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Climate extremes may be more important than climate means when predicting species range shifts

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Abstract

It is well known that temperatures across the globe are rising, but climatic conditions are becoming more variable as well. Forecasts of species range shifts, however, often focus on average climatic changes while ignoring increasing climatic variability. In particular, many species distribution models use space-for-time substitution, which focuses exclusively on the effect of average climatic conditions on the target species across a geographic range, and is blind to the possibility of range-wide population collapse with increasing drought frequency, drought severity, or climate effects on other co-occurring species. Relegated to assessments of broad demographic patterns that ignore underlying biological responses to increasing climatic variability, this prevalent method of distribution forecasting may systematically underpredict climate change impacts. We compare six models of survival and abundance of a subcanopy tree species, Taxus brevifolia, over 40 years of past climate change to disentangle multiple sources of uncertainty: model formulation, scale of climate effect, and level of biological organization. We show that drought extremes increased Taxus individual- and population-scale mortality across a wide geographic climate gradient, precluding detection of a monotonic relationship with average climate. Individual-scale climatic extremes models derived from longitudinal data had the highest predictive accuracy (82%), whereas mean climate models had the lowest accuracy (< 65%). Our results highlight that conclusions drawn from forecasts of average warming alone likely underpredict climate change impacts by ignoring indicators of range-wide population declines for species sensitive to increasing climatic variability.

Keywords Longitudinal data · Permanent sample plots · Population decline · Smithsonian ForestGEO · Taxus brevifolia · Wind River Forest Dynamics Plot (WFDP)

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1 Introduction

Predicting species range shifts is a central aim of climate impacts research (Parmesan and Yohe 2003), both to identify conservation priorities (VanDerWal et al. 2013, Urban 2015) and to inform coupled global climate models (Stark et al. 2016, Fisher et al. 2018). Changing forest distributions are a particularly large source of uncertainty when predicting future climate (Purves and Pacala 2008) due to the prominent role of forest biomes in regulating global carbon and hydrological cycles (Snyder et al. 2004, Adams et al. 2010), in tandem with the complex biotic and abiotic processes that govern forest dynamics (Franklin et al. 1987, 2002). Distribution forecasts in forests must therefore consider the suite of changes associated with global warming: gradually increasing average temperatures can allow species adaptation (Davis and Shaw 2001), for example, while extreme climate events (e.g., drought) can lead to rapid die-offs due to strains on traits that developed under historic ranges of variability (Breshears et al. 2005, McDowell et al. 2008, Allen et al. 2010, Chevin et al. 2013). Though climatic extremes are projected to grow in severity and frequency with continued climate change (Easterling et al. 2000, Field et al. 2012, Dai 2013), many species distribution models remain focused on average climate changes (e.g., Sitch et al. 2008).

The confounding roles of non-climatic factors, including trophic interactions (Bentz et al. 2010, Wisz et al. 2013), tree neighborhoods (Larson et al. 2015, Ettinger and HilleRisLambers 2017), and disturbance history (Lenoir et al. 2010, Wason and Dovčiak 2017), are gaining attention in efforts to reduce uncertainty persistent in distribution forecasting (Thuiller 2004, Buisson et al. 2010). Likewise, recent research has demonstrated species responses to shifting climate patterns, not just average climate changes, associated with global warming (Parmesan et al. 2000, Knapp et al. 2008). Nonetheless, models of species distributional shifts tend to ignore these confounds and distinctions (Clark et al. 2011). In particular, the commonly used space-for-time substitution approaches (SFT) assume that species distributions are driven primarily by average climate changes (Elith and Leathwick 2009, Blois et al. 2013). However, species sensitive to climate extremes, such as increased annual drought compared with site averages (Easterling et al. 2000, Condit et al. 2004, Allen et al. 2010), are more vulnerable to increasing drought associated with climate change (Walther 2003, Dai 2013, Das et al. 2013). These species are less able to escape the effects of climate change via migration because interannual variability exists across the entire range (Parmesan et al. 2000, Condit et al. 2004). Increasingly variable climate may therefore contribute to population declines and higher extinction risk (Lenoir and Svenning 2015), but remains unexplored by most distribution models (Clark et al. 2011, Fordham et al. 2012).

The primary approach to distribution forecasting utilizes space-for-time substitution (e.g., climatic niche models, dynamic global vegetation models). These models compare average climate conditions across a species' range to make inferences about climate change-induced shifts in the future (Thuiller 2003). Contemporary relationships between species occurrences and average regional climate are extrapolated to predict future occurrences with climatological change over time. Assumptions of SFT forecasts include the following: (1) species are in equilibrium with climatic and environmental factors; (2) phenotypic variability, evolutionary adaptation, biotic relationships, and disturbance regimes can be ignored (Franklin 2010); and (3) species will shift in tandem with the average climatic niche they currently occupy as it moves with changing climate.

While SFT models can be highly predictive over centennial timescales (Hijmans and Graham 2006, Blois et al. 2013), their usefulness in predicting species responses to climate over the shorter, decadal time frames necessary for managers to develop climate-adaptation strategies has been called into question (Franklin 2010, Brun et al. 2016). For instance, forest communities vary in their spatial patterns throughout geographic ranges, reflecting past community assembly processes (Freund et al. 2014, Birch et al. 2019), but SFT models are blind to population and community dynamics (Fordham et al. 2012, 2013). Importantly, model assumptions may be violated in a climate-change context, as no-analogue climates (Williams and Jackson 2007), novel community assemblages (Suttle et al. 2007, Gilman et al. 2010), and altered disturbance regimes (Littell et al. 2010, Franklin et al. 2016) can disrupt species-environment equilibria.

An alternative approach to SFT is longitudinal modeling, which correlates climatic fluctuations over time with observed temporal population trends to forecast climate-induced range shifts (Clark et al. 2011, Renwick et al. 2018). These models assume: (1) population responses to interannual climate can be extrapolated to long-term climate trends; and (2) phenotypic variability and evolutionary adaptation can be ignored. Unlike SFT, longitudinal models can operate across levels of biological organization to capture individual- and population-level responses to climate. Models able to consider climate effects on individual organisms can disentangle the unique and perhaps contrasting responses of mortality, recruitment, and growth processes (Lutz et al. 2014, Wason and Dovčiak 2017) while controlling for variation in stand age or site productivity (Larson et al. 2008). Likewise, individualized information can increase the power of statistical tests (due to replication being at the level of the individual) and thus detect relationships that may not be apparent with population-level datasets (but see Tredennick et al. 2017). Despite these benefits, limited data and computational power often relegate longitudinal models to describing net demographic patterns at the population scale rather than underlying biological processes.

Space-for-time and longitudinal models alike often recognize climate impacts as range shifts down a climate gradient (i.e., to cooler, wetter climates associated with higher elevations or latitudes; a "warming fingerprint") (Parmesan and Yohe 2003). This pattern is identified via positive species responses (e.g., population increase) at the leading edge of species distributions (i.e., cooler, wetter locations in SFT models; cooler, wetter years in longitudinal models) and/or negative responses at the trailing edge (Gedir et al. 2015, Lenoir and Svenning 2015). When opposite trends are observed, including no distributional shifts or equal shifts up and down the climate gradient (Harsch et al. 2009, Chen et al. 2011, Rapacciuolo et al. 2014), it is concluded that species distributions are unlikely to shift with changing climate. Species' ranges can shift dramatically, however, following die-offs associated with climate extremes (Thomas et al. 2004, VanDerWal et al. 2013). This is particularly evident in forests, where altered drought regimes reduce performance of trees adapted to cooler/wetter sites and those adapted to warmer/drier sites alike, even if mean annual climate stays constant (Walther 2003, Knapp et al. 2008, Anderegg et al. 2013).

We add to ongoing efforts to improve vegetation components of earth system models (Moorcroft 2006, Purves and Pacala 2008) by quantifying the potential for bias in forecasts utilizing climate means to estimate species range shifts. We develop a forecasting ensemble that synthesizes data from a Smithsonian Forest Global Earth Observatory site (ForestGEO; Anderson-Teixeira et al. 2015) and region-wide forest monitoring sites to decouple uncertainty associated with temporal scale of climate effect (relative or average climate differences) from uncertainty related to model formulation. The prediction ensemble (1) compares predictions of longitudinal and SFT models to determine whether species' responsiveness to climate extremes may preclude detection of an average climate effect using the subcanopy gymnosperm, Taxus brevifolia, as an example; and (2) assesses climate effects at the individual and population scales to characterize species responses in terms of biological processes and net demographic change. No model prediction ensemble of which we are aware has compared individual- and population-scale longitudinal models to SFT models, presenting the unique opportunity to also decouple uncertainty related to scale of biological organization from that related to scale of climate effect. We then critically examine the disparate ecological interpretations of each model to identify primary sources of uncertainty in forecasts of distributional change, thereby improving our ability to recognize climate change impacts and forecast future species distributions.

2 Methods

2.1 Species and site data

Pacific yew (Taxus brevifolia Nutt.) is a near-threatened tree species (Thomas 2013) with considerable ecological, social, and economic value. Recent reports show that mortality rates for Taxus in southern Washington State, USA, increased three- to four-fold within the past 80 years (Franklin and DeBell 1988, Busing et al. 1995, Larson and Franklin 2010, Lutz et al. 2014). Shade-tolerant understory tree species like Taxus may be particularly sensitive to extreme drought, as these species are adapted to low light levels and low vapor deficits of the understory microclimate and espouse lower water-use efficiencies than drought-tolerant pioneer species (Harrington and Reukema 1983, Lassoie et al. 1985). In the absence of acute disturbances, diminishing Taxus populations may therefore be an early indicator of broader forest responses to warming and drying climate trends (HilleRisLambers et al. 2015).

We combined two long-term, spatially explicit datasets spanning 690-m elevation to examine Taxus populations within the Pseudotsuga-Tsuga (Douglas-fir/western hemlock) forest zone (Franklin and DeBell 1988) of the Pacific Northwest, USA (Table 1; Fig. 1). In both datasets, all trees ≥ 5-cm diameter at breast height (DBH; 1.37 m) were mapped relative to neighboring trees and revisited at roughly 5-year intervals to track individual survival and sapling recruitment. This protocol enabled the assessment of Taxus survival and population growth over time while accounting for competitive dynamics occurring in local tree neighborhoods. The Wind River Forest Dynamics Plot (WFDP) (Lutz et al. 2013) dataset included 23 years within 4 ha of mature forest in the T.T. Munger Research Natural Area in Washington State, USA. The Pacific Northwest Permanent Study Plot (PSP) (Acker et al. 1998) dataset comprised nineteen 1-ha to 2-ha, mature forest stands containing at least two live Taxus stems in the year of establishment and spanning 24 to 35 years of study (Table 1). All twenty stands have temperate maritime climates (cool, wet winters; warm, dry summers) with a strong elevational gradient: higher elevations experience colder, longer winters and cooler, shorter summers compared with lower elevations (Table 1; Fig. S6).

For each stand, we developed population growth summaries: (1) annual population growth rate, calculated as the net change in abundance of Taxus stems ≥ 5 cm DBH over the study duration; and (2) local extinction time, defined as the number of years from the study end date until fewer than one Taxus tree ha^{-1} would be expected per the observed population growth rate.

Table 1 Site details for the research natural areas (RNA), experimental forest (EF), and other permanent study sites containing at least two live Taxus brevifolia stems. Timespan indicates the duration over which tree data were collected. Maximum Taxus ha^{-1} indicates the population abundance used as a response variable in space-for-time models, population growth (%) indicates annualized net change in Taxus abundance over the study timespan, and local extinction time extrapolates the observed population growth rate using an exponential growth model to determine the number of years until Taxus abundance would be fewer than one tree ha^{-1} following the last year of measurement (final year of timespan) given future climates comparable to historical climates. Overall, populations are gradually declining across the sampled range (mean growth rate = − 0.9%, SD = 1.5%)

Identity	Location	Stand age (year)	Plot Size (ha)	Elevation (m)	Aspect (deg)	Slope (deg)	Maximum Taxus ha^{-1} (n)	Population growth (% year^{-1})	Local extinction time (year)	Study timespan
AB08	White River, WA	750	1	1050	300	11	2	2.5	-	1977–2006
AG05	Nisqually River, WA	650	1	950	260	9	54	0.5	-	1977–2009
AV02	Ohanapecosh River, WA	1000	1	850	125	0–6	2	− 2.7	26	1977–2009
RS01	H.J. Andrews EF, OR	460	1	510	225	35	26	− 0.7	467	1977–2012
RS02	H.J. Andrews EF, OR	460	1	520	315	20	33	− 0.8	438	1978–2009
RS03	H.J. Andrews EF, OR	460	1	950	225	10	70	1.2	-	1978–2009
RS23	H.J. Andrews EF, OR	450	1	1020	45	3–29	79	2.7	-	1978–2009
RS24	Hagan Creek, OR	90	1	610	350	24–31	4	0	-	1978–2011
RS27	H.J. Andrews EF, OR	450	1	790	180	3–9	78	0.2	-	1978–2011
RS28	H.J. Andrews EF, OR	459	1	1060	180	10	8	− 0.9	232	1978–2011
RS29	H.J. Andrews EF, OR	450	1	800	355	27–40	24	0	-	1978–2011
RS30	H.J. Andrews EF, OR	450	1	870	355	3	43	0.8	-	1978–2012
RS31	H.J. Andrews EF, OR	450	1	900	140	0–3	11	− 1.8	134	1978–2012
RS34	H.J. Andrews EF, OR	450	2	820	90–279	3–31	64	1.4	-	1979–2013
RS35	Hagan Creek, OR	130	2.1	460	180–360	19–45	7	1.6	-	1980–2009
RS37	Hagan Creek, OR	130	1	475	90–270	3–35	10	− 1.8	128	1981–2009
RS38	H.J. Andrews EF, OR	450	2.4	500	varied	varied	75	− 0.6	721	1984–2012
TA01	Ohanapecosh River, WA	250	1	670	270	3–9	14	− 0.9	294	1987–2012
TO04	Nisqually River, WA	750	1	640	flat	0	5	0	-	1990–2014
WFDP	T.T. Munger RNA, WA	525	4	368	0–360	0–21	93	− 2.4	189	1994–2017

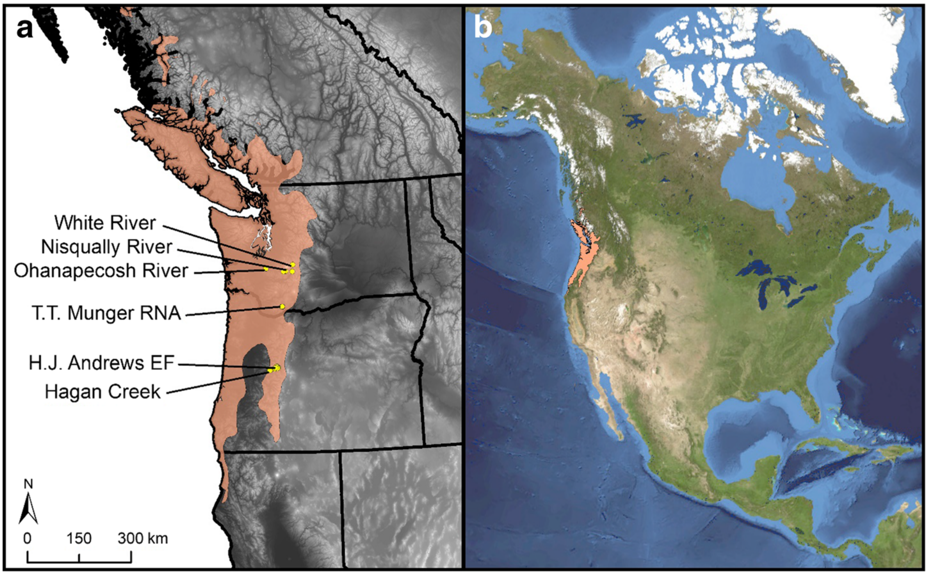

Fig. 1 Locations of Pacific Northwest permanent study sites (**a**) within North America (**b**), including those located within research natural areas (RNA) and experimental forest (EF). Study sites contained between one and six individual forest stands (Table 1), which were analyzed if least two live Taxus brevifolia stems were present in the stand, for a total of 20 stand locations. Orange shading indicates coastal Taxus brevifolia distributional range within the Pseudotsuga-Tsuga (Douglas-fir/western hemlock) forest zone

$$L_j = P_{0,j}\ e^{r_j\ t} \tag{1}$$

This was found by solving for the time parameter (t) of a simple exponential growth model (Eq. 1) for each stand, j, where P_0 is Taxus abundance ha^{-1} in the final study year, r is the observed population growth rate, and L is the local extinction threshold, which we set to 0.99 (less than one tree ha^{-1}).

2.2 Ensemble structure

Our prediction ensemble included six models representing one parametric and one non-parametric model each of individual-level longitudinal, population-level longitudinal, and population-level SFT models (Table 1). We compared parametric and non-parametric formulations to distinguish between those constrained by distributional and homoscedasticity assumptions (parametric) and those more powerful when underlying distributions are unknown (non-parametric). These six model forms have been commonly applied throughout the biogeography and ecology forecasting literature, allowing generalizability to prior research. The ensemble estimated three parameters related to Taxus demography: (1) individual mortality probability/instantaneous mortality probability (both individual-level longitudinal models); (2) population growth (one population-level longitudinal model); and (3) population abundance (both population-level spatial models, one population-level longitudinal model; see Section 2.4).

All models counted trees that were present at study establishment and trees that recruited during the study period (including year of recruitment for longitudinal models).

Individual- and population-level comparisons were only possible using longitudinal models, as SFT models are unable to consider the individual scale. The primary difference between individual and population models was that population-level models quantified abundance or net population growth (i.e., the balance of recruitment and survival), while individual-scale models quantified survival of individual trees. Comparison between the two model types identified how individual survival processes scale up to the population. Agreement between models would suggest that survival (not recruitment) was the predominant process governing population growth and abundance; this is often the case in systems with long-lived species (Silvertown et al. 1993).

We validated models using 10-fold cross-validation following the methods of Cutler et al. (2007), which randomly selects 90% of the data for training at each of ten iterations, allowing all datapoints to be used once for training and once for testing. Using the out-of-sample predictions, we computed (1) model accuracy (variance explained or classification accuracy, where applicable); and (2) mean absolute deviance/mean ratios (MADMR) (Kolassa and Schütz 2007), which is the mean absolute deviance divided by the mean observed response value. MADMR is an alternative to mean absolute percent error (MAPE) that is better suited to handling zeros while remaining scale-free, therefore allowing a direct comparison of error between models built using different units or response values. All statistical analyses were performed using the R version 4.0.2 statistical software (R Core Team 2020).

2.3 Model parameters

2.3.1 Climate

We analyzed Taxus responses to changes in biologically meaningful measures of climate to address recent criticisms of the temperature-driven approach (Stephenson 1998, VanDerWal et al. 2013). Interactions between temperature and precipitation can be important determinants of plant photosynthetic rates and survival (Daniels and Veblen 2003). We therefore used climatic water balance models to calculate drought-related climate covariates of physiological importance to plants (Stephenson 1998, Lutz et al. 2010): snowpack and climatic water deficit (Deficit). In this region, low snowpack has not historically been concomitant with high Deficit, and vice versa. In years when low snowpack and high Deficit happen to cooccur, tree mortality can be increased. Climatic water balance models were made for each site using monthly temperature and precipitation time series from the Parameter-elevation Regression on Independent Slopes Model (PRISM) data set (Daly et al. 2008) at an 800-m spatial resolution following the methods of Hostetler and Alder (2016) and McCabe and Markstrom (2007). Climate values differed between stands but were the same for all trees within a stand.

Longitudinal models captured climate extremes by using maximum modeled annual Deficit anomaly (maximum Deficit) and minimum modeled annual snowpack anomaly (minimum snowpack), which were chosen due to known effects of drought on tree physiology and survival (McDowell et al. 2008, Lian et al. 2020). These values were found by (1) standardizing annual Deficit and snowpack relative to the long-term (1970 to 2017), stand-level averages, thus controlling for different climate averages among sites and expressing climatic extremes relative to those averages; then (2) selecting the maximum Deficit anomaly and minimum snowpack anomaly within each time interval between measurement years per stand.

Space-for-time models captured average climate differences between stands by using mean modeled annual Deficit and mean modeled annual snowpack over the study duration for each stand (Table 1). These values were standardized across all stands to generate climatic units that would be comparable with longitudinal models. We also ran SFT models with maximum Deficit anomaly and minimum snowpack anomaly observed during the study timeframe (calculated by the same methods as for longitudinal models) to ensure that standardization procedures did not change model inferences (no meaningful differences; see Supplemental Information Tables S1, S2).

2.3.2 Abiotic and biotic covariates

To isolate the effects of climate, all six models controlled for the effects of elevation (m) and biotic interactions among forest trees, and individual-level models additionally included log-transformed tree DBH to control for density-independent size asymmetries in survival. Elevation was standardized across the range to express relative differences between stands; elevation was measured at the stand scale and was therefore considered to be the same for each tree within the same stand (i.e., for individual-level models).

To control for prevailing biotic interactions, we calculated woody species richness (number of species) and the Hegyi crowding index (Eq. 2) (Hegyi 1974, Biging and Dobbertin 1995), which quantifies the potential for competitive interactions among trees. The Hegyi index, H, is the distance- and diameter-weighted sum of all tree neighbors, j, within a 10-m radius of focal tree, i. The 10-m radius for calculating the Hegyi index and species richness was chosen based on previously identified interaction distances in similar forests (Das et al. 2008, Lutz et al. 2014, Das et al. 2018).

$$\mathrm{H_i} = \sum \frac{\mathrm{DBH_j}}{\left(1 + \mathrm{Distance_{ij}}\right)\left(\mathrm{DBH_i}\right)} \tag{2}$$

Separate Hegyi values were calculated for conspecific neighbors and heterospecific neighbors based on previous research indicating these have distinct effects (Lutz et al. 2014). For individual-level models, neighborhood covariates were standardized per stand to express relative differences between individuals within each stand over time, and to control for site-specific differences in productivity; for population-level longitudinal models, these were standardized across all stands to express relative differences between stands over time across the entire geographic range; for SFT models, we chose the maximum neighborhood covariate values observed per stand over the study timeframe, then standardized across all stands to express relative differences between stands (but not changing over time).

2.4 Model formulations

2.4.1 Individual-level longitudinal models

We tested generalized linear mixed models (parametric) and Cox survival analysis (semi-parametric). For both models, the interaction between maximum Deficit and minimum snowpack was tested and retained if significant at $\alpha = 0.05$. Though our analysis included stand-level (not individual-tree level) climate values, tree-specific Hegyi and richness parameters produced functional sample sizes equal to tree abundance per model (see sample sizes below).

To model individual mortality probabilities, we created generalized linear mixed models (GLMM; Eq. 3; lme4 package; Bates et al. 2015):

$$\hat{p}_{i,j} = \frac{e^{\beta_{0,i}+X'_{1,i,t}\times\theta_1+X'_{2,j,t}\times\theta_2+X_{3,j}\times\theta_3+X_{4,i,t}\times\theta_4}}{1+e^{\beta_{0,i}+X'_{1,i,t}\times\theta_1+X'_{2,j,t}\times\theta_2+X_{3,j}\times\theta_3+X_{4,i,t}\times\theta_4}} \tag{3}$$

where $\hat{p}$ is a Bernoulli distributed random variable representing tree mortality probability for individual, i, at site, j, which is related (using the Logit link) to sets of tree neighborhood (X'_1) and climate covariates (X'_2) at time, t, plus elevation (X_3), and tree DBH (X_4), with corresponding vectors of coefficients (θ) describing the individual effects of each covariate on survival probability. We included tree-specific random effects to allow intercepts to vary for each individual (i.e., accounting for repeated measures over time; β; n = 1256). Validation metrics were calculated using a classification threshold of 0.053, which was obtained by optimizing sensitivity and specificity of model predictions (Fig. S1).

To model individual mortality hazard (left-censored, meaning that non-zero mortality hazard existed for a period before the study conception), we used a Cox analysis (Eq. 4; rms and simPH packages; Gandrud 2015, Harrell Jr. 2020):

$$\lambda_{i,j,t} = \lambda_{0,i,t}\, e^{X'_{1,i,t}\times\theta_1+X'_{2,j,t}\times\theta_2+X_{3,j,t}\times\theta_3+X_{4,i,t}\times\theta_4} \tag{4}$$

where instantaneous mortality probability (i.e., mortality hazard; λ) for individual, i, at time, t, is a function of the linear combination of time-specific neighborhood, climate, elevation, and DBH covariates scaled by an unspecified baseline hazard function, λ_0. Because Cox regression is a time-to-event model, we ensured that data availability did not bias this model by restricting the dataset to trees residing in the eleven stands with exactly six discrete time steps, between which the number of years spanned 4 to 6 (mode = 5; total timespan = 24 to 30 years). Generalized estimating equations were used to create robust standard errors and account for repeated measures of each tree over time (n = 888) (Therneau et al. 2013). Repeated measures were present because all time-series were combined into a single risk set to allow individual tree mortality hazard to be calculated in the context of all observed climate covariate values over time.

2.4.2 Population-level longitudinal models

We compared an autoregressive linear mixed model (AR1; parametric) with Random forests (non-parametric). To model population abundances (continuous variable), we built an autoregressive linear mixed model (Eq. 5; lme4 package; Bates et al. 2015):

$$y_{j,t} = y_{j,t-1} + X'_{1,j,t}\times\theta_1 + X'_{2,j,t}\times\theta_2 + X_{3,j}\times\theta_3 \tag{5}$$

where y is tree abundance per hectare within each forest stand, j, for year, t, modeled as a function of tree abundance in the previous year (y_{t-1}) plus tree neighborhood, climate, and elevation covariates (n = 20). The interaction between maximum Deficit and minimum snowpack was tested and retained if significant at $\alpha = 0.05$. We allowed the intercept and slope of tree abundance in the previous year (y_{t-1}) to vary randomly with tree stand to account for disparate initial population sizes at each stand, thus preventing dynamics at stands with the highest Taxus abundances from driving model outcomes.

To model population growth (expressed categorically as increasing, stable, or decreasing; n = 20), we used Random forests (randomForest and rfPermute packages; Liaw and Wiener 2002, Archer 2020). Random forests is a machine learning extension of Classification and Regression Trees (CART) that creates an ensemble of many classification trees (or regression trees, if response is continuous; trees n = 5000). The ensemble is created by (1) bootstrap aggregation of data to create parallel trees; then (2) random permutation of predictor covariate placements at each tree node, where predictors at earlier tree nodes are assumed to have a stronger relationship with the response than predictors placed at later nodes. Interactions between covariates are captured implicitly by the branching structure of each tree. The predictive abilities of covariates are quantified by variable importance ranks, which are established on the basis of percent decrease in classification accuracy (or in regression, percent increase in mean squared error) when predictors are placed at earlier nodes along decision trees (i.e., modeled having stronger relationship with response variable). Total classification accuracy (or in regression, variance explained) by Random forests refers to the ensemble model. P values for covariates were attained by permuting the response variable 100 times to produce a null distribution of variable importance, against which the importance metric generated by the original tree ensemble was compared and assessed at $\alpha = 0.05$.

2.4.3 Population-level space-for-time models

We compared a simple linear model (parametric) with Random forests (non-parametric). Because no time component was considered by these models, the response variable was maximum tree abundance per hectare that was observed over the study timeframe (though minimum and mean were tested and produced similar results).

To model population abundances (continuous variable; n = 20), we used a simple linear regression model (Eq. 6):

$$y_j = X'_{1,j} \times \theta_1 + X'_{2,j} \times \theta_2 + X_{3,j} \times \theta_3 \tag{6}$$

where y is maximum tree abundance per hectare within each forest stand, j, over the study period modeled as a function of tree neighborhood, climate, and elevation covariates. The interaction between mean Deficit and mean snowpack was tested and retained if significant at $\alpha = 0.05$ (stats package; R Core Team 2020).

To model population abundances (continuous variable; n = 20), we used Random forests (randomForest and rfPermute packages; Liaw and Wiener 2002, Archer 2020). Rather than building classification trees, we regressed Taxus maximum abundance at each site on the site-specific climatic, neighborhood, and elevation covariates (described in Section 2.4.2). Total variance and P values were obtained as previously described.

3 Results

3.1 Summary

3.1.1 Climate

Between 1977 and 2017, all sites showed increasing modeled annual Deficit, decreasing modeled annual snowpack, and high interannual variability for both (Fig. S6; $P < 0.05$ for all sites' climatic trends). These trends are projected to continue with warmer temperatures and more variable precipitation (Littell et al. 2010, Dalton et al. 2013). Climatic anomalies showed roughly similar trends as annual Deficit and snowpack, but statistical significance was equivocal among sites at $\alpha = 0.05$ (increasing high Deficit anomaly: 5% sites; decreasing low snowpack anomaly: 25% sites). Overall, Deficit became higher on average, with higher extremes in the most recent decade, while snowpack became lower on average and with generally lower extremes (Fig. S6).

3.1.2 Tree populations

Average Taxus abundance declined overall (mean annual population growth rate = − 0.09%, SD = 1.46%). The highest declines (− 2.4% to − 2.7% year^{-1}) were evident at the WFDP and Ohanapecosh River, Washington (Fig. 1; Table 1), where Taxus is projected to become locally extinct within 189 and 26 years, respectively. Taxus distributions did not show a clear warming fingerprint: stands at the leading edge of the mean climate gradient (i.e., higher elevations and latitudes) did not have higher population growth rates than those at the trailing edge (Tables 1 and 3). However, two of the three highest elevation sites (> 1000 m) showed positive population growth (Table 1), and individual tree survival was enhanced at higher elevations (Table 3).

Climate extremes (i.e., anomalies) were more important than climate means for predicting Taxus individual survival and population growth. Longitudinal models showed that climate extremes had strong negative relationships with Taxus survival and population growth, which appear to have obscured a relationship with average climate that may otherwise have been evident in SFT models. Consequently, Taxus' relationship with climate was only apparent in longitudinal models. The relative climate, individual-scale Cox models had the highest predictive accuracy of the six models tested (81.8%; Table 2) and among the lowest error rates (MADMR = 0.08; Table 2).

3.2 Ensemble details

3.2.1 Individual-level longitudinal models

Individual-tree mortality probability (GLMM) and mortality hazard (Cox) were increased by low elevations, high conspecific and heterospecific neighbor density (Hegyi indices), high

Table 2 Results of 10-fold cross-validated model performance for generalized linear mixed model (GLMM; individual scale), Cox survival analysis (Cox; individual scale), 1st order autoregressive linear mixed model (AR1; population scale), simple linear model (SLM; population scale), and Random forests (population scale). Accuracy is classification accuracy (GLMM, Random forests$_a$), concordance (Cox), or percent variance explained (i.e., R^2; AR1 and Random forests$_b$). Two accuracy metrics are given for the AR1 model: marginal R^2 (first number; related to fixed climate and competition effects) and conditional R^2 (second number; related to random autoregressive effects). Mean absolute deviance/mean ratio (MADMR) is scaled by the units of each model's response variable to allow direct comparison of error betwee error)

Model	Validation				
	MADMR	Accuracy (%)	Mortality (n)	Survival (n)	Sample size (n)
Longitudinal					
GLMM	1.84	67.8	314	942	1256
Cox	0.08	81.8	250	638	888
AR1	0.06	1.8 / 99.0	-	-	20
Random forests$_a$	1.05	70.6	-	-	20
Space-for-time					
SLM	0.66	53.0	-	-	20
Random forests$_b$	0.48	59.0	-	-	20

Deficit, and low snowpack (Table 3). Even after accounting for tree density and elevation (i.e., average climate) effects, high Deficit and low snowpack extremes increased mortality. In both models, an interaction between snowpack and Deficit showed that survival was highest when snowpack was high and Deficit was low (Figs. S2, S3), but that high snowpacks could not ameliorate Deficit effects after Deficit surpassed ~ 2.7 SD. Predictive accuracy was 14% higher for Cox models than GLMM (Table 2). Models showed similar significance and direction of effects for each variable, except for species richness (increased mortality probability but not hazard).

3.2.2 Population-level longitudinal models

In agreement with individual-level models, the AR1 population model identified that small Taxus populations were related to higher maximum Deficit (Table 3). Though not significant at $\alpha = 0.05$, Random forests reflected the pattern of Taxus population decline with moderately high Deficits (1–3 SD) and at lower elevations (< 0 SD; Fig. S4). In contrast with individual-level models, small Taxus populations were related to low species richness and low heterospecific neighbor density. Random forests accuracy was comparable to that of individual-level GLMM at 70.6%. AR1 accuracy overall was highest ($R^2 = 99.5\%$; Table 2), but this came almost entirely from random effects (autoregression; conditional $R^2 = 99.0\%$) and predictive abilities of fixed effects was low (i.e., climate, neighborhood, and elevation covariates; marginal $R^2 = 1.8\%$).

3.2.3 Population-level space-for-time models

Average climate covariates were not predictive in either model. SLM and Random forests agreed that small Taxus populations were associated with low species richness and low conspecific neighbor density (Fig. S5). Predictive accuracy was 6% higher for Random forests than SLM, but both SFT models had lower accuracy than longitudinal models (Table 2).

4 Discussion

Our study highlights the importance of ensemble forecasting by demonstrating how different models can lead to contradicting inferences: because Taxus was more sensitive to climate extremes than climate means, SFT models suggested stable Taxus demography, while longitudinal models predicted population declines with continued climate change. Conclusions drawn from longitudinal models are most consistent with observed Taxus declines in recent decades (Table 1). These findings illustrate how sensitivity to climate extremes creates uncertainty in species distribution models relying on climate means by obscuring unidirectional shifts along a geographic climate gradient (Lenoir et al. 2010, Boisvert-Marsh et al. 2014). Considering the many oversimplifications and assumptions that are violated by SFT models in a climate change context (Williams and Jackson 2007, Franklin 2010, Fordham et al. 2013), longitudinal model predictions that account for climatic variability and allow explicit consideration of biological mechanisms are likely to be more useful for developing species conservation and climate change mitigation strategies (Iverson and McKenzie 2013).

Though we used a temperate tree species as an example, climate extremes can induce population declines across taxa (George et al. 1992, Parmesan et al. 2000, Carey and

Table 3 Model coefficients for generalized linear mixed model (GLMM; individual scale), Cox survival analysis (Cox; individual scale), 1st order autoregressive linear mixed model (AR1; population scale), simple linear model (SLM; population scale), and Random forests (population scale). Coefficients for Random forests$_a$ indicate mean decrease accuracy, and percent increase mean squared error for Random forests$_b$, for each variable. Species richness and Hegyi values were calculated within a 10-m radius of each tree; for population-scale models, maximum Hegyi and richness values were chosen to represent each stand. Deficit and snowpack values indicate climate extremes for longitudinal models (i.e., anomalously high Deficit or low snowpack observed within each timestep), and climate means over the entire study for space-for-time models. P values are represented as follows: < 0.1°, < 0.05*, < 0.01**, and < 0.001***. Dashes indicate variable was not included in models

Model	Covariates							
	Elevation	Diameter	Species Richness	Conspecific Hegyi	Heterospecific Hegyi	Deficit	Snowpack	Deficit*Snowpack
Longitudinal								
GLMM	− 0.456***	0.111	0.126*	0.287***	0.148*	0.895***	− 1.807***	0.578**
Cox	− 0.886***	0.202	0.121	0.382***	0.202*	0.518°	− 2.895***	1.768***
AR1	0.626	-	1.438*	0.441°	0.871*	− 0.718**	0.181	-
Random forests$_a$	14.808°	-	17.491°	11.256	10.706	4.558	− 5.892	-
Space-for-time								
SLM	− 0.986	-	25.769*	39.546*	10.318	− 1.675	− 5.831	-
Random forests$_b$	− 12.160	-	35.153**	51.614**	18.381°	− 2.123	0.470	-

Alexander 2003, Matthews and Marsh-Matthews 2003). Conclusions about SFT forecasting methods are thus generalizable to the extent that other species share vulnerabilities with Taxus, including thermo-sensitivity, low phenotypic plasticity, sessility, and dispersal limitation (Svenning et al. 2008, Bertrand et al. 2011, HilleRisLambers et al. 2015). For example, abundance declines are most often observed for non-vagile and thermo-sensitive animals (e.g., lizards and amphibians; Carey and Alexander 2003, Dubos et al. 2020), whereas distributions of highly motile animals (e.g., birds) often shift in accordance with a warming fingerprint (Lenoir and Svenning 2015). Likewise, species lacking the phenotypic plasticity required to rapidly respond to short-term fluctuations can less effectively acclimate to climatic extremes (Agrawal 2001, Chevin et al. 2013). When these species are also sessile or dispersal-limited, populations across the range are likelier to succumb to the negative effects of climate extremes (Coulson et al. 2001, Urban 2015).

Observed tree species' range shifts disproportionately fail to show a strong warming fingerprint, suggesting that these Taxus dynamics may represent other temperate tree species particularly well. For instance, the leading edges of a majority (79%) of terrestrial plant ranges have expanded with their changing climate envelope (Lenoir and Svenning 2015), while only half (52%) of treelines have done the same (Harsch et al. 2009, Zhu et al. 2012). Trees are often subject to lagged responses that are asynchronous with the rate of warming (Bertrand et al. 2011), likely due to species interactions (Suttle et al. 2007, Das et al. 2018), recruitment or dispersal limitations (HilleRisLambers et al. 2015), and disturbance legacies (Wason and Dovčiak 2017). We add to this body of work to show there is potential for widespread declines if species with these characteristics are also sensitive to climate extremes over regional scales. These factors together support the interpretation that tree range expansion is unlikely to keep pace with climate warming (Grabherr et al. 1995). It is therefore inappropriate to conclude that species ranges will remain stable with climate change based on SFT model outcomes incongruent with a warming fingerprint, as instead, we might expect range-wide crashes due to increasingly variable climate patterns (Neumann et al. 2017).

Synchronous responses across scales of biological organization support the interpretation that sensitivity to climate extremes may promote range-wide declines. Individual mortality processes were manifest as population declines at the stand scale, even after accounting for elevation gradients and biotic relationships. Recruitment of young trees was not sufficient to offset the increased mortality observed during periods of drought (HilleRisLambers et al. 2015), highlighting the importance of mortality processes in driving demography of long-lived and/or recruitment-limited species, particularly in temperate forests (Silvertown et al. 1993, Lutz and Halpern 2006, Bertrand et al. 2011). Sensitivity to climate extremes suggests stronger local competition during drought (Clark et al. 2011, Das et al. 2011, Urban et al. 2012, Furniss et al. 2020), which was supported by increased individual mortality with high neighbor crowding (Hegyi indices; Table 3). Sensitivity to Deficit could also suggest limited drought tolerance of established individuals (Voelker et al. 2018), resulting in physiological stress and concomitant vulnerability to forest pests (Mattson and Haack 1987, McDowell et al. 2008, Gaylord et al. 2013). In the absence of disturbances such as fire and pest epidemics that can accelerate forest decline (Bentz et al. 2010, Davis et al. 2019), these factors may together explain gradual declines that occur despite species being well-adapted to average climatological conditions (Bréda et al. 2006).

Taxus decline predicted by our longitudinal models joins the growing body of work demonstrating negative impacts of increasing drought in forests globally (Breshears et al. 2005, Hutyra et al. 2005, Allen et al. 2010, Neumann et al. 2017). Though not as dramatic as rapid die-offs, gradually declining survival rates can substantially reduce carbon sequestration capacity across forested landscapes (Das et al. 2016). Moreover, increasingly frequent and severe drought in the future (Field et al. 2012, Dai 2013) may result in more rapid population crashes compared with the declines of recent decades (Zhu et al. 2012, Lenoir and Svenning 2015). By ignoring climatic variability and extreme events, reliance on SFT models likely contributes to the growing problem of underestimating habitat loss with changing climate (VanDerWal et al. 2013, Allen et al. 2015).

Reliance on climate means in distribution models creates uncertainty that propagates to estimations of global ecosystem functionality with changing climate (Pan et al. 2013, Allen et al. 2015). In addition to anticipating future habitat for much of terrestrial biodiversity, accurately forecasting forest responses to climate change is necessary to obtaining realistic estimates of climate change itself due to strong regulation of global carbon and hydrological cycles by forests (IPCC 2019). Though some terrestrial components of coupled global climate models are rightly beginning to consider wildfire (Fisher et al. 2018), leading models continue to ignore the possibility of drought-induced population crashes (e.g., maximum stress mortality rate = 1%; Levis et al. 2004, Sitch et al. 2008, Lawrence et al. 2019). Nonetheless, forest loss due to increasing climatic variability may destabilize climate and associated habitat production at regional and global scales (Adams et al. 2010, Stark et al. 2016). Such feedbacks have been noted for western temperate forests in particular (i.e., within the range of Taxus; Garcia et al. 2016, Swann et al. 2018), which tout some of the highest biomass carbon densities in the world (Smithwick et al. 2002, Keith et al. 2009, Lutz et al. 2018, Sillett et al. 2018). Climate extremes-associated Taxus decline support the interpretation that current carbon sinks could become carbon sources with increasingly variable climate (Cox et al. 2000).

5 Conclusions

Our study corroborates the growing understanding that SFT models built on climatic means cannot be relied upon to accurately forecast climate change effects in forests. SFT datasets may still be valuable tools, but individual-based, longitudinal data appear to be better suited to biogeographical forecasting amidst modern climate change. It is increasingly important to supplement SFT datasets with a longitudinal component that reflects underlying biological mechanisms, whether that be observational or experimental (Lutz 2015). If this is not possible, SFT study results could be evaluated by explicitly testing whether climate means are indeed the best predictors of biological responses to changing climate. This could be done by comparing predictive accuracy between (1) SFT models using differences in mean climate across the geographic range as a proxy for longitudinal climate change; and (2) SFT models using differences in variability metrics as the proxy, which may better reflect local climate extremes (e.g., coefficients of variance or derivatives). In either case, reliable forecasts of future species distributions require examination of species responses to average and relative climate changes.

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Code availability Upon request to the corresponding author.

Authors' contributions SJG and JAL conceived the study, SJG designed and performed analyses and wrote the initial manuscript, and SGJ and JAL revised and approved the final manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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