Predicting the risk of mountain pine beetle spread to eastern pine forests: Considering uncertainty in uncertain times

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A B S T R A C T

Since the mountain pine beetle (MPB) breached the Rocky Mountains and first appeared in the province of Alberta, Canada, in alarming numbers in the summer of 2005, it has spread eastward across Alberta at an average rate of 80 km/year. In the absence of aggressive control, the beetle will undoubtedly continue to spread eastward. The spread rate is expected to slow as the leading edge invasion front moves further from significant population sources in the dense pine of the Rocky Mountain foothills into the scattered pine of the boreal plains region. However, the realized rate of spread is uncertain, as it will be regulated by a number of factors, some of which are uncertain (e.g. how an insect behaves in a novel environment), inherently unpredictable (e.g. weather), or under human control (e.g. spread control efforts). Whereas previous studies have examined factors affecting spread individually, we present a synthetic framework that models future spread rates as a function of coupled nonlinear recruitment dynamics that arise from the distinct population phases of MPB, and correlated thermal response functions that are characteristic of the influence of climate and climate change on ecosystem processes. We analyzed the model's behavior under two climatic driving scenarios (drying climate and warming climate) and one forest health scenario (an increase in the ratio of stressed to vigorous trees), with the hypothesis that these scenarios would produce unanticipated outcomes in the severity and timing of beetle outbreaks. Our results showed a classic “tipping-point” model capable of generating sudden, unanticipated behavior, demonstrating that MPB populations may respond very strongly to small changes in climate. The MPB may be the first of many systems to behave in unprecedented ways. The model makes clear that the eastward rate of spread will depend on whether, when, and where the system transitions from the current epidemic state to a new endemic state. However, major uncertainties in the system limit our ability to make robust predictions of spread under natural conditions. The integrating framework presented here provides insight into scientific uncertainties worth targeting for applied research into spread management. In the absence of ability to predict beetle spread, forest management should continue to explore ways of coping with unpredictable disturbances, including adaptive capacity to adjust to transformational ecosystem changes expected under climate change.

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1. Introduction

The mountain pine beetle (Dendroctonus ponderosae Hopkins; hereafter MPB) is an eruptive herbivore native to the pine forests of western North America (Safranyik and Carroll, 2006). Periodic outbreaks cause widespread tree mortality, especially to lodgepole pine (Pinus contorta Dougl. ex Loud. var. latifolia Engelm.) in British Columbia (BC), although most species of Pinus have proved to be adequate hosts. The recent outbreak first became apparent in BC in the late 1990s (Aukema et al., 2006). By 2011, >700 million m³ of trees spread over 18.1 million ha of pine forests had been killed. This represented approximately 50% of the total merchantable pine volume in the province (Walton, 2012).

One of the most remarkable aspects of the current MPB outbreak has been the rapid range expansion into forested areas north and east of the insect’s historical range. It is thought that adult beetles from high-density populations within the historical range dispersed above the canopy into susceptible forests (de la Giroday et al., 2011) previously undisturbed by MPB because of unsuitable climate (Safranyik et al., 1975; Carroll et al., 2004). This dispersal event breached a major geographic barrier, the Rocky Mountains (Robertson et al., 2009; de la Giroday et al., 2012), and there are no obvious barriers to continued range expansion as far as the east coast of North America (Safranyik et al., 2010). Long-range dispersal on the order of hundreds of kilometers is unusual but not unprecedented, as similar flights were reported in the late 1970s, with MPB dispersing from the southern Rocky Mountains across the southern grasslands region as far as the Cypress Hills of southeastern Alberta and southwestern Saskatchewan (Hiratsuka et al., 1982). The current situation, however, is novel, in that the newly infested forests in the north are not isolated pine stands within a large prairie region, but part of a contiguous forest stretching eastward and northward across Canada and the US. Consequently, pine trees throughout the entire northern forest are at risk of new ecological disturbance from the effects of MPB infestation (Nealis and Cooke, 2014).

In 2005, the province of Alberta began an annual program to detect and eliminate MPB populations along the presumed leading edge of the invasion, with the intention of reducing further spread. In spite of the ambitious program, annual tree mortality increased, most notably within the forest zone where lodgepole pine and jack pine (Pinus banksiana Lamb.) hybridize. In 2007, the Canadian Forest Service completed an emergency risk assessment addressing the threat of MPB to Canada’s boreal and eastern pine forests (Nealis and Peter, 2008). The assessment concluded that few biological impediments existed to the expansion of MPB range into these new forests as long as weather conditions permitted its survival. Although climate and forest conditions in these new areas were considered less suitable for MPB than those in the historical range, the assessment determined that MPB populations would persist indefinitely and continue to expand their range, with a high potential for significant disturbance to forests with no similar ecological experience. By 2010, genetic evidence had confirmed, as Cerese (1995) had predicted, that MPB was successfully attacking and reproducing in pure jack pine, the dominant pine species of the boreal forest (Cullingham et al., 2011). The ecological bridge to eastern pine forests had been established. As a result, there was growing concern, in both scientific and public forums, about what this meant for the rest of the boreal and eastern pine forest.

Considerable research on MPB ecology and population dynamics has shown that the MPB population system responds strongly and nonlinearly to thermal conditions, including (1) changes in temperature (Logan and Powell, 2001; Powell and Bentz, 2009; Preisler et al., 2012), (2) spatial variations in synoptic climatic conditions (Carroll et al., 2004; Bentz et al., 2010), and (3) climatic fluctuations occurring throughout the Holocene (Brunelle et al., 2008). The system is regulated by “cross-scale drivers”, whereby small changes in “fast” processes at the local scale can amplify, producing large consequences to “slow” processes operating at the landscape scale (Raffa et al., 2008). Indeed, there is clear evidence that insect-caused forest disturbance can serve as a “tipping element” (Lenton, 2013) affecting Earth’s climate, by causing
forests to switch from a terrestrial sink for carbon to a source of atmospheric CO₂, with clear consequences for global climate change (Kurz et al., 2008; Maness et al., 2013). In addition, evidence suggests that forest structure can influence the dynamics of MPB population growth (Safranyik et al., 1974; Amman and Cole, 1983; Preisler and Mitchell, 1993; MacQuarrie and Cooke, 2011; Sims et al., 2014) and spread (Safranyik et al., 1989, 1992; Heavilin and Powell, 2008; Seidl et al., 2016), implying a reciprocal insect–forest negative feedback loop, in addition to the reciprocal insect–climate positive feedback loop.

Recent research has further confirmed that MPB range expansion in BC has been driven largely by 20th century warming (Carroll et al., 2004; Sambaraju et al., 2012). At the same time, the amount of susceptible forest has also been increasing over the 20th century, with a tripling of pine volumes due to natural growth, fire suppression and selective logging favoring the removal of Douglas-fir and spruce (Taylor and Carroll, 2004), as well as precipitation-driven decreases in wildfires (Meyn et al., 2013). Thus, the independent contribution of warming and increasing pine forests to the extent and intensity of the BC outbreak is not entirely clear. Furthermore, detailed MPB population studies in Canada have shown that the intrinsic dynamics of eruption are similar to the positive density-dependent mechanisms first elucidated by Raffa and Berryman (1983): for an established endemic population to erupt, the beetles must aggregate in sufficient numbers to overcome host tree defenses (Boone et al., 2011). Factors that influence the distribution and vigor of host pine trees can therefore be expected to influence population growth and spread rates.

The rapid changes in the distribution of MPB east of the Rocky Mountains, together with the significant investments made by forest managers in response to the epidemic, raise important questions: what happens next, and how should we respond? The matter is urgent, as MPB is no longer solely a commercial pest management problem. As the MPB poses a real, if not imminent, threat to the eastern white pine (Pinus strobus L.) (Safranyik et al., 2010) and other highly valued eastern pine species, a response under legislation (e.g. Canada’s Plant Protection Act) may become necessary. However, in dealing with a native invasive species, there are legal considerations concerning jurisdiction and whether, when, and how to apply the provisions of the Act to protect these pine species.

The emergency risk assessment by Nealis and Peter (2008), and an update by Nealis and Cooke (2014), were prepared under considerable time pressure to satisfy urgent demand for an appraisal of the MPB threat to the eastern boreal pine forests. These reports examined risk factors for spread individually, without considering the role of nonlinear process interactions among factors, which can precipitate unanticipated outcomes in population dynamics and spread rates. In this paper we present a synthetic framework that models future spread rates across Canada as a function of coupled nonlinear recruitment dynamics that arise from the distinct population phases of MPB, and correlated thermal response functions that are characteristic of the influence of climate and climate change on ecosystem processes. Whereas previous studies have examined MPB spread risk factors individually, we attempt to provide a synthetic perspective on the role of synergistic nonlinear process interactions in expected rates of population growth and spread. This integrating framework provides insight into scientific uncertainties worth targeting for applied research into spread management.

2. Methods

There are two major considerations in any epidemiological monitoring and forecasting problem: (1) ascertaining the status of the system (i.e., the “initial conditions” provided to any simulation model), and (2) determining, through observation and experimentation, the dynamic rules by which the system states evolve.

2.1. System status

2.1.1. Forest tree species and volume data

The distribution of lodgepole and jack pine was first reported by Little (1971). However, the two species hybridize readily, and the hybrids are difficult to distinguish from the pure species (Wheeler and Guries, 1987; Bleiker and Carroll, 2011). Consequently, Cullingham et al. (2012) developed a statistical model, based on tree genetic data, to robustly parameterize the spatial distribution of the two species and their hybrids in the province of Alberta.

Forest inventory practices vary among provinces of Canada. Commercial-grade inventories in Alberta, which do not span all forested portions of the provinces, are considered a proprietary resource. A national-scale data set compiled by Yemshanov et al. (2011) attempts to harmonize some of these major spatial inhomogeneities in inventory coverage, by hybridizing accurate, low-resolution timber inventories with land surface data that are imprecise, but benefit from extensive remote sensing data. The resulting estimate of pine volumes were used as a basis for gauging assets at risk of MPB attack.

2.1.2. Insect survey data

Forest pest surveys were conducted annually by the Forest Insect and Disease Survey (FIDS) unit of the Canadian Forest Service until 1995, using fixed-wing aircraft and a sketch-mapping surveyor to delineate affected polygons and to rate damage levels within these. In 1997, provincial governments took over the responsibility for conducting MPB surveys, and the survey methods diverged accordingly. In BC, where the MPB outbreak had already begun, the BC Ministry of Forests, Lands and Natural Resource Operations employed traditional FIDS methods. In Alberta, which had a “zero tolerance” policy for MPB until 2005, helicopters equipped with global positioning systems (GPS) were used to accurately locate individual clusters of attacked trees, often consisting of a single tree. The Alberta survey data are therefore much more accurate both in terms of spatial georeferencing and infestation levels. Although both provinces aspired to complete provincial coverage, both data sets are subject to undocumented spatial and temporal variations in survey effort. However, when considered over broad spatial scales, these data have been shown to be reliable for large-scale inferences (Aukema et al., 2006; Chen et al., 2015).

When points are represented as pixels in digital maps, pixel representation error can be quite significant when the map scale is broad. A single tree displayed as a single pixel in a 1 megapixel map covering Alberta constitutes a 10 000-fold representation error. As a result, when Alberta point attack data are posted as pixels alongside the BC polygon data, they grossly exaggerate the apparent impact of MPB in Alberta. Such maps are adequate to delineate the approximate distribution of MPB, but inadequate to assess relative impacts in the two provinces. To provide an unbiased perspective on MPB damage in the two provinces, the two data sets were rasterized to a common resolution, allowing impact to be expressed in common units (hectares attacked per 4 km² cell). For BC data, raster cells were weighted according to polygon-wide average infestation rates and areas calculated from the proportion of a polygon infested within each raster cell, assuming an average stem density of 1125 mature stems per hectare, which is typical for beetle-prone lodgepole pine stands (Shore and Safranyik, 1992; Whitehead and Russo, 2005). Data were weighted and calculated for each year in the sequence, and then summed. For Alberta data, the number of attacked trees per point
attack cluster was determined from provincial government records, based on a ground survey, and summed across years within each 4 km² raster cell.

2.2. System dynamics

2.2.1. Current rate of range expansion

For each year of infestation, starting in 2001, the leading edge of the invasion front was defined using a heuristic method developed by operational pest managers (see Nealis and Cooke, 2014). We estimated linear rates of MPB range expansion along two axes, extending from Pine Pass, north of Prince George, BC, (1) north through the Rocky Mountain Trench in BC, and (2) east through the Rocky Mountains into the Slave Lake region of Alberta. These transects ran perpendicular to the radial pattern of range expansion, thus simplifying the task of identifying annual rates of frontal advance (in kilometers per year).

2.2.2. Historical trends in climatic suitability

Safranyik et al. (2010) provided maps of three indices of MPB climatic suitability originally presented in Nealis and Peter (2008). They are (1) an index of seasonality (“L,” Logan et al., 2003), (2) an index of winter survival (“R,” Régnière and Bentz, 2007), and (3) a composite index of summer and winter climatic suitability (“S.” Safranyik et al., 1975; Carroll et al., 2004). Details of computation can be found in the original articles. We illustrate temporal variations in these indices across BC and Alberta, by computing them for five-year increments going back a century. The computations were performed using BioSIM, a standard tool employed to generate spatial maps of MPB climatic suitability (Logan et al., 2003; Safranyik et al., 2010; Bentz et al., 2010). Here, we are interested in low-frequency (i.e. decadal-scale) trends associated with global climate warming and high-frequency (i.e. annual) variability, especially during the development of the current outbreak over the past two decades. Weather perturbations and climate change would then serve as “fast” and “slow,” respectively, vertical deflections in the population recruitment curves described below.

2.2.3. Factors likely to affect future spread

Rates of invasive spread are determined jointly by dispersal rates and population growth rates post-dispersal, each of which are governed by multiple intrinsic and extrinsic factors, including host tree interactions (at tree, stand, and landscape scales) and weather and climate (as outlined above).

2.2.3.1. Dispersal

Aided by wind, MPB can disperse hundreds of kilometers (Jackson et al., 2008), if compelled to do so by population status and stand conditions (Powell and Bentz, 2014). Although dispersal propensities and distances in jack pine may change from those observed to date in lodgepole pine in western Alberta, a greater consideration is whether absolute population densities (number of MPB per hectare) available for dispersal are reduced considerably from the high-volume lodgepole pine of the foothills of western Alberta to the jack pine of the boreal plains region of eastern Alberta. A 10-fold reduction in available trees per hectare should, for example, lead to a 10-fold reduction in the number of insects engaging in long-range dispersal. Therefore, pine volume (mapped as described above) was considered a major risk factor governing the potential for population dispersal and invasive spread.

2.2.3.2. Growth

There is now considerable evidence that growth dynamics vary considerably depending on beetle population densities (Carroll et al., 2006; Boone et al., 2011), weather (Powell and Bentz, 2009), climate (Preisler et al., 2012), and host tree status (Clark et al., 2010; Cudmore et al., 2010). Consequently, we employed a minimalist intrinsic growth model to evaluate the predictability of spread rates under a relatively narrow range of realistic extrinsic microclimatic forcing scenarios (Fig. 1). We hypothesized that the nonlinear dynamics characteristic of MPB populations, coupled with multiple correlated environmental sensitivities (e.g. temperature and drought), would be sufficient to produce eruptive growth in response to relatively mild fluctuations in weather or climate. Our simple baseline model of intrinsic population regulation was inspired by Berryman (1979), who suggested that MPB eruptive dynamics could be described by nonlinear density-dependent recruitment curves. These curves would span the endemic and epidemic population states, describing rising recruitment fueled by cooperation at low densities, which gives way to declining recruitment driven by competition at high densities [Fig. 1, curve a; Raffa and Berryman, 1983]. In support of this premise, using direct measures of host procurement success across population densities, Boone et al. (2011) recently confirmed that MPB population growth rates (as indicated by colonization success) tend to increase for low and rising attack densities, whereas MacQuarrie and Cooke (2011) showed that MPB population growth rates tend to decline for higher and rising attack densities. Together, these suggest a strongly nonlinear relationship between population growth rates and attack rates, as originally hypothesized by Berryman (1979).

We revisited the MPB population data of Carroll et al. (2006) from southern BC to determine whether the cooperation effect identified by Boone et al. (2011) spanned a wide range of attacking densities, from the lowest measurable densities to the detection threshold [at which populations are detectable from a standard fixed-wing aerial detection survey, approximately one tree subjected to a successful mass attack per hectare, or 300–600 adult female MPB per hectare (Carroll et al., 2006)]. If MPB exhibit strong positive feedback at this detection threshold, this could help explain sudden eruptive surges in population growth. Strong feed-
back effects would also favor eruptive behavior due to relatively minor environmental perturbations.

2.2.3.3. Synthetic model. Consistent with Berryman (1979, 1999) we posited the existence of an “endemic niche” of stressed trees with recruitment dynamics that would differ from dynamics of vigorous trees in an “epidemic niche,” which are well-defended against low-density beetle attacks [Fig. 1, curve b]. While recruitment in the epidemic niche is modeled as an inverse parabolic function (as described above), recruitment in the endemic niche is posited to exhibit no positive density-dependent cooperation effect (Raffa and Berryman, 1983; their Fig. 11). The probability of outbreak would then be a composite function of the opportunity for beetle populations residing within the endemic niche to successfully switch their attack focus (through either passive spill-over or an active behavioral switch) to vigorous trees within the epidemic niche (Fig. 1). The closer these recruitment curves are to intersecting above the replacement threshold (zero population growth), the greater the chance of outbreak. In this model, environmental perturbations would influence the recruitment dynamics in both

![Image](https://via.placeholder.com/150)

**Fig. 2.** (a) Volume (m$^3$/ha) of all pine species in western Canada. Source: Yemshanov et al. (2011). The approximate distributions of lodgepole and jack pines according to Little (1971) are also shown, as well as the location of first confirmation of successful mountain pine beetle (MPB) reproduction in jack pine (red circle) (Cullingham et al., 2011). (b) Pine species distributions according to genetic markers, as well as MPB locations (Cullingham et al., 2012). The area within North America under consideration is also shown in the inset.
niches simultaneously. Details of model development are provided in Appendix A.

2.2.3.4. Perturbation analysis. After we had calibrated a basic model of intrinsic nonlinearly density-dependent population growth, we undertook a graphical analysis of the model’s behavior to determine its sensitivity to minor perturbations such as mild drying and warming events and trends (see Appendix A). We examined two climatic driving scenarios (drying climate and warming climate) and one forest health scenario (an increase in the ratio of stressed to vigorous trees) – scenarios known to be relevant to MPB ecology and epidemiology (Raffa et al., 2008; Heavilin and Powell, 2008; Powell and Bentz, 2009; Bentz et al., 2010; Preisler et al., 2012). These scenarios were selected to illustrate how the coupled nonlinear process interactions associated with the population-state dependent behaviors of MPB are likely to be a major source of both sudden changes in eruptive behavior and uncertainty in the timing of critical transitions from the endemic to the epidemic state. This is especially true if the perturbations occur synchronously, and each perturbation increases the probability of outbreak associated with saddle-node bifurcation (i.e. an intersection of the endemic and epidemic population recruitment curves when generation recruitment rates exceed replacement).

We hypothesized that the nonlinear recruitment dynamics characteristic of MPB, coupled with correlated thermal response functions (i.e. combined warming, drying, and increasing moisture stress), would be sufficient to make the severity and timing of emergence of eruptive behavior highly unpredictable. More specifically, we predicted that warming, drying, and forest degradation, would result in vertical, nonlinear, and lateral adjustments to the recruitment curves, respectively. These adjustments would be synchronized and would critically influence the unstable eruption threshold (defined as the point where the epidemic niche recruitment curve intersects the horizontal replacement line), thus determining both occurrence and consequences of an outbreak. Alternatively, if MPB recruitment dynamics were only weakly nonlinear, or if they were not responding sensitively and in a correlated manner to climate warming, then the expected rate of population growth and spread would be considerably lower, less stochastic, and less uncertain.

<table>
<thead>
<tr>
<th>Annual displacement (km/year)</th>
<th>Net displacement (km/5 years)</th>
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<tbody>
<tr>
<td>Year</td>
<td>North</td>
</tr>
<tr>
<td>2001–2002</td>
<td>37</td>
</tr>
<tr>
<td>2003–2004</td>
<td>–187</td>
</tr>
<tr>
<td>2004–2005</td>
<td>124</td>
</tr>
<tr>
<td>2005–2006</td>
<td>–106</td>
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<tr>
<td>2006–2007</td>
<td>187</td>
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<td>2007–2008</td>
<td>–15</td>
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<td>2008–2009</td>
<td>38</td>
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<td>2009–2010</td>
<td>150</td>
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<td>2010–2011</td>
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<td>2011</td>
<td>–155</td>
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<tr>
<td>2002–2006</td>
<td>155</td>
</tr>
<tr>
<td>2007–2011</td>
<td>420</td>
</tr>
</tbody>
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* Values in bold highlight exceptional events (see Section 3.1 in text).
* In these eastern plots, some trees (known as “early faders”) were recorded in the same year as attack (i.e. 2009), whereas normally attack cannot be confirmed until the following year.

Fig. 3. Distribution of trees killed by mountain pine beetle in western Canada between 2002 and 2006 (orange) and between 2007 and 2011 (red). Vectors indicate the general linear distance of spread north (A) and east (B) from the leading edge in 2006 (green) to the leading edge in 2011 (red).
3. Results

3.1. Forest and insect distributions

Pine volumes in western Canada are distributed rather unequally. They reach a peak of several hundred cubic meters per hectare in BC, but taper to a minimum through the Athabasca River Valley of central Alberta, where their distribution is very patchy, rising again in eastern Alberta and Saskatchewan (Fig. 2a). By the summer of 2010, pine trees that had been subjected to successful mass attack could be found throughout the jack pine / lodgepole pine hybrid zone of central Alberta (Fig. 2b), isolated stands

Fig. 4. Accumulated tree mortality by mountain pine beetle between 2002 and 2012, and the leading edge of distribution to 2012, based on areas surveyed annually. Because any one survey unit may be affected year after year as beetles attack and kill new trees, summing area damaged per year in severely damaged stands may exceed the actual area of the survey unit. A composite variable, the hectare-year (ha-y), corrects for this artifact of annual mapping of damage by area. One ha-y is 1 ha damaged in one year; thus 100 ha-y could be 100 ha damaged in one year or 10 ha damaged in 10 years, etc. Calculations are per 4 km² (400 ha) units.

Fig. 5. Long-term MPB survival probability (5-year means) and trend lines [i.e. linear regressions (solid and heavy dashed lines); P < 0.05 in all cases] for four climatic suitability indices (mapped in Fig. 7 in Nealis and Peter, 2008) in western Canada (BC and AB). All indices show increasing climatic suitability for mountain pine beetle. Note the strong, steady increase in summer climatic suitability (Logan Probability (L); open squares) and the repeated sequence of warm winters with improved survival since the mid-1980s (Régnieré Cold Tolerance Survival (R); closed squares). A sharp increase in L in the most recent five-year period compensated for a decrease in R, resulting in a sustained increase in the composite index of climatic suitability (closed circles).

Fig. 6. The effect of MPB attack density on ability to successfully overcome tree resistance (data from Carroll et al., 2006). For operational surveys that are initiated at a threshold of one tree that has been subjected to mass attack per hectare, this threshold corresponds to 300–600 attacking females per hectare (shaded rectangle), implying that change in the probability of successful resistance outside this area will be ignored in operational surveys. Data are plotted on logit-log scale, and the intervals are therefore unequal.
of jack pine within the hybrid zone were successfully colonized, and MPB had crossed the Athabasca River Valley, where the sparsest distributions of pine are located (Fig. 3).

The rate of MPB range expansion over the period 2002–2011 was remarkable (Fig. 3). The rate of spread northward and eastward over the five-year period 2006–2010 was particularly rapid, averaging 80 km/year, but dominated by annual jumps exceeding 100 km in 2006–2007 and 2008–2009 (Table 1). The rate of eastern spread over that time varied between 20 and 229 km/year.

The area currently under attack in Alberta is extensive (Fig. 3); however, the intensity of attack is relatively low. When the level of tree mortality in BC and Alberta is expressed in common units of hectares killed per 4 km² raster cell, the difference in impact in the two provinces becomes much clearer, with far greater losses in BC than in Alberta (Fig. 4). Indeed, the rate of attack on the leading edge of the invasion front is so low that in a large-scale coarse-resolution raster data set no impact is discernible. When the leading edge is plotted on the basis of individual point attacks (red line in Fig. 4), there is a perimeter 100 km wide where no impact can be detected. The MPB epidemic has been described in the mainstream media as a “sea of red”; however, this rhetoric clearly does not apply to the situation in Alberta.

3.2. Distribution of favorable climate over time

Two of the three indices of climatic suitability (Logan’s “L” and Safranyik’s “S”) showed a positive trend over the century, with higher than predicted values for most of the period between 2001 and 2010 (Fig. 5). The index of winter climatic suitability (Régnière’s “R”) would have shown a similar positive trend except for the unusually warm winters recorded in 1901–1915. Overall, the geometric mean of the three indices showed both a positive trend over the century and higher than expected values over the period 1991–2010 – the period of the current outbreak (Fig. 5). The composite index varied roughly threefold, from 0.03 in cool years to 0.1 in warm years. Because the indices are calibrated to proportion survival, this can be interpreted as a threefold difference in the eruptive potential of a MPB population.

3.3. Model analysis

3.3.1. Cooperation effect

We found a highly significant, sharply nonlinear relationship between beetle attack density and the ability of a tree to resist attack (Fig. 6; \( r^2 = 0.77 \)). As the density of attackers drops below...
the operational detection threshold of one tree per hectare [corresponding to 300–600 female MPB per hectare (Carroll et al., 2006)], the probability of successful attacks declines sharply from >90% to ≤50. This clearly demonstrates the characteristic cooperation effect of MPB mass attack responsible for eruptive outbreak behavior as shown in other studies (e.g. Safranyik et al., 1975; Berryman, 1976; Raffa and Berryman, 1983; Berryman et al., 1989; Safranyik and Carroll, 2006; Boone et al., 2011).

3.3.2. Synthetic model of eruption

Throughout its native range, MPB occurs most commonly in the endemic state (Safranyik and Carroll, 2006); however, the infrequent epidemic state draws most attention. The synthetic model (Fig. 7 and Appendix A) suggests a number of ways that extrinsic perturbations to the nonlinear dynamics of recruitment may force the system to erupt to outbreak levels. First, if temperatures warm, either temporarily (in the case of weather) or permanently (in the case of climate warming), the vertical shift in the endemic and epidemic recruitment curves leads to an intersection where \( X_n = X_p \) and \( R_p(X) = R_n(X) > 0 \) [i.e. a saddle-node bifurcation (Fig. 7a)], making an outbreak inevitable. A relatively small rate of warming can produce large consequences, with \( X_p \) growing to \( X_p \) facilitating more than a doubling in the number of attacked trees/ha/year. Second, if vigorously growing trees in the epidemic niche suffer compromised defenses, for example under drought conditions, then the nonlinear shift in \( R_n(X) \) to \( R_p(X) \) leads to a similar result, but with \( X_p \) declining very slightly to \( X_p \) (Fig. 7b), ostensibly due to a vigor-related decline in host suitability. Again, such reductions in tree defenses are known to occur, and in fact may well have occurred in southern BC in the early 2000s (Boone et al., 2011). Third, if vigorously growing trees in the epidemic niche are removed from a stand and replaced with suppressed trees in the endemic niche (i.e. forest degradation), then the decrease in competition in the endemic niche and increase in competition in the epidemic niche may be represented as a convergent lateral shift in \( R_n(X) \) and \( R_p(X) \) to \( R_n(X) \) and \( R_p(X) \), which also generates a saddle-node bifurcation (Fig. 7c), precipitating an outbreak. In this scenario, the growth of MPB populations in the enlarged endemic niche is sufficient to ensure that any populations that switch their host preference in the epidemic niche will subsequently erupt to outbreak levels. Again, small extrinsic forcings on a nonlinear growth process may lead to major consequences if the forcings result in critical saddle-node bifurcations where the endemic and epidemic recruitment curves intersect above \( R = 0 \). This point becomes most evident in the scenario in Fig. 7d, in which only modest vertical, nonlinear, and lateral perturbations to the two niches are required to precipitate an eruption (i.e. saddle-node bifurcation at \( R > 0 \)). When only one of the three effects is in play, a considerable perturbation is required to precipitate outbreak (e.g. the magnitude of the shift in \( R_p(X) \) alone required to reach the saddle-node bifurcation as in Fig. 7a). When all three are in play simultaneously, it is much more likely that the gap between the endemic state \( X_n \) and the epidemic state \( X_p \) will be bridged by a saddle-node bifurcation and the elimination of the unstable eruption threshold \( X_e \).

4. Discussion

4.1. Capacity for unanticipated outcomes

According to our model, minor external perturbations—either alone or in combination—to recruitment of MPB to the endemic or epidemic niche lead to very large changes in outbreak probability. The synthetic model presented in Fig. 7 is a classic “tipping-point” model that is capable of generating sudden, unanticipated behavior due to: (1) nonlinear determinacy, (2) multivariate causality, (3) stochasticity, and (4) uncertainty in model parameterization and specification. The model is highly credible, as the baseline recruitment curves are derived from published curves from a large portion of the native range of MPB (MacQuarrie and Cooke, 2011; Boone et al., 2011), and the modeled responses to rising temperature and moisture stress are consistent with previously published models that have been validated (Powell and Bentz, 2009).

Warming, favoring enhanced beetle survival (vertical shift upward), tends to coincide with drying, favoring enhanced low-density attack success (flexing upward at the low end), which in turn may coincide with accelerated shift of mature trees from vigorous to stressed (lateral shift toward convergence and intersection in recruitment curves). Hence, warm, dry conditions tend to lead to a heightened probability of severe outbreak on multiple counts. We contend that the warming trend (Fig. 5) produced an unprecedented level of MPB impact in BC that emerged extremely rapidly over a few years in the early 2000s (Carroll et al., 2004). Such an extreme response to warm weather and a warming climate could not have been foreseen, as an accurate forecast depends on a quantitative understanding of the level of early-stage eruptive positive feedback, as well as the strength of, and correlation among, numerous MPB thermal responses. While models of Safranyik et al. (1975, 1999) may have been sufficient to alert us, at least qualitatively, to the possibility of heavy impacts in BC (Carroll et al., 2004) and of spread to Alberta (Cerezke, 1995; Logan and Powell, 2001), without a valid quantitative growth model no one could have predicted such unprecedented impacts in BC or such a rapid rate of spread over the Rocky Mountains and across Alberta. With the benefit of hindsight provided by several more recent retrospective analyses across western North America (e.g. Carroll et al., 2006; Régnière and Bentz, 2007; Kurz et al., 2008; Cooke, 2009; Powell and Bentz, 2009; Bentz et al., 2010; MacQuarrie and Cooke, 2011; Boone et al., 2011; Preisler et al., 2012; Sambaraju et al., 2012), we have developed a simple, yet comprehensive, synthetic model of the coupling of nonlinear feedback and correlated nonlinear thermal responses.

To the extent that beetles can disperse long distances, this is a system that will produce scale-crossing behavior, precisely as described by Raffa et al. (2008), with “fast” variables that fluctuate annually capable of producing major consequences (e.g. extensive tree mortality) that are irreversible in the short-run. This tends to amplify the spatial scale over which sudden, unanticipated eruptive behavior occurs.

A key feature of the model is the shape of the cooperation curve, which implies that the eruption threshold may occur at a level lower than the survey threshold for detecting dead trees (Fig. 6), which is roughly one tree that has been subjected to successful mass attack per hectare, or 300–600 attacking females per hectare (Carroll et al., 2006). Hence, accurate assessment of threat timing requires intensive monitoring programs over large areas. Extensive monitoring programs (such as the one used in BC in the 1990s) are less capable of anticipating a population eruption than more intensive monitoring programs (such as the one used in Alberta in the 2000s). The more nonlinear, multivariate, stochastic, and uncertain a system’s dynamics, the more closely the system state needs to be monitored to yield a given level of forecasting accuracy—a familiar lesson from meteorological monitoring, modeling, and forecasting (Lorenz, 1963). In the case of MPB, this further implies that population proxy models derived from operational aerial survey data (e.g. Berryman, 1979, 1999; Trzcinski and Reid, 2009; Powell and Bentz, 2009; MacQuarrie and Cooke, 2011) tend to underestimate the most important aspects of the eruptive dynamic—its nonlinearity, dependence on environmental fluctuations, and uncertainty. Hence, forest managers and forest pest managers require either more intensive population monitoring, or a high capacity to
adapt, given the uncertainty when precise monitoring data are lacking.

4.2. Uncertainty cascade and spread prediction

Despite the relative simplicity of this model, there is considerable uncertainty in its structure and in the parameters governing the intrinsic growth equations and their responses to extrinsic perturbations. Without knowing precisely all the drivers, interactions, and functional parameters, accurate quantitative prediction is not possible in this unstable system. This follows the hypothesis of Thom (1974), the original innovator of catastrophe theory, upon which the cross-scale theory of ecosystem ecology (Holling, 1992) is founded. Catastrophe models provide considerable insight that forest managers and policy-makers might find useful in shaping decisions, but they are incapable of providing precise predictions along specific timelines.

What does a conceptual model of eruptive behavior in the beetle’s historic range tell us about likely population growth and spread rates through the boreal forest of central and eastern Alberta? If, as the spatial models of climatic suitability indicate (Nealis and Peter, 2008; Safranyik et al., 2010), the Alberta environment is generally cooler than that in BC and less favorable to beetle survival, then the curves in Fig. 7 should all shift vertically downward to apply to present-day boreal Alberta, thus decreasing the likelihood that arriving populations can aggregate in sufficient numbers to overcome the eruptive threshold and to grow to a self-sustaining outbreak population. Whether the boreal environment is actually cool enough to forestall an outbreak is an open question in need of detailed quantitative research.

The environment of eastern Alberta is drier than BC as a whole, and more prone to drought (Coops et al., 2012), but not necessarily drier than the study regions used to derive our model (i.e. Montana, Idaho, southern interior BC). The potential for variation in drought to lead to region-specific impacts on the MPB system comprises a second source of uncertainty in the model.

All three indices of climatic suitability for MPB shown in Fig. 5 indicate improving survival probability over the past century. However, the Logan model is based on the concept of adaptive seasonality – the strict requirement for life cycle duration that ensures adult emergence is temporally coincident, thereby maximizing chances for successful mass attacks (Raffa and Berryman, 1983), and phenologically timed to enable offspring to mature to cold-tolerant life stages before winter (Logan and Bentz, 1999; Logan and Powell, 2001; Logan et al., 2003). With excessive warming, adaptive seasonality may degrade and cause an abrupt decline in climatic suitability to MPB (Logan and Powell, 2001; Logan et al., 2003). Although Safranyik et al. (2010) suggested this would be unlikely in the boreal region in the near to medium term, this is a third source of uncertainty in our model.

As the model illustrates, tree defenses are a critical determinant of transition to outbreak. Large areas of boreal jack pine through eastern Alberta and Saskatchewan are affected by dwarf mistletoe (Brandt et al., 1998). The impact of mistletoe infection of jack pine on MPB fitness is not straightforward (Klutsch et al., 2016), and its ultimate influence on MPB recruitment in either the endemic or epidemic niche is unknown. Does a mistletoe infection conform to the scenario in Fig. 7c, involving an increase in the number of trees with heavily impaired defenses? This is a fourth source of uncertainty that is critical in affecting the nonlinear dynamics of eruption.

Cudmore et al. (2010) showed that naïve lodgepole pine produce far more MPB brood than lodgepole pine from regions with a previous history of attack. If such differences can be produced within a species, how might recruitment curves differ across species? Again, this is a fifth major uncertainty affecting the highly nonlinear dynamics of establishment and population growth. A shift in host tree defenses in jack pine will have significant effects on the probability that low-density populations can establish and erupt.

In summary, there are at least five major uncertainties in the shapes and positions of the recruitment curves, affecting the possibility of eruption from endemic to epidemic. The extreme sensitivity of the system’s behavior to correlated perturbations affecting the recruitment curves is depicted in Fig. 7d. To the extent that warm, dry conditions may lead to correlated perturbations, this is a system that is highly unstable and prone to abrupt tipping points.

Population growth dynamics are relevant to spread, as population levels determine the number of dispersers able to travel large distances. We reason from this model that it is impossible to predict with any certainty how long the 80 km/year rate of eastward spread observed thus far (Table 1, Fig. 3) may be sustained. To argue that the eastward rate of spread will drop as the invasion front proceeds away from the high-volume pine and the high-density populations of MPB in west and central Alberta (Fig. 3) provides little information. The economics of MPB impacts changes greatly if the expected rate of spread to the commercially valuable white pine stands in Ontario, 2000 km from the current front, is 80 km/year (25 years) versus 8 km/year (250 years) versus 0.8 km/year (2500 years), and yet it is impossible to reduce the uncertainty in order to predict which estimate is more likely.

Even the short-term rate of spread is unknowable, as eruptions are triggered by stochastic weather and mesoclimatic events modeled in Fig. 5. Furthermore, the long-term rate of spread will depend on the rate of climate warming, which in turn depends on climate sensitivity to greenhouse gas forcing, which is somewhat uncertain, and anthropogenic activity generating greenhouse gases, which is equally uncertain. One can only conclude that the eastward rate of spread in the uncontrolled situation is highly uncertain.

4.3. Knowledge gaps and research priorities

Despite the irreducible uncertainties, additional research may facilitate some forecasting – especially in the medium term over larger aggregations of space and time. More research is required on endemic niche dynamics, nonlinear processes, and state transitions. Any processes thought to be implicated in the dynamics of establishment and eruption by MPB in novel pine habitats should also be targeted for research. This would include processes affecting MPB host location, aggregation, sex ratios, attack success, offspring survival in relation to host tree defenses (e.g. resinosin), resource quality, competition with other subcortical insects, predation, parasitism, disease, and a wide range of complex trophic interactions, both negative and positive, involving other subcortical organisms. The amount of research required is directly related to stakeholders’ tolerance for epidemiological unpredictability.

4.4. MPB as a model system

MPB is often held up as an example of how biotic systems may respond very strongly to small changes in climate. Our model shows mechanistically why this is the case, but is the MPB system representative of other forest pest systems? Is it just the first of many such cases, or is it anomalous? This is an important question that is difficult to broach in a study focusing on MPB alone. However, the model analysis presented here shows how any system that is regulated in this way may exhibit such behavior, and the MPB may be the first of many systems to behave in unprecedented ways (Raffa et al., 2008). Of course, the outbreak of MPB in BC was not only unprecedented, it was far more intense and more
extensive than any previous outbreak by this insect in recorded history, and therefore at this point it is not possible to decide whether this case is representative or anomalous.

5. Conclusion

A major component of risk analysis is the assessment of uncertainty in the component risk factors, including the status of the system and its likely behavior. Thanks to the significant investments in monitoring, we have considerable confidence in the status of the system, in terms of the spatial distribution of beetles and pine trees (Figs. 2–4). However, the same cannot be said for the system dynamics that will determine future populations and spread. The interacting nonlinear relationships between the multiple intrinsic and extrinsic drivers of population fluctuations (Figs. 5–7) make it very difficult to judge whether, when, and where the beetle population might transition to endemcity, resulting in a very slow rate of eastward spread. As risk factors multiply, so do uncertainties. Until the threshold climatic and host conditions required to sustain an eruption can be estimated with precision, spread forecasting will remain imprecise.

Despite the irreducible uncertainties, we hesitate to classify the MPB system as an unmanageable problem. Predictions may be difficult, but insights abound, and management options are clear – especially those options that can accommodate unanticipated outcomes and work within the constraints imposed by irreducible uncertainties. We know that two of the main drivers of MPB population growth and spread are climate and effort invested in spread management, and, at least in theory, these processes are amenable to human control. Although research will unquestionably help to reduce the uncertainty concerning spread rates, there is clearly a considerable amount of irreducible uncertainty that will persist. Forest management should therefore continue to explore ways of coping with unpredictable disturbances, including adaptive capacity to adjust to transformational ecosystem changes expected under climate change. “Plan for surprise” was the major recommendation from spruce budworm research in the 1970s (Clark et al., 1979) and has been recommended to the forest sector ever since. Under transformational change associated with unprecedented levels of 21st century climate warming, the principle of adaptive forest disturbance risk management has never seemed more apt.

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Appendix A. Model development

A.1. Model overview

Fig. 7 presents a simple, hybrid, cooperation-competition model of MPB nonlinear dynamics, consistent with the theoretical multi-

nich modeling framework of Berryman (1979, 1999), but (i) parameterized for a specific forest region [the southern interior of British Columbia (data from Boone et al., 2011), and the central Rocky Mountain region (data from MacQuarrie and Cooke, 2011)], and (ii) perturbed in three different ways (a,b,c), including a fourth scenario, (d), in which the three classes of perturbations (a,b,c) are diminished in degree, and applied simultaneously. The three independent classes of perturbations considered are (a) vertical perturbation, (b) lateral perturbation, (c) nonlinear perturbation, using the terminology, geometry, and graphical methodology of Royama (1992). These scenarios involve the simple shifting of base curves in various directions to determine the consequences for the equilibrium state, which governs whether or not an outbreak occurs.

The core model is fully parameterized, as described below, and the specific nonlinear perturbation illustrated in scenario (c) also derives exactly from this parameterization for the southern interior of British Columbia and the central Rocky Mountain region. The scenarios in (a) and (b) are idealized hypotheticals, as described below, but are highly realistic based on our understanding of the MPB system (see Safranyik and Carroll, 2006). The composite scenario (d) is very probable because the individual effects (a–c) mimic in (d) are all relatively small in degree, and all three are likely to result from climate warming and drought, which we know from the empirical literature (e.g. Safranyik and Carroll, 2006; Preisler et al., 2012 and references therein, and Fig. 5) are likely to result in effects such as (i) enhanced winter survival, (ii) reduced tree growth and survival under intense intra-specific competition for light, water, and nutrients, (iii) drought stress causing tree defense against beetle attack to lapse. All curve fitting and simulations were conducted in R, version 3.2.2 (R Development Core Team, 2016).

A.2. Model parameterization

A.2.1. Epidemic niche recruitment curves: cooperation and competition

The core model was developed by hybridizing two data sets governing two complementary component aspects of MPB eruptive biology: (1) the low-density phase, where host defenses against attacking adults, eggs and young larvae are effective, but may be overcome as a function of increasing attack density leading to enhanced cooperation (Boone et al., 2011); (2) the higher-density phase, where host tree defenses have largely been overcome, and the primary source of nonlinear dynamics is increasing competition for food, increased mortality resulting from phloem-drying at high attack densities, and a propensity to disperse as the number of attackers per surviving tree rises, and emigrants compete for new host trees outside the study area (MacQuarrie and Cooke, 2011). The first data set, for cooperative colonization, was specific to the southern interior region of British Columbia, and is the only high-resolution, multi-year field dataset (2000–2005 inclusive) ever compiled to catch an eruption early in its development. The second dataset, for competitive collapse, derived from crude operational field survey data, covered a broader time period, from the 1930s to the 1980s, and a broader area, including all of the southern Rocky Mountain region in southern BC and northern US. The two datasets are therefore highly complementary, in the manner outlined by Berryman (1979), although not quite orthogonal, due to some overlap in the life stage effects covered. Orthogonalization (see Fleiss et al., 2003) was used to extract “component recruitment curves” for distinct classes of life stages to ensure the two derived component functions could be simply multiplied to produce a composite curve for total generation recruitment as described below.
A2.1.1. Parameter estimation.
A2.1.1.1. Co-operation curve: low-density phase colonization in the epidemic niche (i.e. dominant trees). A log-logit model was employed to describe the effect of attack density on the probability of successfully colonizing a tree, using the data presented in Fig. 2 of Boone et al. (2011). Curves were first fit individually by year, whereas in Boone et al. (2011), years were grouped and the data modeled as a single ensemble (Fig. A1).

In three of the years, the colonization curves were relatively flat (2000, 2001, 2004), and in the other three years the response was strongly sigmoidal (2003, 2003, 2005), consistent with the literature suggesting that these curves shift radically in response to drought conditions (e.g. Safranyik and Carroll, 2006; Preisler et al., 2012). We thus modeled two composite curves, designed to indicate colonization probabilities occurring when tree defenses were intact (vigorous trees) versus compromised (stressed trees), as represented in Fig A2.

The equations of these curves were as follows:

\[ p = -0.56 + 0.56a \text{ [stressed tree]} \]

\[ p = -3.36 + 1.66a \text{ [vigorous tree]} \]

where \( p = \text{logit(probability of attacked tree killed)}, \) and \( a = \text{log, attack density}. \)

We considered this curve to represent all of the mortality that would occur in all life stages (adults, eggs, young larvae, mature larvae, pupae, teneral adults) as a result of host tree defenses. The flexing of this curve would eventually become the basis for the perturbation scenario outlined in Fig. 7c, as discussed below. The vigorous host tree condition here was used as the base condition in the development of scenarios shown in Fig. 7a and b.

A2.1.1.2. Competition curve: High-density phase growth in the epidemic niche (i.e. Dominant trees). Whereas endemic-phase population colonization data are exceedingly rare, epidemic-phase operational field data documenting the peak of an epidemic and its subsequent collapse are exceedingly common. MacQuarrie and Cooke (2011) showed that, across its range, initial forest tree densities have a significant influence on the dynamics of MPB epidemic collapse, with more rapid collapse in more heavily thinned stands. We hypothesized that their generation recruitment curve for stands thinned by basal area cuts would apply to the forests studied by Boone et al. (2011) (Fig. A3):

\[ X_t = \log(x_t) \]

A2.2. Recruitment curve in the endemic niche (i.e. suppressed trees)
The endemic-niche recruitment curves in this model are hypothesized, due to a lack of field data for MPB performance on younger, smaller, suppressed, defense-impaired trees. The shapes follow those of the parameterized epidemic-niche curve, just shifted leftward to reflect increasing levels of competition for a fixed resource. As MPB attack densities rise, there are no cooperative effects at play because these trees are lacking host defenses, and the result is pure competition as densities rise – as demonstrated by Raffa and Berryman (1983) on cut tree bolts.
A.2.3. Full model

The full composite model, including both low-density colonization dynamics in the epidemic niche, competition effects in the epidemic niche, and endemic-niche dynamics, is illustrated in Fig. A4.

Derivation of the model aside, the dynamics of this model are determined strictly by the interaction between the endemic niche recruitment curve (black dotted line) and the epidemic niche curve (purple dashed parabola). Note the y-axis here is now plotted on a log scale, whereas Figs. A1 and A2 used less appropriate linear scales (sensu Royama, 1992).

A.2.4. Core model behavior

The left panel (a) in Fig. A4 indicates the typical dynamic when trees are well hydrated and defense against MPB are fully intact. The right panel (b) indicates the effect of drought on the dynamics of lapsing host tree defenses and subsequent population eruption. The label “Allee effect” (Allee, 1931) refers to the degree of positive slope on the cooperation curve (red) that causes the net recruitment curve (purple dashed) to flex from a strong Allee effect where eruption is not possible (a) to a weak Allee effect, where eruption is inevitable (b). In this model the MPB population converges on either the stable endemic state $X_n$ or the epidemic state $X_p$, depending on the value of $X$. $X_i$ is the unstable equilibrium point, which exists in panel (a), but which disappears through a saddle-node bifurcation in panel (b), as the intersection point between the endemic and epidemic niche curves rises above the horizontal $R = 0$ replacement threshold. The relaxation of host defenses in the epidemic niche in (b) allows MPB situated in the endemic niche to spill over onto trees in the epidemic niche, and attack at sufficient density that positive recruitment occurs. The eventual result is outbreak on dominant trees that superficially appear healthy, but which are drought-stressed and defense-impaired.

A.3. Scenario development

The core model behavior section describes the mechanism by which outbreak is thought to typically occur, through the relaxation of host defenses triggered by drought. However other shifts in the epidemic and endemic niche recruitment curves may produce the same saddle-node bifurcation that precipitates outbreak. Two simpler perturbations that result in this same outcome are (1) an identical vertical shift in the two curves, (2) an opposing lateral shift in the two curves (Royama, 1992). A vertical perturbation occurs when the perturbing agent has the same effect on recruitment regardless of population density, and is thus termed “density-independent”. A lateral perturbation occurs when the perturbing agent has a stronger effect at high density than low density, and is thus termed partially “density-dependent”. Competition for a fixed resource, for example, intensifies if some of this resource is suddenly removed. The result is a stronger impact for higher density populations. In our model scenarios we examine the effect of such vertical and lateral displacements.

A.3.1. Vertical displacements

Assuming all insects are equally poorly sheltered against weather, a sudden, drastic change in temperature will affect all population densities equally, resulting in a vertical perturbation of the recruitment curve. Fig. 5 in the manuscript illustrates how climate warming in Alberta and BC is predicated to lead to
enhanced survival, rising from 0.05 during the interval 1905–85 to 0.1 during the interval 1990–2010. Such a doubling represents a significant increase in survival. In our vertical displacement scenario we examine exactly this change, from a peak recruitment rate of $r = 2.5$ to $r = 5.0$. In this scenario, we assume MPB in the endemic niche and epidemic niche are impacted equally by rising temperatures. Although in reality this may be a simplification, if, say, large dominant trees have thicker bark with greater insulating value.

A.3.2. Lateral displacement

When even-aged pine stands reach crown closure, intraspecific competition for light, water and nutrients intensifies, and suppressed trees die in greater proportion (e.g. Farnden, 1996). Environmental perturbations such as drought, or flooding, or defoliation by foliage grazing insects, can accelerate the process, resulting in a transfer of stems from the dominant to the suppressed class. This change in forest health results in opposing changes in the endemic and epidemic niches. In the endemic niche, MPB feeding competition is alleviated, as the supply of stressed trees rises. In the epidemic niche, MPB feeding competition is intensified, as the supply of healthy trees drops. Thus the recruitment curves shift laterally, and converge on another, as illustrated in the scenario shown in Fig. 7b. This increases the likelihood that MPB in the endemic niche can aggregate in sufficient numbers to overcome host tree defenses in the epidemic niche.

We, unfortunately, have insufficient data on this process to generate a parameterized scenario. Therefore this scenario should be considered hypothetical, albeit qualitatively realistic.

A.3.3. Nonlinear displacement

The nonlinear displacement scenario of Fig. 7c has already been presented as a fully parameterized base case, summarized in Fig A4. It is wholly realistic, as it is a parameterized depiction of MPB in southern BC, during 2000–2005 (from Carroll et al., 2006).

A.3.4. Composite perturbation

All three of the above perturbation effects are likely to emerge under rapid climate warming. Rather than combine all three scenarios simultaneously, which would clearly produce outbreak, we asked by how much we could reduce each of the effects, and still produce an outbreak. That number is less than 1/3. This is why scenario shown in Fig. 7d has the saddle-node bifurcation occurring in such close proximity to $R = 0$. In other words, even 1/3 of the observed warming occurring in the last 20 years might be sufficient to produce MPB outbreak, because global climate acts as a “master switch” governing multiple epidemiological processes simultaneously.

References


