

Changes in blister rust infection and mortality in whitebark pine over time

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Abstract: Whitebark pine (*Pinus albicaulis* Engelm.), a keystone species in subalpine ecosystems of western North America, is under threat across its range from white pine blister rust, mountain pine beetle, fire exclusion, and climate change. Loss of whitebark pine is predicted to have cascading effects on many ecosystem services. We remeasured 115 whitebark pine plots in the Canadian Rocky Mountains to determine whether infection and mortality rates from blister rust were changing over time and (or) latitude. Average rust infection of trees among plots increased from 42% in 2003–2004 to 52% in 2009, while mortality increased from 18% to 28%. In eight plots that have been measured three times, infection increased from 43% of live trees in 1996 to 70% in 2003 and 78% in 2009. Mortality increased from 26% to 65% in the same time period. Overall, infection and mortality have increased 3%/year over the 13 years of the study. Incidence of infection and mortality was highest among plots in the southern part of the study area, particularly on the western side of the Continental Divide. The slowing rates of infection and mortality that we found suggest that some level of natural selection may already be occurring in areas with high levels of both.

Résumé : Le pin à écorce blanche (*Pinus albicaulis* Engelm.), une espèce clé dans les écosystèmes subalpins de l'Ouest de l'Amérique du Nord, est menacé partout dans son aire de répartition par la rouille vésiculeuse du pin blanc, le dendroctone du pin ponderosa, l'exclusion du feu et les changements climatiques. On prévoit que la perte du pin à écorce blanche aurait des répercussions en cascade sur plusieurs services de l'écosystème. Nous avons remesuré 115 places échantillons contenant du pin à écorce blanche dans les montagnes Rocheuses canadiennes pour déterminer si les taux d'infection et de mortalité par la rouille vésiculeuse changeaient avec le temps et la latitude. Le taux moyen d'infection des arbres par la rouille vésiculeuse dans les places échantillons a augmenté de 42% en 2003–2004 à 52% en 2009 tandis que la mortalité a augmenté de 18% à 28%. Dans huit places échantillons qui ont été mesurées trois fois, le taux d'infection est passé de 43% des arbres vivants en 1996 à 70% en 2003 et 78% en 2009. La mortalité a augmenté de 26% à 65% durant la même période. Dans l'ensemble, les taux d'infection et de mortalité ont augmenté de 3% par année durant le cours de l'étude qui a duré 13 ans. L'incidence de l'infection et de la mortalité était la plus forte parmi les places échantillons situées dans la partie sud de la zone d'étude. Le ralentissement que nous avons observé dans l'augmentation des taux d'infection et de mortalité indique qu'un certain degré de sélection naturelle est peut-être déjà à l'œuvre dans les régions où l'infection et la mortalité atteignent des niveaux élevés. [Traduit par la Rédaction]

Introduction

Whitebark pine (*Pinus albicaulis* Engelm.), a keystone species in subalpine ecosystems of western North America, is under threat across the species' range. It is being impacted by white pine blister rust (WPBR), caused by the introduced invasive fungus *Cronartium ribicola* A. Dietr., mountain pine beetle (*Dendroctonus ponderosae* Hopkins, 1902) (MPB), fire exclusion, and climate change (Tomback et al. 2001). Loss of whitebark pine is predicted to have cascading effects on the many ecological processes and species, including provision of high-energy food for wildlife, particularly Clark's nutcracker (*Nucifraga columbiana* (Wilson, 1811)) and grizzly bear (*Ursus arctos* Linnaeus, 1758) (Tomback and Kendall 2001), nurse trees for other species in open terrain (Callaway 1998; Resler and Tomback 2008), and retention of snowpack (Farnes 1990; Tomback et al. 2001).

WPBR impacts whitebark pine by reducing seed availability (canopy kill and direct mortality), seed dispersal, and seedling survival. The rust usually kills the upper, cone-bearing branches before the tree itself (McDonald and Hoff 2001). Nearly all cones are produced in the upper third of the crown, so loss of canopy means loss of seed production (Keane et al. 1994). Seedlings of all sizes may also be infected by WPBR, and once seedlings develop

cankers, the majority die within 3 years (Hoff and Hagle 1990), reducing regeneration. Although MPB prefer the thicker phloem layer of larger diameter trees (>10–12 cm), which create better reproductive conditions (Cole and Amman 1980), even small-diameter whitebark pine trees may be very susceptible to MPB attack because of their proximity to larger diameter stems in multitem clusters (Perkins and Roberts 2003).

WPBR, in particular, has devastated many northern whitebark pine populations and is quickly invading others, making it almost range-wide in its distribution across a diversity of habitat types and plant associations as well as edaphic conditions (Schwandt et al. 2010; Tomback and Achuff 2010, and references therein). MPB outbreaks are widespread in several whitebark pine regions (Gibson et al. 2008). While these, and other, studies have reported on the incidence of WPBR on whitebark pine and subsequent mortality, only a few have reported on rates of change in these variables (Keane and Arno 1993; Smith et al. 2008; GYWPMWG 2010).

Long-term observations are an opportunity to examine how stands and landscapes respond to agents such as WPBR and MPB over time (Geils et al. 2011); for example, rust incidence and tree mortality may vary at different stages of an epidemic, or depending on stand age or other factors. A more complete understanding

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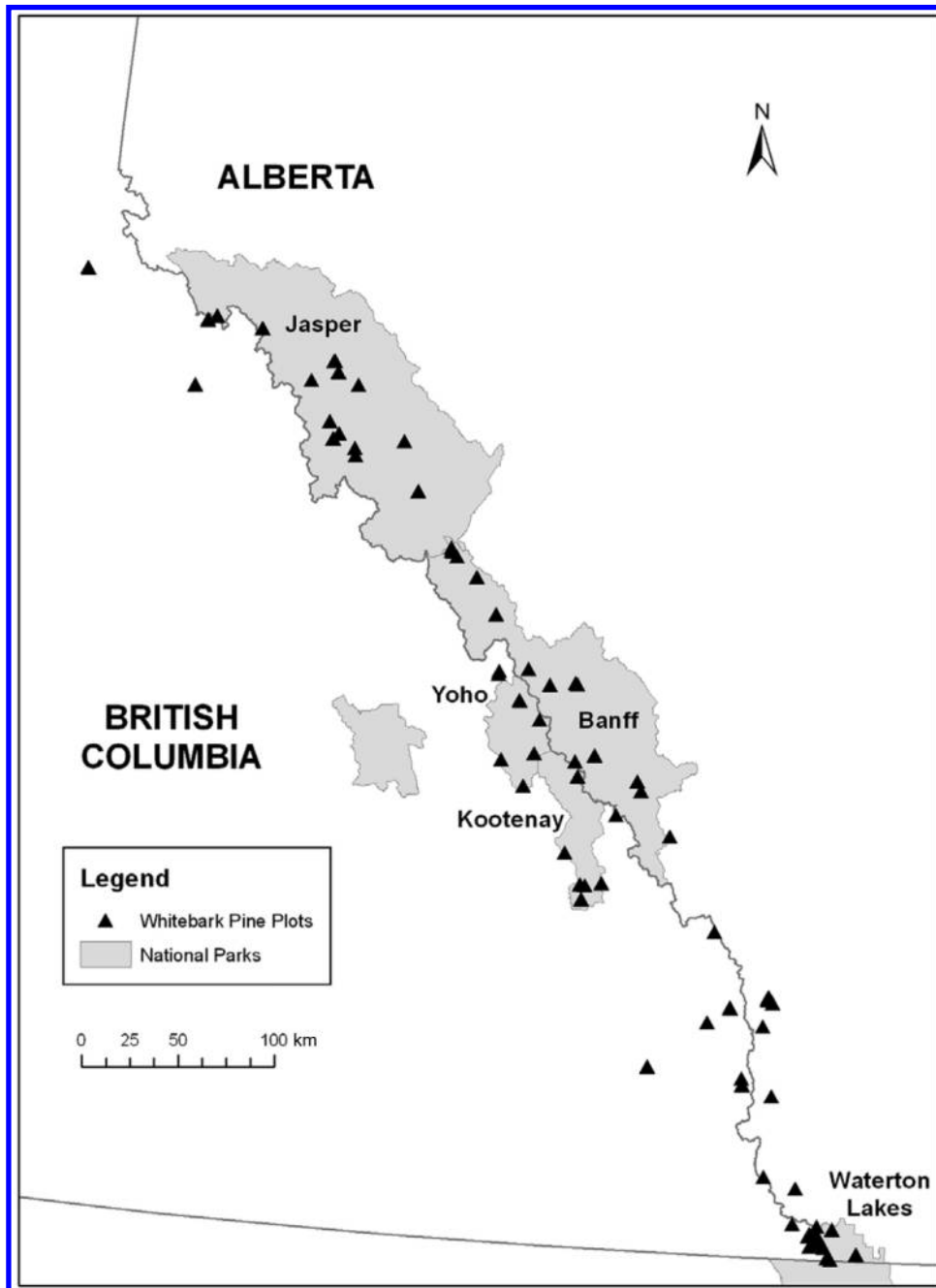
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Fig. 1. Study area for the whitebark pine (*Pinus albicaulis*) survey in the Rocky Mountains of Canada. Each point represents one surveyed plot ($n = 115$).



of the trajectory of the disease over time, and across a broad geographic range, will be critical for management of the species (Keane et al. 2012).

In response to the noted declines, strategies and actions for managing and restoring whitebark pine across its range have been proposed (Schoettle and Sniezko 2007; Aubry et al. 2008; Hunt et al. 2010; Schwandt et al. 2010; Keane et al. 2012) and many agencies are already implementing some of the suggested actions. Accurate assessment of the extent of the problem, including rates of change, is the first step in formulating effective adaptive management strategies (Logan et al. 2008, Keane et al. 2012). To this end, our study sought to determine how infection and mortality rates from blister rust in whitebark pine are changing (i) over time and (ii) across geographical

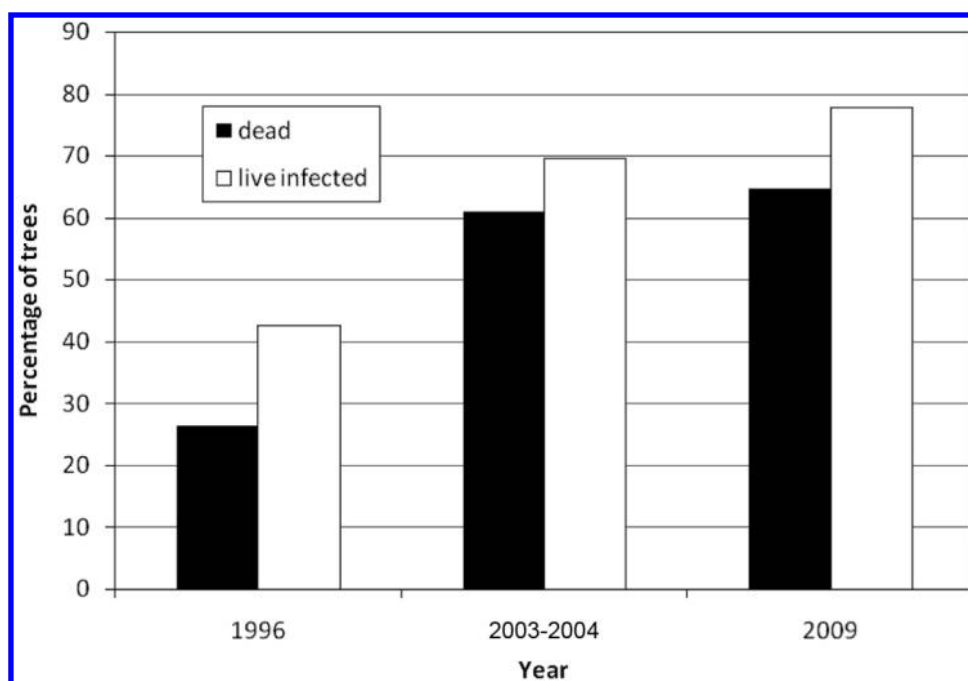
gradients. We then explore the implications of our findings for management of the species.

Methods

Study area and data collection

The study area extended from Waterton Lakes National Park (WLNP), Alberta (49°0'N, 114°2'W), to near McBride, British Columbia (53°20'N, 120°08'W). In 2003 and 2004, we reestablished eight plots that Kendall et al. (1996) had measured in 1996 in WLNP and established 107 new plots to represent as broad a range of habitats within the study area as possible (Smith et al. 2008). While the Kendall plots were not permanently marked in 1996, we were able to resample within the original stands by using geo-

Fig. 2. Incidence of white pine blister rust (*Cronartium ribicola*) and whitebark pine (*Pinus albicaulis*) mortality and infection of living trees for three time periods (1996, 2003–2004, and 2009) in the Canadian Rockies. Number of plots = 8.



graphical coordinates, plot photographs, and azimuths (Smith et al. 2008) and then mark the plots and tag the trees for relocation. Of the 115 plots, 71 are east of the Continental Divide in Alberta and 44 are west of the Divide in British Columbia (Fig. 1). In 2009, we remeasured 114 plots, and in 2010, we remeasured one plot that we could not relocate the previous year.

Methods for establishing plots (10 m × 5 m belt transect) and assessing whitebark pine health were those recommended by Tomback et al. (2005) and utilized in Smith et al. (2008). Within each plot, all whitebark pine trees (height >1.3 m) were marked with numbered aluminum tags. In a tree clump, each stem that originated below 1.3 m was counted as a separate tree if it could be traced separately to ground level (Zeglen 2002). Diameter at breast height was recorded for all trees to the nearest 0.1 cm. Living trees were visually assessed using binoculars for presence-absence of active or inactive branch and stem cankers caused by WPBR. Active cankers had diagnostic orange–yellow aecial blisters containing aeciospores, or empty white spore sacs later in the season. Inactive WPBR cankers were identified by their spindle shape, broken bark, and, because rodents feed on active blister rust cankers, the presence of gnawing or bark stripping. Incidence of infection by blister rust was reported as the percentage of live trees or seedling sites that were infected at the time of each survey (Smith et al. 2011). Canopy kill was measured to the nearest 10% (canopy kill indicates the severity of the infection).

All dead whitebark pine trees, regardless of cause of death (WPBR, MPB, and other causes), were counted in each plot and reported as a percentage of all trees. We could not determine cause of death of most trees (1220) because weathering of the trunks and branches had removed evidence of cankers or beetle galleries. All live whitebark pine ≤1.3 m in each plot were considered seedlings, classified by two height classes (≤50 or >50 cm) and assessed for presence-absence of active or inactive cankers. Both single seedlings and clusters of seedlings germinating from the same spot were counted as only one seedling.

Data analyses

The objective of our analysis was to determine factors that influence infection and mortality rates from blister rust in white-

bark pine including across the geographical range and over time. Spatial and temporal patterns in whitebark pine health were analyzed using four response variables: (i) the percentage of live trees with infection, (ii) the mean percentage of the canopy killed of all live trees, (iii) the percentage of whitebark pine trees in each plot that were dead, and (iv) the percentage of seedlings exhibiting infection. We logit transformed the first three measures to yield a normally distributed response variable. For sites with proportions of 0 or 1, we added or subtracted 0.01, respectively. Data from the first three response variables were analyzed using linear regression. Because the seedling infection data had a large number of zeroes, they were analyzed as presence or absence of seedling infection using logistic regression. The predictor variables for all analyses were divide (east or west of the Continental Divide), latitude (included as a quadratic term), elevation (metres), percent slope, northness (the cosine of the aspect, ranging from 1(north) to -1(south)), eastness (the sine of the aspect), and time (year of sampling). There were no statistically significant correlations among any of the predictor variables at $R < 0.5$ (range 0.01–0.47, $P < 0.05$). In each of these models, we included a random intercept to account for repeated measures at the same plots over time (Breslow and Clayton 1993). We used the procedures *xreg* and *xtlogit* in Stata 10.1 (StataCorp 2007) for the analyses.

Results

Incidence of infection and mortality

In 2009, we assessed a total of 5961 trees >1.3 m across 115 plots. Almost all plots (98%) had at least one tree infected with WPBR. Of these assessed trees, 71% ($n = 4222$) were alive and 29% ($n = 1739$) were dead from all causes. Of the living trees, 44% ($n = 1872$) were infected with WPBR (had active or inactive cankers). Of these infected trees, 18% had active stem cankers that will likely be lethal within a decade. Of the 459 trees for which we could attribute cause of death, 71.7% (329) had definite signs of WPBR (active or inactive cankers), while 28.3% (130) had evidence of MPB infestation (J-shaped galleries). These causes of mortality were 55% and 45%, respectively, in 2003–2004 (Smith et al. 2008). Fifteen (13%) of the plots had no seedlings in 2009. Of the 2732 whitebark pine

≤1.3 m examined, the level of infection was greater for tall (>50 cm) than for short (≤50 cm) seedlings, 25.7% versus 7.6%.

Across plots, rust infection increased from 37% in 2003–2004 to 44% in 2009, while mortality increased from 18% to 28%. The biggest increase in mortality was in the central part of our study area, from 8% in 2003–2004 to 20% in 2009 (Smith et al. 2011), and WPBR continues to be the primary cause of mortality throughout. The largest increase in mortality (16.4% in 2003–2004 to 22.8% in 2009) was in the smallest diameter class (0–4.9 cm diameter at breast height). The mean percentage of the canopy kill of all live trees declined from approximately 19% in 2003–2004 to 10% in 2009 (it was not measured in 1996). The percentage of infected seedlings in each plot decreased slightly from 17% to 15% between 2003–2004 and 2009.

In the eight plots that have been measured three times, infection increased from 43% of live trees in 1996 to 70% in 2003 and 78% in 2009 (Fig. 2). Infection levels increased 4%/year in the first 7 years (Smith et al. 2008), but only 1.3%/year in the 6 years of the second remeasurement interval. The combined total was an increase of 3%/year over the 13 years between 1996 and 2009. The highest increase in mortality occurred between 1996 and 2003–2004 (from 26% to 61%) and then rose slightly to 65% in 2009. Mortality levels increased 5%/year in the first 7 years (Smith et al. 2008), but less than 1%/year during the second interval, for a combined increase of 3%/year over 13 years.

Geographical distribution of infection and mortality over time

Infection and mortality rates varied geographically through the study area. In general, the models for all four response variables were similar (Table 1). As shown by the infection rates reported above, our regression analysis also found that the live tree infection significantly increased over time, was significantly greater on the western side of the Continental Divide, and varied with latitude (Table 1) (overall model $\chi^2_8 = 184$, $P < 0.001$, pseudo- $R^2 = 0.50$, fraction of variance due to random effect = 0.71). Infection levels showed a general nonlinear decrease with latitude (Fig. 3). Specifically, average percentage of trees infected was highest in the southern Rockies (~83%), decreasing to a low in the northern region of Banff National Park (~36%) and then moderately rising in the northern end of the study area in Jasper National Park and McBride, British Columbia (~49%). In general, the models for all four response variables were similar. Live tree infection has significantly increased over time, but was not related to elevation, slope, or measures of aspect (northness, eastness) (Table 1). The degree of canopy kill showed a pattern similar to live trees (overall model $\chi^2_8 = 100$, $P < 0.001$, $R^2 = 0.35$, fraction of variance due to random effect = 0.51). The percentage of WPBR trees in each plot that were dead showed the same pattern for divide and latitude (overall model $\chi^2_8 = 311$, $P < 0.001$, $R^2 = 0.59$, fraction of variance due to random effect = 0.73). The percentage of trees that were dead has also increased over time, but in contrast with the other response variables, the percentage of trees that were dead declined with increasing elevation (Table 1). The presence of infected seedlings in the plots showed the same pattern as live and dead trees (overall model $\chi^2_8 = 24.6$, $P = 0.002$, log likelihood = -117.7, $R^2 = 0.53$, $\chi^2_1 = 5.54$ for test of the significance of the random effect, $P = 0.009$) (Table 1).

Discussion

Infection from WPBR is present in nearly all plots, but the highest levels, and highest rates of increase in tree infection and mortality, were in southwestern Alberta and southeastern British Columbia. The rates of increase in infection and mortality appear to have slowed slightly in the last 6 years, based on plots measured three times in WLN. This may be an artefact of varying times between measurement periods, reduction of plot size from 1996

Table 1. Linear regression models for the logit-transformed mean percentage of (i) live WPBR trees (>1.3 m in height) with infection, (ii) canopy kill, (iii) dead trees, and (iv) the presence of infection on seedlings, where plot is the sampling unit; also reported are the coefficient for each covariate, its standard error, and the test of its significance (eastern plots are the reference category for the divide variable).

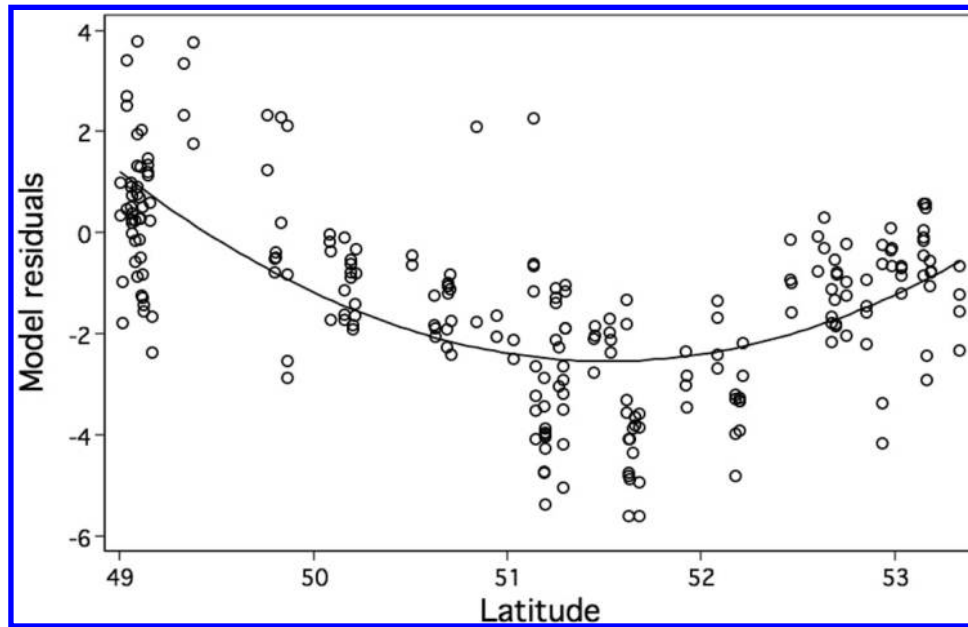
Model and covariate	Coefficient	SE	P
% infection live trees			
Divide	1.41	0.27	<0.001
Latitude	-61.2	9.6	<0.001
Latitude ²	0.59	0.09	<0.001
Elevation	0.00075	0.00115	0.515
Slope	-0.00005	0.00671	0.994
Northness	0.25	0.18	0.163
Eastness	-0.14	0.18	0.408
Sampling year	0.13	0.015	<0.001
Constant	1305	244	<0.001
% mean canopy kill			
Divide	0.31	0.08	<0.001
Latitude	-12	2.8	<0.001
Latitude ²	0.11	0.03	<0.001
Elevation	-0.00055	0.00034	0.101
Slope	0.0026	0.0020	0.189
Northness	0.0014	0.0522	0.978
Eastness	-0.044	0.052	0.390
Sampling year	-0.042	0.007	<0.001
Constant	381	73	<0.001
% dead trees			
Divide	0.62	0.22	0.005
Latitude	-32	7.8	<0.001
Latitude ²	0.31	0.08	<0.001
Elevation	-0.0026	0.0009	0.006
Slope	-0.0028	0.0054	0.611
Northness	-0.027	0.143	0.849
Eastness	0.11	0.14	0.457
Sampling year	0.15	0.01	<0.001
Constant	535	198	0.007
% seedling infection			
Divide	1.91	0.60	0.002
Latitude	-59.4	21.2	0.005
Latitude ²	0.58	0.21	0.005
Elevation	0.0020	0.0023	0.376
Slope	-0.016	0.013	0.239
Northness	0.57	0.36	0.118
Eastness	-0.35	0.35	0.319
Sampling year	-0.25	0.07	0.001
Constant	2022	592	0.001

to 2003–2004 and 2009, or different observers, but given the high infection levels in this part of the study area, most of the trees that are susceptible to WPBR may have already been infected or died, i.e., the population may be “saturated” from an infection standpoint. Therefore, only trees with some resistance persist (the “natural selection” option of Schoettle and Sniezko 2007) and are less likely to become infected unless the environment changes in a way that increases their susceptibility, or the rust becomes more virulent.

While absolute levels of infection and mortality in the central and northern parts of the study area are lower than in the southern part, they do continue to increase. This may indicate that there is greater resistance in the population, or that infection is still spreading, albeit more slowly due to environmental or ecological differences (Smith et al. 2008) along the latitudinal gradient. Given the relatively high rates of infection in the central region, the latter option seems most likely.

We continued to find a higher incidence of infection and mortality on the west side than on the east side of the Continental Divide, reflecting mesoclimatic differences among these regions.

Fig. 3. The number of live whitebark pine (*Pinus albicaulis*) trees that are infected by white pine blister rust (*Cronartium ribicola*) varies by latitude: highest in the southern part of the study area, then dropping significantly in the central Canadian Rockies, and then rising again at the northern part of the study area. The model residuals are the residuals after accounting for all other variables in the model. The line is the fitted line using the model coefficients and the means of the other covariates.



WPBR infection spread is heavily influenced by environmental conditions such as moisture, air temperature, and air circulation (Sturrock et al. 2011), with high hazard conditions of about 48 h of $<20^{\circ}\text{C}$ and 100% humidity producing ideal conditions to form basidiospores, disperse, germinate, and infect white pines (Ostry et al. 2010). These moisture-saturated environments are more typical of our western sites (Smith et al. 2008).

While the percentage of canopy kill declined between measurement periods, it continues to reduce cone production because nearly all cones are produced in the upper third of the crown (Arno and Hoff 1989). The observed decline may reflect (i) the death of the trees from 2003–2004 that had high canopy kill, such that the remaining healthier trees comprise a larger percentage of live trees, (ii) that there were fewer infection events in the intervening years, and (or) (iii) that there was observer variance in classifying the percentage of canopy kill.

Similar to Rochefort (2008), we found that mortality levels decreased with elevation, although our infection levels showed no response to elevation. We hypothesize that the lower mortality levels were due to slower disease development and spread at higher elevations, due to the shorter growing season. However, predicted warmer temperatures at higher elevations may provide favourable conditions for WPBR to spread more rapidly in the future (Larson 2010). Climate warming is also driving recent increases in MPB infestation at higher elevations by lengthening the developmental period and shortening the periods of cold temperatures that kill beetles (Logan and Powell 2001). Also, with climate warming, beetles of different generations are now surviving and killing whitebark pine in a single summer (Bentz et al. 2011). In addition, in some areas, MPB have preferentially selected trees that were infected by WPBR, which may occur more frequently with drought stress (Six and Adams 2007; Bockino and Tinker 2012). High levels of WPBR infection prior to MPB infestation may amplify both disturbances, accelerating the loss of whitebark pine (Gibson et al. 2008; Larson 2010; Sharik et al. 2010). Although our results showed a decrease in mortality from MPB, populations in lodgepole pine (*Pinus contorta* Douglas ex Loudon) have been increasing in the central and northern zones of our study area and are predicted to continue to increase given conservative climate

change scenarios (Carroll et al. 2006), while in the southern part of our study area, previous pine beetle activity already limits the potential for MPB population growth (Dalman 2004).

These two agents (climate warming and MPB) are further fragmenting existing small populations of whitebark pine, increasing the risk of loss of these remnants to wildfires, which are expected to be more intense under a warming climate (Tomback and Achuff 2010). Isolated stands may also be less frequently visited by Clark's nutcrackers, which are the sole disperser of WBP seed (Tomback 1982), thus reducing regeneration. Millar et al. (2012) observed improved growth in whitebark pine trees that survived drought and hypothesized that fitness may be improved with some levels of forest dieback. However, cone production in these stands may be below the predicted threshold for visitation by Clark's nutcrackers (McKinney and Tomback 2007; McKinney et al. 2009; Barringer et al. 2012), reducing dispersal and thus regeneration potential.

Disturbance agents operate on different time scales and frequently affect different demographic stages of populations (Wong 2012), thus complicating the species response. Wong (2012) found that the triple whammy of MPB, WPBR, and various *Ips* spp. of bark beetles reduced whitebark pine basal area significantly, and when regeneration remained low, subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) became dominant in the understory and overstory. Many of the severely impacted stands in our study area may be on a trajectory towards extirpation without active management of competing species and assistance in regeneration.

Infection (44%, range 0%–100%) and mortality (30%, range 0%–90%) levels in plots observed in this study are higher than in surveys a decade earlier in British Columbia (31% infection and 19% mortality: Zeglen 2002; 27% infection and 21% mortality: Campbell and Antos 2000; also see review in Smith et al. 2008). They are also higher than in surveys between 2005 and 2009 in Alberta protected areas (0%–33% infection and 0%–13% mortality: K. Ainsley and A. Benner, unpublished data), but are similar in that the highest levels are in the south. Levels in the Canadian Rockies are higher than in the Greater Yellowstone Ecosystem (mean 20% infection: GYWPMWG 2010) and Washington (mean 22% infection and 31% mortality: Rochefort 2008). The estimated 3%/year in-

crease in mortality in our study is higher than the 2%/year estimated by Keane and Arno (1993).

Management implications

The slowing rates of infection and mortality that we found in our study suggest that some level of natural selection may already be occurring in areas with high levels of both, increasing the importance of protecting these areas from industrial activity, MPB attack, or wildfire. In addition, areas with high canopy kill (thus low cone production) and low natural regeneration will require active management such as collecting and testing seed from potentially blister rust resistant trees, protecting these trees from MPB attack (Smith 2009), and burning areas to improve microsite conditions for planting seedlings (Schwanke and Smith 2010) to maintain whitebark pine populations on the landscape. In areas with lower levels of infection and mortality, less-intensive proactive strategies could be implemented (Schoettle and Sniezko 2007).

The relatively high WPBR infection levels (~49%) near the northern limit of whitebark pine may have implications for natural migration latitudinally as a response to climate warming (Hamann and Wang 2006) or for assisted migration (McLane and Aitken 2012). Continued monitoring of plots in this area is important.

Critical data, such as where whitebark pine mortality and infection are the highest, will inform recovery strategies that must set priorities for recovery efforts and select areas for restoration activities. Whitebark pine is legally listed as Endangered both under The Wildlife Act in the Province of Alberta (Government of Alberta 2010) and under the federal Species at Risk Act (Government of Canada 2012). The species is blue listed by the British Columbia Conservation Data Centre, which is similar to “special concern” or “vulnerable” (British Columbia Conservation Data Centre 2012). The national recovery strategy and action plan is to include population and distribution objectives and methods to monitor the recovery of the species (Government of Canada 2012). In the United States, whitebark pine was assessed as warranting listing as threatened or endangered, but listing was precluded by higher priority actions (U.S. Fish and Wildlife Service 2011). It has been added to the candidate species list and must undergo an annual review.

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