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An Evaluation of a Winter Mortality Model for the Mountain Pine Beetle

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Abstract: The winter mortality of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) larvae caused by temperatures below survivable thresholds and sudden decreases in temperature is among the most influential factors limiting population growth. Due to the importance of winter mortality in the demise of mountain pine beetle infestations, a widely used winter mortality model was developed at the Canadian Forest Service and the United States Forest Service. It predicts lethal temperatures and survival probabilities given temperature time series over the winter season. We present a rare and possibly the first peer-reviewed validation of this winter mortality model, wherein we independently tested the model at a new region in Canada by comparing model predictions to the observed lower lethal temperature thresholds and cold-associated mortality. Model predictions were biologically reasonable but slightly biased. Bias was exacerbated by the inaccurate translation of air temperature data from weather stations to temperatures under the bark where larvae develop. The spatial prediction of relative mortality observed across the study area in Banff National Park was poor—likely because the mountainous terrain presents a difficult prediction challenge when under-bark temperatures are not directly observed. Our results will help inform users of model constraints and how to optimize the accuracy of model predictions.

Keywords: bark beetle; climate; demography; insect; population modeling; cold tolerance; temperature; weather; winter mortality

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1. Introduction

The mountain pine beetle (*Dendroctonus ponderosae* Hopkins) is one of the most destructive forest insects in North America [1,2]. The largest epidemic in recorded history started in central British Columbia in western Canada in the mid-1990s and was fueled by contiguous stands of susceptible hosts and favorable weather, including successive years of mild winter temperatures [3]. By the time the outbreak subsided, the mountain pine beetle had killed over 730 million m^3 of pine in British Columbia, which was approximately 55% of the merchantable pine in the province [4]. Further, in the 2000s, large numbers of beetles from central British Columbia, near the northern extent of the mountain pine beetle's range, dispersed across the Continental Divide and invaded new habitats in north-western Alberta [4]. Mountain pine beetle infestations spread faster than initially anticipated across central Alberta, likely due in part to several years of relatively mild winter temperatures following a main immigration event [4]. The demography of the mountain pine beetle is driven by several positive feedback processes during outbreaks [5–7]; however, cold winter temperatures are known to play a major role in regulating populations [6] and the collapse of some outbreaks has been attributed to extreme cold events [8,9]. Several established infestations in the beetle's recently expanded range east of the Continental Divide in northern Canada began to decline starting in 2018 such that by 2020 outbreak populations were relatively scarce in the region [10]; the collapse of some of these infestations has been attributed to the return of colder winter temperatures.

The primacy of winter cold as a determinant of mountain pine beetle survival has motivated research into the biology of cold-hardening and cold-induced mortality in the mountain pine beetle [8,11–15]. At the time of writing, the Régnière and Bentz winter mortality model [16] was the most detailed and highly cited winter mortality model developed for mountain pine beetle. This model has been widely adopted, partly because it has been incorporated into BioSIM [17,18], an easy-to-use software program that produces outputs of various forest insect models making them accessible to researchers and land managers. The BioSIM software was developed at the Canadian Forest Service to facilitate the deployment of crop and crop-pest models that depend on meteorological inputs. At the core of BioSIM is the ability to read and store large meteorological databases from weather stations and other data sources, the ability to predict meteorological variables at sites of interest using these weather data, and the ability to drive mathematical and simulation models of insect and pest dynamics as a function of meteorological variables. BioSIM has been used by land managers and researchers internationally, especially in the United States and Canada. Although the Régnière and Bentz winter mortality model is included in BioSIM, its source code and inner workings are not easily accessible to users of the software, so these must be extracted from the original research [16].

The structure and functioning of the Régnière and Bentz winter mortality model are physiologically motivated [16]. The model assumes that larvae are in one of three cold hardy states—unhardened, moderately hardened, or fully cold hardened—based on the observed distributions of supercooling points [16]. The supercooling point of an individual is the lowest temperature reached before internal freezing occurs and is considered the minimum lethal temperature for freeze-intolerant insects [19], such as the mountain pine beetle [11]. Each cold hardy state has a probability density and a corresponding cumulative distribution function that represents the likelihood of surviving each temperature (the authors choose the logistic distribution with two parameters—one of which represents the median of the distribution). The transition to and from each state is governed by a dynamic process whereby cold hardiness is gained or lost depending on the temperatures experienced by larvae up to that point [16]. The cold-hardiness metric is continuous, but two cutoffs dictate which of the three states is assigned to each individual larva [16]. The lethal temperature, at which half of all larvae die (LT50), is calculated using a sum of the proportion of individuals in each of the three states multiplied by the median temperature of the distributions associated with each of the three states [16]. The LT50 generated by the model should be closely related to the median supercooling point measured in overwintering mountain pine beetle populations in the field. A survival metric for the population that experiences a given minimum winter temperature can be computed using the sum of each cumulative distribution function evaluated at that temperature weighted (multiplied) by the proportion of individuals in the state that corresponds to each cumulative distribution function. This, however, is not necessarily the survival probability because survival probability is computed as the cumulative minimum survival metric quantified in all time steps up to, and including, the current time step [16]. Time is stepped forward in discrete time steps of 24 h when the model is driven using daily weather data. As input, the model requires daily minimum and maximum temperature time series data. The model does not distinguish between early (LI, LII) and late (LIII, LIV) instar larvae because the study used to parameterize the model found no difference in their supercooling points [16]. However, another study found that late instar larvae survived cold temperatures better than early instar larvae [8]. The data used to parameterize the Régnière and Bentz winter mortality model comprise within-season time series of supercooling points, and model predictions were shown to closely simulate the observed seasonal trends. There is also an adjustment that can be made that translates minimum and maximum daily air temperature data to minimum and maximum under-bark temperature [16], which is based on earlier work on the beetle's micro-habitat [20].

Here, we independently test and validate the Régnière and Bentz winter mortality model [16] for use in Canada. Some testing at the Canadian Forest Service of the model's performance from 2007 to 2012 was completed, but the results of the tests were never published and remain in report form [21]. We collected new detailed demographic and physiological data at a single site as well as demographic data across a wider range of sites in Banff National Park to test the Régnière and Bentz winter mortality model. We found that the winter mortality model predicted best when driven by observed under-bark temperature time series; the translation of air temperatures to predicted under-bark temperatures exacerbated biases in predictions in our data. When the Régnière and Bentz winter mortality model was driven using air temperature data that were translated to predicted under-bark temperatures, it produced reasonable predictions of relative survivorship across winter seasons, but the accuracy of predictions of spatial variation in larval survival within winter seasons was poor.

2. Materials and Methods

Our study sites were in Banff National Park, which is in southwestern Alberta, adjacent to British Columbia, in western Canada (Figure 1). The region is mountainous and dominated by lodgepole pine (*Pinus contorta* Douglas var. *latifolia* (Engelm.)) at lower elevations with limber pine (*Pinus flexilis* E. James) and whitebark pine (*Pinus albicaulis* Engelm.) present at higher elevations. Other coniferous trees that are common in the park are Douglas fir (*Pseudotsuga menziesii* var. *glauca*), subalpine fir (*Abies lasiocarpa* (Hooker) Nuttall), and white spruce (*Picea glauca* (Moench) Voss). Only the pine species are suitable hosts for the mountain pine beetle. Mountain pine beetle infestations were observed primarily in lodgepole pine at low or middle elevations in the park (Figure 1). Our study occurred during the declining phase of the large outbreak in western Canada. The mountain pine beetle is endemic in Banff National Park, and the area is also subject to long-distance dispersal of mountain pine beetles from periodic outbreaks in southern British Columbia.

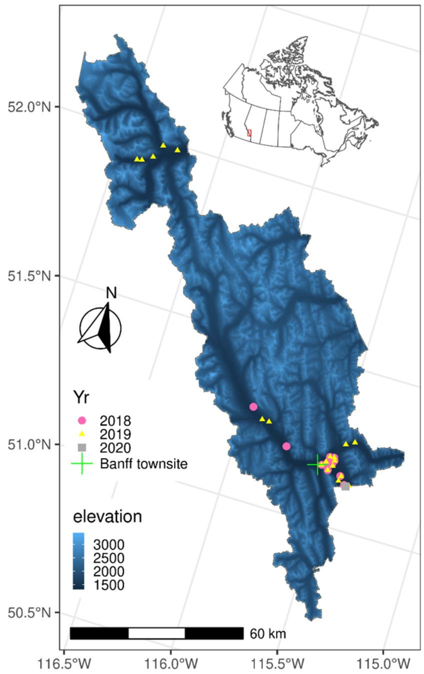

Figure 1. The location of study region (red rectangle in inset map of Canada in upper right) and study sites at which mountain pine beetle demographic data were collected within Banff National Park in Alberta, Canada. The research sites are labeled according to the year in which the sampled cohort of beetles would emerge from natal host trees based on a one-year life cycle.

2.1. Detailed Assessment of Winter Mortality Model in 2019/2020

In mid-September 2019, we established a site near the southern border of Banff National Park to assess the Régnière and Bentz mountain pine beetle winter mortality model (site labeled 2020 in Figure 1). We selected five lodgepole pine trees that were attacked in the 2019 growing season.

Under-bark temperatures were recorded hourly from 18 September 2019 to 2 March 2020 at 1.3 m on the north and south aspects of each of the five sample trees using Onset Hobo MX2302A temperature loggers (Onset Computer Corporation, Bourne, MA, USA). Temperature probes were inserted between the phloem and xylem, where the mountain pine beetle develops. One logger that was on one of the resisted trees failed to record throughout the winter, leaving us with hourly temperature data for the north and south aspects of four trees, or eight temperature time series. Daily minimum and maximum temperatures, which are required for the Régnière and Bentz winter mortality model, were extracted from these data, resulting in sixteen temperature time series.

Mountain pine beetle demographic data were collected in the fall (24 November 2019) prior to the coldest winter temperatures and in late winter (5 March 2020) after the coldest winter temperatures occurred. The supercooling capacity of larvae was also determined in late winter (see below).

We counted the number of entrance holes, maternal (egg) galleries, and larval galleries in a 15 × 15 cm bark sample removed with a mallet and chisel from the north and south sides of each tree at approximately 1.3 m on the bole. The number of individuals in each life stage and their life status (alive, dead) was determined for each sample. Discolored larvae were easily identified as dead and moving larvae were classified as alive. Samples that contained putatively healthy-looking but immobile larvae were brought back to the laboratory and held at 21 °C in a sealed bag until their life status could be determined. In the late-winter sample, we found that two of our five sample trees had resisted attack (i.e., beetles pitched out, no brood produced) [6], and demographic samples were not taken from these trees. Due to cold temperatures in the late-winter sample, we inadvertently cut and damaged some larvae with our chisels and could not definitively determine the life status of healthy colored larvae that we injured: these individuals were classified as damaged.

In late winter, we measured the supercooling points of larvae from each of the three successfully attacked sample trees. Individual larvae were placed in 1.5 mL Eppendorf tubes and shipped overnight on ice to the Pacific Forestry Centre in Victoria, British Columbia, where their supercooling points were determined upon arrival using the methods of Bleiker and Smith [12]. Each larva was secured with vacuum grease to an AWG30 Type T (copper/constantan) thermocouple inserted in a shell vial secured in a 13 mm by 100 mm test tube. Test tubes were immersed in a Glacier G50 ethanol bath controlled by a Haake PC200 circulator (Thermo Fisher Scientific, Waltham, MA, USA), and the temperature was decreased by 1 °C per minute. The temperature of each larva was recorded every second with a USB TC-08 data logger (Pico Technology, Cambridgeshire, UK). The lowest temperature immediately preceding the exotherm associated with the latent heat of crystallization was recorded as the SCP [22].

2.2. Winter Mortality in 2017/2018 and 2018/2019

Parks Canada and the Canadian Forest Service collaboratively collected demographic data in infested trees in the national parks within Alberta in 2017/2018 and 2018/2019. Demographic data were collected as described above from 10 sample trees at each site (10 sites in 2017/2018; 15 sites in 2018/2019) in late April of each year. Ten trees per site were selected at random in accordance with standard sampling protocols established collaboratively between Parks Canada and the Canadian Forest Service for mountain pine beetle population surveys in national parks. This sample size was chosen to balance the reduction in the effect of inter-tree variation and sampling cost. For each study site in which demographic data were collected, the proportion of all living larvae and dead larvae counted on each side of each tree that were alive was calculated and then averaged across all trees at each site to produce a site-level average survival proportion estimate. Samples that contained no brood insects (living or dead) were excluded from the study.

2.3. Winter Mortality Model Predictions

Predictions of the Régnière and Bentz winter mortality model were obtained in three ways: firstly, the model was coded in a computing language to facilitate model runs driven using observed under-bark temperature time series; secondly, it was run in daily mode from within BioSIM v. 11 [18]; thirdly, it was run in annual mode within BioSIM. The second and third approaches rely on air temperatures predicted using daily meteorological data within BioSIM and then upon a method for estimating under-bark temperatures from predicted air temperatures that is used within BioSIM's implementation of the Régnière and Bentz model.

For detailed daily predictions driven using observed under-bark temperature data from Hobo temperature loggers, we coded the Régnière and Bentz winter mortality model in the R computing language [23] (first approach). The model was coded based on Régnière and Bentz's description of the model [16], with small changes due to errors in the original manuscript conveyed by personal communication from Jacques Régnière. We checked that the model coded in R was equivalent to the implementation in BioSIM given the same inputs of under-bark temperature, by extracting the predicted maximum and minimum under-bark temperature time series from the BioSIM implementation of the Régnière and Bentz winter mortality model in the daily mode (Appendix A). Then we used these predicted under-bark temperature time series to drive our R implementation of the Régnière and Bentz model. The output obtained from the R implementation was identical to the output obtained from BioSIM for each of the three trees that contained mountain pine beetle larvae at our detailed study site.

For locations of our study trees that were fitted with Hobo temperature loggers, we also obtained predictions from the Régnière and Bentz winter mortality model in the daily mode produced by running BioSIM (second approach). When the Régnière and Bentz model is deployed within BioSIM in this way, one can obtain daily predictions of under-bark temperatures, survival probabilities, cold hardening levels, and the LT50. For each site at which we estimated survival proportions in the 2017/2018 and 2018/2019 seasons, we ran the Régnière and Bentz winter mortality model in BioSIM in the annual mode (third approach) to obtain predicted survival probabilities.

2.4. Statistical Analyses

The only life stage encountered during sampling was the larval stage, and we calculated larval survival proportions in two ways to assess total and recent mortality. We calculated total survival proportions by counting the number of larval galleries in each 15 × 15 cm sample and the number of living larvae in the sample. Total survival was the quotient of living larvae over the count of larval galleries. The logic behind this measurement is that each larval gallery must have had a mountain pine beetle larva in it at one time even if it was not there at the time of sampling. Therefore, the quotient of living larvae over the count of larval galleries accounts for all mortality that occurred after larval emergence from eggs. The second method for quantifying larval survival was to divide the count of living larvae in each sample by the sum of living and dead larvae in the sample. This statistic is more reflective of the proportion of larvae that escaped recent mortality events, since larval corpses did not have time to decay or to be consumed by scavengers. Calculating survival proportion in this way allowed us to determine which proportion of the total mortality was due to recent mortality events and thus likely cold-associated mortality. All predictions of the winter mortality models were compared to survival proportion statistics calculated using the latter approach described above. Survival proportions were calculated at the site level by averaging across all tree-level survival probabilities at each site.

Satterthwaite adjusted *t*-tests were used to test the null hypothesis that the predicted lethal temperatures at which half of all larvae die (LT50s) were from the same population (were statistically equal) as observed supercooling points. Similarly, the same Satterthwaite adjusted *t*-tests were used to test the null hypothesis that predicted logit-transformed survival probabilities were from the same population (were statistically equal) as logit-transformed observed survival proportions.

Major axis linear regressions were used to compare observed under-bark temperatures to those predicted using the Régnière and Bentz winter mortality model deployed within BioSIM. Major axis regressions were used instead of standard linear regressions because both the predicted and observed temperatures likely contained errors. When predictor variables are observed with error, standard linear regressions are not appropriate [24].

Although observed survival proportions and predicted survival probabilities likely both contained error, major axis regressions were not used in regressions of observed survival proportions as a function of predicted survival probabilities, because the data were not well represented by a bivariate normal distribution. Instead, we used standard linear regressions to assess the relationship between predicted survival probabilities and observed survival proportions. Statistical analyses were conducted in R (Version 4.1.2, R Core Team, Vienna, Austria [23]); the lmodel2 R package (Version 1.7-3) [24] was used for major axis regressions; figures were made using the ggplot2 package (Version 3.4.2) [25] in R.

3. Results

Figures and analyses pertaining to our detailed evaluation of the Régnière and Bentz winter mortality model in the 2019/2020 winter season will be presented first. Then, the survival probabilities predicted by the winter mortality model and observed survival proportions will be compared for the 2017/2018 and 2018/2019 winter seasons.

3.1. Detailed Assessment of Winter Mortality Model in 2019/2020

Recent larval mortality, assumed to be caused by cold, accounted for only 16% of total larval mortality in the fall demographic sample (Figure 2a and Table 1), whereas recent mortality presumed to be associated with cold comprised 45% of total mortality in the late-winter demographic sample (Figure 2b and Table 1). Thus, recent mortality that was likely due to cold temperatures accounted for less than half of the total larval mortality that we observed even after the coldest part of the winter.

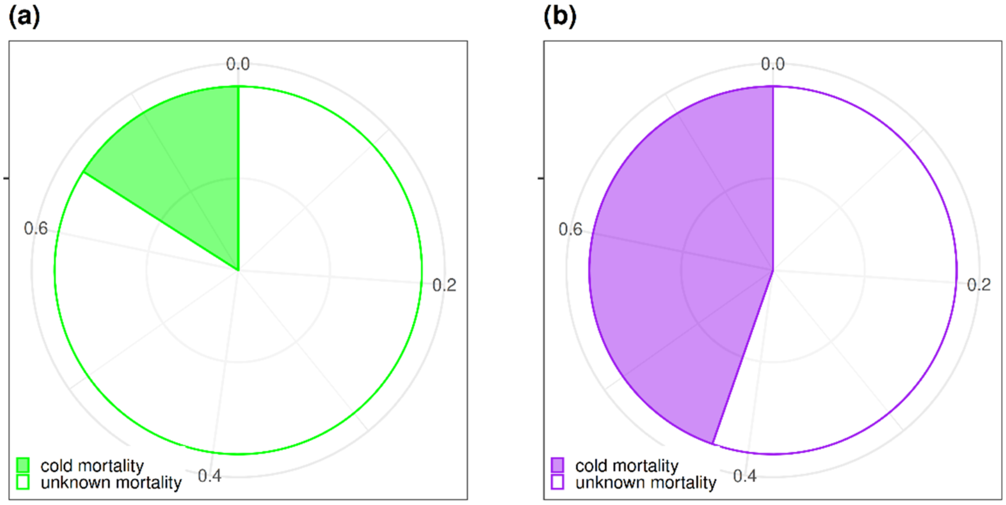

Figure 2. The proportion of total mortality in mountain pine beetle larvae attributable to cold weather (**a**) based on demographic samples taken in the fall season on 24 November 2019 and (**b**) based on demographic samples taken near the end of winter on 5 March 2020. The mortality proportions shown in each case are cumulative mortality calculated up to the sampling date. In both seasons, most larval mortality at the site occurs because of processes unrelated to cold weather, although a larger proportion of the total mortality in the late-winter demographic sample is caused by cold. The data on which the pie charts are based are provided in Table 1.

Table 1. Summary of mountain pine beetle demographic data collected from 15 × 15 cm bark samples at 1.3 m on the north and south sides of sample trees at the 2020 research site used for a detailed assessment of the Régnière and Bentz (2007) winter mortality model.

Sample Time	Tree ID	Side	Entrance Holes	Maternal Galleries	Larval Galleries	Living Larvae	Damaged Larvae [1]	Dead Larvae
Fall	3810	N	3	8	22	17	0	2
		S	1	7	5	2	0	0
Fall	9970	N	1	8	14	4	0	1
		S	0	9	117	17	0	2
Fall	9971	N	2	6	2	2	0	1
		S	1	5	24	1	0	0
Fall	9972 [2]	N	1	0	0	0	0	0
		S	1	0	0	0	0	0
Fall	9973 [2]	N	0	0	0	0	0	0
		S	0	0	0	0	0	0
Late winter	3810	N	2	7	34	0	0	2
		S	1	6	17	0	0	0
Late winter	9970	N	1	4	26	4	1	2
		S	2	6	59	27	2	3
Late winter	9971	N	2	3	4	0	1	3
		S	3	5	66	17	3	15

[1] Larvae that were damaged at the time of sampling whose life status (live, dead) could not be definitively determined (see text). [2] Trees resisted (i.e., pitched out) attack and were not sampled in late winter.

When we used under-bark temperatures from Hobo temperature loggers to drive the Régnière and Bentz winter mortality model, the predicted lethal temperatures at which fifty percent of individuals are expected to die (LT50) align reasonably well with the observed distribution of supercooling points (SCPs) in larvae collected in late winter (Figure 3a) based on a visual assessment. However, we rejected the hypothesis that observed SCPs were equal to predicted LT50s (Figure 3b) based on a two-sample Satterthwaite (unequal variances) *t*-test: $t = 3.6363$, $df = 31.417$, *p*-value = 0.000979.

Visually, survival probabilities predicted by the Régnière and Bentz winter mortality model aligned well with the proportion of counted living and dead larvae that were alive (Figure 3c,d). For the fall sampling date, we failed to reject the hypothesis that the observed (logit-transformed) proportion of larvae that were alive and the predicted (logit-transformed) survival probability were equal using a two-sample Satterthwaite *t*-test: $t = 0.95619$, df = 5.8111, *p*-value = 0.377. Conversely, for the late-winter sample taken, we rejected the hypothesis that the observed (logit-transformed) proportion of larvae that were alive and the predicted (logit-transformed) survival probability were equal using a two-sample Satterthwaite *t*-test: $t = -3.499$, df = 3.0082, *p*-value = 0.03934. Therefore, when the Régnière and Bentz winter mortality model is driven using observed under-bark temperatures, it predicts lethal temperatures, at which fifty percent of larvae are expected to die (LT50s), which are slightly higher than observed supercooling points and survival probabilities that are slightly lower than observed survival proportions in the late winter.

We also tested the performance of the Régnière and Bentz winter mortality model when it is deployed within the BioSIM software environment, which is how most users make predictions using the model. The output of the Régnière and Bentz winter mortality model within BioSIM can then be compared to the output of the Régnière and Bentz model when it is driven using observed under-bark temperature time series (Figure 4). The results are superficially similar, but LT50s predicted within BioSIM occur at consistently warmer temperatures than those predicted using observed under-bark temperatures in the latter half of the winter season (Figure 4a). Survival probabilities predicted within BioSIM are consistently lower than those predicted using under-bark temperatures in the latter half of the winter (Figure 4b), which is consistent with higher LT50s. Thus, in the 2019/2020 winter season, the Régnière and Bentz winter mortality model's underprediction of the survival probability is exacerbated when the air temperatures predicted in BoSIM are used as the basis for its predictions.

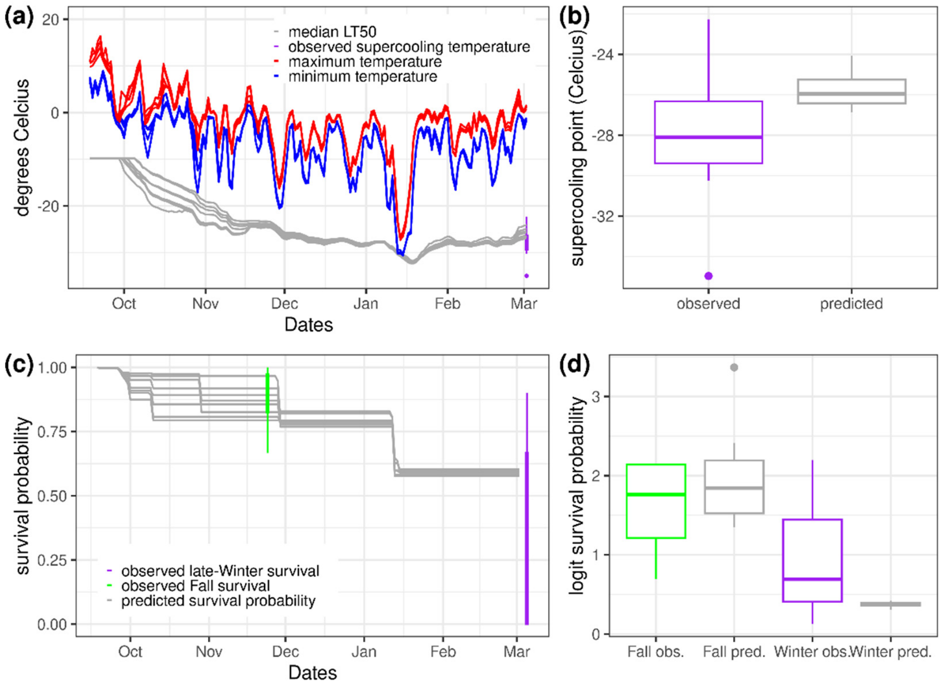

Figure 3. The predictive skill of the Régnière and Bentz winter mortality model when it is driven by observed under-bark temperatures measured at 1.3 m on the north and south sides of four sample trees (eight time series): (**a**) The observed under-bark daily time series of temperature minima and maxima and the LT50 predicted by the Régnière and Bentz winter mortality model. (**b**) The LT50 predicted by the Régnière and Bentz winter mortality model and the observed supercooling points of 29 larvae sampled in late winter 2020. (**c**) Winter survival probability predicted by the Régnière and Bentz winter mortality model compared to observed larval survival in the fall (24 November 2019) and late winter (5 March 2020). (**d**) The logit-transformed observed survival proportions and probabilities predicted by the Régnière and Bentz winter mortality model. In all panels, boxplots are shown, wherein the horizontal line represents the median, and the upper and lower edges of the boxes represent the seventy fifth, and twenty fifth percentiles.

Why then does the Régnière and Bentz winter mortality model make different predictions when based on predicted air temperatures from BioSIM than it does when based on observed under-bark temperature data? A comparison of the observed under-bark temperatures and those predicted using BioSIM provides evidence that the discrepancy between LT50s and survival probabilities predicted using the two approaches is due to the under-bark daily maximum temperatures predicted by BioSIM that are significantly higher than the observed daily maximum temperatures (Figure 4a). The statistical significance of the bias in the daily maximum under-bark temperatures predicted within BioSIM can be assessed using major axis linear regressions, which show that the observed daily maximum under-bark temperatures are consistently 2 to 4 °C lower than those predicted within BioSIM (Figure 4c and see intercept estimates in Table 2).

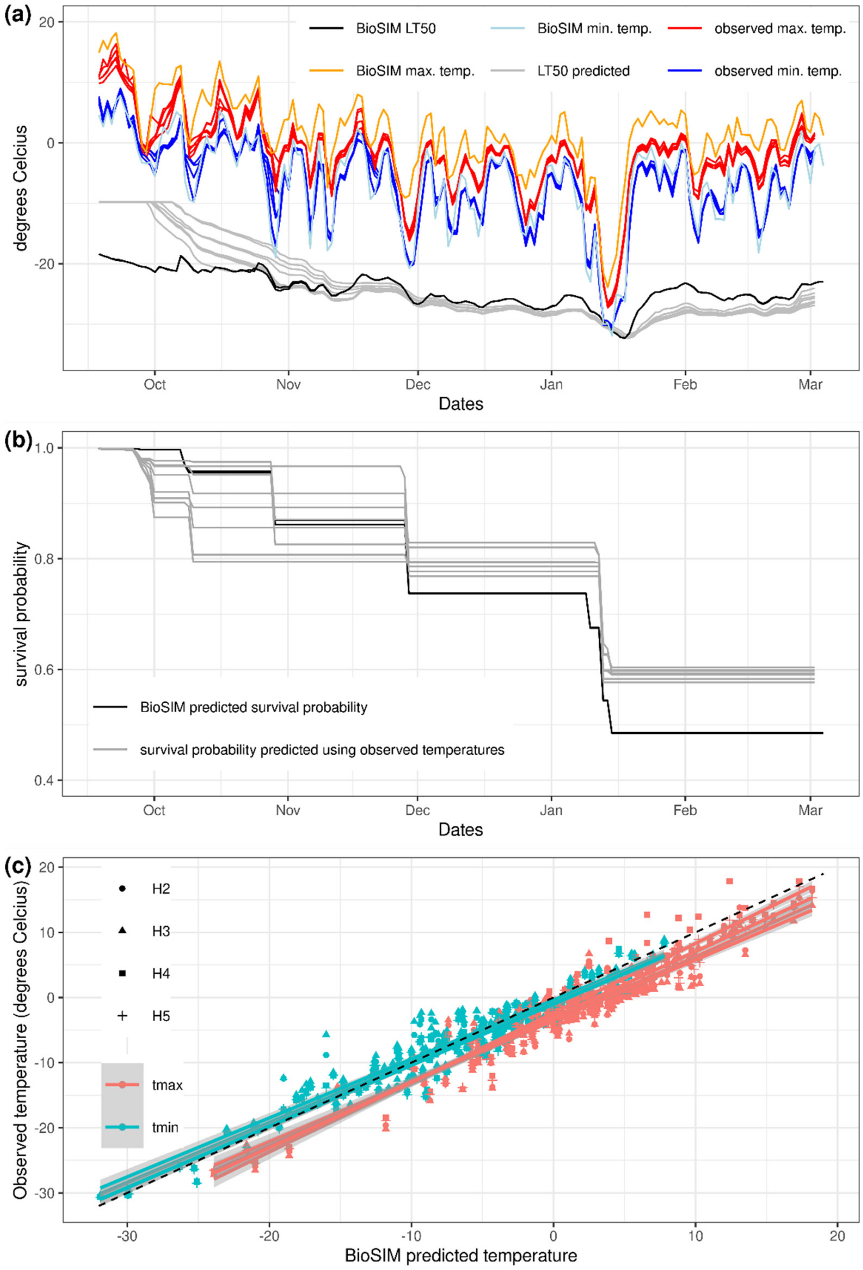

Figure 4. Comparisons of predictions of the Régnière and Bentz winter mortality model when it is driven by observed under-bark temperatures measured at 1.3 m on the north and south sides of four sample trees and when the under-bark adjustment is selected within BioSIM and estimated using predicted air temperatures: (**a**) A comparison of observed under-bark temperatures, predicted under-bark temperatures using BioSIM, and the LT50 predicted by the Régnière and Bentz model driven by observed under-bark temperatures (eight time-series) and predicted under-bark temperatures within BioSIM software (two distinct time-series). (**b**) A comparison of survival probabilities predicted by the Régnière and Bentz model when it is driven using observed and predicted (BioSIM) under-bark temperatures. (**c**) Regressions of observed under-bark temperatures against under-bark temperatures predicted using the Régnière and Bentz winter mortality model in BioSIM (regression statistics in Table 2).
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Table 2. Regression statistics for major axis linear regressions of under-bark maxima and minima temperatures predicted in BioSIM using the Régnière and Bentz (2007) winter mortality model (see Figure 4c) and observed under-bark temperatures measured on the north and south sides of four sample trees. The intercepts are always negative with 95% confidence intervals (CI) that do not overlap zero, which indicates a negative bias of observed temperatures relative to predicted under-bark temperatures (observed temperatures are lower). The typical goodness of fit tests of a standard linear regression are not used in major axis linear regressions, so *F*-values and *p*-values are not provided.

Logger	Type	Intercept (95% CI)	Slope (95% CI)	R^2	Sample Size
H2	Maximum temperature	−3.505 (3.596, −3.419)	1.020 (0.970, 1.072)	0.903	167
	Minimum temperature	−0.492 (−0.798, −0.170)	0.965 (0.918, 1.013)	0.907	167
H3	Maximum temperature	−3.643 (−3.742, −3.549)	0.991 (0.936, 1.048)	0.882	167
	Minimum temperature	−0.072 (−0.400, 0.275)	0.955 (0.905, 1.007)	0.892	167
H4	Maximum temperature	−2.460 (−2.549, −2.376)	1.117 (1.068, 1.169)	0.921	167
	Minimum temperature	−0.810 (−1.064, −0.547)	0.971 (0.932, 1.012)	0.936	167
H5	Maximum temperature	−3.039 (−3.113, −2.967)	1.039 (0.998, 1.083)	0.935	167
	Minimum temperature	−0.776 (−1.036, −0.505)	0.971 (0.932, 1.012)	0.932	167

3.2. Winter Mortality in 2017/2018 and 2018/2019

In addition to our detailed assessment of the predictions of the Régnière and Bentz winter mortality model using observed under-bark temperatures in the 2019/2020 winter season, we compared the observed survival proportions and survival probabilities predicted using the Régnière and Bentz model (annual mode) within BioSIM more broadly across Banff National Park in the 2017/1018 and 2018/2019 winter seasons. There is a significant positive linear relationship between the survival proportions and predicted probabilities of survival when comparisons are made across years (Figure 5a and Table 3). However, when predictions were made across space within the 2017/2018 winter season (Figure 5b and Table 3), and within the 2018/2019 winter season (Figure 5c and Table 3), there was not a positive linear relationship between the predicted survival probabilities and observed survival proportions. This can be seen by inspecting the regression slopes in Table 3: within both the 2017/2018 winter season and the 2018/2019 winter season, the slopes of the regressions of observed survival proportions regressed against predicted survival probabilities were not statistically different from zero (Table 3).

Table 3. Regression statistics for standard (not major axis) linear regressions of probabilities of winter survival predicted in BioSIM using the Régnière and Bentz (2007) winter mortality model and observed larval survival (see Figure 5).

Regression	Intercept (95% CI)	Slope (95% CI)	R^2	*F*-Value	Sample Size	*p*-Value
Across seasons	−0.253 (−0.043, −0.462)	1.358 (0.830, 1.886)	0.59	28.790	22	2.982×10^{-5}
Within 2017/2018	0.417 (−1.122, 1.956)	0.078 (−2.954, 3.109)	0.00	3.483×10^{-3}	10	0.954
Within 2018/2019	0.208 (−0.213, 0.628)	−0.413 (−1.955, 1.130)	0.03	0.355	12	0.564

Interestingly, the points in Figure 5a are mostly below the dashed line (one-to-one line). Thus, the Régnière and Bentz model predicts survival probabilities that are higher than observed survival proportions. This finding contradicts our finding for the detailed dataset collected in the 2019/2020 season, which showed that the Régnière and Bentz model predicted survival probabilities that were lower than observed survival proportions in that year.

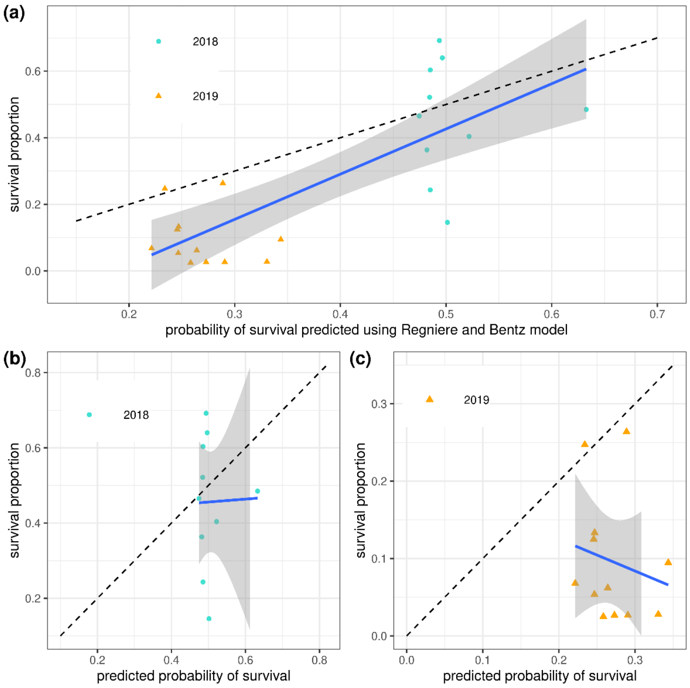

Figure 5. Comparisons of site-level observed surviving proportion of mountain pine beetle larvae and survival probabilities predicted using the Régnière and Bentz model within BioSIM (annual mode): (**a**) Comparisons between observed proportions of larvae that survived and predicted probabilities of survival across winter seasons show a positive linear relationship. (**b**) The lack of a statistical relationship between observed survival proportions and predicted survival probabilities within the 2017/2018 winter season. (**c**) The lack of a statistical relationship between observed survival proportions and predicted survival probabilities within the 2018/2019 winter season (see Table 3 for regression statistics). In all three panels, the grey-shaded regions are standard errors of fitted regressions, the dashed lines are the one-to-one line (corresponding to perfect prediction), and blue lines correspond to best fit linear regressions.

4. Discussion

In the paragraphs that follow, we discuss five findings of this study: Firstly, we found that when the Régnière and Bentz winter mortality model was driven using measured under-bark temperatures in the 2019/2020 winter season, it simulated winter survival probabilities that were slightly too low and LT50s that were slightly too high relative to our observations in 2019/2020. Secondly, when air temperature predicted in BioSIM using nearby weather stations drove the Régnière and Bentz winter mortality model, the biases in model predictions relative to our observations in 2019/2020 were exacerbated due to biased model translation of air temperatures to under-bark temperatures. Thirdly, the predictions of the Régnière and Bentz winter mortality model implemented in BioSIM with air temperatures predicted from weather station data as the basis for model predictions roughly followed the observed trend in mortality across the 2017/2018 and 2018/2019 seasons. Fourthly, in contrast to our third finding, predictions using the BioSIM approach aligned poorly with observed winter mortality proportions when compared across space within the 2017/2018 season and within the 2018/2019 season. Finally, survival probabilities predicted by the Régnière and Bentz winter mortality model were lower than observed survival proportions in 2019/2020 but generally higher than observations in 2017/2018 and 2019/2020, which leads naturally to a discussion of the limitations of the current study as a validation test of the Régnière and Bentz winter mortality model.

We have provided evidence that the predictions of the Régnière and Bentz winter mortality model deviated from observed supercooling points and larval survival proportions at the end of winter 2019/2020. However, our series of one sample date for supercooling points, and two sample periods for winter mortality measurements, is insufficient to assess the quality of the within-season trend predicted by the model. Moreover, the dataset used to formulate the model comprised a more exhaustive time series of samples of larval supercooling points collected within seasons [11] than the present study. Therefore, although the observed larval survival proportions and larval supercooling temperatures in the 2019/2020 winter differed from their analogs predicted by the Régnière and Bentz winter mortality model, the differences were not large enough and our dataset is not extensive enough to invalidate the utility of the model—especially when it is driven using observed under-bark temperatures.

The Régnière and Bentz winter mortality model was developed using measured under-bark temperatures [16] and relies on an accurate representation of this micro-climate. Therefore, we expected superior model performance when the winter mortality model was driven using measured under-bark temperatures compared to when it was informed using weather station data. Accordingly, we found that when the winter mortality model was informed using air temperature data predicted within BioSIM, the predicted LT50s were warmer and the predicted survival probabilities were lower than when under-bark temperatures were used. This finding implies that the easy deployment of the Régnière and Bentz winter mortality model in BioSIM comes at the expense of accuracy because micro-habitats, like the under-bark environment inhabited by bark beetle larvae, are difficult to predict using air temperatures [26]. For example, the under-bark temperature of trees could be strongly affected by incident solar radiation, bark thickness, the moisture of tree tissues, and their volume. Many of these variables may vary over time in a way that does not depend directly on air temperature, thereby decreasing the accuracy with which under-bark temperatures can be predicted using air temperatures.

In addition to revealing the problem of biased predictions when weather station air temperature data were used to drive the Régnière and Bentz winter mortality model in 2019/2020, our data also provided insight into the mechanism within the model that was associated with reduced predictive performance. Specifically, overly high predicted maximum daily under-bark temperatures resulted in a simulated greater loss of cold hardiness in larvae, which resulted in higher simulated mortality at warmer temperatures and lower survival probabilities than when the model was driven using observed under-bark temperatures. It is important to note, however, that the Régnière and Bentz model does adjust air temperatures derived from weather station data to predict under-bark temperatures [16]. In its original form, the adjustment accounts only for elevation but not for tree mass, bark thickness, phloem moisture, or any other factor that might influence under-bark temperature [20]. In addition, in the BioSIM implementation of the Régnière and Bentz winter mortality model, a constant is used to account for the effect of solar radiation in the model component that translates air temperature to under-bark temperature on the south side of the bole. We contend that this constant should likely vary based on geographic location due to the effects of slope aspect, topography, latitude, and season [20]. Thus, the air temperature to under-bark temperature conversion method employed in BioSIM is too simple to accurately predict under-bark temperature across a wide geographic range or across wide variations in tree characteristics.

We observed wide inter-tree variation in mountain pine beetle larval survival in our detailed study in 2019/2020. The wide variation between subpopulations suggests that BioSIM-based predictions might be more comparable to pooled survival estimates calculated by joining populations within individual trees into a site-level population before the calculation of survival. This highlights a fundamental difference between the scale of prediction in BioSIM, which is at the site level, versus the tree-level prediction of the original Régnière and Bentz winter mortality model [16]. In the future, the difference in the spatial scales of weather variables predicted using BioSIM, and the Régnière and Bentz winter mortality model could be reconciled by using statistical approaches that account for spatial variation in parameter values, or using other methodologies that allow for downscaling of predictions from the site to the sub-site level.

In our analysis of a larger spatial and temporal distribution of sites in 2017/2018 and 2018/2019, we found that, although the BioSIM implementation of the Régnière and Bentz winter mortality model provided reasonable estimates of relative mortality proportions from year to year, it did not predict the observed mortality proportions well across our study landscape within the 2017/2018 season nor within the 2018/2019 season. We suspect that poor prediction over space was caused by meteorological interactions with the complex topography of our mountainous study region. The air temperature prediction approach within BioSIM accounts for adiabatic lapse rates with increases in altitude [18], so there is some consideration for the effect of terrain height. However, even with this adjustment, the prediction of meteorological variables in mountainous regions is difficult due to complicated weather patterns, including atmospheric inversions and orographic effects. Our study represents an exceedingly difficult validation challenge for the version of the Régnière and Bentz winter mortality model implemented within BioSIM. This leads us to caution forest managers from relying on model predictions in mountainous landscapes.

In this study, we have used observational data to test the predictions of the Régnière and Bentz winter mortality model. Our study can be subdivided into our detailed assessment at one study site in 2019/2020 and a broader but less detailed assessment across more study sites in 2017/2018 and 2018/2019. The data and predictions from the detailed portion of our study and from the broader analysis are similar enough to permit comparison between them. We found that, in our detailed analysis (2019/2020), the Régnière and Bentz winter mortality model underpredicted the proportions of larvae that survived the winter. Conversely, in the broader study, the Régnière and Bentz winter mortality model overpredicted the proportions of larvae that survived the winter in both years, but especially in 2018/2019. We are uncertain what may have caused this reversal of biases between the earlier two seasons and the later winter season, but we can say that populations were much larger in the earlier years than in the later years. Intraspecific competition due to higher under-bark population densities can increase mortality beyond the isolated effects of cold temperatures on mountain pine beetles [27]. Similarly, other demographic factors including predators and parasitoids can be important for collapsing mountain pine beetle populations [28], but these were not included in our analysis, although they may have limited survival in 2017/2018 and 2018/2019 more than in 2019/2020. It is also possible that a larger dataset would reveal that the bias reversal was in fact just part of the model's prediction error that would average out to zero if data were collected over more years or with a larger dataset.

An important component of the validation of any model is an assessment of bias. It is, therefore, natural to wonder whether the predictions of the Régnière and Bentz winter mortality model are biased relative to the observed survival proportions. Unfortunately, the number of years in our study, the number of study sites, and the geographical range across which our sites were distributed are insufficient for us to conclusively determine whether the predictions of the Régnière and Bentz winter mortality model as implemented in BioSIM are biased relative to the observed demographic data. We can, however, say that the spatial predictions of winter mortality proportions within the 2017/2018 and 2018/2019 years are not correlated with winter survival proportions derived from demographic data at the spatial scale we considered in this study. Therefore, in the context of predictions across the mountainous landscape of our study, the importance of assessing bias is eclipsed by the lack of precision of spatial predictions.

5. Conclusions

Our results illustrate that, when under-bark temperature measurements were available, the Régnière and Bentz winter mortality model made biologically reasonable predictions that captured the dynamic aspect of seasonal changes in larval cold hardiness. Nonetheless, our tests of the Régnière and Bentz winter mortality model exposed two weaknesses. The first of these weaknesses is that the model's translation of air temperatures to under-bark temperatures can produce inaccurate estimates of daily maximum under-bark temperatures. This weakness resulted in the model's underestimation of the survival probability relative to the observed survival proportions in 2019/2020. The second weakness is poor predictions in mountainous terrain. This weakness resulted in a lack of a statistical relationship across space within winter seasons between the observed proportions of larvae that survived the winter and larval survival probabilities predicted by the model. Although the Régnière and Bentz winter mortality model remains useful for predicting the relative impacts of winter mortality across seasons, we hope that this study will increase the awareness of its limitations in the context of the spatial prediction of winter mortality in a complex topography and for prediction in the absence of under-bark temperature measurements.

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Data Availability Statement: The data presented in this study are openly available in Dryad at [https://doi.org/10.5061/dryad.31zcrjdvn].

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Conflicts of Interest: The authors are research scientists employed in the Canadian Forest Service, which is the same organization that employs the authors of BioSIM and one of the creators of the winter mortality model that is the subject of this manuscript (Jacques Régnière). However, the original creators of the mountain pine beetle winter mortality model tested in this study had no role in the design of this study nor in the collection, analyses, or interpretation of the data. The original creators of the model also did not preview the manuscript prior to submission and, therefore, had no influence on its writing or on our decision to submit the results for publication.

Appendix A

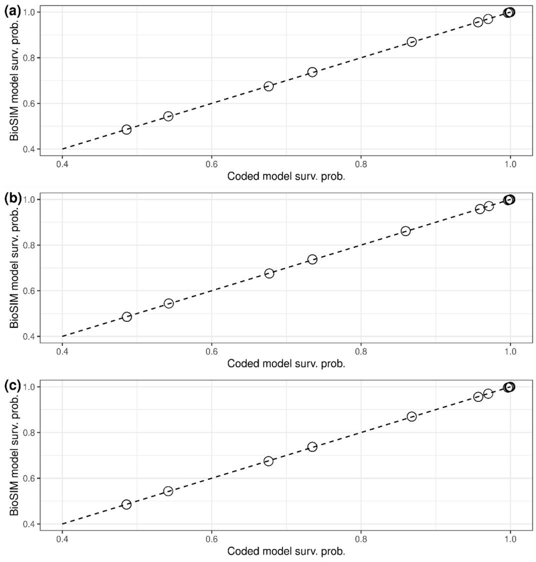

Figure A1. Comparisons of predictions of winter survival probability from the Régnière and Bentz winter mortality model when it is deployed within the BioSIM software environment in which under-bark temperatures are estimated using predicted air temperatures and when the same predicted air temperatures are used to drive the version of the model that we coded in R for (**a**) tree ID number 3810; (**b**) tree ID number 9970; (**c**) tree ID number 9971 at the study site, wherein we conducted a detailed test of the Régnière and Bentz winter mortality model in 2019/2020. In all panels, open circles are data points with x and y coordinates given respectively by predictions of the Régnière and Bentz winter mortality model coded in R, and the BioSIM released version of the same winter of the model.

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