Journal of Environmental Management 373 (2025) 123654

Contents lists available at ScienceDirect

Journal of Environmental Management

journal homepage: www.elsevier.com/locate/jenvman

Research article

A spatial triage of at-risk conifer forests to support seed collection efforts and sustainable forestry

James H. Thorne [a], Jessie M. Godfrey [a,b], Ryan M. Boynton [a], Kristen D. Shapiro [a], Michelle A. Stern [a], Camille Pawlak [c,d], Matthew Ritter [c], Hyeyeong Choe [e,f,*]

[a] Department of Environmental Science and Policy, University of California, One Shields Ave, Davis, CA, 95616, USA
[b] Environmental Horticulture and Water Resources Management, University of California Cooperative Extension, 224 W Winton Ave #134, Hayward, CA, 94544, USA
[c] Biological Science Department, California Polytechnic University San Luis Obispo, San Luis Obispo, CA, 93407, USA
[d] Department of Geography, University of California Los Angeles, CA, 90095, USA
[e] Department of Agriculture, Forestry and Bioresources, Seoul National University, Seoul, 08826, Republic of Korea
[f] Research Institute of Agriculture and Life Sciences, Seoul National University, Seoul, 08826, Republic of Korea

ARTICLE INFO

Keywords:
Climate change risk
Pinus ponderosa
Reforestation
Seed collection
Operational priorities
Spatial prioritization

ABSTRACT

At-risk conifer stands growing in hot, arid conditions at low elevations may contain the most climate change-adapted seeds needed for sustainable forestry. This study used a triage framework to identify high-priority survey areas for *Pinus ponderosa* (Pipo) within a large region, by intersecting an updated range map with a map of seed zones and elevation bands (SZEBs). The framework assesses place-based climate change and potential wildfire risks by rank-order across 740 potential collection units. The study separately combined three operational measures of cone priority SEZBs from a government reforestation nursery in California – current inventory, target seed supply levels, and areas with high seed demand – to create operational SZEB priority rankings. Combining the risk and operational SZEB rankings permitted an overall priority ranking of survey areas, and road extents within each SZEB's Pipo area indicate accessibility. Pipo's California range covers 62,456.9 km^2, which intersects 740 of 1212 total SZEBs. Of these, 43 have high climate exposure under baseline (1980–2010) conditions, and 139 more become highly exposed by the end of the century. Of these 182 highly climate-exposed SZEBs, our index of high-intensity fire risk indicates 42 were also at high risk of stand replacing fire at the beginning of the 2023 fire season. Of these 42, only 4 are currently represented in the seed lot inventory. In contrast, the top 73 operational priority SZEBs all have relatively low risk rankings. Integrating models of landscape risk with operational seed collection priorities can direct collection efforts to high-risk stands before those are lost, and improve spatial coverage in seed bank inventories. The triage framework can provide spatial guidance for cone crop surveying efforts, and has the potential to improve forest nursery and field management. Triage elements can be updated or added to provide more comprehensive tracking over time. For example, wildfire perimeters and seed inventories could be updated annually and fuels reduction treatments, cone crop survey routes, annual assessments of cone crop condition, and additional seedbanks (e.g. for the USDA Forest Service) could be included.

1. Introduction

Pinus ponderosa Douglas ex Lawson & C. Lawson (Pipo/ponderosa pine) is an integral and often dominant component of reference state dry forests in California and across Western North America. It tolerates a fire-prone landscape with short fire return intervals of roughly 5–20 years (Keeley, 2012; Van de Water and Safford, 2011) and its highly flammable litter (Fonda et al., 1998; Fonda and Varner, 2004) promotes fires that may kill seedlings of other species (Williamson and Black, 1981) while relatively thick bark at early growth stages helps Pipo's own seedlings survive (van Mantgem and Schwarz, 2003; Steady et al., 2019). A traditional host species for bark beetle with the opportunity for coevolution (Amman, 1973), Pipo is often able to fend off infestation with monoterpene-rich resin production and delivery (Kane and Kolb,

* Corresponding author. Department of Agriculture, Forestry and Bioresources, College of Agriculture and Life Sciences, Seoul National University, 1 Gwanak-ro, Gwanak-gu, Seoul, 08826, Republic of Korea.
E-mail address: hy.choe@snu.ac.kr (H. Choe).

https://doi.org/10.1016/j.jenvman.2024.123654
Received 13 May 2024; Received in revised form 23 October 2024; Accepted 5 December 2024
Available online 27 December 2024
0301-4797/

2010; Sturgeon, 1979).

However, Pipo range has declined relative to its historic range over the last century (Thorne et al., 2008; Haffey et al., 2018; Davis et al., 2019). Some of this decline is due to management choices like fire suppression, that tend to favor more shade tolerant firs and cedars (Safford and Stevens, 2017). Some of this decline is due to several vulnerabilities amplified by climate change, which interact with each other and land management (Pausas and Keeley, 2021). Drought (Asner et al., 2015; Fettig et al., 2019, Kolb and Robberecht, 1996), bark beetle (Raffa et al., 2008), and fire regimes (Hagmann et al., 2021; Laurent et al., 2019; Westerling et al., 2006; Williams et al., 2023) are all deviating from the historic norms that shaped Pipo physiology and morphology, as well as the structure and composition of Pipo forests (Keeley, 2012; Stephens et al., 2015). The challenge and opportunity now, is for thoughtful post-disturbance reforestation interventions (North et al., 2019) to mitigate the impacts of climate change (Xu and Prescott, 2024), restore these forests (Davis et al., 2019; Steele et al., 2022), and increase the numerous ecological and societal benefits they provide (Dore et al., 2010; Fettig, 2018; Marcille et al., 2020). Seed collection is at the start of this reforestation pipeline.

Conifer seed inventories across the western US are insufficient to accommodate currently needed or anticipated reforestation efforts (Fargione et al., 2021). This holds true in California. California's Department of Forestry and Fire Protection recently completed a preliminary Assessment of Needs (AON) for its statewide seedbank (California Department of Forestry and Fire Prevention, 2023). The AON considered the conifer seed needed to secure reforestation on 25% of all forested landscapes for which the state of California is responsible. It found that the need considerably exceeds current inventory and Pipo is among the species with greatest assessed deficit (~10,000 bushels).

Because Pipo has an extensive distribution (Graham and Jain, 2005), the species itself may not be highly vulnerable to climate change (Potter et al., 2017), but stands at the lowest, hottest, and driest locations that it occupies, are at risk. High mortality has been observed at trailing edge locations across the species' range (Allen and Breshears, 1998; Negron et al., 2009; McDowell et al., 2009). Climatic conditions may also be less favorable for establishment and growth at trailing edge locations (Breshears et al., 2008; Hill et al., 2023). Following a stand-replacing disturbance, like the high severity fires increasing in size and frequency across California (Miller and Safford, 2012; Miller et al., 2012), many conifers in arid locations may be unable to regenerate naturally (Clark et al., 2021; Davis et al., 2019; Pozner et al., 2022; Rother and Veblen, 2016; Stevens-Rumann and Morgan, 2019; Stewart et al., 2021). Further, when an order comes into a nursery for seed or seedlings, a nursery manager checks the location of the request and, traditionally, tries to use seed from the same area or one nearby to fill the request. However, there is some acceptance of transferring seed/seedlings from lower elevation source locations to higher elevation planting locations as a form of climate-anticipating reforestation (St. Clair et al., 2022). As remaining low-elevation, hot and dry stands may be the best available sources for climate-optimized seed (Martínez-Berdeja et al., 2019; St. Clair et al., 2022), the urgency to collect from these at-risk locations increases. In sum, our approach addresses the potentially amplifying demand for seed from low elevation stands, to prepare for a future in which at-risk seed sources may no longer persist.

Nurseries tasked with reforestation in California use a map that splits the state into seed zones and 500-foot (152.4 m) elevation bands. Seed zones were originally drawn in 1946 (Fowells, 1946), and have gone through several revisions, the most recent in 1970 (Buck et al., 1970). There are 87 seed zones and 1212 seed zone x 500-foot (152.4 m) elevation bands (hereafter, "SZEBs") across California. These spatial units have been used to catalog the collection locations of conifer seed lots stored in nursery freezers, and in selecting seed lots to fill orders for seed or seedlings.

Our primary objective with this work was to provide a geographic selection analysis that can help to target, or triage (Bottrill et al., 2008), searches for Pipo seed by ranking risks to SZEBs from climate change and severe wildfire, as well as operational factors like seed demand for each seed zone (CAL FIRE's internal assessment) and the current inventory (California Department of Forestry and Fire Prevention, 2023)). We conducted an assessment of the SZEBs that contain the most environmentally at-risk Pipo and combined it with a rank order of seed need to generate a mapped ranking of priority areas for scouting Pipo seed crops across California. To do so required answering the following questions.

1) What is the existing range of Pipo in California and what SZEBs does the range intersect?
2) What is the relative risk from climate change and high-intensity wildfire for the extent of ponderosa pine in each SZEB?
3) What is the relationship between environmental risks and operational seed needs?
4) And, what are the highest priority scouting areas for Pipo in California?

2. Materials and methods

We developed a geospatial dataset and protocol that uses climate change risk, fire risk, and operational considerations (supply and demand), to target the collection of additional Pipo seed. We first generated a best-available, observation-based map of Pipo's distribution within California using several high-quality vegetation datasets. We then projected climate exposure to each grid cell across the identified Pipo range for a single climate model and emissions scenario through the end of the century. Climate risk and a proxy for high intensity fire risk were then combined into a rank-ordered overall risk category for each SZEB that intersected with the identified Pipo range. The final step in our selection process was to compare the SZEB risk rankings with three rankings for seed supply and demand at the LA Moran Reforestation Center, CAL FIRE's tree nursery in Davis, California. Once all SZEBs were ranked, as described in more detail below, we assessed access to show how the framework might be used to further efficiencies in scouting for and collecting Pipo seed. Because the SZEB framework currently uses Standard metrics for distance and elevation, we use feet and miles in some of the following calculations.

2.1. Ponderosa pine range map development

We wanted a map that portrays a single species' range, rather than one based solely on vegetation types that might contain the species. The reasons for this were to quantify our rankings as accurately as possible and ensure that all SZEB areas that intersect with the Pipo range were included. The map aims to err towards including rather than excluding potential range so as to capture as many stands as possible but exclude areas where the species is not found, to make the scouting effort more efficient. Although errors of commission (inaccurately assigning presence to our species range map) were not desirable (Di Marco et al., 2017), errors of omission (inaccurately assigning absence to our map) were even less desirable as they could eliminate high-risk seed sources from the assessment.

We constructed the Pipo range map for California by combining data from several vegetation surveys. The primary source used was a digitized Pipo range map (Pawlak et al., 2023) derived from the Griffin & Critchfield (G & C) atlas of California tree ranges (Griffin and Critchfield, 1972). We then updated the range by removing and adding locations using a series of other spatial data.

To refine the G & C digitization and remove raster cells unlikely to include Pipo, we first excised any raster cells outside its California elevation range of 150 m–2300 m as noted in the Jepson Flora of California (Hickman, 1993). We also excised grid cells which intersected with tree or shrub California Wildlife Habitat Relationship (CWHR) types from the most recent statewide vegetation map Fire and Resources

Assessment Program (FRAP, 2016) for which Pipo was not noted in the type description as a typical species (California Department of Fish and WildlifeBiogeographic Data Branch, 2021). Excised CWHR types included (e.g.) Alpine Dwarf Shrub (ADS), Alkali Desert Scrub (ASC), and Chamise-Redshank Chaparral (CRC; full list in SM Appendix 2).

This process removed large sections of the Pipo range map. To ensure we didn't exclude any extents, we then added areas with more recent or detailed datasets. We started by comparing the range map with 39 vegetation maps compiled by the California Department of Fish and Wildlife's (CDFW) VegCAMP, the Vegetation Classification and Mapping Program), which includes surveys by the National Park Service (NPS). If Pipo areas in a vegetation map intersected with the G & C base layer, we reviewed associated survey reports (SM Table 1) and added in any vegetation type polygons for which Pipo was a documented component. If survey reports were absent or vague, we assigned presence to CDFW/NPS survey vegetation types by conservatively interpreting the vegetation type descriptions in A California Manual of Vegetation (Sawyer et al., 2009) and/or confirming with expert opinion. An excel file that tracks the source of Pipo presence assignment for these surveys is available as SM Table 1.

We then added in point observation data from herbarium records and 18 vegetation and forest plot surveys from numerous sources (e.g. California state vegetation mapping, National Park Service Inventory and Mapping, and USDA Forest Service mapping and monitoring programs) assembled over the last several decades (SM Table 2).

Finally, if Pipo was specifically labeled in polygons from the Wieslander vegetation type maps from the 1930s (Thorne and Le, 2016), we also added back in those polygons. A complete list of our sources appears in Supplemental Tables for polygon and point data (SM Tables 1 and 2) and a text document describing our decision protocols is included as Supplemental text (SM Appendix).

2.2. Climate change risk index

For the climate change risk assessment, we applied a place-based climate exposure analysis that portrays variable risk within a specific vegetation type's range to the newly defined Pipo range (Thorne et al., 2015, 2018, 2020; Muñoz-Sáez et al., 2021; Choe and Thorne, 2019; Hidalgo-Triana et al., 2023). Data for ten hydro-climatic variables were generated using downscaling to 270 m grid resolution and the Basin Characterization Model (BCMv8, Flint et al., 2021) for a baseline time period (1981–2010) and for three future time periods (2010–2039, 2040–2069, and 2070–2099). The BCM variables used were the annual 30-year averages for: minimum temperature (tmin), maximum temperature (tmax), precipitation (ppt), potential evapotranspiration (pet), actual evapotranspiration (aet), climatic water deficit (cwd), snowpack (pck), groundwater recharge (rch), runoff (run), and soil water storage (str).

For historical precipitation and air temperature we used data from the Parameter Regression on Independent Slopes Model (PRISM; Daly et al., 2008). PRISM data has the highest accuracy for precipitation and high accuracy for temperature among five gridded renditions of California's historical climate, when compared to 1231 California weather stations (Stern et al., 2022). We statistically downscaled PRISM data from 4-km to 270-m (Thorne et al., 2020). For the future, we selected a relatively hot and dry global climate model (MIROC-ESM; Watanabe et al., 2011) and a high emissions scenario (Representative Concentration Pathway RCP 8.5; Thorne et al., 2020). Selection of a hot and dry future is a conservative approach, if future warming is less, or future precipitation more than in the model we selected, those should, theoretically, reduce direct climate stress on ponderosa pine. However, we cannot be assured of this, and so the selection of a hot and dry future is a conservative approach when considering a risk ranking for climate change stress.

Data from all time periods were extracted for 100,000 randomly selected points across California. The points were tagged as being within or beyond the Pipo range, and were inputted to a principal component analysis to define California's two-dimensional hydro-climatic space, which includes the Pipo range. From here, the baseline time period climate of each Pipo grid cell was ranked according to the frequency with which that climate occurred across grid cells in the ponderosa pine range. Climates found up to 80% of the time in the 1980–2010 period were considered not climatically stressful. Those occurring only 5% of the time were considered climatically stressful and classed as climate risky parts of the Pipo range.

The future climate projected for each grid cell was ranked using the baseline climate frequency class. When a cell's climate in one of the three future time periods became climate conditions found in only the 5% least-frequent baseline conditions, or fell outside all baseline climates (non-analog, NA), we classified the cell as climate risky. Any cells that fell or transitioned into climate conditions between stable and risky (80–95%) were classified as moderately risky. The average exposure score of all Pipo grid cells in each SZEB was then calculated for each of the 4 time periods using a zonal mean, and the mean value from each time period was classified into not stressful, moderately stressful, or highly stressful, and assigned to the SZEB.

The frequency distribution generated by this climate exposure analysis is two-tailed. A climate can be infrequent across a species' range because it is on the wet/cold end of the distribution or the hot/dry end of the distribution. To focus our results away from areas with starting conditions on the wet and cold end of the range, we used the distributions of tmin and ppt in the baseline time period (1980–2010) to move the coldest 10% and the wettest 10% of SZEBs to the bottom of our rankings (assigning a value of 0).

Although we did not want to exclude any areas which might have recently supported Pipo from the range maps used to define its climate space, we also did not want to prioritize areas for cone scouting recently burned at high severity or currently occupied by human land uses. High severity burn areas were identified using the Monitoring Trends in Burn Severity dataset for 1984–2021 (MTBS, 2022) and the Rapid Assessment of Vegetation Condition After Wildfire (RAVG) dataset for 2022 (U.S. Forest Service, 2023). Areas occupied by human land uses were identified using the FRAP Fveg map (FRAP: Fire and Resources Assessment Program, 2016). After removing areas burned at high severity or currently occupied by human land uses like Urban (URB) and Pasture (PAS), any SZEBs with 1 grid cell or less remaining were also bumped to the bottom of our rankings (assigned a value of 0).

Due to either wet/cold conditions or low areas, a total of 184/740SZEBs were limited to the lowest climate risk category regardless of their climate exposure values. Before any high severity burn or land use types were removed, 47/740 SZEBs were represented by a single grid cell. We did not incorporate the same wet/cold limitation into the wildfire rankings (below) but we did incorporate the same high burn severity and land use/area-based limitation.

Our final ranking of climate change exposure risk assigned a value of 0–5, as follows: 0 = low exposure or limited priority; 1 = never exceeds moderate exposure; 2 = high exposure by 2070–2099; 3 = high exposure by 2040–2069; 4 = high exposure by 2010–2039; and 5 = high exposure in the baseline time period 1980–2010.

2.2.1. High-severity wildfire risk index

To assess the risk of high intensity fire to each grid cell, we generated a proxy for potentially high fuel loads or stand densities by comparing the years since an area last burned to the historic fire return interval. The assumption is that landscapes which are overdue for a burn, relative to pre-colonization fire frequencies, are at higher risk.

We used two fields from a preexisting Fire Return Interval Departure (FRID) dataset (Safford et al., 2014). These fields were Time Since Last Fire (TSLF), updated through 2021 at the time of this analysis, and mean reference fire return interval (meanRefFRI). To accommodate fires from 2022, we combined the data in the FRID TSLF field with all fire-impacted cells in the RAVG raster for 2022 (U.S. Forest Service,

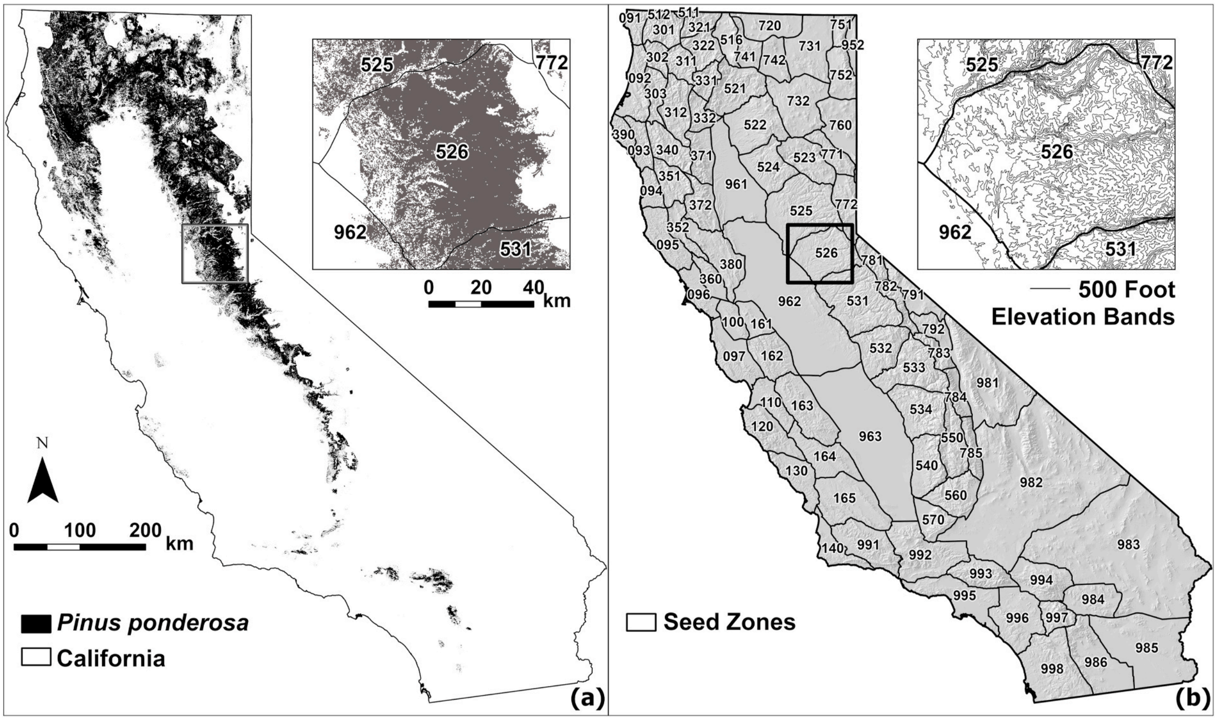


Fig. 1. The 2023 range map for ponderosa pine in California (a) and the seed zones and elevation bands used in nursery seed lot catalogs (b). Numbers on the right-hand image are the identification number of each seed zone.

2023), setting these cells to a TSLF value of 1 and adding 2 to all TSLF data derived from the FRID dataset. We then used the following formula 1 - (TSLF/meanRefFRI) to estimate relative fuel accumulation, and assess the risk to each cell within the identified Pipo range. A few cells could not be assigned as they didn't have an underlying fire return interval value. These cells are coded with values of −999.

We then calculated a mean value for the Pipo grid cells within each SZEB, first converting any negative values (i.e. within the range of precolonization fire return intervals) to zeros so that very large negative values would not render means meaningless. SZEBs with one Pipo grid cell or less were bumped down in the rankings into a "very low" high intensity fire risk category, regardless of mean relative fuel load values.

The final wildfire risk ranking assigned a value of 0–3 to each SZEB as follows. If the resulting mean value for all Pipo grid cells in a SZEB was less than or equal to 0 then, on average for that SZEB, the most recent fire was within the range of precolonization fire return intervals and the final wildfire risk ranking was 0 = very low. If the resulting mean value was less than or equal to 0.33 but greater than 0, then the mean time since last fire was up to 1.5 x the precolonization fire return interval and the ranking was 1 = low. If the resulting mean value was less than or equal to 0.67 but greater than 0.33, then the mean time since last fire was 1.5–3 x the precolonization fire return interval and the ranking was 2 = moderate. If the resulting value was greater than 0.67, then the mean time since last fire was more than 3x (up to ~10x) the precolonization fire return interval and the ranking was 3 = high.

2.2.2. Combining climate and wildfire intensity risk

We created a combined risk index by adding the climate change risk index and the high-severity wildfire risk index at the SZEB level. This created a ranking from 0 to 8, representing the various combinations of risk, with 0 being very low and 8 being high.

2.3. Operational needs assessment

To better integrate the risk assessment with ongoing nursery practices, we developed three indices of operational seed needs: seed zones from which the LAMRC receives a high number of seed or seedling requests; a CAL FIRE estimate of the bushels of seed needed to reforest 25% of non-industrial privately-held forested lands (California Department of Forestry and Fire Prevention (2023); and, a ranking of the bushels of ponderosa seed available per SZEB in the LAMRC's inventory. These categories represent priorities that the LAMRC already considers when determining areas for cone crop scouting.

The following describes the rankings in each index:

High-demand seed zones – Based on the number of requests, we ranked seed zones as: High = 1 or Low = 0.

Reforestation targets – We ranked the estimated number of bushels (a term deriving from the volume of the baskets used when collecting conifer cones, equal to about 0.04 m^3) needed for reforesting conifer extents in each SZEB as follows: 0 needed = 0; 0–10 = 1; 11–50 = 2; or >50 bushels = 3.

Inventory – We ranked the Pipo seed in the inventory in terms of bushels as: 0 = 4; 0–10 = 3; 10–50 = 2; 50+ = 1.

Combining operational needs to rank-order ponderosa SZEBs – We added the three categories together to create an index from 0 to 8, representing different combinations of operational priority for seed collection.

2.4. Overall rank order analysis

We used the SZEB rank values for combined climate and fire risk and then combined operational priority to rank-order all 740 SZEBs. We sorted the table (SM Table 3) first by risk and then by operational priority, high-to-low. This resulted in a sequentially ranked series for the 740 ponderosa SZEBs. The table can also be used to rank order the SZEBs according to any of the individual or combination of metrics—climate, fire, and/or the three operational categories.

2.5. Post ranking SZEB access analyses

We used Open Street Map (OpenStreetMap contributors, 2024) to calculate both the linear extent of roads within the ponderosa range of

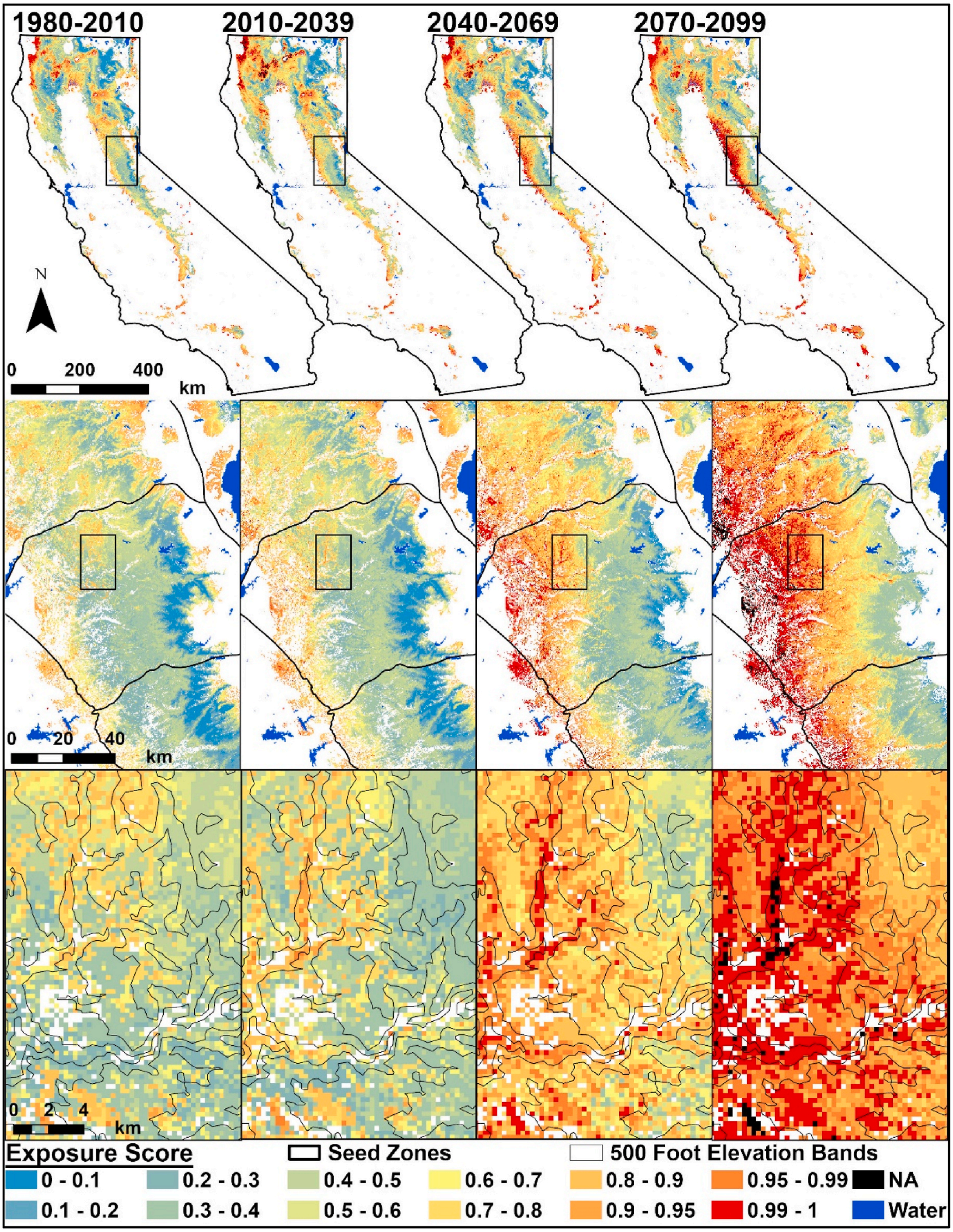


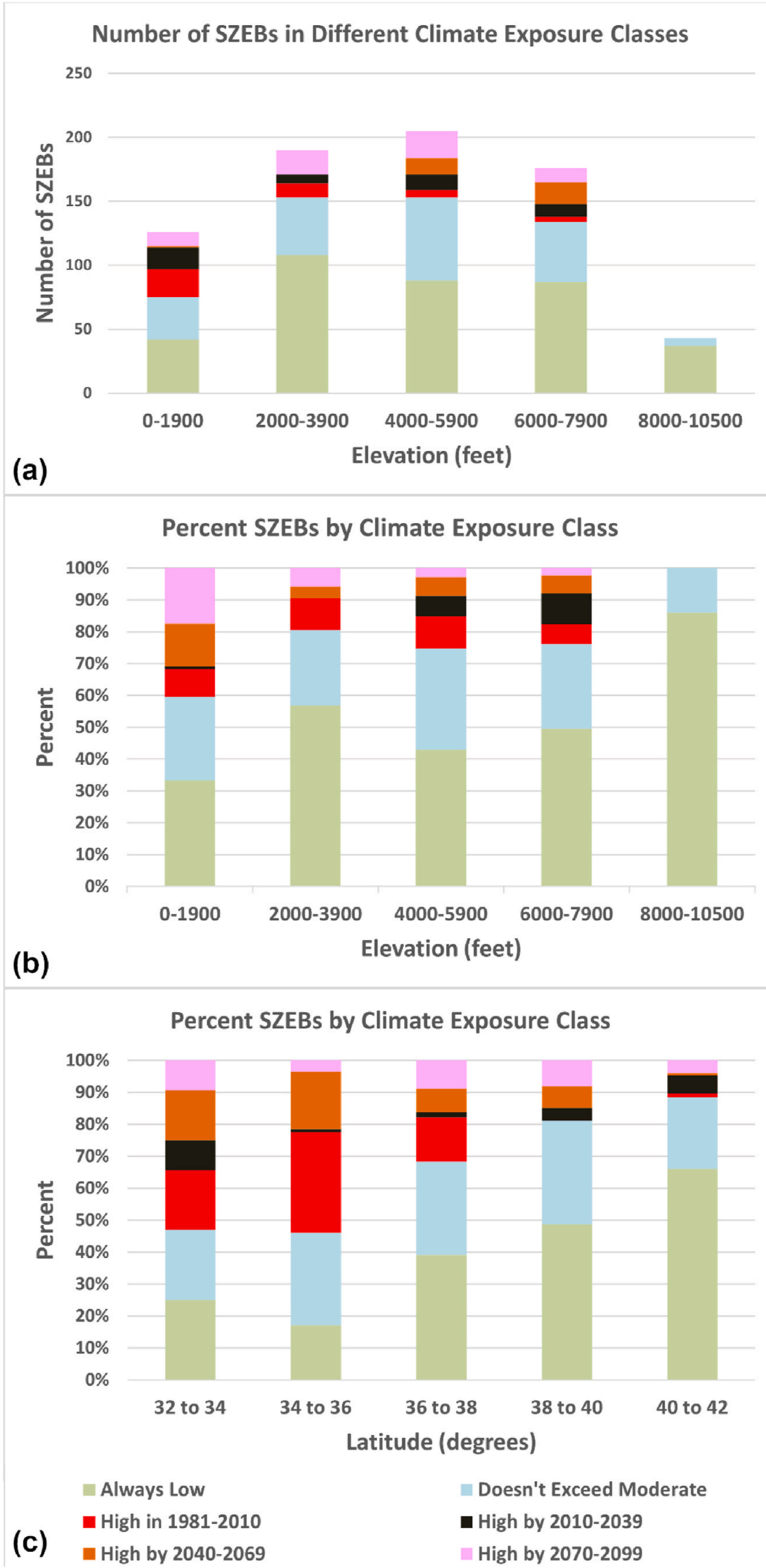
Fig. 2. Climate change exposure score for ponderosa pine's range in 4 time periods. Increasing levels of high climate exposure are particularly evident in the southern and lower-elevations of the range. The high exposure found in the northwest represents areas that are the 10% wettest and coolest of the range in the baseline time period.

each SZEB and the area within 100m of a road. This can be used to evaluate accessibility among similarly priority-ranked SZEBs. We also show an example of how aerial imagery can be used to confirm that stands are still extant in areas that are identified as high priority SZEBs for cone scouting.

3. Results

3.1. Ponderosa pine range

Pipo range in California covers 62,456.9 km^2 and intersects with 740 SZEBs (Fig. 1). The extent of Pipo within a SZEB ranged from 519.9 to



(caption on next page)

Fig. 3. The number and percentage of SZEBs in different classes of climate stress according to elevation (a & b) and by latitude (c). The red band and above show the number or percentage of SZEBs that have high climate exposure ranking from 2010 (red). to 2040 (black), to 2070 (brown), to 2100 (pink). A total of 51 SZEBs (40.5%) below 2000' (610 m) are highly exposed during this time. The pattern is similar for SZEBs in the 2000–4000' (to 1219 m), 4000–6000' (to 1829 m), and 6000–8000' (to 2438 m) elevations, with 19.4, 25.4, and 23.9% of their respective SZEBs showing high climate stress by 2100. An average of 52.5% of the SZEBs in southern California, between 32 and 36° latitude, have high climate exposure from now to the end of the century, compared to an average of 20.9% for those north of 36° latitude, which includes most of the Sierra Nevada Mountains.

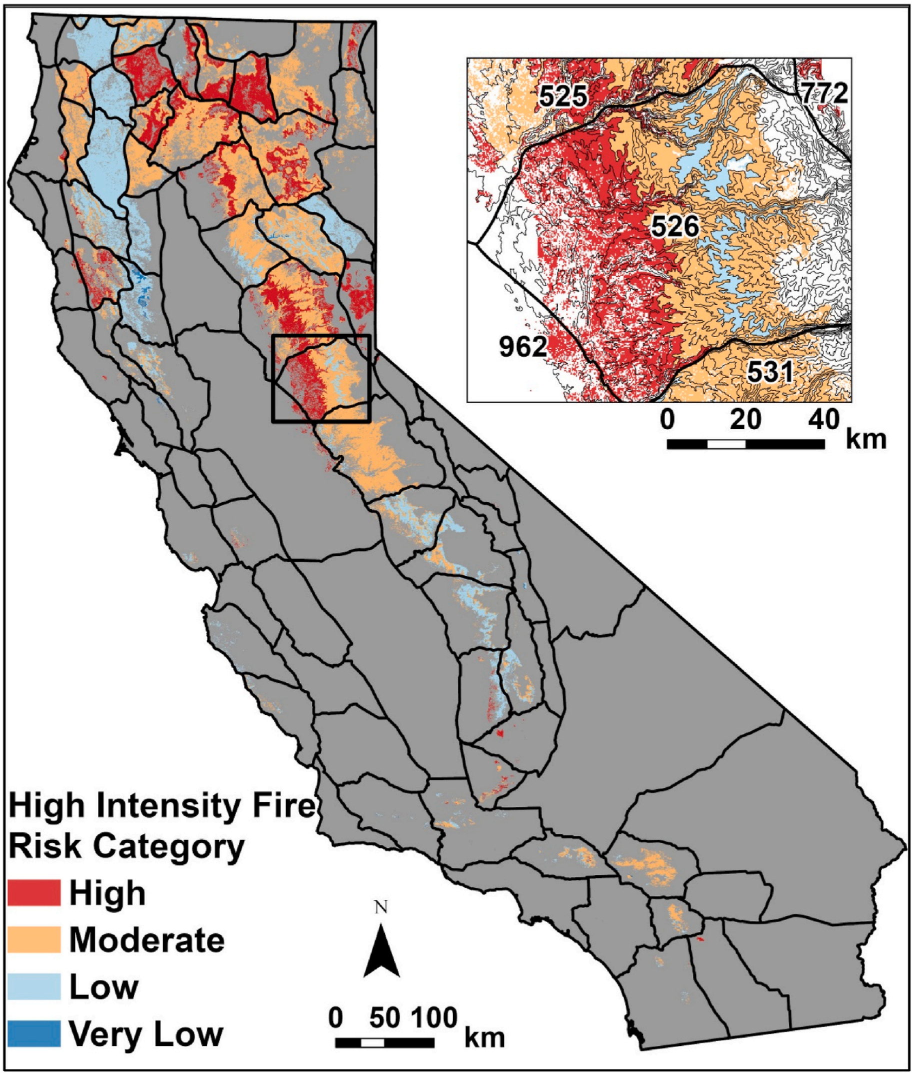


Fig. 4. Spatial ranking of high fire intensity risk to ponderosa pine cone crop collection areas. The map shows SZEBs within the ponderosa pine range assumed to have high fuel loads based on time since last fire relative to pre-colonization fire return intervals. The priorities have been classed into four levels with highest priority shown in red.

0.027 km^2. Results for all SZEBs and metrics in this section are provided in SM Table 3.

3.2. Climate exposure

By end-century, 182/740 ponderosa pine (24.6%) SZEBs are in the high climate risk category for climate exposure. In the baseline time period, 43 SZEBs were already at the hot dry margin. Another 46 SZEBs enter this category by 2040, 31 more by 2070, and 62 more by 2099 (Fig. 2).

Of Pipo's 126 SZEBs in the 0–2000′ elevation band, 22 are at high climate risk in the baseline time period (1980-2010), with 17 more projected to move into high climate stress conditions by 2040; an additional 12 join them by 2100, bringing the total number of low elevation Pipo SZEBs to 51 (40.5%) by end-century (Fig. 3; Supplemental Table 3). The remainder stay in low or moderate projected climate stress. However, the progression of climate stress moving uphill can be detected in that these elevation extents show a higher proportion of SZEBs entering high climate stress by end-century, relative to the number currently in high exposure.

3.3. Fuels and wildfire risk

For wildfire intensity risk, 135 of Pipo's 740 SZEBs are in the highest risk category, including 32 of the 126 below 2000' (25%). Similar numbers of SZEBs at high wildfire risk extend through elevations up to 8000' (Fig. 4).

Eleven SZEBs have the highest risk profile for both wildfire and climate, five in the 2000–4000′ elevation and six between 4000 and 8000' (SM Table 3). An additional 65 SZEBs are in moderate wildfire risk

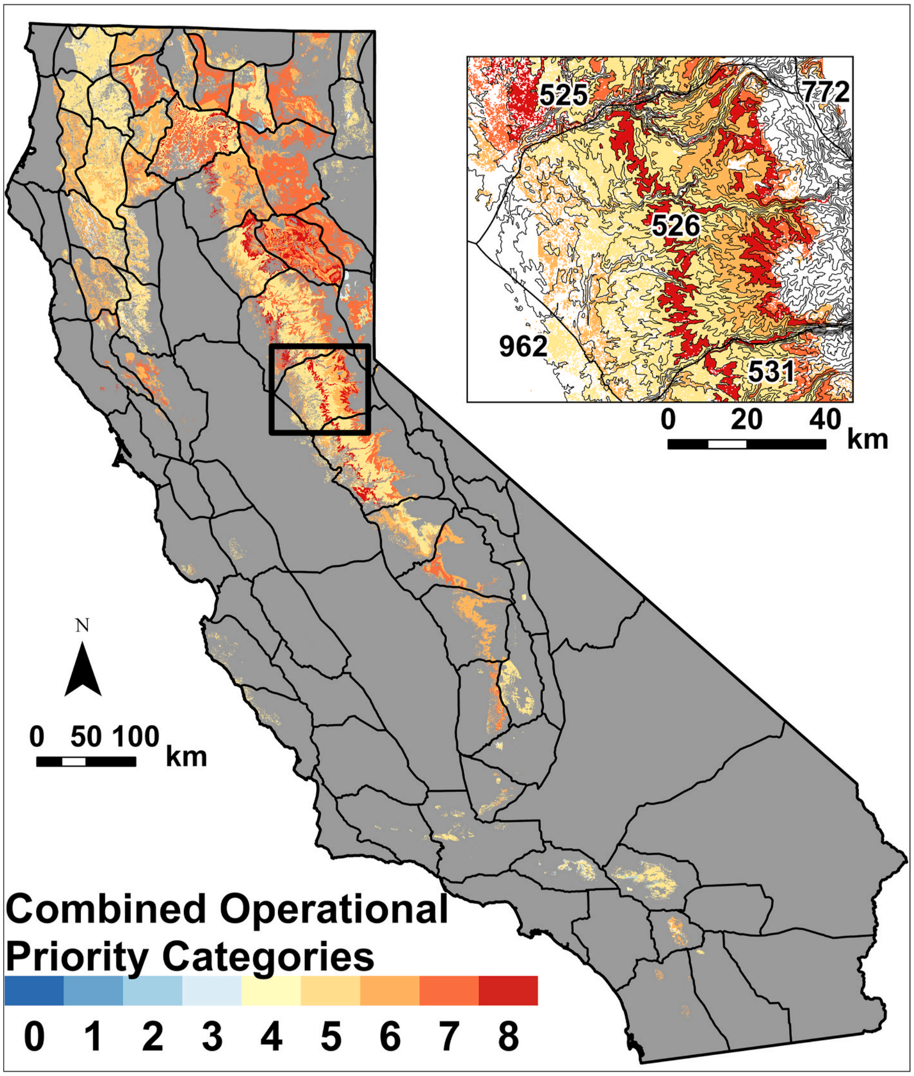


Fig. 5. Spatial ranking of operational priority for ponderosa pine cone crop collection areas. The map shows the combination of three operational priorities used in determining seed collection field efforts by the LA Moran Reforestation Center (seed orders, anticipated seed need for reforestation of private, non-industrial lands, and current supply of seed lots in the repository. The map units shown are the 740 seed zone elevation bands (SZEBs) containing the range of ponderosa pine overlaid by outlines of all seed zones (main map) and/or elevation bands (inset). The priorities have been classed into nine levels with highest priority shown in red.

and high climate risk. These SZEBs are distributed with 25 between 0 and 2000′, 10 from 2000 to 4000′, 20 in the 4000–6000′ range and 10 above 6000'. Finally, 35 SZEBs have low wildfire intensity risk, but high climate exposure, 30 of which are between 2000 and 4000'.

3.4. Operational priority rankings

250 Pipo SZEBs are in seed zones where landowner demand for seed has historically been high.

Of the 740 total Pipo SZEBs, 76 are expected to require more than 50 bushels of seed to reforest 25% of their forested areas and another 137 are expected to need 10–50 bushels.

655 of the 740 SZEBs have no seed supply in the LAMRC inventory and 26 more have low supplies, <10 bushels.

Combining operational priorities identifies 13 SZEBs in the highest of 8 operational need classes, 60 in the 2nd highest class, and 211 in the 3rd highest class (Fig. 5).

3.5. Combined ranking framework

The final categorical combination ranks all Pipo SZEBs for both risk and operation (Fig. 6). The top 11 SZEBs in the highest climate-fire risk category (8), fall into operational priority category 6 (of 8) or lower. Similarly, the top 13 SZEBs in the highest operational priority category fall into relatively low climate-fire risk categories, although 4 fall into our highest fire risk class. Summing these 24 SZEBs in independently ranked highest climate risk, fire risk, or operational priority categories, 23 have no seed in the inventory.

We used available road datasets to assess road lengths within the Pipo range, which covers 107,632 km. A 100m buffer on these roads shows that 17,100 km^2 of Pipo range could potentially be viewed from the roads (e.g. Fig. 7). There are 45 SZEBs with no roads in Pipo. Among the others, mean road extent is 155 km. Among the SZEBs with the highest combined climate and wildfire risk, road access in their Pipo areas ranges from 0 to 120 km. Among the 13 SZEBs with highest operational priority, road access ranges from 12 to 1251 km.

Of the top 11 priority SZEBs for climate-fire, roads in their Pipo extents that measure more than 1 km are found in 7, with lengths from 2 to 22 km. The 13 highest operational priority Pipo areas in SZEBs all have road access, ranging from 0.29 to 120 km lengths.

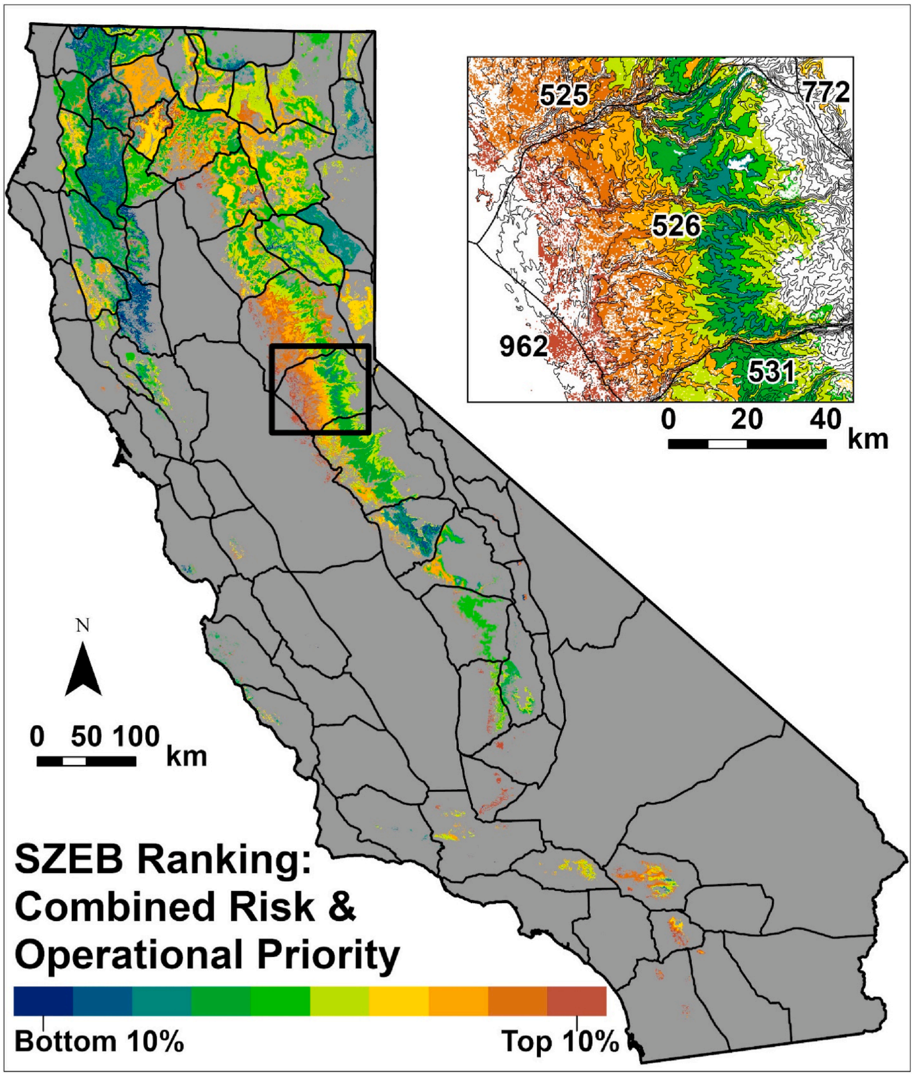


Fig. 6. Spatial ranking of combined risk and operational priorities for ponderosa pine cone crop collection areas. The map shows seed zone elevation bands (SZEBs) containing ponderosa pine range order-ranked from 1 to 740 by the combination of climate exposure risk, wildfire risk and three operational priorities (seed orders, anticipated seed need for reforestation of private, non-industrial lands, and current supply of seed lots in the repository. Here the 740 SZEBS are classed into 10% intervals, with the 74 highest-priority SZEBs shown in red. *Post-ranking analysis: road access and visual inspection.*

4. Discussion

Overall, there is a poor overlap between SZEBs at high risk and those with high operational priority. This is exacerbated by the low numbers of seed lots in the LAMRC's overall seed inventory. In particular, areas in the Transverse ranges and southern California already exhibit high levels of risk, and are poorly represented in the state's seed inventory. It is possible that federal or private timber companies' seed banks for Pipo have better representation for these areas, but this study did not have access to those records, pointing to the need to build a comprehensive inventory of seed lots in repository, particularly with regards to intensifying climate change trends.

The spatial pattern of projected stressful climate exposure across Pipo range is consistent with general observations that vegetation shifts upslope (Breshears et al., 2008) and that tree species show varying levels of latitudinal migration in North America (Sharma et al., 2022). This phenomenon is widely observed in California, for Pipo (Thorne et al., 2008; Hill et al., 2023), other tree species (Wright et al., 2016), and for 4426 native plant species in California, whose ranges have moved upslope an average of 13 m over the past century (Wolf et al., 2016). Overall, we found that about 40% of the Pipo range in SZEBs below 2000′ is either already in or will be in high climate exposure by end-century, while 52% of California's mountain region Pipo in the southern third of the state (south of 36° latitude) are already or will be at high levels of climate stress by end century. Ponderosa pine's lower elevation and latitudinal range retractions are represented here by high climate exposure advancing upslope and into the 36–38° latitude zones over the remainder of this century (Fig. 3).

The projected increase in climate stress to California Pipo stands at southern and lower elevation locations provides incentive to ensure remaining stands are surveyed for cone crops; a motivation that increases when considering the rapid expansion of wildfire extents over the past decade (California Department of Forestry and Fire Prevention, 2022), operational seed needs, low seed inventories, and the potential genetic value of seed lots from low elevations for use in climate change anticipatory reforestation, wherein trees originating from hotter and drier locations may be better adapted to future hotter and drier conditions expected to occur at the planting site (Xu and Prescott, 2024).

The updated Pipo range map is the base for this study. We used Pipo presence data to define the boundaries of land supporting the species, and it was across this range that we assessed climate exposure and high-intensity wildfire risk. Our mapping process of first cutting Griffin &

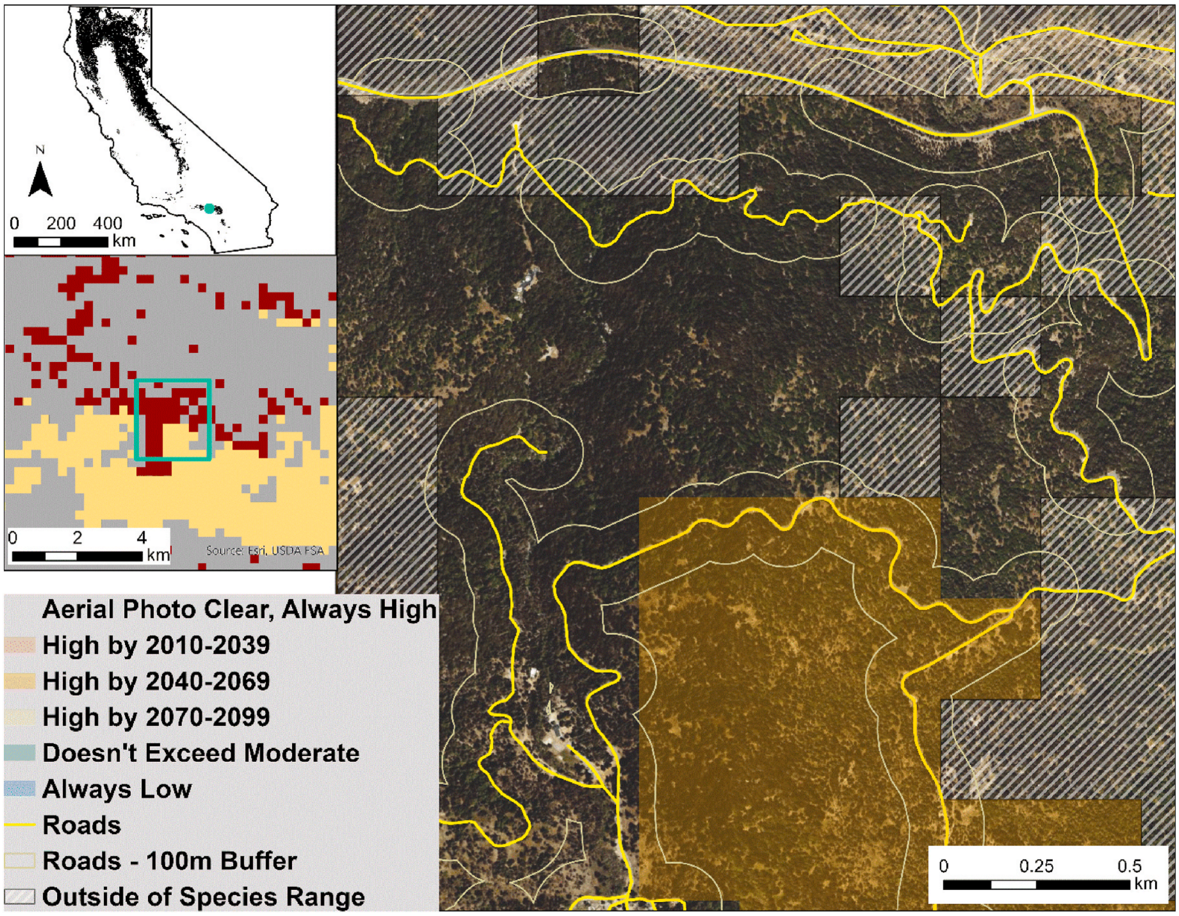


Fig. 7. Screening prior to sending a cone crop survey. The figure shows part of seed zone 994 (upper left); lower left shows the areas within (red and tan) and outside *Pinus ponderosa* range (grey). The large image shows a high-priority ranked area comprising 3 elevation bands from 3500 to 5000'. Their overall ranking (out of 740 SZEBs) is 66th, 35th and 122nd. The aerial imagery shows these stands have not been recently lost to disturbance. The roads show 18 km of vehicle access to assess potential cone crops. The roads traverse areas with high current climatic exposed (aerial imagery unobscured) and an area projected to be highly exposed in the 2040–2069 time period (tan). Road length would permit roadside scouting of 5.4 km^2, indicated by the 100m buffer. If forest in the cross hatching is found to have mature Pipo stands, those could be added to the range map. Once a survey was conducted in this area, notes on stand condition, potential future cone crop sites, and other field data could be added to the GIS for future years.

Critchfield's Pipo range map (1972) by its minimum elevation given in the California flora (150 m, Hickman, 1993), then adding areas where subsequent surveys detected the species, may have excluded some low-elevation stands in southern California, if those had not been surveyed after 1972. The same lower cutoff at higher latitudes, the range spanning from 32 to 42° latitude, likely includes the majority of ponderosa stands. Although we did not further examine lands below 150 m in southern California, much of those lands are heavily used by humans, which we removed from range map when we removed landcover types including urban and agriculture (SM Appendix 2).

New technologies in forestry are improving mapping precision and accuracy, including drones for mapping post-wildfire vegetation growth (Young et al., 2022) and LiDAR and hyperspectral imagery for mapping structure and species across increasingly large areas (Qin et al., 2022). Spatial modeling of single species' ranges across large areas has predominantly relied on statistical models including wide-ranging plot--based efforts (Riley et al., 2021) and hybrid projects that combine satellite imagery and plot data (e.g LEMMA GNN; https://lemma.forestry.oregonstate.edu/data). Our approach contrasts by compiling multiple map- and point-based records that represent true-positive presence locations, which for California represents the first updated Pipo range map in 52 years (Griffin and Critchfield, 1972). We primarily used this approach in order to explore the spatial patterns of climate stressors within the known range. This place-based approach aligns with the need of forest management to understand how climate change stress varies across the lands they manage, which can inform the selection of adaptation management strategies including prioritizing areas to scout for cone crops. The range map also provides a spatial baseline for further range modifications from additional surveys and monitoring, particularly given the rapid increase in mapping technologies, geospatial computing capacity and inventory approaches.

The integration of remote sensing that can identify forest structure, fuels, and productivity of individual stands within the mapped Pipo range also represents a promising way to further improve the assessment of risks within an existing range. Operationally, inclusion of these types of data, as well as local knowledge, may already be possible for individual national forests or at sub-watershed scales. Foresters planning seed collection campaigns within their areas of responsibility may have the opportunity to incorporate such data. For example, they may also already be familiar with zones in their areas that are more or less productive for Pipo, or in which other risk factors such as bark beetles (Raffa et al., 2008) should be considered.

The operationalization of climate-adaptive reforestation also requires integrating anticipated future conditions and ecological forecasts which can benefit from technologies like GPS to better record the locations of collected seed lots, rather than the large areas encompassed in SZEBs. Seed lots registered with stand level precision would permit more precise assessment of which seed lots are best suited for climate-adaptive planting (Young et al., 2020), and would be a suitable addition to web-based tools such as the Climate Adaptive Seed Tool (https://reforestationtools.org/climate-adapted-seed-tool/) or the seed lot selection tool (St Clair et al., 2022; https://seedlotselectiontool.org/sst/) that assist reforestation practitioners. However, even while incorporating more accurate methods and technologies going forward, it is also necessary to retain legacy seed lot records that historically recorded seed lot locations using the Bureau of Land Management's Public Lands Survey System subdivisions of Township Range and Section (TRS; FGDC.gov, https://www.fgdc.gov/standards/projects/cadastral/index_html), whose minimum area covers one square mile. For example, 738 (66%) of the LAMRC's seed lot inventory in 2022 are registered only by TRS localities, 15 seed lots by latitude and longitude, the remaining locations are by place or person name, and 14% of its 334 Pipo seed lots were collected in 1980 or earlier.

Spatial risk-ranking of SZEBs addresses one step of the reforestation cycle at which climate change and other factors can be incorporated, the seed collection step. Because these stands are predominantly at low and hot elevations, their seeds may also be needed for climate adaptive planting (Young et al., 2020; St. Clair et al., 2022) by matching them to sites where future conditions will be as hot as the low elevation sites where the seeds were collected are today. Some site-specific variability in ponderosa traits may be genotype- or location-specific (Martínez-Berdeja et al., 2019; Ramírez-Valiente et al., 2021). To ensure that these evolved traits are represented in seed inventories for future plantings, increased seed collection efforts are needed, particularly for areas at high risk of loss and that are underrepresented in the current seed inventory.

5. Conclusions

Reforestation nurseries manage complex programs to collect, accession, and store seed; process orders and select seed lots; and grow and distribute appropriate seedlings for field operations. These processes are challenged by a warming climate, changes in precipitation patterns and wildfires. We examined one of the first steps in reforestation operations by combining CAL FIRE's LA Moran Reforestation Center's seed inventory with climate change projections and risk of high-intensity wildfire for the seed zone elevation bands that make up the spatial units the nursery uses. We found spatial prioritization for ponderosa pine based on risk identified areas not identified when using nursery operational priorities related to seed supply and demand. Combining individual objectives in rank-ordered classes permits the incorporation of risk-based metrics into route-planning for cone crop surveys. Additionally, use of road networks and aerial imagery permits pre-field assessment of whether ponderosa stands are accessible and still extant in areas that are selected. Overall low inventories of seed and increasing risk make incorporating such efficiencies a useful contribution to the early steps in the reforestation process.

Further efficiencies in scouting for cones could include keeping records of routes travelled during surveys, areas surveyed, stands observed, and observations of the level of cone production by species on a yearly basis. Similarly, spatial updates of wildfire and potentially other types of tree mortality (e.g. bark beetle attacks) could improve the efficiency of seed collection efforts.

CRediT authorship contribution statement

James H. Thorne: Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Jessie M. Godfrey:** Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis, Data curation. **Ryan M. Boynton:** Writing – review & editing, Visualization, Investigation, Data curation. **Kristen D. Shapiro:** Writing – review & editing, Formal analysis, Data curation. **Michelle A. Stern:** Writing – review & editing, Investigation, Formal analysis. **Camille Pawlak:** Writing – review & editing, Resources. **Matthew Ritter:** Writing – review & editing, Resources. **Hyeyeong Choe:** Writing – review & editing, Investigation, Formal analysis.

Funding

This work was supported by CAL FIRE [grant number 8GG21805].

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: James Thorne reports financial support was provided by California Department of Forestry and Fire Protection. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors would like to thank Denia Troxell, Kuldeep Singh, Katherine Bolte, and James Scheid with the Lewis A. Moran Reforestation Center in Davis, California for facilitating access to their seed bank inventory and guidance throughout the project. We thank Joe Stewart and Jessica Wright for content discussions. We would also like to thank Steve Ostoja from the USDA Climate Hub for earlier support in the development of the framework.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2024.123654.

Data availability

We have shared the link to our data in the supplementary material.

References

Allen, C.D., Breshears, D.D., 1998. Drought-induced shift of a forest–woodland ecotone: rapid landscape response to climate variation. Proc. Natl. Acad. Sci. USA 95, 14839–14842. https://doi.org/10.1073/pnas.95.25.14839.

Amman, G.D., 1973. Population changes of the mountain pine beetle in relation to elevation. Environ. Entomol. 2 (4), 541–548. https://doi.org/10.1093/ee/2.4.541.

Asner, G.P., Brodrick, P.G., Anderson, C.B., Vaughn, N., Knapp, D.E., Martin, R.E., 2015. Progressive forest canopy water loss during the 2012-2015 California drought. Proc. Natl. Acad. Sci. USA 113 (2), 249–255. https://doi.org/10.1073/pnas.1523397113.

Bottrill, M.C., Joseph, L.N., Carwardine, J., Bode, M., Cook, C., Game, E.T., Grantham, H., Kark, S., Linke, S., McDonald-Madden, E., Pressey, R.L., Walker, S., Wilson, K.A., Possingham, H.P., 2008. Is conservation triage just smart decision making? Trends Ecol. Evol. 23 (12), 649–654. https://doi.org/10.1016/j.tree.2008.07.007.

Breshears, D.D., Huxman, T.E., Adams, H.D., Zou, C.B., Davison, J.E., 2008. Vegetation synchronously leans upslope as climate warms. Proc. Natl. Acad. Sci. USA 105 (33), 11591–11592. https://doi.org/10.1073/pnas.0806579105.

Buck, J.M., Adams, R.S., Cone, J., Conkle, M.T., Libby, W.J., Eden, C.J., Knight, M.J., 1970. California tree seed zones. USDA Forest Service, San Francisco and Division of Forestry. Department of Conservation, California Resources Agency, Sacramento, CA.

California Department of Fish and Wildlife, Biogeographic Data Branch, 2021. California Wildlife Habitat Relationship System. Version 10.1.24. Sacramento, CA. (Accessed 4 May 2023).

California Department of Forestry and Fire Prevention, 2023. Reforestation Services Program 2023 Assessment of Needs for the State Seed Bank. California Department of Forestry & Fire Protection, Sacramento, CA.

California Department of Forestry and Fire Prevention, 2022. The fire and resource assessment program (FRAP) fire perimeters database [WWW document] URL [https://frap.fire.ca.gov/frap-projects/fire-perimeters/. . Accessed January 2023.

Choe, H., Thorne, J.H., 2019. Transboundary climate adaptation strategies are needed for east asian temperate forests. Climatic Change 156, 51–67. https://doi.org/10.1007/s10584-019-02493-8.

Clark, J.S., Andrus, R., Aubry-Kientz, M., Bergeron, Y., Bogdziewicz, M., Bragg, D.C., Brockway, D., Cleavitt, N.L., Cohen, s, Courbaud, B., Daley, R., Das, A.J., Dietze, M., Fahey, T.J., Fer, I., Franklin, J.F., Gehring, C.A., Gilbert, G.S., Greenberg, C.H., Guo, Q., HilleRisLambers, J., Ibanez, I., Johnstone, J., Kilner, C.L., Knops, J., Koenig, W.D., Kunstler, G., LaMontagne, J.M., Legg, K.L., Luongo, j, Lutz, J.A., Macias, D., McIntire, E.J.B., Messaoud, Y., Moore, C.M., Moran, E., Myers, J.A., Myers, O.B., Nunez, C., Parmenter, R., Pearse, S., Pearson, S., Poulton-Kamakura, R., Ready, E., Redmond, M.D., Reid, C.D., Rodman, K.C., Scher, C.L., Schlesinger, W.H., Schwantes, A.M., Shanahan, E., Sharma, S., Steele, M.A., Stephenson, N.L., Sutton, S., Swenson, J.L., Swift, M., Veblen, T.T., Whipple, A.V., Whitham, T.G., Wion, A.P., Zhu, K., Zlotin, R., 2021. Continent-wide tree fecundity driven by indirect climate effects. Nat. Commun. 12, 1242. https://doi.org/10.1038/s41467-020-20836-3.

Davis, K.T., Dobrowski, S.Z., Higuera, P.E., Holden, Z.A., Veblen, T.T., Rother, M.T., Parks, S.A., Sala, A., Maneta, M.P., 2019. Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration. Proc. Natl. Acad. Sci. USA 116 (13), 6193–6198. https://doi.org/10.1073/pnas.1815107116.

Daly, C., Halbleib, M., Smith, J.I., Gibson, W.P., Doggett, M.K., Taylor, G.H., Curtis, J., Pasteris, P.P., 2008. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. Int. J. Climatol. 28, 2031–2064.

Di Marco, M., Watson, J.E.M., Possingham, H.P., Venter, O., 2017. Limitations and trade-offs in the use of species distribution maps for protected area planning. J. Appl. Ecol. 54 (2), 2–411. https://doi.org/10.1111/1365-2664.12771.

Dore, S., Kolb, T.E., Montes-Helu, M., Eckert, S.E., Sullivan, B.W., Hungate, B.A., Kaye, J. P., Hart, S.C., Koch, G.W., Finkral, A., 2010. Carbon and water fluxes from ponderosa pine forests disturbed by wildfire and thinning. Ecol. Appl. 20 (3), 663–683. https://doi.org/10.1890/09-0934.1.

Fargione, J., Haase, D.L., Burney, O.T., Kildisheva, O.A., Edge, G., Cook-Patton, S.C., Chapman, T., Rempel, A., Hurteau, M.D., Davis, K.T., 2021. Challenges to the reforestation pipeline in the United States. Frontiers in Forests and Global Change 4 (8). https://doi.org/10.3389/ffgc.2021.629198.

Fettig, C.J., 2018. Socioecological impacts of the western pine beetle outbreak in southern California: lessons for the future. J. For. 117 (2), 138–143. https://doi.org/10.1093/jofore/fvy029.

Fettig, C.J., Mortenson, L.A., Bulaon, B.M., Foulk, P.B., 2019. Tree mortality following drought in the central and southern Sierra Nevada. California, U.S. Forest Ecology and Management 432, 164–178. https://doi.org/10.1016/j.foreco.2018.09.006.

Flint, L.E., Flint, A.L., Stern, M.A., 2021. The basin characterization model-a regional water balance software package. In: United States Geological Survey Techniques and Methods 6-H1, p. 85. https://doi.org/10.3133/tm6H1.

Fonda, R.W., Belanger, L.A., Burley, L.L., 1998. Burning characteristics of western conifer needles. Northwest Sci. 72, 1–9.

Fonda, R.W., Varner, J.M., 2004. Burning characteristics of cones from eight pine species. Northwest Sci. 78 (4), 322–333.

Fowells, H.A., 1946. Forest seed collection zones in California. USDA Forest Service, California forest and Range Experimental Station. Forest Research Note 51.

FRAP: Fire and Resources Assessment Program, 2016. GIS Data. California Department of Forestry and Fire Protection, Sacramento, CA. https://frap.fire.ca.gov/mapping/gis-data(note:thevegetationmap. is listed as FVEG on this website).

Graham, R.T., Jain, T.B., 2005. Ponderosa Pine Ecosystems. USDA Forest Service General, Pacific Southwest Research Station, Berkeley, CA. Technical Report PSW-GTR-198.

Griffin, J.R., Critchfield, W.B., 1972. The Distribution of Forest Trees in California. USDA Forest Service Research Paper, Pacific Southwest Research Station, Berkeley, CA.

Haffey, C., Sisk, T.D., Allen, C.D., Thode, A.E., Margolis, E.Q., 2018. Limits to ponderosa pine regeneration following large high-severity forest fires in the United States Southwest. Fire Ecology 14, 143–163. https://doi.org/10.4996/fireecology.140114316.

Hagmann, R.K., Hessburg, P.F., Prichard, S.J., Povak, N.A., Brown, P.M., Fulé, P.Z., Keane, R.E., Knapp, E.E., Lydersen, J.M., Metlen, K.L., Reilly, M.J., Sánchez Meador, A.J., Stephens, S.L., Stevens, J.T., Taylor, A.H., Yocom, L.L., Battaglia, M.A., Churchill, D.J., Daniels, L.D., Falk, D.A., Henson, P., Johnston, J.D., Krawchuk, M.A., Levine, C.R., Meigs, G.W., Merschel, A.G., North, M.P., Safford, H.D., Swetnam, T. W., Waltz, A.E.M., 2021. Evidence for widespread changes in the structure, composition, and fire regimes of western North American forests. Ecol. Appl. 31 (8). https://doi.org/10.1002/eap.2431.

Hickman, J.C., 1993. The Jepson Manual: Higher Plants of California. University of California Press, Berkeley, CA.

Hidalgo-Triana, N., Solakis, A., Casimiro-Soriguer, F., Choe, H., Navavro, T., Perez-Latorre, A.V., Thorne, J.H., 2023. The high climate vulnerability of western Mediterranean forests. Sci. Total Environ. 895, 164983. https://doi.org/10.1016/j.scitotenv.2023.164983.

Hill, A.P., Nolan, C.J., Hemes, K.S., Cambron, T.W., Field, C.B., 2023. Low-elevation conifers in California's Sierra Nevada are out of equilibrium with climate. Proceedings of the National Academy of Sciences Nexus 2.2, pgad004. https://doi.org/10.1093/pnasnexus/pgad004.

Kane, J.M., Kolb, T.E., 2010. Importance of resin ducts in reducing ponderosa mortality from bark beetle attack. Oecologia 164, 601–609. https://doi.org/10.1007/s00442-010-1683-4.

Keeley, J.E., 2012. Ecology and evolution of pine life histories. Ann. For. Sci. 69, 445–453.

Kolb, P.F., Robberecht, R., 1996. High temperature and drought stress effects on survival of Pinus ponderosa seedlings. Tree Physiol. 16 (8), 665–672. https://doi.org/10.1093/treephys/16.8.665.

Laurent, P., Mouillot, F., Moreno, M.V., Yue, C., Ciais, P., 2019. Varying relationships between fire radiative power and fire size at a global scale. Biogeosciences 16, 275–288. https://doi.org/10.5194/bg-16-275-2019.

Marcille, K.C., Morgan, T.A., McIver, C.P., Christensen, G.A., 2020. California's Forest Products Industry and Timber Harvest, 2016. USDA Forest Service, Portland, OR. Pacific Southwest Research Station. General Technical Report PSW-GTR-994.

Martínez-Berdeja, A., Hamilton, J.A., Bontemps, A., Schmitt, J., Wright, J.W., 2019. Evidence for population differentiation among Jeffrey and Ponderosa pines in survival, growth and phenology. For. Ecol. Manag. 434, 40–48, 10.1016/j.foreco.2018.12.009.

McDowell, N.G., Allen, C.D., Marshall, L., 2009. Growth, carbon-isotope discrimination and drought-associated mortality across Pinus ponderosa elevational transect. Global Change Biol. 16 (1), 399–415. https://doi.org/10.1111/j.1365-2486.2009.01994.x.

Miller, J.D., Safford, H., 2012. Trends in wildfire severity: 1984 to 2010 in the Sierra Nevada, modoc plateau, and southern cascades, California, USA. Fire Ecology 8, 41–57. https://doi.org/10.4996/fireecology.0803041.

Miller, J.D., Skinner, C.N., Safford, H.D., Knapp, E.E., Ramirez, C.M., 2012. Trends and causes of severity, size, and number of fires in northwestern California, USA. Ecol. Appl. 22, 184–203. https://doi.org/10.1890/10-2108.1.

Muñoz-Sáez, A., Choe, H., Boynton, R.M., Elsen, P.R., Thorne, J.H., 2021. Climate exposure shows high risk and few climate refugia for Chilean native vegetation. Sci. Total Environ. 785, 147399. https://doi.org/10.1016/j.scitotenv.2021.147399.

MTBS, 2022. MTBS Data Access: Fire Level Geospatial Data. MTBS Project (USDA Forest Service/U.S. Geological Survey), 2017, July - 2022). http://mtbs.gov/direct-download.

Negron, J.F., McMillin, J.D., Anhold, J.A., Coulson, D., 2009. Bark beetle-caused mortality in a drought-affected ponderosa pine landscape in Arizona, USA. Forestry Ecology and Management 257 (4), 1353–1362. https://doi.org/10.1016/j.foreco.2008.12.002.

North, M.P., Stevens, J.T., Greene, D.F., Coppoletta, M., Knapp, E.E., Latimer, A.M., Restaino, C.M., Tompkins, R.E., Welch, K.R., York, R.A., Young, D.J.N., Axelson, J. N., Buckley, T.N., Estes, B.L., Hager, R.N., Long, J.W., Meyer, M.D., Ostoja, S.M., Safford, H.D., Shive, K.L., Tubbesing, C.L., Vice, H., Walsh, D., Werner, C.M., Wyrsch, P., 2019. Tamm Review: reforestation for resilience in dry western U.S. forests. For. Ecol. Manag. 432. https://doi.org/10.1016/j.foreco.2018.09.007.

OpenStreetMap contributors, 2024. Shapefile extract from Geofabrik download server. Retrieved from. https://www.geofabrik.de/data/download.html. (Accessed 1 February 2024).

Pausas, J.G., Keeley, J.E., 2021. Wildfires and global change. Front. Ecol. Environ. 19, 387–395. https://doi.org/10.1002/fee.2359.

Pawlak, C.C., Love, N.L.R., Yost, J.M., Fricker, G.A., Doremus, J.M., Ritter, M.K., 2023. California's native trees and their use in the urban forest. Urban For. Urban Green. 89, 128125. https://doi.org/10.1016/j.ufug.2023.128125.

Potter, K.M., Crane, B.S., Hargrove, W.W., 2017. A United States national prioritization framework for tree species vulnerability to climate change. N. For. 48, 275–300. https://doi.org/10.1007/s11056-017-9569-5.

Pozner, E., Bar-On, P., Livne-Luzon, S., Moran, U., Tsamir-Rimon, M., Dener, E., Schwartz, E., Rotenberg, E., Tatarinov, F., Preisler, Y., Zecharia, N., Osem, Y., Yakir, D., KleinT, 2022. A hidden mechanism of forest loss under climate change: the role of drought in eliminating forest regeneration at the edge of its distribution. For. Ecol. Manag. 506, 119966. https://doi.org/10.1016/j.foreco.2021.119966.

Qin, H., Zhou, W., Yao, Y., Wang, W., 2022. Individual tree segmentation and tree species classification in subtropical broadleaf forests using UAV-based LiDAR, hyperspectral, and ultrahigh-resolution RGB data. Remote Sensing of Environment 280, 113143. https://doi.org/10.1016/j.rse.2022.113143.

Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., Romme, W.H., 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. Bioscience 58, 501–517. https://doi.org/10.1641/B580607.

Ramírez-Valiente, J.A., del Blanco, L.S., Alía, R., Robledo-Arnuncio, J.J., Climent, J., 2021. Adaptation of Mediterranean forest species to climate: lessons from common garden experiments. J. Ecol. 110, 1022–1042. https://doi.org/10.1111/1365-2745.13730.

Riley, K.L., Grenfell, I.C., Finney, M.A., Wiener, J.M., 2021. TreeMap, a tree-level model of conterminous US forests circa 2014 produced by imputation of FIA plot data. Sci. Data 8, 11. https://doi.org/10.1038/s41597-020-00782-x.

Rother, M.T., Veblen, T.T., 2016. Limited conifer regeneration following wildfires in dry ponderosa pine forests of the Colorado Front Range. Ecosphere 7, e01594. https://doi.org/10.1002/ecs2.1594.

Safford, H.D., Stevens, J.T., 2017. Natural Range of Variation (NRV) for Yellow Pine and Mixed Conifer Forests in the Sierra Nevada, Southern Cascades, and Modoc and Inyo National Forests. USDA Forest Service, California, USA. Pacific Southwest Research Station. General Technical Report PSW-GTR-256, Albany, CA.

Safford, H.D., Van de Water, K.M., 2014. Using Fire Interval Departure (FRID) Analysis to Map Spatial and Temporal Changes in Fire Frequency on National Forest Lands in California. USDA Forest Service, Albany, CA. https://doi.org/10.2737/PSW-RP-266. Pacific Southwest Research Station. Research Paper PSW-RP-266.

Sawyer, J.O., Keeler-Wolf, T., Evens, J.M., 2009. A Manual of California Vegetation. California Department of Fish and Game, Scaramento, CA.

Sharma, S., Andrus, R., Bergeron, Y., Bogdziewicz, M., Bragg, D.C., Brockway, D., Cleavitt, N.L., Courbaud, B., Das, A.J., Dietze, M., Fahey, T.J., Franklin, J.F., Gilbert, G.S., Greenberg, C.H., Guo, Q., Hille Ris Lambers, J., Ibanez, I., Johnstone, J. F., Kilner, C.L., Knops, J.M.H., Koenig, W.D., Kunstler, G., LaMontagne, J.M., Macias, D., Moran, E., Myers, J.A., Parmenter, R., Pearse, I.S., Poulton-Kamakura, R., Redmond, M.D., Reid, C.D., Rodman, K.C., Scher, C.L., Schlesinger, W.H., Steele, M. A., Stephenson, N.L., Swenson, J.J., Swift, M., Veblen, T.T., Whipple, A.V., Whitham, T.G., Wion, A.P., Woodall, C.W., Zlotin, R., Clark, J.S., 2022. North American tree migration paced by climate in the West, lagging in the East. In:

Proceedings of the National Academy of Sciences, vol. 119, e2116691118. https://doi.org/10.1073/pnas.2116691118, 3.

St Clair, J.B., Richardson, B.A., Stevenson-Molnar, N., Howe, G.T., Bower, A.D., Erickson, B.J., Ward, B., Bachelet, D., Kilkenny, F.F., Wang, T., 2022. Seedlot selection tool and climate-smart restoration tool: web-based tools for sourcing seed adapted to future climates. Ecosphere 13, 5. https://doi.org/10.1002/ecs2.4089.

Steady, W.D., Partelli-Feltrin, R., Johnson, D.M., Sparks, A.M., Kolden, C.A., Talhelm, A. F., Lutz, J.A., Boschetti, L., Hudak, A.T., Nelson, A.S., Smith, A.M.S., 2019. The survival of Pinus ponderosa saplings subjected to increasing levels of fire behavior and impacts on post-fire growth. Fire 2 (2), 23. https://doi.org/10.3390/fire2020023.

Steele, Z.L., Jones, G.M., Collins, B.M., Green, R., Koltunov, A., Purcell, K.L., Sawyer, S. C., Slaton, M.R., Stephens, S.L., Stine, P., Thompson, C., 2022. Mega-disturbances cause rapid decline of mature conifer forest habitat in California. Ecol. Appl. 33 (2), e2763. https://doi.org/10.1002/eap.2763.

Stephens, S.L., Lydersen, J.M., Collins, B.M., Fry, D.L., Meyer, M.D., 2015. Historical and current landscape-scale ponderosa pine and mixed conifer forest structure in the Southern Sierra Nevada. Ecosphere 6 (5), 79, 0.1890/ES14-00379.1.

Stern, M.A., Flint, L.E., Flint, A.L., Boynton, R.M., Stewart, J.A.E., Wright, J.W., Thorne, J.H., 2022. A comparison of historical gridded climate datasets and the implications for uncertainty in hydrological modeling. J. Hydrometeorol. 23, 293–308.

Stevens-Rumann, C.S., Morgan, P., 2019. Tree regeneration following wildfires in the western US: a review. Fire Ecology 15. https://doi.org/10.1186/s42408-019-0032-1.

Stewart, J.A.E., van Mantgem, P.J., Young, D.J.N., Shive, K.L., Preisler, H.K., Das, A.J., Stephenson, N.L., Keeley, J.E., Safford, H.D., Wright, M.C., Welch, K.R., Thorne, J. H., 2021. Effects of postfire climate and seed availability on postfire conifer regeneration. Ecol. Appl. 31 (3). https://doi.org/10.1002/eap.2280.

Sturgeon, K.B., 1979. Monoterpene variation in ponderosa pine xylem resin related tow estern pine beetle predation. Evolution 33 (3), 803–814. https://doi.org/10.2307/2407647.

Thorne, J.H., Boynton, R.M., Flint, L.E., Flint, A.L., 2015. The magnitude and spatial patterns of historical and future hydrologic change in California's watersheds. Ecosphere 6 (2), 1–30. https://doi.org/10.1890/ES14-00300.1.

Thorne, J.H., Choe, H., Stine, P.A., Chambers, J.C., Holguin, A., Kerr, A.C., Schwartz, M. W., 2018. Climate change vulnerability assessment of forests in the southwest USA. Clim. Change 148 (3), 387–402. https://doi.org/10.1007/s10584-017-2010-4.

Thorne, J.H., Gogol-Prokurat, M., Hill, S., Walsh, D., Boynton, R.M., Choe, H., 2020. Vegetation refugia can inform climate-adaptive land management under global warming. Front. Ecol. Environ. 18 (5), 281–287. https://doi.org/10.1002/fee.2208.

Thorne, J.H., Le, T.N., 2016. California's historic legacy for landscape change, the wieslander vegetation type maps. Madrono 63 (4), 293–328, 10.312./0024-9637-63.4.293.

Thorne, J.H., Morgan, B.J., Kennedy, J.A., 2008. Vegetation change over sixty years in the Central Sierra Nevada, California, USA. Madrono 55 (3), 223–237. https://doi.org/10.3120/0024-9637-55.3.223.

U.S. Forest Service, 2023. Rapid Assessment of Vegetation Condition after Wildfire (RAVG) Thematic Percent Change in Composite Burn Index (CBI-4). Raster Dataset. Online link: https://data.fs.usda.gov/geodata/rastergateway/ravg/index.php. Downloaded:4/1/23.

Van de Water, K.M., Safford, H.D., 2011. A summary of fire frequency estimates for California vegetation before euro-American settlement. Fire Ecology 7, 26–58. https://doi.org/10.4996/fireecology.0703026.

van Mantgem, P., Schwartz, M., 2003. Bark heat resistance of small trees in Californian mixed conifer forests: testing some model assumptions. For. Ecol. Manag. 178 (3), 341–352. https://doi.org/10.1016/S0378-1127(02)00554-6.

Watanabe, S., Hajima, T., Sudo, K., Nagashima, T., Takemura, T., Okajima, H., Nozawa, T., Kawase, H., Abe, M., Yokohata, T., Ise, T., Sato, H., Kato, E., Takata, K., Emori, S., Kawamiya, M., 2011. MIROC-ESM 2010: model description and basic results of CMIP5-20c3m experiments. Geosci. Model Dev. (GMD) 4, 845–872. https://doi.org/10.5194/gmd-4-845-2011.

Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W., 2006. Warming and earlier spring increase western US forest wildfire activity. Science 313, 940–943. https://doi.org/10.1126/science.1128834.

Williams, J.N., Safford, H.D., Enstice, N., Steel, Z.L., Paulson, A.K., 2023. High-severity burned area and proportion exceed historic conditions in Sierra Nevada, California, and adjacent ranges. Ecosphere 14 (1), e4397. https://doi.org/10.1002/ecs2.4397.

Williamson, G.B., Black, E.M., 1981. High temperature of forest fires under pines as a selective advantage over oaks. Nature 293, 643–644.

Wolf, A., Zimmerman, N.B., Anderegg, W.R.L., Busby, P.E., Christensen, J., 2016. Altitudinal shifts of the native and introduced flora of California in the context of 20th-century warming. Global Ecol. Biogeogr. 25, 418–429. https://doi.org/10.1111/geb.12423.

Wright, D.H., Nguyen, C.V., Anderson, S., 2016. Upward shifts in recruitment of high-elevation tree species in the northern Sierra Nevada, California. Calif. Fish Game 102, 17–31. https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=123646&inline.

Xu, W., Prescott, C.E., 2024. Can assisted migration mitigate climate-change impacts on forests? For. Ecol. Manag. 556 (1), 121738. https://doi.org/10.1016/j.foreco.2024.121738.

Young, D.J., Koontz, M.J., Weeks, J., 2022. Optimizing aerial imagery collection and processing parameters for drone-based individual tree mapping in structurally complex conifer forests. Methods Ecol. Evol. 13, 1447–1463. https://doi.org/10.1111/2041-210X.13860.

Young, D.J., Blush, T.D., Landram, M., Wright, J.W., Latimer, A.M., Safford, H.D., 2020. Assisted gene flow in the context of large-scale forest management in California, USA. Ecosphere 11, e03001. https://doi.org/10.1002/ecs2.3001.