Shifting Roles of Predisposing Agents, Spatial Contagion, And Accessible Host Quality Drive Phase Transitions of An Irruptive Herbivore

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Shifting roles of predisposing agents, spatial contagion, and accessible host quality drive phase transitions of an irruptive insect herbivore

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Abstract – 250 Limit (249 currently)

Irruptive forest insects such as bark beetles undergo intermittent outbreaks that cause landscape-scale tree mortality. Despite their enormous economic and ecological impacts we still have only limited understanding of the dynamics by which populations transition from normally stable endemic to irruptive densities. We investigated density-dependent changes in mountain pine beetle reliance on stressed hosts, host selection, spatial configuration of attacks, and the interaction of host selection and spatial configuration by performing a complete census of lodgepole pine across six stands and six years. Additionally, we compared the dynamics of mountain pine beetle with those of other bark beetles. We found that as population size increased, reliance on stressed trees decreased and new attacks shifted to larger trees with thicker phloem and higher growth rates that can support higher offspring production. Moreover, the spatial configuration of beetle-attacked trees shifted from random to spatially aggregated. Further, we found evidence that beetle utilization of larger trees was related to aggregation behavior as the size of tree attacked was positively correlated at 10-25 m, within the effective distance of pheromone-mediated signaling. In contrast, non-irruptive bark beetle species did not exhibit such density-dependent spatial aggregation at the stand scale or switches in host selection behavior. These results identify how density-dependent linkages between spatial configuration and host utilization can converge to drive population transitions from endemic to irruptive phases. Specifically, a combination of stand-level spatial aggregation, behavioral shifts, and higher quality of attainable hosts defines a critical threshold beyond which continual population growth becomes self-driving.

Introduction

Irruptive insect herbivores cause significant tree mortality globally (Peltonen et al. 2002; Anderegg et al. 2015; Hicke et al. 2016) and can ultimately lead to pervasive shifts in ecosystem dynamics and services (McDowell et al. 2020). Population fluxes of forest insects are integral components of disturbance regimes and can promote heterogeneity (Turner et al. 2004), biodiversity (Beudert et al. 2015), and ecosystem services (Thom and Seidl 2016). Yet, several recent largescale outbreaks coupled with warming temperatures and severe droughts have caused unprecedented tree mortality in historically impacted and relatively novel locations (Williams and Liebhold 2006; Jepsen et al. 2008; Allen et al. 2015; Seidl et al. 2017). These shifting regimes have led to substantial economic and environmental losses (Kurz et al. 2008; Hicke et al. 2012; Chang et al. 2012; Seidl et al. 2015). Both the frequency and severity of irruptions by some native species are increasing due to climate change and land use alteration (Ayres and Lombardero 2000; Seidl et al. 2017; Biedermann et al. 2019).

Outbreaks of forest insects can occur in periodic intervals (Royama 1992; Berryman 1996; Kendall et al. 1999; Bjornstad and Grenfell 2001) or intermittently in response to pulses of resource availability or bioclimatic suitability (Powers et al. 1999; Aukema et al. 2006; Økland and Bjørnstad 2006). The likelihood and extent of irruptions are often mediated by competing negative and positive feedbacks (Berryman 1987; Raffa et al. 2008; Biedermann et al. 2019). Negative feedbacks include resource depletion (Økland and Berryman 2004; Økland and Bjørnstad 2006), host defenses (Boone et al. 2011, Howe et al. 2020), and natural enemies (Turchin 1999; Dwyer et al. 2004; Cobbold et al. 2009). Positive feedbacks include cooperative host utilization, predator escape, and improved mate finding (Larsson et al. 2000, Liebhold and

Tobin 2008, Kausrud et al. 2012). Once populations transition past crucial thresholds positive feedbacks can become dominant and generate self-driving population growth (Berryman 1987).

Despite our extensive knowledge of the basic biology and emergent landscape patterns of irruptive forest insects, relatively little is known about the processes by which they transition from their endemic to irruptive phases. For example, we do not have a good understanding of how the spatial dynamics of infestation trees within a stand interact with host selection behavior, tree defenses, and endogenous drivers. Consequently, models that examine the dynamics of outbreak spread are not timely for applying effective mitigation measures.

The most destructive forest insects worldwide are bark beetles that colonize the subcortical tissues of the main stems of conifers. Bark beetle species that colonize live tree stems can be broadly grouped into three groups, those that colonize lower-stems and are functionally parasitic in that they don't typically kill trees (lower-stem hereafter) (Gregoire 1985), irrupt in response to a pulse of resources (pulse-driven hereafter) (Øklund and Bjørnstad 2006, Aukema et al. 2016), or breach cross-scalar thresholds to undergo self-driving growth (threshold-limited hereafter) (Berryman 1987, Raffa et al. 2008). Irruptive bark beetles (i.e., those that are pulse-driven or threshold-limited) exhibit long endemic phases during which populations are low and colonize trees that are either dead or highly stressed. Such hosts are poorly defended but also nutritionally sub-optimal. This endemic phase can be followed by rapid transitions from incipient to epidemic phases (Safranyik and Carroll 2006). Lower-stem bark beetles generally do not undergo outbreaks, except in rare cases where they are introduced to new regions (Yan et al. 2004). At the landscape-scale, population transitions of irruptive bark beetles are often synchronous across large areas and driven by high temperatures and drought (Aukema et al. 2008; Marini et al. 2012; Preisler et al. 2012; Kolb 2016; Seidl et al. 2016; Hart et al. 2017;

Sommerfeld et al. 2018). At the stand scale, population increases can be driven by increasing tree age, biotic and abiotic stressors, and high tree density.

Mountain pine beetle (*Dendroctonus ponderosae* Hopkins) occurs throughout western North America. It is most closely associated with lodgepole pine (*Pinus contorta* Douglas), but can utilize most *Pinus* spp. in its range (Meddens et al. 2012). Successful colonization causes tree mortality within one to two years, and beetles can usually reproduce in a tree for only one generation (Safranyik and Carroll 2006). Brood production is directly related to tree diameter and phloem thickness (Amman and Cole 1983, Safranyik and Carroll 2006). Pines possess sophisticated multimodal defenses that can usually resist attacks, often resulting in attack abandonment or beetle mortality (Raffa et al. 2005). Beetles can avoid these defenses by entering only highly stressed trees during lengthy low-density periods. Alternatively, beetles can overcome trees of almost any vigor class once their populations are high (Waring and Pitman 1985, Boone et al. 2011, Williams et al. 2018). The ability of large populations to utilize healthy trees is driven by pheromone-mediated mass attacks by which high numbers of beetles can overcome otherwise efficacious defenses (Raffa and Berryman 1983, Blomquist et al. 2010). Low populations are typically unable to elicit mass attacks.

The population dynamics, attack behavior, and spatial spread of epidemic mountain pine beetle populations are relatively well described (Aukema et al. 2006; Preisler et al. 2012; Cooke and Carroll 2017). However, the critical transition from the endemic to irruptive phase remains understudied for several reasons. First the broad scale of these ecosystems necessitates extensive aerial surveys for monitoring and surveillance, but aerial surveys primarily detect tree mortality where populations have already transitioned past the endemic phase. Second, despite the importance of external landscape scale drivers such as climate, population transitions occur at the

stand level. Furthermore, local drivers, such as biotic agents that impair tree defenses are not necessarily detectable or manifested at large spatial scales. Third, the transition from net negative feedback, where population growth is limited to low-vigor trees and below thresholds needed to overcome vigorous trees, to positive feedback (self-sustaining population growth) can occur rapidly, further complicating attempts to capture dynamics at either the landscape or stand scales.

Although there is substantial information on how certain agents impair host defenses at the tree level, we have little understanding of how prior stressors, beetle attack behavior, and host availability interact to either constrain endemic populations or foster phase transitions. Prior work suggests potential variation in the clustering of attacks (Safranyik and Carroll 2006; Bleiker et al. 2014), and that lower-stem colonizing bark beetle species or mistletoe (Klutsch et al. 2014) may create a low-vigor niche for endemic mountain pine beetle populations (Smith et al. 2011). However, few studies have attempted to integrate the spatial and mechanistic components of endemic-irruptive phase transitions (Koopmans 2011).

Our objective was to explore four facets of an irruptive herbivore's stand and tree level interactions that putatively tilt net feedbacks from negative to positive and hence initiate outbreaks. Specifically, we test whether: a) beetle reliance on prior stress agents, b) host utilization, c) spatial distribution of attacks, and d) the interaction of spatial distribution of attacks and size of attacked trees changes with local population density. Further, we compare these threshold-limited attack dynamics and interactions with pulse-driven, and lower-stem bark beetles in the same system. We hypothesize that behavioral shifts putatively concentrate beetle populations so as to maximize the likelihood of success of pheromone-mediated mass attacks, allow beetles to overcome defenses of previously inaccessible vigorous trees, and utilize nutritionally high-quality trees that enhance brood production.

Methods

Site Establishment

Six mature lodgepole pine (*Pinus contorta* Douglas) stands at two sites (Angstad Creek, Aberdeen Plateau) in southern British Columbia were randomly selected to monitor beetle populations for 3-6 years (Boone et al. 2011). Candidate stands were first identified from forest inventory maps ([forest inventory methods \[link\]](#)) and were considered for study if they: 1) were located within areas of historically suitable climate for mountain pine beetle (Safranyik and Carroll 2006; Safranyik et al. 2010); 2) contained no mountain pine beetle activity observable from aerial surveys ([aerial survey methods \[link\]](#)) but did have endemic reproducing populations verified by on-site observations; 3) were at least 10 km away from recorded tree mortality caused by epidemic mountain pine beetle; and 4) were at least 1 km away from each other. Stands A and B were established in 2000, stands D and E in 2001, stand F in 2002, and stand G in 2003. Stands A, B, and F were located at Angstad Creek and stands D, E, and G were located on the Aberdeen Plateau (Figure 1).

Variable radius plots (Avery and Burkhart 2002) were installed in each stand at a density of 1 plot/ha and mensurational characteristics were quantified. The stands averaged 15.3 ha, with 1265 trees/ha, and were comprised of 90.3% lodgepole pine. The average age of lodgepole pines was approximately 100 years, the mean basal area was 40.75 m²/ha, and the mean diameter at breast height (DBH) was 22.65 cm (Boone et al. 2011).

Site Monitoring

For the duration of the study (2000-2005), presence/absence of bark beetle attack was assessed for every tree within the stands (an estimated 110,000 trees). At each site, a 25 x 50 m

grid was established as a reference and the stems of all trees were assessed for evidence of attack (Carroll et al. 2006). All trees within a stand were censused at four-week intervals from June-September. All trees were censused for evidence of beetle attack, and upon confirmation of attack, were spatially referenced and their characteristics and condition were assessed. Potential conditions that could impair tree vigor (e.g. physical damage, root or foliar infections, etc.) were recorded (Supplemental Table 1). For every attacked tree, a small amount of bark was removed ($<225 \text{ cm}^2/\text{tree}$) to confirm beetle activity and species identification. For trees in which some or all beetles had completed development and dispersed, the timing of attack (i.e., year) was estimated based on condition of the phloem, presence of subcortical beetles, and the condition of remaining foliage (Supplemental Table 2) (Carroll et al. 2006). DBH was measured for each attacked tree ($n=5287$) while mean annual increments at 5 years ($n=2320$), phloem thickness ($n=834$), and tree height ($n=2589$), were measured for a subsample of trees.

For the purposes of these analyses, we separated bark beetles into three guilds: threshold-limited species, i.e., mountain pine beetle ($n=5,320$ attacked trees); pulse-driven species, i.e., *Ips pini* Say ($n=140$ attacked trees); and lower-stem bark beetle species that included *D. murrayanae* Hopkins ($n=206$ attacked trees), *D. valens* LeConte ($n=35$ attacked trees), *Hylurgops* spp. (*H. porosus* LeConte & *H. rugipennis* Mannerheim; $n=478$ attacked trees), *Orthotomicus latidens* LeConte ($n=1099$ attacked trees), and *Pseudips mexicanus* Hopkins ($n=1906$ attacked trees). Further, in lieu of definitive counts of beetle population size, we assume that the number of attacked trees/ha is highly correlated with local population size since a complete census of beetles is not possible.

Non-baited flight intercept panel traps (Schmitz 1984) were placed at regular intervals (8-18/site) in each stand and checked approximately every ten days from late May until September

during the above years. Because total trap catch numbers over the course of the study were low (257 mountain pine beetles, 102 *Ips pini*, and 953 lower-stem bark beetles), a common problem when sampling endemic populations without pheromones (Krause et al. 2018), these data were not incorporated into analyses.

Analyses

All data wrangling and analyses were conducted in R (4.0.2) using R Studio (1.3.1073). The relevant R packages include: tidyverse for wrangling and visualizations (Hadley et al. 2019); sf for plotting spatial data with ggplot (Pebesma 2018); spatstat for examining point process models (Baddeley et al. 2015); ggeffects for visualizing predicted least squares fits for interactions (Ludecke 2018), vegan for multivariate analyses (Oksanen et al. 2020), and factoMiner/factoextra for visualizing multivariate analyses (Kassambara and Mundt 2020).

Are there density dependent shifts in beetle reliance on prior stressors?

Beetle reliance on prior stressors as a function of population size was analyzed using linear and generalized linear models. Linear models were used to compare the proportion of trees/stand with either prior or no prior stressors (e.g. mistletoe, physical deformities, lower-stem bark beetle attack; Supplemental Table 1) with a covariate of $\log_{10}(\text{number of attacked trees/ha})$. Generalized linear models (with logit link function) were used to compare the likelihood that an attacked tree had either a prior stressor (“1”) or no prior stressor (“0”), with a covariate of $\log_{10}(\text{number of attacked trees/ha})$. Thus, linear models were conducted on a per-stand basis while generalized linear models were conducted with a response on a per-tree basis and a predictor on a per-stand basis. The appropriateness of each model was assessed graphically. The apparent breakpoint in the sigmoidal relationship between the probability an attacked tree had a

prior stressor and population density for threshold-limited bark beetles (Figure 2D) is due to the properties of log-transformed values below and above 1.

Are there density dependent shifts in host utilization?

Changes in beetle host utilization (e.g., beetles attacking larger trees) as a function of population size were analyzed for each guild using linear models. Three linear models were fit with responses of: DBH, 5-year mean annual increment, and phloem thickness, with a covariate of the $\log_{10}(\text{number of attacked trees/ha})$. Model assumptions were assessed graphically for all model fits. The residuals from linear model constructed for 5-year mean annual growth increment exhibited a fair amount of heteroscedasticity and were not normally distributed. However, in our analyses, heteroscedasticity is largely due to the uneven sampling scheme (i.e. larger values of x have more observations) and no simple transformations easily fixed the residuals, so we report the original non-transformed linear models. Relationships between host selection by each bark beetle guild and tree characteristics including prior injury or disease, tree height, DBH, 5-year mean annual increment, phloem thickness, and population size, was explored using principal components analysis (PCA). Hypothesis testing was performed using permutational multivariate analysis of variance (PERMANOVA), with Bray-Curtis as the distance metric. Screeplots are provided in Supplemental Figure 1.

Are there density dependent shifts in the spatial configuration of attacked trees?

The spatiotemporal dynamics of bark beetle attacks were assessed both graphically (i.e., x-y plots for each stand/year) and by describing the distribution of attacked trees with a transformed Ripley's K-function (L-function hereafter). More specifically, we tested whether the

distribution of attacked trees was more aggregated (positive spatial correlation) or inhibited (negative spatial correlation) than random. Further, we did not assume that there was an equal chance of observing a beetle attack throughout our observation window because each censused area was embedded within a larger stand to diminish possible edge effects (Carroll et al. 2006) and the spatial distribution of tree size was likely not homogenous (see for example, Matasci et al. 2018, for within stand variability of lodgepole pine basal area at 30 m² across BC). As a result, all L-functions were fit with an inhomogeneous process.

Hypothesis testing for each stand/year was conducted through the following process. First, duplicate attacks (i.e., trees attacked by multiple bark beetles of the same guild) were removed (threshold-limited: max.=2; pulse-driven: max.=2; lower-stem: max.=6). Next, we created a realization of the joint density of all trees attacked by bark beetles. Originally, separate densities were fit for each ‘marked’ point (i.e., each guild of beetle), but since the significance bands were not visually distinguishable from the joint density significance bands, the joint density was used for ease of processing and because we are operating under the assumption that trees within a stand are equally likely to be attacked by beetles from each guild. Joint densities were realized with smoothing parameters of $\sigma=50$, $\sigma=15$, and $\sigma=5$ that correspond to null hypotheses of the underlying spatial distribution of available low-vigor trees. Significance bands were calculated by simulating 999 realizations of an inhomogeneous Poisson process based on each realized joint density. We then compared the observed L-function to the simulated significance bands. Portions of each observed L-function higher or lower than the significance bands were significantly (p-value < 0.001) more aggregated or inhibited than random. We provide a step-by-step walkthrough of this process in Supplemental Figure 2. Further, we supplemented our graphical interpretation of each point pattern using a nearest neighbor

approach, the Clark-Evans aggregation index (Clark and Evans 1954), with 999 simulations (Supplemental Figure 3).

Are there interactions between size of tree attacked and spatial configuration of attacks?

Spatial correlation of size of tree attacked was analyzed by fitting a conditional mean summary function, $E(r)$, for each stand (Schlather et al. 2004). This approach allowed us to test the spatial correlation of a continuous ‘marked’ point pattern (conceptually similar to a semivariogram). Significance was assessed with an envelope with 999 simulations. E-functions were fit using attacks from all bark beetles since the function behaves better when points are approximately evenly spaced. The summary function for stand B was fit based on attacks from 1999-2003, since we were primarily interested in describing the spatial dependence of the early stages of aggregation and not stand-level irruption.

Results

Overall, from 1999-2005 we observed 9204 trees attacked by bark beetles, 58% of which were attacked by mountain pine beetle ($n=5340$ trees), 2% by *Ips* ($n=140$ trees), and 40% by lower-stem bark beetles ($n=3724$ trees). At the beginning of the time series in 1999, there were only 19 attacked trees, and by 2005 there were 3411. The number of trees attacked by each guild varied substantially among and within stands over time (Table 1).

Density-dependent shifts in mountain pine beetle dependence on prior stress agents

Mountain pine beetles predominantly attacked trees with prior stressors when their populations were low, but not when their populations were high (Figure 2A; slope=-0.22;

F_{1,29}=9.59; p-value=0.004). The probability that a tree attacked by mountain pine beetle had a prior stressor decreased as the beetle population size increased (Figure 2D; odds ratio=0.01; $\chi^2_{(1)}$ =1224.96; p-value < 0.001). That is, likelihood odds that an attacked tree had a prior stressor decreased by 0.99 for each ten-fold increase in the number of attacked trees/ha. From 1999-2005, 20% of trees attacked by mountain pine beetle (70% if Stand B in 2005 is removed) had prior stressors.

Density-dependent shifts in size, growth rates, and phloem thickness of trees attacked by mountain pine beetles

As mountain pine beetle populations increased, beetles attacked larger trees (Figure 3A; slope=1.37, F_{1,5652}=119.3; p-value<0.001); however, there was substantial unexplained variability (R²=0.02). Likewise, at higher populations mountain pine beetles attacked trees with higher growth rates (Figure 3B; slope=0.21; F_{1,2349}=242.6; p-value<0.001), which explained ~10% of the observed variability (R²). Additionally, at higher populations, mountain pine beetle attacked trees with thicker phloem (Figure 3C; slope =0.74; F_{1,880}=145.7; p-value<0.001), which explained the greatest amount of variability (R²=0.14), although this sample size was smaller. Population size did not affect height of trees attacked (F_{1,2686}=3.8; p-value=0.051). In total, these density-dependent shifts in host selection were associated with beetles attacking trees that were on average, larger, with faster growth rates, and with thicker phloem (Figure 3D; PERMANOVA; F_{2,2291}=172.82; p-value < 0.001). However, these characteristics explained little of the observed variability attributable to differences among bark beetle guilds (R²=0.1) and was better explained by among-site differences (R²=0.26).

Density-dependent shifts in the spatial distribution of trees attacked by mountain pine beetle

From 1999-2005, trees attacked by mountain pine beetles increased exponentially in three of six stands and shifted from putatively random to aggregated (Figure 4A; stands A, B, & F). Changes in spatial distribution were not apparent in two stands (Figure 4B; stands D & G) or in the case of stand E, were not likely a result of within-stand dynamics (Figure 4B) (Carroll et al. 2006). In stands A, B, and F, the spatial pattern of trees attacked by mountain pine beetle shifted from no spatial structure to significant positive spatial correlation (i.e., aggregation; p -value < 0.001) as mountain pine beetle populations increased (interpretation of the observed $L(r)$ - r functions for each stand-year: Figure 5; all observed $L(r)$ - r functions: Supplemental Table 3). Moreover, the shift from random to aggregated attacks appeared to occur between 2 and 4 attacked trees/ha (Figure 5; grey box). In stand A, the pattern of attacked trees at the beginning of the spatial transition (2001-2003) also exhibited significant negative spatial correlation (i.e., inhibition) at ~50 m. There was weak evidence of similar patterns in B-2001 and D-2003. As populations continued to increase, there was no significant spatial inhibition. This pattern indicated that during the beginning of the transition from random to aggregated, mountain pine beetles attacked trees in discrete clusters, while at higher population levels, mountain pine beetle attacks did not occur in discrete clusters and were more evenly distributed throughout the stand.

Interactions between the spatial pattern and characteristics of attacked trees

Size of trees attacked by mountain pine beetles exhibited significant positive spatial correlation in all of the stands where the distribution of beetle attacks shifted from putatively random to aggregated. In stands A, B, and F, tree size attacked was significantly positively correlated at distances of 5-25 m, and corresponded to beetles attacking trees that were 1-2 cm

larger than the stand average (Figure 6). Additionally, there was further significant positive correlation around 50 m in stands A and B, while there was significant negative correlation around 50 m in stand F.

Density dependent relationships in reliance on prior stressors, host utilization, and spatial aggregation for pulse-driven and lower-stem bark beetles

Pulse-driven and lower-stem bark beetles exhibited different dynamics than mountain pine beetle. Although, pulse-driven beetles (i.e., *I. pini*) exhibited a similar decreasing relationship between population size and reliance on prior stressors (Figure 2B; slope=-0.18; $F_{1,22}=4.5$; p-value=0.045), there was no relationship between population size and the probability that an attacked tree had a prior stressor (Figure 2E; $\chi^2_{(1)}=0.97$; p-value = 0.34). Lower-stem bark beetles always preferred stressed trees and increasing population size was positively related to prior stressors (Figure 2C; slope=0.20; $F_{1,30}=10.96$; p-value=0.002). Correspondingly, there was no relationship between population size of lower-stem bark beetles, i.e., *D. murrayanae*, *D.*, *Hylurgops* spp. (*H. porosus* & *H. rugipennis*), *Orthotomicus latidens*, or *Pseudips mexicanus*, and the probability that an attacked tree had a prior stressor (Figure 2F; $\chi^2_{(1)}=0.12$; p-value = 0.88). Additionally, increasing populations of pulse driven bark beetles attacked smaller trees (Figure 3A; slope=-2.5; $F_{1,204}=6.17$; p-value=0.01) and increasing populations of lower-stem bark beetles attacked slower-growing trees (Figure 3B; slope=-0.08; $F_{1,5414}=94.95$; p-value<0.001). Pulse-driven bark beetles did not attack faster growing trees or trees with thicker phloem and lower-stem bark beetles did not attack larger trees or those with thicker phloem as population size increased.

Spatial aggregation dynamics of pulse-driven and lower-stem bark beetles exhibited different patterns than mountain pine beetle (Figure 4A-B). Increasing populations of both pulse-driven and lower-stem bark beetles did not exhibit significant positive spatial correlation as compared to an inhomogeneous null distribution (Figure 5), except for lower-stem beetles in D-2003. In most stand/year combinations, the spatial distribution of lower-stem bark beetles was best approximated by a random distribution based on a joint density with $\sigma=15$ (Supplemental Table 3). In other words, trees attacked by lower-stem beetles were randomly distributed within small patches (~20-50 m).

Discussion

Threshold-limited irruptive insect species persist during endemic periods and when appropriate conditions arise transition to an epidemic phase where populations become self-amplifying. For the mountain pine beetle, prior stressors within some host trees provide an endemic niche for sustained reproduction, but reliance on this resource decreases as populations increase. Furthermore, a critical stand-level population threshold exists that separates endemic from incipient/irruptive population phases. The spatial distribution of attacks shifts from random to clustered as aggregation pheromones attract large numbers of beetles that redirect to nearby trees. As their population densities increase, mountain pine beetles begin to colonize larger, thicker-phloemed trees, which yield more offspring (Amman and Cole 1983, Graf et al. 2012), thus driving positive feedback. In contrast, pulse-driven and lower-stem bark beetles did not show density-dependent changes in reliance on prior stressors, host selection, spatial distribution, or their interactions. Jointly, these results underscore the importance of low-vigor trees for the persistence of endemic populations of tree-killing bark beetles, sources of positive feedbacks

driving the onset and expansion of irruptive populations, and key traits differentiating irruptive from nonirruptive species within a closely related taxonomic group.

Previous observations and models suggest that the random spatial pattern of attacks at low population densities reflects the similarly relatively random distributions of stressors and susceptible trees within stands (Logan et al. 1998; Powell et al. 1999; Safranyik and Carroll 2006; Koopmans 2011). Since colonized trees are usually only available for one beetle generation, they represent a resource pulse that is removed from the pool of available hosts. However, once populations of some bark beetle species are high, they can successfully colonize trees adjacent to those they have filled to capacity (Gara and Coster 1968, Geiszler et al. 1983, Mitchell and Preisler 1991, Preisler and Mitchell 1993). This switching behavior greatly increases beetles' chances of initiating mass attacks on entered trees during outbreaks, but is less likely to succeed when populations are low (Raffa and Berryman 1983; Boone et al. 2011). Switching behavior is mediated by initial attraction to a tunneling beetle in a focal tree by long-range aggregation pheromones (Blomquist et al. 2010) followed by short-range anti-aggregation pheromones that orient beetles to adjacent trees once an optimal attack density is reached (Hunt and Borden 1990; Gitau et al. 2013). The distance of observed significant spatial correlation in this study falls within the effective radius in which this switching behavior occurs (Geiszler and Gara 1978, Geiszler et al. 1980). The likelihood that the beetles maintained by sources of chronic stress on trees can breach the irruptive threshold to cause largescale mortality is influenced by regional bioclimatic conditions, synchrony of neighboring populations, and the availability and connectivity of suitable hosts across the landscape (Peltonen et al. 2002; Logan et al. 2003; Aukema et al. 2006; Safranyik and Carroll 2006; Raffa et al. 2008; Preisler et al. 2012).

Our results also contribute to our understanding of the relative contributions of stand and regional drivers to population transitions, but disentangling them remains difficult. For example, based on the numeric increases of pulse-driven and lower-stem bark beetles in all stands, the region-wide drought that began in 1999 (SPEI Database) likely increased the availability of low-vigor trees throughout our study area. This apparent resource-pulse led to mountain pine beetle population phase transitions at Angstad Creek (stands A, B, and F), but not Aberdeen Plateau (increases in stand E likely resulted from of immigration for reasons described earlier). This suggests that either the apparent resource pulses at the Aberdeen Plateau stands were insufficient to support transitions, or perhaps that the large populations of early-season lower-stem beetles in stands D and G outcompeted the late-season mountain pine beetle for food and space within low-vigor trees (Rankin and Borden 1991; Safranyik et al. 1999) and thus had an overall antagonistic rather than facilitatory effect. Thus, at the landscape-level, it may appear that extreme bioclimatic stressors inevitably lead to population phase transitions, but at the stand-level, such predictions may fail to materialize due to local effects of host-availability or competition.

It is well known that mountain pine beetles are associated with large trees during their irruptive phase (Amman 1969, Safranyik and Carroll 2006; Raffa et al. 2008). This association can sometimes be interpreted as a global preference for large trees, and hence that removing large trees can prevent outbreaks. However, we have shown that beetles at endemic densities primarily attack smaller stressed and suppressed trees and only after transitioning past a critical density primarily attacked trees that are larger, have higher growth rates, and contain thicker phloem (Figure 3A-C). Further, the high spatial correlation of attacks on larger trees (Figure 6) highlights the extent to which local aggregation among neighboring trees facilitates changes in host utilization. Our results do not preclude the possibility of an underlying environmental

gradient that may contribute to observed patterns, but the convergence of significant interactions among tree size, aggregation, and decreased reliance on prior stressors at similar distances and population densities makes that explanation less likely. Further, these patterns were only observed in stands where aggregation resulted from within-stand dynamics. Collectively, these observations support a density-dependent model of beetle host selection in which endemic beetles avoid well-defended hosts but epidemic beetles exploit them (Wallin and Raffa 2004; Boone et al. 2011; Powell et al. 2012; Lindgren and Raffa 2013; Burke and Carroll 2017).

The interaction of spatial, behavioral, and ecological processes that govern endemic persistence and phase transitions we describe here is generalizable to other tree-killing bark beetles. However, the specific features that structure the endemic niche vary among geographic regions, host-tree, and beetle species. For example, mountain pine beetle endemic populations in some regions are largely maintained in trees affected by wildfire or fungi (Nebeker et al. 1995; Powell et al. 2012). Similarly, endemic populations of southern pine beetle (*Dendroctonus frontalis* Zimmermann) are maintained largely in lightning-struck trees that are distributed relatively randomly, but subsequent outbreaks show high contagion (Coulson et al. 1983; Martinson et al. 2013). Also, European spruce beetles (*Ips typographus* L.) disperse over large distances to locate trees downed by storm damage, generating strong Allee effects at low densities, but can transition into outbreaks depending on the amount and spatial configuration of windthrown trees (Liebhold and Tobin 2008; Kausrud et al. 2012). Douglas-fir beetles (*Dendroctonus pseudotsugae* Hopkins) typically prefer low-vigor or dead hosts (Furniss 1981, Powers et al. 1999; 2016), but increased tree mortality can occur following defoliator outbreaks, again with the scale of beetle outbreaks varying with the dispersal ability and intensity of different defoliator species (Hadley and Veblen 1993; Schaupp et al. 2008; Negron et al. 2014).

In each of these cases, transition from endemic to eruptive phases involves an integration of stand-level biotic or abiotic stressors, largescale region-wide stressors, and plasticity in beetle host selection behavior, with attributes of stand- and landscape- scale stressors and species-specific behavior generating system-specific dynamics (Raffa et al. 2008; Stephenson et al. 2019; Ward and Aukema 2019).

For most bark beetle species, system-specific properties preclude the behavioral shift needed to generate self-amplifying dynamics (Raffa et al. 2008). For example, *I. pini* in this study showed only minor decreases in reliance on prior stressors as its population increased, similar to the minor decreases in reliance on lower stem beetle-fungal complexes it shows in red pine (*Pinus resinosa* Sol. Ex Aiton) in Wisconsin (Aukema et al. 2010). Likewise, *I. grandicollis* Eichhoff colonized large numbers of jack pine (*Pinus banksiana* Lamb.) following defoliation by *Choristoneura pinus* Freeman, and *Ips confusus* Wood & Bright colonized large numbers of pinyon pine (*Pinus edulis* Engelm.) following drought, but in both cases bark beetle populations subsided when the stress declined (Wallin and Raffa 2001; Raffa et al. 2008).

These results have several implications to improved management of bark beetles. First, empirically quantifying the threshold at which populations shift from stress-dependent to self-driving growth allows managers to target their efforts accordingly. This threshold provides a useful juncture beyond which stand-level management strategies are less likely to contain populations, short of aggressive large-scale sanitizing cuts. Second, identifying related density-dependent changes in host utilization provides opportunities for proactive management plans such as thinning from below (i.e., removing suppressed trees). Such strategies are likely to be particularly important for preventing outbreaks in large-scale commercial forestry settings. Further, our results provide guidance for the monitoring and modeling of beetle populations. For

example, the critical phase threshold we quantify occurs below or near the density at which tree mortality is likely to be detected by aerial surveys (Cooke and Carroll 2017). Thus, models based on aerial detection data are more useful for understanding the spread of outbreaks rather than factors that drive their onset. Also, unbaited traps did not prove to be useful at low beetle densities. Together these results indicate that integrated aerial, pheromone-based, and ground surveys are required for effective monitoring and management.

There are several limitations to our study. First, mensurational data were not collected on all trees or in a sufficiently high-resolution grid, both of which could benefit more formal point process models. Such data could also help partition the extents to which interactions between the size and clustering of attacked trees arise from beetle switching behavior or an underlying environmental gradient. Further, high-resolution marked point process models with temporal autocorrelation are still in their infancy (Diggle 2013; Badley and Turner 2016). Such models could help account for the temporal dependence among years within the same stand and help disentangle interactions among bark beetle groups.

Thresholds and density-dependent feedbacks are critical components of the phase transitions of irruptive insect species (Roffey and Popov 1968). In bark beetle systems, cross-scalar interactions of spatial colonization pattern, host availability, host quality, and herbivore behavior serve as both important inputs and outputs of population dynamics. External drivers such as biotic stressors can add momentum to the system, thus allowing populations to transition between ‘quasi-stable’ population states (Lindgren and Raffa 2013). These interacting processes merit further investigation to better inform management by improving predictions of when and where irruptive insects will undergo population transitions and under what circumstances they are most amenable to intervention if desired.

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483

484 **Declarations**

485 We declare no conflicts of interest.

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- 664

Figure Captions

Figure 1: Location of sites within British Columbia and mensurational characteristics ($\pm$ SE when noted). DBH corresponds to diameter at breast height, and %LPP to the percent of lodgepole pine in a given stand.

Figure 2: Density dependent relationships between the stand-scale proportion of attacked trees with prior stressors (A-C) and the tree-scale probability an attacked tree contains a prior stressor (D-F) for three beetle guilds, the threshold limited mountain pine beetle (A,D); pulse-driven *Ips pini* (B,E), and lower-stem beetles (C,F). Points in all panels correspond to the proportion of attacked trees with prior stressors per stand. Colors denote beetle species. A detailed list of prior stressors is provided in Supplemental Table 1.

Figure 3: Relationships between A) diameter at breast height; B) 5-year mean annual increment; and C) phloem thickness vs. the number of attacked trees/ha; and D) the characteristics associated with trees attacked by each guild. Colors denote species. Lines (A-C) are fit with least-squares and only shown for significant relationships ($\alpha=0.05$). Points (D) correspond to principal components analysis of trees attacked by each guild. Screeplots are provided in Supplemental Figure 1.

Figure 4: Spatial dynamics of trees attacked by mountain pine beetle from 1999-2005, separated into A) those stands where patterns of attacked trees shifted from random to aggregated; and B) those stands where transitions either did not occur (stands D & G), or presumably occurred because of immigrating beetles (Carroll et al. 2006). Points correspond to each attacked tree and colors denote beetle species. Observed L(r)-r functions are provided for each year/stand/guild in Supplemental Figure 3.

Figure 5: Dynamics of spatial aggregation as a function of increasing population size, depicting our interpretation of each observed $L(r)$ - r function (Supplemental Figure 3). Points correspond to each year-stand combination and colors denote species. Shapes denote our confidence in the interpretation where X denotes point patterns with too few observations to interpret, open circles denote point patterns where there was not significant aggregation, circles with crosses denote point patterns that were significant, but barely, and filled circles denotes point patterns where there was significant evidence of aggregation. The grey vertical box denotes the proposed aggregation threshold. Since our interpretations may be construed as subjective, we provide an alternative nearest-neighbor approach in Supplemental Figure 4.

Figure 6: Conditional spatial correlation of tree size at each stand. Curves are fit with all species since the conditional mean behaves better with equally spaced distances and the curve for stand B corresponds to 1999-2003 since we are primarily interested in the initial aggregation phase.

Supplemental Figures

Figure 1: Screeplots for principal components analysis, depicting A) the variability explained by each dimension; and the factors contributing to the B) 1st, C) 2nd, and D) 3rd dimensions.

Figure 2: Walkthrough of hypothesis testing process given a small (200 x 200 m) window from stand A in 2005. The example is testing whether the distribution of trees attacked by mountain pine beetle is more (aggregation) or less (inhibition) spatially correlated than randomly distributed points (Poisson) based on the underlying joint density of beetle attacks. Point color denotes bark beetle guild for threshold limited (i.e., mountain pine beetle; black) and lower-stem (yellow). Gradient color denotes intensity of the joint density and is depicted on different scales for each null hypothesis. Scales are not shown because the relative intensity is more important than the realized values.

Figure 3: Alternative hypothesis testing for the spatial configuration of attacked trees based on A) a nearest-neighbor approach (Clark Evan's Aggregation Index) and B) how our interpretations of observed L(r)-r functions compares. Colors denote bark beetle guild. Shapes in **A** correspond to significance assessed at the $\alpha=0.01$ level where filled circles denote significant and open circles denote not significant. Shapes in **B** correspond to our interpretation of the observed L(r)-r functions, where filled circles denote significant aggregation, circles with crosses denote weak significant aggregation (i.e., the observed L(r)-r function barely exceeded the significance bands), open circles denote no significant aggregation, and X's denote stand/year/guild combinations where there were fewer than 5 attacked trees.

722 **Supplemental Tables**

723 **Supplemental Table 1:** Criteria used to estimate the number of years since initial complete (A)
724 or partial (B) attacks by bole-infesting bark beetles on lodgepole pine trees. Adopted from Carroll
725 et al. (2006).

726 **Supplemental Table 2:** Distribution of prior stressors A) in each stand, and B) the number of
727 trees with at least 0, 1, 2, 3, or 4 stressors.

728 **Supplemental Table 3:** Observed L(r)-r functions for each guild/stand/year combination.
729 Patterns not shown contained less than five attacked trees. Panels for each point pattern
730 correspond to different null hypotheses of the underlying spatial distribution of available host
731 trees. We provide our interpretation of whether each pattern exhibits significant aggregation or
732 inhibition in the right-hand columns.

Figures

Stand	Elevation (m)	Area (ha)	Age (yrs±SE)	Density (trees/ha±SE)	Basal Area (m ² /ha±SE)	DBH (cm±SE)	%LPP
A	1163	16.7	110.5 (1.52)	1265 (252.9)	41.5 (6.9)	22.8 (0.61)	92.5
B	1121	17.6	116.5 (1.18)	1273 (190.4)	43.9 (6.7)	24.1 (0.58)	94.5
D	1384	13.0	119.2 (1.97)	1325 (153.2)	37.0 (4.1)	21.5 (0.63)	90.4
E	1346	7.9	90.7 (2.56)	1257 (249.6)	37.6 (5.9)	21.2 (0.91)	90.6
F	1204	11.9	148.9 (1.55)	807 (148.4)	30.6 (5.3)	28.2 (0.80)	80.1
G	1426	14.9	108.6 (0.58)	1424 (115.0)	49.6 (4.4)	22.5 (0.43)	94.2

Figure 1

Location of sites within British Columbia and mensurational characteristics (±SE when noted). DBH corresponds to diameter at breast height, and %LPP to the percent of lodgepole pine in a given stand.

Figure 2

Density dependent relationships between the stand-scale proportion of attacked trees with prior stressors (A-C) and the tree-scale probability an attacked tree contains a prior stressor (D-F) for three beetle guilds, the threshold limited mountain pine beetle (A,D); pulse-driven *Ips pini* (B,E), and lower-stem beetles (C,F). Points in all panels correspond to the proportion of attacked trees with prior stressors per stand. Colors denote beetle species. A detailed list of prior stressors is provided in Supplemental Table 1.

Figure 3

Relationships between A) diameter at breast height; B) 5-year mean annual increment; and C) phloem thickness vs. the number of attacked trees/ha; and D) the characteristics associated with trees attacked by each guild. Colors denote species. Lines (A-C) are fit with least-squares and only shown for significant relationships ($\alpha=0.05$). Points (D) correspond to principal components analysis of trees attacked by each guild. Screeplots are provided in Supplemental Figure 1.

Figure 4

Spatial dynamics of trees attacked by mountain pine beetle from 1999-2005, separated into A) those stands where patterns of attacked trees shifted from random to aggregated; and B) those stands where transitions either did not occur (stands D & G), or presumably occurred because of immigrating beetles (Carroll et al. 2006). Points correspond to each attacked tree and 685 colors denote beetle species. Observed $L(r)$ - r functions are provided for each year/stand/guild in Supplemental Figure 3.

Figure 5

Dynamics of spatial aggregation as a function of increasing population size, depicting our interpretation of each observed $L(r)-r$ function (Supplemental Figure 3). Points correspond to each year-stand combination and colors denote species. Shapes denote our confidence in the interpretation where X denotes point patterns with too few observations to interpret, open circles denote point patterns where there was not significant aggregation, circles with crosses denote point patterns that were significant, but barely, and filled circles denote point patterns where there was significant evidence of aggregation. The grey vertical box denotes the proposed aggregation threshold. Since our interpretations may be construed as subjective, we provide an alternative nearest-neighbor approach in Supplemental Figure 4.

Figure 6

Conditional spatial correlation of tree size at each stand. Curves are fit with all species since the conditional mean behaves better with equally spaced distances and the curve for stand B corresponds to 1999-2003 since we are primarily interested in the initial aggregation phase.

Supplementary Files

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