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Multi-Scale Integration of Tree Recruitment and Range Dynamics in a Changing Climate

Paige E. Copenhaver-Parry
George Fox University, pparry@georgefox.edu

Charles J. W. Carroll
Colorado State University

Patrick H. Martin
University of Denver

Matthew V. Talluto

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Paige E. Copenhaver-Parry[1] iD | Charles J. W. Carroll[2] | Patrick H. Martin[3] iD | Matthew V. Talluto[4] iD

[1]Department of Biology, George Fox University, Newberg, Oregon, USA

[2]Department of Forest and Rangeland Stewardship, Colorado State University, Fort Collins, Colorado, USA

[3]Department of Biological Sciences, University of Denver, Denver, Colorado, USA

[4]Department of Ecohydrology, Leibniz Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany

Correspondence
Paige E. Copenhaver-Parry, Department of Biology, George Fox University, 414 N. Meridian St., Newberg, OR 97132, USA.
Email: pparry@georgefox.edu

Abstract

Aim: The rate and magnitude of climate-induced tree range shifts may be influenced by range-wide variation in recruitment, which acts as a bottleneck in tree range dynamics. Here, we compare range predictions made using standard species distribution models (SDMs) and an integrated metamodelling approach that assimilates data on adult occurrence, seedling recruitment dynamics, and seedling survival under both current and future climate, and evaluate the degree to which information provided by seedling data can improve predictions of range dynamics.

Location: The interior west region of the United States.

Time period: 1990–2015.

Major taxa studied: Five widespread conifer tree species.

Methods: We used a previously published metamodelling framework to combine information from SDMs of adult tree occurrence and sub-models describing seedling recruitment dynamics and seedling survival into a single set of predictions for the probability of occurrence for each species. The integrated framework links sub-models to a SDM to generate cohesive predictions that consider information and uncertainty contained in all datasets. We then compared predictions from the integrated model to SDM predictions.

Results: Integration of seedling information served primarily to improve characterization of model uncertainty, particularly in regions where recruitment may be limited by temperatures that exceed seedling tolerance. Integration constrained response curves very slightly across most climate gradients, particularly across temperature gradients. These differences were primarily attributable to the isolated effects of temperature on seedling survival and not to recruitment dynamics.

Main conclusions: Our results indicate that range-wide variation in recruitment both now and in the future is most uncertain along the edges of occupied regions, which increases uncertainty in projections of future species occurrence along range margins. Overall, the broad-scale climatic dependence of the regeneration niche appears weaker than that of the adult climatic niche, and this enhances uncertainty in predicting range-wide responses of these species to climate change.

KEYWORDS
Bayesian, climate change, demography, life stage, range dynamics, recruitment, species distribution modelling, tree seedlings, western United States

1 | INTRODUCTION

Rapid range shifts have been observed for many species in recent decades and are expected to increase under continued climate change (Boisvert-Marsh, Perie, & De Blois, 2014; Kelly & Goulden, 2008; Monleon & Lintz, 2015). In many cases, range shifts appear to follow complex dynamics that are largely inconsistent with expectations based on warming as the primary driver, and recent research efforts have emphasized the need to better understand the complex suite of mechanisms that underlie range dynamics (Alexander et al., 2018; Rumpf, Hulber, Zimmermann, & Dullinger, 2018; Wason & Dovciak, 2017). Range dynamics ultimately arise from variation in demographic rates (e.g., growth, mortality, recruitment) that determine population growth rates and dictate the environments in which a species can persist (Normand, Zimmermann, Schurr, & Lischke, 2014; Schurr et al., 2012). Understanding the demographic processes that underlie range dynamics is important and necessary for addressing a wide variety of ecological problems, such as biodiversity decline, and for accurately forecasting species range shifts in response to climate change.

Variation in demographic rates across populations and environmental gradients can generate disequilibrium between species occurrence and broad-scale environmental conditions such as climate due to source–sink population dynamics, recruitment limitation, and time-delayed extinction (Holt, 2009; Jackson, Betancourt, Booth, & Gray, 2009; Svenning & Sandel, 2013). These effects may be particularly pronounced in long-lived plants such as trees, which rely upon successful dispersal, colonization and establishment over multiple, long generations to shift their ranges (Renwick & Rocca, 2015; Talluto, Boulangeat, Vissault, Thuiller, & Gravel, 2017; Zhu, Woodall, & Clark, 2012). There is general agreement that trees will respond to warming by shifting their ranges upward in elevation and latitude, and indeed this pattern has been observed across many forest systems (e.g., Lenoir, Gegout, Pierrat, Bontemps, & Dhote, 2009; Murphy, VanDerWal, & Lovett-Doust, 2010; Smithers, North, Millar, & Latimer, 2018). Yet, variation in the rate and magnitude and, in some cases, the direction of range shifts indicates that variation in underlying demographic responses to a complex suite of climate variables that may not tightly covary with temperature, such as precipitation, may be an important determinant of how tree range shifts occur (e.g., Bykova, Chuine, Morin, & Higgins, 2012; Crimmins, Dobrowski, Greenberg, Abatzoglou, & Mynsberge, 2011; Serra-Diaz et al., 2015). In particular, the rate and magnitude of range shifts may be influenced by range-wide, climate-induced variation in recruitment, which acts as a critical bottleneck in tree range dynamics (Canham & Murphy, 2016; Conlisk et al., 2017; Corlett & Westcott, 2013).

Juveniles of many tree species show reduced survival and high environmental sensitivity relative to adults, and thus occupy narrower niches, particularly along moisture gradients (Bykova et al., 2012; Grubb, 1977; Jackson et al., 2009; Smithers et al., 2018). Indeed, in comparisons of adult and juvenile tree distributions, seedlings have often been found to occupy a climatic subset of the adult distributional area, with limited colonization beyond range margins and in certain core areas (Bell, Bradford, & Lauenroth, 2014; Murphy et al., 2010; Zhu et al., 2012). Within species ranges, juveniles are largely restricted to sites beneath existing forest canopies, particularly in water-limited systems, underscoring the sensitivity of juveniles to moisture limitation and the differences in climatic tolerance between juveniles and adults (Bell et al., 2014; Dobrowski et al., 2015; Smithers et al., 2018). The restricted biotic and abiotic environments under which recruits can successfully establish may drive variation in recruitment rates across a species' range that is inconsistent with its shifting climate envelope (reviewed in Copenhaver-Parry, Shuman, & Tinker, 2017).

At the same time, transplant experiments beyond range margins for a variety of temperate tree species generally indicate that range margins correspond not only with bioclimatic limits on establishment, but also with insufficient seed production (Hargreaves, Samis, & Eckert, 2014; Lee-Yaw et al., 2016). Likewise, other lines of evidence indicate that low adult density and correspondingly low seed availability at high elevation range margins contribute to recruitment limitation and lagged range shifts (Conlisk et al., 2017; Kroiss & HilleRisLambers, 2015). Recruitment dynamics, therefore, are influenced by both the environmental conditions under which juveniles can establish and survive, and in which adults can survive and reproduce – collectively termed the regeneration niche (Grubb, 1977). Characterizing the climatic dependence of the regeneration niche requires an integrated understanding of both juvenile and adult climatic niches and recruitment rates across a broad gradient of climatic conditions (Kroiss & HilleRisLambers, 2015). As such, species distribution models that characterize only the climatic niches of adult trees ignore important limitations on demographic processes including recruitment, and static comparisons of adult and seedling distributions do not provide an integrated understanding of the conditions under which propagules can be both produced and successfully establish.

In this study, we apply a recently developed, integrated metamodelling framework (Talluto et al., 2016) to directly assimilate juvenile and adult tree climatic niches and recruitment rates into a cohesive framework for projecting current and future ranges. We assimilate data from experimental and observational datasets of seedlings and adults of five dominant tree species in the Rocky Mountain region of the western US, and project future ranges while accounting for underlying variation in recruitment in response to climate. Our approach directly integrates information on the conditions under which seedlings can continually establish and persist with patterns of adult occupancy, enabling inference directly and simultaneously informed by data spanning multiple life stages. Our specific aims were to compare species range predictions made using a standard species distribution modelling (SDM) approach and our integrated approach under both current and future climate, and to determine whether the additional information provided by integrating seedling data can be used to generate more robust predictions of species range dynamics.

2 | METHODS

2.1 | Data

Adult occurrence records and seedling abundance records were extracted from the U.S. Forest Service Forest Inventory and Analysis (FIA) database for the five most abundant and broadly distributed tree species in the Interior West region of the US, which encompasses the states of Arizona, New Mexico, Colorado, Utah, Wyoming, and Montana (Figure 1). The five focal species (*Abies lasiocarpa*, *Picea engelmannii*, *Pinus contorta*, *Pinus ponderosa*, *Pseudotsuga menziesii*) dominate the majority of forested area in the study region (Copenhaver-Parry & Bell, 2018; Peet, 1981). Shade tolerance generally declines from high to low elevations, with higher-elevation montane species (*A. lasiocarpa* and *Picea engelmannii*) exhibiting high shade tolerance and lower elevation montane and woodland species (*Pinus contorta*, *Pinus ponderosa*, *Pseudotsuga menziesii*) exhibiting moderate to low shade tolerance (Niinemets & Valladares, 2006). We utilized all Phase 2 FIA plots (visited ground plots) within the study region in which data were collected according to the standardized sampling design; plots that utilized other sampling designs in either of the most recent two inventories were excluded. While FIA data are not restricted to naturally regenerating forests, plantations make up only a negligible portion of the forested area within our study area (Chen, Pan, Hayes, & Tian, 2017), and thus all forested plots inventoried according to the standardized design were deemed acceptable for inclusion in our analysis. The standardized FIA sampling design includes measurement of all adult trees [diameter at breast height (DBH) ≥ 12.7 cm] within four 7.3-m-radius subplots, and tabulation of all seedlings (diameter at root collar ≤ 2.54 cm and height ≥ 15.24 cm) within four 2.1-m-radius microplots nested within subplots (O'Connell et al., 2015). While these size thresholds correspond poorly with age due to dramatic variation in seedling growth rates across species and growing conditions, age–height relationships from other studies suggest that seedlings of slower-growing species such as *A. lasiocarpa*, *Picea engelmannii*, and *Pseudotsuga*

menziesii may range from 8 to 35 years old, while seedlings of faster-growing species including *Pinus contorta* and *Pinus ponderosa* may range from 4 to 25 years old (Urza & Sibold, 2007). We summed data from the four subplots and four microplots to estimate occurrence and abundance of adults and seedlings at the plot level.

The occurrence of adult trees indicates long-term persistence of species within a given location, but seedling occurrence may fluctuate over time in response to transient dynamics or pulsed recruitment patterns (Renwick & Rocca, 2015). Thus, evaluating the occurrence or abundance of seedlings at a single point in time in relation to climate may not realistically reflect the climatic regeneration niche, which may be better characterized as the climatic conditions under which seedling recruitment can be sustained over time (Holt, 2009). To better capture sustained recruitment within our models, we utilized seedling count data from the two most recent repeat FIA inventories to estimate the change in seedling counts over time at each plot. For most of the study area, only two FIA inventories have been completed. These data record variation in seedling counts over time in response to the full suite of environmental influences that may affect recruitment including climate, density dependence, and microenvironment, and were used to parameterize the recruitment dynamics sub-model (see Section 2.2). Further, these data may reflect environmental influences on any stage of recruitment, including dispersal, germination, growth, and establishment.

To incorporate additional mechanistic information into the integrated model and to better inform environmental relationships, we integrated an additional dataset characterizing the specific relationship between temperature and seedling survival. To isolate the effect of temperature on seedling survival, experimental data on seedling survivorship across a 6° range of mean annual temperature were used to parameterize the seedling survival sub-model (see Section 2.2). These data come from a series of experimental common gardens established in Colorado in 2014 to isolate the effects of temperature on tree seedling performance while minimizing differences in moisture, light, soils, topography, exposure, and local
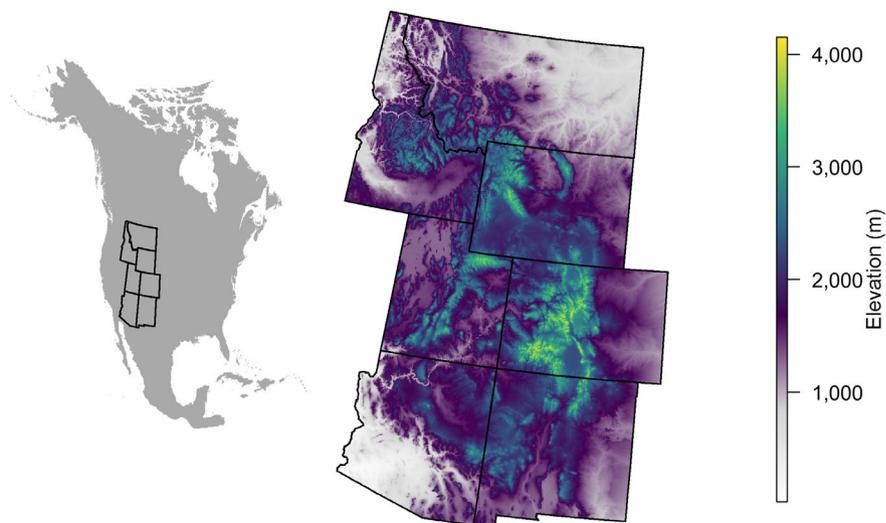
FIGURE 1 A topographic depiction of the study area, which encompasses the interior west region of the US and includes the states of Idaho, Montana, Wyoming, Utah, Colorado, Arizona, and New Mexico [Colour figure can be viewed at wileyonlinelibrary.com]

adaptation (see Carroll, Knapp, & Martin, 2017 for full details). One-year-old seedlings were planted within each garden, and growth and survivorship were monitored monthly for 3 years. Seedlings were watered throughout the experiment to reduce transplant shock and mortality.

Climate data for model fitting were extracted from the U.S. Forest Service Moscow Forest Sciences Laboratory (MFSL) down-scaled gridded climate dataset, available at a 30-arc second resolution (Rehfeldt, 2006). We utilized a 30-year climate normal (1961–1990) for a suite of temperature and precipitation variables representing established seasonal and annual climatic controls on the occurrence of the focal species (Table 1; Copenhaver-Parry & Bell, 2018). Variable selection for each focal species was based on the model selection approach described in Copenhaver-Parry and Bell (2018). Briefly, multiple sets of seasonal and annual temperature and precipitation variables with a correlation of < .7 were considered in the modelling approach and were evaluated in models with a variety of interaction structures. All models evaluated included main effects and various combinations of quadratic effects and bivariate interactions. Models with different combinations of covariates and interaction structures were compared based on true skill statistic (TSS; Allouche, Tsoar, & Kadmon, 2006), specificity, and sensitivity. The covariate combinations and interaction structures that maximized performance across these metrics were retained for subsequent modelling efforts. Ultimately, four climate covariates along with various subsets of their interactions and quadratic terms were used to model all of the species (Table 1).

Downscaled future climate projections from the HADCM3 (Hadley Centre Coupled Climate Model version 3) coupled climate model were used for model projections (Pope, Gallani, Rowntree, & Stratton, 2000). Projections from both the A2 and B2 emissions scenarios were used to contrast range projections under scenarios with high (A2) and intermediate (B2) levels of economic development and population growth (Nakicenovic, 2000). All projected data were for the nominal 11-year period surrounding 2090 (2085–2096).

TABLE 1 The final selected climate covariates included degree days less than 0°C (*DD0*), the temperature differential between mean maximum temperature in the warmest month and mean minimum temperature in the coldest month (*TDiff*), growing season precipitation (April–September; *GSP*), and winter precipitation (mean annual precipitation minus *GSP*; *WINP*), along with various combinations of quadratic terms and bivariate interactions. Out-of-sample area under the receiver operating curve (AUC) estimates generated for the naïve and integrated models are based on mean model predictions and U.S. Forest Service Forest Inventory and Analysis (FIA) adult occurrence data

Species	Main effects	Quadratic terms	Interaction terms	AUC	
				Naïve	Integrated
Abies lasiocarpa	*DD0*	$DD0^2$	$DD0 \times WINP$	.9304	.9303
	TDiff	$WINP^2$	$GSP \times TDiff$		
	GSP		$GSP \times WINP$		
	WINP				
Picea engelmannii	*DD0*	$DD0^2$	$DD0 \times TDiff$	.9200	.9200
	TDiff	$WINP^2$	$DD0 \times WINP$		
	GSP		$GSP \times TDiff$		
	WINP		$GSP \times WINP$		
Pinus contorta	*DD0*	$DD0^2$	$DD0 \times TDiff$	.8880	.8880
	TDiff	$TDiff^2$	$DD0 \times WINP$		
	GSP	GSP^2	$GSP \times WINP$		
	WINP				
Pinus ponderosa	*DD0*	$DD0^2$	$DD0 \times TDiff$	.8746	.8761
	TDiff	$TDiff^2$	$GSP \times DD0$		
	GSP	GSP^2	$DD0 \times WINP$		
	WINP		$GSP \times TDiff$		
			$TDiff \times WINP$		
			$GSP \times WINP$		
Pseudotsuga menziesii	*DD0*	$DD0^2$	$DD0 \times TDiff$	.8577	.8586
	TDiff	$TDiff^2$	$GSP \times DD0$		
	GSP		$DD0 \times WINP$		
	WINP		$GSP \times TDiff$		
			$GSP \times WINP$		

2.2 | Modelling approach

We used the framework outlined in Talluto et al. (2016), which operates by first constructing an SDM using occurrence and environmental data (hereafter "naïve SDMs", indicating that they are informed only by presence–absence data), and by then further informing the parameters of this model using sub-models that relate species performance to the same variables used to calibrate the SDM. Here, we build SDMs using occurrences of adult trees, and then further constrain these with sub-models using data for seedlings at two different scales, considering (a) seedling survival using smaller-scale experimental results and (b) seedling recruitment dynamics, using data from the FIA. These sub-models are constructed using the same or similar environmental variables as the SDM – for example, seedling survival was modelled as a function of degree days less than 0°C (see below), and this variable was also present in the SDMs. The final model is constructed as a hierarchical Bayesian model incorporating the information from all sub-models; thus, it is possible to use the environmental relationships from the sub-models as informative priors when parameterizing the relationship between the probability of occurrence and the environment for the SDM. The end result of this process is an integrated SDM (sensu Talluto et al., 2016) that predicts the probability of occurrence for each species while incorporating information and uncertainty from all three sources. Below, we describe the three sub-models in detail, and the procedures used to account for the change in scales between the sub-models and the integrated SDM.

2.2.1 | Species distribution model

We used a generalized linear model (GLM) with Bernoulli errors and a logistic link function to model the probability of occurrence of adult trees as a function of climate, following a standard SDM approach. Although other models can provide greater flexibility for SDMs (e.g., generalized additive models [GAMs], random forests, etc.; Elith & Leathwick, 2009), we chose a simpler approach to minimize model overfitting due to the ultimate goal of using the model to generate future predictions. Moreover, the GLM structure has the additional advantage of being straightforward for incorporating multiple data sources (Talluto et al., 2016). We fit a separate model for each species, which took the form:

$$\text{logit}(\phi_i) = \alpha_i + \beta_i E_{\text{informed}} + \gamma_i E_{\text{uninformed}}$$

where ϕ_i is the probability of presence of species i, α_i is an intercept parameter, and β_i and γ_i are vectors of slope parameters (hereafter we drop the i subscript for simplicity; all equations are species specific unless otherwise noted). The Es are matrices of climate covariates, which can either be informed by additional sub-models as in the case of the integrated models or uninformed as in the naïve SDM. Climate covariates (Table 1) were standardized prior to model fitting to aid model convergence and comparison of coefficients. Model likelihood was assessed using the FIA adult tree presence/absence data:

$$y \sim \text{Bernoulli}(\phi)$$

where y is a vector of presences and absences. For the naïve models, we used simple regularizing priors (Gelman, Jakulin, Pittau, & Su, 2008):

$$\alpha \sim \text{Cauchy}(0,5)$$

$$\beta \sim \text{Cauchy}(0,2.5)$$

$$\gamma \sim \text{Cauchy}(0,2.5)$$

For the integrated model, parameters relating to informed covariates (i.e., β) were instead modelled using a hierarchical likelihood function integrating information from the two additional datasets. This was accomplished by simulating presence–absence datasets $y_{\text{recruitment}}$ and y_{survival} following Talluto et al. (2016). The procedures for how these datasets were generated are specified in the sub-model sections below. These simulated datasets were then incorporated into the model assuming a pseudo-likelihood similar to that used for the naïve SDM:

$$y_{\text{recruitment}} \sim \text{Bernoulli}(\phi_{\text{recruitment}})$$

$$\phi_{\text{recruitment}} = \alpha + \beta E_{\text{informed}}$$

The survival sub-model had an identical structure.

2.2.2 | Recruitment dynamics sub-model

We fit a simple discrete-time model based on the Ricker model for discrete population dynamics (Ricker, 1954) to estimate the population growth rate of seedlings using the seedling counts from FIA repeat survey data. Following the approach of Thuiller et al. (2014), re-arrangement and log-transformation of the classic Ricker model was used to model the change in seedling counts between surveys as a function of the intrinsic population growth rate and seedling density:

$$\hat{r} = r + b \times N_t$$

$$\log\left(\frac{N_{t+1}}{N_t}\right) \sim \text{Normal}(\hat{r}, \sigma_r)$$

where $\hat{r}$ is the estimated log change in population size among survey periods, σ_r is the standard deviation of $\hat{r}$, N_t is the seedling count at the initial survey, N_{t+1} is the seedling count at the second survey, r is the intrinsic population growth rate, and b is a density dependence parameter. We further modelled the intrinsic population growth rate r as a function of climate, such that:

$$r = \exp\left(\frac{\alpha_r + \beta_r E_{\text{informed}}}{\Delta t}\right)$$

where a_r is the recruitment model intercept, β_r is a slope vector for the recruitment model, E_{informed} is the same covariate matrix used in the SDM, and Δt is the number of years between surveys. All parameters used regularizing priors as in the naïve SDM.

Because the recruitment model was fit at a different scale than the SDM, for the purpose of integration it was necessary to make a theoretical assumption as to how seedling recruitment dynamics relate to occurrence. We used the concept of the fundamental niche as the environmental conditions under which a species can maintain positive intrinsic growth rates (Holt, 2009) to link the recruitment dynamics sub-model and the occurrence data by using the sub-model to predict recruitment rates at the same locations as the calibration occurrence data. Thus, for each Markov chain Monte Carlo (MCMC) iteration we computed a value of r at each location in the FIA dataset and then assigned a presence (1) where $r > 0$ or absence (0) where $r <= 0$ in the simulated $y_{\mathrm{recruitment}}$ dataset.

2.2.3 | Seedling survival sub-model

We used a second sub-model to estimate the probability of seedling survival as a function of temperature based on experimental seedling data. This model was also fit as a logistic regression, with binary survival across the duration of the experiment as the response variable and the temperature-related variables from the naïve models as well as seedling size as covariates:

$$s \sim \mathrm{Bernoulli}(\rho)$$

$$\mathrm{logit}(\rho) = \alpha_s + \beta_s E_{\mathrm{informed}}$$

where s is a vector of binary survival observations, ρ is the survival probability, and α_s and β_s are intercept and slope parameters, respectively, for the survival model. Because seedlings were watered during the experiment to minimize transplant shock-induced mortality, no precipitation effects were included in the survival sub-model.

To generate simulated presence and absence data to inform the SDM within the integrated model, we selected a simple threshold model to translate survival probability to occurrence; thus, the simulated presence–absence dataset y_{survival} was set to 1 when ρ exceeded this threshold and to 0 otherwise. Our approach to linking these data was based on the assumption that species occurrence relates to the environments under which seedlings can survive. Occurrence thresholds were determined empirically for each species by calculating the survival probability that maximized sensitivity and specificity. This provided a semi-independent means of relating the survival data to the FIA data by selecting thresholds that provided the best empirical fit to FIA-observed presences and absences.

2.2.4 | Calibration of integrated model

We calibrated the integrated models in a Bayesian framework using a MCMC algorithm. The integrated model estimates the posterior distributions of model parameters based on simultaneous evaluation of the probability of all three occurrence datasets (i.e., observed occurrences used in the naïve model as well as simulated occurrence datasets from the sub-models) given the metamodel and model priors and allows uncertainty from all sub-models to propagate to the final predictions (Talluto et al., 2016). This uncertainty propagation includes uncertainty from the integration process itself, as the simulated occurrence datasets from the recruitment dynamics and survival sub-models enter the model as random variables that vary as a function of model parameters, and thus are re-generated at each MCMC iteration.

All models were fit using the LaplacesDemon package in R (R Core Team, 2017; Statisticat, LLC, 2017). The naïve model and sub-models were fit using random-walk metropolis, and the integrated model was fit with automated factor slice sampling. Convergence was evaluated based on the acceptance rate, Monte Carlo standard error, effective sample size, Hellinger distance as a measure of stationarity, and visual inspection of trace plots. All models were run for at least 100,000 iterations and thinned to every 50th value. The first 50% of samples were discarded as burn-in, and the remaining 50% were retained for further analysis and inference. Models were fit on a random 50% subset of available data, and the remaining data were reserved for model evaluation.

2.3 | Model evaluation and prediction

Naïve and integrated models were evaluated by computing the area under the receiver operating curve (AUC) using the AUC package in R (Ballings & Van den Poel, 2013). AUC evaluates the ability of a model to discriminate between presences and absences without invoking a probability threshold (Manel, Williams, & Ormerod, 2001). We calculated out-of-sample AUC using the posterior predictive means generated with reserved data.

Naïve and integrated models were used to predict the current occurrence probability of the focal species across the study region based on gridded climate data. Predictions were made using the joint posterior distribution of each model. Prediction uncertainty was characterized by the standard error of the mean of the posterior predictive distribution. All predictions were mapped within 100 km of current forested area, which represents a generous estimation of the maximum distance tree species might be capable of migrating by 2090 (Clark, 1998; Corlett & Westcott, 2013). Naïve and integrated model predictions under both current and future climate were compared based on comparison of response curves, visual inspection of mapped predictions, differences in uncertainty, and a comparison of the geographic overlap and distances between the geographic centres for mapped predictions. Geographic overlap was calculated using Schoener's D statistic, a measure of the proportional geographic overlap of two predictions as an index ranging from 0 to 1 (Roder & Engler, 2011). Geographic centres of predicted distributions were calculated using the COGravity function within the SDMTools package in R (VanDerWal, Falconi, Januchowski, Shoo, & Storlie, 2014).

3 | RESULTS

3.1 | Model validation

Model fit based on out-of-sample estimates of AUC was high for all models and species (AUC = .858–.930), indicating that both the naïve
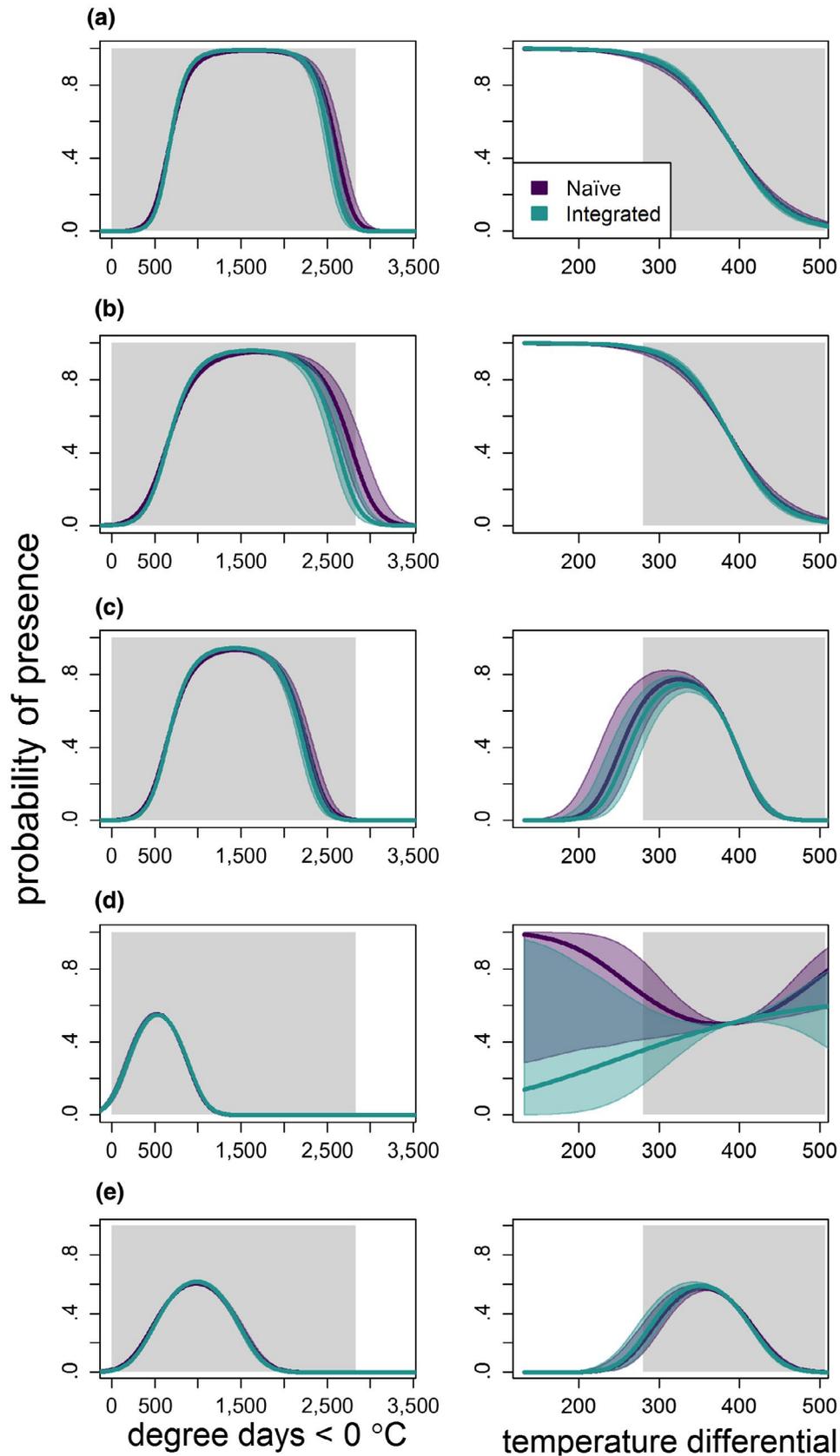
FIGURE 2 Response curves for *Abies lasiocarpa* (a), *Picea engelmannii* (b), *Pinus contorta* (c), *Pinus ponderosa* (d), and *Pseudotsuga menziesii* (e) across the temperature variables used in the naïve (purple) and integrated (turquoise) models. Lines represent posterior mean predictions, and the coloured shaded regions around each line represent 95% credible intervals. The grey region corresponds with the range of data over which the models were fitted [Colour figure can be viewed at wileyonlinelibrary.com]

and integrated models were effective at discriminating between presences and absences in the adult occurrence data (Table 1). Differences in AUC between naïve and integrated models were negligible for all species, despite the additional seedling data that were included in the integrated models.

3.2 | Climatic niches

Differences between integrated and naïve response curves were minimal across all species. However, response curves for the integrated models did capture a narrower set of suitable climatic conditions compared to those from the naïve models (Figure 2; see Supporting Information Appendix S1: Figures S1.1–S1.5). In nearly all cases, coefficient estimates from the naïve models were slightly smaller in magnitude than coefficient estimates from integrated models (Figure 3), indicating that the additional information provided by seedling recruitment and survival data served to constrain the climatic niches slightly. The most notable differences in climatic niches occurred across temperature gradients (Figure 2). In general, higher-elevation species showed the most divergent response curves between the naïve and integrated models across a degree-days < 0°C

gradient, with naïve response curves shifted slightly toward warmer temperatures. Lower-elevation species response curves diverged more notably with temperature differential. Temperature differential responses predicted by the integrated and naïve models diverged substantially for *Pinus ponderosa* (Figure 2d); for this species, the naïve model predicted an upward response curve, while the integrated model predicted a curvilinear response curve across the range of sensible temperature differentials, with the probability of presence increasing toward larger temperature extremes. For all species and response curves, there was a high degree of overlap in uncertainty between the naïve and integrated models.

Comparisons of main effects coefficients from sub-models demonstrate that constraints to climatic niches within the integrated model arise predominantly from the response of seedling survival to temperature variation, while recruitment dynamics estimated using observational field data were largely invariant to climatic variation across all climate variables (Figure 3). In most cases, recruitment dynamics sub-model parameters did not differ significantly from zero (Figure 3). In contrast, climate coefficients estimated by the seedling survival sub-models showed several significant temperature effects (Figure 3). Specifically, the effect of temperature differential was
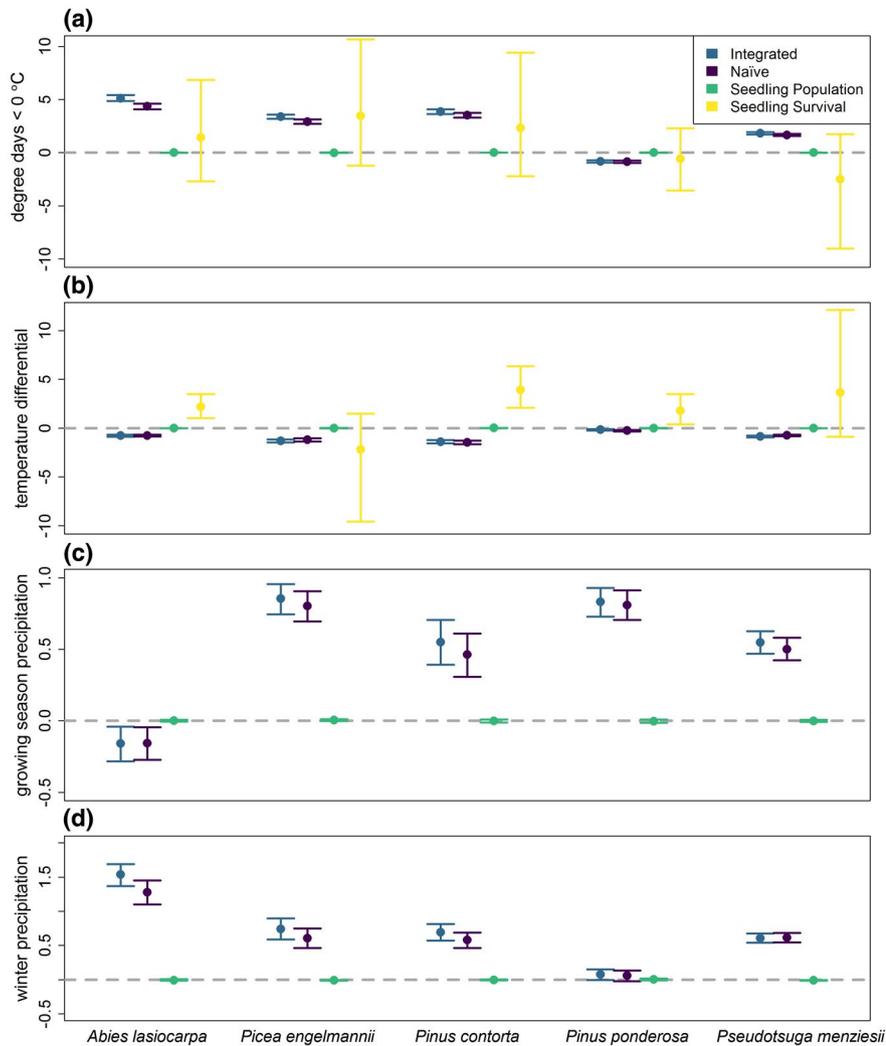
FIGURE 3 Coefficient estimates from the naïve model, integrated model, seedling recruitment sub-model, and seedling survival sub-model for the four main climate effects: degree days <0°C (a), temperature differential (b), growing season precipitation (c), and winter precipitation (d). Points represent posterior means, and bars correspond with 95% credible intervals. Only temperature effects were included in the seedling survival sub-model [Colour figure can be viewed at wileyonlinelibrary.com]

significant and large for *Pinus ponderosa*, *A. lasiocarpa*, and *Pinus contorta*, although these effects were also estimated with broad credible intervals indicating a high degree of uncertainty.
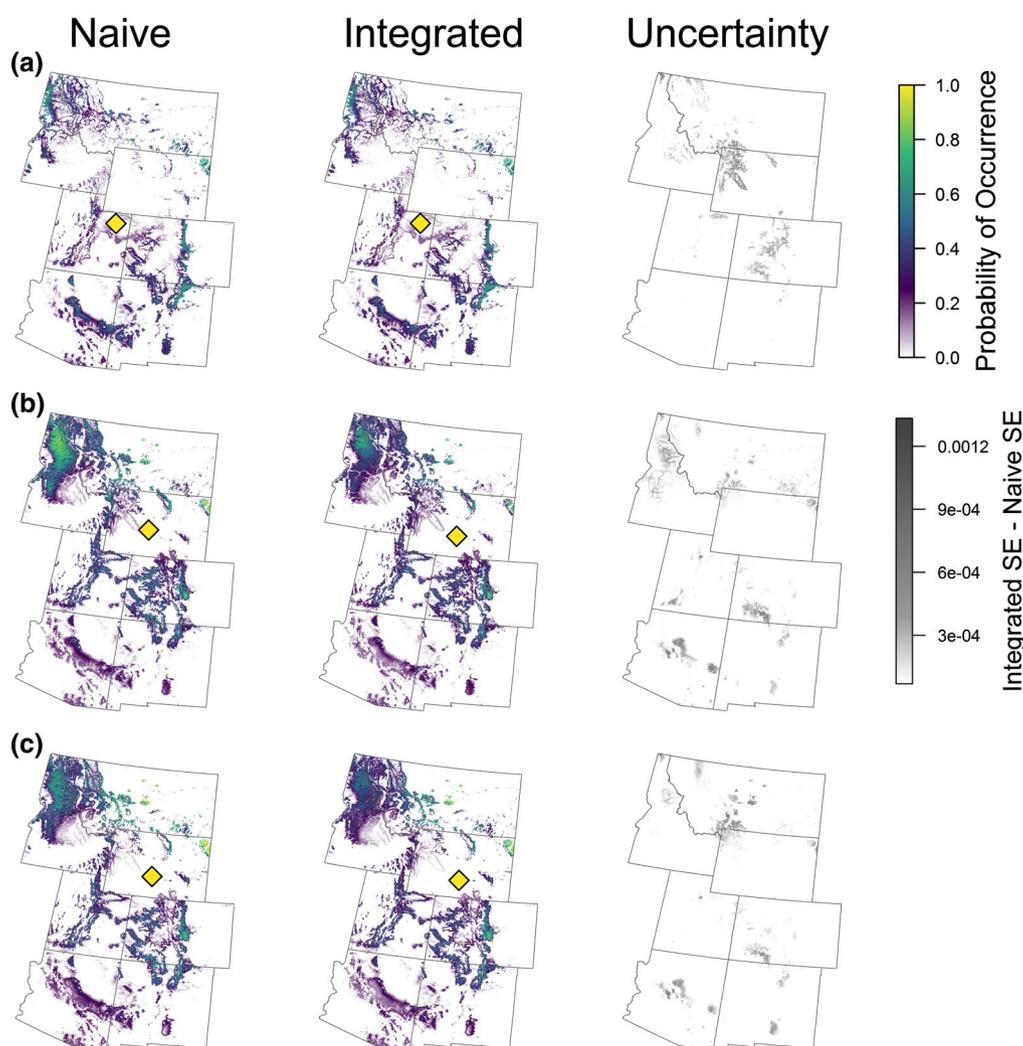
3.3 | Current range predictions

Consistent with response curves, current range predictions from the naïve and integrated models differed minimally for all species (Figures 4 and 5; Supporting Information Appendix S1: Figures S1.6–S1.8). In all cases, geographic overlap in mapped range predictions between models was nearly 100% (99.91–99.97%). Geographic centres did not differ significantly between naïve and integrated models for any species (Supporting Information Appendix S1: Table S1.1). Across all species, differences in uncertainty in mapped predictions were positive, indicating that integrated model predictions had greater uncertainty than naïve model predictions. Differences in uncertainty were generally greatest in areas along the edges of occupied regions, such as in low-elevation regions for subalpine species

and in higher-elevation regions for montane and woodland species, and in the southernmost regions of the study area (Figures 4 and 5; Supporting Information Appendix S1: Figures S1.6–S1.8). These uncertainty differences were magnified for *A. lasiocarpa*, for which uncertainty in integrated model predictions was substantially higher than uncertainty in naïve model predictions across the forested region of the study area and particularly along southern and eastern range margins (Figure 5).

3.4 | Future range predictions

Future range predictions under 2090 projected climate indicate range contractions within the study area for high-elevation montane and subalpine species (*A. lasiocarpa*, *Picea engelmannii*, *Pinus contorta*), and range expansions for lower-elevation species (*Pseudotsuga menziesii*, *Pinus ponderosa*; Figures 4 and 5; Supporting Information Appendix S1: Figures S1.6–S1.8). Predicted range shifts are more severe under the A2 scenario than the B2 scenario

FIGURE 4 *Pinus ponderosa* range predictions for the naïve model, integrated model, and the difference between posterior prediction standard errors (Uncertainty) under current climate (a), predicted 2090 climate under the A2 emissions scenario (b), and predicted 2090 climate under the B2 emissions scenario (c). The geographic centres of the predicted distributions are marked (yellow diamonds). Predictions are mapped across the interior west region of the US [Colour figure can be viewed at wileyonlinelibrary.com]
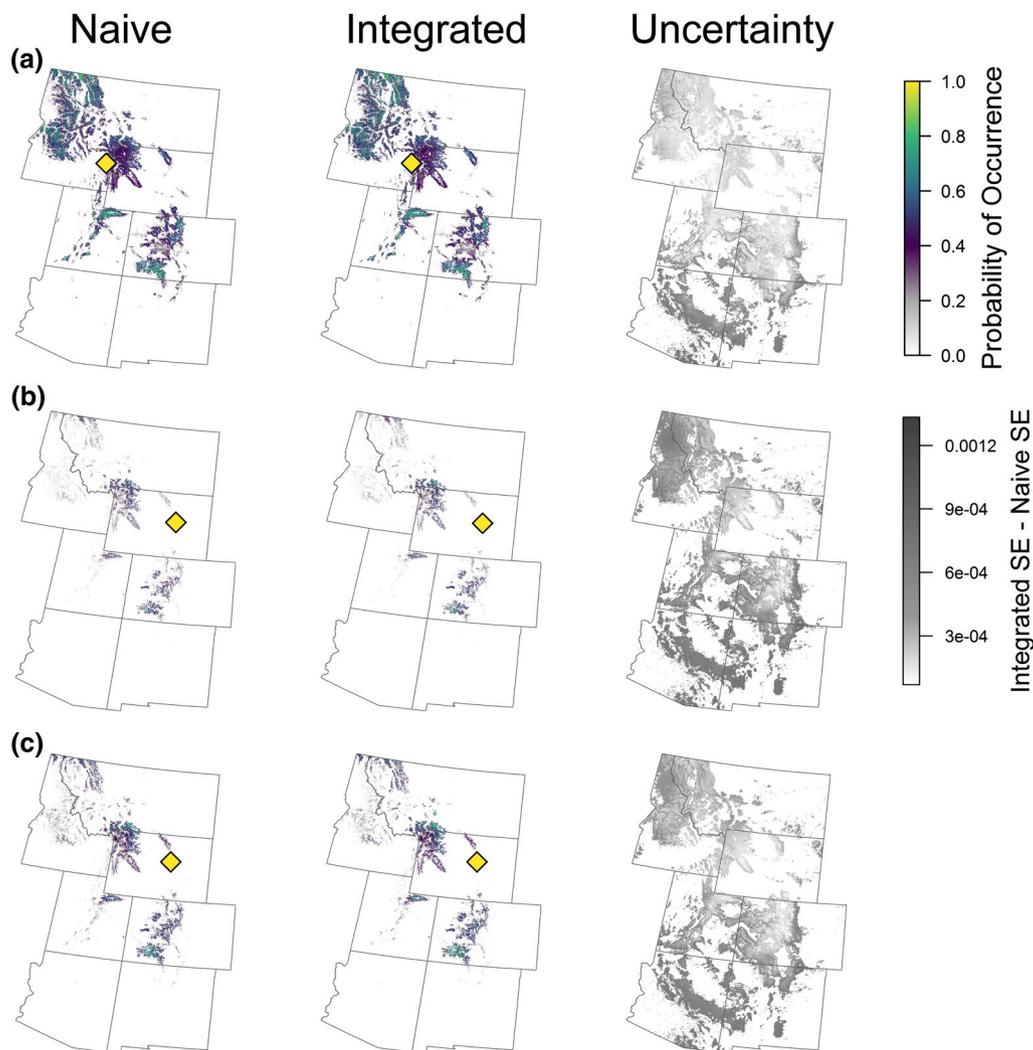
FIGURE 5 *Abies lasiocarpa* range predictions for the naïve model, integrated model, and the difference between posterior prediction standard errors (Uncertainty) under current climate (a), predicted 2090 climate under the A2 emissions scenario (b), and predicted 2090 climate under the B2 emissions scenario (c). The geographic centres of the predicted distributions are marked (yellow diamonds). Predictions are mapped across the interior west region of the US [Colour figure can be viewed at wileyonlinelibrary.com]

for all species. The small differences in range predictions between naïve and integrated models are magnified under future climate, particularly for lower-elevation species such as *Pinus ponderosa* (Figure 4). In the northern portion of *Pinus ponderosa*'s range, the integrated models predict a lower probability of presence than the naïve models and less total occupied area. This corresponds with key differences in temperature differential response curves between naïve and integrated models.

Differences in geographic centres between naïve and integrated models remained non-significant under future climate (Supporting Information Appendix S1: Table S1.1). Geographic overlap declined slightly, but remained at nearly 100% for all species under both scenarios (B2: 99.67–99.89%; A2: 99.12–99.87%). Differences in uncertainty between naïve and integrated models were also magnified under future climate for all species and were always positive, indicating greater uncertainty in integrated model predictions than naïve model predictions (Figures 4 and 5; Supporting Information Appendix S1: Figures S1.6–S1.8). Trends in prediction uncertainty

differences across species and between the naïve and integrated models were similar between current range predictions and future range predictions.

4 | DISCUSSION

4.1 | Impacts of recruitment on range predictions

Our comparison of naïve and integrated models reveals few major qualitative differences in response curves or range predictions when accounting for recruitment. Overall, integration of seedling information served primarily to improve characterization of model uncertainty, especially in regions where seedling recruitment may be limited due to temperatures that exceed seedling tolerance, and constrained most response curves very slightly, particularly across temperature gradients. These differences were primarily attributable to the effects of temperature on seedling survival and not to recruitment dynamics estimated from field inventories (Figures 2 and

3). These findings are consistent with other studies that have failed to identify strong climate signals in seedling abundance patterns across species ranges (Canham & Murphy, 2016; Dallas & Hastings, 2018), highlighting the importance of both habitat suitability and the abundance of adult trees and seedlings in quantifying the regeneration niche.

Investigations of the decoupling of tree population dynamics, seedling abundance, and tree density from climate in temperate forests (Canham & Murphy, 2016; Dallas & Hastings, 2018; Thuiller et al., 2014) suggest that seedling abundance patterns may be poorly predicted by climate in part due to density dependence. Conspecific density dependence appears pervasive among temperate forest trees and has been demonstrated to have strong impacts on recruitment dynamics (Zhu, Woodall, Monteiro, & Clark, 2015). Negative conspecific density dependence may reduce the abundance of seedlings and/or slow recruitment dynamics when species are abundant. Conversely, positive conspecific density dependence may increase seedling abundance and/or accelerate recruitment dynamics when seedling densities are low (Zhu et al., 2015). In both cases, resultant recruitment dynamics would be characterized by intrinsic growth rates that deviate from expectations based on climatic suitability. These density-dependent effects may be particularly pronounced within the strongly successional forests in the western US and are a likely mechanism to explain the non-significant response of recruitment dynamics to range-wide variation in climate observed in our study.

Another potential explanation for the decoupling of recruitment dynamics from climate could relate to the climatic buffering effect of the forest canopy, which modulates the climatic conditions experienced by seedlings, particularly those of shade-tolerant species that establish beneath dense canopies (De Frenne et al., 2013; Lenoir, Hattab, & Pierre, 2017). This effect can generate microclimate conditions that deviate substantially from the coarse-scale climate characterized by the gridded climate data utilized in our models. Few studies have directly evaluated the influence of microclimate on range-wide variation in recruitment due primarily to limited availability of climate data at sufficiently fine spatial scales, but available investigations suggest that estimates of survival may be higher when microclimate is considered due to a dampening of climatic extremes, and that the strength of this effect is strongly related to canopy density (De Frenne et al. 2013; Kroiss & HilleRisLambers, 2015; Lenoir et al., 2017). At the same time, existing evidence suggests that non-climatic microsite conditions including edaphic factors and competition may have stronger effects on recruitment than microclimate (Kroiss & HilleRisLambers, 2015). Future efforts to characterize range-wide recruitment dynamics would likely benefit from spatially extensive, detailed environmental data at scales most relevant to seedlings.

The effects of temperature on seedling survival as estimated within the seedling survival sub-models generally indicate improved seedling survival for high-elevation species in cooler environments, which are also associated with smaller temperature extremes, and potentially higher survival of lower-elevation species in warmer environments, consistent with the geographic distributions of these species (Figure 3). However, climate effects on seedling survival were estimated with high uncertainty in the survival sub-model. Uncertainty is likely partially attributable to the smaller sample size associated with the experimental seedling dataset; as evidence of this, the degree of uncertainty in coefficient estimates increased as species abundance in the dataset declined. Simultaneously, seedlings of these species may exhibit low temperature sensitivity, resulting in broad and uncertain temperature responses. Indeed, physiological responses to temperature variation in the common garden data utilized in the survival sub-model showed low temperature sensitivity in conifer seedlings (Carroll et al., 2017).

The broad uncertainty in seedling survival responses explains the increased uncertainty associated with integrated model predictions relative to naïve model predictions, particularly along elevational and latitudinal range margins (Figures 4 and 5, Supporting Information Appendix S1: Figures S1.6–S1.8). Variation in uncertainty differences across species can primarily be explained by the degree to which temperature responses estimated by the seedling sub-models deviate from those estimated by the naïve SDM; where the models agree, uncertainty is reduced, and where the models diverge, uncertainty increases. Uncertainty differences were greatest for shade-tolerant species like *A. lasiocarpa* (Figure 5). For this species, seedlings – which establish beneath the canopy – experience substantially different temperature and moisture conditions than those that characterize the regional climate, which may explain the greater divergence in estimated temperature responses between the naïve SDM and the seedling sub-models than estimated for less shade-tolerant species.

The spatial patterns of uncertainty differences have important implications for anticipating climate-induced range shifts, as tracking climate change would require species to increase recruitment at and beyond cool range margins and to exhibit recruitment declines at warm range margins (Corlett & Westcott, 2013; Kelly & Goulden, 2008; Monleon & Lintz, 2015). Comparisons of adult and juvenile climatic niches within our study region have failed to provide evidence of climate tracking, but instead have identified patterns consistent with recruitment limitation at both warm and cool range margins (Bell et al., 2014; Dobrowski et al., 2015). This finding may be explained by the restricted climatic niche of seedlings relative to adult conspecifics, owing to the greater sensitivity of seedlings to moisture stress, temperature extremes, and shading (Canham & Murphy, 2016; Dobrowski et al., 2015; Jackson et al., 2009). This pattern is also consistent with observations of pronounced migration lags of up to *c.* 130 km in latitude or 60 m in elevation among tree species in the Rocky Mountains (Gray & Hamann, 2013). Similarly, our results demonstrate that areas along the edges of occupied regions are characterized by the greatest uncertainty in occurrence probabilities both now and in the future. Collectively, these findings suggest that considerable uncertainty exists in the ability of recruitment increases beyond cool range margins to compensate for expected recruitment declines at warm range margins, which indicates the potential for substantial future migration lags.

4.2 | Evaluation of modelling approach

Our model evaluation results (Table 1) and range predictions (Figures 4 and 5, Supporting Information Appendix S1: Figures S1.6–S1.8) indicate that the integrated models successfully discriminated between presences and absences in the adult occurrence data while simultaneously integrating information from the seedling sub-models and propagating uncertainty from the sub-models to the integrated model. The primary benefit of integration in this context was to improve characterization of uncertainty in current and future range predictions. In locating regions of uncertainty under both current and future climates, our integrated models represent a substantial improvement in applied utility over traditional niche modelling approaches, which are often limited by poor characterization of uncertainty and limited predictive accuracy due to a reliance on purely correlative environment–occurrence relationships and a lack of ecological mechanism (Addison et al., 2013; Dormann, 2007; Dormann et al., 2012). Indeed, incorporating demographic information into SDMs has been shown to improve niche estimates and predictive accuracy in a variety of integrated or hybrid modelling approaches (Merow et al., 2014; Pagel & Schurr, 2012; reviewed in Fletcher et al., 2019). However, these improvements are only realized in contexts where demographic and occurrence information agree; in contexts where demography is weakly or negatively correlated with species occurrence probability, integrating these divergent sources of information will generally serve to increase uncertainty in estimates and predictions (Talluto et al., 2016). This latter phenomenon has been consistently identified in widespread forest tree species, for which demography and occurrence probabilities appear to be decoupled, particularly in populations at carrying capacity in which alternative processes, such as density dependence, may better explain demographic rates (Bin et al., 2016; Dallas & Hastings, 2018; Thuiller et al., 2014). While our modelling approach did not directly account for density dependence or other non-climatic factors that may influence carrying capacities, spatial evaluation of model uncertainty can be used to identify regions and populations where species may not respond to climate change in the manner expected based upon occurrence–environment relationships – a task for which SDMs based only on presence–absence data are inadequate. These regions may indicate target locations for activities intended to better anticipate and manage the effects of climate change including demographic monitoring and assisted migration (Aitken, Yeaman, Holliday, Wang, & Curtis-McLane, 2008; McLachlan, Hellmann, & Schwartz, 2007).

At the same time, this modelling approach and resultant inferences have several important limitations. First, the mean coefficient estimates resulting from the integrated model deviate little from the estimates of the naïve model, indicating that the posterior estimates of the integrated models were driven largely by the adult occurrence data with little contribution from the seedling data. The limited contribution of the seedling data can be explained by (a) the non-significant responses of seedling recruitment dynamics to climate, and (b), the small sample size associated with the experimental seedling survival data. Variation in sample sizes and the amount of information contained within different datasets present a limitation for integrated modelling approaches such as the one applied here, and the best approach for accommodating data disparity remains unclear (Fletcher et al., 2019). A variety of weighting approaches may be utilized, but they may contribute to an undesirable trade-off between bias and precision. While beyond the scope of this current study, future applications of this model and other integrated models would benefit from a clearer understanding of the impact of weighting approaches on integrated models (Fletcher et al., 2019).

Second, our models did not account for a number of potentially important ecological processes that are likely to impact range dynamics under future climate including biotic interactions, seed dispersal, and adaptation. While competitive interactions between tree species have been demonstrated to have limited influence on species occurrence patterns within our study region (Copenhaver-Parry & Bell, 2018), seedling recruitment may be particularly sensitive to density dependence. Our models likely reflect this effect in non-significant responses of recruitment dynamics to climate, yet substantial changes to forest structure in the future either through disturbance, land-use change, or climate-induced mortality events may alter the density dependence landscape in a way that modifies recruitment–climate relationships (Dobrowski et al., 2015; Honnay et al., 2002; Kroiss & HilleRisLambers, 2015; Liang, Dubeneck, Gustafson, Serra-Diaz, & Thompson, 2018). Similarly, adaptation is a likely response to climate change among our focal species, which exhibit strong local adaptation in traits along temperature gradients, and may shift the climatic niches of seedlings, which will be the first to display phenotypes consistent with climate change-induced adaptations (Aitken et al., 2008). Both of these processes violate the assumption of stationary relationships with climate and have the potential to generate future range dynamics that deviate from the predictions of the integrated models (Hampe, 2004; Kubisch, Degen, Hovestadt, & Poethke, 2013). These limitations are not easily overcome with existing data, and ultimately require a level of caution and humility when interpreting and applying model predictions, particularly under future climate (Dormann, 2007).

Our results are also limited by the availability of repeat survey data. Our recruitment dynamics sub-model was calibrated on repeated measurements from two time points at each inventory plot separated by an average of 5 years, which may be insensitive to the high temporal variability of masting, disturbance, and climate in western forests (Renwick & Rocca, 2015; Serra-Diaz et al., 2015). However, our use of a discrete-time recruitment dynamics model based on two time points likely represents an improvement over previous characterizations of seedling niches based upon a single time point (e.g., Bell et al., 2014; Dobrowski et al., 2015; Monleon & Lintz, 2015), and our modelling approach provides a flexible framework within which to integrate additional data as new seedling inventory data become available.

4.3 | Conclusions

The rate and magnitude of tree range shifts under future climate are likely to depend strongly upon the climatic dependence of the

regeneration niche. In western forests, tree species are already lagging their climatic niches (Gray & Hamann, 2013), and comparisons of adult and juvenile niches indicate the potential for range contractions (Bell et al., 2014). Our results indicate that range-wide variation in recruitment both now and in the future is most uncertain along the edges of occupied regions, which increases uncertainty in projections of future species occurrence along range margins. Further, recruitment dynamics when considered at this scale appear to be only weakly related to coarse-scale climate, and the manner in which non-climatic factors will alter recruitment dynamics under future climate remains unclear. Overall, our findings suggest that the broad-scale climatic dependence of the regeneration niches of western forest trees may be weaker than that of the adult climatic niche, and that this enhances uncertainty in predicting range-wide responses of these species to climate change.

DATA ACCESSIBILITY STATEMENT

All forest inventory data utilized in this study are publicly available from the USDA Forest Service Forest Inventory and Analysis Database (https://www.fia.fs.fed.us/tools-data/); precise plot locations were made available for this study through a non-disclosure agreement with the USDA Forest Service and are not publicly available. Current and future climate data are available from the USDA Forest Service Rocky Mountain Research Station Moscow Forestry Science Laboratory (https://forest.moscowfsl.wsu.edu/). Data from the seedling experimental gardens utilized in this study are available on FigShare at the following https://doi.org/10.6084/m9.figshare.8977289. All code associated with model construction and model fitting is available as an R package from a public GitHub repository (https://github.com/mtalluto/tree_seedling_metamodel).

ORCID

Paige E. Copenhaver-Parry iD https://orcid.org/0000-0001-8774-670X

Patrick H. Martin iD https://orcid.org/0000-0003-2025-4289

Matthew V. Talluto iD https://orcid.org/0000-0001-5188-7332

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BIOSKETCH

The authors are quantitative and plant community ecologists interested in investigating how ecological processes that span multiple spatio-temporal scales, including physiology, demography, and species interactions, contribute to biodiversity patterns. We work primarily in forest ecosystems and within the context of global change, applying quantitative methods to better anticipate the effects of climate change on forest patterns and processes across scales.

SUPPORTING INFORMATION

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