West coast U.S. tree species show stronger evidence for shifts in density than range

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ABSTRACT

Climate change is associated with shifts in the geographic range of trees and other taxa globally. In North America and elsewhere tree species' ranges are expected to shift at rates of meters to kilometers annually. However, empirically detecting a shift in the range of a tree species may be difficult due to the lack of quality long-term regional or national data. Evidence of range shifts is further confounded by apparently contradictory findings from separate studies that use different methods to evaluate species responses. In this study we examine U.S. Forest Service Forest Inventory Analysis plot revisit data in the states of California, Oregon, and Washington to examine shifts in the ranges and densities of tree species relative to values of temperature, precipitation, and maximum and minimum vapor pressure deficit (VPD) using a design-based estimation technique. We also examine changes in these four climate variables for years before and between plot visits. We found that the ranges for 49 tree species seldom shifted in the 10-year period of plot remeasurements, but depending on the climate variable considered, between seven and ten out of 30 species did exhibit density shifts, generally increasing in plots that were initially cooler, drier, and had lower VPD. Overall, plots increased in temperature and VPD values between time periods while they generally experienced declines in precipitation. These changes were frequently not constant across species plots. Temperature and precipitation values were often negatively associated with first visit values (cooler and wetter plots disproportionately warmed and dried). Maximum and minimum VPD generally increased most at plots with initially higher VPD values. These results indicate that the geographical range of U.S. west coast tree species may not change as quickly as their ecological niches geographically shift, although changes in species densities within their ranges may already be underway. The results also indicate that changes in environmental conditions may differ among and within species' ranges.

1. Introduction

The rate of vegetation change between 2000 BCE and now is faster than any other time period within the past 18,000 years and is likely caused by human impacts on plant species (Mottl et al., 2021). Scientists have documented recent range shifts for a variety of terrestrial and marine taxa that correspond to a changing climate; e.g., latitudinal or elevation range shifts or changes in densities or cores within ranges (Lenoir and Svenning, 2015). For tree species, proximate climate-related drivers of range shifts may reduce species' ranges. These drivers include insect and disease outbreaks and an increase in wildfire prevalence (Weed et al., 2013, Jolly et al., 2015, Stanke et al., 2021). Species range shifts can occur in climatically unexpected directions such as towards lower elevations or latitudes (Lenoir et al., 2010). For trees, such shifts

may be due to anthropogenic causes aside from climate change (e.g., fire suppression; Minnich et al., 1995, Dolanc et al., 2014). Although tree-range modeling broadly indicates that North American tree species should directionally migrate towards previously cooler regions (McKenney et al., 2007, Iverson et al., 2008, Loarie et al., 2009) and distributional shifts within ranges appear widespread (Murphy et al., 2010, Fei et al., 2017), there is scant empirical evidence that ranges are currently directionally shifting towards previously cooler regions (Zhu et al., 2012, Sittaro et al., 2017, Woodall et al., 2018).

Modeling studies indicate that many tree species' ranges in North America may shift substantially in the coming decades (McKenney et al., 2007, Iverson et al., 2008). Serra-Diaz et al. (2014) modeled climate-related range shifts for eight oak (*Quercus*) and pine (*Pinus*) species in California over the next 80 years and estimated that range-shift

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velocities would be affected by terrain, with species inhabiting relatively flat terrain experiencing faster range shifts than those in steep terrain. Loarie et al. (2009) found the same topographical relationship for the speed of temperature change within biomes, with mountainous biomes shifting on average by 0.08 km/yr while flatter biomes (mangroves, deserts, grasslands) shifting by 1.26 km/yr over the next 80 years. It is imperative that we determine whether tree species (and others) can shift their ranges with sufficient speed to match the changes underway in their niche space; otherwise, species may face substantial range contractions (McKenny et al., 2007, Iverson et al., 2008) and require management interventions to overcome dispersal barriers.

Empirically detecting shifts in tree species' distributions and ranges is challenging because few programs exist that collect tree plot data across many years using a geographically widespread and probabilistically-based sample design with consistent measurement protocols. Sampling designs and data-collection protocols enacted by governments, research institutions, or other organizations may change over time, lack methodological consistency across political boundaries, and/or not sample plots probabilistically. Consequently, several analytical approaches have been used to evaluate evidence of recent tree species range shifts.

One method compares the distribution of seedlings or saplings relative to adults (Zhu et al., 2012, Monleon and Lintz, 2015, Sittaro et al., 2017, Woodall et al., 2013, 2018). The Migration Hypothesis proposed by Zhu et al. (2014) predicts that seedling ranges may shift into previously unoccupied but newly favorable areas and out of regions that have become unsupportive of that life stage. This type of analysis has been done primarily by examining plot occupancy by seedlings or saplings and adult trees within longitudinal strips and estimating means of range limits for each age type. Latitude serves as a proxy for a climate-change signal in these studies, and may be justified as models (McKenney et al., 2007, Iverson et al., 2008) indicate that climate change may be expected to result in poleward shifts. However, seedling or saplings and adult tree distributions do not necessarily behave as predicted when analyses of their distributions are performed using revisit data. Sittaro et al. (2017) found evidence of seedling ranges shifting northward at a more rapid pace than adults, but they did not find that seedling ranges extended farther north than the ranges of adults. Woodall et al. (2018) similarly found seedlings south of adults. Zhu et al. (2014) proposed the Turnover Hypothesis to explain observed patterns: warmer and wetter conditions could increase turnover rates, promoting elevated rates of mortality and recruitment. Their analysis of 65 species in the eastern United States supported the Turnover Hypothesis over the Migration Hypothesis. Regardless, using the longitudinal strip method, Zhu et al. (2012) and Woodall et al. (2013, 2018) compared differences in the distributions between seedling/sapling and adult populations in the eastern United States but did not find evidence that the ranges of many species were shifting northward (but see Sittaro et al., 2017).

Another approach for evaluating species' responses to a changing climate is to quantify distribution shifts within ranges towards more habitable range edges instead of quantifying range edge changes (Kelly and Goulden, 2008). Murphy et al. (2010) and Fei et al. (2017) found shifts in plot abundance and occupancy within tree species' ranges in the eastern United States northward (Murphy et al.) or northward and/or westward (Fei et al.). Although these analyses do not capture changes in species' geographical extents, they may be more sensitive to initial shifts in distribution. However, observing distributional shifts within ranges instead of shifts in range edges may indicate that a species lacks the ability to adjust to climatic shifts (Liang et al., 2018).

Monleon and Lintz (2015) used a design-based analysis approach to estimate mean seedling vs. mature tree distributions across California, Washington, and Oregon along gradients of elevation, latitude, and average temperatures of sample plots. Across species they found seedlings to inhabit cooler plots (based on plot means of temperatures from 1970 to 2000) than mature trees. They favored the use of average plot temperature over latitude or elevation as it directly reflected plot

temperatures instead of serving as a proxy of temperature. Their findings appear to contradict those of Zhu (2012) and Woodall et al. (2013, 2018) who did not find similar range shifts. Stanke et al. (2021) similarly utilized design-based estimates of data from the U.S. Forest Service Forest Inventory and Analysis Program (FIA) to establish that relative densities of eight western tree species were declining, but their analysis did not directly examine the declines alongside environmental variables.

As described above, previous studies have utilized different techniques for assessing the evidence of tree species distribution responses to a shifting climate. Some findings, such as species range expansion with seedlings trailing adults (Fei et al., 2017, Sittaro et al., 2017, Woodall et al., 2018), appear counterintuitive or contradictory. The Lenoir and Svenning (2015) literature review concluded that multifaceted approaches are needed when forecasting biodiversity responses to climate in order to provide comprehensive assessments of shifts in species' ranges. They recommend that researchers examine the responses at trailing and leading edges of species' ranges as well as the "optimum" within-range habitat (i.e., abundance). They also recommend that these features be examined along latitudinal, elevational, and longitudinal gradients.

The goal of this analysis was to evaluate the evidence of tree species distribution changes across the states of Washington, Oregon, and California, USA, over a 10-year period. Similar to Monleon and Lintz (2015), this study capitalizes on the probabilistic FIA sampling design. It develops design-based estimates to examine changes in two metrics: a "range shifts" is the difference in first and second visit means of occupied plots' climate variable values, and a "density shift" is the difference in mean climate variable values between plots that had more and fewer trees of a given species between visits. The four climate variables investigated are total annual precipitation and mean annual temperature, minimum vapor pressure deficit (VPD), and maximum VPD. We selected total annual precipitation and mean annual temperature for this analysis as these variables have previously been examined relative to species movement (Colwell et al., 2008, Zhu et al., 2012, Sittaro et al., 2017). Our two VPD metrics, although derived from temperature, may more directly relate to tree physiology in forested regions (Breshears et al., 2013, Eamus et al., 2013, Liu et al., 2020, Lu et al., 2022), as VPD is a direct measure of atmospheric desiccation strength (Grossiord et al., 2020). Our secondary analysis goal was to examine our assumptions about environmental change at plots, which we approached by assessing differences in climate variables values between visits. We created a data visualization dashboard (dashboard; https://tinyurl.com/yc8cf4k9/) so that users may explore analysis outcomes, compare results under different analysis scenarios, and examine data by and across species.

2. Methods

This study relies on U.S. National Forest Inventory datasets for all forestland in California, Washington, and Oregon, USA. The field data were collected by the FIA which generally defines forestland as an area greater than 4,050 m^2 at least 10 percent stocked or potentially stocked with tree species, excluding urban and agricultural land uses (Reams et al., 2005). Since 2000, the FIA sampling design consists of a spatially balanced probability sample (McRoberts, 2005, Reams et al., 2005) The standard density of FIA plots is one ground plot every 24 km^2. Plots were initially measured in California and Oregon between 2001 and 2010 while Washington plots were measured between 2002 and 2011. FIA plots in the Pacific Northwest are sampled every ten years whereas elsewhere in the country plots may be sampled on a five-year basis (Thompson, 2015). We only had access to remeasurement data between 2011 and 2019, or nine year-pairs of measurements for California and Oregon and eight for Washington (2012–2019). Consequently, the general plot sampling intensity for Oregon and California is one plot every 26.7 km^2 and one plot every 30 km^2 for Washington. Within the three states there were different plot densification efforts which increased the number of overall strata. We post-stratified the FIA plots

into 25 strata based on these sample densities and ancillary information (e.g., land classification, ownership). We used the strata and associated weights when estimating range and density shift estimates (Appendix).

The total sample size was 42,963 plots, of which 21,905 were forested and 2,745 could not be measured, either because the landowner denied access or because the plots were unsafe to reach or occupy (Fig. 1). Plots were configured with three points spaced 36.6 m from a fourth center point and offset 120°. Plots containing forest land were installed and measured by field crews. At each of the four points within a plot, trees with stem diameter greater than or equal to 12.7 cm were tallied in a 7.32 m radius circular subplot (total area 672.5 m²). Crews also measured larger trees in macroplots (18 m radius including the subplot at its center) and seedlings and saplings microplots (2.1 m diameter plots within subplots). For most species, stem diameter was measured at 1.37 m above the ground. Bechtold and Scott (2005) provide plot design details and measurement protocols.

2.1. Data

The plot and tree data for this analysis were obtained from the Pacific Northwest Forest Inventory and Analysis Database (https://www.fs.usda.gov/pnw/page/pnw-fia-inventory-data/, accessed August 2022). Specifically, we relied on the TREE, PLOT, and COND tables. We imported the data into R 4.0.5 (R Core Team, 2021). The analysis makes use of all FIA plots in the sample regardless of whether they were occupied by target species. We summarized the tree data to tally the number of live trees present for each species during each visit.

We only included tree data from plots in Oregon, Washington, and California that were visited twice between 9 and 11 years apart (2001–2009 and 2011–2019). We included all individual trees with diameters greater than 12.7 cm and excluded all trees $\geq$ 18.3 m (60 feet) from plot centers. For the range-shift analysis we included macroplot data but excluded trees $\geq$ 7.3 m (24 feet) from plot centers with DBH values greater than 61.0 cm (24 in.) and < 76.2 cm (30 in.). FIA data collection protocols differentially tally these trees in plots depending on the regions in which the plots were located (Thompson, 2015). In the density-shift analysis we excluded all macroplot trees to standardize interpretations of tree density. We removed *Prunus emarginata* from the analysis as this species often exhibits a shrub growth form. We also removed all trees that had been erroneously included in earlier surveys

(e.g., they were located outside of plots). We coded *Abies shastensis* as *Abies magnifica* because *A. shastensis* is a variety of *A. magnifica*.

We included only those trees that were alive during both visits, alive at the first visit and then dead at the second, and those that reached a DBH greater than 12.7 cm in the plot by the second visit. We reviewed all trees that had species name changes between visits to determine which species identification was correct. In the absence of other information, we selected the species name from the second visit as a species name change requires crew members to intentionally change the species code from what was recorded at the first visit.

Some larger-diameter trees appeared during the second visit but were not coded as missed during the first visit. If the diameter of these trees was greater than 12.7 cm plus the 99th percentile of the amount of growth observed for that species, they were coded as alive during both periods; otherwise, they were coded as ingrowth.

For the range-shift analysis, a plot containing a species was coded as having the species present during both visits, completely dying out, or appearing as ingrowth within the plot. If first-visit alive trees were dead by the second visit but ingrowth of the same species appeared, the plot was coded as containing the species alive for both visits. For the density change analysis, the number of live trees for a species was considered during the first and second visit and a plot was labeled as having more, fewer, or the same number of live trees across visits.

We validated species identifications by comparing occupied plot distributions against species range maps. Species ranges were checked against the United States Department of Agriculture Natural Resources Conservation Service PLANTS database (https://plants.usda.gov, accessed August 2022) and specimen record locations provided by Discover Life (https://www.discoverlife.org/, accessed August 2022).

2.2. Analysis

Our analysis progression is depicted in Fig. 2. To summarize, we first obtained climate variable values for all FIA plots, for both the first and second visit periods. We then conducted the range shift and density shift analyses. Finally, we examined between-visit changes in climate variables.

For each of the FIA plots used in the analysis we obtained estimated values for total annual precipitation and mean annual temperature, minimum VPD, and maximum VPD from the spatially gridded (800 m)
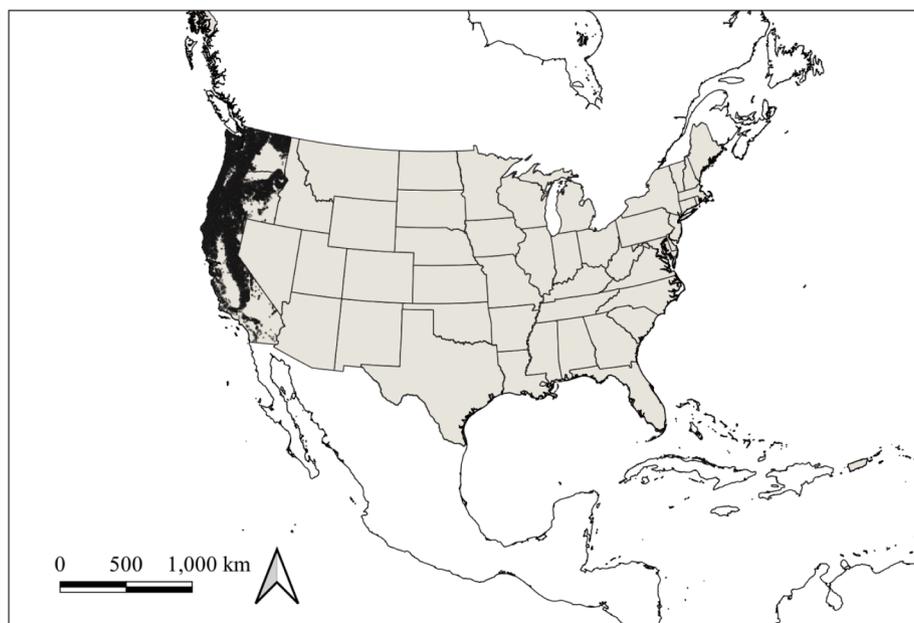
Fig. 1. Distribution of 21,905 forested FIA plots in the states of Oregon, Washington, and California.
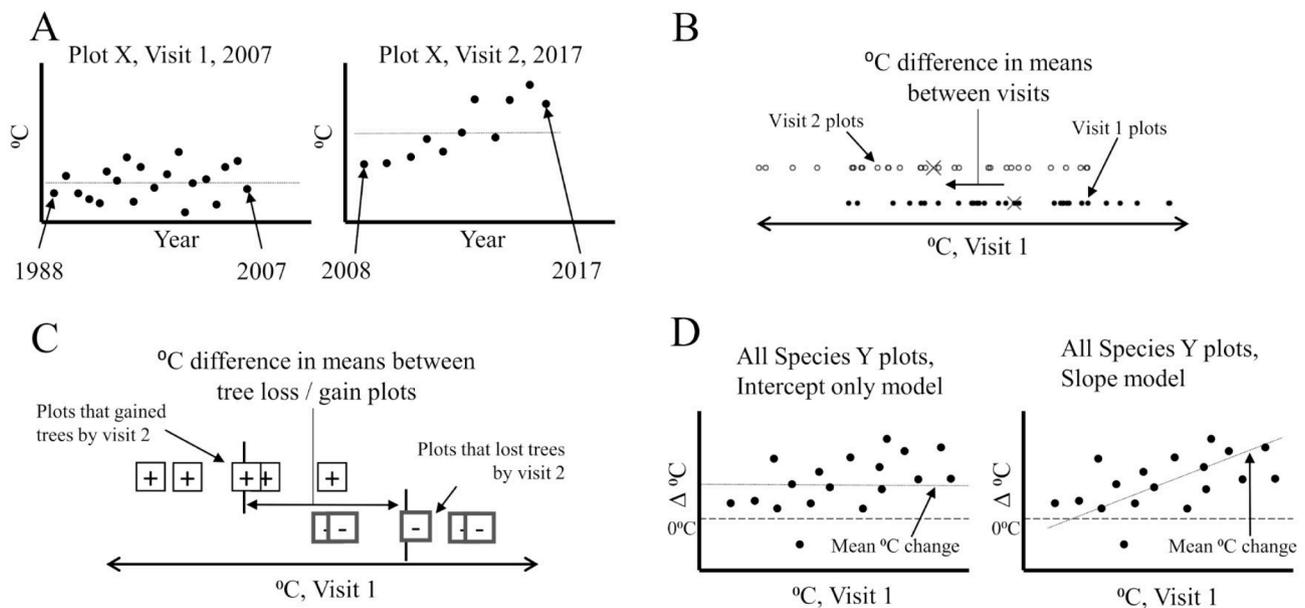
Fig. 2. Analysis steps. A: Find mean of climate variable value (here: temperature) for visit 1 and 2 values for each FIA plot (e.g., the dashed lines in Plot X). B: Conduct range shift analysis for each species of interest. Range shift = mean of climate variable values for the population of plots occupied in visit 2 minus those occupied in visit 1. C: Conduct density shift analysis for each species of interest. Density shift = mean of climate variable values for plots that gained individuals minus those that lost individuals. D: Climate variable values across species-occupied plots. For each species we examined how plot climate variable values changed between the two visits and related to visit 1 values. For subplots B, C, and D, examples portray results for a single species and plot x axes use climate variable values from the visit 1 year (see text for explanation).

parameter-elevation regressions on independent slopes model (PRISM; Daly et al., 2008). Minimum and maximum VPD represent annual averages of daily minimum and maximum values (Daly et al., 2015, https ://prism.oregonstate.edu/). We drew from PRISM output for 1981–2019. For each plot we calculated the mean climate variable value for the 20 years up to and including the first-visit year, and a second mean for the values for the ten years between the first and second visit, including the second visit's year (first- and second-visit value, Fig. 2A). We utilized 20 years of climate data for the first-visit value to capture longer-term climatic trends instead of short-term anomalies. We did not use more than 20 years' data for the first-visit estimates as PRISM data prior to 1981 are of potentially lower quality (https://prism.oregons tate.edu/). Although we found mean climate variable values for the first and second visit, the range and density shift analysis outcomes reported here only make use of the first-visit values. The range shift analysis compares, for instance, the mean of the first-visit temperature values for plots that were occupied at visit 2 minus those that were occupied at visit 1 (Fig. 2B). We assumed that first-visit climate variable values would relate to conditions ten years later. Specifically, for temperature, we assumed that plots have warmed in an approximately linear and constant fashion across species' ranges. We did not know whether precipitation, maximum VPD, or minimum VPD would consistently positively or negatively change across species' ranges. We therefore explored each species' plot changes in climate variable values between the first and second visit relative to first visit values (Fig. 2D).

The range and density shift analyses followed standard survey sampling estimation procedures (Särndal et al., 1992) from a continuous population perspective (Cordy, 1993). For the range-shift analysis we estimated the difference in the population means of climate variable values for each species (Fig. 2B). The two populations are those plots occupied during the first or second visit. We calculated the mean for each visit as an approximate design unbiased estimator of the weighted-domain sampling mean for plots (eqn 8, Appendix; Scott et al., 2005). The weighted domains were derived from the different plot sampling intensities of the 25 strata (see above). The estimated difference of the two means is calculated as the difference between their respective

domain ratio estimators (Wolter, 1985; eqn 15, Appendix). We employed the same or similar equations as Monleon and Lintz (2015) to obtain estimates of the variance and confidence intervals (eqns 16 and 17, Appendix).

We used a Generalized Least Squares (GLS) approach to estimate the mean difference in climate variable values among all species as the average of individual species' differences, weighted by the inverse of the estimated covariance matrix. We obtained the variance–covariance matrix through bootstrapping because data for the covariance matrix were sparse and species were not independent (multiple species may occupy a single plot; see GLS equations 18 and 19 in the Appendix).

The density-shift analysis made use of the same procedure as described above, estimating a statistic of the difference between two ratios, the weighted domain sampling means of climate variable values. The analysis diverged from the original procedure in that it found the difference in means for a climate variable between plots that had more and fewer individuals by the second plot visit (Fig. 2C).

Our range and density shift analyses did not control for multiple comparisons: "Non-significant" species responses, i.e., those with confidence intervals overlapping zero, do not necessarily imply a lack of response (Type-II error), and "significant" responses (i.e., 95% confidence intervals do not include zero) may be spurious (Type-I error). In the Results we refer to these "significant" species as evidencing a shift in their range or density. We encourage readers to interpret these "significant" individual responses as suggesting that patterns potentially, but do not necessarily, exist. Although we discuss possible responses for individual species, our overall analysis findings consider the number of species with 95% confidence intervals that excluded zero and not the individual species. Since species' responses were not independent, we performed a permutation test for each climate variable examined in the range and density shift analyses to determine false error rates. Each test involved 10,000 iterations of random sampling without replacement from climate parameter values for forested plots. We used the results to determine the probability of observing specified numbers of "significant" findings, both for an individual climate variable analysis and across range and density shift analyses.

We examined the difference between first and second visit climate variable values for plots occupied by each species (Fig. 2D). Since species' occupied plots are geographically unevenly distributed, the analysis sought to account for spatial autocorrelation of climate variable values for FIA plots while allowing for some flexibility in model form by creating and comparing two linear spatial error models (R package spatialreg, Bivand and Piras, 2020; Bivand et al., 2021). We derived spatial point neighborhoods by using Gabriel graphs (Matula and Sokal, 1980) and assessed the spatial autocorrelation in models with Moran's I test. For both models the plot-level changes in the values for a selected climate variable served as a dependent variable. The models differed in that one was an intercept-only model while the other also included a slope parameter associated with the first visit climate variable values (Fig. 2D). For each species and metric we selected between the two models by comparing model AIC values; the intercept model was preferred (i.e., more parsimonious) unless the slope model was better supported ($\Delta AIC = 0$, AIC difference greater than 3).

2.3. Data visualization

Our dashboard (https://tinyurl.com/yc8cf4k9/) enables viewers to compare different analyses, observe maps of species plot distributions, and view displays of climate variable values by species. The dashboard also includes range and density analysis results that use second-visit climate variable values instead of first visit values, and allows the visualization of results that use bootstrap variance estimation instead of the Taylor linearization method approximation.

3. Results

3.1. Range shift analysis

During the two visits 49 species occupied 15,390 plots in total with each species occupying at least 54 plots at each visit (Table 1). Of the 49 species, 29 were gymnosperms. We observed little concurrence in species' range shifts across climate variables. Two of the 13 species with apparent range shifts for at least one climate variable exhibited shifts in more than one variable (*Pinus ponderosa*, maximum and minimum VPD; *Quercus agrifolia*, temperature and minimum VPD).

Three species evidenced range shifts for temperature (Fig. 3). During the second visit *Pseudotsuga menziesii* and *Quercus douglasii* occupied, on average, previously warmer plots (positive change), while *Quercus agrifolia* occupied previously cooler plots (negative change). Three findings out of 49 at $\alpha = 0.025$ may be due to chance alone (permutation test $p = 0.068$).

Chamaecyparis lawsoniana was the only species with a precipitation range shift (Fig. 3). It exhibited a shift towards plots that previously received more annual precipitation (i.e., wetter plots). Three species demonstrated range shifts for maximum VPD. *Picea sitchensis* and *Pinus ponderosa* exhibited range shifts towards plots with initially lower maximum VPD values while *Notholithocarpus densiflorus* shifted towards plots with higher VPD values. Unlike the other three range-shift analyses, the minimum VPD analysis found seven species with range shifts. Six shifted towards plots with initially lower minimum VPD values (*Acer macrophyllum, Alnus rubra, Quercus agrifolia, Pinus monticola, Pinus ponderosa, and Quercus chryolepsis*). *Arbutus menziesii* shifted towards plots with initially greater minimum VPD values. Seven apparent range shifts out of 49 for one or more of the four climate variables examined is unexpected by chance (permutation test $p = 0.004$).

The across-species GLS mean and 95% confidence interval for the range shift temperature (mean = 0.002 °C, 95% CI = -0.004 °C to 0.007 °C), precipitation (mean = -0.451 mm, 95% CI = -1.430 mm to 0.528 mm), maximum VPD (mean = 0.003 hPa, 95% CI = -0.005 hPa to 0.010 hPa), and minimum VPD (mean = -0.002 hPa, 95% CI = -0.004 hPa to < 0.001 hPa) all encompassed zero which indicated that we found no evidence for an overall range shift towards regions that were

Table 1

Species included in the analysis. The Remained Occupied, Extirpated, and Colonized columns indicate, respectively, the number of FIA plots per species that were occupied during both visits, were occupied during the first visit but not the second, and were occupied during the second visit but not the first. The columns Lost and Gained are the number of plots that lost or gained conspecifics.

Species	Remained Occupied	Extirpated	Colonized	Lost	Gained
Abies amabilis	1130	33	41	365	494
Abies concolor	1874	142	80	752	721
Abies grandis	1642	126	112	544	693
Abies lasiocarpa	684	90	39	320	266
Abies magnifica	561	18	21	200	165
Abies procera	383	18	40	83	151
Chamaecyparis lawsoniana	77	8	4	17	14
Chamaecyparis nootkatensis	110	2	6	24	23
Juniperus californica	62	2	3	5	8
Juniperus occidentalis	965	55	48	130	295
Larix occidentalis	985	74	71	278	207
Calocedrus decurrens	1240	89	62	309	360
Picea engelmannii	658	91	46	221	214
Picea sitchensis	233	36	28	92	62
Pinus albicaulis	173	30	8	77	41
Pinus attenuata	61	22	16	43	22
Pinus contorta	2058	198	135	885	868
Pinus jeffreyi	608	29	14	144	154
Pinus lambertiana	876	115	38	227	121
Pinus monticola	538	66	67	159	144
Pinus ponderosa	4374	207	232	1238	1425
Pinus sabiniana	171	24	14	41	46
Pinus monophylla	190	13	3	56	49
Pseudotsuga menziesii	7898	371	360	2673	2731
Sequoia sempervirens	238	2	4	48	84
Taxus brevifolia	195	25	11	44	33
Thuja plicata	1388	73	99	220	473
Tsuga heterophylla	2585	160	203	823	1120
Tsuga mertensiana	724	19	30	184	246
Acer macrophyllum	853	88	88	237	297
Aesculus californica	69	10	5	25	17
Alnus rubra	1128	190	158	663	458
Alnus rhombifolia	63	8	3	28	19
Arbutus menziesii	754	85	49	314	157
Betula papyrifera	66	14	4	45	16
Chrysolepis chrysophylla	289	56	39	120	108
Cornus nuttallii	66	29	18	30	26
Fraxinus latifolia	54	3	11	13	29
Notholithocarpus densiflorus	611	39	32	279	258
Populus tremuloides	98	21	8	60	23
Populus balsamifera	149	19	18	30	42
Quercus agrifolia	188	11	6	65	33
Quercus chrysolepis	791	60	30	228	283
Quercus douglasii	335	5	0	68	60
Quercus garryana	321	13	11	89	107
Quercus kelloggii	805	91	42	327	171
Quercus lobata	60	2	0	9	5
Quercus wislizeni	184	23	13	86	68
Umbellularia californica	256	8	21	39	117

Note: Native species not reported above because, for the range shift analysis, they occupied<50 plots: *Cupressus bakeri, Cupressus sargentii, Cupressus macnabiana, Juniperus osteosperma, Juniperus scopulorum, Larix lyallii, Picea breweriana, Pinus balfouriana, Pinus coulteri, Pinus flexilis, Pinus muricata, Pinus radiata, Pinus sylvestris, Pinus washoensis, Pinus longaeva, Pseudotsuga macrocarpa, Sequoiadendron giganteum, Torreya californica, Acer negundo, Acer platanoides, Ailanthus altissima, Betula occidentalis, Eucalyptus globulus, Fraxinus velutina, Juglans hindsii, Liquidambar styraciflua, Malus fusca, Platanus racemosa, Populus fremontii, Prosopis glandulosa, Prunus virginiana, Prunus avium, Quercus engelmannii, Robinia pseudoacacia,* and *Olneya tesota.*
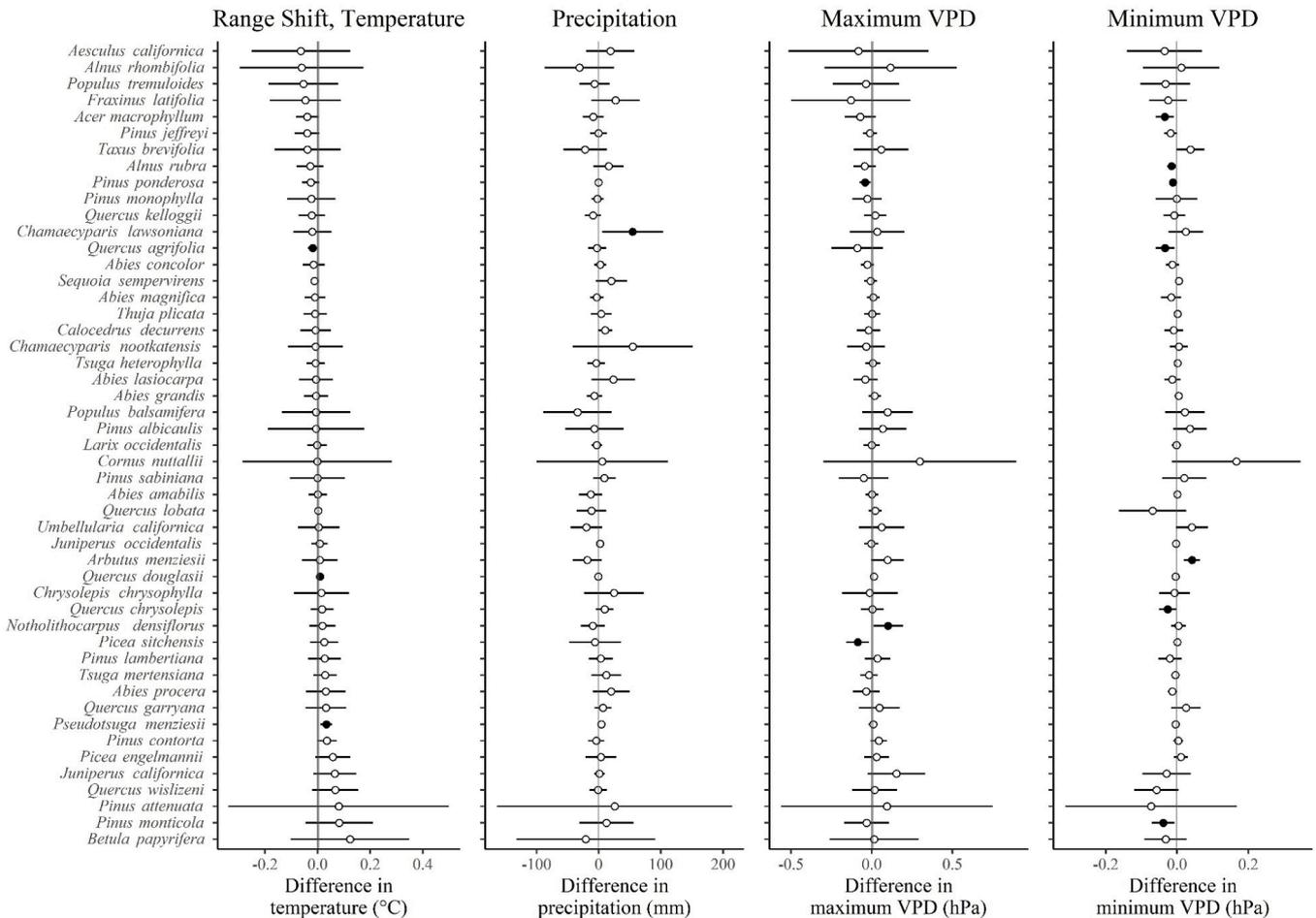
Fig. 3. Estimated range-shift temperature, precipitation, maximum VPD, and minimum VPD differences between plot measurements for 49 species. Changes in the mean of species plot values (circles) greater than zero indicated that the species inhabited warmer, wetter, or had higher VPD value plots during the second visit. Horizontal lines are species-specific 95% confidence intervals; filled circles indicate that the confidence intervals do not include zero. Plots include a vertical band representing the 95% GLS confidence interval for estimates of the overall difference in climate variable values across species.

previously warmer/cooler, wetter/drier, or had higher/lower VPD. The GLS confidence interval bands are difficult to see in Fig. 3 as they are narrow relative to the spread of findings for individual species.

3.2. Density change analysis

Thirty species each inhabited at least 60 plots that exhibited changes in the number of conspecifics between visits (Table 1). Twenty of those species were gymnosperms. We observed a high degree of concurrence across climate variables in species' responses for the density shift analysis. Eleven of 16 species with at least one climate variable density shift also shifted for one or more other variables (five species for two variables, four species for three variables, two species for four variables; Fig. 4).

The difference in mean temperature for *Pinus contorta* and *Pseudotsuga menziesii* was positive, which is consistent with a density shift towards previously warmer areas (Fig. 2C). Eight species (*Abies concolor, Abies grandis, Abies magnifica, Calocedrus decurrens, Pinus ponderosa, Thuja plicata, Acer macrophyllum,* and *Quercus kelloggii*) had negative density shifts, consistent with a shifting towards areas that were previously cooler. Eight of the ten species exhibiting temperature-associated density shifts were gymnosperms.

Seven species exhibited negative density shifts for precipitation (*Abies concolor, Abies grandis, Pinus contorta, Pseudotsuga menziesii, Arbutus menziesii, Quercus garryana, Quercus kelloggii*). One species, *Quercus douglasii,* shifted positively towards previously wetter areas.

Maximum and minimum VPD respectively had five and seven species with negative density shifts towards initially lower VPD plots. *Pinus contorta* and *Pseudotsuga menziesii* exhibited maximum VPD density shifts towards initially higher-VPD plots, and *Arbutus menziesii, Pseudotsuga menziesii,* and *Quercus douglasii* appeared to exhibit similar shifts for minimum VPD. The permutation analysis found that one or more climate variables with seven or more significant findings was unlikely due to chance alone at α = 0.025 (permutation test $p < 0.001$). Gymnosperms included four out of eight, one out of seven, and four out of ten species associated with precipitation, maximum VPD, and minimum VPD respectively.

The overall GLS range-shift estimates for temperature and precipitation were negative in both cases, with confidence intervals that did not include zero (temperature mean = -0.061 °C, 95% CI = -0.112 °C to −0.011 °C; precipitation mean = -31.8 °C, 95% CI = -45.3 °C to −18.3 °C). GLS results for Maximum and minimum VPD differed in that their intervals did contain zero (maximum VPD mean = -0.005 hPa, 95% CI = -0.020 hPa to 0.010 hPa; minimum VPD mean < 0.001 hPa, 95% CI = -0.064 hPa to 0.065 hPa). Unlike Fig. 3, these four GLS confidence interval ranges are visible when plotted (Fig. 4).

3.3. Plot changes in precipitation and temperature

When we examined the mean change (intercept-only model) in climate variables for species' plots, we found that temperature, maximum VPD, and minimum VPD increased for a majority of species
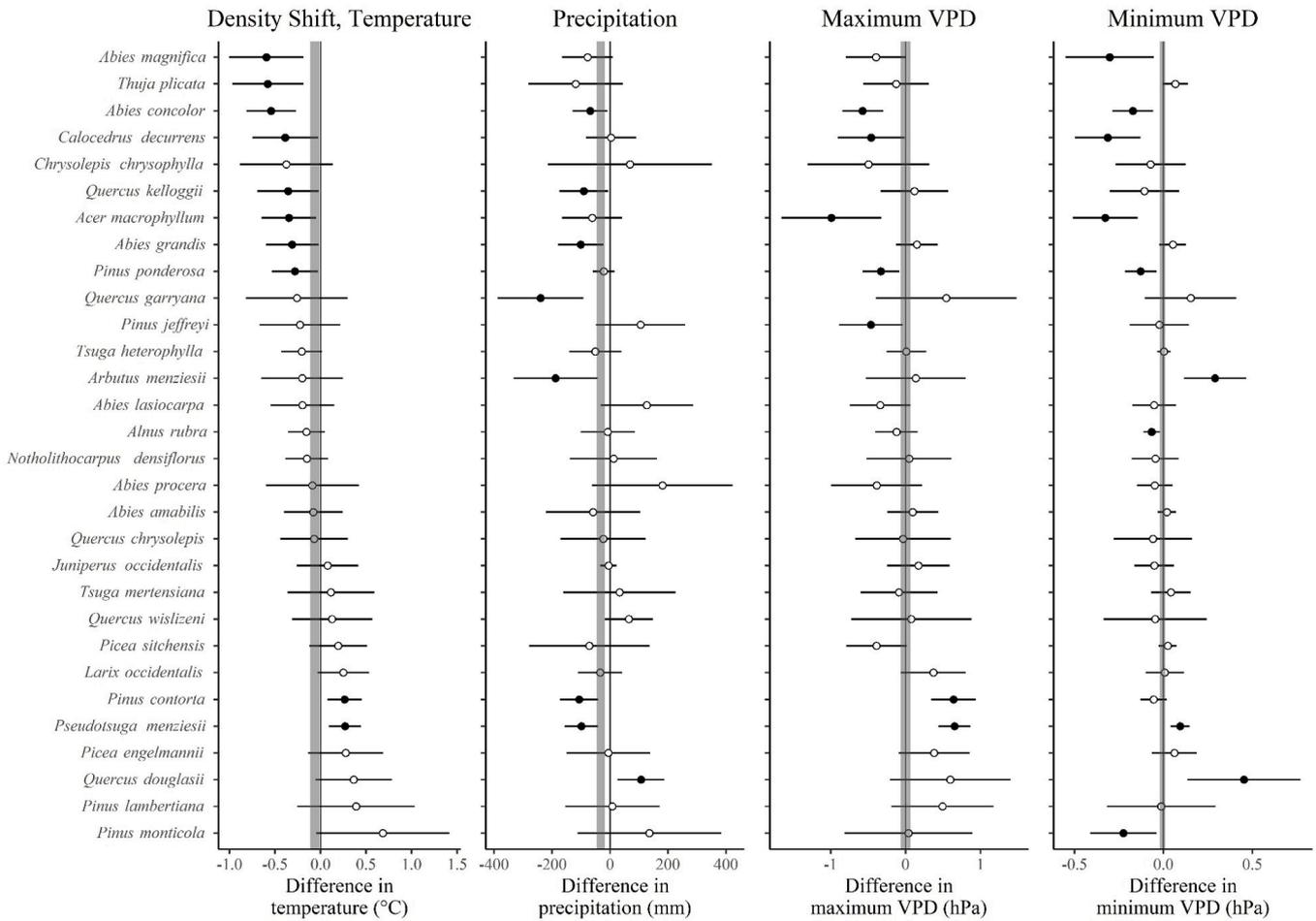
Fig. 4. Estimated density shifts by temperature, precipitation, maximum VPD, and minimum VPD for 30 species. Mean changes (circles) greater than zero indicated that more trees for a species were found in warmer/wetter/higher VPD plots (and/or fewer trees were found in cooler/drier/lower VPD plots) on average during the second plot visits. Horizontal lines are species-specific 95% confidence intervals; filled circles indicate that the confidence intervals do not include zero. All plots include a vertical band representing the 95% GLS confidence interval for estimates of the overall difference in climate variable values between plots with more and fewer trees.

while precipitation generally decreased (Table 2, dashboard). While most intercept-only spatial error models for temperature were significantly positive (α = 0.025), 29 of the 49 species were better modeled with negative slopes indicating that temperature changes may have been greater at initially cooler plots. Most (27 out of 35) significant intercept-only models for precipitation were negative, indicating that precipitation generally declined between visits. Like the analyses for

temperature, 32 species' plots were better fit with a slope, and most of those (26) were negative, indicating that precipitation declined most at the plots which initially had the highest precipitation amounts.

For all but one species, maximum and minimum VPD increased (significant intercept-only values) or did not significantly change. Most (41) minimum VPD models were better fit with a positive slope as were 21 maximum VPD models, indicating that VPD generally increased more at plots with greater initial values. Seven maximum VPD models were better fit with a negative slope. Readers may view individual species' plot climate variable changes geographically and relative to other variables in the dashboard.

3.4. Additional results

We found as many or more significant species results when the analysis relied on second-visit plot temperature or precipitation values instead of first-visit values, or used bootstrap confidence interval estimates instead of the Taylor linearization approximation approach. Some species reported above exhibited confidence intervals that included zero under these other scenarios (dashboard). We are not reporting these results further for purposes of brevity and clarity.

4. Discussion

We did not find strong evidence of tree species range shifts associated

Table 2

Summary of estimated changes in plot temperature, precipitation, and maximum and minimum VPD across species' ranges between the first and second visits (see text). The column Metric is the mean positive or negative change (+Δ, -Δ) in the climate variables. Intercept is the number of species with significant (p < 0.025) intercept estimates for intercept-only models. The columns Slope + and Slope- report the number of species' plots which were better modeled with positive and negative slope terms, respectively, with the initial visit climate variable value serving as the model's independent variable.

Metric	Intercept	Slope +	Slope -
+ΔTemperature	37	0	25
−ΔTemperature	3	0	4
+ΔPrecipitation	8	1	6
−ΔPrecipitation	27	1	26
+ΔVPD Maximum	44	21	5
−ΔVPD Maximum	1	0	2
+ΔVPD Minimum	48	41	0
−ΔVPD Minimum	0	0	0

with the four climate variables examined. Few species exhibited shifts in plot means towards initially warmer/cooler/lower VPD or wetter/drier/higher VPD plots. Those which did appear to shift generally did so for only one out of the four climate variables, possibly indicating that their results were spurious. The GLS confidence intervals reinforced that there were no overall across-species shifts within the climate variables. However, our findings for minimum VPD did appear to differ from the other three climate variables, as more species than expected by chance exhibited range shifts towards plots with initially lower minimum VPD values.

Species densities appeared to shift along climate variable gradients. Following the ten-year remeasurement period, several species exhibited mean within-plot density shifts towards plots that were previously cooler, drier, and/or had lower VPD values. The GLS temperature and precipitation findings for the density change analysis indicated that, across species and within plots that experienced changes in tree numbers, overall densities were shifting towards previously cooler or drier plots. The GLS did not find an overall density shift direction for maximum or minimum VPD.

The spatial error analysis confirmed that mean temperatures generally increased across all plots, although the increases were neither consistent across species nor uniform among species' plots. For a majority of species, initially cooler plots exhibited greater warming. Precipitation on average declined across species' ranges and was often associated with greater declines at initially wetter plots. A shift in a species' density towards initially drier plots may reflect a shift towards plots that experienced an increase (or less of a decrease) in precipitation.

Unlike temperature and precipitation, maximum and minimum VPD change was often positively associated with first-visit plot VPD values. This was especially pronounced for minimum VPD, where virtually all species' plot values disproportionately increased at plots that initially had higher VPD values.

Vapor pressure deficit should increase exponentially alongside linear increases in temperature (Breshears et al., 2013, Grossiord et al., 2020). Vapor pressure deficit may serve as a principal driver of mesic forest physiological stress and affect ecosystem production, although disentangling the effects of VPD from soil moisture, precipitation, and temperature can be challenging (Eamus et al., 2013, Williams et al., 2013, Stovall et al., 2019, Liu et al., 2020, Lu et al., 2022). We do not have an explanation for why our species range shift analysis for minimum VPD detected as many "significant" species as it did, particularly given that we did not see a similar pattern for maximum VPD. It is possible that of the four climate variables, it best captured a gradient certain species were sensitive to. We have not encountered literature differentiating the impacts of maximum vs. minimum VPD on plant species, especially expressed as annual means.

Our findings are roughly consistent with those from other empirically based analyses of species' responses to climate change in North America. Tree species' ranges in eastern North America, as quantified, do not appear to be shifting (Zhu, 2012, Sittaro, 2017, Woodall, 2018), although the density of species within their ranges may be (Fei et al., 2017, Murphy et al., 2010). Murphy et al., found that eastern U.S. tree species' densities were greatest ("leaning" distributions; Breshears et al., 2008) towards the northern (i.e., assumed cooler, but see Fig. 1A in Fei et al., [2017]) margins. Fei et al. (2017) found that changes in moisture appeared to be a stronger driver of species' density shifts than temperature, and that angiosperm densities appeared more related to moisture than temperature while gymnosperms were the opposite. We are not drawing conclusions about gymnosperm or angiosperm responses in this study as comparatively few of our species exhibited density shifts.

Density analysis results for two species were at odds with findings from Monleon and Lintz (2015). We found that plot densities were generally increasing in cooler plots for *Abies concolor* and *Calocedrus decurrens*. However, Monleon and Lintz (2015) found that the seedlings of these species occupied warmer plots on average than mature trees. The Turnover Hypothesis (Fei et al., 2017) may account for the

discrepancy, as potentially seedlings of both species may be germinating but failing to survive in previously warmer, wetter plots. Another explanation is that, given that their ranges broadly overlap, this study may be detecting drought and insect-related mortality of these species in the Sierra Nevada (USDA Office of Communications, 2016), a relatively warm and dry portion of their ranges (dashboard).

Species range shift models indicate that, given predicted and observed climatic changes, we should expect tree species' ranges to shift over time (Iverson et al., 2008, Serra-Diaz et al., 2014). The west coast states of the continental United States have experienced conditions that generally differed from those in the 20*th* century, which may affect species distributions. All three states have been experiencing increasing frequencies of droughts (Ficklin et al., 2015), wildfires (Westerling et al., 2006), and impacts from pests in non-coastal mountain ranges (Hicke et al., 2016). Hydrologic regimes have shifted in all three states, with longer summer and fall periods of minimal precipitation (Holden et al., 2018), smaller snowpacks, and shorter snowpack durations (Mote et al., 2018). Temperatures have generally increased in all three states (Westerling et al., 2006, Abatzoglou, 2014). We therefore presume that many of the species we examined are experiencing conditions that make persistence in many places more difficult. However, aside from our examination of minimum VPD, our analyses failed to detect a meaningful number of species range shifts.

There may be several non-exclusive explanations for our lack of range-shift detection. One explanation is that our analysis lacked statistical power. We were seeking evidence of range shifts based on revisited plots containing new species or entirely lacking their previous inhabitants of a given species. We attempted to detect an overall change based on these plot-level changes following a revisit period of 10 years. The revisit time period may have been too short given the range-shift metric we were applying. Monleon and Lintz (2015) may have detected initial range-shifts by examining seedlings which then failed, within our study's timeframe, to manifest as colonization by trees.

A second explanation is that geographical shifts in tree species' ranges may be constrained if species ranges abut and intermingle with other tree species ranges. Zhu et al. (2012), Sittaro et al. (2017), and Woodall et al. (2018) performed range-shift analyses in eastern North America and similarly did not find strong evidence of plot occupancy range shifts of trees. This same constraint may enable within-range density shifts, observed in this study and by Fei et al. (2017) and Murphy et al. (2010). Liang et al. (2018) modeled the ability of trees to migrate in the northeastern US given existing forest cover and fragmentation. They found that it was unlikely that species could shift their ranges fast enough to match the velocity of change in their ecological niche location associated with projected climate change effects. They explain that it may be difficult for seeds to disperse into previously marginal habitat and germinate under an existing forest canopy and successfully compete for light against existing seedlings. Even with substantial disturbance, Liang et al., hypothesize that existing seed banks may out-compete incoming seeds. Similarly, existing seedbanks may enable density increases at the favorable margins of a species' range.

A final explanation is that our range-shift analysis used possibly useful but incomplete metrics. Monleon and Lintz (2015) established that examining species shifts in west-coast USA states with previous plot temperature averages was likely superior to using elevation or latitude as proxies for climate change. Our species range-shift examination relied on a similar temperature metric and examined range-shifts relative to three other climate metrics. It may be that metrics such as minimum VPD better capture climatic stresses that more directly drive range shifts, while temperature and precipitation may generally serve as more indirect metrics for species. Other metric possibilities include pathogen and wildfire extent (e.g., using information similar to Hicke et al., 2016) and species-specific habitat measures (e.g., land use habitat modification; Lenoir et al., 2010).

We believe that species with atypical findings for the density change

analysis highlight certain issues and complexities that confound broad-scale interpretations of our findings. One issue is that a species may experience different ecological pressures across its range. For instance, we found that *Pinus contorta* and *Pseudotsuga menziesii* both shifted in density towards previously warmer and drier areas with higher maximum VPD. Both species appeared to experience, on average, a greater decrease in precipitation in initially wetter plots. We found the density shifts towards initially warmer plots with higher maximum VPD surprising. *P. contorta* is expected to lose habitat in the future as a consequence of climate change (Coops and Waring, 2011), although subspecies may respond differently from one another and may potentially be able to undergo range expansion (Oney et al., 2013). Similarly, Bell and Gray (2016) found that warmer and wetter regions were conducive for positive changes in *P. menziesii* biomass while different factors elsewhere in the species range promoted biomass increases. Another confounding factor is that *P. menziesii* is an intensively managed species, and its management may affect its observed range and density. Therefore, our range shift and density shift analysis results for these species (and others) may be overly simplistic, as our results likely blend the effects of different regional ecological pressures (Lenoir et al., 2010; Lenoir and Svenning, 2015). In effect, given the broad geographic sample of plots, our overall findings for some species may be potentially misleading as they result from the summary of numerous sub-regional associations (i.e., Simpson's Paradox).

An issue complicating interspecific generalizations or comparisons is that species may encounter different environmental pressures. *Quercus douglasii* exhibited a density shift towards initially wetter plots, unlike other species with "significant" density shifts related to precipitation. This shift may have been predominantly driven by drought conditions, as precipitation generally decreased across its plots and previously drier sites may have been more susceptible to drought stress. We note for this species that regions with the lowest initial precipitation (see dashboard) matched areas of dieback (see Fig. 1 in McLaughlin et al., 2020). Additionally, the actual response of the species may have been driven mainly or in part by changes in subsurface hydrology in addition to changes in precipitation (McLaughlin et al., 2020). We find several considerations here: Observed changes in precipitation were neither unidirectional across species' ranges nor always constant across plots within species' ranges. Thus, changes in precipitation may indeed be affected by climate change, but regionally precipitation may be affected to different degrees or in different directions (positive or negative change). Plots inhabited by *Quercus douglasii* experienced a decrease in precipitation while other species experienced (often uneven) increases in precipitation. Also, the actual ecological pressures affecting distribution changes likely differ by species and may be imperfectly associated with changes in mean annual temperature, VPD, or total annual precipitation.

We anticipate that future FIA plot revisit data sets will enable analyses with greater ability to detect and quantify changes in species' ranges. More time will pass for the environment to change and for species to respond. Future FIA plot revisit data will help detect range shifts if indeed we are searching too soon for a signal from overly coarse presence/absence data. In the meantime, the revisit data offer many avenues for exploring potential drivers of range changes for individual species, such as the prevalence and distribution of pests and diseases, impacts of fire and harvest, regional differences in tree growth, and size- or age-related mortality patterns.

5. Conclusion

These findings indicate that the ranges of tree species within the contiguous west coast states of the U.S. have not exhibited profound shifts relative to the temperature, precipitation, and VPD metrics used in this study, although the density for some species may be changing within the ranges they currently inhabit. There may be several reasons why we did not observe shifts in tree species ranges. Given the expected changes in geographical niches, these findings may point towards contractions in species ranges (McKenney et al., 2007).

Our summaries of species range and density shifts across large geographical areas in relation to plot precipitation and temperature values hopefully provide useful large-scale information to managers and researchers. The findings are probably best interpreted at the level of individual species, which we hope our dashboard facilitates, in combination with autecological information.

CRediT authorship contribution statement

Jeremiah D. Groom: Data curation, Methodology, Software, Formal analysis, Writing – original draft, Visualization. **Vicente J. Monleon:** Conceptualization, Software, Resources, Methodology, Writing – review & editing.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Jeremiah D. Groom reports financial support was provided by Oregon Department of Forestry. Jeremiah D. Groom reports financial support was provided by Oregon State University Institute for Natural Resources.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.121262.

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