



Status of Whitebark Pine in the Greater Yellowstone Ecosystem

A Step-Trend Analysis with Comparisons from 2004 to 2023



Field crew surveying at a long-term monitoring transect on the Bridger-Teton National Forest.
NPS / E. SHANAHAN

Status of whitebark pine in the Greater Yellowstone Ecosystem: A step-trend analysis with comparisons from 2004 to 2023

Science Report NPS/SR—2025/328

Erin Shanahan , Rob Daley , Lydia Druin , Kristin Legg 

National Park Service
Greater Yellowstone Inventory and Monitoring Network
2327 University Way, Suite 2
Bozeman, MT 59715

Please cite this publication as:

Shanahan, E., R. Daley, L. Druin, and K. Legg. 2025. Status of whitebark pine in the Greater Yellowstone Ecosystem: A step-trend analysis with comparisons from 2004 to 2023. Science Report NPS/SR—2025/328. National Park Service, Fort Collins, Colorado.
<https://doi.org/10.36967/2313989>

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Abstract

Whitebark pine (*Pinus albicaulis*) is a high-elevation conifer of the northern Rocky Mountains and the Pacific Northwest. This slow-growing, long-lived conifer influences critical ecosystem functions in subalpine environments, including snow capture, landscape stability, soil amelioration, and overall forest health and resilience. Moreover, its nutritious seeds feed the federally threatened grizzly bear (*Ursus arctos*), Clark’s nutcracker (*Nucifraga columbiana*), red squirrel (*Tamiasciurus hudsonicus*), and other species. However, whitebark pine is declining in high-elevation forests due to several factors: a nonnative pathogen (white pine blister rust, *Cronartium ribicola*), unprecedented mountain pine beetle (*Dendroctonus ponderosae*) outbreaks, wildfire, and drought. The ensuing mortality, particularly of large, mature trees, has reduced cone production and compromises this species’ essential ecosystem services. Consequently, in 2023, the U.S. Fish and Wildlife Service listed the whitebark pine as federally threatened. Given these long-standing concerns, the Greater Yellowstone Network has been monitoring whitebark pine as part of the Interagency Whitebark Pine Monitoring Program since 2004. The monitoring program represents a tri-state, cross jurisdictional effort to track whitebark pine population condition and trends on National Park Service, U.S. Forest Service, and Bureau of Land Management lands in the region. This report documents the prevalence of blister rust infection, tree mortality, and recruitment of whitebark pine during the fifth time-step period, from 2020 to 2023 and compares it with prior time-step periods spanning 2008 to 2019. We found that estimates of blister rust infection continue to increase, using both an improved Bayesian modeling approach and the initial design-based ratio estimator. Based on model estimates, 47% of all whitebark pine in the Greater Yellowstone Ecosystem (GYE) are infected with blister rust. Furthermore, 47% of trees observed with cones or cone scars were infected with blister rust. We continued to observe tree size shifting towards smaller diameters following the mid-2000s mountain pine beetle outbreak and subsequent wildfire and disease activity across the ecosystem. This remains a critical concern given that 94% of cone-producing trees have larger diameters. Tree mortality continues to stabilize after peaking from 2008 to 2011, with 226 new trees reported dead during 2020 to 2023. Tree recruitment persists throughout the ecosystem, with 280 more trees growing past the > 1.4 m height threshold for tagging and monitoring—more than the number of new trees tagged over the previous 2016 to 2019 period. Changes in the GYE whitebark pine population are tracked through continued annual monitoring and regular trend reporting.

Why Monitor Whitebark Pine?

Whitebark pine (*Pinus albicaulis*) is an upper subalpine conifer of the northern Rocky Mountains and the Sierra Nevada Mountains north to the Cascades in the Pacific West. It is a keystone species that strongly influences community assembly and productivity of high-elevation ecosystems (Tomback et al. 2001). Whitebark pine is considered a “pioneer” species due to its tolerance of harsh environmental conditions and ability to establish and persist where other species cannot, due in part to its unique relationship with its primary seed distributor, Clark’s nutcracker (*Nucifraga columbiana*). In doing so, whitebark pine can alter microclimates and enable species such as subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) to more readily establish (Tomback et al. 1993). Additionally, the highly nutritious seeds of whitebark pine trees are seasonal forage for a variety of wildlife, including grizzly bears (*Ursus arctos horribilis*), red squirrels (*Tamiasciurus hudsonicus*), Clark’s nutcrackers, and a variety of granivorous small mammals.

Throughout its historical range, whitebark pine has significantly decreased as a major component of high-elevation forests due to multiple factors, including the nonnative white pine blister rust (*Cronartium ribicola*, hereafter blister rust), endemic mountain pine beetle (*Dendroctonus ponderosae*), as well as changing disturbance regimes and climate. Because of persistent, high mortality across its range, the U.S. Fish and Wildlife Service listed whitebark pine as a federally threatened species under the Endangered Species Act in 2023 (USFWS 2021; Federal Register 2022). Of significant concern is the loss of large diameter mature, cone-producing whitebark pine trees and the associated ecosystem services they provide. Understanding these challenges to whitebark pine—not only at the tree- and stand-level, but also at a landscape scale—is critically important to conserving and managing this iconic subalpine conifer in the Greater Yellowstone Ecosystem (GYE).



Whitebark pine (in the background) grows on high mountain slopes.

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Monitoring Program Purpose and Objectives

To track the health status of whitebark pine in the intermountain region, several agencies have collaborated through the [Greater Yellowstone Coordinating Committee](#) since 2004 to implement the Greater Yellowstone Ecosystem Interagency Whitebark Pine Monitoring Program, led by the National Park Service's Greater Yellowstone Inventory and Monitoring Network. This report summarizes the past four years (2020–2023) of whitebark pine health status and trend monitoring in the GYE in comparison with the previous four time-steps: Time-Step 1 (2004–2007), Time-Step 2 (2008–2011), Time-Step 3 (2012–2015), and Time-Step 4 (2016–2019). This represents our fourth step-trend (Trend 4) report on whitebark pine health status in the GYE.

The objectives of the Greater Yellowstone Ecosystem Interagency Whitebark Pine Monitoring Program follow:

1. Assess trends in the proportion of live whitebark pine trees (> 1.4 m tall) infected with blister rust.
2. Document blister rust infection severity and changes over time by the occurrence and location on the tree of new and persisting infections.
3. Assess trends in mortality of whitebark pine trees and describe contributing mortality factors.
4. Document the recruitment of whitebark pine into the reproductive population and assess multiple factors that influence overall recruitment success over time.

Contribution to Regionwide Management

Over the past two decades, the long-term Interagency Whitebark Pine Monitoring Program has developed a comprehensive understanding of the health, demography, and disturbance response of whitebark pine in the GYE. Key disturbances include blister rust, pests—such as the mountain pine beetle—and shifting fire regimes. Data generated from this dynamic and expanding program are used in the following ways:

- Support data-driven management decisions on public lands, including but not limited to national parks, national forests, Bureau of Land Management forests, and designated wilderness areas across the western United States.
- Inform and guide restoration activities and planning strategies.
- Support conservation and research on whitebark pine, including enhanced understanding of population health and a collective understanding of whitebark pine ecology.
- Substantiate conservation actions throughout the GYE and across the distribution of whitebark pine in western North America.

Importantly, this interagency protocol has been adopted and adapted by other federal and state entities as they commence monitoring activities across the broader range of five-needle pines. Long-term monitoring programs are particularly useful for long-lived species like whitebark pine, as population trends and responses to restoration activities are more effectively observed across extensive time periods compared to shorter, < 5-year programs (Leirfallom et al. 2015; Murray et al. 2021). As such, the cross jurisdictional Interagency Whitebark Pine Monitoring Program is uniquely positioned to provide information over a sustained timeframe at a landscape scale. Accumulating data across three states, three national parks, five national forests, and three Bureau of Land Management regions leads to more efficient, constructive, and informed management decisions, all crucial tenets for threatened species conservation. Additionally, ongoing tracking of tree health helps identify potentially rust-resistant individuals, which is a high priority in conservation efforts (Schoettle et al. 2019; Tomback et al. 2022), as well as reproducing trees that can supplement cone collection for restoration activities, such as direct seeding or planting (Tomback et al. 2022).

Methods

The complete methods for this long-term effort are published in the [*Interagency Whitebark Pine Monitoring Protocol for the Greater Yellowstone Ecosystem*](#) (GYWPMWG 2011), as well as in Article 5 ([Methods](#)) of the *Whitebark Pine Monitoring in the Greater Yellowstone Ecosystem* online article series.

In summary, 176 permanent 10 × 50 m belt transects were established within 150 pure whitebark pine stands and mixed stands supporting whitebark pine and other conifer species between 2004 and 2007 (Figure 1). We used a design-based statistical sampling method that allows inference of the monitoring results to the mapped population of whitebark pine in the GYE. All live, > 1.4 m tall trees were permanently tagged to enable long-term monitoring of individuals on a four-year rotating schedule. Whitebark pine stand transects were divided into four different panels, each sampled in a different year, so that all transects were sampled at least once every four years (Table 1).

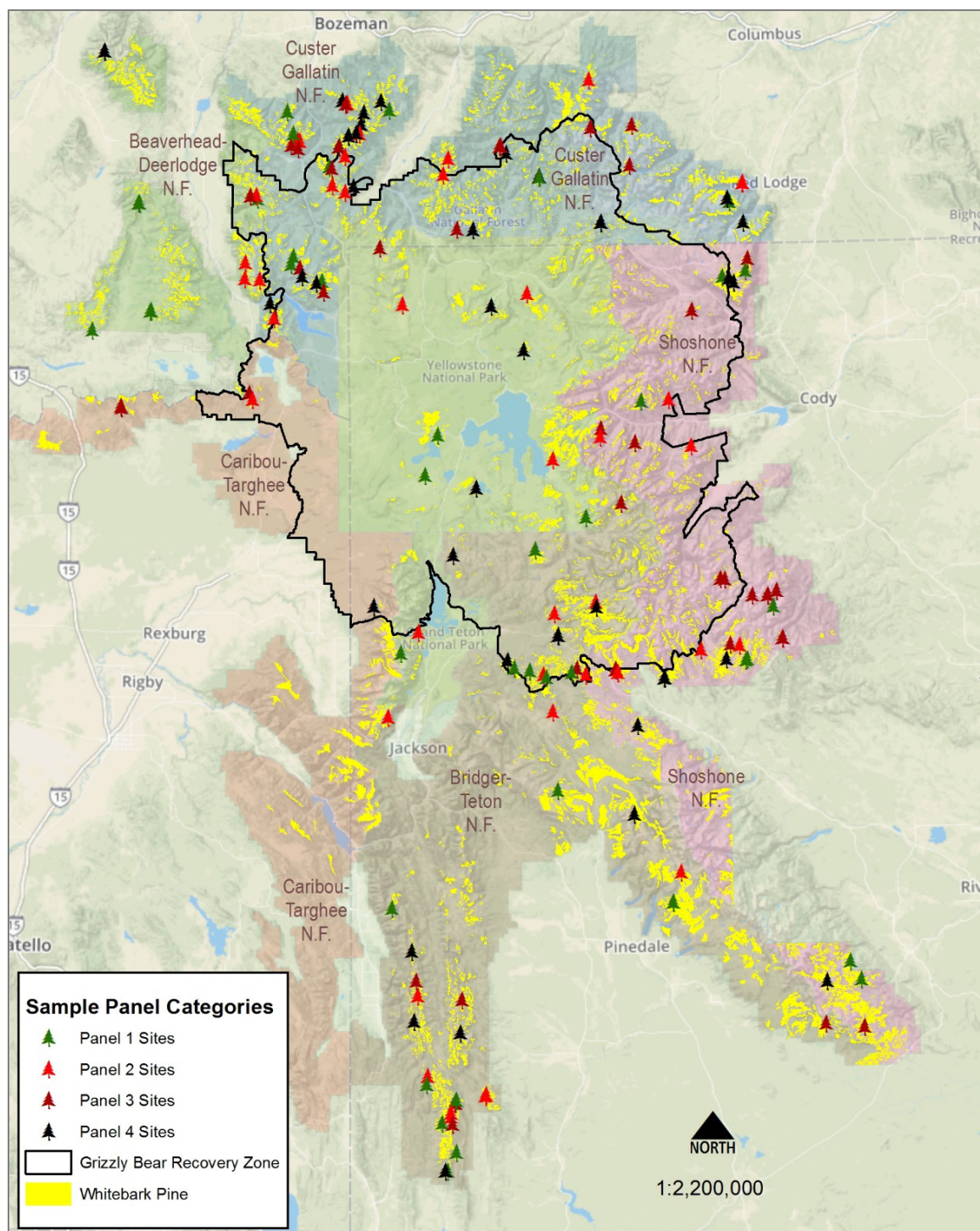


Figure 1. The study area for the Interagency Whitebark Pine Monitoring Program in the Greater Yellowstone Ecosystem (shown as the shaded zones), which has sites spanning Montana, Wyoming, and Idaho. Sites were randomly selected from known stands of whitebark pine, shown in yellow, and assigned panel membership (given by green, red, brown, or black tree icons) to distinguish revisit schedule during each four-year time period.

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Table 1. Revisit schedule during each time-step based on panel membership for the Interagency Whitebark Pine Monitoring Program. The schedule includes full surveys, shown in green, and mortality only surveys, shown in orange. Mortality only surveys were completed during a mountain pine beetle epidemic, occurring primarily in Time-Step 2.

Time-Step	Year(s)	Panel 1 (43 Transects)	Panel 2 (45 Transects)	Panel 3 (44 Transects)	Panel 4 (44 Transects)
1	2004–2007	Set up surveys and document initial health status	Set up surveys and document initial health status	Set up surveys and document initial health status	Set up surveys and document initial health status
2	2008	Blister rust and mortality surveys	–	Mortality only surveys	–
	2009	–	Blister rust and mortality surveys	–	Mortality only surveys
	2010	Mortality only surveys	–	Blister rust and mortality surveys	–
	2011	–	Mortality only surveys	–	Blister rust and mortality surveys
3	2012	Blister rust and mortality surveys	–	Mortality only surveys	–
	2013	–	Blister rust and mortality surveys	–	Mortality only surveys
	2014	–	–	Blister rust and mortality surveys	–
	2015	–	–	–	Blister rust and mortality surveys
4	2016	Blister rust and mortality surveys	–	–	–
	2017	–	Blister rust and mortality surveys	–	–
	2018	–	–	Blister rust and mortality surveys	–
	2019	–	–	–	Blister rust and mortality surveys
5	2020	Blister rust and mortality surveys	–	–	–
	2021	–	Blister rust and mortality surveys	–	–
	2022	–	–	Blister rust and mortality surveys	–
	2023	–	–	–	Blister rust and mortality surveys
6	2024	Blister rust and mortality surveys	–	–	–

Table 1 (continued). Revisit schedule during each time-step based on panel membership for the Interagency Whitebark Pine Monitoring Program. The schedule includes full surveys, shown in green, and mortality only surveys, shown in orange. Mortality only surveys were completed during a mountain pine beetle epidemic, occurring primarily in Time-Step 2.

Time-Step	Year(s)	Panel 1 (43 Transects)	Panel 2 (45 Transects)	Panel 3 (44 Transects)	Panel 4 (44 Transects)
6 (cont.)	2025	–	Blister rust and mortality surveys	–	–
	2026	–	–	Blister rust and mortality surveys	–
	2027	–	–	–	Blister rust and mortality surveys

Objective 1: Status of Blister Rust Using Advancements in Analytical Methodologies

Previous analysis of blister rust prevalence for Trends 1 and 2 utilized a design-based ratio estimator. While the use of a ratio estimator was appropriate for the time frame spanning 2004 to 2015, recent advances in statistical methodologies have greatly improved our ability to incorporate the numerous factors influencing whitebark pine health and to more accurately assess status and trends. In the Trend 3 report (2016–2019), we introduced a Bayesian hierarchical occupancy model-based approach that has the flexibility to account for the multiple sources of variation in a field-based, observational monitoring program such as ours (e.g., tree size, elevation, transect and stand membership). With the inclusion of a model-based analysis, we increase our ability to effectively detect change using a repeat survey framework.

Maintaining the protocol’s relevancy is especially critical given threats to the species’ survival and the protocol’s use by several other agencies that also track whitebark pine health. While the Bayesian model improves accuracy by using more contemporary and adaptable approaches, we include the standard ratio estimator for past and current trend report comparisons. Additionally, though we intend to utilize the Bayesian model for trend estimations going forward, should there be a lack of future funding resources that prohibit our ability to access skilled statisticians to assist with this more advanced analysis technique, we can continue to rely on the ratio estimator to provide credible and valuable information on trend status (i.e., increases or decreases in blister rust).

Objective 2: Infection Severity

Infection severity affects whitebark pine reproduction. The reproductive output of persisting whitebark pine populations in the GYE is vitally important for the long-term, natural, and assisted restoration of the species (Tomback et al. 2022). As such, blister rust infections, also referred to as cankers, situated on the bole of a tree have long been considered a more detrimental and immediate threat to overall tree health than infections in the canopy. Damage caused by infections located anywhere on the bole can severely restrict reproductive functionality and capacity (McDonald and Hoff 2001).

Following the interagency whitebark pine monitoring protocol, blister rust infections are recorded by location in the canopy (branches) and on the bole (trunk). However, recent work has revealed that blister rust detection probability varies by observer depending on the metric; high agreement among observers is evident for general infection presence or absence (i.e., a tree is infected or not), whereas consensus decreases considerably when identifying location-based infections (i.e., is the infection in the bole or canopy; Shanahan et al. 2021; Wright and Irvine 2017). Nevertheless, this second objective continues to provide important information for the potential trajectory of whitebark pine health and reproductive productivity in the future.

Objective 3: Mortality

To determine whitebark pine mortality, we survey all belt transects to reassess the life status of permanently tagged trees > 1.4 m tall. A ratio estimator is used to evaluate the proportion of trees that died between time-steps and all potential mortality-influencing conditions (blister rust, mountain pine beetle, fire, and others) are recorded.

Objective 4: Recruitment

Given the extensive loss of mature whitebark pine across its range, the persistence of this important conifer will be characterized by the species' ability to replace itself on the landscape (e.g., ratio of mortality to recruitment), while maintaining genetic diversity sufficient to support resilient, viable populations into the future. Thus, regeneration and recruitment are crucial components in determining whitebark pine population trajectories. While the terms recruitment and regeneration are often used interchangeably in forestry, we define recruitment as the sum of factors influencing the addition of whitebark pine to the reproducing population (Helms 1998); regeneration is one factor.

The monitoring program assesses recruitment and recruitment potential across the range of established transects. Whereas recruitment documents the presence of live, five-needle pines, recruitment potential is distinguished by a broader scope of metrics, both tangible (e.g., cone production) and conceptual (e.g., upper live canopy volume, infection of non-reproducing trees, infection location of both reproducing and non-reproducing trees, competition for resources, etc.). Taken together, these two components, recruitment, and recruitment potential, collectively influence prospective whitebark pine survival at the landscape-level.

We estimate the upper live canopy volume for all live, tagged whitebark pine trees as one measure of recruitment potential. While male pollen cones are found in the lower extremities of a tree, female cone production on whitebark pine predominantly occurs in the upper branches. This may be an adaptive trait that evolved with the tree's primary seed disperser, the Clark's nutcracker, whereby cones in the tops of a tree are easier to detect for birds as they fly above the canopy. Trees that are of reproductive age and size, and those that are older, larger, and with healthy, intact canopies have greater potential to produce more cones than smaller individuals with less upper canopy volume. While many factors can influence upper canopy volume (e.g., size/age, environmental damage, fire, competition, and more), blister rust infection can have a significant impact on cone production potential. Blister rust cankers kill cone bearing branches, and cankers located on the bole of an infected tree can cause entire portions of the tree to die by restricting the flow of water and

photosynthates. Top kill is a common result of a bole canker infection due to damage from the fungal growth underneath the bark or from rodent or insect girdling that prevents nutrients from reaching parts of the tree distal to the canker, or from both causes.

Three critical tenets of recruitment are germination, growth, and survival into the reproducing population. Information on successful seed germination under highly variable, natural circumstances is sparse; however, research has demonstrated that newly emerged, five-needle pine seedlings are an indicator of sustained seed caching behavior by Clark's nutcrackers (within 1–2 years; Larson 2009) and that emergent seedlings tend to be ephemeral in nature. Mortality in this size class is considered common and typically the result of environmental factors such as desiccation from sun and heat exposure, smothering from sloughing tree bark, and/or rodent predation (Larson 2009; Pansing et al. 2017). Similarly, there is a dearth of knowledge on the proportion of germinated individuals that survive long enough to establish and grow into the reproducing population. Size is a strong determining factor in survival and the presence of larger trees in an area (i.e., recruiting individuals taller than emergents) is an indication that survival and establishment have been successful in the past (Larson 2009). Our regeneration counts, therefore, help inform recruitment.

To quantify the multiple influencing factors on whitebark pine recruitment, then, we collect a variety of metrics. We track trees as they are added to the tagged tree population (e.g., grew above the > 1.4 m tall threshold). We record the number of live ≤ 1.4 m tall five-needle pine trees within the boundaries of the 10×50 m monitoring transects—small tree counts are generalized to all five-needle pines because whitebark pine cannot readily be distinguished from limber pine (*Pinus flexilis*) without cones or genetic analysis. We note the number and productivity (e.g., number of cones per tree) of cone producing trees. We consider conceptual indicators of recruitment potential by incorporating estimates of upper live canopy volume (where cones are produced), infection status, and infection position (canopy or bole) of both non-reproducing and reproducing trees. Currently data are presented as simple summary statistics. However, the development of more advanced analytical techniques is underway for this critical aspect of whitebark pine health.



Examining a five-needle pine seedling on a plot.

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Results

Results from Time-Step 5 (2020 to 2023) are reported for each monitoring objective, including comparisons with Time-Steps 1 to 4.

Objective 1: Status of Blister Rust

We estimated the presence of blister rust in the GYE whitebark pine population with two methods: the design-based ratio estimator (Lohr 2010) and the Bayesian hierarchical occupancy model (Shanahan et al. 2021). Both results follow the previously observed trend of incremental (albeit not statistically significant) increases in blister rust, with the Bayesian model indicating blister rust prevalence in Time-Step 5 at 47% of whitebark pines infected throughout the GYE ($p = 0.47$; Table 2; Figure 2). This is the highest percentage of trees detected with blister rust infection since the inception of the monitoring program.

Table 2. Estimated white pine blister rust infection proportion, based on a design-based ratio estimator, or prevalence, based on a Bayesian hierarchical occupancy model, for whitebark pine in the Greater Yellowstone Ecosystem. Estimates are reported with standard deviation, along with 95% confidence intervals (design-based estimator) or credible intervals (Bayesian model). Due to refinements in the monitoring data, estimates for Time-Steps 1–4 have been updated from previously reported results.

Estimation Method	Time-Step	Infection Proportion or Prevalence	95% Confidence or Credible Interval
Design-based estimator	T1 (2004–2007)	0.19 (SD = 0.037)	0.13–0.26
	T2 (2008–2011)	0.20 (SD = 0.036)	0.12–0.26
	T3 (2012–2015)	0.17 (SD = 0.040)	0.09–0.25
	T4 (2016–2019)	0.18 (SD = 0.039)	0.10–0.25
	T5 (2020–2023)	0.20 (SD = 0.042)	0.11–0.28
Bayesian hierarchical occupancy model	T1 (2004–2007)	0.41 (SD = 0.040)	0.34–0.49
	T2 (2008–2011)	0.38 (SD = 0.038)	0.31–0.46
	T3 (2012–2015)	0.32 (SD = 0.035)	0.26–0.39
	T4 (2016–2019)	0.40 (SD = 0.041)	0.31–0.48
	T5 (2020–2023)	0.47 (SD = 0.040)	0.39–0.55

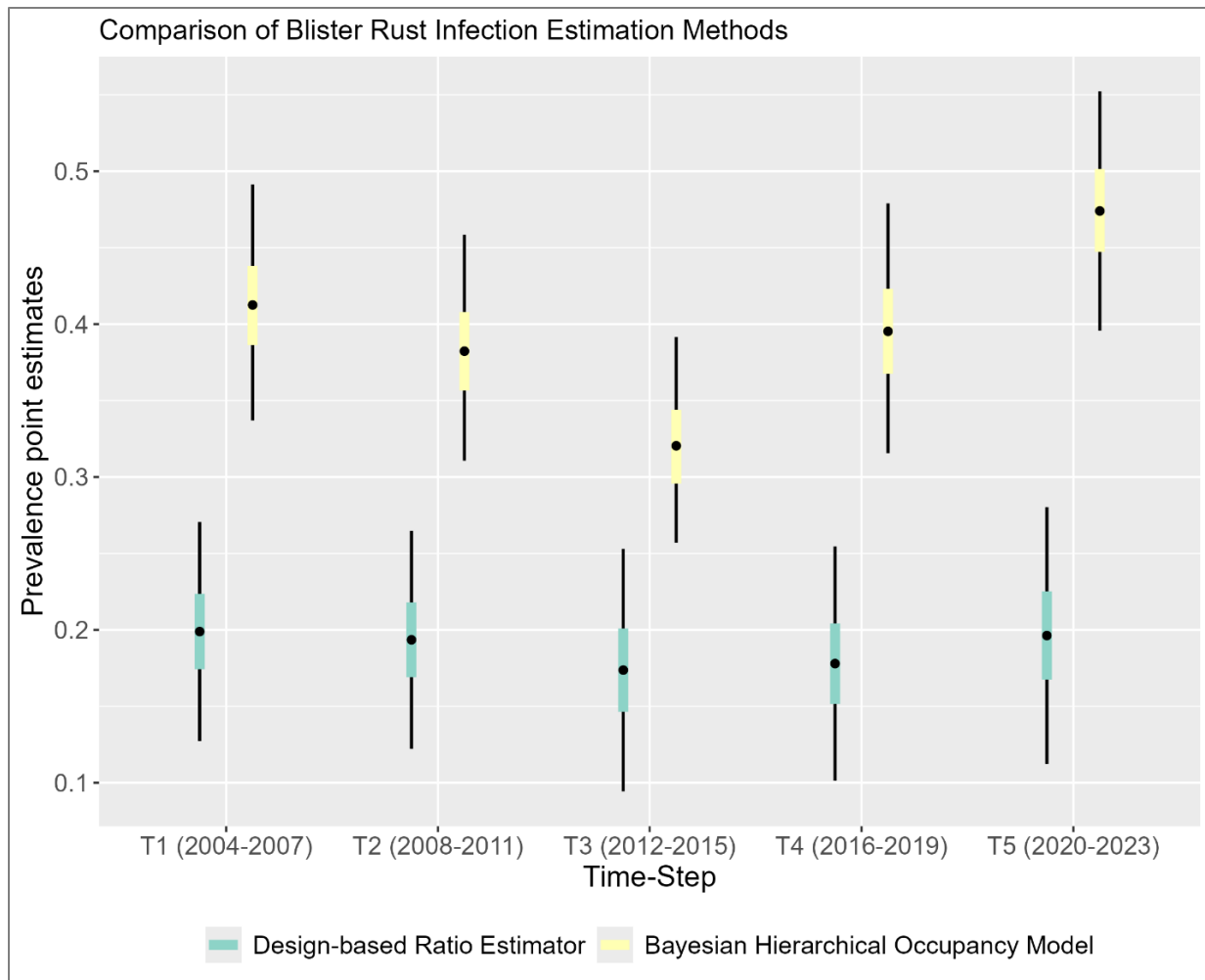


Figure 2. Comparison of estimated white pine blister rust infection prevalence in whitebark pine between 2004 and 2023 using two different approaches. The design-based ratio estimator is the lower series of estimates in green, and the Bayesian hierarchical occupancy model is the upper series of estimates in yellow. This figure was adapted from Shanahan et al. (2021) for estimating white pine blister rust infection prevalence in whitebark pine in the Greater Yellowstone Ecosystem across the previous four time-steps, spanning 2004–2019 and updated to include Time-Step 5 results.

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The Bayesian model accounts for detection error as well as tree- and site-level heterogeneity (i.e., tree size, elevation, transect and stand membership), and as a result, we expect reported results of blister rust prevalence and detection probability to change subtly, even for previous time periods, as the monitoring data are refined, tree sizes are remeasured and updated, observer precedence is assessed, and new observers survey trees. For this reason, Bayesian hierarchical occupancy model results reported herein will differ slightly from previously published estimates (e.g., in Shanahan et al. 2021).

Objective 2: Infection Severity

During Time-Step 5, 1,186 of the 3,744 total living tagged trees (~32%) were observed with blister rust infection (Figure 3). Cankers located only in the canopy (canopy only) occurred in 44% of infected trees (523 trees), while bole cankers were observed in 56% of infected trees (663 trees). Trees recorded with both bole and canopy infections are included in the bole infected category.

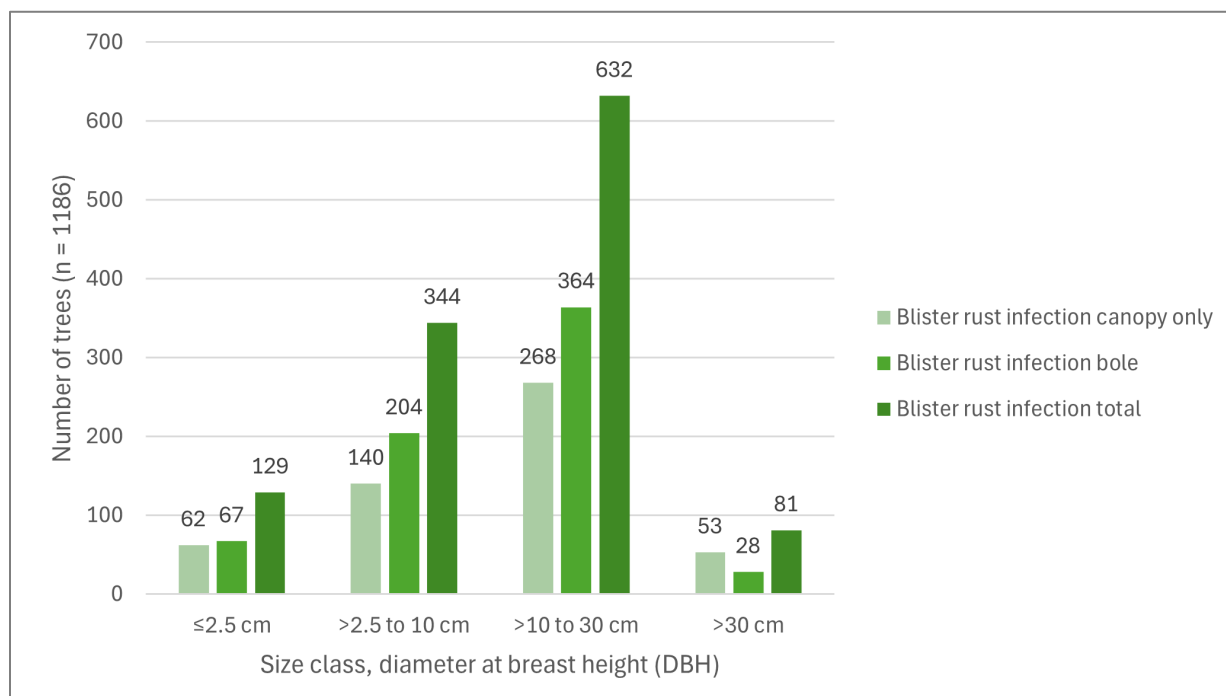


Figure 3. Number of live, tagged whitebark pine trees infected with blister rust during 2020–2023 on Greater Yellowstone Ecosystem monitoring transects, by size class. The “Blister rust infection bole” category includes trees with bole-only and trees with coinciding bole and canopy infections. Of 1186 total infected trees, 523 had infections in the canopy only, and 663 had bole or bole + canopy infections.

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These observations represent an increase in the number of trees recorded with infections between Time-Step 4 (1,001 trees in 2016–2019) and Time-Step 5 (2020–2023). In Time-Step 4, 27% of living trees were recorded with infections, while in Time-Step 5, 32% were documented with infections.

We have continued to record changes in tree infection status and changes in infection location over the past two decades of the monitoring program. Tables 3 and 4 describe if and how infection status and location have changed between Time-Step 1 and Time-Step 5 and between Time-Step 4 and Time-Step 5. In Time-Step 1 (2004–2007), we observed 1,083 trees with blister rust symptoms, of which 446 trees (approx. 41%) were still alive and infected by the end of Time-Step 5 (2020–2023), showing significant mortality of those trees over that time period. In Time-Step 4 (2016–2019), we recorded cankers on 1,001 trees, with 712 trees (approx. 84%) remaining alive and infected through Time-Step 5.

Table 3. Number of live whitebark pine trees changing or not changing their white pine blister rust infection status category over time on Greater Yellowstone Ecosystem monitoring transects. Tree count for each status category is calculated from either Time-Step 1 (2004–2007) or Time-Step 4 (2016–2019) to the most recently completed monitoring time period, Time-Step 5 (2020–2023). The time between sampling a given tree from Time-Step 1 to Time-Step 5 was anywhere from 13 to 19 years, depending on when a tree was originally tagged. Changes between Time-Steps 4 and 5 occurred over a shorter 4-year interval.

Infection Status	Time-Step 1 → Time-Step 5 (<i>n</i> = 2,851)	Time-Step 4 → Time-Step 5 (<i>n</i> = 2,840)
Uninfected → Uninfected	1,647	1,633
Uninfected → Infected	640	370
Infected → Infected ^A	446	712
Infected → Uninfected	118	125

^A Note that the count of trees remaining infected between time-steps is diminished significantly by the number of infected trees that died between time-steps.

Table 4. Number of live whitebark pine trees changing or not changing their white pine blister rust infection location category over time on Greater Yellowstone Ecosystem monitoring transects. Tree count for each location category is calculated from either Time-Step 1 (2004–2007) or Time-Step 4 (2016–2019) to the most recently completed monitoring time period, Time-Step 5 (2020–2023). The time between sampling a given tree from Time-Step 1 to Time-Step 5 was anywhere from 13 to 19 years, depending on when a tree was originally tagged. Changes between Time-Steps 4 and 5 occurred over a shorter 4-year interval.

Infection Location	Time-Step 1 → Time-Step 5 (<i>n</i> = 446)	Time-Step 4 → Time-Step 5 (<i>n</i> = 712)
Canopy only → Canopy only	109	160
Canopy only → Bole	234	93
Bole → Canopy only	17	53
Bole → Bole	86	406

Some whitebark pine trees recorded with blister rust infection are later recorded without any sign of infection. Over the 13 to 19 year interval between Time-Steps 1 and 5 (from year of tagging in Time-Step 1 to year of surveying in Time-Step 5), a total of 118 trees (26%) no longer had observed blister rust cankers. Over the four-year period between Time-Steps 4 and 5, a total of 125 trees (15%) recorded as infected in Time-Step 4 were noted as uninfected by Time-Step 5. We are confident that with our 0.85 (95% CI = 0.81–0.89) detection rate for presence or absence of infection (Wright and Irvine 2017), it is reasonable to expect that many trees initially observed with some level of blister rust infection, then subsequently documented without infection, may no longer have active blister rust cankers.

Based on our monitoring data, trees with bole-only or canopy-only infections seem to transition to uninfected status more frequently than trees that have coinciding bole and canopy infections. For

instance, we observed 111 trees initially infected in Time-Step 1 and 121 trees initially infected in Time-Step 4 with either bole- or canopy-only blister rust cankers that were later documented as uninfected in Time-Step 5. In contrast, for trees with corresponding infections in the bole and canopy, only seven trees in Time-Step 1 and four trees in Time-Step 4 were documented as uninfected in Time-Step 5. This suggests a higher potential for infection pruning, dormancy, or apparent recovery in trees with blister rust cankers when infected in only the canopy or the bole—but not both. Observation error, where an infection was present but not detected at a subsequent survey, could be influencing these results to some degree. While further research is needed to elucidate the mechanisms underlying this phenomenon, long-term monitoring can help detect these and similar transitional infection changes, alerting managers to the location of potential blister rust-resistant individuals outside of what is currently known.

Objective 3: Whitebark Pine Mortality



Dead whitebark pine trees on the Bridger-Teton National Forest in 2023.

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In Time-Step 5, we observed an additional 226 dead tagged trees since Time-Step 4. We estimate the proportion of monitored whitebark pine trees > 1.4 m tall that died during Time-Step 5 at $0.048 (\pm 0.012)$. Of the Time-Step 5 dead trees, only eight had signs of mountain pine beetle

infestation and all were ≥ 27.5 cm diameter at breast height (DBH). From 2008, the year of the first revisits to tagged trees, to the end of surveys in 2023, a total of 1,944 tagged trees have died. This equates to a cumulative mortality of 0.29 (± 0.049) since monitoring began in 2004 (Table 5). Our ongoing assessments of tree mortality show a continued stabilization after peak mortality occurred during a mountain pine beetle epidemic in Time-Step 2 (Figure 4).

Table 5. Estimates of cumulative whitebark pine mortality within the Greater Yellowstone Ecosystem using the design-based ratio estimator. Estimates are reported with standard deviation, along with 95% confidence intervals. Cumulative mortality is defined as the estimated proportion of trees experiencing mortality from 2004 to the conclusion of the most recent time period in 2023. The establishment period during Time-Step 1 (2004–2007) is not reported because this time period consisted exclusively of initial surveys and tagging all live trees on the transects, with no surveying for dead trees.

Time-Step	Cumulative Mortality Estimate	95% Confidence or Credible Interval
T2 (2008–2011)	0.21 (SD = 0.042)	0.12–0.29
T3 (2012–2015)	0.24 (SD = 0.044)	0.16–0.33
T4 (2016–2019)	0.27 (SD = 0.050)	0.17–0.37
T5 (2020–2023)	0.29 (SD = 0.049)	0.19–0.38

Seventeen monitored transects have had trees affected by wildfire since 2004. Fourteen trees observed in Time-Step 5 had evidence of fire effects (e.g., bole charring or fire scars); 13 of these trees were dead. It is important to note that many dead trees recorded with fire effects also had signs of mountain pine beetle infestation and/or blister rust infection.

Although the mountain pine beetle epidemic that began during the early 2000s subsided in the GYE starting around 2011 (Shanahan et al. 2016), our long-term monitoring continues to document periodic infestations in the tagged tree population. In Time-Step 5, only one live, tagged tree was documented with signs of mountain pine beetle attack. However, over recent years, monitoring program field crews, along with forest managers from other agencies, have observed a qualitative increase in mountain pine beetle activity throughout the study area. Active attacks and recent mortality were encountered more frequently in locations on the Bridger-Teton, Shoshone, and Caribou-Targhee National Forests, and within Grand Teton National Park (Bockino et al. 2023). Climatic conditions favoring mountain pine beetle population growth, including an increase in the number of growing degree days, as well as increased annual water deficits that further contribute to tree stress have been building since 1980 (Figure 5; Carroll et al. 2004). As such, conditions in the GYE may be trending toward another epidemic-level event, if infestations continue to escalate in the remaining stands of larger diameter whitebark pine trees (e.g., > 10 cm DBH; Bockino et al. 2023).

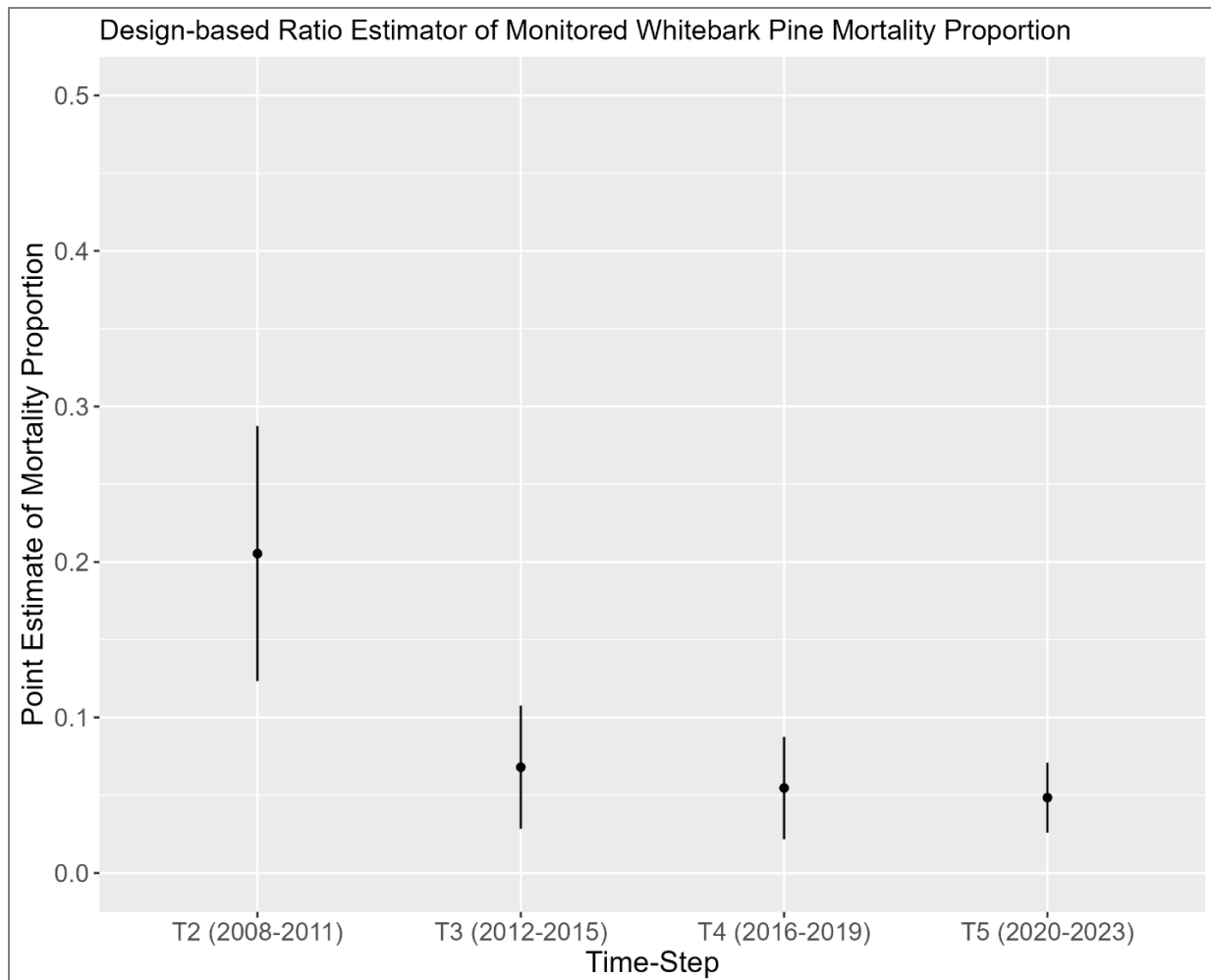


Figure 4. Whitebark pine tree mortality occurring within monitored stands in the Greater Yellowstone Ecosystem in each given time-step, not cumulative rates over time. Time-Step 1 (2004–2007) is not reported because this time period consisted of initial surveying and tagging live trees, with no surveying for dead trees.

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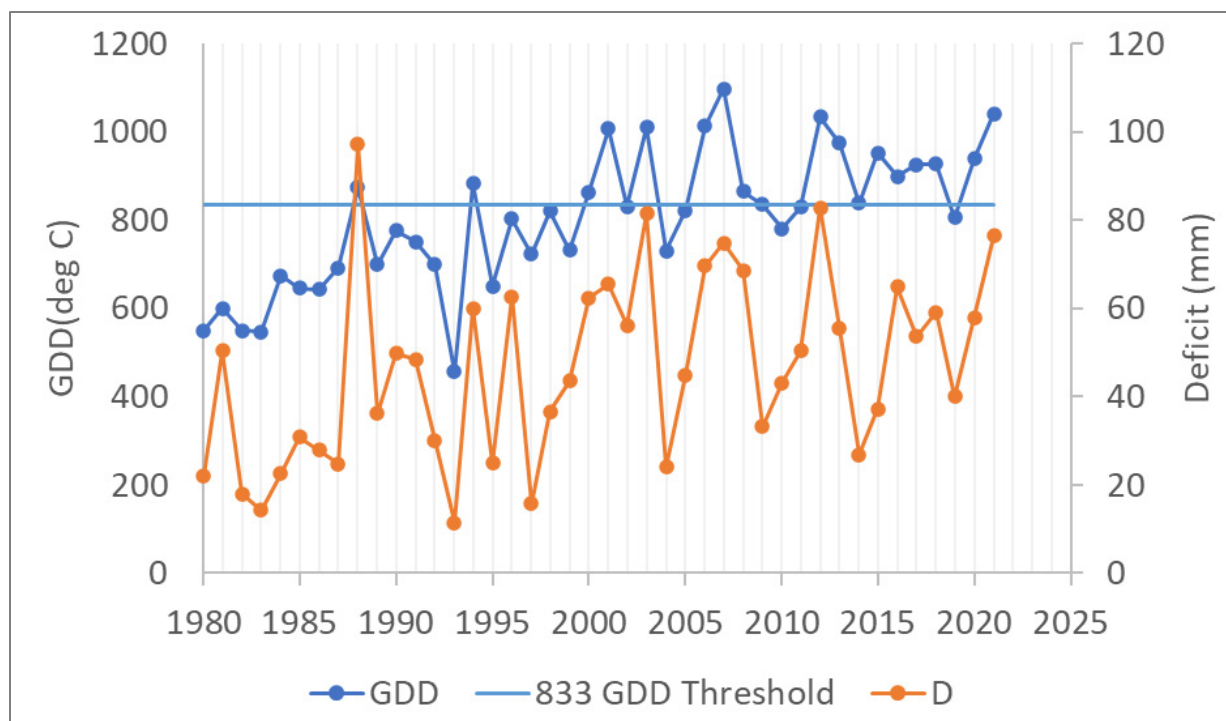


Figure 5. Annual cumulative growing degree days (GDD; degrees Celsius) and annual moisture deficit (D; mm) between 1980 and 2021. This time period spans extensive whitebark pine mortality in the early 2000s, peaking in 2009, as well as increased mortality observed more recently from 2019 to 2022. These changing environmental conditions can facilitate increased mountain pine beetle populations, potentially leading to future outbreak scenarios. The blue horizontal line represents the 833 cumulative growing degree day threshold for univoltine (one generation per year) mountain pine beetle reproduction, after Carroll et al. (2004).

NPS / D. THOMA

Objective 4: Whitebark Pine Recruitment



Emergent five-needle pine seedling.

NPS / E. SHANAHAN

As part of our monitoring effort, we measured recruitment through a variety of metrics, including newly tagged trees, regeneration in the understory, cone-producing trees, and upper live canopy volume.

Newly Tagged Trees

After initial plot establishment and tree tagging from 2004 to 2007, an additional 965 trees passed 1.4 m in height and were thus incorporated into the monitored tree cohort from 2008 to 2023. This is an average of 60 new trees tagged per year and includes 280 trees added in Time-Step 5 (Table 6). These latest additions follow an increasing trend in the number of new trees (> 1.4 m tall) entering monitoring, with Time-Step 5 having the second-highest number of new trees tagged since Time-Step 2 ($n = 286$; Table 7).

Table 6. Five-needle pine trees that reached the > 1.4 m tall threshold between 2020 and 2023 on Greater Yellowstone Ecosystem transects. These trees were tagged and added to the monitored tree population.

Year	New Trees Added in Time-Step 5			
	Panel 1	Panel 2	Panel 3	Panel 4
2020	56	–	–	–
2021	20	53	–	–
2022	–	–	54	–
2023	–	–	8	89

Table 7. Five-needle pine trees that reached the > 1.4 m tall threshold and subsequently entered the monitored population on Greater Yellowstone Ecosystem transects, by Time-Step. From 2008 to 2023, 965 trees were newly tagged after passing the height threshold.

Time-Step	New Trees Added
T1 (2004–2007)	N/A
T2 (2008–2011)	286
T3 (2012–2015)	159
T4 (2016–2019)	240
T5 (2020–2023)	280

Regeneration: Five-Needle Pine Understory

The number of understory trees (those < 1.4 m in height and thus not tagged for monitoring) are counted in each belt transect during survey visits. In Time-Step 5, the average density of understory trees was 58 trees per 500 m² over 172 transects. Understory trees on four transects were not counted due to the presence of snow covering all or a portion of the 10 × 50 m area. Counts per transect ranged from a minimum of 0 to a maximum of 480 understory trees. The average density of trees (58 whitebark pine per 500 m²) represents a minor increase over a previously stable density of approximately 52 trees per 500 m² from 2008 to 2019.

The total count of understory trees observed with blister rust in Time-Step 5 was 188 trees, or 2% of the total count of all understory trees (Table 8). While this number may imply a substantial increase in understory infection rates when compared to the 40 trees (< 1%) observed with blister rust in Time-Step 4, the number of blister rust-infected understory trees has been highly variable across all five time periods since monitoring began in 2004 (e.g., Time-Step 1 = 107 trees; Time-Step 2 = 102 trees; Time-Step 3 = 55 trees). Visible signs of blister rust, such as needle spotting, on seedlings and smaller trees is difficult, time-consuming, and not as accurate compared to identifying infection on larger and older cohorts. Nonetheless, our long-term monitoring program will continue to advance our understanding of blister rust prevalence in the understory and thus the potential for these trees to grow into mature, cone-bearing members of the population.

Table 8. Blister rust infection status of understory five-needle pine trees (≤ 1.4 m tall) in Time-Step 5 (2020–2023) for all monitoring transects in the Greater Yellowstone Ecosystem, by panel.

Panel	Small Trees ≤ 1.4 m Tall ($n = 9918$)			
	Blister Rust Absent	Blister Rust Present	Infection Status Unknown	Total
1	2,726	110	11	2,847
2	1,480	26	49	1,555
3	2,906	21	14	2,941
4	2,543	31	1	2,575

Due to difficulties differentiating early blister rust infection and other damaging agents in a field setting, we are likely underestimating blister rust prevalence within five-needle pine understory trees. One of the initial signs of blister rust infection is yellow/brown spotting on needles. However, this condition can also be caused by other injuries or conditions such as needle cast spotting from a variety of fungi (*Bifusella linearis*, *Bifusella saccate*, *Lophodermella arcuate*, *Lophodermella nitens*; Funk 1985; Figures 6, 7, and 8) or environmental damage, such as heat exposure and lack of adequate soil moisture.

Older, and often larger understory trees that have been infected longer tend to have more obvious signs of blister rust, such as visible aecia spores (Figure 9) or an array of the five indicators of infection (flagging, chewing, swelling, roughened bark, oozing sap).



Figure 6. Spotting on the needles of a young limber pine tree from blister rust. This was the result of a controlled infection in a greenhouse setting.
USFS / A. SCHOETTLE



Figure 7. Blister rust damage on a whitebark pine, possibly due to drought.
MONTANA STATE UNIVERSITY / M. LAVIN



Figure 8. Needle cast spotting (*Bifusella saccate*) on limber pine.
USFS / STALEY



Figure 9. Fruiting body of aecia spores caused by blister rust on a < 1.4 m tall understory five-needle pine tree. The sweet-tasting spores attract rodents and insects, which feed on cankers, often girdling the affected area.

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Cone-Producing Trees

Since monitoring began in 2004, we have observed 1,499 whitebark pine trees with cones, 94% of which had a diameter at breast height (DBH) > 10 cm. As of 2023, 512 of these reproducing trees (34%) have died. In Time-Step 5, 532 of 3,744 trees (14.2%) were observed with cones, which is consistent with the approximately 13% observed cone-bearing trees in Time-Step 4. The overwhelming majority (approximately 80%) of these trees had a DBH of > 10 to ≤ 30 cm (Table 9). For the 118 trees > 30 cm DBH surveyed in Time-Step 5, over 60% were observed with cones. Cone-producing trees in Time-Step 5 were most often observed with one to five cones ($n = 269$ trees) or cone scars ($n = 125$ trees), whereas only ~26% of cone-producing trees were observed with six to ten cones (13.2%) or more than ten cones (12.8%). Due to the nature of the revisit schedule, where trees are only observed once every four years, trees may be cone-producing individuals but not observed with cones at the time of each survey visit, which may lead to an underestimation of reproductive trees in the Greater Yellowstone Ecosystem.

Table 9. Size class distribution of whitebark pine trees documented as reproducing in Time-Step 5 (2020–2023) on monitoring transects in the Greater Yellowstone Ecosystem transects, by panel.

Size Class (Diameter at Breast Height)	Number of Reproducing Whitebark Pine Trees by Size Class in Time-Step 5 (<i>n</i> = 532)				
	Panel 1	Panel 2	Panel 3	Panel 4	Total
≤ 2.5 cm	0	0	2	0	2
> 2.5 to ≤ 10 cm	6	5	7	11	29
> 10 to ≤ 30 cm	79	107	162	80	428
> 30 cm	27	11	20	15	73

Reproductive trees, typically those with a DBH > 10 cm, have previously experienced heavy mountain pine beetle infestations and subsequent mortality in and around Time-Step 2 (2008–2011). Since then, the number of cone-producing trees with signs of active mountain pine beetle infestation has continued to drop, from nine trees in Time-Step 4 to only two trees in Time-Step 5. However, the proportion of cone-producing whitebark pine trees with blister rust infections has remained steady, with nearly half of cone-producing trees observed exhibiting symptoms of active blister rust infections in Time-Step 5 (*n* = 251 trees; 47%).

Recruitment Potential: Upper Live Canopy Volume

In Time-Step 5, 3,348 surveyed whitebark pine trees had a live upper canopy volume of at least 1% (Table 10). Of these trees with live upper canopy, 75% had live canopy volumes > 75%. In contrast, 390 trees (approximately 10%) had no remaining live canopy volume, and of these, 267 trees (approximately 68%) were infected with blister rust. Trees with diminishing or no live canopy volume, which can be caused by bole cankers among other reasons, are likely unable to successfully produce cones (Figure 10).

Table 10. Percentage of upper canopy volume that is alive for living whitebark pine trees monitored on Greater Yellowstone Ecosystem transects during Time-Step 5 (2020–2023), by size class. Trees with 0% upper live canopy volume will not produce cones, while those with < 25% upper live canopy volume are unlikely to successfully reproduce.

Upper Live Canopy Volume	Number of Trees by Size Class (Diameter at Breast Height, DBH)					Total Number of Trees
	≤ 2.5 cm	> 2.5 to 10 cm	> 10 to 30 cm	> 30 cm	No DBH Data	
0%	61	164	160	5	0	390
> 0 to 25%	50	62	53	5	1	171
> 25 to 50%	58	66	68	6	0	198
> 50 to 75%	151	146	137	24	0	458
> 75 to 100%	933	723	792	70	3	2,521



Figure 10. Whitebark pine tree with a significant bole canker. The tree has been completely girdled by rodents feeding on the aecia spores and sweet tasting sap. While trees can live for decades with blister rust infection, once the bole of the tree has been girdled to this extent, the upper canopy and portion of the bole distal to the canker will eventually die within a few years.

NPS / E. SHANAHAN

Live, Tagged Tree Size Distributions over Time

After the mountain pine beetle epidemic in Time-Step 2, whitebark pine in the Greater Yellowstone Ecosystem experienced a shift to smaller-sized trees (Shanahan et al. 2016). The size distribution observed in Time-Step 5 reinforces this trend, with further declines observed in larger size classes (Figure 11). This overall shift to smaller-sized trees occurred due to high mortality in the larger size classes coupled with a steady increase in small trees reaching 1.4 m tall, boosting the count of tagged trees with a DBH of ≤ 2.5 cm.



Figure 11. Tree size class distribution for live whitebark pines in the Greater Yellowstone Ecosystem documented through the Interagency Whitebark Pine Monitoring Program from 2004 to 2023.

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The Future of Whitebark Pine

Mountainous regions provide many vital ecosystem services. For instance, they store critical winter precipitation, support biodiversity, provide refugia during warming periods, and offer humans unique recreational opportunities. Conditions in these regions serve as fundamental indicators of environmental change over time (Oldfather et al. 2025; Elsen et al. 2020). Safeguarding these essential ecological functions depends on maintaining the integrity of high-elevation ecosystems.

Whitebark pine is an integral component of alpine and subalpine environments in the Greater Yellowstone Ecosystem. The January 2023 listing of this species under the Endangered Species Act recognizes its widely understood importance in these environments (Federal Register 2022). In addition to whitebark pine's value to wildlife and promoting early forest succession, by far one of its most critical roles is tied to water. These hardy subalpine trees provide surface area to promote snow drift capture and prolong snow retention in scattered tree islands. As winter precipitation and snowpack continue to decline in mountainous regions across western North America (Mote et al. 2018; Pederson et al. 2011), our ability to manage water resources grows increasingly uncertain (Musselman et al. 2021). Therefore, the need to protect, promote, and restore whitebark pine intensifies as disturbance events (e.g., mountain pine beetle outbreaks and blister rust) expand across the landscape (Pansing et al. 2020; Cardinal et al. 2022). Long-term monitoring addresses this need by documenting changing population trends in response to ongoing and episodic disruptions that can lead to unintended shifts in ecosystem stability. Monitoring also helps uncover new threats to whitebark pine communities, offering valuable insights to land and resource managers.

For more than two decades, the long-term Interagency Whitebark Pine Program has rigorously quantified vital demographic rates critical to understanding the long-term population viability of whitebark pine within the Greater Yellowstone Ecosystem and across its broader range. With this information in hand, resource managers can make informed decisions on how to most effectively allocate limited resources—such as time, funding, personnel, and planting stock—to better safeguard vulnerable whitebark pine populations into the future.

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National Park Service
U.S. Department of the Interior



Science Report NPS/SR—2025/328
<https://doi.org/10.36967/2313989>

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1201 Oakridge Drive, Suite 150
Fort Collins, CO 80525