



Status of Whitebark Pine in the Greater Yellowstone Ecosystem

A Step-Trend Analysis with Comparisons from 2004 to 2015

Natural Resource Report NPS/GRYN/NRR—2017/1445



ON THE COVER

Ramshorn Peak in the southern end of the Absaroka Mountain Range on the Shoshone National Forest”
Photograph by NPS/ERIN SHANAHAN

Status of Whitebark Pine in the Greater Yellowstone Ecosystem

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Executive Summary

Background and Objectives

Whitebark pine (*Pinus albicaulis*) is a foundation and keystone species in upper subalpine environments of the northern Rocky Mountains that strongly influences the biodiversity and productivity of high-elevation ecosystems (Tomback et al. 2001). Throughout its historical range, whitebark pine has decreased significantly as a major component of high-elevation forests. As a result, it is critical to understand the challenges to whitebark pine—not only at the tree and at the stand level, but also as these factors influence the distribution of whitebark pine across the Greater Yellowstone Ecosystem (GYE).

In 2003, the National Park Service (NPS) Greater Yellowstone Inventory and Monitoring Network identified whitebark pine as one of twelve significant natural resource indicators or vital signs. This designation initiated a long-term, collaborative monitoring program of whitebark pine in the GYE. The objectives of the monitoring program are to

1. assess trends in the proportion of live whitebark pine trees (>1.4 m tall) infected with white pine blister rust (*Cronartium ribicola*; blister rust)
2. document blister rust infection severity by the occurrence and location on the tree of new and persisting infections and assess how infection severity is changing over time
3. assess trends in mortality of whitebark pine trees and describe contributing factors of mortality
4. document the recruitment of understory whitebark pine into the reproductive population and assess the multiple factors that influence regeneration and recruitment success overtime

In this report we summarize the past 12 years (2004–2015) of whitebark pine status and trend monitoring in the GYE divided into three time-steps: Time-Step 1 (2004–2007; herein referred to as Time 1), Time-Step 2 (2008–2011; herein referred to as Time 2), and Time-Step 3 (2012–2015; herein referred to as Time 3).

Summary of Results

Objective 1: Blister Rust Infection Proportions

The proportion of live whitebark pine trees infected with blister rust in the GYE in Time 1 was estimated at 0.21 (0.03 SE). In Time 2 the estimation was 0.22 (0.02 SE). In Time 3, we estimated the proportion of live trees infected with blister rust to be 0.20 (0.03 SE). We detected no significant change

in the proportion of trees infected in the GYE among the three time-steps.

Objective 2: Blister Rust Infection Severity

At the end of Time 3, we found that 25% (942 trees) of live, tagged trees (3,716) were infected with blister rust. Trees with only canopy cankers represented 37% (343) of the total number of trees infected with blister rust, whereas trees with bole cankers comprised 63% (599) of the infected sample. A bole infection is more consequential than a canopy canker, as it compromises not only the overall longevity of the tree, but its functional capacity for reproductive output as well (Kendall and Arno 1990; Campbell and Antos 2000; McDonald and Hoff 2001; Schwandt and Kegley 2004).

In addition, we chronicled when a change or transition in infection location (canopy or bole) occurred in infected trees among time-steps. We found that 60% (237) of trees recorded with canopy cankers in Time 1 transitioned to bole cankers by Time 3. For this Time 1 to Time 3 comparison, revisits were separated by 4 to 11 years, depending on the transect and its assigned panel revisit schedule. For Time 2 to Time 3, which had a more consistent revisit interval of 4 years for all transects on all panels, only 12% (98) of canopy cankers transitioned to bole cankers. Additionally, once an infection was identified as occurring in the bole of a tree, the likelihood of that same tree exhibiting only a canopy canker at a subsequent visit (bole → canopy ‘transition’), was low. This information demonstrates the value of long-term monitoring to evaluate the implications of the severity of blister rust infection through time.

Objective 3: Whitebark Pine Mortality

We estimate the proportion of whitebark pine >1.4 m tall in the GYE that have died between 2008 and 2015 to be 0.26 (0.03 SE). The peak of mortality occurred from 2008 to 2011 when mountain pine beetle populations were at epidemic levels (Shanahan et al. 2014). Approximately 60% (902) of the dead tagged trees had signs of mountain pine beetle activity and the majority of these were >10 cm DBH. Wildland fire has also had an impact on whitebark pine. Fourteen of the transects have been burned and 249 tagged trees died, with signs of fire.

Objective 4: Whitebark Pine Recruitment

Reproducing trees made up approximately 26% (963) of the total live, tagged cohort of trees (3,716) at the end of Time 3. Of these, 43% (411) were infected with blister rust and

16% (154) had sign of mountain pine beetle. In Time 3, the average density of small trees ≤ 1.4 m tall was 51 understory trees per 500 m² (Time 1 = 37, Time 2 = 53). Raw counts of these understory individuals ranged from 0 to 521 small trees per transect. In addition, 447 trees were added to the tagged tree cohort by the end of 2015. These newly tagged trees reached a height of >1.4 m tall and were therefore added to the sample.

Throughout the past decade in the GYE, monitoring has helped document demographic shifts in whitebark pine forests in response to insect, pathogen, wildland fire, and other disturbance events. Blister rust infection is ubiquitous but variable across the region. And while we have documented mortality of whitebark pine, we have also recorded considerable recruitment. We provide this second step-trend report to characterize the current status and trends in the health of whitebark pine in the GYE.

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Introduction

Whitebark pine (*Pinus albicaulis*) forests are biologically significant components of high elevation regions in the United States northern Rocky Mountains. From an ecological perspective, whitebark pine is a keystone species that creates microhabitats for other vegetation (Keane and Arno 1993) and is an important food source for a variety of wildlife (Tomback et al. 2001). In some locations, it also traps winter snow, which helps to regulate hydrologic processes in the spring and summer (Arno and Hoff 1990; Weaver 2001). Whitebark pine is located primarily above 2400 m. It is found on over 800,000 ha in Yellowstone and Grand Teton National Parks and five surrounding national forests that are collectively identified as the Greater Yellowstone Ecosystem (GYE; Tomback et al. 1993; Shanahan et al. 2014). In addition to its ecological importance, whitebark pine is one of the most socially relevant and iconic tree species inhabiting high mountain ranges in the GYE. It is considered a symbol of a primitive America, a legacy of public land stewardship, and an ambassador for the conservation of subalpine environments (Tomback et al. 2001).

Currently, the long-term persistence of whitebark pine in the GYE is uncertain. Studies show a decline in the abundance of whitebark pine across the western United States as anthropogenic warming alters forest disease agents, drought duration, and fire regimes (Westerling et al. 2011; MacFarlane et al. 2013; Chang et al. 2014; Buotte et al. 2016). Recent estimates from aerial surveys (2009) documented greater than 80% mortality of overstory whitebark pine throughout the GYE (MacFarlane et al. 2013). While ground-based surveys implemented by the National Park Service's Greater Yellowstone Inventory and Monitoring Program (monitoring program) found similar estimates of mortality in the larger size class of trees that typically comprise the overstory population of whitebark pine, mortality rates across the range of size classes were estimated to be between 18% and 36%. Across the range of size classes, primary mortality factors include exotic white pine blister rust (blister rust; *Cronartium ribicola*), native mountain pine beetle (*Dendroctonus ponderosae*), and wildland fire (Shanahan et al. 2014).

Introduced in 1910, blister rust has resulted in severe declines in whitebark pine populations throughout their range (Kendall and Arno 1990; Keane and Arno 1993; Tomback and Achuff 2010). The life cycle of blister rust is complex. It requires high relative humidity and mild temperatures in the late summer for the production of basidiospores (reproductive cells) and the successful spread of infecting spores from

intermediary host species (*Ribes* spp, *Castilleja* spp., and *Pedicularis* spp.) to whitebark pine (Van Arsdell et al. 1956; Hoff and Hagle 1990; McDonald et al. 2006). Whitebark pine stands in the moister environment of Glacier National Park, Montana, have been devastated by blister rust (Kendall and Arno 1990), whereas the impacts of blister rust in the GYE have been limited by an overall drier and colder environment (Campbell and Antos 2000; Koteen 2002; Larson 2011). Blister rust infection or cankers can cause the death of upper canopy cone-bearing branches, thus negatively impacting seed-production; cankers found on the lower portions of the bole will eventually kill an infected tree (Smith and Hoffman 2000; Koteen 2002; Newcomb 2003).

Mountain pine beetle life cycles have been linked to weather and climate (Raffa et al. 2008; Logan et al. 2010; Raffa et al. 2013), with populations typically held in check by low winter temperatures (Amman 1973). However, mountain pine beetle populations can exponentially increase in response to longer warm season temperatures by producing multiple broods in a single year (Logan et al. 2010). Previous periods of warming in the 1930s, 1970s, and 1980s resulted in epidemic mountain pine beetle levels, with populations declining to endemic levels following the return to cooler temperatures (both winter and summer) and the depletion of host resources (Logan et al. 2010). Many conifers have defenses that serve to protect them against bark beetle attacks (Raffa and Berryman 1983; Shrimpton 1978; Boone et al. 2011), yet these mechanisms can be compromised under high temperatures and seasonal drought stress (Berg et al. 2006; Raffa et al. 2008; Bentz et al. 2010; Preisler et al. 2012). It is possible for a healthy tree to pitch out (reject by producing extra pitch) the first invaders, but trees subjected to a range of physiological stresses (drought, defoliation, age) may have reduced defensive abilities, which enable attacking mountain pine beetles to overcome protective thresholds (Raffa et al. 2005; Raffa et al. 2008).

Wildland fire is yet another contributor to whitebark pine mortality in the GYE. As climatic changes augment drought severity across the western United States, the probability of wildland fire is expected to increase (Westerling et al. 2011). While wildland fire has historically been an important component for the maintenance of whitebark pine forests (Arno 1986), but predicted warming trends may increase the frequency and severity of fire events to the detriment of high elevation whitebark stands (Keane et al. 2016). In addition to the loss of genetically valuable individuals (Keane et al.

2016), remaining populations may be reduced to densities that preclude natural re-establishment.

This long-term monitoring program provides a unique opportunity to investigate the biotic and abiotic interactions that affect whitebark pine health through time. The first step-trend analysis (Shanahan et al. 2014) documented status and trends in whitebark pine health between the initial establishment period, 2004 to 2007 (Time 1), and the first revisit survey period, 2008 to 2011 (Time 2). This second step-trend analysis summarizes trends across the three periods 2004–2007, 2008–2011, and 2012–2015 (Time 3). It is imperative that we continue to improve our understanding of whitebark pine response to a changing climate. As the whitebark pine monitoring program moves forward, our ability to document persistent and emerging patterns in whitebark pine health continually expands. This science-based knowledge increases our capacity to provide relevant and contemporary health parameters to land managers who are responsible for the protection and conservation of whitebark pine in the GYE. In addition, information gleaned from this monitoring program can be extrapolated to other areas that support whitebark pine populations.

Report Objectives

Thus far, we have completed three time-steps following the objectives outlined in the *Interagency Whitebark Pine Monitoring Protocol for the Greater Yellowstone Ecosystem* (GYWPMWG 2011). The intent of this trend report is to

1. Describe the estimated proportion of live whitebark pine trees (>1.4 m tall) infected with blister rust across the three time-steps and assess changes in blister rust infection over time.
2. Document blister rust infection severity by the occurrence and location of new and persisting infection by the end of 2015 and evaluate the rate at which infection transitioned from canopy to bole cankers between the three time-steps.
3. Determine mortality of whitebark pine trees within Time 2, Time 3, and cumulatively from 2008 to 2015, and describe contributing factors of mortality
4. Document the recruitment of understory whitebark pine into the reproductive population.

Methods

In this section we briefly describe the methods used in the whitebark pine long-term monitoring program. For a more in-depth explanation of these processes, refer to the inter-agency whitebark pine monitoring protocol (GYWPMWG 2011).

Stand and Transect Selection

We define whitebark pine stands as a contiguous area of forest with whitebark pine as the dominant or co-dominant

component. We identified stands from photo interpretation of vegetation habitat (Dixon 1997) and stand composition cover maps (GYWPMWG 2011). We selected stands randomly from a sample frame of approximately 10,770 mapped whitebark pine stands ≥ 2.0 ha in the Greater Yellowstone Ecosystem (GYE) (Dixon 1997; Landenburger et al. 2008; Figure 1). Stands were divided into four panels with differing revisit schedules (described in more detail in *Revisit Schedule*, below). We used a probabilistic, two-stage cluster design,

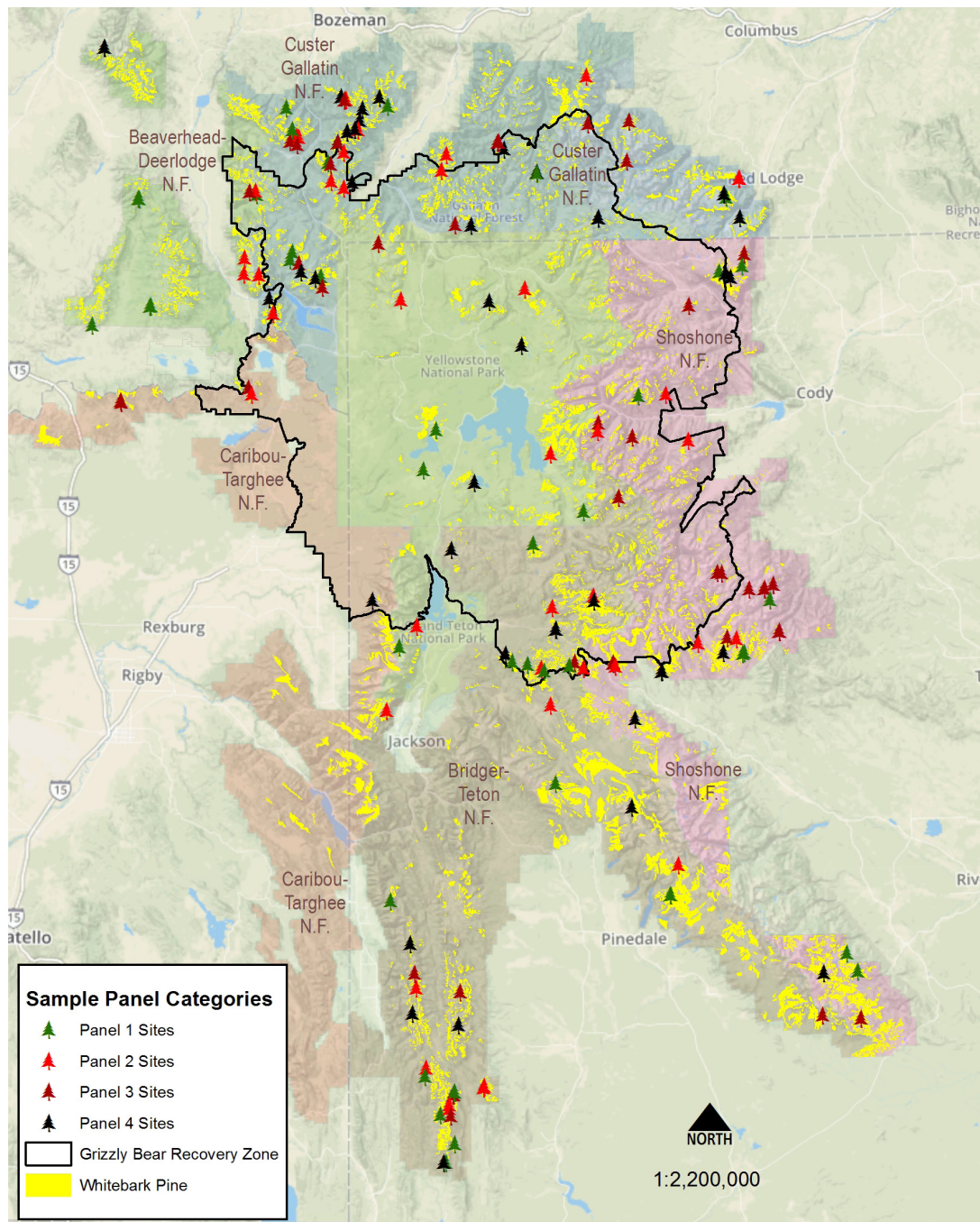


Figure 1. Inter-agency Whitebark Pine Monitoring Program study area in the Greater Yellowstone Ecosystem (all shaded regions).

where whitebark pine stands were the primary sample units and 10 × 50 m transects were the secondary sample units within selected stands (Lohr 2010). One or two transects were randomly placed within the delineated boundary of a stand (stands that had two transects installed were used to evaluate within stand variation). If a minimum of one live whitebark pine tree >1.4 m tall was observed, a transect was established and permanently monumented in order to facilitate relocation of the transect for future revisits.

Transect Establishment and Metrics

From 2004 to 2007 (Time 1), 176 permanent transects in 150 whitebark pine stands were established. All live, whitebark pine trees >1.4 m tall located within transect boundaries were marked with a numbered aluminum tag. A total of 4,768 individual trees >1.4 m tall were permanently tagged. We documented multiple attributes for every tagged tree (Table 1).

Tree status: If a tree had all brown needles or was devoid of needles, it was classified as dead in the year that this condition was observed (any year from 2008 to 2015).

Cones: We added the presence or absence value (Y/N) of cone production as an additional metric in 2007. Then in 2013, we began tracking reproduction and the number of cones produced per tree using a binning system (0, 1–5, 6–10, >10). This information could be used to assess how

blister rust infection in the canopy or bole of an infected tree affects overall cone production and/or to evaluate the amount of potential seed source available for future regeneration.

Blister rust cankers: We examined trees for blister rust infection and recorded the location of blister rust infections (canopy or bole) for each tagged tree. A canopy canker was defined as any infection occurring within the canopy of a tree ≥5 cm distal from the main bole of the tree. A bole canker was an infection on the main trunk of the tree or within 5 cm of the bole along peripheral branches.

Tree health codes: While the monitoring program does not assign cause of death to a given tree, we do report observed indicators that are associated with tree mortality.

Understory counts: Trees ≤1.4 m tall that occurred within the boundaries of the belt transect were tallied and evaluated for the presence/absence of blister rust.

We noted additional information at transects, including UTM coordinates of beginning, center, and end points of the belt transect (Figure 2), elevation, habitat type (from Steele et al. 1983), and cover type (from Mattson and Despain 1985).

Revisit Schedule

After 2007, stands were randomly assigned to one of four panels, each consisting of 44 transects. Revisits to each stand

Table 1. Whitebark pine tree attributes documented during surveys in the Greater Yellowstone Ecosystem.

Attribute	Description
clump membership	number and letter
DBH	measured at 1.4 m above the ground
height	height bins 1 = ≤5 m, 2 = >5 m to ≤10 m, 3 = >10 m
tree status	live = green needles still present recently dead = red or brown needles remaining on tree (only measured during subsequent revisit surveys) dead = tree is completely denuded of needles (only measured during subsequent revisit surveys)
cone count bins	initiated in 2007 as Y/N cone count bins initiated 2013 = 0, 1–5, 6–10, >10 S = cone scar(s) but no visible current-year cones
blister rust cankers	number and location in the canopy of the tree = upper third, middle third, or lower third number and location on the bole of the tree = upper third, middle third, or lower third
number of blister rust indicators	flagging, rodent chewing, swelling, roughened bark, and oozing sap
upper tree canopy volume	percentage of canopy in the upper one third of the foliage that is alive
mountain pine beetle indicators	pitch tubes, frass, or J-shaped galleries
tree health codes	can have multiple per tree such as dead top, fading crown, fire, etc.
understory counts	tally of understory trees (≤1.4 m tall); evidence of blister rust = present, absent, unknown

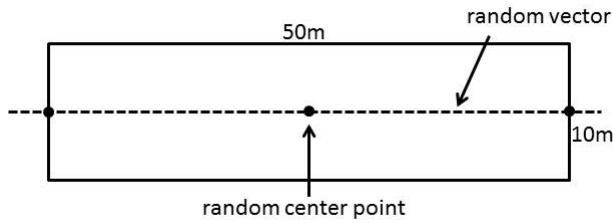


Figure 2. Belt transect layout for whitebark pine monitoring in the Greater Yellowstone Ecosystem. Permanent markers were placed at the two end points and the center point.

Survey Schedule		Time 1	Time 2				Time 3				Continued Monitoring 2016 Forward
Sample Panel	Transects per Panel	2004 thru 2007	2008	2009	2010	2011	2012	2013	2014	2015	
1	43	initial surveys for all 176 transects	br & mort		mort only		br & mort				
2	45			br & mort		mort only		br & mort			
3	44		mort only		br & mort		mort only		br & mort		
4	44			mort only		br & mort		mort only		br & mort	

Figure 3. Panel sampling revisit schedule (br = blister rust, mort = mortality) for monitoring whitebark pine in the Greater Yellowstone Ecosystem. All transects were visited every two years for mortality and every four years for blister rust status. Starting in 2014, after the mortality of live, tagged trees sharply declined, monitoring was restored to a four-year interval schedule documenting changes in blister rust and mortality.

in a panel were planned on a rotating, two- or four-year schedule (Figure 3). Following initial blister rust infection, it takes approximately four years to visually detect infection (McDonald and Hoff 2001). Therefore, field crews evaluated trees for blister rust infection every four years. Over the course of the mountain pine beetle outbreak (2008–2013), all transects were surveyed every two years to document mortality.

Tagged trees included in our investigation had two to five observations between 2004 and 2015. After Time 1, we tagged any whitebark pine tree within the boundary of a transect that attained a height of >1.4 m tall, recorded all attributes of the tree, and added it to the tagged tree cohort for long-term monitoring.

Data Management and Statistical Analyses

We trained field observers to carry and use a detailed data recording guide to help ensure legible, valid entries and maximize the quality of recorded values. Network personnel entered data from field data sheets into a Microsoft Access database on a regular basis throughout the field season using a customized data entry form that included a cascading system of data validation controls. We subjected data to rigorous quality assurance and quality control (QA/QC) procedures as outlined in the protocol (GYWPMWG 2011). Due to minor retroactive updates to the master database as part of ongoing quality controls, there may have been an insignificant amount of variability (typically <1% difference) when comparing data reported in previous years.

All analyses and corresponding figures used Microsoft Excel and the statistical computing language R (R Development Core Team 2015) specific to each objective. We have presented some of the results described in this trend report as preliminary findings in past versions of the Interagency Whitebark Pine Monitoring Program (monitoring program) annual reports (e.g., GYWPMWG 2015). This document provides results for the full 12 years of data collection and analysis in order to present a complete assessment of changes over time across the sample frame.

Objective 1

Describe the estimated proportion of live whitebark pine trees (>1.4 m tall) infected with blister rust across the three time-steps and assess change in the estimate over time.

We estimated the proportion of trees infected with blister rust in the sampled portion of 10,770 whitebark pine stands identified in the GYE. We used a combined ratio estimator on the live, tagged trees at the end of each time-step. A combined ratio estimator is appropriate for estimating a proportion from data collected using a stratified (e.g., Grizzly Bear Recovery Zone and administrative unit) two-stage cluster sample (Lohr 2010). The probabilistic sampling design allows inferences to the entire sampled population of mapped whitebark in the GYE. In addition, we evaluated three scenarios using a subset of sampled stands to investigate the potential infection rates given the inclusion and/or exclusion of known dead and newly tagged trees (Table 3 in Results provides a more detailed description).

To investigate the evidence of a change in the proportion of stands infected with blister rust, a nonparametric Wilcoxon Signed Rank test was used (`wilcox.test` in R). In stands that had two established belt transects (26 stands had two belt transects established in order to investigate within-stand variation), we calculated the overall average proportion for the stand to account for the potential lack of independence of belt transects nested within stands. We excluded stands that had transects without any live, tagged trees (due to complete mortality of all originally tagged trees), which explains the decrease in stand number with each consecutive time-step.

Objective 2

Document blister rust infection and severity by location on the tree of new and persisting infection at the end of 2015 and evaluate the rate at which infection transitioned from canopy to bole cankers.

We recorded infection status (uninfected or infected) for

each live, tagged tree. In addition to tracking status, we documented whether blister rust cankers occurred in the canopy or on the bole. We reported canker locations in two categories: branch only or bole (bole includes those trees that have blister rust infection occurring in both the branch and bole). We compared changes in canker position between Time 1, Time 2, and Time 3 in order to assess changes in infection severity. From one time-step to the next, infection status can remain static (uninfected → uninfected or infected → infected), or change (uninfected → infected or infected → uninfected). Due to the random panel assignment following initial surveys in the transect establishment period (Time 1), resurvey for individual trees varied by time-step. For the Time 1 to Time 2 comparison, the interval for individual tree resurvey was anywhere from 1 to 7 years. For the Time 1 to Time 3 comparison, the resurvey interval varied from 4 to 11 years. For the Time 2 to Time 3 comparison, all trees analyzed were resurveyed on a 4-year interval. The number of trees used in the analysis for each time-step follows:

- 3,795 trees tagged in Time 1 that were still alive in Time 2
- 3,270 trees tagged in Time 1 that were located and still alive in Time 3
- 3,554 trees tagged in Time 1 or Time 2 that were still alive in Time 3

We will present a more thorough investigation of canker transition in a future report that models infection transition as it relates to DBH, time, and a DBH-time interaction.

Objective 3

Determine cumulative mortality rates of whitebark pine trees from 2008 to 2015, with factors influencing mortality.

To determine whitebark pine mortality, we resurveyed all belt transects to identify which of the permanently tagged trees >1.4 m tall were still alive. We compared the total number of live, tagged trees to the total number of dead, tagged trees, both cumulatively and at the end of each time-step. We identified all potential mortality-influencing conditions, including blister rust, mountain pine beetle, fire, and others. In addition, we evaluated the change in distribution of DBH size classes in whitebark pine populations as a result of mortality.

We used a combined ratio estimator to calculate the proportion of mortality for overall mortality across the GYE at the end of 2015 and between Time 2 and Time 3. Strata with low sample sizes were combined so that there were at least two transects within each stratum (e.g., sites within an Admin-

istrative Unit inside or outside of the Grizzly Bear Recovery Zone were aggregated by Administrative Unit if a stratum had only one transect).

Objective 4

Document the recruitment of understory whitebark pine into the reproductive population and assess the multiple factors that influence regeneration and recruitment success overtime.

To investigate the proportion of live, reproducing tagged trees, we divided the total number of positively identified live, cone-bearing trees by the total number of live trees

remaining in the tagged tree sample at the end of each revisit time-step. To approximate the average density of recruitment trees per stand, we summed trees ≤ 1.4 m tall by stand (within the 500 m² transect area) and divided by the total number of stands. Some stands were precluded from the ≤ 1.4 m tall survey due to lingering snow cover. Where there were two belt transects per stand (26 cases), we averaged the count of small trees over the two belt transects for one stand total. We did not report the average small tree count for Time 1; these data were unreliable because the trees were originally counted regardless of partial snow cover in this time period.



**Whitebark pine survey crew in 2016 with the Madison Range, Custer Gallatin National Forest, in the background.
Photo NPS/ERIN SHANAHAN**

Results

The following results are based on data collected by the monitoring program in Time 1, Time 2, and Time 3. Comparisons between time-steps are dependent upon the objective being addressed.

Objective 1: Blister Rust Infection Proportions

We estimated the proportion of live trees infected with white pine blister rust in the Greater Yellowstone Ecosystem (GYE) (Table 2):

- Infected proportion in Time 1 was 0.21 (0.03 SE)
- Infected proportion in Time 2 was 0.21 (0.02 SE)
- Infected proportion in Time 3 was 0.19 (0.03 SE)

There was no significant change in the proportion of trees infected in the GYE between the three time-steps. We conclude that the overall proportion of whitebark pine trees infected with blister rust at the end of Time 3 (2015) remains in the range of 0.13 to 0.25 (SE 0.03) in the GYE (Table 2 and Figure 4).

Fifty-two percent (72) of stands exhibited a decrease in the proportion of trees infected from Time 2 to Time 3, 25% (34) of stands showed an increase, and 23% (32) remained unchanged. Overall, we estimated a 7% decrease in the mean percentage of trees infected with blister rust within a stand from Time 2 to Time 3 ($n = 138$, Wilcoxon Signed Rank Test). Figure 5 reflects the changes in the proportion of trees infected with blister rust at the stand level.

Table 2. Design-based ratio estimates for the proportion of trees infected with blister rust in the Greater Yellowstone Ecosystem. Transects without any live, tagged trees are excluded from this analysis; therefore, the number of transects decreased with each consecutive time-step.

Time-Step	No. of transects	No. of stands	No. of live trees	Proportion of transects infected	Combined ratio estimates		
					Proportion of live trees infected	Standard Error (SE) for proportion of live trees infected	Confidence Interval (CI) for proportion of live trees infected
2004–2007 [T1]	176	150	4746	0.81	0.21	0.03	[0.14, 0.27]
2008–2011 [T2]	172	146	4210	0.84	0.21	0.02	[0.16, 0.26]
2012–2015 [T3]	162	138	3689	0.79	0.19	0.03	[0.13, 0.25]

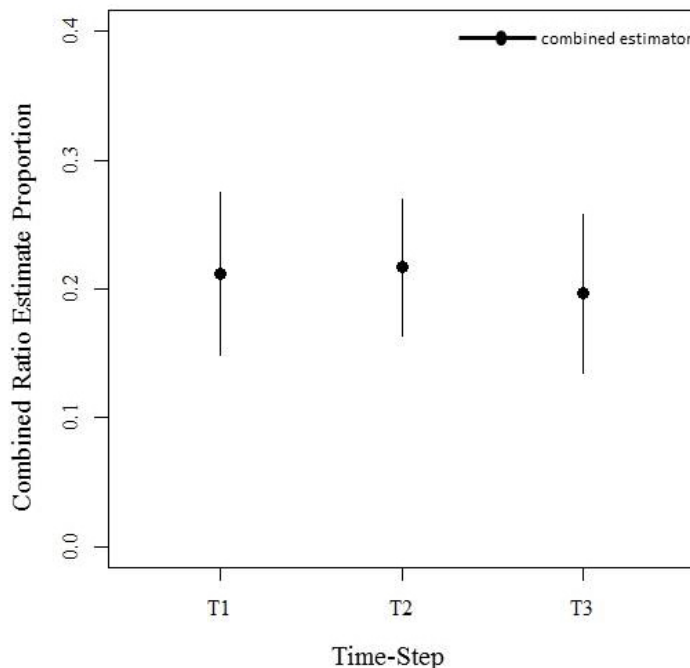


Figure 4. Trends in the proportion of trees infected with blister rust in the Greater Yellowstone Ecosystem, based on combined ratio estimates for each of three time-steps. T1 = 2004–2007, T2 = 2008–2011, T3 = 2012–2015.

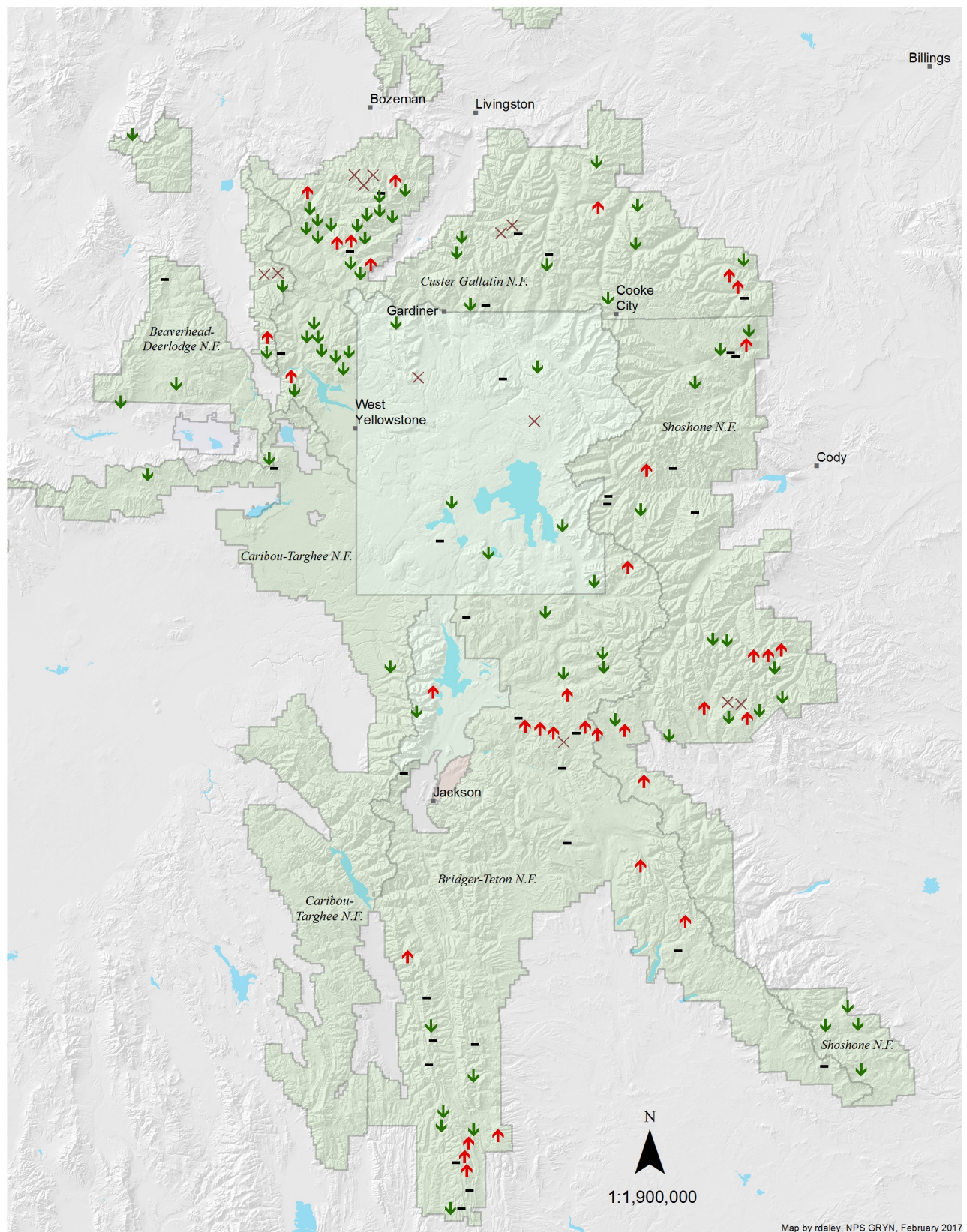


Figure 5. Change in the proportion of whitebark pine trees infected with blister rust within each of the stands with remaining live, tagged trees between Time 2 and Time 3 in the Greater Yellowstone Ecosystem. Twenty-five percent of stands (34 total stands) had increased infection (↑), 52% of stands (72 total stands) had a decrease in infection (↓), and 23% of stands (32 total stands) "-" had no change in infection.

Whitebark pine forests have experienced many dynamic changes over the past decade. To properly represent these changes, we calculated the combined ratio estimator using three additional data subset scenarios. Each scenario corresponds to an alternative outcome had mortality not occurred at such a substantial degree (Subset 3, 4) and/or new trees not been added to the sample (Subset 2, 3) between 2008 and 2015 (Table 3). We recognized that all four of these scenarios may have influenced our reported overall estimate for blister rust infection in the GYE, and we therefore undertook further analysis to investigate this potential bias. Data Subset 1 reflects the current, on-the-ground conditions of the monitoring transects, where dead trees have been removed from the sample and newly tagged trees have been added to the sample.

We found no significant difference in the proportion of trees infected with blister rust using a combined ratio estimator under four different scenarios that included or excluded known tagged dead or newly tagged trees (Table 4). All estimates were within 4% of each other and fell well within the current 14% to 26% estimated infection rate within the GYE (excluding the standard error).

Objective 2: Blister Rust Infection Severity

At the end of Time 3, we found that 25% (942 trees) of the live, tagged trees (3,716) were infected with blister rust. This included eight newly tagged trees documented with blister rust infections. In addition, we documented whether blister rust cankers occurred in the canopy or on the bole. A bole infection is considered more consequential than a canopy canker as it compromises not only the overall longevity of the tree, but its functional capacity for reproductive output as well (Kendall and Arno 1990; Campbell and Antos 2000;

McDonald and Hoff 2001; Schwandt and Kegley 2004). Trees with infections only in the canopy made up approximately 37% (343 trees) of the total number of trees infected with blister rust at the end of Time 3. Trees with bole cankers comprised 63% (599 trees; this included trees with combination bole and canopy cankers) of the infected sample. Of the documented reproducing trees (963), 43% (411) were infected with blister rust.

Infection Status and Transition—Time 1 to Time 3 and Time 2 to Time 3

Long-term monitoring tracks infection status and severity (i.e., location on the tree) through time for all live, tagged whitebark pine trees. Among the possible changes in infections status, only the change from Uninfected → Infected declined substantially during Time 2 → Time 3 (Table 5). It should be noted that the Time 1 to Time 3 comparison does not take into account any infection status change that may have occurred within Time 2.

In addition to the overall proportion of infection, we chronicled if and when infection location changed or transitioned in the canopy and bole of infected trees between time-steps. As with infection status, infection location can stay the same (canopy → canopy or bole → bole) or transition (canopy → bole or bole → canopy) over the time-step period. Again, we assigned trees infected with both canopy and bole cankers to the bole canker category for this analysis. Not surprisingly, we found that over a longer time interval of four to eleven years, as expressed in the Time 1 to Time 3 comparison, 60% of canopy cankers transitioned to the bole (Table 6). In addition, we found that once an infection occurs in the bole, the likelihood of it transitioning back to a canopy canker is low (Table 6).

Table 3. Description of data inclusions and exclusions for each of the four data subset scenarios used to calculate the proportion of whitebark pine trees infected with blister rust in the Greater Yellowstone Ecosystem.

Ratio estimator data subset scenarios	Dead tagged trees in Time 2 and Time 3	Newly tagged trees in Time 2 and Time 3
Subset 1 *	Excluded	Included
Subset 2	Excluded	Excluded
Subset 3	Included	Excluded
Subset 4	Included	Included

*Subset 1 was used to calculate and report on the current status of blister rust in the Greater Yellowstone Ecosystem.

Table 4. Estimated proportion of whitebark pine trees infected with blister rust in the Greater Yellowstone Ecosystem in Time 2 and Time 3 using a combined ratio estimator for the four possible data subset scenarios.

Time	Subset	Estimate	SE
Time 2	Subset 1 *	0.22	0.03
	Subset 2	0.23	0.03
	Subset 3	0.24	0.03
	Subset 4	0.22	0.03
Time 3	Subset 1 *	0.20	0.03
	Subset 2	0.22	0.03
	Subset 3	0.22	0.03
	Subset 4	0.20	0.03

*Subset 1 was used to calculate and report on the current status of blister rust in the Greater Yellowstone Ecosystem.

Table 5. Infection status and change in infection status between time-steps for tagged whitebark pine trees in the Greater Yellowstone Ecosystem. “n” represents the number of tagged trees that remained alive between the time-step comparisons. Due to the random panel assignment following transect establishment in Time 1, resurvey for individual trees varied by time-step. The interval for individual tree resurvey was anywhere from one to four years for the Time 1 to Time 2 comparison, five to twelve years for the Time 1 to Time 3 comparison, and four years for the Time 2 to Time 3 comparison.

Infection status	Time 1 → Time2 (n = 3,795)	Time 1 → Time3 (n = 3,270)	Time 2 → Time3 (n = 3,554)
Uninfected → Uninfected	64% (2,418)	66% (2,169)	69% (2,435)
Uninfected → Infected	11% (423)	10% (343)	4% (150)
Infected → Infected	21% (780)	18% (574)	22% (784)
Infected → Uninfected	6% (174)	6% (184)	5% (185)

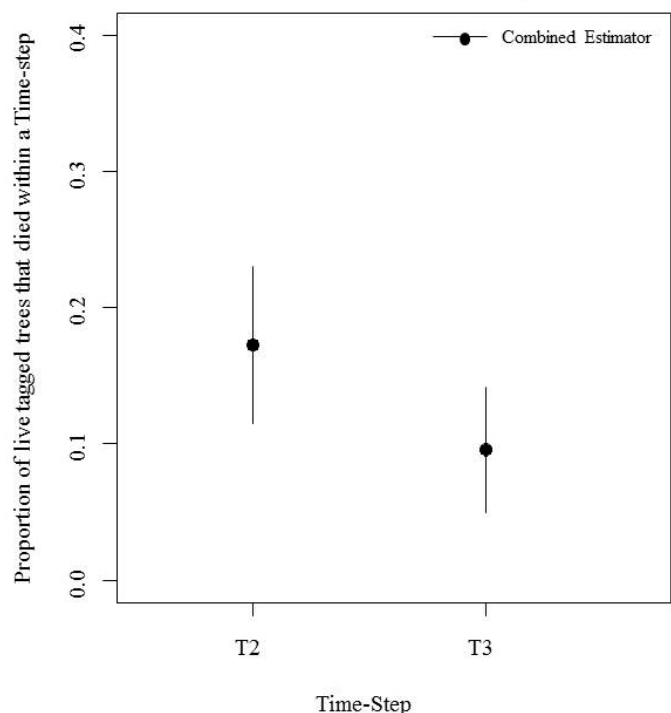
Table 6. Infection location and change in infection location between time steps. “n” represents the number of tagged trees that remained alive and infected between the time-step comparisons. Due to the random panel assignment following transect establishment in Time 1, resurvey for individual trees varied by time-step. The interval for individual tree resurvey was anywhere from one to four years for the Time 1 to Time 2 comparison, five to twelve years for the Time 1 to Time 3 comparison, and four years for the Time 2 to Time 3 comparison

Infection location	Time 1 → Time2 (n = 613)	Time 1 → Time3 (n = 574)	Time 2 → Time3 (n = 784)
Canopy → Canopy	36% (245)	27% (157)	30% (237)
Canopy → Bole	32% (235)	60% (237)	12% (98)
Bole → Bole	30% (280)	28% (163)	53% (416)
Bole → Canopy	2% (20)	9% (17)	4% (33)

Objective 3: Whitebark Pine Mortality

We estimated the proportion of dead whitebark pine trees across all size classes to be 0.26 in the GYE (0.03 SE) by the end of Time 3, using a combined ratio estimator. Documented mortality of trees decreased in Time 3 to a rate of 0.09 (0.02 SE) compared to the 0.17 (0.03 SE) mortality recorded during Time 2 (Figure 6). These estimates were derived from the total number of live, tagged trees starting at the beginning of each time-step.

Figure 6. Estimated mortality of whitebark pine trees greater than 1.4 m tall in the Greater Yellowstone Ecosystem, using a combined ratio estimator comparing Time 2 and Time 3. The total number of live trees was different at the beginning of each time-step (T2≈ 4,700, T3≈ 4,000); therefore, these estimates are distinct for each four-year period, rather than cumulative.



By the end of Time 3, 29% (1,502) of the tagged trees had died; 99% of the dead trees were from the original live, tagged trees cohort in Time 1. Approximately 32% (481) of the dead trees showed evidence of mountain pine beetle infestation only. The majority (902) of trees killed with evidence of mountain pine beetle were within the >10 to 30 cm DBH size class. Blister rust was the only associated factor for 14% (203) of the dead trees. Dead trees with sign of blister rust varied in size class but were predominantly in the >2.5 cm to 10 cm size class range. A total of 8% (121) of dead trees were documented with only fire scars. The remaining 46% (697) of trees died with evidence of a combination of factors, such as fire, mountain pine beetle, or blister rust,

or with other factors such as structural or animal damage (Figure 7).

Live, Tagged Tree Distribution History

With the mortality following the mountain pine beetle outbreak and other factors, we documented a shift in the size class distribution for the live, tagged tree cohort to smaller DBH trees (Figure 8; Shanahan et al. 2016).

We have observed a shift to smaller size classes of trees among the three time-steps (Table 7). The mean tree DBH has decreased from 13.22 cm in Time 1 to 9.09 cm in Time 3 (Table 7; Shanahan et al. 2016).

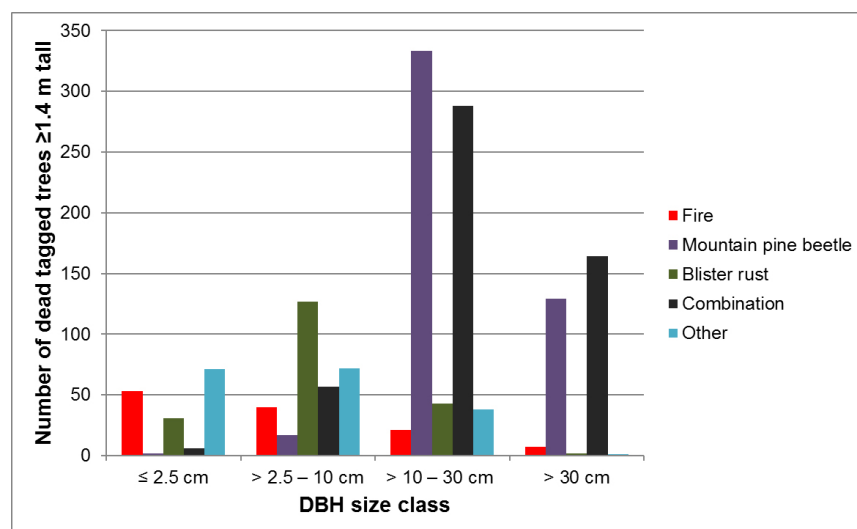


Figure 7. Cumulative mortality of tagged whitebark pine trees in the Greater Yellowstone Ecosystem from 2008 through the end of Time 3 (2015) by DBH size class and by indicators: fire, mountain pine beetle, blister rust, or other (i.e., wind throw, animal damage). The “combination” category refers to the simultaneous occurrence on a given dead tree of two or more of the three main indicators: mountain pine beetle, blister rust, and fire.

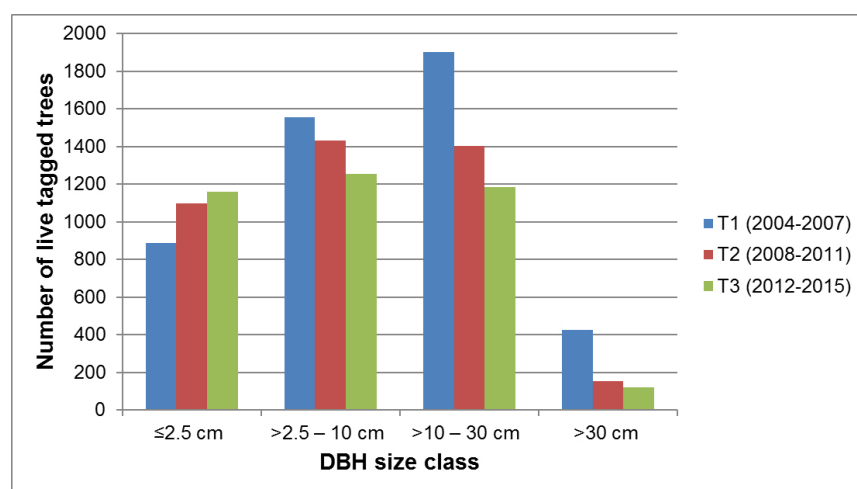


Figure 8. Size class distribution for live, tagged trees over the course of the 12-year whitebark pine monitoring program in the Greater Yellowstone Ecosystem.

Table 7. Summary statistics for Diameter at Breast Height (DBH; cm) values for all live, tagged whitebark pine trees monitored in the Greater Yellowstone Ecosystem for each time-step.

Time-Step	Min	1st Quartile	Median	Mean	3rd Quartile	Max
T1	1	4	10	13.22	19.5	126.5
T2	1	3	8	10.77	15.5	95
T3	1	2	6.5	9.09	13	95

Objective 4: Whitebark Pine Recruitment

We assessed recruitment by tracking the number of new whitebark pine trees added to the tagged tree sample, the number of cone-producing trees, and by recording seedlings and saplings in the understory. In Time 3, an additional 160 trees were tagged that grew to >1.4 m tall since Time 2. This brought the total count of newly tagged trees added since initial transect establishment to 447 (including the 287 trees that were added in Time 2).

Cone-Producing Trees

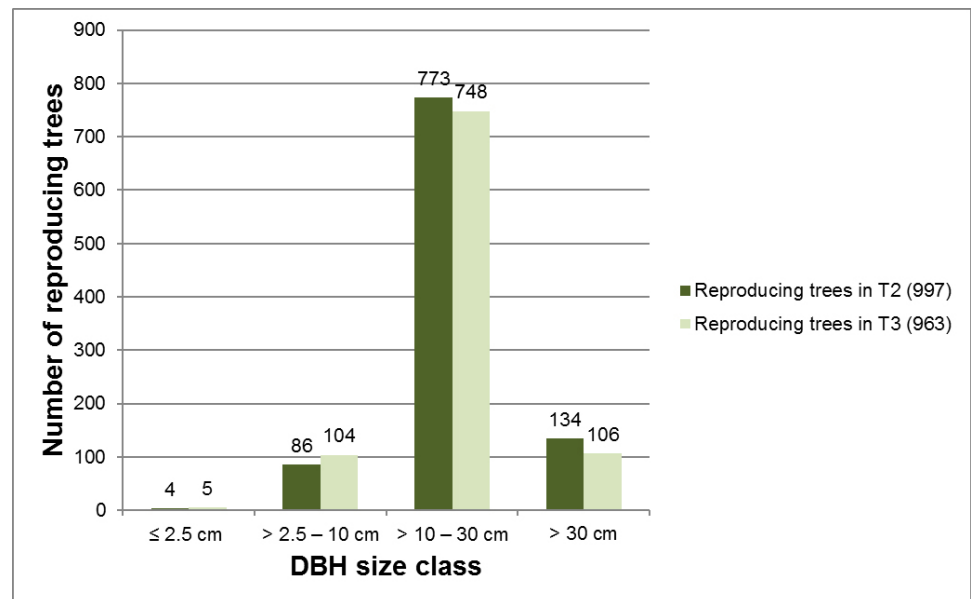
Known reproducing trees made up approximately 26% (963 trees) of the total live, tagged trees at the end of Time 3 (Figure 9). In Time 2, 997 trees were recorded as reproducing. We report this as a conservative estimate because we recognize that due to the panel revisit schedule, this metric may not be observed if the panel that a tree is assigned is not visited while a tree is exhibiting signs of reproduction. Although we documented reproduction across all four size classes, the smaller-DBH trees usually did not produce as many cones. These typically younger trees tended to have

fewer canopy branches and less overall canopy volume compared to their larger-DBH counterparts. A total of 74% (2,753) had no observable signs of cone scars, cones, or conelets. Of the reproducing trees, 43% (411) had blister rust infections with 54% (220) of these infections located on the bole. One hundred and fifty-four (16%) reproducing trees had sign of mountain pine beetle.

Understory Seedlings and Saplings

Differentiating between whitebark pine and limber pine (*Pinus flexilis*) seedlings or saplings is problematic given the absence of cones or cone scars. Therefore, understory summaries in this report may include individuals of both species when they are sympatric in a stand. In Time 3, the density of trees ≤ 1.4 m tall averaged 51 understory trees per 500 m², which was similar to the density reported for Time 2, of 53 per 500 m². Raw counts of these understory individuals ranged from 0 to 521 small trees per belt transect (Figure 10). We documented <1% (80) of these small trees as having some level of blister rust infection.

Figure 9. Number of live, reproducing, tagged whitebark pine trees in the Greater Yellowstone Ecosystem in Time 2 (997) compared to the number in Time 3 (963), differentiated by DBH size class.



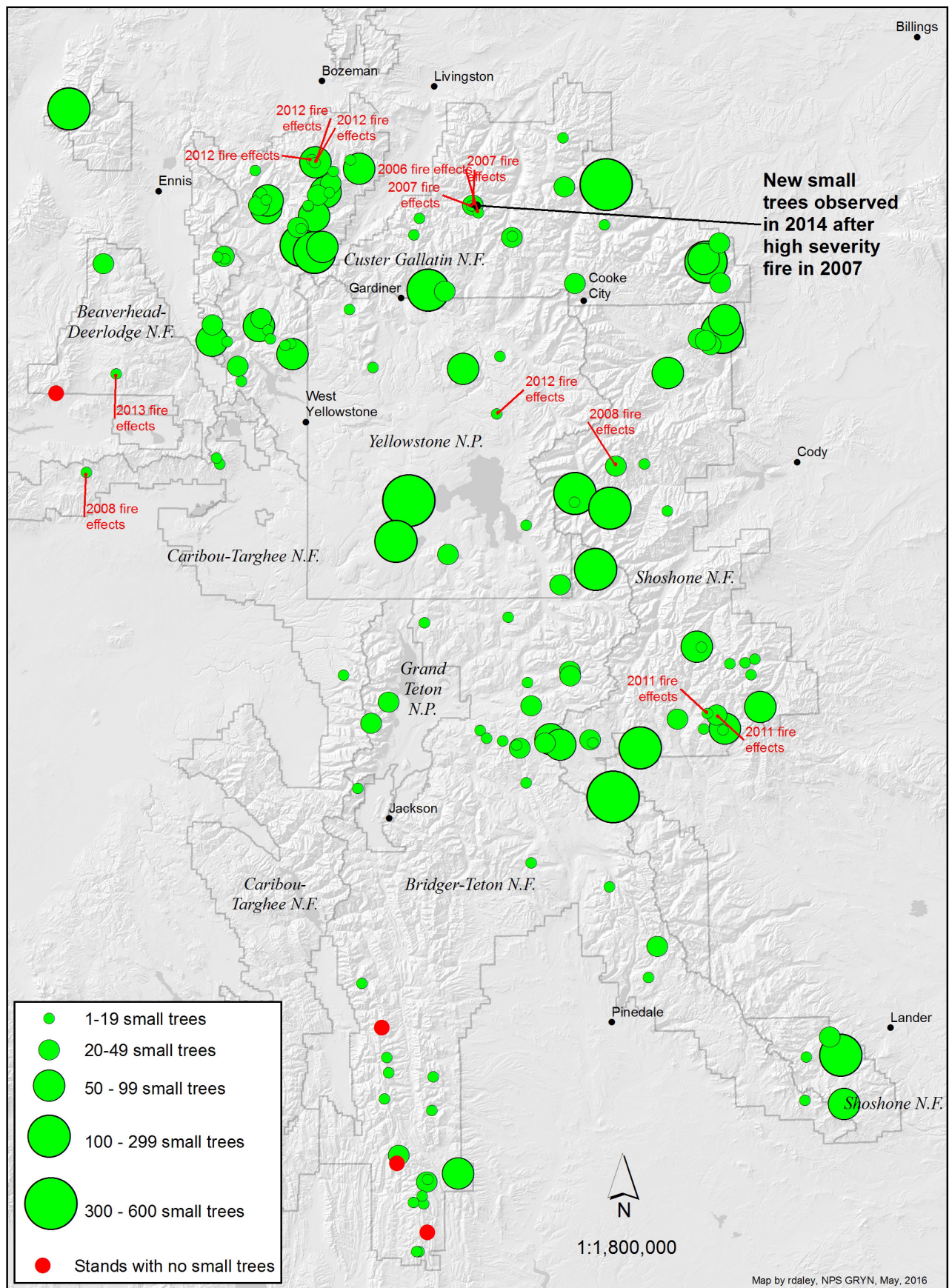


Figure 10. Average count of whitebark pine trees (per 500 m²) less than 1.4 m tall in stands monitored from 2004 through 2015 in the Greater Yellowstone Ecosystem.

Discussion

Blister Rust Infection Proportions

The estimated proportion of whitebark pine trees infected with blister rust in the Greater Yellowstone Ecosystem (GYE) was similar across all three time-steps (2004–2007, 2008–2011, 2012–2015). The overall percentage of whitebark pine trees >1.4 m tall that were infected with blister rust in the GYE continues to range between 14% and 26%. While variation (increases and decreases) in blister rust infection occurred across the monitoring transects and resulted in shifts in the proportion of trees infected for the majority (77%) of stands, we detected no significant difference in the overall blister rust infection rate among the time-steps. We recognized that the mortality that occurred over the course of the three time-steps had the potential to impact our reported estimate of the proportion of trees infected with blister rust in the GYE. To address this concern, we calculated estimates for three alternative scenarios of exclusion and inclusion, described in Table 3, in addition to the estimate conveyed in this report. Results from these three scenarios demonstrate that the death of 29% (1,502) of the originally tagged trees did not affect the rate of infection in the GYE, nor did the addition of 447, predominantly uninfected new trees. The greatest difference between any of the scenarios presented in Tables 3 and 4 was no greater than 4% and not statistically significant. Trees with or without blister rust showed evidence of mountain pine beetle (Shanahan et al. 2016) and fire in relatively equal numbers.

Blister Rust Infection Severity

While we did not observe a discernable change in the proportion of trees infected with blister rust in the GYE, we documented infection transitioning from canopy to bole. This kind of transition may be a potentially more informative indicator of individual tree health and the overall population trajectory with regard to the impacts of blister rust infection. By the end of Time 2, 58% (698 of 1,203) of infected tagged trees were infected in the bole (Shanahan et al. 2014), compared to approximately 63% (599 of 942) of bole infected trees at the end of Time 3. Over the 12-year monitoring period, 60% (237) of the trees that remained alive and infected transitioned from a less lethal (canopy) form of infection to one considered more detrimental (bole) to the health status of the tree. Cones are produced on the outer branches in the upper canopy of whitebark pine; portions of a branch that are distal to an active canker are often precluded from vital nutrients necessary to sustain normal tree function, healthy foliage, and cone production (Maloney et al. 2012).

As a result, death of infected upper branches can occur and negatively impact cone production. Maintaining our long-term monitoring program and adhering to the panel revisit schedule will allow us to investigate the dynamic nature of infection transition. Continued evaluation of this metric is a more informative indicator of individual tree health. It will also enable us to better predict the overall whitebark pine population trajectory as it relates to the persistent impacts of blister rust infection.

Whitebark Pine Mortality

Mortality of whitebark pine occurred across all DBH size classes. By the end of Time 3, we estimated the proportion of whitebark pine >1.4 m tall in the GYE that had died since Time 1 to be 0.26 (0.03 SE). While mortality of tagged trees continued in Time 3, it occurred at a reduced rate of 9%, compared to the mortality of tagged trees documented in Time 2 (17%; Figure 6). While we continued to record dead trees with signs of mountain pine beetle in Time 3, we suspect that many of these trees were likely attacked during Time 2 but not recorded as dead until two years later when they were revisited according to their panel schedule (Figures 3 and 7). Very few new or active mountain pine beetle attacks were observed on the monitoring transects during Time 3. Blister rust was the sole attribute in 14% of the total number of dead, tagged trees by the end of Time 3.

Along with mountain pine beetle and blister rust, whitebark pine stands have also been affected by wildland fires across the ecosystem. Fire-influenced mortality increased two-fold during Time 3, from a total of 6 burned stands in Time 2 to 14 in Time 3. The majority of these fire events were stand replacing, where all trees within the fire perimeter were killed. A cumulative total of 254 dead, tagged trees were documented as fire affected. Under projected climate change conditions, wildland fire events are predicted to increase in the GYE (Westerling et al. 2011). Consequently, we expect an increase in the number of stands affected by fire into the future.

Over the course of the monitoring program, a distinct shift in the size class distribution of live, tagged trees was evident (Figure 8 and Table 7). The initially tagged sample had almost equal numbers of trees ≤ 10 cm DBH and trees > 10 cm DBH. The ensuing mortality since establishment resulted in a shift to smaller size classes (≤ 10 cm DBH) and potentially fewer cone-bearing trees in the GYE (Figure 9). Given that blister rust is thought to be more detrimental to smaller

trees (Tomback et al. 1995), this finding suggests that, in the coming decades, blister rust may become the most probable cause of whitebark pine mortality in the GYE (Shanahan et al. 2016).

Whitebark Pine Recruitment

Although approximately 29% (1,502) of the tagged trees have died, we observed reproducing trees, regeneration in the understory, and recruitment on the majority of monitoring transects. We documented 26% (963) of the live, tagged trees as cone producing. Regeneration varies dramatically across the 176 belt transects. Counts of whitebark pine trees ≤ 1.4 m tall ranged from 0 to 521 trees per 500 m² belt transect (Figure 10). Our estimates suggest that there were 51 five-needle pines ≤ 1.4 m tall per 0.04 ha. In addition, by the end of Time 3, we tagged an additional 447 new trees within the belt transects that had grown into the >1.4 m tall height category.

Interactions between Factors Influencing Mortality

In addition to our annual and trend reports, we recently published a study (Shanahan et al. 2016) that analyzed the associations between observed mortality in relation to tree-level variables, including duration and location of blister rust, mountain pine beetle, tree size, potential interactions between tree size, blister rust, and mountain pine beetle, and water availability. In this study, tree and disease variables were linked to stand level estimates of water availability, calculated with gridded climate data and a water balance model that accounts for sub grid cell variations in slope, aspect and soil water holding capacity. Our findings describe how

warming temperatures from 2006 to 2008 that likely released temperature constraints on beetle development (Shanahan et al. 2016) contributed to the mountain pine beetle outbreak that caused extensive mortality described in this study. We demonstrated that larger DBH whitebark pine were preferentially attacked and subsequently killed by mountain pine beetle, which resulted in a regionwide shift to smaller DBH trees (Figure 8 of this trend report; Shanahan et al. 2016). When infected with blister rust, these smaller DBH trees experience higher mortality than their larger infected cohorts do. We found no evidence for an interactive effect between blister rust and mountain pine beetle on whitebark pine mortality (see Shanahan et al. 2016, page 9, Figure 3). This interactive effect had been previously suggested by other studies of whitebark pine in the GYE (Bockino and Tinker 2012; Dooley and Six 2015). We also observed that greater water availability positively influenced survival in trees attacked by mountain pine beetle (see Shanahan et al. 2016, page 11, Figure 4), improving the tree's ability to pitch out beetles by strengthening its resin response. These conclusions suggest that preferential planting in locations that have higher water availability and lower relative humidity (less conducive to the spread of blister rust) may confer a survival advantage in the face of a warmer and drier future. With continued monitoring, we expand our understanding of whitebark pine survival and mortality as it relates to pathogens, insect outbreaks, and climatic effects. This information improves our overall understanding of the biophysical influences on whitebark pine with the purpose of advancing conservation efforts in the GYE.

Conclusions

Throughout the past decade in the GYE, monitoring has helped document shifts in whitebark pine forests as they have been impacted by insect, pathogen, wildland fire, and other events. Blister rust infection is ubiquitous but spatially variable in the ecosystem and infection proportions are variable across the region (Figure 11). The proportion of whitebark pine trees >1.4 m tall that died across the GYE at the end of Time 3 was 0.26 (0.03 SE). It is important to note that estimates presented here reflect data collected from ground-based monitoring efforts that assess mortality status across all size (height and DBH) classes as opposed to other studies that report higher estimates of mortality based on aerial and remote sensing detection that focus exclusively on canopy occupying trees (Logan et al. 2010; McFarlane et al. 2013).

Mortality of overstory cohorts in many stands throughout the GYE has prompted considerable interest and emphasized the need for investigating the growth of the whitebark pine understory. An effort to track this metric was piloted over the course of Time 3. As we initiate the fourth time-step, we will begin collecting data to accurately assess recruitment of small trees into the >1.4 m height category using nested plots within the 10 × 50 m permanent transects.

The monitoring program continues to impart meaningful information to the broader regional assessment of trends in the health and status of whitebark pine. The monitoring program acts as an important resource for a variety of organizations embarking on five-needle pine monitoring. It has provided contemporary data both regionally and on a landscape level where other populations of whitebark pine persist. Data from the program have been used by multiple organizations and private entities:

- local US Forest Service and Bureau of Land Management districts have used the data to assess the “wilderness character” of surrounding public land
- the U.S. Geological Survey Interagency Grizzly Bear Study Team have included the data as part of their food synthesis report (Interagency Grizzly Bear Study Team 2013)
- the program provides science-based data to the U.S. Fish and Wildlife Service in their listing consideration for whitebark pine under the Endangered Species Act, including annual updates to population health (USFWS 2011)
- the data are used for baseline infection status and other health metrics for the Whitebark Pine Strategy for the GYE (GYCCWPS 2011)
- the program fulfills numerous data requests for other investigations on whitebark pine health, many of which have been related to climate change (Chang et al. 2014; Buermeyer et al. 2016; Hansen et al. 2016)

We provide this second step-trend report to improve understanding of the state of whitebark pine in the GYE. Many aspects of whitebark pine health are highly variable across the range of its distribution in the GYE. Through sustained implementation of the monitoring program, we will continue efforts to document and quantify whitebark pine forest dynamics as they arise under periodic upsurges in insect, pathogen, fire episodes, and other climatic events in the GYE. Since its inception, this monitoring program perseveres as one of the only sustained long-term efforts conducted in the GYE with the singular purpose to track the health and status of this prominent keystone species.

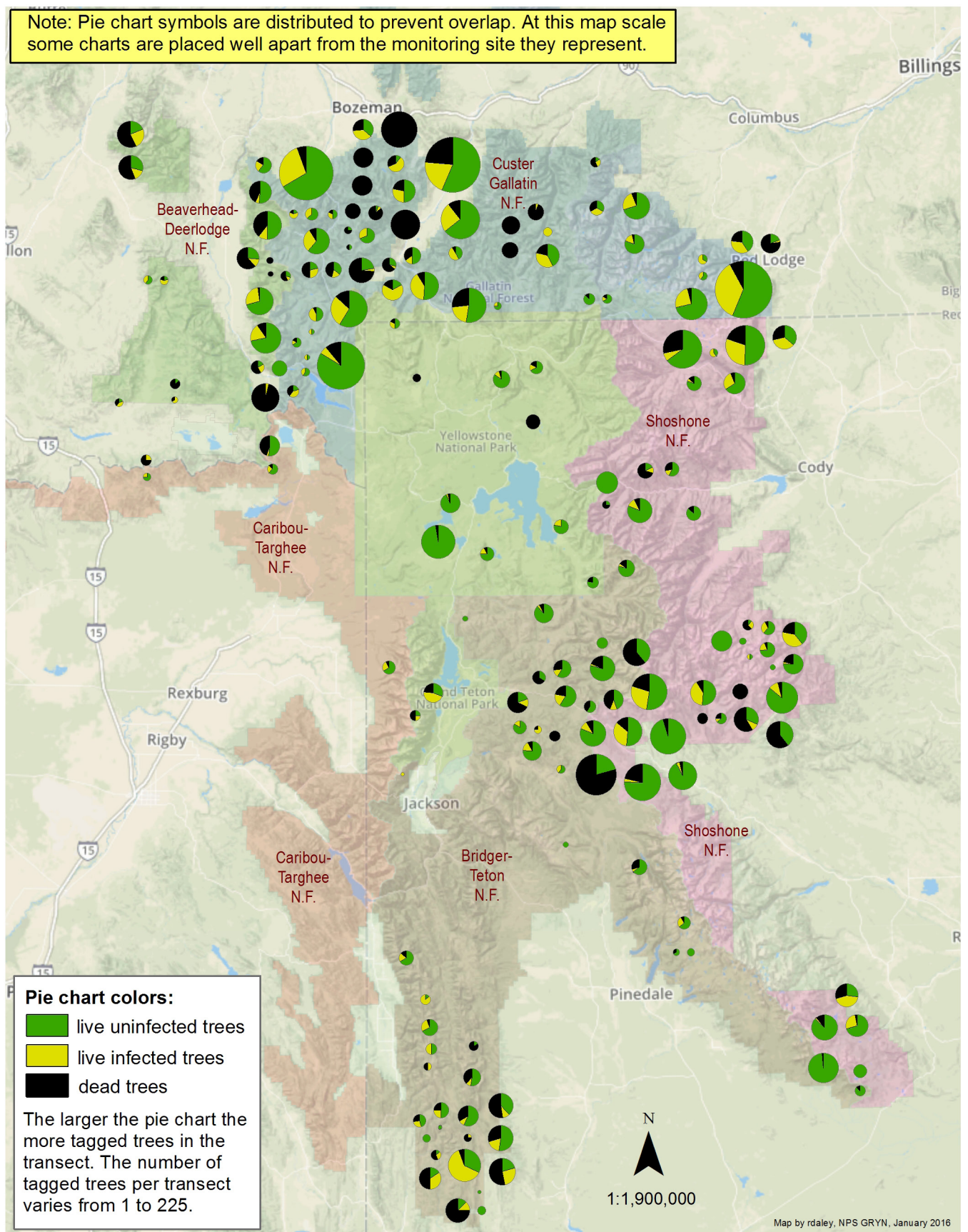


Figure 11. Distribution of blister rust-infected whitebark pine trees in sampled transects in the Greater Yellowstone Ecosystem at the end of 2015.

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