A species' response to spatial climatic variation does not predict its response to climate change

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The dominant paradigm for assessing ecological responses to climate change assumes that future states of individuals and populations can be predicted by current, species-wide performance variation across spatial climatic gradients. However, if the fates of ecological systems are better predicted by past responses to in situ climatic variation through time, this current analytical paradigm may be severely misleading. Empirically testing whether spatial or temporal climate responses better predict how species respond to climate change has been elusive, largely due to restrictive data requirements. Here, we leverage a newly collected network of ponderosa pine tree-ring time series to test whether statistically inferred responses to spatial versus temporal climatic variation better predict how trees have responded to recent climate change. When compared to observed tree growth responses to climate change since 1980, predictions derived from spatial climatic variation were wrong in both magnitude and direction. This was not the case for predictions derived from climatic variation through time, which were able to replicate observed responses well. Future climate scenarios through the end of the 21st century exacerbated these disparities. These results suggest that the currently dominant paradigm of forecasting the ecological impacts of climate change based on spatial climatic variation may be severely misleading over decadal to centennial timescales.

climate change | tree growth | prediction

Anthropogenic climate change is impacting biodiversity and ecological communities globally, altering their ability to provide the ecosystem functions and services on which humanity depends (1). Documenting and predicting these impacts has been a research priority for decades (2–4); however, predicting how climate change may impact specific ecological entities and processes remains challenging. In most cases, predictions of this sort are based on statistical relationships between some ecological phenomenon and spatial variation in climatic conditions. A particularly common application of this approach uses species' current geographic occurrence patterns to predict their future distribution (i.e., species distribution models, SDMs; 5, 6), though it can also be used to predict any ecological phenomenon that varies across space (e.g., species' abundance, community composition, a demographic vital rate, ecosystem services). Regardless of the ecological variable of interest, this approach rests upon the assumption that the observed response to spatial climatic variation is predictive of the response to changing climate through time (7). For example, if the individual growth rate of a species increases with temperature across its geographic range, this assumption results in the expectation that growth in all populations will increase as temperatures rise in the future. Similarly, if growth rates are highest in the center of a species' temperature range, the expectation is that future warming will result in growth increases in colder parts of the range, and growth declines in warmer parts of the range (i.e., the "leading edge" and "trailing edge" of a species' distribution; 8). However, substituting spatial variation for temporal variation in this way is known to be problematic in some cases (7, 9–15) and could be misleading. For example, if populations are tightly adapted to local historical climatic conditions, then increasing temperatures could lead to population declines for each population across the range, and not to leading and trailing range edges. Alternatively, spatial gradients in other important nonclimatic environmental factors (e.g., soil nutrients, competitive environment, land management) could decouple species-wide patterns of performance variation from climatic variation (15). Nevertheless, using spatial variation across species' distributions to make predictions could be justified if errors are small enough that species-wide responses to spatial climatic variation yield informative coarse-scale predictions. Determining the degree of mismatch between predictions based on ecological responses to spatial climatic variation versus in situ climatic variation through time is therefore critical to evaluating the assumptions underlying the currently dominant approaches to forecasting biodiversity responses to climate change (7, 12, 13).

Significance

Most predictions of how species will respond to climate change assume that performance variation across spatial climatic gradients predicts how individuals and populations will respond to climate change through time. Here, we use a new network of tree-ring growth time series collected from across the distribution of ponderosa pine to demonstrate that this assumption is false and produces severely misleading predictions.

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Assessing the scope and consequences of these potential mismatches requires data that capture both how an ecological phenomenon varies across spatial climatic gradients (hereafter the *species-wide response*), and how the same phenomenon varies through time in response to in situ climatic variation (hereafter the *population-level response*). While most ecological datasets are too limited in either extent or duration to accomplish this, spatial networks of biogenic time series, like the annual growth rings of temperate tree species, provide a rare opportunity (16). Tree rings can be used to assess both how quickly a species grows at a given location, as well as how individual performance has varied through time in response to past climatic variation. With time-series data collected from many individuals in many populations across a species' geographic distribution, aggregated population-level responses to temporal climatic variation can be compared against species-wide performance variation across spatial climatic gradients. This makes it possible to determine whether populations have responded to currently changing climatic conditions in a manner consistent with species-wide responses to spatial climatic variation (scenario *i*, Fig. 1*A*) or instead whether population responses contrast in slope (scenario *ii*, Fig. 1*A*) or sign (scenario *iii*, Fig. 1*A*) relative to expectations from species-wide patterns.

Here, we use ponderosa pine [*Pinus ponderosa, sensu lato*; (17, 18)] in western North America as a case study for comparing species-wide responses to spatial climatic variation against population-level responses

to temporal climatic variation. This study system is particularly well-suited for the purpose: western North America experienced relative climatic stability for much of the 20th century before a consistent warming trend began in the early 1980s (Fig. 2*A*). Because high-quality historical climate data are available across the region throughout this period, it is possible to leverage the prewarming stable period to model trees' responses to both spatial and temporal climatic variation and compare model predictions to observed responses after secular warming began (Fig. 2*A*). Individual ponderosa pines live 100 to 1,000 y, providing performance time series that span this transition from climatic stability to secular warming. Further, ponderosa pine is a common subject for tree-ring analyses because of the species' clearly defined annual growth rings and climatic sensitivity (19). These climate sensitivities, coupled with the dramatic gradients spanned by its highly disjunct geographic distribution (2 to 17 °C mean annual temperature, 100 to 2,500 mm mean annual precipitation), make ponderosa pine a suitable subject for comparing population-level versus species-wide climate responses and evaluating how differences might influence forecasts of future performance.

We collected tree-ring samples from 23 populations of ponderosa pine, located across much of the *sensu lato* species' geographic and climatic distribution in the western United States (Fig. 1*C* and *SI Appendix*, Table S1; 20). Because we sampled all suitable individuals within a plot of fixed size, these data are representative of each population, in contrast to traditional dendrochronological
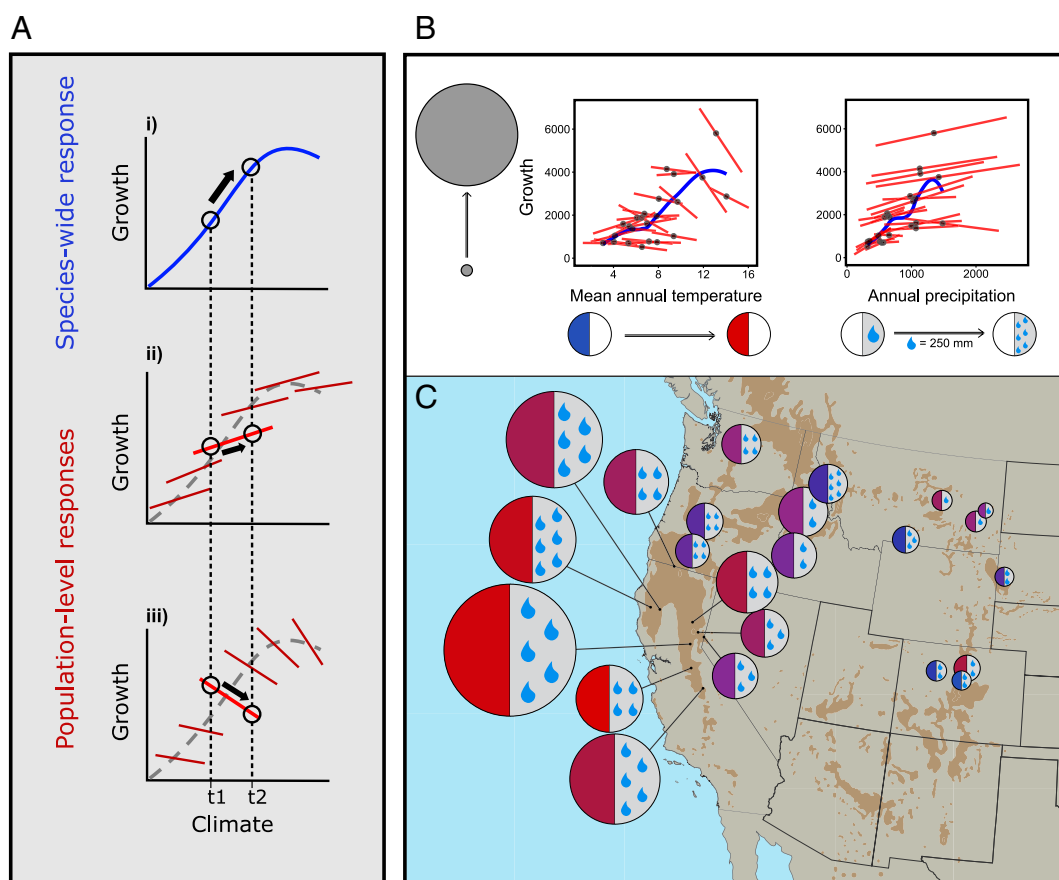

Fig. 1. Contrasting responses to spatial versus temporal climatic variation result in dramatically different predictions of future growth. (*A*) Three scenarios of how species-wide responses to spatial climatic variation (blue line, gray dashed lines) could differ from responses of populations to interannual climatic variation (red lines): (*i*) *matching responses*, in which species-wide and population-level responses are identical; (*ii*) *mismatched slopes*, in which responses differ in their strength, but match in sign; and (*iii*) *mismatched signs*, in which species-wide and population-level responses are directionally opposed. When climate changes from t_1 to t_2, each scenario yields different predicted growth responses. (*B*) Observed climate-growth relationships across 23 ponderosa pine (*P. ponderosa s.l.*) populations. Black points indicate long-term mean climate and growth (BAI, mm^2) for each study site; blue lines are locally-weighted regressions illustrating the species-wide spatial climate-growth relationship. Each red line indicates the linear relationship between interannual climatic variation and growth within a single population. (*C*) Study sites were distributed across the geographic and climatic distribution of ponderosa pine, spanning gradients in mean growth rate (size of circle) and average climatic conditions, indicated inside each circle (see axis legends, panel *B*).
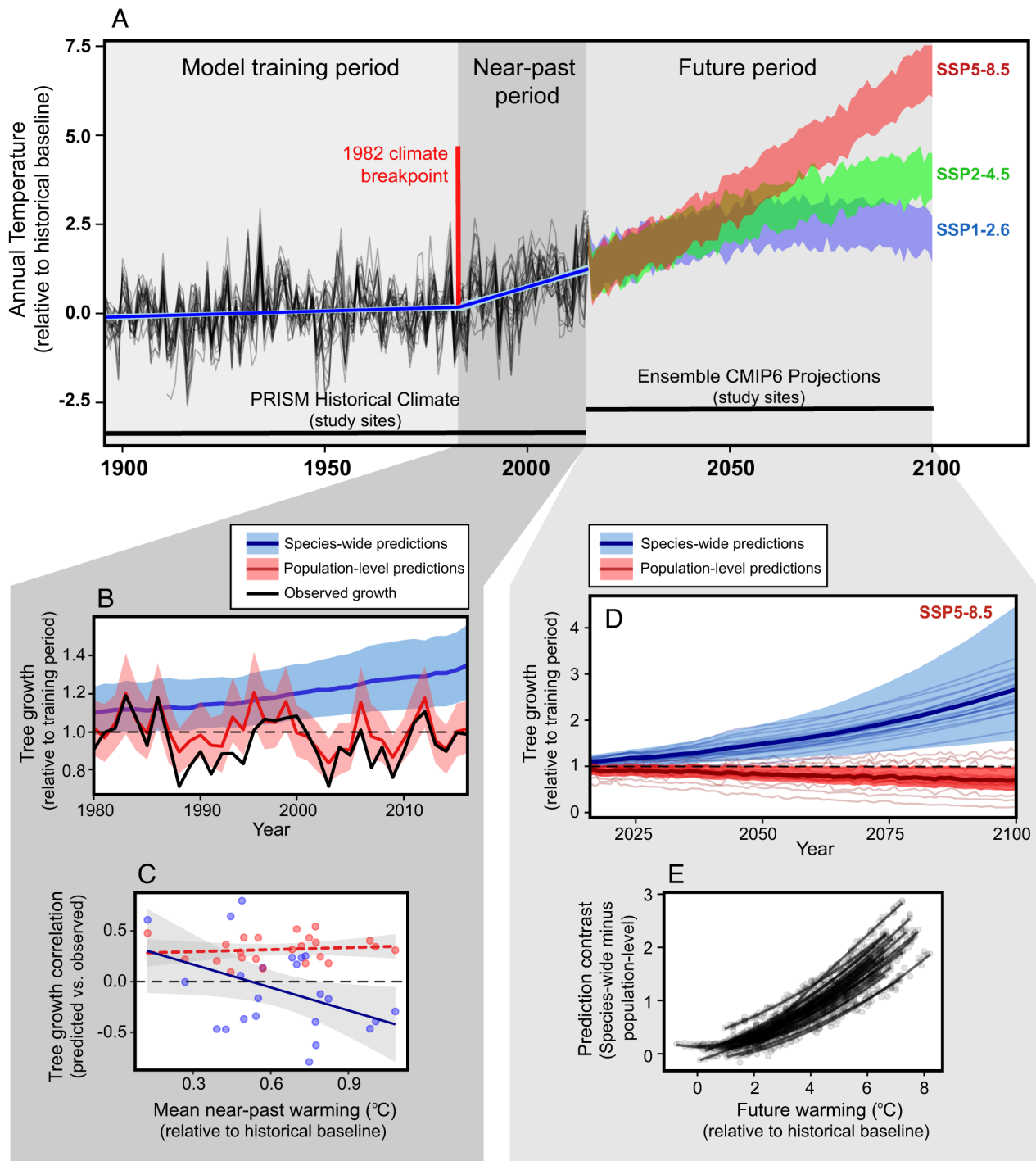
Fig. 2. Population-level climate responses better predicted observed growth trends during the near-past period of climate change, and yield forecasts that diverge substantially from those generated using the species-wide response. (*A*) Mean annual temperature anomalies (°C) at each of our 23 study sites relative to 1900 to 1950 historical baselines, based on PRISM historical climate data (black lines) and three CMIP6 future climate scenarios (SSP1-2.6, blue; SSP2-4.5, green; SSP5-8.5, red). A breakpoint regression analysis (blue line) of these historical climate time series found a significant breakpoint in 1982, used to define the boundary between model training and near-past prediction time periods. (*B*) Mean posterior growth predictions and 95% credible intervals during the near-past period, for species-wide predictions (blue) and population-specific predictions (red), compared to observed growth during the same period (black line), averaged across all study sites. Supplementary materials contain predictions for each site. (*C*) Correlations between predicted and observed growth (Pearson's *r*), in relation to mean warming recorded at each site over the near-past period. (*D*) Divergence between species-wide (blue) and population-level (red) growth predictions under the SSP5-8.5 scenario. Heavy lines and shading indicate mean posterior predictions and 95% credible intervals across all sites, respectively; light lines indicate mean posterior predictions for each site. (*E*) Contrasts between species-wide and population-level predictions, as a function of projected future warming at each site (black points and lines).

sampling focusing only on individuals likely to be highly sensitive to climatic fluctuations (21). We used standard dendrochronological methods to prepare and crossdate samples before measuring the radial distance between annual growth rings. We then converted these radial increments (mm) to basal area increments (BAIs)

(mm^2) using field-measured and back-calculated tree diameters; hereafter, "growth" refers to BAIs (with units mm^2 y^{-1}; see Materials and Methods). To quantify both species-wide and population-level climate responses, we used a generalized linear mixed model to predict each tree's annual growth prior to the onset of climate

warming (1900 to 1982) as a function of 1) spatially varying mean climatic conditions, capturing species-wide variation in average growth rate and 2) time-varying climatic variables, capturing aggregated population-level variation in annual growth rates (using PRISM climate data; see Materials and Methods; 22). We also incorporated the effect of individual tree size on growth into the model; see Materials and Methods for further details. We applied this model to ask which statistically-inferred response better predicted observed growth following the onset of climate warming (1982 to 2015), by comparing model-predicted responses to spatial versus temporal climatic variation to observed growth over the same period. Finally, we used a range of CMIP6 future climate scenarios (23) to contrast these growth predictions through the end of the 21st century.

The model presented here treats ponderosa pine as a single unit; however, there is an emerging recognition that the Pacific and interior varieties (var. *ponderosa* and var. *scopulorum*; 24) represent distinct lineages that may be more closely related to other species than to one another (17, 18). Recent molecular work has identified further genetic structuring comprising up to four potential species layered on this Pacific—interior distinction (17, 18). To explore the degree to which this taxonomic uncertainty might modify observed species-wide growth responses, we fit an additional model variant that incorporated interactions between spatially varying climate and Pacific versus interior population origin (Supplementary Materials and Methods).

Growth Responses to Climatic Variation Differ across Space versus through Time

The data show that species-wide responses to spatial climatic variation and population-level responses to temporal climatic variation are opposite in sign with respect to temperature but not precipitation. We found evidence of a strong species-wide, positive relationship between mean growth rate and spatial variation in mean temperature and precipitation (Fig. 1 *B* and *C*), such that trees grew faster in warmer and wetter locations. In contrast, populations show 1) negative relationships between interannual variation in growth rate and temperature, and 2) weakly positive relationships between interannual variation in growth rate and precipitation that are stronger at the driest locations (Fig. 1 *B* and *C* and *SI Appendix,* Fig. S1). Thus, at the sensu lato species level, warmer regions were associated with faster growth, whereas at the population level, warmer years were associated with slower growth. This sign difference in the relationship between spatial and temporal variation in temperature is consistent with our scenario *iii* (Fig. 1*A*). However, with respect to precipitation, these relationships differed only in magnitude, consistent with our scenario *ii* (Fig. 1*A*).

Species-Wide Spatial Patterns Do Not Predict Growth Responses to Recent Climate Change

These contrasting responses resulted in divergent predictions in response to a secular warming trend in the near-past (1982 to 2015), such that the species-wide response predicted increased growth, whereas population-level responses predicted decreased growth (Fig. 2*B* and *SI Appendix,* Fig. S2). Comparing these near-past predictions to observed growth trends over the same period showed that population-level responses to interannual climatic variation predicted actual growth trends substantially better than the species-wide response to spatial climatic variation. The predictive performance of the species-wide response declined with the amount of warming a site experienced ($r = -0.42$, $P = 0.04$), such that these predictions correlated negatively with observed

growth above ~0.5 °C of warming (Fig. 2*C*). This demonstrates that predicting a species' response to climate change based on spatial variation in performance can yield directionally incorrect predictions of how growth may change over a timeframe as short as 40 y. A few recent studies have found similarly contrasting responses to spatial versus temporal environmental variation (13, 25–28), implying that this type of space-for-time prediction could be misleading. Here, we have directly tested this implication by asking whether responses to spatial climatic variation across a species' distribution accurately predict actual observed responses to changing climate.

Future Climate Change Exacerbates Divergence between Predictions

The finding that species-wide patterns fail to predict actual responses on short decadal timescales raises concern about the accuracy of predictions made over the longer timescales that are typically used when forecasting species' responses to climate change, e.g., to the end of the 21st century (3). To examine this, we extended our projections of ponderosa pine's performance out to the end of the century (2015 to 2100) under a range of future CMIP6 climate scenarios (SSP1-2.6, SSP2-4.5, SSP5-8.5; 21). We found that in all future climate scenarios, the responses to spatial versus temporal climatic variation predict dramatically different performance trajectories (Fig. 2*D* and *SI Appendix,* Figs. S3 and S4). Under the SSP5-8.5 scenario, forecasts based on the response to spatial climatic variation indicated growth increases of up to 300%, compared to projected growth declines in most populations when forecasts were based on the response to interannual climatic variation (Fig. 2*D*). Notably, across populations, the degree to which the two predictions diverged depended strongly on the amount of future warming projected at the study site, with the largest divergences occurring with the greatest projected warming (Fig. 2*E* and *SI Appendix,* Figs. S3 and S4).

Discussion

This study provides a rare empirical test of whether the impact of recent climate change can be predicted by a species' relationship to spatial climatic variation; we find that it cannot. Our results indicate that such spatially based predictions run the risk of being directionally incorrect, with important consequences for any conservation planning and management action they might inform (4, 6). Further, we demonstrate that an alternative approach leveraging time-series data matches observed growth responses to climate change quite well. While our analyses focus on a small taxonomic sample, the literature suggests that these results and their implications may be relevant for many species and for the practice of ecological forecasting generally. For example, contrasting responses to spatial versus temporal climatic variation have been documented in several other tree species, including in eastern North America (13, 29), suggesting that our findings may be relevant outside of the semiarid temperate landscapes occupied by ponderosa pine. Further, several recent studies have reported similarly contrasting responses across space versus through time in a much wider variety of contexts [e.g., demographic rates of perennial bunchgrasses (30), patterns of pathogen-driven forest mortality (31), vital rates of regional bird populations (26, 27, 32), and population growth rates of an endemic alpine plant (33)]. Our findings suggest that in all these cases, ecological responses to climate change on decade-to-century timescales cannot be accurately predicted by responses to spatial environmental variation.

This conclusion is particularly concerning given the wide application and acceptance of spatial models and other space-for-time substitutions for predicting the ecological impacts of climate change (6, 34). Just in the context of tree growth, there are several recent examples of studies using spatial patterns to forecast future growth or related performance metrics (e.g., refs. 35–39). Even more prevalent are large-scale and high-profile forecasts of biodiversity responses to climate change based on correlative relationships between species' occurrence patterns and spatial climatic variation (2, 3, 40–45). A growing body of work has begun documenting cases where observed responses to climate are at odds with such spatially based predictions (30, 46–52). Contrasting ecological responses across space versus through time could be contributing to these mismatches between predicted and observed responses to climate change. However, we emphasize that our findings do not constitute a direct test of SDMs but are rather a conceptually analogous test of a key assumption underlying their application to ecological forecasting. A test of SDM predictions based on spatial versus temporal climatic variation would require data on how species' occurrence patterns have changed through time. We also emphasize that it is not straightforward to compare forecasts of individual growth against forecasts of an occurrence-based SDM, as individual growth rates and probability of occurrence are two different ecological metrics that have been shown to not closely track one another (11, 51). Nonetheless, our finding that spatial and temporal climate responses are not interchangeable, taken in context with corroborating work in other systems (26, 27, 30–33), suggests that the conceptual basis for using SDMs and other similar spatial methods for ecological forecasting might in many cases not be sound.

Taxonomic uncertainty and intraspecific variation in climatic tolerances further complicate attempts to predict species' responses to climate change. Recent work has improved the performance of species distribution and other similar models by incorporating variation in functional traits (53, 54) or dividing species into subspecific groups (55–58). However, these approaches still rely on responses to spatial climatic variation and thus risk ignoring the kinds of spatial versus temporal mismatches highlighted by our findings here. Further, there is considerable uncertainty about the taxonomic scale on which climatic tolerances vary, which likely depends on many factors including the relative amount of spatial versus temporal climatic variation and biogeographic history experienced by the organism in question (59, 60). Here, an analysis of the impact of taxonomic uncertainty on ponderosa pine's climate responses revealed heterogeneity in the mismatch between spatial versus temporal climate responses. Specifically, we found that spatial variation in temperature had a stronger positive effect on mean growth rate among populations of the Pacific variety (var. *ponderosa*) than among interior populations (var. *scopulorum*; *SI Appendix,* Fig. S7). However, a strong statistical interaction between mean annual temperature and mean annual precipitation indicated that this heterogeneity was contingent on the amount of precipitation that populations experience. This differed between varieties; Pacific populations experience wetter conditions than interior populations, facilitating a stronger positive response to spatial variation in temperature (*SI Appendix,* Fig. S7). This suggests that mismatched responses to spatial versus temporal temperature variation is at least partially contingent upon mean precipitation conditions, which differ between the two varieties. In contrast, we found no consistent differences between varieties in their responses to temporal climatic variation—warmer-than-average local conditions led to reduced growth for all populations (*SI Appendix,* Figs. S1 and S8). This analysis of subspecific varieties did not ameliorate mismatches between spatial versus temporal growth responses or their future predictions but rather revealed an additional layer of complexity wherein these mismatches may be partially contingent on additional climatic dimensions and/or intraspecific variation. Hence, our conclusion that spatially derived climate responses fail to reliably predict population-level responses to climate change through time remains robust to intraspecific variation in climate responses and taxonomic uncertainty in this study system.

Over time periods longer than a few decades, whether population-level predictions based on responses to in situ temporal variation in climate continue to be more accurate than predictions based on the response to spatial climatic variation depends on a variety of processes including plasticity, evolutionary adaptation, and migration (8, 61, 62). An emerging body of work has indicated that individual tree growth responses to interannual climate variability may change through time as trees are exposed to different ranges of climatic conditions (63–66). Unfortunately, this sort of plasticity is likely to accelerate growth declines as trees experience conditions beyond the range of variability to which they are adapted (63, 67, 68). Thus, predictions of future tree growth based on static, linear relationships between interannual climatic variation and growth, including our predictions, may be overly optimistic and in fact underestimate future growth declines. For example, recent megadrought conditions in the western United States could induce negative growth responses beyond those predicted by past climate sensitivities. This could be reflected in several of our study populations that experienced near-past growth declines beyond those predicted by our model's population-level response (*SI Appendix,* Fig. S2). Whether transgenerational plasticity could shift climate sensitivities through parental effects on offspring phenotypes is currently unknown (69, 70). However, given increasing climatic variability and the complexity of environmental cues, any such parental effects have a high likelihood of being detrimental rather than helping to compensate for declining performance (70). Over longer timescales, evolutionary adaptation to changing conditions could compensate for declining performance, through selection for either higher mean growth rates or different climate sensitivities (61, 71, 72). However, this evolutionary rescue seems unlikely to result in meaningful change over the time period we examine here, given the rapid pace of climate change relative to the slow demographic rates of long-lived tree species (72–75). Adaptive responses to climate change could be accelerated or otherwise facilitated by migration of genotypes better-suited to current and future climatic conditions (61, 76). However, naturally occurring tree dispersal already lags behind the pace of climate change (50) and may be further hindered by human land use, biotic interactions, or other factors that limit range shifts. Thus, while plasticity, adaptation, and migration are important processes in determining species' future trajectories, it is unclear whether they have the capacity to substantially alter the results or implications of the work we present here over the projection timeframe.

To improve ecological forecasting, there is an urgent need to better understand where and when we need to incorporate temporal variation into our forecasts of future ecological states—including not only tree growth but also species' distributions, ecosystem productivity, and other socially valuable ecological phenomena. Building a predictive understanding of mismatched ecological responses to temporal versus spatial climatic variability will be especially important as climate change alters past environmental correlations to produce locally and globally novel climate regimes (77, 78). Critically important work in this area aiming to move beyond the current spatially based paradigm by integrating different sources of ecological information has already been fruitful (56, 79–81). Ultimately, improving our ability to make accurate, reliable forecasts will require systematic exploration of ecological

mismatches between space and time, as well as further development of data, methods, and models for incorporating both sources of variability.

Materials and Methods

Study Species. Ponderosa pine (*P. ponderosa s.l.*) is widely distributed in western North America throughout a highly disjunct range that encompasses a tremendous breadth of climatic conditions, with mean annual temperatures ranging from 0 to 15 °C and 200 to 2,100 mm of mean annual cumulative precipitation (Fig. 1). The most commonly used taxonomy recognizes two varieties of *P. ponderosa*, var. *scopulorum* and var. *ponderosa*–the interior and Pacific varieties, respectively (24). The most recent molecular work has found evidence of more complex taxonomic structuring within ponderosa pine (17, 18), indicating at least four lineages. However, these finer taxonomic divisions do not seem to align with differences in climate sensitivities (19, 55) and do not yet have precisely defined geographic boundaries, preventing the confident assignment of populations to these taxonomic units without genetic analyses. Hence, the analyses presented in the main body of this manuscript treat the *P. ponderosa* as a single unit, with supplementary analyses of how the Pacific–interior distinction impacts climate responses.

Tree-Ring Data.

Data collection. We selected study populations from across the distribution of *P. ponderosa s.l.*, following the niche-based methodology proposed by Perret and Sax (20). We used curated and taxonomically verified botanical records compiled in the Conifer Database (82) to bound the climate space occupied by *P. ponderosa s.l.* across its geographic distribution. This climate space was defined by a set of seven climatic variables previously used to model the climatic niches of pines and other conifer species (20, 83). We limited site selection to public lands managed by the United States Forest Service or the Bureau of Land Management. Further criteria were that sites were free of obvious recent disturbance (e.g., timber harvest, thinning or other stand management, recent fire), were a minimum of one kilometer from high-traffic roadways, and were not located on either particularly steep slopes or along drainages. Wherever possible, we selected sites such that they corresponded with one of the Conifer Database botanical records used to build the species' climatic niche model. This site selection procedure resulted in 24 study sites, spread across the states of Arizona, California, Colorado, Idaho, Montana, Oregon, and Montana (Fig. 1 and *SI Appendix*, Table S1).

We used a consistent plot- and survey-based approach to collect tree-ring samples at each study site. Specifically, we established a 25-m by 25-m square plot in a representative portion of the stand at each site. Within this plot, we measured each ponderosa pine's bole diameter at 1.4 m above ground level (i.e., diameter at breast height, DBH), assessed its general condition and vigor, recorded the presence or absence of new cones, and recorded any evidence of pathogens (e.g., sap flows, needle blight). Using a Haglöf increment borer, we collected two 4.3-mm diameter cores from each tree greater than 15 cm DBH in the plot. One core was collected at breast height (140 cm), and the other was collected as close to the ground as possible given available equipment and the individual tree's setting. In cases where there were fewer than 15 suitable trees on a plot, we sampled additional trees at increasing distances from the plot center. For 10 sites, we could not establish a fixed plot due either to excessive understory growth or site terrain characteristics. For these sites, trees were sampled at increasing distances from the intended plot location (i.e., an n-tree sampling design; (84)). Sampling was conducted during the 2018 growing season between June and October.

Sample preparation. All increment cores were mounted, sanded, and visually cross-dated according to standard dendrochronological methods (85). We then measured the width in millimeters of each growth ring in every core sample using 2,400 dpi digital scans and the computer program CooRecorder (86). We verified year assignments of the measured tree ring series using CDendro (87) and the "dplR" package in R 3.6.3 (88, 89). Specifically, we used 20-y lagged interseries correlations to identify dating and measurement errors across all series per site. These errors were iteratively identified and corrected until all interseries correlations between 20-y segments were above 0.60. Both core samples for each tree were used during visual and statistical cross-dating, but only samples extracted from breast height were retained for growth analyses. For one site, located outside of Show Low, Arizona, a high rate of missing and false rings prevented confident

assignment of a year of formation to growth rings. This site was excluded from all subsequent analyses. We used field-measured DBH for each tree to convert these ring width timeseries to annual BAIs, a procedure that controls for the influence of increasing tree bole diameter on annual ring widths (90). In total, this yielded 339 tree growth time series from 23 sites (*SI Appendix*, Table S1).

Analyses.

Climate data. We associated BAI time series for each tree at each site with PRISM LT81m historical monthly climate time series spanning the years 1900 to 2015 (22). For each year, we summarized monthly climate data into eight seasonal periods spanning the growing season of the previous year through the end of the current year. In each of these seasons, we calculated mean maximum monthly temperature and cumulative precipitation. To characterize the general climatic regimes at each site, we calculated mean annual temperature and mean annual cumulative precipitation in 30-y moving windows, as well as across the length of the entire time series. These climatic variables are similar to those used in growth analyses for ponderosa pine and other species (13, 19, 21, 91–93). Exploratory analyses indicated that interannual growth was more strongly correlated with these seasonal climatic variables than annual climatic variables. Some analyses have also included composite measures of moisture availability like vapor pressure deficit (e.g., refs. 18 and 75) or climatic moisture deficit (e.g., ref. 76), usually derived from a combination of temperature and precipitation measurements. Though these composite variables can be quite informative, we opted to include only mean and maximum temperatures and cumulative precipitation to limit model complexity and ease interpretation.

Substantial climate change has already been reported across western North America over the past several decades (94–97). In order to identify when warming began in the climate time series at each of our study sites, we used a breakpoint regression analysis to assess how secular trends in annual temperature anomalies relative to 1900 to 1950 means have changed across the full time series (1900 to 2015). Breakpoints identified by this analysis were used to divide growth and climate time series into "prewarming" and "postwarming" periods in subsequent analyses. These analyses were conducted using the "segmented" package in R3.6.3 (98).

Growth model. We were interested in describing two aspects of growth variation in our dataset: 1) species-wide variation in average growth rate associated with spatially varying long-term mean climate and 2) population-specific variation in annual growth associated with time-varying climatic variables. In order to do this, we used a hierarchical generalized linear mixed model implemented in a Bayesian framework to model annual BAI during the prewarming period as a function of a tree's size in the preceding year, spatially varying mean climatic conditions, and time-varying seasonal climate variables:

$$BAI_{t,s,y} \sim \beta_0 + \gamma_{0,t,s} + \beta_1 BA_{t,s,y-1} + \gamma_{1,s} BA_{t,s,y-1} + \beta_{2i} CN_{i,s}$$
$$+ \beta_{3j} TA_{j,s,y} + \gamma_{2j,s} TA_{j,s,y} + \beta_{4j} PA_{j,s,y} + \gamma_{3j,s} PA_{j,s,y} + \varepsilon. \quad [\mathbf{1}]$$

In this model, the BAI in year *y* of tree *t* at site *s* is modeled as the linear combination of that tree's basal area (*BA*) in the previous year, *y-1*, long-term mean climate variables (*CN*) that vary between sites *s*, and annual climate variables (*TA, PA*) that vary across years *y* and sites *s*. *CN* terms indicate long-term mean climatic conditions over the length of the model training period. Beta terms (β) indicate estimated fixed effects describing species-wide responses, whereas gamma (γ) terms indicate random effects varying across sites *s* or trees *t*. Hence, β_0 is the species-wide intercept (average BAI), whereas $\gamma_{0,t,s}$ is a random modification of the species-wide intercept for each tree *t* nested in each site *s*. This random intercept modification accounts for growth variation between sites and between trees within a site caused by nonclimatic factors like soil characteristics, topography, stand density, and disturbance histories. *BA* was back-calculated for each tree in every year using the field-measured DBH and ring width time series data, then standardized relative to the mean tree size at each site. Because the influence of tree size on BAI can vary widely, we included a site-level random slope modifier on this term ($\gamma_{1,s}$). The index *i* varies from one to three, denoting one of two long-term mean climate variables *CN*, mean annual temperature and mean annual precipitation, as well as their interaction. The β_{2i} coefficients then capture the species-wide relationship between mean climatic conditions and BAI. The index *j* indicates one of eight seasonal periods ranging from the previous year's growing season through the end

of the current growing season in year y. Thus, the parameters β_{3j} and β_{4j} describe the fixed species-wide effect of mean monthly maximum temperatures (TA) and cumulative precipitation (PA), respectively, during each period j. The parameters $\gamma_{2j,s}$ and $\gamma_{3j,s}$ capture population-specific deviations from the species-level response to each of the same seasonal predictors. Because growth increments are always greater than zero, with a variance proportional to the mean, we used a Gamma distribution with a logarithmic link function and an estimated dispersion parameter q to describe the model error distribution. Because the logarithmic link function required the dependent variable to be positive and nonzero, we added the minimum observed ring width in each series to any missing rings in that series (i.e., years that were identified via cross-dating when no wood formation occurred in the sample). We did this instead of adding an arbitrarily small constant in order to preserve differences between individual trees in an ecologically realistic way.

Past work has indicated that population-specific growth sensitivities to interannual climatic variation vary predictably with the mean temperature and precipitation conditions at a site (13, 19). Because we were interested in estimating both species-wide and population-level climate responses, we accounted for population-specific variation in climate sensitivities by adding in the site-level random slope modifiers $\gamma_{2j,s}$ and $\gamma_{3j,s}$. In addition, recent work has questioned the assumption of stationarity in climate responses through time that underlies a substantial portion of the dendrochronological literature (63–66). Because this work indicates that the climate sensitivities of a single tree may change through time as climate changes, we fit our model using only climate and growth data from the prewarming period identified in our exploratory analyses of climate time series.

The high dimensionality of these random effects (γ terms) in our growth model made it difficult to obtain stable coefficient estimates using traditional frequentist methods. Hence, we implemented the growth model in a Bayesian framework, using minimally informative priors, in the "brms" package in R 3.3.0 (99). We assessed model convergence using R-hat statistics for the posterior distribution of each parameter and model fit by comparing the distribution of the training data to the distribution of the mean posterior predictions of those observations, across the entire dataset and by each site individually. For each site, we compared model fitted to observed values by calculating the SD, Pearson's r, and root mean squared error of the model's mean posterior predictions, visualized in a Taylor diagram (*SI Appendix*, Fig. S5). In addition, we plotted these site-level fitted values and their 95% credible intervals as growth time series for visual comparison to observed values (*SI Appendix*, Fig. S6).

Subspecific model variant. To explore whether the taxonomic uncertainty associated with subspecific delineations within *P. ponderosa s.l.* influences inferred species-wide growth responses, we fit an additional model that included interactions between variety (Pacific versus interior) and spatially varying mean climate. Populations in California, Oregon, Washington, and Idaho were categorized as belonging to the Pacific variety (*P. ponderosa* var. *ponderosa*), and populations in Montana, South Dakota, and Colorado as belonging to the interior variety (*P. ponderosa* var. *scopulorum*). Because population-level random effects were already included in the modeled response to time-varying climate, we did not include interactions between variety identity and the seasonal, time-varying climate predictors. This model indicated that the spatial climate responses of the Pacific variety (var. *ponderosa*) matched that of those of *P. ponderosa s.l.*, whereas the interior variety (var. *scopulorum*) had a weaker response to spatially varying temperature (*SI Appendix*, Fig. S7). However, we also found a strong statistical interaction between mean annual temperature and mean annual precipitation; because interior populations occupy a colder and drier range of climates than Pacific populations, we cannot attribute intraspecific heterogeneity in these climate responses to taxonomy alone. In contrast, we found no consistent differences between varieties in population-level responses to temporal climatic variation (*SI Appendix*, Fig. S8). Because this model variant did not resolve mismatches between spatial versus temporal climate responses and generated

similar predictions from both, we used the "sensu lato" model for all subsequent analyses and results.

Near-past predictions. To evaluate whether observed growth better matched predictions derived from species-wide or population-specific climate responses, we predicted growth at each site in response to observed climatic conditions after the onset of warming. These predictions were made based on species-wide versus population-specific responses separately. Specifically, for species-wide responses, observed 30-y rolling mean climate normals in the post-warming period were entered into the model CN terms, while setting all other climate effects at zero, such that the predicted effect of changing climate depended upon the estimated values of β_{2i}. For population-specific responses, observed post-warming seasonal climate values were substituted into TA and PA terms, while keeping all other climate effects at zero, such that the predicted effect of changing climate depended upon the estimated values of β_{3j}, β_{4j}, γ_{2j}, and γ_{3j}. In these postwarming predictions, we used observed tree sizes $BA_{t,s,y}$ so that model-predicted growth could be directly compared against observed growth. We used Pearson's correlation coefficient between the observed and predicted growth series for each tree in the dataset to quantify their correspondence. For species-wide predictions, we converted observed growth series to 30-y rolling means to match the scale of variability in the predicted series.

Future projections. We then used the growth model to project future tree growth using climate projections from the CMIP6 ensemble dataset for future scenarios SSP1-2.6, SSP2-4.5, and SSP5-8.5 (23) downscaled and extracted using ClimateNA 7.3.0 (100). We aggregated monthly climate projections to recreate the same mean, annual, and seasonal climate variables used in fitting the growth model (Eq. 1). We used these future climate data to project growth through the end of the 21st century for each tree by forcing the model with the species-wide versus population-level responses to climate variation separately, as described above. To make species-wide growth projections, we entered future 30-y mean annual temperature and precipitation projections into the CN term in our growth model, while setting the effects of annual climate variables TA and PA to zero. For population-specific projections, we set the effects of CN model terms to zero, and entered in projected future TA and PA time series. Both projection types were made with all modeled random effects, with tree size BA set to the mean observed value in the model fitting period. All model predictions were made using 2,000 posterior draws of model parameters, which we summarized with mean posterior predictions and 95% credible intervals.

Data, Materials, and Software Availability. Tree ring timeseries data have been deposited in Dryad (DOI: 10.5061/dryad.x3ffbg7rj). Previously published data were used for this work (22, 100). All other data are included in the manuscript and/or *SI Appendix*.

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