Check for updates

Ecological Monographs, 91(1), 2021, e01437
© 2020 by the Ecological Society of America

Translocation experiment reveals capacity for mountain pine beetle persistence under climate warming

David N. Soderberg,[1,2,5] Karen E. Mock,[1,2] Richard W. Hofstetter,[3] and Barbara J. Bentz[1,4]

[1] *Wildland Resources Department, Utah State University, 5230 Old Main Hill, Logan, Utah 84322 USA*
[2] *Ecology Center, Utah State University, 5205 Old Main Hill, Logan, Utah 84322 USA*
[3] *School of Forestry, College of Engineering, Forestry and Natural Sciences, Northern Arizona University, Flagstaff, Arizona 86011 USA*
[4] *U.S. Forest Service, Rocky Mountain Research Station, 860 N. 1200 E, Logan, Utah 84321 USA*

Citation: Soderberg, D. N., K. E. Mock, R. W. Hofstetter, and B. J. Bentz. 2021. Translocation experiment reveals capacity for mountain pine beetle persistence under climate warming. Ecological Monographs. 91(1):e01437. 10.1002/ecm.1437

Abstract. Predicting species response to climate change is a central challenge in ecology, particularly for species that inhabit large geographic areas. The mountain pine beetle (MPB) is a significant tree mortality agent in western North America with a distribution limited by climate. Recent warming has caused large-scale MPB population outbreaks within its historical distribution, in addition to migration northward in western Canada. The relative roles of genetic and environmental sources of variation governing MPB capacity to persist in place in a changing climate, and the migratory potential at its southern range edge in the United States, have not been investigated. We reciprocally translocated MPB populations taken from the core and southern edge of their range, and simultaneously translocated both populations to a warmer, low-elevation site near the southern range boundary where MPB activity has historically been absent despite suitable hosts. We found genetic variability and extensive plasticity in multiple fitness traits that would allow both populations to persist in a warming climate that resembles the thermal regime of our low-elevation site. We demonstrate, for the first time, that supercooling points in MPBs are influenced both by genetic and environmental factors. Both populations reproduced with seasonally appropriate univoltine generation times at all translocated sites, and bivoltinism was not observed. The highest reproductive success occurred at the warmest, out-of-range low-elevation site, suggesting that southward migration may not be temperature limited.

Key words: bivoltinism; climate change; cold-hardening; diapause; genetic variation; local adaptation; mountain pine beetle; phenotypic plasticity; reciprocal translocation; supercooling.

Introduction

There is scientific consensus that climate is rapidly changing, with dramatic effects to ecosystems globally (IPCC 2014). Because climate is an enduring selective agent on traits that shape species distributions and population success, population persistence in a rapidly changing climate will depend on the degree of heritable variation and phenotypic plasticity in environmentally regulated traits (Bradshaw 1965, Sgrò et al. 2016). Heritable trait variation underlies a population's ability to adapt to new conditions through selection. Phenotypic plasticity is the extent to which an individual genotype can produce different phenotypes under a range of environments, and populations with sufficient plasticity may persist in changing environments without genetic adaptation through natural selection. However, phenotypic plasticity itself is a heritable trait with variation subject to selection (Via and Lande 1985, Schlichting and Pigliucci 1998). In addition to persistence in place through trait adaptation or plasticity (Babin-Fenske et al. 2008, Merilä and Hendry 2014), range shifts via migration to new habitats can be a viable response to rapidly changing environmental conditions (Chen et al. 2011). Indeed, northern boundaries of multiple species have expanded with recent climatic changes that include rapid warming at higher latitudes (Hickling et al. 2006, Parmesan 2006, Morley et al. 2017), although less is known about responses of populations at low-latitude margins of species distributions. To more fully understand and predict responses to future climatic changes, including the potential for population persistence in place, an understanding of range-determining factors and trait responses, such as adaptive potential and phenotypic plasticity, is critical (Gienapp et al. 2008).

Forested ecosystems cover ~30% of the global land surface area (FAO 2018) and are undergoing dramatic changes in response to climate change (Allen et al.

Manuscript received 11 December 2019; revised 13 May 2020; accepted 17 August 2020. Corresponding Editor: John J. Battles.
[5] E-mail: davidsoderberg@gmail.com

2010), with much of this change mediated by insect-caused mortality (Hicke et al. 2015, Seidl et al. 2017). The mechanisms that lead to tree mortality are complex, and include climate-related impacts on tree physiological responses, biotic and abiotic disturbances, and increasingly, their interactions (Anderegg et al. 2015). The mountain pine beetle (*Dendroctonus ponderosae* Hopkins; Coleoptera: Curculionidae, Scolytinae; MPB) is an ecologically and economically significant tree mortality agent (Grégoire et al. 2015) that can reverse the role of forests from carbon sinks to carbon sources, at least in the short term until regrowth occurs (Hansen et al. 2014, Arora et al. 2016). MPB, a species native to western North America with an expansive range extending from Baja California Norte, Mexico into western Canada (Cooke and Carroll 2017, Dowle et al. 2017), feeds and reproduces within the inner bark (i.e., phloem) of *Pinus* species, causing tree death at landscape scales when population levels are high (Raffa et al. 2008).

The distribution of *Pinus* species in western North America extends both northward and southward beyond the known historical distribution of MPB, and northward range expansion has recently occurred as a result of changing climate in British Columbia and Alberta, Canada (de la Giroday et al. 2012, Sambaraju et al. 2019). At the southern limit of the historical distribution in central and southern Arizona (AZ) in the USA, MPBs are found in the closely related and hybridizing high-elevation species *P. flexilis* (James) and *P. strobiformis* (Engelmann) (Bentz and Hansen 2017, Menon et al. 2018), yet MPB is limited or absent in lower elevation *Pinus* species (e.g., *P. ponderosa* Dougl. ex P. & C. Laws.) south of the Grand Canyon, AZ (McHugh et al. 2003, Gaylord et al. 2006, Lynch et al. 2006, Williams et al. 2008). Although multiple *Pinus* species are found in mainland Mexico and further south, MPB is considered rare to absent south of the U.S. border (Wood 1982, Cibrián-Tovar et al. 1995). Recently, however, several MPBs were found in a dead *P. strobiformis* in Chihuahua Mexico just south of the AZ border (Armendáriz-Toledano et al. 2017). While it is clear that increases in temperatures have permitted MPB migration northward in Canada (Carroll et al. 2004, Sambaraju et al. 2012, 2019), factors delimiting the southern edge of the MPB distribution in the United States are unknown.

MPB survival is significantly affected by thermal regimes that influence multiple physiological traits including development rates and thresholds (Régnière et al. 2012), prepupal diapause (Bentz and Hansen 2017), and cold-hardening (Bentz and Mullins 1999, Rosenberger 2017). These traits facilitate appropriate overwintering seasonality, generation time, and an adult emergence that is synchronous and seasonally appropriate for mass aggregation on well-defended live host trees (Logan and Bentz 1999, Safranyik and Carroll 2006). Local heritable adaptation and plasticity in traits that influence generation time have been shown in populations from different latitudes using common garden laboratory studies (Bentz et al. 2001, 2011, Bracewell et al. 2013, Bentz and Hansen 2017). The applicability of these results to field populations and the role of the observed variation in population response to a changing climate remain unclear. Field translocation experiments between contrasting environments are a particularly powerful approach for characterizing the extent of genetic and environmental sources of variation in traits influencing population persistence in a changing climate (Kawecki and Ebert 2004, Hoffmann and Sgrò 2011, Nooten and Hughes 2017). Translocation experiments can also be used to describe the role of environmental factors (e.g., temperature) in defining geographic distributions (Case et al. 2005, Gaston and Fuller 2009).

We implemented a reciprocal field translocation experiment to assess MPB response to native and novel environments, and to evaluate the relative roles of genetic effects (g, i.e., variation due to differences in source population), environmental sources of variation (E, i.e., differences due to phenotypic plasticity), and their interaction (gE) in several thermally regulated traits. We used two MPB source populations, one from the core and one from the southern, low-latitude edge of the species distribution (Fig. 1). We also simulated a warming climate by transplanting each population to a warmer, low-elevation *Pinus* forest near the southern distribution boundary where MPB activity has historically been absent (Gaylord et al. 2006, Lynch et al. 2006, Williams et al. 2008). By comparing the relative fitness of the two source populations in three sites (near the core of the species distribution, near the southern distribution edge, and just beyond the current southern distribution) we investigated (1) the response of two MPB populations to warming temperatures, (2) the potential for population persistence in a changing climate, and (3) the potential for thermal regimes to define the southern MPB distribution boundary and constrain expansion southward. In addition to the field translocation experiment, we evaluated responses of the same two populations in a laboratory common garden to compare responses to fluctuating vs. constant temperatures and relate the results from field and laboratory-based experiments.

Methods

Study system

Except for a short adult dispersal period, the MPB life cycle occurs in the phloem beneath the outer bark of *Pinus* host trees. Adult emergence and flight typically occur in mid-summer, and following acceptance of a new susceptible host tree, MPB release aggregation pheromones that attract conspecifics. Aggregation and attacks on a single tree that occur within a few days can overwhelm the tree's resinous defenses, allowing successful entry through the outer bark into the phloem (Raffa

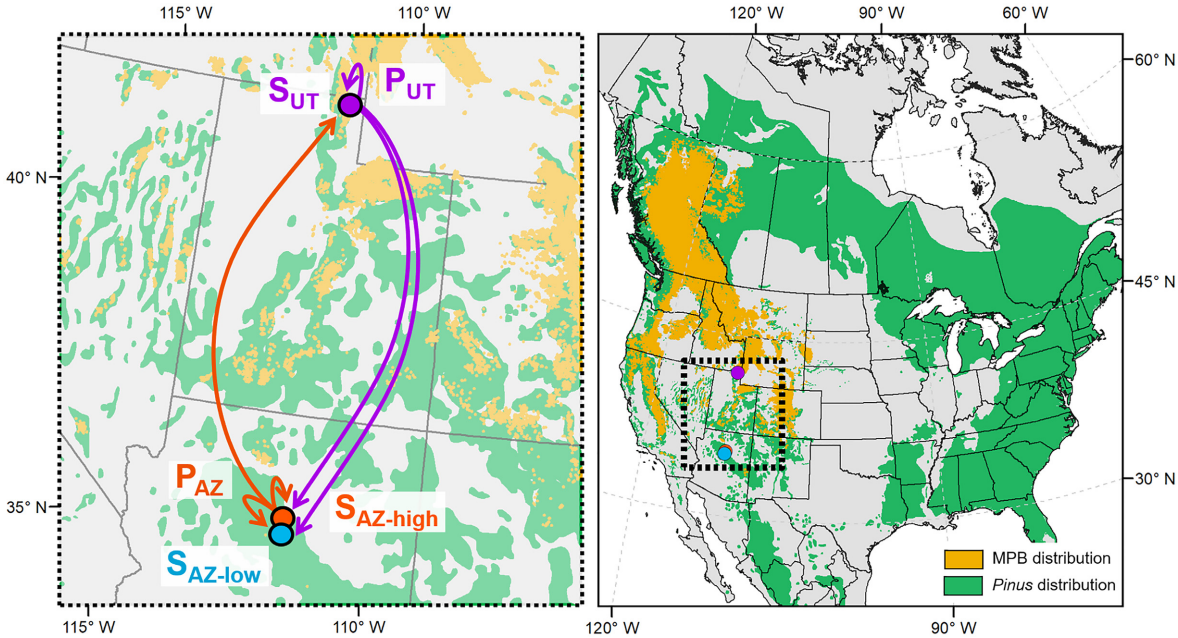

FIG. 1. Distribution of mountain pine beetle (United States [USDA Forest Service, Regional State and Private Forestry]; British Columbia, Canada [https://www.for.gov.bc.ca/ftp/HFP/external/publish?Aerial_Overview/]; Alberta, Canada [mountain pine beetle detailed Aerial Survey Data, Forest Health and Adaptation Section, Government of Alberta]) and *Pinus* (Little 1971; https://www.fs.fed.us/database/feis/pdfs/Little/aa_SupportingFiles/LittleMaps.html) within North America, which includes recent population expansion in British Columbia and Alberta, Canada (right). Design of the field translocation experiment in the southwestern United States (left). Mountain pine beetle were reciprocally translocated between sites in Utah (S_{UT}) and Arizona ($S_{AZ\text{-}high}$), as well as to their original source sites. Mountain pine beetle from both sites were also translocated to a third site ($S_{AZ\text{-}low}$). Insect groups used in these experiments were designated P_{AZ} and P_{UT}, referring to source populations.

et al. 1993). Synchronous adult emergence from previously infested trees facilitates this mass aggregation (Logan and Bentz 1999). Adults mate and females excavate vertical galleries in the phloem, laying eggs while simultaneously propagating the spores of symbiotic fungi that are carried on the body, in the gut, and in the maxillary mycangia (Whitney 1982, Bleiker and Six 2009). Larvae mine horizontally in the phloem, cutting off nutrient and water transport along the tree bole (Amman 1978), feeding on mycelial growth of the inoculated fungi (Adams and Six 2007), which provides a nutritional benefit to developing larvae (Bentz and Six 2006, Myrholm and Langor 2015). Although the MPB-fungus symbioses are complex and not fully understood, success and survival of both MPB and its fungal associates are enhanced by fungal neutralization of host defenses (Solheim 1995, Six and Wingfield 2010). Following mating, oviposition and development through at least four instars, MPB typically overwinter as a prepupae before eclosing into an adult that undergoes a maturation period prior to emergence from the tree. A single generation typically requires one year from tree attack to brood adult emergence, although two years (i.e., semivoltine) may be required in cold habitats (Bentz et al. 2014). Seasonally appropriate emergence timing during summer is critical to population success (Logan and Bentz 1999, Safranyik and Carroll 2006). Populations with observed generation times of less than a year (i.e., bivoltine) are rare, and not considered self-sustaining in climates within the current MPB distribution (Bentz et al. 2014, Bentz and Powell 2014, but see Mitton and Ferrenberg 2012).

Temperature is the primary driver of MPB development time, and ultimately adult emergence synchrony and generation time, as it influences development rates, thresholds, and other strategies including diapause that control seasonality (Bentz et al. 1991, Règniére et al. 2012, Bentz and Hansen 2017). Cold temperatures can also have a direct and significant negative impact on population success when cold-hardening acclimation is not sufficient (Bentz and Mullins 1999, Rosenberger 2017). Variation in body size, which can be positively correlated with fecundity and dispersal (Reid 1958, Honěk 1993, Elkin and Reid 2005, but see Amman 1972), can also be influenced by temperature (Amman 1972, Atkinson 1994, Bentz et al. 2011). MPB populations often exhibit female-biased sex ratios, in large part due to differential mortality of males in the larval stages during stressful thermal extremes (Lachowski and Reid 2014, James et al. 2016). MPB has an extensive range in western North America, and field studies showed that some thermally regulated fitness traits (i.e., larval cold-hardening, adult size, time to complete a generation) vary geographically among populations (Bentz and

Mullins 1999, Bentz et al. 2014). Common garden laboratory experiments further demonstrated that observed differences among latitudinally separated populations in diapause induction, generation time and adult size were due to genetic adaptation and environmentally induced plastic responses (Bentz and Hansen 2017). Lacking is an integrated evaluation of the relative roles of genetic variance (g), environmental effects (E), and their interaction (gE) in observed patterns of geographic variation in multiple thermally regulated fitness traits. The role of thermally regulated traits in limiting the southern distribution of MPB in the southwestern United States is also unclear.

Experimental design and setup

We conducted a reciprocal translocation experiment in the field to assess MPB response to native and novel environments, assessing the relative contributions of genetic (g) and environmental (E) variation in multiple fitness traits. We investigated individual traits related to development time, adult size, and survival, and demographic fitness traits representing adult emergence synchrony and reproductive success. We reciprocally translocated a "core range" population (P_{UT}), originating from an infested *P. flexilis* in a northern Utah (UT), USA site (Logan Canyon; S_{UT}), and a "southern range" population (P_{AZ}), originating from an infested *P. flexilis–P. strobiformis* hybrid at a high-elevation central AZ, USA site (Lockett Meadow; $S_{AZ\text{-}high}$) (Table 1; Fig. 1). Our high-elevation AZ site is in a zone of extensive *P. strobiformis* and *P. flexilis* introgression (Menon et al. 2018). Both populations were reared in bolts of the natal tree species at their native and translocated sites. Additionally, both populations were reared at a third site (Centennial Forest; $S_{AZ\text{-}low}$). $S_{AZ\text{-}low}$ is at a low-elevation in the region of the southern distribution, is dominated by *P. ponderosa* (ex Dougl. Ex P. & C. Laws.), and MPB activity is absent in the historical record (Gaylord et al. 2006, Lynch et al. 2006, Williams et al. 2008). In addition to the field sites, we reared the same two source populations (P_{UT} and P_{AZ}) in laboratory incubators, in natal tree species bolts, under constant temperatures of 18° and 25°C, to compare population trait response between field and laboratory settings.

MPB collection, tree harvest, and bolt infestation

For both field and laboratory experiments, we felled MPB-infested trees on 21 June 2016 from the S_{UT} site and on 4 May 2016 from the $S_{AZ\text{-}high}$ site (Table 1). Cut bolts (~46 cm long) were harvested from one tree at each of the S_{UT} and $S_{AZ\text{-}high}$ sites. Bolt ends were sealed with paraffin wax and transported to the Rocky Mountain Research Station (RMRS) Laboratory in Logan, UT where they were placed at ambient room temperature to allow adults to emerge naturally. Adult beetles were collected daily and stored in Petri dishes lined with distilled water-moistened filter paper at 4°C for up to approximately 10 d. To rear the next generation of beetles we also harvested three live, healthy trees of the same species at each site, cut them into ~46 cm long bolts, and sealed the cut ends with paraffin wax to retain moisture and deter fungal contamination. Bolts were stored at 4°C for up to 3 weeks. The uninfested experimental bolts from each site were randomized among the three field sites and the two temperatures in the laboratory study.

We determined the sex of emerged adult beetles using the morphologically distinct seventh tergite (Lyon 1958). To avoid potential genetic differences in development time among emerging adults, and to standardize for cohort density, we used beetles that emerged during the time beginning just before and throughout peak emergence from natal bolts. Experimental bolts of the same species were infested by drilling a small hole vertically into the phloem at the anatomical bottom of the bolt, inserting first a female then a male beetle, and stapling a mesh screen over each hole to prevent beetle escape. To minimize potential maternal effects due to host species (Burke and Carroll 2017), P_{UT} were reared in *P. flexilis* and P_{AZ} in *P. flexilis/ strobiformis* hybrids that were harvested from the same locations as infested bolts (Table 1). Individuals were randomized by sex and mating pairs were infested 6 cm apart, with 10–13 pairs per bolt depending on bolt circumference. Following infestation, bolts were inverted to allow for natural upward gallery excavation. Infested bolts were either transported to field sites or placed in laboratory incubators as described in *Field and Laboratory experiments.*

TABLE 1. Field sites and *Dendroctonus ponderosae* population source locations.

Site	Source population	Host tree	Location	Latitude (°N)	Longitude (°W)	Elevation (m)
S_{UT}	P_{UT}	*Pinus flexilis*	Logan Canyon, Wasatch-Cache NF, UT	41.9319	111.447	2,204
$S_{AZ\text{-}high}$	P_{AZ}	*Pinus strobiformis/ flexilis* hybrid	Lockett Meadow, Coconino NF, AZ	35.3586	111.6208	2,604
$S_{AZ\text{-}low}$			Centennial Forest, Coconino NF, AZ	35.1498	111.7156	2,106

Note: United States Forest Service, National Forest (NF) locations where *D. ponderosae* populations (P) were collected in Utah (UT) and Arizona (AZ). Collection sites (S) were also used as the field sites for the reciprocal translocation experiment. Live trees for rearing each population were harvested within 4 km of the collection/rearing sites.

Field experiments

Experiment setup.—For the field reciprocal translocation experiment, we enclosed infested bolts individually in escape-proof netting (Rothco, MPN 8088) and within 24 h of infestation, suspended each bolt ~1 m above the ground in wooden A-frame structures with metal covers at each location (Table 1; Appendix S1: Fig. S1). Prior to infestation bolts were randomly distributed to their respective treatment groupings. Nine bolts infested with the P_{UT} population and nine bolts infested with the P_{AZ} population (18 bolts total per site) were placed at each of the three sites (54 bolts total). Bolt location was randomized among three A-frame structures at each site such that there was an equal number of P_{UT} and P_{AZ} infested bolts per A-frame (six bolts per structure) (Appendix S1:: Fig. S1). Field experiments were initiated as follows: S_{UT} on 30 July 2016; $S_{AZ\text{-high}}$ on 10 August 2016; $S_{AZ\text{-low}}$ on 11 August 2016.

To capture thermal conditions at each field site, temperature probes were inserted into the phloem on the south aspect of each infested bolt and temperatures were recorded hourly over the duration of MPB development and emergence (i.e., August 2016 to August 2017; CR1000, Campbell Scientific, Logan, Utah, USA). To describe environmental effects, growing degree hours (GDH) >10° and <0°C (i.e., cumulative heat and cold units) and weekly maximum and minimum temperatures were calculated for each bolt beginning on 12 August 2016.

MPB collection and trait measurements.—Adult brood emergence at each site was monitored at least twice weekly throughout emergence and daily during the weeks of peak emergence. We collected individuals by bolt and transported them on ice to either Northern Arizona University, Flagstaff, AZ, or the RMRS Laboratory in Logan, UT. Generation time for each individual was calculated as the time difference between bolt infestation and brood adult emergence. Generation time includes the time duration for mating, oviposition, egg, larval, pupal, and teneral adult (pre-emergent) development, in addition to a facultative prepupal diapause. We considered generation time resulting in seasonally appropriate (i.e., summer) adult emergence to represent higher relative fitness than a generation time resulting in aseasonal emergence. Adult emergence synchrony is important to successful mass attacks and colonization of new host trees (Logan and Bentz 1999). We define emergence synchrony as the standard deviation in generation time across all individuals of a population at a site, where a lower standard deviation suggests greater emergence synchrony and therefore greater fitness (see *Statistical Analyses*). Reproductive success, a direct measure of fitness representing number of offspring produced, was calculated as the number of emerged brood adults per bolt divided by the number of successful galleries within the bolt, thereby compensating for uneven mating success and subsequent brood production among bolts. A parent gallery was considered successful (and therefore included in the count) if the gallery length was greater than 10 cm (Eidson et al. 2018), assuming that galleries less than 10 cm were the result of failed copulation by the inserted mating pair. The subset of bolts sampled for cold-hardening were not included in the determination of reproductive success, as the removal of larvae altered the number of emerged brood.

To measure larval cold-hardening, individual larvae were collected from three infested bolts per population at each field site three times throughout the annual generation: (1) late November/early December 2016, (2) late January/early February 2017, and (3) late March/early April 2017. To account for temperature variability due to bolt aspect, we randomly sampled MPB larvae on three aspects (north, southwest, and southeast) along the bolt circumference, with each population at each site sampled from all three aspects (one aspect per bolt) each sampling period. To extract larvae, the outer bark and phloem were removed using a 15-cm hole saw, and the wound was sealed with paraffin wax. Larvae were placed in Petri dishes with filter paper and transported directly or overnight-shipped on ice to the RMRS Laboratory in Logan, UT. Larval instar was determined based on head capsule width (P_{UT}: Logan et al. 1998; P_{AZ}: B. J. Bentz, *unpublished data*).

Supercooling points (i.e., the temperature of hemolymph crystallization; Lee 1989) of larvae were analyzed within 24 h of collection. Supercooling points of collected larvae were measured following the protocol of Bentz and Mullins (1999). Briefly, the temperature of individual larvae was monitored while the environmental temperature was lowered at a rate of ~1.5°C/minute. The supercooling point of each larvae was estimated as the lowest recorded temperature prior to tissue freezing, which was observed as an increase in temperature (≥0.5°C) caused by the exothermic latent heat of crystallization. MPB typically has four larval instars prior to pupation, and we observed some combination of larval instars 2, 3, and 4 in cold-hardening samples taken in the fall, winter and spring at each site. No other life stages were observed during sampling for this study. To assess population source and environmental differences in life stage development, we calculated a "developmental index" by averaging instar number (i.e., instars 2, 3, 4) across all observed individuals at each field site and seasonal sampling period.

Adult pronotal width was measured and sex determined (Lyon 1958) for 6,251 individuals (65% of total emerged brood adults). Individuals were collected for sex determination and size measurement at least every 4 d, and every 2 d during peak emergence. We measured pronotal width as a proxy for size (Kozol et al. 1988) using an ocular micrometer to the nearest 0.01 mm.

Laboratory experiments

We reared each population in laboratory incubators at a constant 18°C and 25°C with a 12 h : 12 h photoperiod (Appendix S1: Fig. S2). Optimal larval development in the laboratory occurs at ~25°C for P_{UT} (Régnière et al. 2012) and ~27°C for P_{AZ} (McManis et al. 2018). 18°C was used because it is the lowest temperature, in either population, where the majority of individuals can develop directly to the adult stage without induction of a facultative prepupal diapause (Bentz and Hansen 2017). Induction of the prepupal diapause would delay development, and because the two populations differ in diapause intensity (Bentz and Hansen 2017), the developmental delay would generate confounding differences between the populations. Four infested bolts of each population were reared at 18°C and three bolts for each population were reared at 25°C. Adult emergence from individual bolts was monitored daily. Generation time for each individual brood adult and reproductive success per bolt were measured as described in *Field experiments*. Sex and pronotal size (mm) of 1,532 individuals (31% of total emerged brood adults) were measured as described above, collected from a weekly random population subsample.

Statistical analysis

We tested for differences in fitness traits due to genetic (i.e., g, source population), environmental (i.e., E, rearing site/temperature), and genetic-by-environmental interaction (i.e., gE) effects. Our model is hierarchically structured with normal distributions and is described as follows:

$$y_{ijkl}^{(m)} = \mathrm{g}_{ik}^{(m)} + \mathrm{E}_{jk}^{(m)} + \mathrm{gE}_{ijk}^{(m)} + e_{ijkl}^{(m)}$$

where $\mathrm{g}_{jk}^{(m)}$ represents the genetic effect of the ith population in the kth bolt for the mth trait, $\mathrm{E}_{ik}^{(m)}$ represents the environmental effect of the jth environment in the kth bolt for the mth trait, $\mathrm{gE}_{ijk}^{(m)}$ is the interaction between the genomic effect of the ith population in the kth bolt and the environmental effect of the jth environment in the kth bolt for the mth trait, and $e_{ijkl}^{(m)}$ is the residual error associated with the lth observation of the kth bolt of the jth population in the ith environment for the mth trait.

The model parameters g, E, and gE were drawn from normal distributions centered around the mean and estimated variances of our data. Specifically

$$\mu\mathrm{g}_{ik}^{(m)} \ \mathrm{Normal}\left(\mu\mathrm{g}_i, \mathrm{g}\sigma^2\right)$$

$$\mu\mathrm{E}_{ik}^{(m)} \ \mathrm{Normal}\left(\mu\mathrm{E}_i, \mathrm{E}\sigma^2\right)$$

$$\mu\mathrm{E}_{ijk}^{(m)} \ \mathrm{Normal}(\mu\mathrm{gE}_i, g\mathrm{E}\sigma^2).$$

The model parameters were given normal, uninformative priors with wide distributions. Specifically

$$\mu\mathrm{g}_i, \mu\mathrm{E}_j, \mu\mathrm{gE}_{ij} \ \mathrm{Normal}(0, 1{,}000).$$

With the exception of the variance parameters, which were given modest, Student t prior distribution. Specifically

$$\mathrm{g}\sigma^2, \mathrm{E}\sigma^2, \mathrm{gE}\sigma^2 \ \mathrm{Student}(0, 10).$$

We conducted all analyses in R version 3.3.2 (R Core Team 2018) by computing Bayesian hierarchical models (accounting for variation between bolt replicates) for all fitness traits via Markov chain Monte Carlo (MCMC) sampling. Packages rstanarm (Gabry and Goodrich 2016) and brms (Bürkner 2017, 2018) were used to compute four MCMC chains for 2,000 iterations, discarding the first 1,000 iterations as burn-in and sampling each iteration thereafter. All models were checked graphically for convergence and Rhat ($\hat{r}$) values (i.e., the Gelman-Rubin convergence diagnostic (Gelman and Rubin 1992)), a ratio of variation within and between MCMC chains, were equal to 1, indicating thorough MCMC sampling and convergence of the posterior distributions.

To evaluate synchrony in the timing of adult emergence (i.e., the absolute value of the number of days wherein 1 standard deviation of a population has emerged), we used the posterior distribution of the standard deviation of the generation time parameter (see Bolstad and Curran 2016). Generation times of all individuals within a population at a site were used, and a lower standard deviation implied greater emergence synchrony and therefore greater fitness.

Using Bayesian MCMC estimates, a median estimate and quantified uncertainty were derived for each model parameter. The median effect size (ES) and 95% Bayesian credible intervals ($\mathrm{CI}_{\mathrm{Bayes}}$) were then calculated as the median difference in model parameter estimates between populations, bounded by the range of values indicating the equal-tail 95% credible interval of the true parameter estimate, given the data. ES describes the magnitude of difference between populations, and the marginal probability (MP) is the probability that a population's fitness trait estimate is statistically different (greater or less than, given the direction of the ES) than the comparison population. MP was estimated by calculating the total number of parameter MCMC estimates greater (or less) than the test comparison, divided by the total number of MCMC estimates. In the results, differences between source populations are considered significant or credible when MP > 95% (Ellison 2004).

Results

Field site temperature profiles

As expected, based on GDH heat and cold units (Fig. 2a) and observed maximum and minimum phloem

temperatures (Fig. 2b), $S_{AZ\text{-}low}$ was the warmest site and S_{UT} the coldest (Appendix S2: Table S1). On average, phloem temperatures at $S_{AZ\text{-}low}$ were warmer than S_{UT} in the summer (3.3°C), fall (4.8°C), winter (8.0°C), and spring (6.5°C). Overall, $S_{AZ\text{-}low}$ was an average of 5.5°C warmer than S_{UT} across the duration of the study. Within sites, bolt phloem temperatures did not differ between populations with respect to heat and cold units (Appendix S2: Table S2).

Reproductive success

In the field experiment, we found genetic effects on reproductive success, except at $S_{AZ\text{-}high}$ (Fig. 3a; Table 2). P_{UT} reproductive success was greater than P_{AZ} when reared at its native site (S_{UT}), but P_{AZ} reproductive success was not different from P_{UT} reproductive success at $S_{AZ\text{-}high}$ (Table 2; Appendix S3: Table S1). Both P_{UT} and P_{AZ} had greater reproductive success at $S_{AZ\text{-}low}$, the warmer and lower elevation out-of-range site, than at their natal sites. In the field, there were environmental effects for both populations, with the exception of P_{UT} reared in $S_{AZ\text{-}high}$. Both populations had increased success at $S_{AZ\text{-}low}$, relative to $S_{AZ\text{-}high}$, and the southern population had a decrease in reproductive success at S_{UT} relative to $S_{AZ\text{-}high}$. The range of environmental effects on reproductive success were greater in P_{AZ} (effect size = 6.98 to 15.21) than P_{UT} (effect size = −0.36 to 4.52), and also greater than genetic effects (effect size = −0.34 to 6.28) (Table 2). In the laboratory reproductive success of both populations was greater at 18°C compared to 25°C (Fig. 4a; Table 3; Appendix S3: Table S2).

Generation time

For both populations at all field sites adult emergence occurred at seasonally appropriate times in the summer (Fig. 5). P_{UT} at the $S_{AZ\text{-}low}$ site was the earliest to emerge (median = July 24, 2017) and P_{AZ} at the S_{UT} site was the latest to emerge (median = August 28, 2017). Generation time, even at the warmest site ($S_{AZ\text{-}low}$), required ~ one year from the time bolts were infested and placed at each site. Bivoltinism (i.e., two generations in a single year) was not observed at any site. Sites were checked periodically between December and June, and the first observed adult emergence occurred on 27 June at the warm $S_{AZ\text{-}low}$ site, with median emergence at this site on 24 July. Therefore, the fastest generation time for an individual was 322 d, although the median time was 349 d.

We observed genetic differences in generation time in both the field and laboratory experiments. In the field experiment, P_{AZ} developed slower than P_{UT} at all sites (median difference 10.5–15.7 d; Fig. 3b; Table 2; Appendix S3: Table S1), and P_{AZ} also developed slower than P_{UT} at both 18° and 25°C in the laboratory experiment (median difference 15.7–39.2 d; Fig. 4b; Table 3; Appendix S3: Table S2). The slower P_{AZ} generation time was associated with larger male and female adult progeny size in both the field and laboratory (Figs. 3, 4; Appendix S4: Fig. S1, Tables S2, S3). Adults of both populations were larger at 18°C compared to 25°C in the laboratory (Appendix S4: Fig. S1; Table S3).

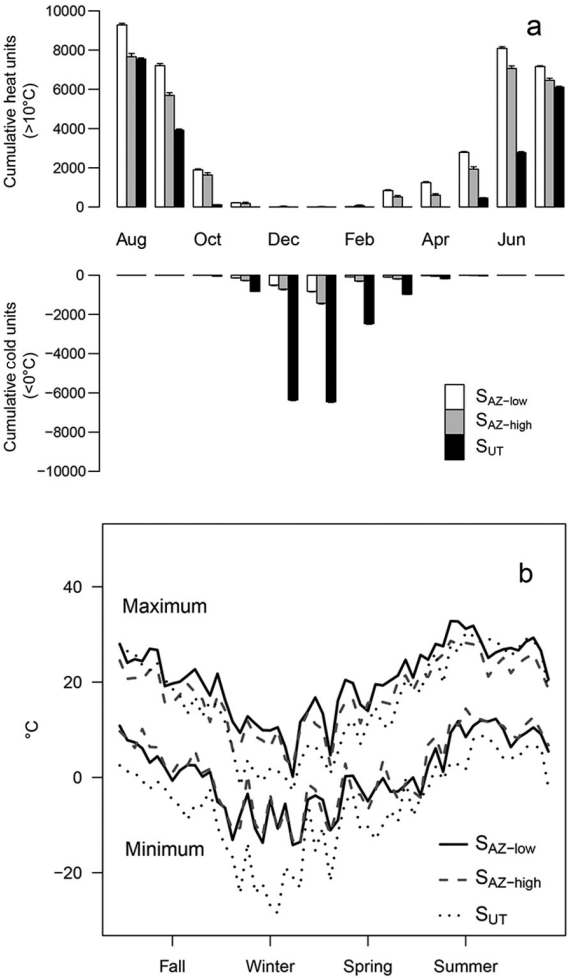

FIG. 2. (a) Cumulative heat (growing degree hours >10°C) and cold (<0°C) units based on phloem temperatures of infested bolts at three field sites (S_{UT}, $S_{AZ\text{-}high}$, $S_{AZ\text{-}low}$; nine bolts per population per site). Temperatures are shown in chronological order of mountain pine beetle generation time (i.e., August 2016 through July 2017). Shown are the mean (and SE) among 18 bolts at each site. (b) Weekly maximum and minimum phloem temperatures at the S_{UT}, $S_{AZ\text{-}high}$, and $S_{AZ\text{-}low}$ field sites during the study from August 2016 to August 2017. See Table 1 for field site information.

Environmental effects on generation time were also observed in both populations in the field and laboratory experiments. In the field experiment, the median generation time of P_{UT} was 35 d faster at the $S_{AZ\text{-}low}$ site and 29.3 d faster at $S_{AZ\text{-}high}$ than at S_{UT}, and 5.7 d faster at $S_{AZ\text{-}low}$ than $S_{AZ\text{-}high}$ (Table 2; Appendix 3: Table S1). P_{AZ} median generation time was 31.1 d faster at $S_{AZ\text{-}low}$ and 31.7 d faster at $S_{AZ\text{-}high}$ than at S_{UT}. P_{UT} generation time differed between the two warmest sites, $S_{AZ\text{-}high}$ and $S_{AZ\text{-}low}$, but P_{AZ} generation time did not differ between

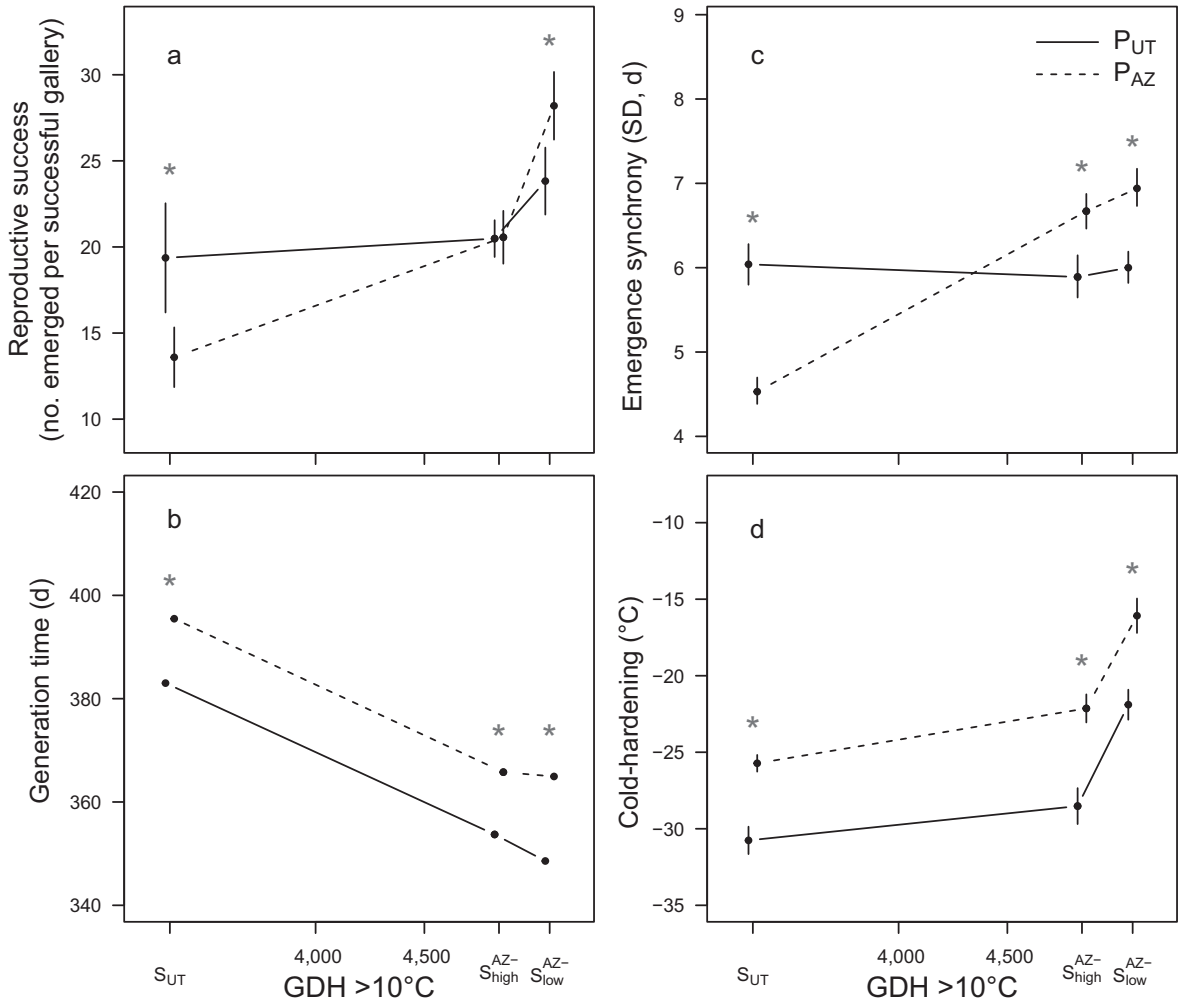

FIG. 3. Fitness trait reaction norms of two mountain pine beetle populations, P_{UT} and P_{AZ}, when reared in the field at the S_{UT}, $S_{AZ\text{-}high}$, and $S_{AZ\text{-}low}$ sites (see Table 1). Sites are plotted in order of latitude and relative bolt phloem growing degree-hour (GDH) accumulations >10°C. Shown are the mean (and 95% CI_{freq}, CI_{Bayes} for emergence synchrony) among nine bolts per population at each site. Asterisks are shown where genetic differences (i.e., due to source population) were credibly different (>95% MP) at a field site (see Table 2). Panels present mountain pine beetle fitness traits of (a) reproductive success, (b) generation time (time from infestation to emergence), (c) emergence synchrony (defined as standard deviation of generation time), and (d) supercooling point.

these sites (Table 2). P_{UT} generation time was also different between 18°C and 25°C in the laboratory experiment, but P_{AZ} generation time did not differ (Table 3; Appendix 3: Table S2). Our results demonstrate both genetic and environmental effects on generation time. Environmental effects observed between the coldest and warmest sites (effect size = 29.3–35.0) were two to three times greater than genetic effects (effect size = 10.5–15.7). Genetic-by-environment interactions were only different between the warmer $S_{AZ\text{-}low}$ and $S_{AZ\text{-}high}$ sites and 18°C and 25°C laboratory temperatures (Tables 2, 3).

Emergence synchrony

In the field experiment, emergence synchrony (i.e., low standard deviation) was greatest for P_{AZ} at the S_{UT} site, and the least in P_{AZ} at $S_{AZ\text{-}low}$ (Fig. 3c; Table 2; Appendix S3: Table S1). Effects due to the environment were only observed for P_{AZ}, which was less synchronous at $S_{AZ\text{-}high}$ and $S_{AZ\text{-}low}$ than at S_{UT}. Genetic effects on emergence synchrony were observed at all sites, with P_{UT} showing less emergence synchrony than P_{AZ} at S_{UT}, but greater emergence synchrony at both $S_{AZ\text{-}high}$ and $S_{AZ\text{-}low}$ than P_{AZ}. In the laboratory study, genetic effects in emergence synchrony were also observed, although in this setting P_{UT} exhibited environmental effects between 18° and 25°C while P_{AZ} synchrony was not different between these two temperatures (Fig. 4c; Table 3; Appendix S3: Table S2). Emergence synchrony was greater in the field experiment for both populations relative to the laboratory experiment. In the field experiment, genetic effects on P_{UT} emergence synchrony were

TABLE 2. Field experiment Bayesian model fitness trait comparison estimates: reproductive success, generation time, emergence synchrony, and supercooling point.

	Reproductive success (no. emerged)		Generation time (d)		Emergence synchrony (SD d)		Supercooling point (°C)	
Field experiment population, and site	ES (95% CI_{Bayes})	MP (%)	ES (95% CI_{Bayes})	MP (%)	ES (95% CI_{Bayes})	MP (%)	ES (95% CI_{Bayes})	MP (%)
Environment (E)								
P_{UT}								
$S_{AZ\text{-}low}$ vs. $S_{AZ\text{-}high}$	4.15 (0.46, 7.69)	**98.5**	−5.7 (−8.5, −2.8)	**100**	0.11 (−0.20, 0.43)	75.6	7.30 (3.28, 11.75)	**100**
$S_{AZ\text{-}high}$ vs. S_{UT}	−0.36 (−0.36, 3.90)	56.6	−29.3 (−32.3, −26.3)	**100**	−0.14 (−0.49, 0.20)	79.5	−0.00 (−0.05, 0.05)	71.1
$S_{AZ\text{-}low}$ vs. S_{UT}	4.52 (1.62, 7.32)	**100**	−35.0 (−38.0, −32.1)	**100**	−0.04 (−0.33, 0.27)	59.4	−0.00 (−0.05, 0.05)	**99.9**
P_{AZ}								
$S_{AZ\text{-}low}$ vs. $S_{AZ\text{-}high}$	8.21 (5.39, 10.99)	**100**	−0.5 (−3.3, 2.3)	62.4	0.27 (−0.03, 0.58)	**96.5**	5.00 (0.79, 9.01)	**98.7**
$S_{AZ\text{-}high}$ vs. S_{UT}	6.98 (4.37, 9.48)	**100**	−31.1 (−34.0, −28.3)	**100**	2.31 (1.88, 2.39)	**100**	4.05 (−0.24, 8.20)	**96.9**
$S_{AZ\text{-}low}$ vs. S_{UT}	15.21 (12.54, 17.90)	**100**	−31.7 (−34.5, −28.6)	**100**	2.41 (2.14, 2.69)	**100**	9.08 (4.78, 13.3)	**99.9**
Source population (g)								
P_{UT} vs. P_{AZ}								
S_{UT}	6.28 (3.71, 9.24)	**100**	−12.4 (−15.3, −9.2)	**100**	1.50 (1.22, 1.79)	**100**	−3.78 (−7.85, 0.59)	**96.2**
$S_{AZ\text{-}high}$	−0.34 (−3.98, 3.57)	57.0	−10.5 (−13.4, −7.7)	**100**	−0.78 (−1.10, −0.45)	**100**	−6.72 (−10.95, −2.65)	**99.7**
$S_{AZ\text{-}low}$	−4.42 (−7.22, −1.58)	**100**	−15.7 (−18.7, −12.9)	**100**	−0.94 (−1.23, −0.66)	**100**	−4.42 (−8.49, −0.20)	**98.1**
Relative environmental effects (gE)								
P_{UT} vs. P_{AZ}								
$S_{AZ\text{-}low}$ vs. $S_{AZ\text{-}high}$	−4.10 (−8.68, 0.42)	**96.3**	−5.2 (−9.3, −1.1)	**99.7**	−0.17 (−0.61, 0.26)	73.2	2.27 (−3.22, 8.37)	78.9
$S_{AZ\text{-}high}$ vs. S_{UT}	−6.48 (−11.03, −2.05)	**99.9**	1.8 (−2.1, 6.0)	81.0	−2.28 (−2.72, −1.85)	**100**	−2.99 (−9.00, 3.00)	85.1
$S_{AZ\text{-}low}$ vs. S_{UT}	−10.64 (−14.58, −6.80)	**100**	−3.3 (−7.6, 0.8)	94.6	−2.44 (−2.86, −2.04)	**100**	−0.66 (−6.46, 5.23)	59.2

Notes: Field experiment Bayesian model estimates testing the genetic (g; P_{UT}, P_{AZ}), environmental (E; $S_{AZ\text{-}low}$, $S_{AZ\text{-}high}$, S_{UT}), and genetic-by-environmental (gE) effects of mountain pine beetle fitness traits of reproductive success (number emerged per successful gallery), supercooling point, generation time (time from infestation to emergence), emergence synchrony (defined as the standard deviation of generation time), and supercooling point. The median effect size (ES) and 95% Bayesian credible intervals (CI_{Bayes}) are shown. The marginal probability (MP) is the probability that pairwise comparisons are statistically different, given the direction of the ES. Values in bold represent comparison estimates that are credibly different (MP > 95%).

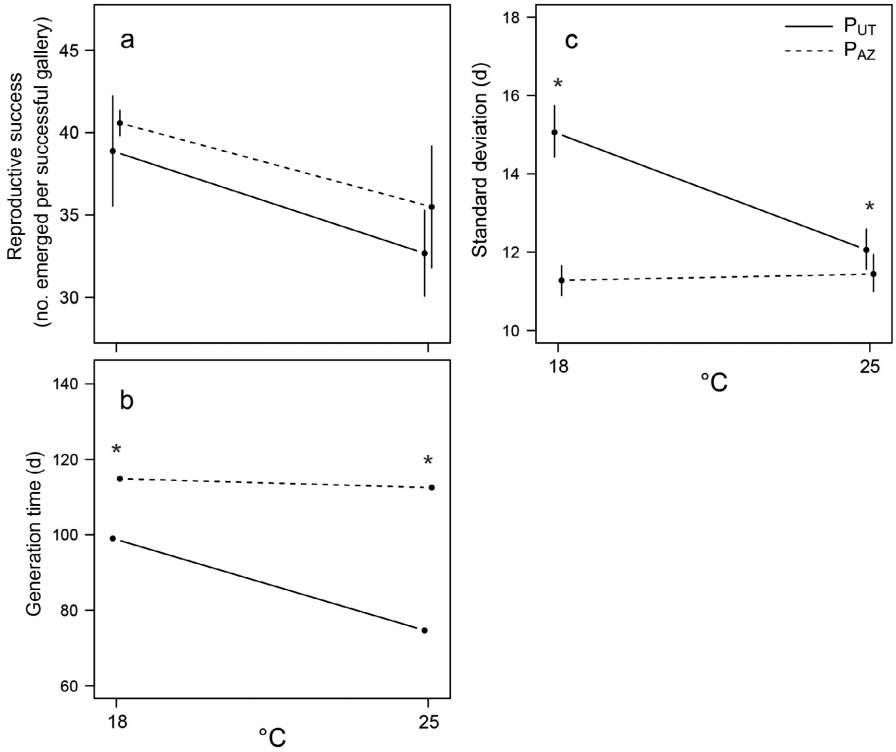

FIG. 4. Fitness trait reaction norms of two mountain pine beetle populations, P_{UT} and P_{AZ}, when reared in the laboratory at two constant temperatures (18°C and 25°C) and a 12 h : 12 h photoperiod. Shown are the mean (and 95% CI_{freq}, CI_{Bayes} for emergence synchrony) model estimates among four bolts per population at 18°C and three bolts per population at 25°C. Asterisks are shown where genetic differences (i.e., due to source population) were credibly different (>95% MP) at a laboratory temperature (see Table 3). Panels present mountain pine beetle fitness traits of (a) reproductive success, (b) generation time (time from infestation to emergence), and (c) emergence synchrony (defined as standard deviation of generation time).

TABLE 3. Laboratory experiment Bayesian model fitness trait comparison estimates: reproductive success, generation time, and emergence synchrony.

Laboratory experiment		Reproductive success (no. emerged)		Generation time (d)		Emergence synchrony (SD d)	
Population	Temperature (°C)	ES (95% CI_{Bayes})	MP (%)	ES (95% CI_{Bayes})	MP (%)	ES (95% CI_{Bayes})	MP (%)
Environment (E)							
P_{UT}	25 vs. 18	−5.94 (−10.37, −1.76)	**99.4**	−24.1 (−31.1, −18.6)	**100**	−2.99 (−3.84, −2.21)	**100**
P_{AZ}	25 vs. 18	−3.95 (−7.99, −0.12)	**97.9**	−1.3 (−8.0, 5.1)	62.4	0.17 (−0.41, 0.77)	62.4
Source population (g)							
P_{UT} vs. P_{AZ}	18	−1.13 (−4.97, 2.76)	72.4	−15.7 (−21.8, −9.7)	75.4	3.79 (3.04, 4.56)	**100**
	25	−3.18 (−7.48, −1.29)	91.8	−39.2 (−45.8, −32.6)	50.2	0.62 (−0.04, 1.32)	**99.7**
Relative environmental effects (gE)							
P_{UT} vs. P_{AZ}	25 vs. 18	2.05 (−3.72, 7.82)	75.1	−23.6 (−32.8, −14.2)	**100**	−3.17 (−4.19, −2.17)	**100**

Notes: Laboratory experiment Bayesian model estimates testing the genetic (g; P_{UT}, P_{AZ}), temperature (E; 18°, 25°C), and genetic-by-environmental (gE) effects of mountain pine beetle fitness traits of reproductive success (number emerged per successful gallery), generation time (time from infestation to emergence), and emergence synchrony (defined as the standard deviation of generation time). The median effect size (ES) and 95% Bayesian credible intervals (CI_{Bayes}) are shown. The marginal probability (MP) is the probability that pairwise comparisons are statistically different, given the direction of the ES. Values in bold represent comparison estimates that are credibly different (MP > 95%).

greater than environmental effects, although environmental effects were greater than genetic effects in P_{AZ} (Table 2). Genetic-by-environment interactions were different between all field and laboratory contrasts, except between the warmer field sites $S_{AZ\text{-low}}$ and $S_{AZ\text{-high}}$ (Tables 2, 3).

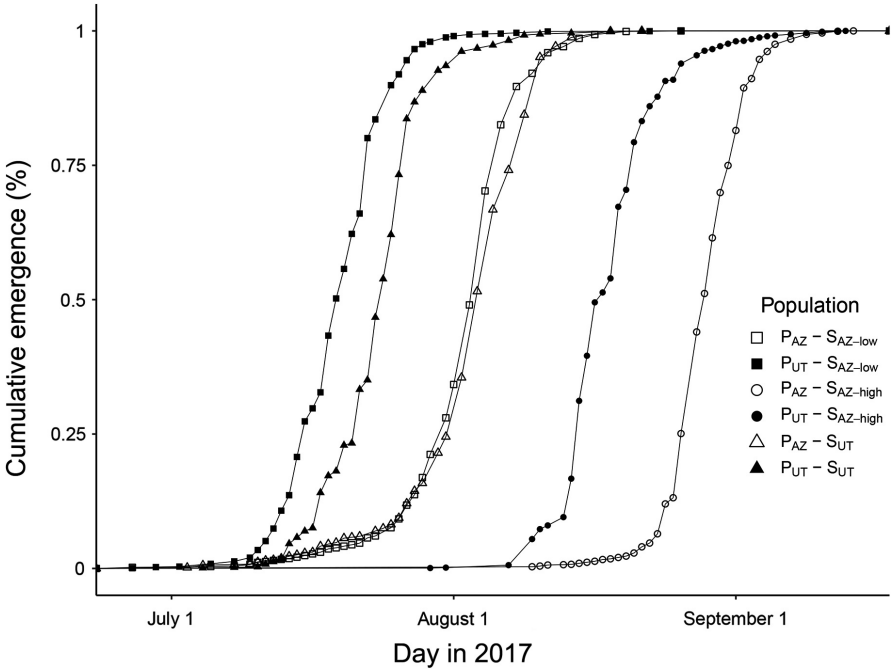

FIG. 5. Emergence timing of two mountain pine beetle populations, P_{UT} and P_{AZ}, from infested bolts placed at three field sites (S_{UT}, $S_{AZ\text{-}high}$, $S_{AZ\text{-}low}$) (see Table 1). Field experiment initiation dates: S_{UT}, 30 July 2016; $S_{AZ\text{-}high}$, 10 August 2016; $S_{AZ\text{-}low}$, 11 August 2016.

Cold-hardening

Samples of both P_{UT} and P_{AZ} contained a majority of fourth instars in the fall and winter samples at $S_{AZ\text{-}low}$ (Fig. 6; Appendix S5: Table S1). A majority of fourth instars was not observed at the S_{UT} and $S_{AZ\text{-}high}$ sites until the spring sample. Development was therefore faster for both populations at the warmest site, $S_{AZ\text{-}low}$, and both populations overwintered at this site as a 4th instar. Overwinter life stages were a mix of third and fourth instars at the two cooler sites. P_{UT} supercooling points were well below minimum temperatures at the three field sites (Appendix S5: Fig. S1). By contrast, P_{AZ} supercooling points were closer to winter minimum temperatures, particularly at the S_{UT} site. Female proportion in the P_{UT} population was greater at the coldest site (S_{UT}) compared to the intermediate temperature site ($S_{AZ\text{-}high}$), and the same trend was observed in the P_{AZ} population (Appendix S5: Fig. S3; Tables S3, S4).

In the fall samples, supercooling points of P_{UT} instar 3 and instar 4 were different at the $S_{AZ\text{-}high}$ and S_{UT} sites, and among all P_{AZ} instars at the S_{UT} site (Appendix S5: Table S2). There were no differences in supercooling points among the instars in the winter and spring 2017 sample periods at all sites (Appendix S5: Table S2). We analyzed genetic and environmental sources of variation on cold-hardening using only winter samples, and all individuals in these samples were pooled by site and population.

Based on winter samples, we found genetic variation in supercooling points at all sites, with P_{AZ} supercooling points higher than P_{UT} at all sites (Fig. 3d; Table 2). Environment also had an effect, and for both populations supercooling points were the lowest at the coldest site (S_{UT}) and highest at the warmest site ($S_{AZ\text{-}low}$), although no difference in supercooling point was observed for P_{UT} between $S_{AZ\text{-}high}$ and S_{UT}. Genetic-by-environment interactions were not different. The effect sizes of genetic (3.78–6.72) and environmental (4.05–9.08) sources of variation in cold-hardening were similar (Table 2).

DISCUSSION

Predicting responses to climate change remains a central challenge in ecology, particularly for impactful species such as MPB that have the potential to affect large geographic regions. Understanding and ultimately predicting such responses requires the use of controlled experiments that tease apart specific trait-based responses to environmental changes. Here we used a reciprocal translocation experiment to mimic a changing climate and characterize the fitness response of MPB populations in a single generation. In general, we found that MPB populations are highly resilient to single-generation changes in climate regimes, displaying sustained or amplified reproductive success, with trait variation attributable to both population genetic differences and environmental plasticity.

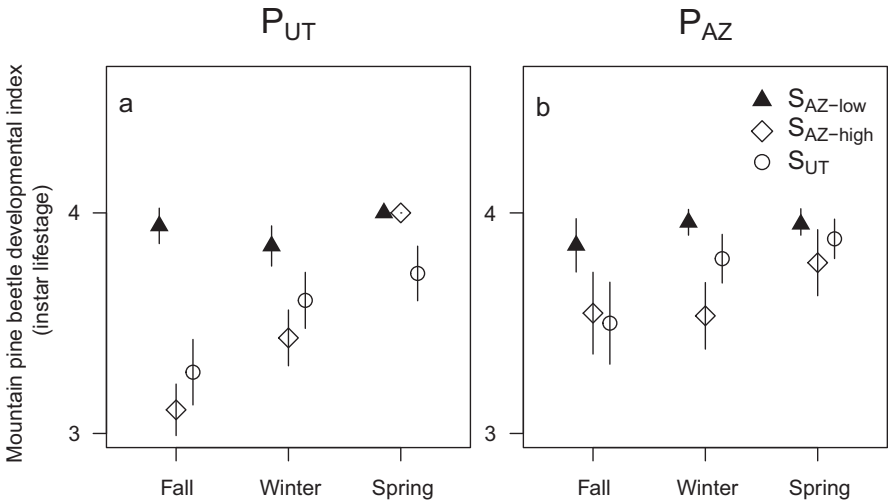

FIG. 6. Mountain pine beetle developmental index (based on four larval instars) in the fall (i.e., November) 2016, winter (i.e., February) 2017, and spring (i.e., March and April) 2017 at three field sites S_{UT}, $S_{AZ\text{-}high}$, and $S_{AZ\text{-}low}$ (see Table 1). Shown are the mean (and 95% CI_{freq}) among three bolts of the (a) P_{UT} and (b) P_{AZ} populations.

Reproductive capacity and climate change

Our findings demonstrate that MPBs originating from high-elevation sites in the core (P_{UT}) and southern (P_{AZ}) areas of its range are capable of reproducing with synchronous, univoltine, and seasonally appropriate adult emergence when reciprocally translocated. Reproductive success combined with seasonally appropriate adult emergence in the reciprocal environments indicates that both populations are capable of survival and reproduction in novel climates. P_{AZ} had greater reproductive success (20.5 adults per gallery) in its warmer natal environment than in the colder reciprocal environment (13.6 adults per gallery), suggesting local adaptation, although P_{UT} reproductive success in the two environments was similar (~20 adults per gallery; Fig. 3a). Most importantly, both populations had their greatest reproductive success at the warmest site that was at a lower elevation than the current MPB range in AZ. The warm out-of-range site was on average 5.5°C warmer than the coldest study site, which is greater than the projected mean temperature increase in *Pinus* and MPB habitat through 2040 (see Bentz et al. 2019). These results suggest persistence and potentially increased MPB population success under warming climatic conditions that provide similar seasonal patterns as our study sites.

Despite favorable thermal conditions and suitable host trees, MPB activity has been historically absent at warm, low-elevation sites in AZ (McHugh et al. 2003, Gaylord et al. 2006, Lynch et al. 2006, Williams et al. 2008), suggesting that factors other than direct temperature effects are operating at low-elevations at the southern U.S. edge of the species range. While abiotic factors are considered important to expansion of species northern range boundaries (MacArthur 1972, Brown et al. 1996, Normand et al. 2009), biotic factors have been suggested mechanisms that constrain species range limits near southern boundaries (Kaufman 1995, Sax 2001, Gross and Price 2008). For MPB, these biotic factors may include resource competition (Berryman 1974, Coulson 1979, Rankin and Borden 1991), semiochemical interference with other phloephagous bark beetles (Sánchez-Martínez and Wagner 2002, Negron et al. 2009, Hofstetter et al. 2012), differential impacts of temperature on the symbiotic fungal community (Six and Bentz 2007, Moore and Six 2015), insect (Reeve 1997, Turchin et al. 1999) and avian predation (Steeger et al. 1998), host tree growth and vigor (Raffa and Berryman 1982), and host tree chemistry that can inhibit MPB development and aggregation pheromone synthesis (Erbilgin and Raffa 2000, Franceschi et al. 2005). Assessing these interactions, specifically the role of competition among phloephagous bark beetles in attack and colonization of southwestern type ponderosa pine, warrants further investigation.

Generation time and diapause

As expected for ectotherms, generation time was dramatically affected by temperature in our field and laboratory experiments, with effect sizes of 3–4 weeks in several contrasts. Both genetic and environmental variation influenced generation time, although the effect sizes for environmental variation were generally two to three times greater. Both source populations had faster generation times at the warmest relative to coldest field sites, and in the laboratory P_{UT} generation time was fastest at the warmest constant temperature. Genetic factors were also prevalent. P_{UT}, which evolved at the site with the fewest GDH > 10°C, developed faster than P_{AZ} at all three field sites and both temperatures in the laboratory. The evolution of rapid generation times is not

uncommon for species adapted to cold habitats (Sgrò et al. 2016). The patterns we observed are also consistent with counter-gradient variation wherein genetic influences on a trait oppose environmental influences, thereby minimizing phenotypic change along a geographic gradient (Conover and Schultz 1995). In MPB, the longer generation time of southern populations is likely a result of selection pressure to maintain univoltinism (Logan and Bentz 1999, Bentz et al. 2014). P_{AZ} adults were also larger than P_{UT} adults across all field sites and constant temperatures in the laboratory, which is consistent with the hypothesis that longer development time should produce larger adult size (Roff 1992), although we cannot rule out nutritional affects due to the host tree. Generation time and adult size are also influenced by MPB fungal symbionts (Bentz and Six 2006, Bleiker and Six 2014), which may have been lost or gained in shifts to the novel environments. A better understanding of fungal associates of the two MPB populations and their resiliency to thermal changes is needed.

The greatest difference in generation time between the two populations occurred at the warm, out-of-range site where P_{UT} generation time was almost 16 d faster than P_{AZ}. The genetic-by-environment interactions between the two warmest field sites and the two laboratory temperatures also highlights the differential responses of P_{UT} and P_{AZ} to the warmest environment. In contrast to the evolved rapid generation time of P_{UT}, P_{AZ} evolved at a relatively warm site where a relaxed generation time is considered an adaptation for maintaining seasonality (Bentz et al. 2001, Bracewell et al. 2013, Bentz et al. 2014). Instead of reducing generation time, warming can maintain or increase the time required to complete a generation in populations such as P_{AZ} with plastic physiological responses that include diapause (Forrest 2016, Buckley et al. 2017). Diapause is a common trait for maintaining synchrony, and one that is often locally adapted (Denlinger 2002).

Differences in induction cues and the intensity of a facultative prepupal diapause have been previously shown for northern UT and central AZ MPB populations, suggesting local adaptation for this trait that is induced by cool temperatures and serves to reduce the probability that the cold-intolerant pupal stage will occur during winter (Bentz and Hansen 2017, Bleiker and Smith 2019). Results from our translocation experiment, however, suggest that this prepupal diapause is likely not driving the observed heritable variation in generation time or the lack of P_{AZ} plasticity at the warmest sites. At the warmest site both populations overwintered as majority late-stage larvae or prepupae and remained in these stages at least through our last sample date in early April, most likely in diapause. Moreover, northern UT MPB populations have a greater diapause intensity and duration than central AZ beetles (Bentz and Hansen 2017), suggesting that generation time in P_{UT} individuals would have been longer if prepupal diapause was the delaying factor. Heritable differences in generation time between the source populations in our translocation experiment must instead occur in either the pupal or teneral adult life stage. McManis et al. (2018) found few differences in egg and larval development times between central AZ and northern UT populations in a laboratory environment, and observed that central AZ pupae developed at warmer temperatures than northern UT pupae. Pupal development of AZ populations at a warmer temperature would tend to speed up rather than slow down generation time at the warmer sites. Therefore, we concur with McManis et al. (2018) that the likely life stage responsible for delayed generation time in P_{AZ}, relative to P_{UT}, is the teneral adult.

An obligatory or facultative reproductive diapause in teneral adults has been observed or suggested for multiple *Dendroctonus* species (Ryan 1959, Chansler 1967, Langor and Raske 1987, Safranyik et al. 1990, McKee and Aukema 2015). Observed adult diapause in these species occurs during winter. An adult winter diapause in *D. ponderosae* was suggested by Lester and Irwin (2012), but has not been verified. A winter adult diapause would not, however, explain the generation time differences we observed between the two populations in our study, as both overwintered as late-stage larvae and prepupae. Although it has not been investigated for any *Dendroctonus* species, summer adult diapause is common among Coleoptera and other Curculionidae (Masaki 1980). For example, optimal summer adult diapause developmental temperatures in the weevil *Hypera brunneipennis* were in the range of 20–25°C (Madubunyi 1978). In another example, locally adaptive adult diapause was observed in the moth *Mamestra brassicae*, where summer diapause was virtually absent in northern populations and both its incidence and duration increased in populations at southern locations (Masaki 1980). Our results suggest that MPB has a previously unidentified teneral adult summer diapause that is manifest in the P_{AZ}, but not P_{UT} population. Genetic-by-environment interactions that also support this hypothesis include (1) in the field, P_{AZ} generation time did not differ between the two warmest sites, although P_{UT} generation was accelerated at the warmest site; (2) in the laboratory, P_{AZ} generation time did not differ between the two constant temperatures, but P_{UT} generation time was accelerated at the warmest temperature; and (3) in the laboratory, P_{AZ} generation time did not vary across temperatures but P_{AZ} adult size was larger at 18°C compared to 25°C. This result suggests that a warm temperature-induced diapause delayed P_{AZ} adult development but did not affect its size, similar to a phenomena observed in grasshoppers (Buckley et al. 2015). An evolved adult summer diapause that serves to relax development time during long growing seasons, thereby maintaining univoltinism as we observed, could be maladaptive if a reduction in generation time is more advantageous as climate warms (Forrest 2016).

Emergence synchrony

Synchrony of adult emergence from brood trees is critical to successful MPB mass attacks on trees (Logan and Bentz 1999, Safranyik and Carroll 2006). Variation in emergence synchrony was influenced by source population in both the field and laboratory experiments. Emergence synchrony of P_{UT} was less (i.e., greater standard deviation) than P_{AZ} at the coolest site and also at the coolest temperature (18°C) in the laboratory. P_{UT} emergence synchrony was not influenced by environmental variation among field sites but, in the laboratory emergence synchrony, declined at 18°C relative to 25°C. The opposite trend was observed for P_{AZ} where environmental variation did not influence synchrony in the laboratory, but did in the field. In the laboratory, low emergence synchrony in P_{UT} at 18°C could be due to a portion of the population entering the facultative prepupal diapause, whereas 18°C is above the upper threshold for prepupal diapause induction in P_{AZ} (Bentz and Hansen 2017). If some P_{UT} individuals entered the prepupal diapause in the laboratory and some did not, a larger standard deviation in emergence timing, as was observed, would occur. In P_{AZ} the lack of environmental variation in emergence synchrony in the laboratory mirrors the negligible variation in generation time across temperatures in the laboratory, suggesting, as described above, a role for warm temperature-induced adult diapause. The large differences in genetic and environmental effects on the two populations that differ between the field and laboratory, including greater emergence synchrony in the field relative to the lab, suggest that environmental cues in the field environment are important to synchrony, and that population response to fluctuating vs. constant temperatures differs (Colinet et al. 2015).

Cold-hardening

In recent years, warming temperatures have facilitated MPB persistence at high elevations (Weed et al. 2015, Buotte et al. 2016) and expansion northward in Canada (Carroll et al. 2004, Sambaraju et al. 2012, Goodsman et al. 2018), causing enormous impacts to ecosystem goods and services (Morris et al. 2018). A critical trait affecting such persistence and expansion is cold-hardening, which allows overwintering life stages to survive ambient temperatures well below freezing. Cold-hardening in the MPB involves the production of antifreeze compounds, including glycerol, in response to thermoperiodic cues (Bentz and Mullins 1999, Fraser et al. 2017, Thompson et al. 2019), dynamic processes that occur with high energetic cost (Danks 1987, Lee 1989). Supercooling points in MPB, indicative of the extent of cold-hardening, have been shown to differ geographically among populations in the field (Bentz and Mullins 1999), as has been observed in many other insect species with large geographic distributions (Kukal and Duman 1989, Shintani and Ishikawa 2002, Elkinton et al. 2017). However, studies on the degree of heritability and plasticity for this trait are limited, and absent for MPB. Here we were able to demonstrate, for the first time, that supercooling points in MPBs are influenced both by genetic and environmental factors, with similar effect sizes. In our winter sample, P_{UT}, originating from the coldest of the three sites, had supercooling points that were consistently lower than P_{AZ} at all three field sites, indicating an evolved capacity for greater cold-hardening. Genetic adaptation of P_{AZ} to relatively warm winter conditions was evident in its reduced supercooling capacity, compared to P_{UT}, across all sites. Moreover, when compared to the similar reproductive success of the two populations in the laboratory, low reproductive success of P_{AZ} at the coldest site was likely due to inadequate cold-hardening and excess winter mortality. The higher proportion of females in both populations at the coldest site also suggests that males were more susceptible to stressful thermal extremes (Lachowski and Reid 2014, James et al. 2016). Supercooling points in both source populations were consistently highest at the warmest sites illustrating how environmental conditions can dictate facultative metabolic investment in antifreeze compounds (Lee 1989).

Fitness benefits of cold-hardening occur when supercooling points are low enough to allow survival, so the degree of cold-hardening must be considerably lower than the average winter temperatures at a site. Although the relatively high supercooling points in P_{AZ} at S_{UT} did not preclude reproductive success in this particular year, average mid-winter P_{AZ} supercooling points were 2.72°C warmer than the lowest recorded minimum phloem temperature at the S_{UT} site. By contrast, P_{UT} average mid-winter supercooling points were 2.25°C colder than the lowest minimum temperature at the S_{UT} site. This finding indicates that northward movement of P_{AZ} is likely to require adaptive evolution to persist through colder winters. Climate change has already increased minimum temperatures in northern latitudes (Easterling et al. 1997), which will reduce the amount of adaptive evolution necessary for persistence of migrants from warmer climates. P_{UT} supercooling points in the middle of winter at the warmest site were 7.6°C colder than the lowest minimum temperature at that site, reflecting an unnecessary and maladaptive energetic investment in cold-hardening. However, as climate change is also expected to increase temperature variability (Stouffer and Wetherald 2007), apparent overinvestment in supercooling may serve as an adaptive buffer in highly variable years.

Conclusion

Pinus habitat within the MPB range is projected to increase by 1–3°C between the periods 1981–2010 and 2011–2040 depending on season, latitude, and elevation (Bentz et al. 2019). A central question in ecology is how the changing environmental conditions will influence

population persistence and range shifts. Using a reciprocal translocation experiment with populations representative of the core and southern edge of the MPB distribution, we found evidence for local adaptation and extensive plasticity in key fitness traits that will sustain population persistence in these regions as temperatures warm. Our results indicate a low likelihood of MPB extinction with warming temperatures that are within the seasonal thermal regime of our study, as survival followed by natural selection in subsequent generations will facilitate future adaptation to warming environments. However, range retraction of suitable host trees as a result of warming temperatures could affect MPB persistence at its southern range.

Both source populations showed their greatest reproductive success at a site that is at a lower elevation than the current MPB range in AZ, and was warmer than both sources. Absence of MPB activity in the historical records from this low-elevation site suggests that factors other than direct temperature effects are controlling population presence and spread southward in low-elevation *Pinus*. *Pinus* also extend south of the United States into Mexico and Central America, but MPB activity in these areas has been limited or absent. Our results suggest a capacity for MPB to persist with warming in *Pinus* hosts found in the core of its range and high-elevation *Pinus* in its southern range, although migration further south into Mexico may be hampered by the fragmented occurrence of high-elevation pines (Menon et al. 2018). The potential to expand into lower elevation forests at the southern range edge, and further southward, may also be limited, but likely by biotic interactions rather than direct temperature effects.

Neither population developed on a bivoltine lifecycle, even at the warm, low-elevation and out-of-range site where both populations overwintered in the last larval instar prior to pupation. These results support previous studies suggesting that a cold-induced prepupal diapause limits MPB bivoltine lifecycles in habitats with relatively cold winter temperatures (Bentz et al. 2014, Bentz and Powell 2014). Moreover, multiple results from our study suggest that MPBs from the high-elevation AZ site have a warm-induced adult summer diapause that was not manifest in UT beetles and has likely evolved to maintain univoltinism and seasonality in the prolonged growing season at this site. The potential for bivoltinism, therefore, will be dictated by the different cues that induce diapause in the two populations. Loss of seasonality and population success may also occur if diapause cues are disrupted in a warming climate. As warming continues, an understanding of limits to the observed plasticity and genetic variation in multiple traits will be required to project future thermal regimes that maintain seasonality (Bentz et al. 2019) and allow population persistence and expansion.

Acknowledgments

Jim Vandygriff and Matt Hansen provided assistance with collection of *D. ponderosae*-infested and non–infested trees, laboratory rearing, and field assembly. We thank Dr. Monica Gaylord, Danny DePinte, and John Anhold for their help with field assembly and winter collections in Arizona. We also thank Zach Gompert, Justin Runyon, and Justin deRose for providing comments on an earlier version of the manuscript, and to William Pearse for statistical help. The experiment was designed by B. Bentz, K. Mock, and R. Hofstetter. D. Soderberg, B. Bentz, and R. Hofstetter implemented the field experiment and collected data. D. Soderberg conducted the statistical analysis and led the writing of the manuscript with assistance from B. Bentz and K. Mock. We thank USDA Forest Service Rocky Mountain Research Station and the Quinney College of Natural Resources at Utah State University for financial support.

Literature Cited

Adams, A. S., and D. L. Six. 2007. Temporal variation in mycophagy and prevalence of fungi associated with developmental stages of *Dendroctonus ponderosae* (Coleoptera: Curculionidae). Environmental Entomology 36:64–72.

Allen, C. D., A. K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Vennetier, T. Kitzberger, A. Rigling, D. D. Breshears, and E. H. Hogg. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259:660–684.

Amman, G. D. 1972. Some factors affecting oviposition behavior of the mountain pine beetle. Environmental Entomology 1:691–695.

Amman, G. D. 1978. The biology, ecology, and causes of outbreaks of the mountain pine beetle in lodgepole pine forests. Pages. 39–53 *in* A. A. Berryman, G. D. Amman, and R. W. Stark, editors. Theory and practice of mountain pine beetle management in lodgepole pine forests: symposium proceedings; 1978 April 25–27. University of Idaho, Forest, Wildlife and Range Experiment Station. Pullman, Washington, USA.

Anderegg, W. R., et al. 2015. Tree mortality from dought, insects, and their interactions in a changing climate. New Phytologist 208:674–678.

Armendáriz-Toledano, F., V. Torres-Banda, and G. Zúñiga. 2017. The current status of *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae: Scolytinae) in Mexico. The Coleopterists Bulletin 71:565–570.

Arora, V. K., Y. Peng, W. A. Kurz, J. C. Fyfe, B. Hawkins, and A. T. Werner. 2016. Potential near-future carbon uptake overcomes losses from a large insect outbreak in British Columbia, Canada. Geophysical Research Letters 43:2590–2598.

Atkinson, D. 1994. Temperature and organisms size—a biological law for ectotherms? Advances in Ecological Research 3:1–58.

Babin-Fenske, J., M. Anand, and Y. Alarie. 2008. Rapid morphological change in stream beetle museum specimens correlates with climate change. Ecological Entomology 33:646–651.

Bentz, B. J., R. R. Bracewell, K. E. Mock, and M. E. Pfrender. 2011. Genetic architecture and phenotypic plasticity of thermally regulated traits in an eruptive species, *Dendroctonus ponderosae*. Evolutionary Ecology 25:1269–1288.

Bentz, B. J., and E. M. Hansen. 2017. Evidence for a prepupal diapause in the mountain pine beetle (*Dendroctonus ponderosae*). Environmental Entomology 1:175–183.

Bentz, B. J., A. M. Jönsson, M. Schroeder, A. Weed, R. A. Wilcke, and K. Larsson. 2019. *Ips typographus* and *Dendroctonus ponderosae* models project thermal suitability for intra and inter–continental establishment in a changing climate. Frontiers in Forests and Global Change 2:1.

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

Bentz, B. J., J. A. Logan, and J. C. Vandygriff. 2001. Latitudinal life history variation in *Dendroctonus ponderosae* (Coleoptera: Scolytidae) development time and size. Canadian Entomologist 133:375–387.

Bentz, B. J., and D. Mullins. 1999. Ecology of mountain pine beetle (Coleoptera: Scolytidae) cold hardening in the intermountain west. Environmental Entomology 28:577–587.

Bentz, B. J., and J. A. Powell. 2014. Mountain pine beetle seasonal timing and constraints to bivolinism (A comment on Mitton and Ferrenberg, "Mountain Pine Beetle Develops an Unprecedented Summer Generation in Response to Climate Warming). American Naturalist 184:787–796.

Bentz, B. J., and D. L. Six. 2006. Ergosterol content of fungi associated with *Dendroctonus ponderosae* and *Dendroctonus rufipennis* (Coleoptera: Curculionidae, Scolytinae). Annals of the Entomological Society of America 99:189–194.

Bentz, B. J., J. Vandygriff, C. Jensen, T. Coleman, O. Maloney, S. Smith, A. Grady, and G. Schen-Langenheim. 2014. Mountain pine beetle voltinism and life history characteristics across latitudinal and elevational gradients in the western United States. Forest Science 60:434–449.

Berryman, A. A. 1974. Dynamics of bark beetle populations: towards a general productivity model. Environmental Entomology 3:579–585.

Bleiker, K. P., and D. L. Six. 2009. Competition and coexistence in a multi–partner mutualism: Interactions between two fungal symbionts of the mountain pine beetle in beetle-attacked trees. Microbial Ecology 57:191–202.

Bleiker, K. P., and D. L. Six. 2014. Dietary benefits of fungal associates to an eruptive herbivore: potential implications of multiple associates of host population dynamics. Environmental Entomology 36:1384–1396.

Bleiker, K. P., and G. D. Smith. 2019. Cold tolerance of mountain pine beetle (Coleoptera: Curculionidae) pupae. Environmental Entomology 48:1412–1417.

Bolstad, W. M., and J. M. Curran. 2016. Bayesian inference for standard deviation. *In* W. M. Bolstad and J. M. Curran, editors. Introduction to Bayesian statistics. Third edition. John Wiley & Sons, Inc.

Bracewell, R. R., M. E. Pfrender, K. E. Mock, and B. J. Bentz. 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.

Bradshaw, A. D. 1965. Evolutionary significance of phenotypic plasticity in plants. Advances in Genetics 13:115–155.

Brown, J. H., G. C. Stevens, and D. M. Kaufman. 1996. The geographic range: size, shape, boundaries, and internal structure. Annual Review of Ecology and Systematics 27:597–623.

Buckley, L. B., A. J. Arakiki, A. F. Cannistra, H. M. Kharouba, and J. G. Kingsolver. 2017. Insect development, thermal plasticity and fitness implications in changing, seasonal environments. Integrative and Comparative Biology 57:988–998.

Buckley, L. B., C. R. Nufio, E. M. Kirk, and J. G. Kingsolver. 2015. Elevational differences in developmental plasticity determine phenological responses of grasshoppers to recent climate warming. Proceedings of the Royal Society B 282:20150441.

Buotte, P. C., J. A. Hicke, H. K. Preisler, J. T. Abatzoglou, K. F. Raffa, and J. A. Logan. 2016. Climate influences on whitebark pine mortality from mountain pine beetle in the Greater Yellowstone Ecosystem. Ecological Applications 26:2505–2522.

Burke, J. J., and A. L. Carroll. 2017. Breeding matters: Natal experience influences population state–dependent host acceptance by an eruptive insect herbivore. PLoS ONE https://doi.org/10.1371/journal.pone.0172448.

Bürkner, P. C. 2017. brms: An R package for Bayesian multilevel models using Stan. Journal of Statistical Software 80:1–28.

Bürkner, P. C. 2018. Advanced Bayesian multilevel modeling with the R package brms. R Journal 10:395–411.

Carroll, A. L., S. W. Taylor, J. Régnière, and L. Safranyik. 2004. Effects of climate change on range expansion by the mountain pine beetle in British Columbia. Mountain Pine Beetle Symposium: challenges and solutions (30–31 October 2003). Pages 223–232 *in* T. L. Shore, J. E. Brooks, and J. E. Stone, editors. Mountain Pine Beetle Symposium: challenges and solutions, October 30–31, 2003, Kelowna, British Columbia, Canada. Information Report BC–X–399. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia.

Case, T. J., R. D. Holt, M. A. McPeak, and T. H. Keitt. 2005. The community context of species' borders: Ecology and evolutionary perspectives. Oikos 108:28–46.

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

Chen, I., J. K. Hill, R. Ohlemüller, D. B. Roy, and C. D. Thomas. 2011. Rapid range shifts of species associated with high levels of climate warming. Science 333:1024–1026.

Cibrián-Tovar, D., J. T. Méndez-Montiel, R. Campos-Bolanos, H. O. Yates, and J. Flores-Lara. 1995. Insectos forestales de México/Forest Insects of Mexico. Universidad Autonoma de Chapingo, Mexico City, Mexico.

Colinet, H., B. J. Sinclair, P. Vernon, and D. Renault. 2015. Insects in fluctuating thermal environments. Annual Review of Entomology 60:123–140.

Conover, D. O., and E. T. Schultz. 1995. Phenotypic similarity and the evolutionary significance of countergradient variation. Trends in Ecology and Evolution 10:248–252.

Cooke, C. J., and A. L. Carroll. 2017. Predicting the risk of mountain pine beetle spread to eastern pine forests: Considering uncertainty in uncertain times. Forest Ecology and Management 396:11–25.

Coulson, R. N. 1979. Population dynamics of bark beetles. Annual Review of Entomology 24:417–447.

Danks, H. V.1987. Insect dormancy: an ecological perspective. Biological Survey of Canada (Terrestrial Arthropods), Ottawa, Ontario, Canada.

de la Giroday, H. C., A. L. Carroll, and B. H. Aukema. 2012. Breach of the northern Rocky Mountain geoclimatic barrier: initiation of range expansion by the mountain pine beetle. Journal of Biography 39:1112–1123.

Denlinger, D. L. 2002. Regulation of diapause. Annual Review of Entomology 47:93–122.

Dowle, E. J., R. R. Bracewell, M. E. Pfender, K. E. Mock, B. J. Bentz, and G. J. Ragland. 2017. Reproductive isolation and environmental adaptation shape the phylogeography of mountain pine beetle (*Dendroctonus ponderosae*). Molecular Ecology 26:6071–6084.

Easterling, D. R., et al. 1997. Maximum and minimum temperature trends for the globe. Science 277:364–367.

Eidson, E., B. J. Bentz, and K. E. Mock. 2018. Low offspring survival in mountain pine beetle infesting the resistant Great Basin bristlecone pine supports the preference–performance hypothesis. PLoS ONE 13:e0196732.

Elkin, C. M., and M. L. Reid. 2005. Low energy reserves and energy allocation decisions affect reproduction by mountain pine beetles, *Dendroctonus ponderosae*. Functional Ecology 19:102–109.

Elkinton, J. S., J. A. Lombardo, A. D. Roehrig, and T. J. McAvoy. 2017. Induction of cold hardiness in an invasive herbivore: The case of hemlock woolly adelgid (Hemiptera: Adelgidae). Environmental Entomology 46:118–124.

Ellison, A. M. 2004. Bayesian inference in ecology. Ecology Letters 7:509–520.

Erbilgin, N., and K. F. Raffa. 2000. Opposing effects of host monoterpenes on responses by two sympatric species of bark beetles to their aggregation pheromones. Journal of Chemical Ecology 26:2527–2548.

Food and Agriculture Organization. 2018. Global forest resources assessment 2010. FAO Forestry Paper No. 163. FAO, Rome, Italy.

Forrest, J. R. 2016. Complex responses of insect phenology to climate change. Current Opinion in Insect Science 17:49–54.

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

Fraser, J. D., T. R. Bonnett, C. I. Keeling, and D. P. Huber. 2017. Seasonal shifts in accumulation of glycerol biosynthetic gene transcripts in mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae), larvae. PeerJ 5:e3284.

Gabry, J., and B. Goodrich. 2016. rstanarm: Bayesian Applied Regression Modeling via Stan. R package version 2.9.0–3. https://CRAN.R-project.org/package=rstanarm

Gaston, K. J., and R. A. Fuller. 2009. The sizes of species' geographic ranges. Journal of Applied Ecology 46:1–9.

Gaylord, M. L., T. E. Kolb, K. F. Wallin, and M. R. Wagner. 2006. Seasonality and lure preferences of bark beetles (Curculionidae: Scolytinae) and associates in a northern Arizona ponderosa pine forest. Environmental Entomology 35:37–47.

Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences (with discussion). Statistical Science 7:457–511.

Gienapp, P., C. Teplitsky, J. S. Alho, J. A. Mills, and J. Merilä. 2008. Climate change and evolution: disentangling environmental and genetic responses. Molecular Ecology 17:167–178.

Goodsman, D. W., G. Grosklos, B. H. Aukema, C. Whitehouse, K. P. Bleiker, N. G. McDowell, R. S. Middleton, and C. Xu. 2018. The effect of warmer winters on the demography of an outbreak insect is hidden by intraspecific competition. Global Change Biology 24:3620–3628.

Grégoire, J. C., K. F. Raffa, and B. S. Lindgren. 2015. Chapter 15 - Economics and politics of bark beetles. Pages 585–613 *in* F. E. Vega and R. W. Hofstetter, editors. Bark beetles. Academic Press.

Gross, S. J., and T. D. Price. 2008. Determinants of the northern and southern range limits of a warbler. Journal of Biography 27:869–878.

Hansen, M. C., et al. 2014. Monitoring conterminous United States (CONUS) land cover change with web-enabled Landsat data (WELD). Remote Sensing of Environment 140:466–484.

Hicke, J. A., J. H. A. Meddens, and C. A. Kolden. 2015. Recent tree mortality in the western United States from bark beetles and forest fires. Forest Science 62:141–153.

Hickling, R., D. B. Roy, J. K. Hill, and C. D. Thomas. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. Global Change Biology 12:450–455.

Hoffmann, A. A., and C. M. Sgrò. 2011. Climate change and evolutionary adaptation. Nature 470:479–485.

Hofstetter, R. W., M. L. Gaylord, S. Martinson, and M. R. Wagner. 2012. Attraction to monoterpenes and beetle-produced compounds by syntopic *Ips* and *Dendroctonus* bark beetles and their predators. Agricultural and Forest Entomology 14:207–215.

Honěk, A. 1993. Intraspecific variation in body size and fecundity in insects: A general relationship. Oikos 66:483–492.

IPCC Climate Change 2014. 2014. Synthesis report. *In*Core Writing Team, R. K. Pacharui, and L. A. Meyer. Cambridge University Press, Cambridge, UK.

James, P. M., J. K. Janes, A. D. Roe, and B. J. Cooke. 2016. Modeling landscape-level spatial variation in sex ratio skew in the mountain pine beetle (Coleoptera: Curculionidae). Environmental Entomology 4:790–801.

Kaufman, D. M. 1995. Diversity of New World mammals: universality of the latitudinal gradient of species and bauplans. Journal of Mammalogy 76:322–334.

Kawecki, T. J., and D. Ebert. 2004. Conceptual issues in local adaptation. Ecology Letters 7:1225–1241.

Kozol, A. J., M. P. Scott, and J. F. Traniello. 1988. The American burying beetle, *Nicrophorus americanus*: studies on the natural history of a declining species. Psyche 95:167–176.

Kukal, O., and J. G. Duman. 1989. Switch in the overwintering strategy of two insects and latitudinal differences in cold hardiness. Canadian Journal of Zoology 67:825–827.

Lachowski, L. E., and M. L. Reid. 2014. Developmental mortality increases sex–ratio bias of a size–dimorphic bark beetle. Ecological Entomology 39:300–308.

Langor, D. W., and A. G. Raske. 1987. Reproduction and development of the eastern larch beetle, *Dendroctonus* Simplex LeConte (Coleoptera: Scolytidae), in Newfoundland. Canadian Entomologist 119:985–992.

Lee, R. E. 1989. Insect cold hardiness: to freeze or not to freeze. How insects survive low temperatures. BioScience 39:308–312.

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

Little, E. L. 1971. Atlas of United States trees. Volume 1. Conifers and important hardwoods. Miscellaneous Publication 1146. U.S. Department of Agriculture, Forest Service, Washington, D.C., USA.

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

Logan, J. A., B. J. Bentz, J. C. Vandygriff, and D. L. Turner. 1998. General program for determining instar distributions from head capsule widths: example analysis of mountain pine beetle data. Environmental Entomology 27:555–563.

Lynch, H. J., R. A. Renkin, R. L. Crabtree, and P. R. Moorcroft. 2006. Insect–fire interactions in Yellowstone National Park: The influence of historical mountain pine beetle (*Dendroctonus ponderosae*) activity on the spatial pattern of the 1988 Yellowstone fires. Ecosystems 9:1318–1327.

Lyon, R. L. 1958. A useful secondary sex character in *Dendroctonus* bark beetles. Canadian Entomologist 90:582–584.

MacArthur, R. H. 1972. Geographical ecology: patterns in the distribution of species. Harper & Row, New York, New York, USA.

Madubunyi, L. C. 1978. External environmental factors regulating imaginal diapause in *Hypera brunneipennis*. Annals of the Entomological Society of America 71:37–39.

Masaki, S. 1980. Summer diapause. Annual Review of Entomology 25:1–25.

McHugh, C. W., T. E. Kolb, and J. L. Wilson. 2003. Bark beetle attacks on ponderosa pine following fire in Northern Arizona. Environmental Entomology 12:7–22.

McKee, F. R., and B. H. Aukema. 2015. Successful reproduction by the eastern larch beetle (Coleoptera: Curculionidae) in the absence of an overwintering period. Canadian Entomologist 147:602–610.

McManis, A. E., J. A. Powell, and B. J. Bentz. 2018. Developmental parameters of a southern mountain pine beetle (Coleoptera: Curculionidae) population reveal potential source of latitudinal differences in generation time. Canadian Entomologist 151:1–15.

Menon, M. J. C., et al. 2018. The role of hydridization during ecological divergence of southwestern white pine (*Pinus strobiformis*) and limber pine (*P. flexilis*). Molecular Ecology 27:1245–1260.

Merilä, J., and A. P. Hendry. 2014. Climate change, adaptation, and phenotypic plasticity: the problem and the evidence. Evolutionary Applications 7:1–14.

Mitton, J. B., and S. M. Ferrenberg. 2012. Mountain pine beetle develops an unprecedented summer generation in response to climate warming. American Naturalist 179:163–171.

Moore, M. L., and D. L. Six. 2015. Effects of temperature on growth, sporulation, and competition of mountain pine beetle fungal symbionts. Microbial Ecology 70:336–347.

Morley, J. W., R. D. Batt, and M. L. Pinsky. 2017. Marine assemblages respond rapidly to winter climate variability. Global Change Biology 23:2590–2601.

Morris, J. L., et al. 2018. Bark beetles as agents of change in social–ecological systems. Frontiers in Ecology and the Environment 16:S34–S43.

Myrholm, C. L., and D. W. Langor. 2015. Assessment of the impact of symbiont *Ophiostomatales* (Fungi) on mountain pine beetle (Coleoptera: Curculionidae) performance on a jack pine (*Pinaceae*) diet using a novel in vitro rearing method. Canadian Entomologist 148:68–82.

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

Nooten, S. S., and L. Hughes. 2017. The power of the transplant: direct assessment of climate change impacts. Climatic Change 144:237–255.

Normand, S., U. A. Treier, C. Randin, P. Vittoz, A. Guisan, and J. Svenning. 2009. Importance of abiotic stress as a range-limited determinant for European plants: insights from species responses to climatic gradients. Global Ecology and Biogeography 18:437–449.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics 37:637–669.

R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org

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

Raffa, K. F., and A. A. Berryman. 1982. Physiological differences between lodgepole pines resistant and susceptible to the mountain pine beetle and associated microorganisms. Environmental Entomology 11:486–492.

Raffa, K. F., T. W. Phillips, and S. M. Salom. 1993. Strategies and mechanisms of host colonization by bark beetles. Pages 102–128 *in* T. Schowalter, and G. Filip, editors. Beetle-pathogen interactions in conifer forests. Academic, San Diego, California, USA.

Rankin, L. J., and J. H. Borden. 1991. Competitive interactions between the mountain pine beetle and the pine engraver in lodgepole pine. Canadian Journal of Forest Research 21:1029–1036.

Reeve, J. D. 1997. Predation and bark beetle dynamics. Oecologia 112:48–54.

Régnière, J., J. A. Powell, B. J. Bentz, and V. Nealis. 2012. Effects of temperature on development, survival and reproduction of insects: Experimental design, data analysis and modeling. Journal of Insect Physiology 58:634–647.

Reid, R. W. 1958. The behavior of the mountain pine beelte, *Dendroctonus monticolae* Hopkins, during mating, egg laying, and gallery construction. Canadian Entomologist 90: 505–509.

Roff, D. A. 1992. The evolution of life histories: theory and analysis. Chapman and Hall, New York, New York, USA.

Rosenberger, D. W. 2017. Cold tolerance of mountain pine beetle among novel eastern pines: A potential for trade-offs in an invaded range? Forest Ecology and Management 400:28–37.

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

Safranyik, L., and A. L. Carroll. 2006. The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. Pages 3–66 (Chapter 1) *in* L. Safranyik, and W. R. Wilson, editors. The mountain pine beetle: a synthesis of biology, management, and impacts on lodgepole pine. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia, Canada.

Safranyik, L., C. Simmons, and H. J. Barclay. 1990. A conceptual model of spruce beetle population dynamics. Information Report BC–X–316. Forestry Canada, Pacific Forestry Centre, Victoria, British Columbia, Canada.

Sambaraju, K. R., A. L. Carroll, and B. H. Aukema. 2019. Multiyear weather anomalies associated with range shifts by the mountain pine beetle preceding large epidemics. Forest Ecology and Management 438:86–95.

Sambaraju, K. R., A. L. Carroll, J. Zhu, K. Stahl, D. Moore, and B. H. Aukema. 2012. Climate change could alter the distribution of mountain pine beetle outbreaks in western Canada. Ecography 35:211–223.

Sánchez–Martínez G., and M. R. Wagner. 2002. Bark beetle community structure under four ponderosa pine forest stand conditions in northern Arizona. Forest Ecology and Management 170:145–160.

Sax, D. F. 2001. Latitudinal gradients and geographic ranges of exotic species: implications for biogeography. Journal of Biography 28:139–150.

Schlichting, C., and M. Pigliucci. 1998. Phenotypic evolution: a reaction norm perspective. Sinauer Associates, Sunderland, Massachusetts, USA.

Seidl, R., et al. 2017. Forest disturbances under climate change. Nature Climate Change 7:395–402.

Sgrò, C. M., J. S. Terblanche, and A. A. Hoffmann. 2016. What can plasticity contribute to insect responses to climate change? Annual Review of Entomology 61:433–451.

Shintani, Y., and Y. Ishikawa. 2002. Geographic variation in cold hardiness of eggs and neonate larvae of the yellow-spotted longicorn beetle *Psacothea hilaris*. Physiological Entomology 24:158–164.

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

Six, D. L., and M. J. Wingfield. 2010. The role of phytopathogenicity in bark beetle-fungus symbioses: a challenge to the classic paradigm. Annual Review of Entomology 56:255–272.

Soderberg, D. 2020. Translocation experiment reveals capacity for mountain pine beetle persistence under climate warming. Dryad data set. https://doi.org/10.5061/dryad.bnzs7h47g

Solheim, H. 1995. Early stages of blue–stain fungus invasion of lodgepole pine sapwood following mountain pine beetle attack. Canadian Journal of Botany 73:70–74.

Steeger, C., M. Machmer, and B. Gowans. 1998. Impact of insectivorous birds on bark beetles: a literature review. Pandion Ecological Research Report, Ymir, British Columbia, Canada.

Stouffer, R. J., and R. T. Wetherald. 2007. Changes of variability in response to increasing greenhouse gases. Part 1: Temperature. Journal of Climate 20:5455–5467.

Thompson, K. M., D. P. Huber, and B. W. Murray. 2019. Autumn shifts in cold tolerance metabolites in overwintering adult mountain pine beetles. bioRxiv.

Turchin, P., A. D. Taylor, and J. D. Reeve. 1999. Dynamic role of predators in population cycles of a forest insect: an experimental test. Science 285:1068–1071.

Via, S., and R. Lande. 1985. Genotype-environment interaction and the evolution of phenotypic plasticity. Evolution 39:505–522.

Weed, A. S., M. P. Ayres, and B. J. Bentz. 2015. Population dynamics of bark beetles. Pages 157–176 *in* F. Vega and R. Hofstetter, editors. Bark beetles: biology and ecology of native and invasive species. Elsevier Academic Press, Cambridge, Massachusetts, USA.

Whitney, H. S. 1982. Relationships between bark beetles and symbiotic organisms. Pages 183–211 *in* J. B. Mitton and K. B. Sturgeon, editors. Bark beetles in Northern American conifers. University Press, Austin, Texas, USA.

Williams, K. K., J. D. McMillin, T. E. DeGomez, K. M. Clancy, and A. Miller. 2008. Influence of elevation on bark beetle (Coleoptera: Curculionidae, Scolytinae) community structure and flight periodicity in ponderosa pine forests of Arizona. Environmental Entomology 37:94–109.

Wood, D. L. 1982. The role of pheromones, kairomones, and allomones in the host selection and colonization behavior of bark beetles. Annual Review of Entomology 27:411–446.

Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecm.1437/full

Data Availability

Additional supporting information may be found online at: Data are available from the Dryad Digital Repository (Soderberg 2020): https://doi.org/10.5061/dryad.bnzs7h47g.