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Forest Structure, Health, and Mortality in Two Rocky Mountain Whitebark Pine Ecosystems: Implications for Restoration

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ABSTRACT: Whitebark pine (*Pinus albicaulis* Engelm.) forests in western North America are increasingly threatened by the exotic pathogen white pine blister rust (*Cronartium ribicola* J.C. Fisch.). Whitebark pine is designated a high priority species on the candidate list of Endangered or Threatened species, spurring activity to monitor the rust infection and develop restoration strategies. We surveyed two major whitebark pine ecosystems (Northern Divide Ecosystem [NDE], including Glacier National Park, and Greater Yellowstone Ecosystem [GYE], including Yellowstone National Park) to quantify stand density, structure, species composition, blister rust infection, and mortality. We compared ecosystems based on these variables and suggest alternative restoration strategies. Overall stand densities were similar between the two ecosystems; however, NDE forests had only 79 live whitebark trees ha⁻¹ compared to 274 in the GYE. Rust infection, crown kill, and mortality were all significantly greater in NDE forests. Nearly 75% of all whitebark trees in the NDE were dead, and approximately 90% of the remaining whitebark were infected with rust. These high infection and mortality levels suggest that planting rust-resistant whitebark seedlings should be a high-priority restoration strategy in the NDE. Conversely, nearly 30% of large seed-bearing whitebark remain uninfected in the GYE, indicating that avian seed dispersal should be reasonably dependable during good cone years in that ecosystem. Our study preceded a recent bark beetle (*Dendroctonus ponderosae* Hopkins) epidemic, and provides a comparison of rust-infected whitebark communities in two major ecosystems under virtually beetle-free conditions, and establishes a baseline for assessing impacts of beetles in the future.

Index terms: *Cronartium ribicola*, *Pinus albicaulis*, restoration, white pine blister rust, whitebark pine

INTRODUCTION

Whitebark pine (*Pinus albicaulis* Engelm.) grows in the highest and coldest mountain environments in western North America, ranging from central British Columbia south to central California, and from the Pacific coastal mountains east to the Rocky Mountains of Alberta, Montana, and Wyoming. Whitebark is considered a keystone species in high-elevation communities, serving as the “glue” that holds them together structurally and functionally (Tomback and Kendall 2001). A unique feature of this species is that it obligately depends on Clark’s nutcracker (*Nucifraga columbiana* Wilson) to disperse and “plant” its large, wingless seeds (Tomback 1982). Nutcrackers use their sturdy beaks to pry seeds from tightly closed whitebark cones, deposit them in a sublingual pouch, and then transport them to widely dispersed cache sites for later consumption. Some of the cached seeds are not recovered, and subsequently germinate and become established as whitebark seedlings.

In the Rocky Mountains, whitebark pine occurs in mixture with Douglas-fir (*Pseudotsuga menziesii* var. *glauca* [Beissn.] Franco), lodgepole pine (*Pinus contorta* Douglas var. *latifolia* [Engelm.] Critchfield), subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.), and Engelmann spruce

(*Picea engelmannii* Parry ex Engelm.) in the lower and middle portion of its elevational range, but becomes a climax dominant on high, cold, and exposed sites (Arno and Weaver 1990). Historically, this species was relatively little affected by either insect or disease agents. However, since the exotic pathogen, white pine blister rust (*Cronartium ribicola* J.C. Fisch.), was introduced into British Columbia in the early 1900s, the disease has inexorably spread to the east and south (McDonald and Hoff 2001). Currently, some level of infection appears across much of whitebark’s range, with near-total infection in some populations (Hoff et al. 2001). In 2011, the U.S. Fish and Wildlife Service placed whitebark pine as a high priority on the candidate species list of Endangered or Threatened species (U.S. Fish and Wildlife Service 2011). Managers in both U.S. and Canadian national parks are alarmed at the rate of spread and intensity of the infection, spurring activity to monitor the disease and develop restoration strategies. Two areas in the U.S. Rocky Mountains are of special concern – the Northern Divide Ecosystem (NDE), including Glacier National Park and the adjacent Flathead National Forest, and the Greater Yellowstone Ecosystem (GYE), including Yellowstone National Park and the adjacent Gallatin and Shoshone National Forests. Monitoring in the NDE has found infection levels approaching 90 percent in some whitebark popula-

tions (Kendall and Keane 2001). In the GYE, the apparent importance of whitebark pine seeds to grizzly bears (*Ursus arctos*) elevates concerns about potential impacts of blister rust infection in that ecosystem (Mattson and Reinhart 1997).

Whitebark pine is faced with multiple challenges to its long-term persistence, including white pine blister rust (Hoff et al. 1980; Kendall and Keane 2001; Tomback and Achuff 2010), mountain pine beetles (*Dendroctonus ponderosae* [Hopkins]) (Logan and Powell 2001; Gibson et al. 2008), successional replacement by shade-tolerant conifers (Arno 1980; Murray et al. 2000), and potential impacts of climatic change (McKenney et al. 2007; Logan et al. 2010). However, our study focused solely on white pine blister rust, for several reasons. First, blister rust is currently the most widespread and pernicious threat across whitebark's range. Second, mountain pine beetle-infested trees and beetle-caused mortality were rarely encountered during field sampling in our study; Rochefort (2008) also reported infrequent mountain pine beetle activity in her survey of whitebark pine communities in Mount Rainier and North Cascades National Parks. While bark beetle activity is currently at epidemic levels in some whitebark communities (including the GYE), it is a recent and ongoing phenomenon. Hence, this study provides a comparison of rust-infected whitebark communities in two major ecosystems under virtually beetle-free conditions, and establishes a baseline for assessing impacts of beetles in the future. Successional replacement of whitebark by shade-tolerant conifers is also a concern, but it is only a very gradual threat in some ecosystems (Arno 1980). Finally, climatic change may profoundly affect whitebark communities, both directly through physiological effects on regeneration and survival, and indirectly through influences on blister rust, bark beetles, fire regimes, and succession (Hamann and Wang 2006; Logan et al. 2010). However, assessing these potential effects and complex relationships was not part of our study.

This study had three primary objectives: (1) describe and quantify stand density, structure (trees ha⁻¹ by diameter class),

species composition, blister rust infection, and mortality in two major whitebark pine ecosystems (NDE and GYE), (2) compare ecosystems based on these variables, and (3) suggest alternative restoration strategies based on differences between ecosystems.

METHODS

Study Area and Sampling Design

Sampling was conducted in two study areas (ecosystems), the NDE in northwestern Montana and the GYE in southwestern Montana/northwestern Wyoming (Figure 1; U.S. Geological Survey 1999). We used a two-stage design to select sampling locations within each ecosystem. Research sites within an ecosystem were identified based on known occurrence or a high probability of occurrence of whitebark pine, presence of mature (i.e., cone-bearing) whitebark pine trees, reasonable access, and representation of a range of forest communities. Presence of mature trees was required for a complementary study on seed production and predation (McKinney et al. 2009), and reasonable access was defined as a location within 16 km of a trailhead. Forest communities in both ecosystems were comprised of whitebark pine, lodgepole pine, subalpine fir, Engelmann spruce, and Douglas-fir in various combinations and relative abundances. Elevation of research sites ranged from 1806 to 2181 m in the NDE and from 2546 to 2978 m in the GYE. Field data were collected from June to September, 2004–2006.

Each research site (NDE $n = 10$ sites, GYE $n = 8$ sites) was established by delineating rectangular boundaries 100-m wide by ≥ 200 -m long within a contiguous forest stand (site area: min = 2 ha, max = 7 ha, mean = 2.6 ha). We then subdivided sites into 1-ha squares (100 m \times 100 m) to increase efficiency and provide better control over sampling. For the second level of the sampling design, we selected random azimuths and established two 10 m \times 50 m (500-m²) belt transects within each hectare of each research site. We counted, measured, or evaluated the variables necessary to summarize the density,

structure, species composition, and health of the whitebark pine community within the belt transects at each research site. Because our sampling design used a combination of subjectivity and probability, statistical inference from our results is limited to the sampled forest stands.

Only trees large enough to potentially bear cones (i.e., ≥ 7 cm dbh (breast height = 1.3 m)) were sampled. Each sample tree was recorded for species, diameter, live (healthy or rust infected), percentage crown kill (if infected), or dead (cause). All live whitebark pine trees were visually inspected for blister rust infection symptoms. A tree was classified as infected if active or inactive branch or stem cankers were identified, and uninfected if not (Hoff 1992). Crown kill was estimated to the nearest 5% for all infected trees. Additional stand descriptors that were estimated, calculated, or measured include: canopy cover (%), canopy height (m), and basal area (cross-sectional area; BA, m² ha⁻¹). Canopy cover was estimated to the nearest 5% in four cardinal directions at the midpoint of each transect using a convex forest densitometer. Canopy cover readings were first averaged for each transect and then across transects to obtain an overall site mean. Canopy height was measured to the nearest 1 m. Basal area was calculated for each tree from the measured diameter and then summed by transect, species, and research site to obtain basal area by species and for all species combined.

Data Analyses

Prior to analyses, we summarized data at the research site and ecosystem level. A significance level of $P = 0.05$ was assumed for subsequent hypothesis testing. Tests for violations of assumptions were investigated, and all necessary data transformations were made. We used S-Plus 7.0 (Insightful Corporation 2005), SPSS 10.0 (SPSS 1999), and Microsoft Excel (Microsoft Corporation 2003) for all statistical analyses and computations.

We summarized forest conditions for each ecosystem using standard descriptors, in-

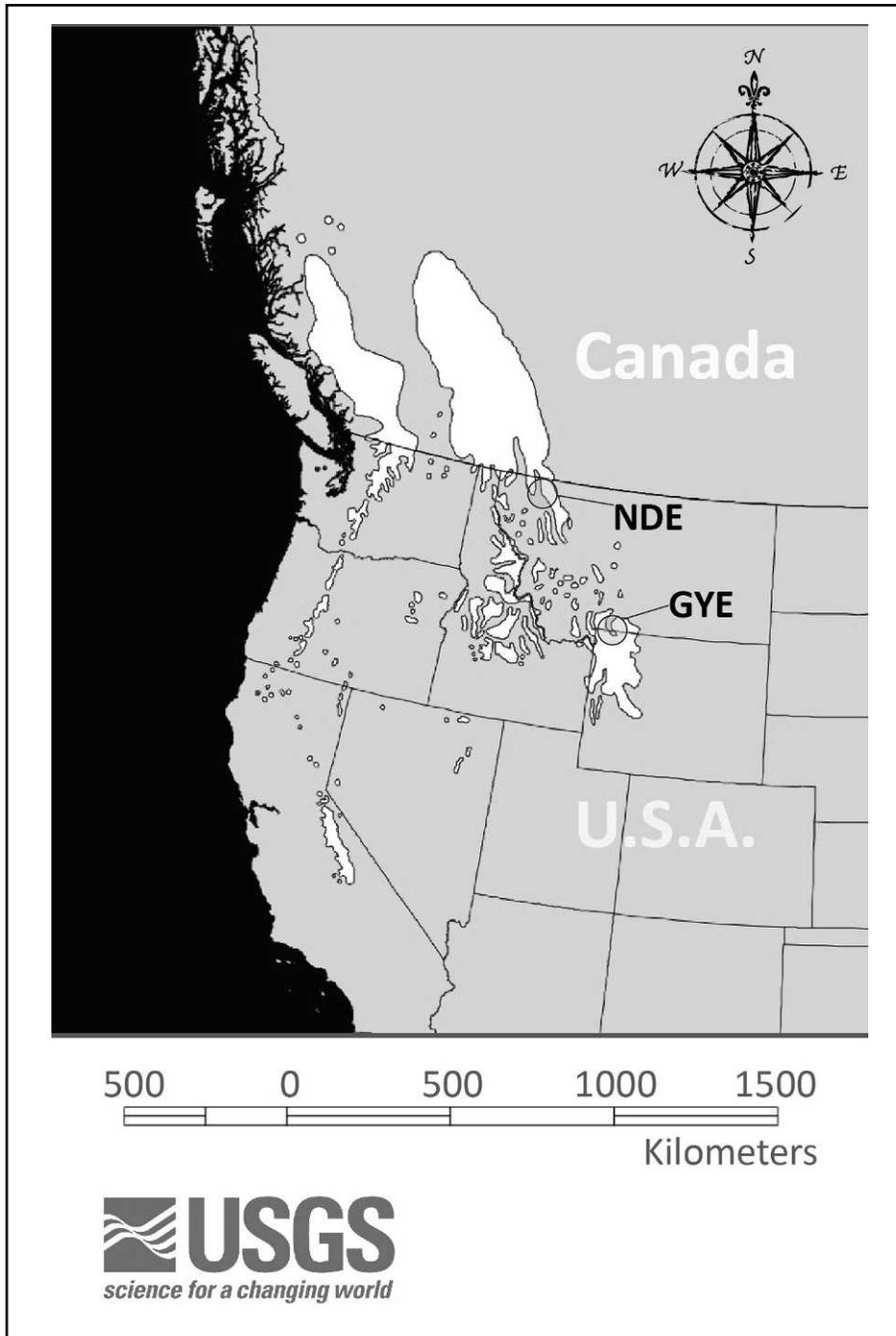


Figure 1. Distribution of whitebark pine in white (USGS 1999), and location of the two study ecosystems (NDE, Northern Divide Ecosystem; GYE, Greater Yellowstone Ecosystem) 2004–2006.

cluding tree density (trees ha⁻¹ ≥ 7 cm dbh), relative density (%), structure (trees ha⁻¹ by 5-cm diameter class), basal area (BA, m² ha⁻¹), canopy cover (%), and canopy height (m). Additional variables summarized for whitebark pine only included blister rust infection of live trees (%), crown kill of infected trees (%), and mortality (%).

Independent sample *t*-tests were used to determine whether NDE forests differed from GYE forests in terms of basal area, forest canopy cover, and canopy height. We compared forest health conditions between the two ecosystems using a MANOVA test to confirm if observed sharp whitebark pine declines in the NDE were reflected in

greater population mean vectors for blister rust infection, crown kill, and mortality. Crown kill was natural log-transformed to meet assumptions of normality.

We further assessed forest conditions by comparing several sets of tree distributions, first between and then within ecosystems. Specifically, we compared histograms of trees ha⁻¹ by 5-cm diameter classes for all species combined using a departure index (Menning et al. 2007). Using this index, a test distribution (e.g., all trees in the NDE) was compared with a reference distribution (e.g., all trees in the GYE). The resulting index, called the Departure Index (DI), provides information about the magnitude, location, and direction of departure of the test tree distribution, if any, from the reference distribution. A positive DI value indicates the test distribution is right-skewed compared to the reference distribution, and a negative value indicates that the test distribution is left-skewed. The magnitude of the DI indicates how far the test distribution is shifted relative to the reference. The DI always has an absolute range of 2 (from minimum to maximum) owing to the inclusion of a scaling factor of 2. This is a desirable attribute because it allows direct comparison of results from one analysis to another. Finally, information about the reference distribution is given by the maximum and minimum values of a DI analysis. For example, if the reference distribution follows a normal distribution (i.e., it is symmetrical), then possible DI values will range from -1 to +1 because compared to the symmetrical reference distribution, the test distribution could depart equally left (1) or right (+1) (see Menning et al. 2007 for a full discussion).

In addition to the DI, we also calculated the Kullback-Leibler (K-L) Criterion (Burnham and Anderson 2002) to measure the absolute difference between the two tree distributions for each pair-wise comparison – the greater the K-L value, the greater the difference between the two distributions. The K-L Criterion is similar to the DI in that it reports the magnitude of difference between two ordered distributions. It differs from the DI, however, in that it does not identify where the differences occur. Instead, all differences are reported as

positive and absolute, regardless of where they occur in the distributions (Menning et al. 2007). We included the K-L Criterion as a means to corroborate the DI results. Similar comparisons between ecosystems were then conducted for live whitebark pine trees only.

We also used the Departure Index and K-L Criterion to assess forest conditions within each ecosystem. For each ecosystem, we compared the distribution of dead whitebark pine trees (the test distribution) with the distribution of live whitebark pine trees (the reference distribution) to evaluate the magnitude and direction of change in size distributions between dead and live trees. This allowed us to identify whether mortality was independent of tree size and then to compare relative changes between ecosystems.

RESULTS

We quantified density, structure, basal area, species composition, canopy cover, canopy height, blister rust infection, crown kill, and tree status (live or dead) based on measurement and evaluation of 4496 trees (2404 in the NDE; 2092 in the GYE).

Forest Conditions

Overall stand densities were similar between the two ecosystems in terms of whitebark pine, other species, and all species combined (Table 1, Figure 2A). Mean values for dead whitebark pine basal area, other conifer species basal area, canopy cover, and canopy height also did not differ between the two ecosystems (Table 2). However, the NDE had significantly lower

live whitebark pine basal area compared to the GYE (Table 2). NDE forests also had only 79 live whitebark pine trees ha⁻¹ compared to 274 live whitebark ha⁻¹ in the GYE (Figure 2B). Conversely, there were 230 dead whitebark trees ha⁻¹ in the NDE, but only 77 dead whitebark ha⁻¹ in the GYE.

Comparisons of tree distributions, using the GYE as the reference distribution and the NDE as the test distribution, showed that forest structure was similar between the two ecosystems when all species were considered, somewhat different for live whitebark pine only, and the most different for dead whitebark pine only (Table 3, Figure 3).

Tree diameter class distributions were strongly left-skewed in the GYE (reference distribution) for all three groups of trees (i.e., all species, live whitebark pine, dead whitebark pine), meaning there were proportionally more small trees than large trees (Table 3, Figure 3). When the NDE was compared to the GYE, negative DI values indicate that an even greater proportion of trees were in the smaller size classes in this ecosystem. Nearly two-thirds (65%) of live whitebark pine in the NDE fell in the two smallest diameter classes (Figure 3). This contrasts sharply with the GYE, where only 40% of live trees were in the two smallest classes. The distribution of dead whitebark pine in the NDE was similarly dominated by small trees (66% in the first two size classes), compared to 27% in the two smallest classes in the GYE.

Within-ecosystem comparisons in the NDE showed little difference between dead whitebark pine (test) and live whitebark

(reference) distributions (K-L Criterion = 0.033, Figure 4). The distribution of live trees was left-skewed (D.I. range -0.32, 1.68), while the distribution of dead trees was skewed even slightly further left (D.I. value = -0.004) because of a higher proportion of dead trees in the smallest size class (Figure 4). The cumulative proportion of live and dead trees was essentially equal in this ecosystem for trees <17 cm dbh (live = 0.65, dead = 0.66), and correspondingly for trees ≥17 cm dbh (live = 0.35, dead = 0.34) (Figure 4).

Diameter distributions of dead (test) and live (reference) whitebark pine within the GYE differed more than the corresponding distributions within the NDE (K-L Criterion = 0.067, Figure 4). The distribution of live trees was skewed left (D.I. range -0.53, 1.47), whereas the distribution of dead trees shifted right, toward larger trees (D.I. value = 0.15). Whitebark pine trees were more evenly distributed across size classes in the GYE than the NDE (Figure 4). Only 38% and 27% of the live and dead trees, respectively, were contained within the two smallest size classes. Thus, about two-thirds of all whitebark pine in the GYE were ≥17 cm dbh, compared to only about one-third in the NDE (Figure 4). Mortality was not even across the distribution, with heavier mortality in the mid and large size classes in this ecosystem (Figure 4).

Infection, Crown Kill, and Mortality

The relative health of the whitebark pine component of these high-elevation forest communities varied dramatically between the two ecosystems. Based on an analysis of site-level mean values, population mean vectors for rust infection, crown kill, and mortality were significantly different between the NDE and GYE (MANOVA Wilks' Lambda $F_{3,14} = 9.806, P = 0.001$), and pair-wise comparisons demonstrated significantly greater infection ($F_{1,16} = 10.403, P = 0.005$), crown kill ($F_{1,16} = 14.633, P = 0.001$), and mortality ($F_{1,16} = 12.663, P = 0.003$) in NDE forests. On a trees ha⁻¹ basis at the ecosystem level (i.e., irrespective of site), about 74% of all whitebark pine trees in the NDE were dead, compared to only 22% in the GYE, and approximately 92% of the live

Table 1. Density of whitebark pine (live + dead), other conifer species, and all species combined; and relative density (%) of whitebark pine and other species in whitebark pine communities in the Northern Divide Ecosystem (NDE, $n = 10$) and Greater Yellowstone Ecosystem (GYE, $n = 8$), Rocky Mountains, USA, 2004–2006.

Ecosystem	Whitebark pine		Other species		All species trees ha ⁻¹
	trees ha ⁻¹	%	trees ha ⁻¹	%	
NDE	309	34	605	66	914
GYE	352	42	476	58	828

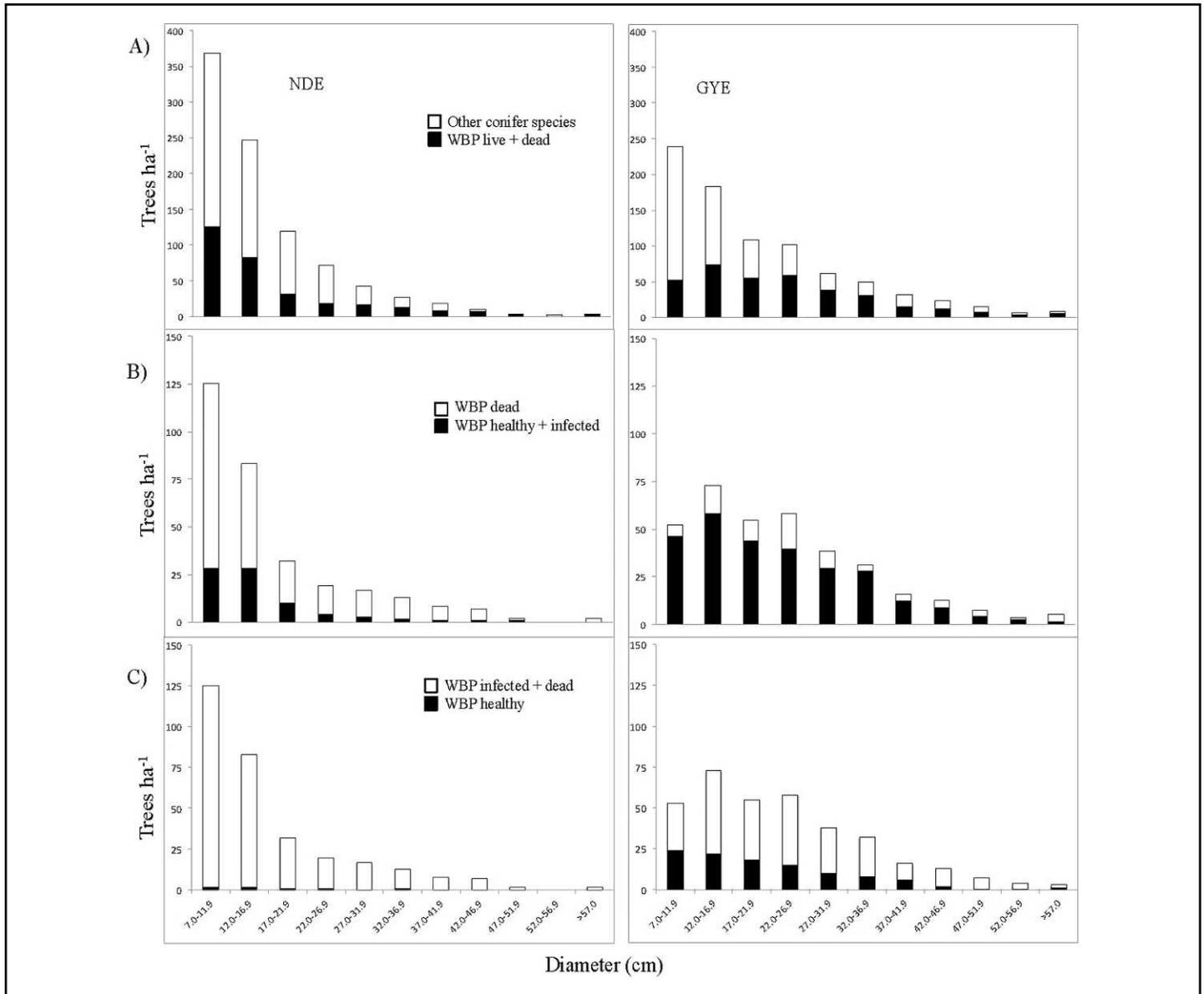


Figure 2. Tree distributions in the Northern Divide Ecosystem (left panels) and Greater Yellowstone Ecosystem (right panels), Rocky Mountains, USA, 2004–2006, by 5-cm diameter classes, for: A) all trees (whitebark pine live + dead and other species), B) whitebark live (healthy + infected) and whitebark dead, and C) whitebark (healthy) and whitebark (infected + dead).

	Ecosystem		Two sample t-test results		
	NDE	GYE	df	t	P
Basal area $m^2 ha^{-1}$					
Whitebark pine live	1.96 (0.65)	14.54 (2.45)	16	5.48	< 0.05
Whitebark pine dead	7.24 (2.17)	7.15 (2.06)	16	0.03	> 0.05
Other conifer species	15.29 (4.26)	15.15 (4.22)	16	0.02	> 0.05
Canopy cover %	64.2 (6.1)	48.9 (8.7)	16	1.37	> 0.05
Canopy height m	13.8 (2.2)	13.7 (1.1)	16	0.04	> 0.05

Table 3. Comparison of tree diameter distributions between the Greater Yellowstone Ecosystem (reference) and Northern Divide Ecosystem (test), Rocky Mountains, USA, 2004–2006, in order of increasing difference. A negative Departure Index value indicates that the test distribution was left-skewed (higher proportion of small trees) relative to the reference distribution.

	Departure Index		Kullback-Leibler criterion
	Range	Value	
All tree species	-0.41, 1.59	-0.15	0.0405
Live whitebark	-0.53, 1.47	-0.21	0.0805
Dead whitebark	-0.67, 1.33	-0.36	0.2236

whitebark in the NDE were infected with blister rust compared to about 62% in the GYE (Figure 5). Furthermore, virtually all large whitebark pine (i.e., trees ≥ 37 cm dbh) that we investigated in the NDE were infected, whereas about 28% of the large whitebark trees in the GYE remained uninfected (Figure 5).

DISCUSSION

Based on sampling 18 elevationally and geographically dispersed research sites, tree density, structure, and species composition were relatively similar in

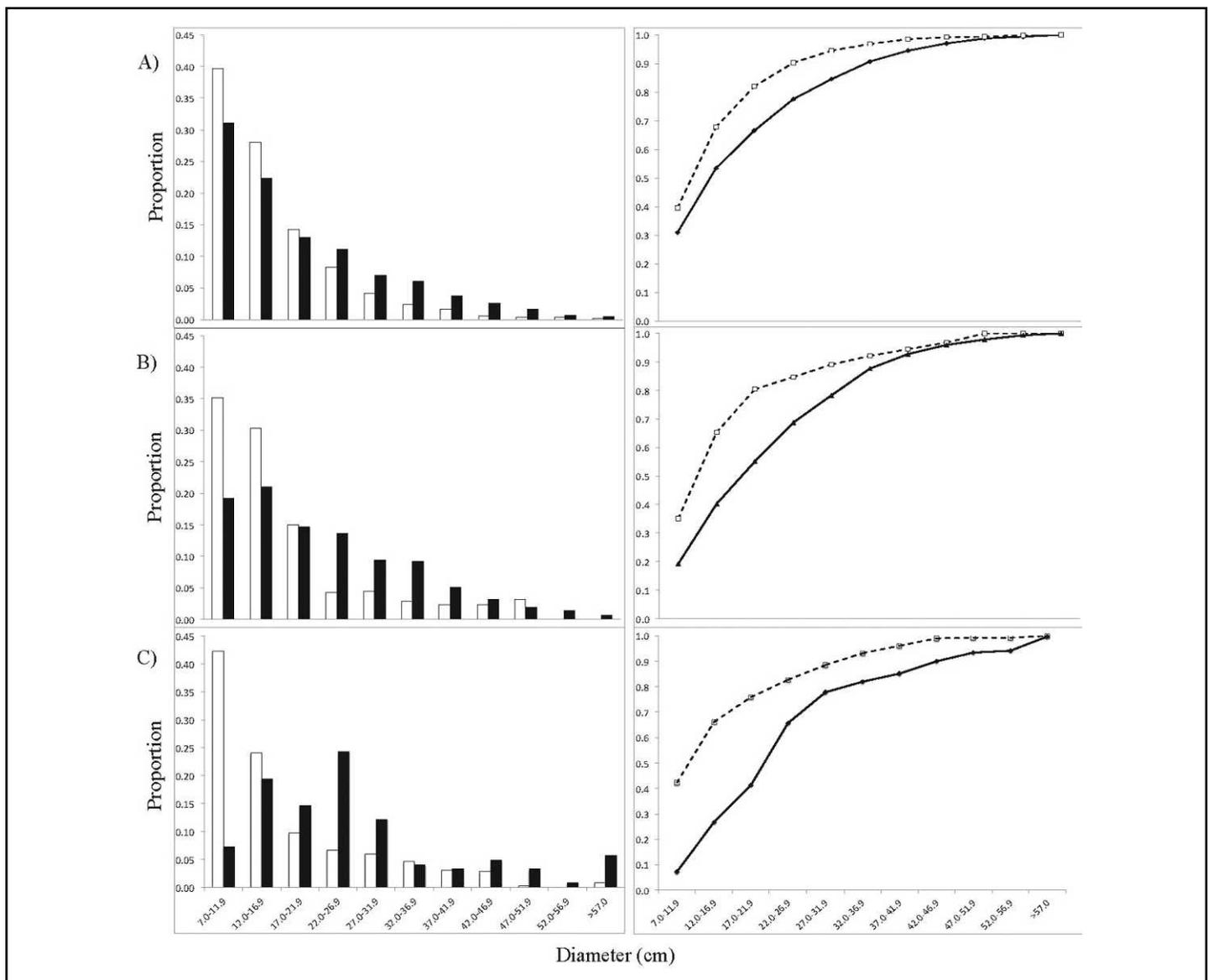


Figure 3. Tree distributions in the Northern Divide (open bars) and Greater Yellowstone (solid bars) Ecosystems, Rocky Mountains, USA, 2004–2006, by 5-cm diameter classes, for: A) all tree species, B) live whitebark pine trees, and C) dead whitebark pine trees. Left panels are histograms and right panels are cumulative histograms.

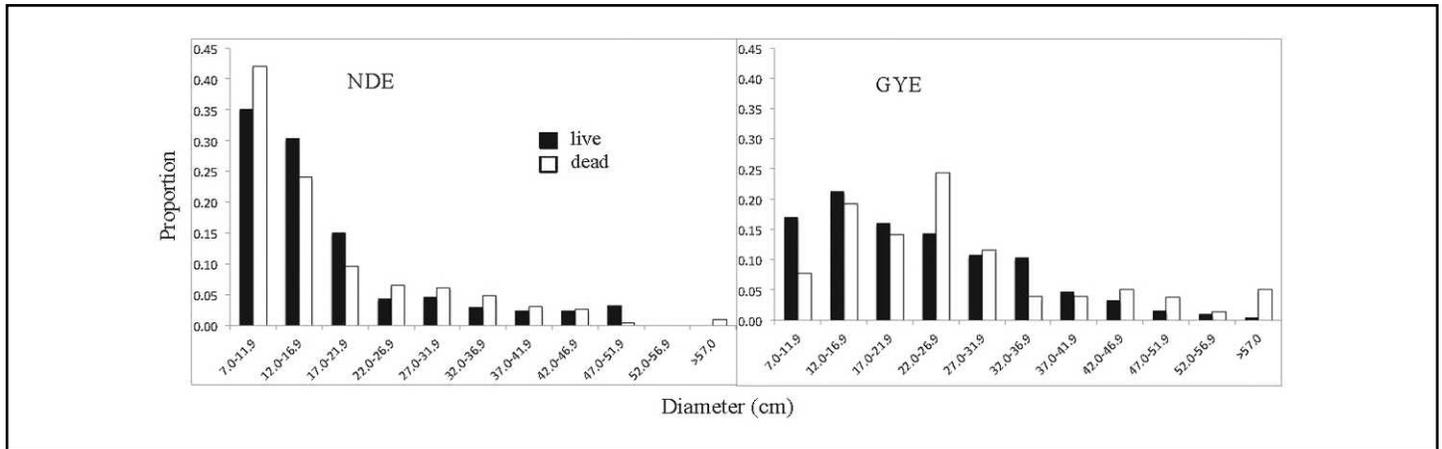


Figure 4. Distributions of live and dead whitebark pine trees by 5-cm diameter classes for the Northern Divide and Greater Yellowstone Ecosystems, Rocky Mountains, USA, 2004–2006.

two major Rocky Mountain whitebark pine ecosystems, the Northern Divide Ecosystem and the Greater Yellowstone Ecosystem. This study was not designed to provide a comprehensive random sample of the whitebark pine populations across these expansive ecosystems, but rather a representative survey of forest conditions in each. Whitebark pine densities ranged from 309–352 trees ha⁻¹ in both ecosystems, while densities of all tree species combined ranged from 828–914 trees ha⁻¹. Furthermore, tree distributions (trees ha⁻¹ by 5-cm dbh classes) of both whitebark pine and all species combined showed only modest differences between ecosystems. However, the relative health and functionality of the whitebark pine component varied dramati-

cally when evaluated by categories of live, infected, and dead (Tables 1 and 2, Figure 2). Nearly three-fourths of the whitebark pine in the NDE were dead, and over 90% of the remaining live trees were infected with blister rust (Figure 5). In contrast, less than one-fourth of the whitebark in the GYE were dead, and about 60% of the live trees were infected. Furthermore, far fewer small- and mid-sized trees were infected in the GYE (Figure 2C), and nearly 30% of large seed-bearing trees remained uninfected in this ecosystem (Figure 5). The significantly lower levels of infected and dead whitebark pines observed in the GYE, which is about 400 km south of the NDE, are consistent with the reported decrease in intensity of rust infection with

decreasing latitude suggested by Kendall and Keane (2001).

By way of regional comparison, Rochefort (2008) reported whitebark pine mortality of 33% and 24% in Mount Rainier and North Cascades National Parks, respectively. Approximately 20% of the remaining live whitebark trees in Mount Rainier and 49% of the trees in the North Cascades were infected. Across the two national parks, 52% of whitebark were dead or infected, substantially lower numbers than were reported by Kendall and Keane (2001) for northwestern Montana, and substantially lower than we found for the NDE in this study. However, the 24% mortality reported by Rochefort (2008) for North Cascades National Park was nearly identical to the 22% that we found in the GYE. The 49% infection level in North Cascades was well lower than the 62% we observed in the GYE, perhaps because Rochefort’s (2008) data were based on surveys conducted six to eight years before our sampling took place and included slightly smaller trees (minimum of 2.5-cm dbh vs. 7-cm dbh in our study), which tend to have lower infection rates.

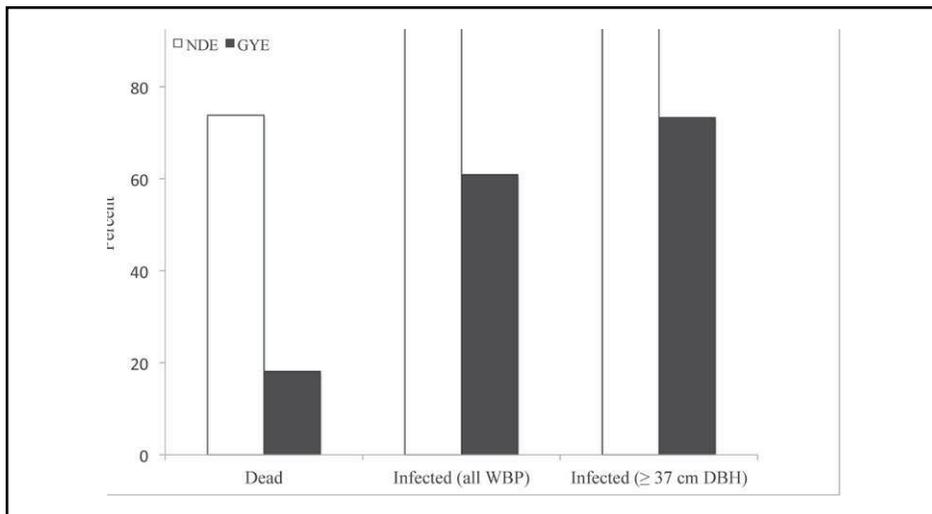


Figure 5. Percent dead, infected, and large (>37 cm dbh) infected whitebark pine in the Northern Divide and Greater Yellowstone Ecosystems, Rocky Mountains, USA, 2004–2006.

While our results show that whitebark pine communities in the GYE have substantial health problems, conditions there are not yet critical. In contrast, whitebark communities in the NDE are in a precarious situation by any measure. The virtual absence of uninfected, large (≥ 37 -cm dbh) cone-bearing trees in the NDE makes the

sustainability of that system even more tenuous. Whitebark communities in the GYE may very well be on a similar rust infection trajectory as those in the NDE, but have not been exposed to blister rust infection as long because of their considerably greater distance from the point of the pathogen's introduction in southwest British Columbia. However, fundamental differences in current mortality, blister rust infection levels, and cone production potential between whitebark pine communities in the NDE and GYE suggest that different restoration strategies will be needed to address characteristics and conditions unique to each ecosystem at this time. For example, McKinney et al. (2009) reported evidence indicating that Rocky Mountain stands with less than about $5 \text{ m}^2 \text{ ha}^{-1}$ of live whitebark pine basal area provide too little cone production to reliably attract nutcracker seed dispersal. Barringer et al. (2012) found a similar relationship between cone production and nutcracker occurrence in Alberta (Canada), Montana, and Wyoming, but reported a slightly lower level of live whitebark basal area ($\geq 2 \text{ m}^2 \text{ ha}^{-1}$) for similar levels of nutcracker occurrence. Because of the highly specialized mutualistic relationship between whitebark pine and Clark's nutcracker (Hutchins and Lanner 1982; Tomback 1982), the pine has no compensatory mechanism to regenerate itself if the relationship breaks down. For this reason, managers have devised methods for collecting cones from uninfected trees, extracting and processing seeds, and raising rust-resistant whitebark seedlings in the nursery. Planting these rust-resistant seedlings should be a high-priority restoration strategy in the NDE, where live whitebark basal areas average $< 2 \text{ m}^2 \text{ ha}^{-1}$. Conversely, the relatively high whitebark pine basal areas (i.e., approximately $15 \text{ m}^2 \text{ ha}^{-1}$) that remain in the GYE indicate that nutcracker seed dispersal should be reasonably dependable during good cone years in that ecosystem. Applying silvicultural cutting and prescribed burning treatments (where administratively acceptable) that open up the forest canopy and reduce the density of shade-tolerant competitors could increase nutcracker seed-caching opportunities and further promote whitebark seedling establishment in the GYE. But two developing influences complicate these

apparently preferred restoration strategies for each ecosystem. First, the mountain pine beetle has rapidly emerged as a major mortality agent in whitebark communities, particularly in the GYE (Logan et al. 2010). The immediate concern is that many stands may have too few live, cone-bearing size whitebark trees remaining after blister rust infection and beetle attack to attract nutcrackers for critical seed-dispersal services. This threshold has already largely been passed in the NDE. Another especially consequential impact is that beetles kill whitebark pine trees regardless of rust resistance. The longer-term concern is that rust-resistant trees will be killed before cones can be gathered and their seeds extracted and stored for future restoration purposes. In this way, the mountain pine beetle threatens the genetic diversity necessary for sustaining whitebark pine into an uncertain future. Indeed, this scenario may be playing out now in the GYE given the current bark beetle epidemic that is decimating whitebark pine. Thus, there is an urgency associated with planting rust-resistant whitebark pine seedlings in that ecosystem also. Another strategy, allowing certain lightning-ignited backcountry fires to burn – consistent with human safety, infrastructure, and other ecosystem concerns – would create additional sites for seed-caching by nutcrackers while reasonable numbers of cone-bearing whitebark pine still remain. Rust-resistant seed could also be hand-sown in burned-over areas, although ongoing research suggests that probabilities of germination and establishment using this method will likely be quite low (Schwandt et al. 2011). Both of these strategies would increase whitebark pine abundance and rust-resistance within the GYE population.

It has been seven years since our surveys concluded. A recent review of range-wide whitebark decline and restoration strategy (Keane et al. 2012) indicates that both blister rust and mountain pine beetle have increased in the GYE, but that this region has historically had low levels of both agents relative to other regions. The increases in blister rust and pine beetle in the GYE have not been equivalent, however. Surveys by the Greater Yellowstone Monitoring Group suggest that blister rust

infection has increased by approximately 5% from their 2004–2007 survey cycle (similar to our 2004–2006 survey period) to the 2008–2011 survey cycle (GYWPMWG 2012). In contrast, mountain pine beetle activity has increased dramatically. A 2009 Landscape Assessment aerial survey indicates at least some level of beetle activity in 90% of GYE whitebark stands (reported in Bockino and Tinker 2012). The situation in the NDE is quite different. The very high rust infection levels of 60%–80% and mortality levels $> 90\%$ in some areas reported in this and other NDE studies (Kendall and Keane 2001; Keane et al. 2012) leave little room for dramatic change, and the consensus is that whitebark status in the NDE has changed little since our surveys. There is a current effort underway at the University of Montana Spatial Analysis Laboratory, however, to map whitebark pine across the NDE (R. Keane, fire ecologist, USFS Missoula Fire Sciences Laboratory, pers. comm.).

This study summarizes and compares forest structure, health, and mortality in two major whitebark pine ecosystems in the U.S. Rocky Mountains. It profiles conditions strongly influenced by the decades-long presence of blister rust as a primary mortality agent, and provides a baseline for assessing impacts of the mountain pine beetle – an emerging mortality factor in whitebark communities, particularly in the GYE. Our study demonstrates that there is no single appropriate restoration strategy, *per se*. It also suggests that restoration strategies that are currently appropriate for existing conditions in the NDE and GYE may not be so in the future, given the recent emergence of mountain pine beetles and the largely unknown effects (direct and indirect) of potential climatic change. However, a recent range-wide, state-of-knowledge symposium illustrated the depth and breadth of research focused on whitebark pine (Keane et al. 2011). For example, advances in genomics, better understanding of cone predator/seed dispersal/stand structural relationships, advances in nursery culturing techniques, and updated planting guidelines collectively provide both direction and information for managers to design more effective and site-specific restoration strategies for

the future.

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