

Quantifying the demographic vulnerabilities of dry woodlands to climate and competition using rangewide monitoring data

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Citation: Shriver, R. K., C. B. Yackulic, D. M. Bell, and J. B. Bradford. 2021. Quantifying the demographic vulnerabilities of dry woodlands to climate and competition using rangewide monitoring data. *Ecology* 102(8):e03425. 10.1002/ecy.3425

Abstract. Climate change is expected to alter the distribution and abundance of tree species, impacting ecosystem structure and function. Yet, anticipating where this will occur is often hampered by a lack of understanding of how demographic rates, most notably recruitment, vary in response to climate and competition across a species range. Using large-scale monitoring data on two dry woodland tree species (*Pinus edulis* and *Juniperus osteosperma*), we develop an approach to infer recruitment, survival, and growth of both species across their range. In doing so, we account for ecological and statistical dependencies inherent in large-scale monitoring data. We find that drying and warming conditions generally lead to declines in recruitment and survival, but the strength of responses varied between species. These climate conditions point to geographic regions of high vulnerability for particular species, such as *Pinus edulis* in northern Arizona, where both survival and recruitment are low. Our approach provides a path forward for leveraging emerging large-scale monitoring and remotely sensed data to anticipate the impacts of global change on species distributions.

Key words: *climate; competition; demography; Forest Inventory and Analysis; integral projection model; Juniperus osteosperma; Pinus edulis.*

INTRODUCTION

Changing climate, disturbance regimes, and human activity are expected to reshape the distribution of forest and woodland species across the globe, potentially transforming the structure of these ecosystems (McDowell et al. 2018). Although mortality of overstory plants is often the most obvious indicator of declining forest and woodland health (e.g., Millar and Stephenson 2015), the resilience and long-term viability of tree species in the face of environmental change will be determined not only by survival of existing individuals, but also the recruitment and growth of new individuals that drive population recovery and spread; that is, resilience (Jackson et al. 2009). Evidence of declining forest health and resilience due to declining recruitment is increasingly common (Petrie et al. 2017, Stevens-Rumann et al. 2018). Yet anticipating where forest and woodland species may be most vulnerable to environmental change is often hampered by a lack of understanding of how rates of survival, growth, and, most notably, recruitment vary across a species range and the role of both abiotic

conditions and biotic interactions in driving them (Sirén and Morelli 2020).

Demographic processes are recognized to be critical to understanding species range shifts and ecosystem state changes in response to climate change (Briscoe et al. 2019). But efforts to estimate how plant recruitment, survival, and growth vary across large spatial scales are limited, in part because many traditional demographic inference approaches (e.g., Caswell 2001) do not typically accommodate diverse data structures and the ecological/statistical dependences inherent to large spatial data. Instead, plant demographic analyses have typically placed the onus on researchers to mark and return to individuals and independently measure each demographic transition in the field, making it logistically challenging to scale data collection to larger areas. At the same time, there has been an explosion of diverse data sets from large-scale field monitoring and remote sensing (e.g., forest inventories, lidar) with the potential to revolutionize our understanding of spatiotemporal plant demographic processes and their population consequences. Yet, these data sources rarely provide data on both survival and recruitment at the individual-scale resolution required for traditional demographic modeling approaches. Harnessing the power of these data sets will require flexible modeling approaches that can link detailed, individual demographic data with additional

Manuscript received 11 December 2020; revised 8 February 2021; accepted 21 March 2021. Corresponding Editor: Brett T. McClintock.

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data sources that describe how demographic processes drive changes in abundance and population structure across large landscapes and over decades (Shriver et al. 2019).

Here, we develop an approach to infer the range-wide recruitment, survival, and growth rates of two widespread dry woodland species using large-scale U.S. Department of Agriculture (USDA) Forest Service Forest Inventory and Analysis (FIA) data (Bechtold and Patterson 2005). Because FIA plots encompass nearly the entire range of many tree species, they present a unique opportunity to understand how demographic rates vary across a species' range and identify where populations may be most vulnerable to changing climate and disturbance. But FIA data also present a number of challenges (see Methods for full explanation), most notably accounting for ecological dependencies in quantifying recruitment. Specifically, seedlings are not tagged but simply counted; thus the fate (growth/survival) of existing seedlings are not independently quantified from new recruits. We overcome this challenge by developing an integrated population modeling approach that accounts for ecological dependencies while also accounting for spatial autocorrelation and sharing information across plots in a rigorous way.

METHODS

FIA data

We developed our demographic models using the publicly available FIA database.² 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 here, but full details on the FIA program and sampling design can be found in Bechtold and Patterson (2005).

We focus our analyses on two widespread dry woodland species in the Colorado Plateau and Great Basin regions: *Pinus edulis* (hereafter PiEd) and *Juniperus osteosperma* (hereafter JuOs). Nearly the entire ranges of both 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 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 2,013 plots with 16,951 tagged PiEd individuals, and 2,380 JuOs plots with 25,105 tagged JuOs individuals. All PiEd and JuOs individuals >15.24-cm (6 in.) in height are surveyed. Within each plot, all adult trees of >12.7-cm (5 in.) diameter are assigned unique tags and tracked within four, 7.32-m (24 ft.) -radius subplots. All saplings of <12.7- and >2.54-cm (1 in.) diameter are assigned unique tags and tracked within four, 2.07-m (6.8 ft.) -radius microplots within the larger adult plots.

Finally, seedlings of <2.54-cm diameter are counted within the same microplots as the saplings. Two censuses were conducted 10 yr apart in each plot. In some cases, additional plot surveys occurred between the standard 10-yr interval. These additional surveys were excluded because they were sporadic and not standardized across the data set. 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.

Demographic modeling

Data on adult and sapling growth and survival are collected at the individual level. Individual plants >2.54-cm diameter are tagged, and as a result the growth and survival of an individual plant can be tracked over the census interval. We built growth (i.e., change in diameter size) and survival models following the well-developed generalized linear model functional forms common for plant demography models (Merow et al. 2014). Individual diameter size change is modeled as normal distribution truncated at zero ($T[0, \infty)$) according to

$$z_{i,t+1} \sim \text{Normal}(u_{i,t+1}, \sigma^2) T[0, \infty) \quad (1)$$

$$u_{i,t+1} = \alpha_{(z)} z_{i,t} + \mathbf{X}_{d[i]} \mathbf{b}_{(z)} + \omega_{d[i]} \quad (2)$$

where $z_{i,t}$ is the size of plant i ($i = 1 \dots J$) in the first census (t), $u_{i,t+1}$ is expected mean size at the second census, 10 yr later ($t + 1$), $\alpha_{(z)}$ is a regression coefficient for plant size, $\mathbf{X}_{d[i]}$ is a vector of plot-level environmental covariates for plot d ($d = 1 \dots D$) where individual i is located, $\mathbf{b}_{(z)}$ is a vector of environmental regression parameters specific to the size model, indicated by the subscript (z), $\omega_{d[i]}$ is a plot-level spatial random effect, and σ is a standard-deviation parameter describing individual variation not explained by covariates and random effect.

Similarly, survival probability is modeled as

$$s_{i,t+1} \sim \text{Bern}(p_{i,t+1}) \quad (3)$$

$$\text{logit}(p_{i,t+1}) = \alpha_{(s)} z_{i,t} + \mathbf{X}_{d[i]} \mathbf{b}_{(s)} + \epsilon_{d[i]} \quad (4)$$

where $p_{i,t+1}$ is the probability of survival for individual i from t to $t + 1$, $z_{i,t}$ is again the size of plant i in the first census (t), $\alpha_{(s)}$ is a regression coefficient for plant size on survival, $\mathbf{b}_{(s)}$ is a vector of environmental regression parameters specific survival, and $\epsilon_{d[i]}$ is a plot-specific spatial random effect for each individual i .

Spatial random effects were fit using a predictive process model (Banerjee et al. 2008, Latimer et al. 2009). Predictive process models address the computational challenges of fitting spatial models to large data sets by reducing point locations (i.e., plots) to a lesser number of constituent knots that encapsulate the landscape of

²<http://www.fia.fs.fed.us/>.

spatially autocorrelated processes not explained by covariates. In the case of growth random effects,

$$\boldsymbol{\omega}^* \sim \text{MVN}(0, \Sigma^*) \quad (5)$$

$$\Sigma_{k,k'}^* = \tau_{(z)} e^{-\phi_{(z)} \delta_{k,k'}} \quad (6)$$

$$\boldsymbol{\omega} = \Sigma \Sigma^{*-1} \boldsymbol{\omega}^* \quad (7)$$

$$\Sigma_{d,k} = \tau_{(z)} e^{-\phi_{(z)} \delta_{d,k}} \quad (8)$$

$\boldsymbol{\omega}^*$ is a K -length vector of random effects ($\boldsymbol{\omega}^* = \omega_1^*, \omega_2^* \dots \omega_K^*$) associated with each knot (k). Σ^* is a K by K covariance matrix where each element is a correlation among knots weighted by distance, $\delta_{k,k'}$. ϕ is a parameter describing the rate at which correlations decay as a function of distance (km), and τ is an error term. $\boldsymbol{\omega}$ is a D -length vector of random effects for each plot ($\omega_d = \omega_1, \omega_2, \dots, \omega_D$). The underlying knot-based spatial landscape is then linked back to specific plots using Eq. 7, where Σ is a D by K cross-covariance matrix that describes the spatial relationship between plots and knots using Eq. 8, where $\delta_{d,k}$ is the distance (km) between each the fuzzed location of plot (d) and knot (k) pair. We settled on an exponential spatial kernel after initial explorations of spatial autocorrelation patterns using independent random effects. Given available time, alternative spatial autocorrelation structures could be explored. Although model fit will improve as the number of knots increase, the choice of the number of knots is a trade-off of model fit and computational efficiency. We follow the recommendations of Latimer et al. (2009) (i.e., 100–400 knots for ~4,000 plots) by using 200 knots in a landscape of ~2,000 plots (per species) with locations assigned to maximize coverage of FIA plot locations using the “cover.design” function in the “fields” package (v. 9.6) in R (Nychka and Furrer 2017). See package documentation for detailed explanation of coverage criteria and swapping algorithm.

FIA data present several challenges for estimating recruitment rates. First, unlike the growth and survival of saplings and adults, the recruitment, growth, and survival of seedlings is never directly observed. All conifers <2.54-cm diameter and >15.25-cm height are simply counted, making it impossible to separate new recruits from the fate of preexisting seedlings directly. In other words, the change in the count from census to census represents both new recruitment, but also the survival and growth of existing plants. Although this data structure does not preclude inference on the underlying reproduction/recruitment rate, it is incompatible with most traditional statistical approaches (e.g., Poisson generalized linear models) for estimating plant reproduction and recruitment, which require clearly identifying the reproductive output (e.g., seeds) of existing individuals and the fate of these propagules. Second, the search area for seedlings is small given the low density of seedlings

(especially in many dry forests and woodlands), and considerably smaller than the area adult trees are measured over (~12× smaller). This presents a challenge for estimating recruitment because as the number of individuals in a plot declines separating the true signal of environmental and spatial processes from noise introduced by sampling and demographic stochasticity is increasingly difficult. This may be particularly problematic for tree species exhibiting spatially and temporally heterogeneous seedling distributions, such as woodland tree species (Bell et al. 2014).

To address these challenges, we developed an integrated size-structured population modeling approach that shares available information among our different data sets (i.e., growth, survival of adults and saplings and counts of seedlings) and across FIA plots to infer the growth and survival of seedlings along with the reproductive output of existing trees leading to new recruits. In the absence of individual-level data, previous studies have often relied on estimating possible recruitment rates by calculating the level of recruitment needed to maintain a set population growth rate (e.g., $\lambda = 1$) given set growth and survival rates (Needham et al. 2016). Our approach builds on this work by estimating the recruitment rate needed to explain changes in the number of untagged plants given likely growth and survival rates based on individual data. Thus, we can produce data-driven estimates of recruitment rates without assuming a set population growth rate a priori.

Because the fate of all tagged individuals in the first census (i.e., any individual >2.54 cm) is already known, our goal is to build a model that describes the fate of all untagged individuals. Untagged individuals include all plants <2.54 cm and any plants that were not tagged in the first census, but reached the minimum tagged size (2.54 cm) by the second census. All untagged plants could comprise existing plants previously <2.54 cm or new recruits.

We model the number of untagged plants in a plot as conditionally negative binomial parameterized in terms of mean and dispersion terms:

$$\mathbf{c}'_{d,t+1} \sim \text{Neg. Binomial}(\mathbf{n}'_{d,t+1} \cdot a, \kappa) \quad (9)$$

where $\mathbf{c}'_{d,t+1}$ is a 5×1 vector of the counts of all untagged plants in plot d at the second census $t + 1$. $\mathbf{n}'_{d,t+1}$ is a 5×1 vector of area standardized occurrence rates. a is the total plot area in which plants were counted, and κ is a dispersion parameter. We also explored a Poisson sampling distribution; however, early model checking indicated a negative binomial was more appropriate. Each element in $\mathbf{c}'_{d,t+1}$ represents the counts of individuals in each 2.54-cm (or 1 in.) diameter class up to 12.7 cm. Although the choice of diameter class is flexible, we use the natural choice of 2.54-cm diameter classes for all trees because the FIA data set already lumps any plants <2.54 cm into a single class. Only

plants <12.7 cm (i.e., size classes 1–5) were considered in untagged plant counts because untagged plants larger than this are more likely a result of previously missed observations than growth and recruitment from the smallest classes. $\mathbf{n}'_{d,t+1}$ is defined as

$$\mathbf{n}'_{d,t+1} = \mathbf{A}_{d,t} \mathbf{n}_{d,t} \quad (10)$$

where $\mathbf{A}_{d,t}$ is a 5×30 ($h = 1 \dots 5, j = 1 \dots 30$) discretized integral projection model (IPM) kernel (i.e., a matrix projection model with 2.54-cm size classes) describing all the pathways by which an existing plant could lead to an untagged plant (survival/growth of existing plants <2.54 cm and new reproduction from existing plants). Although typically IPMs are presented as continuous-state integrals that are then discretized for computation, we introduced this discretization up front for clarity and to reduce notation (see Ellner and Rees 2006, Merow et al. 2014 for detailed IPM explanation and notation). $\mathbf{n}_{d,t}$ is a 30×1 vector of area standardized rates of occurrence of all plants in the first census in each 2.54-cm bin, derived from the empirical counts each species.

$\mathbf{A}_{d,t}$ is made up by the two different pathways by which untagged plants may appear: (1) the growth/survival of plants that were <2.54 cm in the previous census, and (2) recruitment arising from reproduction of existing trees:

$$A_{h,j} = \overbrace{g_{h,1} \cdot s_1}^{11.1} + \overbrace{r_h \cdot f_j}^{11.2} \quad (11)$$

The first term (11.1) describes the fate of individuals <2.54 cm at time t . $g_{h,1}$ are growth transition probabilities describing the movement of individuals in size class 1 to size classes 1 to 5. s_1 is the survival probability of individuals in size class $j = 1$ at time t . In the second term (11.2), f_j describes the number of new recruits produced per existing plant in each 2.54-cm size class ($j = 1 \dots 30$; i.e., 0 to 76.2 cm), and r_h is the probability new recruits will transition to size class h by the second census. Note each element in Eq. 11 would also be indexed by plot (d) and census interval (t), but we have omitted this for clarity.

Like tagged plants, $g_{h,1,d}$ is defined by a truncated normal distribution function, but here it is a discretized kernel to account for size class binning. For a given plot d ,

$$g_{h,1,d} = \frac{(\Phi(\text{Upper}_h | u_d, \sigma^2) - \Phi(\text{Lower}_h | u_d, \sigma^2))}{(1 - \Phi(0 | u_d, \sigma^2))} \quad (12)$$

where Φ indicates a cumulative normal function with mean u_d and variance σ^2 evaluated at the upper and lower size limit of size bin h (Doak et al. 2021). The final term renormalizes the truncated kernel to strictly positive size values to prevent biologically impossible transitions to negative sizes. u_d is the same function used for the growth of tagged individuals (see Eqs. 1 and 2), but

in this case individual size ($z_{i,t}$) is approximated by the midpoint of bin $j = 1, m_1$:

$$u_d = \alpha_{(z)} m_1 + \mathbf{X}_d \mathbf{b}_{(z)} + \omega_d \quad (13)$$

$s_{1,d}$ is also based on the same survival function used for tagged plants, again approximated by the midpoint of bin $j = 1, m_1$:

$$s_{1,d} = \text{logit}(p_{1,d}) = \alpha_{(s)} m_1 + \mathbf{X}_d \mathbf{b}_{(s)} + \varepsilon_d \quad (14)$$

r_h uses a Gaussian kernel (normalized to sum to 1) to estimate the probability of any new recruit reaching size classes 1–5 as

$$r_h = N(m_h | \nu, v^2) / \sum_{i=1}^5 N(m_i | \nu, v^2) \quad (15)$$

Finally, the parameter of primary interest is the number of new recruits in each plot d , produced per existing tree of size j in the plot (d), $f_{j,d}$, defined according to

$$\log(f_{j,d}) = \alpha_{(f)} m_j + \mathbf{X}_d \mathbf{b}_{(f)} + \gamma_d \quad (16)$$

where m_j is the midpoint of each of the size classes, and $\alpha_{(f)}$ is a regression parameter describing the effect of size on reproduction. $\mathbf{b}_{(f)}$ are regression parameters describing the impact of size on reproductive output, and γ_d is a spatial random effect again defined by a predictive process (see Eqs. 5–8) with its own parameters $\phi_{(f)}$ and $\tau_{(f)}$.

Covariates

Based on previous research in dry woodland ecosystems, covariates were selected to summarize the effects of moisture availability (MA), heat stress (HS), and neighbor density (ND) on the growth, survival, and recruitment (McDowell et al. 2008). Moisture availability was the mean growing season (May to October) available soil water (i.e., >−3.9 MPa) over 40–100-cm depth over the 10-yr census interval. Heat stress was the average temperature over the growing season over the 10-yr census interval. Neighbor 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, $\mathbf{X}_d$:

$$\mathbf{X}_d = [1, \text{MA}_d, \text{MA}_d^2, \text{HS}_d, \text{HS}_d^2, \text{ND}_d]$$

where 1 indicates the intercept term. Although multi-model inference using differing variables and functional form is possible given unlimited time (models take about 5–8 d to fit), we chose instead to focus on a limited set of variables and functional forms that are common to the demographic modeling literature and well supported based on our prior knowledge of the biology of PiEd and JuOs. All covariate parameters were given weakly

informative priors (i.e., Normal(0,5)) (Appendix S1: Table S1).

Heat stress was calculated as the average temperature (C) during the growing season (May–October) over the 10-yr period between the first and second census. Average temperatures were extracted from the Livneh gridded climate data set (Livneh et al. 2015). The Livneh data set provides estimates of daily temperature and precipitation at a ~7-km grid cell across the United States. Because the Livneh data set is only available through 2015, for the limited number of plots that had their second census in 2016 or 2017 the climate conditions were averaged over the 8- or 9-yr period from 2006 or 2007 to 2015.

Soil water availability was calculated using output from SOILWAT2. SOILWAT2 is a daily time-step, multiple soil layer, process-based model of ecosystem water balance that has been shown to perform well in several dryland ecosystems (Bradford et al. 2014). The model was run for 127,443 sites across the western United States on a 1/16th degree grid. This spatial resolution and grid is the same as the underlying climate data (Livneh et al. 2015) that drove the SOILWAT2 simulations.

Soils data for the model were extracted from the ISRIC Wise Global v1.2 data set (Batjes 2012) and consisted of texture (% clay and % sand), gravel (% volume), and matric density (g/cm³) for eight soil layers (10, 20, 40, 60, 80, 100, 150, and 200 cm), or until maximum depth was reached, at each site. Vegetation composition in SOILWAT2, including static estimates of biomass and phenology for different plant function types, were generated using algorithms that account for the effect of temperature and precipitation on these factors (Bradford et al. 2014).

These data were formatted and ingested into the SOILWAT2 ecohydrological model using the rSOILWAT2 (Schlaepfer and Murphy 2018) and rSFSW2 (Schlaepfer and Andrews. 2018) R packages. Soil water available per layer was calculated as the difference between actual volumetric water content (VWC, cm/cm) and the amount of VWC potentially available at a soil water potential threshold of −3.9 MPa.

Neighbor density was calculated as the basal area (m²/ha) in each plot. Basal area data were extracted from the FIA data set from all living trees (regardless of species) in the first census and correcting for differing sampling plot sizes. All covariates were centered and standardized by mean and variance to improve model convergence. Models were fit using the original, raw data scale (inches) for plant size, and results were converted to metric units.

Computation

We fit our models with Hamiltonian Monte Carlo (HMC) using the “rstan” package (Stan Development Team 2020). Models were run with three chains and 2,000 iterations each, 1,000 of which were warmup.

Parameter convergence was monitored visually and using convergence statistics ($\hat{R}$). Stan code is in Data S1: StanCode.stan.

Model checking

We validated and tested model results in three ways. First, we simulated a data set with the same structure as the FIA data using known parameter values, and fit our model to ensure the true parameter values were recovered within estimated posterior distributions. Second, we conducted posterior predictive checks of within-sample data and calculated posterior *P*-values to test that our predictions from our model were no more extreme than the observed data. Finally, for each species we withheld all size, survival, and seedling count data in 10% of plots. Because the spatial domain of our data sets encompasses the extant range of each species, withheld data provide validation of the model's ability to predict vital rates at new locations within this range, including information from both covariates and spatial random effects. These withheld data were used for out-of-sample validation, where we calculated the degree of predictive accuracy using linear correlations, root-mean-squared error normalized by the range of the response variable (NRMSE), and coverage of our 95% confidence intervals (CIs). Coverage calculates the proportion of out-of-sample data points that lie within a specified credible interval based on the logic that the proportion from an accurate model should be similar to the specified credible interval or better (i.e., a 95% CI should contain 95% or more of observations). Finally, we determined the proportion of explained variation because of fixed and random effect for each vital rate at the plot scale using multilevel R^2 (Gelman and Pardoe 2006).

RESULTS

Vital rates

Recruitment output increased on average with tree diameter for both PiEd and JuOs (Fig. 1, Appendix S1: Fig. S5). PiEd survival rates declined on average with increasing tree diameter, and JuOs survival increased (Fig. 1; Appendix S1: Fig. S5). However, size effects on survival in both species were somewhat weak. Both PiEd and JuOs diameter growth declined with increasing tree diameter on average (Fig. 1; Appendix S1: Fig. S5), but this decline in growth increment may not represent a decline in total carbon uptake given the radial geometry of trees.

To understand how demographic rates vary across climate and geographic space, we estimated posterior mean demographic rates for an average diameter individual (21-cm PiEd, 31-cm JuOs) using the observed moisture availability, heat stress, and neighbor density in each plot as well as spatial random effects. This allowed us to quantify and visualize how vital rates change with each

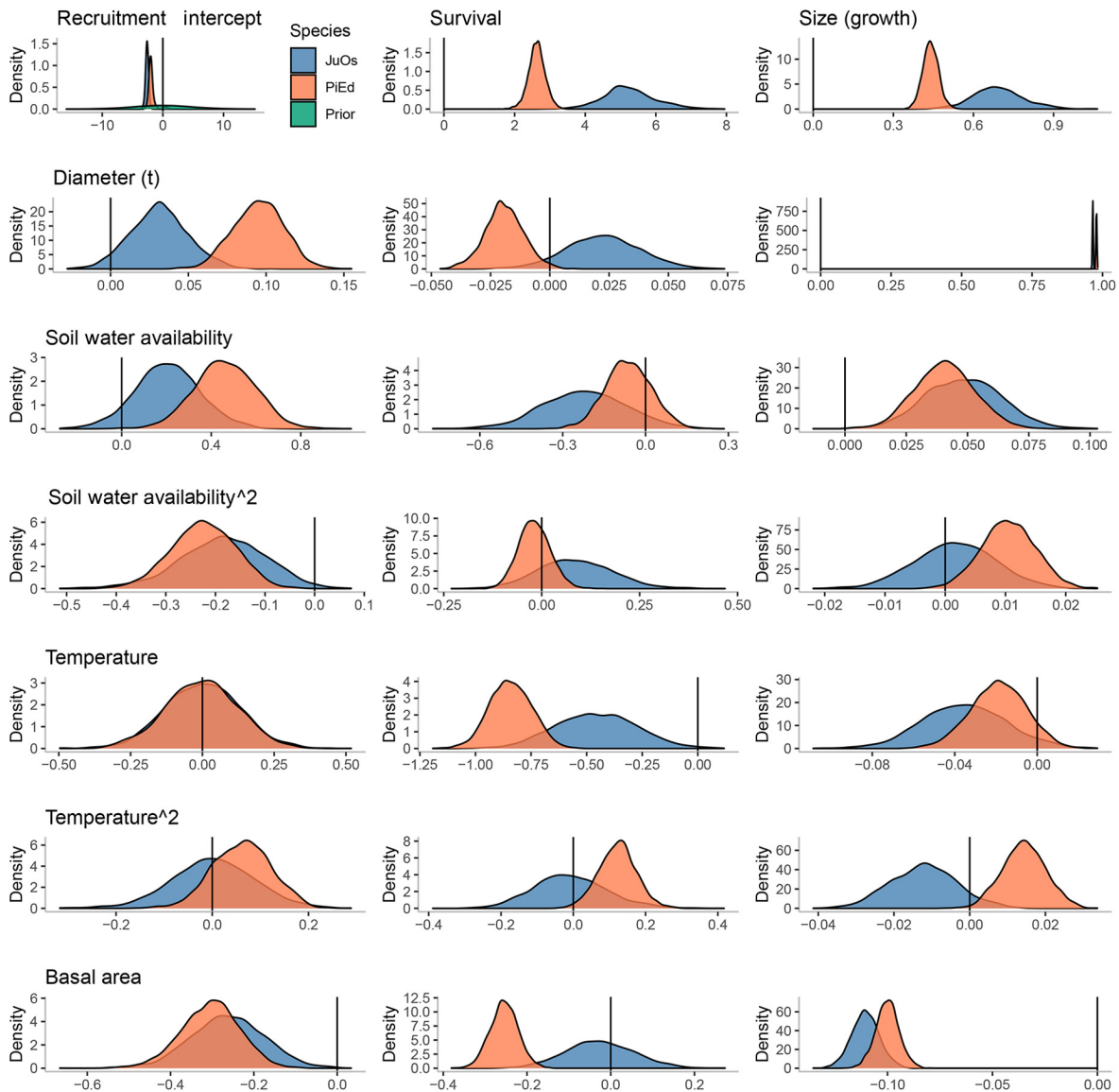


FIG. 1. Marginal posterior plots for all covariate parameters for recruitment rate (column 1), survival probability (column 2), and growth (column 3) models. Within each panel both PiEd (orange) and JuOs (blue), as well as the prior distribution (green) are shown in the first panel (top, left) to illustrate the degree of parameter learning from the data. The same prior was used for all covariate parameters for both species, but the prior is omitted from the remaining panels for a clearer view of posterior distributions.

climate variable, while still taking into account the considerable spatial variability that can be introduced from other climate conditions (e.g., a dry–warm vs. dry–cool plot) and unaccounted for environmental conditions (i.e., random effects).

Climate and competition

Model results indicate consistent responses in both JuOs and PiEd recruitment to climate. In both species, recruitment increased, on average, as moisture availability increased, saturating or declining slightly in the

wettest conditions (Figs. 1–3). JuOs and PiEd recruitment decreased with increasing neighbor density, but there was little to no clear effect of heat stress on recruitment rates (Fig. 1).

Posterior mean probabilities of survival were far more variable across plots for PiEd (0.2–1) than JuOs (0.98–1; Figs. 2, 3). In fact, the number of observations of JuOs mortality not associated with fire or harvest was only 153 individuals (0.6% of 25,015), compared to 1,597 (9.4% of 16,951) for PiEd. In contrast to recruitment, increasing heat stress led to clear declines in survival. JuOs and PiEd individuals in the coolest plot are

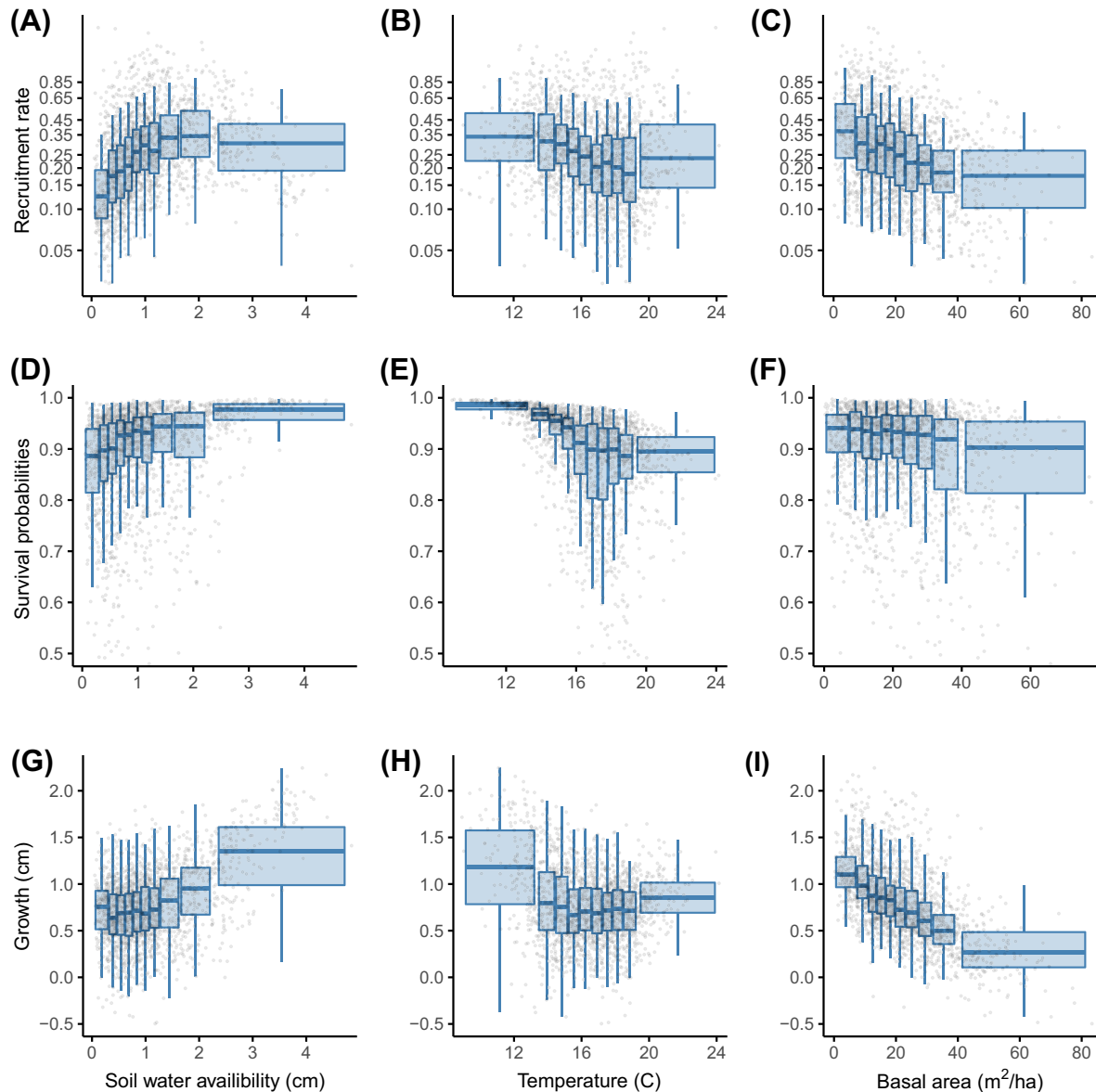


FIG. 2. Response of *Pinus edulis* (PiEd) recruitment rate (A, B, C), survival probability (D, E, F), and growth (G, H, I) to soil water availability, temperature, and basal area. Posterior mean estimates of a 21-cm-diameter individual for each plot (points) are aggregated into boxplots. Each boxplot spans a width of climate space (x-axis) that includes 10% of the total plots; that is, each contains an equal number of plots. Boxplot heights along the y-axis span the spatial variability in plots created by additional climate conditions and plot random effects.

expected to have 10-yr survival probabilities near 1. PiEd survival rates declined by 10–15% in the driest conditions, and JuOs survival declined ~1%. Plots with higher neighbor density had lower PiEd survival (Figs. 1, 2), but JuOs showed no consistent survival changes across the gradient in neighbor density (Figs. 1, 3). Both species showed declines in survival with decreasing moisture availability, but these trends were weaker than heat stress with coefficient 95% CI for linear and quadratic terms overlapping with 0 (Fig. 1; Appendix S1: Table S3, S4).

Diameter growth increased on average for PiEd with increasing moisture availability and declining temperatures (Fig. 2). In contrast, JuOs showed weaker diameter growth response to moisture availability and no growth change with warmer temperatures (Figs. 1, 3). Both species showed clear and consistent declines in growth with increasing neighbor density (Figs. 1–3).

At a fixed, average tree diameter size, climate and competition covariates explained 28% (14–45%) of the variation in PiEd recruitment rates, 38% (30–47%) of the variation in survival probabilities, and 54% (47–61%) of

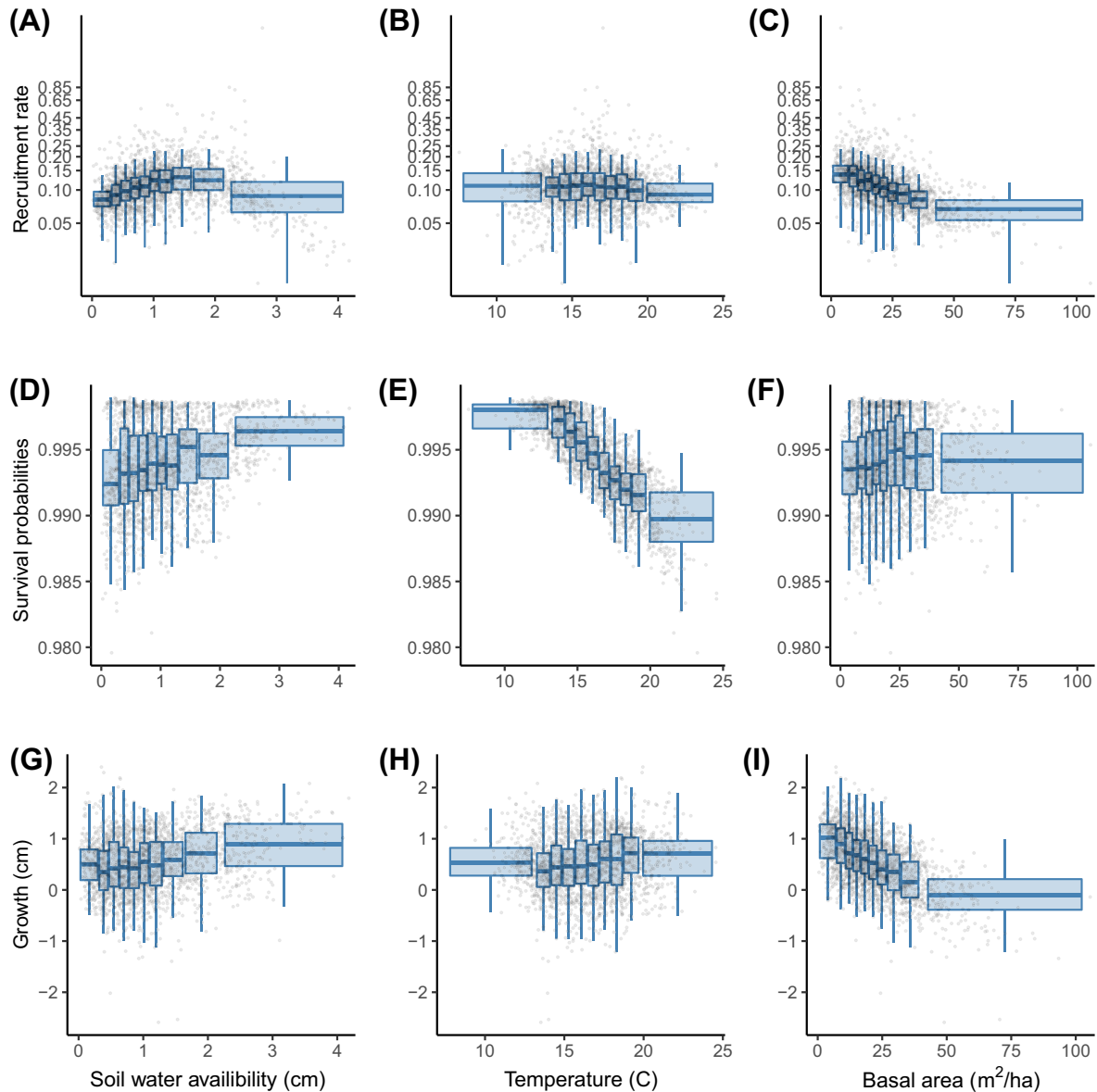


FIG. 3. Response of *Juniperus osteosperma* (JuOs) recruitment rate (A, B, C), survival probability (D, E, F), and growth (G, H, I) to soil water availability, temperature, and basal area. Posterior mean estimates of a 31-cm-diameter individual for each plot (points) are aggregated into boxplots. Each boxplot spans a width of climate space (x-axis) that includes 10% of the total plots; that is, each contains an equal number of plots. Boxplot heights along the y-axis span the spatial variability in plots created by additional climate conditions and plot random effects.

the variation in growth. For JuOs, climate and competition explained 35% (10–67%) of the variation in recruitment rates, 56% (16–91%) of the variation in survival probabilities, and 28% (17–37%) of the variation in growth. These values are consistent with other plant demographic modeling, which has found the random effects regularly explain >50% of variation in demographic rates (Clark et al. 2010, Czachura and Miller 2020).

Geography

We found limited evidence of consistent responses of either species' demographic rates to single geographic gradients (latitude, longitude, elevation), except increasing survival at high latitudes/elevations and declining growth at high elevations in JuOs (Fig. 4; Appendix S1: Figs. S6, S7). However, we did find clear hotspots, including low survival and recruitment in

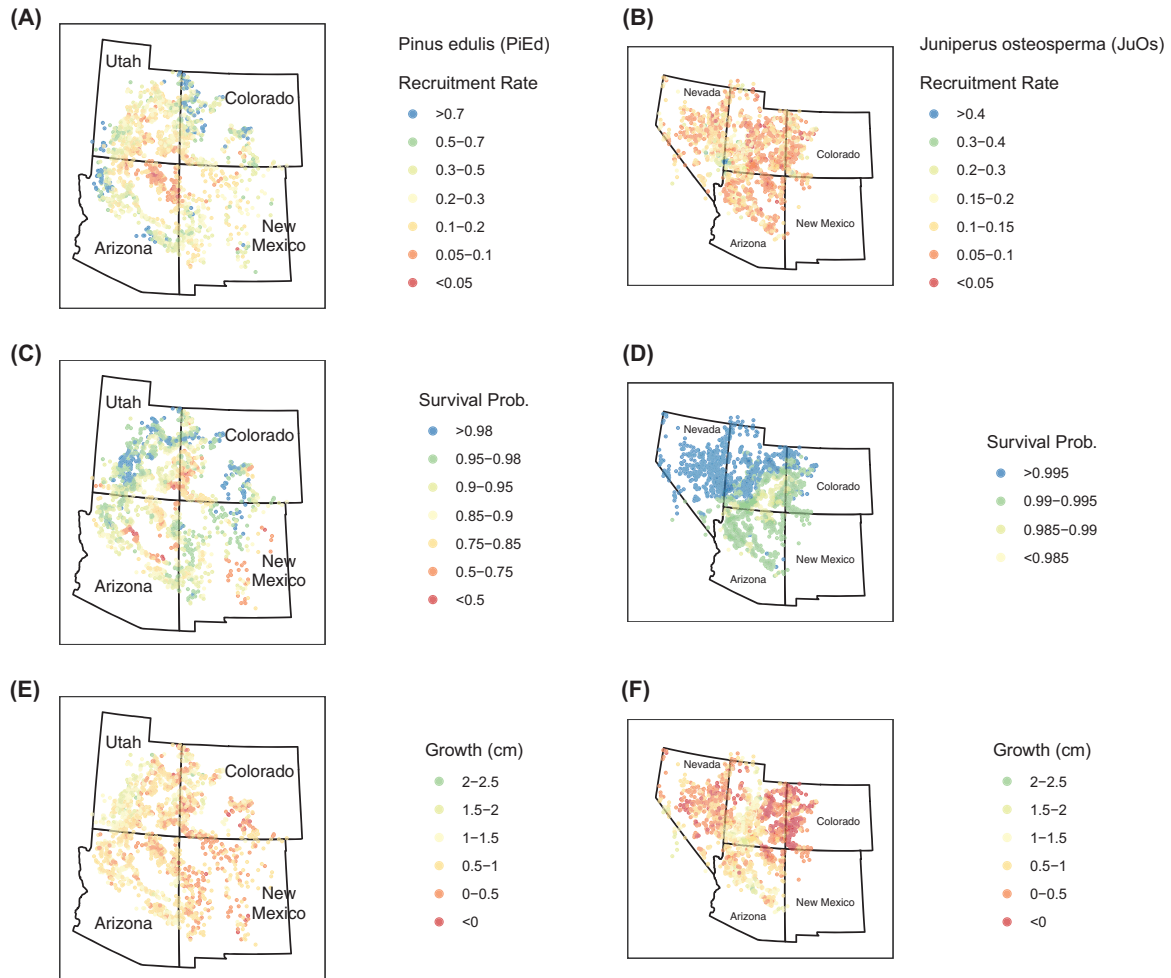


FIG. 4. Spatial variation in recruitment rate (A, B), survival probability (C, D), and growth (E, F) for *Pinus edulis* (PiEd; A, C, E) and *Juniperus osteosperma* (JuOs; B, D, F). Posterior mean estimates of a 21-cm (PiEd) and 31-cm (JuOs) diameter individual's recruitment rate, survival probability, and growth at all plots (points) in response to covariates and random effects. Note, points are fuzzed plot locations from publicly available Forest Inventory and Analysis (FIA) data.

PiEd in the four corners and lower survival and higher recruitment for JuOs in southwest Utah driven by both covariates and unexplained environmental conditions captured by random effects. We also found regions of high survival for both JuOs and PiEd in their north-western range, with survival generally declining toward their central and southern range (Fig. 4; Appendix S1: Figs. S6, S7).

Model checking

The model fit to simulated data was able to recover all “true” process parameters within estimated posterior distributions, and only the “true” recruitment size kernel mean and standard deviation (ν and ν), fell outside 95% CI for estimated parameters (Appendix S1: Table S2).

This weaker indefinability in the recruitment size kernel may result from kernel normalization, which can result in equifinality where multiple parameter combinations yield the same kernel shape.

Posterior parameter trace plots and convergence statistics indicate that parameters converged, but there was somewhat higher $\hat{R}$ values ($1.1 < \hat{R} < 1.2$) for three intercept parameters (PiEd recruitment, JuOs growth and survival) resulting from challenges separating the universal intercept term from spatial random effects (Appendix S1: Table S2, S3). Within-sample posterior predictive P -values indicate good agreement between observed data and model predictions (see supplemental figures). Predictions generated by demographic models are no more extreme than observed data ($0.05 < P < 0.95$) for all vital rates except JuOs size

($P = 0.998$). This lack of agreement between observed and predicted JuOs size data is primarily driven by large deviations in a small number of plots (Appendix S1: Fig. S15). Out-of-sample validation also indicates generally good agreement between model predictions and withheld observations (see supplemental figures). However, because spatial random effects generally account for 40–60% of explained variation in demographic rates, the success of out-of-sample predictions is driven by both covariates and spatial random effects. We found very high correlations (0.99), low NRMSE (0.02), and good coverage (0.974 and 0.959) with the size models for both species. Survival predictions at out-of-sample plots had lower correlations (0.34, 0.04); JuOs had somewhat lower NRMSE (0.09) than PiEd (0.29), but both had good coverage (0.996, 0.992). Finally, out-of-sample prediction correlation for the number of untagged plants (i.e., fecundity and recruitment) were higher for PiEd (0.71) than JuOs (0.45), although both species had relatively low NRMSE values (0.06 and 0.07, respectively). High coverage values (0.991, 0.998, respectively) for both species indicates that predictive intervals captured all of the observed data points, likely due in part to the overdispersion of the negative binomial observation model (see Appendix S1 for full details).

Somewhat low linear correlations (despite low NRMSE) between predicted and observed survival and fecundity are likely due in part to mismatches in the scale of climate covariates and plots. They also reflect the challenge of predicting which individual trees will survive or die even in instances when population-level survival is highly predictable.

DISCUSSION

Our approach offers a promising step forward in leveraging nontraditional spatiotemporal data sets to understand the link between plant demographic rates and large-scale abundance and distribution patterns (Briscoe et al. 2019). An explosion of large-scale monitoring and remote-sensing data sets provide exciting opportunities to understand the drivers of species abundance and distributions, but these data sets are rarely fully compatible with traditional demographic modeling approaches. For example, in our study, FIA data provide detailed information on individual growth and survival, yet recruitment of new individuals was not directly observed. To overcome this, we developed integrated modeling approach that simultaneously inferred the fate of existing seedling as well as new seedlings entering the population through recruitment. Using FIA data and novel demographic inference approaches, we found that variation in abiotic climate conditions (heat stress and moisture availability) and biotic conditions (neighbor density) can both help explain variation in the recruitment, survival, and growth of woodland species across their range. Similar modeling approaches that link individual- and population-scale data provide exciting

opportunities to improve our understanding and predictions of how individual demographic rates translate into population changes over time and across landscapes (Plard et al. 2019, Shriver et al. 2019).

PiEd exhibited a much greater variability in survival rates, and greater sensitivity of survival to heat stress and moisture availability than JuOs. This finding complements a growing body of work that has found regional mortality in pinyon pine species associated with drought, and link the higher mortality rates in pinyon pine, compared to juniper species, to differences in physiological responses to drought and susceptibility of PiEd to pine beetle during drought (McDowell et al. 2008). In addition, our finding that survival declined in both JuOs and PiEd with increasing temperatures support physiological findings that, in addition to drought, extreme heatwaves are an important driver of mortality of pinyon species across their range (Adams et al. 2009), although considerably less is known about the physiological mechanisms of JuOs mortality. Finally, we found evidence of declining survival in PiEd in larger-diameter individuals. Previous work has noted relatively high survival among PiEd and JuOs seedlings and saplings and little change in PiEd survival in larger individuals (Pelt et al. 1990), and others have found declining survival in mature PiEd individuals, likely due to greater drought and bark beetle susceptibility in water-stressed large-diameter trees (Floyd et al. 2009). Similar to survival, our findings of increased diameter growth with greater moisture availability and reduced diameter growth with warm growing season temperature in PiEd are consistent with dendrochronology work that found higher growth rates in years with greater moisture availability and lower vapor pressure deficit (Truettner et al. 2018). However, this work also found similar moisture and vapor pressure deficit sensitivities in JuOs growth over time, whereas we found little evidence of JuOs diameter growth sensitivity to spatial climate variables.

Considerably less is known about environmental conditions that drive PiEd and JuOs recruitment (Hartsell et al. 2020). Consistent with findings from other semi-arid tree species (including PiEd), we found that increasing moisture is generally associated with increasing recruitment in both JuOs and PiEd (Petrie et al. 2017, Redmond et al. 2018, Stevens-Rumann et al. 2018). But we also found evidence that recruitment rates may level off, or begin to decline, in the wettest conditions. Evidence that increasing average temperatures were associated with declining recruitment were more equivocal, with modest declines in PiEd recruitment, but no clear response in JuOs. These patterns provide hypotheses for further investigation to tease apart the climate drivers and physiological mechanisms controlling recruitment at local scales.

Our model results demonstrate that FIA data, and other large monitoring data sets, can be valuable sources for understanding how demographic rates vary across tree species ranges, but there are key limitations

associated with these data sets, as other studies have noted. First, the relatively small plot sizes and sparsity of individuals in plots can make demographic rate inference more difficult, and the degree to which larger climate conditions explain plot-level variation can vary (as seen in fixed vs. random explained variation estimates). Gelfand et al. (2013) present a creative approach for scaling and fitting IPMs in the face of this sparsity by aggregating plots into climate bins, but as the authors note this approach is not as well suited for biogeographic studies where identifying both climate and geographic patterns of demographic rates is of interest, as is the case in many management contexts. We present a complementary approach that allows us to begin to understand biogeographic patterns of demographic rates, although this comes at the additional computational cost needed to fit spatial random effects. An additional limitation associated with inferring climate sensitivities from FIA data is the limited number of resampling intervals, just one interval throughout much of the western United States. This presents a challenge for separating spatial and temporal climate effects and understanding how demographic rate climate sensitivities may change across species range (Klesse et al. 2020).

Together our results indicate that warm and dry conditions are associated declines in survival and recruitment and increasing demographic vulnerabilities of PiEd and JuOs. This suggests that continued warming and drying, as is expected throughout the southwest United States (Bradford et al. 2020), could lead to increasing vulnerabilities of dry woodlands across their range, but continued monitoring is needed to confirm how well spatial climate relationships predict demographic rates over time. Quantitatively assessing the likelihood of forest decline at different locations given current demographic rates will require integrating these demographic vulnerabilities into population models, and will be the focus of future work. We also find potential opportunities for management to alleviate the impacts of climate change. Increases in tree density leads to notable declines in all vital rates (except JuOs survival). Managed reductions in tree density could provide an opportunity to increase individual growth and decrease the risk of widespread mortality (Bradford and Bell 2017). Similarly, increases in recruitment associated with declining density could provide a natural compensatory mechanism enabling resilience of some populations following mortality events.

ACKNOWLEDGMENTS

This work was supported by the U.S. Geological Survey North Central Climate Adaptation Science Center. We thank the USDA Forest Service Forest Inventory and Analysis program for maintaining the large network of forest inventory plots supporting this research. We thank Caitlin Andrews for her assistance in preparing climate covariates and Cory Merow for feedback on this manuscript. Any use of trade, firm, or product name is for descriptive purposes only and does not imply

endorsement by the U.S. Government. Full Code available on Zenodo, <https://doi.org/10.5281/zenodo.4792318>.

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