

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42

Supporting Information for

Tree rings reveal the transient risk of extinction hidden inside climate envelope forecasts

Margaret E. K. Evans*^{1†}, Sharmila M. N. Dey^{2†}, Kelly A. Heilman^{1†}, John R. Tipton³, R. Justin DeRose⁴, Stefan Klesse⁵, Emily L. Schultz⁶, John D. Shaw⁷

¹ Laboratory of Tree-Ring Research, University of Arizona, Tucson, Arizona, USA 85721.

² Department of Earth and Planetary Sciences, Harvard University, Cambridge, Massachusetts, USA 02138.

³ Statistical Sciences Group, Los Alamos National Laboratory, Los Alamos, New Mexico, USA 87545.

⁴ Department of Wildland Resources and Ecology Center, Utah State University, Logan, Utah, USA 84322.

⁵ Forest Dynamics, Swiss Federal Institute for Forest, Snow, and Landscape Research WSL, 8903 Birmensdorf, Switzerland.

⁶ Department of Biology, Colorado Mountain College, Breckenridge, CO, USA 80424.

⁷ Riverdale Forestry Sciences Lab, Rocky Mountain Research Station, USDA Forest Service, Riverdale, Utah, USA 84405.

† These authors contributed equally to this work

Corresponding author: Margaret Evans

Email: mekevans@arizona.edu

This PDF file includes:

Supporting text
Figures S1 to S13
Tables S1 to S3
SI References

43 **Supporting Information Text**

44

45 **Biodiversity Forecasting with Occurrence Data**

46

47 Predicting the impact of climate change on biodiversity has been dominated for the last twenty
48 years by an approach that associates a species' occurrence (either presence-absence or
49 presence-only data) with climate at those locations. The principle is illustrated in Fig. S1 with
50 respect to a single temperature variable. In practice, this statistical model, known as a *species*
51 *distribution model (SDM)*, *climate envelope model*, or *ecological niche model*, is created using
52 many climate (or other predictor) variables at once. Excellent reviews of the methods are found in
53 (1–3). The statistical model is then used to predict or forecast change in the species' geographic
54 distribution with changing climate. In the single-variable example of temperature, with warming,
55 the species' probability or rate of occurrence is predicted to increase at relatively cool locations
56 (the *leading edge*) and decline at warmer locations (the *trailing edge*; Fig. S1B).

57

58 **Climate responses across scales**

59

60 In order for climate envelope or SDM predictions of range dynamics to actually come to pass,
61 lower-level demographic variables, such as population size or density (abundance), population-
62 level growth rate, or the net effect of individual-level vital rates (including growth, survival, and
63 birth rates) should respond similarly to changing climate, either matching the entire response,
64 including breadth (solid lines, Fig. S2), or, if more limited in breadth, they should reflect the local
65 slope of the species-scale climate response curve (dashed lines, Fig. S2). Ecological theory
66 supports this assumption: the *center-periphery hypothesis* predicts that individual-level
67 performance and population-level growth rate decline from the center to the edge of a species'
68 geographic and environmental distribution (Fig. S2). Under the *abundant-center hypothesis* and
69 *Whittaker's continuum concept*, it is expected that a species' abundance is greatest at the center
70 of its ecological niche (*i.e.*, climatic tolerances; Fig. S2). Though we note – these theoretical
71 expectations concern time-averaged responses to spatial variation in climate (not responses to
72 time-varying climate). Further, range dynamics in the real world are complicated by the lack of
73 correspondence between position in geographic and environmental space – climatically average
74 (or extreme) conditions are found throughout species' geographic distributions (4–6).

75

76 Climate response curves at different biological scales (individual, population, and species) and in
77 response to spatial vs. temporal climate variation are influenced by a variety of different
78 ecological processes. Further, they can take on a variety of shapes beyond a Gaussian, bell-
79 shaped curve (unimodal, symmetric; Fig. S10A).

80

81 *Individual Scale.* Focusing on the scale of an individual organism, the phenotypic response of a
82 single genotype to different environmental conditions is termed by population geneticists its
83 *reaction norm*. A time series of an individual's growth rate is an example of a single genotype
84 expressing different phenotypes (growth rates) when exposed to different conditions (interannual
85 climate variation and any other differences between years). This interannual variation in growth is
86 the result of *phenotypic plasticity*. *Thermal performance curves*, plastic responses to different
87 temperature conditions, have been the subject of heightened interest in the context of
88 anthropogenic warming (7). They are understood to be bounded at both a minimum and
89 maximum value – organismal functionality goes to zero below a minimum temperature and above
90 a maximum temperature (the *critical thermal maximum*). Between the minimum and maximum
91 lies an optimum – a temperature at which individual-level physiological functioning reaches its
92 peak. This thermal response curve may be symmetric (Gaussian) or left- or right-skewed (Fig.
93 S10A). If skewed, the response may be approximated by a linear function across much of the
94 range of temperatures to which the organism is regularly exposed and hence adapted (Fig.
95 S10B). Other climate response curves at the individual scale may be saturating. For example,
96 performance in plants may be a saturating function of soil moisture – increasing to a plateau,
97 above which additional soil moisture leads to neither increased nor decreased performance (Fig.
98 S10A).

99

100 *Population scale.* Climate response curves at the population scale, involving population size,
101 density, or growth rate as responses, emerge as the net result of five demographic processes or
102 *vital rates*: birth, death, immigration, emigration, and (in structured populations) changes in age,
103 size, or developmental stage. Different vital rates may be affected by climate differently, even in
104 an opposite manner – known as *demographic compensation*. The net effect of a climate variable
105 on population growth rate is a function of its effect on each vital rate and the sensitivity of
106 population growth rate to changes in each vital rate. Additionally, population-scale climate
107 response curves reflect community dynamics, including competition between species, facilitative
108 or mutualistic interactions, food web (consumer-resource) relationships, disturbance processes,
109 source-sink dynamics, and community sorting (e.g., priority effects).

110

111 *Species Scale.* At the scale of a species' geographic distribution, climate response curves reflect
112 all the above processes. In addition, it is widely recognized that climatically suitable habitat may
113 not be occupied because the species' rate of dispersal may prevent (limit) it from colonizing a
114 given location (*dispersal limitation*). In fact, all these processes (plasticity, demography,
115 competition and other interspecific interactions, disturbance processes, evolution, dispersal, etc.)
116 operate at all scales all the time. Different sources of data, with different temporal and spatial

117 extent and resolution, offer more or less insight into direct cause-effect relationships and which
118 processes are important influences on pattern at each scale.

119

120 **Study species**

121

122 *Pinus edulis* Engelm. (Colorado, common, or two-needle piñon) is a small-statured, slow-growing,
123 stress-tolerant pine that can survive more than 500 years. It is endemic to the Colorado Plateau
124 of the southwestern U.S. states of Arizona, Colorado, New Mexico, and Utah, where potential
125 evapotranspiration exceeds precipitation in most months (8). Because it occurs across a wide
126 range of elevation (1400-2700 m), *P. edulis* grows under a wide range of temperature conditions
127 (mean annual temperature [MAT] of 4-17° C; Fig. S3). There is a gradient of monsoon moisture
128 (in July and August, Fig. S11) increasing from north to south across *P. edulis*' distribution (8).

129

130 **Tree-Ring Data**

131

132 Tree-ring data were derived from increment cores sampled in the U.S. Forest Service Forest
133 Inventory and Analysis (FIA) Program's spatial network of permanent sampling plots, during
134 forest inventories between 1995 and 2013 (especially 1995-1997; (9, 10). Samples were
135 processed to generate annually resolved time series at the University of Arizona Laboratory of
136 Tree-Ring Research and at Utah State University, following standard dendrochronological
137 protocols (9, 11): mounted on grooved boards, sanded to a fine polish, crossdated to assign a
138 year of formation to each growth ring, and measured on a calibrated sliding stage micrometer.
139 Year assignments were verified using COFECHA (12) before any analyses of the ring width time
140 series. Start dates of the time series ranged from 1530 to 1983, but data analysis was limited to
141 the period for which gridded climate data products are available (1895-1995).

142

143 **Regression modeling of tree-ring width**

144

145 We used a Bayesian hierarchical regression model to evaluate the predictions of Hypotheses 1
146 vs. 2 about patterns of variation in *P. edulis*' performance with variation in climate across space
147 and time. This model predicted the log-transformed width of growth rings as a function of tree size
148 and climate variables. Tree size (stem diameter at root collar, DRC) was included as a predictor
149 because ring widths are known to change with tree size – radial growth increments are wide
150 when a tree is small and become narrower as a tree becomes larger (13). Starting with the DRC
151 measurement at the time that an increment core was sampled (available from the FIA database),
152 DRC was back-calculated based on the tree-ring time series, generating an inferred DRC for
153 every tree in every year. In addition to these fixed effects, we specified random tree effects – *i.e.*,

154 a modification of the model intercept specific to each tree – capturing heterogeneity among trees
155 in average growth rate not explained by site-specific mean annual temperature (MAT) and mean
156 annual precipitation (MAP) data.

157 Both spatially varying and spatio-temporally varying climate predictors were included in
158 models of *P. edulis* growth, the first to capture how growth varies across spatial gradients of
159 climate and the second to capture plastic responses to interannual climate variability (*i.e.*,
160 reaction norms). Both types of climate predictors were created from time series of monthly, 4-km
161 resolution climate data downloaded from the PRISM Climate Group (14) for the period 1895-
162 2018. Climate normals, which vary strictly across space, were created by averaging monthly
163 mean temperature and summing monthly precipitation of each year (January-December), then
164 averaging across years to calculate mean annual temperature (MAT) and mean annual
165 precipitation (MAP). To make time-varying climate predictors, the time series of monthly climate
166 data were aggregated across a twelve-month time frame (previous September to current August)
167 and four biologically relevant seasons: fall (September through October of the previous year),
168 winter (previous November through the current year's March), spring (current year April through
169 June) and monsoon (July through August). These four seasonal climate variables represent two
170 wet seasons, one warm (monsoon) and one cold (winter), along with two warm, dry seasons
171 (spring, fall; Fig. S11). Responses to time-varying climate were modeled as linear, which is
172 traditional in dendrochronology (11, 13). While a few recent analyses of tree-ring data have
173 shown nonlinearity in responses to climate (15, 16), and some reaction norms (*e.g.*, thermal
174 response curves) are theoretically expected to peak between minimum and maximum climate
175 values (7), field-observed values of performance vs. climate may be adequately predicted with a
176 linear response across the historic, field-observed range of variability of climate, as described
177 above, in "*Climate Responses across Scales*" (see Fig. S10B).

178 Though we had specific hypotheses to test (Fig. 1), it is important to verify that the model
179 structure corresponding to those hypotheses adequately describes variation in *P. edulis*
180 performance across space and time, *i.e.*, is not outcompeted by alternative models. We report
181 here the fit to data of ten alternative Bayesian hierarchical regression models (Table S2), which
182 included different combinations of climate predictors (normals, time-varying) and different
183 methods of scaling during standardization (*i.e.*, centering and scaling of predictors to a mean of
184 zero and standard deviation of one). Specifically, time-varying climate predictors were
185 standardized using either global or local scaling. Global scaling compares temperature or
186 precipitation at a given site each year to the global average for that variable across both space
187 and time, whereas local scaling compares each year's climate to the local site average for that
188 variable. Locally scaled variables thus reflect climate anomalies relative to average conditions at
189 each site. The hypothesis under global scaling is that a temperature of 10° C and temperature
190 variation of 1° C has the same effect on all trees throughout the geographic distribution, whereas

191 the hypothesis under local scaling is that a temperature of 10° C may be relatively cool at the
192 warm edge of the distribution and relatively warm at the cool edge of the distribution, and that the
193 effect of climate variability is best described relative to what trees are adapted to at a given
194 location. Hence, the fit of data to models with globally vs. locally scaled climate predictors
195 represents a secondary test comparing the hypotheses that climate responses are best described
196 at the species scale (Hypothesis 1) vs. population or individual scale (Hypothesis 2).

197 The ten models are generally ordered from simpler to more complex. Model 1 tested the
198 hypothesis that the climate normals MAP and MAT alone are sufficient to explain variation in *P.*
199 *edulis* growth. Model 2 repeated Model 1 with the addition of tree size. Model 3 tested the
200 hypothesis that time-varying climate, in addition to climate normals and tree size, explain growth
201 variation, using globally scaled, 12-month cumulative precipitation and average temperature.
202 Models 4-6 tested alternative seasonal time-varying climate predictors (both precipitation and
203 temperature), which were globally scaled (Table S2). Models 7 and 8 test the hypothesis that the
204 climate normals MAP and MAT do not significantly influence *P. edulis* growth (by removing them),
205 with Model 7 using global scaling and Model 8 local scaling of the time-varying climate predictors.
206 Model 9 tested the same seasonal climate predictors as Model 6, using local scaling for the time-
207 varying predictors. Model 10 was unique in testing the use of both locally and globally scaled
208 versions of the time-varying climate predictors of Model 6. All models included all two-way
209 interactions between predictors, and all but Model 1 included the effect of tree size (Table S2).

210 Regression modeling was implemented using R, RStudio, and STAN (17), in the
211 computational environment of VICE and the Discovery Environment of CyVerse
212 (www.cyverse.org). Markov chain Monte Carlo simulations were run with 3 chains of 5000
213 iterations each, discarding the first 1000 iterations as warmup, resulting in 12,000 posterior
214 samples. Convergence was assessed using visual inspection of traceplots and Gelman-Rubin
215 diagnostics (18). Models were fit with a randomly selected 80% of the growth ring measurements
216 and were validated with the remaining 20% of these held-out data using the root mean squared
217 error (MSE) of model-predicted tree-ring width under a 5-fold cross-validation procedure. In
218 addition, a full data fit using the approximate leave-one-out (elpd) information criterion (19–21);
219 Fig. S9) was used to evaluate model performance. Model fit was also assessed visually using
220 posterior predictive checks (18). The model fit statistics showed that seasonal time-varying
221 climate variables predict *P. edulis*'s growth variability better than 12-month time-varying climate
222 variables (Models 5 and higher fit better than Model 4), and that local scaling outperforms global
223 scaling of the time-varying climate variables (Model 9 compared to Model 6, and Model 8
224 compared to Model 7; Fig. S9). Further, the inclusion of both climate normals and time-varying
225 climate variables is supported (Model 9 fit the data better than Models 8 and 7; Fig. S9). Among
226 the ten models fit to the ring-width data, two rose to the top in terms of low MSE and elpd: Models
227 9 and 10 (Fig. S9). We selected Model 9 as the preferred best-fit model, which included MAP and

228 MAT, four seasonal time-varying climate predictors - spring and fall temperatures and winter and
229 monsoon precipitation - and all 2-way interactions between fixed effects.

230 The posterior predictive distribution diagnostics for Model 9 (pointwise posterior
231 predictive credible intervals, probability integral transform overlay, and probability integral
232 transform q-q plots; Fig. S12) illustrate a good fit to the bulk of the data but show some evidence
233 of misfit for very small and very large tree-ring width observations. We plotted model residuals as
234 a function of each of the time-varying climate predictors to check for systematic misfit that might
235 result from modeling log-transformed ring widths as a linear response of interannual climate
236 variation. The residuals showed no trend with respect to spring or fall temperature variation or
237 monsoon precipitation variation among years, but there was some trend in the residuals with
238 respect to variation in winter precipitation (blue trend lines, Fig. S13). There is a modest pattern of
239 more extreme negative residuals at both the lowest and highest observed values of winter
240 precipitation, indicating that the model tends to over-predict growth ring widths in the driest and
241 wettest winters, respectively (Fig. S13B). Noticeable in all four panels of Fig. S13 are data points
242 with strong negative residuals (the cloud of points below most of the rest of the residuals, in each
243 panel) – these are cases where observed growth ring widths are much smaller than the
244 predictions of the model. These are the year and tree combinations in which a growth ring was
245 not produced, which we replaced with 0.001 mm (the smallest non-zero observation in our data),
246 since the log of zero is undefined. Part of the trend in the residuals in Fig. S13B seems to arise
247 from the association of the “missing ring” years with low values of winter precipitation. In other
248 words, missing rings tend to be produced when winter precipitation is low. The trend of negative
249 residuals at high values of winter precipitation suggests that there may be some leveling off
250 (saturation) of the response of tree growth to the highest values of winter precipitation, as
251 discussed above in “*Climate Responses across Scales*” (see Fig. S10A). Overall, this trend in
252 residuals is modest and we considered linear responses to climate to be adequate to describe the
253 variation in the data. A future improvement to modeling tree ring widths would be to use a Tobit or
254 other mixture model to better capture the conditions that drive the formation of missing rings.

255 Because Model 9 performed well across predictive metrics and showed good evidence of
256 fit from the posterior predictive diagnostic plots, the output of Model 9 was used for testing
257 Hypotheses 1 vs. 2 and to create Fig. 2-3 and Fig. S4-S7. We note that across all ten models, the
258 effects of climate were consistent in sign and magnitude, lending confidence in the robustness of
259 these effects to alternative model structures.

260

261 **Climate responses**

262

263 All estimated fixed effects (including interactions) from Model 9 are shown in Fig. S4. In a soil
264 moisture-limited species (*P. edulis*), we expected to see higher-than-average growth in both

265 cooler-than-average years and locations (Fig. 1D) because lower rates of evaporation with lower
266 temperatures should weaken soil moisture-limitation of growth. Instead, the negative effect on *P.*
267 *edulis*' growth of interannual variability in temperature ($\beta_{\text{springtemp}} = -0.0965$, 95%CI = -0.1076 – -
268 0.0857 and $\beta_{\text{falltemp}} = -0.0723$, 95%CI = -0.826 – -0.0618) is contrasted by a positive effect of
269 spatial variation in mean annual temperature ($\beta_{\text{MAT}} = 0.2083$, 95% CI = 0.1661 – 0.2506). Further,
270 there is a significant positive interaction between the climate normals (fig. S4, $\beta_{\text{MAT*MAP}} = 0.0438$,
271 95% CI = 0.0097 – 0.0775), indicating that as mean annual temperature increases, the positive
272 influence of mean annual precipitation ($\beta_{\text{MAP}} = 0.2355$, 95% CI = 0.1940 – 0.2771) on growth
273 increases (and *vice versa*). Hence, growth rates of *P. edulis* are greatest at warmer-than-average
274 sites, but especially those that are also wetter-than-average (blue lines, Fig. 2C-D). This may best
275 be interpreted in terms of Liebig's law of the minimum. Among wetter-than-average sites, where
276 soil moisture is less limiting, the influence of another limiting factor becomes evident: trees at cold
277 but relatively wet sites are still unable to grow rapidly (blue lines, Fig. 2A-B), whereas those at
278 warm but relatively wet sites can. We summarize *P. edulis*' observed climate-growth relationships
279 in abstract form in Figure S8B, in contrast to the predicted climate-growth relationships in fig.
280 S8A.

281 Finally, negative model-predicted responses to greater-than-average winter precipitation
282 are seen at a very small number of cold, wet locations (e.g., blue lines, Fig. 3A; Fig. S6C), which
283 may represent high-elevation sites where a year of deep snowpack can limit the growing season
284 and hence tree growth.

285

286

References

287

288

1. J. Franklin, *Mapping Species Distributions: Spatial Inference and Prediction* (Cambridge University Press, 2010).

289

2. A. T. Peterson, *et al.*, *Ecological Niches and Geographic Distributions (MPB-49)* (Princeton University Press, 2011).

290

3. J. Elith, J. R. Leathwick, Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annu. Rev. Ecol. Evol. Syst.* **40**, 677–697 (2009).

292

293

294

4. S. Pironon, *et al.*, Geographic variation in genetic and demographic performance: new insights from an old biogeographical paradigm. *Biol. Rev.* **92**, 1877–1909 (2017).

295

296

5. M. Bontrager, *et al.*, Adaptation across geographic ranges is consistent with strong selection in marginal climates and legacies of range expansion. *Evolution* **75**, 1316–1333 (2021).

297

298

6. S. Pironon, *et al.*, The ‘Hutchinsonian niche’ as an assemblage of demographic niches: implications for species geographic ranges. *Ecography* **41**, 1103–1113 (2018).

299

300

7. M. J. Angilletta Jr., Thermal Adaptation: A Theoretical and Empirical Synthesis. *Therm. Adapt. Theor. Empir. Synth.* 1–302 (2009).

301

302

303

<https://doi.org/10.1093/acprof:oso/9780198570875.001.1>.

304

8. R. F. Miller, *et al.*, The ecology, history, ecohydrology, and management of pinyon and juniper woodlands in the Great Basin and Northern Colorado Plateau of the western United States. *Gen Tech Rep RMRS-GTR-403 Fort Collins CO US Dep. Agric. For. Serv. Rocky Mt. Res. Stn. 284 P 403* (2019).

305

306

307

9. R. J. DeRose, J. D. Shaw, J. N. Long, Building the Forest Inventory and Analysis Tree-Ring Data Set. *J. For.* **115**, 283–291 (2017).

308

309

10. W. A. Bechtold, P. L. Patterson, Editors, The enhanced forest inventory and analysis program - national sampling design and estimation procedures. *Gen Tech Rep SRS-80 Asheville NC US Dep. Agric. For. Serv. South. Res. Stn. 85 P 080* (2005).

310

311

312

11. J. Speer, *Fundamentals of Tree Ring Research* (2010).

313

12. R. L. Holmes, Computer-Assisted Quality Control in Tree-Ring Dating and Measurement. (1983).

314

315

13. H. C. Fritts, *Tree Rings and Climate* (Academic Press, 1976).

316

14. PRISM Climate Group, Oregon State University. (2004). Available at: <https://prism.oregonstate.edu/>.

317

318

15. M. P. Dannenberg, E. K. Wise, W. K. Smith, Reduced tree growth in the semiarid United States due to asymmetric responses to intensifying precipitation extremes. *Sci. Adv.* **5**, eaaw0667 (2019).

319

320

321

16. J. Gantois, New tree-level temperature response curves document sensitivity of tree growth to high temperatures across a US-wide climatic gradient. *Glob. Change Biol.* **28**, 6002–6020 (2022).

322

323

324

17. Stan Development Team, *Stan User’s Guide*, 2.32.

325

18. A. Gelman, D. B. Rubin, Inference from Iterative Simulation Using Multiple Sequences. *Stat. Sci.* **7**, 457–472 (1992).

326

327

19. A. Vehtari, A. Gelman, J. Gabry, Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Stat. Comput.* **27**, 1413–1432 (2017).

328

329

20. A. Gelman, X.-L. Meng, H. Stern, POSTERIOR PREDICTIVE ASSESSMENT OF MODEL FITNESS VIA REALIZED DISCREPANCIES. *Stat. Sin.* **6**, 733–760 (1996).

330

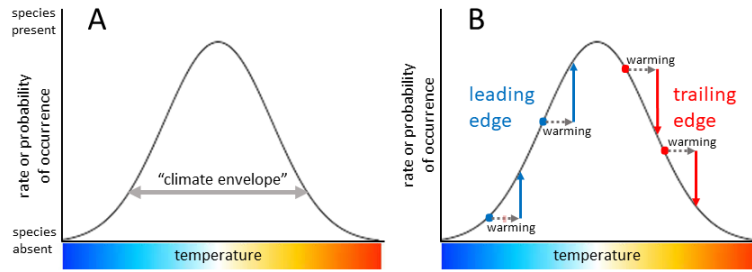
331

21. J. Gabry, D. Simpson, A. Vehtari, M. Betancourt, A. Gelman, Visualization in Bayesian workflow. *J. R. Stat. Soc. Ser. A Stat. Soc.* **182**, 389–402 (2019).

332

333

- 334 22. E. L. Little, *Atlas of United States trees* (U.S. Dept. of Agriculture, Forest Service, 1971).
- 335 23. T. Dallas, R. R. Decker, A. Hastings, Species are not most abundant in the centre of their
336 geographic range or climatic niche. *Ecol. Lett.* **20**, 1526–1533 (2017).
- 337 24. T. A. Dallas, A. Hastings, Habitat suitability estimated by niche models is largely unrelated
338 to species abundance. *Glob. Ecol. Biogeogr.* **27**, 1448–1456 (2018).
- 339 25. B. J. McGill, Trees are rarely most abundant where they grow best. *J. Plant Ecol.* **5**, 46–51
340 (2012).
- 341 26. G. Midolo, C. Wellstein, S. Faurby, Individual fitness is decoupled from coarse-scale
342 probability of occurrence in North American trees. *Ecography* **44**, 789–801 (2021).
- 343 27. M. F. Oldfather, D. Ackerly, Linking demography and microclimate across the range of an
344 alpine plant in (ESA, 2017).
- 345 28. T. Bohner, J. Diez, Extensive mismatches between species distributions and performance
346 and their relationship to functional traits. *Ecol. Lett.* **23**, 33–44 (2019).
- 347 29. K. C. Baer, J. L. Maron, Ecological niche models display nonlinear relationships with
348 abundance and demographic performance across the latitudinal distribution of *Astragalus*
349 *utahensis* (Fabaceae). *Ecol. Evol.* **10**, 8251–8264 (2020).
- 350 30. M. Bernal-Escobar, D. Zuleta, K. J. Feeley, Changes in the climate suitability and growth
351 rates of trees in eastern North America. *Ecography* **2022**, e06298 (2022).
- 352 31. M. L. DeMarche, *et al.*, Latitudinal gradients in population growth do not reflect
353 demographic responses to climate. *Ecol. Appl.* **31**, e2242 (2021).
- 354 32. J. M. Diez, I. Giladi, R. Warren, H. R. Pulliam, Probabilistic and spatially variable niches
355 inferred from demography. *J. Ecol.* **102**, 544–554 (2014).
- 356 33. M. F. Oldfather, M. J. Koontz, D. F. Doak, D. D. Ackerly, Range dynamics mediated by
357 compensatory life stage responses to experimental climate manipulations. *Ecol. Lett.* **24**,
358 772–780 (2021).
- 359 34. J. Pagel, *et al.*, Mismatches between demographic niches and geographic distributions are
360 strongest in poorly dispersed and highly persistent plant species. *Proc. Natl. Acad. Sci.* **117**,
361 3663–3669 (2020).
- 362 35. W. Thuiller, *et al.*, Does probability of occurrence relate to population dynamics?
363 *Ecography* **37**, 1155–1166 (2014).
- 364 36. S. M. Amburgey, *et al.*, Range position and climate sensitivity: The structure of among-
365 population demographic responses to climatic variation. *Glob. Change Biol.* **24**, 439–454
366 (2018).
- 367 37. U. Bradter, *et al.*, Decomposing the spatial and temporal effects of climate on bird
368 populations in northern European mountains. *Glob. Change Biol.* **28**, 6209–6227 (2022).
- 369 38. P. Gaüzère, V. Devictor, Mismatches between birds' spatial and temporal dynamics reflect
370 their delayed response to global changes. *Oikos* **130**, 1284–1296 (2021).
- 371 39. F. La Sorte, T. Lee, H. Wilman, W. Jetz, Disparities between observed and predicted
372 impacts of climate change on winter bird assemblages. *Proc. Biol. Sci.* **276**, 3167–74 (2009).
- 373

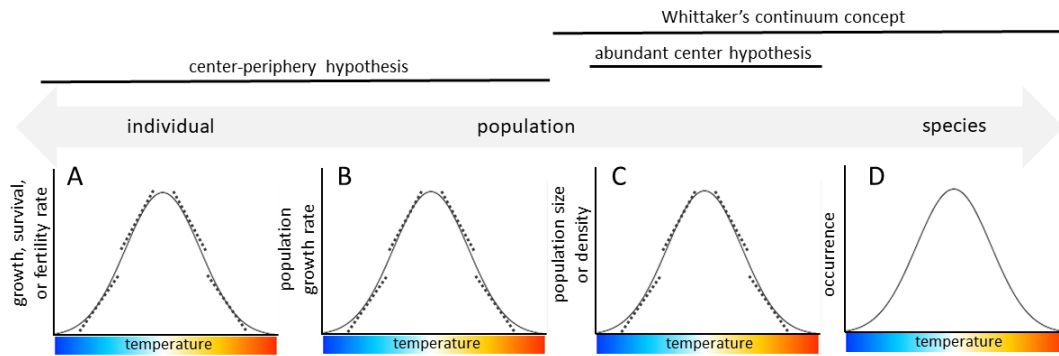


374

375 **Fig. S1.** Conceptual illustration of (A) a species' climate envelope, inferred from presence-
 376 absence or presence-only data, with respect to a single dimension of climate (a temperature
 377 variable). This species-level climate response is then used to project (B) the effect of climate
 378 change (warming) on the species' rate or probability of occurrence.

379

380

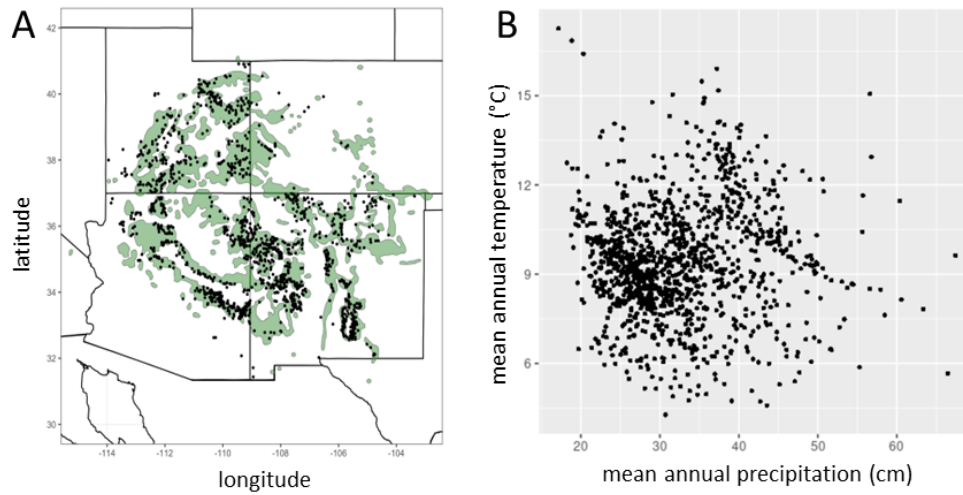


382

383 **Fig. S2.** Responses to temperature variability at the (A) individual, (B-C) population, and (D)
 384 species scale. The use of climate envelope models to forecast change in species' distributions
 385 effectively assumes that climate responses are the same across scales, as illustrated here. Solid
 386 lines indicate a scenario in which individual- and population-scale climate responses are equal in
 387 breadth to the species-scale response; dashed lines indicate the case where individual- and
 388 population-scale climate tolerances are narrower than species-scale climate tolerances, but they
 389 match in local slope (the sign of the response). Ecological theories that support the assumption of
 390 scale-invariant climate responses are placed above the biological scale axis.

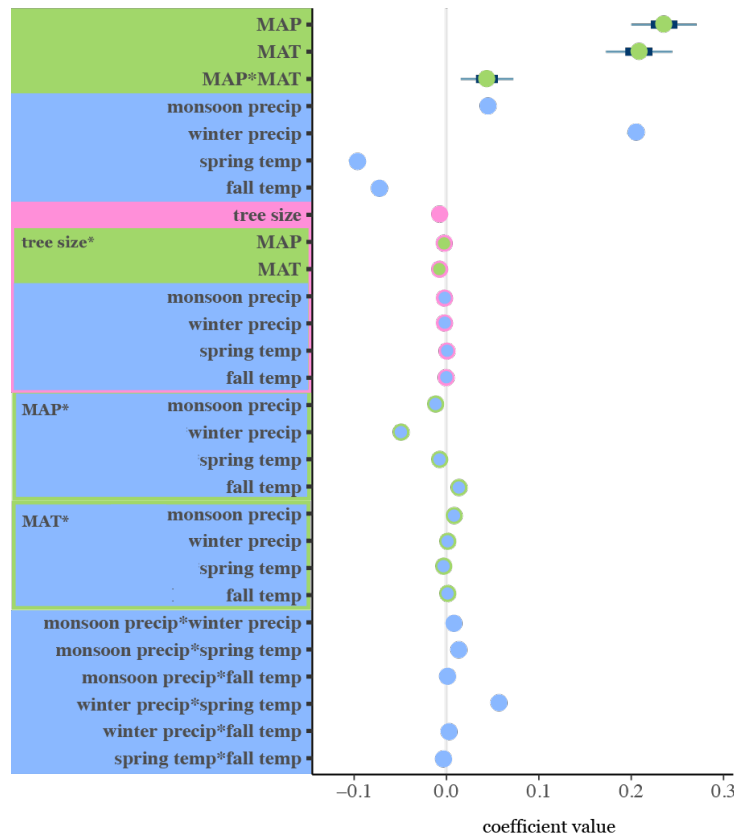
391

392



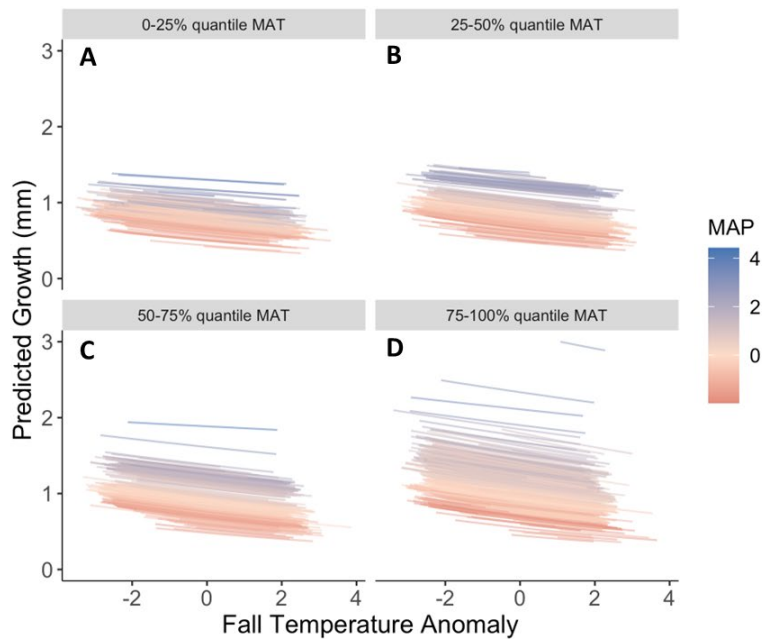
394

395 **Fig. S3.** Location in (A) geographic and (B) climate space of the 977 U. S. Forest Service Forest
396 Inventory and Analysis (FIA) plots in the U. S. states of Arizona, New Mexico, Colorado, and Utah
397 where *Pinus edulis* increment cores were collected. Green in panel A is the geographic
398 distribution of *Pinus edulis*, as defined in the atlas of U. S. trees (22).



400

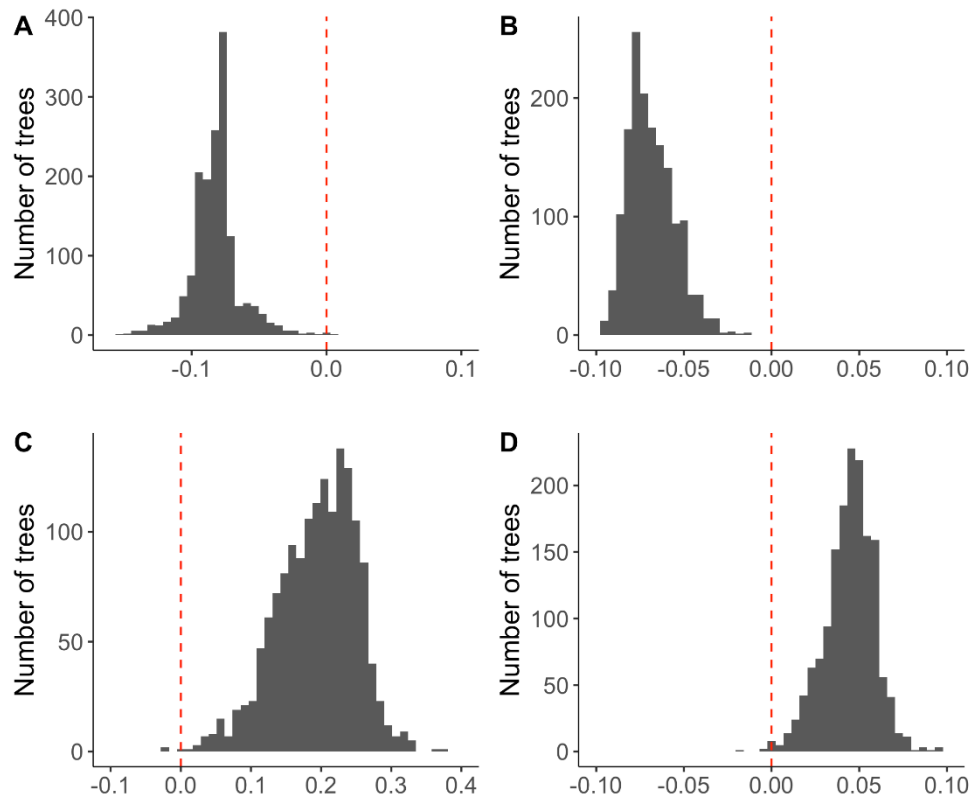
401 **Fig. S4.** Estimates of effects from a multiple regression model of *P. edulis* growth (model 9 in
 402 Table S2). Each dot-whisker shows the Bayesian posterior distribution of a model parameter
 403 (posterior mean +/- 95% central density). Predictors were centered and scaled, with the exception
 404 of tree size. Main effects are color-coded into three groups: climate normals (green), time-varying
 405 climate variables (blue), and tree size (pink). Two-way interaction effects are color-coded
 406 accordingly both in the y-axis label and the dot-whisker.



408

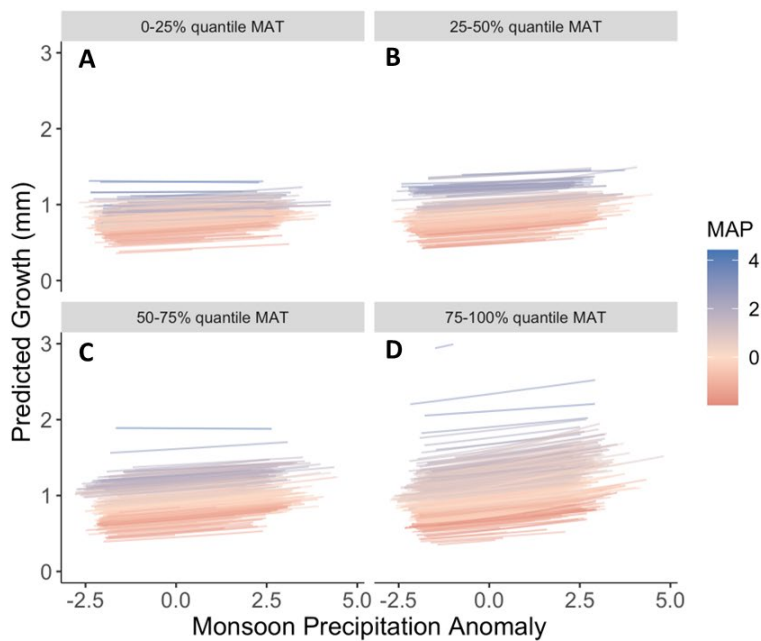
409 **Fig. S5.** Model-predicted responses to fall temperature variability of all 1,558 common pinon trees
 410 in the dataset, at locations that vary from cool to warm (quantiles of mean annual temperature
 411 [MAT], averaged over the period 1895-2018), with each response colored by the mean annual
 412 precipitation (MAP) at that location, from dry (red) to wet (blue). Fall temperature is the average of
 413 monthly average temperatures September-October of the previous calendar year, locally scaled,
 414 *i.e.*, anomalies relative to site-specific average fall temperature. Responses are plotted for a
 415 constant tree size of 20 cm.

416



417

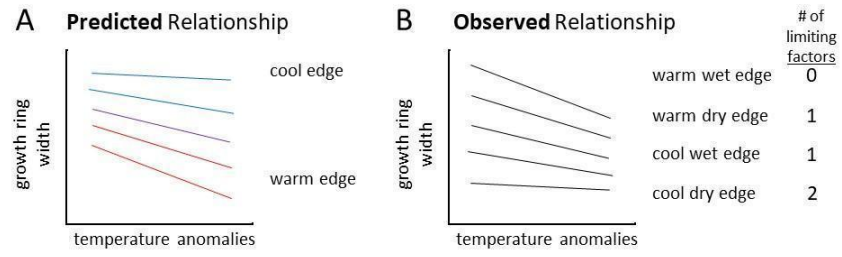
418 **Fig. S6.** Histograms of the sensitivity of the growth of 1,558 *Pinus edulis* trees to four time-
 419 varying climate predictors: (A) spring and (B) previous fall temperature, and (C) winter and (D)
 420 monsoon precipitation. These sensitivities correspond to the slopes of the lines in Fig. 2, Fig. S5,
 421 Fig. 3, and Fig. S7, respectively, although here the slope is change in *log-transformed* growth-ring
 422 width in response to variation in each climate predictor.



424

425 **Fig. S7.** Model-predicted responses to monsoon precipitation variability of all 1,558 common
 426 pinon trees in the dataset, at locations that vary from cool to warm (quantiles of mean annual
 427 temperature [MAT], averaged over the period 1895-2018), with each response colored by the
 428 mean annual precipitation (MAP) at that location, from dry (red) to wet (blue). Monsoon
 429 precipitation is the sum of precipitation in July and August of the current calendar year, locally
 430 scaled, *i.e.*, anomalies relative to site-specific average monsoon precipitation. Responses are
 431 plotted for a constant tree size of 20 cm.

432

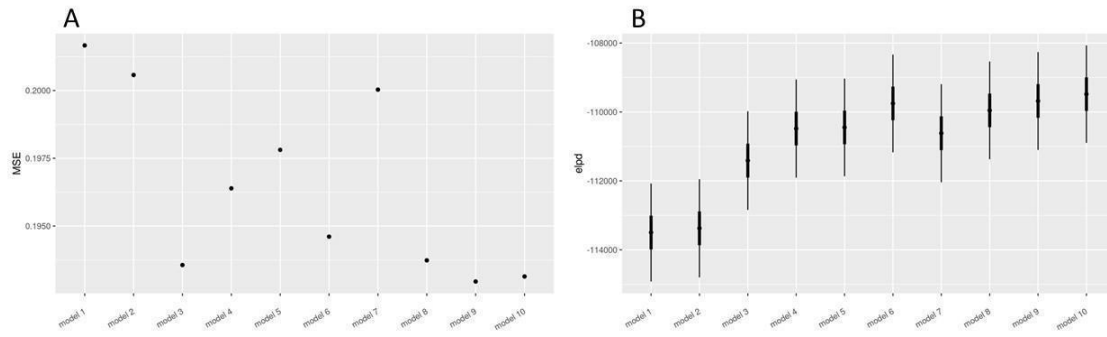


433

434 **Fig. S8.** Predicted vs. observed relationships between tree growth and interannual temperature
435 variability across the distribution of a (A) hypothetical soil moisture-limited species (as in Fig. 1E),
436 and (B) *Pinus edulis*.

437

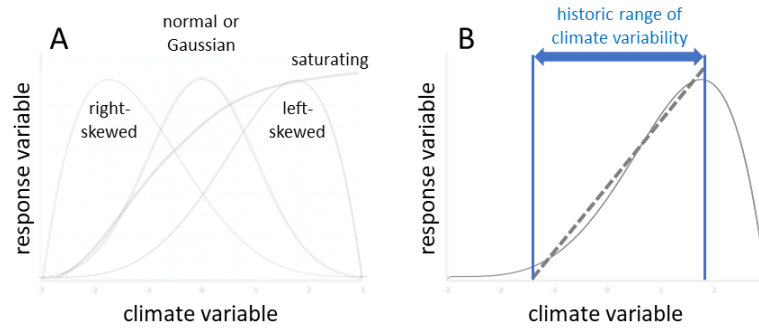
438



439

440 **Fig. S9.** Fit of ten alternative regression models to *Pinus edulis* tree-ring width data, with respect
441 to (A) root mean squared error (MSE) and (B) approximate leave-one-out information criterion
442 (elpd). All ten models are detailed in Table S2.

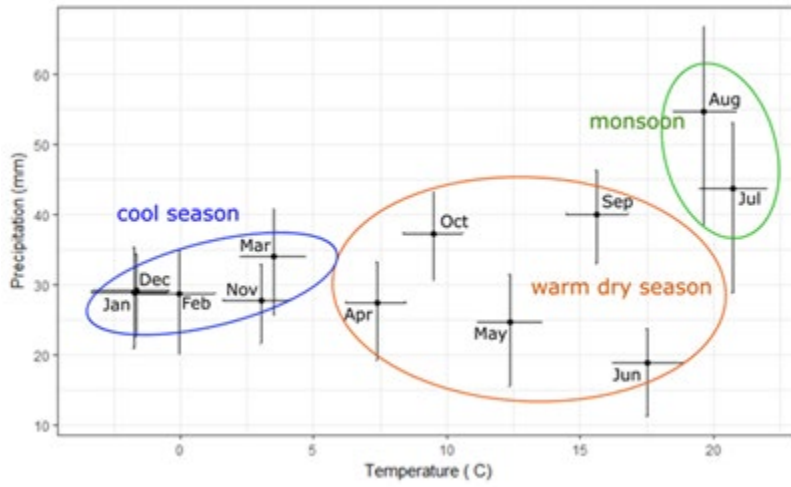
443



444

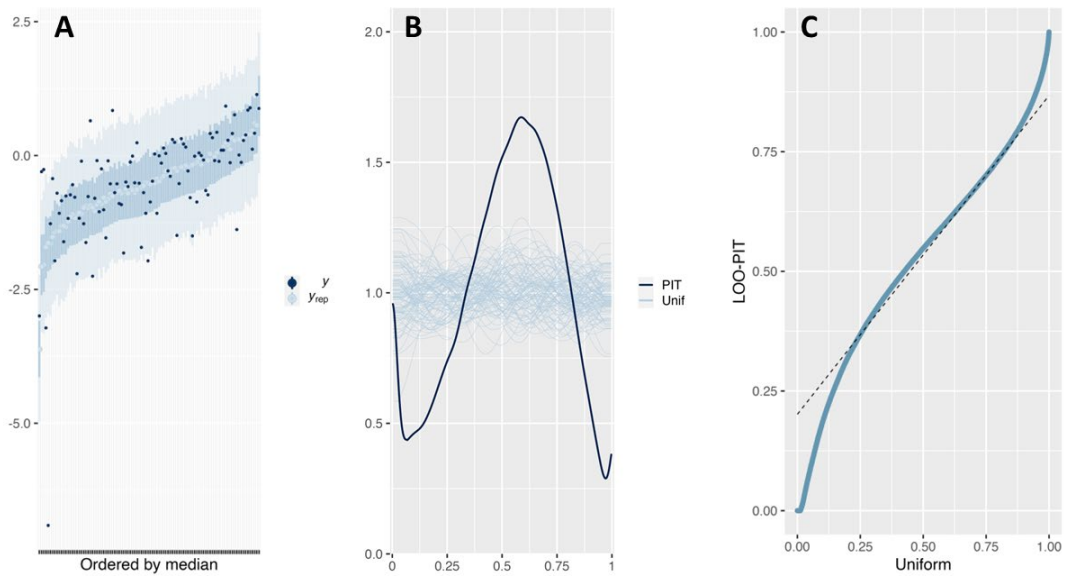
445 **Fig. S10.** Climate responses (A) may take a variety of shapes, from symmetric to skewed to
446 saturating. (B) A skewed response may be fit to field-collected data with a line, *i.e.*, across the
447 range of climate variability to which an organism is regularly exposed and therefore adapted.

448



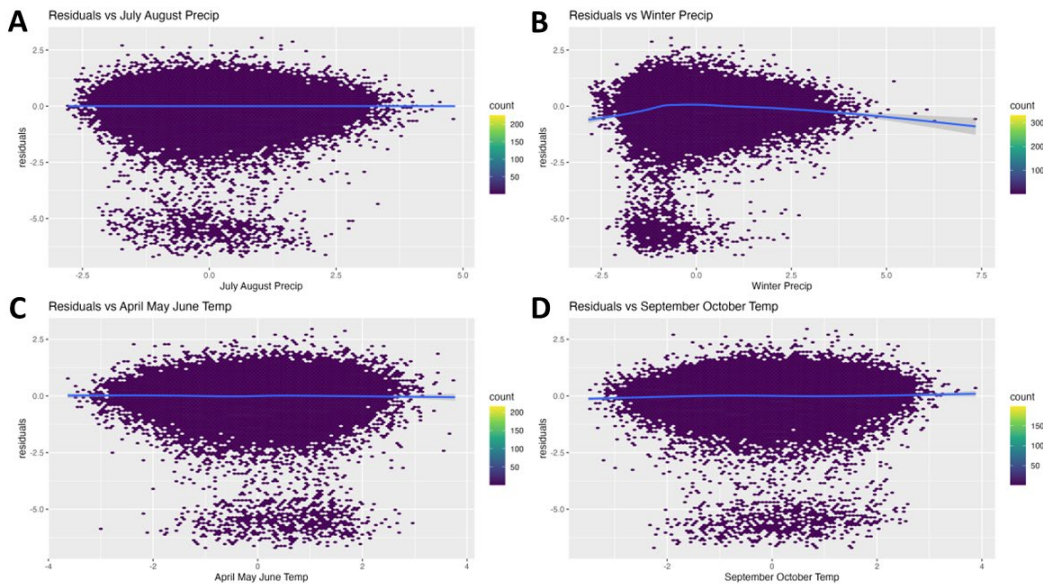
449

450 **Fig. S11.** Average monthly temperature and precipitation at U. S. Forest Service Forest Inventory
451 and Analysis plot locations where *Pinus edulis* is present, based on PRISM 4-km resolution
452 climate data.



454

455 **Fig. S12.** Posterior predictive diagnostics for Model 9. (A) The 50% and 90% posterior predictive
 456 intervals for a subset of log tree-ring widths, ordered by posterior predictive mean (y_{exp}). Dark
 457 points are the observed log ring widths (y), which mostly fall within the 50% or 90% posterior
 458 predictive intervals. (B) Smoothed density of posterior predictive samples of log ring width in light
 459 blue and a smoothed density of observed log ring widths in dark blue. (C) Leave-one-out quartile-
 460 quartile plot of posterior predictive mean vs. observed log ring width.



462

463 **Fig. S13.** Residuals of model 9 plotted against the four time-varying climate predictors: (A)
 464 monsoon precipitation, (B) winter precipitation, (C) spring temperature, and (D) previous fall
 465 temperature. A generalized additive model fit to the residuals in each panel, shown with a blue
 466 line, evaluates trend in model residuals.

467 **Table S1.** Corroborating evidence of scale-dependent climate responses: mismatches between
468 individual-level vital rates (*e.g.*, growth, survival, fertility, recruitment), population-level growth rate
469 or abundance, and species-level occurrence, probability of occurrence, or climatic suitability
470 derived from occurrence data in the recent literature. The citation is followed by a description of
471 the scope of the data (organism, spatial and temporal replication, location), then the type of data
472 analyzed, or variables estimated from data, then a description of the mismatch, reproduced from
473 the title or abstract of the citation or summarized succinctly. Where possible, we list (in
474 parentheses) whether the study considered spatial vs. temporal variation in the individual- and
475 population-level variables. Species-level variables (*e.g.*, climatic suitability) vary only across
476 space (with some exceptions). Citations are grouped into four categories: those addressing 1) the
477 abundant center hypothesis or 2) center-periphery hypothesis, those 3) analyzing individual-level
478 performance variation across space and time and fitting a demographic model to estimate
479 population-level growth rate, and 4) those that explicitly consider distinct variation across space
480 vs. time. This list of citations is surely incomplete, and alternative placement of a given paper into
481 a different category is possible.

Citation	Study organism, sample size, (location)	Individual	population	species	Description of mismatch
Abundant center hypothesis					
Dallas et al. 2017 (23)	1109 bird species, 81 mammal species, 63 fish species, 166 tree species (the Americas)		abundance (spatial)	geographic distribution, climatic niche	species are not most abundant in the center of their geographic distribution or climatic niche
Dallas & Hastings 2018 (24)	246 mammal species, 148 tree species (USA)		abundance (spatial)	climatic suitability	climatic suitability estimated by niche models is largely unrelated to species abundance
Center-Periphery Hypothesis					
McGill 2012 (25)	15 tree species (eastern North America)	growth (spatial variation in 46-yr average rate)	abundance (spatial)		trees are rarely most abundant where they grow best
Midolo et al. 2021 (26)	66 tree species (North America)	growth (spatial variation)		probability of occurrence	individual fitness is decoupled from coarse-scale probability of occurrence
Oldfather & Ackerly 2017 (27)	16 populations of a perennial plant, years 2014-2017 (one mountain range, California, USA)	growth, survival, and recruitment (spatial and temporal variation)	population growth rate (spatial and temporal variation)		vital rates and population growth rate do not decline from the center to the edges of the species' elevational range
Pironon et al. 2017 (4)	review of 248 empirical studies (all taxa)	genetic variation, growth, survival, recruitment	genetic variation, abundance, population growth rate	geographic distribution, climatic niche	demographic vital rates, population size, and population growth rate follow center-periphery expectations in only 20-30% of studies
Bohner & Diez 2019 (28)	59 tree species (western USA)	growth, survival, and recruitment (spatial variation in 10-yr average rates)	population density (spatial)	probability of occurrence	extensive mismatches between peak probability of occurrence and peak population density or individual-level demographic rates
Demographic (vital) rates					
Baer and Maron 2020 (29)	11 populations of a perennial plant, years 2013-2016	growth, survival, fecundity,	abundance, population growth rate	climatic suitability	positive (but nonlinear) relationship between a) climatic suitability vs. b) abundance and demographic performance

	(Utah and Idaho, USA)	germination (spatial and temporal variation)	(spatial and temporal variation)		(latitudinal gradient, range center to range edge)
Bernal-Escobar et al. 2022 (30)	37 species of trees, 558 populations (eastern North America)	growth (spatial and temporal variation, moving window 30-year average growth rate)		climatic suitability (spatial and temporal variation, moving window 30-year probability of occurrence)	changes in individual growth rate were negatively correlated with changes in climatic suitability
DeMarche et al. 2021 (31)	3 species of perennial plants, 5-7 populations per species, years 2015-2018 (Oregon and Washington, USA)	growth, survival, fecundity, recruitment (spatial and temporal variation treated as equivalent)	population growth rate (spatial and temporal variation)		latitudinal gradients in performance are not predictive of either local or species-wide responses to climate; population growth rate is lower at cool and wetter locations, but is lower in warmer and drier years; opposite response across space vs. time (latitudinal gradient from center to northern edge of their distributions)
Diez et al. 2014 (32)	perennial plant, 6 populations (one watershed, eastern USA)	growth, survival, and recruitment (spatial and temporal variation treated as equivalent)	abundance, population growth rate (spatial variation)	occurrence	demographic suitability did not predict occurrence, but demographic suitability and abundance were positively correlated
Oldfather et al. 2021 (33)	perennial plant, 9 populations (elevation gradient, one mountain range, California, USA)	growth, survival, recruitment (spatial and temporal)	population growth rate (spatial and temporal)		lack of concordance between spatial patterns of population growth rate with climate gradients and the response of population growth rate to experimental climate manipulations; cool-edge populations did not respond positively to warming
Pagel et al. 2020 (34)	26 perennial plant species (South Africa)	3,617 records of survival, fecundity, and recruitment	population growth rate (spatial)	occurrence	mismatches between demographic suitability (population growth rate) and observed geographic distributions
Pironon et al. 2018 (6)	2 short-lived herbaceous plants; 11 and 20 populations per species (Europe,	growth, survival, fecundity, recruitment (spatial and	population growth rate (spatial and temporal)	occurrence	occurrence and performance niches cannot be assumed to be the same

Thuiller et al. 2014 (35)	California, USA) 108 tree species (western USA, Quebec, France, Switzerland)	temporal) basal area (spatial and temporal)	population growth rate, carrying capacity, and abundance	probability of occurrence	population growth rate was negatively correlated with probability of occurrence, while carrying capacity and abundance were positively correlated with probability of occurrence
---------------------------	---------------------------------------------------------------------------------	------------------------------------------------	----------------------------------------------------------	---------------------------	----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------

Space vs. Time not equivalent

Amburgey et al. 2018 (36)	one species of frog, 746 populations at 27 locations, 3-22 years (North America)	fertility (spatial and temporal)	population growth rate (spatial and temporal)	climatic distribution	sensitivity of population growth rate to interannual climate variability changes in sign across the climatic distribution for some climate variables and not others
Bradter et al. 2022 (37)	39 bird species, 1756 survey routes, years 1996-2018 (Fennoscandia)		abundance (spatial and temporal)		the assumption of equivalent species' response to spatial and temporal variation in climate was seldom met
Gaüzère & Devictor 2021 (38)	124 bird species, 2133 sites, years 2001-2012 (France)		abundance (spatial and temporal)		quantified and mapped differences between spatial vs. temporal variation in abundance
La Sorte et al. 2009 (39)	227 bird species, 404 locations, 26 years (North America)		body mass (spatial and temporal)	occupancy (spatial and temporal)	trends of species richness, body mass, and occupancy through time differed significantly from spatially derived predictions, questioning space-for-time substitution

484 **Table S2.** Ten regression models predicting growth ring width variation of *Pinus edulis* as a
 485 function of tree size and climate variables. A numerical label and all main effects are listed for
 486 each model, as well as the type of scaling used for time-varying predictors (G for global scaling or
 487 L for local scaling). Seasons were defined as monsoon (m; Jul-Aug), winter (w; Nov-Mar), spring
 488 (s; Apr-Jun), and fall (f; Sep-Oct). Values of the model fit statistics root mean squared error (MSE)
 489 and leave-one-out (elpd) validation are shown in Fig. S9.

490

Model	Tree Size	Climate Normals	Time-varying Climate	Scaling
1		✓		
2	✓	✓		
3	✓	✓	12-month precip and temp	G
4	✓	✓	12-month temp, mw precip	G
5	✓	✓	mw precip, mw temp	G
6	✓	✓	mw precip, sf temp	G
7	✓		mw precip, sf temp	G
8	✓		mw precip, sf temp	L
9	✓	✓	mw precip, sf temp	L
10	✓	✓	mw precip, sf temp	G, L

491

492

493

494

495

496 **Table S3.** Model-fit statistics (deviance and AIC) for generalized additive models (GAMs) of *Pinus*
 497 *edulis*' occurrence in the U.S. Forest Inventory and Analysis plots of Arizona, Colorado, New
 498 Mexico, and Utah as a function of the climate conditions at plot locations (variables listed). GAMs
 499 were fit with five, four, and three knots (k).

500

Climate Variable	Deviance			AIC		
	k=5	k=4	k=3	k=5	k=4	k=3
Mean Annual Temperature	252.85	254.76	254.47	288.96	289.32	287.7
Mean Annual Precipitation	294.76	296.05	299.84	331.09	331.67	334.4
Monsoon Precipitation	289.94	302.46	302.98	327.88	337.39	337.68
Winter Precipitation	299.73	302.46	302.98	336.14	337.39	337.68
Fall Temperature	257.7	258.14	257.85	293.28	292.83	291.21
Spring Temperature	257.54	258.02	257.85	292.65	292.21	290.63

501