



Range-wide population assessments for subalpine fir indicate widespread disturbance-driven decline

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ARTICLE INFO

Keywords:

Subalpine fir
Abies lasiocarpa
Mortality
Disturbance

ABSTRACT

Subalpine forests in western North America are threatened by rapid climate change, increased activity by endemic and exotic insects and diseases, and changing wildfire regimes. The interactive effects of these stressors have resulted in pronounced population declines in many subalpine tree species; however, a systematic assessment of the status and trends of subalpine forests is lacking. Subalpine fir (*Abies lasiocarpa*) is a widespread species across the western United States, with documented population declines in many parts of its distribution. Here we use subalpine fir as an initial leverage point to build a more complete understanding of subalpine forest baseline conditions and responses to environmental change. Specifically, we leverage the USDA Forest Service Forest Inventory and Analysis (FIA) database to (1) ask how subalpine fir populations are changing across the species' distribution in the western US, (2) assess the drivers of recent subalpine fir population trends, and (3) explore whether those changes imply generalized species-wide and/or system-wide decline. We found that subalpine fir abundance and basal area are declining concurrently across ~ 62% of the species' distribution, and increasing across ~ 19%. Range-wide, we estimated 25.02 ± 2.74 % subalpine fir mortality between 2000 and 2009 and 2010–2019 FIA inventory periods, with higher mortality concentrated in the eastern Oregon Cascades, central Idaho, and parts of southern Colorado. High regeneration density did not predict positive population trajectories, which were instead associated with higher rates of adult recruitment. While the importance of different mortality agents varied substantially between ecoregions, 83.4% of total range-wide mortality was related to fire or biological disturbance. Declining subalpine fir basal area coincided with declines in the basal area of other co-occurring tree species in 39% of subalpine forest area, and with increases in conspecific basal area in 22% of forest area. Fire disturbance was the single largest cause of subalpine fir mortality; however, even where subalpine fir fire mortality was high, mortality among other species was primarily caused by insects. Our results suggest that subalpine fir declines across large portions of the western United States are driven by forest disturbance, and that declines in subalpine fir populations may be indicative of negative change in subalpine forest systems broadly.

1. Introduction

Forests globally are being impacted by multiple stressors, including changing wildfire regimes (Jolly et al., 2015; Moritz et al., 2012) biotic disturbances (Patacca et al., 2022; Shaw et al., 2022), and climate change (Allen et al., 2015; Allen et al., 2010). In western North America, subalpine forests (i.e., abiotically limited high-elevation communities with upper bounds defined by the forest-alpine ecotone and lower bounds by denser montane forest; Millar and Rundel, 2016) have recently experienced rapid climatic warming (Pepin et al., 2022),

dramatic changes in snow amount and duration (Siirila-Woodburn et al., 2021), high rates of insect and disease damage (Davis et al., 2022; MacLauchlan, 2016), and wildfire events that are unprecedented in recent millennia (Higuera et al., 2021). The interactive effects of these stressors have reduced subalpine tree populations in many regions of the western United States. Whitebark pine (*Pinus albicaulis*), for example, has suffered population declines range-wide due to a combination of diseases, insects, changing wildfire regimes, and climate change (Aguilera et al., 2021), leading to a recent decision to list the species as threatened under the United States Endangered Species Act (US Fish &

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<https://doi.org/10.1016/j.foreco.2023.121128>

Received 24 March 2023; Received in revised form 15 May 2023; Accepted 17 May 2023

Available online 26 May 2023

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Wildlife Service, 2022). Other species facing similar sets of stressors include other high-elevation five-needle pines (e.g., *Pinus flexilis*, *P. aristata*, *P. longaeva*; Goeking and Windmuller-Campione, 2021; Smith et al., 2015), lodgepole pine (*P. contorta*; Smith et al., 2015), aspen (*Populus tremuloides*; Singer et al., 2019), Engelmann spruce (*Picea engelmannii*; DeRose et al., 2013), and subalpine fir (*Abies lasiocarpa*; Andrus et al., 2021; Harvey et al., 2021; Lalande et al., 2020).

Accelerated rates of environmental change at high elevations are projected to negatively impact subalpine forest systems (Andrus et al., 2021; Dirnböck et al., 2011; Dudley et al., 2021), potentially threatening the many important services they provide. Besides containing an estimated 11% of forest carbon stocks in the western United States (USDA Forest Service, 2022), subalpine forests provide important habitat and resources for many wildlife species (Costello et al., 2014), regulate hydrological processes of snow accumulation, ablation, and melt (Gleason et al., 2013; López-Moreno and Stähli, 2008; Troendle and King, 1987), and provide many social and cultural values (Davis, 2018; Hand and Lawson, 2018). Despite this, subalpine forest systems have been the subject of less research attention compared to lower-elevation forest types, possibly due to their lower timber product value (USDA Forest Service, 2022) and their distribution primarily in protected areas where management action is restricted (Smith and Gray, 2021). However, improving our understanding of how subalpine systems respond to global change is becoming increasingly important as the social value of forests shifts from resource extraction to other ecosystem services (Bengston, 1994).

Subalpine fir in the western United States provides an excellent initial leverage point to build a more complete understanding of subalpine forest baseline conditions and responses to environmental change. The species is widespread through the mountains of western North America, forming an important component of subalpine forests in most mountain ranges outside of the California Sierra Nevada and western Great Basin (Alexander et al., 1990). Similarly to other subalpine tree species, subalpine fir populations are suffering declines in many parts of this broad distribution (Andrus et al., 2021; Davis et al., 2022; Harvey et al., 2021; Lalande et al., 2020; Reich et al., 2016; Smith et al., 2015). In the mountains of Colorado, for example, elevated subalpine fir mortality and subsequent population declines have recently been linked to spatiotemporal patterns of moisture availability and drought (Smith et al., 2015; Harvey et al., 2021), climate change impacts on seedling establishment (Andrus et al., 2021; Andrus et al., 2018), and interactions between climate stress and damage by insects and diseases (Reich et al., 2016; Lalande et al., 2020). However, these drivers and their effects likely vary substantially across the large geographic distribution of subalpine fir. For example, substantial subalpine fir mortality has been reported in the Pacific Northwest due to outbreaks of the non-native balsam woolly adelgid (*Adelges piceae*). However, the insect's distribution throughout the rest of subalpine fir's range is poorly characterized, and can be difficult to diagnosis prior to late-stage crown symptoms (Davis et al., 2022; Hicke et al., 2023; Hrinkevich et al., 2016; Mitchell and Buffam, 2001).

This diversity and variability in the drivers of subalpine fir decline highlights the current lack of a range-wide population status and trends assessment. Such a synthesis could provide insight into broad-scale patterns in the responses of subalpine forest systems generally to environmental change, given the species' large geographic distribution and ecological importance. In the United States, the only dataset that can provide the combination of tree-level detail and large spatial extent necessary to do this is the USDA Forest Service Forest Inventory and Analysis (FIA) database. The FIA program has established more than 355,000 monitoring points across the United States using a balanced and randomized sampling design; where these points intersect forestlands (as defined by the FIA program; Burrill et al., 2015), individual trees are inventoried, measured, and tracked through time on 126,000 permanent plots. While FIA data are typically used to comprehensively assess present and prospective conditions of renewable resources on forests and

rangelands in the United States, they are also uniquely suited for analyses of tree demography, forest ecosystem vulnerability, and underlying change drivers on regional to national spatial scales (e.g., Anderegg et al., 2022; Bell et al., 2014; Fitts et al., 2022; Schultz et al., 2021; Shriver et al., 2022).

In this study, we leverage the FIA database to (1) ask how subalpine fir populations are changing across the species' entire distribution in the western United States, (2) assess the drivers of recent subalpine fir population trends, and (3) explore whether those changes imply generalized species-wide and/or system-wide decline. We use repeat FIA inventories to calculate decadal changes in subalpine fir abundance and basal area, as indicators of population trajectories. We further quantify the rates and sources of subalpine fir mortality between inventories using tree-level information recorded in the FIA database, and assess the regeneration potential of populations using information on seedling and sapling density and recruitment. Finally, we compare subalpine fir population trends and mortality rates to those of other co-occurring tree species to investigate the broader ecosystem context of observed trends in subalpine fir populations.

2. Methods

2.1. Forest inventory data

Since its beginning in 1929, the FIA program has collected data necessary to determine the status and trends of forest resources in the United States (Burrill et al., 2015). In 1999, the FIA program began implementing a nationally-consistent random sampling design comprised of permanent monitoring plots distributed across all land ownership and forest types, with an average plot remeasurement period of 10 years in the western United States (Bechtold and Patterson, 2005). Forest land is defined as patches at least 0.4 ha in size with at least 10% cover of tree species currently or recently, and no non-forest land use (e.g., mowing or intensive grazing). Each plot is composed of four 7.32 m radius subplots, within which all trees greater than 12.7 cm diameter at breast height (DBH) are inventoried, measured, and assigned a unique identifier used to track individuals between remeasurements. Trees smaller than 12.7 cm DBH, including seedlings, are inventoried on 2.07 m radius microplots nested within subplots. In Oregon, Washington, and California, larger trees (DBH greater than 76 cm in western OR and western WA; DBH greater than 61 cm in eastern OR, eastern WA, and CA) are inventoried on additional 18 m radius macroplots around existing subplots. In addition to tree species, diameter, and many other physical measurements, FIA field crews identify and record tree-level damage resulting from insects, diseases, or other causes, as well as a putative cause of mortality for all recently dead trees. For complete descriptions of FIA sampling design, measurement protocol, and estimation methods, refer to the FIA field manual (USDA Forest Service, 2022), Burrill et al. (2015), and Bechtold and Patterson (2005).

2.2. Population status and trends

To gain a range-wide sample, we identified all FIA plots that contained subalpine fir or corkbark fir (*Abies lasiocarpa* var. *arizonica*) in either the most recent or previous measurement. In all subsequent area-based estimates, we considered a plot occupied by subalpine fir if it contained one or more individuals with a DBH greater than 2.54 cm. This criterion is more inclusive than using FIA-assigned forest types or abundance or basal area thresholds, and likely overestimates occupancy relative to other methods. However, given the large distribution of subalpine fir and the ecological diversity it encompasses, we opted for this simple approach that could be easily and consistently applied in all contexts. We assigned each occupied plot to one of six ecological provinces following Bailey's ecoregion classifications (Cleland et al., 2007; Fig. 1). To describe the climate space occupied by subalpine fir in each ecological province, we associated exact plot coordinates with

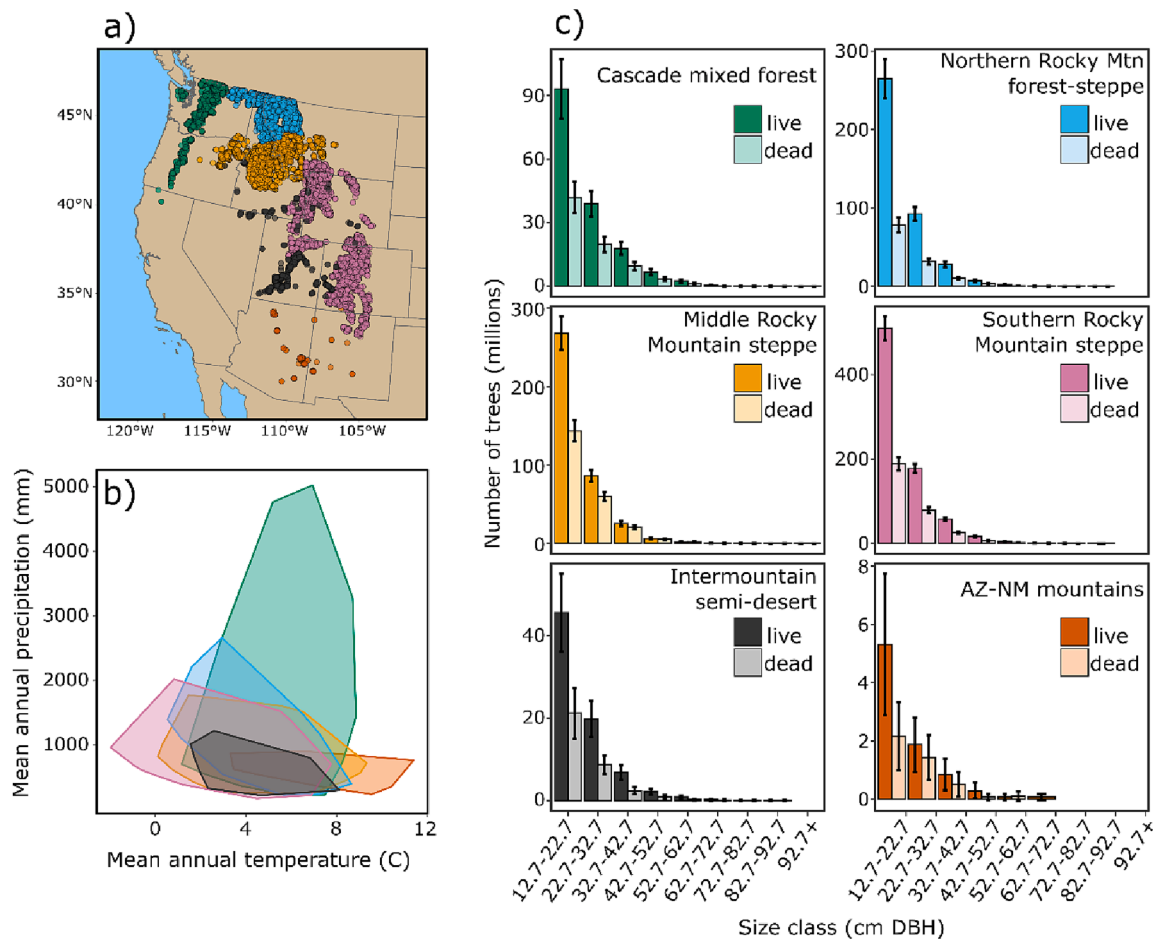


Fig. 1. The (a) geographic, (b) climatic, and (c) size distribution of subalpine fir in each of the 6 ecological provinces occupied by the species (colors corresponding between panels). (a) The geographic distribution of FIA plots containing subalpine fir between 2000 and 2019 (locations approximate; see Methods). (b) Minimum convex hull climate spaces bounding subalpine fir FIA plots in each ecological province. Mean annual temperature (x-axis) and mean annual precipitation (mm) correspond to the period between remeasurements for each FIA plot (2000–2009 and 2010–2019 for most plots). (c) Estimated current size class distributions of live and dead subalpine fir. Panels and colors correspond to ecological provinces, with dark bars indicating live trees in a size class, and light bars indicating dead trees. Estimates are based on FIA sampling design, with error bars indicating the sampling error of each estimate.

1980–2010 climate normals from ClimateNA (Wang et al., 2016), capturing the time period when most plots were established (Burrill et al., 2015). All plot locations shown in figures and contained in supplementary data files are approximate, due to statutory limitations on the publication of actual FIA plot locations. Within each ecological province, we estimated the abundance and basal area of live and dead subalpine fir in 12.7 cm DBH size classes following the estimation procedures of Bechtold and Patterson (2005), modified from implementation in the ‘rFIA’ package (Stanke et al., 2020; see Supplementary Materials Appendix S1) in R 4.2.1 (R Core Team, 2022).

We assessed subalpine fir population trends through time using similar procedures (Bechtold and Patterson, 2005; Stanke et al., 2020; Supplementary Materials Appendix S1) to estimate change in both abundance and basal area within smaller ecoregion subsections (Cleland et al., 2007) occupied by the species. Change was estimated between the 2000–2009 and 2010–2019 inventory periods using the “temporally invariant” method (Bechtold and Patterson, 2005; Stanke et al., 2020). Using this method, population estimates for each time point contain data from multiple years spanning the entire ten-year remeasurement period. While temporally binning measurements in this way does smooth trends through time, it also substantially reduces estimated uncertainty, especially across smaller areas containing fewer FIA plots (Bechtold and Patterson, 2005). Because Wyoming transitioned to the annualized plot remeasurement scheme later than other states, we estimated abundance and basal area change in the state between the most recent measurement

and the last previous periodic inventory in 2002 (Thompson et al., 2005). Individual trees within plots were linked between periodic and annual inventories in Wyoming using recorded distance and azimuth relative to plot centers; because these were not recorded for saplings, all population change estimates were calculated for trees larger than 12.7 cm DBH. Finally, to assess whether subalpine fir population trends reflect those of other associated tree species, we repeated our estimation for all species that co-occurred with subalpine fir. These conspecific estimates were limited to subalpine fir’s range, such that they reflect forest status and trends only where subalpine fir occurs.

2.3. Mortality and regeneration

We estimated subalpine fir mortality within each ecoregion subsection as the percent and density per hectare of estimated total live trees greater than 12.7 cm DBH in the 2000–2009 inventory that had died by the 2010–2019 inventory. Because FIA plots were remeasured approximately once every 10 years, this metric can be interpreted as a decadal mortality rate. We did not annualize our mortality estimates in order to avoid implying that mortality was constant over our study period, given the spatial and temporal heterogeneity of forest disturbance events. However, we assessed variation in decadal mortality rates through time at the ecological province scale using plot remeasurements from each survey year between 2011 and 2019. Because splitting inventories by survey year substantially reduced the sample size in each estimate, we

did not repeat this analysis at the ecoregion subsection scale. FIA field crews assign a putative cause of death for every mortality tree on a plot (*i.e.*, FIA variable 'TREE:AGENTCD'), differentiating between broad classes of mortality agents (*e.g.*, fire, insects, diseases, harvest, competition). We used this tree-level information to estimate the contribution of each mortality agent to total mortality within each ecoregion subsection and within larger ecological provinces.

We assessed regeneration of subalpine fir populations by estimating (1) adult recruitment as the number of trees that entered the greater than 12.7 cm DBH size class between inventory periods, and (2) the density of saplings (individuals between 2.54 and 12.7 cm DBH) present during the initial inventory period. Because trees smaller than 12.7 cm DBH were not tracked between periodic and annual inventories in Wyoming, these latter estimates excluded that portion of subalpine fir's distribution. We used linear quantile regression to quantify the relationship between these two estimates, and used pairwise bootstrapping as implemented in the R package 'quantreg' (Koenker, 2023) to assess the significance and fit of these relationships. We repeated this analysis for the next smaller size class by comparing sapling recruitment (number of trees entering the 2.54 to 12.7 cm DBH size class) to the initial density of seedlings (individuals smaller than 2.54 cm DBH and at least 15 cm tall).

2.4. Disturbance

Information on the distribution and impact of physical and biotic forest disturbances is contained in the FIA database in several different ways. Because we were specifically interested in how forest disturbances of all types and magnitudes impact population trajectories, we chose to use tree-level mortality agents (*i.e.*, FIA variable 'TREE:AGENTCD') as indicators of disturbance (Fitts et al., 2022). In this case, we considered a plot disturbed if it had one or more remeasured subalpine fir assigned the corresponding mortality agent code. As a result, we likely overestimate disturbed area relative to other approaches that incorporate a severity threshold (*e.g.*, using plot condition classes; Fitts et al., 2022) by including misidentified mortality. However, this is consistent with our approach for determining subalpine fir occupancy, and has the additional advantage of detecting low-severity disturbances. With this inclusive criterion, we used plot expansion factors to calculate the percentage of subalpine fir forested area within ecoregion subsections that experienced either fire or biological disturbance between

remeasurements. Biological disturbance encompassed mortality from either insects or diseases, which we combined because of difficulties in determining the proximate cause of mortality when both are present.

3. Results

3.1. Population status and trends

In the 2010–2019 inventory period, subalpine fir occurred in 5,614 FIA plots across an estimated 12.6 ± 0.14 million ha (total $\pm$ standard error) in six ecological provinces (Cleland et al., 2007; Fig. 1a). Across its entire distribution, the species occupied a mean annual temperature range of -3 to 11 degrees Celsius, and a mean annual precipitation range of 366 to 4650 mm. The climate space occupied by subalpine fir within each ecological province was fairly consistent, with the exception of the Cascade Mixed Forest province, which experienced far more precipitation than other provinces (Fig. 1b). Where it occurred, live subalpine fir density was highest in the Northern Rocky Mountain Forest-Steppe province (91.93 ± 3.94 trees per occupied hectare), followed by the Intermountain Semi-Desert province (90.93 ± 9.00 trees per occupied hectare). Density of dead subalpine fir was highest in the Intermountain Semi-Desert province (14.99 ± 2.68 trees per occupied hectare), followed by the Middle Rocky Mountain Steppe province (14.18 ± 0.65 trees per occupied hectare). Across all ecological provinces, subalpine fir populations followed an approximate negative exponential relationship between tree size and abundance (*i.e.*, a "reverse-j" size distribution), while the proportion of dead to live individuals increased with tree size (Fig. 1c).

Range-wide, the number of subalpine fir larger than 12.7 cm DBH decreased between 2000 and 2009 and 2010–2019 inventories by $12.13 \pm 1.08\%$, while basal area declined by $8.81 \pm 0.93\%$. Variation in these trajectories at the ecoregion subsection scale was distributed such that 62.1% of subalpine fir's occupied area experienced declines in both abundance and basal area, and 19.3% experienced increases in both measures. 12.7% of the species' occupied area saw declining abundance but increasing basal area, and *vice versa* for the remaining 5.9% (Fig. 2, Table S1). The magnitude of these changes also varied substantially, with the largest declines in parts of the Cascade Mixed Forest and Middle Rocky Mountain Steppe ecological provinces, and the largest increases scattered across the Northern and Southern Rocky Mountain provinces (Fig. 3, Fig. S5). Change estimates for all ecoregion subsections can be

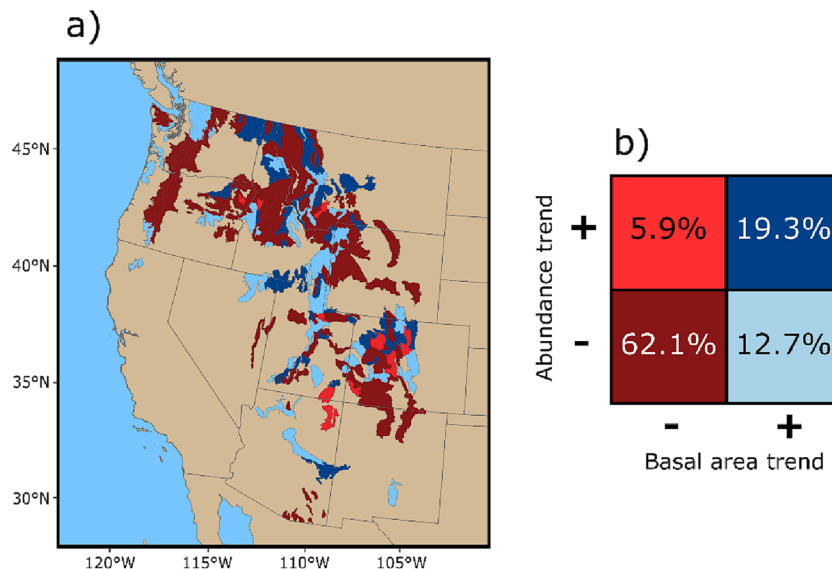


Fig. 2. Subalpine fir population trends estimated between 2000 and 2009 and 2010–2019 inventory periods for individuals with a measured diameter greater than 12.7 cm. Panel (a) shows ecoregion subsections occupied by subalpine fir, colored according to the combination of basal area and abundance trends, as shown in panel (b). Percentages in panel (b) indicate the proportion of forest area occupied by subalpine fir that falls within each change category.

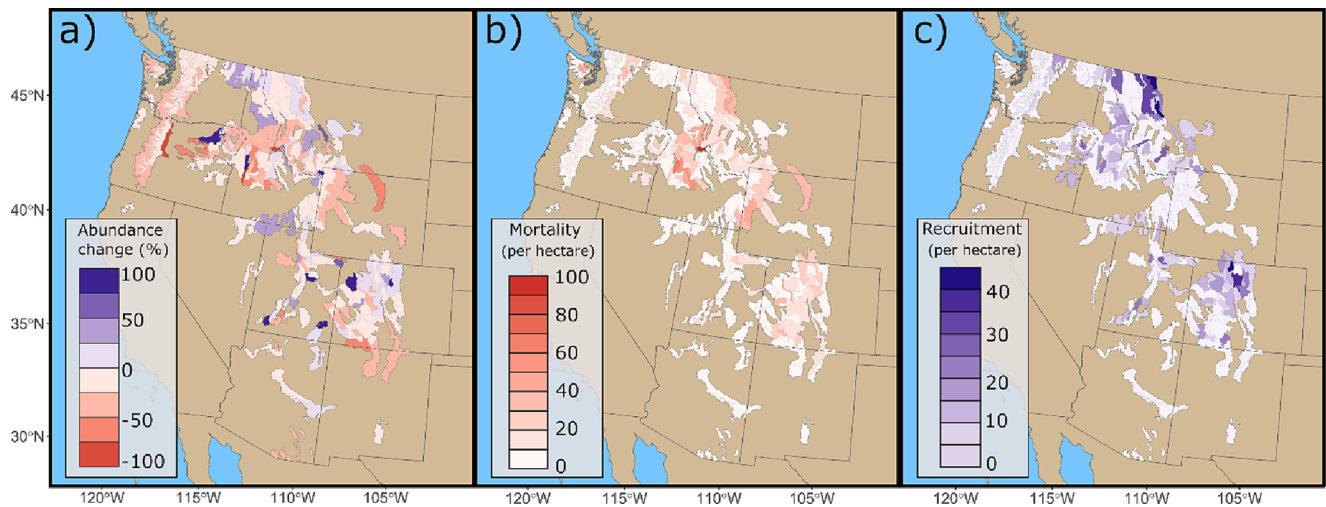


Fig. 3. Estimated change in adult subalpine fir abundance within occupied ecoregion subsections between 2000 and 2009 and 2010–2019 inventories (a), with corresponding mortality (b) and recruitment (c) densities (trees per hectare). All estimates are for trees with measured diameter greater than 12.7 cm.

found in Supplementary Materials Appendix S1 and Appendix S2.

3.2. Mortality and regeneration

Range-wide, we estimated 25.02 ± 2.74 % subalpine fir mortality between 2000 and 2009 and 2010–2019 inventories, on an individual tree basis. This mortality was not evenly distributed, with high mortality (greater than 50% between remeasurements) concentrated in the eastern Oregon Cascades, central Idaho, and parts of southern Colorado (Fig. 4a). We found that percent mortality was substantially lower in other regions (e.g., northern Colorado, northern Rockies), even when mortality occurred with relatively high density (Fig. 3, Fig. 4). We also found differences between ecological provinces in how variable mortality was through time (Fig. 4b). In particular, mortality was more consistent between years in the Southern Rocky Mountain Steppe (coefficient of variation (CV) = 11.7%) than any other province, and highest in the AZ-NM Mountain (CV = 57.6%) and Intermountain Semi-Desert (CV = 34.5%) provinces.

Tree-level mortality agents indicated that 83.4% of mortality was disturbance-related, with fire responsible for 36.8%, disease responsible for 24.5%, and insects responsible for 22.1% of total range-wide mortality (Fig. 4c). However, the contribution of each mortality agent varied substantially among ecological provinces. For example, while fire was the dominant subalpine fir mortality agent in the Middle Rockies, Pacific Northwest, and Intermountain Semi-desert provinces, insect and diseases were much larger sources of mortality in the southern Rockies and AZ-NM mountains (Fig. 4c).

Sapling density during the initial 2000–2009 inventory period and adult recruitment density between inventory periods ranged from 0 to 719.4 trees per hectare and 0–48.4 trees per hectare, respectively (Fig. 5a). In 78 ecoregion subsections (37%), we found no adult recruitment despite non-zero sapling density in the initial inventory. The slope of linear regressions between sapling density and adult recruitment increased with the data quantile considered (Fig. 5a). For example, the estimated slope of the 0.50 quantile (i.e., the median slope) was 0.04, whereas the slope was 0.11 for the 0.95 quantile. Positive adult abundance trends were associated with higher quantiles and steeper slopes between sapling density and subsequent adult recruitment (Fig. 5a). Seedling density during the initial inventory and subsequent sapling recruitment ranged from 0 to 5388.7 and 0–257.5 trees per hectare, respectively. Quantile slopes were lower than those for saplings and adults, and were not associated with adult abundance trends (Fig. 5b).

3.3. Disturbance

Range-wide, 7.4% of subalpine fir forests experienced fire mortality between 2000 and 2009 and 2010–2019, compared to 28.9% that experienced biological disturbance (i.e., insect and/or disease) mortality (Fig. 6). At the ecoregion subsection scale, fire-disturbed area was heavily right-skewed, with many regions experiencing very little to zero fire disturbance. However, most ecoregions experienced mortality from biological disturbances, with estimates ranging from 0 to 100% of subalpine fir forests impacted. Despite the smaller total disturbed area, mortality from fire per unit area disturbed accumulated at a rate approximately four times higher than mortality from biological disturbances (fire mortality: $\beta = 1.29$, $R^2 = 0.65$; insect/disease mortality: $\beta = 0.33$, $R^2 = 0.36$; Fig. 6c).

3.4. Interspecific comparisons

The majority of FIA plots containing subalpine fir during the 2010–2019 inventory period were assigned a primary condition with the “Engelmann spruce/subalpine fir”, “Subalpine fir”, “Lodgepole pine”, or “Douglas fir” forest types (i.e., FIA variable COND:FORTYPCD; Fig. S1). Accordingly, the most common species co-occurring on plots with subalpine fir were Engelmann spruce (*Picea engelmannii*), lodgepole pine (*Pinus contorta*), and Douglas fir (*Pseudotsuga menziesii*; Fig. S2). Comparing basal area trajectories between subalpine fir and all other combined co-occurring tree species yielded four possible combinations (Fig. 7): trajectories can have the same sign (both positive or both negative), or they can be mismatched (one positive and the other negative). Range-wide, declining subalpine fir basal area coincided with declines in the basal area of all other co-occurring tree species in 39.3% of forested area. Similarly coupled basal area increases occurred in 20.8% of forested area. Subalpine fir was in decline while other species increased in 21.7% of forest area, and the opposite was true in the remaining 18.2% (Fig. 7a). Where subalpine fir was in decline, fire was the most important mortality agent for the species; however, declines among other species were driven by very high insect mortality (greater than 50 trees killed per hectare; Fig. 7b). In particular, where all species except subalpine fir were in decline, insects were by far the largest source of mortality (71.4 ± 2.6 trees killed per hectare; Fig. 7b).

4. Discussion

Our analyses indicate that subalpine fir populations are in decline across much of the species’ distribution. Over the past decade, subalpine

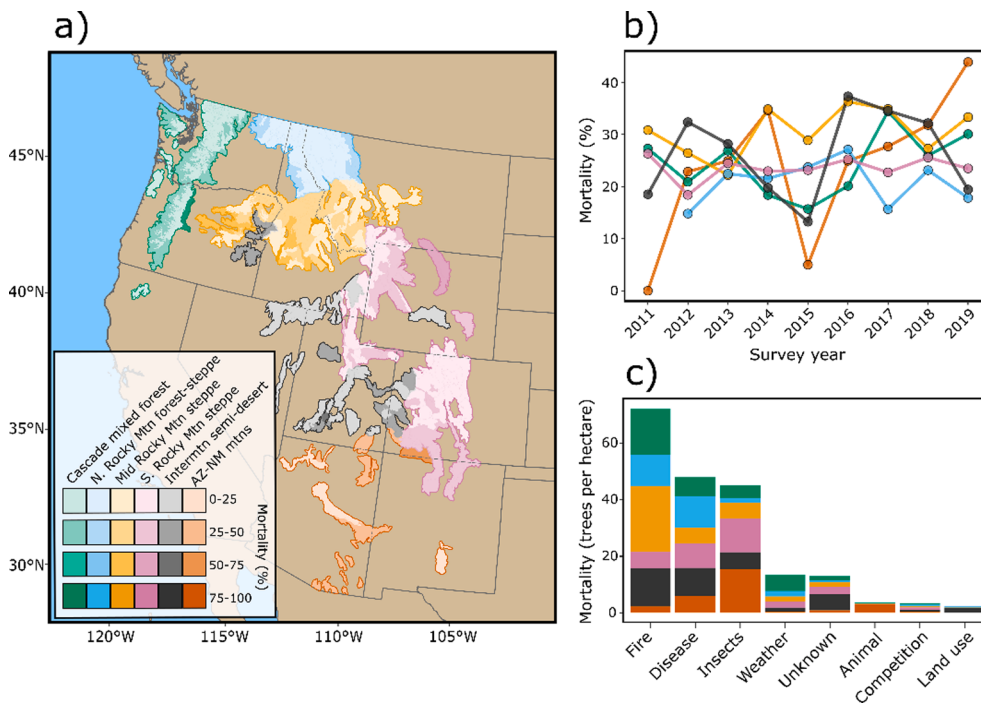


Fig. 4. Estimated mortality rates of adult (DBH greater than 12.7 cm) subalpine fir between 2000 and 2009 and 2010–2019 inventories. Colors in panel (a) correspond with ecological provinces, with darker colors indicating higher mortality. Panel (a) mortality estimates are inclusive of all data from both inventory periods. Panel (b) shows how mortality rates estimated between inventory periods vary based on each year's annual survey; y-axis represents an approximate decadal mortality rate. Point and line colors in panel (b) correspond with ecological provinces shown in (a). Panel (c) shows the contributions of field-assigned mortality agents (x-axis) to overall adult mortality (trees per hectare) within each ecological province (bar color) across complete inventory periods.

fir abundance and basal area have decreased concurrently in 62% of subalpine fir forests across the western United States, while increasing concurrently in only 19% (Fig. 2). Declines were dramatic in some regions (e.g., east side of the Oregon Cascades, central Idaho), with subalpine fir abundance declining by more than 75% from 2000 to 2009 levels. These steep population declines coincided with very high subalpine fir mortality, especially in regions where fire and biological disturbances (i.e., insects and diseases) were particularly prevalent (Fig. 3, Fig. 4). Indeed, most subalpine fir mortality range-wide was disturbance-related, with the importance of specific disturbance types and mortality agents varying substantially. Range-wide, fire and biological disturbances accounted for more than 80% of total subalpine fir mortality (Fig. 3), while the contributions of other sources like competition, harvest, and severe weather were minor. We found that the effects of fire and biological disturbance differed substantially, such that mortality accumulated approximately four times as rapidly with forest area impacted by fire compared to biological disturbances (Fig. 6C). This likely reflects subalpine fir's low fire tolerance and the diffuse nature of insect and disease mortality. However, tree mortality from biological disturbance agents has also been shown to alter fuel load and flammability in subalpine forest systems (Collins et al., 2012; Jenkins et al., 2008; Jolly et al., 2012; Jorgensen and Jenkins, 2011; Shaw et al., 2022), potentially increasing wildfire risk and severity during and after outbreaks. This suggests that some amount of biological disturbance may be obscured by subsequent fire, and that the population- and landscape-scale consequences of biological disturbance may be underestimated by focusing solely on direct mortality impacts.

While these results are concerning for subalpine fir populations that are experiencing protracted declines, regeneration may offset elevated mortality at larger scales and within certain landscapes. Among live trees in all six ecological provinces, we found the classic “reverse-j” size distribution (i.e., an approximate negative exponential relationship between tree size and abundance) thought to be indicative of a stable demographic structure (Fig. 1; Goeking and Windmuller-Campione, 2021; Rubin et al., 2006). Depending on the rate and distribution of mortality and recruitment, this abundance of smaller trees may be enough to balance mortality within larger size classes (Rubin et al., 2006). Indeed, we found that subalpine fir increased in both abundance

and basal area across a substantial portion of its distribution (19% of occupied area), especially in regions with relatively high density of new adult recruitment (Fig. 2, Fig. 3). In contrast, other subalpine tree species like Great Basin bristlecone pine (*Pinus longaeva*) and foxtail pine (*P. balfouriana*) have recently been found to have uniform size distributions, indicating a potential shortage of younger trees and suggesting an inability to balance mortality among larger, older size classes (Goeking and Windmuller-Campione, 2021).

However, our findings also suggest that regeneration density in itself is insufficient to guarantee a positive outcome for subalpine fir. Indeed, we found that a substantial portion of the species' distribution had no adult recruitment between inventories despite adequate initial sapling density (Fig. 5a). Ecoregion subsections in this group had uniformly negative population trajectories, whereas positive population trajectories were associated with the highest sapling – adult recruitment rates (Fig. 5a). Whether individuals recruit into the next-larger size class is a function of diameter growth rate and survival, which themselves may vary with climate, stand structure, disturbance, and many other factors. Assessing these relationships would form the basis of a full demographic transition model; while outside the scope of this study, future work along these lines could help us gain a more mechanistic understanding of subalpine fir population trajectories. For example, recent work by Schultz et al. (2021) and Shriver et al. (2022) used FIA data to train integral projection models, which they applied to questions about climate, competition, and disturbance effects on tree species' demographic vital rates and geographic distributions.

Other recent studies focusing on subalpine fir decline have found similar patterns to those we present here, with variation in mortality rates and causes likely reflecting differences in methods and scale. For example, across ecoregion subsections covering most of the Colorado portion of the Southern Rocky Mountain ecological province (i.e., ecoregions M331F - M331I; Cleland et al., 2007), we estimated an average of $20.58 \pm 5.21\%$ subalpine fir mortality between 2000 and 2009 and 2010–2019 FIA inventories (Supplementary Materials Appendix S2). In comparison, two recent studies covering approximately the same region estimated 24% and 37% subalpine fir mortality (Harvey et al., 2021, and Lalande et al., 2020, respectively). These higher mortality rates may reflect a longer time period than the one we consider:

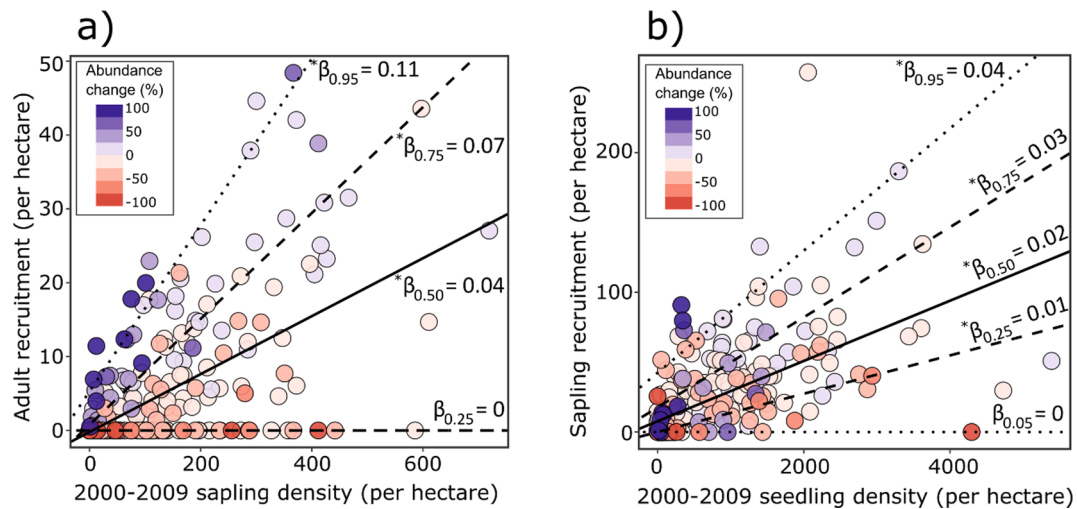


Fig. 5. Relationships at the ecoregion subsection scale between subalpine fir regeneration density and recruitment into larger size classes. Panel (a) shows the relationship between the density of saplings (defined as individuals between 2.54 and 12.7 cm DBH) in the 2000–2009 inventory period and adult (DBH greater than 12.7 cm) recruitment density between 2000 and 2009 and 2010–2019 inventories. Panel (b) shows the relationship between seedling (DBH < 2.54 cm) density in the 2000–2019 inventory period and sapling recruitment density between inventories. In both panels, black lines are linear quantile regressions, with β coefficients indicating the estimated slope of the corresponding quantile. Asterisks indicate that estimated slope coefficients are significant at the $p < 0.05$ level. Point color corresponds to the estimated percent change in adult abundance within each ecoregion subsection between 2000 and 2009 and 2010–2019 inventory periods.

Harvey et al. (2021) calculated tree-level mortality based on individuals estimated to be alive in the year 2000 that were dead during 2015–2016 sampling (i.e., a 15–16 year window), whereas Lalande et al. (2020) calculated the incidence of mortality based on a single plot measurement (i.e., potentially including mortality that occurred more than 10 years prior). Differences could also be due to a focus on areas with prior known and documented subalpine fir decline or temporal smoothing resulting from our temporally indifferent estimation (Bechtold and Patterson, 2005). Andrus et al. (2021) also provide subalpine fir mortality estimates at a smaller spatial scale, focusing on Niwot Ridge, Colorado, and found decadal mortality rates between 4.8% and 10.1%, depending on the specific timeframe (modified from Andrus et al., 2021). Our mortality estimate for the same region (M3311b – North Front Range subsection; Cleland et al., 2007) falls in this range, at $6.45 \pm 1.84\%$. These comparisons provide useful context for our change and mortality estimates, which are at a larger scale than other studies of subalpine fir decline (e.g., Andrus et al., 2021; Davis et al., 2022; Harvey et al., 2021; Lalande et al., 2020; Reich et al., 2016; Smith et al., 2015). While varying study designs, time periods considered, and analytical methods may contribute to differences between our mortality estimates and prior studies, these differences seem minor and suggest that large-scale sampling efforts like the FIA program are able to accurately detect trends identified by smaller-scale studies.

More broadly, our results suggest that subalpine fir could serve as an indicator of negative change in subalpine forest systems. Where subalpine fir is in decline, populations of other species are approximately twice as likely to also be in decline (Fig. 7). However, the reverse is not true; where subalpine fir basal area is increasing, other species are just as likely to experience declines as not (Fig. 7). This may be the result of different mortality drivers between species. For example, in regions experiencing general declines (i.e., decreasing basal area across all subalpine tree species), the largest mortality source for subalpine fir is fire, whereas mortality of other species is dominated by insects. Insect mortality is similarly the largest source of mortality by far in areas where subalpine fir populations are on positive trajectories, but other species are in decline (Fig. 7b). This suggests that the major mortality sources for subalpine fir across its distribution either directly impact other co-occurring tree species (e.g., fire disturbance) or may be associated with factors impacting other tree species (e.g., drought impacts, insects and diseases). However, declines in other species appear to be driven by

host-specific insect mortality (Fig. 7b), such that positive subalpine fir population trends give little insight into the trajectories of other species.

Cross-scale interactions between species-specific discriminant disturbances (e.g., host-specific insects and diseases) and other non-discriminant change drivers (e.g., wildfire, drought) may also be important components of overall forest change. For example, in a mixed subalpine fir – Engelmann spruce stand, a severe spruce beetle (*Dendroctonus rufipennis*) outbreak may cause Engelmann spruce mortality while having no direct detrimental effects on subalpine fir. Similarly, in the same context a severe balsam woolly adelgid infestation could cause very high subalpine fir mortality while leaving Engelmann spruce untouched (Davis et al., 2022; Hicke et al., 2023). However, in each case, resulting foliar drying and dead fuel loading increases the subsequent risk of more severe wildfire (Chadbourn, 2020; Jenkins et al., 2008; Jorgensen and Jenkins, 2011). This non-discriminant disturbance will impact all tree species present, regardless of whether they were affected by the initial insect outbreak, with severity more likely to be influenced by stand structural attributes than by species identity. Though outside the scope of the current study, additional work investigating how the presence of host-specific biological disturbance agents influences the trajectories of non-host tree species could help disentangle these interactions. This could be accomplished using additional forest health data contained in the FIA database. Specifically, living tree damages could be used to assess the presence of host-specific biological disturbance agents, and associated with subsequent forest disturbances. Because the work we present here was focused on disturbance impacts on subalpine fir population trajectories, we chose to use tree-level information on proximate mortality agents to define disturbances, rather than living tree damages or disturbance condition classes. While this allowed us to detect and quantify the effects of low-severity forest disturbances (Fitts et al., 2022), using these other aspects of the FIA database for similar purposes could lead to differing pictures of the distribution and impact of disturbances (Fitts et al., 2022; Mortenson et al., 2015; Randolph et al., 2021). For example, multiple concurrent or sequential disturbances are masked by focusing only on proximate mortality agents; while information on damage to living trees could discern these compound disturbances, it cannot be used to calculate their effects on mortality.

Outside of the FIA program, airborne or spaceborne remotely-sensed data can also be used to quantify the distribution and impact of forest

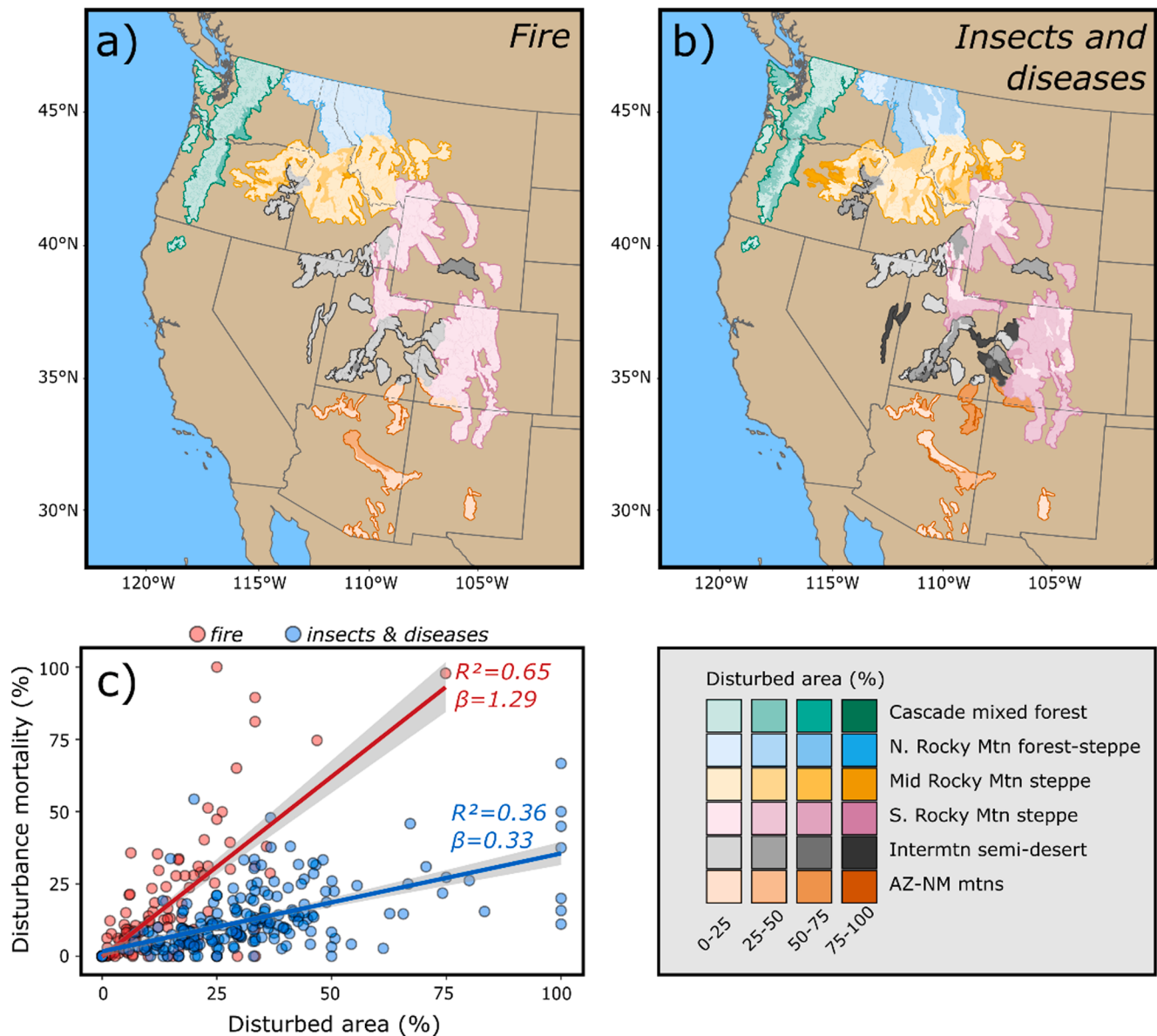


Fig. 6. The proportion of subalpine fir forest area impacted by fire (a) and insect/disease (b) mortality, by ecological province and ecoregion subsection. Colors in panels (a) and (b) indicate ecological provinces, and color darkness indicates the proportion of forest area containing subalpine fir impacted by each disturbance. Panel (c) shows the relationship between the amount of disturbed area (as a proportion of total forest area within an ecoregion subsection) and mortality caused by fire (red line and points) and insects/disease (blue line and points). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

disturbance (Senf et al., 2017). Indeed, most work to date quantifying the extent of subalpine fir decline on regional or larger scales in western North America has used Aerial Detection Survey (ADS) data in some capacity (e.g., Harvey et al., 2021; Lalande et al., 2020; Reich et al., 2016). These data can provide information about disturbance extent, distribution, and severity over vast areas with finer temporal resolution than plot-based estimates, providing an important monitoring tool for rapid disturbance detection (Hermosilla et al., 2015; Kennedy et al., 2015; Senf et al., 2017). However, because large-scale remotely sensed data are limited in their ability to provide tree-level information, attributing tree mortality to precise biological agents is difficult, often requiring integration with forest inventory or other plot-level data (Kennedy et al., 2015; Meigs et al., 2015; Meigs et al., 2011). Further work exploring how plot-based and remotely sensed forest disturbance datasets complement one another under differing conditions (e.g., landscapes, forest types, disturbance intensities, agent identities) would greatly improve our ability to monitor and predict changes in forest

ecosystems broadly. For example, forest inventory data could be used to identify vulnerable regions for specific species or forest types, within which disturbance events could be comprehensively assessed using satellite remotely sensed data and attributed to likely causal agents with aerial detection information and field validations. These assessments could then be used to guide and inform subsequent targeted field efforts, with the goal of establishing a collaborative and consistent change detection and monitoring framework.

Moving forward, building a predictive framework for how changing disturbance regimes may impact subalpine and other forest systems in the context of changing climates requires two principal advances. First, we need to improve our understanding of how individual tree species respond to physical and biological forest disturbances under different climatic conditions. While our approach here focuses on forest disturbance impacts on general population trajectories, work examining the interacting effects of changing climate and specific disturbance types on underlying demographic vital rates (e.g., mortality, recruitment,

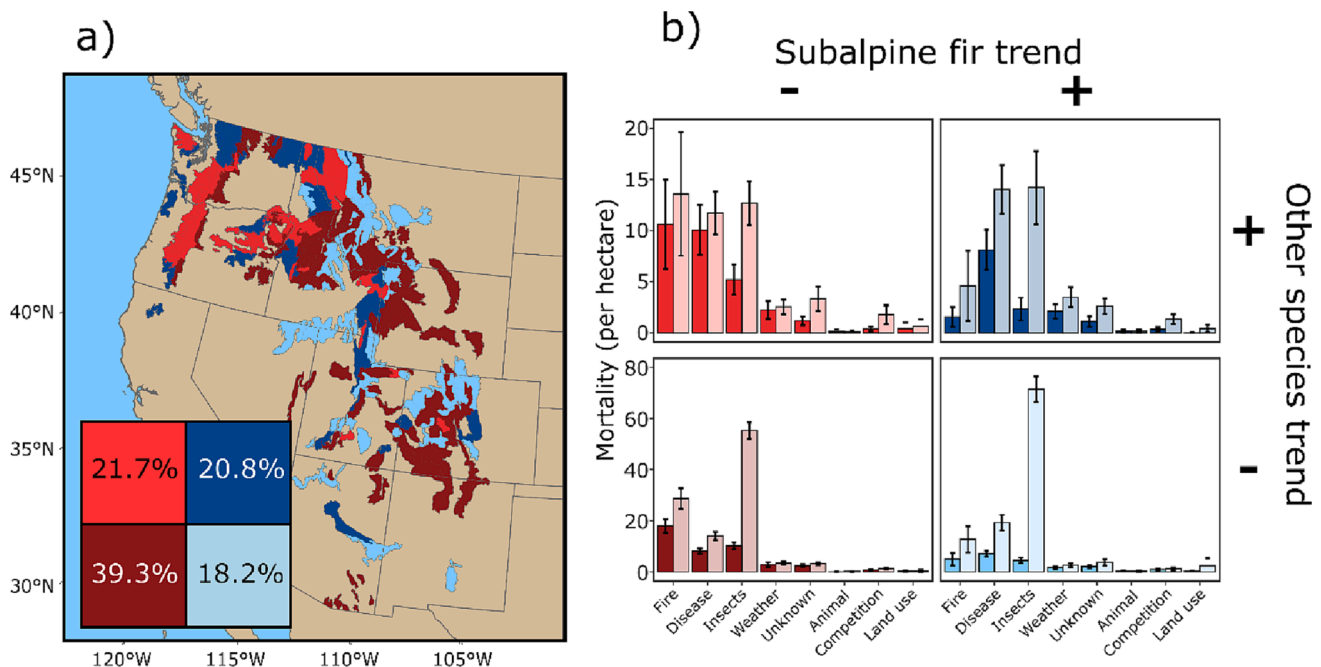


Fig. 7. Trends in subalpine fir basal area compared to the trends observed in other co-occurring species. Panel (a) shows the geographic distribution of ecoregion subsections containing subalpine fir, colored according to the combination of trends in the basal area of subalpine fir and other co-occurring species (b). Panel (a) inset shows the percent of subalpine fir forest area that falls into each basal area change category. Panel (b) shows the estimated mortality (trees per hectare) of subalpine fir (dark bars) and other co-occurring species (light bars) in each basal area change category caused by field-recorded mortality agents, with error bars indicating the estimate sampling error. Note that the two rows in panel (b) have different y-axis scales.

growth) is critically important. For example, recent work has found that warmer conditions are associated with elevated tree mortality for several species across disparate forest types (*Juniperus monosperma*, *J. osteosperma*, *J. scopulorum*, *Picea mariana*, *Pinus contorta*, *P. edulis*, *P. monophylla*, *Populus tremuloides*; Schultz et al., 2021; Shriver et al., 2022; Zhang et al., 2015). However, while warmer conditions were also associated with lower recruitment for a subset of these species, they had no impact on others (e.g., *Pinus edulis*; Schultz et al., 2021) and were even associated with elevated recruitment for one species (*Populus tremuloides*; Zhang et al., 2015). This suggests that future population trajectories may vary widely among species, driven by differences in their abilities to balance increasing mortality with new regeneration. Second, we thus need to build a comparative framework for assessing how these interspecific differences in species' demographic responses may lead to ecosystem restructuring or reassembly (*sensu* Seidl and Turner, 2022) under projected future climate and disturbance regimes. An important consideration in this area is that physical disturbance and biological disturbance agents are themselves subject to direct climate change effects (Lehmann et al., 2020; Shaw et al., 2022). Our hope is that the population assessments that we present here become a building block toward such a framework for subalpine forests that can be adapted and applied consistently to other forest types and ecosystems broadly.

CRediT authorship contribution statement

Daniel L. Perret: Conceptualization, Resources, Supervision, Writing – original draft, Writing – review & editing. **David M. Bell:** Conceptualization, Resources, Writing – review & editing. **Andrew N. Gray:** Conceptualization, Resources, Supervision. **John D. Shaw:** Conceptualization, Writing – review & editing. **Harold S.J. Zald:** Conceptualization, Resources, Supervision, Writing – review & editing.

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.

Data availability

FIA data publicly available; analysis code all contained in supplement and on corresponding author's GitHub repository.

Acknowledgements

This work was supported by interagency agreement 21-IA-11261959-058 between the USDA Forest Service Pacific Northwest Research Station and the DOE Oak Ridge Institute for Science and Education. This research was supported by the USDA Forest Service, Pacific Northwest Research Station, and the Western Wildland Environmental Threat Assessment Center. We thank the field crews, information management, and analytical staff responsible for collection and quality assurance of the USDA Forest Service Forest Inventory and Analysis Program. We further thank L. Lowrey and J. Halofsky for insightful and helpful discussion about this study. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official USDA or U.S. Government determination or policy.

Data Statement

FIA data are freely available for download from the USDA Forest Service FIA DataMart (<https://apps.fs.usda.gov/fia/datamart/datamart.html>). Climate data used in this study are freely available from ClimateNA (<https://climatenas.com/>). All code used for manipulating data, performing analyses, and generating figures is stored on the corresponding author's GitHub repository (<https://github.com/daniel-perret/SubalpineFirDecline>).

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