

1 **The signature of endemic populations in the spread of**  
2 **mountain pine beetle outbreaks**

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6 **Abstract** The mountain pine beetle (MPB) is among the most destructive eruptive  
7 forest pests in North America. A recent increase in the frequency and severity of  
8 outbreaks, combined with an eastward range expansion towards untouched boreal  
9 pine forests, has spurred a great interest by government, industry and academia into  
10 the population ecology of this tree-killing bark beetle. Modern approaches to studying

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11 the spread of the MPB often involve the analysis of large-scale, high resolution datasets  
12 on landscape level damage to pine forests. This creates a need for new modelling tools  
13 to handle the unique challenges associated with large sample sizes and spatial effects.  
14 In two companion papers (Koch *et al.*, 2020, JRSI; and Koch *et al.*, 2020, EEST),  
15 we explain how the computational challenges of dispersal and spatial autocorrelation  
16 can be addressed using separable kernels. In this paper, we use these ideas to capture  
17 nonstationary patterns in the dispersal flights of MPB. This facilitates a landscape-  
18 level inference of subtle properties of MPB attack behaviour based on aerial surveys  
19 of killed pine. Using this model, we estimate the size of the cryptic endemic MPB  
20 population, which formerly has been measurable only by means of costly and time-  
21 intensive ground surveys.

22 **Keywords** mountain pine beetle · endemic · nonstationary · redistribution · kernel ·  
23 modelling

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53

## 1 Introduction

The mountain pine beetle (MPB) *Dendroctonus ponderosae* Hopkins (Coleoptera Curculionidae), is a tree-killing species of bark beetle native to pine forests of Western North America. Each year for a short period in summer, adult MPB seek to complete their life cycle by attacking a suitable living host pine. During attacks, MPB bore into the bark, introducing fungal pathogens in the process, and ultimately girdle the tree (Taylor et al. 2006). Death follows swiftly for a pine whose defence systems fail to eject these attackers. When an attack succeeds, MPB use the host to feed and reproduce, laying eggs in galleries excavated underneath its bark.

A successful attack often leads to a MPB outbreak, in which local populations rise dramatically and large numbers of healthy pine are attacked over a period of several years. These outbreaks are major disturbance agents of pine forests, so mathematical models to explain their origin and how they spread across the landscape are of great interest to forest ecologists.

With few exceptions, the adult MPB die after reproduction, and their progeny emerge as teneral adults the following summer to begin a new life cycle. This semelparity, and the approximately linear relationship between reproductive success and host death, are mathematically convenient properties when constructing models to track year-to-year changes in MPB populations. For example if a total of  $B$  beetles have attacked a stand containing  $H$  susceptible pines, killing a fraction  $\phi(B)$  of them, then a rough estimate of the MPB population emerging in the next year is  $\lambda\phi(B)H$ , where  $\lambda > 0$  represents average per-stem productivity.

76 Modellers sometimes exploit this relationship to project outbreak dynamics ahead  
77 to future years (Heavilin and Powell 2008), and to explore ecological factors in  
78 population growth (Aukema et al. 2008). However, two major complications in MPB  
79 dynamics become apparent when attempting to link the host mortality fraction  $\phi(B)$   
80 with the underlying beetle population (Nelson et al. 2008). First, any spatially explicit  
81 model for  $\phi(B)$  must account for dispersal flights, which allow localized outbreaks to  
82 spread into nearby areas. Second,  $\phi(B)$  must reflect the eruptive and nonlinear nature  
83 of MPB population growth. We review these aspects briefly below, before introducing  
84 a new mathematical approach to the modelling problem.

### 85 1.1 Dispersal flights

86 In modelling the evolution of an outbreak over multiple years it is often convenient to  
87 track the beetle population in discrete time, where  $B_t$  is the value of  $B$  in year  $t$ . Such  
88 models cannot easily relate  $B_{t+1}$  and  $\lambda\phi(B_t)H$  without incorporating dispersal. Flights  
89 of the MPB allow it to escape depleted stands, spark outbreaks in neighbouring areas,  
90 and expand its range (de la Giroday et al. 2012). By modelling  $B_t$  as the outcome of  
91 a spatially explicit dispersal event, we are better equipped to capture these interesting  
92 and important ecological phenomena, and achieve a higher precision in fitting  $\phi(B)$   
93 to data.

94 A variety of MPB dispersal models can be found in the literature (*e.g.* Goodsman  
95 et al. 2016; Preisler et al. 2012; Aukema et al. 2008; Heavilin and Powell 2008),  
96 but most make two simplifying assumptions out of mathematical convenience: that

97 movements occur in all directions with equal probability (isotropy); and that patterns  
98 of redistribution do not vary with spatial location (stationarity).

99 The main novelty in the methods presented here is that we drop both of these  
100 assumptions. Our dispersal model has the flexibility to capture directed and location-  
101 dependent (anisotropic and nonstationary) events. It is meant as a phenomenological  
102 alternative to dynamical systems based approaches to the same problem (*e.g.* Garlick  
103 et al. 2011; Powell and Bentz 2014; Powell et al. 2018), but with a simpler math-  
104 ematical representation that borrows computationally efficient methods from spatial  
105 statistics. Our mathematical approach is based on ideas presented in two companion  
106 papers; on covariance structure (Koch et al. 2020a), and redistribution kernels (Koch  
107 et al. 2020b).

## 108 1.2 Colonization curves

109 The colonization curve, function  $\phi(B)$ , should be highly nonlinear to accommodate  
110 the distinct behaviours exhibited in different phases of MPB populations (Berryman  
111 1978). During the incipient-epidemic phase, attacks occur at densities low enough  
112 to be defended by hosts, so cooperative efforts in overcoming these defences leads  
113 to a positive density dependence (Allee effect) in  $\phi(B)$  (Boone et al. 2011). How-  
114 ever, as the number of attacking individuals rises, the MPB enters epidemic and  
115 post-epidemic phases, in which the density dependence turns negative as a result of  
116 scramble competition (Woodell and Peters 1992).

117 Empirical data on  $\phi(B)$  therefore reveals an S-shaped, or sigmoid relationship  
118 (Raffa and Berryman 1983). This form is reminiscent of the familiar type-III func-

119 tional responses for parasitism behaviour (Holling 1959), and indeed many aspects of  
120 MPB population dynamics are well described by this parasitoid-prey systems theory  
121 (Goodsman et al. 2016). In Section 2, we show how these functions can be adapted  
122 to model MPB population growth, generalizing the models of Heavilin and Powell  
123 (2008) and Koch et al. (2020b).

### 124 1.3 Aerial Overview Surveys

125 The extent to which a model can be complexified is limited by the amount and quality  
126 of data available for fitting and validation. Thus while the ideas outlined above lead to  
127 sophisticated population models, they also demand an unusually large spatial dataset  
128 for parameter inference. For this reason, we demonstrate our methods in an analysis  
129 of data from the Aerial Overview Survey (AOS) in British Columbia (BC).

130 The AOS maintains an annual record of the spatial patterns of insect damage to  
131 forests in BC. Operators fly in fixed-wing aircraft over most of the forested land in the  
132 province each summer, logging the locations of damage (and the presumed cause) as  
133 polygon and point data on maps, which are then digitized and published online.

134 These data are sometimes dismissed as too imprecise for detailed population  
135 modelling, since the process of visual observation and manual delineation of damaged  
136 areas is prone to human error (*e.g.* Kautz 2014; Wulder et al. 2006). Nevertheless,  
137 because the AOS covers such an impressively large extent and timeline of forest  
138 damage patterns in BC, a considerable body of landscape-level MPB research draws  
139 from the AOS and its predecessor, the Forest Insect and Disease Survey (*e.g.* Aukema

140 et al. 2006; Robertson et al. 2009; Chen and Walton 2011; Reyes et al. 2012; Sambaraju  
141 et al. 2012; Chen et al. 2015a,b).

#### 142 1.4 Paper Outline

143 We show in Section 2 how a generalization of the Heavilin and Powell (2008) model  
144 allows us to relate data from the AOS with ground surveys of MPB activity. We use  
145 these ideas in Section 3 to demonstrate the remarkable amount of information that  
146 can be extracted – with the right modelling tools – from the AOS alone.

147 In particular our model accurately estimates the size of the cryptic, low-density  
148 endemic MPB population using only spatial data on outbreaks. This is remarkable  
149 given that pine mortality caused by the endemic phase happens at levels far below  
150 the operational detection threshold of the AOS (Cooke and Carroll 2017). Studies  
151 of endemic MPB more typically rely on intensive ground surveys of attacked pine  
152 (*e.g.* Boone et al. 2011; Bleiker et al. 2014). Our model estimates the rate of endemic  
153 attacks using only AOS data on outbreak-level pine mortality.

154 This is important because, in comparison to more reliable ground survey methods,  
155 aerial survey programs such as the AOS are a far less expensive and time-consuming  
156 means of monitoring MPB activity over large geographical areas. Note that similar  
157 datasets are available for the neighbouring province of Alberta (AB), in which a highly  
158 consequential MPB range expansion is currently underway.

159 Section 2.1 introduces the model by reviewing a popular mathematical repre-  
160 sentation for the colonization curve  $\phi(B)$ , before introducing several refinements in  
161 Sections 2.2-2.4. Our representation of dispersal flight is then introduced Section

162 2.5, and an error model suitable for the AOS dataset is proposed in Section 2.6. We  
 163 demonstrate the model in Section 3 by fitting to data on outbreaks of the MPB in BC  
 164 during the years 2006-2008.

## 165 2 Methods

166 Our case study covers a pine-rich region of roughly 10,000 km<sup>2</sup>, centered over the  
 167 Merritt Timber Supply Area (TSA) of Southern BC (Figure 1). We divided this into a  
 168 1 hectare (ha) resolution grid (*sensu* Aukema et al. 2006) to form a 1000 x 1000 lattice  
 169 of cells, with matching layers provided by the province (<http://www.hectaresbc.org>)  
 170 on wildfire, cutblocks, and topography.

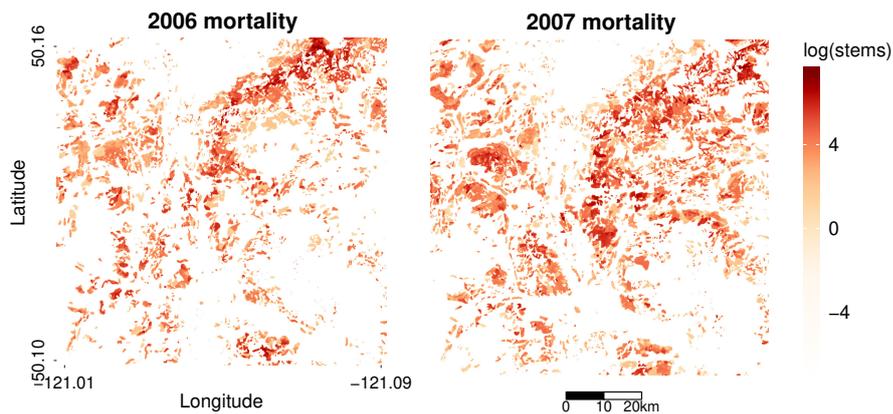


Fig. 1: Hosts killed by MPB ( $\phi_{i,t}H_{i,t}$ , in stems/ha) in the summers of 2006-2007. AOS data on damage severity were rasterized to approximate susceptible host mortality ( $\phi_{i,t}$ ). Host density  $H_{i,t}$  was derived from pine volume estimates in Beaudoin et al. (2014), as described in Appendix 1.1

171 As we are interested in how dispersal patterns are related to outbreak development,  
 172 we analysed the attack years 2006-2008, in which a large number of pine-leading stands  
 173 would see transitions from endemic to epidemic behaviour (the incipient-epidemic  
 174 population phase). This period captures the peak of an epidemic in the Merritt TSA  
 175 (in terms of basal area damaged) at a time when around one out of four cells in the  
 176 area exhibited crown-fade due to MPB activity.

177 Our analysis tracks four state variables, indexed by year ( $t$ ) and location ( $i$ ): Only  
 178 two of them are measured in practice: pine mortality ( $\phi_{i,t}$ ) and host density ( $H_{i,t}$ ,  
 179 in stems/ha) (Appendices 1.1–1.2); The others, MPB density *pre*-dispersal  $\tilde{B}_{i,t}$  and  
 180 *post*-dispersal  $B_{i,t}$  (in females/ha), are latent variables, inferred by the model but  
 181 never directly observed (Table 1).

location $i$	vectorized	definition	units	type
$H_{i,t}$	<b><math>H_t</math></b>	pre-attack susceptible pine density	stems/ha	observed
$\phi_{i,t}$	<b><math>\phi_t</math></b>	proportion of $H_{i,t}$ killed by MPB	unitless	
$\tilde{B}_{i,t}$	<b><math>\tilde{B}_t</math></b>	emerging MPB density (pre-dispersal)	females/ha	latent
$B_{i,t}$	<b><math>B_t</math></b>	MPB attack density (post-dispersal)		

Table 1: Notation for state variables in the MPB attack dynamics model. Indexing is by year  $t$  and location  $i$ , and boldface denotes the vector of all  $n$  locations, *e.g.*

$$\boldsymbol{\phi}_t = (\phi_{1,t}, \phi_{2,t}, \dots, \phi_{n,t})'$$

182 In the remainder of Section 2 we construct a model connecting these four state  
 183 variables. We start in Section 2.1 by extending the red-top model of Heavilin and

184 Powell (2008), interpreting its attack parameters in a new light. We then link this  
185 attack model to novel submodels describing four important components of MPB  
186 population dynamics (Nelson et al. 2008): stand susceptibility, endemic populations,  
187 reproduction, and dispersal (Sections 2.2-2.5, respectively). Finally, in Section 2.6 we  
188 describe the data and statistical methodology used for fitting the full model, before  
189 presenting our results and connecting them to empirical findings from the MPB  
190 literature in Sections 3-4.

## 191 2.1 Attack dynamics ( $\phi$ )

192 Our equation for pine mortality  $\phi_{i,t}(B_{i,t})$  generalizes the red-top model of Heavilin  
193 and Powell (2008) to better match the types of colonization curves fitted in Cooke  
194 and Carroll (2017). The red-top model is best introduced by focusing at first on a  
195 particular location and year; so for notational convenience we omit the subscripts  $i$   
196 and  $t$  until they are needed again in Section 2.4. Thus, for  $i$  and  $t$  fixed, we relate the  
197 attack density  $B$  (females/ha) to pine mortality  $\phi$  by:

$$\text{proportion of } H \text{ killed} = \phi(B) = \frac{B^\kappa}{a^\kappa + B^\kappa} \text{ where } a > 0, \kappa > 0. \quad (1)$$

198 Parameter  $a$  is the half-saturation value, or attack density (in females/ha) at which  
199 50% mortality occurs, and  $\kappa$  is a shape parameter controlling the density dependence.  
200 The special case  $\kappa = 2$  recovers the red top model of Heavilin and Powell (2008) (after  
201 multiplying both sides by  $H$ ). Other  $\kappa$  values reflect alternative regimes of density  
202 dependence. Larger  $\kappa$  and/or  $a$  values coincide with a stronger defensive response by

203 pines. When  $\kappa \leq 1$ , the Allee effect vanishes, reflecting compromised defences, as  
 204 might occur, for example, during a drought.

205 Parameter estimation becomes simpler if Equation (1) can be made linear in its  
 206 parameters. Observing that the odds-ratio of pine mortality  $\phi/(1 - \phi)$  is  $(B/a)^\kappa$ , we  
 207 can take logarithms to get a linear equation on the logit-log scale:

$$\text{logit}(\phi) = -\kappa \log(a) + \kappa \log(B), \quad (2)$$

208 where  $\log(B)$  is the logarithm of attack density, and  $\log(a)$  the density (on the log  
 209 scale) at which one half of susceptible hosts are expected to be colonized.

210 This also happens to be the mathematical form of the colonization curve fitted in  
 211 Cooke and Carroll (2017) to the data reported in Boone et al. (2011) on attacked pines  
 212 in our study area. Their analysis estimated  $\hat{\kappa} = 1.66$  for the 2 years leading up to 2006.  
 213 In years prior, a much lower value (0.56) was estimated, suggesting that environmental  
 214 stressors on pine may have relaxed the Allee effect and bolstered endemic populations  
 215 to spark the large-scale outbreaks of 2006-2008 (Figure 1).

216 Once started, outbreaks are not easily stopped. Irruptions in MPB populations are  
 217 accompanied by behavioural changes in which host-preference switches from stressed  
 218 to healthy pine (Carroll et al. 2006). This allows population growth to continue even  
 219 after pine vigour recovers from a period of stress. Above a certain density threshold,  
 220  $B_T$ , the MPB have sufficient numbers to cooperatively attack a healthy pine (a mass  
 221 attack), releasing them from the ordinary pressures of the Allee effect and marking  
 222 the beginning of the incipient-epidemic phase.

223 The nature of this density dependence is reflected by the (equivalent) equations  
 224 (1) and (2). The case  $\kappa > 1$ , corresponding to attacks on healthy pine, is illustrated

graphically in Figure 2. We discuss two features of this curve below, the incipient-epidemic transition point ( $B_T$ ) and mass attack number ( $m_A$ ). We report on their estimates in Section 3.

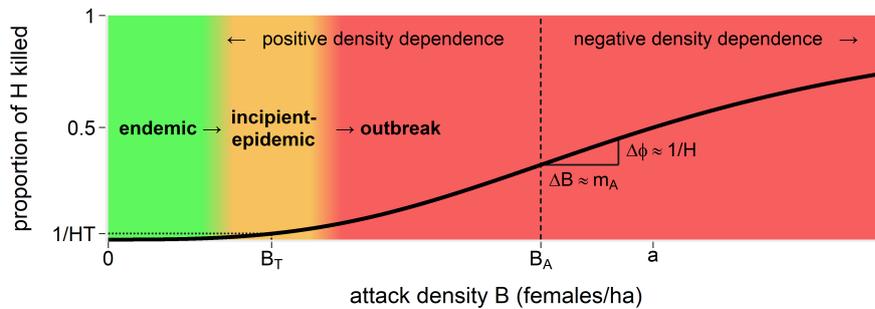


Fig. 2: Host mortality as a function (Equation 1) of MPB attack density  $B$  for  $\kappa = 3$ . Above the inflection point ( $B_A$ ) is a regime of negative density dependence. When  $B \approx 0$ , the endemic population is too small to mass-attack healthy pine. When  $B$  rises to the incipient-epidemic transition point  $B_T$ , mass attacks become feasible and the MPB are released from the endemic phase. At moderate densities, each attacked pine accounts for  $\approx m_A$  beetles. At higher densities, intraspecific competition leads to diminishing returns and negative density dependence

### 2.1.1 The incipient-epidemic transition ( $B_T$ )

Empirical data from our study area suggest that a density of  $\hat{B}_T \approx 300$ -600 females/ha is sufficient to initiate the incipient-epidemic phase in an area of  $T = 15.3$  ha (Carroll

et al. 2006).  $B_T$  is of course scale dependent; Amman (1984) estimated a quite different transition point at the  $T = 40.5$  ha scale.

However, given any scale of interest, and given the values of  $\kappa$  and  $a$ ,  $B_T$  can be estimated via equation (1). This is done by setting  $\phi(B_T) = 1/HT$  (i.e. assuming a single host death in the specified area,  $T$ ) and inverting (1) to get:

$$B_T = \frac{a}{\sqrt[\kappa]{HT - 1}}. \quad (3)$$

### 2.1.2 The mass attack number ( $m_A$ )

The number of MPB aggregating during attacks is carefully moderated by pheromones. This allows the beetle to optimize its reproductive success in mass attacks, by attacking in numbers high enough to overcome tree defenses, but low enough to avoid crowd competition (Taylor et al. 2006). For example, Raffa and Berryman (1983) reported an optimum of around 61 attackers/m<sup>2</sup>, implying that a tree with 5.5 m<sup>2</sup> of bark available for attack (typical of the pine-leading stands in our study area) would have an optimum around 340 females/stem.

Under ideal conditions for MPB attack, this optimal density will presumably match the average attack density per attacked tree, which we call the *mass attack number*  $m_A$  (in females/stem). This average is approximated by the slope of  $\phi(B)$  near its inflection point  $B_A = a\sqrt[\kappa]{(\kappa - 1)/(\kappa + 1)}$  (where  $\phi''(B_A) = 0$ ), since, at this intermediate density,  $\phi(B)$  is nearly linear, and increases with  $B$  at rate  $\phi'(B_A) \approx 1/(m_A H)$ . From (1) we can therefore compute the approximation:

$$m_A \approx 1/(\phi'(B_A)H) = \frac{4B_A\kappa}{H(\kappa^2 - 1)}. \quad (4)$$

## 2.2 Stand susceptibility ( $a$ )

Although (3) and (4) both depend nonlinearly on  $\kappa$ , both equations scale linearly with the half-saturation value  $a$ . Stands that are highly susceptible to MPB attack have lower values (requiring fewer attacking beetles to initiate an outbreak), and vice versa. We can therefore interpret  $a$  as a simple measure of susceptibility to attack.

One can expect  $a$  to vary with environmental factors, such as weather, and stand characteristics, such as pine density. These factors have a complex and nuanced relationship with susceptibility (Preisler et al. 2012), and a clear biology-based model for this relationship is lacking. To avoid overcomplicating our model, we simply take the best linear approximation on the logit-log scale, writing  $\mathbf{x}\boldsymbol{\beta} = -\kappa \log(a)$  for a set of unknown regression parameters  $\boldsymbol{\beta} = (\beta_1, \dots, \beta_{n_\beta})$  and covariates  $\mathbf{x} = (x_1, \dots, x_{n_\beta})$ .

Thus in equation (2) for the mortality log-odds,  $\logit(\phi)$ , we swap out the intercept term with a linear predictor. Similar regression models, such as in Aukema et al. (2008) and Preisler et al. (2012), have been useful for identifying environmental factors that have a significant ( $\beta_k \neq 0$ ) effect on outbreak occurrence. For our purposes  $\boldsymbol{\beta}$  simply serves as a (location-wise) correction of  $a$  through which to estimate MPB population sizes, so we do not focus on the  $\beta_k$  or their effect sizes in our analysis. However, interested readers will find the full set of linear regression covariates listed in Appendix 1.2.

### 2.3 Endemic populations ( $\epsilon$ )

The (aspatial) red-top model of Heavilin and Powell (2008) has no endemic equilibrium: low density populations are viewed as unstable, tending to extinction, and occurring only by means of immigrations from a reservoir of distant outbreaks appearing stochastically across the landscape. However, empirical data (*e.g.* Boone et al. 2011; Bleiker et al. 2014) suggest that resident endemic populations are widespread and persistent. These low-density populations subsist on a small number of defensively compromised pines and an assemblage of secondary bark beetle species that assist in the colonization of weakened trees.

We introduce a stable endemic equilibrium into the red-top model (Equation 1) by adding a small positive term  $\epsilon > 0$  (in females/ha) to the post-dispersal MPB population ( $B$ ) in the red-top model at all sites/years prior to attack. Specifically, with the addition of endemic beetles the attack function  $\phi(B)$  becomes:

$$\text{proportion of } H \text{ killed} = \phi(B + \epsilon) = \frac{(B + \epsilon)^\kappa}{a^\kappa + (B + \epsilon)^\kappa} \text{ where } \epsilon > 0, \quad (5)$$

which, on the log-scale, produces  $\text{logit}(\phi) = -\kappa \log(a) + \kappa \log(B + \epsilon)$ .

This constant introduces a spatially uniform background level of MPB. Should an in-flight from a neighbouring outbreak occur, its density is added to the endemic cohort  $\epsilon$ , and the combined population attacks pines according to Equation (1). The effect of  $\epsilon$  is therefore to boost the effective size of spreading populations, increasing the likelihood that an incipient-epidemic transition will succeed in sparking a local outbreak.

289 In the absence of immigrating MPB, the endemic population is too small to attack  
 290 healthy pines, so it instead seeks out defensively weakened trees. Because this pool  
 291 of suitable hosts is ephemeral and extremely small compared to  $H$ , these endemic  
 292 MPB incur a much higher flight-establishment mortality cost than do outbreaking  
 293 populations: Taylor et al. (2006) estimates the generation mortality of endemic MPB  
 294 at 97.5%. Assuming most of this loss can be attributed to the search flight, the  
 295 rate of attack on defensively weakened hosts under this model would be  $(1 - 0.975)\epsilon$   
 296 females/ha (or slightly above), with the healthy pine population variable  $H$  unaffected.

297 However, if an endemic population joins with a cohort of immigrating outbreak-  
 298 level MPB, suitable hosts suddenly become abundant, and the flight-establishment  
 299 losses should drop accordingly. The generation mortality in populations capable of  
 300 mass-attacks is thought to lie in the range 80-98.6% (Taylor et al. 2006; Amman  
 301 1984). We assume that these losses mostly occur as a result of tree defences and  
 302 crowd-competition. Unlike search flight losses, the latter are subsumed into  $\phi(B)$   
 303 under the model (1). Therefore, we estimate the total number of attacking beetles  
 304 at a given site as the sum of  $\epsilon$  and any MPB (local or immigrant) originating from  
 305 mass-attacked trees.

#### 306 2.4 Reproduction ( $\lambda$ )

307 Reproduction connects subsequent years, so we must now make the dependence of  
 308 our model variables on time and location explicit. In the red-top model, reproduction  
 309 is summarized by  $\tilde{B}_{i,t} = \lambda_{t-1}\phi_{i,t-1}H_{i,t-1}$ . This expresses that  $\tilde{B}_{i,t}$ , the density of

310 (non-endemic) mature MPB emerging in year  $t$  at location  $i$ , is proportional to the  
 311 number of mass-attacked stems in year  $t - 1$ .

312 The productivity parameter  $\lambda_{t-1}$  specifies the average number of female MPB  
 313 brood to emerge from each attacked tree in the year following an attack. This counts  
 314 only those individuals that hatch, survive to maturity, and engage in search flights for  
 315 new hosts. Note that by aggregating demographic information to the level of the tree  
 316 (and year), we forego some precision. However this formulation simplifies the model  
 317 considerably, summarizing in a single constant the many MPB within-tree growth and  
 318 development processes that cannot be observed in aerial surveys (Berryman 1974).

319 Under this model, productivity  $\lambda_t$  is not identifiable from data on  $\phi_{i,t}$  and  $H_{i,t}$   
 320 without knowledge of  $a_{i,t}$ . So we instead fixed the value of  $\lambda_t = \lambda$  in all years to a  
 321 plug-in estimate of  $\lambda = (2/3)(250) = 166.7$  (females/stem) suggested by empirical  
 322 productivity data for epidemic phase MPB (Cole, W. and Amman 1969, Fig. 9), and  
 323 assuming a 1:2 male-female sex ratio (Reid 1962). This productivity value is consistent  
 324 with a 90% generation mortality rate, calculated using the brood production regression  
 325 in (Safranyik 1988, eq. 14) on the mean diameters (Carroll et al. 2006) and heights  
 326 (Safranyik and Linton 1991) of pine in our study area.

327 Although a time (and space) dependent  $\lambda$  would be more realistic, it would compli-  
 328 cate the model considerably. We do however allow all other process model parameters  
 329 to vary with time (*e.g.*  $\epsilon_t$ ,  $\kappa_t$ ,  $\beta_t$ , and the parameters of  $D_t$ ), estimating them sepa-  
 330 rately for each year in our analysis. Variations in productivity are therefore reflected in  
 331 changing stand susceptibility  $a_{i,t}$ , which varies both spatially and temporally through  
 332  $\beta_t$  and the local covariates  $x_{i,t}$  (Table 2).

submodel	vector	contents	definition	units
		$\kappa_t$	density dependence shape value	unitless
attack	$\theta_{\phi_t}$	$\lambda$	beetle production per attacked host	females/stem
		$\epsilon_t$	emerging endemic MPB population level	females/ha
		$a_{i,t}$	half-saturation / susceptibility value	females/ha
		$\beta_t$	linear regression coefficients for $a_{i,t}$	-
dispersal	$\theta_{D_t}$	$\Delta_{k,t}$	pWMY kernel: angle, shape and range	-
error	$\theta_{V_t}$	$\sigma_t^2$	marginal variance	unitless
		$\rho_t$	Gaussian autocorrelation range (x and y)	km

Table 2: Parameters of the generalized red-top model ( $\theta_t$ ), organized into categories of attack ( $\theta_{\phi_t}$ ), dispersal ( $\theta_{D_t}$ ), and error ( $\theta_{V_t}$ ). All except for  $\lambda$  are fitted to data separately by year ( $t$ ). For dispersal, a 5-parameter product-WMY (pWMY) kernel (Appendix 2) is assigned to each of  $m = 625$  data blocks, indexed by  $k = 1, \dots, m$ . A vector of 44 regression coefficients ( $\beta_t$ ) defines stand susceptibility through the linear model  $\kappa_t \log(a_{i,t}) = \mathbf{x}_{i,t} \beta_t$  for local covariates  $\mathbf{x}_{i,t}$  (Appendix 1.3), where  $i$  indexes location.

### 333 2.5 Dispersal ( $\tilde{B} \rightarrow B$ )

334 Dispersal can be represented in population models using redistribution kernels (Neu-  
335 bert et al. 1995). These are functions,  $D_t$ , specifying a probability distribution for  
336 location following movement events. If the emerging MPB population  $\tilde{B}_{t,i}$  is observed  
337 at  $n$  spatial locations,  $D_t$  specifies an  $n \times n$  matrix ( $\mathbf{D}_t$ ) whose  $i, j^{th}$  entry  $[D_t]_{ij}$  is  
338 the expected proportion of the population  $\tilde{B}_{t,j}$  that will move to cell  $i$  in the course  
339 of dispersal (Appendix 2). Thus, after adding the endemic MPB, the expected attack  
340 density is  $\mathbb{E}(B_{i,t}) = \epsilon_t + \sum_j ([D_t]_{ij} \tilde{B}_{t-1,j})$ . The equivalent matrix-vector equation

341  $\mathbb{E}(\mathbf{B}_t) = \epsilon_t \mathbf{I} + \mathbf{D}_t \tilde{\mathbf{B}}_t$  allows us to drop the cumbersome location indices ( $i$ ), so we  
 342 will use this simplified notation whenever possible.

343 The  $i^{\text{th}}$  entry of  $\mathbb{E}(\mathbf{B}_t)$  estimates the density of attackers, sometimes called beetle  
 344 pressure, at stand location  $i$  in year  $t$ . Beetle pressure is a common feature of MPB  
 345 outbreak risk models (*e.g.* Wulder et al. 2006; Preisler et al. 2012), where it expresses  
 346 proximity to infestations by a weighted sum of severity values or presence/absence  
 347 indicators in a neighbourhood of the target stand. The weights in this calculation are  
 348 provided by the kernel function  $D_t$ .

349 The choice of  $D_t$  therefore reflects assumptions about how MPB redistribute in  
 350 search of new hosts. Ad-hoc assignments of weights to  $[D_t]_{ij}$  often suffices in simpler  
 351 predictive models (*e.g.* Kärvelo et al. 2014; Kunegel-Lion et al. 2019) but, whenever  
 352 possible, it is desirable to choose a kernel derived from models of the physical flight  
 353 process (Nelson et al. 2008).

354 Our flight model approximates the Whittle-Matérn-Yasuda (WMY) kernel family  
 355 (Yasuda 1975), which describes diffusive movements through complex habitat (Koch  
 356 et al. 2020b). Included in this family are a number of distinct isotropic kernels that  
 357 have been advocated in previous studies of similar datasets (*e.g.* Turchin and Thoeny  
 358 1993; Heavilin and Powell 2008; Goodsmann et al. 2016). Figure 3 (middle) is one  
 359 example, arising from diffusion with constant settling.

360 We calculate the  $[D_t]_{ij}$  values using pWMY kernels, which in addition to closely  
 361 approximating the WMY, easily incorporate anisotropic (directed) movement patterns  
 362 (Figure 3, right) as might be expected from the effect of local winds (Ainslie and  
 363 Jackson 2011) and patchy habitat (Powell et al. 2018).

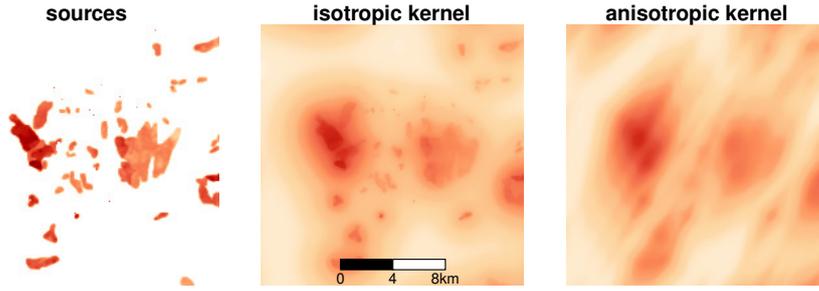


Fig. 3: MPB density pre-dispersal (left) and post-dispersal (middle and right) for two models of MPB flight patterns: an isotropic Bessel kernel (middle) with parameters from Goodsman et al. (2016), and an anisotropic pWMY kernel (right) parametrized to resemble the Bessel, but with the addition of a northeast-facing directionality

Writing  $\delta_{ij} = (x_i - x_j, y_i - y_j)'$  for the vector difference between the x-y coordinates at locations  $i$  and  $j$ , the equation of the anisotropic pWMY kernel is:

$$D_t(\delta_{ij}; \alpha, \rho_x, \nu_x, \rho_y, \nu_y) = c D_W(d_{ij}^x; \rho_x, \nu_x) D_W(d_{ij}^y; \rho_y, \nu_y),$$

where  $(d_{ij}^x, d_{ij}^y)' = \mathbf{R}_\alpha \delta_{ij}$ , and  $D_W(d; \rho, \nu) = (d/\rho)^\nu K_\nu(d/\rho)$ , (6)

364 where  $K_\nu$  denotes the  $\nu^{th}$  order modified Bessel function of the second kind,  $\mathbf{R}_\alpha$  is the  
 365 standard 2D rotation matrix for angle  $\alpha$ , and  $c$  is the kernel normalization constant.  
 366 The parameters of this kernel are explained in detail in Appendix 2.

367 Importantly, the pWMY can be computed far more quickly than the WMY. Com-  
 368 putational simplicity allows different dispersal patterns to be quickly fitted at different  
 369 sites within a dataset. In our study area, this revealed a complex pattern of direction-  
 370 ality (nonstationarity) that varies depending on the position of the source population.

371 Nonstationarity in dispersal patterns over a large geographic area is unsurprising  
 372 in light of work by Powell and Bentz (2014), whose differential-equation based move-  
 373 ment model connects environmental cues to direction and motility in MPB flights.  
 374 Recognizing the importance of this nonstationarity, but lacking high-resolution data  
 375 on its cues, we opted for a novel phenomenological model that combines multiple  
 376 stationary (pWMY) kernels to form a nonstationary one.

377 We fitted each pWMY kernel to a relatively small square geographical area (a  
 378 block) before combining them by computing a weighted average of their fitted values,  
 379 with weights inversely related to distance from the block centroid (Figure 4). The  
 380 effective contribution of each kernel to beetle pressure  $\mathbb{E}(B_t)$  is therefore restricted  
 381 to a neighbourhood (dashed outer line in Figure 4, right) of the block over which it  
 382 was fitted (solid line).

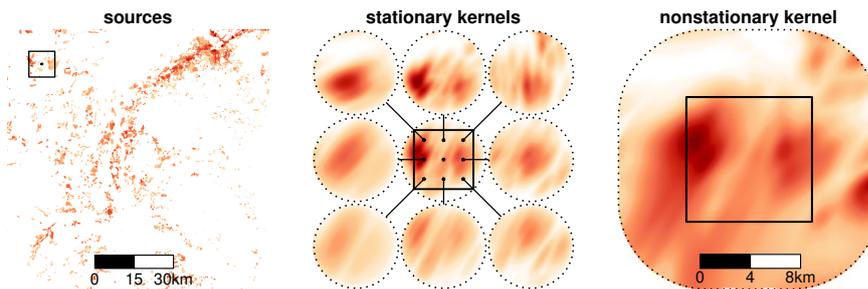


Fig. 4: A nonstationary flight pattern estimation scheme: stationary kernels are separately fitted to small overlapping blocks of data (at left, a block and its centroid). Expected beetle pressure (detail, at right) is computed as the distance-weighted average of nearby kernel predictions. The middle panel shows the nearest 9 block centroids and their kernel predictions before averaging

383 The resulting nonstationary dispersal model is itself a redistribution kernel, so we  
384 refer to it as  $D_t$  (with associated matrix  $D_t$ ). Its explicit mathematical form is derived  
385 in Appendix 2.

386 The virtue of this approach is that it captures complex (nonstationary) dispersal  
387 patterns by means of simpler stationary kernels, whose parameters can be fitted  
388 rapidly by well-established techniques over small neighbourhoods within which a  
389 stationarity assumption is reasonable. Moreover, there is no requirement for detailed  
390 environmental data, such as the stand density values used by Powell and Bentz (2014).  
391 Movement patterns are instead estimated directly from the available attack data.

392 Our construction of  $D_t$  used a total of 625 pWMY kernels in a  $25 \times 25$  grid arrange-  
393 ment of blocks, each of size  $10 \times 10$  km. Since each pWMY kernel captures only the  
394 local flight patterns within its respective block, we chose a distance-weighting func-  
395 tion (Appendix 5.2) that assigns zero weight beyond the centroid-to-corner distance  
396 within a block (7.1 km). This scheme tracks movements up to 14.2 km, a reasonable  
397 upper bound on self-powered dispersal given laboratory studies suggesting fewer than  
398 10% of MPB are capable of flight beyond this distance (Shegelski et al. 2019).

399 To avoid overparameterizing an already complicated model – and lacking data on  
400 wind patterns – we assumed that atmospherically-driven flight events (such as those  
401 documented by Jackson et al. 2008) were rare enough to ignore. Furthermore, although  
402 both block size and the number of blocks can be viewed as tuning parameters for the  
403 dispersal model, we assigned them ad-hoc values in this case to (roughly) coincide with  
404 the aforementioned self-powered dispersal limitations of MPB, rather than attempting  
405 to optimize them via model selection.

406 Some edge effects are unavoidable with this modelling strategy. For example,  
407  $[D_t]_{ij}$  values for a location coinciding with a block centroid will be determined  
408 almost entirely by the data within that single block, whereas for a location halfway  
409 between block centroids, the  $[D_t]_{ij}$  values are influenced by data from two (or more)  
410 overlapping blocks – a much larger geographical extent. We believe, however, that this  
411 type of inconsistency pales in comparison to the roughcast assumption of stationary  
412 and isotropic dispersal patterns.

## 413 2.6 Model-fitting

### 414 2.6.1 Data

415 Pine density  $H_t$  was estimated using the model output of Beaudoin et al. (2014) for the  
416 year 2001, after adjusting for losses due to wildfire, logging, and pest damage incurred  
417 during the intervening years (Appendix 1.1). For simplicity we did not attempt to  
418 model regeneration, but rather assume that changes in density due to growth were  
419 small enough to ignore over the period 2001-2008.

420 Pine mortality data are drawn from the AOS of the Merritt TSA (Figure 1) for the  
421 attack years 2006-2008. These were rasterized by standard methods (Appendix 1.2)  
422 to produce a  $1000 \times 1000$  grid of sample locations at a 1 ha resolution, matching the  
423 geometry of the pine density dataset. To avoid edge effects in dispersal calculations,  
424 we excluded a  $\approx 10$ km buffer at the edge of this grid from the response data, forming  
425 the (logit-transformed) vector  $\phi_t$  from the subgrid of dimensions  $893 \times 893$  centered  
426 on this region (a within-year sample size of 797,449 points).

### 2.6.2 Statistical model

A redistribution kernel is a probabilistic model – it connects MPB damage patterns to the *expected* density of attackers arriving next year at each location  $\mathbb{E}(\mathbf{B}_t)$ . Variations of  $\mathbf{B}_t$  about this mean should therefore be modeled as error. Investigations into ecological dispersal by Preston (1948) and Limpert et al. (2001) inform us these errors are likely to be lognormally distributed. Assuming,  $(\mathbb{E}(B_{i,t}) - B_{i,t}) \stackrel{iid}{\sim} \text{lognormal}(0, \tilde{\sigma}_t^2)$ , we can summarize Sections 2.1-2.5 in the equation:

$$\underbrace{\text{logit}(\boldsymbol{\phi}_t)}_{\text{pine mortality log-odds}} = \underbrace{\mathbf{X}_t \boldsymbol{\beta}_t}_{\text{susceptibility}} + \underbrace{\kappa_t \log(\boldsymbol{\epsilon}_t \mathbf{I} + \lambda \mathbf{D}_t (\boldsymbol{\phi}_{t-1} \odot \mathbf{H}_{t-1}))}_{\text{beetle pressure}} + \underbrace{\mathbf{Z}_t}_{\text{error}} \quad (7)$$

where  $\mathbf{X}_t = (\mathbf{x}'_{1,t}, \dots, \mathbf{x}'_{n,t})'$  is the (covariate) data matrix for year  $t$ , and  $\mathbf{Z}_t$  is the vector of process errors arising from  $\mathbf{B}_t$ . The logit and log functions are applied elementwise, and the symbol  $\odot$  denotes elementwise multiplication. This slight abuse of notation allows us to suppress the location indices  $i$  and write the complete model (7) in terms of length- $n$  vector operations.

Under the lognormal assumption,  $\mathbf{Z}_t$  is mean-zero multivariate normal (MVN), with a variance  $\kappa_t \tilde{\sigma}_t^2$  that scales with the strength of the density dependence in  $\phi(B)$ . We assume that measurement error introduces an additional mean-zero MVN random vector appearing additively on the logit scale of (7). Since these errors are presumably independent of  $\mathbf{B}_t$ , their effect (by standard MVN theory) is to simply increase the variance of  $\mathbf{Z}_t$ . Thus, ignoring any autocorrelation (for now), we could write  $\mathbf{Z}_t \sim \text{MVN}(\mathbf{0}, \sigma_t^2 \mathbf{I})$ , where  $\sigma_t^2$  is the sum of the variances from process and measurement error.

447 For simplicity we ignored temporal autocorrelation by treating each year of data  
 448 in the analysis as independent, as is commonly done in large-scale MPB outbreak  
 449 analyses (*e.g.* Heavilin and Powell 2008; Goodsmann et al. 2016). While this is not  
 450 ideal, it avoids the difficulties associated with aligning consecutive years of raster  
 451 data containing a large number of slight positional errors (Wulder et al. 2009), while  
 452 simplifying the error model both mathematically and computationally.

453 Spatial autocorrelation, on the other hand, is more easily corrected using covari-  
 454 ograms (Chilès and Delfiner 2012). For computational efficiency we used the Gaussian  
 455 covariogram, which generates a covariance matrix  $V_t$  (to replace  $\sigma_t^2 \mathbf{I}$  above) based  
 456 on  $\sigma_t^2$  and a pair of correlation range parameters,  $\rho_t$ . In this model, the logarithm of  
 457 the likelihood function for observations of  $\phi_t$ , given  $\phi_{t-1}$  and  $X_t$  is proportional to:

$$\mathcal{L}(\theta_t | \mathbf{Z}_t) = -\log(\det(V_t)) - \mathbf{Z}_t' V_t^{-1} \mathbf{Z}_t \quad \text{where } \theta_t = (\theta_{\phi_t}, \theta_{D_t}, \theta_{V_t}) \quad (8)$$

458 with  $\mathbf{Z}_t$  as defined in (7), and model parameters  $\theta_t$  organized into components of  
 459 attack dynamics,  $\theta_{\phi_t} = (\kappa_t, \lambda, \epsilon_t, \beta_t)$ ; error,  $\theta_{V_t} = (\sigma_t^2, \rho_t)$ , and dispersal  $\theta_{D_t} =$   
 460  $(\Delta_{1,t}, \dots, \Delta_{625,t})$ ; as in Table 2. The model can now be fitted to data by maximum likeli-  
 461 hood estimation (MLE), which finds the maximizer of (8), called  $\hat{\theta}_t = (\hat{\theta}_{\phi_t}, \hat{\theta}_{D_t}, \hat{\theta}_{V_t})$ .

462 Our estimation method for  $\theta_t$  is based on the 2-step algorithm described in Cru-  
 463 jeiras and Van Keilegom (2010), but with a blockwise approach to approximating  
 464 the large number of parameters in  $\theta_{D_t}$ . Each of the 625 pWMY kernels is fitted in-  
 465 dependently to the data in its block, before being combined to form the nonstationary  
 466 kernel matrix  $\hat{D}_t$ . By assuming  $D_t \approx \hat{D}_t$ , estimation of the remaining parameters  $\theta_{\phi_t}$   
 467 and  $\theta_{V_t}$  then becomes straightforward using generalized least squares (GLS) based

468 methods (Chilès and Delfiner 2012). Simulations indicated that our approach yields  
469 unbiased and reasonably precise estimates of  $\theta_t$  (Appendix 3).

### 470 **3 Results**

471 The estimated endemic densities and attack curve shapes in all three years (Figure  
472 5) matched closely with ground surveys of our study area during the period 2001-  
473 2005. We estimated  $\epsilon_t$ , the endemic contribution, at 388, 279, and 566 (females/ha),  
474 respectively, for the years 2006 – 2008. Note that these densities are well above  
475 what is considered normal for the endemic phase (Safranyik and Carroll 2006), as  
476 they represent populations before flight-establishment loss. After correcting for this  
477 loss (97.5%), our estimates suggest a range of 7 – 14 attackers/ha in endemic-only  
478 populations, similar to the ranges reported in Boone et al. (2011) and Bleiker et al.  
479 (2014).

480 A density dependence in attack was detected in all years, with  $\kappa$  estimated at 1.69,  
481 1.32, and 1.67. Note that the estimates in 2006 and 2008 very nearly matched the  
482 value of 1.66 reported by Cooke and Carroll (2017) for pooled colonization curve  
483 data from the preceding years 2002-2003 and 2005 (Figure 5). This indicates that  
484 not only is density dependence detectable from stand-level AOS data (in the absence  
485 of failed attack counts) – supporting the findings of Goodsman et al. (2016) on Allee  
486 effects – but also that the precise shape of the attack curve in (9) can be estimated  
487 from aerial data on  $\phi_t$  and  $H_t$  alone. This includes both the Allee and compensatory  
488 (crowd competition) effects highlighted in Figure 2.

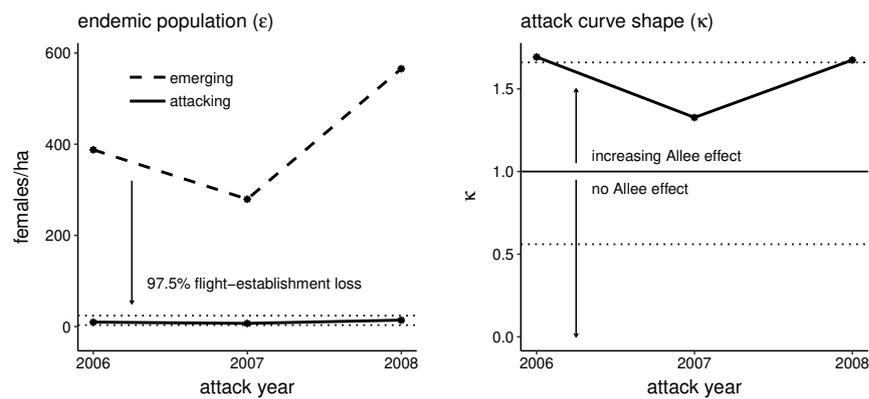


Fig. 5: Fitted attack parameters. At left, estimates of the endemic population and expected attack rates lying within the range (dotted lines) reported in Boone et al. (2011). At right, estimates of the attack curve shape compared with reference levels from Cooke and Carroll (2017) (dotted lines)

489 Estimates of stand susceptibility  $a_{i,t}$  varied across the landscape, being spatially  
 490 dependent on  $\mathbf{x}_{i,t}$ . Locations unsuitable to MPB (such as unforested areas) tended  
 491 to assume extremely large  $a_{i,t}$  values whereas areas with optimal habitat for MPB  
 492 assumed much smaller ones.

493 Restricting our attention to optimal stands only – *i.e.* those having a density of 800-  
 494 1500 stems/ha and aged > 80 yrs (Carroll et al. 2006), representing around 150,000  
 495 locations – the observed distribution of susceptibility values can be compared to  
 496 empirical data from similar outbreaks. For example the modes of the estimated  $m_{A_{i,t}}$   
 497 values over these optimal stands were centered at 336, 932, and 480 females/stem,  
 498 for the years 2006-2008 respectively (Figure 6). This is reasonably consistent with

499 the 300-617 females/stem range observed in our study area by Safranyik and Linton  
 500 (1991) during a previous outbreak in 1984.

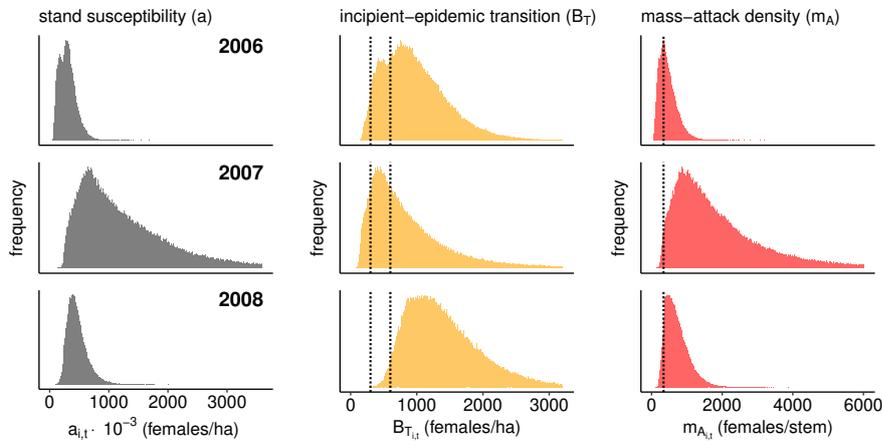


Fig. 6: Histograms of estimated susceptibility ( $a_{i,t}$  left) in stands optimal for MPB in the years 2006-2008, and two associated quantities: (middle) the beetle pressure required for one mass attack per 15 ha, with dotted lines indicating an empirical range (Cooke and Carroll 2017); and the mass attack number (right), with a dotted line indicating the optimum of Raffa and Berryman (1983).

501 Using data on average diameters and attack heights for these optimal stands  
 502 (23cm, Carroll et al. 2006; and 11.36m, Safranyik and Linton 1991; respectively), we  
 503 estimated a typical bark area of  $5.5 \text{ m}^2/\text{stem}$  (Safranyik 1988, eq. 6). Our typical per- $\text{m}^2$   
 504 observed attack density ( $m_{A_{i,t}}/5.5$ ) therefore lay in the range of 61-170 females/ $\text{m}^2$ .  
 505 Note that the lower end of this range (observed in 2006) coincides exactly with the  
 506 optimal attack density measured by Raffa and Berryman (1983) (Figure 6, right).

507 This shows that 2006 was a year of strong population growth for MPB, with a  
 508 relatively low threshold for outbreak emergence ( $B_T$ ), and mass attack numbers ( $m_A$ )  
 509 centred at or near the optimum for brood production. Populations continued to expand  
 510 through the next two years, with a large number of incipient epidemic transition  
 511 events, followed by a collapse. Our model indicates that in optimal habitat, these  
 512 events typically happened when MPB attack densities increased through the range  
 513 427-1114 of females/ha (the modes of the estimated  $B_{T_{i,t}}$  by year; Figure 6, middle).  
 514 This agrees with empirical observations by (Cooke and Carroll 2017) of a transition  
 515 point in the 300-600 range during the five years leading up to 2006, and indicates that  
 516  $B_T$  values spiked as the epidemic neared collapse in 2008.

517 On dividing the  $B_{T_{i,t}}$  values in Figure 6 by our estimates for  $\epsilon_t$ , and taking medians,  
 518 we find that a factor of 2.5 – 3.2 increase in the endemic population was typically  
 519 sufficient to initiate an outbreak. These findings support the observation of Carroll  
 520 et al. (2006) that the incipient-epidemic transition point seems to occur at a level  
 521 slightly above the density required to mass-attack a single pine. Our model expresses  
 522 this quantity by the ratio  $B_{T_{i,t}}/m_{A_{i,t}}$ , whose median values (in optimal MPB habitat)  
 523 were 2.2, 0.5, and 2.0 in the years 2006-2008, respectively.

524 Flight events under the fitted model are summarized by the block-wise redistribu-  
 525 tion kernel estimates. Our pWMY kernels identified a large number of highly directed  
 526 (anisotropic) dispersal events in all years. The grid of fitted dispersal kernel param-  
 527 eters ( $\hat{\theta}_{D_{k,t}}$ ) that generate  $\hat{D}_t$  (Figure 7) resembles a smooth vector field, raising some  
 528 interesting questions as to the driving forces behind these patterns.

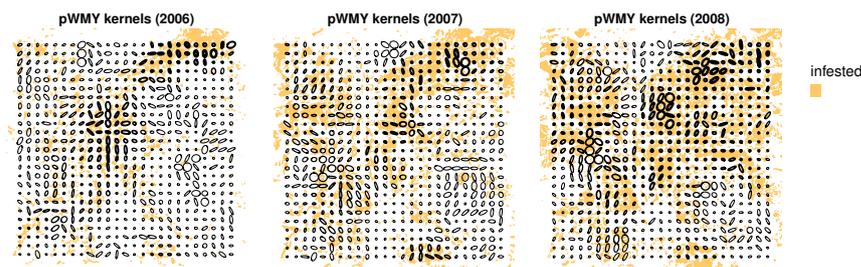


Fig. 7: Diffusion ellipses summarizing the angle and effective range corresponding to each of the 625 fitted pWMY parameter sets used to construct  $\hat{D}_t$  for each year. Each ellipse inscribes a contour of constant density for dispersal from its centre. Line thickness is scaled to match the estimated number of MPB displaced, emphasizing major outbreak centres. Infestations from the previous year are shaded to indicate the spatial distribution of source populations. Uninfested areas tended to produce small ellipses – these should be viewed as uninformative, as the model had no data from which estimate flight patterns in those blocks.

529 The combination of these stationary fitted kernels to form the nonstationary kernel  
 530 ( $\hat{D}_t$ ) brings into focus a complex landscape of MPB movement patterns (Figure 8),  
 531 illustrating how detailed information on beetle pressure can be recovered from AOS  
 532 data by rethinking the usual modelling assumptions about dispersal.

533 Note that our model was constructed for parameter inference, rather than predic-  
 534 tions of future outbreak locations. However, our methodology for estimating beetle  
 535 pressure could easily be adapted to serve a forecasting role. We illustrate the idea in  
 536 Figure 9, where the empirical value of  $B_T = 450$  (the midpoint of the range reported  
 537 in Cooke and Carroll 2017) is used as threshold for outbreak development. The plot

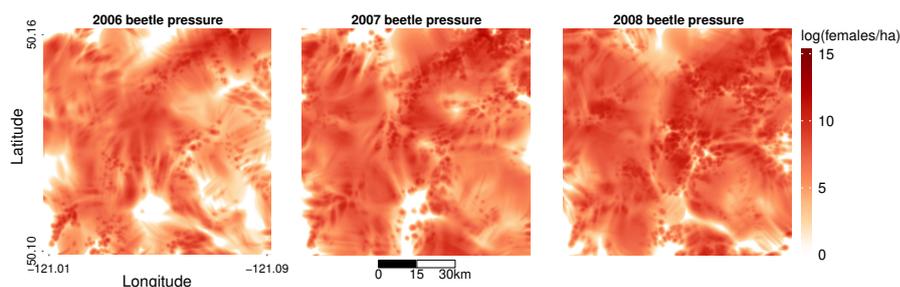


Fig. 8: Heatmaps of  $\log(\lambda \hat{D}_t (\phi_{t-1} \odot H_{t-1}))$ , the fitted beetle pressure values arising from flight events in the years 2006-2008 (excluding endemic MPB).  $\hat{D}_t$  is the moving average of predictions from a  $25 \times 25$  grid of local stationary models, each fitted to a local subset of the data

538 shows how our model delineates infested areas under two different scenarios; the first  
 539 with no endemic population, and the second with  $\epsilon_t$  set to its estimated value from  
 540 2006. Notice that neither  $a_{i,t}$ ,  $\kappa_t$  nor  $\theta_{V_t}$  is needed for this classification.

541 The true positive rate in the training year 2006 was 93.5%, and in the forecast  
 542 for 2007 it improved to 98.0%. By including the endemic population in our beetle  
 543 pressure estimates, the contours of the infestation predictions broadened, sometimes  
 544 by several kilometres. This improved detection rates substantially (true positive rate  
 545 in 2006 without the endemic component: 71%; and in 2007: 84%).

#### 546 4 Discussion

547 The S-shaped colonization curves that characterize the non-linearity of MPB attack  
 548 dynamics (*e.g.* Raffa and Berryman 1983; Boone et al. 2011) are usually fitted to field  
 549 data on individual attacked trees, so they relate attack density to the mortality among

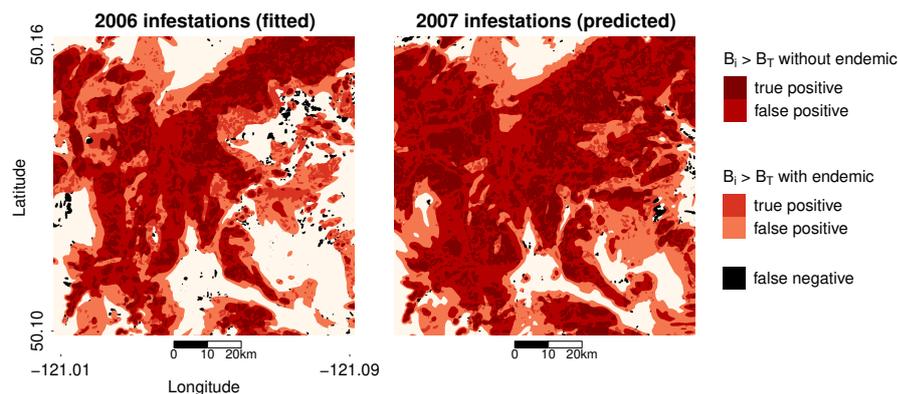


Fig. 9: Infested locations and next-year forecasts using the equation  $\hat{\mathbf{B}}_t = \hat{\epsilon}_t + \hat{\mathbf{D}}_t \tilde{\mathbf{B}}_t$  from Section 2.5. Using the fitted values of  $\hat{\epsilon}_t$  and  $\hat{\mathbf{D}}_t$  from the training year 2006 (left), locations were classified as infested (shaded) if the predicted beetle pressure exceeded  $B_T = 450$ . Using these same parameters along with the observed attack damage and pine density in 2006, we then predicted infestations in 2007 (right). For comparison, an endemic-free estimate is also plotted (darker shaded regions) by replacing  $B_{i,t}$  with  $B_{i,t} - \epsilon_t$ . The effect is to withdraw the contours of infested areas inward, considerably limiting the estimated spread.

550 pines undergoing attack. This is a conditional probability model. For example, the  
 551 model of Cooke and Carroll (2017) has the form:

$$\text{logit}(\text{Pr}(\text{pine mortality} \mid \text{attack})) = A + \kappa \log(N_a) = (A - \kappa \log(c)) + \kappa \log(B) \quad (9)$$

552 where  $A$  is an dimensionless intercept; and  $N_a$  is the number of stems attacked within  
 553 the study plot, which we expect to scale according to  $cN_a \approx B$  with the attack density  
 554  $B$  (in females/ha).

555 Our model, however, is based on aerial data, from which failed attacks cannot  
556 be resolved. In (2), we therefore related  $B$  to the *unconditional* probability of stand  
557 level mortality  $\Pr(\text{pine mortality} \mid \text{attack}) \Pr(\text{attack})$ , which we called  $\phi$ . Notice that  
558 when  $\Pr(\text{attack}) = 1$ , both the red-top model of Heavilin and Powell (2008) and our  
559 generalization (1) coincide exactly with (9). In reality, attack rates will be much lower,  
560 so in the high-level description (1) we assumed that the logit-linear relationship (9)  
561 remains after aggregating mortality data at the 1 hectare scale. Our results supported  
562 this assumption, with estimates of  $\kappa$  in close agreement with the field data reported  
563 by Cooke and Carroll (2017).

564 In Section 2.1 we showed how, via stand-susceptibility ( $a$ ), this  $\kappa$  value is mathe-  
565 matically linked to the mass attack number ( $m_A$ ) and the incipient-epidemic transition  
566 point ( $B_T$ ). Our comparison of point estimates for these parameters with empirical  
567 data from previous years showed reasonably good agreement, supporting the theory  
568 behind formulae (3) and (4). This illustrates one way in which our model can be used  
569 to study ecological questions about MPB attack dynamics at the level of the individual  
570 tree, while using only (stand-level) AOS data for parameter fitting.

571 For instance, the observed increase in  $B_T$  in 2008, along with the elevated  $m_A$   
572 levels in 2007-2008, can be attributed to host depletion, as MBP tend to select pine of a  
573 certain phloem, size, and vigour class for colonization (Shrimpton and Thomson 1985;  
574 Cole and McGregor 1983; Raffa and Berryman 1983). As the preferred hosts become  
575 scarce, MPB are thought to balance increasing fitness costs by first intensifying mass  
576 attacks on the few that remain (Lewis et al. 2010), thus effectively increasing  $m_A$

577 above its optimal level. Similarly, a scarcity of suitable mass-attack targets can be  
578 expected to make spontaneous eruptions from the endemic phase less likely.

579 Furthermore, our results on  $\epsilon_t$  shed a mathematical light on how outbreaks might  
580 sporadically arise across the landscape – if environmental conditions were to double  
581 or triple the number of injured/weakened pines available to the endemic population,  
582 this could allow it to grow to the point of exceeding  $B_T$  in the absence immigrating  
583 MPB – in accordance with the theory of Berryman (1978), and the explanation of  
584 Cooke and Carroll (2017) as to the origin of the outbreaks analysed in Section 3.

585 In-flights of MPB are equally important to understanding MPB outbreak dynamics.  
586 This is clear from the large number of spatial regression studies pointing to beetle  
587 pressure as the single most significant factor in outbreak development (*e.g.* Aukema  
588 et al. 2008; Preisler et al. 2012; Sambaraju et al. 2012). However there remains  
589 little consensus in the modelling literature on how best to represent beetle pressure  
590 mathematically.

591 As we explained in Section 2.5, beetle pressure simply expresses our modeling  
592 assumptions about MPB dispersal; Different modelling approaches handle this prob-  
593 lem in different ways. With few exceptions (such as Powell and Bentz 2014; Powell  
594 et al. 2018) forecasting models tend to reconstruct beetle pressure in a heuristic way,  
595 by defining infestation indicator variables that are summed over local spatial neigh-  
596 bourhoods (see *e.g.* Shore et al. 2000; Aukema et al. 2008; Robertson et al. 2009;  
597 Kunegel-Lion et al. 2019). Many attack dynamics regression models also employ  
598 this trick (*e.g.* Zhu et al. 2010; Preisler et al. 2012; Sambaraju et al. 2012; Kärverno  
599 et al. 2014), and indeed a stationary and isotropic kernel-based representation (as in

600 Heavilin and Powell 2008; Goodsmann et al. 2016) is simply a refinement that finds a  
601 biology-based shape (and range) for the filter. Our method refined this idea further,  
602 in a novel way, by introducing directedness and location-dependence by means of a  
603 weighted combination of stationary kernels.

604 As we observed in a previous study (Koch et al. 2020b), the precision gained  
605 through the use of anisotropic kernels appears to far outweigh the drawbacks associated  
606 with the introduction of additional dispersal parameters. Moreover, we believe our  
607 refined flight model shows promise not only in formulating beetle pressure (as we  
608 do here), but as a tool for studying nonstationary dispersal processes more generally.  
609 Future work might look for connections between  $\theta_{D_{k,t}}$  and environmental drivers such  
610 as prevailing wind direction, as a means of studying the dispersal process itself. For  
611 example, one could analyse whether patterns of directionality might arise in reaction  
612 to population density, both of beetles and hosts, similar to work by Powell and Bentz  
613 (2014) (we thank an anonymous reviewer for these suggestions).

614 Though we did not analyse the kernel parameters ( $\theta_{D_t}$ ) in detail, it is worth re-  
615 marking that in most of the pWMY kernels a leptokurtic pattern of dispersal was  
616 favoured over the simpler Gaussian model of bio-diffusion. This highlights the versa-  
617 tility of the pWMY in modelling different flight mechanisms (Koch et al. 2020b), and  
618 suggests that a wide range of MPB flight behaviours are realized across the landscape:  
619 including both the fat-tailed patterns, proposed by Goodsmann et al. (2016) and Turchin  
620 and Thoeny (1993); and the Gaussian, suggested by Heavilin and Powell (2008).

621 Note that the model-fitting procedure of Section 2.6 was constructed to study  
622 attack dynamics (at least) one year after they occur, not to predict them in future

623 summers, nor is our estimate of stand susceptibility  $a_{i,t}$  (as a log-linear function of  
624 local covariates) intended for extrapolation. A more judicious choice of covariates  
625 whose values can be projected in time (combined with a significance-based covariate  
626 selection) would be needed in a predictive risk model for MPB damage. Nonetheless  
627 we think the framework in (7) – and in particular the nonstationary approach to  
628 dispersal – will be helpful in building model-based solutions to management and  
629 forecasting problems.

630 We illustrated this briefly in the next-year classification example of Figure 9.  
631 Note that our high detection rates lie near the level mentioned in Fettig et al. (2014)  
632 for stabilizing outbreaks by mitigation measures (such as cut and burn). However  
633 with high recall comes a high false positive rate (low precision); Moreover the 2007  
634 prediction required information on pre-dispersal density that is typically not available  
635 until *after* the attack summer being predicted – recall that  $\tilde{\mathbf{B}}_t$  is derived from crown  
636 fade data with a one-year lag. One possible solution would be to iterate equation (7)  
637 with simulated error to produce a suite of multi-year forecasts under various scenarios  
638 of stand susceptibility and process error, an idea we plan to explore in future work.

639 Figure 9 illustrates an important consequence of the ubiquity of endemic MPB  
640 in their natural range: it increases the potential for outbreaks to spread. The potential  
641 for range expansion may be therefore be underestimated if the endemic contribution  
642 to MPB outbreaks is ignored. This will be of particular relevance in contemporary  
643 areas of concern, such as the Boreal forest in Alberta (Safranyik et al. 2010). The  
644 establishment of endemic populations in these areas should be closely monitored, as

our results show that they have the potential to accelerate the spread of outbreaks, and thus speed the range expansion of the MPB.

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