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Variable Demographic Patterns Interact With Disturbance and Climate to Shape Limber Pine Population Viability

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ABSTRACT

Limber pine (*Pinus flexilis*) is an important five-needle pine that has received far less research attention than its close taxonomic relative, whitebark pine (*Pinus albicaulis*). Recent, severe, and widespread decline of whitebark pine portends a similar fate for limber pine. While mountain pine beetle (*Dendroctonus ponderosae*) outbreaks are likely responsible for the vast majority of limber pine mortality, their possible role as disturbance agents on demographic processes in these forests is unknown. In this study, we examine the long-term persistence of a limber pine woodland located in the Greater Yellowstone Ecosystem. Dendroecological methods were employed to reconstruct establishment dates, death dates, cause of death, and the driver of growth variability for 81 limber pines. Over the past ~800 years, recruitment was characterized as episodic, with peaks occurring in the 13th and 17th centuries consistent with multi-decadal pluvial periods. Over the past two centuries, mortality was much more continuous, but with pulses centered on the 1880s, 1960s, and early 2000s. Mortality of over half the limber pine since ~1860 can be directly attributed to the mountain pine beetle. Mortality peaked during the 1960s, but was found in trees up to 800+ years old. Variability in limber pine growth was strongly and consistently driven by spring moisture availability. The balance between continuous and episodic demographic processes in the face of mounting disturbance pressure over time is likely to further bottleneck the population, potentially decreasing limber pine population viability.

Keywords: climate change adaptation, generalist, Greater Yellowstone Ecosystem, limber pine, mountain pine beetle, *Pinus flexilis*, population dynamics, surrogate species

INTRODUCTION

Limber pine (*Pinus flexilis*) exhibits such a wide ecological amplitude that it could be considered a poster-child for generalist species. It has a huge geographic range, and unlike any of the other five-needle pines it occurs across the elevation gradient of forests in the interior western United States in proportion with its common associates (Windmuller-Campi-

one and Long 2016). Limber pine's close taxonomic relative, whitebark pine (*Pinus albicaulis*), is commonly cited as a species in peril (USFWS 2020), largely due to combined impacts from the native mountain pine beetle (*Dendroctonus ponderosae*), the invasive white pine blister rust (*Cronartium ribicola*), and compounding influences of climate change (Resler and Tomback 2008; Rochner et al. 2021). While broadly more generalist than whitebark pine, limber pine is not immune to

these threats. Indeed, the species is highly vulnerable to both the mountain pine beetle and white pine blister rust. Recent work has indicated that range-wide mortality in limber pine is approaching similar levels as was seen in whitebark pine two decades ago due to mountain pine beetle (Goeking and Windmuller-Campione 2021). Although limber pine plays a similar functional role as whitebark pine in high-elevation ecosystems, it has received much less research interest (Means 2011; Schoettle et al. 2019). To address this, we examine patterns of establishment, growth, and mortality in a limber pine woodland.

The primary dispersal mechanism for limber pine is seed collectors (Hutchins and Lanner 1982), specifically the Clark's nutcracker (*Nucifraga columbiana*), which likely play a large role in the massive ecological amplitude (Lanner and Vander Wall 1980). However, the establishment and survival of cached seeds depend on the autecological characteristics of limber pine. While limber pine is intolerant of shade, its tolerance to other environmental stressors is high (Steele 1990), such that seed caches in the open areas, such as recently dis-

turbed sites, are more likely to establish and recruit to the overstory. This may be why limber pine is often cited as a post-fire invader; however, fire does not guarantee establishment (Dawe et al. 2020). Limber pine can also be incredibly long-lived: It is not uncommon to find lower elevation trees in excess of 700 years, and higher elevation trees in excess of 1,000 years old (MacDonald and Case 2005). Indeed, some remarkable limber pine (live and dead) exist in the west, preserved by a combination of their longevity (high resin content, exposed sites), and also their remoteness.

To better understand the potential for limber pine population decline or persistence we sampled a putative limber pine “ghost woodland” within the Greater Yellowstone Ecosystem that had what appeared to be substantial levels of mortality (figure 1). We used dendroecological techniques to reconstruct establishment dates, mortality dates, and drivers of growth variability. While this limber pine population seems to have been threatened by the recent mountain pine beetle outbreak that began in the early 2000s, not unlike that seen in whitebark pine, perhaps this kind of disturbance is a

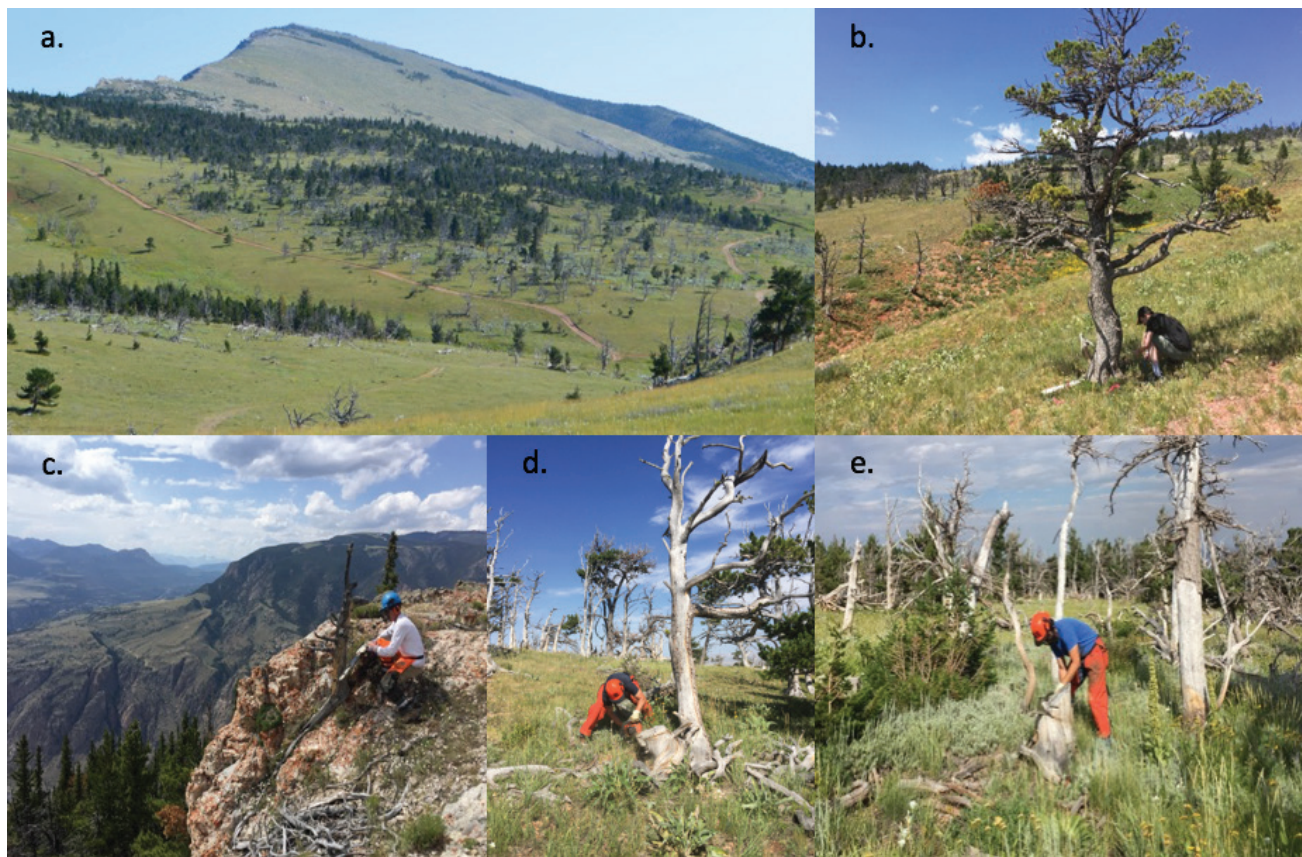


Figure 1. Pictures of the Bald Ridge study area: (a) view of the limber pine woodland and ridge extent, (b) example of live limber pine, (c) western edge of the study area, (d) & (e) sampling dead limber pine.

normal part of population dynamics. To address this possibility, we ask the following questions: 1) Were dates of mortality continuous or episodic, and was the recent mountain pine beetle outbreak the primary cause? 2) Was reconstructed recruitment continuous or episodic? 3) What climatic factors influenced growth variability, were they temporally stable, and were establishment or mortality patterns driven by these climatic factors?

METHODS

Study Area and Sample Selection

Bald Ridge is a gently east-sloping fault block with a relatively open canopy woodland of limber pine (44.789°N, 109.338°W, 2330 m elevation), in the Shoshone National Forest near Cody, WY (figure 1). Substantial mortality was apparent at this site, putatively caused by the recent mountain pine beetle outbreak. This site is south-facing with minimal soil development. To capture the influence of climate on tree growth, we sought trees from this site that were greater than 10 cm in diameter at breast height and appeared to be, or have been, open grown, such that we would minimize the effects of possible density-dependent competition on growth.

Tree-Ring Data Collection and Chronology Development

We collected two cores per tree, roughly perpendicular to each other at or near ground level but sometimes resorted to a higher point on the stem (up to 60 cm) because of root buttressing, branches, or other obstructions. We also recorded tree status (live or dead), coring height, diameter at coring height, and GPS location. In addition to cores, we also collected full cross-sections near the root collar of snags and sub-fossil wood. We mounted, sanded, and dotted the samples using standard procedures (Speer 2010). While dotting the samples, we used visual crossdating methods, which allowed for the identification of potential dating errors and missing rings prior to measurement and statistical crossdating. We measured tree-ring widths with a Velmex Unislide Measure J2X system with 0.001 mm precision. To verify our crossdating we used COFECHA (Holmes 1983). We verified the annual resolution of every tree reported in our results through crossdating. To develop a site chronology for climate response we detrended each series using a cubic smoothing spline, averaging with a robust mean, and applying an autoregressive model in *dplR* (Bunn 2008). We used the residual chronology in all climate-growth analyses.

Establishment Dates and Death Dates

We were confident we could estimate establishment dates for many of the limber pine samples despite a tendency for heart rot in the species. To estimate the number of rings to the pith for all samples that did not reach tree center, we used either the Duncan (1989) or the Applequist (1958) methods for cores and cross-sections, respectively. We chose the best estimates (i.e., oldest and most confident pith date) made from all measured series for each sample (two per tree in most cases) and binned these into bi-decadal groups for graphical analysis.

We recorded dates of death for any limber pine in which we had strong evidence for the waney edge, that is, that the outside ring was the last year of growth, indicated by either smooth outer wood or the presence of bark (figure 2). We noted how confident we were in the outside ring being indicative of the date of death. We chose the best estimate (i.e., latest, and most confident) made from all measured series for a given tree (two per tree in most cases). We also noted the presence or absence of blue-stain fungi in the entirety of the present sapwood of the dead samples, when sapwood was present, as a proxy for indicating that the tree was putatively killed by the mountain pine beetle.

Climate Growth Relationships

We evaluated climate-growth relationships between the residual chronology and monthly precipitation and maximum monthly temperature. Climate data extracted from the Partial Regression on Independent Slopes Model dataset (PRISM 2018) was used in the R package *treeclim* (Zang and Biondi 2015). We evaluated monthly and seasonal (3, 6, and 12-month) summed (precipitation) or averaged (temperature) responses under the assumption that precipitation was the primary driver, and temperature the secondary, based on substantial preliminary testing (Meko et al. 2011). We then tested for temporal stability in response to the primary growth driver using an evolving correlation analysis that started with a 30-yr moving window that increased by one year in each iteration with significance at the $P < 0.05$ level based on bootstrapped confidence bounds (Biondi 1997).

RESULTS

We crossdated and measured 120 tree-ring series from 63 trees sampled on Bald Ridge to build an initial limber pine chronology. The inter-series correlation was 0.561, and

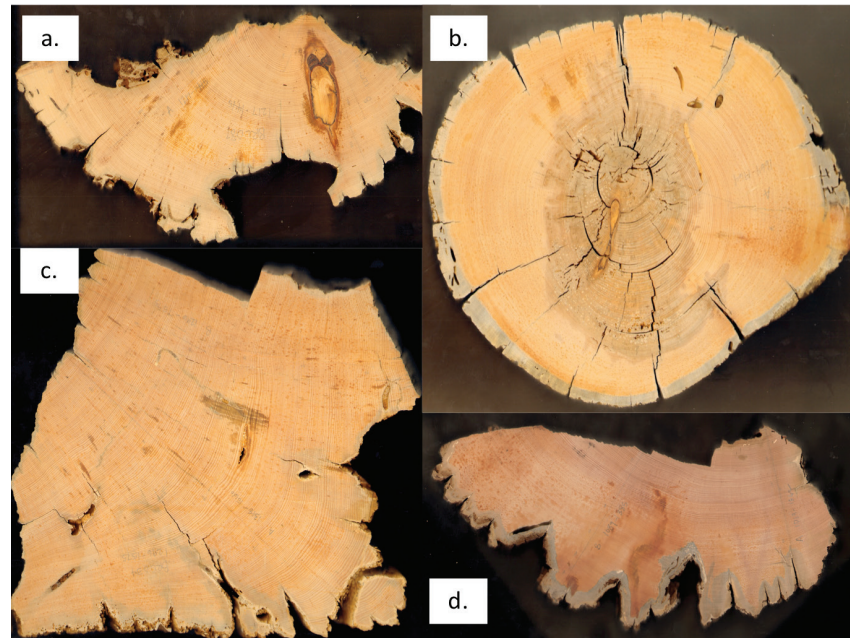


Figure 2. Examples of limber pine cross-sections. (a) Cross-section without indication of outside ring or sapwood, but inside curvature sufficient for the determination of an establishment date. (b) More recently killed tree with a wavy edge, blue-stain in the sapwood, and a pith. (c) Very old cross-section with no outside ring, no sapwood, and no way to determine establishment date. (d) Very old cross-section with no outside edge, weathering that could be mistaken for sapwood, and no way to determine establishment date.

average standard deviation was 0.285. Mean length for all series was 307 years with a total of 36,901 rings measured. We used this chronology to crossdate 18 additional trees, for 81 trees in total. Of those, 30 were alive, and 51 were dead. Fifty-three percent of the trees contained the pith ($n = 43$, five live and 38 dead trees). Twenty-four trees without the pith had curvature sufficient to estimate the number of rings to the pith. Of the dead trees with evidence of the wavy edge, we confirmed date of death for 18 limber pines. The

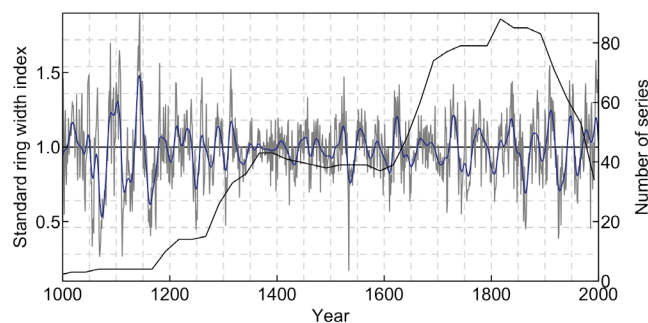


Figure 3. Standard limber pine chronology for Bald Ridge plotted to accentuate year-to-year and multi-decadal variability in ring width. Dark blue line is a 20-year cubic smoothing spline. Secondary axis indicates the number of tree-ring series in the chronology.

full limber pine chronology for Bald Ridge covered the period (965–2018, figure 3).

We obtained confirmed mortality dates for only 2% ($n = 18$) of the total limber pine sampled. A large majority of the dead limber pine with confirmed death dates (77%; 14 of 18 trees) died from mountain pine beetle attack, presumed by the presence of blue-stain fungi in the sapwood. While the mountain pine beetle-caused mortality peaked in the 1960s, its presence in the sapwood of limber pine across the site at Bald Ridge suggested it has been a disturbance agent in this system continuously for the last millennium (figures 4 and 5).

We estimated establishment dates from 81% ($n = 66$) of the limber pine sampled. The average estimated number of rings to the pith was 22.3. The oldest establishment date was 965, and the most recent occurred in the 1940s (figure 5). The oldest live tree establishment date was 1648. Over the past approximate millennium, establishment of limber pine at Bald Ridge was characterized by pulsed recruitment primarily in the 1300s, and from the 1600s through the mid-1700s (figure 5). Of the trees used to estimate establishment dates, 28 (42%) had evidence of blue-stain in the sapwood. None of the live trees had blue-stain in their sapwood.

Variability in limber pine ring width at Bald Ridge was positively correlated with precipitation over the historical in-

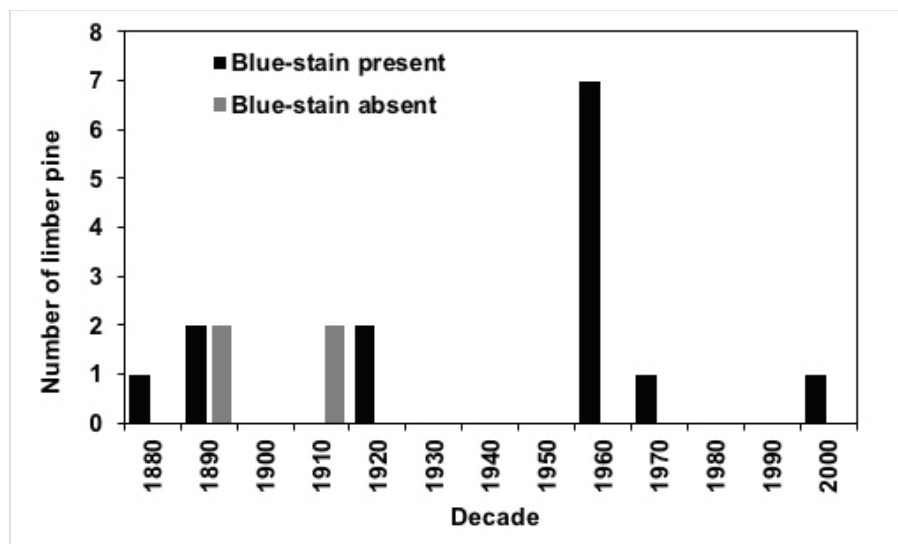


Figure 4. Number of limber pine by decadal bin that have a confirmed date of death. Black-filled bars indicate that blue-stain was found in the sapwood of the sample, while gray-filled bars indicate no blue-stain. Gaps indicate no observations from that time period.

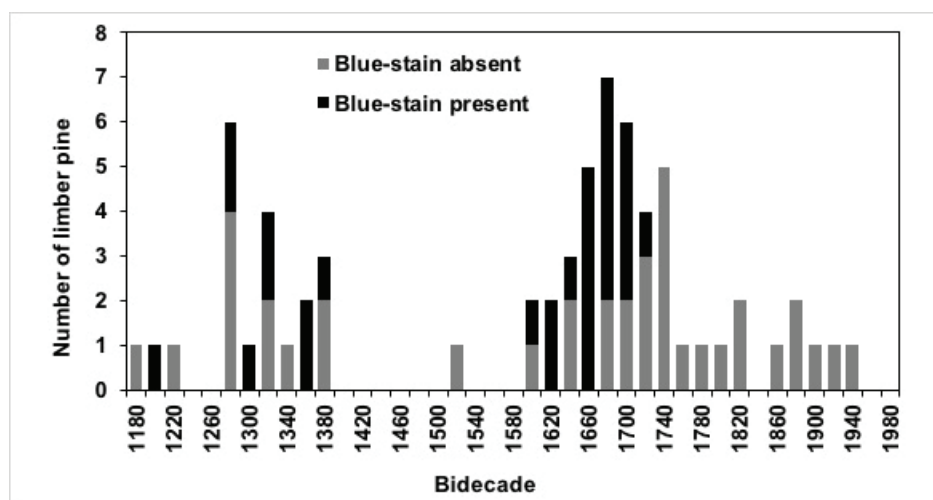


Figure 5. Number of limber pine established by bidecadal bin at Bald Ridge. Black-filled bars indicate that blue-stain was found in the sapwood of the sample, while gray-filled bars indicate no blue-stain or no sapwood. Gaps indicate no observations from that time period.

strumental record (1896-2017). After variability in growth due to precipitation was accounted for, temperature explained no further variation (figure 6). Month-by-month limber pine growth could be explained by growing season precipitation during May, and cool season January precipitation (i.e., snowpack). Seasonal accumulation of precipitation explained more variability in limber pine growth, specifically the water-year ending in May of the growing season (figure 6). Sim-

ilar to monthly results, the strongest relationships to seasonal precipitation peaks occurred in the cool season (i.e., January) and growing season spring (i.e., May; figure 7). The positive relationship between limber pine growth and monthly May precipitation was statistically significant ($P < 0.05$) and temporally stable over the historical record of climate (figure 7). However, growth relationships with cool-season precipitation were not temporally stable over the same period; we identi-

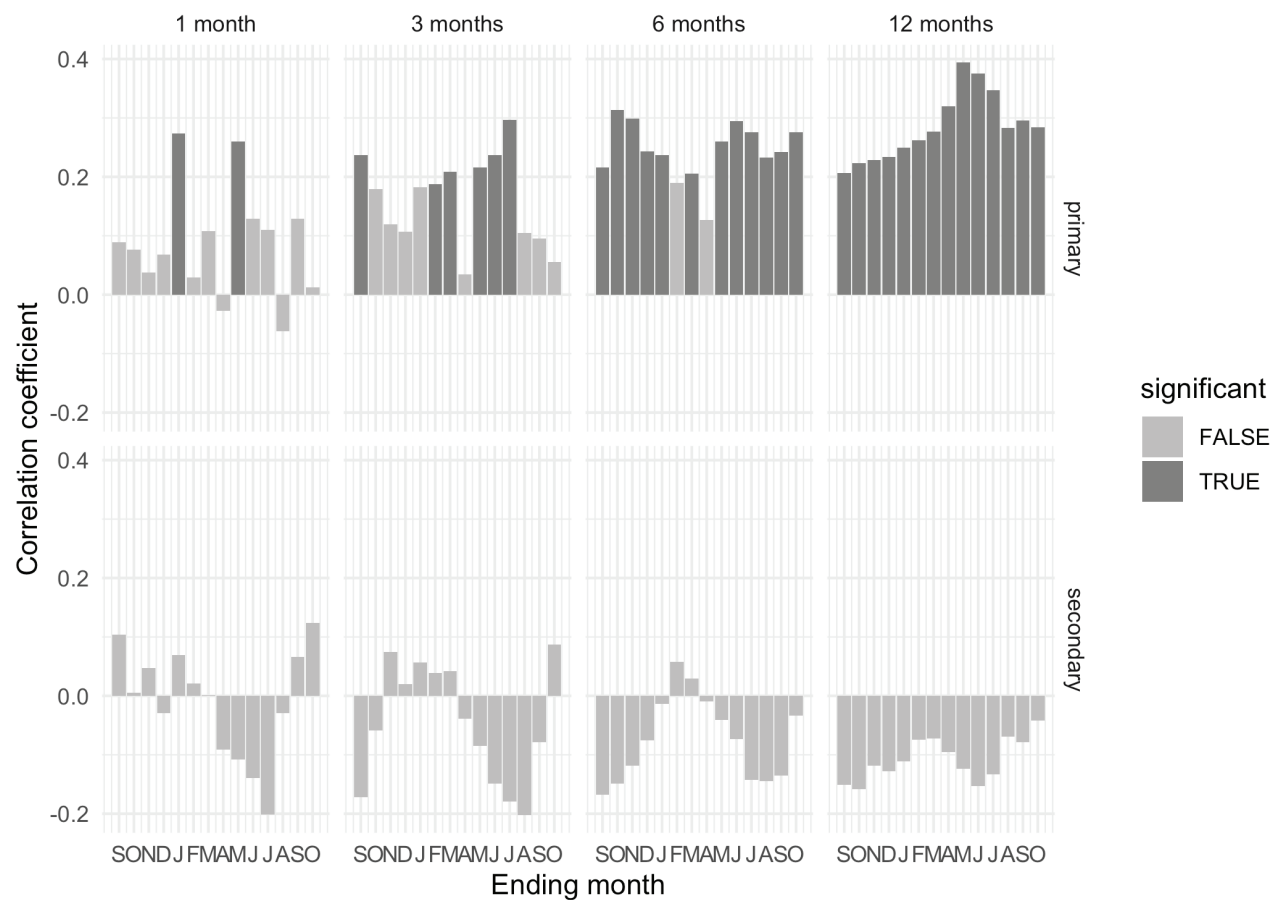


Figure 6. Monthly and seasonal (3, 6, and 12-month) correlations between the Bald Ridge residual chronology and precipitation as the primary variable (top panels), and maximum temperature data as the secondary variable (bottom panels). Significance at the 95% confidence level is indicated by shaded bars.

fied a shift from a negative cool-season response (previous November and December) to a positive cool-season response (current January) during the mid-20th century (figure 7).

DISCUSSION

For at least the last millennium a limber pine woodland has occupied the Bald Ridge site. Over this period episodic establishment, coupled with continual mortality and moisture-driven growth, has resulted in relatively continuous population dynamics. Although our data were not sufficient to ascertain whether the mountain pine beetle-caused mortality had increased in recent decades, it is clear mountain pine beetle has been killing limber pine on Bald Ridge for as long as we have been able to infer based on the presence of blue-stain fungi. One possibility for the lack of recent mountain pine

beetle-killed limber pine was our sampling approach which could have been inadvertently focused on older specimens (i.e., trees larger than 10 cm in diameter at breast height), and therefore created a bias against recently dead trees. Regardless, background mortality rates were very low, averaging 1.6% per decade over the relatively short period of reconstructed death dates (~1880-2000). The visible presence of standing dead and down limber pine in this “ghost woodland,” begs the question, was the observed mortality a normal part of disturbance processes in limber pine systems, or does it portend a more challenging future for the species?

By far the biggest contributor to the observed mortality at Bald Ridge has been the mountain pine beetle, but this disturbance agent has been around for millennia (Brunelle et al. 2008) at endemic and epidemic levels. However, outbreaking mountain pine beetle populations might be increasingly

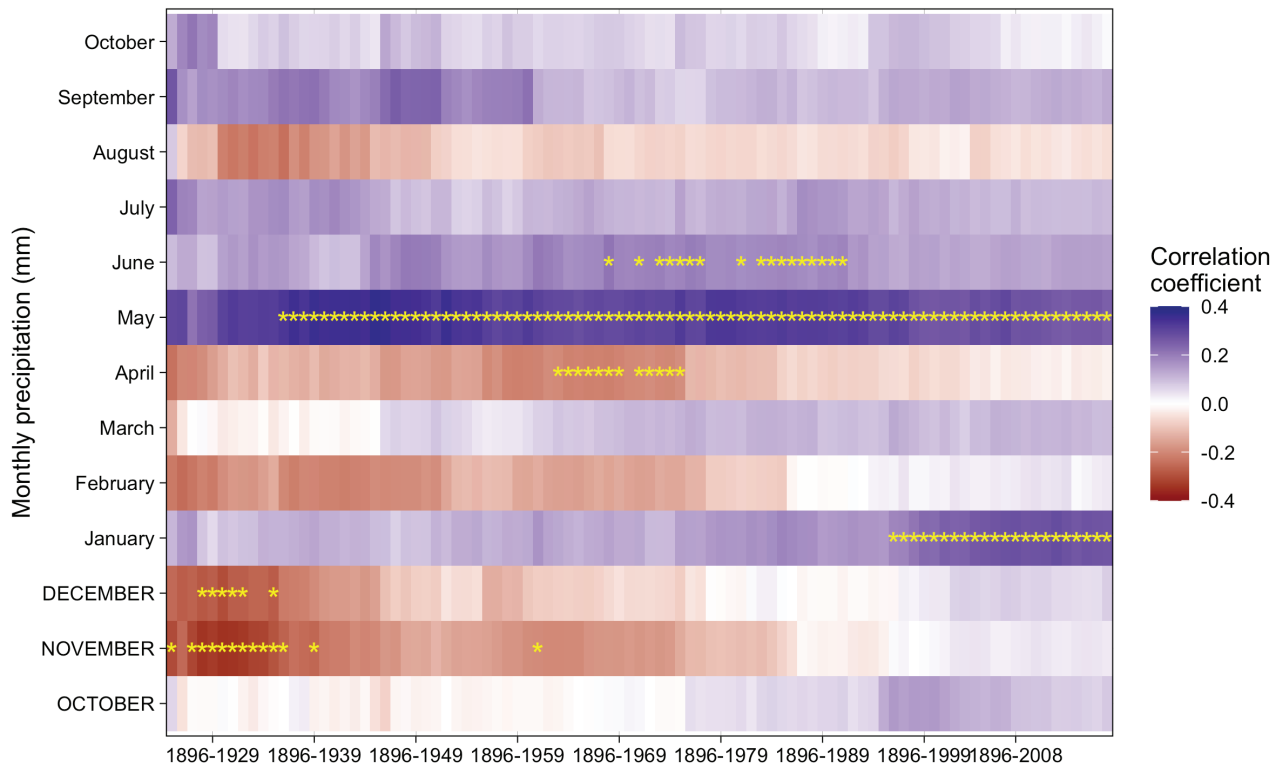


Figure 7. Evolving correlation response window between the residual Bald Ridge chronology and monthly precipitation starting at the earliest time period (1896-1929 CE) and repeated for increments of one year until the final time period 1896-2015. Months in all caps indicate previous year. Yellow stars indicate significance of correlation for the evolving response window at the $p < 0.05$ level.

likely at higher elevations due to climate change (Raffa et al. 2008), but limber pine exists across all elevations in its geographic range where climate may not have been historically limiting for the mountain pine beetle. If this is the case, it may help explain why limber pine at Bald Ridge have been affected by mountain pine beetle for centuries. Despite the susceptibility of limber pine to mountain pine beetle, older trees, and survivors of mountain pine beetle outbreaks, do persist on harsh sites.

Because climate-growth analyses indicated that ring width variability at Bald Ridge responded to seasonal precipitation, it can serve as a moisture proxy going back in time. In contrast to continuous mortality, largely from mountain pine beetle, pulses of successful establishment appear to have been coincident with wet climatic periods (figures 3 and 7), at least during some decades, despite assumed similar levels of pressure by Clark's nutcracker and other seed predators over time. While there may have been limber pine establishment since the 1940s, our sampling approach (increment cores) would have precluded trees too young (small) to extract cores, and

might partially explain limited establishment in the previous ~80 years. Similarly, although we were able to reconstruct pith dates for over 80% of the trees sampled, patterns in establishment dates may differ had we captured a higher percentage of the population.

Moisture conditions were the primary driver of tree growth; water-year (12-month), particularly spring precipitation, was the dominant climatic factor influencing growth variability at the Bald Ridge site. We found that drought stress (high temperature and low precipitation) limits growth in limber pine, which was consistent with previous studies (Kipfmüller and Salzer 2010). The changing cool season precipitation signal suggests more precipitation is being delivered as rain, rather than snow over time, providing less of a potential negative effect of late-lying snowpack on growth, and increased opportunity for soil moisture to contribute to enhanced growth. One of the primary factors in tree growth, photosynthetic capacity, is responsive to moisture availability, and higher temperatures limit respiration rates in trees. It is likely that the generally exposed nature of our Bald Ridge

site resulted in increased solar radiation over the course of the growing season that would effectively control the availability of soil moisture, thereby limiting annual ring-width increment. As we look to the future of limber pine, these observations will be important to consider as we head into a time period with likely more drought, increased temperatures, and less frequent and/or more variable wet periods (Westerling et al. 2011).

Overall, the balance between continuous mortality, episodic establishment, and climate driven growth variability in the face of mounting mountain pine beetle pressure and increasing precipitation variability is likely to impinge upon limber pine population viability. Introduced pathogens, specifically white pine blister rust, also threaten limber pine forest health, although there is some indication of genetic resistance (Snieszko et al. 2016). Still, the existence of many persistent and old limber pines at Bald Ridge indicate the species is likely to persist, yet. These longer-lived, slower-growing specimens may also represent the seed source for future generations of limber pine as climate changes. Across a broad ecological amplitude, the presence of many live trees, including such long-lived survivors, could make limber pine populations a resource for maintaining the function of five-needle pines in the face of rapid environmental change. Our dendroecological results constitute a better understanding of limber pine ecology, including the mechanisms behind survival and mortality of individuals, that would benefit management of the Greater Yellowstone Ecosystem and other montane and subalpine limber pine forests in the interior west.

Using dendrochronological methods with limber pine is not without its limitations. It is widely known that individuals of advanced age (often the most sought-after specimens) are likely to be rotten in the center, making estimates of establishment dates difficult. Our intensive sampling approach was able to remedy this as we ended up with quite a large number of samples with the pith or near pith growth rings, enabling us to make a reasonable estimate of the number of rings to the pith (figure 2). Given the potential for long tree-ring chronologies of limber pine, it is surprising there are so few efforts to build reconstructions with this species (but see Case and MacDonald 1995; Axelson et al. 2009). While often characterized as variable in their climate signal (Kipfmüller and Salzer 2010), limber pine can be excellent and stable recorders of past climatic variability. Their ecological amplitude, longevity, and landscape placement all make them ideal candidates for the development of long tree-ring chronologies. Such chronologies, as seen with our study, can provide useful information on long-term demographics, disturbance, and climate drivers in limber pine populations.

This particular study aids in improving our understanding of limber pine ecology, and can be used to guide our management of the species into the future. As we think about climate change adaptation, and the conservation, preservation, or restoration of five-needle pines, we suggest that, as a textbook generalist, limber pine has untapped potential to help us maintain five-needle pines on our western landscapes. Whether that is the promotion of extant populations, the release of pine from more successful overstory competitors, or its use as a 'surrogate' to fill recently vacated niches of functionally similar species (e.g., whitebark pine), we need to look more closely at the adaptation potential of limber pine.

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