Chapter 6
Individual-Based Modeling: Mountain Pine Beetle Seasonal Biology in Response to Climate

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Contents

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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

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

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

Issues surrounding the effects of climate on the distribution and performance of species have been investigated by a range of methods, including correlative approaches such as climate matching or species distribution modeling (Elith and Leathwick 2009) that correlate presence/absence observations with climatic and geographic variables and extrapolate the results to novel regimes. Mechanistic approaches include more detailed (if less comprehensive) process modeling (Sutherst and Bourne 2009; Régnière et al. 2012a). In this chapter, we present a prototype mechanistic IBM that describes in detail the fitness (population growth rate) responses of MPB to temperature, based on understanding of the 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.

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 glyc-
110 erol 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).

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;

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

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

6.3.1 Objects

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

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

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

6.3.2 Development, Reproduction, Variability

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

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

6.3.3 Survival

A constant "attrition" rate s, representing all mortality not specifically described, is applied at the creation of new eggs. The main cause of dynamic mortality in the model is exposure to cold. All eggs, pupae, and teneral adults are assumed to be killed as soon as temperature drops below -18 ℃. Larval cold tolerance is modeled following Régnière and Bentz (2007). The probability distribution of cold tolerance is a population trait that varies over time in response to temperature. The proportion of the larval population in one of three states, each with its SCP distribution, is calculated from the daily series of minimum/maximum temperatures. A composite distribution of SCP is compiled each day. Probability of cold mortality is based on this distribution and daily minimum temperature. The maximum mortality rate experienced by larvae is applied to each super-individual at the end of larval development.

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

6.3.4 Attack

The beetle population is initialized using a Gaussian distribution of attacks over time on the forest's defenseless focus trees. Mean date (t_0) and standard deviation (σ_0) of the initial attacks are specified as inputs. The number of females per m² of bark in this initial attack is $n_0 + a_{\max}(F_0 \times F_d - 1)$, so that when a single focus tree ($F_0 = 1/F_d$) is used, the model simulates an incipient outbreak with an initial density of n_0 females m⁻² of bark. Females in the initial attack lay eggs, generating the brood adults that will attack new host trees at emergence.

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

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

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

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

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

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

The daily number of attacking beetles killed by tree defenses is

$$A = a_0 F_a, \tag{6.3}$$

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

6.4 Calibration/Validation

6.4.1 Seasonality of Adult Emergence

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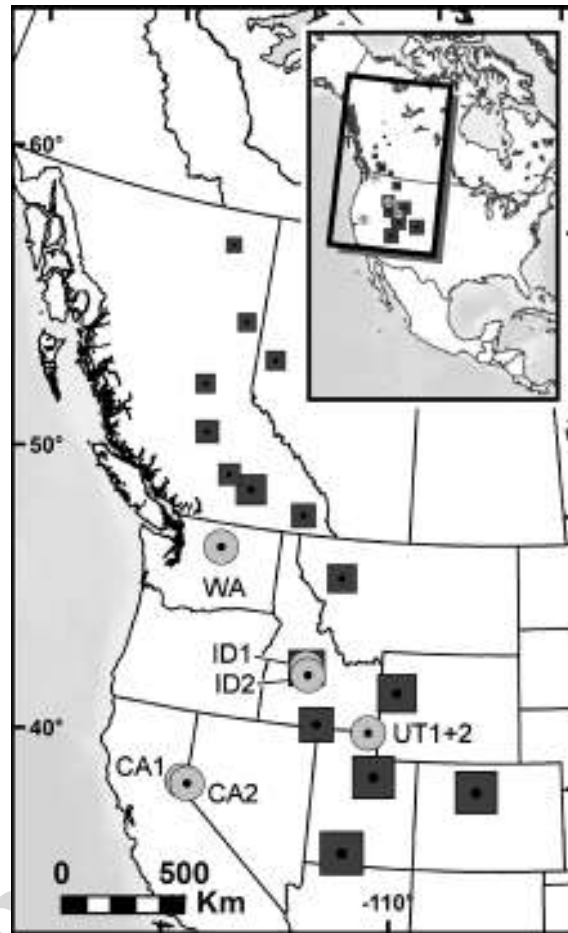

276   Our model requires as input daily minimum and maximum temperatures,
277 and these were extracted from the observed hourly temperature records. We
278 calculated bark temperatures by averaging north- and south-aspect daily mini-
279 mum and maximum observations and developed a phloem microclimate 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
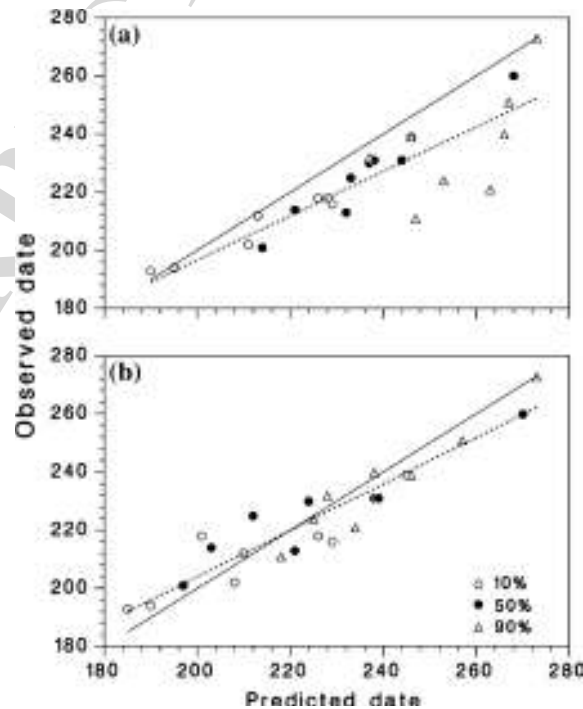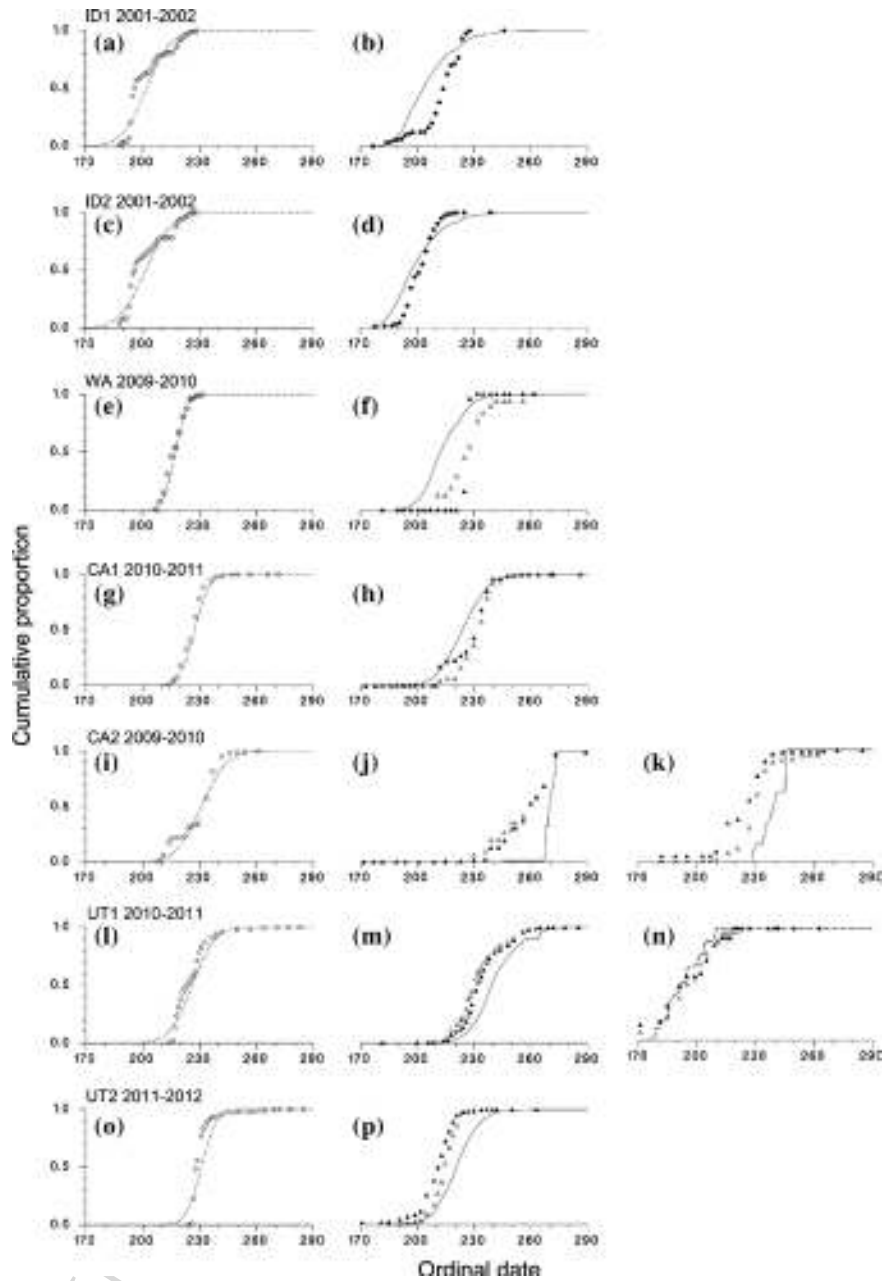
Fig. 6.3 Comparison of observed and simulated mountain pine beetle emergence in seven locations and years. The figure is divided in three columns. On the left are the observed (*white circle*) and Gaussian (*dotted line*) attack patterns (model input) for each plot-year. In the center are the observed (*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

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

6.4.2 Fitting to Observed Annual Growth Rates

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

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

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

This provided a means to complete our time series of daily minimum and maximum phloem temperature to cover the period 1986–2010.

Using this daily minimum and maximum phloem temperature time series as input, the model was run in outbreak mode, using a simulated annealing algorithm to estimate the value of the attrition survival parameter ($s = 0.43$) and initial infestation size in 1986 ($F_0 = 0.03$ km^2) on the basis of minimum sum of squared deviations between observed and simulated total forest area killed over time. Other parameter values were fixed ($F_s = 2800$ km^2; $F_d = 75{,}000$ trees km^{-2}; $a_0 = 5$ attacks day^{-1} m^{-2}; $a_{max} = 120$ attacks m^{-2}; $T_e = 18$ °C; $N_0 = 60$ attacks; $t_0 = 200$, $\sigma_0 = 5$ days, and $\alpha = 40$).
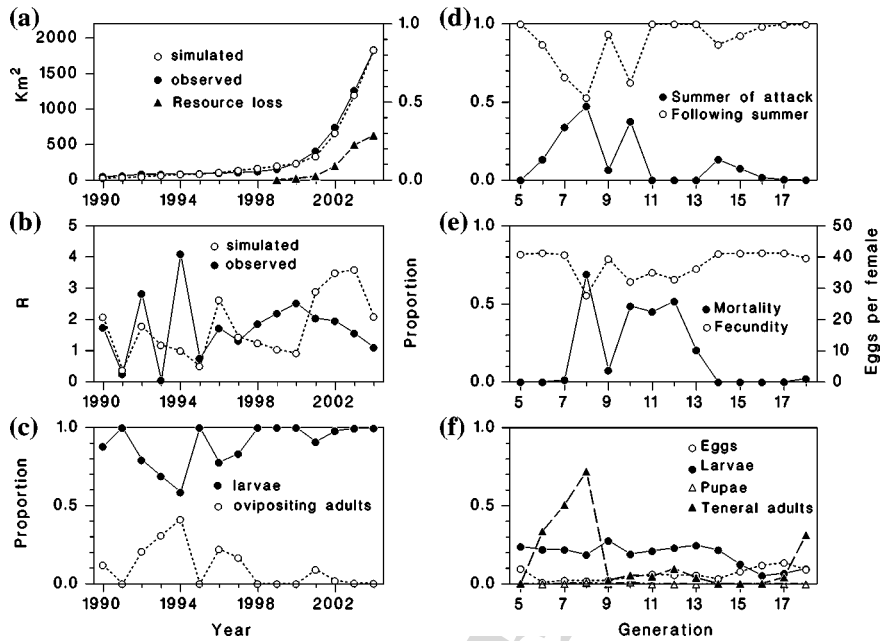
Fig. 6.4 Observed (*white circle*) and simulated (*black circle*). **a** Infestation size (also, value of survival from resource-loss S_l *black triangle*); **b** annual infestation growth rates; **c** proportion of overwintering individuals in larval stages (*black circle*) or as ovipositing adults (*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

The resulting predicted and observed cumulative forest mortality (km^2) were highly correlated ($r = 0.997$; Fig. 6.4a). The annual outbreak area growth rates (Fig. 6.4b), however, were not significantly correlated with the simulated annual growth rates of successful attacks ($r = 0.12$, $P = 0.67$; Fig. 6.4b), although average observed (1.733 ± 1.014) and simulated (1.757 ± 1.006) growth rates were nearly identical ($P = 0.95$). The model is set up to assume an exact correspondence between the number of successful MPB attacks and tree mortality because the density of successful attacks per tree is constant, all trees are equally likely to be attacked and killed, and there is no spatial variation in tree density. In nature, none of these are constant, and deviations between beetle population performance and tree mortality rates may vary accordingly. Growth rates were significantly reduced by resource-loss in the last 2 years of the simulated outbreak through Eq. (6.1), as the total area killed (F_k) approached total forest size, estimated here at $F_s = 2800$ km^2 (black triangle in Fig. 6.4a). Model results indicate that most individuals 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 ($0.03 \text{ km}^2 \times 75,000 \text{ trees km}^{-2} = 2250$ 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 % ($a_0/a_{max} = 5/120$).

6.5 Model Behavior

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^2 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 $T_e = 18$ ℃. 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 ℃.
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
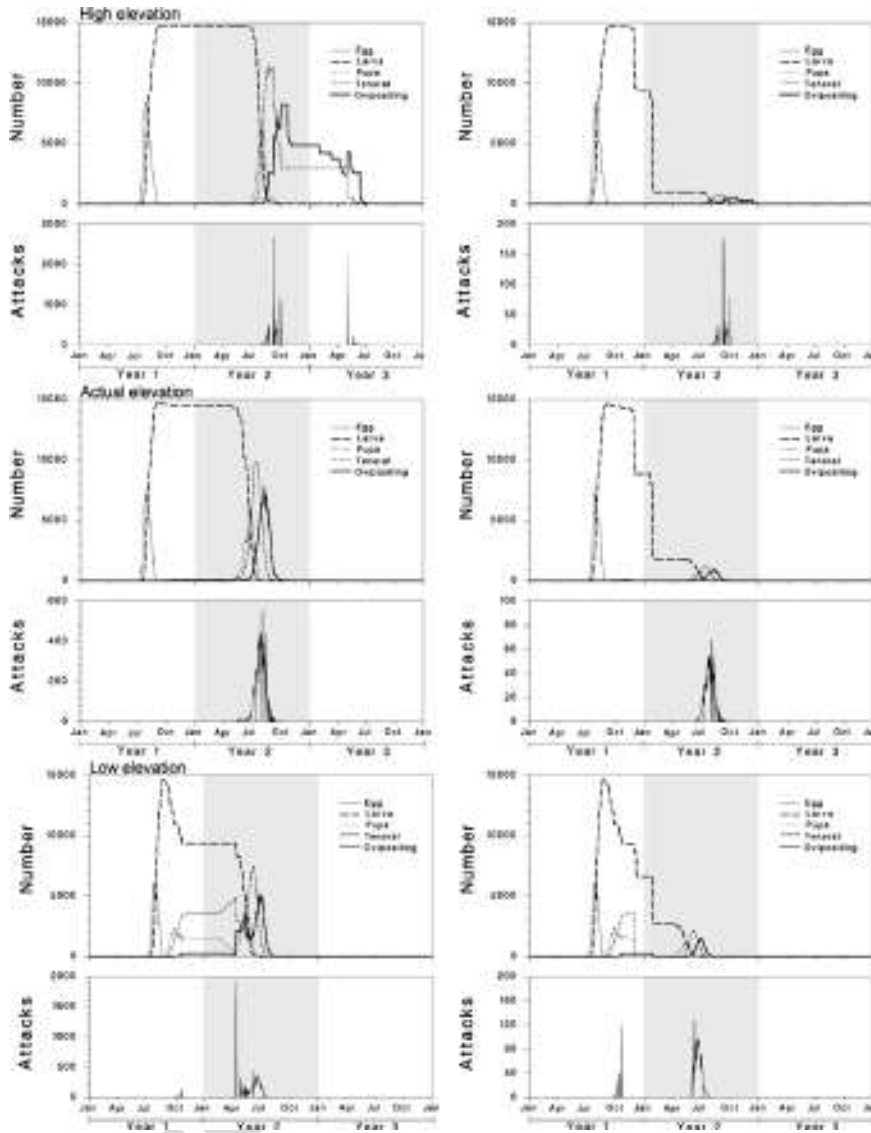
Fig. 6.5 Predicted life stage frequencies and attack timing following a Gaussian initial attack centered on July 17 (day 200 ± 5 days). Temperature was estimated for three elevations at the latitude and longitude of Jasper, Alberta, Canada (52.88°N, −118.07°E): 1500 m (*top row* of 4 panels), 1062 m (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, resulting
416 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).

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

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

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

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

The modeled changes in MPB survival and recruitment rates over time and space described here were caused by corresponding changes in observed thermal regimes, in particular extreme minimum and mean annual temperatures (Fig. 6.6k, l), and to a lesser extent mean maximum temperatures (Fig. 6.6m). There was also a slight increase in precipitation over the years (Fig. 6.6n), but because of a gradual increase in mean annual temperature this did not translate to a change of aridity, calculated as the annual sum of monthly differences between potential evapotranspiration and precipitation (Fig. 6.6o).
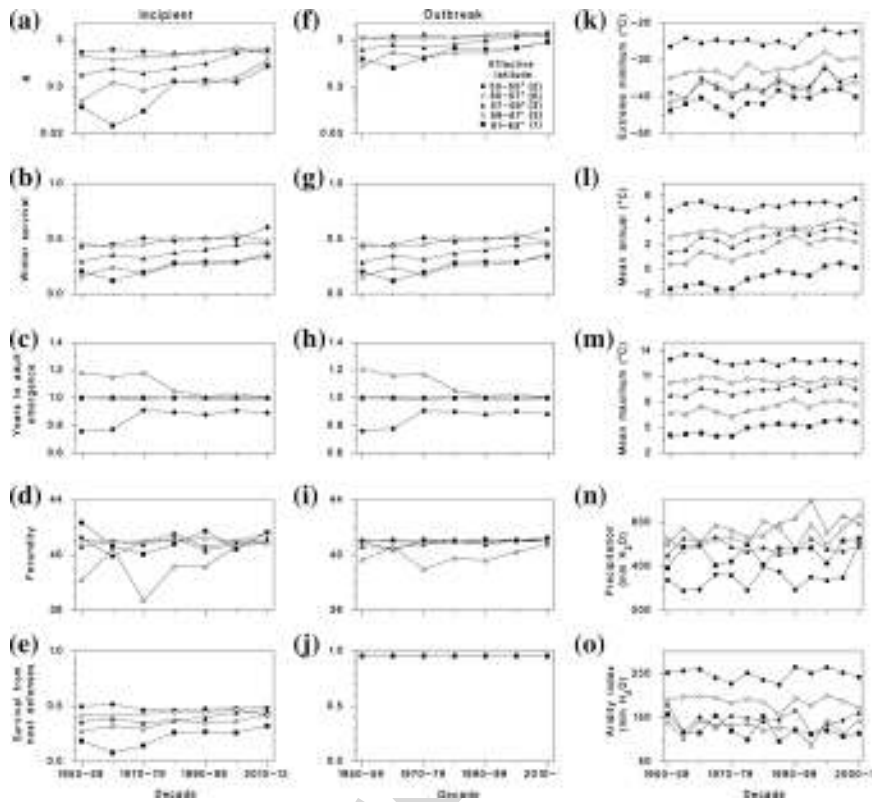
Fig. 6.6 Decadal average model inputs and outputs in incipient and outbreak modes for an array of 15 locations in western North America over the period 1951–2012. Sites grouped into five effective latitude classes of 2° (number of sites per class in parentheses). *Left column* incipient mode. *Center 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

6.6 Climate Change

Simulated past and future (1961–2100) daily minimum and maximum temperatures on a 201 × 193 grid over North America were obtained from the Canadian Regional Climate Model (CRCM) version 4.2.0 runs ADJ and ADL (Music and Caya 2007). These runs are based on the Intergovernmental Panel on Climate Change (IPCC) A2 emissions scenario (IPCC 2007), which has been realistic thus far given actual emissions estimates (Raupach et al. 2007). The IPCC A2 is intermediate between Representative Concentration Pathway RCP6 and RPC8.5 scenarios (IPCC 2013).
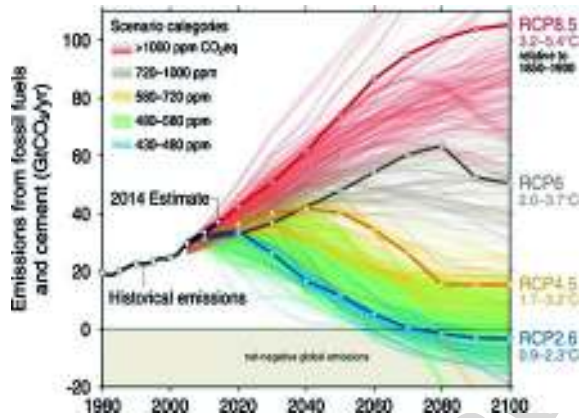
501 From these data, 30-year normals were computed for several decades in
502 the interval 1961–2050, and the "delta" method (differences between modeled
503 decadal normals and the reference 1981–2000) was used to generate unbiased dec-
504 adal sets of 30-year normals into the future. We used as model 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.
516 gov/srtm/version2_1/SRTM30/; Accessed 6 January 2015). Because of the sto-
517 chastic nature of the model and of weather inputs when generated from normals,
518 each model run was replicated 10 times, and model output was averaged over rep-
519 licates and years. From these averaged outputs, maps were generated by universal
520 kriging with elevation provided by the input DEM as external drift variable. Log
521 population growth rates were used for interpolation. Model output was masked
522 using polygons that estimate the twentieth century distributions of pine habitat in
523 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
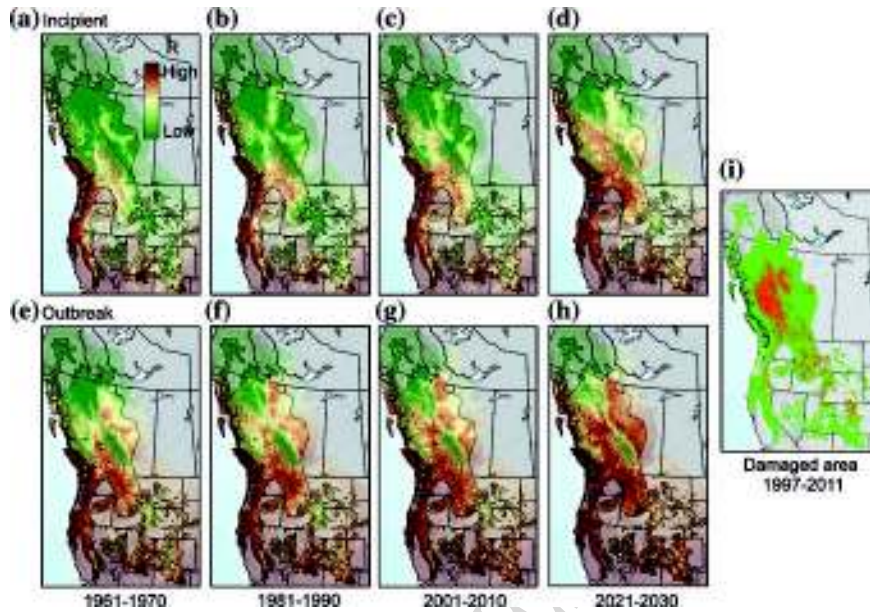
Fig. 6.7 Incipient (**a–d**) and outbreak (**e–h**) population growth rates during 1961–1970 (**a**, **e**), 1981–1990 (**b**, **f**), 2001–2010 (**c**, **g**), and expected in 2021–2030 (**d**, **h**). **i** Map overlaying areas affected by mountain pine beetle in western North America, 1997–2011 (*red*) 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

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

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

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

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

6.7 Modeling Conclusions

Our integrated model of phenology and cold tolerance provides a tool to evaluate climate influences on the invasiveness of MPB, a native insect limited in distribution by climate. Simulations illustrate important consequences of climate on MPB dynamics. When run across a latitudinal gradient, winter survival and the
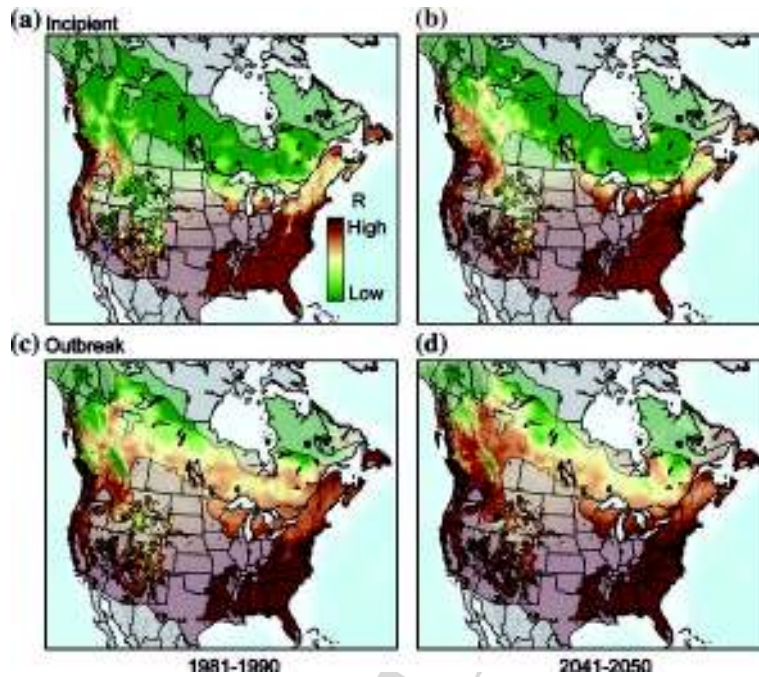
Fig. 6.8 Incipient (**a**, **b**) and outbreak (**c**, **d**) MPB population growth rates during 1981–1990 and expected in 2041–2050 in North America north of Mexico. Model output is masked with the twentieth century distribution of all pine species (U.S. Geological Survey 1999)

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

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

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

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

6.8 IBM as Generalized Modeling Approach for Insect Disturbance Modeling

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

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

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

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

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

6.9 IBM as a Scaling Strategy for Insect Disturbance Modeling

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

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

At still larger scales, IBMs offer an opportunity for resolving unlikely dispersal events with potentially large consequences, as in the dispersal episode that led to MPB crossing the Rockies from BC to Alberta (de la Giroday et al. 2012). In deterministic spatial modeling approaches it is very difficult to resolve a low-probability event such as long-distance dispersal via storm cells. In a deterministic model of outbreak progression, low-probability events would become small magnitude certainties driving unrealistically rapid outbreak propagation. However, in an IBM, low-probability events are resolved as infrequent samples of individuals. Low-probability events appear as tails in a distribution in deterministic models, but in an IBM low-probability events are samples of mostly zero. When an event that could trigger an outbreak occurs however, individual beetles could be dispersed realistically to distant locations, allowing an IBM to simulate continental-scale events.

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

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