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The effect of warmer winters on the demography of an outbreak insect is hidden by intraspecific competition

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Abstract

Warmer climates are predicted to increase bark beetle outbreak frequency, severity, and range. Even in favorable climates, however, outbreaks can decelerate due to resource limitation, which necessitates the inclusion of competition for limited resources in analyses of climatic effects on populations. We evaluated several hypotheses of how climate impacts mountain pine beetle reproduction using an extensive 9-year dataset, in which nearly 10,000 trees were sampled across a region of approximately 90,000 km^2, that was recently invaded by the mountain beetle in Alberta, Canada. Our analysis supports the hypothesis of a positive effect of warmer winter temperatures on mountain pine beetle overwinter survival and provides evidence that the increasing trend in minimum winter temperatures over time in North America is an important driver of increased mountain pine beetle reproduction across the region. Although we demonstrate a consistent effect of warmer minimum winter temperatures on mountain pine beetle reproductive rates that is evident at the landscape and regional scales, this effect is overwhelmed by the effect of competition for resources within trees at the site level. Our results suggest that detection of the effects of a warming climate on bark beetle populations at small spatial scales may be difficult without accounting for negative density dependence due to competition for resources.

KEYWORDS
bark beetle, climate change, density dependence, dynamics, insect, outbreak, population ecology

1 | INTRODUCTION

Warmer climates have been associated with recent increases in the severity, frequency, and extent of devastating bark beetle outbreaks (Aukema et al., 2008; Bentz et al., 2010; Logan & Powell, 2001; Safranyik et al., 2010), yet information is lacking to date on the potential interaction between a changing climate and negative density dependence in bark beetles. Such systems include the aggressive mountain pine beetle, which underwent climate-facilitated range expansion in the 2000s in Canada when beetles from an epidemic in British Columbia blew over the Rocky Mountains and became established in north-western Alberta, a region where they had not historically been present (Robertson, Neson, Jelinski, & Wulder, 2009). Like in many bark beetle systems (Bentz et al., 2010;

Lesk, Coffel, D'Amato, Dodds, & Horton, 2017), winter temperatures are a key determinant of mountain pine beetle's annual population levels and distribution (Aukema et al., 2008; Bentz et al., 2010; Logan & Powell, 2001; Safranyik, 1978; Safranyik et al., 2010).

In addition to the limiting effects of cold winter temperatures on the insect's survival, its reproductive success is also subject to over-compensating negative density dependence (Ricker-type negative density dependence) due to competition among larvae feeding under the bark of host trees (Berryman, 1974; Berryman & Pienaar, 1973; Raffa & Berryman, 1983). The objective of this study was to determine if climatic variation, and in particular cold winter temperatures, interacts with negative density dependence in the mountain pine beetle and to elucidate the nature of climatic interactions with nonlinear demography. To determine the effect of climate on mountain pine beetle reproduction and its interaction with negative density dependence driven by larval competition, we fitted variations of a generalized Ricker equation (Berryman & Lima, 2006):

$$X_{t+1} = \theta X_t e^{g\left(1-\left(\frac{X_t}{K}\right)^{\omega}\right)}, \tag{1}$$

in which X_t and X_{t+1} represent population density at time t and time $t+1$; θ is a density-independent multiplicative factor impacting reproduction (e.g. winter mortality); g modulates fecundity; K is the carrying capacity, and ω is an empirical nonlinear competition parameter (Berryman & Lima, 2006). Note that in the classical Ricker model, $\theta = 1$ and $\omega = 1$. The linearized version of eqn 1 gives the natural logarithm of the *per capita* reproductive rate per generation:

$$Ln(R_{t+1}) = \alpha - \beta X_t^{\omega}, \tag{2}$$

wherein $R_{t+1} = X_{t+1}/X_t$, $\alpha = Ln(\theta) + g$, and $\beta = g/K^{\omega}$. The linearized generalized Ricker equation (eqn 2) is easier to fit to data using a robust generalized linear mixed modeling approach than the original equation (eqn 1). Moreover, the ways in which climatic variation impacts demography can be easily visualized using eqn 2.

We expected that climatic variation impacts the parameters in eqn 1 and so prior to model fitting we formulated four hypotheses that describe how climate may impact eqn 2 and hence population dynamics over time. In the first hypothesis (H1), we predicted that variation in winter temperatures may impact the density-independent probability of overwinter survival represented by the multiplicative constant (θ) in eqn 1. In that case, we expected α in eqn 2 to change and the line that represents the right hand side of eqn 2 to move vertically (Figure 1a). Thus, according to H1, variation in overwinter survival will lead to random intercepts (α_r) that vary across years and sites (random intercepts model). In our second hypothesis (H2), we predicted that climatic variability may impact fecundity as represented by the growth rate parameter (g in $\alpha = Ln(\theta) + g$, and $\beta = g/K^{\omega}$). In this case, α and β will increase as g increases, resulting in a teeter-totter or compensatory effect because of the negative sign on β (Figure 1b). The overcompensatory effect would lead to variation in intercepts (α_r) and slopes (β_r) across sites and years (random intercepts and slopes). In the third hypothesis (H3), we predicted that climatic variability may impact the carrying capacity parameter (K) by impacting the quality or quantity of resources under the bark of host trees. Such variation in the carrying capacity would lead to changes of the slope (β) of the line, but not its height (Figure 1c). This third hypothesis would lead to a random slopes model (β_r). In the fourth case (H4), climate simultaneously impacts overwinter survival (through θ in $\alpha = Ln(\theta) + g$) and the under-bark carrying capacity (through K in $\beta = g/K^{\omega}$), leading to slopes and heights that vary (Figure 1d) but which are not necessarily negatively correlated. Like H2, H4 would lead to slopes and intercepts that vary across years (random intercepts and slopes).

We compared our four hypotheses of how climate impacts the nonlinear demography of mountain pine beetle reproduction by fitting multiple models to a 9-year dataset (2008–2016) in which nearly 10,000 trees across most of the recently invaded range in Alberta, Canada were sampled. We demonstrate that warmer winter
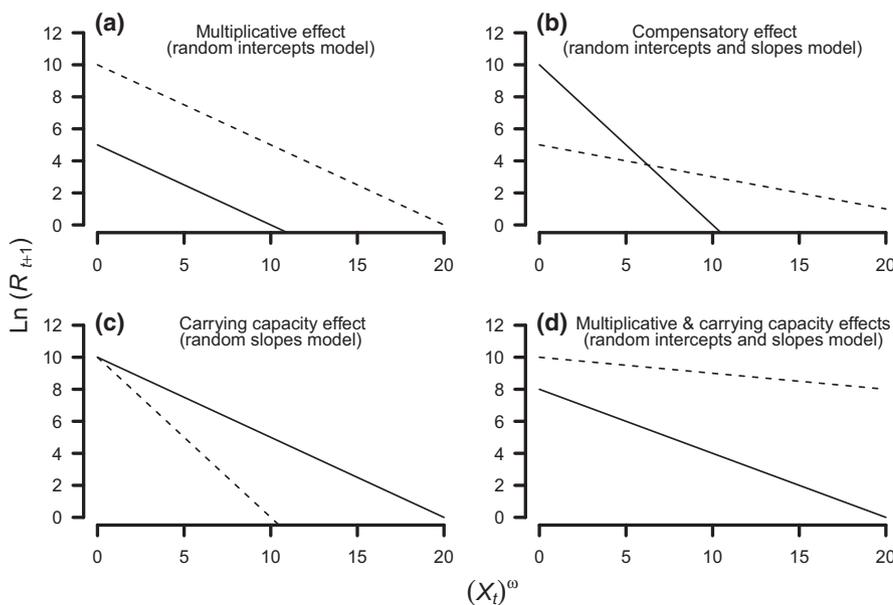

FIGURE 1 Four hypotheses for how climate may impact density dependent mountain pine beetle reproduction as represented by the generalized Ricker model: (a) Hypothesis 1 (H1) represents a multiplicative effect in which climatic variation raises or lowers the natural logarithm of per capita productivity. (b) Hypothesis 2 (H2) represents a compensatory dynamic in which climatic variation leads to a teeter-totter effect. (c) In hypothesis 3 (H3) climatic variability impacts the carrying capacity, which results in a change in the slope of the line. (d) Hypothesis 4 (H4) represents a combination of multiplicative and carrying capacity effects

temperatures lead to a consistent increase in mountain pine beetle reproductive rates that is evident at the larger spatial scales of our analysis but overwhelmed by the effect of negative density dependence at the smaller spatial scales. A warming trend in winter temperatures in Alberta coincides with an increase in mountain pine beetle reproduction within trees as well as its unprecedented range expansion to the north and east of previous range limits.

2 | MATERIALS AND METHODS

2.1 | Study species, data, and location

Successful adult mountain pine beetle attack of host trees leads to the death of tree tissues around developing brood, which in the case of mass attacked trees, ultimately results in tree death. The typical life cycle takes 1 year to complete, but can take more or less time depending on temperature. Most of the life cycle is completed under the bark except for dispersal when young adults emerge from the natal host in the summer to colonize new host trees and lay eggs. Although any life stage can potentially overwinter, larvae are thought to be the most cold tolerant stage (Régnière & Bentz, 2007; Rosenberger, Aukema, & Venette, 2017). Overwinter mortality accounts for the largest fraction of mountain pine beetle mortality (Amman & Cole, 1983).

Recently, the mountain pine beetle significantly expanded its range eastward in Canada. Historically, the beetle's range in Canada was largely limited to west of the Rocky Mountains in central British Columbia; however, multiple times in the 2000s, large numbers of beetles from an outbreak in central British Columbia moved across the Continental Divide and invaded north-eastern British Columbia and west-central Alberta (Safranyik et al., 2010). The mountain pine beetle is well-established in this new region and is now close to the Saskatchewan border in northern Canada.

The provincial management agency, Alberta Agriculture and Forestry, monitors mountain pine beetle populations annually in the spring. Surveyors select up to 20 attacked trees per site, and cut four disks (10.16 cm diameter or 4 inches) of sapwood with the bark attached using a hole saw fitted to a gas powered drill. Two disks are removed from each of the north and south sides of the stem around 1.3 m above the ground. The bark is removed from each disk and the number of entrance holes (typically one entrance hole per attacking female beetle) and the number of living and dead insects in each life stage are counted. Data are pooled at each site and the number of living insects at each site is divided by the total number of entrance holes at that site. This r-value is a measure of mountain pine beetle's potential productivity at each sample site and is used to guide management decisions. From 2008 to 2016 over 1000 sites were surveyed in this way resulting in nearly 10,000 sampled trees in mountain pine beetle's recently expanded range in Alberta (Figure 2a).

We calculated a tree-level estimate of mountain pine beetle reproduction by dividing the number of living insects sampled in each tree by the number of entrance holes for that tree. We excluded any trees that successfully resisted attack. Resinosis can
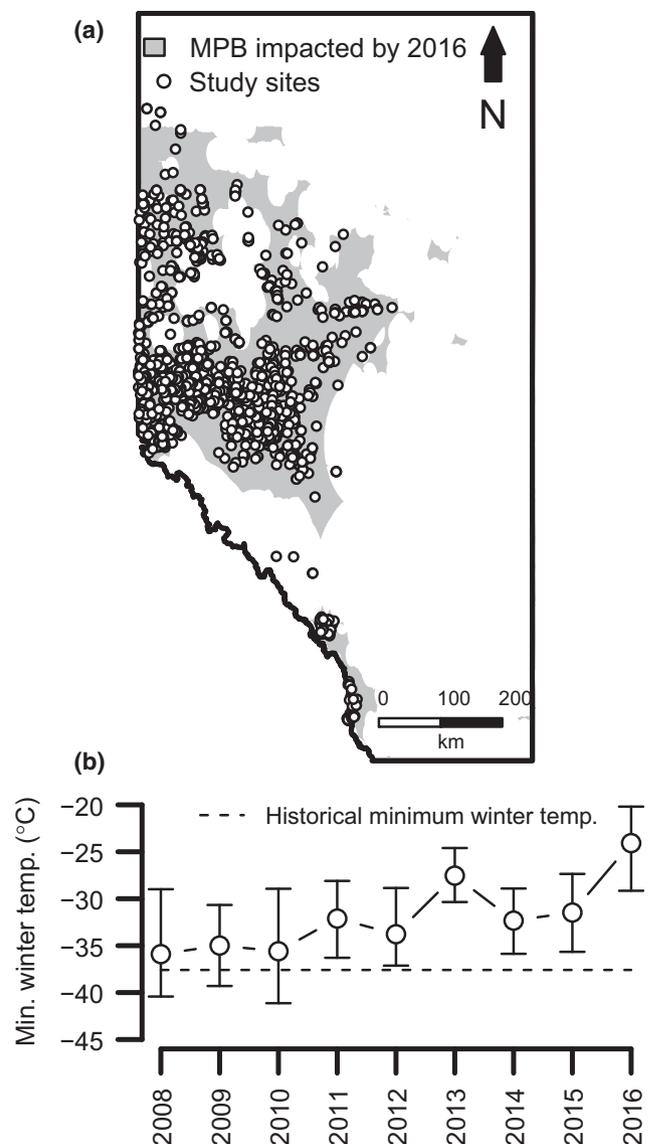

FIGURE 2 A map of Alberta showing (a) the maximum extent of mountain pine beetle attacked trees that were attacked in 2015 or before along with the point locations of study sites surveyed by Alberta Agriculture and Forestry between 2008 and 2016. (b) averaged minimum temperatures across all study sites compared to the historical average minimum winter temperatures in the region from 1980 to 2007

deter attacking parents and drown eggs and sometimes young larvae in the summer shortly after attack; however, within a few weeks of attack, it is usually evident if the tree has succumbed to attack based on the progression of parent galleries and the presence of developing larvae. Thus, we considered trees without any larvae or pupae, living or dead present at the time of sampling in the spring to have resisted mountain pine beetle attack and excluded them from the analysis. Observations without any entrance holes were also excluded as we considered them to be false zeros resulting from the relatively small surface area sampled (each sampled tree was visually observed to have been attacked by mountain pine beetles prior to sampling). We compared the four hypotheses of how climate

impacts the nonlinear dynamics of mountain pine beetle reproduction by fitting the models that represented them to the extensive dataset described above.

Temperature data and model estimates of winter mortality in mountain pine beetle larvae were obtained using BioSIM software (Régnière, St-Amant, & Béchard, 2014). Temperature data are drawn from a daily temperature database of regional daily temperatures collected at weather stations. The raw weather station data used in our analysis are available at ftp://ftp.cfl.scf.rncan.gc.ca/regniere/Data/Weather/Daily/. BioSIM then interpolates the weather station data to produce estimates of weather at user-specified spatial locations and time frames. All of the data that we used in our analysis are available at article landing page (see online Supporting information S1).

2.2 | Statistics

We computed mountain pine beetle reproductive success at the tree level by dividing the number of living individuals in the four disks sampled per tree by the number of entrance holes occurring on the disks. We assumed that each entrance hole corresponds to a male–female pair and thus to the density of the parent generation attacking the tree X_t. We also assumed that each counted living individual was a member of the progeny generation from parent beetles that attacked and mated the previous summer (less than a year prior to the survey date) rather than a member of the progeny of parents that attacked more than 1 year prior to the survey date.

The appropriate statistical models for counts of individuals per sample of a given surface area are Poisson or negative binomial distributions. We found that the data were overdispersed relative to the Poisson distribution for a given mean and so we assumed that the number of living offspring counted per tree (X_{t+1}) was a negative binomially distributed random variable with a mean of μ_{t+1} and an overdispersion parameter of q. A zero inflation model however, was necessary because the frequency of zeros in our data exceeded the number expected under the negative binomial distribution. Thus, the base model that we fitted to our data was a generalized linear model with a log-link,

$$Ln(\mu_{t+1}) = Ln(f(\cdot)), \qquad (3)$$

with an additional binomially distributed component to account for extra zeros. We assume that the probability of additional zeros that are not expected under the negative binomial distribution is a fixed parameter (this is the zero inflation parameter in the zero-inflated generalized linear mixed model).

In eqn 3, $f(\cdot)$ is a function of the relevant predictor variables and parameters that represent one of the hypotheses in our candidate set of models. For the generalized Ricker model, $f(\cdot)$ is equivalent to eqn 1 and, thus,

$$Ln(\mu_{t+1}) = Ln(X_t) + \alpha + g\sqrt{X_t(K)^{-1}}, \qquad (4)$$

in which $\omega = 1/2$, which has been justified empirically for bark beetles in prior work (Berryman, 1974). We allowed the carrying

capacity parameter to vary with tree diameter at 1.3 m above the ground (diameter at breast height-DBH) and we assumed that carrying capacity was linearly proportional to DBH ($K = \varphi DBH$) and so eqn 4 becomes

$$Ln(\mu_{t+1}) = Ln(X_t) + \alpha + \beta\sqrt{X_t(DBH)^{-1}}, \qquad (5)$$

in which $\beta = g/\sqrt{\varphi}$.

We assumed that variation in climate, much like environmental stochasticity, leads to normally distributed perturbations to the parameters in the generalized Ricker equation (eqn 1). Thus, the appropriate mixed effects model assuming that the additive random effects are normally distributed $\left(\alpha_r \sim N\left(0, \sigma_\alpha^2\right) \text{ and } \beta_r \sim N\left(0, \sigma_\beta^2\right)\right)$ can be written as:

$$Ln(\mu_{t+1}) = Ln(X_t) + \alpha + \alpha_r + (\beta + \beta_r)\sqrt{X_t(DBH)^{-1}}. \qquad (6)$$

The random slope and random intercept model above represents the hypothesis of a climatic effect on both the intercept and slope (H2 and H4). The other two hypotheses for how climate interacts with the generalized Ricker growth equation can be obtained by setting the random slope term to zero to represent only the multiplicative effect (H1), or by setting the random intercept term to zero to represent only the carrying capacity effect of climate (H3).

We fitted each of the models above assuming that each random parameter is nested such that the random parameter varies by year, by project (management area) within year, and by site within project within year. The variations of statistical models described above resulted in three candidate models to be compared. We fitted each of these models to the data and compared their performance using Akaike (1981) information criterion (AIC). Lower AIC values indicate lower information loss by the model and more efficient representation of the processes that gave rise to the data (Akaike, 1981). All analyses were conducted using R statistical software (R Core Team, 2017) and generalized linear mixed models were fitted in R using the glmmADMB package (Fournier et al., 2012; Skaug, Fournier, Bolker, Magnusson, & Nielsen, 2016). The code for our analyses are can be downloaded from the article landing page (see online Supporting information S2).

2.3 | Effect of winter mortality

To test for the effect of winter mortality on the survival of mountain pine beetle larvae after competition, we included a probability of winter survival in our models based on a cold-tolerance model for mountain pine beetle (Régnière & Bentz, 2007). The probability of winter survival (p_{surv}) was included in our models as a fixed effect as follows

$$Ln(\mu_{t+1}) = Ln(X_t) + \eta Ln(p_{surv}) + \alpha + \alpha_r + (\beta + \beta_r)\sqrt{X_t(DBH)^{-1}}, \qquad (7)$$

in which η is a parameter that corrects for bias in the predicted probability of winter survival and all other parameters are defined

with reference to eqn 6. We obtained site and year specific estimates of the probability of winter survival for each of study site locations using BioSIM software (Régnière et al., 2014). Using the AIC model selection approach, we compared models that explicitly included winter survival as a function of winter temperatures to models that represented climatic variability using random effects.

2.4 | Verification of model validity

To verify the reliability of our findings based on our best selected model, we performed a number of model checks including testing for spatial and temporal autocorrelation of model residuals. To perform the tests for spatial autocorrelation in each year of our study, we obtained the response residuals (observed - fitted) of our best model and fitted a spline correlogram using the ncf package in R (Bjornstad, 2018) as a function of distance between points in our dataset. Spatial autocorrelation of residuals was determined at the site level as we did not have coordinates for individual trees in the study, but we did have the latitudes and longitudes of sites. To test for temporal autocorrelation in our residuals, we averaged our residuals within years and then used the acf function (autocorrelation function) in R to determine whether residuals were correlated across time lags. If spatial or temporal correlation were present, it would reduce the reliability of our findings.

2.5 | Effect of tree species

As the mountain pine beetle expanded its range east in Canada, it moved into a region where the ranges of lodgepole and jack pines overlap and the two species hybridize (Cullingham et al., 2011). To determine whether the expansion eastward into new host types impacted mountain pine beetle reproduction in a way that would invalidate our results, we subsetted our data according to whether infestations were in areas dominated by lodgepole pine or in areas where jack pine and jack pine hybrids occur as predicted by historical range maps (Little & Viereck, 1971). We then repeated our statistical analysis as described above in each region to estimate parameters and select the optimal models.

3 | RESULTS

Our data most strongly support the generalized Ricker model with random intercepts and slopes (AIC = 22150.4, fixed df = 10) which corresponds to H2 or H4; the random intercepts only model (H1) had an intermediate level of support (AIC = 22154.0, fixed df = 7) and the random slopes only generalized Ricker model (H3) was least supported (AIC = 22261.2, fixed df = 7). The generalized Ricker model with random intercepts and slopes did not distinguish compensatory effects (H2) from a combination of multiplicative effects and carrying capacity effects (H4), but we prefer the latter. If the primary effect of climate were on mountain pine beetle fecundity (H2: g in eqns 1 and 2), we would expect the random slopes and

intercepts to be negatively correlated. The estimated random intercepts and slopes of our preferred model are positively correlated (see Supporting information S3 Figure A3.1), which suggests that the climatic effect on nonlinear dynamics is due to a combination of multiplicative and carrying capacity effects (H4). Our general findings did not change when we split our data into regions dominated by lodgepole pine and regions divided by hybrids of jack pine and lodgepole pine and by pure jack pine (see Supporting information S4).

When the generalized ricker model with random effects is amended to include the winter survival probability of mountain pine beetle (multiplicatively), the model performance is improved for all variations on the random effects (lower AICs), and the random slopes and intercepts model (AIC = 22117.4, fixed df = 11) is preferred over the random slopes only model (AIC = 22209.2, fixed df = 8) and the random intercepts only model (AIC = 22120.6, fixed df = 8). The bias-corrected curves (see Supporting information S5 for description of bias correction) that represent the model favored by our data represent the dominant negative trend in beetle productivity with increasing beetle density well (Figure 3). Moreover, the model fit at the site level explains 94% of the variation in our observed data (Figure 4) and model residuals lack significant spatial or temporal autocorrelation (see Figure A3.2, and A3.3 in Supporting information S3).

The effect of winter mortality as a function of cold winter temperature changes depending on spatial scale of analysis. At the site level, the effect of winter mortality is overpowered by that of negative density dependence (Figure 5a), but at larger spatial scales (coarser resolutions of analysis), the effect of winter cold on the probability of survival becomes more evident and the effect of within tree competition (negative density dependence) becomes less pronounced (Figure 5b and c).

The importance of minimum winter temperatures as drivers of mountain pine beetle reproductive potential is reflected in similar temporal patterns in the time series of minimum winter temperatures and the time series of estimated intrinsic growth rates at the provincial (landscape scale) in this study (Figure 6a). A strong correlation between minimum winter temperature and intrinsic mountain pine beetle reproductive rates is evident (Figure 6b) and exists even when the temperature and beetle data are detrended (examining the residuals of the smoothers fitted in panel a) indicating that winter temperature deviations from the overall trend are also important drivers of mountain pine beetle reproduction (Figure 6c).

4 | DISCUSSION

The primary effect of spatial and temporal climatic variation on nonlinear mountain pine beetle demography is through a multiplicative effect which raises and lowers the natural logarithm transformed *per capita* reproductive rate vertically in our graphical representations with an additional small carrying capacity effect (variation in the slopes of our linearized version of the generalized Ricker model).
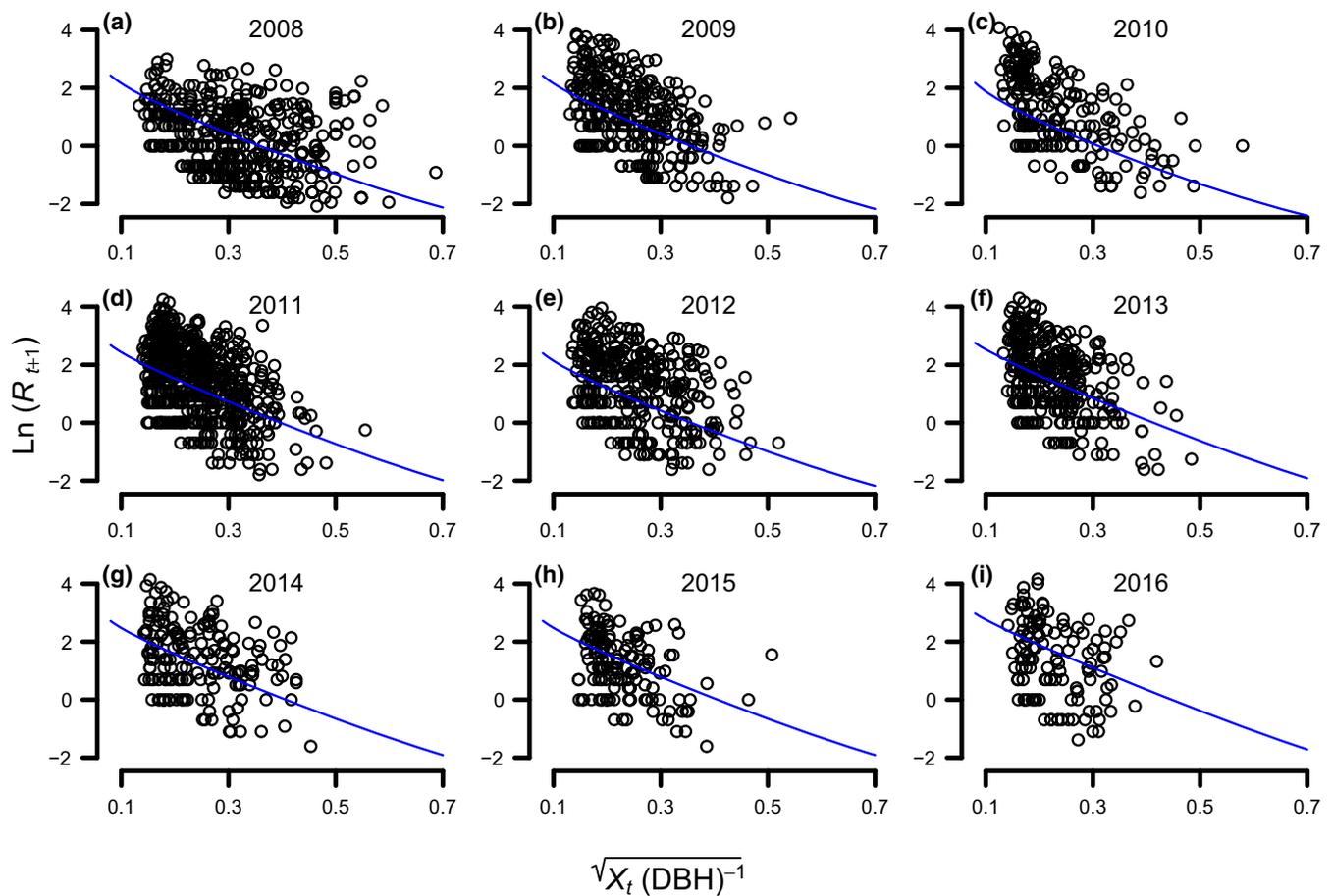
FIGURE 3 Model fits of the generalized Ricker model that was most strongly supported by the data. The model features random slopes and intercepts and a multiplicative effect of winter mortality on reproduction. Model fits are shown for survey years 2008–2016 (a)-(i). Lines in the plots are bias-corrected (see Supporting information S5 for description of bias correction) model fits for the natural logarithm of per capita reproductive rate. The vertical axis $\left(\text{Ln}(R_{t+1}) = \text{Ln}(X_{t+1}) - \text{Ln}(X_t)\right)$ is the natural logarithm of living offspring produced per male–female pair and so observations in which no living offspring were produced are not plotted (necessitating the bias correction). Values on the horizontal axis are $\sqrt{X_t(\text{DBH})^{-1}}$, in which X_t is the number of male–female pairs and DBH is the diameter at breast height of the host tree
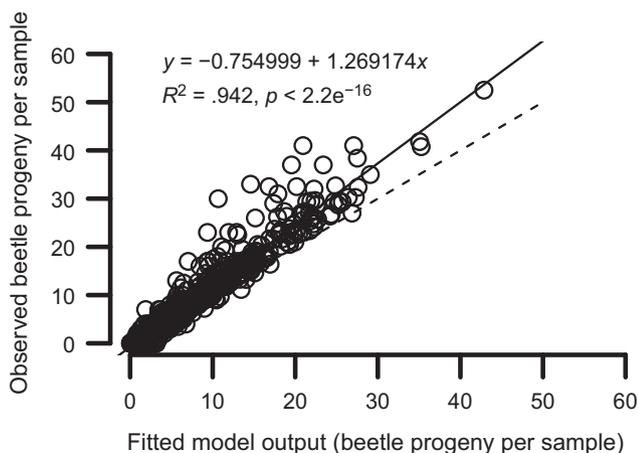

FIGURE 4 Our best-fitted model in comparison to observations with a fitted linear regression (solid line) to illustrate the strength of the relationship and the quality of the model. The dashed line is the one-to-one line, along which points should fall if the fitted model were entirely unbiased

Our analysis confirms that the winter survival of juvenile bark beetles maturing under the bark is a likely driver of the dominant multiplicative effect. Models featuring process-based representations of mountain pine beetle winter survival probability as a function of winter temperatures outperformed models without explicit representations of winter mortality. Notably, however, our demonstration of the importance of winter temperatures in mountain pine beetle demography was facilitated by accounting for negative density dependence due to competition for resources under the bark. This was particularly apparent at the smaller spatial scales of our analysis in which the effect of cold winter temperatures on mountain pine beetle survival was obscured by the stronger effect of negative density dependence.

Warmer winter temperatures have previously been implicated in the mountain pine beetle reproduction through cold-induced mortality in smaller scale studies (Bentz & Mullins, 1999; Régnière & Bentz, 2007) and have been also been shown to affect the area of the landscape impacted by mountain pine beetles (Aukema et al., 2008).
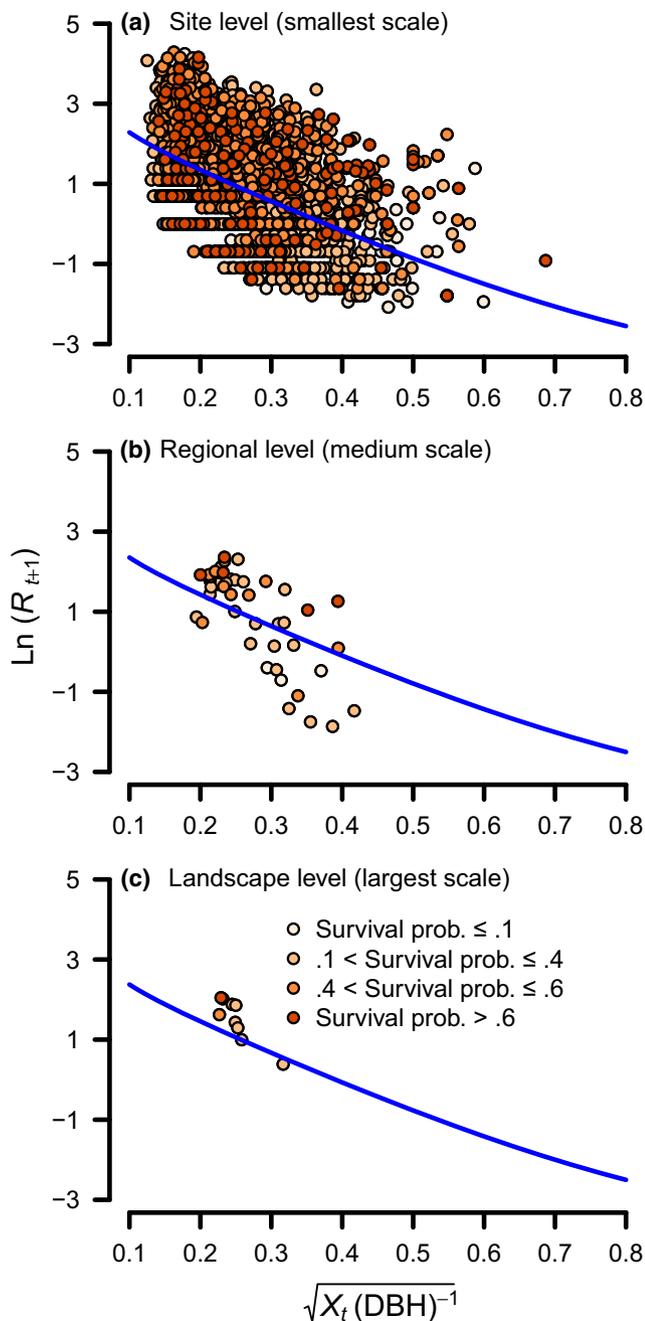
FIGURE 5 Plots showing the relative importance of cold-induced winter mortality, modeled as the probability of winter survival, and density dependence as drivers of the natural logarithm transformed per capita productivity (Ln(R_{t+1})) at (a) the site level, (b) the regional scale (management area), and (c) the landscape scale. The blue curves are the bias-corrected overall model fits (see Supporting information S5 for description of bias correction) of our best model ignoring random effects

FIGURE 6 Time trends in (a) minimum winter temperatures estimated in regions across Alberta, Canada, and mountain pine beetle intrinsic growth rates within regions across Alberta as estimated using our best fitting generalized Ricker model that excludes the explicit winter survival probability component of the model. Smoothers are fitted to both time series and shaded regions show the 95% CI for the smoother fits. Also shown are (b), the correlation between intrinsic mountain pine beetle reproductive rates and minimum winter temperature, and (c), the correlation between the detrended mountain pine beetle reproductive rates and detrended minimum winter temperatures (residuals of smoother fits)

Previous studies that have confirmed the importance of winter temperatures in mountain pine beetle dynamics (Aukema et al., 2008; Sambaraju et al., 2012) have linked minimum winter temperatures to the forested area impacted by mountain pine beetles, which is a proxy for popul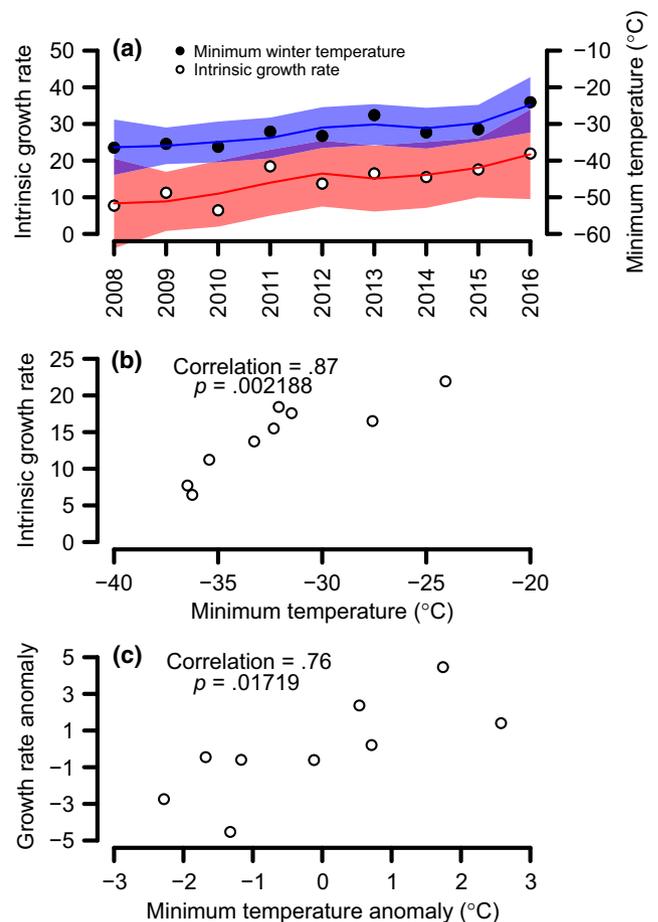ation size rather than a direct measure of reproduction. To our knowledge, no previous study has shown empirically that increasing trends in winter temperature over time result in increased mountain pine beetle productivity as such an analysis requires an extensive multiyear dataset in which mountain pine beetle reproduction is directly measured like the one we analyzed in the current study. We demonstrate both a clear increase in minimum winter temperatures over time and a concurrent increase in mountain pine beetle productivity over the same time period in our study region.

Our study focused on the effect of cold temperatures on mountain pine beetle survival as lethal winter temperatures have been shown to be dominant drivers of mountain pine beetle demography (Amman & Cole, 1983; Aukema et al., 2008; Bentz & Mullins, 1999; Régnière & Bentz, 2007; Safranyik, 1978). In addition, a dynamic

process-based model of cold-hardening and survival of mountain pine beetle has been developed (Régnière & Bentz, 2007), enabling its inclusion in the context of the generalized Ricker population model that we used in the current study.

Using a population dynamics approach as we have done makes it more difficult to include climatic variables that impact bark beetle demography in ways that are less understood, than it would be if we used a strict multiple regression approach (challenges of multicollinearity notwithstanding). For this reason, we have not included a suite of climatic variables in our models that are likely also important determinants of mountain pine beetle demography. Indeed, this is a limitation of our methodology. An advantage of using a model that more accurately captures nonlinear demography that we exploited in the current study is that it enables a biologically motivated statement of hypotheses and a more process-based understanding of how climate may impact biologically relevant parameters in the demographic model.

Modeling studies have emphasized the importance of warming winters in determining the future range of bark beetles (Bentz et al., 2010; Lesk et al., 2017). Our empirical results confirm that warming trends are positively impacting mountain pine beetle reproduction. Globally, minimum temperatures are increasing at a faster rate than maximum temperatures (Easterling et al., 1997; Vose, Easterling, & Gleason, 2005) and both minimum and maximum temperatures are projected to continue to increase as the climate warms throughout this century (IPCC, 2014). As a result, we anticipate higher mountain pine beetle reproduction within trees under climate warming, which will enable beetles to more easily surpass outbreak thresholds, leading to more frequent and more widespread mountain pine beetle outbreaks across North America.

Despite the importance of warming minimum temperatures, the signal of negative density dependence was so strong at the site level in our data that it obscured the effects of cold temperatures on winter mortality. Thus, although warmer winters increase the survival of juvenile mountain pine beetles (Régnière & Bentz, 2007; Rosenberger et al., 2017), we have shown that this can lead to severe competition due to overcrowding, which can decelerate population growth—sometimes before all susceptible host trees have been exploited by mountain pine beetles or other *Dendroctonus* bark beetles (Aukema, Mckee, Wytrykush, & Carroll, 2016; Goodsman, Cooke, & Lewis, 2017). In such climatic regimes, sustained bark beetle outbreaks will depend on their dispersal from overcrowded regions to escape the deleterious consequences of negative density dependence.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.