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Climate change and range expansion of an aggressive bark beetle: evidence of higher beetle reproduction in naïve host tree populations

Timothy J. Cudmore[1], Niklas Björklund[2], Allan L. Carroll[3] and B. Staffan Lindgren[1]*

[1]Natural Resources and Environmental Studies Institute, University of Northern British Columbia, Prince George, BC, Canada; [2]Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden; and [3]Department of Forest Sciences, University of British Columbia, Vancouver, BC, Canada

Summary

1. Hosts may evolve defences that make them less susceptible and suitable to herbivores impacting their fitness. Due to climate change-driven range expansion, herbivores are encountering naïve host populations with increasing frequency.

2. Aggressive bark beetles are among the most important agents of disturbance in coniferous forest ecosystems. The presence of bark beetle outbreaks in areas with a historically unsuitable climate, in part a consequence of climate change, provided an opportunity to assess the hypothesis that the mountain pine beetle *Dendroctonus ponderosae* has higher reproductive success in lodgepole pine *Pinus contorta* trees growing in areas that have not previously experienced frequent outbreaks.

3. We felled and sampled mountain pine beetle-killed trees from historically climatically suitable and unsuitable areas, i.e. areas with and without a historical probability of frequent outbreaks. Reproductive success was determined from a total of 166 trees from 14 stands.

4. Brood productivity was significantly affected by climatic suitability class, such that mean brood production per female increased as historical climatic suitability decreased.

5. *Synthesis and applications*. The current study demonstrates that the mountain pine beetle has higher reproductive success in areas where its host trees have not experienced frequent beetle epidemics, which includes much of the current outbreak area in north central British Columbia. This increased productivity of mountain pine beetle is likely to have been a key reason for the rapid population buildup that resulted in unprecedented host tree mortality over huge areas in western Canada. The outbreak thus provides an example of how climate change-driven range expansion of native forest insects can have potentially disastrous consequences. Since an increased reproductive success is likely to accelerate the progression of outbreaks, it is particularly critical to manage forests for the maintenance of a mosaic of species and age classes at the landscape level in areas where host tree populations are naïve to eruptive herbivores.

Key-words: climate change, climatic suitability class, co-evolution, lodgepole pine, mountain pine beetle, range expansion, reproductive success, selection pressure, suitability, susceptibility

Introduction

The geographical distributions of most insect species are constrained by their climate tolerances. Global climate change is likely to alter the range of areas potentially suitable for habitation (Rosenzweig *et al.* 2007), as evidenced by a rapidly increasing number of reports showing significant recent range shifts toward higher latitudes and higher elevations (Williams & Liebhold 2002; Rosenzweig *et al.* 2007; Jepsen *et al.* 2008; Raffa *et al.* 2008).

The mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae: Scolytinae), is the most destructive bark beetle in mature lodgepole pine *Pinus contorta* Dougl. Ex Loud.var. *latifolia* Engelm. forests in western North America (Wood 1963; Safranyik, Shrimpton & Whitney 1975; Amman *et al.* 1977; Safranyik & Carroll 2006). It is considered the most destructive of all western forest insects (Furniss & Carolin 1977), affecting an average of 50,000 ha per year of forested lands in British Columbia alone (Wood & Unger

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*Corresponding author: E-mail: lindgren@unbc.ca

1996). Large epidemics occur periodically (Taylor *et al.* 2006), in which more than 80% of host trees over 10-cm diameter at breast height (dbh) may be killed over large expanses (Safranyik 1988a). In the current outbreak in western Canada, the cumulative area affected (including 'trace' infestations, i.e. < 1% mortality in a given area) since the beginning of the outbreak in the mid- to late1990s had reached approximately 13 million ha by the end of 2008 (Fig. 1a; Kurz *et al.* 2008). The infestation has also spread into areas further north and at higher elevations than recorded previously (Carroll *et al.* 2004).

Prior to 1970, mountain pine beetle infestations occurred most commonly in the southern half of British Columbia (east of 122° longitude and south of 54° latitude) as well as in southwestern Alberta in Canada, and in 12 of the western states in the United States (Safranyik & Carroll 2006). The distribution of the mountain pine beetle is not limited by the range of its primary host tree, lodgepole pine, which extends into the Yukon and the Northwest Territories. Instead, it is excluded from higher latitudes and elevations by adverse climatic conditions (Amman 1973; Safranyik 1978). In fact, Safranyik (1978) found that Hopkins Bioclimatic Law (Hopkins 1919), which states that every 1°N latitude increase is roughly equivalent to 120 m increase in elevation, applies extremely well to the range of mountain pine beetle in terms of altitudinal and latitudinal boundaries. In a meta analysis of previous outbreaks Björklund & Lindgren (2009) confirmed the strong influence of elevation and latitude on mountain pine beetle attack dynamics. For instance, near the northern margin of the beetle's historic range, the altitudinal limit for beetle survival is roughly 750 m

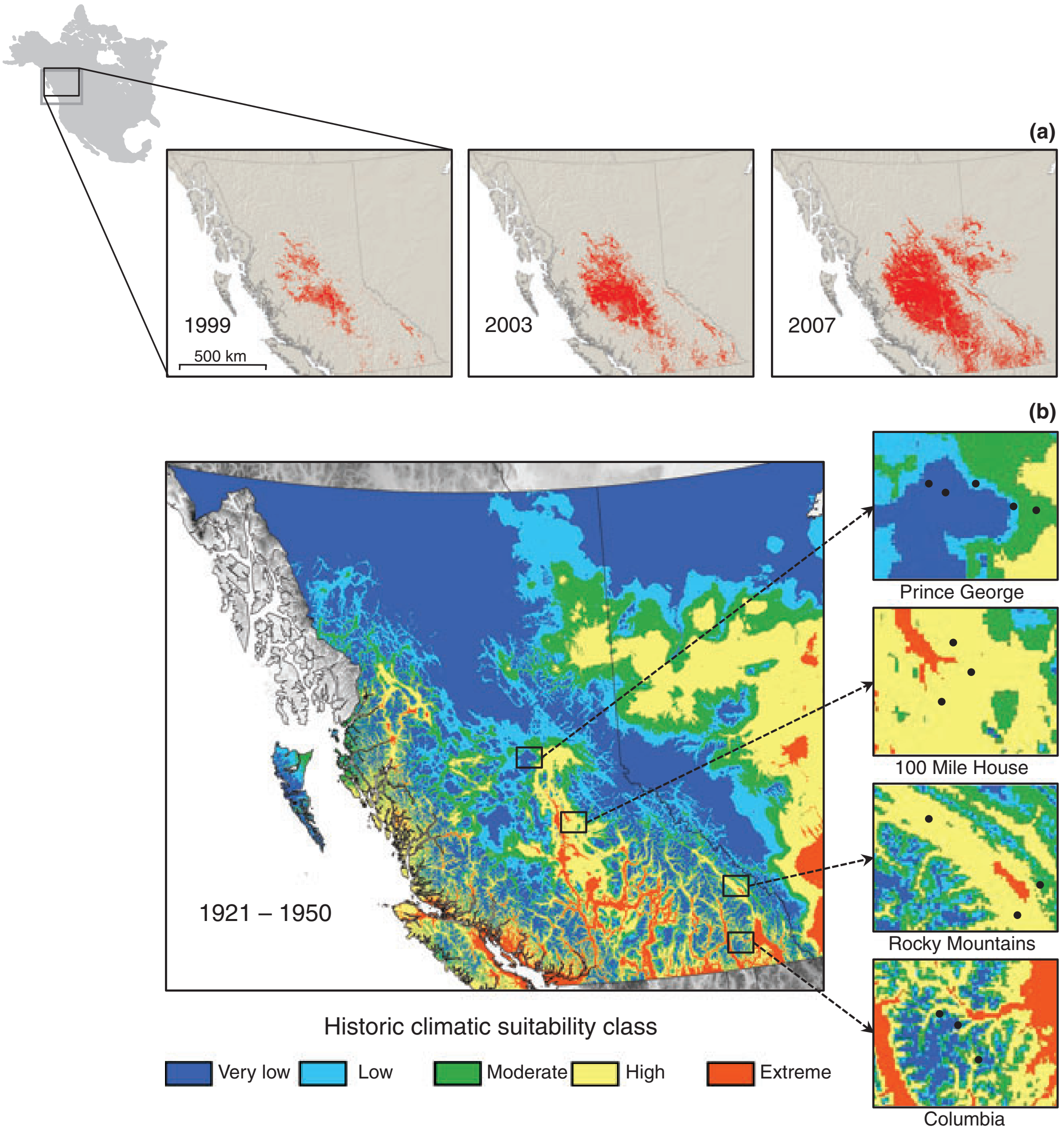

Fig. 1. (a) Development of the mountain pine beetle *Dendroctonus ponderosae* outbreak in western Canada from 1999 to 2007 [infestations indicated in red (data courtesy of the British Columbia Ministry of Forests and Range, and Alberta Sustainable Resources Development)], and (b) the distribution of historic climatic suitability classes (CSCs) during 1921 to 1950 (adapted from Carroll *et al.* 2004); extreme CSCs indicate climatically optimal habitat, whereas very low CSCs denote climatically unsuitable habitats. Insets indicate regions sampled; points indicate locations of individual sample stands.

above sea level, while at the southern margin the altitudinal limit is approximately 3650 m (Struble & Johnson 1955).

The current mountain pine beetle outbreak in western Canada encompasses its historic range, but is now also prevalent in areas where outbreak populations have not been previously recorded (Taylor *et al.* 2006) because of an unsuitable climate (Carroll *et al.* 2004). For example, the portion of the current outbreak that was initiated in Tweedsmuir Provincial Park (Aukema *et al.* 2006) falls into the latter category (Fig. 1b). The presence of outbreaks in areas with a historically unsuitable climate provides an opportunity to assess the potential impact of long-term exposure to bark beetle-caused mortality on lodgepole pine–bark beetle interactions. No such assessment has been made previously.

Based on work by Safranyik *et al.* (1975), Carroll *et al.* (2004) developed a model of climatic suitability to the mountain pine beetle. The model determines climatic suitability based on four primary variables: (i) sufficient degree-day accumulations for the beetle to maintain a synchronized, univoltine life cycle, (ii) the occurrence of lethal winter minimum temperatures, (iii) temperatures during the dispersal period, and (iv) spring precipitation deviation (see http://warehouse.pfc.forestry.ca/pfc/25051.pdf for details). Using historic climatic conditions and a spatially explicit climate-driven simulation tool to account for elevation, slope and aspect (BioSIM) (Régnière 1996), the model produces maps of historic climatic conditions (in 64-ha cells) relevant to the mountain pine beetle (Fig. 1b). Carroll *et al.* (2004) generalized their climatic suitability index into five climatic suitability classes (CSCs): very low, low, moderate, high and extreme. Prior to 1970, no mountain pine beetle infestation had been recorded in either 'very low' or 'low' CSCs (Safranyik *et al.* 1975; Carroll *et al.* 2004). When overlaying mountain pine beetle infestation data on historic climatic suitability maps, Carroll *et al.* (2004) reported an expansion in the range of climatically suitable habitats, as well as an increase (at an increasing rate) in the number of infestations since 1970 in previously climatically unsuitable habitats.

Conifers are well defended against herbivory by both constitutive and induced defences (Franceschi *et al.* 2005). In the Pinaceae, these defences have evolved at least in part as a consequence of adaptive pressure brought to bear by eruptive bark beetles and their symbiotic bluestain fungi. Where eruptive populations have not been present, or at least not frequent, it is conceivable that defence capabilities at the population level would be relatively low (Herms & Mattson 1992), resulting in 'defence-free space' (Ghandi & Herms 2010; Raupp, Shrewsbury & Herms 2010). Specifically, lodgepole pine was shown to differ with respect to their defensive monoterpenes in areas with and without historic mountain pine beetle presence (Clark 2008); however, the effects on insect reproduction have never been studied.

This study was conducted to investigate potential differences in mountain pine beetle productivity as a function of historic climatic suitability in areas with high host tree abundance in British Columbia. We assessed the hypothesis that due to long-term interactions in areas where the climate has been historically favourable for the mountain pine beetle, host trees will be less suitable for reproduction than in areas where the beetle has not frequently reached epidemic levels in the past. More specifically, we tested the prediction that the suitability of trees for the mountain pine beetle, as indicated by brood productivity, should decline with increasing frequency and intensity of outbreaks. We used historic climatic suitability classification (Carroll *et al.* 2004) to test this prediction, as a higher reproductive rate in naïve hosts could lead to more severe outbreaks. This would in turn have significant implications for the importance of host population management at the landscape level.

Materials and methods

Data were collected in 2005 and 2006. Those collected in 2005 were a subset of a more extensive study on the effect of host diameter on susceptibility and suitability for the mountain pine beetle (Björklund *et al.* 2009). Data from 2006 were generated specifically to test our prediction. Thus, the methods described below differ slightly between years.

STUDY SITES

We attempted to establish study sites in areas that were historically climatically unsuitable (i.e. very low or low CSCs) or suitable (i.e. moderate, high or extreme) to mountain pine beetle. Sampling was conducted in two geographic regions (northern and southern British Columbia) during the summer of 2005, and in two additional regions (intermediate in latitude to the above) during the summer of 2006 (Fig. 1b). In 2005, trees were sampled in the Prince George Forest District (approx. 53·9°N, 123·5°W) and in the Rocky Mountain Forest District (approx. 49·5°N, 116·2°W).

As all forest land in British Columbia has been classified into biogeoclimatic zones based on macroclimate, vegetation and soils (Meidinger & Pojar 1991), it is possible to use this classification scheme to minimize variation relating to local environmental factors among selected research sites. Thus, we included two biogeoclimatic zones, Sub-Boreal Spruce (SBS) (Meidinger, Pojar & Harper 1991) and Engelmann Spruce-Subalpine Fir (ESSF) (Coupé, Stewart & Wikeem 1991) in the current study as a means of minimizing within-region variation and to facilitate comparison of beetle population parameters among regions. Thus, within each Forest District, sampling was confined as much as possible to the same biogeoclimatic subzone (BGCSZ) (Meidinger & Pojar 1991). Stands in the Prince George Forest District were in the Sub-Boreal Spruce dry-warm subzone (Meidinger, Pojar & Harper 1991) and in 'very low', 'low', and 'moderate' historic climatic suitability classes based on 1921–1950 climate normals (Table 1; Fig. 1b) (Carroll *et al.* 2004). This time interval was selected as representative of climatic conditions prior to the current rapid warming trend (e.g. IPCC 2007). Stands in the Rocky Mountain District were in the Engelmann Spruce-Subalpine Fir dry-mild subzone (Coupé *et al.* 1991) and in 'moderate' and 'high' CSCs based on 1921–1950 climate normals. Given present day climatic conditions (i.e. means during 1981–2007), both the Prince George and Rocky Mountain Forest District stands were in either 'moderate' or 'high' CSCs (see Table 1; Fig. 1b).

In 2006, study sites were identified by conducting an intersection of three spatial data layers using a geographic information system. These layers were historic CSC, biogeoclimatic subzone, and recent mountain pine beetle infestation as recorded from aerial surveying. Only polygons where this intersection was ≥10 ha were considered. Sampling was conducted in the 100 Mile House Forest District

Table 1. Summary data for the stands sampled in all four regions (2005 and 2006). Pine mortality is the % killed of available lodgepole pine in the stand. Historic climatic suitability classes are based on 1921–1950 climate normal, while current classes are based on the period 1981–2007 (Carroll *et al.* 2004)

Forest district	Elevation (m)	Climatic suitability class		Biogeo-climatic subzone	# Plots (for stand data)	# Felled trees	Mean age	Pine (%)	Pine mortality (%)
		Historic	Current						
Prince George	781	Very low	High	SBSdw	8	15	111	75	32
	850	Moderate	High	SBSdw	9	21	151	79	45
	883	Very low	Very low	SBSdw	8	15	89	97	39
	938	Low	High	SBSdw	7	11	146	68	57
	898	Low	High	SBSdw	8	16	148	82	58
Rocky Mountain	1491	High	High	ESSFdm	4	8	111	91	64
	1756	Moderate	Moderate	ESSFdm	7	10	103	92	34
	1473	High	High	ESSFdm	8	10	109	99	37
100 Mile House	976	High	High	SBSdw	6	10	120	90	62
	956	High	High	SBSdw	4	10	120	99	73
	1003	High	High	SBSdw	10	10	122	94	69
Columbia	1870	Low	Low	ESSFdk	4	10	152	81	14
	1640	Moderate	Moderate	ESSFdk	6	10	160	60	35
	1775	Low	Low	ESSFdk	4	10	138	63	36

(approx. 52·0°N, 121·2°W) and the Columbia Forest District (approx. 51·1°N, 116·3°W). Stands in the 100 Mile House District were in the Sub-Boreal Spruce dry-warm subzone (Meidinger, Pojar & Harper 1991), i.e. the same as the 2005 stands in the Prince George Forest District, but in 'high' historic CSCs (Table 1; Fig. 1b). Stands in the Columbia Forest District were in the Engelmann Spruce-Subalpine Fir dry-cool subzone (Coupé *et al.* 1991) and in 'low' and 'moderate' historic CSCs (Table 1; Fig. 1b) (Carroll *et al.* 2004). Stands in the dry-mild subzone, i.e. the subzone of the Rocky Mountain Forest District stands sampled in 2005, were not available, so we considered these subzones equivalent for the purpose of this study.

STAND SELECTION AND SAMPLING

In 2005, five lodgepole pine-leading stands, 80 years or older, and of similar density, in the Prince George Forest District and three in the Rocky Mountain Forest District were sampled. All stands were at least 1 km apart. A baseline was installed at a randomly selected angle from a point of commencement. Transects off the baseline were then established at randomly selected distances between 80 and 150 m by selecting numbers from a random number table, and a minimum of eight variable radius plots per stand were established at random distances along these transects. Each plot was surveyed using a prism with a basal area factor of 4, and tree species, dbh, and attack status were recorded for each tree over 7·5-cm dbh.

In 2006, using the same selection criteria as described above, three stands in the 100 Mile House Forest District and three in the Columbia Forest District were sampled. Four to ten variable radius plots per stand (see Table 1 for exact numbers) were established using randomly selected distances from points where trees were felled (see below). From each of these points, transects were installed at 90°, 180°, 270°, and 360°. A variable radius plot was established at a random distance, between 80 and 150 m, along any or all of these bearings, as long as they fell within the stand. Each plot was surveyed using a prism with a basal area factor of 4, and the same information was collected as in 2005. Percentage mortality, diameter distribution, and species composition of each stand were determined from the plot data.

SAMPLE-TREE SELECTION

To maintain an equal representation of diameters for each sample stand, six (2005) or five (2006) trees from each of the two diameter classes, 25–30 cm and > 30 cm, were selected if available. Only trees in those diameter classes that met the following criteria were chosen for felling: beetles had completed their development and emerged from the tree; there were no major wounds, scars or forks which might influence the vigour of trees at the time of attack; and trees were a minimum of 50 m from edges of stands, lakes or any open area to prevent edge effects.

In 2005, three trees were selected and felled for sampling at each plot. If the correct diameter class was not available among trees within a given plot, the closest appropriate tree to the plot centre along the transect to the next plot was felled. In 2006, the three trees closest to each plot centre were selected and felled for sampling.

BROOD SAMPLING

After felling, the attacked portion of the bole, defined as the distance from the base of the tree to the highest pitch tube and/or gallery start, was cut into three equal segments. The sampling unit was a 15 × 30-cm rectangle (Safranyik 1968) cut in the bark at the midpoint of each of the three segments.

On each segment, gallery start and pupal chamber densities were obtained by peeling off the outer bark on the north aspect of the bole, where attack densities tend to be highest (Safranyik & Carroll 2006), to reveal the starting point of each gallery within the sample square, as well as each individual pupal chamber. All values were standardized and expressed as the number per square metre.

DATA ANALYSES

The mean number of brood beetles produced per m^2 was calculated for each tree from the mean gallery start and pupal chamber densities per tree from the three segments. A mixed model ANOVA was conducted to analyse the effects of historic climate (CSC) and attack density on mountain pine beetle brood production, with biogeoclimatic zone and stand as random variables. A Levene's test ($P < 0{\cdot}05$) indicated the need for a square root transformation of the data to satisfy the assumption of homogeneity of variances ($P = 0{\cdot}774$).

The level of significance was set at $\alpha = 0{\cdot}05$ for all statistical tests. Data were analysed using SYSTAT 12 (Systat Software, Inc., Port Richmond, CA, USA). Graphs of untransformed data were created using SigmaPlot 6.0 (Systat Software, Inc.).

Results

SITE AND STAND CHARACTERISTICS

The overall species composition varied among stands, but was considered comparable for the purpose of this analysis since lodgepole pine was dominant (60–99%) in all stands (Table 1). Percentage mortality of available lodgepole pine was highest in the 100 Mile House Forest District (69%), followed by the Prince George Forest District (67%), Rocky Mountain Forest District (55%) and Columbia Forest District (28%) (Table 1).

BROOD PRODUCTION

The mean number of brood beetles produced per attacking female was significantly affected by historic climatic suitability class ($F = 8{\cdot}79$, df = 3, 8·8, $P = 0{\cdot}005$) (Fig. 2), increasing as suitability decreased. There was a significant negative effect of attack density on brood productivity, as expected ($F = 22{\cdot}68$, df = 1, 13·7, $P < 0{\cdot}001$). There was no significant interaction between historic climatic suitability class and attack density ($F = 0{\cdot}709$, df = 3, 79·7, $P = 0{\cdot}549$) (Fig. 3).

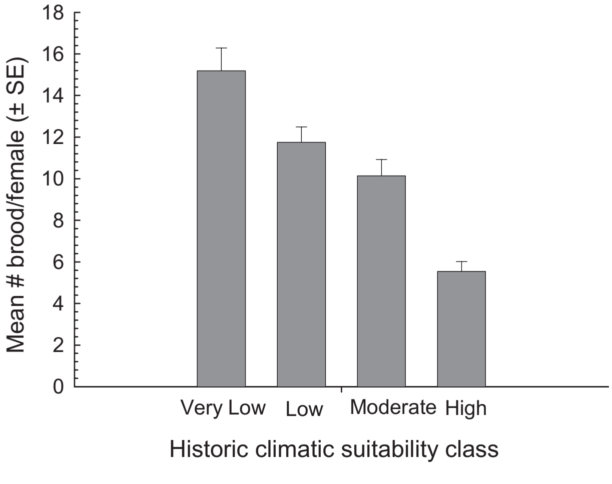

Fig. 2. Effect of historic climatic suitability class (Carroll *et al.* 2004) on the number of brood beetles produced per female. The effect was highly significant ($F = 4{\cdot}358$, df = 3327, $P = 0{\cdot}005$).

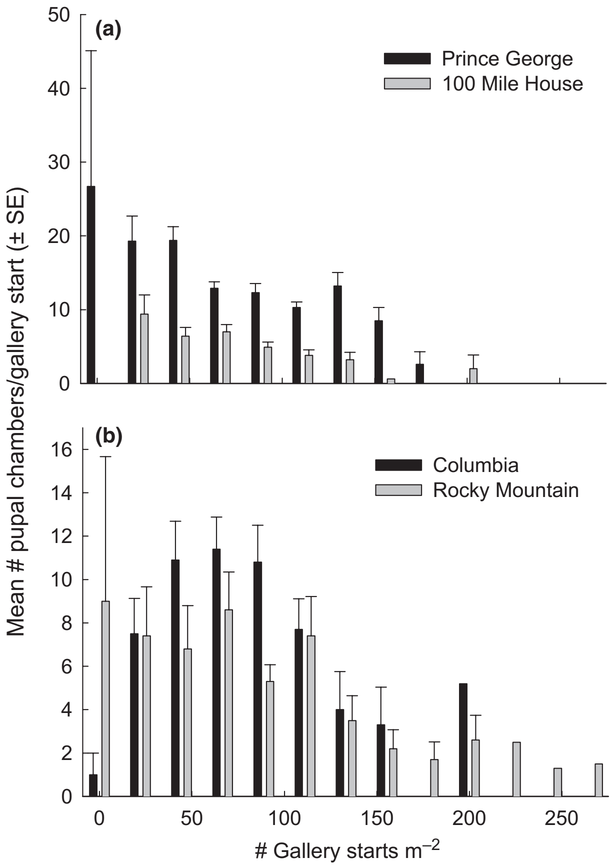

Fig. 3. Brood beetle production per female at different gallery start densities comparing sites in historically suitable (grey bars) and unsuitable (black bars) (Carroll *et al.* 2004). (a) Stands in the Sub-Boreal Spruce biogeoclimatic zone; (b) Stands in the Engelmann Spruce-Subalpine Fir biogeoclimatic zone. Note differing *y*-axis scales.

Discussion

Research into the effects of climate on mountain pine beetle populations has led to the prediction that the beetle's range will expand further north and to higher elevations based on current climate change modelling (Logan & Powell 2001; Carroll *et al.* 2004). According to the Intergovernmental Panel on Climate Change Fourth Assessment Report, even with significant mitigation efforts global mean temperature is expected to rise by several degrees by the end of the 21st century (IPCC 2007). A 3 °C change in mean annual temperature would correspond to a 300–400-km latitudinal shift in isotherms, or 500 m in elevation (Hughes 2000). Logan & Powell (2001) predicted that a warming of 2·5 °C would result in a 7° northward shift in climatically suitable habitats, and render much of the boreal forest suitable to the mountain pine beetle.

Range expansion by native forest insects as a result of a changing climate may have significant consequences for forest managers by increasing areas prone to potential broad-scale disturbance and/or altering insect–host tree interactions and limiting the capacity to predict pest behaviour based on empirical relationships. Overall, our results indicate that the mountain pine beetle has a higher reproductive success in lodgepole pine forests that have not previously experienced significant infestation due to climatic limitations than in areas where the insect has putatively exerted evolutionary pressures on its host through periodic outbreaks. Much of the most extensive lodgepole pine mortality in north central British Columbia during the current outbreak occurred west of 122° longitude, an area dominated by historically unsuitable climatic conditions (Carroll *et al.* 2004). In the absence of limiting climatic conditions, e.g. lethal winter temperatures or unsuitably cool summers, the higher rate of reproduction in areas with historically unsuitable climatic conditions may be a key reason for the observed rapid population buildup with resulting unprecedented host tree mortality over huge areas (Kurz *et al.* 2008), demonstrating the critical importance of managing forests for a mosaic of species and age classes at the landscape level.

We found surprisingly high brood productivity in areas with historically unsuitable climate. Safranyik (1988b) found an average of 5·2 brood beetles per female, and Reid (1963) found an average emergence of 6·6 beetles per female (calculated from table IV). These results are consistent with ours in areas with high historic climate suitability (Fig. 2), but much lower than in areas with low historic climatic suitability. Both Safranyik (1988b) and Reid (1963) conducted their studies during incipient epidemics, when mostly large diameter trees are attacked, whereas our study was conducted during a severe outbreak. Thus, we expected lower average productivity as attack densities, and hence intraspecific competition, would be expected to be higher during epidemics. Instead we found that brood productivity increased as historic climate suitability decreased, and in stands with very low historic suitability the brood production was more than twice as high as in stands with high suitability (Fig. 3).

The average attack densities in trees from areas with historically unsuitable climates (very low or low; 71·5 ± 4·57 SEM) did not differ from those in areas with historically suitable climate (moderate and high; 70·1 ± 3·34 SEM). These means are close to what Berryman *et al.* (1985) determined to be the optimal attack density ($\sim$75 attacks m^{-2}). Furthermore, although the percentage pine mortality in the Columbia Forest District was much lower than the other three regions, attack densities remained similar (72·0 ± 3·24 SEM vs. 70·4 ± 7·77 SEM in all other stands). Consequently, our assumption that 'beetle pressure' at the tree-level may be considered similar in all stands appears valid. Tree-level beetle pressure may be viewed as a function of the local population available to respond to aggregation pheromones produced by beetles in the process of colonization of a tree, and hence contributing to the rate of attack on that tree. The rate of attack is in turn critical in determining final attack density (Raffa & Berryman 1983).

The mean elevation for the sites in the Columbia Forest District was higher than in the Rocky Mountain Forest District, and normally this would be a cause for lower productivity (Amman 1973); however, productivity in these stands was as high or higher at equivalent attack densities (Fig. 3b). In addition, all sites but one in the other three forest districts are currently suitable ('moderate' or 'high') CSCs (based on the 1981–2007 data), while two of the Columbia sites have remained 'low', and the third site has remained 'moderate' (Table 1). Therefore, the productivity observed in the Columbia stands would probably have been even higher, and similar to the Prince George sites, had the current climate become more suitable.

The interaction between bark beetles and their host trees is ancient, and can be traced back to the Triassic Period (Sturgeon & Mitton 1982). Given that mountain pine beetle productivity was higher in areas that were historically climatically unsuitable, it may be argued that in regions where outbreaks are absent, or at least infrequent and of low intensity, e.g. at high elevations (Amman 1973), host tree populations are generally more suitable for beetle reproduction. The relationship between mountain pine beetle and lodgepole pine can be viewed as a predator–prey adaptation (Berryman *et al.* 1985) as mountain pine beetles must kill their host to survive. Therefore, the most susceptible trees are most likely to be taken out of the gene pool during outbreaks (Yanchuk, Murphy & Wallin 2008). In areas where the beetle and lodgepole pine have coexisted, the most susceptible and suitable trees may have been selected against over time. Furthermore, the highest brood production will be in the most suitable trees, generating more intense outbreaks, which in turn may result in stronger selection pressure against other such 'high beetle-producing' trees. Resulting stands would thus be primarily comprised of less susceptible and suitable genotypes. Although the most susceptible and suitable trees would have been selected against, the remaining genotypes would still sustain outbreaks, as seen in our historically climatically suitable areas. Lodgepole pine reproduces at a very young age, and cone persistence and serotiny would mean that even killed trees could contribute to the future genepool, albeit at a lower rate (Raffa & Berryman 1987).

Higher brood productivity in lodgepole pine trees in areas with historically unsuitable climate may be due to higher suitability as a result of quantitatively or qualitatively lower defences expressed by host trees, or higher quality resources for beetle development. The terpenoid defences employed by species of Pinaceae are evolutionarily very old, and likely to have arisen as a consequence of interactions with numerous organisms, including bark beetles (Franceschi *et al.* 2005). Defence is costly, however, and in populations where selection pressures are low, it is likely that plants would minimize the allocation of resources to defence, which would come at the expense of growth (Herms & Mattson 1992). Clark (2008) showed that lodgepole pine from regions not previously exposed to mountain pine beetle differed significantly in terms of their defensive monoterpenes when compared to those in areas exposed to periodic beetle outbreaks, lending support to our findings. Similarly, populations of ponderosa pine that have suffered from heavy bark beetle-caused mortality have a greater frequency of trees containing higher concentrations of the toxic monoterpene limonene (Sturgeon 1979).

Phloem thickness, which positively affects brood productivity (Amman 1972), did not differ among CSCs (data not shown), but the relative nutrient content may have been higher in phloem tissue in lower CSC classes, i.e. these trees may have been more favourable for brood development. Phloem compression may differ among trees depending upon their growth rates, and therefore the amount of actual phloem tissue may differ in trees with the same recorded phloem thickness (Cabrera 1978). Alternatively, trees in populations exposed to frequent mountain pine beetle outbreaks may have high levels of polyphenols, e.g. tannins, phenylpropanoids, etc. (Hemingway, McGraw & Barras 1977), that reduce the digestibility of the available nutrients. This was not tested in this study, but

Clark (2008) found a weaker secondary resinosis response by trees from outside the mountain pine beetle's historic range than in trees from within its normal distribution.

Although many animals tend to be relatively specialized and sedentary at the extreme margins of their geographic range (Thomas *et al.* 1999), the results of our study suggest that the productivity of mountain pine beetle within historically climatically marginal habitats is actually higher than that associated with its historic range. Interestingly, several previous studies of insects that have expanded their geographical ranges show increased dispersal tendencies at the cost of lower productivity (Hughes, Hill & Dytham 2003; Hanski *et al.* 2004; Simmons & Thomas 2004). The mobility of individuals in newly established populations tends to decrease with increasing habitat connectivity (Hanski *et al.* 2004). The high connectivity between areas with high and low historic CSCs in our study area suggests that we should not expect decreased productivity due to increased investment in dispersal.

Our study shows that for the mountain pine beetle the number of brood beetles produced per parent is higher in forests where it has not previously existed at epidemic levels in recorded history when compared with forests where it has frequently reached outbreak levels in the past. Forests that have not suffered historic outbreaks could be considered 'naïve' to mountain pine beetle. This situation may be likened to that of exotic insects and diseases invading new ecosystems and becoming more successful there than in the native ecosystem. For example, the emerald ash borer, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), is relatively rare in Asia, where it is endemic and Manchurian ash *Fraxinus mandshurica* Rupr. is its primary host (Schaefer 2005). Unlike in Asia, this insect kills even healthy trees on high-quality sites in North America (Poland & McCullough 2006), indicating that North American ashes lack defences as a result of a lack of a coevolutionary history with this insect. Thus, there is evidence to suggest that exotic and invasive pests tend to be more destructive than native pests (Liebhold *et al.* 1995; Niemelä & Mattson 1996). Invasive species (and species at the margin of an expanded range such as mountain pine beetle in this case) may be successful because they are interacting with trees that have not evolved specific defence mechanisms, and there may be a lack of natural predators. Although the mountain pine beetle is not an exotic pest in the geographic regions sampled in our study, it could be considered as invasive because it is moving into and inhabiting an area it previously did not occupy at epidemic levels (Krcmar-Nozic, Wilson & Arthur 2000; Carroll *et al.* 2004). It is likely that it did occupy some or all of these areas at endemic (i.e. sub-outbreak) levels. However, endemic mountain pine beetle populations characteristically exist at very low densities, and are restricted to scattered moribund host trees that have been compromised by other factors such as among-tree competition, wind/snow damage or parasite/pathogen infection (Safranyik & Carroll 2006). It is very unlikely that endemic mountain pine beetle populations could impose selection pressures upon the defensive mechanisms of lodgepole pine. Since the invasion into geographic regions where host trees have not coexisted with the insect is similar to the situation with exotic species, it is not unreasonable to attribute some of the success that mountain pine beetle has in naïve forests to the same causes.

Range expansion due to climate change has been demonstrated for a vast number of species and the result of the current study provides the first evidence, to our knowledge, that native insect species may have a much higher reproductive success in previously unoccupied regions. This indirect effect of climate change may lead to a rapid population buildup with extreme host mortality as a consequence, and should be taken into account in models that evaluate the impacts of climate change and predict the progression of outbreaks. Increased reproductive success is likely to accelerate the progression of outbreaks. Therefore, it is particularly critical to manage forests for the maintenance of a mosaic of species and age classes at the landscape level in areas where host tree populations are naïve to eruptive herbivores.

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