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# Complexities in predicting mountain pine beetle and spruce beetle response to climate change

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## 1 Introduction

Bark beetle (Coleoptera: Curculionidae, Scolytinae) life processes, as with all insects, depend on the environment. Insect growth, development, and survival are directly influenced by temperature (Bale et al., 2002; Régnière, Powell, Bentz, & Nealis, 2012) and precipitation (Reid & Ahn, 2020), as are the host trees essential for their survival (Rehfeldt, Crookston, Warwell, & Evans, 2006). Many bark beetle species within the genus *Dendroctonus* require complete or partial tree death for offspring production. Large and vigorous trees with thick phloem provide the most resources for developing brood (Amman, 1972), although they generally have greater levels of defense that require larger numbers of beetles to overcome and kill (Boone, Aukema, Bohlmann, Carroll, & Raffa, 2011). Warm temperatures and decreased precipitation can reduce tree defenses enabling fewer attacking beetles to overwhelm and kill potential host trees, thereby indirectly favoring population success (Anderegg et al., 2015). Changing thermal regimes can also directly influence the number of beetles available to attack and overwhelm host trees through effects to winter survival and cohort synchrony (Bentz & Jönsson, 2015). Relative to long-term trends, temperature and precipitation norms have been changing in recent decades because of atmospheric changes in climate. Globally, temperature and vapor pressure deficit are increasing (www.ipcc.ch). In the past several decades, tree mortality due to bark beetles in temperate forests of western North America has been extensive (Hicke, Xu, Meddens, & Egan, 2020), and in some cases, the increased mortality has been attributed to indirect (Fettig, Mortenson, Bulaon, & Foulk, 2019; Hart, Veblen, Schneider, & Molotch, 2017; Kolb et al., 2019) and direct (Berg, Henry, Fastie, De Volder, & Matsuoka, 2006; Buotte et al., 2016; Lesk, Coffel, D'Amato, Dodds, & Horton, 2017; Pettit, Voelker, DeRose, & Burton,

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2020; Sambaraju, Carroll, & Aukema, 2019) effects of reduced precipitation and warming temperatures.

Temperature directly effects bark beetles through: (1) development and growth rates, (2) the induction, development, and termination of diapause, and (3) mortality from extreme temperatures. Development rates and thermal thresholds are key traits that drive generation time and have evolved to match appropriate life stages with the seasons and synchronize adult emergence for the mass aggregation needed to overwhelm defenses of host trees where brood develop (Hansen, Bentz, & Turner, 2001; Logan & Bentz, 1999). Diapause, a resting state, is also an important synchronizer of bark beetle cohorts in multiple species and provides a means for surviving adverse conditions such as extreme cold or heat (Doležal & Sehnal, 2007; Gent, Wainhouse, Day, Peace, & Inward, 2017; Hansen, Bentz, Powell, Gray, & Vandygriff, 2011; Inward, Wainhouse, & Peace, 2012; Langor & Raske, 1987; Schebeck et al., 2017). Metabolic production of compounds that serve to protect tissues during extreme cold (i.e., cold hardening) has also evolved in bark beetle species inhabiting temperate forests (Bentz & Mullins, 1999; Lombardero, Ayres, Ayres, & Reeve, 2000; Zhao et al., 2021). Multiple thermally regulated physiological traits are therefore integrated to maintain bark beetle seasonality and survival in temperate forests, where the timing of adult emergence and overwintering life stages are critical. For species that can cause landscape-scale tree mortality, including many *Dendroctonus* species, these traits play important roles in population outbreak initiation and growth, and subsequent tree mortality. Many *Dendroctonus* species also have distributions that extend across widely varying environmental conditions, generally following the distributions of their host trees, resulting in the potential for adaptive differentiation in environmentally determined traits.

Two species with extensive distributions across North America are *Dendroctonus rufipennis* Kirby (spruce beetle, SB) and *D. ponderosae* Hopkins (mountain pine beetle, MPB). Both species are native to North America and are known for their capacity to cause landscape-scale tree mortality. During the past several decades, the two species killed ∼2.4 billion trees across ∼2.3 Mha in the western United States (US) (Hicke et al., 2020). SB colonizes and feeds on many *Picea* species in North America (Kelley & Farrell, 1998; Wood, 1982), although susceptibility varies among species. For example, blue spruce (*Pi. pungens* Engelm.) is a less suitable host to SB than Engelmann spruce (*Pi. engelmannii* Parry ex Engelm.) (Ott, Fettig, Munson, Runyon, & Ross, 2021). MPB attacks and reproduces in *Pinus*, and although a majority of the *Pinus* species within the MPB range are suitable for attack and reproduction (Wood, 1982), attacks on *P. longaeva* are rare (Bentz, Hood, Hansen, Vandygriff, & Mock, 2017) and brood survival is extremely limited (Eidson, Mock, & Bentz, 2018). Unlike SB that is found across the range of *Picea* in North America north of Mexico, the MPB range does not extend to the southern, northern, or eastern extent of North American *Pinus* (Fig. 1). MPB is considered rare to absent in mainland Mexico, although several dead MPBs were recently found in a dead *P. strobiformis* Engelm. just south of the Arizona, USA border (Armendáriz-Toledano, Torres-Banda, & Zúñiga, 2017). Warming temperatures have played a major role in the recent and rapid MPB migration northward in British Columbia and eastward into Alberta, Canada, since

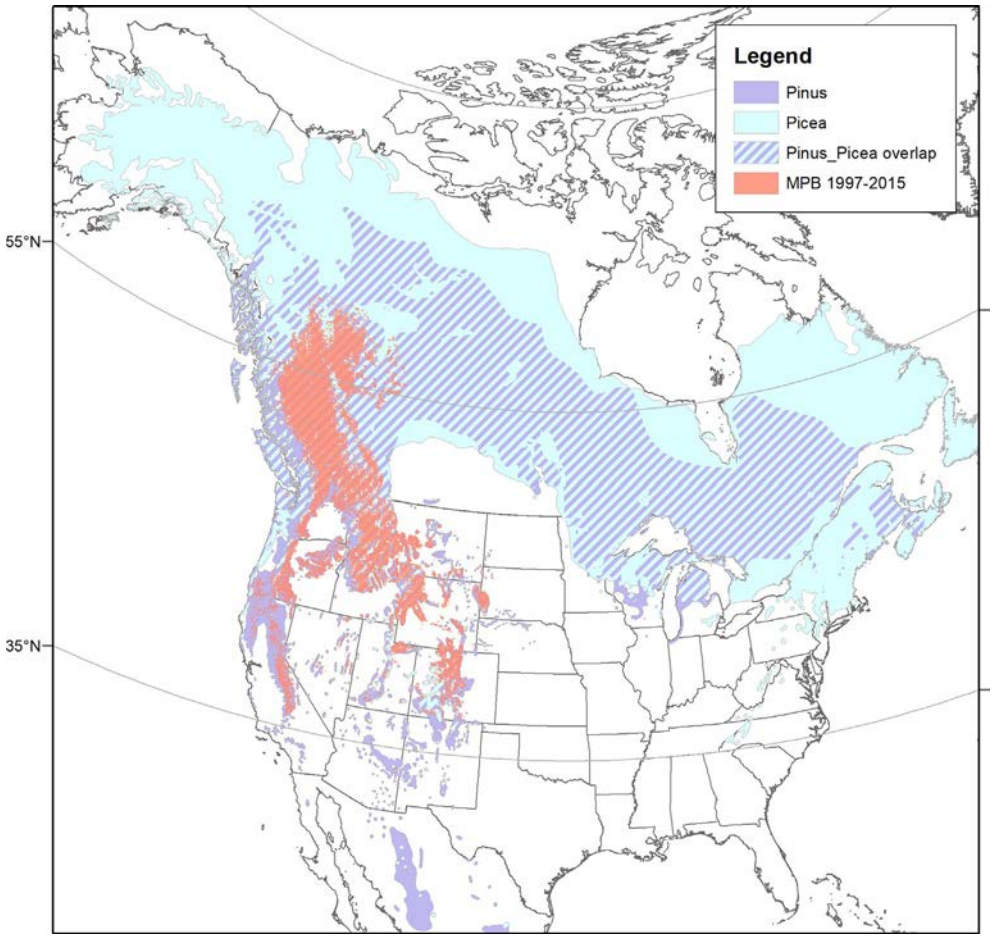


**FIG. 1** Distribution of mountain pine beetle (MPB) *Pinus* host species and the extent of MPB population activity during 1997 to 2015. Prior to 1999, the majority of MPB activity was south of ~54°N and expansion northward has occurred. The spruce beetle (SB) distribution is considered to be coincident with the distribution of *Picea* in North America, north of Mexico. SB is not found in Mexico (Cibrián Tovar, Méndez Montiel, Campos Bolaños, Yates, & Flores Lara, 1995). Depicted *Pinus* and *Picea* distributions are based on Little (1971) and the area estimated to have presence of MPB-killed trees is based on aerial detections (United States: USDA Forest Service, Regional State and Private Forestry; British Columbia, Canada: https://www.for.gov.bc.ca/ftp/HFP/external/!publish/Aerial_Overview/); Alberta, Canada: Mountain Pine Beetle Detailed Aerial Survey Data, Forest Health and Adaptation Section, Government of Alberta.

the late 1980s (Cullingham et al., 2011) (Fig. 1), a migration that has been ongoing for ~12,000 years following glaciation during the Pleistocene (Mock et al., 2007).

At the Last Glacial Maximum (LGM, ~18,000 BP), ice sheets covered Canada and parts of the northern USA (Clark et al., 2009). Following the LGM, postglacial colonization of Canada by *Picea* and *Pinus* from Pleistocene refugia occurred and associated bark beetle species have been continually tracking their host tree migrations. Pollen and macrofossil records indicate that *Picea* postglacial colonization occurred from refugia south of the

glacial margin in the eastern and western USA, in addition to refugia in Beringia north of the glacial margin (Anderson, Hu, Nelson, Petit, & Paige, 2006; Jackson, Webb, Anderson, et al., 2000; Whitlock & Bartlein, 1997). Genetic analysis reveals that SB closely tracked its hosts during postglacial recolonization and the SB distribution currently includes all of Canada, with clear genetic diversity resulting from colonization that originated from the multiple refugia (Maroja, Bogdanowicz, Wallin, Raffa, & Harrison, 2007). Postglacial colonization by *Pinus* occurred from multiple refugia in the western US and nonglaciated islands on the west coast of BC, Canada (Godbout, Fazekas, Newton, Yeh, & Bousquet, 2008; Richardson, Brunsfeld, & Klopfenstein, 2002). Glacial refugia for MPB have also been identified, and they suggest that MPB postglacial migration in British Columbia, Canada, likely occurred from refugia in the western USA (Cullingham et al., 2019; Dowle et al., 2017). A lack of a confirmed refugia north of the glacial margin, as in SB, has potentially slowed MPB colonization of pines that extend further north and east in western Canada than the current MPB distribution. The MPB distribution has therefore been considered limited by direct climate effects on population success rather than availability of host trees (Safranyik et al., 2010).

In addition to migration into previously glaciated areas in Canada, climate fluctuations during and following the Pleistocene caused shifts in MPB and SB distributions within the USA. These shifts were driven by barriers for gene flow among tree populations (e.g., Willyard et al., 2017). Reproductive isolation among bark beetle populations followed leading to local adaptation, an important evolutionary outcome of multiple glacial refugia and secondary contact post-glaciation. The phylogeographic patterns we see today in multiple bark beetle species are reflective of these postglacial processes (Bracewell, Pfrender, Mock, & Bentz, 2013; Cognato, Harlin, & Fisher, 2003; Havill, Cognato, Del-Val, Rabaglia, & Garrick, 2019; Kelley, Mitton, & Paine, 1999; Maroja et al., 2007; Mock et al., 2007). In SB and MPB, local adaptation and phenotypic and genetic differences have been detected among populations in several thermally dependent life history traits, likely a combination of postglacial processes and environmental variability across their distributions (Bentz, Bracewell, Mock, & Pfrender, 2011; Bentz, Logan, & Vandygriff, 2001; Bracewell et al., 2013; Cullingham et al., 2019; Davenport, 2020; Dowle et al., 2017; Soderberg, Mock, Hofstetter, & Bentz, 2020).

Due to the complex and integrated physiological traits involved, predicting future population success in a changing climate requires an understanding of not only the timing and thermal sensitivity of multiple life history traits but also the geographic variability among populations in these traits. It is clear that climate change can result in both beneficial and maladaptive phenological shifts in insects depending on life history complexity (Forrest, 2016; Valtonen et al., 2014). We review the knowledge base of development rates, diapause, and cold hardening in SB and MPB, two economically and ecologically important *Dendroctonus* species. The potential influence of changing temperatures on these traits and ultimately population survival and success in an uncertain future climate is discussed, in addition to management implications. Potential tree mortality caused by these species will depend on a match between the new climate and their evolved, thermally dependent traits.

## 2 Development rates and thresholds

Bark beetles have complete metamorphosis, with developmental stages that begin with oviposition and an egg stage, multiple larval instars, a pupal phase, a teneral (sexually immature) adult stage, and a mature adult (Fig. 2). Development thresholds and rates for each stage are temperature-dependent and can vary among life stages within a species (Bentz & Jönsson, 2015). The shape of a development rate—temperature curve for ectotherms is nonlinear with a low temperature development threshold, an upper threshold beyond which development ceases, and a temperature in between the two thresholds where a maximal development rate occurs (Deutsch et al., 2008). Using phloem sandwiches (i.e., phloem encased by transparent material to allow observation) in the laboratory at constant temperatures, life stage-specific development rates of eggs, larvae, and pupae have been described for SB populations from central Utah (hereafter SB) (Hansen et al., 2001; Hansen et al., 2011), MPB from northern Utah and central Idaho (hereafter MPB_N) (Bentz, Logan, & Amman, 1991; Régnière et al., 2012), and a MPB population from central Arizona (hereafter MPB_S) (McManis, Powell, & Bentz, 2018). Acknowledging that the experiments were conducted at different times and temperatures, comparing development rates between the species provides insight into similarities and differences between the two *Dendroctonus* species and the two geographically separated MPB populations.

SB and MPB typically develop through four larval instars. In both species, eggs and larval instars 1 and 2 have lower developmental thresholds, between 5°C and 7°C, than later life stages (Fig. 3). The instar 3 low threshold for development is slightly higher, and in both species, completion of the 4th instar (i.e., pupation or eclosion to the pupal stage) is restricted below ~15°C depending on temperatures during earlier stages. Completion of SB pupae (i.e., eclosion to the adult stage) was observed as low as 5.5°C, although MPB pupae were not examined at constant temperatures below 10°C. Although


**FIG. 2** Life stages of mountain pine beetle and spruce beetle: (A) eggs, (B) early instar larval mining, (C) late instar larvae, (D) prepupa, (E) pupa and teneral adults, and (F) adult mountain pine beetle *(top)* and spruce beetle *(bottom)*. *Photo Credits: (A) W. Ciesla, Forest Health Management International, Bugwood.org; (B) E. Eidson, Idaho Department of Lands; (C, D, E) B. Bentz, Rocky Mountain Research Station; (F) O'Donnell & Cline, E. Vallery, Bugwood.org.*

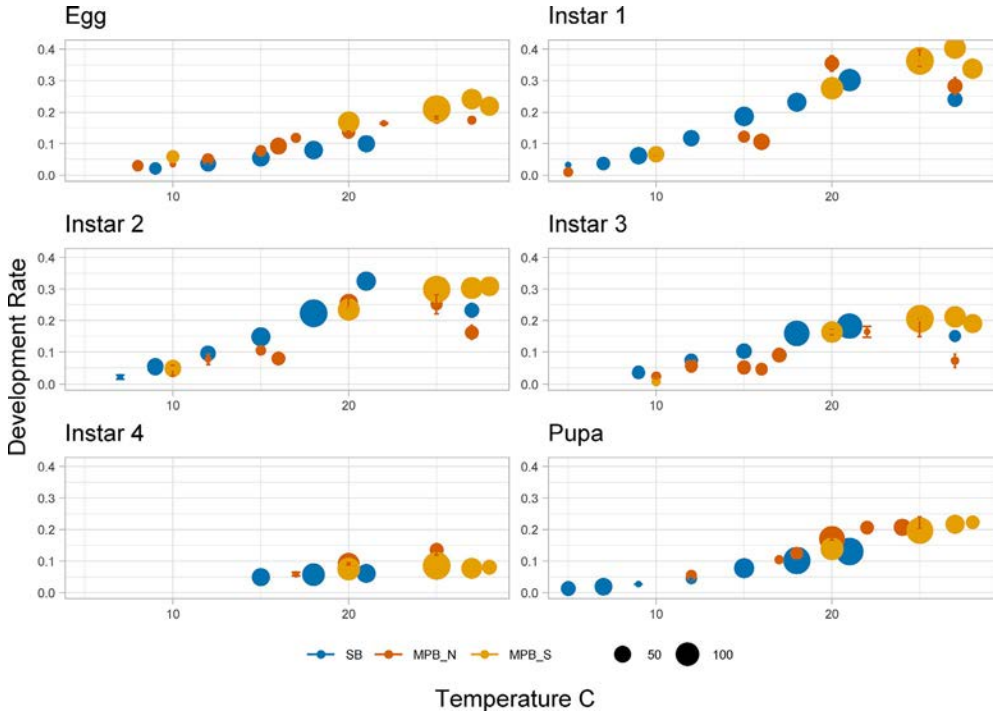


**FIG. 3** Life stage-specific developmental rates (mean ± SE) of spruce beetle (SB) from a central Utah population, mountain pine beetle (MPB) from northern Utah and central Idaho (MPB_N), and MPB from central Arizona (MPB_S). Experiments were conducted at a range of constant temperatures. Size of point is relative to number of individuals tested at each temperature.

data on all life stages are not available, development time between the species differed by less than 5 days for a given life stage-constant temperature combination between 15°C and 25°C (Hansen et al., 2001; McManis et al., 2018). Based on the available data, SB and MPB_N development rates peak in the range 20°C to 25°C for all life stages (also see Hansen et al., 2011 and Régnière et al., 2012). Although determining upper developmental thresholds is difficult, experiments with MPB_S were successfully conducted at higher temperatures, and the data suggest this population has maximal development and an upper temperature threshold slightly higher than both SB and MPB_N, but less than 29°C where all individuals died (McManis et al., 2018). Development of the sexually immature teneral adult into a sexually mature adult is also difficult to study because there is no known external character that distinguishes the transition. Therefore, the rate from a teneral to mature adult emergence from a tree remains undetermined for both species.

## 3 Diapause

Diapause is a common strategy used by insects to synchronize individual development within a population and to survive seasonally predictable adverse environmental conditions such as winter and summer temperatures, and seasonal drought.

Characterized by a neuro-hormonally regulated reduction in metabolic activity, diapause is a developmental arrest that can be either facultative or obligatory (Tauber, Tauber, & Masaki, 1986). Diapause induced by specific environmental conditions is termed facultative. In this circumstance, diapause will not be induced and manifest if those conditions are not encountered by the insect. Alternatively, obligatory diapause is fixed to seasonal changes regardless of environmental conditions. Developmental delays resulting from diapause are not simply present or absent, but instead have a distribution of rates across temperatures similar to development rates (Danks, 2007; Gray, Logan, Ravlin, & Carlson, 1991; Hansen et al., 2011). Temperature and photoperiod are considered the most common diapause cues in insects (Denlinger, 2002). Because *Dendroctonus* develop beneath the bark of host trees, thermoperiod rather than photoperiod has been considered a critical cue and laboratory testing found no evidence of a photoperiod effect for the SB prepupal diapause (Hansen et al., 2001; Hansen et al., 2011). Although MPB larvae have recently been shown to have photosensitivity (Wertman, Bleiker, & Perlman, 2018), the role of photoperiod in diapause states of the two species remains unclear.

## 3.1 Prepupal diapause

SB and MPB both have a facultative prepupal diapause invoked by temperatures below 12°C to 17°C experienced during late-stage larval instars (i.e., instars 3 and 4) (Bentz & Hansen, 2017; Hansen et al., 2011). Prepupa is a substage at the end of instar 4 prior to pupation marked by the cessation of feeding and construction of a pupal chamber (Fig. 2). The prepupal diapause serves to halt development as temperatures cool, thereby reducing the likelihood that the cold-intolerant pupal stage occurs during winter (Amman, 1973; Bleiker, Smith, & Humble, 2017). Prepupal diapause appears to be induced more often in SB than in MPB, likely due to the cooler SB habitats and early summer adult flight that results in the occurrence of late-stage instars during late summer and early fall when diapause-inducing temperatures are likely. In contrast, the timing of MPB attack and oviposition, and generally warmer conditions in MPB host types, result in a variety of life stages, including prepupa, overwintering (Amman, 1973; Bentz & Mullins, 1999; Lester & Irwin, 2012; Reid, 1962; Soderberg et al., 2020). Despite the flexibility in MPB lifecycle timing and variety of overwintering life stages, late stage larvae and prepupae are the most common and considered among the life stages most resistant to cold-induced mortality (see *Cold Hardiness* section).

Laboratory studies have demonstrated a SB prepupal diapause in populations from Utah (Hansen et al., 2001) and British Columbia, Canada (Dyer & Hall, 1977), and field studies in Alaska (Werner & Holsten, 1985) and Colorado (Massey & Wygant, 1954) documented the prevalence of instar 4 (presumably, prepupae) during winter, consistent with prepupal diapause. In contrast, there is substantial variation in the presence of the MPB prepupal diapause phenotype within a population, and also among geographically separated populations (Bentz & Hansen, 2017). In laboratory experiments, a greater proportion of MPB_S exposed to constant 17°C pupated, compared with MPB_N individuals reared at

the same constant temperature. These results indicate that more MPB_N than MPB_S were induced into a prepupal diapause at 17°C. MPB_N, with colder habitats, also has a greater duration of prepupal diapause than MPB_S (Bentz & Hansen, 2017). The large variation within and among MPB populations in induction cues and diapause developmental timing likely contributed to a historical lack of recognition of this diapause state (Logan & Bentz, 1999; Safranyik & Carroll, 2006). Moreover, laboratory experiments on MPB historically focused on northern populations (Bentz et al., 1991; Régnière et al., 2012; Safranyik & Whitney, 1985) which have an easily induced and relatively hard to terminate prepupal diapause that was interpreted as a simple high temperature threshold to complete instar 4.

## 3.2 Teneral adult diapause

In addition to a prepupal diapause, SB has a diapause during the teneral adult stage facilitating synchronized and seasonally appropriate adult emergence (Safranyik, Simmons, & Barclay, 1990; Schebeck et al., 2017). The SB adult diapause is terminated by a period at cool temperatures (i.e., winter) and is considered requisite for reproductive viability (Davenport, 2020; Safranyik et al., 1990). Unlike SB, an adult diapause in MPB has only recently been suggested. Although the diapause identified in SB occurs in the teneral (i.e., prereproductive) adult, Lester and Irwin (2012) proposed that post-reproductive MPB adults (i.e., parent adults) in Oregon overwintered in a state of endogenous metabolic suppression providing possible evidence for a diapause in that life stage.

More recent research suggests that prereproductive MPB adults (i.e., teneral adults) may also have a diapause state. Motivation for investigating a teneral adult diapause in MPB was based on common garden rearing studies using the MPB_N and MPB_S populations that showed total development time between the two populations can differ by up to 70 days depending on the constant temperature (Bracewell et al., 2013; Soderberg et al., 2020). Yet, in a laboratory setting, life stage-specific development rates of all MPB_N and MPB_S life stages were found to be similar with teneral adult rates unknown (see *Development Rate and Thresholds*) (Fig. 3). These results suggest a developmental delay in MPB_S teneral adults, potentially representing a diapause state. Preliminary evidence indicates the MPB_S teneral adult diapause state manifests as reduced respiration at warm temperatures, suggesting delayed sexual maturity (Hansen et al. unpublished). The MPB_S adult diapause likely serves to maintain the appropriate timing of adult emergence and reproductive viability despite the increased thermal input at more southern locations.

Similar to SB, MPB_S teneral adult diapause begins in summer, appears to be terminated by relatively cool temperatures, and facilitates appropriate and seasonal lifecycle timing (Fig. 4). MPB adult diapause, however, seems to only manifest in MPB_S and, unlike SB, is easy to terminate and is relatively short in duration. For example, a constant temperature of 25°C appears to induce adult diapause in MPB_S under laboratory conditions and transfer to constant 15°C appears to complete diapause within just a few days. In contrast, SB collected in British Columbia needed 50–75 days of constant 2°C to complete adult diapause (Bleiker & Willsey, 2020).

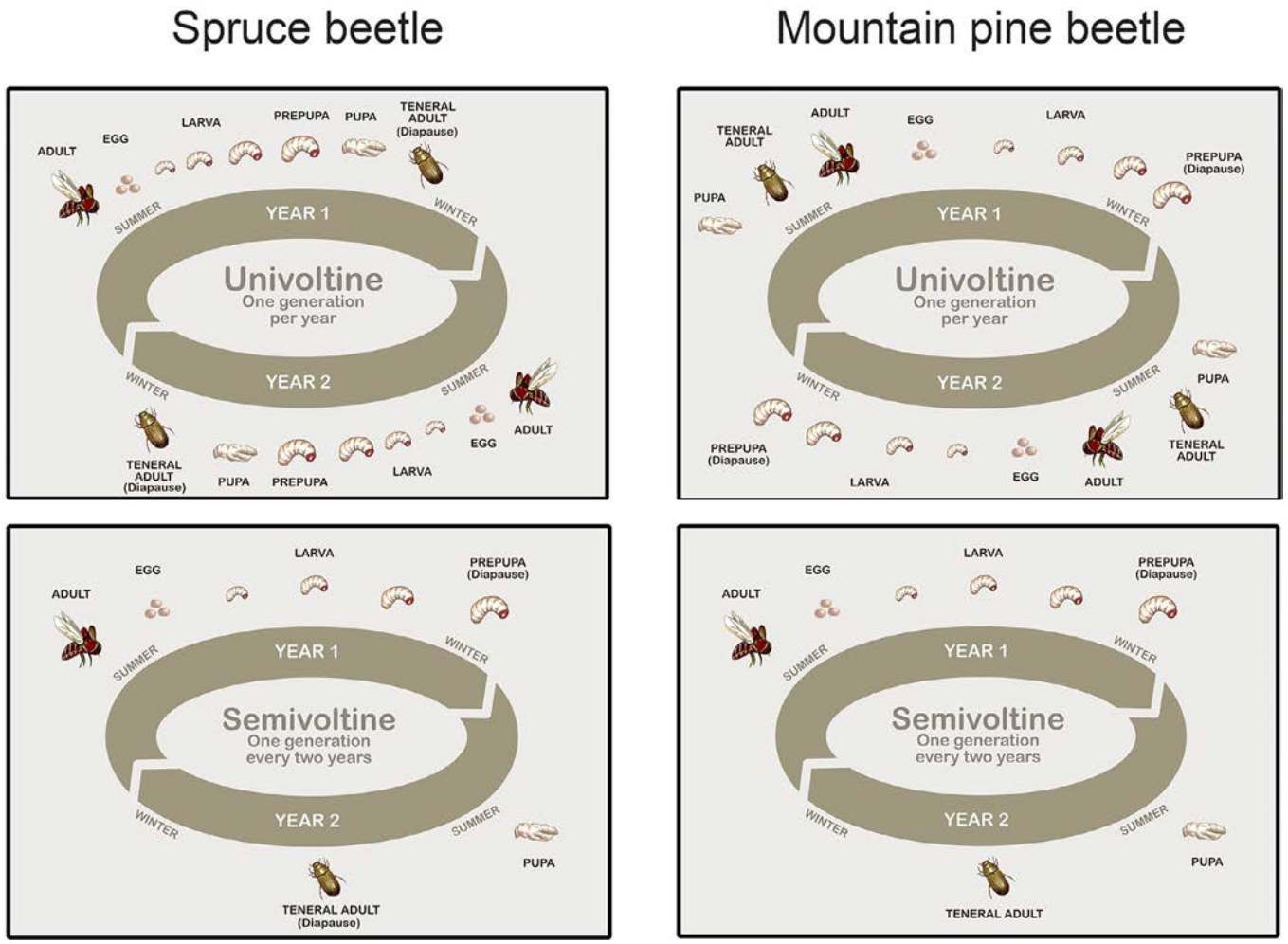


**FIG. 4** Optimal lifecycles for spruce beetle are univoltine (one generation per year) and semivoltine (one generation every 2 years). Historically, semivoltine lifecycles were ubiquitous for spruce beetle with univoltine lifecycles occurring only in warm locations or years with exceptionally warm summers. In a spruce beetle univoltine lifecycle, the prepupal diapause is averted and winter is spent as a diapausing teneral adult that emerges as a mature adult the following early summer. In a spruce beetle semivoltine lifecycle, the first winter is spent as a diapausing prepupa and the second winter as a diapausing teneral adult. Mountain pine beetle lifecycles are more variable than spruce beetle and shown are potential scenarios for each voltinism type. Adults typically emerge in the middle of summer, and late stage larvae and diapausing prepupae are the most common overwintering life stages. At the highest elevations and in cool years, a semivoltine mountain pine beetle lifecycle can occur that is similar to a spruce beetle semivoltine lifecycle. As in the mountain pine beetle univoltine lifecycle, the overwintering life stage can vary, although the second winter is typically spent as a teneral adult. Not uncommonly, mountain pine beetles at high elevations encounter conditions intermediate between those conducive to the univoltine and semivoltine cycles. This can result in fractional voltinism with variable and unpredictable lifestage timing.

## 3.3 Diapause effects on lifecycle timing

SB habitat (i.e., *Picea* forests which generally occur at high elevation) is relatively cool, and conditions typically induce prepupal diapause before the first winter (Dyer & Hall, 1977; Hansen et al., 2001). Pupation occurs early the second summer, followed a few weeks later by eclosion to the teneral adult. The remainder of that summer is spent as a diapausing teneral adult, and cool temperatures the second winter complete diapause development (Bleiker & Willsey, 2020). Emergence of mature adults occurs early the third summer, resulting in a semivoltine lifecycle (i.e., one generation in 2 years) (Fig. 4). In locations or years with warm summers, SB avert the facultative prepupal diapause and the first winter is spent as a diapausing teneral adult, resulting in a univoltine lifecycle (Fig. 4).

Semivoltinism has historically been the typical lifecycle across the range of SB, and the adult diapause was considered obligate and required for reproductive maturity. Recent research, however, suggests some SB populations have individuals that are reproductively viable without exposure to cold temperatures, indicating variability in the adult diapause phenotype. The nondiapausing phenotype is uncommon with a higher proportion of nondiapausing SB teneral adults in more southerly populations (Davenport, 2020; Schebeck et al., 2017). McKee and Aukema (2015) also found that some adults in a *D. simplex* LeConte population at the southern extent of its range reproduced without overwintering, in contrast to previous reports that the adult diapause in this species was obligatory. Davenport (2020) also found that SB adult emergence did not correlate with reproductive maturity, not surprising given the affinity of SB brood and parent adults to overwinter at the base of trees which reduces mortality from lethal winter temperatures and woodpecker predation (Knight, 1961). Moreover, field results in Colorado suggest that cold requirements for termination of the SB teneral adult diapause may be relatively short in duration, as diapause was terminated in some individuals before the end of winter, potentially satisfied by cold temperatures in the fall and early winter (Davenport, 2020).

In MPB, generation time is typically either univoltine or semivoltine, although fractional voltinism can occur in years with unseasonal thermal regimes (see *Potential climate change effects on population persistence and expansion*). The thermal range over which MPB hosts occur is greater than SB hosts and a variety of MPB life stages can overwinter (Bentz et al., 2014; Bentz & Mullins, 1999; DeLeon, Bedard, & Terrell, 1934; Lester & Irwin, 2012). This suggests that relative to SB, MPB lifecycle timing is less controlled by diapause in the prepupal and teneral adult life stages. As in SB, however, when invoked a prepupal diapause can prevent further development to the cold-intolerant pupal stage during winter, thereby maintaining univoltinism and limiting the possibility for bivoltinism. In MPB_S, a teneral adult diapause serves to delay adult maturation and emergence, thus maintaining a timely univoltine lifecycle in warmer conditions (Soderberg et al., 2020). A teneral adult diapause phenotype has not been observed in the cooler habitats of MPB_N. Although more research is needed, if the MPB_S teneral adult diapause is obligatory, as in SB, it could be maladaptive as climate warms (Forrest, 2016).

In both species, some portion of parent adults survive and can make a second attack the same or following year after overwintering. In addition, semivoltine beetles emerge earlier than univoltine beetles (Bentz et al., 2014; Hansen et al. unpublished) and re-emerged parents are among the first to fly in the early summer (Hansen & Bentz, 2003). Along with attacks from new adults, these events can result in overlapping cohorts in both species.

## 4 Cold hardening

In addition to diapause, SB and MPB cold harden to survive adverse environmental conditions. Both species have the capacity to supercool, wherein individuals survive below freezing temperatures by accumulating cryoprotectants (Bentz & Mullins, 1999; Bonnett et al., 2012; Miller & Werner, 1987; Rosenberger, Aukema, & Venette, 2017). SB and MPB are freeze-intolerant species and metabolism of cryoprotectants, including glycerol, reduces supercooling points to avoid ice crystal formation within tissues (Bentz & Mullins, 1999; Miller & Werner, 1987). The accumulation of cryoprotectants begins in the autumn with cooling temperatures (Fraser, Bonnett, Keeling, & Huber, 2017), and the lowest supercooling points are found in the middle of winter (Bentz & Mullins, 1999; Lester & Irwin, 2012; Rousseau, Bauce, Lavallée, & Guertin, 2012). Individuals are considered most susceptible to cold mortality in the autumn and spring, prior to and following maximum supercooling yet when rapid drops in temperature can occur. Supercooling capacity can vary by life stage. In MPB, eggs, pupae, and new brood adults are less cold tolerant than larval instars (Bleiker et al., 2017; Bleiker & Smith, 2019; Thompson, Huber, & Murray, 2020), and the instar 4/prepupal stage is considered the most cold hardy (Rosenberger et al., 2017; Safranyik & Linton, 1998). SB overwinters as a prepupa and teneral adult, and the two life stages appear to have similar cold hardening capacities (Miller & Werner, 1987).

Cold hardening is a metabolically expensive process (Lee, 1989). Different levels of investment into supercooling among life stages within and between species reflect genetic adaptations for maintaining appropriate seasonality, minimizing investment in life stages that rarely overwinter. That is, development rates and diapause generally synchronize the most cold-tolerant life stages for overwintering. Completion of SB reproductive diapause requires overwintering, which serves to maintain population synchrony and seasonality (Bleiker & Willsey, 2020; Davenport, 2020; Schebeck et al., 2017). Given that semivoltine life cycles overwinter as brood adults, it is not surprising this life stage has extensive capacity to cold harden. In contrast, MPB brood adults are not a common overwintering life stage, and energy toward cold hardening in this life stage is minimized (Thompson et al., 2020). Similarly, variation in investment among populations within each species that have adapted to warm versus cold climates would also be expected. In a translocation experiment, MPB_N had supercooling points that were consistently lower than MPB_S regardless of the temperatures at the sites where the two populations were reared. These results indicate a genetic adaptation for greater cold hardening in larvae of MPB_N, a population that has evolved in a significantly colder area than MPB_S (Soderberg et al., 2020). Geographic variation in SB cold hardening has not been investigated.

## 5 Potential climate change effects on population persistence and expansion

Warming temperatures associated with climate change will influence SB and MPB population persistence through effects to development, diapause, and cold hardening. Development rates and diapause regulate generation time and voltinism in both species, and cold hardening influences survival. Observed plasticity in these traits (Bentz et al., 2011; Bentz & Hansen, 2017; Davenport, 2020; Hansen et al., 2001; Soderberg et al., 2020) will allow populations to track environmental changes at least in the short term, or until environmental conditions exceed the capacity of existing plasticity. Individual development rates will likely not evolve in the next few decades, but as the local climate warms, more time will be spent at temperatures that result in faster development. Due to the nonlinearity of development rate curves, populations inhabiting environments with temperatures that are already close to their maximal development rate may be pushed into thermal regimes that result in slower development or death (Deutsch et al., 2008). In contrast, populations in environments that are cooler than maximal will likely have accelerated development with warming. For SB and MPB, maximal life stage-specific development rates occur in the range 20°C to 28°C. Not surprisingly, there is substantial variation in summer and winter temperatures across the ranges of both species in North America. Based on downscaled temperature projections at a $\sim$50 km $\times$ 50 km grid scale (see Bentz et al., 2019 for details), the estimated summer mean temperatures in pine habitats across the range of MPB averaged 15.3°C during the period 1981–2010 (Fig. 5). Summer temperatures in spruce habitat across North America during the same time period averaged 13.1°C. In many habitats, therefore, both SB and MPB are generally living in climates that are cooler than their maximal development, and warming is therefore likely to accelerate egg, larval and pupal development during summer. Warmer and longer summers are already influencing the probability of univoltine generations in SB throughout its range, and MPB at high elevations.

Although most habitats may have mean summer temperatures below that for peak development, habitats at the warmest extremes, in addition to warm microhabitats within stands, could approach or exceed maximal development temperatures of both species as climate warms. For example, south side temperatures of tree boles can be substantially warmer than north side temperatures (Bolstad, Bentz, & Logan, 1997; Hansen et al., 2001), and seasonal temperatures can be substantially warmer in habitats at southern range edges (Soderberg et al., 2020). In these areas, continually warming temperatures will likely push development into thermal regimes that slow development or cause death. Shifts along the development rate curves in the warmest habitats will likely manifest as disruptions to seasonality with cold intolerant life stages overwintering (Régnière, Bentz, Powell, & St-Amant, 2015). These "development traps" can occur when cues are disrupted and additional generations are attempted but fail (Van Dyke, Bonte, Gotthard, & Maes, 2015). In addition to development rate, diapause in multiple life stages in both species can regulate adult emergence and generation timing but may also be disrupted by inappropriate cues.

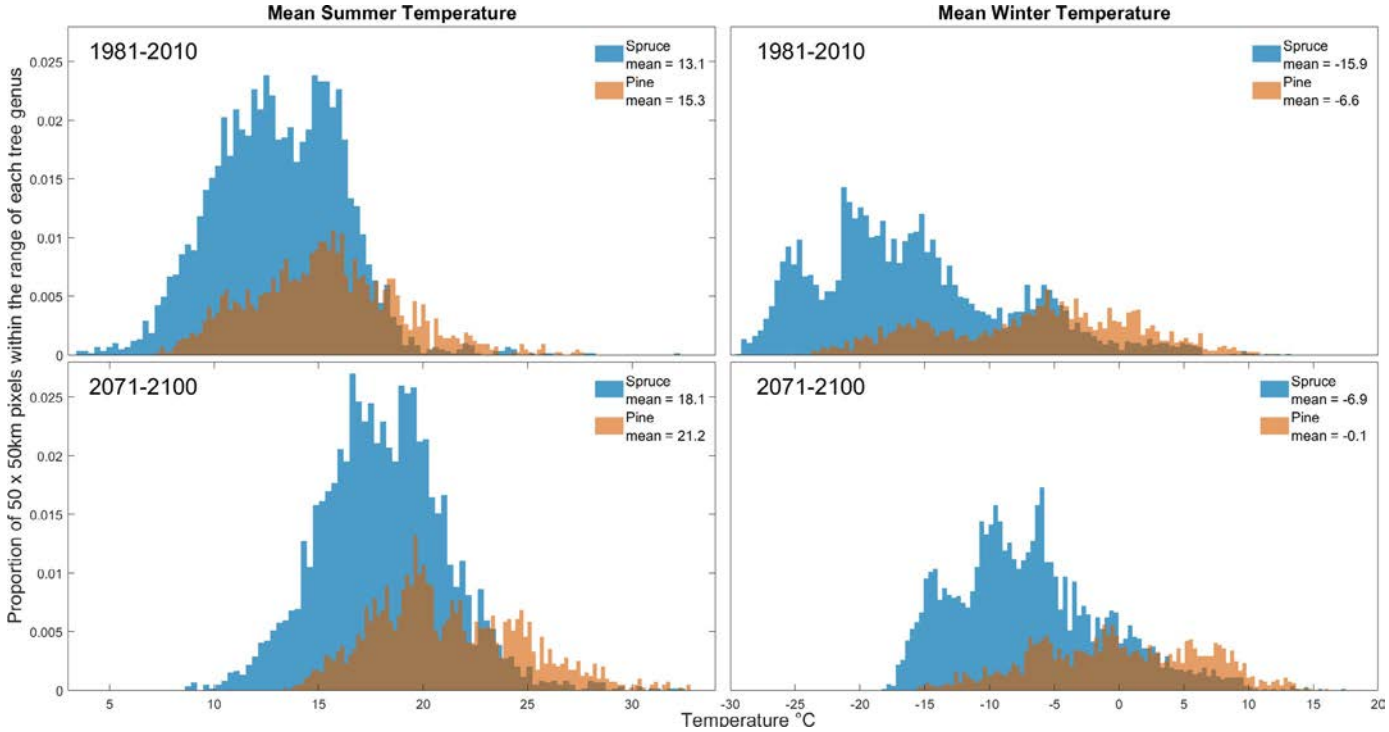


**FIG. 5** Mean summer (June, July, August) and winter (December, January, February) temperatures across the ranges of mountain pine beetle *Pinus* hosts and spruce beetle *Picea* hosts (see Fig. 1) in historic (1981–2010) and future (2071–2100) periods. Shown is the proportion of ~50 × 50 km pixels within the range of each tree genus representing a given average temperature. Temperature projections are from regionally downscaled global climate model scenarios produced within the CORDEX project (http://www.cordex.org, grid of ~50 × 50 km pixels). Pine (*Pinus*) and spruce (*Picea*) distributions for the 50 × 50 km grids were extracted from the North America Land Cover Characteristics spatial database (https://lta.cr.usgs.gov/glcc/na_int). See Bentz et al. (2019) for details.

Recent warming is allowing shifts from semivoltinism to univoltinism in both SB and MPB (Bentz et al., 2014; Berg et al., 2006). In SB, atypically warm summers result in several factors that contribute to univoltinism: (1) earlier adult flight and attack which expose brood to more of the summer season, (2) faster development of eggs and larvae, as described above, and (3) aversion of the facultative prepupal diapause (Hansen et al., 2011). Shorter generation time can result in an exponential increase in population size and thus increased tree mortality (Berg et al., 2006; Hansen & Bentz, 2003). In MPB, semivoltine lifecycles occur at the highest elevations, and warming temperatures also result in an increased proportion of univoltine rather than semivoltine MPB, with associated tree mortality (Bentz et al., 2014; Buotte et al., 2016; Perkins & Swetnam, 1996). It is important to note that neither species has been observed to successfully complete two generations in a single year (i.e., bivoltine).

Although bivoltinism has not been observed (Bentz & Powell, 2014; Soderberg et al., 2020), when re-emerged parents or semivoltine brood emerge in early June, MPB can complete a generation in a single warm summer. Brood adults emerge during autumn of the same year, resulting in overlapping cohorts and sister broods (Bentz et al., 2014; DeLeon et al., 1934; Reid, 1962). Completion of a second generation over winter, however, has been constrained by cold autumn and winter temperatures that reduce development time and potentially invoke a prepupal diapause (Bentz et al., 2014; Bentz & Powell, 2014; Soderberg et al., 2020). In SB, a cold-terminated obligatory adult diapause has constrained completion of a generation over summer (Schebeck et al., 2017). If the nondiapausing SB adult phenotype is selected for in a population, warm spring and summer temperatures could result in an earlier adult flight of overwintering adults and completion of a SB generation between late spring and early fall. Similar to MPB, however, cold temperatures in the fall and winter would invoke the SB prepupal diapause and restrict completion of a generation the following winter thereby preventing a bivoltine lifecycle. Although more research is needed, if the MPB_S teneral adult diapause is obligatory, as in most SB populations, it could be maladaptive if bivoltinism is more advantageous as climate warms (Forrest, 2016). Warming temperatures also have the potential to delay termination of both the prepupal and adult diapauses, which require a cold period for termination, thereby increasing the heat units required for emergence in addition to increased variation in adult emergence timing (Bosch & Kemp, 2003). For both species, a bivoltine lifecycle is likely to occur only if autumn and winter temperatures warm catastrophically. Autumn and winter temperatures must be consistently above ~15°C to avoid a prepupal diapause and ensure development rates that promote rapid progression to the adult stage (Hansen et al., 2011; Bentz & Powell, 2014; also see *Development Rates and Thresholds* and *Diapause*). Temperatures are predicted to increase by the end of the century favoring SB and MPB winter survival and univoltinism (Bentz et al., 2010; Bentz et al., 2019), but it appears unlikely they will warm enough to allow rapid development during winter to accomplish two generations in a year (Fig. 5). Instead, depending on the geographic location, short-term projected warming could result in fractional or asynchronous voltinism when diapause cues are disrupted.

In historical climates, stable or synchronous voltinism in temperate insects such as SB and MPB is hypothesized to have occurred with thermal regimes that produced either univoltinism or semivoltinism (Hansen et al., 2011; Powell & Logan, 2005; Régnière et al., 2015). When temperatures move thermal regimes outside the stable bands, but not far enough to reach another region of stable, integer voltinism (i.e., bi-, uni- or semivoltinism), fractional or asynchronous voltinism is predicted to occur ( Jenkins, Powell, Logan, & Bentz, 2001). In other words, in the temperate climates of both species the appropriate timing of life stages is critical to ensure adult emergence and attacks of new trees occur synchronously and during the appropriate time of year. This seasonality is considered adaptive (Logan & Bentz, 1999), and evolved development rates and diapause in both species serve to maintain a stable and seasonal voltinism that increases the likelihood of successful attacks on new trees and population growth. Weather has likely disrupted seasonality in some years within the range of both species, particularly in thermally marginal habitats. For example, a year with cool summer temperatures in a central Idaho pine forest disrupted MPB_N seasonality when temperatures were between thermal regimes for univoltinism and semivoltinism, coinciding with a population crash (Powell & Logan, 2005). These regimes are also likely when winter temperatures warm, but not enough to avert a cold-induced diapause and speed development to the adult phase, what Van Dyke et al. (2015) call a 'lost generation'. Similar disruptions and a loss of seasonality are likely to occur in some future habitats as climate variability and warming increase. Given the extensive range of both species and local adaptation to historical climates, outcomes will vary geographically.

Using a mechanistic demographic model developed for MPB_N (Bentz & Powell, 2014; Powell & Bentz, 2009), worst-case climate projections (i.e., RCP 8.5) estimate a loss of univoltine seasonality in the next 20 years (i.e., 2011–2040 time period) for about 20% of the MPB_N habitat in the western United States that previously supported a univoltine lifecycle (Bentz et al., 2019). With projected increases of summer temperatures between 5°C and 9°C by the end of the century, 77% of previously univoltine habitat is estimated to no longer be suitable due to excessive warmth and disruption of diapause and seasonality. Increasing population success is predicted, however, in previously unoccupied habitats further north in western Canada (Bentz et al., 2019; Régnière et al., 2015). Of the areas where univoltinism was predicted to be lost by the end of the century, only 17% were predicted to move into a thermal band that would be suitable for successful bivoltinism, all of which were confined to low elevation pine forests at southern extremes in the western US (Bentz et al., 2019). As described above and highlighted in a recent field translocation study, the timing of cold temperatures in the fall and winter is responsible for preventing bivoltinism and maintaining univoltinism, even in areas where average temperatures are more than 5°C warmer than historical parts of the range (Soderberg et al., 2020). Cold autumn and winter temperatures halt development beyond the prepupal phase until spring, resulting in a univoltine lifecycle. Basing predictions of future population success on average temperatures, therefore, is ill-advised. In addition, *P. ponderosa*, which is the dominant pine at the lowest elevations of the southern range extent in Arizona, US, is host

to many *Dendroctonus* and *Ips* species (Wood, 1982) which are strong competitors of MPB, likely also limiting the potential for MPB success in these forests. Although a model for projecting loss of seasonality in SB is not currently available, a rigid diapause state in two life stages decreases the probability of fractional voltinism with warming, at least until selection increases the proportion of the nondiapause adult phenotype.

## 6 Management implications of climate change-affected population dynamics

It is clear that changing climate will influence SB and MPB population success and that the effects will vary geographically due to substantial genetic differences and local adaptation in multiple thermally regulated traits. In high elevation pine systems, for example, a shift from predominant semivoltinism to univoltinism has accelerated MPB-caused host mortality (Buotte et al., 2016), and runs of unusually warm summers resulted in a predominance of the SB univoltine cycle and synchronous, regionalized outbreaks (Berg et al., 2006). Therefore, a primary concern for managers is anticipating years wherein the univoltine cycle will prevail in areas where the semivoltine cycle has historically been typical. Predicting areas where fractional voltinism and likely population collapse will occur is also important as these areas may need no management intervention. Phenology models can be used for these events using contemporaneous weather as input (Bentz et al., 2010, Bentz et al., 2019). Given genetic variability among populations in thermally regulated traits, however, regionally specific models are needed but not readily available. For example, genotypic variation in diapause expression is likely to result in widely ranging timing of emergence and attacks on new hosts as temperatures warm, and thereby confound scheduling of management activities such as deployments of monitoring traps, trap trees, and semiochemical repellents. With advance knowledge of beetle success resulting from year-to-year weather, managers can prioritize areas for mitigation using known control methods such as those outlined in Fettig, Gibson, Munson, and Negrón (2014) and Chapter 11. New tools such as novel semiochemicals (e.g., Hansen et al., 2019) give managers expanded capabilities to protect high value host trees from infestation regardless of changes in beetle population dynamics resulting from climate disruption. Cooke and Carroll (2017) also provide a framework for analyzing climate-driven MPB spread into novel areas of Canada, highlighting the need for managers to be prepared for unpredictable disturbances.

Managing for resistance and resilience to future disturbances is an emerging theme in climate-adapted forest management (Halofsky et al., 2018), with prescriptions to increase heterogeneity of age classes and species composition within and across landscapes (Bentz et al., 2005). Vegetation management that removes susceptible host size classes and reduces basal area moderates beetle-caused mortality at the stand-level, but only at sub-epidemic beetle population levels (Hansen, Negron, Munson, & Anhold, 2010;

Windmuller-Campione & Long, 2015). Epidemic populations can result in widespread mortality among mature trees regardless of density management history, particularly when conducted at sub-watershed scales. In fact, post-outbreak stand conditions can be similar among managed and unmanaged stands (Hansen et al., 2010; Vandygriff et al., 2015). Perhaps more relevant to climate disruption and heightened risk of widespread outbreaks is the need for creating stand- and landscape-scale resilience to beetle outbreaks (Windmuller-Campione & Long, 2015). Stand structure and composition that is associated with resistance to SB and MPB have been extensively studied, and resilience to future disturbances can be promoted through silviculture and timed regeneration of desired species (Long, Windmuller-Campione, & DeRose, 2018).

## 7 Conclusions

Future warming trends throughout the century are expected to diminish the likelihood of cold-induced winter mortality in both species, particularly at high elevations and latitudes, and in areas that have been historically cold (Bentz et al., 2010; Bentz et al., 2019; Weed, Bentz, Ayres, & Holmes, 2015). While this may increase population success in some areas, disrupted seasonality and fractional voltinism will likely occur in areas of the western US historically on the margin of thermal suitability. Fractional voltinism is maladaptive and can result in collapse of local populations. Phenotypic and genetic variability in development and diapause rates will likely function to avoid complete extirpation, at least in the short term, although model results and observations suggest that univoltine MPB population success will be greater at more northern latitudes in Canada compared to southern latitudes in the USA as temperatures continue to warm. Future warming will also increase the probability of univoltine individuals across elevations and latitudes of both species. It is unlikely, however, that enough warming will occur during autumn and winter to disrupt evolved diapause states and development rates and allow for bivoltine lifecycles within major portions of both species' ranges. Moreover, the likelihood for this is greater for MPB than SB and potentially greater at southern compared to northern latitude sites. Finally, direct climate disruption impacts on SB and MPB population success must also consider indirect impacts. It is critical to understand effects of changing climate on host tree defense capacity and future distributions (see Chapters 4–6) and cascading effects throughout community associates including fungi, bacteria, and mites (Garnas, 2018; see Chapter 10).

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