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RESEARCH ARTICLE

Dry forest decline is driven by both declining recruitment and increasing mortality in response to warm, dry conditions

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Abstract

Aim: Anticipating when and where changes in species' demographic rates will lead to range shifts in response to changing climate remains a major challenge. Despite evidence of increasing mortality in dry forests across the globe in response to drought and warming temperatures, the overall impacts on the distribution of dry forests are largely unknown because we lack comparable large-scale data on tree recruitment rates. Here, our aim was to develop range-wide population models for dry forest tree species (pinyon pine and juniper), quantifying both mortality and recruitment, to better understand where and under what conditions species range contractions are occurring.

Location: Western United States.

Major taxa studied: Two pinyon pine (*Pinus* spp.) and three juniper (*Juniperus* spp.) species.

Methods: We developed range-wide demographic models for five species using forest inventory data from across the western United States and estimated population trends and climate vulnerability.

Results: We find that four of the five species are declining in parts of their range, with *Pinus edulis* having the largest proportion of populations declining (24%). Population vulnerability increases with aridity and temperature, with up to ~50% of populations declining in the warmest and driest conditions. Mortality and recruitment were both essential to explaining where populations are declining.

Main conclusions: Our results suggest that dry forest species are undergoing an active range shift driven by both changing recruitment and mortality, and that increasing temperatures and drought threaten the long-term viability of many of these species in their current range. While four of the five species examined were experiencing some declines, *P. edulis* is currently most vulnerable. Management actions such as reducing tree density may be able to mitigate some of these impacts. The framework we present to estimate range-wide demographic rates can be applied to other species to determine where range contractions are most likely.

KEYWORDS
climate change, demography, FIA, forest decline, pinyon-juniper, range shifts

1 | INTRODUCTION

Observations of mass mortality in tree species across the globe have raised alarm about the long-term viability of many extant forests in the face of climate change and other anthropogenic stressors (Aleixo et al., 2019; Allen et al., 2010; Hammond et al., 2022; McDowell et al., 2020; Ury et al., 2021). This concern has been particularly acute in many dryland forest regions (Mátyás et al., 2018; Petrie et al., 2017; Williams et al., 2010), which cover >10 million km^2 across the globe (Bastin et al., 2017). For example, pinyon-juniper woodlands in the western United States have experienced some of the most notable mortality events (Breshears et al., 2005; Campbell et al., 2020; Meddens & Hicke, 2014), and typically make up the warmest, driest limit of forests in this region (Urza et al., 2020). If warming, drying, or increasing disturbance lead to permanent declines of dominant tree species in these regions, declining species are unlikely to be replaced by other trees and instead may lead to ecosystem state changes from forests to shrub and grasslands, with lasting implications for ecosystem services and biodiversity (Anderegg et al., 2013; McDowell et al., 2016; Reichstein et al., 2013).

Despite increasing observations of mass mortality events in dry forests, the long-term viability of extant populations often remains uncertain. This is in large part because we lack comparable data on recruitment of new trees, although several studies have suggested that tree recruitment may be diminished under climate change, especially in dry areas (Davis et al., 2019; Petrie et al., 2017; Stevens-Rumann et al., 2018). Recruitment data are essential to estimate population trends and determine where new individuals gained through regeneration are not compensating for those lost through mortality. Areas where mortality exceeds recruitment are vulnerable to population decline and eventual range shifts. Historically, estimating recruitment rates in response to environmental conditions over broad spatial scales has been difficult or impossible. While recruitment data are regularly collected in small spatial scale demographic studies, recruitment is not easily observable from most large-scale data sources (e.g., remote sensing products), and not directly measured with tagged individuals in national forest inventories (e.g., Forest Inventory and Analysis, FIA). However, recent advances in inference approaches (Schultz et al., 2022; Sharma et al., 2022; Shriver et al., 2021) provide an opportunity to estimate demographic rates, including recruitment, of tree species across wide geographic areas using large scale monitoring data and identify the abiotic and biotic conditions explaining demographic performance. Recruitment and survival data can then be integrated to estimate current population trends (i.e., population growth rates, λ), enabling identification of regions of population vulnerability at range-wide scales that were previously not possible, and link vulnerability to temperatures, drought, and density-dependent effects (e.g., competition, pathogens).

In pinyon-juniper woodlands, a widespread dry forest type in the western United States, incidences of mass mortality have been clearly linked to tree physiological responses to increasing drought and heat stress (Breshears et al., 2009; McDowell et al., 2008). In addition to increasing temperatures and prolonged drought, pinyon-juniper woodlands have also experienced widespread increases in tree and basal area density over the 20th century (Filippelli et al., 2020; Miller et al., 2019). Current high basal area densities could further exacerbate the demographic impacts of drought and increasing temperatures by increasing competition and pathogen risk, exacerbating declines in survival, recruitment, and growth. However, the impacts of stand basal area density on the demographic performance of pinyon-juniper across broad scales are not well understood. If demographic rates decline sufficiently with increasing density (i.e., negative density dependence), natural or managed reductions in tree density could ameliorate the negative impacts of changing climate on demographic performance (Bradford & Bell, 2017). Alternatively, if the impacts of negative density dependence are weak compared to the direct impacts of increasingly warm and dry conditions, then populations may be especially vulnerable to decline regardless of management interventions.

Demographic population models are a powerful tool for understanding how the survival, growth and reproduction of individuals lead to population-level trajectories, yet efforts to estimate the population trends of plants over large spatial extents have historically been limited. Here, we overcome this challenge using novel approaches to infer tree survival, recruitment and growth parameterized from FIA data (Shriver et al., 2021). Combining these demographic rates together in structured population models, we estimate existing population trends of two pinyon pine and three juniper species in the western United States and identify how population vulnerability varies across environmental gradients. We quantify the population growth response of each species to soil water availability, temperature, and basal area density gradients to understand the potential impact of future increases in heat and moisture stress. Further, our modelling approach explicitly acknowledges conditions beyond average climate such as soil characteristics and biotic interactions likely explain a significant portion of variability in demographic performance, and captures and propagates this spatial heterogeneity throughout our analyses with spatial random effects. Using this approach, we: (a) estimate the proportion of sampled populations that are declining; (b) quantify how population growth rates vary across climate, density, and geographic gradients; and (c) identify the relative role of both recruitment and mortality in driving the vulnerability of dry forests.

2 | METHODS

2.1 | Forest inventory data

We developed our demographic models using the publicly available FIA database (http://www.fia.fs.fed.us/). FIA is a systematic and standardized survey of forested regions in the entire United States, including both public and private lands. We describe relevant details of the sampling design below, but full details on the FIA programme and sampling design can be found in Bechtold and Patterson (2005).

We focus on five widespread dry woodland species in the Rocky Mountain and Great Basin regions: *Pinus edulis* (PiEd), *Pinus monophylla* (PiMo), *Juniperus osteosperma* (JuOs), *Juniperus monosperma* (JuMo), and *Juniperus scopulorum* (JuSc). Nearly the entire ranges of these species are within the United States, thus FIA data provide a near complete survey of their range-wide dynamics. Because our primary focus was quantifying population trajectories and demographic rates of each species and linking these to climate across their range, we excluded all plots in which fire mortality or tree harvesting occurred. This resulted in a total of 578 to 2,013 plots and 3,225 to 25,105 individuals per species (Supporting Information Table S1). All individuals greater than 15.24 cm (6 in.) in height are surveyed. Within each plot, all adult trees greater than 12.7 cm (5 in.) diameter at breast height (DBH) are assigned unique tags and tracked within four 7.32 m (24 ft.) radius subplots. All saplings <12.7 and >2.54 cm (1 in.) DBH are assigned unique tags and tracked within four 2.07 m (6.8 ft.) radius microplots within the larger adult plots. Finally, seedlings <2.54 cm DBH are counted within the same microplots as the saplings. Two censuses were conducted 10 years apart in each plot. In some cases, additional plot surveys occurred between the standard 10-year interval. These additional surveys were excluded because they were sporadic and not standardized across the dataset. The exact timing of the initial censuses varied by state and region within state (typically 10–20% of plots in each state are surveyed each year) but occurred between 2000 and 2007.

2.2 | Structured population model

To quantify how the vulnerability of populations of each tree species varied across its range, we developed structured population models (integral projection models, IPMs) for each species in each plot in which that species occurred. The IPM for each plot, species is formulated as:

$$n(m')_{d,t+1} = \int K(m'|m)_{d,t} n(m)_{d,t}\, dm \tag{1}$$

where $n(m)_{d,t}$ is the population size structure of a focal species in plot d at time t, $K(m'|m)_{d,t}$ is a kernel that describes the redistribution of individuals of that species from size m to m' based on underlying demographic processes. $K(m'|m)_{d,t}$ is made up of four demographic processes

$$K(m'|m)_{d,t} = G(m'|m)_{d,t} * S(m)_{d,t} + F(m)_{d,t} * R(m') \tag{2}$$

where $G(m'|m)_{d,t}$ is a growth kernel describing transitions from diameter size m to m' in plot d at time t. $S(m)_{d,t}$ is a function describing the survival rates of individuals of size m, $F(m)_{d,t}$ is a function describing the number of new recruits produced by individuals of size m, and $R(m')$ is a kernel describing the size distribution of new recruits.

The growth kernel, $G(m'|m)_{d,t}$ was a normal density function, truncated at 0, where the probability of transitioning to any size, m', was

$$G(m'|m)_{d,t} = Normal(m' \mid \mu(m)_{d,t}, \sigma^2) T[0,] \tag{3}$$

$$\mu(m)_{d,t} = \alpha_{(g)} m + \mathbf{X}_{d,t} \mathbf{b}_{(g)} + \omega_d \tag{4}$$

where $\alpha_{(g)}$ is a parameter describing the effect of tree diameter size on size transitions (i.e., whether growth increases or decreases with tree size), $\mathbf{X}_{d,t}$ is a design matrix including all environmental covariates (see below), $\mathbf{b}_{(g)}$ is a vector of parameters describing the effect of environmental covariates on size transitions, and ω_d is a spatial random effect for each plot d that accounts for all other factors that would influence growth, but are not directly accounted for by covariates. Finally, σ^2 describes individual-level variability in size transitions.

Survival is formulated as a logistic function

$$\text{logit}(S(m)_{d,t}) = \alpha_{(s)} m + \mathbf{X}_{d,t} \mathbf{b}_{(s)} + \varepsilon_d \tag{5}$$

where similar to above $\alpha_{(s)}$ is a parameter describing the effect of tree diameter size survival, $\mathbf{X}_{d,t}$ is a design matrix including all environmental covariates, $\mathbf{b}_{(s)}$ is a vector of parameters describing the effect of environmental covariates on survival, and ε_d is a spatial random effect specific to survival for each plot d.

And finally, recruitment (which integrates all the processes leading to new recruits including seed production, germination, and establishment) is

$$\log(F(m)_{d,t}) = \alpha_{(f)} m + \mathbf{X}_{d,t} \mathbf{b}_{(f)} + \gamma_d \tag{6}$$

2.3 | Demographic model fitting

Demographic models for growth, survival and recruitment described above were fit using an integrated model that shared individual-level information (survival and size of individual saplings and adults) and population-level information (counts of seedlings). Individual-level survival data were assigned a Bernoulli likelihood, plant size (i.e., growth) a Gaussian likelihood, and negative binomial likelihood was used for seedling counts (Shriver et al., 2021). All covariates were assigned vague, zero-centred priors. Spatial random effects were fit using a predictive-process model (Banerjee et al., 2008). Predictive-process models overcome the computational burden of fitting spatial random effects to large datasets with a dimension reduction approach that reduces the large number of plots into a smaller number of constituent knots that summarize the landscape of spatially autocorrelated processes. The number of knots used for each species was approximately 10% of the total plot number (Supporting Information Table S1). Demographic model convergence and fit was assessed using convergence statistics (R-hat), posterior predictive checks, and out-of-sample predictions with withheld data. Full details of demographic model fitting can be found in Shriver

et al. (2021) and demographic parameter estimates are in Supporting Information Appendix S1.

2.4 | Covariates

As described in Shriver et al. (2021) covariates were selected to summarize the effects of moisture availability (MA), heat stress (HS) and neighbour basal area density (ND) on the growth, survival and recruitment. Moisture availability was the estimated mean growing season (May to October) available soil water (i.e., moisture that can be extracted from the soil until soil water potential reaches −3.9 MPa) between 40 and 100 cm depth over the 10-year census interval. Heat stress was the average temperature over the growing season over the 10-year census interval. Gridded climate data were extracted from the Livneh climate dataset (Livneh et al., 2015). Climate data were then paired with soils data from ISRIC Wise Global dataset v1.2 (Batjes, 2012) to create estimates of soil water availability using SOILWAT2 (Bradford et al., 2014). Neighbour density was the basal area density of all living trees in the plot at the first census. We considered both linear and quadratic effects of the two climate related covariates yielding a matrix of covariates, $\mathbf{X}_{d,t}$:

$$\mathbf{X}_{d,t} = \left[1, MA_{d,t}, MA_{d,t}^2, HS_{d,t}, HS_{d,t}^2, ND_{d,t}\right]$$

2.5 | Analysis

To understand how population growth rates (λ) change across environmental and geographic gradients we calculated equilibrium λ (i.e., at stable size distribution) for each FIA plot location and species. Assuming stands are at equilibrium size structure helps remove the potential influence of past disturbance and management, which impacts population structure and thus population-level recruitment and survival, but are transient and do not represent a direct impact of climate. We calculated λ assuming both extant basal area in the plot and under a climate-only scenario (i.e., zeroing out density effects) to quantify the direct impacts of environmental conditions on λ without the influence of density dependence. λ for each plot was determined by discretizing the continuous IPM using 1-cm diameter size classes and calculating the dominant eigenvalue of the discretized matrix. Smaller size class binning was assessed but were found to have little impact on λ despite significantly increasing computation time (Supporting Information Figure S1). Growth transition probabilities were determined by integrating over the size bin m' using a truncated normal cumulative distribution function, assuming a starting point at the midpoint of the size bin for m. Similarly size specific recruitment and survival rates were determined for each discretized size bin using the midpoint of the size bin for m. To determine how populations' growth and vulnerability varied across climate gradients we calculated the proportion of all plots with growing populations (i.e., $\lambda > 1$) in bins representing 10% quantiles across each covariate. This approach allowed us to display variability in three ways. First, the proportion of plots within a climate bin with growing populations ($\lambda > 1$) captures spatial heterogeneity not explained by focal climate variables (e.g., proportions close to 1 or 0 indicate similar responses among all plots), as we might expect that even in the most extreme conditions other, unaccounted for, environmental conditions captured by the spatial random effects such local topo-edaphic conditions could influence population growth rates. Second, uncertainty in the proportion of plots with growing populations (represented as a box and whiskers) captures model uncertainty carried through from the posterior estimates of demographic rates. Finally, examining how the proportion of growing populations changes across covariate bins allowed us to understand how population vulnerability shifts in response to climate while acknowledging the uncertainties listed above.

To understand the importance of recruitment and mortality in driving population vulnerability we calculated population-level recruitment and mortality rates. For recruitment, this was done by finding the total reproductive output assuming the population was at its stable size distribution. Similarly, mortality was determined as by calculating one minus the total population survival rate assuming the population was at stable size distribution. In both cases posterior median population-level recruitment and mortality rates were calculated and then we used the median recruitment and mortality rate across all populations as a baseline for comparing above or below 'typical' recruitment and mortality rates.

3 | RESULTS

For both pinyon species and two of the three juniper species, at least some proportion of their populations are likely declining (Figure 1). However, there was considerable variability across species. The greatest proportion of declining populations was found in PiEd, where we estimated 24% (8–66%, 95% credible interval [CI]) of plots had declining populations, with 76% increasing. We found somewhat lower but still notable numbers of declining populations in PiMo (4%, 0–30% CI), JuMo (5%, 0–22% CI), and JuSc (3%, 0–27% CI). No populations of JuOs were found to be declining based on posterior estimates of population growth rates (0%, 0–3% CI).

The vulnerability of all species increased in drier soil moisture conditions, reflected by lower proportions of plots supporting stable or growing populations ($\lambda > 1$) in drier conditions (Figure 2). However, the influence of moisture conditions varied considerably among species. Few, if any, JuOs populations were declining (Figure 2g), while ~50% of PiEd populations were declining in the driest conditions under extant stand density (Figure 2a). Between 10% and 30% of the populations of the remaining species (PiMo, JuMo, JuSc) were found to be declining in the driest conditions. Vulnerability also increased across all species with increasing average growing season temperature at extant stand densities; however, the vulnerability of pinyon species (PiEd, PiMo, Figure 2b,e) stabilized and did not increase beyond ~16 °C. Similar to soil moisture conditions, the magnitude of vulnerability to temperature differed by species, with few if any populations declining in JuOs (Figure 2h), compared to ~35% of PiEd

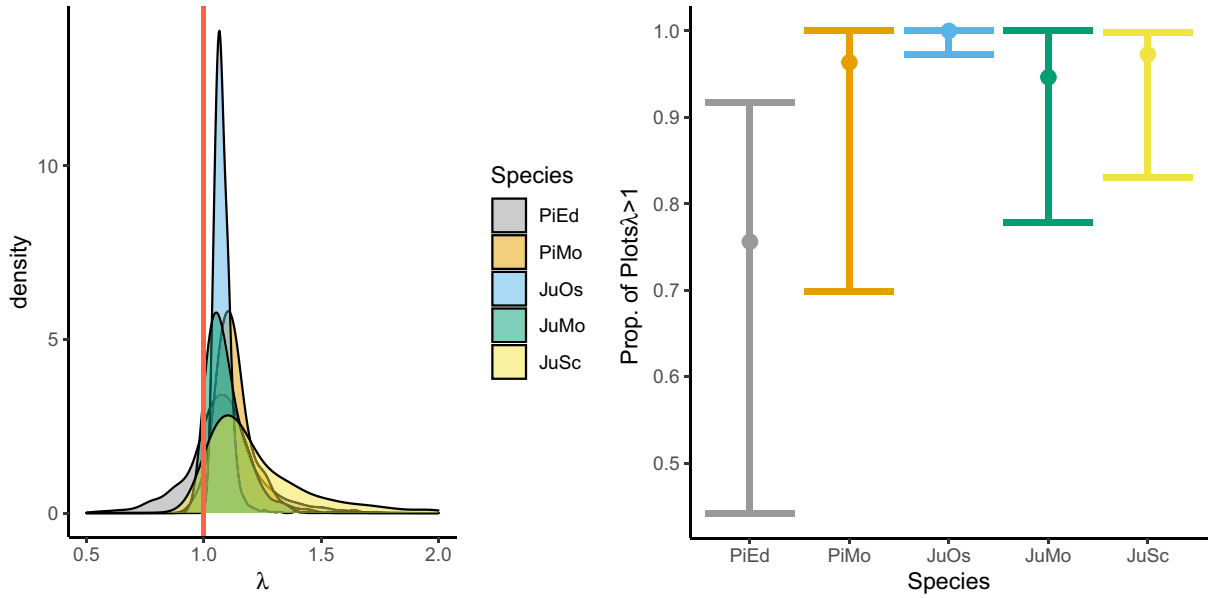

FIGURE 1 Estimates of population growth (λ) across the range of five species of pinyon and juniper. Density plots (left) use posterior median estimate of 10-year population growth rate for each Forest Inventory and Analysis (FIA) plot in which the species occurred. Estimates of the proportion of plots with stable or growing populations ($\lambda > 1$) (right) with error bars summarizing the 95% CI from model uncertainty. PiEd, *Pinus edulis*; PiMo, *Pinus monophylla*; JuOs, *Juniperus osteosperma*; JuMo, *Juniperus monosperma*; JuSc, *Juniperus scopulorum*.

populations declining in the warmest conditions (Figure 2b). The responses of woodland species to stand density were much more idiosyncratic. The proportion of growing populations of PiEd, JuOs, and JuSc declined with increasing basal area density, while PiMo and JuMo population growth did not display a clear relationship with basal area (Figure 2, right column).

Climate vulnerabilities combined with spatial random effects led to geographic regions with lower population growth rates (λ) and thus greater population vulnerabilities (Figure 3). For example, PiEd populations were consistently estimated to be declining in the central part of its range, in the Four Corners region (i.e., the intersection of Arizona, Utah, Colorado, and New Mexico), as well as in southern New Mexico. In contrast, PiMo populations were estimated to be declining in the north-west part of its range, western Nevada, and portions of south-west Utah, while populations are estimated to be growing rapidly in north-east Nevada. JuMo had lower rates of population growth at its southern limit, in particular south-western and south-eastern parts of its range in Arizona, New Mexico and West Texas, while more northern populations are stable or growing. JuSc populations were estimated to be declining or growing more slowly in Arizona and New Mexico, and increasing rapidly in northern parts of its range in Montana. Finally, JuOs showed no clear geographic pattern, with populations growing throughout its range.

Both low levels of recruitment and elevated rates of mortality were needed to explain declines in nearly all populations of each species (Figure 4). Of the populations of PiEd that were found to be declining, 86% were experiencing both below median population-level recruitment and above median population-level mortality, while only 12% were experiencing above median mortality alone and 2% were experiencing below median recruitment alone. Similarly, 100% of declining PiMo and JuMo populations and 94% of JuSc had both below median recruitment and above median mortality. Finally, no JuOs populations were found to be declining based on posterior median estimates of λ.

4 | DISCUSSION

Combining range-wide estimates of recruitment and survival in pinyon and juniper species in the western United States, we found that four of the five species are declining in some part of their range and warm and dry conditions are associated with increasing population vulnerability. While mortality events have been documented in warm, dry, low-elevation woodlands throughout western North America, our results are the first to document the response of new tree recruitment across several woodland species at similar spatial extents and to combine mortality and recruitment together to quantify population trajectories. Further, we found that data on mortality and recruitment are both essential to explain population declines, indicating that understanding and estimating recruitment is likely essential to fully anticipate forest vulnerability in response to global change.

Our results suggest that population vulnerability is likely to increase as warming and drying due to anthropogenic climate change continues, potentially leading to contractions of low-elevation woodlands and state-changes to grass and shrublands. We found consistent declines in population growth as conditions warm and dry in nearly all species; however, there is considerable variability

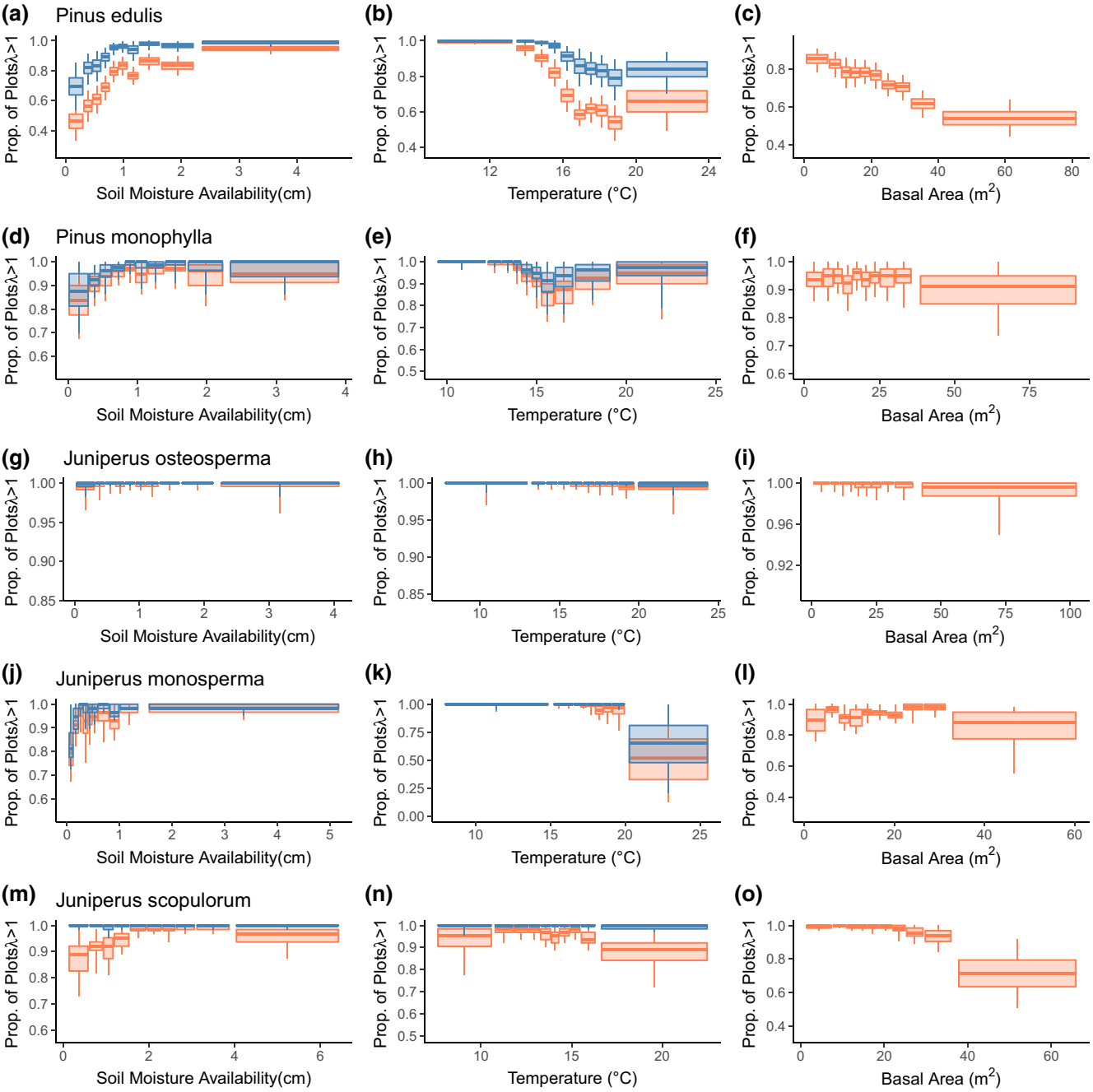

FIGURE 2 Proportion of all Forest Inventory and Analysis (FIA) plots with stable or growing populations ($\lambda > 1$) across climate and tree density conditions. *Pinus edulis* (PiEd; a–c), *Pinus monophylla* (PiMo; d–f), *Juniperus osteosperma* (JuOs; g–i), *Juniperus monosperma* (JuMo; j–l), *Juniperus scopulorum* (JuSc; m–o). Orange boxes indicate vulnerability under extant tree density conditions and blue is climate-only (density basal area of zero). Whisker lengths along *y* axis indicate model uncertainty (95% credible interval). Box plot widths each span 10% of all FIA plots for each species along *x* axis.

among species with about half of PiEd populations in the warmest and driest locations declining ($\lambda < 1$), while in other species (PiMo, JuMo, and JuSc) ~10–20% of populations are declining in the warmest and driest conditions. While it is worth noting that our results represent spatial relationships between demographic rates, population growth, and climate conditions, studies exploring temporal increases in aridity and temperatures at individual sites have noted similar changes in survival, reproductive output, and recruitment and in some cases linked these responses to physiological mechanisms (Breshears et al., 2005; Redmond et al., 2012; Wion et al., 2020). Our findings provide clear evidence that vulnerability to increasing aridity observed at local scales is likely to impact both pinyon-juniper survival and recruitment range-wide leading to increasing vulnerability of low-elevation woodlands.

We found consistent increases in vulnerability across species, although there was considerable variability in the magnitude of

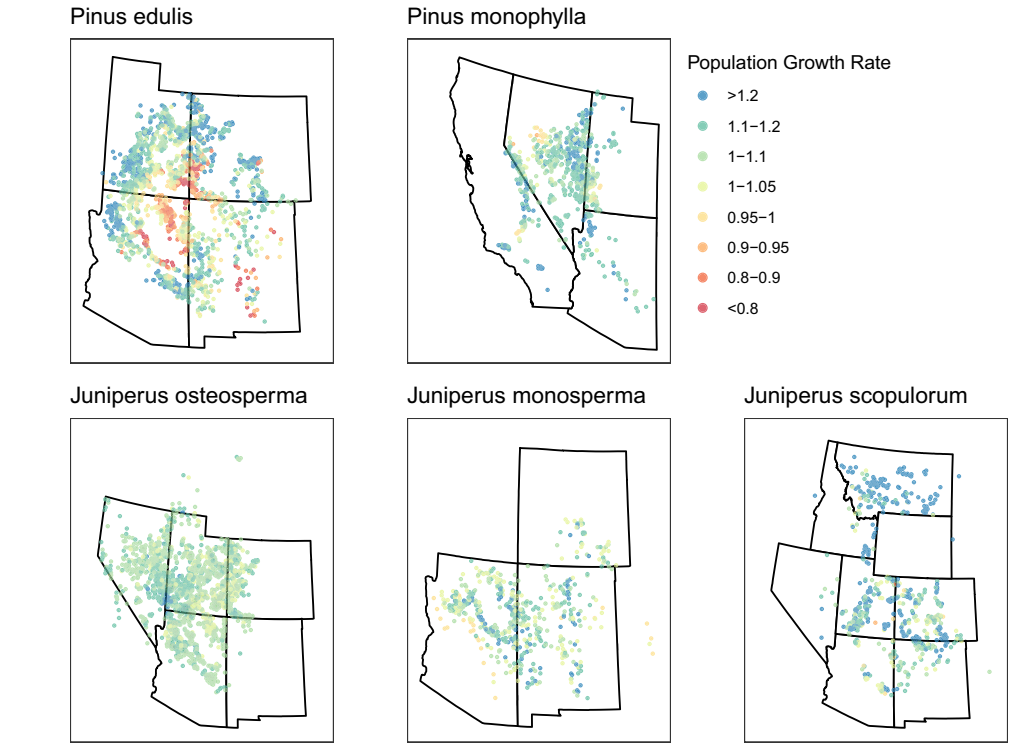

FIGURE 3 Spatial variation in population vulnerability of five species of pinyon and juniper. Maps of 10-year population growth rate (λ) using posterior median estimates of λ. Values < 1 indicate declining populations.

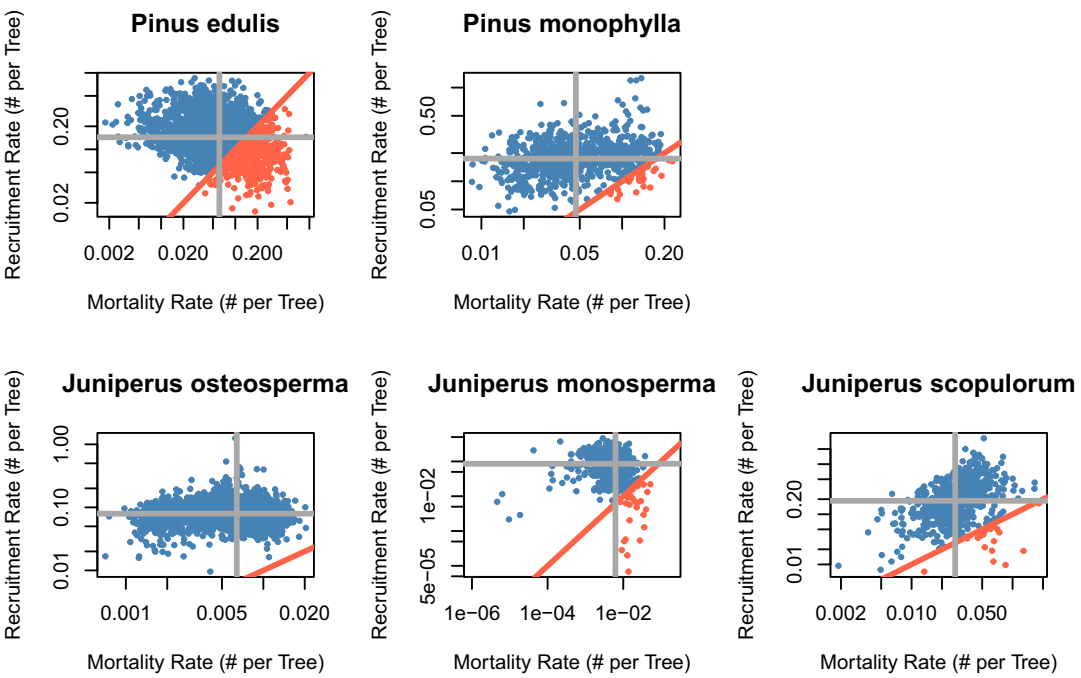

FIGURE 4 10-year recruitment and mortality rates for five species of pinyon and juniper indicating population vulnerability driven by both mortality and recruitment. In each species blue points indicate populations estimated to be growing based on recruitment and mortality rates, and orange points are declining populations. The orange line indicates the threshold between growing and declining populations. Grey lines indicate the median recruitment (horizontal) and mortality rate (vertical) across all populations. Points are based on posterior median estimates of 10-year recruitment and mortality for each population. Note, the *x* axis for *Juniperus monosperma* (JuMo) has been truncated, removing two populations with low mortality rates from the figure, to more clearly display remaining populations.

vulnerability. Overall, pinyon species (PiEd and PiMo) appear more vulnerable than juniper species to warm and dry conditions over our study period (2000–2017), with the greatest proportion of populations declining in PiEd (~50% in the driest conditions). This finding aligns with previous physiological and demographic work that suggested that pinyon pines are likely to be less tolerant of drought and warming conditions than junipers (McDowell et al., 2008), as well as mortality events that have occurred over the last 20 years in these species (Allen et al., 2010). Similar recent research has also noted that demographic performance of PiEd declines in warming, drying conditions helping to drive changes in the lower elevation range limit of PiEd, while the limits on upslope expansion were less clear but likely driven by interacting abiotic and biotic factors (Schultz et al., 2022). Climate sensitivities of PiEd cone production and survival have been well documented, in particular prolonged drought and warming have been associated with mortality events in both PiEd and PiMo (Breshears et al., 2005; Greenwood & Weisberg, 2008; Redmond et al., 2012, 2018; Wion et al., 2020). While historically junipers have been thought to be more drought tolerant (McDowell et al., 2008) and have experienced relative stability compared to pinyons (Stanke et al., 2021), recent intense hot-droughts in northern Arizona and southern Utah led to mortality and canopy dieback in junipers, most notably in JuOs and JuMo (Kaibab National Forest, 2021; Kannenberg et al., 2021). Overall, our knowledge of the climate drivers of PiEd has advanced significantly since mortality events in the early 2000s; however, considerably less is known about the drivers of population dynamics in PiMo and juniper species (Hartsell et al., 2020). Our findings indicate that while juniper populations may be more resistant, increasing temperatures and aridity are still likely to lead to increased population vulnerability. Finally, FIA sampling design may also contribute to differences in the total magnitude of vulnerability observed. FIA forest surveys are limited to areas with >10% tree cover (Bechtold & Patterson, 2005). While this captures most of the range of these species it may miss the lowest range limits of some juniper species, which often occur in open savanna conditions that are not typically classified as 'forest land', suggesting that we could be missing the warmest and driest conditions in which these species occur and thus underestimating their vulnerability.

While climate change is expected to alter the composition and structure of forests globally (Anderegg et al., 2020; McDowell et al., 2020), the loss of low elevation, dry woodlands is particularly notable as declines in pinyon, juniper, and other low elevation species would likely lead to a larger state-change from forested ecosystems to grass or shrublands (Mátyás, 2010; Mátyás et al., 2018; McDowell et al., 2016; Urza et al., 2020). Historically, dry woodlands have expanded into lower elevations in the western United States and globally throughout much of the 19th and 20th centuries driven by domestic grazing, fire suppression, climate fluctuations, and other land use practices (Miller et al., 2019; Scholes & Archer, 1997). This expansion impacted rangeland ecosystem services, but also created one of the largest global terrestrial carbon sinks during this period (Ahlstrom et al., 2015). Observations of population vulnerability with increasing temperatures and declining soil moisture observed here and in other studies may indicate that low-elevation woodlands are reaching a tipping point where contraction occurs in areas of historic expansion. This would have critical ecological impacts on local and global carbon cycling, and there is increasing risk of conversion of contracting woodlands to invasive dominated systems (at least temporarily) rather than simply converting back to native grass and shrublands (Flake & Weisberg, 2021; Williams et al., 2017).

Our results indicate that for some species historically high woodland tree densities, driven in part by a century of fire exclusion and other land use practices, could be exacerbating vulnerability created by warming and drying conditions. We found negative effects of increasing tree density on PiEd, JuOs and JuSc; however, these negative effects of density were not clearly apparent in PiMo or JuMo. This variability among species may reflect the complexity of density dependence in dry forests. While a number of studies have indicated that density is likely to interact with drought and warming temperatures to increase vulnerability, others have found no effect of density, or even the potential positive impacts driven by facilitation, with magnitude and strength of density effects changing across climate conditions, species, and life stage (Greenwood & Weisberg, 2008; Looney et al., 2012; Meddens et al., 2015; Urza et al., 2019). Still previous work and our own results suggest a growing opportunity to increase dry forest resistance to changing climate through silvicultural approaches (Bradford & Bell, 2017; Bradford et al., 2022). In general, development of management practices to promote climate resistance and resilience in pinyon-juniper woodlands lags behind more productive forest ecosystems, often focusing on increasing understory productivity or fuel reduction rather than forest health per se. Significant work is still needed to determine where, how, and for what species reductions in tree density may improve the health of pinyon-juniper woodlands.

While mortality of adult canopy trees is often the most visible sign of increasing population vulnerability, our results indicate that data on mortality and recruitment are both needed to fully anticipate population vulnerability. This finding supports recent calls to develop mechanistic, demographic range models to predict shifts in the distribution and abundance of plant species as well as an increasing focus on the drivers of plant recruitment and regeneration (Ehrlén & Morris, 2015; Evans et al., 2016; Petrie et al., 2016; Sharma et al., 2022). Yet, the biggest barrier to developing range-wide demographic models is typically a lack of detailed demographic data at large spatial scales and logistical challenges associated with collecting such data. Our integrated population modelling approach provides one potential path forward to address these challenges (Shriver et al., 2021). As an increasing number of new large-scale spatial datasets emerge (e.g., lidar, structure from motion), creating flexible demographic modelling approaches that can accommodate multiple, often non-traditional, data sources will be critical to anticipating plant responses to global change over large spatial scales.

5 | CONCLUSIONS

Anticipating where species are most likely to be vulnerable to climate change remains a major challenge for ecologists. Using a novel

range-wide demographic modelling approach and forest inventory data we found that four of five pinyon-juniper species in the western United States are declining in some part of their range. Our results indicate that range contractions are likely ongoing in many parts of the historic pinyon-juniper range. In particular, *Pinus edulis* (PiEd) is most vulnerable with > 50% of populations declining in the warmest and driest conditions. But our findings of strong density dependence in many species indicates that managed reductions in tree density could slow or reverse this decline in some cases. The novel approach we present for demographic range models can be used to anticipate the vulnerability of other species and forecast coming range shifts.

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DATA AVAILABILITY STATEMENT

Raw FIA data are publicly available at https://apps.fs.usda.gov/fia/datamart/datamart.html. Data used for this paper can be found in Noel et al. (2022) (https://doi.org/10.5066/P9FIGKFM). Demographic model results for each species and code to reproduce population analysis and figures can be found on Zenodo with DOI https://doi.org/10.5281/zenodo.6862819.

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BIOSKETCH

The authors' research collaboration seeks to understand the vulnerability of dry forests to climate change, including increasing temperatures and drought, anticipate where change in forest structure and composition may occur, and identify management actions to mitigate impacts on forests.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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