1. Conceptual diagram of non-mutually exclusive climatic, landscape and trophic factors that increase individually or jointly the likelihood of bark beetle outbreak. Conditions are typically inadequate for beetles to overcome constraints on population growth, and only a narrow set of conditions allows populations to pass through an 'eruptive window'. Beyond this threshold, beetles generate substantial positive feedback, and lower-scale constraints commonly exert less effect. Each of the factors shown can reduce the corresponding constraint, increasing that portion of the portal. The relative importance of each factor in transitioning from endemic to eruptive dynamics varies among systems.

toxins, structures such as resin ducts and glands provide conduits for delivering allelochemicals, and autonecrosis confronts beetles with physical suberization, localized toxin accumulation and nutrient starvation. Both physical and chemical defences can be constitutive or induced (Franceschi *et al.*, 2005). Induced resinosis can inhibit attraction to pheromones produced by entering beetles (Erbilgin *et al.*, 2006). Induced chemical responses include increasing concentrations from tolerable to toxic levels, changing relative abundances, often with disproportionately high biosynthesis of the more toxic compounds, and producing new compounds not detectable in constitutive tissue (Huber *et al.*, 2004; Raffa *et al.*, 2005; Keeling and Bohlmann, 2006). A wide variety of biotic and abiotic stresses have been shown to reduce tree defences and increase the incidence of attack (Lombardero *et al.*, 2000b; Boone *et al.*, 2011; Hart *et al.*, 2014).

Third, temperature both imposes severe limitations on beetles' geographic ranges and is an important driver of their abundance (Trân *et al.*, 2007; Powell and Bentz, 2009). Temperature influences voltinism, within-generation synchrony and seasonality, and ultimately survival. Interactions between temperature and developmental

parameters can be particularly critical in some tree-killing bark beetles because synchronous emergence can foster their ability to overcome tree defences jointly (Bentz *et al.*, 1991).

Fourth, predators and competitors play important roles. Predators, such as woodpeckers, beetles and flies can exert high mortality (Schroeder and Weslien, 1994; Turchin *et al.*, 1999). Several parasitic insects attack bark beetles, but they typically cause less mortality than to other herbivore guilds, due to protection by bark. Competitors often exert high costs on beetle reproduction (Reeve *et al.*, 1998). The predominant competitors are other bark beetles and wood borers, often those that specialize on dead or highly stressed trees. Competition can arise from moderately aggressive species exploiting a common stressed-tree resource, or from a diverse guild of saprophages exploiting trees killed by primary bark beetles. Alongside these trophic interactions, particular assemblages of symbionts can strongly influence beetle reproduction (Bleiker and Six, 2007; Hofstetter *et al.*, 2007).

Several features of the conditions required for transition from endemic to eruptive dynamics are pertinent to climate

change. First, the drivers and constraints (Fig. 10.1) interact. For example, warming temperature can benefit beetles directly, but also influences the composition of symbionts (Addison *et al.*, 2013) and stresses trees through lower soil moisture and higher vapour pressure deficit. Likewise, the importance of interspecific competition depends on population phase; specifically, whether beetles are restricted to stressed trees or extend into healthy trees (Powell *et al.*, 2012). Second, these processes operate across scales. For example, the efficacy of individual tree defence is influenced by higher-scale factors such as forest structure, weather and long-distance dispersal of attacking beetles (Simard *et al.*, 2012). Third, once conditions allow populations to rise past the eruptive threshold, positive feedback can persist even after the eliciting driver has been relaxed. Fourth, single drivers are often insufficient to carry populations past the eruptive threshold, despite their individual importance. For example, when temperatures in coastal Alaska are warm and dry enough for *Dendroctonus rufipennis* to transition from semivoltine to univoltine development, outbreaks become likely (Werner and Holsten, 1985; Berg *et al.*, 2006; Sherriff *et al.*, 2011). Yet outbreaks are rare among the univoltine *D. rufipennis* populations of interior Alaska and the Great Lakes region, probably because of a combination of dry conditions that favour competitors and cold winters in Alaska and forest heterogeneity and natural enemies in the Great Lakes region (Haberkern *et al.*, 2002; Werner *et al.*, 2006).

When anticipating the effects of climate change, it is helpful to recognize there are precedents for other anthropogenic activities raising innocuous bark beetle–microbial complexes to severe pest status. The most dramatic cases arose when beetle–fungal complexes were introduced by humans into areas in which native trees had not co-evolved and host resistance was lacking (Gibbs, 1978; Sun *et al.*, 2013). Other examples include habitat manipulations that yielded more susceptible, homogeneous forest structures (Jactel and Brockerhoff, 2007) and fragmentation that directly benefited

bark beetles or reduced prey tracking by predators (Coulson *et al.*, 1999; Ryall and Fahrig, 2005).

10.3 Effects of Climate Change on the Frequency and Severity of Outbreaks

Attributing unusually large outbreaks to human-caused climate change requires several conditions. First, temperature and precipitation changes need to be related to human activities, which is well established in many analyses (IPCC, 2007; Barnett *et al.*, 2008). Second, the frequency and severity of outbreaks need to be correlated with climatic changes, which has been shown both within historical ranges (Berg *et al.*, 2006; Logan and Powell, 2009; Sherriff *et al.*, 2011; Creeden *et al.*, 2014), and northward and elevational expansions (Carroll *et al.*, 2004; Logan *et al.*, 2010; Sambaraju *et al.*, 2012; Weed *et al.*, 2013) by several species. Third, association of outbreaks with climatic variables is most compelling when it can be linked mechanistically to processes known to affect insect development, behaviour and reproduction. The direct and indirect effects of temperature (Section 10.3.1) and drought (Section 10.3.2) on multiple features of bark beetle performance are quite pronounced, and are becoming increasingly understood.

10.3.1 Effects of temperature on bark beetle synchronicity, seasonality and survival

Temperature is a significant driver of bark beetle life history traits that promote synchrony of vulnerable life stages with appropriate seasons (i.e. seasonality) and tolerance of adverse environmental conditions. For those species that require coordinated attacks to overcome tree defences, temperature can further influence population success through the synchronous emergence of adults (Logan and Bentz, 1999). Many physiological processes throughout multiple life stages can influence synchrony, seasonality

and survival (Table 10.1), including: (i) thermal thresholds and rates of development; (ii) diapause; and (iii) cold hardening. Because these temperature-dependent traits are shaped by natural selection to provide optimal fitness in a given environment, they vary among and within species that are distributed across large climatic ranges. Climate change will directly influence bark beetle populations through these traits.

Developmental thresholds and rates

Low and high thresholds bound the thermal range for insect development and are important factors in population survival and growth that vary among and within species (Deutsch *et al.*, 2008). Examining low and high temperature thresholds is complicated, however, by non-linearities that influence survival at temperature extremes (Régnière *et al.*, 2012). Low thermal thresholds for development can be important population synchronizing factors when they differ among life stages, particularly in species that live in cool habitats (Bentz *et al.*, 1991). When development in older life stages (i.e. prepupae) only occurs at high temperatures, yet development in younger life stages (i.e. eggs and early instars) can occur at low temperatures, development is halted in older individuals while continuing in younger ones as temperatures cool. Later-hatching individuals can 'catch up' with those oviposited first, promoting synchronization of life stages across a population (Bentz *et al.*, 1991). High thermal thresholds for development and temperatures that result in the fastest development are also important, yet unknown for most bark beetle species. Optimal development rates are between 27 and 30°C for *D. frontalis* (Wagner *et al.*, 1983), and near 28°C for *Dendroctonus simplex* (McKee and Aukema, 2015a), yet *D. ponderosae* development declines above 25°C (Régnière *et al.*, 2012). A rise in development rate with increasing temperature up to some maximum, followed by a rapid decline, is common in insects, and has important implications for population response in a warming climate. Species already living at or near their thermal maximum (i.e. small 'thermal

safety margin') may be more impacted by climate warming as temperatures exceed optimal thresholds, especially those with sharp declines in development rate at temperatures above the optimum. Populations in cooler environments typically have thermal optima higher than their current environment (i.e. large 'thermal safety margin') relative to populations in warmer environments (Deutsch *et al.*, 2008), and therefore initially respond positively to warming temperatures. For example, at many cool, high-elevation sites, recent temperature increases remain in the thermal range of increasing development rate for *D. ponderosae*, resulting in a decrease in generation time. At warm, low-elevation sites, however, historical temperatures were already at or near the threshold for optimal development and increased warming has had little effect on generation time (Bentz *et al.*, 2014).

Although warming temperatures can shorten the generation time of some individuals (Werner and Holsten, 1985; Hansen *et al.*, 2001; Bentz *et al.*, 2014), evolved development rates and thresholds limit where and how fast this occurs. For example, although *D. ponderosae* may complete a generation in a single summer when temperatures are warm and attacks occur early (DeLeon *et al.*, 1934; Bentz *et al.*, 2014), few adults are typically present in early summer, and development rates and thresholds limit the capacity to produce a second generation across winter (Bentz and Powell, 2014). The complexity of bark beetle temperature-dependent physiology that has evolved to promote population success across varying environments complicates predictions of response to future climatic conditions. New thermal regimes in some habitats may reduce outbreaks of some species, yet changes in other habitats may favour them. A detailed understanding of development rates, thresholds and diapause will be required to make useful predictions.

Diapause

Diapause is the most common strategy by which insects gain protection from regular periods of adverse environmental

Table 10.1. Temperature-dependent life history parameters that can influence response to climate change and contribute to phenotypic plasticity and heritable variation in bark beetles.

Parameter	Definition	Relationship among bark beetles	Ecological significance	References
Development rate	Rate for completion of a life stage	Development rate shows a parabolic relationship with temperature, increasing from T_{\min} to T_{opt} , then dropping rapidly to T_{\max} . Can vary among life stages within a species and among species	Influences seasonality and voltinism	1, 9, 12, 15, 18, 22, 23
Optimal developmental threshold T_{opt}	Temperature at which insects experience most rapid development	Varies among species	Populations currently living in environments that are on average cooler than their T_{opt} can respond to climate warming with increased development and potentially decreased generation time	1, 9, 15, 18, 22, 23
Maximum developmental threshold T_{\max}	Temperature above which development ceases	Varies among species	Populations living in warm environments may approach T_{\max} faster with climate warming than those in cool environments	1, 9, 15, 18, 22, 23
Minimum developmental threshold T_{\min}	Lowest temperature at which development continues	Often higher in later life stages than early life stages	Differences among life stages can promote seasonality and adult emergence synchrony	1, 9, 15, 18, 23
Diapause, facultative	Dormancy elicited by environmental cues	Prepupal and adult dormancies in many species	Promotes seasonality and dictates the number of generations per year. Increased probability of being averted with climate warming, resulting in reduced generation time	3, 4, 6, 8, 9, 10, 12, 13, 16, 21
Diapause, obligate	Dormancy that is a requisite component of life history	Adult reproductive dormancy in several species	Promotes seasonality and synchrony of adult emergence	5, 12, 19, 20
Cold hardening	Accumulation of cryoprotectant compounds to reduce supercooling point (SCP), the temperature at which mortality occurs	Freeze intolerance is universal among species. SCPs vary seasonally and among and within species	Species that overwinter under bark have lower SCPs than those that overwinter in soil. SCPs vary seasonally in cold relative to warm habitats. Soil inhabiting species may be affected negatively by reduced snowpack	2, 7, 11, 14, 17

Notes: ¹Bentz *et al.* (1991); ²Bentz and Mullins (1999); ³Birch (1974); ⁴Christiansen (1971); ⁵Clark (1974); ⁶Doležal and Sehnal (2007); ⁷Gehrken (1984); ⁸Gehrken (1985); ⁹Hansen *et al.* (2001); ¹⁰Inward *et al.* (2012); ¹¹Koštál *et al.* (2011); ¹²Langor and Raske (1987); ¹³Lester and Irwin (2012); ¹⁴Lombardero *et al.* (2000a); ¹⁵McKee and Aukema (2015a); ¹⁶McKee and Aukema (2015b); ¹⁷Miller and Werner (1987); ¹⁸Régnière *et al.* (2012); ¹⁹Ryan (1959); ²⁰Safranyik *et al.* (1990); ²¹Scott and Berryman (1972); ²²Wagner *et al.* (1983); ²³Wermelinger and Seifert (1998).

conditions, and by which individuals are seasonally synchronized (Tauber *et al.*, 1986). Diapause has been demonstrated or suggested to occur in multiple bark beetles, although only a small proportion of species have been investigated. When diapause is induced by specific environmental conditions, it is termed facultative. Alternatively, obligatory diapause occurs regardless of environmental conditions. Facultative or obligatory diapause in the adult stage has been observed or suggested for eight bark beetle species, and a facultative larval/prepupal diapause has been found in three species (Table 10.1). Some species, including *D. rufipennis*, have both an adult and a prepupal diapause. The obligatory adult reproductive diapause provides protection from cold, and the larval/prepupal diapause aids in synchronicity and seasonality, and also reduces the probability that cold-sensitive pupae are not present during winter. The facultative nature of the prepupal diapause provides flexibility, allowing beetles to shift between semivoltinism and univoltinism depending on environmental conditions. If oviposition occurs during a cool summer, prepupal diapause is elicited and the first winter is spent as a prepupa and the second as an adult, resulting in a semivoltine life cycle. If conditions are warm during the first summer, the prepupal diapause is averted and a univoltine life cycle results. A facultative, rather than obligatory, diapause will increase the probability of decreased generation time when warming associated with climate change reduces the occurrence of dormancy in the first year.

Cold hardening

Arrested development, either via diapause or simple quiescence, does not ensure overwinter survival. Bark beetles rely on supercooling for overwintering success. The capacity to supercool has been found in all bark beetle species investigated (Table 10.1), and a physiological independence between cold hardening and diapause occurs in at least some species. As in other insects, cold hardening and diapause can, but need not, co-occur. Bark beetles are freeze-intolerant,

meaning they cannot survive ice formation within their tissues (Lee, 1991). Supercooling to survive subfreezing temperatures is accomplished by accumulating antifreeze proteins and low molecular weight polyols and sugars (Table 10.1). Supercooling points (i.e. the temperature at which mortality occurs) are often much lower than the temperatures experienced, can be highly variable at a given point in time, and are higher in southern than in northern populations, most likely a genetic adaptation to local climate (Bentz and Mullins, 1999; Lombardero *et al.*, 2000a). Species that inhabit colder areas exhibit seasonality in cold-hardening and cryoprotectant accumulation, with the greatest supercooling capacity in winter (Bentz and Mullins, 1999), whereas species in warm habitats show little seasonal variation in cold-hardening capacity (Lombardero *et al.*, 2000a). Overwintering behaviour can also play a role in seasonality and intensity of supercooling, whereby species that typically overwinter under the bark have supercooling points lower than those of species that overwinter in the soil (Table 10.1). Overwintering in the soil can also result in a shift in the seasonality of supercooling, whereby cold-hardiness is greatest during autumn when there is a lack of snow cover (Lombardero *et al.*, 2000a). A diminishing snow pack, which is predicted in a changing climate, could remove an important thermal buffer for many species that overwinter in the soil or beneath the bark of trees' lower stems. In general, increasing minimum temperatures associated with climate change can release populations from the constraint of periodic cold temperature extremes (Régnière and Bentz, 2007; Preisler *et al.*, 2012; Sambaraju *et al.*, 2012). It is important to note, however, that winter temperatures are not necessarily a constraint for populations across the range of all species (Trân *et al.*, 2007; Weed *et al.*, 2015). In addition, for some species, continued increases in minimum winter temperature could actually be detrimental if temperatures warmed to the extent that metabolic activity was accelerated and stored resources were depleted (Irwin and Lee, 2003).

Effects of temperature on community associates

Temperature also affects bark beetles indirectly through impacts on their microbial associates. In addition to the microorganisms described above, various species of nematodes and mites are commonly phoretic on bark beetles (Cardoza *et al.*, 2008). Although the impact of temperature on the complex web of interactions among bark beetle microbial associates is not well known, it has been shown that certain ophiostomatoid fungi have different temperature-dependent thresholds and development rates (Hofstetter *et al.*, 2007; Rice *et al.*, 2008), thereby allowing the beetles to exist across a broad range of environmental conditions. Varying temperatures among and within years appears to maintain the presence of two important fungal associates of *D. ponderosae* (Addison *et al.*, 2013). The influence of climate change on natural enemies that have adapted life history strategies, such as diapause, to coincide developmental timing with their prey/hosts (Reeve, 2000) will also need to be considered.

10.3.2 Effects of drought and temperature on conifer physiology, defence and detection by beetles

Rising temperatures and regional precipitation decreases will increase drought stress on many coniferous forests by increasing evaporative demand or vapour pressure deficit (Williams *et al.* 2012; Breshears *et al.*, 2013). During drought, many conifers close stomata to prevent extreme negative water potentials that cause air emboli in xylem cells (i.e. cavitation) and consequently reduce sapwood hydraulic conductance (Martínez-Vilalta *et al.*, 2004; Choat *et al.*, 2012). Some conifers experience frequent occurrence and repair of cavitation in leaves and twigs, via mechanisms that remain poorly understood (Brodersen and McElrone, 2013). Protection of xylem from cavitation by stomatal closure reduces photosynthesis to near zero during severe drought (Plaut *et al.*, 2012; Koepke and Kolb,

2013), which suggests alteration of tree carbon balance.

Drought impacts on conifer carbon balance are complex. Mild drought typically has little impact on non-structural carbohydrate (NSC) concentrations (Gruber *et al.*, 2011), or can increase concentrations of specific tissues when carbohydrate use (sink strength) is reduced more than the supply from photosynthesis (source strength; Sala *et al.*, 2012). This increase in tissue NSC concentration during mild drought increases the soil-to-plant water potential gradient, and consequently plant water uptake, thus serving as a drought resistance mechanism (Pallardy, 2008).

In contrast to mild drought, severe prolonged droughts often deplete NSC concentration of conifer tissues. Isohydric conifers that sharply reduce stomatal conductance to prevent cavitation, the 'wait-it-out strategy' (Mitchell *et al.*, 2013), are prone to NSC depletion and carbon starvation (McDowell *et al.*, 2008). For example, experimental severe drought reduced NSC concentration of *Pinus edulis* sapling leaves and branches by 30–50% (Adams *et al.*, 2013b; Anderegg and Anderegg, 2013), *Picea abies* sapling roots by 85% (Hartmann *et al.*, 2013b) and *Pinus radiata* seedlings by 48% (Mitchell *et al.*, 2013). Consistent with carbon starvation, sapwood NSC concentration was almost entirely depleted during drought-induced mortality of mature *Pinus sylvestris* (Galiano *et al.*, 2011). Mechanisms by which severe drought reduces conifer NSC concentration are not fully understood, but probably involve: long periods of near-zero photosynthesis during continuing tissue respiration; canopy defoliation; disruption of starch conversion to sugar; and impeded carbohydrate translocation among tissues (Breshears *et al.*, 2009; Sala *et al.*, 2010; Galiano *et al.*, 2011; Adams *et al.*, 2013b; Hartmann *et al.*, 2013a). Moreover, rising temperature accelerates carbon starvation during drought because warming increases the maintenance costs of tissue respiration (Zhao *et al.*, 2013).

Resin synthesis depends on NSC supply to polyphenolic parenchyma cells in xylem and phloem because carbon is the dominant elemental component of resin (Franceschi

et al., 2005). Stored NSC is used to synthesize both constitutive (Gaylord *et al.*, 2013) and induced (Guérard *et al.*, 2007) resin defences. Decreases in induced resin flow during stresses that reduce photosynthesis suggest an important role of new carbon assimilation for induced defence (Lewinsohn *et al.*, 1993; Lombardero *et al.*, 2000b; Wallin and Raffa, 2001; Wallin *et al.*, 2003). Mature conifers that have survived severe drought and associated bark beetle attacks often have more abundant or larger xylem resin ducts than trees that have died (Kane and Kolb, 2010; Gaylord *et al.*, 2013). Thus, climate changes affecting NSC availability seem likely to alter conifer resin defence.

Drought has non-linear impacts on quantities of conifer resin, consistent with the growth differentiation balance hypothesis (GDBH). The GDBH predicts that moderate water stress increases resin quantity because growth is constrained more than NSC supply from photosynthesis, thereby providing surplus NSC for resin synthesis (Herms and Mattson, 1992). In contrast, GDBH predicts that severe water stress reduces the supply of NSC to all carbon sinks, including resin synthesis, due to decreased photosynthesis while NSC is depleted by tissue respiration. The GDBH has been supported for mature conifers by demonstration of a variable role of drought on the resin quantity of *Pinus taeda*, depending on the relative impact of drought on photosynthesis and within-tree carbon sink strength (Dunn and Lorio, 1993; Lorio *et al.*, 1995; Reeve *et al.*, 1995). Application of the GDBH to climate change suggests that increased frequency of moderate water stress will enhance resin quantity, whereas increased frequency of severe water stress, as is predicted during climate change for many water-limited forests (Vose *et al.*, 2012), will reduce resin quantity. These relationships can be complex, however, because in some cases trees respond to drought with both reduced growth and increased susceptibility to bark beetles (Rolland and Lemperiere, 2004). An additional complication is that drought can result in less cambial growth, so that separate from increasing tree susceptibility, drought could reduce the

food quality for developing beetles in successfully attacked trees.

Climate change also may alter resin defences indirectly via changes in tree growth. Manipulative experiments (Way and Oren, 2010) and modelling (Luo *et al.*, 2008) show that warming and increased precipitation generally increase tree growth, whereas warming and reduced precipitation or water availability decrease growth. Elevated atmospheric carbon dioxide concentration increases the growth of young conifers via increased photosynthesis (Franks *et al.*, 2013) and also increases resin quantity for non-suppressed trees by providing more NSC for resin synthesis (Novick *et al.*, 2012). Tree growth and size are related positively to both resin flow (Davis *et al.*, 2012; Westbrook *et al.*, 2013) and tree survival of some bark beetle attacks (Waring, 1983; Negrón *et al.*, 2009). Thus, physical resin defence may increase with climate warming via faster tree growth in cool mesic and boreal forests whose growth is currently limited most strongly by low temperature (Boisvenue and Running, 2006; Littell *et al.*, 2010). In contrast, physical resin defence likely will decrease with climate warming in xeric forests where intensification of drought stress decreases tree growth (Williams *et al.*, 2010). Physical resin defence may be altered further during climate change via increases in air and phloem temperatures that decrease resin viscosity and consequently increase resin volumetric flow rate from beetle attack wounds (Gaylord *et al.*, 2007).

Little is known about how warming and drought affect the chemical constituents of conifer resin defences. Most investigations used seedlings rather than larger trees. In controlled manipulations, moderate drought stress yielded the highest constitutive monoterpene cyclase activity in *Abies* seedlings (Lewinsohn *et al.*, 1993). In contrast, the highest induced concentrations in response to simulated attack were in well-watered seedlings (Lewinsohn *et al.*, 1993). Experiments on *Pinus* and *Picea* seedlings have produced mixed results, with reports of both small (Lusebrink *et al.*, 2011) and large (Turton *et al.*, 2003) changes in monoterpene

quantities and composition in response to experimentally induced water stress. In one of few investigations of mature trees, experimentally induced water stress on *P. taeda* increased concentrations of resin monoterpenes, especially α - and β -pinene, but decreased concentrations of resin acids (Hodges and Lorio, 1975). This change in resin composition was suggested to increase beetle detection of stressed trees, promote beetle aggregation and reduce tree physical defence via reduction in resin viscosity and crystallization rate (Hodges and Lorio, 1975).

Warming and increasing drought intensity may influence bark beetle detection of stressed trees via a change in attraction cues. Bark beetles use a combination of visual, tactile, auditory, gustatory and olfactory cues to select trees for attack (Raffa and Berryman, 1982a; Wood, 1982; Strom *et al.*, 2001). Tree monoterpenes, volatile organic compounds and ethanol are olfactory attractants for some bark beetles (Kelsey and Joseph, 2001; Seybold *et al.*, 2006; Miller and Rabaglia, 2009). Drought stress could alter tree quantity and/or composition of these attractants (e.g. Manter and Kelsey, 2008), which in turn could signal tree stress to bark beetles.

Cavitation of water in sapwood is another potential signal of conifer stress that may be altered by climate change-induced drought. Sapwood cavitation causes ultrasonic acoustic emissions that are detectable with transducers at the bark surface (Rosner *et al.*, 2006). Some bark beetles respond to ultrasonic acoustic waves at frequencies similar to those produced by sapwood cavitation during drought (Rudinsky and Michael, 1972). The hypothesis that acoustic emissions from sapwood cavitation signal tree stress to bark beetles has not been tested adequately.

10.3.3 Effects of temperature and drought and their interactions on recent outbreaks

There is substantial empirical evidence for climate influences on recent bark beetle outbreaks in North America, particularly *D.*

ponderosae, *D. rufipennis*, *D. frontalis*, and *Ips confusus* LeConte. Studies in the USA and Canada have relied on aerial surveys from forestry agencies, archived records of outbreaks (e.g. Hebertson and Jenkins, 2008) and dendrochronological analyses (e.g. Berg *et al.*, 2006; Campbell *et al.*, 2007). Ideally, studies include variables that represent each of the major influences of climate discussed previously. In practice, a range of climate variables has been used, from simple climate variables to outputs of climate suitability models (e.g. Preisler *et al.*, 2012).

The influence of climate on bark beetle outbreaks has been documented in several respects. First, observed range expansion of outbreaks has been linked to climate (Section 10.4.1). Second, temperature increases that provide more favourable conditions for the beetles, and drought stress that provides more susceptible hosts, have facilitated outbreaks within historical ranges (Berg *et al.*, 2006; Rouault *et al.*, 2006; Aukema *et al.*, 2008; Raffa *et al.*, 2008). Warmer winters and higher year-round temperatures benefit beetles directly and have been identified as facilitating outbreaks (Aukema *et al.*, 2008; Powell and Bentz, 2009; Marini *et al.*, 2012; Preisler *et al.*, 2012; Creeden *et al.*, 2014). Drought conditions exert stress on host trees, reducing their defences and thus facilitating outbreaks (Raffa *et al.*, 2008; Creeden *et al.*, 2014; Hart *et al.*, 2014). In some cases, the effect of drought can be spatially explicit, such as when drier sites provide the basis for initial population increases that can subsequently transition into regional outbreaks (Kaiser *et al.*, 2014). The seasonal timing of water stress can also be important (Thomson and Shrimpton, 1984; Hebertson and Jenkins, 2003; Raffa *et al.*, 2008; Preisler *et al.*, 2012). Populations of non-aggressive beetle species are closely tied to drought effects on host susceptibility during both their rising and falling phases (Raffa *et al.*, 2008). In contrast, relief from drought does not terminate outbreaks of aggressive species when populations have exceeded a critical threshold (Raffa *et al.*, 2008; Creeden *et al.*, 2014). Third, unfavourable temperatures can lead to declines in outbreaking populations of aggressive bark beetles. For

example, low winter temperatures appear to have reduced *D. ponderosae* populations in British Columbia in the 1980s (Safranyik and Linton, 1991; Stahl *et al.*, 2006) and early 1930s (Bentz *et al.*, 2011). Unusually low summer temperatures (without low winter temperatures) reduced building populations of *D. ponderosae* in Idaho in 1993 (Logan and Powell, 2009; Creeden *et al.*, 2014). Declines of several *D. ponderosae* outbreaks did not occur under unfavourable climate conditions, however, suggesting roles of other factors, such as host depletion (Creeden *et al.*, 2014).

There are several key areas in which our knowledge remains relatively limited. In particular, studies of actual beetle population responses, rather than just killed trees, to climate change would increase the confidence of findings. The lack of such observations over larger spatial extents and/or longer periods, and also at the critical fine scales at which populations first rise, makes it difficult to delineate thresholds. Likewise, we have little understanding of how climate change will influence disturbance interactions. For example, anticipated changes in temperature and precipitation regimes are projected to increase the frequency and severity of wildfires (Westerling *et al.*, 2011). By itself, wildfire injury is unlikely to elicit large-scale outbreaks (Hood and Bentz, 2007; Davis *et al.*, 2012; Powell *et al.*, 2012). However, as climatic drivers increasingly raise beetle populations and exert region-wide stress on host trees, the likelihood that immediate population increases following fire could transition into outbreaks through their combined and interacting effects may increase.

10.4 Effects of Climate Change on Bark Beetle Range Expansion and Population Dynamics in New Habitats

When evaluating how relationships between plants and herbivores may respond to climatically induced herbivore range shifts, it is useful to delineate three general types of regime change: (i) increased and more

persistent establishment in areas where host trees historically experienced only intermittent exposure (semi-naïve); (ii) establishment in areas dominated by a historical host tree species but where local tree populations had experienced little or no pressure (naïve host); and (iii) movement into new areas that contain tree species that had not experienced prior exposure and are connected via suitable host type to historically unexposed biomes (naïve novel host). It is most useful to base degrees of historical interaction and reproductive range on evidence of actual beetle development in hosts, as opposed to just sedimentation layers, because advective transport can randomly deposit large numbers of insects (Jackson *et al.*, 2008; de la Giroday *et al.*, 2011) and thus generate false positives.

10.4.1 Recent changes in latitudinal, elevational and host species ranges of bark beetles

To avoid local extinction during rapidly changing climate, organisms must migrate to more favourable habitats, respond with phenotypic plasticity in thermally dependent traits and/or adapt genetically to changing conditions (Hoffmann and Sgrò, 2011). The distribution of many tree-killing bark beetles is currently limited by climate, rather than host trees (Bentz *et al.*, 2010; Weed *et al.*, 2013), allowing opportunities for expansion of outbreak populations with warming, particularly to the north (Carroll *et al.*, 2004; Tr an *et al.*, 2007; Cullingham *et al.*, 2011; de la Giroday *et al.*, 2012). Although few studies have been conducted on bark beetles, phenotypic plasticity is evident when beetles are reared in different environments, such as thick versus thin phloem (Haack *et al.*, 1987), across environments and different temperatures (Bentz *et al.*, 2011; Bracewell *et al.*, 2013) and among years with different thermal patterns (Bentz *et al.*, 2014). Continued warming, however, could exceed the range of plastic tolerance for some species and occur faster than potential adaptation, even within

insects that have relatively short generation times. Given sufficient time, genetic variation and strong selection, populations could further adapt to novel thermal regimes and affect outbreak risk (Björkman *et al.*, 2011). The potential for necessary changes in bark beetle species at the genetic level, however, is poorly understood.

Two common responses of ectotherms to elevated temperature are movement into higher elevations and movement into higher latitudes (Parmesan, 2006). Bark beetles are no exception, and there are well-documented examples involving several species (Table 10.2). Increases in both winter and year-round temperatures have contributed to northward (Carroll *et al.*, 2004; Tr an *et al.*, 2007; Safranyik *et al.*, 2010; Sambaraju *et al.*, 2012) and elevational (Logan and Powell, 2001; Logan *et al.*, 2010) movement of *D. ponderosae*, including into forest types that have experienced no or infrequent beetle activity in the past. Similarly, increasing winter minimum temperatures in New Jersey have allowed the persistence of

outbreak-level populations of *D. frontalis* (Weed *et al.*, 2013).

10.4.2 Anticipating trophic interactions with host trees and natural enemies in semi-naïve and naïve habitats

In addition to the direct effects of temperature, a wide range of trophic interactions will influence the extent to which insect populations establish, spread and undergo outbreaks in newly or increasingly accessed habitats. These drivers include multiple components of plant–insect relationships, interactions with natural enemies such as predators, parasitoids and competitors, and mediation of these relationships by beetles' symbionts. Our ability to predict how these relationships will affect beetle performance in changing climate scenarios is poor, but our understanding of outbreak dynamics in historical ranges (Fig. 10.1) can provide a useful framework.

Table 10.2. Range expansions of bark beetles, and population dynamics in new habitats, associated with climate change.

Species	Region	Shift in latitude, elevation and/or host species	References
<i>Dendroctonus ponderosae</i>	Western North America	Upward shift in elevation, permitting increased access to high-elevation five-needle pines	Logan and Powell (2001); Carroll <i>et al.</i> (2004); Hicke <i>et al.</i> (2006); Bentz <i>et al.</i> (2010); Logan <i>et al.</i> (2010); Raffa <i>et al.</i> (2013)
<i>D. ponderosae</i>	Western Canada	North and eastward shifts, permitting access to jack pine	Cerezke (1995); Jackson <i>et al.</i> (2008); Robertson <i>et al.</i> (2009); Cudmore <i>et al.</i> (2010); Safranyik <i>et al.</i> (2010); Cullingham <i>et al.</i> (2011); de la Giroday <i>et al.</i> (2011, 2012); Sambaraju <i>et al.</i> (2012)
<i>Dendroctonus brevicomis</i>	Western USA	Modelled future range expansion and contraction predictions	Evangelista <i>et al.</i> (2011)
<i>Dendroctonus frontalis</i>	Southern USA	Northward range expansion	Ungerer <i>et al.</i> (1999); Waring <i>et al.</i> (2009)
<i>D. frontalis</i>	Eastern USA	Northern expansion of outbreaks in New Jersey pinelands	Weed <i>et al.</i> (2013)
<i>Dendroctonus mexicanus</i>	South-western USA	Northward range expansion	Moser <i>et al.</i> (2005); Waring <i>et al.</i> (2009)
<i>Ips pini</i>	Western USA	Modelled future range expected to decrease generally	Evangelista <i>et al.</i> (2011)

Range responses to climate change have been most studied in *D. ponderosae*, so we focus on this system as a case study. Forest types in the northern Rocky Mountains show strong elevational gradients (Logan and Powell, 2001). Middle elevation stands are typically dominated by lodgepole pine, which transition into non-host species such as spruce and fir, and higher elevations are dominated by five-needled pine species such as whitebark pine. Over the periods for which data are available, most mortality caused by *D. ponderosae* was to lodgepole pine, with only intermittent and comparatively brief impacts on whitebark pine during unusually warm periods (Logan and Powell, 2001; Jewett *et al.*, 2011). As unfavourable conditions such as cold temperatures returned, beetle populations either declined below detectable levels or became locally extirpated (Logan *et al.*, 2010). During recent years, however, continuous high temperatures have been accompanied by continuous *D. ponderosae* reproduction and high tree mortality in stands dominated by five-needled pines (Logan *et al.*, 2010).

In mixed stands that provided equivalent environmental conditions, lodgepole pines had higher total concentrations of constitutive phloem monoterpenes than whitebark pines (Raffa *et al.*, 2013). Differences in inducible defences were even more striking. When trees were challenged with simulated attack by *D. ponderosae*–*Grosmannia clavigera* complexes, lodgepole pine showed much greater induced biosynthesis of monoterpenes. Resin flow in response to natural attacks was also more substantial in lodgepole pines. There were also differences in the composition of phloem chemicals that related to beetle performance. Whitebark pines had higher concentrations of the pheromone precursor (Blomquist *et al.*, 2010) (–)- α pinene and the pheromone synergist (Miller and Borden, 2000) myrcene, and lower concentrations of the repellent (Sturgeon and Mitton, 1986) limonene and lower induced concentrations of the pheromone inhibitor 4-allylanisole (Emerick *et al.*, 2008) than whitebark pine. Collectively, these results suggest that whitebark pine is relatively poorly equipped

to prevent mass attacks from being elicited by pioneer beetles, and to resist attacks under way. Overall, both the tree defence and temperature sides of the portal in Fig. 10.1 appear to widen with anticipated climate change, making continued outbreaks in high-elevation ecosystems more likely.

Host selection behaviour adds an additional, and complicating, dimension to beetle–host relationships. In the above mixed stands, beetles entered more lodgepole than whitebark pines, despite the latter's inferior defences. Thus, there appears to be a lag time between increased access to a less defended tree and increased behavioural orientation toward it. Although beetles may not prefer whitebark pines, they readily accept them. For example, in no-choice laboratory assays, beetles entered both trees equally, and in stands dominated by whitebark pine, natural entry rates were equivalent. These results resemble findings from other systems that delineate the timespans and complexity of host switching by herbivorous insects (Singer and McBride, 2010). Presumably, there will be increased selection for orientation toward whitebark pine if warm temperature regimes persist.

We currently have little information on how a third constraint in Fig. 10.1, predators, competitors and symbionts, compares between lodgepole and whitebark pine habitats. The little data available suggest that predators and competitors may, like the herbivore, display lags in their host-searching behaviours. These insects find beetle-killed trees by exploiting volatile plumes containing mixtures of bark beetle pheromones and tree compounds (Wood, 1982). In the mixed stands described above, numbers of the major predator and competitor species were equivalent in unbaited traps on unattacked lodgepole and whitebark pines (Raffa *et al.*, 2013). However, more of these predators and competitors were caught on lodgepole than on whitebark pines in which *D. ponderosae* were tunnelling. Additional behavioural studies are needed to determine how prevalent and persistent this pattern is, and whether *D. ponderosae* attacking whitebark pines may experience partial escape from natural enemies. In addition, the relative

abundances of predators and competitors in lodgepole versus whitebark pine stands are unknown.

The second type of regime change, establishment in areas predominantly covered by the same, but historically unexposed, host species (naïve habitats), has also been observed with *D. ponderosae* (Safranyik and Carroll, 2006; Safranyik *et al.*, 2010). Large-scale outbreaks in the predominantly lodgepole pine forests of southern British Columbia have been well documented over the past several hundred years. The beetle's historical distribution was limited by cold temperatures to the north and the geophysical barrier of the Rocky Mountains to the east (Carroll *et al.*, 2004; Sambaraju *et al.*, 2012). More recently, beetles have moved farther north, where they have caused extensive mortality to lodgepole pines (Carroll *et al.*, 2004; Sambaraju *et al.*, 2012). Additionally, these high populations provided the source for windborne eastward dispersal in enormous and probably unprecedented numbers (Bartell *et al.*, 2008; Jackson *et al.*, 2008). Beetles recently breached the Rocky Mountains in west-central Alberta and are now causing high mortality in the lodgepole pine forests of western Alberta (de la Giroday *et al.*, 2012).

As with increased beetle access to high-elevation stands, we have little knowledge of trophic interactions in regions recently accessed by *D. ponderosae*. However, the available data indicate beetle reproduction is higher in historically unexposed than exposed lodgepole pine habitats (Cudmore *et al.*, 2010). Naïve lodgepole pine appears to be both more susceptible and of higher quality for beetle development (Fig. 10.2). This is consistent with limited prior selection pressure imposed by *D. ponderosae* on these trees. Furthermore, lodgepole pines in areas that did not historically experience beetle outbreaks had higher levels of the pheromone precursor α -pinene (Clark *et al.*, 2010) and lower overall concentrations of induced monoterpenes (Clark *et al.*, 2010, 2014). This suggests host trees in naïve habitats are both more likely to facilitate mass attacks and less able to defend themselves. Thus, it appears that both the left and lower margins

of the eruptive window in Fig. 10.1 will be more favourable to *D. ponderosae* in naïve lodgepole pine habitats under anticipated climate regimes.

Information comparing natural enemy and competitor complexes between lodgepole pines in historically versus recently infested regions is not available. Likewise, our knowledge of the microbial associates in historically exposed versus unexposed regions is limited. Both the relative abundance of the ophiostomatoid fungi (Rice *et al.*, 2008) and the complex of bacteria (Adams *et al.*, 2013) associated with *D. ponderosae*-lodgepole pine complexes

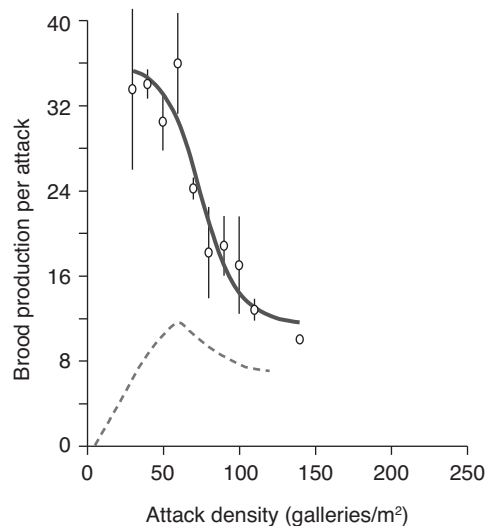


Fig. 10.2. Mean (\pm SE) number of mountain pine beetle offspring per female in relation to the density of attacking females determined from 10 to 12 mass attacked lodgepole pines within each of 8 infestations assessed in 2008 near Grande Prairie, Alberta, Canada (A.L. Carroll, unpublished data). The same relationship for mountain pine beetle attacking lodgepole pine within its native range (north-eastern Oregon, USA (from Raffa and Berryman, 1983)) is shown as a dashed line. Lodgepole pines in the naïve zone are both more susceptible, evidenced by the peak of the solid line occurring much farther to the left than the peak of the dashed line, and are also of higher substrate quality (phloem thickness, nutrients, symbiont activity, etc.), evidenced by any point past the peak of the dashed line being higher than that of the solid line.

appear to differ between British Columbia and Alberta, but the biological significance is unknown.

With increased temperatures, *D. ponderosae* is also undergoing the third type of regime change, spread into entirely new (naïve, novel host) habitats (Logan and Powell, 2001; Safranyik *et al.*, 2010). Lodgepole pine naturally hybridizes with jack pine in sections of Alberta, and both hybrid and pure jack pines are being killed (Cullingham *et al.*, 2011). Jack pine extends eastward through the boreal forest and connects with eastern white pine and red pine in the Great Lakes region. This raises the prospect of a 'native invasive' whereby anthropogenically altered climate rather than direct human transport provides the bridge (Erbilgin *et al.*, 2013; Lusebrink *et al.*, 2013). Models of temperature suitability for beetles yield variable predictions (Bentz *et al.*, 2010; Safranyik *et al.*, 2010).

In estimating how trophic interactions will influence *D. ponderosae* in habitats dominated by naïve host species, we consider in sequence host-plant relationships, forest structure and natural enemies and symbionts (Fig. 10.1). Table 10.3 provides data on the same host compounds evaluated in the lodgepole versus whitebark pine

comparison. Several trends emerge. First, the naïve novel tree species, especially in the Great Lakes region, appear more amenable to *D. ponderosae*'s mass attack behaviour than the historical species (Erbilgin *et al.*, 2013; Raffa, 2014; Clark *et al.*, 2014). For example, jack pine has a higher per cent composition of α -pinene than lodgepole pine. Further, none of the pheromone inhibitor, 4-allylanisole, was found in jack pine. Concentrations of myrcene, a pheromone synergist, appear within the range of lodgepole pine. Red pine has higher concentrations of α -pinene than lodgepole pine and no detectable levels of 4-allylanisole. Eastern white pine had higher levels of α -pinene and lower levels of 4-allylanisole than lodgepole pine. A second trend is that there is substantial intraspecific variation between regions. Interestingly, Alberta lodgepole pine had higher concentrations of α -pinene, that is, were more jack pine-like, than the British Columbia, Oregon or Wyoming populations, and Alberta jack pine had lower concentrations, that is, were more lodgepole pine-like, than the jack pines in Wisconsin. This is consistent with the hybridization by these species in Alberta. With regard to inducibility, midwestern pines show pronounced biosynthesis of monoterpenes and

Table 10.3. Composition (%) of volatiles known to affect bark beetle signalling in lodgepole versus midwestern pines.

Pine species (region)	Host volatile			Reference
	α -pinene	Myrcene	4-Allylanisole	
Lodgepole (central southern British Columbia)	5.26	0.73	Not tested	Boone <i>et al.</i> (2011)
Lodgepole (eastern central British Columbia and western central Alberta)	7.09	2.98	Not tested	Clark <i>et al.</i> (2014)
Lodgepole (north-western Wyoming)	3.27	3.96	1.05	Powell and Raffa (2011)
Lodgepole (north-eastern Oregon)	2.92	1.66	Not tested	Raffa and Berryman (1982b)
Lodgepole (western central Alberta)	23.26	2.00	Not tested	Erbilgin <i>et al.</i> (2013)
Jack (eastern central Alberta)	58.42	2.16	Not tested	Clark <i>et al.</i> (2014)
Jack (eastern northern Alberta)	58.12	1.09	Not tested	Erbilgin <i>et al.</i> (2013)
Jack (central Wisconsin)	71.04	3.83	0.00	Aukema <i>et al.</i> (2010)
Red (central Wisconsin)	60.66	0.41	0.00	Aukema <i>et al.</i> (2010)
Eastern white (central Wisconsin)	64.45	1.98	0.42	Aukema <i>et al.</i> (2010)

phenolics in response to fungi vectored by the bark beetles native to this region (Raffa and Smalley, 1995). However, Clark *et al.* (2014) found that induced monoterpene biosynthesis to mountain pine beetle-associated fungi was lower in jack pine than in southern British Columbia lodgepole pine. So, while naïve novel host species have evolved defences to local ophiostomatoid fungi, it is unclear whether those defences are effective against *D. ponderosae* and its associated microorganisms. An additional feature that could potentially increase tree susceptibility in the boreal forest and Great Lakes region is biotic stress caused by a native outbreak defoliator, *Choristoneura pinus pinus* Freeman, which reduces defences in jack pine (Wallin and Raffa, 2001; Colgan and Erbilgin, 2011) and root beetles (*Hyllobius*, *Hylastes*) and associated fungi that impair defences in red pine (Klepzig *et al.*, 1996; Aukema *et al.*, 2010).

It is not known whether the structure of midwestern boreal forests will be as conducive to outbreaks as that of Rocky Mountain lodgepole pine forests (Fig. 10.1, upper margin). Lodgepole forests tend to be dense, of low species diversity and of relatively even age structure (Taylor and Carroll, 2004). Boreal forests tend to be much more fragmented, with jack pines often distributed patchily amid aspen, prairie and other habitats (Safranyik *et al.*, 2010). These structural features decrease the likelihood of synchronous, landscape-scale outbreaks. Additionally, if jack pines in the region have relatively thinner phloem or smaller diameters, that could limit brood production in killed trees. Although much more research is needed, preliminary considerations suggest this element of the eruptive window might be narrowed.

Another factor that could potentially help narrow the eruptive window of *D. ponderosae* in midwestern forests is the abundance of predators and competitors. Overall, predator and competitor loads of midwestern beetles appear to be higher than those of western beetles (Table 10.4). The transcontinentally distributed *D. rufipennis* provides a case study for appraising inter-regional effects. In this system, predator and competitor loads are much higher in the

Midwest. Table 10.4 probably underestimates the increased competitor load that invading *D. ponderosae* would encounter, because the primary tree-killing bark beetle of midwestern pines, *Ips pini*, is a secondary beetle, i.e. competitor, where it overlaps *D. ponderosae*. Also, a survey of *Monochamus* (Cerambycidae) species (Miller *et al.*, 2013), which can be significant competitors and facultative predators of tree-killing bark beetles (Dodds *et al.*, 2001), reported a mean trap catch 1.5 times higher in Wisconsin and Michigan than in seven western states and provinces. The extent to which these communities would influence *D. ponderosae* in new habitats, however, is unknown. An important question concerns how strongly natural enemies in midwestern forests are attracted to *D. ponderosae*'s pheromones. If they are abundant but not attracted to the newly arrived pest, their effect could be diminished. We currently lack data on these predators' responses to the transverbenol produced by female *D. ponderosae*, but at least three local bark beetles (*D. rufipennis*, *D. simplex* and *Dendroctonus valens*) produce frontalin, which male *D. ponderosae* emit. The major predators in upper midwestern forests are highly attracted to this compound (Aukema and Raffa, 2005). Another factor that could improve attraction to *D. ponderosae* is that secondary arrival by *I. pini* results in the emission of ipsdienol, which attracts predators that subsequently feed on *D. ponderosae* (Boone *et al.*, 2008). A second question concerns the phenological synchrony between *D. ponderosae* and natural enemies in midwestern forests. For example, *D. ponderosae* typically attacks trees in mid to late summer, whereas most predators in Wisconsin are active earlier in the season (Aukema *et al.*, 2000). This asynchrony could potentially provide *D. ponderosae* with some escape from the high populations of predators there.

10.5 Conclusions

1. Both mechanistic understanding of the key processes affecting bark beetle population dynamics, and epidemiological

Table 10.4. Predator and competitor loads of bark beetles in western versus midwestern North America. Studies that were designed deliberately to manipulate ratios of predators and prey were omitted; direct comparisons or meta-analyses were not applicable due to interspecific and methodological differences. Table 10.4a = arrival; Table 10.4b = emergence.

(a)

Location	Primary bark beetle	Predators/ beetle	Competitors/ beetle	Reference	Sampling method
Western region					
Interior Alaska	<i>Dendroctonus rufipennis</i>	Not sampled	2.00	Werner <i>et al.</i> (2006)	Pheromone traps
British Columbia	<i>Dendroctonus ponderosae</i>	0.01	Not sampled	Miller <i>et al.</i> (2005)	Pheromone traps
North-eastern Oregon	<i>Dendroctonus pseudotsugae</i>	0.04	Not sampled	Ross and Daterman (1995)	Pheromone traps
North-eastern Oregon	<i>D. pseudotsugae</i>	0.14	Not sampled	Ross and Daterman (1997)	Pheromone traps
North-eastern Oregon	<i>D. pseudotsuga</i> , <i>D. brevicomis</i>	0.02	0.07	Zhou <i>et al.</i> (2001)	Pheromone traps
West-central Montana	<i>D. ponderosae</i>	0.67	1.25	Boone <i>et al.</i> (2008)	Pheromone traps
North-western Wyoming	<i>D. ponderosae</i>	0.06	2.54	Raffa <i>et al.</i> (2013)	Unbaited funnel traps
North-western Wyoming	<i>D. ponderosae</i>	0.00	0.01	Powell <i>et al.</i> (2012)	Pheromone traps
North-eastern Utah	<i>D. ponderosae</i>	Not sampled	2.37	Lerch (2013)	Unbaited panel traps
Great Lakes region					
North-eastern Minnesota	Mostly <i>Dendroctonus simplex</i> , some <i>D. rufipennis</i>	0.99	3.25	Gandhi <i>et al.</i> (2009)	Pheromone traps
Northern Minnesota, Wisconsin, Michigan	<i>Dendroctonus rufipennis</i>	204.50	402.25	Haber Kern and Raffa (2003)	Pheromone traps
Wisconsin	<i>Ips pini</i>	2.12	0.09	Aukema and Raffa (2004)	Attraction to infested bolts
Wisconsin	<i>I. pini</i> , <i>Ips grandicollis</i>	0.10	Not sampled	Erbilgin <i>et al.</i> (2002)	Pheromone traps
Wisconsin	<i>I. pini</i>	1.59	Not sampled	Erbilgin and Raffa (2000)	Infested bark disks
Wisconsin	<i>I. pini</i>	0.71	0.06	Raffa (1991)	Pheromone traps

continued

analyses relating tree mortality to environmental factors, provide strong evidence that outbreaks are largely driven by weather. These include both direct and host-mediated effects. Specifically, warm temperatures can

reduce overwintering mortality and shorten generation times, and severe drought and warm temperatures impose physiological stresses on trees that can impede their defence systems.

Table 10.4. *continued.*

(b)

Location	Primary bark beetle	Predators/ beetle	Competitors/ beetle	Reference	Sampling method
Western region					
Interior Alaska	<i>D. rufipennis</i>	0.35	4.02	Gara <i>et al.</i> (1995)	Emergence from infested logs
Coastal Alaska	<i>D. rufipennis</i>	0.06	2.02	Gara <i>et al.</i> (1995)	Emergence from infested logs
Great Lakes region					
Northern Minnesota, Wisconsin, Michigan	<i>Dendroctonus rufipennis</i>	1.9	2003.00	Haberkern <i>et al.</i> (2002)	Emergence from infested logs

2. Several species of eruptive bark beetles exhibit bimodal population dynamics, such that if their numbers surpass a critical threshold, their growth becomes self-sustaining, even after initial inciting conditions are relaxed. Because most climate change models predict not only changes in mean temperature and precipitation but also more frequent extreme events, species that exhibit such threshold behaviour are particularly likely to undergo regime changes, with increased environmental and socio-economic impacts.

3. There is substantial evidence that recent anthropogenic changes in climate have increased the frequency and magnitude of outbreaks by some bark beetle species. Due to temperature-dependent physiological constraints, however, response to continued climatic changes will vary among and within species.

4. In addition to increased impacts within historical regions, some tree-killing bark beetles are surviving better at higher latitudes and elevations than in the past, accessing new regions in which host species historically had little exposure and accessing new regions with historically unexposed host species. In the latter cases, native bark beetles pose the risk of behaving as invasive species, linked to new biomes by climate change rather than human transport.

5. We currently lack the information needed to predict how bark beetles will behave in naïve habitats. Current

population models yield different results, in part because we are just beginning to quantify phenotypic plasticity and genetic variation within species. In general, tree resistance is lower in regions that had little or no prior exposure than in historical ranges. We have only marginal information on beetle behavioural preferences. It also appears that midwestern forests may harbour richer competitor and predator communities than western conifer forests, but direct comparisons have not been performed.

6. Although there is substantial knowledge on the genetics, physiology, behaviour and ecology of bark beetles, our ability to project this information on to future temperature and precipitation regimes in historical habitats, the spread, survival and population dynamics of beetles in newly accessed regions, and the socio-economic impacts of these alterations, is limited. Indeed, one of the major consequences of climate change is increased uncertainty.

Acknowledgements

KFR was supported by NSF (DEB-0816541), the University of Wisconsin Graduate School through the Beers-Bascom Fellowship and the University of Wisconsin College of Agricultural and Life Sciences. ALC was supported by the Future Forest Ecosystems

Science Council of British Columbia. JAH was supported by the USGS Climate Research and Development Program through the Western Mountain Initiative and USDA NIFA (2013-67003-20652). BHA was supported by the USFS Evaluation Monitoring Program (12-DG-1142000-1478) and the University of Minnesota College of Food, Agriculture, and Natural Sciences.

References

- Adams, A.S., Adams, S.M., Currie, C.R., Gillette, N.E. and Raffa, K.F. (2010) Geographic variation in bacterial communities associated with the red turpentine beetle (Coleoptera, Curculionidae). *Environmental Entomology* 39, 406–414.
- Adams, A.S., Aylward, F., Adams, S.M., Erbilgin, N., Aukema, B.H., *et al.* (2013a) Metagenome of bacterial communities associated with mountain pine beetles and their host trees. *Applied Environmental Microbiology* 79, 3468–3475.
- Adams, H.D., Germino, M.J., Breshears, D.D., Barron-Gafford, G.A., Guardiola-Claramonte, M., *et al.* (2013b) Nonstructural leaf carbohydrate dynamics of *Pinus edulis* during drought-induced tree mortality reveal role for carbon metabolism in mortality mechanism. *New Phytologist* 197, 1142–1151.
- Addison, A.L., Powell, J.A., Six, D.L., Moore, M. and Bentz, B.J. (2013) The role of temperature variability in stabilizing the mountain pine beetle-fungus mutualism. *Journal of Theoretical Biology* 335, 40–50.
- Anderegg, W.R.L. and Anderegg, L.D.L. (2013) Hydraulic and carbohydrate changes in experimental drought-induced mortality of saplings in two conifer species. *Tree Physiology* 33, 252–260.
- Aukema, B.H. and Raffa, K.F. (2004) Does aggregation benefit bark beetles by diluting predation? Links between a group-colonization strategy and the absence of emergent multiple predator effects. *Ecological Entomology* 29, 129–138.
- Aukema, B.H., and Raffa, K.F. (2005) Selective manipulation of predators using pheromones: responses to frontalin and ipsdienol pheromone components of bark beetles in the Great Lakes region. *Agricultural and Forest Entomology* 7, 193–200.
- Aukema, B.H., Dahlsten, D.L. and Raffa, K.F. (2000) Exploiting behavioral disparities among predators and prey to selectively target pests: maximizing bark beetle, predator removal during semiochemically based trap-out. *Environmental Entomology* 29, 651–660.
- Aukema, B.H., Werner, R.A., Haberkern, K.E., Illman, B.L., Clayton, M.K., *et al.* (2005) Quantifying sources of variation in the frequency of fungi associated with spruce beetles: implications for hypothesis testing and sampling methodology in bark beetle–symbiont relationships. *Forest Ecology and Management* 217, 187–202.
- Aukema, B.H., Carroll, A.L., Zheng, Y., Zhu, J., Raffa, K.F., *et al.* (2008) Movement of outbreak populations of mountain pine beetle: influence of spatiotemporal patterns and climate. *Ecography*, j.2007.0906-7590.05453.
- Aukema, B.H., Zhu, J., Moeller, J., Rasmussen, J. and Raffa, K.F. (2010) Interactions between below- and above- ground herbivores drive a forest decline and gap-forming syndrome. *Forest Ecology and Management* 259, 374–382.
- Barnett, T.P., Pierce, D.W., Hidalgo, H.G., Bonfils, C., Santer, B.D., *et al.* (2008) Human-induced changes in the hydrology of the Western United States. *Science* 319, 1080–1083.
- Bartell, N.V., Lindgren, S., Cooke, J., Davis, C., Mock, K., *et al.* (2008) Using genetic analyses to infer mountain pine beetle population structure and dispersal patterns in British Columbia and Alberta. *British Columbia Journal of Ecosystems and Management* 9, 140–142.
- Bentz, B.J. and Mullins, D.E. (1999) Ecology of mountain pine beetle (Coleoptera: Scolytidae) cold hardening in the Intermountain West. *Environmental Entomology* 28, 577–587.
- Bentz, B.J. and Powell, J.A. (2014) Mountain pine beetle seasonal timing and constraints to bivoltinism: a comment on Mitton and Ferrenberg (2012). *The American Naturalist* 184, 787–796.
- Bentz, B.J., Logan, J.A. and Amman, G.D. (1991) Temperature-dependent development of the mountain pine beetle (Coleoptera: Scolytidae) and simulation of its phenology. *Canadian Entomologist* 123, 1083–1094.
- Bentz, B.J., Regniere, J., Fettig, C.J., Hansen, E.M., Hayes, J.L., *et al.* (2010) Climate change and bark beetles of the western United States and Canada: direct and indirect effects. *Bioscience* 60, 602–613.
- Bentz, B.J., Bracewell, R.R., Mock, K.E. and Pfrender, M.E. (2011) Genetic architecture and phenotypic plasticity of thermally-regulated traits in an eruptive species, *Dendroctonus ponderosae*. *Evolutionary Ecology* 25, 1269–1288.
- Bentz, B.J., Vandygriff, J.C., Jensen, C., Coleman, T., Maloney, P., *et al.* (2014) Mountain pine beetle voltinism and life history characteristics across latitudinal and elevational gradients

- in the western United States. *Forest Science* 60(3), 434–449.
- Berg, E.E., Henry, J.D., Fastie, C.L., De Volder, A.D. and Matsuoka, S.M. (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, M.C. (1974) Seasonal variation in pheromone-associated behavior and physiology of *Ips pini*. *Annals of the Entomological Society of America* 67, 58–60.
- Björkman, C., Kindvall, O., Höglund, S., Lilja, A., Barring, L., et al. (2011) High temperature triggers latent variation among individuals: oviposition rate and probability for outbreaks. *PLoS ONE* 6, e16590.
- Bleiker, K.P. and Six, D.L. (2007) Dietary benefits of fungal associates to an eruptive herbivore: potential implications of multiple associates on host population dynamics. *Environmental Entomology* 36, 1384–1396.
- Blomquist, G.J., Figueroa-Teran, R., Aw, M., Song, M.M., Gorzalski, A., et al. (2010) Pheromone production in bark beetles. *Insect Biochemistry and Molecular Biology* 40, 699–712.
- Boisvenue, C. and Running, S.W. (2006) Impacts of climate change on natural forest productivity – evidence since the middle of the 20th Century. *Global Change Biology* 12, 862–882.
- Boone, C.K., Six, D.L. and Raffa, K.F. (2008) The enemy of my enemy is still my enemy, competitors add to predator load of a tree-killing bark beetle. *Agricultural and Forest Entomology* 10, 411–421.
- Boone, C.K., Aukema, B.H., Bohlmann, J., Carroll, A.L. and Raffa, K.F. (2011) Efficacy of tree defense physiology varies with bark beetle population density: a basis for positive feedback in eruptive species. *Canadian Journal of Forest Research* 41, 1174–1188.
- Boone, C.K., Adams, A.S., Bohlmann, J., Keefover-Ring, K., Mapes, A.C., et al. (2013) Bacteria associated with a tree-killing insect reduce concentrations of plant defense compounds. *Journal of Chemical Ecology* 39, 1003–1006.
- Bracewell, R.R., Pfrender, M.E., Mock, K.E. and Bentz, B.J. (2013) Contrasting geographic patterns of genetic differentiation in body size and development time with reproductive isolation in *Dendroctonus ponderosae* (Coleoptera: Curculionidae, Scolytinae). *Annals of the Entomological Society of America* 106, 385–391.
- Brand, J.M., Bracke, J.W., Markovetz, A.J., Wood, D.L. and Browne, L.E. (1975) Production of verbenol pheromone by a bacterium isolated from bark beetles. *Nature* 254, 136–137.
- Breshears, D.D., Myers, O.B., Meyer, C.W., Barnes, F.J., Zou, C.B., et al. (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.
- Breshears, D.D., Adams, H.D., Eamus, D., McDowell, N.G., Law, D.J., et al. (2013) The critical amplifying role of increasing atmospheric moisture demand on tree mortality and associated regional die-off. *Frontiers in Functional Plant Ecology*, doi:10.3389/fpls.2013.00266.
- Brodersen, C.R. and McElrone, A.J. (2013) Maintenance of xylem network transport capacity: a review of embolism repair in vascular plants. *Frontiers in Plant Science* 4, 1–11.
- Campbell, E.M., Alfaro, R.I. and Hawkes, B. (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.
- Cardoza, Y.J., Moser, J.C., Klepzig, K.D. and Raffa, K.F. (2008) Multipartite symbioses among fungi, mites, nematodes, and the spruce beetle, *Dendroctonus rufipennis*. *Environmental Entomology* 37, 956–963.
- Carroll, A.L., Taylor, S.W., Régnière, J. and Safarynyk, L. (2004) Effects of climate change on range expansion by the mountain pine beetle in British Columbia. In: Shore, T., Brooks, J.E. and Stone, J.E. (eds) *Mountain Pine Beetle Symposium: Challenges and Solutions*, 30–31 October 2003, Kelowna, British Columbia. Information Report BC-X-399. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, pp. 223–232.
- Cerezke, H.F. (1995) Egg gallery, brood production, and adult characteristics of mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera, Scolytidae), in three pine hosts. *Canadian Entomologist* 127, 955–965.
- Choat, B., Jansen, S., Brodribb, T.J., Cochard, H., Delzon, S., et al. (2012) Global convergence in the vulnerability of forests to drought. *Nature* 491, 752–755.
- Christiansen, E. (1971) Laboratory study on factors influencing pre-imaginal development in *Hylobius abietis* L. (Coleoptera: Curculionidae). *Norsk Entomologisk Tidsskrift* 18, 1–8.
- Clark, E.L., Carroll, A.L. and Huber, D.P.W. (2010) Differences in the constitutive terpene profile of lodgepole pine across a geographical range in British Columbia, and correlation with historical attack by mountain pine beetle. *The Canadian Entomologist* 142, 557–573.

- Clark, E.L., Pitt, C., Lindgren, B.S., Carroll, A.L. and Huber, D.P.W. (2014) Comparison of lodgepole and jack pine constitutive and induced resin chemistry: implications for range expansion by the mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera: Curculionidae). *PeerJ* 2, e240.
- Clark, E.W. (1974) Reproductive diapause in *Hylobius pales*. *Annals of the Entomological Society of America* 68, 349–352.
- Colgan, L. and Erbilgin, N. (2011) Tree-mediated interactions between the jack pine budworm and a mountain pine beetle fungal associate. *Ecological Entomology* 36, 425–434.
- Coulson, R.N., McFadden, B.A., Pulley, P.E., Lovelady, C.N., Fitzgerald, J.W., *et al.* (1999) Heterogeneity of forest landscapes and the distribution and abundance of the southern pine beetle. *Forest Ecology and Management* 114, 471–485.
- Creeden, E.P., Hicke, J.A. and Buotte, P.C. (2014) Climate, weather, and recent mountain pine beetle outbreaks in the western United States. *Forest Ecology and Management* 312, 239–251.
- Cudmore, T.J., Bjorklund, N., Carroll, A.L. and Lindgren, B.S. (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.
- Cullingham, C.I., Cooke, J.E., Dang, S., Davis, C.S., Cooke, B.J., *et al.* (2011) Mountain pine beetle host–range expansion threatens the boreal forest. *Molecular Ecology* 20, 2157–2171.
- Davis, R.S., Hood, S. and Bentz, B.J. (2012) Fire-injured ponderosa pine provide a pulsed resource for bark beetles. *Canadian Journal of Forest Research* 26, 2022–2036.
- Davis, T.S. and Hofstetter, R.W. (2011) Reciprocal interactions between the bark beetle-associated yeast *Ogataea pini* and host plant phytochemistry. *Mycologia* 103, 1201–1207.
- de la Giroday, H.M.C., Carroll, A.L., Lindgren, B.S. and Aukema, B.H. (2011) Incoming! Association of landscape features with dispersing mountain pine beetle populations during a range expansion event in western Canada. *Landscape Ecology* 26, 1097–1110.
- de la Giroday, H.-M.C., Carroll, A.L. and Aukema, B.H. (2012) Breach of the northern Rocky Mountain geoclimatic barrier: initiation of range expansion by the mountain pine beetle. *Journal of Biogeography* 39, 1112–1123.
- DeLeon, D., Bedard, W.D. and Terrell, T.T. (1934) Recent discoveries concerning the biology of the mountain pine beetle and their effect on control in western white pine stands. *Journal of Forestry* 32, 430–436.
- Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., *et al.* (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America* 105, 6668–6672.
- Diguistini, S., Want, Y., Liao, N.Y., Taylor, G., Tanguay, P., *et al.* (2011) Genome and transcriptome analyses of the mountain pine beetle-fungal symbiont *Grosmannia clavigera*, a lodgepole pine pathogen. *Proceedings of the National Academy of Sciences of the United States of America* 108, 2504–2509.
- Dodds, K.J., Graber, C. and Stephen, F.M. (2001) Facultative intraguild predation by larval Cerambycidae (Coleoptera) on bark beetle larvae (Coleoptera: Scolytidae). *Environmental Entomology* 30, 17–22.
- Doležal, P. and Sehnal, F. (2007) Effects of photoperiod and temperature on the development and diapause of the bark beetle *Ips typographus*. *Journal of Applied Entomology* 131, 165–173.
- Dunn, J.P. and Lorio, P.L. Jr (1993) Modified water regimes affect photosynthesis, xylem water potential, cambial growth, and resistance of juvenile *Pinus taeda* L. to *Dendroctonus frontalis* (Coleoptera: Scolytidae). *Environmental Entomology* 22, 948–957.
- Emerick, J.J., Snyder, A.I., Bower, N.W. and Snyder, M.A. (2008) Mountain pine beetle attack associated with low levels of 4-allylanisole in ponderosa pine. *Environmental Entomology* 37, 871–875.
- Erbilgin, N. and Raffa, K.F. (2000) Effects of host tree species on attractiveness of tunneling pine engravers, *Ips pini* (Coleoptera, Scolytidae), to conspecifics and insect predators. *Journal of Chemical Ecology* 26, 823–840.
- Erbilgin, N., Nordheim, E.V., Aukema, B.H. and Raffa, K.F. (2002) Population dynamics of *Ips pini* and *Ips grandicollis* in red pine plantations in Wisconsin: within- and between-year associations with predators, competitors, and habitat quality. *Environmental Entomology* 31, 1043–1051.
- Erbilgin, N., Krokene, P., Christiansen, E., Zeneli, G. and Gershenson, J. (2006) Exogenous application of methyl jasmonate elicits defenses in Norway spruce (*Picea abies*) and reduces host colonization by the bark beetle *Ips typographus*. *Oecologia* 148, 426–436.
- Erbilgin, N., Ma, C., Whitehouse, C., Shan, B., Najjar, A., *et al.* (2013) Chemical similarity between historical and novel host plants promotes range expansion of the mountain pine beetle in a naive host ecosystem. *New Phytologist* 201, 940–950.

- Evangelista, P.H., Kumar, S., Stohlgren, T.J. and Young, N.E. (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.
- Faccoli, M. and Schlyter, F. (2007) Conifer phenolic resistance markers are bark beetle antifeedant semiochemicals. *Agricultural and Forest Entomology* 9, 237–245.
- Franceschi, V.R., Krokene, P., Christiansen, E. and Krekling, T. (2005) Anatomical and chemical defenses of conifer bark against bark beetles and other pests. *New Phytologist* 167, 353–376.
- Franks, P.J., Adams, M.A., Amthor, J.S., Barbour, M.M., Berry, J.A., *et al.* (2013) Sensitivity of plants to changing atmospheric CO₂ concentration: from the geological past to the next century. *New Phytologist* 197, 1077–1094.
- Galiano, L., Martinez-Vilalta, J. and Lloret, F. (2011) Carbon reserves and canopy defoliation determine the recovery of Scots pine 4-yr after a drought episode. *New Phytologist* 190, 750–759.
- Gandhi, K.J.K., Gilmore, D.W., Haack, R.A., Katovich, S.A., Krauth, S.J., *et al.* (2009) Application of semiochemicals to assess the biodiversity of subcortical insects following an ecosystem disturbance in a sub-boreal forest. *Journal of Chemical Ecology* 35, 1384–1410.
- Gara, R.I., Werner, R.A., Whitmore, M.C. and Holsten, E.H. (1995) Arthropod associates of the spruce beetle *Dendroctonus rufipennis* (Kirby) (Col., Scolytidae) in spruce stands of the south-central and interior Alaska. *Journal of Applied Entomology* 119, 585–590.
- Gaylord, M.L., Kolb, T.E., Wallin, K.F. and Wagner, M.R. (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.L., Kolb, T.E., Pockman, W.T., Plaut, J.A., Yopez, E.A., *et al.* (2013) Drought predisposes piñon-juniper woodlands to insect attacks and mortality. *New Phytologist* 198, 567–578.
- Gehrken, U. (1984) Winter survival of an adult bark beetle *Ips acuminatus* Gyll. *Journal of Insect Physiology* 30, 421–429.
- Gehrken, U. (1985) Physiology of diapause in the adult bark beetle, *Ips acuminatus* Gyll., studied in relation to cold hardiness. *Journal of Insect Physiology* 31, 909–916.
- Gibbs, J.N. (1978) Intercontinental epidemiology of Dutch elm disease. *Annual Review of Phytopathology* 16, 287–307.
- Gruber, A., Pirkebner, D., Florian, C. and Oberhuber, W. (2011) No evidence for depletion of carbohydrate pools in Scots pine (*Pinus sylvestris* L.) under drought stress. *Plant Biology*, doi:10.1111/j.1438-8677.2011.00467.x.
- Guérard, N., Maillard, P., Bréchet, C., Lieutier, F. and Dreyer, E. (2007) Do trees use reserve or newly assimilated carbon for their defense reactions? A ¹³C labeling approach with young Scots pines inoculated with a bark-beetle-associated fungus (*Ophiostoma brunneo ciliatum*). *Annals of Forest Science* 64, 601–608.
- Haack, R., Wilkinson, R. and Foltz, J. (1987) Plasticity in life-history traits of the bark beetle *Ips calligraphus* as influenced by phloem thickness. *Oecologia* 72, 32–38.
- Haber Kern, K.E. and Raffa, K.F. (2003) Phloeophagous and predaceous insects responding to synthetic pheromones of bark beetles inhabiting white spruce stands in the Great Lakes Region. *Journal of Chemical Ecology* 29, 1651–1663.
- Haber Kern, K.E., Illman, B.L. and Raffa, K.F. (2002) Bark beetles and fungal associates colonizing white spruce in the Great Lakes region. *Canadian Journal of Forest Research* 32, 1137–1150.
- Hammerbacher, A., Schmidt, A., Wadke, N., Wright, L.P., Schenider, B., *et al.* (2013) A common fungal associate of the spruce bark beetle metabolizes the stilbene defenses of Norway spruce. *Plant Physiology* 162, 1324–1336.
- Hansen, E.M., Bentz, B.J. and Turner, D.L. (2001) Physiological basis for flexible voltinism in the spruce beetle (Coleoptera: Scolytidae). *The Canadian Entomologist* 133, 805–817.
- Hart, S.J., Veblen, T.T., Eisenhart, K.S., Jarvis, D. and Kulakowski, D. (2014) Drought induces spruce beetle (*Dendroctonus rufipennis*) outbreaks across northwestern Colorado. *Ecology* 95, 930–939.
- Hartmann, H., Ziegler, W., Kolle, O. and Trumbore, S. (2013a) Thirst beats hunger – declining hydration during drought prevents carbon starvation in Norway spruce seedlings. *New Phytologist*, doi:10.1111/nph.12331.
- Hartmann, H., Ziegler, W. and Trumbore, S. (2013b) Lethal drought leads to reduction in nonstructural carbohydrates in Norway spruce tree roots but not in the canopy. *Functional Ecology* 27, 413–427.
- Hebertson, E.G. and Jenkins, M.J. (2003) Historic climate factors associated with major avalanche years on the Wasatch Plateau, Utah. *Cold Regions Science and Technology* 37, 315–332.
- Hebertson, E.G. and Jenkins, M.J. (2008) Climate factors associate with historical spruce beetle (Coleoptera: Curculionidae) outbreaks in Utah and Colorado. *Environmental Entomology* 37, 281–292.

- Hermes, D.A. and Mattson, W.T. (1992) The dilemma of plants – To grow or defend. *Quarterly Review of Biology* 67, 283–335.
- Hicke, J.A., Logan, J.A., Powell, J. and Ojima, D.S. (2006) Changing temperatures influence suitability for modeled mountain pine beetle (*Dendroctonus ponderosae*) outbreaks in the western United States. *Journal of Geophysical Research-Biogeosciences* 111(G2), G02019.
- Hodges, J.D. and Lorio, P.L. Jr (1975) Moisture stress and composition of xylem oleoresin in loblolly pine. *Forest Science* 21, 283–290.
- Hoffmann, A.A. and Sgrò, C.M. (2011) Climate change and evolutionary adaptation. *Nature* 470, 479–485.
- Hofstetter, R., Dempsey, T., Klepzig, K. and Ayres, M. (2007) Temperature-dependent effects on mutualistic, antagonistic, and commensalistic interactions among insects, fungi and mites. *Community Ecology* 8, 47–56.
- Hood, S.M. and Bentz, B. (2007) Predicting post-fire Douglas-fir beetle attacks and tree mortality in the Northern Rocky Mountains. *Canadian Journal of Forest Research* 37, 1058–1069.
- Huber, D.P.W., Ralph, S. and Bohlmann, J. (2004) Genomic hardwiring and phenotypic plasticity of terpenoid-based defenses in conifers. *Journal of Chemical Ecology* 30, 2399–2418.
- Inward, D.J.G., Wainhouse, D. and Peace, A. (2012) The effect of temperature on the development and life cycle regulation of the pine weevil *Hyllobius abietis* and the potential impacts of climate change. *Agriculture and Forest Entomology* 14, 348–357.
- IPCC (Intergovernmental Panel on Climate Change) (2007) *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK, and New York.
- Irwin, J.T. and Lee, R.E. Jr (2003) Cold winter micro-environments conserve energy and improve overwintering survival and potential fecundity of the goldenrod gall fly, *Eurosta solidaginis*. *Oikos* 100, 71–78.
- Jackson, P.L., Straussfogel, D., Lindgren, B.S., Mitchell, S. and Murphy, B. (2008) Radar observation and aerial capture of mountain pine beetle, *Dendroctonus ponderosae* Hopk. (Coleoptera: Scolytidae) in flight above the forest canopy. *Canadian Journal of Forest Research* 38, 2313–2327.
- Jactel, H. and Brockerhoff, E.G. (2007) Tree diversity reduces herbivory by forest insects. *Ecology Letters* 10, 835–848.
- Jewett, J.T., Lawrence, R.L., Marshall, L.A., Gessler, P.E., Powell, S.L., *et al.* (2011) Spatio-temporal relationships between climate and whitebark pine mortality in the Greater Yellowstone Ecosystem. *Forest Science* 57, 320–335.
- Kaiser, K.E., McGlynn B.L. and Emanuel, R.E. (2014) Ecohydrology of an outbreak: mountain pine beetle impacts trees in drier landscape positions first. *Ecohydrology* 6, 444–454.
- Kane, J.M. and Kolb, T.E. (2010) Importance of resin ducts in reducing ponderosa pine mortality following bark beetle attack. *Oecologia* 164, 601–609.
- Keeling, C.I. and Bohlmann, J. (2006) Genes, enzymes and chemicals of terpenoid diversity in the constitutive and induced defence of conifers against insects and pathogens. *New Phytologist* 170, 657–675.
- Kelsey, J.G., Peck, R.G. and Niwa, C.G. (2001) Response of some scolytids and their predators to ethanol and 4-allylanisole in pine forests of central Oregon. *Journal of Chemical Ecology* 27, 697–715.
- Kelsey, R.G. and Joseph, G. (2001) Attraction of *Scolytus unispinosus* bark beetles to ethanol in water-stressed Douglas-fir branches. *Forest Ecology and Management* 144, 229–238.
- Klepzig, K.D., Smalley, E.B. and Raffa, K.F. (1996) Combined chemical defenses against an insect–fungal complex. *Journal of Chemical Ecology* 22, 1367–1388.
- Klepzig, K.D., Adams, A.S., Handelsman, J. and Raffa, K.F. (2009) Symbioses, a key driver of insect physiological processes, ecological interactions, evolutionary diversification, and impacts on humans. *Environmental Entomology* 38, 67–77.
- Koepke, D.F. and Kolb, T.E. (2013) Species variation in water relations and xylem vulnerability to cavitation at a forest-woodland ecotone. *Forest Science* 59, 524–535.
- Košťál, V., Doležal, P., Rozsypal, J., Moravcová, M., Zahradníčková, H., *et al.* (2011) Physiological and biochemical analysis of overwintering and cold tolerance in two Central European populations of the spruce bark beetle, *Ips typographus*. *Journal of Insect Physiology* 57, 1136–1146.
- Langor, D.W. and Raske, A.G. (1987) Reproduction and development of the eastern larch beetle, *Dendroctonus simplex* Leconte (Coleoptera: Scolytidae) in Newfoundland. *The Canadian Entomologist* 119, 985–992.
- Lee, R.E. (1991) Principles of insect low temperature tolerance. In: Lee, R.E. and Denlinger, D.L. (eds) *Insects at Low Temperature*. Chapman and Hall, New York, pp. 17–46.

- Lee, S., Kim, J.J. and Breuil, C. (2006) Pathogenicity of *Leptographium longiclavatum* associated with *Dendroctonus ponderosae* to *Pinus contorta*. *Canadian Journal of Forest Research* 36, 2864–2872.
- Lerch, A. (2013) Mountain pine beetle dynamics and lodgepole and ponderosa pine mortality following wildfire in the Uinta Mountains of northern Utah. MSc thesis, University of Wisconsin-Madison.
- Lester, J.D. and Irwin, J.T. (2012) Metabolism and cold tolerance of overwintering adult mountain pine beetles (*Dendroctonus ponderosae*): evidence of facultative diapause? *Journal of Insect Physiology* 58, 808–815.
- Lewinsohn, E., Gijzen, M., Muzika, R.M., Barton, K. and Croteau, R. (1993) Oleoresinosis in grand fir (*Abies grandis*) saplings and mature trees. Modulation of this wound response by light and water stresses. *Plant Physiology* 101, 1021–1028.
- Lieutier, F., Yart, A. and Sallé, A. (2009) Stimulation of tree defenses by Ophiostomatoid fungi can explain attack success of bark beetles on conifers. *Annals of Forest Science* 66, 801–823.
- Lindgren, B.S. and Raffa, K.F. (2013) Evolution of tree killing in bark beetles (Coleoptera: Curculionidae): trade-offs between the maddening crowds and a sticky situation. *The Canadian Entomologist* 145, 471–495.
- Littell, J.S., Oneil, E.E., Mckenzie, D., Hicke, J.A., Lutz, J.A., *et al.* (2010) Forest ecosystems, disturbance, and climatic change in Washington State, USA. *Climatic Change* 102, 129–158.
- Logan, J.A. and Bentz, B.J. (1999) Model analysis of mountain pine beetle (Coleoptera: Scolytidae) seasonality. *Environmental Entomology* 28, 924–934.
- Logan, J.A. and Powell, J.A. (2001) Ghost forests, global warming and the mountain pine beetle (Coleoptera: Scolytidae). *American Entomologist* 47, 160–173.
- Logan, J.A. and Powell, J.A. (2009) Ecological consequences of climate change altered forest insect disturbance regimes. In: Wagner, F.H. (ed.) *Climate Change in Western North America: Evidence and Environmental Effects*. University of Utah Press, Salt Lake City, Utah.
- Logan, J.A., Macfarlane, W.W. and Willcox, L. (2010) Whitebark pine vulnerability to climate-driven mountain pine beetle disturbance in the Greater Yellowstone ecosystem. *Ecological Applications* 20, 895–902.
- Lombardero, M.J., Ayres, M.P., Ayres, B.D. and Reeve, J.D. (2000a) Cold tolerance of four species of bark beetle (Coleoptera: Scolytidae) in North America. *Environmental Entomology* 29, 421–432.
- Lombardero, M.J., Ayres, M.P., Lorio, P.L. and Ruel, J.J. (2000b) Environmental effects on constitutive and inducible resin defences of *Pinus taeda*. *Ecology Letters* 3, 329–339.
- Lorio, P.L. Jr, Stephen, F.M. and Paine, T.S. (1995) Environment and ontogeny modify loblolly pine response to induced acute water deficits and bark beetle attack. *Forest Ecology and Management* 73, 97–110.
- Luo, Y., Gerten, D., Lemaire, Parton, W.J., Weng, E., Zhou, X., *et al.* (2008) Modeled interactive effects of precipitation, temperature, and [CO₂] on ecosystem carbon and water dynamics in different climatic zones. *Global Change Biology* 14, 1986–1999.
- Lusebrink, I., Evenden, M.L., Blanchet, F.G., Cooke, J.E.K. and Erbilgin, N. (2011) Effect of water stress and fungal inoculation on monoterpene emission from an historical and a new pine host of the mountain pine beetle. *Journal of Chemical Ecology* 37, 1013–1026.
- Lusebrink, I., Erbilgin, N. and Evenden, M.L. (2013) The lodgepole x jack pine hybrid zone in Alberta, Canada, a stepping stone for the mountain pine beetle on its journey east across the boreal forest? *Journal of Chemical Ecology* 39, 1209–1220.
- McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, 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.
- McKee, F.R. and Aukema, B.H. (2015a) Influence of temperature on the reproductive success, brood development, and brood fitness of the eastern larch beetle, *Dendroctonus simplex* LeConte. *Agricultural and Forest Entomology* 17, 102–112.
- McKee, F.R. and Aukema, B.H. (2015b) Successful reproduction by eastern larch beetle progeny in the absence of an overwintering period. *The Canadian Entomologist* (in press).
- Manning, C.G. and Reid, M.L. (2013) Sub-lethal effects of monoterpenes on reproduction by mountain pine beetles. *Agricultural and Forest Entomology*, doi:10.1111/afe.12013.
- Manter, D.K. and Kelsey, R.G. (2008) Ethanol accumulation in drought-stressed conifer seedlings. *International Journal of Plant Science* 169, 361–369.
- Marini, L., Ayres, M.P., Battisti, A. and Faccoli, M. (2012) Climate affects severity and altitudinal distribution of outbreaks in an eruptive bark beetle. *Climatic Change* 115, 327–341.
- Martínez-Vilalta, J., Sala, A. and Piñol, J. (2004) The hydraulic architecture of Pinaceae – a review. *Plant Ecology* 171, 3–13.

- Miller, D.R. and Borden, J.H. (2000) Dose-dependent and species-specific responses of pine bark beetles (Coleoptera, Scolytidae) to monoterpenes in association with pheromones. *The Canadian Entomologist* 132, 183–195.
- Miller, D.R. and Rabaglia, R.J. (2009) Ethanol and (-)- α -pinene: attractant kairomones for bark and ambrosia beetles in the southeastern US. *Journal of Chemical Ecology* 35, 435–448.
- Miller, D.R., Lindgren, B.S. and Borden, J.H. (2005) Dose-dependent pheromone responses of mountain pine beetle in stands of lodgepole pine. *Environmental Entomology* 34, 1019–1027.
- Miller, D.R., Dodds, K.J., Eglitis, A., Fettig, C.J., Hofsetter, R.W., *et al.* (2013) Trap lure blend of pine volatiles and bark beetle pheromones for *Monochamus* spp. (Coleoptera, Cerambycidae) in pine forests of Canada and the United States. *Journal of Economic Entomology* 106, 1684–1692.
- Miller, L.K. and Werner, R.A. (1987) Cold-hardiness of adult and larval spruce beetles *Dendroctonus rufipennis* (Kirby) in interior Alaska. *Canadian Journal of Zoology* 65, 2927–2930.
- Mitchell, P.J., O'Grady, A.P., Tissue, D.T., White, D.A., Ottenschlaeger, M.L., *et al.* (2013) Drought response strategies define the relative contributions of hydraulic dysfunction and carbohydrate depletion during tree mortality. *New Phytologist* 197, 862–872.
- Morales-Jimenez, J., Zuniga, G., Ramirez-Saad, H.C. and Hernandez-Rodriguez, C. (2012) Gut-associated bacteria throughout the life cycle of the bark beetle *Dendroctonus rhizophagus* Thomas and Bright (Curculionidae, Scolytinae) and their cellulolytic activities. *Microbial Ecology* 64, 268–278.
- Moser, J.C., Fitzgibbon, B.A. and Klepzig, K.D. (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.
- Negrón, J.F., McMillin, J.D., Anhold, J.A. and Coulson, D. (2009) Bark beetle-caused mortality in a drought-affected ponderosa pine landscape in Arizona, USA. *Forest Ecology and Management* 257, 1353–1362.
- Novick, K.A., Katul, G.G., McCarthy, H.R. and Oren, R. (2012) Increased resin flow in mature pine trees growing under elevated CO₂ and moderate soil fertility. *Tree Physiology* 10.1093/treephys/tpr133.
- Pallardy, S.G. (2008) *Physiology of Woody Plants*. Academic Press, New York.
- Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* 37, 637–669.
- Plaut, J.A., Yepez, E.A., Hill, J., Pangle, R., Sperry, J.S., *et al.* (2012) Hydraulic limits preceding mortality in a pinon-juniper woodland under experimental drought. *Plant, Cell, Environment* 35, 1601–1617.
- Powell, E.N. and Raffa, K.F. (2011) Fire injury reduces inducible defenses of lodgepole pine against mountain pine beetle. *Journal of Chemical Ecology* 37, 1184–1192.
- Powell, E.N., Townsend, P.A. and Raffa, K.F. (2012) Wildfire provides refuge from local extinction but is an unlikely driver of outbreaks by mountain pine beetle. *Ecological Monographs* 82, 69–84.
- Powell, J.A. and Bentz, B.J. (2009) Connecting phenological predictions with population growth rates for mountain pine beetle, an outbreak insect. *Landscape Ecology* 24, 657–672.
- Preisler, H.K., Hicke, J.A., Ager, A.A. and Hayes, J.L. (2012) Climate and weather influences on spatial temporal patterns of mountain pine beetle populations in Washington and Oregon. *Ecology* 93, 2421–2434.
- Raffa, K.F. (1991) Temporal and spatial disparities among bark beetles, predators, and associates responding to synthetic bark beetle pheromones, *Ips pini* in Wisconsin. *Environmental Entomology* 20, 1665–1679.
- Raffa, K.F. (2014) Terpenes tell different tales at different scales: glimpses into the chemical ecology of conifer–bark beetle–microbial interactions. *Journal of Chemical Ecology*, doi:10.1007/s10886-013-0368-y.
- Raffa, K.F. and Berryman, A.A. (1982a) Gustatory cues in the orientation of *Dendroctonus ponderosae* (Coleoptera: Scolytidae) to host trees. *Canadian Entomologist* 114, 97–104.
- Raffa, K.F. and Berryman, A.A. (1982b) Physiological differences between lodgepole pines resistant and susceptible to the mountain pine beetle and associated microorganisms. *Environmental Entomology* 11, 486–492.
- Raffa, K.F. and Berryman, A.A. (1983) The role of host plant resistance in the colonization behavior and ecology of bark beetles. *Ecological Monographs* 53, 27–49.
- Raffa, K.F. and Smalley, E.B. (1995) Interaction of pre-attack and induced monoterpene concentrations in conifer defense against bark beetle–microbial complexes. *Oecologia* 102, 285–295.
- Raffa, K.F., Aukema, B.H., Erbilgin, N., Klepzig, K.D. and Wallin, K.F. (2005) Interactions among conifer terpenoids and bark beetles across multiple levels of scale, an attempt to understand links

- between population patterns and physiological processes. *Recent Advances in Phytochemistry* 39, 80–118.
- Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., *et al.* (2008) Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *Bioscience* 58, 501–517.
- Raffa, K.F., Powell, E.N. and Townsend, P.A. (2013) Temperature-driven range expansion of an irruptive insect heightened by weakly coevolved plant defenses. *Proceedings of the National Academy of Sciences of the United States of America* 110, 2193–2198.
- Reeve, J.D. (2000) Complex emergence patterns in a bark beetle predator. *Agricultural and Forest Entomology* 2, 233–240.
- Reeve, J.D., Ayers, M.P. and Lorio, P.L. Jr (1995) Host suitability, predation, and bark beetle population dynamics. In: Cappuccino, N. and Price, P.W. (eds) *Population Dynamics: New Approaches and Synthesis*. Academic Press, San Diego, California, pp. 339–357.
- Reeve, J.D., Rhodes, D.J. and Turchin, P. (1998) Scramble competition in the southern pine beetle, *Dendroctonus frontalis*. *Ecological Entomology* 23, 433–443.
- Régnière, J. and Bentz, B. (2007) Modeling cold tolerance in the mountain pine beetle, *Dendroctonus ponderosae*. *Journal of Insect Physiology* 53, 559–572.
- Régnière, J., Powell, J., Bentz, B. and Nealis, V. (2012) Effects of temperature on development, survival and reproduction of insects: experimental design, data analysis and modeling. *Journal of Insect Physiology* 58, 634–647.
- Rice, A., Thormann, M. and Langor, D. (2008) Mountain pine beetle-associated blue-stain fungi are differentially adapted to boreal temperatures. *Forest Pathology* 38, 113–123.
- Robertson, C., Nelson, T.A., Jelinski, D.E., Wulder, M.A. and Boots, B. (2009) Spatial-temporal analysis of species range expansion: the case of the mountain pine beetle, *Dendroctonus ponderosae*. *Journal of Biogeography* 36, 1446–1458.
- Rolland, C. and Lempriere, G. (2004) Effects of climate on radial growth of Norway spruce and interactions with attacks by the bark beetle *Dendroctonus micans* (Kug., Coleoptera: Scolytidae): a dendroecological study in the French Massif Central. *Forest Ecology and Management* 201, 89–104.
- Rosner, S., Klein, A., Wimmer, R. and Karlsson, B. (2006) Extraction of features from ultrasound acoustic emissions: a tool to assess the hydraulic vulnerability of Norway spruce trunkwood? *New Phytologist* 171, 105–116.
- Ross, D.W. and Daterman, G.E. (1995) Response of *Dendroctonus pseudotsugae* (Coleoptera, Scolytidae) and *Thanasimus undatulus* (Coleoptera, Cleridae) to traps with different semiochemicals. *Journal of Economic Entomology* 88, 106–111.
- Ross, D.W. and Daterman, G.E. (1997) Using pheromone-baited traps to control the amount and distribution of tree mortality during outbreaks of the Douglas-fir beetle. *Forest Science* 43, 65–70.
- Rouault, G.L., Candau, J.-N.L., Lieutier, F.O., Nageleisen, L.-M., Martin, J.-C., *et al.* (2006) Effects of drought and heat on forest insect populations in relation to the 2003 drought in Western Europe. *Annals of Forest Science* 63, 613–624.
- Rudinsky, J.A. and Michael, R.R. (1972) Sound production in Scolytidae: chemostimulus of sonic signal by the Douglas-fir beetle. *Science* 175, 1386–1390.
- Ryall, K.L. and Fahrig, L. (2005) Habitat loss decreases predator-prey ratios in a pine-bark beetle system. *Oikos* 110, 265–270.
- Ryan, R.B. (1959) Termination of diapause in the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins (Coleoptera: Scolytidae), as an aid to continuous laboratory rearing. *The Canadian Entomologist* 91, 520–525.
- Safranyik, L. and Carroll, A.L. (2006) The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. In: Safranyik, L. and Wilson, W.R. (eds) *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, pp. 3–66.
- Safranyik, L. and Linton, D.A. (1991) Unseasonably low fall and winter temperatures affecting mountain pine beetle and pine engraver beetle populations and damage in the British Columbia Chilcotin Region. *Journal of the Entomological Society of British Columbia* 88, 17–21.
- Safranyik, L., Simmons, C. and Barclay, H.J. (1990) A conceptual model of spruce beetle population dynamics. *Forestry Canada Information Report BC-X-316*.
- Safranyik, L., Carroll, A.L., Regniere, J., Langor, D.W., Riel, W.G., *et al.* (2010) Potential for range expansion of mountain pine beetle into the boreal forest of North America. *Canadian Entomologist* 142, 415–442.
- Sala, A., Piper, F. and Hoch, G. (2010) Physiological mechanisms of drought-induced tree mortality are far from being resolved. *New Phytologist* 186, 274–281.

- Sala, A., Woodruff, D.R. and Meinzer, F.C. (2012) Carbon dynamics in trees: feast or famine? *Tree Physiology* 10.1093/treephys/tp143.
- Sambaraju, K.R., Carroll, A.L., Zhu, J., Stahl, K., Moore, R.D., *et al.* (2012) Climate change could alter the distribution of mountain pine beetle outbreaks in western Canada. *Ecography* 35, 211–223.
- Schmidt, A., Nagel, R., Krekling, T., Christiansen, E., Gershenzon, J., *et al.* (2011) Induction of isoprenyl diphosphate synthases, plant hormones and defense signalling genes correlates with traumatic resin duct formation in Norway spruce (*Picea abies*). *Plant Molecular Biology* 77, 577–590.
- Schroeder, L.M. and Weslien, J. (1994) Reduced offsprung production in bark beetle *Tomicus piniperda* in pine bolts baited with ethanol and alpha-pinene, which attract antagonistic insects. *Journal of Chemical Ecology* 20, 1429–1444.
- Scott, B. and Berryman, A. (1972) Larval diapause in *Scolytus ventralis* (Coleoptera: Scolytidae). *Journal of the Entomological Society of British Columbia* 69, 50–53.
- Scott, J.J., Oh, D.-C., Yuceer, M.C., Klepzig, K.D., Clardy, J., *et al.* (2008) Bacterial protection of beetle–fungus mutualism. *Science* 322, 63.
- Seybold, S.J., Huber, D.P.W., Lee, J.C., Graves, A.D. and Bohlmann, J. (2006) Pine monoterpenes and pine bark beetles: a marriage of convenience for defense and chemical communication. *Phytochemistry Review* 5, 143–178.
- Sherriff, R.L., Berg, E.E. and Miller, A.E. (2011) Climate variability and spruce beetle (*Dendroctonus rufipennis*) outbreaks in south-central and southwest Alaska. *Ecology* 92, 1459–1470.
- Simard, M., Powell, E.N., Raffa, K.F. and Turner, M.G. (2012) What explains landscape patterns of tree mortality caused by bark beetle outbreaks in Greater Yellowstone? *Global Ecology and Biogeography* 21, 556–567.
- Singer, M.C. and McBride, C.S. (2010) Multitrait, host-associated divergence among sets of butterfly populations, implications for reproductive isolation and ecological speciation. *Evolution* 64, 921–933.
- Six, D.L. (2003) Bark beetle–fungus symbiosis. In: Miller, T. and Kourtzis, K. (eds) *Insect Symbiosis*. CRC Press, Boca Raton, Florida, pp. 99–116.
- Six, D.L. and Wingfield, M.J. (2011) The role of phytopathogenicity in bark beetle–fungus symbioses: a challenge to the classic paradigm. *Annual Review of Entomology* 56, 255–272.
- Stahl, K., Moore, R.D. and McKendry, I.G. (2006) Climatology of winter cold spells in relation to mountain pine beetle mortality in British Columbia, Canada. *Climate Research* 32, 13–23.
- Strom, B.L., Goyer, R.A. and Shea, P.J. (2001) Visual and olfactory disruption of orientation by the western pine beetle to attractant-baited traps. *Entomologia Experimentalis et Applicata* 100, 63–67.
- Sturgeon, K.B. and Mitton, J.B. (1986) Allozyme and morphological differentiation of mountain pine beetles *Dendroctonus ponderosae* Hopkins associated with host tree. *Evolution* 40, 290–302.
- Sun, J., Lu, M., Gillette, N. E. and Wingfield, M.J. (2013) Red turpentine beetle, innocuous native becomes invasive tree killer in China. *Annual Review of Entomology* 58, 293–311.
- Tauber, M.J., Tauber, C.A. and Masaki, S. (1986) *Seasonal Adaptations of Insects*. Oxford University Press, New York, p. 411.
- Taylor, S.W. and Carroll, A.L. (2004) Disturbance, forest age dynamics and mountain pine beetle outbreaks in BC: a historical perspective. In: Shore, T.L., Brooks, J.E. and Stone, J.E. (eds) *Challenges and Solutions: Proceedings of the Mountain Pine Beetle Symposium*. Kelowna, British Columbia, Canada, 30–31 October 2003. Canadian Forest Service, Pacific Forestry Centre, Information Report BC-X-399, pp. 41–51.
- Thomson, A.J. and Shrimpton, D.M. (1984) Weather associated with the start of mountain pine beetle outbreaks. *Canadian Journal of Forest Research* 14, 255–258.
- Trần, J.K.I., Ylioja, T., Billings, R.F., Régnière, J. and Ayres, M.P. (2007) Impact of minimum winter temperatures on the population dynamics of *Dendroctonus frontalis*. *Ecological Applications* 17, 882–899.
- Turchin, P., Taylor, A.D. and Reeve, J.D. (1999) Dynamical role of predators in population cycles of a forest insect: an experimental test. *Science* 285, 1068–1071.
- Turtola, S., Manninen, A., Rikala, R. and Kainulainen, P. (2003) Drought stress alters the concentration of wood terpenoids in Scots pine and Norway spruce seedlings. *Journal of Chemical Ecology* 29, 1981–1995.
- Ungerer, M.J., Ayres, M.P. and Lombardero, M.J. (1999) Climate and the northern distribution limits of *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae). *Journal of Biogeography* 26, 1133–1145.
- Vose, J.M., Peterson, D.L. and Patel-Weynand, T. (eds) (2012) Effects of climatic variability and change on forest ecosystems: A comprehensive science synthesis for the U.S. forest sector. USDA General Technical Report PNW-GTR-870. USDA, Portland, Oregon.
- Wagner, T.L., Gagne, J.A., Sharpe, P.J.H. and Coulson, R.N. (1983) A biophysical model of

- southern pine beetle, *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae) development. *Ecological Modelling* 21, 125–147.
- Wallin, K.F. and Raffa, K.F. (2001) Effects of folivory on subcortical plant defenses: Can defense theories predict interguild processes? *Ecology* 82, 1387–1400.
- Wallin, K.F., Kolb, T.E., Skov, K. and Wagner, M.R. (2003) Effects of crown scorch on ponderosa pine resistance to bark beetles in northern Arizona. *Environmental Entomology* 32, 652–661.
- Waring, K.M., Reboletti, D.M., Mork, L.A., Huang, C.H., Hofstetter, R.W., *et al.* (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.
- Waring, R.H. (1983) Estimating forest growth and efficiency in relation to tree canopy age. *Advances in Ecological Research* 13, 327–354.
- Way, A. and Oren, R. (2010) Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data. *Tree Physiology* 30, 669–688.
- Weed, A.S., Ayres, M.P. and Hicke, J.A. (2013) Consequences of climate change for biotic disturbances in North American forests. *Ecological Monographs* 84, 441–470.
- Weed, A.S., Bentz, B.J., Ayres, M.P. and Holmes, T.P. (2015) Geographically variable response of *Dendroctonus ponderosae* to winter warming in the western United States. *Landscape Ecology*, doi:10.1007/s10980-015-0170-z.
- Wermelinger, B. and Seifert, M. (1998) Analysis of the temperature dependent development of the spruce bark beetle *Ips typographus* (L.) (Col., Scolytidae). *Journal of Applied Entomology* 122, 185–191.
- Werner, R.A. and Holsten, E.H. (1985) Factors influencing generation times of spruce beetles in Alaska. *Canadian Journal of Forest Research* 15, 438–443.
- Werner, R.A., Raffa, K.F. and Illman, B.L. (2006) Insect and pathogen dynamics. In: Chapin, F.S. III, Oswood, M., Van Cleve, K., Viereck, L.A. and Verbyla, D. (eds) *Alaska's Changing Boreal Forest*. Oxford University Press, Oxford, UK, pp. 133–146.
- Westbrook, J.W., Resende, M.F.R., Munoz, P., Walker, A.R., Wegrzyn, J.L., *et al.* (2013) Association genetics of oleoresin flow in loblolly pine: discovering genes and predicting phenotype for improved resistance to bark beetles and bioenergy potential. *New Phytologist*, doi:10.1111/nph.12240.
- Westerling, A.L., Turner, M.G., Southwick, E.A.H., Romme, W.H. and Ryan, M.G. (2011) Continued warming could transform Greater Yellowstone Ecosystem fire regimes by mid-21st century. *Proceedings of the National Academy of Sciences of the United States of America* 108, 13165–13170.
- Williams, A.P., Allen, C.D., Millar, C.I., Swetnam, T.W., Michaelsen, J., *et al.* (2010) Forest responses to increasing aridity and warmth in the southwestern United States. *Proceedings of the National Academy of Sciences of the United States of America* 107, 21289–21294.
- Williams, A.P., Allen, C.D., Macalady, A.K., Griffin, D., Woodhouse, C.A., *et al.* (2012) Temperature as a potent driver of forest drought stress and tree mortality. *Nature Climate Change*, doi:10.1038/NCLIMATE1693.
- Wood, D.L. (1982) The role of pheromones, kairomones, and allomones in the host selection behavior of bark beetles. *Annual Review of Entomology* 27, 411–446.
- Zhao, J., Hartmann, H., Trumbore, S., Ziegler, W. and Zhang, Y. (2013) High temperature causes negative whole-plant carbon balance under mild drought. *New Phytologist*, doi:10.1111/nph.12400.
- Zhou, J.L., Ross, D.W. and Niwa, C.G. (2001) Kairomonal response of *Thanasimus undatulus*, *Enoclerus spegeus* (Coleoptera, Cleridae), and *Temnochila chlorodia* (Coleoptera, Trogositidae) to bark beetle semiochemicals in eastern Oregon. *Environmental Entomology* 30, 993–998.