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Comparative species assessments of five-needle pines throughout the western United States

Sara A. Goeking [a,*], Marcella A. Windmuller-Campione [b]

[a] USDA Forest Service Rocky Mountain Research Station, 507 25th Street, Ogden, UT 84401, United States
[b] Department of Forest Resources, University of Minnesota, 1530 Cleveland Ave. N, St. Paul, MN 55108, United States

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ABSTRACT

Five-needle white pine species provide important ecosystem services throughout the western U.S., and many of these species have become susceptible to stressors including warmer temperatures, insect epidemics, nonnative disease, and altered disturbance regimes. The objective of this study was to characterize recent broad-scale demographic patterns, including species abundance (i.e., numbers of individuals, tree density, size-class distributions, recruitment, growth rates, mortality rates, and causes of mortality, for the six species of five-needle pine that occur in the western US. We used the U.S. Forest Service's Forest Inventory and Analysis (FIA) dataset, spanning greater than 10 years, to quantify demographic status and trends for each species. FIA data were compiled from a probabilistic sample design and consistent analysis framework that included not only the dominant community types of five-needle pines, but also all other forest community types, which have previously been demonstrated to encompass abundant regeneration of five-needle pine species. Our analysis revealed similar trends for whitebark and limber pines: both species exhibited increased levels of mortality that are occurring faster than growth of surviving trees, as well as abundant regeneration in forest types that are not dominated by five-needle pines. Although limber pine has experienced lower mortality rates than whitebark pine, it nonetheless showed signs of decline that are comparable to broad-scale indicators exhibited by whitebark pine 10 years prior. In contrast to whitebark and limber pines, Great Basin bristlecone and foxtail pine mortality rates were relatively low, and their populations exhibited a flat diameter distribution except for restricted recruitment from seedling to sapling size-classes. Our findings suggest that five-needle white pine species would benefit not only from increased seedling recruitment, but also from enhanced recruitment among older and larger age and size classes. Thus, it may be important to apply a variety of management strategies – including artificial regeneration with disease-resistant seedlings, direct seeding, and early intervention to decrease competition that may allow natural regeneration to achieve recruitment inter large size-classes – and also apply silviculture techniques to forest types that may be dominated by other species. The consistent monitoring conducted by FIA can allow future assessment of the demographic trajectory of each five-needle pine species, and thus can help prioritize management and restoration priorities, both within communities dominated by five-needle pines and in other community types that may be important targets for silvicultural interventions or restoration treatments.

1. Introduction

Interacting and compounding impacts from multiple stressors have placed a spotlight on five-needle white pine species in North America and the need to increase our understanding of the stand development and regeneration dynamics of these species. The six species of five-needle white pines that occur in the western US and are commonly grouped together are whitebark pine (*Pinus albicaulis* Engelm.), limber pine (*P. flexilis* James), Rocky Mountain bristlecone pine (*P. aristata* Engelm.), Great Basin bristlecone pine (*P. longaeva* D.K. Bailey), southwestern white pine (*P. strobiformis* Engelm.), and foxtail pine (*P. balfouriana* Balf.). Although five-needle white pine species occur across western North America, we have limited knowledge of their community composition and structure across much of their range. Compared to more productive and commercially important tree species, there has been limited research until recently from a western science

* Corresponding author.
E-mail addresses: sara.goeking@usda.gov (S.A. Goeking), mwind@umn.edu (M.A. Windmuller-Campione).

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perspective. However, Indigenous communities hold generational knowledge of the species' silvics and management; Augare-Estey (2011) shares knowledge about the cultural significance of whitebark pine within the Blackfoot Confederacy community and how this knowledge may aid in maintenance and restoration of the species. First, traditional ecological knowledge of whitebark pine and disturbance may help address existing knowledge gaps. Second, awareness of public perception of various restoration strategies within indigenous communities may increase chances of support and even elicit assistance such as identification of sites for restoration or cone collection (Augare-Estey, 2011).

There is a growing body of literature on the threats and interacting impacts of the invasive and nonnative white pine blister rust (*Cronartium ribicol*a J.C. Fisher), mountain pine beetle (*Dendroctonus ponderosae* Hopkins), and other stressors on whitebark pine (Cleaver et al., 2015; Gibson et al., 2008; Tomback et al., 2011). For example, whitebark pine covers 18% of the land area within the Greater Yellowstone Ecosystem (GYE), where Macfarlane et al. (2013) estimate that almost half of the whitebark pine has experienced severe mortality. While there is less extensive research available for the other five-needle white pine species, various mortality agents have killed about 24% of limber pine within limber pine forest types in the Central and Southern Rocky Mountains, with another 26% in declining health (Cleaver et al., 2015). Even more alarming, approximately half (51%) of all standing whitebark pines were dead as of 2016, with mortality continuing to increase (Goeking and Izlar, 2018). These levels of mortality have caused a great level of concern among natural resource managers with whitebark pine being recommended for listing as a threatened species in 2020 (USDI, 2020).

Concerns over the threats to five-needle pines have led scientists and natural resource managers to gather data on current stand conditions including mortality levels, regeneration, and growth across the range of the individual five-needle pine species. Many of these species are considered poor competitors and are therefore minor components of productive sites, whereas they are able to dominate harsh sites such as treeline environments where other species cannot survive (Tomback et al., 2011). Within treeline ecosystems, five-needle white pines are considered both foundational and keystone species: as foundation species, they define community structure and alter microclimates at treeline sites, and as keystone species, they serve as a food source to multiple animal species (Logan et al., 2010; Tomback et al., 2011).

While each of the five-needle white pines are the dominant species within their own respective community type, they are also observed as minor components across a wide range of forest communities below treeline, and regeneration is occurring in those other communities. Understanding how stand dynamics and community structure vary across all sites where five-needle pines occur, including stands where they are minor components, requires extensive sampling effort. Additionally, comparative assessment of five-needle pine species and their susceptibility to stressors requires consistent sampling across their geographic ranges. For example, in contrast to other five-needle pines, Great Basin bristlecone and foxtail pine have been observed to have chemical defenses increasing resistance to mountain pine beetle (Bentz et al., 2017; Eidson et al., 2017); broad-scale assessments can help determine the extent to which Great Basin bristlecone is maintaining more stable population levels than other five-needle pines following the recent beetle epidemic.

The objective of this study was to characterize recent demographic patterns, including species abundance (i.e., numbers of individuals), size-class distributions, recruitment, growth rates, mortality rates, and mortality causes, for the six species of five-needle pine that occur in the western US. In this study, we expanded the focus of previous regional and species-specific assessments to all five-needle white pine species throughout the western US. We relied on the extensive, probabilistic sampling network implemented by the US Forest Service's Forest Inventory and Analysis (FIA) Program, which has been used to conduct species assessments for whitebark pine and limber pine. Previous studies have used FIA data to assess whitebark pine's size-class distributions, growth, mortality, and regeneration, finding that regeneration of this species was more common in other forest community types (e.g. lodgepole pine, Douglas-fir, and Engelmann spruce forest types) (Goeking et al., 2019; Goeking and Izlar, 2018). Similarly, Windmuller-Campione and Long (2016) utilized the same database, and observed limber pine occurring with twenty-two different overstory species and presence of limber pine regeneration in many different forest community types. By utilizing a similar approach to those previous studies, we set out to achieve a greater understanding of the demographic dynamics of each of the different five-needle white pines not only within their dominant community type but in all forest community types where those species occur, which may illuminate important additional targets to consider for silvicultural intervention or restoration treatments.

2. Materials and methods

Our comparative species assessments relied on data collected by the US Forest Service's Forest Inventory and Analysis program, as presented in the publicly available FIA database, FIADB (Burrill et al., 2018). As an ongoing monitoring program, FIA collects data from a nationwide, probabilistic network of permanent monitoring plots across all ownership categories and forest types, with average plot spacing of about 5 km and a remeasurement cycle of 10 years in the western US (Bechtold and Patterson, 2005). Use of this dataset ensured that data collection and analysis methods occur in a consistent manner, across all forest types and for all species.

We based our estimates of current, broad-scale species indicators on the most recent available FIA data in eleven western states. FIA estimates are based on multiple years of data such that all plots, over an entire measurement cycle, contribute to the estimate (Bechtold and Patterson, 2005). Within the FIADB, the nominal year associated with each estimate is the last full year of data collection. We selected 2019 for our estimates of five-needle pine attributes, and these estimates were based on an entire 10-year cycle of data collected between 2010 and 2019. For our comparisons of broad-scale indicators between two time periods, the latter time period consisted of the most recent available data (2010–2019). For many states (Arizona, Colorado, Idaho, Montana, and Utah), the earlier time period represented data collected no later than 2009. However, due to delayed implementation of permanent plots in some states, the earliest estimates available from other states included data collected later: California and Oregon include data collected in 2010; Washington includes data collected through 2011; and Nevada, New Mexico, and Wyoming include data collected through 2012. This timeframe resulted in data collected during some years being included in both time periods, e.g., Washington's 2011 estimates are based on data collected in 2002–2011 and 2019 estimates are based on data collected in 2010–2019. However, moving-window estimation is statistically conservative because it dampens any apparent trends over time, and any significant changes over time are likely larger than estimated (see Bechtold and Patterson, 2005, Ch. 5). In our results, we refer to the later time period as 2010–2019 and the earlier time period as pre-2010.

The methods described here are a brief summary of the field protocols and data compilation techniques used by FIA. For a complete and more detailed explanation of FIA's data collection protocols, database, and estimation procedures, please see USDA (2019), Burrill et al. (2018), and Bechtold and Patterson (2005), respectively. Field plots consisted of four 7.3-m radius subplots, with one central subplot and three additional subplots located at azimuths of 120, 240, and 360 degrees from the central subplot. On each subplot, several measurements were collected on all trees that are at least 12.7 cm in diameter at breast height (DBH). Tree-level measurements included species, live/dead status, DBH, height, and many others (see USDA, 2019). Additionally, damages such as those caused by insects or disease were recorded for live trees, and mortality causal agents were recorded for dead trees that died since the previous measurement (i.e., within the previous 10 years).

Regeneration was assessed within 2.1-m radius microplots, which constitute a subset of each of the four subplots (USDA, 2019). Within each microplot, the same suite of measurements that were collected for live trees were measured for all live saplings, which were defined as stems at least 2.5 cm DBH. For all softwood species, including pines, seedlings were defined as stems less than 2.5 cm DBH but at least 15.2 cm in length (i.e., height in the case of vertical stems), and the number of seedlings of each species was recorded on each microplot (USDA, 2019). Given the extremely slow growth rates of some of these species, seedlings may be several years to decades old (Tomback et al., 1993). Thus, the lack of data on individuals less than 15.2 cm in length represents an unmeasured age-class whose influence on future age structure will not be observed for several years.

Both growth and mortality were quantified in units of volume per year. Net growth represents the total growth volume of surviving trees, minus the volume of trees that died, over a specified time period. Mean annual tree growth was calculated as the difference in tree volume between two measurements divided by the remeasurement period in years (Burrill et al., 2018), which was typically 10 years. For trees without a previous measurement, growth was estimated based on the width of the most recent 10-year increment of tree rings, as determined by coring the tree with an increment bore, divided by 10 years to get an annual growth rate (USDA, 2019). Mean annual tree mortality was estimated as the volume of trees that died within the 10 years prior to measurement divided by 10. We compared net growth among the six five-needle pine species, and also compared growth and mortality for individual diameter classes for all species. Based on preliminary results that showed high mortality of whitebark and limber pines, we also compared net growth of these two species by ecological section (Cleland et al., 2007) to determine whether any mortality hotspots existed.

Broad-scale estimates of the number of trees, mean annual growth, and mean annual mortality for each species were obtained from the online EVALIDator tool (USDA, 2020). The EVALIDator tool represents a user-friendly implementation of FIA's design-based estimators, which rely on a probability-based sample as well as post-stratified estimators for variance reduction purposes (Bechtold and Patterson, 2005; McRoberts, 2010). This design-based estimation process also enables unbiased estimation of standard errors, which we used to identify differences among groups or time periods (e.g., change in the number of seedlings over time). In this study, we used EVALIDator to estimate the following metrics: number of live trees by species and 5.1-cm (2-inch) diameter size class; number of dead trees by species, size class, and mortality causal agent; number of seedlings by species and forest type; mean annual growth by species, size class, and ecological section; and mean annual mortality by species and size class. We also used EVALIDator to produce sampling errors for all of these estimates, where one sampling error is an approximate 68% confidence interval (USDA, 2020).

Any estimates for a particular species were based only on plots where that species was present. To illustrate where each species occurs, we downloaded data from the FIA Data Mart (USDA, 2021); linked data tables representing plot-level, stand-level, and tree- or seedling-level information in a relational database; and queried the entire western US for occurrences of any of the six five-needle pine species included in this analysis. Although most estimates of broad-scale attributes were obtained from the online EVALIDator estimation tool (USDA, 2020), as described above, density of each five-needle white pine species was instead estimated from data downloaded from the FIA Data Mart (USDA, 2021). We used tree-level expansion factors to calculate the number of live trees per hectare, for each species at each plot where it occurs and constrained to trees 12.7 cm DBH or larger, and then calculated mean and median number of trees per hectare among all plots where each species occurs. The reason we used this method rather than EVALIDator is because EVALIDator produces estimates of tree density (number of trees per unit area) on the basis of total forest area rather than area where a particular species occurs.

3. Results & discussion

The number of plots with any five-needle pine species present varied from 23 plots with foxtail pine to 1572 plots with whitebark pine present (Fig. 1). Because data were collected from FIA's probability-based sample across all forest types, the number of plots with each five-needle pine species present corresponded to that species' prevalence across the landscape. After whitebark pine, limber pine was the most abundant five-needle pine species, and both species were widespread across the western US. Great Basin bristlecone and foxtail pine were the least abundant and widespread. Foxtail pine is known to occur in two disjunct populations in California, one in the southern Sierra Nevada and the other in northern California's Klamath Mountains (Tomback et al., 2011), although only the southern population was represented in the FIA dataset, i.e., it did not occur on any FIA plots within its northern population.

The percentage of total trees that are dead suggests that some five-needle pine species have been – and are – more vulnerable to recent threats than others (Table 1). Range-wide estimates based on FIA's probabilistic sample indicate that the relative proportion of dead vs. live trees is relatively stable for foxtail pine, Rocky Mountain bristlecone, and Great Basin bristlecone. Southwestern white pine percentages have increased from 15% to 21% dead, mainly due to fire-caused mortality in the largest size classes (see Section 3.5).

3.1. *Has the number of live or dead trees of each five-needle pine species changed appreciably over the past two decades?*

In contrast to the other five-needle pine species, the percentage of all standing limber pine and whitebark pine trees that were dead has increased substantially in recent years. For limber pine, this percentage increased from 34% to 42% over the past decade, and for whitebark pine, from 43% to 54% (Table 1). A previous Resource Planning Act assessment based on FIA data (Oswalt et al., 2019) provided longer-term context for these percentages. As of 1999, only 12% of standing whitebark pines were dead (Oswalt et al. 2019), while that number increased to 51% as of 2016 (Goeking and Izlar, 2018), and to 54% as of 2019 (Table 1). For limber pine, the percentage of standing trees that are dead increased from only 8% in 1999 to 38% as of 2015 (Oswalt et al., 2019) and now to 42% as of 2019 (Table 1). Note that the current proportion of all standing limber pines that are dead (42%) is now approximately the same as the proportion of dead whitebark pine prior to 2010 (Table 1).

One possible explanation for such different percentages of dead trees among five-needle pine species is that species with no major changes in the proportion of dead vs. live trees are less susceptible to stressors that have caused recent high mortality of other species. For example, the chemical resistance of Great Basin bristlecone and foxtail pine to

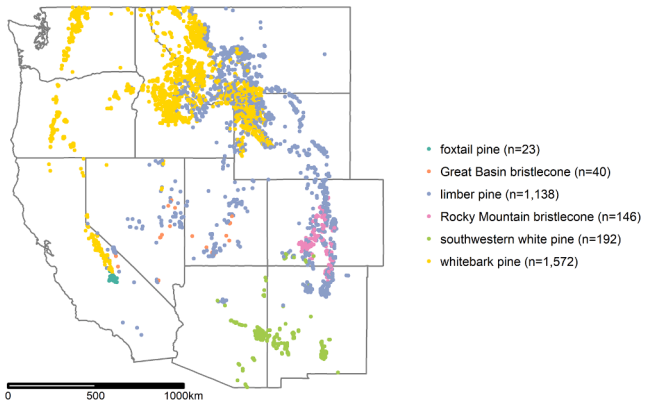

Fig. 1. Distribution of 5-needle pine species at permanent forest monitoring plots monitored by the US Forest Service's Forest Inventory & Analysis Program. Locations are approximate (n = number of plots with species present).

Table 1
Total number of live and dead trees in 2000–2009 and 2010–2019.

Species	Time period	Number of live trees[1]	Number of dead trees[1]	Total number of trees	Percent of total that are dead	Mean (median) live tree density[2]
Whitebark pine	2000–2009	353,104,855	261,714,695	614,819,550	42.6%	330 (178)
	2010–2019	277,086,183	326,005,359	603,091,542	54.1%	319 (149)
Limber pine	2000–2009	160,141,135	80,610,097	240,751,232	33.5%	173 (60)
	2010–2019	151,749,994	111,264,067	263,014,061	42.3%	164 (60)
Rocky Mountain bristlecone	2000–2009	24,070,039	7,284,599	31,354,638	23.2%	182 (82)
	2010–2019	28,194,684	7,833,609	36,028,293	21.7%	172 (74)
Great Basin bristlecone	2000–2009	7,362,893	1,338,315	8,701,208	15.4%	77 (45)
	2010–2019	8,279,079	1,867,046	10,146,125	18.4%	104 (60)
Southwestern white pine	2000–2009	19,479,515	3,384,132	22,863,647	14.8%	91 (45)
	2010–2019	17,148,564	4,681,646	21,830,210	21.4%	99 (45)
Foxtail pine	2000–2009	4,286,814	910,449	5,197,263	17.5%	81 (45)
	2010–2019	5,354,393	1,109,757	6,464,150	17.2%	96 (77)

[1] Number of live trees ≥ 12.6 cm DBH. Most of the FIA dataset does not include dead trees < 12.6 cm DBH; thus, this size constraint was applied to live trees for comparability.
[2] Density of live trees ≥ 2.5 cm DBH per hectare of forest land with that five-needle pine species present.

mountain pine beetle (Bentz et al., 2017; Eidson et al., 2017) and lower susceptibility of Rocky Mountain bristlecone to insects and pathogens (Schoettle and Coop, 2017) may be contributing to their relatively stable proportions of live vs. dead trees.

The density (trees per hectare) of five-needle pine trees also differed among species. Whitebark pine was the only five-needle pine that occurred at an average conspecific density greater than 200 trees per hectare (Table 1). Mean densities of live whitebark, limber, and Rocky Mountain bristlecone pines decreased slightly during 2010–2019, as compared to the mean density in the previous decade. Although these decreases are not substantial, future decreases in density of these species could represent a change in stand structure and pine nut availability that may have ramifications for other species, such as Clark's nutcrackers, which may reduce seed dispersal from low-density stands as they forage for pine nuts (McKinney et al., 2009). In locations where whitebark and limber pines exist within forest types other than those dominated by whitebark and limber pine, respectively, decreases in density over time also represent shifts in species composition and potentially decreased stand diversity.

3.2. For each species, does the size-class distribution follow the expected reverse-J distribution?

Most of the five-needle pine species exhibited the expected reverse-J size-class distribution (Fig. 2). Given a sufficiently large sample of trees of a particular species, a histogram of the number of trees by diameter class typically followed an approximately negative exponential distribution, known more commonly as the reverse-J distribution (O'Hara, 2002; Rubin et al., 2006). Because there are far more small individuals than larger ones, smaller size-classes can experience high mortality and still contribute to a sustainable population over time. Thus, the reverse-J distribution, alongside other distributions with larger numbers of small versus larger trees, is often interpreted as a sign of a self-replacing population or *meta*-population (O'Hara, 2002; Rubin et al., 2006). Even whitebark and limber pines exhibited the reverse-J size-class distribution (Fig. 2), despite experiencing the highest recent mortality among the western five-needle pines, as summarized below (Section 3.5; Figs. 5 and 7).

In contrast to the other five-needle pine species, Great Basin bristlecone and foxtail pines' populations instead showed a flat, or uniform, size-class distribution (Fig. 2). A uniform size-class distribution can indicate that the species is declining over time due to decreased regeneration (Rubin et al., 2006). For species that follow a reverse-J size-class distribution, mortality of seedlings, saplings, and small trees can be disproportionately high while still allowing sufficient survivorship to recruit individuals into larger size-classes (Leak, 1964). A uniform size-class distribution, in contrast, may be less resilient in the face of chronic stressors such as increased temperature and drought stress because any increase in mortality in a given size-class will directly reduce the potential recruitment to larger size-classes. Thus far, there is insufficient research to determine whether the flat size-class distributions of Great Basin bristlecone and foxtail pines represent lack of resilience versus unique life history characteristics such as low regeneration and high survival. Tree-ring and retrospective analysis of foxtail pines over the past 1000 years shows that mortality of mature trees was unrelated to climate, while seedling recruitment was inversely related to summer temperature (Lloyd, 1997). Similarly, summer moisture is important for seedling regeneration of Great Basin bristlecone pine (Smithers and North, 2020), and subsequent seedling survival was higher and growth rates were slower than for limber pines on the same sites (Smithers et al., 2021). These previous studies show that seedling regeneration of both Great Basin bristlecone and foxtail pines is tied to summer moisture stress, whereas survival of larger individuals is not, which could lead to the flat size-class distribution we observed. Future research could use ongoing monitoring, as well as techniques such as dendrochronological reconstructions of past stand history, to determine whether currently observed size-class distributions are a recent phenomenon indicating lack of resilience versus a unique characteristic of these species.

3.3. Has recruitment of five-needle pines changed significantly over the past two decades?

Recruitment, as measured by the number of live seedlings and saplings and their associated confidence intervals, has not changed substantially for any of the five-needle pines from pre-2010 to 2010–2019 (Fig. 3). Whitebark pine and limber pine exhibited almost no change in the number of seedlings and saplings over this time span; observed changes are within an approximate 68% confidence interval (Fig. 3). Southwestern white pine experienced an increase in seedlings, and a decrease in the number of saplings < 7.6 cm DBH, over the past two decades, although both of these changes are within one 68% confidence interval of the 2010 estimates. Rocky Mountain bristlecone exhibited the opposite trend, with a smaller decrease in seedling numbers and an increase in saplings < 7.6 cm DBH.

Given the slow growth rates of these four species, the stable numbers of seedlings and saplings likely represent consistent survivorship rates of previous recruits over time, in addition to any new recruitment. As mentioned in the previous section, unmanaged tree species are expected to exhibit a reverse-J size-class distribution, and the seedling and sapling size classes (Fig. 3) confirm this expectation.

No sapling-sized individuals of foxtail pine or Great Basin bristlecone were observed on any plots, except for a small number of Great Basin bristlecone saplings pre-2010 (Fig. 3). The fact that no saplings were observed is likely due, at least in part, to the small number of plots with

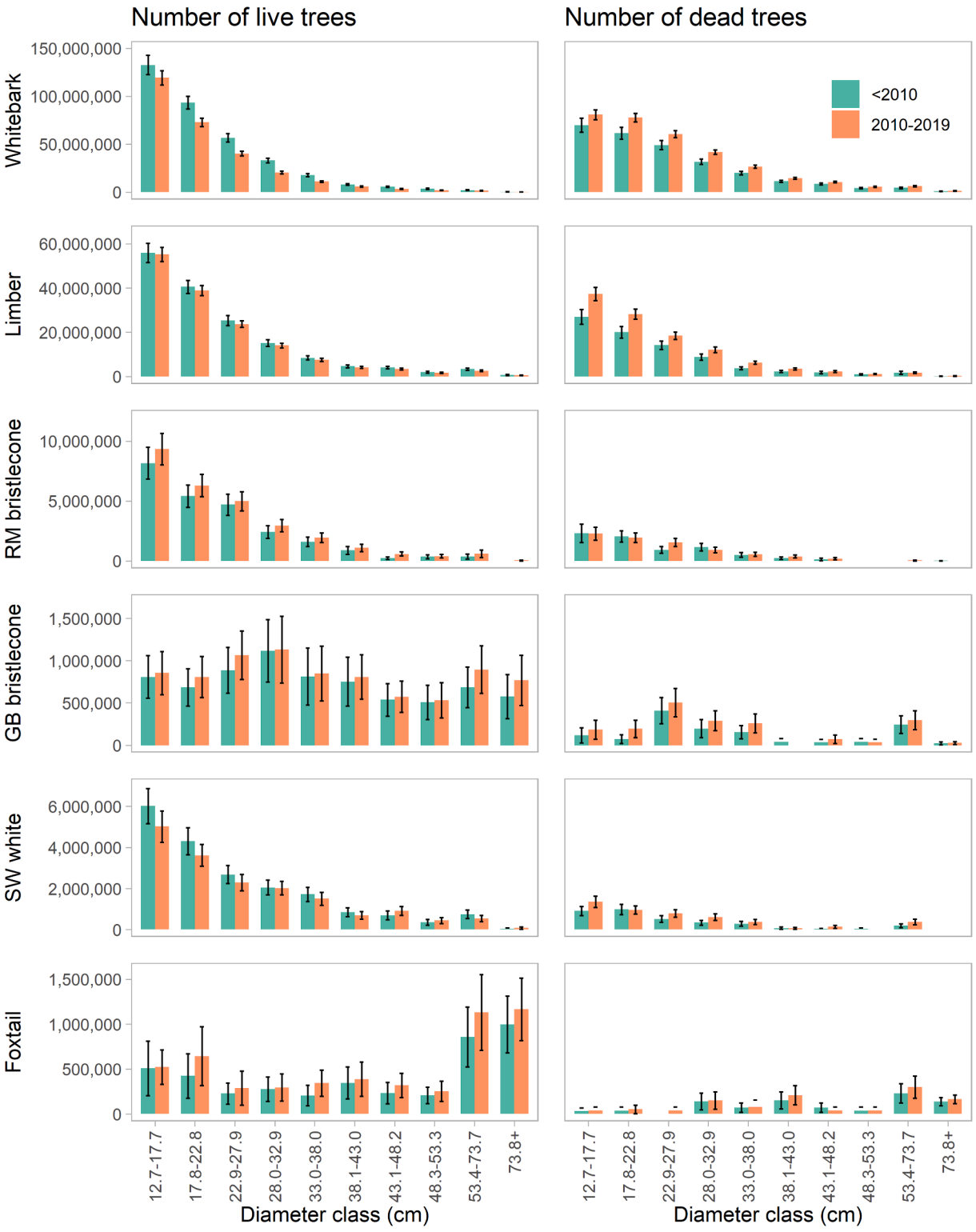

Fig. 2. Number of live and dead trees by species and diameter class, for the pre-2010 sampling period and the 2010–2019 period. Error bars represent an approximate 68% confidence interval. Note differences in scales of y axes. Abbreviations: RM = Rocky Mountain, GB = Great Basin, and SW = southwestern.

these species present (Fig. 1) and the smaller sample area for saplings than for trees 12.7 cm DBH and larger. However, the number of larger trees of these species, as well as the number of seedlings (Fig. 3), suggests that there has been a dip in recruitment to sapling size-classes. The number of seedlings of these species further indicates that seedling recruitment is indeed occurring, but that there may be an important bottleneck in recruitment from seedling to sapling size-classes. Additional research and management trials should be explored to identify treatments that may increase the recruitment of seedlings to saplings for foxtail pine and Great Basin bristlecone.

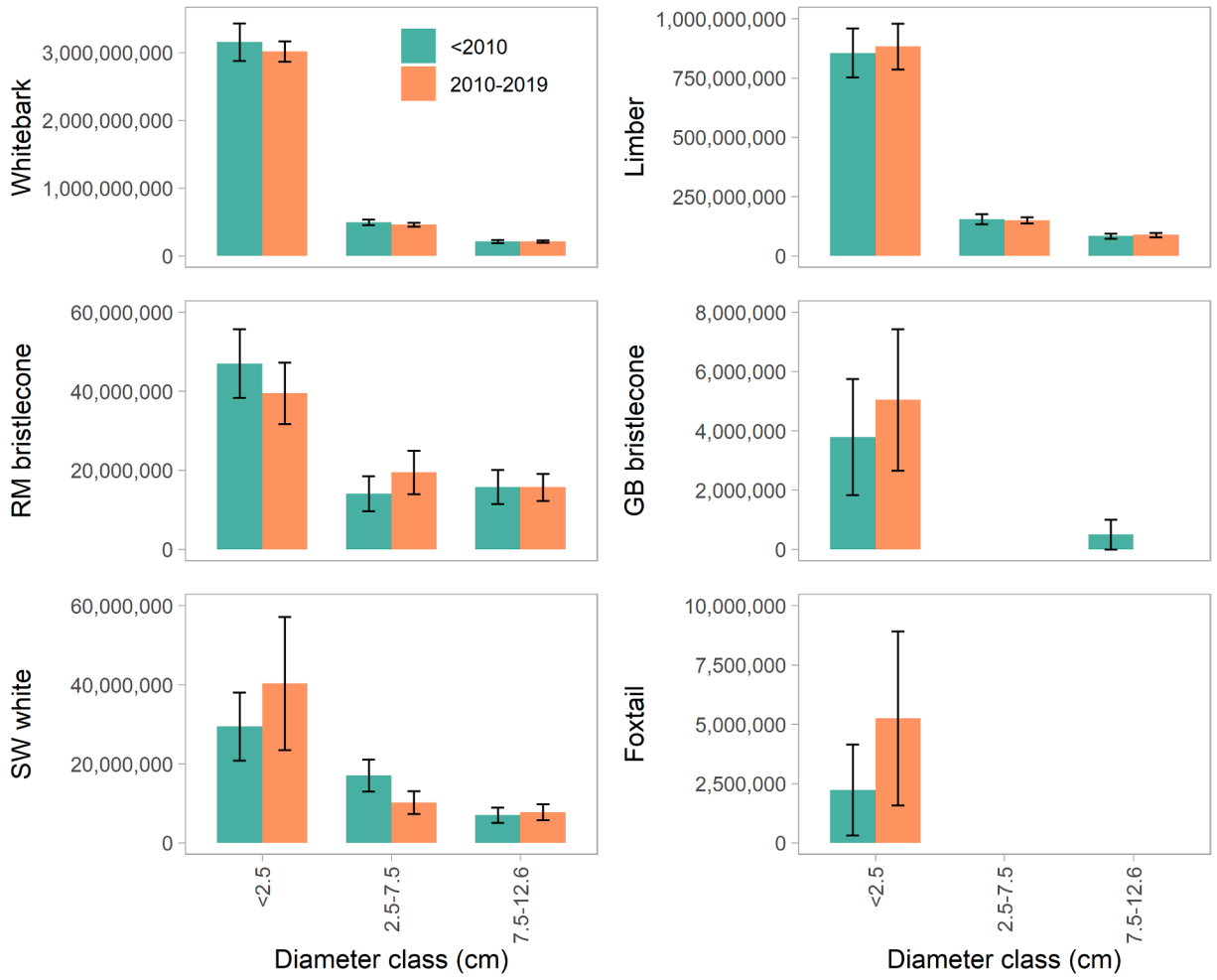

Fig. 3. Number of live seedlings and saplings by species and diameter class, for the pre-2010 sampling period and the 2010–2019 period. Error bars represent an approximate 68% confidence interval. No Great Basin bristlecone or foxtail pines saplings (2.5–12.6 cm DBH) were observed. Note differences in scales of y axes. Abbreviations: RM = Rocky Mountain, GB = Great Basin, and SW = southwestern.

3.4. Is recruitment of seedlings and saplings occurring in specific forest types?

The total number of seedlings of each five-needle pine species varied among overstory forest types (Fig. 4). Whitebark pine, limber pine, and southwestern white pine recruitment occurred most abundantly in forest types dominated by other (non-five-needle pine) species. These results are consistent with those reported in previous studies using FIA data (Goeking et al., 2019; Goeking and Izlar, 2018): whitebark pine seedlings occur most often in the lodgepole pine forest type, and 26% of all whitebark pine seedlings occur in stands with a whitebark pine-dominated overstory.

Limber pine, southwestern white pine, and Great Basin bristlecone exhibited a similar tendency to germinate and reach seedling size (≥30.5 cm length) under canopies dominated by other species (Fig. 4). Stands dominated by Douglas-fir contained more limber pine and southwestern white pine seedlings than any other forest type. About 20% of limber pine seedlings occurred within the limber pine forest type, and less than 18% of southwestern white pine seedlings occurred within the southwestern white pine forest type. Great Basin bristlecone seedlings occurred most often in the Engelmann spruce forest type, and only 19% of Great Basin bristlecone seedlings occurred in bristlecone forest types. However, due to the small number of plots with Great Basin bristlecone (n = 40), and the large associated standard errors (Fig. 4), there is high uncertainty associated with any conclusions about differences in Great Basin bristlecone seedlings among forest types.

Occurrences of Rocky Mountain bristlecone and foxtail pine seedlings differed from the other five-needle pines in that they most commonly occurred within their own forest type (Fig. 4). Almost 75% of all Rocky Mountain bristlecone seedlings occurred in the bristlecone forest type, and foxtail pine seedlings were observed only within the foxtail pine forest type.

3.5. Is recent growth of surviving trees compensating for mortality?

Net growth for five-needle pine species (Fig. 5) indicates species for which growth compensated for mortality (Rocky Mountain bristlecone, Great Basin bristlecone, and foxtail pine); growth is slightly outpaced by mortality (southwestern white pine); or mortality far outpaced growth (limber pine and whitebark pine). The relative amounts of growth and mortality indicate whether populations were stable, increasing, or decreasing. During 2010–2019, net growth of five-needle pine species varied from −4.2% of previous live tree volume per year for whitebark pine to almost +1.0% for Rocky Mountain bristlecone (Fig. 5).

Negative values of net growth for whitebark pine and limber pine demonstrate that mortality outpaced growth of surviving trees during 2010–2019 (Fig. 5). At the broad scales surveyed by FIA's probabilistic sample, negative net growth indicates that these species are declining at a metapopulation scale. Growth and mortality by size-class provide insights into demographic shifts that may occur due to high mortality for some species or size classes (Fig. 6). Whitebark pine and limber pine exhibited similar patterns of growth and mortality by size-class: for both

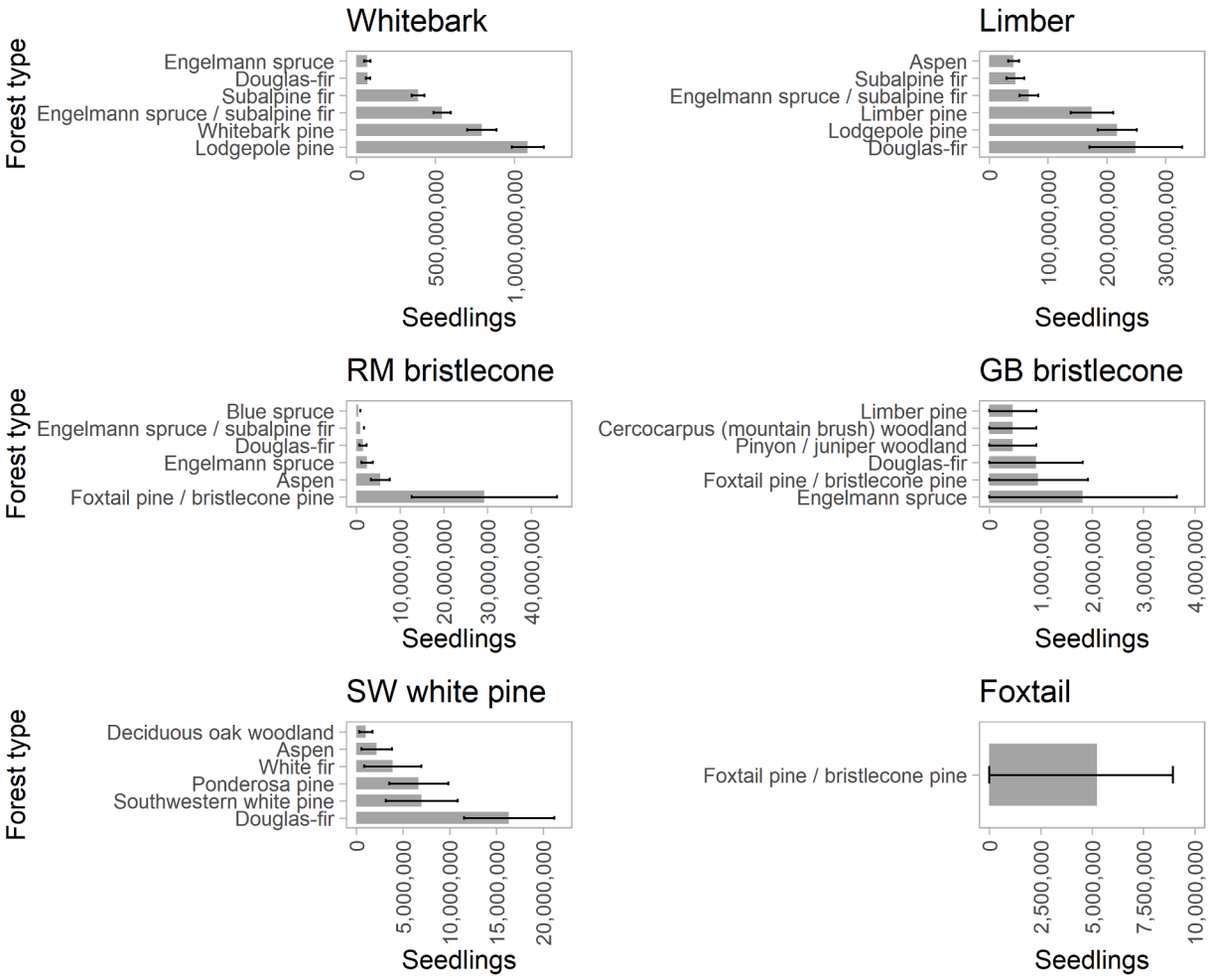

Fig. 4. Number of seedlings of each species of 5-needle pine by forest type. Error bars represent an approximate 68% confidence interval. Abbreviations: RM = Rocky Mountain, GB = Great Basin, and SW = southwestern.

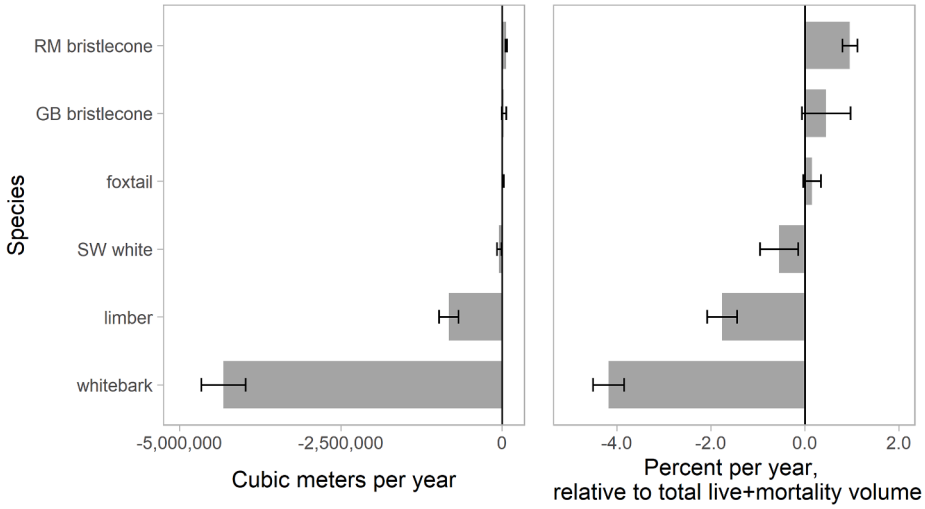

Fig. 5. Net growth (live tree growth minus the volume of trees that died) of each species, expressed in terms of mean cubic volume per year (left) and in terms of the mean annual percentage of live volume plus mortality volume (right). Error bars represent an approximate 68% confidence interval. Abbreviations: RM = Rocky Mountain, GB = Great Basin, and SW = southwestern.

species, mortality significantly exceeded growth for all size classes larger than 17.6 cm DBH (Fig. 6). Although the difference between growth and mortality in size-classes larger than 17.6 cm DBH was smaller for limber pines than for whitebark pines, the amount by which mortality exceeded growth suggests that both species declined appreciably during 2010–2019.

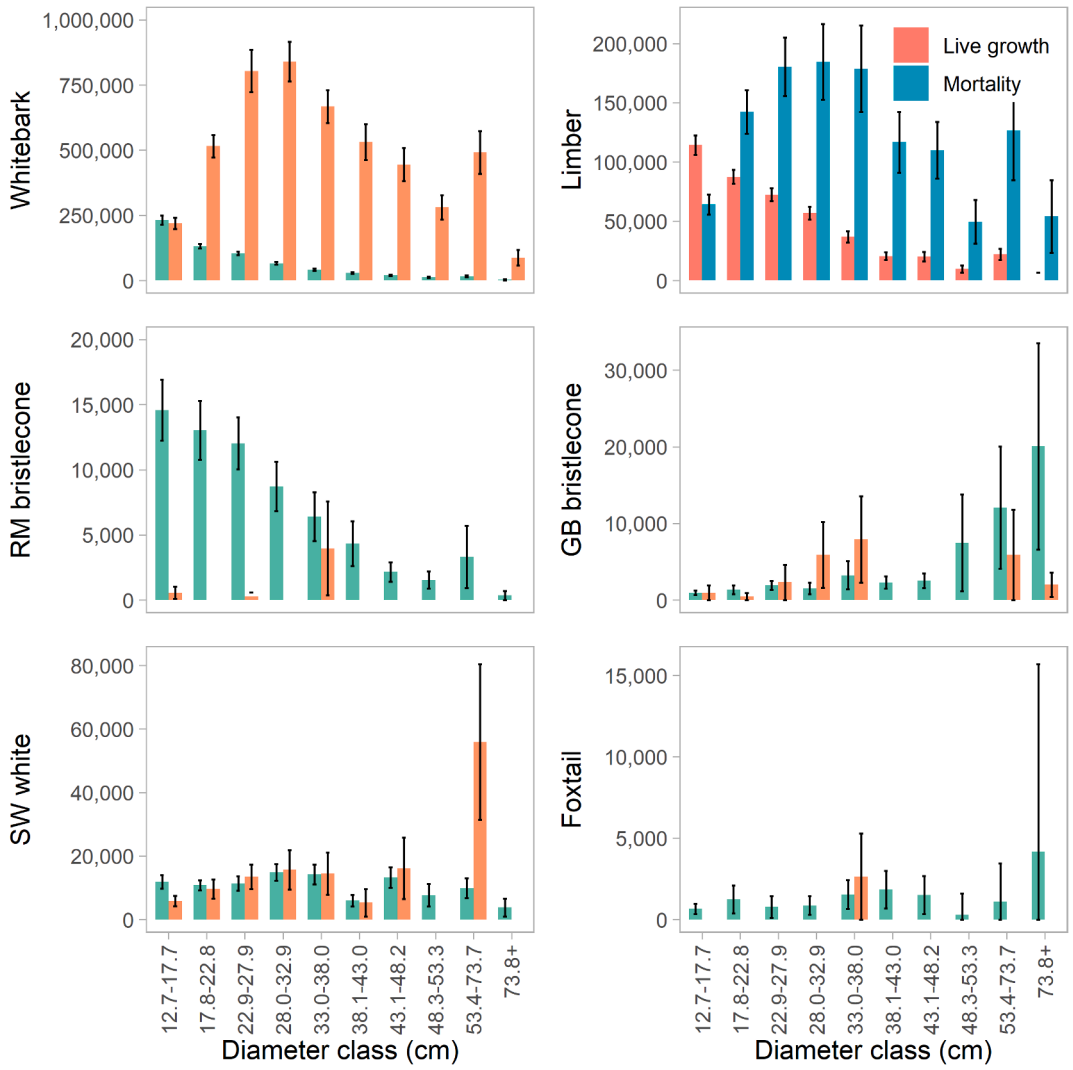

Fig. 6. Growth and mortality of each species, by diameter class, during 2010–2019. Error bars represent an approximate 68% confidence interval.

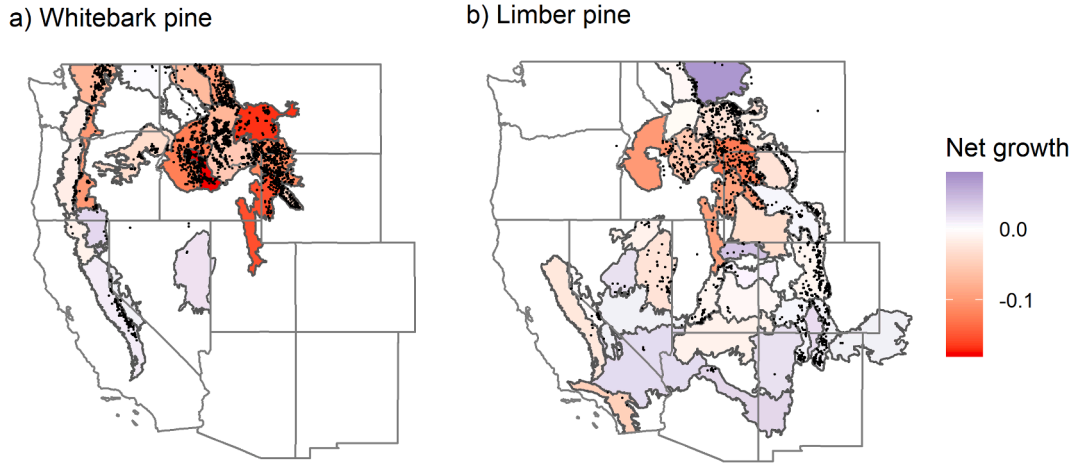

Fig. 7. Mean annual net growth of whitebark pine (a) and limber pine (b) by ecological section. Mean annual net growth is defined as live tree growth minus the volume of trees that died, expressed as mean cubic volume per year as a proportion of live plus mortality volume (e.g., −0.1 represents negative net growth of 10% of live tree volume per year). Points represent approximate FIA plot locations with each respective species present.

For the smallest size-class (12.7–17.6 cm DBH), limber pine growth exceeded mortality by almost a factor of 2, while growth and mortality are approximately equal for whitebark pines (Fig. 6). Although positive (limber pine) or near-zero (whitebark pine) net growth of small trees may seem less ominous than the large negative net growth in larger size classes, it is worth noting that as of 2015, growth of whitebark pines in

this size class exceeded mortality by almost a factor of 2 (see Fig. 5 in Goeking and Izlar, 2018), just as limber pine experienced as of 2019 (Fig. 6, this paper). Thus, between 2015 and 2019, growth of surviving whitebark pines 12.7 to 17.6-cm DBH went from being almost twice as high as mortality to being approximately offset by recent mortality. Similarly, limber pine's 2019 growth and mortality mirrored the 2015 trajectory of whitebark pine, not only in the smallest size class but for larger trees as well (see Fig. 5 in Goeking and Izlar, 2018, and Fig. 6 of this paper).

Given the large negative net growth of whitebark and limber pines, we estimated their net growth rates by ecological section to identify geographic hotspots of mortality vs. growth (Fig. 7). Average annual net growth of whitebark pine was lowest (i.e., most negative) in central Idaho and in the Greater Yellowstone Ecosystem stretching from southwestern Montana to southwestern Wyoming. Net growth of limber pine was relatively low in central Idaho and relatively high in the southern part of its range.

In contrast to whitebark pine and limber pine's large negative net growth rates, the other five-needle pine species experienced survivor growth that approached or even exceeded mortality volumes. Annual net growth of southwestern white pine averaged −0.5% per year during 2010–2019 (Fig. 5). Growth and mortality of southwestern white pine were approximately equal for most size-classes (Fig. 6), with two exceptions. First, growth exceeded mortality in the smallest size-class (12.7 to 17.6 cm DBH). Second, the largest trees (53.3 and 73.4 cm DBH) experienced high mortality (Fig. 6). Increased mortality of the largest southwestern white pine trees may be due to an increase in fire-caused mortality during 2010–2019 compared to the decade prior to 2010 (Fig. 8). Net growth was near zero (i.e., balanced survivor growth and mortality) for foxtail pine and Great Basin bristlecone (Fig. 5).

Rocky Mountain bristlecone is the only one of the six five-needle pine species for which net growth was positive and definitively greater than zero (Fig. 5). Both Great Basin bristlecone and foxtail pine experienced slightly positive net growth (Fig. 5), with very little recent mortality (Fig. 6). Thus, although 15 to 23% of individuals of these species were dead as of 2019 (Table 1), most of those standing dead trees did not die within the previous decade, i.e., they are persistent and potentially long-dead standing trees.

Aside from the increase in fire-caused mortality of southwestern white pines (Fig. 8), mortality causal agents did not change substantially between 2000 and 2009 and 2010–2019. Within both time periods, the most prevalent mortality agents for whitebark and limber pines were insects. Rocky Mountain bristlecone pine's largest cause of mortality was recoded as "unknown," implying that mortality may have been due to subtle (e.g., prolonged drought stress) or interacting factors (e.g., drought stress and disease). One caveat of assigning a single mortality causal agent is that multiple interacting stressors (e.g., drought, insects, disease) may contribute to the death of a tree, and it may be difficult to conclusively pinpoint a single cause of mortality. Further, because FIA plots are measured once every 10 years, it is unlikely that field crews will be at the plot at precisely the right time to know conclusively what killed a tree. Some mortality causes may leave residual evidence, such as galleries beneath a tree's bark that provide clues regarding insect-caused mortality, or blackened trunks that suggest fire. However, for agents such as white pine blister rust, there may be little to no easily observable evidence that disease killed the tree. Thus, it is likely that disease-caused mortality is underestimated relative to other causal agents that may leave more obvious residual evidence.

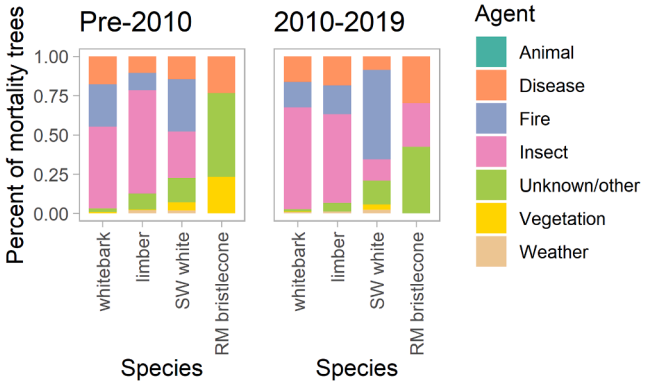

Fig. 8. Number of mortality trees (i.e., trees that died within ten years prior to measurement) by mortality agent, for each species and for the pre-2010 sampling period and the 2010–2019 sampling period. Animal damage was rare enough to not be visible at this scale and consisted of porcupine damage on whitebark and limber pines. Great Basin bristlecone and foxtail pines are not shown due to insufficient sample sizes of mortality trees. Abbreviations: RM = Rocky Mountain and SW = southwestern.

4. Implications for management

Managers and researchers continue to assess mortality levels and the subsequent impacts of mortality on five-needle pine stand dynamics locally, regionally, and across their ranges. The FIADB provides an opportunity to assess mortality, growth, structure, and composition of the different five-needle white pines utilizing the same probabilistic sample design and the same analysis framework, resulting in an objective and broad-scale overview of these species throughout their US ranges. Our analysis observed similar trends for whitebark and limber pines, which both had increased levels of mortality (Fig. 6), negative levels of net growth (Fig. 5), and regeneration observed in forest types other than those dominated by whitebark and limber pines, respectively (Fig. 4). In contrast, Great Basin bristlecone and foxtail pine mortality was relatively low (Fig. 6), and their populations exhibit a flat diameter distribution (Fig. 2) except for restricted recruitment from seedling to sapling size-classes (Fig. 3). The ability to quantify similarities and differences among five-needle pine species can allow for a greater exchange of information related to management strategies.

Management strategies will need to utilize multiple different techniques in the restoration and maintenance of five-needle white pine communities, especially in ecosystems that are experiencing severe declines such as the Greater Yellowstone Ecosystem. One strategy is related to the development of blister rust resistant or resilient planting stock, which is an ongoing effort for several five-needle white pine species (Schoettle et al., 2019; Waring and Goodrich, 2012). Survival and growth of outplanted (artificial regeneration) rust-resistant whitebark pine seedlings has been variable (Cripps et al., 2018; Laufenberg et al., 2020; Lonergan et al., 2014). Cripps and colleagues (2018) observed increased survival after seven in Waterton Lakes National Park for seedlings planted in clustered (60.8% survival of at least one seedlings) compared to those planted as individuals (53%). However, due to multiple logistics including high cost (cost estimated between $1980 and 2400 USD per ha (Tomback et al., 2011), accessibility, and land management agencies' guidelines (planting may be infeasible or restricted in wilderness areas), artificial regeneration is not a feasible option for many locations. Another strategy which also focuses on regeneration in treeline or five-needle pine forest types is the use of direct seeding (DeMastus, 2013; Pansing et al., 2017; Schwandt et al., 2011). Remeasuring an earlier study, Pansing and Tomback (2019) monitored survival of seedlings in caches created through direct seeding and observed 37% survival of at least one seedling per cache by year five.

While active restoration through artificial regeneration will be required, natural regeneration – especially within whitebark pine, limber pine, and southwestern white pine – will be necessary to sustain populations in areas that cannot be artificially planted. Silviculture treatments can facilitate increased survival and growth of natural regeneration and have resulted in variable and inconsistent trends in responses (Keane et al., 2007; Retzlaff et al., 2018). Maher et al. (2018) observed a variable response to active restoration in overstory

whitebark pine trees and no response in whitebark pine regeneration in five whitebark pine silvicultural restoration sites located in Montana, Idaho, and Oregon. Future research is needed to explore different silvicultural tools and techniques that could be applied and monitored within five-needle white pine communities.

Given that natural regeneration may be required to augment active planting, silvicultural strategies should be applied not only to communities dominated by five-needle white pines but also in forest types where these species are a minor component. Southwestern white pine, limber pine, and whitebark pine all had large amounts of regeneration in forest types where they are not the dominant species. Many of these forest types, such as lodgepole pine and Douglas-fir, are actively managed with over a century of silvicultural research in these systems. While historical management of these systems may have focused on production, there continues to be a shift to managing for multiple values and for ecosystem resilience to climate change. One mechanism for increased resilience is increased species diversity, which can also benefit the recruitment of five-needle white pine species given the abundance of five-needle white pine regeneration that has occurred naturally in multiple forest types. If regeneration is already occurring, managers and silviculturists can utilize early intervention through the use of competition control with the goal of increasing recruitment of five-needle pines from seedlings to saplings to overstory trees.

Strategies for restoration or conservation of five-needle white pines are most likely to succeed if management is coordinated across land stewardship entities and political boundaries (Keane et al., 2012). Cross-boundary restoration efforts may also benefit from multidisciplinary, cross-cultural, and traditional knowledge of these species, which in turn can result in broader support and increased collaboration among land stewards, resource managers, and others who value five-needle white pines (Augare-Estey, 2011).

5. Conclusions

While the five-needle white pine species are often grouped together due to their many similarities, we observed differences in demographic structure across the United States utilizing the FIADB. Consistent with many studies, several stressors continued to cause high mortality in whitebark pine and limber pine through 2019. Mortality of whitebark pine continued to exceed growth of surviving trees, and the percentage of trees that are dead is estimated at 54% as of 2019. Limber pine is more widespread and has experienced lower mortality rates than whitebark pine, but nonetheless showed signs of decline that are comparable to broad-scale indicators exhibited by whitebark pine 10 years prior. However, the current demographic structures of other five-needle white pines appear more stable than whitebark and limber pines, with the exception of the uniform size-class distribution and lack of sapling-sized trees of Great Basin bristlecone and foxtail pine. The continual and consistent monitoring conducted by FIA can allow future comparisons and monitoring to quantify the demographic trajectory of each of the individual five-needle pine species and thus to better prioritize management and restoration priorities. The current trajectories of whitebark and limber pine populations warrant prioritization of active management and restoration. Multiple efforts including artificial regeneration of blister rust-resistant seedlings, direct seeding, and early intervention techniques to release natural regeneration will all need to be considered in order to increase the number of seedlings transitioning to saplings and then to mature, seed-bearing overstory trees. However, for each of these techniques and others yet to be tested in these systems, additional research should seek to illuminate stand development processes, and the specific silvicultural actions that are likely to successfully facilitate increased recruitment, within the multiple ecosystems that five-needle white pines call home.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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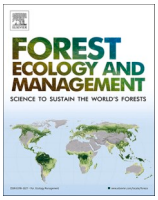

Corrigendum

Corrigendum to "Comparative species assessments of five-needle pines throughout the western United States" [For. Ecol. Manage. 496 (2021) 119438]

Sara A. Goeking [a,*], Marcella A. Windmuller-Campione [b]

[a] USDA Forest Service Rocky Mountain Research Station, 507 25th Street, Ogden, UT 84401, United States
[b] Department of Forest Resources, University of Minnesota, 1530 Cleveland Ave. N, St. Paul, MN 55108, United States

The authors regret that the colours in Figure 6 of the original article were not consistent across all panels. In particular, the colours in upper right panel of Fig. 6 (limber pine) are opposite the colours used in all other panels. We have corrected the colours for all panels in this Corrigendum. Note that the original data and findings remain unchanged.

The authors would like to apologise for any inconvenience caused.

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* Corresponding author.
E-mail addresses: sara.goeking@usda.gov (S.A. Goeking), mwind@umn.edu (M.A. Windmuller-Campione).

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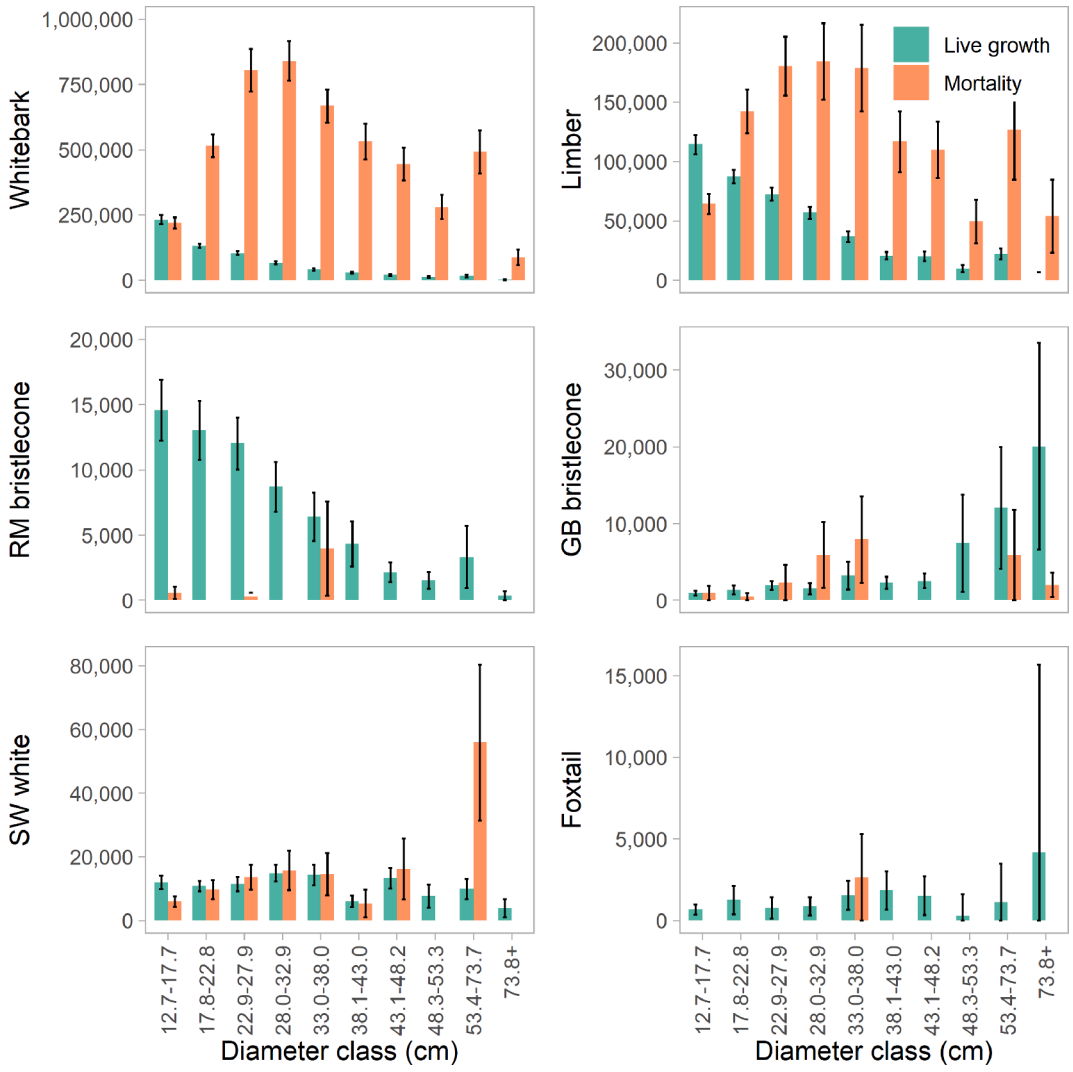
Whitebark
Limber
RM bristlecone
GB bristlecone
SW white
Foxtail
Live growth
Mortality
1,000,000
750,000
500,000
250,000
0
200,000
150,000
100,000
50,000
20,000
15,000
10,000
5,000
30,000
80,000
60,000
40,000
12.7-17.7
17.8-22.8
22.9-27.9
28.0-32.9
33.0-38.0
38.1-43.0
43.1-48.2
48.3-53.3
53.4-73.7
73.8+
Diameter class (cm)