Herbaceous perennial plants with short generation time have stronger responses to climate anomalies than those with longer generation time

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There is an urgent need to synthesize the state of our knowledge on plant responses to climate. The availability of open-access data provide opportunities to examine quantitative generalizations regarding which biomes and species are most responsive to climate drivers. Here, we synthesize time series of structured population models from 162 populations of 62 plants, mostly herbaceous species from temperate biomes, to link plant population growth rates (\(\lambda\)) to precipitation and temperature drivers. We expect: (1) more pronounced demographic responses to precipitation than temperature, especially in arid biomes; and (2) a higher climate sensitivity in short-lived rather than long-lived species. We find that precipitation anomalies have a nearly three-fold larger effect on \(\lambda\) than temperature. Species with shorter generation time have much stronger absolute responses to climate anomalies. We conclude that key species-level traits can predict plant population responses to climate, and discuss the relevance of this generalization for conservation planning.

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Climate change is altering the mean as well as the variance in temperature and precipitation worldwide. These changes in climate are widely recognized as a prime global threat to biodiversity because temperature and precipitation ultimately drive the demographic processes that determine the size and long-term viability of natural populations. Hence, it is critical to evaluate which species are most responsive to climatic drivers, and in which biomes. The urgency to understand the response of species to climate is particularly high for species that cannot buffer against the effects of climate change by migrating, such as sessile species. Among sessile species, numerous plants have short-distance dispersal, and cannot, therefore, shift their ranges fast enough to keep up with the current pace of climate change.

Assuming plant productivity is a proxy of population performance, we expect that precipitation, or its interaction with temperature, predicts plant population growth better than temperature alone. Most plant physiological processes, such as seed germination, tissue growth, floral induction, and seed set, are affected by water availability. Accordingly, precipitation is a key driver of vegetation productivity worldwide. Temperature can also influence these processes, but typically by modulating water availability, as plant growth occurs across a wide range of temperatures (namely between 5 and 40°C). The effect of temporal fluctuations on the growth rate of a population should be proportional to precipitation or temperature anomalies, where anomalies are deviations from mean values.

Precipitation and temperature anomalies are expected to have more pronounced effects in arid and cold biomes than in wet and temperate ones. While species should be adapted to their respective environment, extreme environments impose hard physiological limitations. In arid environments, plants experience water limitation more frequently. Similarly, in cold biomes plants should more frequently experience temperatures that are too low to allow tissue growth. Accordingly, as water availability decreases, precipitation becomes the main factor limiting plant physiological processes. On the other hand, in cold biomes temperature anomalies can be disproportionately important. For example, the temperature has a positive effect on tree growth that increases in explanatory power with altitude. Temperature can also influence these processes, but typically by modulating water availability, as plant growth occurs across a wide range of temperatures (namely between 5 and 40°C).

The overall effect of climate on plant population growth rate. As predicted (H1), the overall effect of precipitation anomalies on a log(λ) was strong (β = 0.031, 95% CI: 0.007–0.054) relative to that of temperature (η = −0.013, 95% CI: −0.036 to 0.009) and their interaction (θ = −0.008, 95% CI: −0.029 to 0.011), which were centered around zero. On average, a year with precipitation one standard deviation above the mean changed λ by +3.3%.

The effect of biome on the response of plants to climate. The meta-regressions testing the response of plant populations to precipitation (H2) and temperature (H3) anomalies were both nonsignificant (Fig. 1). When testing the correlation between WAI and the response of plant populations to precipitation anomalies, only 90.5% of our bootstrap samples had slopes below zero (βmeta = −3.83 × 10−3, 95% CI: −9.47 × 10−5, 1.99 × 10−3). Similarly, we did not find evidence that the mean annual temperature (H4) of the site predicted the response of plant populations to temperature anomalies (Fig. 1b; βmeta = −1.42 × 10−3, 95% CI: −6.62 × 10−3, 1.00 × 10−2).

The effect of generation time on the response of plants to climate. We found strong support for the effect of generation time (H5) on the absolute response of plant populations to climate. As expected, the response of species to climate correlated negatively with generation time (Fig. 2). In these meta-regressions, 100% of simulated βmeta values referring to the effect of precipitation (βmeta = −0.54, 95% CI: −0.63 to −0.44) and temperature (βmeta = −0.40, 95% CI: −0.50 to −0.30) were below zero.

The effect of plant types on estimates of climate effects. The effect of precipitation (P < 0.01), but not temperature (P = 0.97), changed based on organism type according to the ANOVA tests. Tukey’s honestly significant difference test showed a significant difference in the effect of precipitation between herbaceous and graminoid species (Supplementary Tables 2 and 3, Supplementary Fig. 6). We, therefore, re-run separate tests of H2, and H5 excluding the precipitation effect sizes of graminoid species. We excluded graminoid species only because herbaceous species comprised 127 of our 162 populations so that excluding them...
would not provide meaningful inferences. In these additional tests discarding graminoid data, H2 was not supported, and H4 was upheld. In H2, the percentage of simulated $\beta_{\text{meta}}$ values lower than zero was 72%, well below the 90.4% of the full dataset (Supplementary Methods, Supplementary Fig. 7). On the other hand, H4 was upheld, with 100% of $\beta_{\text{meta}}$ below zero (Supplementary Methods, Supplementary Fig. 8).

Discussion

While quantifying population responses to climate drivers has a long history in plant ecology\textsuperscript{22}, there is an urgent need to synthesize our knowledge due to on-going climate change\textsuperscript{4,23}. The availability of open-access data\textsuperscript{24}, a solid understanding of physiological ecology\textsuperscript{25}, and a mature evolutionary theory of life histories\textsuperscript{26} provide opportunities to produce quantitative generalizations regarding plant population responses to climate. In our global synthesis, we found that (H$_1$) precipitation has a stronger effect on population growth rates than temperature and that (H$_4$) plant species with shorter generation time respond more strongly to climate. These generalizations, especially the one on generation time, are relevant to conservation planning and evolutionary theory. However, because the available data is biased towards herbaceous perennials of temperate regions, our results might not be universal.

The large, positive effect of precipitation on a log($\lambda$) and the negative, smaller effects of temperature and its interaction with precipitation are consistent with the importance of water availability on plant population performance\textsuperscript{22} and productivity\textsuperscript{8}. The importance of precipitation as a driver of plant population growth implies highly uncertain ecological forecasts. Climate change projections involving precipitation are much more uncertain than those involving temperature\textsuperscript{23}. Moreover, prediction uncertainty in climate projections is not expected to improve much in the coming decades\textsuperscript{27}. As a result, accounting for this uncertainty will be a fundamental step when crafting ecological forecasts of plant populations (e.g., model uncertainty\textsuperscript{28}).

To our knowledge, our results are the first to show that generation time is linked to population responses to climatic drivers across a large number of species. To our knowledge, the only other study to test for this hypothesis found a similar pattern for...
three amphibian species\textsuperscript{29}. We formulated our hypothesis linking generation time to population responses to climate because in a sample of long-lived plants and animals, Morris et al\textsuperscript{29} found that the long-run population growth rate responds little to increases in the variation of survival and reproduction. Our results are complementary to this seminal study, in that the low sensitivity to climate drivers we found in long-lived species should minimize the variation in yearly population growth rates. Such minimized variation in yearly population growth rates is linked to higher long-run population growth rates\textsuperscript{30–32}. Hence, we demonstrated that it is possible to use plant traits to predict which species will be most sensitive to climate change\textsuperscript{1}. Interestingly, generation time is a fundamental quantity in identifying extinction probability\textsuperscript{33,34}, and therefore, a good news that this trait can also predict the climatic sensitivity of herbaceous plants.

The fact that responses to climate do not change based on biome suggests that plant populations are demographically adapted to cope with climate variation regardless of the average climate. In extreme environments, the stronger effect of climate on the variation of ecosystem processes such as productivity\textsuperscript{14,35} or biomass accumulation\textsuperscript{15,16} is not reflected in demographic patterns. It is, therefore, plausible that adaptations such as investment in survival\textsuperscript{36} or dormancy\textsuperscript{37} are sufficient to decouple physiological processes from demographic patterns. Such de-coupling is crucial because if climate drove larger variance in population growth rates, this would decrease the chances of population persistence. However, because plants appear adapted to local climatic variation, these results do not mean that all biomes will be equally vulnerable to climatic change. Rather, vulnerability to climate change will likely depend on how changes in climate compare to pre-existing climatic variability\textsuperscript{38}.

The geographic and taxonomic bias of our dataset might amplify the relevance of precipitation anomalies, and it therefore may affect the generality of our findings. First, geographic bias potentially underemphasizes the role of temperature, because of our dataset under-samples extremely cold and hot biomes. For example, in cold biomes such as montane or boreal forests, the influence of temperature on growth is larger as the mean annual temperature decreases\textsuperscript{15,16}. On the other hand, the interaction between precipitation and temperature may be larger in hot than in colder biomes\textsuperscript{9}. Therefore, we might expect a strong interaction between precipitation and temperature anomalies where mean precipitation is low and mean temperature high. These conditions should occur, for example, in the subtropical desert or tropical savannas, but only a handful of our studies occur in these biomes (Supplementary Fig. 1). Similarly, the taxonomic bias in our data could also amplify the importance of precipitation anomalies. For example, our dataset contained only two trees and five shrubs. However, woody species have surprisingly effective adaptations to cope with water shortages\textsuperscript{39} and they could therefore be susceptible only to extreme precipitation anomalies. Nevertheless, we note that inferences dominated by herbaceous species comprise most of the biodiversity in temperate forests\textsuperscript{41}, and they have a critical role in the carbon cycle\textsuperscript{12}.

Our findings on the link between short generation times and climatic sensitivity do not automatically translate into climate vulnerability. The observational nature of our data imposes to interpret our findings in light of two caveats. First, our data did not address several of the concurrent factors that contribute to the effects of climate on populations. These include factors such as density-dependence\textsuperscript{3}, trophic interactions\textsuperscript{51}, and anthropogenic drivers\textsuperscript{52}. Second, our results are more relevant to changes in climatic variability than changes in climatic means. When predicting the effects of large changes in climatic means, our nonlinear results (Supplementary Figs. 3–5) show that extrapolation might not be warranted. Besides these two caveats, the conservation literature links short generation times to lower, rather than higher climate vulnerability as indicated by our results\textsuperscript{33,54}. These studies reflect conservation assessments which posit that short generation time should be linked to lower extinction probability\textsuperscript{33}. Short-generation time should also increase the probability of evolutionary rescue\textsuperscript{35}. However, the advantages provided by short generation time might be overridden by the rapid rates of climate change expected. Thus, weighing the positive and negative effects of generation time will leverage our findings to improve the quality of climate change vulnerability assessments.

### Methods

**Demographic data.** To address our hypotheses, we used matrix population models or integral projection models (IPMs) from the COMPADRE Plant Matrix Database (v. 5.0.1\textsuperscript{196} and the PARDINO IPM Database\textsuperscript{57}, which we amended with a systematic literature search. First, we selected density-independent models from COMPADRE and PARDINO which described the transition of a population from 1 year to the next. Among these, we selected studies with at least six annual transition matrices, to balance the needs of adequate yearly temporal replicates and sufficient sample size for a quantitative synthesis. This yielded data from 48 species and 144 populations.

We then performed a systematic literature search for studies linking climate drivers to structured population models in the form of either MPMs or IPMs. We performed this search on ISI Web of Science for studies published between 1997 and 2017. We used a Boolean expression containing keywords related to plant form, structured demographic models, and environmental drivers (Supplementary Methods). We only considered studies linking macro-climatic drivers to natural populations (e.g., transplant experiments and studies focused on local climatic factors such as soil moisture, light due to treefall gaps, etc. were excluded). Finally, we used the same criteria used to filter studies in COMPARE and PARDINO, by selecting studies with at least six, density-independent, annual projection models.
This search brought two additional species, belonging to three additional populations, which we entered in the COMPADRE database. One of the studies included in the search because it contained density-dependent IPMs, also provided raw data with high temporal replication (14–32 years of sampling) for 12 species from 15 populations. Therefore, we reanalyzed these freely available data to produce density-independent MPDs that were directly comparable to the other studies in our dataset (Supplementary Methods). The resulting dataset consisted of 46 studies, 62 species, 162 populations, and a total of 3761 MPMs and 52 IPMs (Supplementary Data 1). The analyzed plant populations were tracked for a mean of 16 (median of 12) annual transitions. To our knowledge, this is the first attempt to produce open-accessed population projection models. However, this dataset is taxonomically and geographically biased. Specifically, among our 62 species, this dataset contains 54 herbaceous perennials (11 of which graminoids), and eight woody species: five shrubs, two trees, and one woody succulent (Opuntia imbricata). Moreover, almost all of these studies were conducted in North America and Europe (Supplementary Fig. 1), in temperate biomes that are cold, dry, or both cold and dry (Supplementary Fig. 1 inset). Our geographic and taxonomic bias reflects the rarity of long-term plant demographic data in general. This dearth of long-term demographic data is particularly evident in the tropics. The ForestGEO network59 is an exception to this rule, but to date, no matrix population models or integral projection models using these data have been published.

We used the MPMs and IPMs in this dataset to calculate the response variable of our analyses: the yearly asymptotic population growth rate ($\lambda$). This measure is one of the most widely used summary statistics in population ecology60, as it integrates the response of multiple interacting vital rates. Specifically, $\lambda$ reflects the population growth rate of a population that would maintain its vital rates constant through time61. This metric therefore distills the effect of underlying vital rates on population dynamics, free of other confounding factors (e.g., transient dynamics arising from population structure62). We calculated $\lambda$ of each MPM or IPM with standard methods63,64. Because our MPMs and IPMs described the demography of a population for a year, we compared the $\lambda$ values of populations that were directly comparable to the other studies in our dataset (Supplementary Fig. 1, inset). Our geographic and taxonomic bias reflected the rarity of long-term plant demographic data in general. This dearth of long-term demographic data is particularly evident in the tropics. The ForestGEO network59 is an exception to this rule, but to date, no matrix population models or integral projection models using these data have been published.

**Climatic data.** To test the effect of temporal climatic variation on demography, we gathered global climatic data. We downloaded 1 km$^2$ gridded monthly values for maximum temperature, minimum temperature, and total precipitation between 1901 and 2016 from CHELSAcuts64, which combines the CRU TS 4.0165, and CHELSA66 datasets. Gridded climatic data are especially suited to estimate annual climatic means67. These datasets include values from 1901 to 2016, which are necessary to cover the temporal extent of all 162 plant populations considered in our analysis. For each study population, we calculated the mean temperature of the minimum and maximum monthly temperatures. We used monthly values to calculate the time series of mean annual temperature and total annual precipitation at each site. We then used this dataset to calculate our annual anomalies for each census year, defined as the 12 months preceding a population census. Our annual anomalies are standardized z-scores. For example, if $X$ is a vector of 40 yearly precipitation or temperature values, $E(X)$ calculates the mean, and $\sigma(X)$ calculates the standard deviation, we compute annual anomalies as $A = (X - E(X))/\sigma(X)$. Therefore, an anomaly of one refers to a year where precipitation or temperature was one standard deviation above the 40-year mean. In other words, anomalies represent how infrequent annual climatic conditions are at a site. Specifically, if we assume that $A$ values are normally distributed, values exceeding one and two should occur every 6 and 44 years, respectively. We used 40-year means because the minimum number of years suggested to calculate climatic averages is 30. Z-scores are commonly used in global studies on vegetation responses to climate68,69, and they reflect the null hypothesis that species are adapted to the climatic variation at their respective sites. Across our populations, the standard deviations of annual precipitation and temperature anomalies change by 300% and 60%, respectively (Supplementary Fig. 2). Thus, a z-score of one refers to a precipitation anomaly of 50 or 160 mm and to a temperature anomaly of 0.5 or 0.8°C. Our null hypothesis posits that species are adapted to these conditions, regardless of the absolute magnitude of the standard deviation in annual climatic anomalies. If this null hypothesis were true, each species would respond similarly to z-scores. Z-scores are more easily interpreted when calculated on normally distributed variables. We found our temperature and precipitation z-scores were highly skewed (skewness above 1) only in, respectively, 2 (for temperature) and three (for precipitation) of our 162 populations. We concluded that this degree of skewness should not bias our z-scores substantially.

To test how the response of plant populations to climate changes based on biome and latitude, we used three climatic drivers. For each study population, we computed a proxy for water limitation, water availability index (WAI), and temperature limitation using mean annual temperature. To compute these metrics, we downloaded data at 1 km$^2$ resolution for mean annual potential evapotranspiration, mean annual precipitation, and mean annual temperature referred to the 1970–2000 period. We obtained potential evapotranspiration data from the CGIAR-CSI consortium (http://www.cgiar-csi.org/). This dataset calculates potential evapotranspiration using the Hargreaves method69. We obtained mean annual precipitation and mean annual temperature from WorldClim70. Here, we used WorldClim rather than CHELSA climatic data because the CGIAR-CSI potential evapotranspiration data were computed from the former. We calculated the WAI values at each of our sites by subtracting mean annual potential evapotranspiration from the mean annual precipitation. Such proxy is a coarse measure of plant water availability that ignores information such as soil characteristics and plant rooting depth. However, WAI is useful to compare water availability among disparate environments, so that it is often employed in global analyses67,71. As our proxy of temperature limitation, we use mean annual temperature. While growing degree days would be a more mechanistic measure of temperature limitation72, this requires daily weather data. However, we could not find a global, downscaled, daily gridded weather dataset to calculate this metric.

The overall effect of climate on plant population growth rate. To test $H_1$, we estimated the overall effect sizes of responses to anomalies in temperature, precipitation, and their interaction with a linear mixed-effect model.

$$\log(\lambda) = a + bP + cT + \delta P T + \epsilon$$

(1)

where $\log(\lambda)$ is the log of the asymptotic population growth rate of plant population $P$ is precipitation, $T$ is temperature. We included random population effects on temperature and the slope of the rainfall–temperature interaction. This allowed for variability in the responses to precipitation and temperature across populations, with no ecologically meaningful (e.g., habitat) differences. Across our populations, the standard deviation in annual precipitation and temperature anomalies change by 300% and 60%, respectively (Supplementary Fig. 2). Thus, a z-score of one refers to a precipitation anomaly of 50 or 160 mm and to a temperature anomaly of 0.5 or 0.8°C. Our null hypothesis posits that species are adapted to these conditions, regardless of the absolute magnitude of the standard deviation in annual climatic anomalies. If this null hypothesis were true, each species would respond similarly to z-scores. Z-scores are more easily interpreted when calculated on normally distributed variables. We found our temperature and precipitation z-scores were highly skewed (skewness above 1) only in, respectively, 2 (for temperature) and three (for precipitation) of our 162 populations. We concluded that this degree of skewness should not bias our z-scores substantially.

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we fit a linear effect of the non-climatic covariate and its interaction with one of the two linear climatic anomalies. Thus, including the linear model in Eqs. 2 and 3, the non-climatic covariates and the covariate interaction models, we tested up to six alternative models for each one of our populations (Supplementary Table 1). We selected the best model according to the Akaike Information Criterion corrected for small sample sizes (AICc). We carried out these and subsequent analyses in R version 3.6.176.

In the populations for which AICc selected one of the model alternatives to the baseline in Eqs. 2 and 3, we calculated the effect size of climate by adding the effect of the new terms to the linear climatic terms. For example, when a quadratic precipitation model was selected, we calculated the effect size of precipitation as $\beta = \beta_1 + \beta_2 x + \beta_3 x^2$. The models including an interaction between temperature and a non-climatic covariate, we evaluated the effect of the interaction at the mean value of the covariate. Therefore, we calculated the effect size as $\beta = \beta_1 + \beta_C E(C)$ for continuous covariates. For categorical variables, we calculated the effect size as $\beta = \beta_0 + \beta_0.5$: that is, we calculated the mean effect size between the two categories. We quantified the standard error of the resulting effect sizes by adding the standard errors of the two terms.

The effect of biome on the response of plants to climate. We used a simulation procedure to run two meta-regressions to test for the correlation between the effect size of climate drivers on $\lambda$, and our measures of water or temperature limitation. These meta-regressions accounted for the uncertainty, measured as the standard error, in the effect sizes of climate drivers. We represented the effect of biome using a proxy of water (WAI) and temperature (mean annual temperature) limitation. For each of our 162 populations, the response data of this analysis were the effect sizes ($\beta$; $\lambda$ values) estimated by Eqs. 2 and 3 or their modifications in case a quadratic or non-climatic covariate model were selected. In these meta-regressions, the weight of each effect size was inversely proportional to its standard error. To test $H_2$ and $H_3$ on how water and temperature limitation should affect the response of populations to climate, we used linear meta-regressions. These two hypotheses tested both the sign and magnitude of the effect of climate. Therefore, we used the effect sizes as a response variable which could take negative or positive values. As predictors, we used population-specific WAI ($H_2$ only for effect sizes quantifying the effect of precipitation), and mean annual temperature ($H_3$ only for effect sizes quantifying the effect of temperature). The null hypothesis of these meta-regressions is that plant species are adapted to the climatic variation at their respective sites. Such an adaptation implies that a precipitation z-score of one should produce effects on log($\lambda$) of similar magnitude and sign across different climates. This should happen across average climatic values that are connected to substantially different absolute climatic anomalies (Supplementary Fig. 2). On the other hand, we hypothesised that at low WAI and MAT values, species are more responsive to z-scores than expected under the null hypothesis.

We performed these two meta-regressions by exploiting the standard error of each effect size. We simulated 1000 separate datasets where each effect size was independently drawn from a normal distribution whose mean was the estimated $\beta$ value, and the standard deviation was the standard error of this $\beta$. These simulated datasets accounted for the uncertainty in the $\beta$ values. We fit 1000 linear models, extracting for each its slope, $\beta_{meta}$. Each one of these slopes had in turn an uncertainty, quantified by its standard error, $\sigma_{meta}$. For each $\beta_{meta}$ we then drew 1000 values from a normal distribution with mean $\beta_{true}$ and standard deviation $\sigma_{meta}$ to simulate the confidence intervals of $\beta_{meta}$. This procedure assumes that the distribution of $\beta_{true}$ values is normally distributed. We performed one-tailed hypothesis tests, considering meta-regression slopes significant when over 95% of simulated values were below zero.

The effect of generation time on the response of plants to climate. To test $H_4$, on how the generation time of a species should mediate its responses to climate, we used a gamma meta-regression. We fitted gamma meta-regressions because our response variables were the absolute effect sizes of precipitation and temperature anomalies, $|\beta|$, which are bounded between 0 and infinity. Test $H_4$, we therefore fitted gamma meta-regressions with a log link, using $|\beta|$ values as response variable and generation time ($T$) as predictor. We calculated $T$ directly from the MPMs and IPMs (Supplementary Methods). We log-transformed $T$ to improve model fit. We carried out these meta-regressions using the same simulation procedure described for testing $H_2$ and $H_3$. We also carried out one-tailed hypothesis tests, by verifying whether 95% of $\beta_{meta}$ values were below zero.

The effect of plant types on estimates of climate effects. We verified whether certain plant types could bias our results by subdividing our species as graminoids, herbaceous perennial plants with long life spans, woody species (shrubs and trees), and succulents. We ran ANOVA tests to verify whether the effect sizes of precipitation and temperature anomalies differed between plant types. We then tested for significant differences in pairwise contrasts between plant types by running Tukey's honestly significant difference tests. We carried out these tests on the average effects of climate in each test accounting for differences in parameter uncertainty. If Tukey's test identified significant differences among plant types, we ran additional tests of $H_4$, excluding the plant type, or plant types, whose response to climate differed.
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