



# 1 Chapter 6

## 2 Individual-Based Modeling: Mountain Pine

### 3 Beetle Seasonal Biology in Response

#### 4 to Climate

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## 6.1 Introduction

Over the past decades, as significant advances were made in the availability and accessibility of computing power, individual-based models (IBM) have become increasingly appealing to ecologists (Grimm 1999). The individual-based modeling approach provides a convenient framework to incorporate detailed knowledge of individuals and of their interactions within populations (Lomnicki 1999). Variability among individuals is essential to the success of populations that are exposed to changing environments, and because natural selection acts on this variability, it is an essential component of population performance.

Initially viewed simply as an alternative modeling technique to classical differential- or difference-based deterministic models of theoretical ecology, IBMs are in fact fundamentally different (De Angelis and Mooij 2005). These models have four essential characteristics: (1) an organism’s life cycle can be depicted in full detail (e.g. thermal responses, behavior, fecundity); (2) variability among individuals of the same life stage, be it caused by genetic or environmental differences, is accounted for; (3) resources exploited by the modeled organisms are explicitly accounted for; and (4) population sizes are represented by integer numbers because they are composed of individuals (Uchmanski and Grimm 1996). An IBM focuses on the fates of individuals with explicitly different traits, and on the biotic and abiotic circumstances to which each responds. The full complexity of an organism’s life cycle can therefore be described and modeled. Such models provide a helpful framework within which to conceptualize and interconnect natural processes, design research, analyze results, and synergistically combine empirical studies and modeling (Van Winkle et al. 1993).

Dealing with individuals simplifies the mathematical formulation of rules and relationships that dictate their responses to environmental conditions or to each other. Individuals can thus differ in many ways, either genetically or because of their environmental context, and it is these differences and their consequences that determine the behavior and the effects of populations on their environment. The object-oriented programming techniques upon which IBMs rest are particularly well suited to discuss adaptation of organisms to varying environmental conditions, because of the property of inheritance from parents and to progeny (Warren and Topping 2001). As is true of all objects in this programming paradigm, specific traits of parents can be passed on, intact or modified, to progeny (children). In a biological context, this occurs when individuals are “copied” at



41 reproduction. Adaptive characteristics that allowed the survival of parents are thus  
42 inherited by their progeny, modifying the relative frequencies of various individual  
43 traits according to their survival and fecundity (fitness) under current environmen-  
44 tal conditions. Thus, the frequency distributions of various traits can change in  
45 simulated populations much as they do in nature.

46 IBMs are well suited to describing the temperature-dependent processes of  
47 organisms sensitive to varying environmental conditions, and can help to model  
48 the responses of populations to a changing climate. Many insect species, including  
49 those deemed pests due to their significant ecological and economic impact, have  
50 been influenced by a changing climate (Bale et al. 2002). Prime examples are bark  
51 beetles in the genus *Dendroctonus* for which a clear connection between weather  
52 and population irruptions and subsequent landscape-scale tree mortality has been  
53 shown (Hansen et al. 2001; Berg et al. 2006; Aukema et al. 2008; Chapman et al.  
54 2012; Preisler et al. 2012; Hart et al. 2014). Changing climatic conditions are  
55 also responsible for a range shift in at least one species, *Dendroctonus pondero-*  
56 *sae*, the mountain pine beetle (MPB). This irruptive species attacks and kills most  
57 *Pinus* species in western North America (Wood 1982). Genetic data suggest that  
58 MPB migrated north following the postglacial Holocene recolonization of British  
59 Columbia by several *Pinus* species (Richardson et al. 2002; Mock et al. 2007;  
60 Godbout et al. 2008; Samarasekera et al. 2012). Recent warming has increased  
61 the speed of this MPB migration into new regions in Alberta, British Columbia,  
62 the Yukon, and Northwest Territories, Canada (Bentz et al. 2010; Safranyik et al.  
63 2010; Cudmore et al. 2010; de la Giroday et al. 2012), with exposure to at least  
64 one new host tree species, jack pine (*Pinus banksiana*) (Cullingham et al. 2011).  
65 Jack pine extends across the boreal forest of Canada and into the northern part of  
66 the mid-western United States, and there is concern about the potential for MPB  
67 to invade eastward across Canada and into central and eastern states (Nealis and  
68 Cooke 2014). Long-lived high-elevation pines (e.g. *P. albicaulis*) with life history  
69 strategies not suited for large-scale disturbance events may also be at risk (Logan  
70 et al. 2010; Tomback and Achuff 2010). Sustained MPB outbreaks are now occur-  
71 ring in high elevation forests where persistent activity was previously constrained  
72 by cold temperatures (Amman 1973; Logan and Powell 2001; Bentz et al. 2011a).  
73 The capacity of MPB to continue expanding into new thermal habitats, however,  
74 remains unclear.

75 Issues surrounding the effects of climate on the distribution and perfor-  
76 mance of species have been investigated by a range of methods, including cor-  
77 relative approaches such as climate matching or species distribution modeling  
78 (Elith and Leathwick 2009) that correlate presence/absence observations with  
79 climatic and geographic variables and extrapolate the results to novel regimes.  
80 Mechanistic approaches include more detailed (if less comprehensive) process  
81 modeling (Sutherst and Bourne 2009; Régnière et al. 2012a). In this chapter, we  
82 present a prototype mechanistic IBM that describes in detail the fitness (popula-  
83 tion growth rate) responses of MPB to temperature, based on understanding of the  
84 insect's developmental and survival responses to temperature, and on the resulting



85 consequences through its interactions with host trees. We realize that many aspects  
86 of MPB life history and the role of hosts at tree and stand scales are not accounted  
87 for within this prototype. However, this “working” model allows us to investigate  
88 climate change effects on the invasiveness of MPB and provides a useful dem-  
89 onstration for the general application of an IBM approach to insect disturbance  
90 modeling.

## 91 6.2 The Insect

92 The behavior and ecology of MPB have been extensively studied (see Safranyik  
93 and Carroll 2006). Most populations across the insect’s range are univoltine (one  
94 generation per year) although 2–3 years can be required in colder environments  
95 or years (Amman 1973; Bentz et al. 2014). Bivoltinism (i.e. two generations in  
96 1 year) appears to currently be limited in MPB due to evolved developmental  
97 thresholds that serve to reduce cold-induced pupal mortality (Bentz and Powell  
98 in press). MPBs develop through four larval instars before pupating and becom-  
99 ing adults. Except for a brief adult flight period, the entire lifecycle is spent in  
100 the phloem, and the host tree is typically killed as part of successful offspring  
101 production. Adults emerge from trees in the summer months to attack new hosts  
102 using a coordinated attack mediated by beetle-produced pheromones. A well-  
103 synchronized adult emergence facilitates mass attack, and is important in the  
104 development of MPB outbreaks because the insects must overcome host defenses  
105 to successfully colonize healthy trees (Raffa et al. 2008). Temperature directly  
106 influences MPB development rate (Bentz et al. 1991; Régnière et al. 2012b), and  
107 stage-specific development thresholds help synchronize adult emergence (Powell  
108 and Logan 2005). Mortality due to extreme cold also conditions MPB population  
109 success (Safranyik and Linton 1998). Cues of declining temperature initiate glycerol  
110 synthesis and lower supercooling points (SCP), increasing MPB larval cold  
111 tolerance (Bentz and Mullins 1999). Before this acclimation occurs or when it is  
112 disrupted by warm periods, significant mortality can occur following cold snaps.  
113 Reproductively active MPB adults also supercool to some extent (Lester and Irwin  
114 2012). In areas where MPB population growth has historically been limited by  
115 cold mortality, warm temperatures associated with climate change have increased  
116 population success and may allow continued population expansion (Stahl et al.  
117 2006; Sambaraju et al. 2012).

## 118 6.3 The Model

119 The influence of climate on MPB population success has been the subject of  
120 considerable modeling attention. Empirically driven, statistical approaches have  
121 been proposed (Safranyik et al. 1975; Aukema et al. 2008; Preisler et al. 2012;



122 Reyes et al. 2012), and mechanistic models have also been developed (Bentz et al.  
123 1991; Gilbert et al. 2004; Régnière and Bentz 2007; Powell and Bentz 2009), to  
124 analyze the role of temperature in MPB population outbreaks using historic and  
125 future climate data (Logan and Bentz 1999; Logan and Powell 2001; Hicke et al.  
126 2006; Bentz et al. 2010; Safranyik et al. 2010). While empirical models have  
127 good descriptive power for the range of conditions for which they were derived,  
128 they need to be used with caution under unobserved multivariate contexts such  
129 as encountered when crossing ecoregional boundaries. In contrast, mechanistic  
130 models are more suitable for predicting MPB population success in novel climate  
131 regimes. Previous mechanistic model development, however, has used frameworks  
132 that don't allow inclusion of processes other than the influence of temperature on  
133 insect development time. For example, Powell and Bentz (2009) were successful  
134 in linking phenology, temperature, and population growth rates; although their  
135 approach is based on cohorts, it is unsuited to linking with other aspects of MPB  
136 life history such as cold tolerance (Régnière and Bentz 2007). MPB has no obli-  
137 gate diapause stage. The age distribution of overwintering populations, and there-  
138 fore, winter survival are thus largely determined by summer phenology. Modeling  
139 cold tolerance requires an individual beetle's history of cold exposure. An IBM  
140 can potentially succeed where other modeling approaches have failed because it  
141 allows life history traits relevant to beetle success to be projected onto individuals  
142 (i.e. age-specific development time, exposure to cold, fecundity), and collaboration  
143 among individuals to overwhelm host responses can be incorporated. We develop  
144 an IBM that integrates the influence of temperature on insect development time  
145 and cold mortality, and their consequences on the interaction between MPB and its  
146 host trees.

147 Our model allows two operating modes: *incipient* or *outbreak*. In the out-  
148 break mode, attacking brood adults lay eggs in successfully attacked trees, and  
149 their progeny are allowed to produce successive generations. Only in the first  
150 year is an input initial attack pattern provided; subsequent timing and intensity of  
151 attacks are determined by the timing of brood adult emergence. This can lead to  
152 overlapping generations (e.g. when the semivoltine descendents of year  $n-1$  and  
153 univoltine descendents of year  $n$  overlap to attack trees in year  $n + 1$ ). As in a  
154 real-world outbreak, very rapidly so many beetle objects are available that brood  
155 trees are overwhelmed almost with impunity as only a small proportion of attacks  
156 are warded off by tree defenses. In incipient mode, new attacks in a single focus  
157 tree are initiated each year, and the number of successful attacks generated by the  
158 progeny of this initial attack in the subsequent year or two (depending on voltin-  
159 ism) is recorded. Thus, each initial attack is allowed only a single generation. The  
160 incipient mode thus describes the process whereby an incipient population subsists  
161 on limited, ephemeral resources, and is unable to develop to the outbreak phase  
162 by mass attacking new hosts. This mode predicts the circumstances under which  
163 incipient populations can become outbreak populations, while the outbreak mode  
164 describes the effect of temperature on the natural course of an outbreak. In both  
165 cases, population growth rate ( $R$ ) is expressed as the ratio of successful attacks in  
166 successive years or generations.



### 167 **6.3.1 Objects**

168 This IBM is nonspatial, in the sense that trees and insects do not have specific  
169 locations in space, and movement is assumed to occur throughout (and only  
170 within) the modeled forest. The model contains four kinds of objects: a forest, two  
171 kinds of host trees, and beetles.

172 The forest is a “container object” that tracks the number and states of tree and  
173 beetle individuals. The forest has a total size,  $F_s$  (km<sup>2</sup>), with tree density  $F_d$  (trees  
174 km<sup>-2</sup>) used solely to determine the number of available host trees. There are two  
175 types of trees: focus and brood, all the same size, differing only in their defen-  
176 sive capability. An area,  $F_0$  (km<sup>2</sup>), of forest containing defenseless focus trees  
177 receives initial beetle attacks. Brood trees are attacked by adults emerging from  
178 these focus trees, and from previously attacked brood trees. Brood trees can ward  
179 off attacks at a constant daily rate of  $a_0$  (beetles m<sup>-2</sup> of bark per day), and support  
180 a maximum number of attacks  $a_{\max}$  (beetles m<sup>-2</sup> of bark), reflecting maximum  
181 colonization density of individual trees. Brood trees whose defense capacity ( $a_0$ )  
182 is exceeded are killed, and their numbers accumulate  $F_k$  over time  $t$  (years). Insect  
183 objects are contained either in focus or brood trees. In this model, only females are  
184 modeled. In MPB, sex ratio varies systematically over the course of an outbreak  
185 (Amman and Cole 1983). While this would be an interesting parameter to explore  
186 because of possible sex-differential mortality and maternal choice of sex ratios, we  
187 chose to use a constant 60 % female sex ratio to create female eggs.

188 Each insect object is distinct in three characteristics, expressed relative to the  
189 population mean: eight uncorrelated stage-specific development rates, potential  
190 fecundity, and larval cold tolerance. Individuals develop, reproduce, and survive  
191 independent of one another, except when the newly emerged adults attack new  
192 hosts. At that time, the number of adults attacking on a given day determines the  
193 probability of survival given host tree defenses. Because the number of individual  
194 beetles becomes very large, especially when the model runs in outbreak mode, a  
195 “super-individual” approach (Scheffer et al. 1995) is used in which beetle objects  
196 represent several individuals with the same characteristics (development rates, age,  
197 potential, and realized fecundity).

### 198 **6.3.2 Development, Reproduction, Variability**

199 Descriptions of MPB thermal responses in development and oviposition were  
200 taken from Régnière et al. (2012b). Development and oviposition are simulated  
201 by a unimodal rate equation with a distinct set of parameters for each life stage  
202 and for egg laying. At creation, each individual is assigned relative development  
203 rates in each of the seven life stages and relative fecundity, represented by eight  
204 random numbers that are drawn from lognormal distributions with means of 1.  
205 Development in successive life stages and oviposition are summed at each time



206 step (4 h). Individuals change stages when their physiological age (starting at 0 for  
207 eggs) reaches a new unit (1: instar 1, 2: instar 2, 3: instar 3, 4: instar 4; 5: pupae, 6:  
208 teneral (unemerged) adult, 7: ovipositing adult) with two exceptions. Teneral adult  
209 emergence can be delayed without further aging if temperature remains below  
210 an emergence threshold,  $T_e = 18^\circ\text{C}$  (Safranyik and Carroll 2006). Adults emerg-  
211 ing on any given day collectively attack new trees and become ovipositing adults.  
212 Ovipositing adults die once they have laid 95 % of their potential fecundity (aver-  
213 age 82 eggs/female), which simulates old age mortality.

### 214 6.3.3 Survival

215 A constant “attrition” rate  $s$ , representing all mortality not specifically described,  
216 is applied at the creation of new eggs. The main cause of dynamic mortality in  
217 the model is exposure to cold. All eggs, pupae, and teneral adults are assumed  
218 to be killed as soon as temperature drops below  $-18^\circ\text{C}$ . Larval cold tolerance is  
219 modeled following Régnière and Bentz (2007). The probability distribution of  
220 cold tolerance is a population trait that varies over time in response to temperature.  
221 The proportion of the larval population in one of three states, each with its SCP  
222 distribution, is calculated from the daily series of minimum/maximum tempera-  
223 tures. A composite distribution of SCP is compiled each day. Probability of cold  
224 mortality is based on this distribution and daily minimum temperature. The maxi-  
225 mum mortality rate experienced by larvae is applied to each super-individual at the  
226 end of larval development.

227 In ovipositing adults, cold tolerance varies seasonally and is modeled in rela-  
228 tion to time of year, independent of temperature. For this purpose we fitted a  
229 cosine function of calendar date to the observations of Lester and Irwin (2012,  
230 their Fig. 5a;  $\text{SCP}_a = -20.2 - 6.09 \cos [2\pi (t/365)^{1.365}]$ ;  $R^2 = 0.946$ ). Adults  
231 exposed to a temperature  $\leq \text{SCP}_a$  die immediately.

### 232 6.3.4 Attack

233 The beetle population is initialized using a Gaussian distribution of attacks over  
234 time on the forest’s defenseless focus trees. Mean date ( $t_0$ ) and standard deviation  
235 ( $\sigma_0$ ) of the initial attacks are specified as inputs. The number of females per  $\text{m}^2$  of  
236 bark in this initial attack is  $n_0 + a_{\text{max}}(F_0 \times F_d - 1)$ , so that when a single focus  
237 tree ( $F_0 = 1/F_d$ ) is used, the model simulates an incipient outbreak with an initial  
238 density of  $n_0$  females  $\text{m}^{-2}$  of bark. Females in the initial attack lay eggs, generat-  
239 ing the brood adults that will attack new host trees at emergence.

240 When an adult emerges from a tree, it joins the day’s collection of emerging  
241 adults ( $n_e$ ) that generate that day’s new attack on surviving host trees in the stand.  
242 All successfully attacked trees are killed. To limit population growth, a proportion



243  $S_l$  of emerging beetles succeeds at finding live hosts to attack while the remainder  
244 is lost. This loss is a function of the proportion of the trees in the forest that have  
245 already been attacked and killed:

246

$$S_l = 1 - \left( \frac{F_k}{F_s \times F_d} \right)^\alpha \quad (6.1)$$

247 where  $F_k$  is the number of trees in the forest that have already been attacked, and  
248  $F_s \times F_d$  is the total number of trees in the forest. The exponent  $\alpha \geq 1$  specifies  
249 how rapidly resource depletion inhibits host encounter. We use  $\alpha = 40$ , large  
250 enough so that the effect of resource exhaustion occurs abruptly as tree mortality  
251 approaches 100 %. Thus, in the simulations produced here,  $\alpha$  is used only to pro-  
252 duce a sudden limit to growth.

253 Total emerging adults attacking new hosts is  $n_a = S_l n_e$ . Our model assumes that  
254 beetles are perfect host finders, consistently aggregating on available hosts and  
255 reaching maximum attack density on those trees before switching. The number of  
256 trees attacked is determined by:

257

$$F_a = \max \left( 1, \frac{n_a}{a_{\max}} \right) \quad (6.2)$$

258 The daily number of attacking beetles killed by tree defenses is

259

$$A = a_0 F_a, \quad (6.3)$$

260 In an incipient outbreak, where beetles emerge from a single focus tree, the pro-  
261 portion of attacking beetles killed by host defenses can be fairly high, as  $A$  can  
262 easily exceed  $n_a$  on any given day. But once  $F_a$  becomes large enough in a devel-  
263 oping outbreak, survival from host defenses is determined solely by the ratio  
264  $a_0/a_{\max}$ .

## 265 6.4 Calibration/Validation

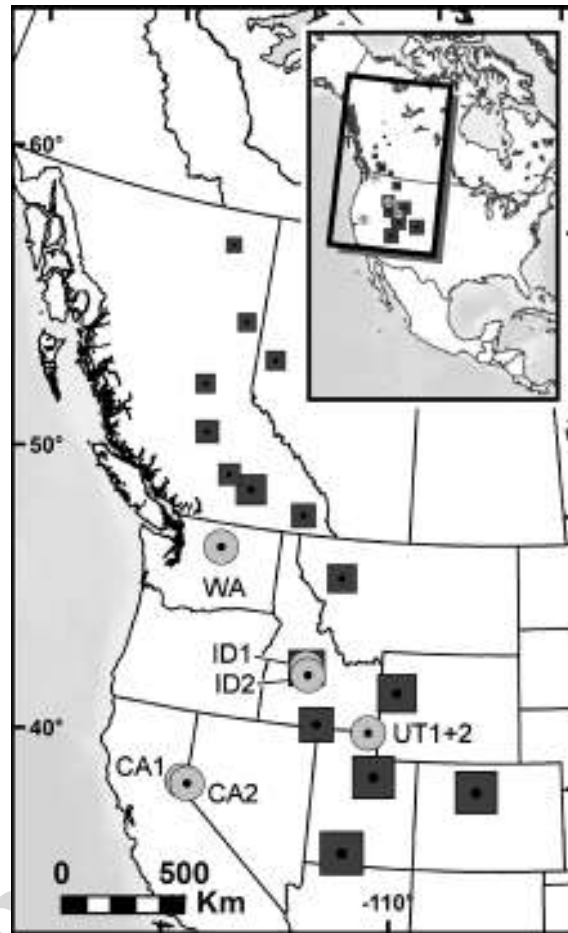
### 266 6.4.1 Seasonality of Adult Emergence

267 We compared output of our model with field observations to verify that the seasonal-  
268 ity it predicted was close to reality. Beetle development time and associated phloem  
269 temperatures were monitored in the field at a range of latitudes and elevations  
270 (Fig. 6.1; Bentz et al. 2014). Beetle attacks and the subsequent emergence of brood  
271 adults were monitored on individual host trees every 1–4 days during the entire  
272 attack period. Hourly phloem temperature records were obtained from the north and  
273 south aspects of tree boles, just under the outer bark, 1.8 m above ground. Hourly  
274 mean air temperature was recorded at each site. These measurements were made  
275 continuously from initiation of attacks to adult emergence 1 or 2 years later.





**Fig. 6.1** Map of western North America illustrating sampling locations for validation of adult emergence phenology (circles, Table 2; Bentz et al. 2014) and simulation of population growth rates between 1950 and 2012 (squares, sizes proportional to elevation)

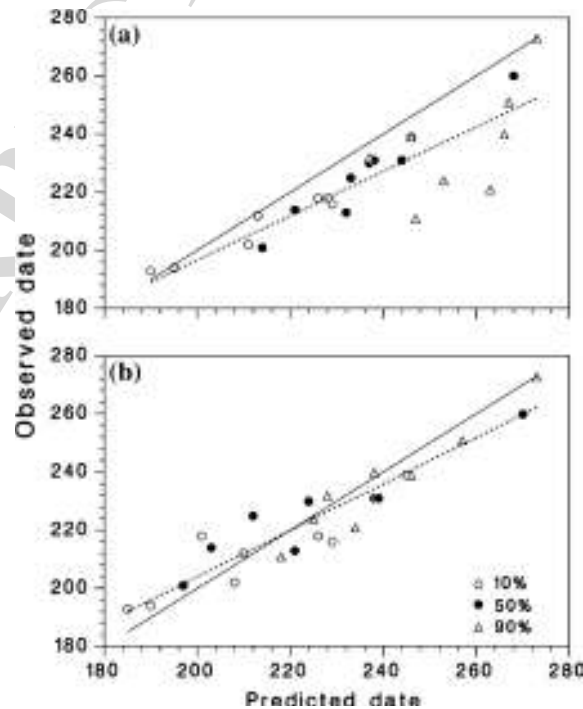


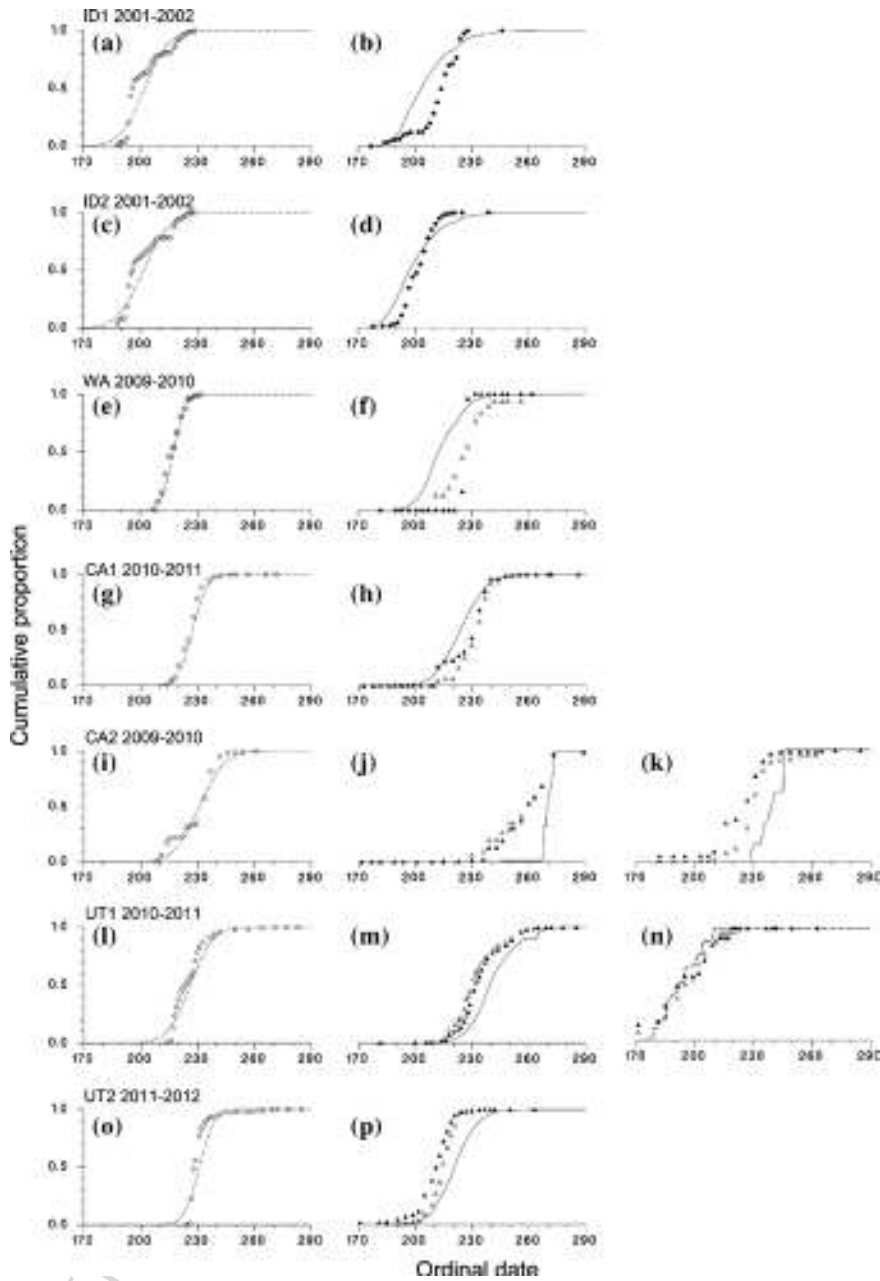
276 Our model requires as input daily minimum and maximum temperatures,  
277 and these were extracted from the observed hourly temperature records. We  
278 calculated bark temperatures by averaging north- and south-aspect daily mini-  
279 mum and maximum observations and developed a phloem microclimate filter  
280 to transform daily minimum and maximum air temperature ( $T_n, T_x$ ) into phloem  
281 temperature ( $T'_n, T'_x$ ). Because phloem temperatures are not usually available,  
282 and air temperatures modified with the microclimate filter will be used in model  
283 application, we present model test results obtained with this input, except when  
284 otherwise mentioned. For each set of MPB attack and emergence observations  
285 (i.e. location and year), the attack data were summarized by calculating the  
286 mean and standard deviation of attack dates, used as model inputs. The model  
287 interpolates between successive minima and maxima and runs on a 4-hr time  
288 step (Allen 1976).



289 The dates when 10, 50, and 90 % emergence were observed in the field were  
290 compared to model-predicted dates. Because an IBM is inherently stochastic,  
291 each simulation was replicated 30 times and results averaged. The dates predicted  
292 by the model, using the published parameters for development rates, variability,  
293 and fecundity (Régnière et al. 2012b), were well-correlated with observations  
294 ( $r = 0.87$ ), but the model-predicted events an average of 12.0 days later than  
295 observed, and the observed–predicted regression line had a slope of 0.76 (sig-  
296 nificantly less than 1; Fig. 6.2a). Based on these results, we made two modifi-  
297 cations to the model. To restrict the duration of the oviposition period, the total  
298 number of eggs laid was limited to 50 % of individuals' potential fecundity, set  
299 to  $\bar{E}_0 = 82$  eggs per female (Régnière et al. 2012b). This reduction was obtained  
300 by trial and error, and may reflect adult mortality not otherwise explicitly consid-  
301 ered in the model. To better represent the observed variability of the adult emer-  
302 gence period, we also reduced the variability of development rates of all immature  
303 stages by half, again by trial and error. It is quite possible that the methods used  
304 to determine insect development rates under laboratory conditions (see Régnière  
305 et al. 2012b) exaggerated their normal variability. These changes increased the  
306 observed–predicted correlation ( $r = 0.94$ ), made the bias nonsignificant (aver-  
307 age 1.2 days), and increased the observed–predicted regression slope to 0.8 (still  
308 significantly less than 1). Given the input initial attack patterns (left column of  
309 Fig. 6.3) and observed air temperatures modified for bark microclimate, modeled

**Fig. 6.2** Relationship between observed and simulated dates of 10, 50, and 90 % cumulative emergence of univoltine adults in 8 site-years in the western United States between 2002 and 2012. **a** Unmodified model; **b** modified model; parameters that describe fecundity and development time variance were altered. *Solid lines* equality; *dotted lines* regression





**Fig. 6.3** Comparison of observed and simulated mountain pine beetle emergence in seven locations and years. The figure is divided in three columns. On the left are the observed (*white circle*) and Gaussian (*dotted line*) attack patterns (model input) for each plot-year. In the center are the observed (*black circle* all orientations; *black triangle* south bole; *white triangle* north bole) and simulated (*Dash line*) univoltine adult emergence patterns in the following summer. On the right, in the case of sites CA2 and UT1, are semivoltine adult emergence patterns 2 years after the initial attack. The dashed line in the right panel for UT1 was generated using north bole temperatures as model input



310 univoltine adult emergence patterns generally agree well with observations (center  
312 and right columns in Fig. 6.3), although emergence timing of semivoltine adults  
313 was less accurate (Fig. 6.3k). The need to reduce developmental variability and  
314 oviposition period to obtain a better fit with field observations suggests that  
315 important development and mortality processes may be missing in our model.  
316 Nevertheless, observed and simulated development times ranged from 400 to  
317 800 days; a precision of <15 days over such a long simulation period is sufficient  
318 to predict climate impacts on MPB seasonality and performance.

#### 319 **6.4.2 Fitting to Observed Annual Growth Rates**

320 Estimates of observed MPB outbreak growth rates obtained from aerial detec-  
321 tion surveys conducted by United States Forest Service for the Sawtooth National  
322 Recreation Area (SNRA), Idaho, were described in Powell and Bentz (2009).  
323 We collected MPB-infested tree phloem and air temperature data at multiple  
324 sites between 18 July 1992 and 15 October 2004, using the methods described in  
325 Sect. 6.3.1, from four sites in the SNRA, forming a continuous thermal record of  
326 daily minimum and maximum temperatures. Assuming that the density of trees is  
327 relatively constant, the area growth rate (calculated as the ratio of area affected  
328 in year  $n + 1$ /area affected in year  $n$ ) approximates the growth rate in number of  
329 MPB-infested trees.

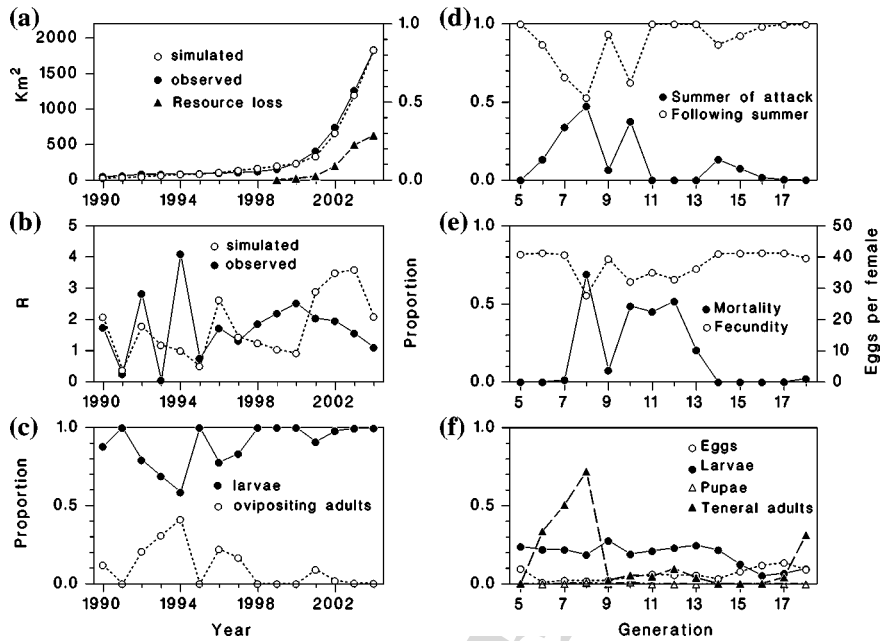
330 Additional daily minimum and maximum air temperature data for the period  
331 lacking phloem temperature observations between 1986 and 2010 were obtained  
332 from the nearest weather stations in the National Climatic Data Center daily  
333 observations databases, using distance-weighted averaging and thermal gradient  
334 approach of BioSIM (Régnière et al. 2014). These records were then transformed  
335 with a multiple regression relating daily air temperature minima and maxima to  
336 observed 1992 phloem temperatures:

337

$$\begin{aligned} T'_n &= 2.55 + 1.00T_n + 0.298(T_x - T_n) \\ T'_x &= 1.88 + 1.04T_n + 0.080(T_x - T_n) \end{aligned} \quad (6.4)$$

338 This provided a means to complete our time series of daily minimum and maxi-  
339 mum phloem temperature to cover the period 1986–2010.

340 Using this daily minimum and maximum phloem temperature time series as  
341 input, the model was run in outbreak mode, using a simulated annealing algo-  
342 rithm to estimate the value of the attrition survival parameter ( $s = 0.43$ ) and ini-  
343 tial infestation size in 1986 ( $F_0 = 0.03 \text{ km}^2$ ) on the basis of minimum sum of  
344 squared deviations between observed and simulated total forest area killed over  
345 time. Other parameter values were fixed ( $F_s = 2800 \text{ km}^2$ ;  $F_d = 75,000 \text{ trees km}^{-2}$ ;  
346  $a_0 = 5 \text{ attacks day}^{-1} \text{ m}^{-2}$ ;  $a_{\max} = 120 \text{ attacks m}^{-2}$ ;  $T_e = 18 \text{ }^\circ\text{C}$ ;  $N_0 = 60 \text{ attacks}$ ;  
347  $t_0 = 200$ ,  $\sigma_0 = 5 \text{ days}$ , and  $\alpha = 40$ ).



**Fig. 6.4** Observed (*white circle*) and simulated (*black circle*). **a** Infestation size (also, value of survival from resource-loss  $S_t$  *black triangle*); **b** annual infestation growth rates; **c** proportion of overwintering individuals in larval stages (*black circle*) or as ovipositing adults (*white circle*); **d** proportion of adults emerging in the year of attack (*black circle*) or in the following year (*white circle*); **e** winter mortality rate of ovipositing adults (*black circle*) and average realized fecundity (*white circle*); **f** winter mortality of immature stages (eggs: *white circle*; larvae: *black circle*; pupae: *white triangle*; teneral adults: *black triangle*). Year is the year of attack. Generation 5 was produced in 1990, with univoltine adults emerging in 1991

348 The resulting predicted and observed cumulative forest mortality ( $\text{km}^2$ ) were  
 349 highly correlated ( $r = 0.997$ ; Fig. 6.4a). The annual outbreak area growth rates  
 350 (Fig. 6.4b), however, were not significantly correlated with the simulated annual  
 351 growth rates of successful attacks ( $r = 0.12$ ,  $P = 0.67$ ; Fig. 6.4b), although aver-  
 352 age observed ( $1.733 \pm 1.014$ ) and simulated ( $1.757 \pm 1.006$ ) growth rates were  
 353 nearly identical ( $P = 0.95$ ). The model is set up to assume an exact correspond-  
 354 ence between the number of successful MPB attacks and tree mortality because  
 355 the density of successful attacks per tree is constant, all trees are equally likely to  
 356 be attacked and killed, and there is no spatial variation in tree density. In nature,  
 357 none of these are constant, and deviations between beetle population performance  
 358 and tree mortality rates may vary accordingly. Growth rates were significantly  
 359 reduced by resource-loss in the last 2 years of the simulated outbreak through Eq.  
 360 (6.1), as the total area killed ( $F_k$ ) approached total forest size, estimated here at  
 361  $F_s = 2800 \text{ km}^2$  (black triangle in Fig. 6.4a). Model results indicate that most indi-  
 362 viduals in the SNRA during the study period spent winter as larvae (Fig. 6.4c).



363 Years with a large proportion of individuals spending winter as ovipositing adults  
364 corresponded to those with a higher proportion of individuals emerging as adults  
365 in the same summer as they were oviposited (Fig. 6.4d;  $r = .86$ ). Winter mortality  
366 among overwintering adults was the main source of variation in realized fecun-  
367 dity (Fig. 6.4e;  $r = -0.96$ ). Winter mortality of eggs and pupae was very low  
368 (Fig. 6.4f) because very few individuals were predicted to spend winter in those  
369 stages. Larval winter mortality averaged only 20 %, but mortality in the teneral  
370 adult stage was highly variable, with high mortality rates associated with years  
371 when a high proportion of individuals reached the ovipositing adult stage in the  
372 summer of attack ( $r = 0.66$ ), as many individuals were unable to emerge prior to  
373 winter. Because in these simulations the initial population was already in outbreak  
374 mode ( $0.03 \text{ km}^2 \times 75,000 \text{ trees km}^{-2} = 2250 \text{ trees}$ ), the number of MPB attack-  
375 ing was well beyond a tree's defensive capacity, and the proportion of attacks  
376 warded off by trees is near constant at 4 % ( $a_0/a_{\max} = 5/120$ ).

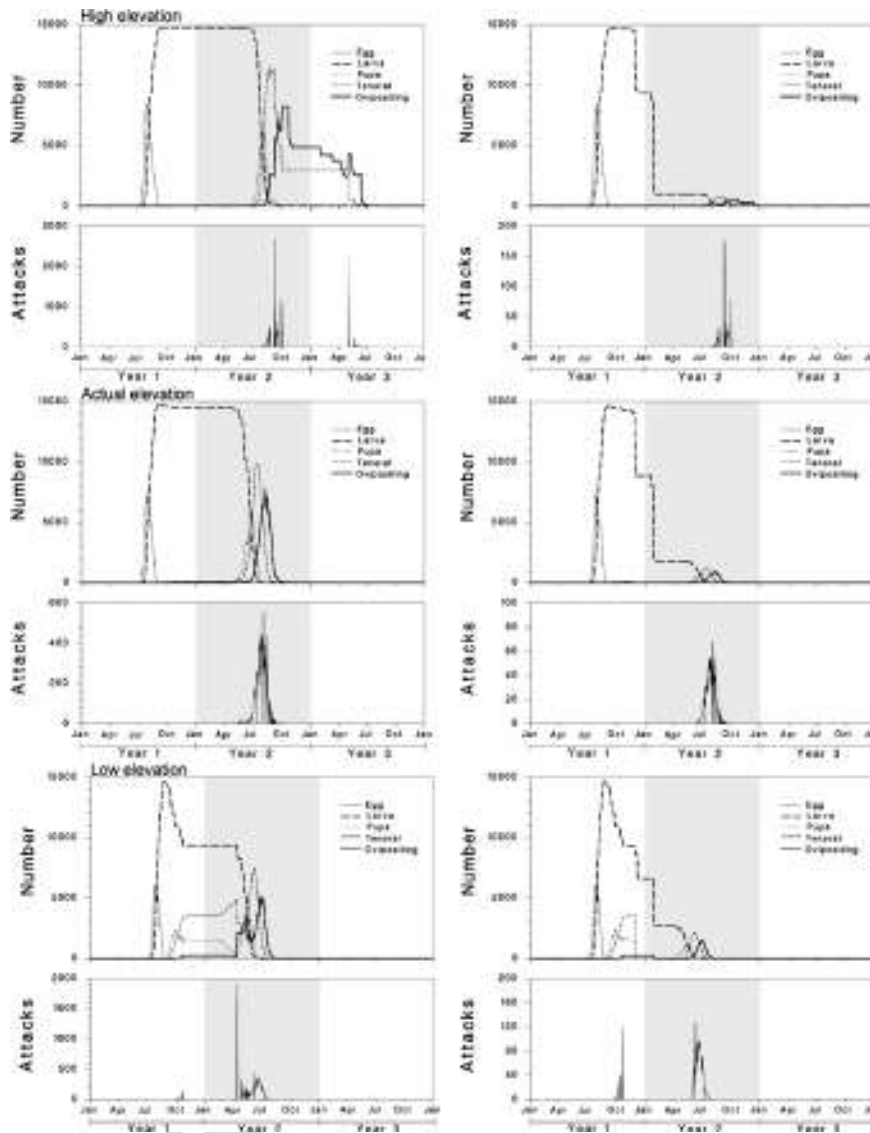
## 377 6.5 Model Behavior

### 378 6.5.1 Seasonality and Elevation

379 We ran the model at three elevations near Jasper, Alberta, where MPB is well  
380 established: one point at Jasper (1062 m), two at the same latitude and longitude  
381 but at fictional elevations: low (400 m) and high (1500 m). Actual weather obser-  
382 vations for the period 2007–2010 were used as input. The nearest Environment  
383 Canada weather station was chosen for each simulation point using BioSIM  
384 (Régnière et al. 2014), compensating for differences in coordinates with regional  
385 latitude, longitude, and elevation thermal gradients.

386 We ran the model in incipient mode using (1) 60 females/m<sup>2</sup> in the initial  
387 attack, with  $t_0 = 200$  (17 July) and  $\sigma_0 = 5$ , (2) attrition survival  $s = 1$ , and (3)  
388 adult emergence threshold  $T_e = 18$  °C. Two different simulations were run: (a) no  
389 winter mortality and (b) winter mortality in all life stages. The distribution of life  
390 stages and adult emergence over time resulting from these simulations are illus-  
391 trated in Fig. 6.5.

392 At the fictional low elevation site, ignoring winter mortality, a very small pro-  
393 portion of adults emerged in October of the initial attack year. The majority of  
394 brood adults emerged the following summer (i.e. univoltine). Some individuals  
395 developed to the teneral adult stage prior to winter, and the predicted emergence  
396 of these individuals was as early as April when temperatures exceeded 18 °C.  
397 However, most individuals spent the winter in the larval and pupal stages and  
398 emerged in July. When cold mortality was applied, overwintering eggs, pupae, and  
399 teneral adults were killed, along with a portion of overwintering larvae. As a result  
400 of this mortality, the relative importance of the first summer's late (October) flight  
401 was inflated. As none of the eggs laid by those late-summer attackers would have  
402 survived winter, their contribution to the population would be null. Mortality of



**Fig. 6.5** Predicted life stage frequencies and attack timing following a Gaussian initial attack centered on July 17 (day  $200 \pm 5$  days). Temperature was estimated for three elevations at the latitude and longitude of Jasper, Alberta, Canada ( $52.88^{\circ}\text{N}$ ,  $-118.07^{\circ}\text{E}$ ): 1500 m (top row of 4 panels), 1062 m (actual elevation, center row) and 400 m (bottom row). Left column: simulations with no winter mortality. Right column: winter mortality in all life stages

403 pupae and teneral adults also eliminated the brood adults that would have emerged  
404 in early spring, leaving only the individuals that spent winter in the larval stages to  
405 contribute to the next summer's brood adult flight in June and July.



406 At the middle elevation (actual elevation of Jasper), all individuals spent win-  
407 ter as larvae, mostly in the 4th instar. Brood adult emergence occurred in July of  
408 the following summer (univoltine). Mortality due to cold did not change the tim-  
409 ing of adult emergence, although the total number of emerging brood adults was  
410 reduced. At the highest elevation, the population also overwintered as larvae, and a  
411 high proportion of individuals emerged in August to October of the following year  
412 (univoltine). The remaining individuals spent the second winter as teneral adults  
413 and emerged 2 years after the initial attack (semivoltine). Many of the univoltine  
414 adults would have overwintered as ovipositing adults. When cold-induced mortal-  
415 ity is added, teneral adults are predicted to die during the second winter, result-  
416 ing in emergence of univoltine beetles only.

417 These simulations illustrate important consequences of climate on MPB  
418 dynamics. First, at low elevation locations where summer development is accel-  
419 erated, but with sufficient cold to kill the most sensitive life stages, brood adults  
420 emerging in late summer of the year of initial attack may not reproduce success-  
421 fully due to mortality of eggs during winter. Ovipositing adults are also likely to  
422 be killed overwinter. Thus, warmer climates can lead to lower overall population  
423 fitness as a result of poor synchrony between winter cold and the most cold-  
424 hardy life stages (larvae). However, in still warmer conditions where winters  
425 are not cold, this effect would disappear. In colder climates with slower summer  
426 development and a mix of univoltine and semivoltine beetles, winter mortality  
427 in the teneral and ovipositing adult stages can also result in high mortality dur-  
428 ing the second winter. These results confirm previous research suggesting that  
429 climates leading to well-synchronized, strictly univoltine phenology are the most  
430 adaptive for the insect (Amman 1973; Safranyik 1978). As winter temperatures  
431 warm, however, complete univoltinism does not appear to be mandatory for  
432 population growth as long as adult emergence remains synchronous (Bentz et al.  
433 2014).

### 434 6.5.2 Latitudinal Gradient

435 We ran the model over the period 1951–2010 at 15 locations along a latitudinal  
436 gradient within the geographical range of lodgepole pine (*P. contorta*), between  
437 Strawberry Point, Utah, USA (37.45°N, -112.34°E, 2695 m) and Fort Nelson,  
438 British Columbia (58.78°N, -122.73°E, 395 m). There was a strong negative  
439 correlation between elevation and latitude among the sites ( $r = -0.90$ ; squares,  
440 Fig. 6.1). The model was run in incipient as well as outbreak mode. Weather  
441 inputs were provided by BioSIM, from the two daily NCDC weather stations  
442 nearest to each simulation point, compensating for differences in latitude, longi-  
443 tude, and elevation with local thermal gradients derived from several nearest nor-  
444 mals-generating weather stations. We provided the same Gaussian initial attack  
445 pattern (mean: 17 July, standard deviation: 5 days) as input. Each simulation was  
446 replicated 30 times and results were averaged to reduce stochastic effects. General



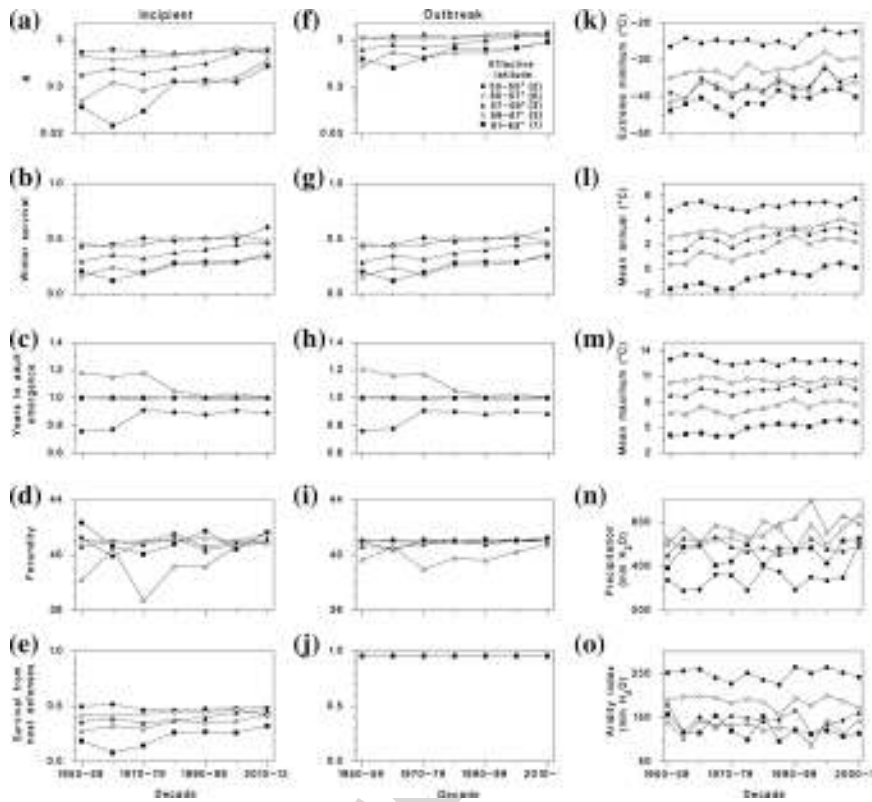


447 Linear Models were used to relate several key output variables (single-generation  
448 population growth rates  $R$ , winter survival  $S_w$ , voltinism, fecundity, and attacking  
449 adult survival from host defenses  $S_h$ ) to year, latitude  $L$ , and elevation  $E$ . For this  
450 analysis, latitude and elevation were combined into a single variable that we called  
451 “effective latitude” ( $L_E = L + kE$ ) where  $k$  transforms elevation into degrees lati-  
452 tude. The value of  $k$  was chosen to maximize the correlation between average  
453 growth rate and  $L_E$  (1°N per 165 m elevation). This value is similar to that esti-  
454 mated by Bentz et al. (2014) using degree hours >15 °C required for completion of  
455 a generation.

456 Simulated growth rates increased significantly between the 1950–1959 and  
457 2010–2012 time periods. In both incipient and outbreak modes, effective latitude  
458 had a negative effect on growth rates, and the increase of population growth rates  
459 through time was most pronounced at the highest effective latitudes (time  $\times$  lati-  
460 tude interactions highly significant in both modes; Figs. 6.6a, f). Winter survival  
461 also increased significantly over time and decreased significantly with effective  
462 latitude (Figs. 6.6b, g). However, no significant interaction was apparent between  
463 effective latitude and time period in either incipient or outbreak mode in the effect  
464 on winter survival. These effects were identical in incipient and outbreak modes.  
465 Year, effective latitude, and their interaction also significantly affected voltinism in  
466 the two simulation modes (Figs. 6.6c, h). These results suggest that MPB popula-  
467 tions across the 15 sites in this latitudinal/elevational gradient have been mostly  
468 univoltine, and increasingly so over the period 1950–2012. This strong tendency  
469 to univoltinism reflects the choice of our simulation locations, all situated within  
470 the main distribution of lodgepole pine. The exceptions to univoltinism occurred  
471 mostly between 1950 and 1980, with 30 % of adults emerging in less than a year  
472 in Cassia, Idaho, USA (42.1°N, –114.1°E, 1965 m), and 20 % as semivoltine in  
473 Vernon, British Columbia (50.35°N, –119.11°E, 1452 m). Realized fecundity did  
474 not change significantly over the simulation period, but dropped significantly with  
475 effective latitude (Figs. 6.6d, i).

476 Fecundity was more variable in incipient mode, probably as a result of the  
477 smaller number of adults surviving host defenses (Figs. 6.6e, j). In incipient mode,  
478 this factor increased significantly over time and declined with effective latitude,  
479 with a significant interaction. However, as expected, outbreak-mode survival from  
480 host defenses was very high and essentially constant. To summarize these results,  
481 a regression model using  $\log S_w$  (winter survival), and  $\log S_h$  (attacking adult  
482 survival from host defenses) as predictors explained 98.6 % of the variation in  $\log$   
483  $R$  between years, locations, and simulation modes.

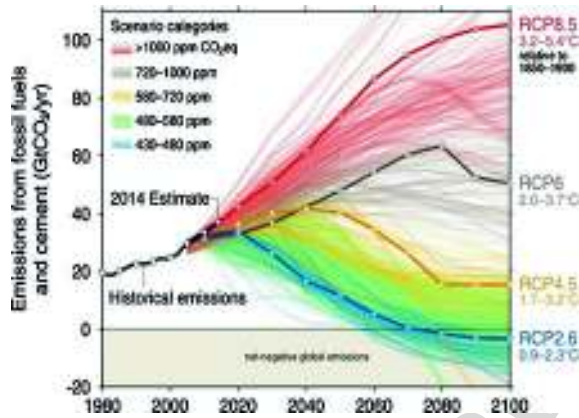
484 The modeled changes in MPB survival and recruitment rates over time and  
485 space described here were caused by corresponding changes in observed ther-  
486 mal regimes, in particular extreme minimum and mean annual temperatures  
487 (Fig. 6.6k, l), and to a lesser extent mean maximum temperatures (Fig. 6.6m).  
488 There was also a slight increase in precipitation over the years (Fig. 6.6n), but  
489 because of a gradual increase in mean annual temperature this did not translate to  
490 a change of aridity, calculated as the annual sum of monthly differences between  
491 potential evapotranspiration and precipitation (Fig. 6.6o).



**Fig. 6.6** Decadal average model inputs and outputs in incipient and outbreak modes for an array of 15 locations in western North America over the period 1951–2012. Sites grouped into five effective latitude classes of  $2^\circ$  (number of sites per class in parentheses). *Left column* incipient mode. *Center column* outbreak mode. *Right column* weather statistics. **a, f** Generation growth rate; **b, g** winter survival (all stages); **c, h** mean number of years to complete a generation (development in 1 year is univoltine); **d, i** realized fecundity; **e, j** survival from host defenses; **k** extreme annual minimum, **l** mean annual and **m** mean maximum air temperature; **n** annual precipitation; and **o** aridity index

## 492 6.6 Climate Change

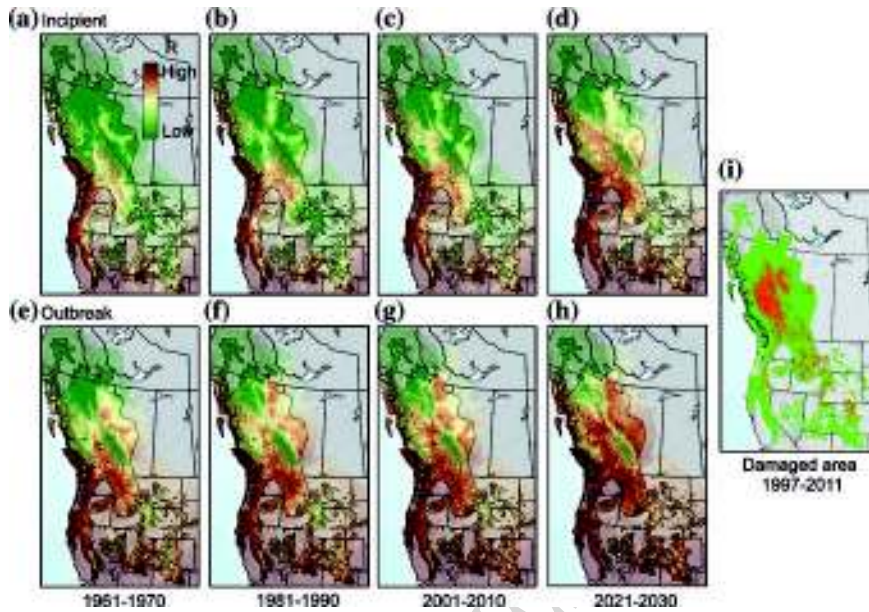
493 Simulated past and future (1961–2100) daily minimum and maximum tempera-  
 494 tures on a  $201 \times 193$  grid over North America were obtained from the Canadian  
 495 Regional Climate Model (CRCM) version 4.2.0 runs ADJ and ADL (Music and  
 496 Caya 2007). These runs are based on the Intergovernmental Panel on Climate  
 497 Change (IPCC) A2 emissions scenario (IPCC 2007), which has been realistic  
 498 thus far given actual emissions estimates (Raupach et al. 2007). The IPCC A2 is  
 499 intermediate between Representative Concentration Pathway RCP6 and RCP8.5  
 500 scenarios (IPCC 2013).



501 From these data, 30-year normals were computed for several decades in  
502 the interval 1961–2050, and the “delta” method (differences between modeled  
503 decadal normals and the reference 1981–2000) was used to generate unbiased dec-  
504 adal sets of 30-year normals into the future. We used as model input 10 years of  
505 observed daily minimum and maximum temperatures for the decades 1961–1970,  
506 1981–1990, 2001–2010, and 10 years of daily values generated stochasti-  
507 cally from climate-changed normals (Régnière and St-Amant 2007) for decades  
508 2021–2030 (normals 2011–2040) and 2041–2050 (normals 2031–2060).

509 Two sets of model output maps were prepared, one for western North America,  
510 and one for the whole continent, north of Mexico. The model was run in incipi-  
511 ent and outbreak modes for 10,000 simulation points located randomly across  
512 western North America, and 30,000 points across the whole of North America  
513 north of Mexico, with increased point density in mountainous areas. Elevations  
514 were obtained from digital elevation models (DEM) at 30 arc-second resolution  
515 obtained from Shuttle Radar Topography Mission SRTM 30 ([http://dds.cr.usgs.gov/srtm/version2\\_1/SRTM30/](http://dds.cr.usgs.gov/srtm/version2_1/SRTM30/); Accessed 6 January 2015). Because of the sto-  
516 chastic nature of the model and of weather inputs when generated from normals,  
517 each model run was replicated 10 times, and model output was averaged over rep-  
518 licates and years. From these averaged outputs, maps were generated by universal  
519 kriging with elevation provided by the input DEM as external drift variable. Log  
520 population growth rates were used for interpolation. Model output was masked  
521 using polygons that estimate the twentieth century distributions of pine habitat in  
522 the United States and Canada (all *Pinus* species mapped by Little 1971).

524 Predicted MPB population growth rates over the distribution of western pine  
525 species increased considerably in every decade between 1961–1970 and 2001–  
526 2010, and are predicted to continue increasing under climate change (Fig. 6.7).  
527 Over the historical period (1961–1970 to 2001–2010), these changes coincided  
528 with changes in the thermal regime (Fig. 6.6). The maps suggest that numerous  
529 forested areas, particularly in south-central British Columbia, coastal regions  
530 and low latitudes and elevations in the United States, have historically had high



**Fig. 6.7** Incipient (a–d) and outbreak (e–h) population growth rates during 1961–1970 (a, e), 1981–1990 (b, f), 2001–2010 (c, g), and expected in 2021–2030 (d, h). i Map overlaying areas affected by mountain pine beetle in western North America, 1997–2011 (red) on the twentieth century distribution of western pines not including jack pine (data compiled by G. Thandi, Natural Resources Canada, and provided by: BC Ministry of Forests, Alberta Environment and Sustainable Resource Development, USDA Forest Service, Natural Resources Canada). Western pine species distribution compiled from U.S. Geological Survey 1999

531 probability of MPB outbreak development. Periodic MPB outbreaks have been  
532 observed in these areas (Preisler et al. 2012). However, factors other than temper-  
533 ature that are not accounted for in our model affect MPB population dynamics.  
534 These include stand density, host tree age and size (Fettig et al. 2007), and mois-  
535 ture conditions that can influence fungal symbionts (Rice et al. 2007), tree defense  
536 capacity, and phloem drying. The latter factor is a major cause of mortality among  
537 MPB immature stages (Cole 1981; Safranyik and Carroll 2006). Along our latitu-  
538 dinal gradient, annual precipitation (Fig. 6.6n) and mean temperature combined  
539 to generate a strong aridity gradient, undoubtedly a factor involved in limiting  
540 MPB population growth rates in the southern proportion of the insect’s range.  
541 Also, MPB developmental responses to temperature in the southwest United States  
542 differ from those in the northern part of the insect’s range (Bentz et al. 2011b)  
543 from which our model parameters were obtained. Therefore, model predictions are  
544 less reliable in these areas. Western pine forests at higher elevations in the United  
545 States and Canada, and at higher latitudes in British Columbia and Alberta his-  
546 torically had a low probability of MPB outbreaks. These areas are predicted to  
547 become increasingly suitable to MPB with climate change. Many of these areas



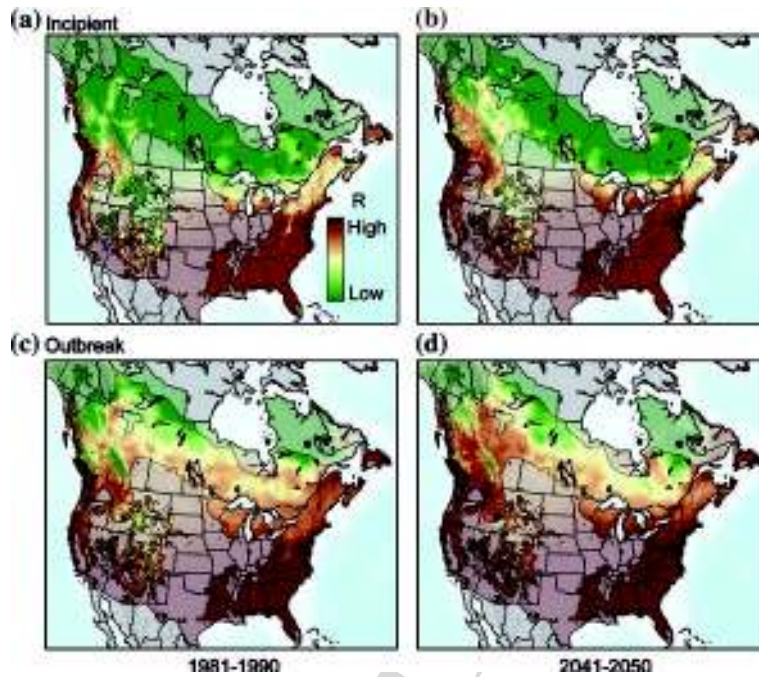
548 are currently experiencing widespread MPB outbreaks (Safranyik et al. 2010;  
549 Meddens et al. 2012; Fig. 6.7i), and the climate change scenario maps (Fig. 6.7d,  
550 h) show that this trend can be expected to continue, with increasing risk in the  
551 Yukon, Northwest Territories, and Alberta.

552 In 2006, MPB populations were observed infesting jack pine in central Alberta  
553 (Cullingham et al. 2011). This population expansion was aided by long-distance  
554 dispersal of beetles from epidemic populations west of the Rocky Mountains  
555 (de la Giroday et al. 2012), and possibly by high reproductive success in naïve  
556 hosts (Cudmore et al. 2010). The current distribution of MPB-caused tree mor-  
557 tality in Alberta (Fig. 6.7i) corresponds well with predicted population growth  
558 rates in outbreak mode, for the period 2001–2010 (Fig. 6.7g). By the middle of  
559 this century, predicted population growth rates will be moderate to high in most of  
560 Alberta, although moderate to low in the northern and eastern Canadian Provinces  
561 where it is actually predicted to decline slightly in the future. These results high-  
562 light the differential effect of temperature on MPB cold tolerance and population  
563 synchrony. Increasing minimum temperatures may result in higher overwinter sur-  
564 vival, but univoltinism will be disrupted when temperatures are too warm (Bentz  
565 et al. 2010; Sambaraju et al. 2012; Bentz and Powell in press). MPB outbreak  
566 potential and population growth is also influenced by stand conditions, measured  
567 using indices of stand structure, volume, density and composition. Safranyik et al.  
568 (2010) found that stands east of Alberta generally have low suitability, and when  
569 combined with our model results suggest that future population growth across the  
570 boreal forest will be less than that recently observed in British Columbia.

571 Incipient model results indicate areas where thermal conditions are highly  
572 conducive to the transition between incipient and outbreak populations, although  
573 population growth is artificially halted in the model. By the middle of this cen-  
574 tury, model predictions suggest that thermal conditions in much of Alberta and  
575 northwestern British Columbia will become more suitable for transition from the  
576 incipient phase, without the need for large surrounding populations. The Canadian  
577 boreal forest and some high elevations areas in the western United States, however,  
578 will not necessarily be suitable for this transition (Fig. 6.8b), although if popula-  
579 tion growth is unconstrained due to other factors, populations will be moderately  
580 successful (Fig. 6.8d). Pine forests in the eastern United States are also predicted  
581 to have high population growth potential by the middle of this century. Suitability  
582 of eastern pines for MPB reproduction is unknown, however, and our process  
583 models of development and cold tolerance are not parameterized for these regions.

## 584 6.7 Modeling Conclusions

585 Our integrated model of phenology and cold tolerance provides a tool to evalu-  
586 ate climate influences on the invasiveness of MPB, a native insect limited in dis-  
587 tribution by climate. Simulations illustrate important consequences of climate on  
588 MPB dynamics. When run across a latitudinal gradient, winter survival and the



**Fig. 6.8** Incipient (a, b) and outbreak (c, d) MPB population growth rates during 1981–1990 and expected in 2041–2050 in North America north of Mexico. Model output is masked with the twentieth century distribution of all pine species (U.S. Geological Survey 1999)

589 ability of adults to overcome host defenses, a consequence of developmental  
590 timing, explained 98.6 % of the variation in population growth between years,  
591 locations, and simulation modes. Winter survival and population growth rates  
592 increased significantly between 1950 and 2012, particularly at the highest effective  
593 latitudes. When run across an elevation gradient, thermal regimes that resulted in  
594 univoltinism and larval overwintering were optimal. Warm summers at the lowest  
595 elevation accelerated development, resulting in adult emergence the year of attack.  
596 Oviposition was late enough in the fall, however, that a high proportion of the life  
597 stages most sensitive to cold were killed during winter, emphasizing the low over-  
598 all population fitness resulting from poor phenological synchrony between win-  
599 ter cold and the most cold-hardy life stages at warmer temperature. Using climate  
600 projections, simulations suggest that much of the central Canadian boreal forest  
601 fits this scenario. Future environmental suitability for population growth and  
602 expansion, as measured by the influence of temperature on MPB physiological  
603 processes, will lie between the relatively low suitability values predicted by the  
604 incipient mode simulations (where host tree defenses play a large role) and the  
605 higher values predicted in outbreak mode (where host defenses are negligible).

606 This prototype mechanistic model illustrates the importance of accounting for  
607 both cold mortality and life-stage-specific phenological details, in full interaction.



608 This is a benefit of this IBM that an aggregated modeling approach could not  
609 have provided. We acknowledge gaps in our understanding of these processes,  
610 including cold tolerance of life stages other than larvae, and constraints on fecun-  
611 dity. Moreover, host tree abundance and connectivity that affect the beetle's host-  
612 finding and mass attack abilities, and important indirect effects of climate on host  
613 trees and MPB community associates, are not currently incorporated in the model.

614 The MPB has been migrating for the past 8000 years, following a northerly  
615 expansion of its host tree species. As temperature increased, expansion has been  
616 extraordinarily rapid in the past few decades, so rapid that no loss of genetic vari-  
617 ability was detected in expanding populations (Samarasekera et al. 2012). Our  
618 model explains the role of weather in this expansion, and predicts that the pace of  
619 population growth in Alberta and northern BC will continue to increase. Thermal  
620 conditions across the boreal forest into eastern Canada will not be as favorable  
621 for population growth. Adaptation in thermally dependent MPB life history traits  
622 to rapid warming could alter this prediction, and should be a high priority topic  
623 for future research. Moreover, IBMs provide an excellent framework for includ-  
624 ing adaptive potential. In addition to expansion north and east in Canada, MPB  
625 could extend its range south into pine forests of Mexico. The MPB is currently  
626 active in high elevation pine forests of southern Arizona. Genetic differences in  
627 developmental parameters between northern and southern populations (Bentz et al.  
628 2011b; Bracewell et al. 2010), however, limit using the current model to predict  
629 MPB invasiveness in the south. Additional processes such as phloem drying in  
630 response to aridity (Cole 1981), and developmental parameters specific to southern  
631 MPB populations, will allow for a comprehensive tool to predict MPB invasive-  
632 ness across the range of pines.

## 633 6.8 IBM as Generalized Modeling Approach for Insect 634 Disturbance Modeling

635 An ongoing argument in ecological literature relates to the generality and utility  
636 of simple versus complex models. Evans et al. (2013) wrote "*Modellers of bio-*  
637 *logical, ecological, and environmental systems cannot take for granted the maxim*  
638 *'simple means general means good'. We argue here that viewing simple models*  
639 *as the main way to achieve generality may be an obstacle to the progress of eco-*  
640 *logical research. We show how complex models can be both desirable and general,*  
641 *and how simple and complex models can be linked together to produce broad-*  
642 *scale and predictive understanding of biological systems". The data requirements*  
643 *of complex models also are a topic of controversy in the literature (e.g. Lonergan*  
644 *et al. 2014; Evans et al. 2014). We do not intend to answer these issues in detail*  
645 *here.*

646 We believe that the choice of approach to model insect disturbance is dictated  
647 by several criteria: the objectives, the prediction precision and extent of specific-  
648 ity sought, the level of detail and specificity available in our understanding of a



649 species' behavior, and the availability of data. While IBMs such as the one devel-  
650 oped here may seem complex, they are in fact relatively simple because they make  
651 reference to few abstract concepts or theoretical constructs that can be very dif-  
652 ficult to parameterize. They rely on adequate understanding of just what data are  
653 needed to capture the essential behavior we need to mimic of nature. As such they  
654 are data hungry, but only to the extent that the demands placed on their specific-  
655 ity and precision are high. In our individual-based modeling of the responses of  
656 the spruce budworm (*Choristoneura fumiferana* Clem.; Cooke and Régnière 1996;  
657 Régnière et al. 2012a), and its congener the western spruce budworm (*C. occi-*  
658 *dentalis*), to climate (Nealis and Régnière 2014), we used an amount of data very  
659 similar to that required for the present MPB IBM. As has been the case here, we  
660 achieved fairly high precision in predictions, as well as a good level of understand-  
661 ing of the fundamental interactions between positive and negative influences of  
662 climate in their ecology. But perhaps the greatest achievement of these models is  
663 that they allow us to identify areas where we do not know enough or where the  
664 most pressing data needs exist. They are also easy to expand to include new pro-  
665 cesses and behaviors, because of their object-oriented nature.

666 For most pests that have significant economic or ecological impact, basic data  
667 are available for the elaboration of IBMs. The great advantage of insect IBM is  
668 that their structure is generalizable. Descriptions of thermal responses (devel-  
669 opment of the various life stages, reproduction), of movement, of interactions  
670 between individuals in competition for resources, and other key processes are  
671 common to most species. The details (life history strategies, number of life stages,  
672 developmental parameters, the most influential factors) vary between species. The  
673 object-oriented programming paradigm underlying IBMs allows for re-use and  
674 straightforward modification of model structures.

675 But the IBM approach to disturbance ecology is far more broadly generaliz-  
676 able. Our model deals with individual insects and trees. In the same manner, a dis-  
677 turbance model can focus on forests as collections of individual stands, each with  
678 its specific traits (size, composition, age, damage level, treatment history, spatial  
679 location). In the end, no matter the modeling approach used, the requirements for  
680 detail and data are directly proportional to the specificity of the questions being  
681 asked, and the degree of precision required of the answers.

## 682 **6.9 IBM as a Scaling Strategy for Insect Disturbance** 683 **Modeling**

684 The IBM approach used here provided a simple framework for integration across  
685 temporal and mechanistic scales. It allowed us to predict MPB population growth  
686 rates, which depend on extreme cold temperatures (at the hourly/daily scale),  
687 nonlinear developmental responses to temperature (at the weekly/monthly scale),  
688 effects of developmental variability (at the seasonal scale) and accumulation  
689 of population momentum to become a full outbreak (at the multi-yearly scale).





690 Description of processes at the scale of individual beetles allowed us to model  
691 emergent properties at broader scales resulting from superposition of individuals,  
692 without pre-ordained or coerced aggregative effects.

693 Our IBM is nonspatial. It operates at the scale of a forest. Individual trees  
694 within the forest are represented however, and the model could therefore include  
695 tree-level effects such as individual host demography, stress history, and moisture  
696 availability. It may be possible to combine the developmental, survival, and repro-  
697 ductive processes included in our model with those describing the kairomonal  
698 interactions underlying the swarming behavior of adult MPB in another IBM  
699 developed by Perez and Dragicevik (2011). However, as pointed out by Powell  
700 and Bentz (2014), spatially explicit prediction at the tree scale is unrealistic. Data  
701 demands that would allow for accurate predictions from mechanistic models  
702 increase exponentially as the scale of prediction decreases. These data demands  
703 include a complete demography and stress status for all trees across a landscape,  
704 and microclimate variables that dictate the shape and directions of odor plumes  
705 from individual host trees. Assuming that pattern prediction at the tree scale is not  
706 required, the IBM approach provides an efficient way to assess the impact of host  
707 demography and stress on MPB outbreaks at stand scale.

708 At a broader scale, the IBM presented here could easily be adapted to include  
709 dispersal of MPB in a matrix of stands comprising a forest or landscape. The cur-  
710 rent limitation on numbers of successful attacks, Eq. (6.3), would need replacing,  
711 since it is the spatially implicit resolution of a spatially explicit process (searching  
712 for new hosts). The situation is analogous to the relationship between an earlier  
713 stand-level outbreak model (Powell and Bentz 2009) and a more recent spatially  
714 explicit outbreak model (Powell and Bentz 2014). Rather than predict a success-  
715 ful search probability within the stand using Eq. (6.3), MPB in a spatial model  
716 must be allowed to disperse from their source stands, whereupon their success in  
717 exceeding attack thresholds can be assessed.

718 The question of how to disperse beetles accurately is not straight forward. In  
719 a simple cellular automaton setting, a constant fraction of beetles can be allowed  
720 to move between adjacent cells. In fact, some large-scale regression approaches  
721 (e.g. Aukema et al. 2008) include the impact of nearby cells and could be used  
722 to parameterize a cellular dispersal model. A more complicated approach would  
723 be to disperse individual beetles in the IBM according to a dispersal kernel, as  
724 was parameterized by Heavilin and Powell (2008). Individual dispersal distances  
725 are generated as samples from the dispersal kernel, which allows for accurate  
726 resolution of dispersal independent of model structure. This differs from a cel-  
727 lular automaton, which inflicts its gridded structure on model results. A more  
728 nuanced dispersal approach is based on ecological diffusion (Powell and Bentz  
729 2014) and includes the effects of available hosts, which serves to slow down  
730 beetle movement in some patches, and presence of non-host areas through which  
731 beetles disperse much more rapidly. Regardless of dispersal specifics, spatial  
732 waves of killed trees will progress from patch to patch as local susceptible hosts  
733 are exhausted and locally produced brood are exported to nearby cells. Exact  
734 rates of dispersal will depend on the precise details of the dispersal mechanism



735 and density of susceptible host trees, similar to other epidemiology models  
736 (Heavilin et al. 2007).

737 At still larger scales, IBMs offer an opportunity for resolving unlikely disper-  
738 sal events with potentially large consequences, as in the dispersal episode that  
739 led to MPB crossing the Rockies from BC to Alberta (de la Giroday et al. 2012).  
740 In deterministic spatial modeling approaches it is very difficult to resolve a low-  
741 probability event such as long-distance dispersal via storm cells. In a determin-  
742 istic model of outbreak progression, low-probability events would become small  
743 magnitude certainties driving unrealistically rapid outbreak propagation. However,  
744 in an IBM, low-probability events are resolved as infrequent samples of individu-  
745 als. Low-probability events appear as tails in a distribution in deterministic mod-  
746 els, but in an IBM low-probability events are samples of mostly zero. When an  
747 event that could trigger an outbreak occurs however, individual beetles could be  
748 dispersed realistically to distant locations, allowing an IBM to simulate continen-  
749 tal-scale events.

750 The drawback of IBMs in space is the sheer computational scale of keeping  
751 track of individuals. IBMs lend themselves to parallel approaches, particularly for  
752 a system such as MPB where the critical effects of temperature on the popula-  
753 tion are all projected onto individuals independently, and relevant calculations can  
754 occur in parallel. However, continental landscapes involve millions of hosts that  
755 produce tens of thousands of beetles. Even with a “super-individual” approach, an  
756 overwhelming number of objects must be tracked. The continental-scale maps that  
757 we prepared here do not constitute a true scaling-up of the MPB outbreak process,  
758 as model runs were completely independent of one another from location to loca-  
759 tion. At least for the near future, explicit spatial modeling of MPB outbreaks with  
760 IBMs is likely to be restricted to forest scales.

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