



The relative contributions of disease and insects in the decline of a long-lived tree: a stochastic demographic model of whitebark pine (*Pinus albicaulis*)



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ABSTRACT

Pathogens and insect pests have become increasingly important drivers of tree mortality in forested ecosystems. Unfortunately, understanding the relative contributions of multiple mortality agents to the population decline of trees is difficult, because it requires frequent measures of tree survival, growth, and recruitment, as well as the incidence of mortality agents. We present a population model of whitebark pine (*Pinus albicaulis*), a high-elevation tree undergoing rapid decline in western North America. The loss of whitebark pine is thought to be primarily due to an invasive pathogen (white pine blister rust; *Cronartium ribicola*) and a native insect (mountain pine beetle; *Dendroctonus ponderosae*). We utilized seven plots in Crater Lake National Park (Oregon, USA) where 1220 trees were surveyed for health and the presence of blister rust and beetle activity annually from 2003–2014, except 2008. We constructed size-based projection matrices for nine years and calculated the deterministic growth rate (λ) using an average matrix and the stochastic growth rate (λ_s) by simulation for whitebark pine in our study population. We then assessed the roles of blister rust and beetles by calculating λ and λ_s using matrices in which we removed trees with blister rust and, separately, trees with beetles. We also conducted life-table response experiments (LTRE) to determine which demographic changes contributed most to differences in λ between ambient conditions and the two other scenarios. The model suggests that whitebark pine in our plots are currently declining 1.1% per year ($\lambda = 0.9888$, $\lambda_s = 0.9899$). Removing blister rust from the models resulted in almost no increase in growth ($\lambda = 0.9916$, $\lambda_s = 0.9930$), while removing beetles resulted in a larger increase in growth ($\lambda = 1.0028$, $\lambda_s = 1.0045$). The LTRE demonstrated that reductions in stasis of the three largest size classes due to beetles contributed most to the smaller λ in the ambient condition. Our work demonstrates a method for assessing the relative effects of different mortality agents on declining tree populations, and it shows that the effects of insects and pathogens can be markedly different from one another. In our study, beetle activity significantly reduced tree population growth while a pathogen had minimal effect, thus management actions to stabilize our study population will likely need to include reducing beetle activity.

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1. Introduction

A growing number of studies have demonstrated that North American forests are experiencing increasing rates of tree mortality associated with pest outbreaks, emerging pathogens, fire

exclusion, and drought (van Mantgem et al., 2009; Weed et al., 2013; Allen et al., 2015; Freer-Smith and Webber, 2015). For instance, recent and notable large-scale mortality has been observed for lodgepole pine (*Pinus contorta*) due to outbreaks of mountain pine beetle (*Dendroctonus ponderosae*) in the Rocky Mountains; for tanoak (*Notholithocarpus densiflorus*) in coastal California due to the rapid spread of the invasive pathogen *Phytophthora ramorum*; and for piñon pines (*Pinus edulis* and *P. monophylla*) experiencing extreme drought in southwestern

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USA (Breshears et al., 2005; Raffa et al., 2008; Chapman et al., 2012; Cobb et al., 2012; Meddens et al., 2015). Often however, causes of mortality are complex and include multiple factors (Franklin et al., 1987; Allen et al., 2015). For instance, although drought appears to be the primary driver of widespread dieback of aspen (*Populus tremuloides*) in North America (Anderegg et al., 2015), other significant contributing factors are widely recognized, including bark beetles, wood borers, and fungal pathogens (Worrall et al., 2010; Marchetti et al., 2011). The recent increase in mortality of red fir (*Abies magnifica* var. *magnifica*) in the Sierra Nevada is attributed to a complex array of abiotic factors (such as decreased snowpack and warmer temperatures) that trigger increases in dwarf mistletoe (*Arceuthobium* spp.), canker-forming fungi (*Cytospora* spp.), root diseases (*Heterobasidion annosum*, *Armillaria ostoyae*), and fir engraver beetle (*Scolytus ventralis*; Heath et al., 2013). Unfortunately, teasing apart the relative contribution of these causal factors is often difficult or impossible.

The kind of data required to assess the relative impacts of pests, pathogens, or climatic factors on tree populations is rare. Ideally, one would have estimates of demographic rates such as survivorship, growth, and fecundity measured on an annual basis which can be used to determine population growth rates (λ) and build demographic models that incorporate the impact of stochastic events (see Morris and Doak, 2002), and at the same time have annual measures of important causal agents of mortality. Given the speed at which many pest and pathogen outbreaks occur, and the difficulty of measuring demographic rates annually on permanently marked trees, there are almost no data sets with the temporal resolution needed to build these kinds of models. Instead, most studies of tree mortality focus on changes in coarse measures of population size or they estimate the amount of mortality seen at only one particular time (e.g., Gibbs et al., 1999; Kizilinski et al., 2002; Metz et al., 2012).

Whitebark pine (*Pinus albicaulis*) is an exceptionally long-lived tree found in high-elevation forests of western North America (Tomback et al., 2001a, 2001b; Fig. 1). Because of the multiple, critical roles that whitebark pine plays in subalpine ecosystems, it is often described as a keystone or foundation species (Ellison et al., 2005; Keane et al., 2011). These roles include the facilitation of succession on harsh sites after disturbances, the delay of snowmelt during the warm season, and the supply of food for wildlife through seed production (Tomback et al., 2001b). Over the past few decades, whitebark pine has experienced high levels of mortality across most of its range, and was recently listed as a candidate species for protection under the Federal Endangered Species Act (U.S. Fish and Wildlife, 2011). The two primary agents of the decline are thought to be the invasive pathogen, *Cronartium ribicola* and the native mountain pine beetle. Accidentally released into North America ca. 1910, *C. ribicola* is of Asian origin and can infect all five-needled pine species. The pathogen requires an alternate host to complete its lifecycle, and these include several members of the *Ribes*, *Castilleja*, and *Pedicularis* genera (McDonald and Hoff, 2001). Infection causes the disease white pine blister rust (hereon called 'blister rust'), which can damage or kill branches or whole trees by girdling branches and boles (McDonald and Hoff, 2001; Geils et al., 2010). Both the degree to which blister rust is fatal for whitebark pine and the speed at which it can progress on an individual tree is not well-understood and appears to vary considerably among regions. Mountain pine beetle can damage or kill whitebark pine by mass attacking individual pine, and episodes of punctuated mortality have been a normal part of the life history of whitebark pine ecosystems (Perkins and Swetnam, 1996). Recently though, mountain pine beetle infestations have increased for whitebark pine, presumably because warmer winters have increased the beetles' ability to reproduce at higher elevations and latitudes where whitebark pine is common (Preisler et al.,

2012; Meigs et al., 2015). In addition, the effects of fire exclusion and climate change are thought to be important factors in the decline of whitebark pine, and these may interact with each other as well as blister rust and mountain pine beetle incidence (Tomback et al., 2011).

Numerous studies have described the prevalence of blister rust and mountain pine beetle on whitebark pine (e.g., Campbell and Antos, 2000; Zeglen, 2002; Hatala et al., 2010; Smith et al., 2013). These studies demonstrate that rates of blister rust infection and mountain pine beetle infestation vary considerably across the range of the pine. For example, Keane and Arno (1993) resurveyed plots in western Montana 20 years after they were established in 1971 and found an average of 42% mortality over that time. In addition, 89% of the live trees remaining were infected by blister rust. In their study, blister rust was observed to be the primary cause of death. Larson (2011) found significant differences in blister rust infection rates between six mountain ranges from southwest Montana to western Oregon ranging from 5% to 66% among sites. Interestingly, Larson (2011) attributed mountain pine beetle as the proximal agent of mortality for 83% of the dead trees he observed, although the potential role of blister rust for increasing mountain pine beetle attack could not be determined. In addition, detecting the presence of blister rust on dead whitebark pines can be difficult and may reduce the precision of retrospective studies. In California, Maloney et al. (2012) found that blister rust incidence varied by region, from 0% in the Great Basin to 24.2% in the Northern Sierra Nevada, though this study does not report on the impacts of mountain pine beetle. In contrast, Millar et al. (2012) found high mortality of whitebark pine in eastern California where there was no evidence of blister rust in the stands they measured. In their study, stands experienced an average of 70% mortality during the period 2007–2010, most of which was attributed to mountain pine beetle. As with many tree taxa undergoing decline, there is no consensus about what constitutes the greatest threat to whitebark pine, but it is clear that the prudent approach will acknowledge that the answer may vary considerably across the range of the tree.

In this study, we use an exceptional data set from Crater Lake National Park in the southern Cascades of Oregon (USA) in which whitebark pine individuals in seven permanent plots (Murray, 2010) were monitored annually for 11 years to determine the rate of population decline and to evaluate the role of blister rust and mountain pine beetle. Over the study period (2003–2014), we monitored 1220 live whitebark pine, including: 956 seedlings (<1.37 m in height) and 264 trees ≥ 1.37 m height. In addition to annual measures of survival and fecundity, each tree was assessed for signs of blister rust and mountain pine beetle. Although our plots were selected to represent the park's various whitebark pine community types (see *Methods*) and do not represent a systematic survey of the park, they present a unique opportunity for estimating the role of pests and pathogens for whitebark pine. We know of only a single other long-term monitoring study with annual resolution for whitebark pine, however that stand – found in a single large plot in Yosemite National Park (see Das et al., 2013) – has almost no blister rust or mountain pine beetle. Blister rust has been infecting host trees in Crater Lake National Park since at least 1936 (Beck and Holm, 2014) and has been the focus of several studies (Murray and Rasmussen, 2003; Murray, 2010; Smith et al., 2011). Mountain pine beetle is a mortality agent for several pine species found in Crater Lake National Park, including lodgepole pine, ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), western white pine (*Pinus monticola*), and whitebark pine (Beck and Holm, 2014). Mountain pine beetle activity has increased markedly in Oregon since ~2010, presumably because of extended dry seasons and warmer temperatures (Preisler et al., 2012; Meigs et al., 2015). With annual monitoring, we are able to ascribe mortality



Fig. 1. Whitebark pine (*Pinus albicaulis*) in Crater Lake National Park. Panel A: typical whitebark pine habitat along the rim of Crater Lake. The prominent peak shown is Hillman Peak (2484 m) and the forests on the slopes are comprised primarily of whitebark pine and mountain hemlock (*Tsuga mertensiana*). Panel B: mature whitebark pine near the rim of Crater Lake. Panel C: stand of whitebark pine in the North Junction area of the park that has experienced high mortality from mountain pine beetle (*Dendroctonus ponderosae*). Many of the trees were infected with blister rust (*Cronartium ribicola*) prior to being attacked by beetles. Photos in panels A and B courtesy of Rob Mutch and the photo in panel C courtesy of Jen Beck.

to a particular agent or combination of agents, and to assess the observation that mountain pine beetle often selects hosts that have blister rust (e.g., Six and Adams, 2007; Bockino and Tinker, 2012), a potentially important contributor to population decline.

Our major goals in this study were to estimate the rate of population decline of whitebark pine in our study plots between 2003 and 2014 and to compare the roles of blister rust and mountain pine beetle in the decline. The approach we took was to construct a size-based matrix model in which survival and fecundity of whitebark pine could be estimated directly from field data. Because measuring size of slow-growing trees is rarely done on an annual basis, we used three measurements of diameter at breast height (dbh) that were taken during the study (2003, 2007, and 2013). Next, to estimate annual growth during all other years, we conducted a separate tree-ring analysis that allowed us to apportion growth using growth-climate relationships. Using our data, we constructed deterministic and stochastic models that incorporated annual variation in survivorship, growth, and fecundity, and used these models to estimate population growth rates (λ) for (1) the ambient condition, (2), a rust-free condition, (3) a beetle-free condition, and (4) a rust- and beetle-free condition. We also use a life table response experiment (LTRE) to evaluate which differences in demographic rates among these conditions contributes to the differences observed in λ .

2. Materials and methods

2.1. The study site

Our study was conducted in Crater Lake National Park which is located in the south-central Cascade Mountains of Oregon (USA)

and covers an area of 74,132 ha. Winters are cool with mean January temperatures of -3.8°C , and summers are warm with mean July temperatures of 12.8°C . Most precipitation falls in the form of snow between November and March (13.3 m mean annual snowfall), while summers are relatively dry. Elevation within the park ranges from 1158 to 2721 m. Vegetation at the lower elevations is dominated by mixed conifer forest, including ponderosa pine, white fir (*Abies concolor*), sugar pine, and incense cedar (*Calocedrus decurrens*). Whitebark pine is restricted to the upper elevations within the park (~ 2080 – 2700 m), primarily along the rim of Crater Lake's caldera, the park's main geographic feature, and on many of the park's mountain peaks (Fig. 1). Whitebark pine is found across ~ 2000 ha within Crater Lake National Park (2.8% of the park's terrestrial base).

Seven permanent plots were established by the National Park Service in the summer of 2003 (Murray, 2010, 2011; Table 1). The general vicinity of each plot was pre-determined to represent the whitebark pine communities present in the park. Next, each plot was placed within the community based on field reconnaissance of the area, then subjectively choosing a plot center location that appeared typical for the vicinity and community (Mueller-Dombois and Ellenberg, 1974). Each plot was circular with a radius of 9.75 m and covered an area of 299 m^2 . Average plot elevation was 2340 m (range 2103–2536 m). Monitoring of plots occurred every summer from 2003 until 2014, except for 2008 due to inadequate staffing in the park. Monitoring of these plots is ongoing.

2.2. Demographic measurements

All trees, both dead and alive, were mapped and given unique alphanumeric identifiers in each of the seven plots. At the start

Table 1

Location and summary data for whitebark pine demography plots in Crater Lake National Park.

Location	Elevation (m)	Slope (%)	Aspect (degree)	Number of trees (2003) ^a	Number of trees (2014) ^a
Cloud Cap	2441	26	165	58	57
Dutton Ridge	2362	20	228	17	15
Llao Rock	2405	31	311	37	31
Mt. Scott	2536	38	190	64	65
North Junction	2103	11	304	35	14
Watchman	2424	50	256	29	25
Wizard Island	2110	45	179–200	15	7

^a Number of trees includes only those living trees that are ≥ 1.37 m in height (i.e., count shown does not include seedlings; see Fig. 2 for seedling data).

of the study all trees were mapped, but only some trees were marked with aluminum tags. Over the course of the study additional trees were given tags so that all trees were tagged by 2011. For trees with heights ≥ 1.37 m, dbh was measured in 2003, 2007, and 2013. For trees < 1.37 m height (“seedlings”), height was measured in these same three years. In addition, all trees, regardless of size, were assessed every year (2003–2014, not including 2008) for a number of conditions: health (healthy, sick, recently dead, and dead); the presence of white pine blister rust; evidence of mountain pine beetle and degree of activity (as indicated by the abundance of pitch tubes); mistletoe infestation; and female cones (presence/absence only). When blister rust was noted, the status of resulting cankers was recorded as either active or inactive. Blister rust cankers were recorded as active if one of the following symptoms were present: resinous surfaces, fungal fruiting structures, or yellow- to orange-colored bark. New, first-year seedlings (“germinants”) were also recorded each year of monitoring. Because many germinants arise from caches left by Clark’s nutcrackers (*Nucifraga columbiana*; Tomback et al., 2001a; Mattson et al., 2005), a cluster of germinants was usually labeled with one unique identifier. In addition, a large mast year occurred in 2009, resulting in a large number of germinants in 2011. Whitebark pine seeds exhibit a germination syndrome in which most seeds have a two-year dormancy before germinating (Tomback et al., 2001a). In one plot (Mt. Scott), marking all caches in 2011 would have been too destructive given the large number of germinants. Instead, all caches in one quarter of the plot were marked and the number of caches across the entire plot were counted, thereby allowing an estimate of the total germinants. In 2012, all germinants surviving from 2011 were marked throughout the entire plot.

2.3. Construction of the ambient matrix models

We constructed sized-based projection matrices for each annual transition. Because plots were not sampled in 2008, we were able to construct nine matrices (i.e., 2003–2007 and 2009–2014). We used five size classes, which included trees in the following categories: (1) < 1.37 m in height (“seedlings”), (2) 0.1–10 cm dbh, (3) 10.1–20 cm dbh, (4) 20.1–40 cm dbh, and (5) > 40 cm dbh. We based our classes partly to be consistent with previous, related studies (van Mantgem et al., 2004; Maloney et al., 2012), but also because our population size was not large enough to confidently estimate survival and growth rates for more size classes. Because dbh of trees were only measured three times during the study (2003, 2007, and 2013), we approximated their sizes in the other years to allow for calculating size-specific growth. To do this, we used standard dendrochronological techniques (Speer, 2010) to assess climate-driven variation in ring-widths to estimate growth in years that we did not measure dbh, rather than assume constant growth between measures (see Appendix A for details). Using our measures of tree size, estimating stasis (the proportion remaining in a class) and growth were relatively straight-

forward, except in the case of growth from Class 4 to Class 5, which was never observed during the 11-yr study. Instead, we used the estimate of growth from Class 3 to Class 4 for this vital rate in each corresponding matrix (year). When doing this, we also reduced stasis of Class 4 by the same amount so as not to inflate survival of Class 4 trees. Retrogression was allowed in our matrices and was observed in a single year (2011–2012) for one class (Class 3 to Class 2). This is not due to shrinkage of trees, but likely due to trees not having permanent tags placed at breast height. This resulted in dbh being measured at slightly different heights from year-to-year, and thus some trees were recorded as smaller than their previous measure. Because we assume that this sampling error could also result in exaggerated, positive growth, we left retrogression in our matrices to compensate.

Fecundity was estimated separately for each of the nine matrices as the average number of germinants per reproductive tree. Cones were never observed on seedlings and rarely on Class 2 trees ($< 2\%$ of trees with cones were in Class 2), so we included fecundity only in Classes 3, 4, and 5. The number of reproductive adults changed across time due to mortality, which meant that fecundity was estimated using different numbers of reproductive plants for each matrix. In addition, because most germinants arise after a two-year dormancy (Tomback et al., 2001a), we used the number of reproductive trees at time $t-2$ when estimating fecundity at time t . However, we could not do this in two cases. In the 2009–10 matrix we used the germinants born in 2010, but, because we did not have field data from 2008, we used reproductive trees from 2007. And, for the 2003–04 matrix, we used the 2003 adults because surveys had not been done in 2002. Lastly, we assumed that larger trees make greater contributions to fecundity than smaller trees. To assess this, we used logistic regression to assess the relationship of tree size (dbh) and the presence of cone production. The logistic regression estimated the probability of cone production for an individual tree, p , as

$$p = \frac{1}{1 + e^{-(2.9684 + 0.0459(\text{dbh}))}}$$

Our model adequately classified cone bearing trees based on their size (AUC = 0.839) and failed to correctly classify a tree as cone bearing at a rate of 13.6%. Using this model, the relative probability of making cones was estimated as 0.037, 0.126, and 0.838 for Class 3, Class 4, and Class 5 trees, respectively. In this estimate, we assume that the largest Class 5 individual is 87 cm dbh, though there was one larger tree which we consider an unusual outlier (i.e., 118 cm dbh). Including the 118 cm tree would have inflated the relative contribution of Class 5 trees. We then used the relative probabilities of making cones to apportion fecundity (i.e., the percentage of germinants) across the size classes.

Whitebark pine is a masting species (Crone et al., 2011) and a large cone production year was noted in 2009 in the study area which resulted in an exceptionally large number of germinants in 2011 (1235 germinants across the seven plots, in contrast with an average of 14.8 germinants across all other years; see Fig. 2). We

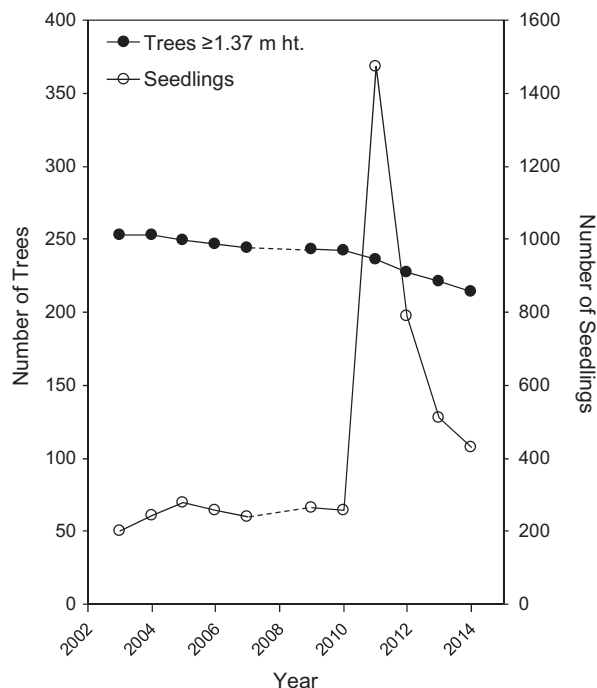


Fig. 2. Total number of whitebark pine found in demography plots monitored from 2003–2014, excluding 2008. Trees (closed symbols) are defined here as ≥ 1.37 m height, and seedlings (open symbols, shown on the second axis) are < 1.37 m height.

suspected that germinants in a large mast year would have lower survivorship than germinants in non-mast years, and this would result in one matrix (2011–12) with very low seedling survivorship that is separate from the matrix with large fecundity (2010–2011). Simulations that randomly select matrices could, without the addition of considerable complexity in the matrix selection process, include large bouts of reproduction followed by artificially high survivorship. Thus, we assessed first year survival of all germinants from 2003 to 2014 other than the mast year (2011 germinants) and estimated the mean rate among years was 62.2%. In contrast, germinants from 2011 had first year survival rates of 44.4% and 49.6% the second year, or 22% survival over the first two years. Given this difference, we first calculated the number of germinants that represented 22% of 1235, our predicted number of individuals after two years (i.e., $1235 \times 0.22 = 271$). Next, we asked what number of germinants would produce 271 germinants had they been subject to 62% survivorship. That is, $435 \times 0.622 = 271$ germinants. Thus, for the 2010–11 matrix we used fecundity rates that result in 435 germinants, and we do not use the 2011 seedlings in seedling survivorship estimates for the 2011–12 and 2012–13 matrices.

2.4. Model variations – assessing rust and beetle impacts

We constructed separate sets of matrices to assess the impact of blister rust, mountain pine beetle, and the combination of both rust and beetles on population growth of whitebark pine. For blister rust, we first removed all individuals from the dataset that showed signs of blister rust in the first year of the transition (matrix). As an example, when estimating demographic rates for the 2003–2004 matrix, we removed all trees that showed signs of blister rust in 2003 (see Knight, 2004 and Farrington et al., 2009 for similar approaches). Any individual that showed signs of blister rust was assumed to be infected by the pathogen for the remainder of the study; we assume that trees do not fully

recover from the rust. Using the “rust-free” trees, we then constructed the nine matrices for each year as described above. This new set of matrices is identical to the ambient matrices in two ways. First, because rust was recorded on only two of 957 seedlings observed, we used the same vital rates for seedlings. Second, because we did not have enough information to assess the impact of blister rust on fecundity, we used the same fecundity rates here as in the ambient matrix.

To assess the impact of mountain pine beetles on population growth of whitebark pine, we constructed another set of annual matrices that excluded those trees that showed signs of beetle (i.e., “beetle-free”). Here, we removed any individual that showed signs of beetle in the first year of the transition (matrix), as in the case of removing blister rust (described above). In addition, we removed trees that showed signs of mountain pine beetle in the second year of the transition and that died before that observation. We did this because mountain pine beetles can attack and kill trees quite rapidly; a tree may not show signs of beetle the first year and yet still be killed by beetles by the second observation. Blister rust, on the other hand, does not kill whitebark pine within the first year of infection and thus we never observed mortality from a newly-infected tree. As with our rust-free matrices, we used demographic rates for seedlings and fecundity from the ambient matrix for our beetle-free matrices. Mountain pine beetle was never observed on seedlings, and we do not have any estimates of how beetles impact fecundity. Lastly, we built a set of nine matrices that excluded individual trees that exhibited blister rust and/or mountain pine beetles using a similar process as that described for our rust- and beetle-free matrices.

2.5. Model analyses

For all of our sets of nine annual matrices – ambient, rust-free, beetle-free, and rust and beetle-free – we conducted a series of identical analyses. First, we calculated a mean matrix from the nine matrices representing the 2003–2007 and 2009–2014 time periods. Using these mean matrices we calculated the deterministic population growth rate (λ), sensitivity values (s_{ij}), where

$$s_{ij} = \partial \lambda / \partial a_{ij}$$

and elasticity values (e_{ij}), where

$$e_{ij} = s_{ij} \times a_{ij} / \lambda$$

and a_{ij} is a given element in the projection matrix associated with a particular s_{ij} . Elasticity values are a measure of how much λ would change by altering one particular demographic rate (a_{ij}).

In addition, we calculated the stochastic population growth rate (λ_s) and 95% confidence intervals by simulation using the “stoch. growth.rate” function in the POPBIO package (Stubben and Milligan, 2007, see also Morris and Doak, 2002) in R (R Development Core Team, 2010). For the stochastic simulations, matrices are selected from the pool of nine annual matrices with replacement, and the population size was simulated over 50,000 years from a starting population of 1 distributed at the stable stage distribution of the mean matrix. Rather than select matrices with equal probability, we attempted to simulate the masting characteristic of whitebark pine. Between 2003 and 2014, two masting events have been noted in the study area (though only one is captured by our study plots), and this frequency is not unlike those found in other studies of whitebark pine (Crone et al., 2011; Sala et al., 2012). Thus, we modified the simulation such that our masting matrix (the 2010–2011 transition) was selected with a probability of 0.182 (i.e., $2 \div 11$ years). All of the other eight matrices had equal probabilities of being selected

during the simulations $((1.0 - 0.182) \div 8 = 0.102)$. We do not include density dependence in any of our model scenarios, which we believe is a reasonable approach because trees in our study population occur at low densities where there is almost no canopy closure, and safe sites for germination are not limiting.

Because λ differed between our scenarios, we also conducted life table response experiments (LTREs) to understand which observed differences in individual demographic rates found between scenarios (e.g., ambient vs. blister rust-free matrices) contributed the most to the observed differences in λ . To do this, we first calculated the difference between all mean matrix elements (\bar{x}) in two scenarios. Next, we calculated the average of each mean matrix element, and then calculated sensitivity values for the mean matrix. Lastly, we multiplied the sensitivity by its corresponding difference (see Caswell, 1989). This product, c_x , is an indication of the relative impact (i.e., contribution) of a change in a particular vital rate on the differences in λ , where, in the case of comparing the ambient to the rust-free matrices

$$c_x = (\bar{x}_{\text{ambient}} - \bar{x}_{\text{rust-free}}) \times S_{ij}$$

LTREs were conducted for pairs of scenarios involving ambient, rust-free, and beetle-free matrices.

3. Results

From 2003–2014, we surveyed 1220 live whitebark pine, including 956 seedlings (Class 1) and 264 trees ≥ 1.37 m height (Class 2 – Class 5) within seven plots in Crater Lake National Park. The total population grew from 455 trees in 2003 to 647 in 2014. Most of this increase was due to a large germination event in 2011 (Fig. 2). In 2011, 1235 new germinants were observed; the number of seedlings in the population increased from 201 in 2003 to a high of 1474 in 2011, then declined to 432 in 2014. We observed an average of 138 germinants (new seedlings) per year, but only 14.8 per year when the 2011 germination event was excluded). For trees ≥ 1.37 m height, the population declined during the 11-yr study from 255 trees to 214 trees, a 16% reduction. This change ($\Delta N = 41$) included mortality of 49 trees and the growth of eight trees from seedlings (Class 1) to Class 2. Of the 49 trees that died, eight trees (17%) were infected with blister rust, 17 were infested with mountain pine beetle (35%), and 17 had both blister rust and mountain pine beetle (35%). Of the seven remaining trees, three (6%) were likely killed due to severe mistletoe infestations, while the remaining four (8%) died of unknown causes. The loss of trees was greatest for the largest class of trees (Class 5), which declined by 44%. The number of Class 3 and 4 trees declined by 25% and 16%, respectively, while Class 2 increased by 3%. Basal area of whitebark pine declined by 30% over the 11 years, from 13.1 m² in 2003 to 9.1 m² in 2014 (Fig. 3). In addition, the plots contained several dead standing trees when they were initiated in 2003. These included four trees in Class 5, two trees in Class 4, four in Class 3, and one in Class 2. These dead trees together represent 0.93 m², which is 10% of the living basal area we found in 2003.

In 2003, 15.6% of trees ≥ 1.37 m in height were infested with blister rust, and by the end of the study, 44.6% of trees were infested (Appendix B). The lower rate of infection found in 2003 may have been due to the relatively late date of surveys in the first field season, when conspicuous blisters are no longer common. Average annual survivorship (stasis and growth combined) of all trees ≥ 1.37 m in height was 97.8% across the study period (Fig. 4). Annual survivorship of healthy, rust-free trees (mean annual survivorship = 98.3%) was not significantly different than survivorship of rust-infested trees (96.5%, Fig. 4; Mann-Whitney,

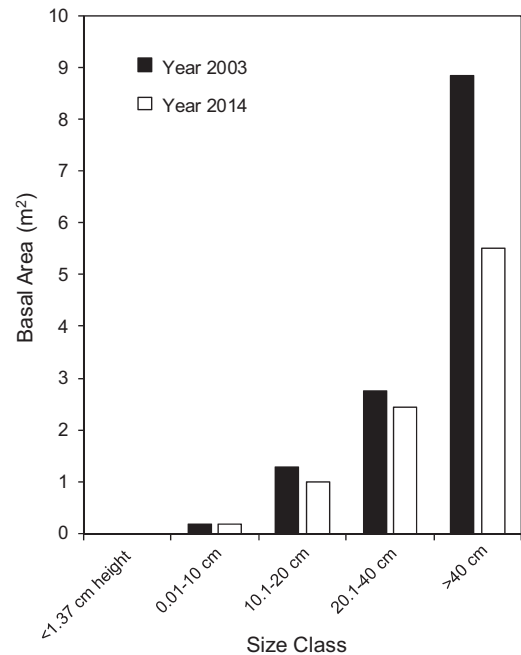


Fig. 3. Change in basal area of whitebark pine found in the demography plots monitored from 2003–2014.

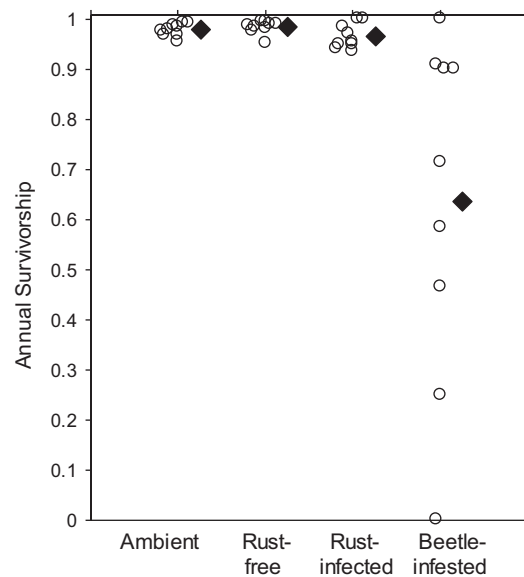


Fig. 4. Annual survivorship (includes stasis and growth) for whitebark pine ≥ 1.37 m height in the demography plots. Each open circle is one year (transition); circles are jittered to make them more visible. Closed black diamonds are mean survivorship values.

$U = 24$, d.f. = 16, $P = 0.159$). The small difference in survivorship was due to an apparent preference by mountain pine beetle for rust-infested trees, and its greater impact on rust-infested trees. Beetles infested rust-infested trees significantly more often than healthy trees (Fig. 5; $U = 1.0$, d.f. = 16, $P = 0.001$). Similarly, beetles were a causal agent of mortality for more rust-infested trees than healthy trees (2.4% vs. 1.1%), though this difference was not significant ($U = 34$, d.f. = 16, $P = 0.596$). Mountain pine beetle was found on an average of 3.6% (± 1.6 SD) of trees ≥ 1.37 m in height,

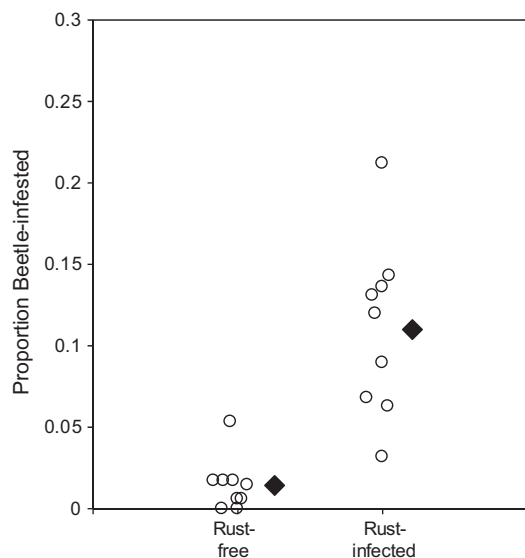


Fig. 5. The proportion of whitebark pine ≥ 1.37 m height in demography plots infested with mountain pine beetle. Each open circle is one year (transition); circles are jittered to make them more visible. Closed black diamonds are mean survivorship values.

though they did not always result in mortality by the next annual survey. Average annual survivorship for beetle-infested individuals was 65% (Fig. 4). Blister rust and mountain pine beetle were both more likely to be found on larger whitebark pine (Appendices C and D). For example, Class 5 trees were four times more likely to be infected with rust than Class 2 trees. Similarly, Class 5 trees were 12 times more likely to be infested with beetles than Class 2 trees.

The mean matrix for whitebark pine using the ambient conditions had a growth rate (λ) of 0.9888 (Table 2), suggesting a 1.1% decline in the population size per year, although the growth rate varied among years of the study (range of $\lambda = 0.9822$ –1.002; see Appendix E). Stasis was highest for Class 2 trees (0.9828), while

Class 4 and 5 had notably lower rates (0.9438 and 0.9539, respectively). The ambient conditions suggest that the largest trees (Class 5) are declining by an average of 4.6% per year. Population growth was most sensitive to changes in Class 2 (Table 3), which resulted from the relatively high survivorship of Class 2 trees. The stochastic model using ambient conditions predicted a mean growth rate (λ_s) of 0.9899, a slight increase over the deterministic growth rate that demonstrates the effect of periodic masting.

The mean matrix using rust-free trees had a growth rate (λ) of 0.9916, a 0.28% increase over the ambient conditions (Table 2, Appendix F). Stochastic simulations indicate λ_s is 0.9930 for rust-free conditions. The 95% confidence intervals for ambient and rust-free conditions overlapped (Fig. 6). In contrast, the mean matrix using beetle-free conditions had a λ of 1.0028, which represents and increase more than five times what was found with the rust-free conditions (Table 2, Appendix G). In addition, the stochastic simulations had a λ_s of 1.0045 with confidence intervals that did not overlap with either the ambient or rust-free estimates (Fig. 6). The scenario that was both rust- and beetle-free gave a $\lambda = 1.0040$ and $\lambda_s = 1.0054$ (Fig. 6). The deterministic λ for this last scenario was 0.0112 greater than the beetle-free scenario, and λ_s was 0.0009 greater than the beetle-free scenario, and the confidence intervals of the two scenarios overlapped with each other and neither included 1.0. As with the ambient scenario, the highest elasticity for the rust-free matrix was for Class 2 (Table 3). In contrast, the largest elasticity for the beetle-free scenario was Class 5 (Table 3). Unlike all other scenarios, the beetle-free scenario had the highest survivorship for Class 5 trees (Table 3).

The LTRE comparing the mean ambient conditions to the no-rust conditions did not reveal any large changes that contributed to a change in λ (Fig. 7), because λ varied little between the two conditions (Table 2, Fig. 7). The largest contribution was for stasis of Class 2 that increased from 0.9828 to 0.9853. In contrast, the ambient conditions varied considerably from the beetle-free conditions (Table 2), and the biggest changes between the mean matrices were found in the stasis of the three largest size classes (Fig. 7). The largest contribution to the change in λ was found, in order, in Class 5, Class 4, and Class 3 (Fig. 7).

Table 2
Projection matrices with average demographic rates for the study period for the ambient condition (top matrix). The middle and bottom matrices show, respectively, average rates without rust-infested individuals (rust-free) and without beetle-infested individuals (beetle-free). The study period was 2003–2014, excluding 2008, so averages are derived from nine annual transitions. Note that growth of whitebark pines is slow, and that trees in the 20.1–40 cm class (Class 4) was never observed during the study period. Thus, we used the growth rate of the 10.1–20 cm class (Class 3) as a proxy for the growth of the 20.1–40 cm class. See text for details.

	<1.37 m ht.	0.01–10 cm	10.1–20 cm	20.1–40 cm	>40 cm
Ambient					
<1.37 m ht.	0.9353	0.0	0.0742	0.2536	1.6902
0.01–10 cm	0.018	0.9828	0.017	0.0	0.0
10.1–20 cm	0.0	0.0103	0.9611	0.0	0.0
20.1–40 cm	0.0	0.0	0.0154	0.9438	0.0
>40 cm	0.0	0.0	0.0	0.0154	0.9539
					$\lambda = 0.9888$
Rust-free					
<1.37 m ht.	0.9353	0.0	0.0742	0.2536	1.6902
0.01–10 cm	0.0018	0.9858	0.0	0.0	0.0
10.1–20 cm	0.0	0.0103	0.9660	0.0	0.0
20.1–40 cm	0.0	0.0	0.0164	0.9541	0.0
>40 cm	0.0	0.0	0.0	0.0164	0.9381
					$\lambda = 0.9916$
Beetle-free					
<1.37 m ht.	0.9353	0.0	0.0742	0.2536	1.6902
0.01–10 cm	0.0018	0.9827	0.0018	0.0	0.0
10.1–20 cm	0.0	0.0104	0.9720	0.0	0.0
20.1–40 cm	0.0	0.0	0.0144	0.9806	0.0
>40 cm	0.0	0.0	0.0	0.0144	0.9959
					$\lambda = 1.0028$

Table 3

Elasticity values associated with the average matrices shown in Table 2 for ambient, rust-free, and beetle-free conditions. The three greatest values in each matrix are bolded.

	<1.37 m ht.	0.01–10 cm	10.1–20 cm	20.1–40 cm	>40 cm
<i>Ambient</i>					
<1.37 m ht.	0.0626	0.0	0.0006	0.0007	0.0022
0.01–10 cm	0.0036	0.6598	0.0004	0.0	0.0
10.1–20 cm	0.0	0.0040	0.1391	0.0	0.0
20.1–40 cm	0.0	0.0	0.0029	0.0617	0.0
>40 cm	0.0	0.0	0.0	0.0022	0.0600
<i>Rust-free</i>					
<1.37 m ht.	0.0619	0.0	0.0007	0.0010	0.0020
0.01–10 cm	0.0037	0.6664	0.0	0.0	0.0
10.1–20 cm	0.0	0.0037	0.1414	0.0	0.0
20.1–40 cm	0.0	0.0	0.0030	0.0780	0.0
>40 cm	0.0	0.0	0.0	0.0020	0.0361
<i>Beetle-free</i>					
<1.37 m ht.	0.0532	0.0	0.0001	0.0003	0.0035
0.01–10 cm	0.0039	0.1882	0.0001	0.0	0.0
10.1–20 cm	0.0	0.0040	0.1232	0.0	0.0
20.1–40 cm	0.0	0.0	0.0037	0.1607	0.0
>40 cm	0.0	0.0	0.0	0.0035	0.4557

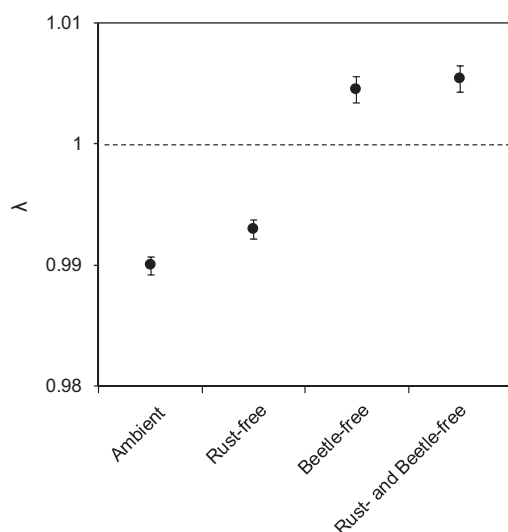


Fig. 6. Stochastic growth rates (λ_s) for whitebark pine in the demography plots. Error bars indicate 95% confidence intervals.

4. Discussion

4.1. Relative importance of mortality agents

Our study suggests the population of whitebark pine in Crater Lake National Park is rapidly declining. Our model, constructed using nine estimates of annual rates of survivorship, growth, and fecundity, predicts that the population is losing ~1.1% of the trees per year. The number of seedlings increased during the study period from 201 to 432, however those gains were not substantial enough to offset mortality of trees, and mortality was highest in the largest classes. For instance, the overall population of trees ≥ 1.37 m in height declined by 15% during the 11-yr study, while the largest class of trees (i.e., trees >40 cm dbh) experienced a 44% loss of individuals. Because of this loss of larger trees, the study population lost $>30\%$ of its total basal area (Fig. 3). The literature on whitebark pine consistently lists blister rust and mountain pine beetle as the primary threats for the species (Keane et al., 2011; U.S. Fish and Wildlife, 2011). However, it has been difficult to estimate the impact of either blister rust or mountain pine beetle for population decline of whitebark pine, and this study is

the first instance in which the relative contributions of these threats have been characterized. We found that blister rust had little impact on population growth during the study period, while mountain pine beetle contributed strongly to population decline. Our study provides a general method to assess multiple stressors on tree populations using a demographic model, and it highlights how different the impacts of important insects and pathogens can be for population growth and structure. In addition, when compared with previous studies, our work also highlights the geographically variable effects of forest insects and pathogens for tree populations, and suggests their interactions with tree hosts are context dependent.

One of the more interesting findings from our study concerned the elasticity analysis, where we found that changes in the stasis of Class 2 (0.01–10 cm dbh) had the most influence on λ in the ambient conditions (Table 3). For trees and other long-lived perennials, elasticity values are usually highest for the largest size classes, as those individuals typically have the highest survivorship and fecundity (e.g., Boucher and Mallona, 1997; Sebert-Cuvillier et al., 2007; Münzbergová et al., 2013). In contrast, survivorship in the population we modeled was highest for Class 2, and the largest trees (Class 5) had an average mortality rate of 4.6% (Table 2). This same general pattern was found in the rust-free scenario, indicating that mortality of large trees is still high enough to reduce the lifetime contribution of those trees. In contrast, the beetle-free scenario produced elasticities that are more typical for trees (Table 3), a reflection of the largest trees having the highest survivorship and fecundity (Table 2). The LTRE demonstrates that, indeed, the increase in survivorship of the three largest classes estimated in the beetle-free scenario contributed the most to the increase in λ (Fig. 7). Overall, these results suggest that beetles are exerting a significant shift on the life history of whitebark pine in the study area.

4.2. Implications for management

Blister rust reduced survivorship of whitebark pine by only 1.8% (Fig. 4) during the study period and reduced population growth by 0.4%; if our model is reflective of the conditions in the study area, removing blister rust entirely would result in a population that is still declining ~0.7% per year given the current rate of beetle-caused mortality (Fig. 6). A beetle-free condition, on the other hand, would result in a population growing ~0.5% per year, primarily because survivorship of beetle-free trees was 56% higher

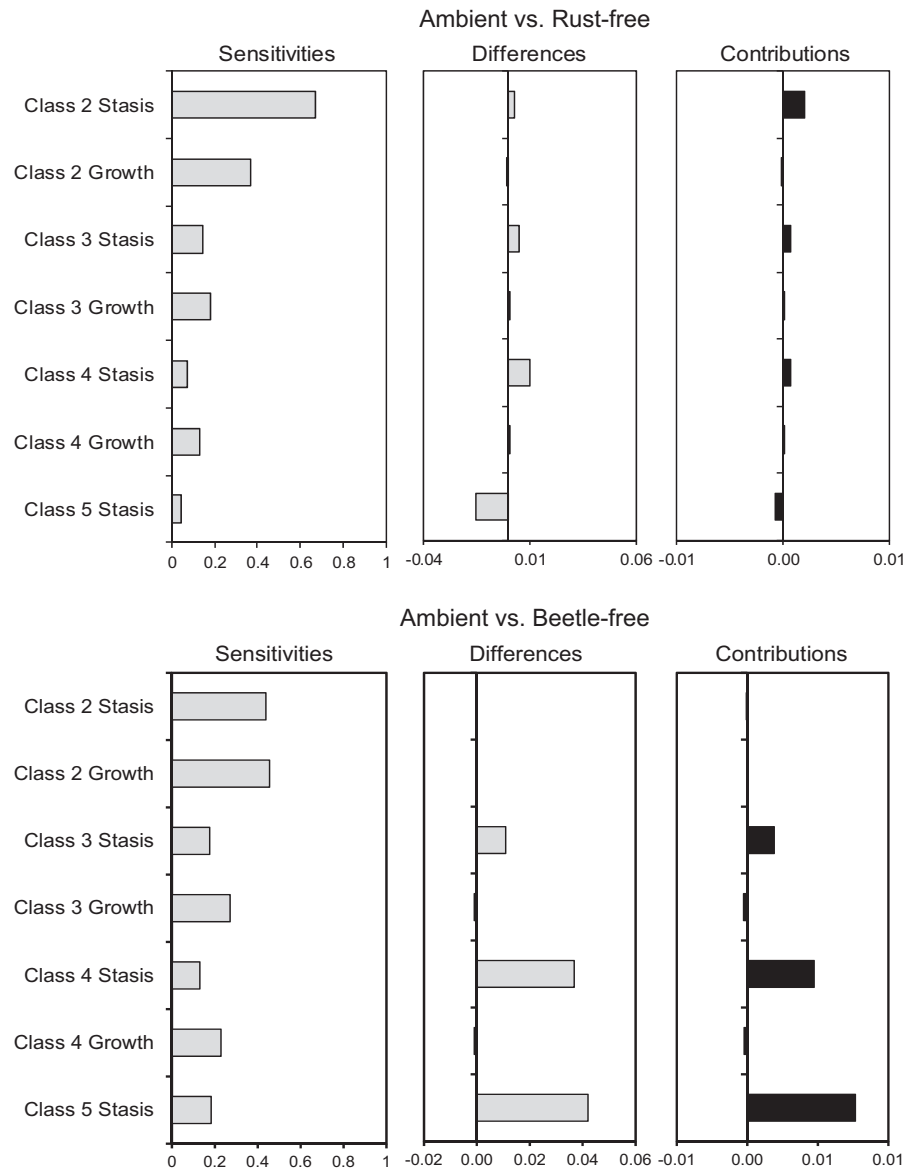


Fig. 7. Results of the LTRE for ambient vs. rust-free conditions and ambient vs. beetle-free conditions. Sensitivity values (s_{ij}) are derived from a matrix of the mean of ambient and rust-free conditions. Differences shown are $\bar{x}_{\text{ambient}} - \bar{x}_{\text{rust-free}}$, and contributions are $c_x = (\bar{x}_{\text{ambient}} - \bar{x}_{\text{rust-free}}) \times s_{ij}$.

than beetle-infested trees. This last conclusion assumes that blister rust continues to only kill 1.8% of trees. Since the current infection rate is 44.6% and has been increasing since 2003 (Appendix B), continued monitoring of our plots is critical to assess the impacts of blister rust. Nonetheless, given the ambient conditions, results suggest management efforts would need to increase survivorship (i.e., stasis) of all three of the largest classes $\sim 3.0\%$ for λ to reach unity. Interestingly, without blister rust, the survivorship of these classes would need to increase by approximately the same amount for the population to remain stable. While our results do not lessen the previously recognized need for continue ongoing efforts to manage blister rust in our study area, they do suggest that effective management scenarios require a reduction of mountain pine beetle attack to levels below what we observed.

The prevalence of blister rust and mountain pine beetle varies considerably across the range of whitebark pine, and as such, the conclusion that mountain pine beetles were most responsible for population decline during our study should not be widely applied for the species as a whole. Rather, our results highlight the variable

nature of insects and pathogen dynamics in both space and time which may be driven by differences in climate, biotic interactions, or both. Nonetheless, mountain pine beetle appears to have been important in the southern Cascades and around our study area since at least 2003. Assessing the same plots we used in our study, but for only the first five years (2003–2007), Murray (2010) concluded that mountain pine beetle was more important than blister rust for tree mortality. In a separate study, Smith et al. (2011) reported that mountain pine beetle was the leading cause of whitebark pine mortality in Crater Lake National Park. Goheen et al. (2002) studied whitebark pine just outside of the northern boundary of the park and estimated that 13% of the mortality was due to mountain pine beetle and 67% to blister rust, however their work was conducted before a recent increase in mountain pine beetle activity (Beck and Holm, 2014). These studies suggest that our study region has had both blister rust and mountain pine beetle for many decades and, at least recently, most observations suggest that mountain pine beetle has been the leading cause of whitebark pine decline in Crater Lake National Parks since 2003.

Mountain pine beetle is an endemic component of whitebark pine ecology across its range (Keane et al., 2011) and observations of their impact on pine have been recorded in our study area since Crater Lake National Park was established in 1902. Recently, however, notable increases in mountain pine beetles have been observed in the Cascades and other parts of western North America (Millar et al., 2012; Preisler et al., 2012; Meigs et al., 2015; Weed et al., 2015). Increases in success of the beetle may be due to warming winter temperatures, which are thought to lead to more frequent univoltine life cycles where cold temperatures normally restrict beetles to a semivoltine cycle (Logan et al., 2010; Preisler et al., 2012; Weed et al., 2015). Within Crater Lake National Park, a marked increase of mountain pine beetle attack on whitebark pine appears to have begun in 2007 during a period of continued increase in minimum winter temperatures (Beck and Holm, 2014). From 2007–2012, mountain pine beetle affected 2.0–4.0 times more area per year than the average annual area affected over the previous five decades (Beck and Holm, 2014). In our study plots, mortality of whitebark pine due to mountain pine beetle did not increase until 2010, perhaps reflecting the amount of time needed for mountain pine beetle to kill trees or the limited ability of our seven plots to capture the full range of conditions within the park. Nonetheless, in an analysis of our models using only pre-2008 data (i.e., using all matrices 2003–2007), the relative contribution of blister rust and mountain pine beetle on population growth remain the same: $\lambda_s = 0.9958$ for ambient conditions, $\lambda_s = 0.9976$ for rust-free conditions, and $\lambda_s = 1.0025$ for beetle-free conditions. Whether mountain pine beetle will continue to have the same impact on whitebark pine populations is unknown and is a crucial question for future work. It is possible that the recent episode of mountain pine beetle attack is now ending. On the other hand, warming conditions predicted to occur in the future may favor greater frequency and longer duration of beetle outbreaks (Preisler et al., 2012; Meigs et al., 2015).

4.3. Caveats and future work

The prevalence of blister rust varies spatially within Crater Lake National Park, and this variability should temper the general application of our model (Murray and Rasmussen, 2003; Smith et al., 2011). Differences in climate between the east and west side of the park is consistent with regional differences between the wet and cool climate of the southwestern Canadian Rockies where blister rust has been most impactful (McDonald and Hoff, 2001; Geils et al., 2010) and the more arid climate in the Northwestern Rocky Mountains where blister rust has not been as important (Gibson et al., 2008; Tomback and Achuff, 2010). In addition, park eradication efforts in of *Ribes*, the alternate hosts for blister rust, from 1937–1949 may have prevented the development of blister rust during the early stages of spread in the park. Two areas that were part of the eradication efforts were near two of our study plots, Cloud Cap and Mt. Scott (Table 1). Murray and Rasmussen (2003) found that transects with *Ribes* supported higher rates of blister rust infection of whitebark pine (12% of live trees) over those without *Ribes* (4% of live trees). In the same study they also failed to find *Ribes* in the Cloud Cap and Mt. Scott areas. Our seven plots contained too few individuals to confidently model each plot separately (Table 1), thus we have not tried to assess spatial variability in population decline across the park. Though combining our plots into one model has its limitations, they are outweighed by the exceptionally long duration of the study. For most trees for which demographic models have been built, the number of transitions used to estimate variability in demographic rates is few. In addition, there are few studies that have recorded the incidence of more than one mortality agent on an annual basis, including the studies used to develop previous models of white-

bark pine (Ettl and Cottone, 2004; Field et al., 2012; Maloney et al., 2012).

The longer-term impacts of blister rust may include the slow deterioration of reproductive success of whitebark pine, which we may not have captured in our study. For instance, blister rust can kill branches without killing the tree, and those branches can be cone-bearing branches resulting in a tree with reduced reproductive potential (McKinney and Tomback, 2007). Our model would not capture this sort of event until the entire tree dies. Given the number of seedlings found in the plots during the study period, we suspect that the population is currently not limited by fecundity. However, this may change if blister rust continues to kill cone-bearing branches of larger trees. In addition, our study indicates that mountain pine beetle is attracted to whitebark pines that are infected with blister rust (Fig. 5; see also Six and Adams, 2007; Bockino and Tinker, 2012), though it is possible we have underestimated this interaction. In our rust-free model, we have removed all the individual trees with rust, which includes trees where beetles may have been attracted to trees because of the presence of blister rust. However, there is some chance that the attraction to rust-infected trees could put uninfected trees at greater risk because beetles are attracted to the general vicinity of the whitebark pine stands. There is no evidence this occurs, either in our study or others, yet we cannot rule it out. Lastly, our model may not capture the full negative impacts of blister rust on whitebark pine survivorship, simply because 11 years may not be long enough to observe higher mortality rates for infected individuals. Given that rust appears to be increasing in our plots, and may have been quite low in the first year (Appendix B), the study populations may represent an early phase of infection. This contrasts with the long history of infection in the park (Beck and Holm, 2014). Continued monitoring of our plots will be essential for resolving this question.

Our main finding relies heavily on being able to estimate demographic rates across the 11-yr study for a population that is both rust- and beetle-free. The method we used of removing either rust-infected or beetle-infested individuals from the data has been demonstrated in several other studies. For instance, Knight (2004) estimated the impact of white-tailed deer (*Odocoileus virginianus*) on the herbaceous perennial, trillium (*Trillium grandiflorum*), by removing individuals that experienced herbivory. Farrington et al. (2009), assessed the relative contribution of deer herbivory and harvesting by people on the herbaceous perennial, American ginseng (*Panax quinquefolius*; see also McGraw and Furedi, 2005). Nonetheless, our approach to evaluating rust-free and beetle-free populations has several potential biases. When removing rust-infected individuals, we assume that trees remaining in the matrices are similar to rust-infected trees, other than that they are disease-free. Potentially, blister rust more often infects weaker trees, with lower rates of survivorship and growth, which would mean our rust-free matrices represent a pool of more robust individuals. If true, our approach would over-estimate the impact of rust on population growth. If, on the other hand, blister rust infects more vigorous trees, then our model would underestimate the impact of blister rust on population growth. Similar biases may arise in assessing beetles on population growth, if indeed beetles preferentially selected weaker or more vigorous trees. Our study and others (Campbell and Antos, 2000; Smith and Hoffman, 2001; but see Tomback and Achuff, 2010) suggest that rust more frequently infects larger trees, and that beetles more often infest larger and rust-infected trees (Bockino and Tinker, 2012), though we cannot assess the relationship of blister rust or beetle incidence with tree vigor. If beetles preferentially attack stressed trees, then our beetle-free matrices reflect the healthier trees in the population. Overall, these issues may reduce the precision of our rust-free and beetle-free models. Nonetheless, given the small impact

of blister rust on whitebark pine survivorship, we feel confident that a rust-free population is one where $\lambda < 1.0$, and that relative impact of the blister rust and mountain pine beetles is well-represented by the models. Notably, our results would not have differed had we considered only trees with active cankers in our rust-free model; if we only removed individuals with active cankers $\lambda = 0.9849$, similar to that found when removing all rust-infected trees (i.e., 0.9916).

Given that we did not measure size (dbh) of trees every year, we estimated annual variation in demographic rates using climate variability as a proxy (see [Appendices A and H](#)). Tree ring growth was significantly correlated with May snow depth and thus we used it to apportion growth in years for which we did not measure tree size. That trees would grow *less* in years that have greater spring snow depth is at first counterintuitive because deep snow might prolong the duration of available water in dry sites. However, it is likely that early growing seasons with heavy snow are characterized by cold soils (i.e., under snow) and low moisture that is still in snow form. Two other studies support this hypothesis. [Daneshgar \(2003\)](#) found strong correlations of whitebark pine growth and low spring snow depth in Mount Rainier and North Cascades National Parks. In contrast, [Daneshgar \(2003\)](#) found tree growth at Crater Lake National Park was not correlated with snow depth, but instead positively correlated with June temperatures. [Peterson and Peterson \(2001\)](#) found strong negative correlations between growth of mountain hemlock and spring snow depth in several sites in the southern Cascades, including Crater Lake National Park. Thus, we consider using spring snow depth a reasonable substitution for tree growth. Nonetheless, future work in our study area would benefit from extending the tree ring chronology to the present, thereby eliminating the need for any proxy.

Besides building better growth estimates for whitebark pine using a current tree ring chronology, there is additional work that would allow for continued development of our model. Estimating demographic rates for a larger number of smaller size classes using a model selection approach would reduce the errors inherent in using only five size classes in which size-specific variation is lost (e.g., [Shriver et al., 2012](#); [Metcalf et al., 2013](#); [Rees et al., 2014](#)). To take this approach, future work will need to estimate sizes of all trees in our plots for all years. In the study presented here, we could not estimate the size for 20 trees (8% of the non-seedling trees) that died during the course of the study, though we were able to confidently place those in a size class. However, because these trees are still standing, growth estimates can be obtained by extracting increment cores from their boles. In addition, our model would benefit from better estimates of the effect of mountain hemlock on whitebark pine demographic rates. Increasing mountain hemlock in whitebark pine stands is an emerging concern in Crater Lake National Park ([Murray, 2007](#); [Beck and Holm, 2014](#)), yet our model cannot be used to address the impact of increased competition for whitebark pine. We suggest studies that estimate the relationship of whitebark pine growth and mountain hemlock density using tree ring studies. In addition, we suggest studies that can estimate the effect of mountain hemlock on whitebark pine seedling abundance, as our observation suggests that high densities of mountain hemlock can preclude whitebark seedling establishment.

4.4. Conclusions

Both pathogens and insect pests can have profound impacts on forested ecosystems (e.g., [Anagnostakis, 1987](#); [Jules et al., 2002, 2014](#); [Orwig et al., 2002](#)), and their impacts are likely to be strongly shaped by changes in climate and, in some regions, exclusion of fire ([Millar and Stephenson, 2015](#)). For many trees, multiple mortality agents are acting in concert, and distinguishing the relative impact

of each is usually impossible. For whitebark pine, it appears that mountain pine beetle has been the primary driver of tree mortality in our study area over the past decade and that any management aimed at increasing the population size of whitebark pine would need to track and address tree mortality due to both mountain pine beetle and blister rust. Lastly, our study presents a potential method for addressing population-level effects of multiple mortality agents for trees, and it illustrates the nature of the intensive field study required to estimate demographic rates such that pest and pathogen effects can be compared.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2016.09.022>.

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