Spatial replication should be prioritized to advance our understanding of population responses to climate

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Running head: spatial replicates estimate climate effects

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Abstract

Understanding the responses of plant populations dynamics to climatic variability is frustrated by the need for long-term datasets that capture demographic responses to a range of climates. Here, we advocate for new studies that prioritize spatial over temporal replication, but without inferring the effect of temporal climatic gradients from spatial climatic gradients – as usually done in the so called "space-for-time substitutions". Rather, we advocate to estimate the effects of climate by sampling replicate populations in locations with similar climate. We first use data analysis on spatial locations in the conterminous USA to assess how far apart spatial replicates should be from each other to minimize temporal correlations in climate. We find that spatial locations separated by 250 Km have moderate (0.5) correlations in annual precipitation. Second, we use simulations to demonstrate that spatial replication can lead to substantial gains in the range of climates sampled during a given set of years so long as the climate correlations between the populations are at low to moderate levels. Third, we use simulations to quantify how many spatial replicates would be necessary to achieve the same statistical power of a single-population, long-term data set under different strengths and directions of spatial correlations in climate between spatial replicates. Our results indicate that spatial replication is an untapped opportunity to study the effects of climate on demography and to rapidly fill important knowledge gaps in the field of population ecology.

Keywords: climate vulnerability assessment, power analysis, sampling design, sample size, forecast, population growth rate, demography, Space-for-Time substitution.

INTRODUCTION

Understanding the responses of biodiversity to climate drivers is necessary to mitigate and adapt to climate change (Urban et al., 2016). In recent years, there are several examples of successful and directly applicable forecasts that predict the effects of climatic drivers on ecological variables (Grevstad et al., 2022; Harris et al., 2018; Hartman et al., 2020). There has been slower progress in predicting the effects of climate on populations and their demography, which is necessary to assess species extinction risk (Mace et al., 2008) and predict range shifts (Schurr et al., 2012). Previous studies suggest that it takes 20-25 years of data to sufficiently describe the relationship between climate and demography (Teller et al., 2016; Tenhumberg et al., 2018). This large replication is necessary to sample a wider range of climatically extreme years (Tenhumberg et al. 2018) and to increase statistical power in the presence of noise caused by non-climate factors (e.g., variation in biotic and abiotic conditions).

Beyond improving our forecasting skill, we have important knowledge gaps in population ecology that must be filled, and we cannot wait 20-25 years to acquire missing information about understudied species and regions. For example, our recent synthesis brought to our attention that knowledge on climate-demography relationships for plants is particularly poor for the species-rich tropics, and for species with extreme generation times (Compagnoni et al., 2021). We need immediate research targeting these locations and plant life histories. As the vast majority of plant ecologists are at young career stages, we need to engage Doctoral Researchers and Postdoctoral Associates in this field of research. However, this will not happen if we require projects to have a duration of two decades.

It is our opinion that new studies should prioritize spatial over temporal replication to assess the demographic responses of a species to climate. Having both spatial and temporal data allows collecting a high sample size in a relatively short period of time. Spatial sampling increases our statistical power because it increases the range of climates that can be sampled across a short

period of time, allowing us to "see through the noise" caused by non-climatic factors. The range of climates sampled can be maximized by censusing populations far enough that the correlation of yearly climatic anomalies among them is low.

Here, we are not advocating a "space-for-time substitution", but simply to prioritize spatial versus temporal replication. Space-for-time substitution studies use spatial gradients that differ dramatically in climate to infer temporal links between climate and population dynamics (Blois et al., 2013). Here, we are instead advocating to replicate sampling across populations that occur in similar climates, and to use this spatial data as a *replicate* of the same temporal process. This recommendation relies on the assumption that in similar environments, plant populations should respond similarly to climate anomalies. For example, the effect of hot or cold years on the growth rate of populations all located at the upper elevational limit of a species' range should be similar in sign and magnitude (Kleinhesselink & Adler, 2018; Morley et al., 2017). There are already many studies that sample populations across species' ranges in order to capture different climates (e.g. Doak & Morris, 2010; Kleinhesselink & Adler, 2018; Merow et al., 2014; Sheth & Angert, 2018). However, to our knowledge, no plant population study has yet prioritized spatial replication across sites with similar climatic conditions to study climate-demography relationships.

In this manuscript, we examine in detail the opportunities provided by spatial replication when studying climate-demography relationship through data analysis and simulation. First, we assess how far apart populations must be from each other to attenuate temporal correlations in climate, by quantifying the relationship between the distance between spatial locations and their correlation in annual precipitation and temperature. We do this using gridded climatic data from the conterminous USA. Second, we consider how sampling design can maximize the range of climates captured during a study by estimating how the range of climates sampled changes depending on the climate correlations between the populations (i.e., which is based on the distance between populations) and the study duration (between five and 30 years). Third, we use simulation to

quantify the statistical power of a climate-demography relationship across sampling designs that vary in the number of spatial and temporal replicates, and the strength and direction of spatial correlations in climate between populations. In this simulation, we also address cases in which populations respond differently to climate, or have different degrees of temporal demographic variability. Based on these results, we make recommendations for new demographic research.

METHODS

Spatial correlation in climate

To understand how spatial correlation in climates depends on the distance between sites, we estimate the spatial correlation of annual climate in the conterminous USA, a large and climatically heterogeneous region of the world. We downloaded monthly temperature and precipitation data for the conterminous United States from the CHELSA database (Karger et al., 2017, 2018). We used CHELSA data, because it is accurate on varied topographic terrain. Such gridded data also provides systematic spatial coverage, and when used for annual means, it correlates strongly with weather station data (Behnke et al., 2016). We downloaded data following a regular grid of 0.5 degrees, for a total of 3253 locations, from 35 years, between 1979 and 2013. For each point along this grid, we calculated annual temperature means, annual precipitation sums, and computed their standardized yearly anomalies (z-scores, henceforth "anomalies"). We analyzed the decay of correlation between these temperature and precipitation anomalies using five reference locations. We picked these locations subjectively, attempting to choose the most distant points in the conterminous United States. These locations were in the Southwestern coast, Northwestern coast, Northeast Coast, Southeast coast, and in the center of the United States.

For each of these five reference locations, we calculated the correlation between its 35 annual temperature and precipitation anomalies, and the same anomalies observed at the other 3252 locations. We plotted the correlation between climatic anomalies versus the distance from the reference location. We produced heatmaps showing the correlation of the climatic anomalies with the reference locations.

Range of climates sampled with different sampling designs

We performed simulations to understand how the range of climate anomalies sampled changes as temporal replication increases when sampling one site, or multiple sites with different spatial correlation in climatic anomalies. We estimated the range of climatic anomalies sampled at a single site using a normal distribution:

$$\boldsymbol{X} \sim Normal(0,1), \qquad (1a)$$

$$\boldsymbol{Range}_x = \frac{Max(\boldsymbol{X}) - Min(\boldsymbol{X})}{2}, \qquad (1b)$$

where **X** is a vector of climate anomalies at the site. The length of **X** is *n*, which is the temporal replication of the study. The standard deviation in Eq. 1a is one, reflecting that we are simulating a series of anomalies. To obtain $\boldsymbol{Range_X}$, the expected range of **X** values (Eq. 1b), we simulated Eq. 1a 1000 times across *n* values ranging from two to 30 in increments of one. We calculated the mean of $\mathbf{Range_X}$ across these 1000 replicate simulations.

We estimated the range of climatic anomalies sampled at two sites drawing values from a multivariate normal distribution,

$$\boldsymbol{X} \sim MVN(\mathbf{0}, \begin{bmatrix} 1 & \rho \\ \rho & 1 \end{bmatrix}), \qquad (2)$$

where **X** is an *n* by 2 matrix, MVN indicates the values in **X** follow a multivariate normal distribution, and ρ is the correlation between the climatic anomalies of two sites. We simulated **X** 1000 times across a series of ρ values of 0, 0.5, 0.95, and one. We simulated *n* values that went from two to 30 in increments of one.

Statistical power for climate-demography relationship with different sampling designs

We used simulations to quantify the statistical power of the relationship between climate and population growth rate for different spatio-temporal sampling designs and different spatial

correlations in climate. First, we simulated the linear relationship between log population growth rates and a normally distributed climatic anomaly at one site using:

$$\boldsymbol{X} \sim Normal(0,1), \qquad (3a)$$

$$\hat{Y}_i = \beta_0 + \beta_1 X_i, \qquad (3b)$$

$$Y_i \sim Normal(\hat{Y}_i, \varepsilon), \qquad (3a)$$

where $\boldsymbol{X}$ is a vector of size *n* of normally distributed climatic anomalies, $\hat{Y}_i$ is the average prediction of the model, β_0 the intercept of the linear model, β_1 is the slope, and Y_i represents the natural logarithm of a population growth rate at year *i*. We used a log population growth rate because we have synthetic estimates of climatic effects on this variable (Compagnoni et al., 2021), because this variable is the central focus of demographic theory (Caswell, 2001; Lewontin & Cohen, 1969; Sibly & Hone, 2002), and because log population growth rate is normally distributed, facilitating simulations and their interpretation by the reader. We simulated the process in Eq. 3 1000 times, assuming study durations, *n*, of 20, and 30 years. For this and subsequent simulations we used a β_1 value of 0.05, and a ε value of 0.15. Our choice of β_1 reflects the effect size of precipitation anomalies on log population growth rate that we estimated across 162 plant populations (Compagnoni et al., 2021). The choice of our ε reflects the median standard deviation of the log population growth rate estimated on the same 162 populations.

Then, we expanded this model to accommodate spatial replicates whose climatic anomalies were correlated to different degrees. To do so, the simulated process was

$$\boldsymbol{X} \sim MVN(\mathbf{0}, \begin{bmatrix} 1 & \rho \\ \rho & 1 \end{bmatrix}), \qquad (4a)$$

$$\hat{Y}_{ip} = \beta_0 + \beta_1 X_{ip}, \qquad (4b)$$

$$Y_{ip} \sim Normal(\hat{Y}_{ip}, \varepsilon), \qquad (4c)$$

where ρ isthe correlation between the climatic anomalies of two sites, and subscript p refers to each site. We simulated the process described in Eq. 4 1000 times using study durations, n, of three and five years, correlations ρ of 0.95 and 0.5, 0, and -0.5 and a number of spatial replicates of two, 10, 20, 30, 40, and 50. When the number of spatial replicates exceeded two, we divided the populations in two subsets, and assigned each subset to one of the two series of climatic anomalies simulated by Eq. 4a. For example, when spatial replicates were 50, we subdivided these replicates in two groups of 25 replicates. Note that replicates within each group experienced identical climate. We used low values for n to reflect that the median length of demographic studies of plants is four years (Salguero-Gómez et al., 2015). This sampling effort likely reflects the length of many PhD programs. We calculated power as the proportion of the 1000 simulations for which β_1 had a p-value below 0.05. We performed a power analysis not because we expect investigators to perform null hypothesis tests relying on p-values. Rather, our power analysis is a simple, intuitive way to quantify how the uncertainty of model estimates is influenced by the sampling design.

The power estimate described above assumed that β_1, in Eq. 3-4b, were the same for each population. We have limited information to evaluate whether there is variation across populations in β_1. A few studies report changes in β_1 values across populations, but many of these studies sampled populations with different average climates (Iler et al., 2019; Sletvold et al., 2013; Tye et al., 2018). Nevertheless, as it is possible for β_1 to vary spatially, we address the sensitivity of our power estimates to spatial variation in β_1. To do so, we modified the simulations presented in Eq. 4. We simulated a nested sampling design in which different populations are sampled in groups of three that experience identical β_1 or ε values. In these simulations, equation 4a contains ρ values equal to one. In the first sensitivity analysis, each group of three populations has a different β_1 value, so that

$$\beta_{1g} \sim Normal(\mu = 0.05, \sigma), \qquad (5)$$

where β_{1g} are the effect sizes for group g of three populations, and the values suggest a mean β_{1g} value of 0.05 with a standard deviation of σ. We tested three values of σ: 0.007, 0.0125, and 0.025.

Note that in the largest σ value, over 5% of β_{1_g} values are expected to be lower than zero. We explored the change in statistical power introduced by Eq. 5 simulating three years of data, and a number of populations going from a minimum of three to a maximum of 48, in increments of three.

RESULTS

Spatial correlation in climate

Annual temperature anomalies are strongly correlated even at relatively large (e.g. 500 Km) distances. The correlation between precipitation anomalies is less strong, and it decays more rapidly with distance (Fig. 1, Fig. S1-4). However, on average the correlation does not approach zero until the distance from the reference location is at least 750 Km for precipitation (Fig. S3) and 1000 Km for temperature (Fig. S2). The distance to reach a correlation of 0.5 is approximately at least 100 Km for both precipitation (Fig. S1) and temperature (Fig. S2). Interestingly, we find that the climate of the reference point on the Southwestern US coast tended to correlate less strongly with the rest of the locations in the US (Fig. S2).

Range of climates sampled with different sampling designs

Spatial replication can lead to substantial gains into the range of climates sampled during a given set of years so long as the climate correlations between populations are at low to intermediate levels. To reach a range of ±2 standard deviation at a single site, one would on average need 27 years of data. This number of years decreases to 20 when using two sites whose climate has correlation 0.9, and 15 when two sites have correlations 0.5 (Figure 2).

Statistical power for climate-demography relationship with different sampling designs

Our power analysis indicates that spatial replication greatly increases the power to detect a relationship between climate and population growth rate (Fig. 3). The statistical power of very long time series for a single site is comparable to that of datasets with high spatial replication. This holds even when the climate of the spatial replicates has a high correlation (e.g. correlation 0.95, Fig. 3). 20 and 25 temporal replicates with one spatial replicate provides a statistical power of about 30 and

40%, respectively. These two statistical powers are reached by just three temporal replicates with, respectively, 10 and 20 spatial replicates experiencing highly correlated climate (0.5, 0.95). Still assuming high climatic correlations, statistical power exceeds 40% when the temporal replication increases to five years. Lower climatic correlation between populations slightly increases statistical power: going from a climatic correlation of 0.95 to zero can increase power by over 10% when temporal replicates are three (Fig. 3).

Assuming variation in the effect of climate on demography (represented by β_1 values) did not noticeably affect statistical power (Fig. S5). Statistical power remained unchanged presumably because the average β_1 is still 0.05.

DISCUSSION

Until recently, understanding the response of plant species to temporal climatic gradients has relied on either long-term monitoring efforts, which are extremely rare (Salguero-Gómez et al., 2015, 2016), or on responses of plant populations to spatial climate gradients ("space-for-time substitutions", Blois et al., 2013), which are affected by several confounding factors (Damgaard, 2019). Fortunately, our power analysis shows that we can propel our understanding of species responses to climate using spatial replicates that come from sites with similar climate (i.e., similar long-term average climates). Moreover, dividing spatial replicates by large distances (e.g. 100 Km) ensures climates are not perfectly correlated. Such imperfect correlation allows for sampling a larger range of climates sampled in a shorter timeframe, further compounding gains in statistical power. We believe this finding could foster progress in global climate change vulnerability assessments, near-term demographic forecasts, and ecological understanding in general. Based on our results, we provide suggestions on sampling designs leveraging spatial replication.

The golden standard for vulnerability assessments relies on population dynamics and demography (Mace et al., 2008). In order to understand which life-histories and which geographic regions will be most affected by climate change, we need more demographic studies that quantify climate-demography relationships. Our power analysis shows that three years of data from ten spatial replicates have the same statistical power as 20 years of data at a single site. The ability to obtain estimates of climate effects in such a short time will likely enable covering the taxonomic, geographic, and life-history biases present in our current data (e.g. Compagnoni et al., 2021).

A benefit of increased spatial replication is that it allows scientists to reach adequate inferences in as little as three years, which will facilitate ecological understanding via iterative (yearly) forecasts. Forecasts can promote ecological understanding when they are tested repeatedly across successive iterations (Dietze et al., 2018). For example, performing model selection on three years of data from 20 separate plant populations might suggest growing season precipitation is a

good predictor of demographic performance. A way to test this inference is to forecast the demography of these 20 populations after the third year of data collection. These forecasts provide each year with 20 out-of-sample data points to test whether growing season precipitation outperforms other predictors. Successive out-of-sample tests might end up changing initial inferences: for example, supporting predictors other than growing season precipitation (e.g. vapor pressure deficit), different model structures (e.g. including density dependence), or motivating changes in data collection efforts.

Spatial replicates are particularly suited to address two mechanisms that could confound climate-demography relationship: species interactions, and microsite variation. First, species interactions mediated by conspecific and heterospecific densities are known to be a key component of population and community dynamics (Chesson, 2000). As a consequence, a growing body of research emphasizes the role of the indirect effects of climate mediated through heterospecific abundances (Adler et al., 2012; Gilman et al., 2010; Suttle et al., 2007). Understanding these effects relies on estimates of conspecific and heterospecific densities which, however, are hard to perform: conspecific effects are attenuated by observation error, which leads to “regression dilution” (Detto et al., 2019; Knape & de Valpine, 2011). However, regression dilution is weaker as the range of densities increases. In the short term, variation in conspecific densities is likely to be much greater across space than time. Spatial replicates are therefore ideal to capture a wide range of conspecific and heterospecific densities. The result is that spatial replication facilitates the estimation of conspecific and heterospecific effects which can be used to project the effect of indirect climatic effects. Second, climate effects on populations should be modulated by soil conditions (Lindell et al., 2022; Nicolè et al., 2011). Reaching a general understanding on this subject could be achieved by stratifying spatial replicates by soil type, and fitting hierarchical models on the resulting data.

To exploit the opportunities provided by spatial replication, investigators should sample sites that can be considered as independent samples (e.g., populations not connected by dispersal).

However, even when sites are separated by relatively large distances, factors other than climate (e.g. outbreaks of natural enemies) could result in spatially autocorrelated vital rates. Therefore, it is prudent for investigators to plan on estimating the spatial autocorrelation among spatial replicates. A previous study suggests that to estimate spatial autocorrelation, replicates should be disposed at random through the landscape, rather than according to regular sampling designs (Fortin et al., 1989). If detected, explicit modeling of spatial autocorrelation within linear models can increase statistical power and decrease parameter uncertainty (Zuur et al., 2009).

In our simulations, we have ignored the possibility for spatial replicates to have unequal residual variance. We did so because unequal residual variance is both unlikely to occur, and it will not affect the average estimates of climatic effects. Unequal variance is not likely because population growth rate increases in temporal variance only at range edges (Csergő et al., 2017; Sexton et al., 2009). Therefore, if spatial replicates come from similar environmental conditions, changes in variance among spatial replicates should be small. However, even in the case residual variance is variable among spatial replicates, this issue is only relevant for probabilistic predictions of single data points (Gelman et al. 2020). When such predictions are the objective, the issue of unequal variance can be ameliorated using weighted least squares regression (Gelman et al., 2020).

Perhaps the most important limitation of spatial replication is for species with small ranges with few extant populations. There are many examples of species with extremely small ranges (Thorne et al., 2009), and with few (Colas et al., 2001) or just one (Jones et al., 1995) extant populations. In these cases, climate vulnerability assessments will necessarily rely have to rely on other methods to quantify climate sensitivity.

While our manuscript has focused on plants, the benefits of spatial replication extends also to animals with short dispersal distances. Just like in plants, the quantification of climate sensitivity in animals suffers from important geographic and taxonomic biases (Paniw et al., 2021). Moreover, while demographic research in animals tend to be more short term than for plants, spatial replicates

290 are typically one or few at most (Salguero-Gómez et al., 2016). These considerations suggest that the
291 potential of spatial replication to aid the study of climate sensitivity in animals could be
292 underexploited. However, spatial replication in animals would be practical only for species with
293 relatively low dispersal ability.

294 The spatially replicated sampling we propose here is a practical solution to estimate climate-
295 demography relationships and rapidly fill important knowledge gaps in the field of population
296 ecology. The current dearth of long-term data almost certainly stems from the difficulty of
297 maintaining data collection efforts under the most common funding schemes, which typically last
298 three to seven years. In the time frame relevant to working on a PhD thesis, it might be possible to
299 observe 20 populations across three years, and achieve the same power for estimating climate-
300 demography relationships that was thought to only be possible with decades-long sampling.
301 Monitoring 20 or more populations simultaneously is a large task for a single researcher. However,
302 such spatial replication might become more feasible with modern methods and through
303 collaborative research networks. For example, the demography of some populations can be sampled
304 effectively with small unmanned aerial vehicles (e.g. Bogdan et al., 2021). Moreover, observation
305 networks for demographic data already exist: for example, PlantPopNet collects data from 46
306 populations of *Plantago lanceolota* around the world (Villellas et al., 2021). We believe that the
307 sampling choices we advocate in this article will contribute to the maturation of population ecology
308 and its links to conservation science, functional ecology, and macro-ecology.

309

310 **Acknowledgements**

311 AC, SE, and TMK were supported by the Alexander von Humboldt Foundation under the framework
312 of the Humboldt Professorship, and by the Helmholtz Recruitment Initiative of the Helmholtz
313 Association (both to TMK). This work was inspired during the sAPROPOS (Analysis of PROjections of
314 POpulationS) working group led by Roberto Salguero-Gómez and TMK at the German Centre for

Integrative Biodiveristy Research (iDiv), which is funded by the German Research Foundation (FZT-118-202548816).

Data Sharing and Data Accessibility. The climatic data used in this article is the CHELSA dataset version 1.2, which is available at http://dx.doi.org/doi:10.5061/dryad.kd1d4.

REFERENCES

Adler, P. B., Dalgleish, H. J., & Ellner, S. P. (2012). Forecasting plant community impacts of climate variability and change: When do competitive interactions matter? *Journal of Ecology*, *100*, 478–487.

Behnke, R., Vavrus, S., Allstadt, A., Albright, T., Thogmartin, W. E., & Radeloff, V. C. (2016). Evaluation of downscaled, gridded climate data for the conterminous United States. *Ecological Applications*, *26*(5), 1338–1351. https://doi.org/10.1002/15-1061

Blois, J. L., Williams, J. W., Fitzpatrick, M. C., Jackson, S. T., & Ferrier, S. (2013). Space can substitute for time in predicting climate-change effects on biodiversity. *Proceedings of the National Academy of Sciences*, *110*(23), 9374–9379. https://doi.org/10.1073/pnas.1220228110

Bogdan, A., Levin, S. C., Salguero-Gómez, R., & Knight, T. M. (2021). Demographic analysis of an Israeli Carpobrotus population. *PLOS ONE*, *16*(4), e0250879. https://doi.org/10.1371/journal.pone.0250879

Caswell, H. (2001). *Matrix Population Models: Construction, Analysis and Interpretation.* Sinauer Associates, Inc.

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, 343–366.

Colas, B., Olivieri, I., & Riba, M. (2001). Spatio-temporal variation of reproductive success and conservation of the narrow-endemic Centaurea corymbosa (Asteraceae). *Biological Conservation*, *99*(3), 375–386. https://doi.org/10.1016/S0006-3207(00)00229-9

Compagnoni, A., Levin, S., Childs, D. Z., Harpole, S., Paniw, M., Römer, G., Burns, J. H., Che-Castaldo, J., Rüger, N., Kunstler, G., Bennett, J. M., Archer, C. R., Jones, O. R., Salguero-Gómez, R., & Knight, T. M. (2021). Herbaceous perennial plants with short generation time have stronger responses to climate anomalies than those with longer generation time. *Nature Communications*, *12*(1), 1824. https://doi.org/10.1038/s41467-021-21977-9

Csergő, A. M., Salguero-Gómez, R., Broennimann, O., Coutts, S. R., Guisan, A., Angert, A. L., Welk, E., Stott, I., Enquist, B. J., McGill, B., Svenning, J.-C., Violle, C., & Buckley, Y. M. (2017). Less favourable climates constrain demographic strategies in plants. *Ecology Letters*, *20*(8), 969–980. https://doi.org/10.1111/ele.12794

Damgaard, C. (2019). A Critique of the Space-for-Time Substitution Practice in Community Ecology. *Trends in Ecology & Evolution*, *34*(5), 416–421. https://doi.org/10.1016/j.tree.2019.01.013

Detto, M., Visser, M. D., Wright, S. J., & Pacala, S. W. (2019). Bias in the detection of negative density dependence in plant communities. *Ecology Letters*, *22*(11), 1923–1939. https://doi.org/10.1111/ele.13372

Dietze, M. C., Fox, A., Beck-Johnson, L. M., Betancourt, J. L., Hooten, M. B., Jarnevich, C. S., Keitt, T. H., Kenney, M. A., Laney, C. M., Larsen, L. G., Loescher, H. W., Lunch, C. K., Pijanowski, B. C., Randerson, J. T., Read, E. K., Tredennick, A. T., Vargas, R., Weathers, K. C., & White, E. P. (2018). Iterative near-term ecological forecasting: Needs, opportunities, and challenges. *Proceedings of the National Academy of Sciences*, *115*(7), 1424–1432. https://doi.org/10.1073/pnas.1710231115

Doak, D. F., & Morris, W. F. (2010). Demographic compensation and tipping points in climate-induced range shifts. *Nature*, *467*(7318), 959–962. https://doi.org/10.1038/nature09439

Fortin, M.-J., Drapeau, P., & Legendre, P. (1989). Spatial Autocorrelation and Sampling Design in Plant Ecology. *Vegetatio*, *83*(1/2), 209–222.

Gelman, A., Hill, J., & Vehtari, A. (2020). *Regression and Other Stories*. Cambridge University Press.

Gilman, S. E., Urban, M. C., Tewksbury, J., Gilchrist, G. W., & Holt, R. D. (2010). A framework for community interactions under climate change. *Trends in Ecology & Evolution*, *25*(6), 325–331.

Grevstad, F. S., Wepprich, T., Barker, B., Coop, L. B., Shaw, R., & Bourchier, R. S. (2022). Combining photoperiod and thermal responses to predict phenological mismatch for introduced insects. *Ecological Applications*, *32*(3), e2557. https://doi.org/10.1002/eap.2557

Harris, D. J., Taylor, S. D., & White, E. P. (2018). Forecasting biodiversity in breeding birds using best practices. *PeerJ*, *6*, e4278. https://doi.org/10.7717/peerj.4278

Hartman, M. D., Parton, W. J., Derner, J. D., Schulte, D. K., Smith, W. K., Peck, D. E., Day, K. A., Del Grosso, S. J., Lutz, S., Fuchs, B. A., Chen, M., & Gao, W. (2020). Seasonal grassland productivity forecast for the U.S. Great Plains using Grass-Cast. *Ecosphere*, *11*(11), e03280. https://doi.org/10.1002/ecs2.3280

Iler, A. M., Compagnoni, A., Inouye, D. W., Williams, J. L., CaraDonna, P. J., Anderson, A., & Miller, T. E. X. (2019). Reproductive losses due to climate change-induced earlier flowering are not the primary threat to plant population viability in a perennial herb. *Journal of Ecology*, *107*(4), 1931–1943. https://doi.org/10.1111/1365-2745.13146

Jones, W. G., Hill, K. D., & Allen, J. M. (1995). Wollemia nobilis, a new living Australian genus and species in the Araucariaceae. *Telopea - Journal of Plant Systematics*, *6*, 173–176. https://doi.org/10.7751/telopea19953014

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, *4*(1), 1–20. https://doi.org/10.1038/sdata.2017.122

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2018). *Data from: Climatologies at high resolution for the earth's land surface areas* (Version 1, p. 7266827510 bytes) [Data set]. Dryad. https://doi.org/10.5061/DRYAD.KD1D4

Kleinhesselink, A. R., & Adler, P. B. (2018). The response of big sagebrush (Artemisia tridentata) to interannual climate variation changes across its range. *Ecology*, *99*(5), 1139–1149. https://doi.org/10.1002/ecy.2191

Knape, J., & de Valpine, P. (2011). Effects of weather and climate on the dynamics of animal population time series. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1708), 985–992. https://doi.org/10.1098/rspb.2010.1333

Lewontin, R. C., & Cohen, D. (1969). On population growth in a randomly varying environment. *Proceedings of the National Academy of Sciences*, *62*(4), 1056–1060.

Lindell, T., Ehrlén, J., & Dahlgren, J. P. (2022). Weather-driven demography and population dynamics of an endemic perennial plant during a 34-year period. *Journal of Ecology*, *110*(3), 582–592. https://doi.org/10.1111/1365-2745.13821

Mace, G. M., Collar, N. J., Gaston, K. J., Hilton-Taylor, C., Akçakaya, H. R., Leader-Williams, N., Milner-Gulland, E. J., & Stuart, S. N. (2008). Quantification of Extinction Risk: IUCN's System for Classifying Threatened Species. *Conservation Biology*, *22*(6), 1424–1442. https://doi.org/10.1111/j.1523-1739.2008.01044.x

Merow, C., Latimer, A. M., Wilson, A. M., McMahon, S. M., Rebelo, A. G., & Silander, J. A. (2014). On using integral projection models to generate demographically driven predictions of species' distributions: Development and validation using sparse data. *Ecography*, *37*(12), 1167–1183. https://doi.org/10.1111/ecog.00839

Morley, J. W., Batt, R. D., & Pinsky, M. L. (2017). Marine assemblages respond rapidly to winter climate variability. *Global Change Biology*, *23*(7), 2590–2601. https://doi.org/10.1111/gcb.13578

Nicolè, F., Dahlgren, J. P., Vivat, A., Till-Bottraud, I., & Ehrlén, J. (2011). Interdependent effects of habitat quality and climate on population growth of an endangered plant. *Journal of Ecology*, *99*(5), 1211–1218. https://doi.org/10.1111/j.1365-2745.2011.01852.x

Paniw, M., James, T. D., Archer, C. R., Römer, G., Levin, S., Compagnoni, A., Che-Castaldo, J., Bennett, J. M., Mooney, A., Childs, D. Z., Ozgul, A., Jones, O. R., Burns, J. H., Beckerman, A. P., Patwary, A., Sanchez-Gassen, N., Knight, T. M., & Salguero-Gómez, R. (2021). The myriad of complex demographic responses of terrestrial mammals to climate change and gaps of knowledge: A global analysis. *Journal of Animal Ecology*, *n/a*(n/a). https://doi.org/10.1111/1365-2656.13467

Salguero-Gómez, R., Jones, O. R., Archer, C. R., Bein, C., de Buhr, H., Farack, C., Gottschalk, F., Hartmann, A., Henning, A., Hoppe, G., Römer, G., Ruoff, T., Sommer, V., Wille, J., Voigt, J., Zeh, S., Vieregg, D., Buckley, Y. M., Che-Castaldo, J., … Vaupel, J. W. (2016). COMADRE: A global data base of animal demography. *Journal of Animal Ecology*, *85*(2), 371–384. https://doi.org/10.1111/1365-2656.12482

Salguero-Gómez, R., Jones, O. R., Archer, C. R., Buckley, Y. M., Che-Castaldo, J., Caswell, H., Hodgson, D., Scheuerlein, A., Conde, D. A., Brinks, E., de Buhr, H., Farack, C., Gottschalk, F., Hartmann, A., Henning, A., Hoppe, G., Römer, G., Runge, J., Ruoff, T., … Vaupel, J. W. (2015). The COMPADRE Plant Matrix Database: An open online repository for plant demography. *Journal of Ecology*, *103*(1), 202–218. https://doi.org/10.1111/1365-2745.12334

Schurr, F. M., Pagel, J., Cabral, J. S., Groeneveld, J., Bykova, O., O'Hara, R. B., Hartig, F., Kissling, W. D., Linder, H. P., Midgley, G. F., Schröder, B., Singer, A., & Zimmermann, N. E. (2012). How to understand species' niches and range dynamics: A demographic research agenda for biogeography. *Journal of Biogeography*, *39*(12), 2146–2162. https://doi.org/10.1111/j.1365-2699.2012.02737.x

Sexton, J. P., McIntyre, P. J., Angert, A. L., & Rice, K. J. (2009). Evolution and Ecology of Species Range Limits. *Annual Review of Ecology, Evolution, and Systematics*, *40*(1), 415–436. https://doi.org/10.1146/annurev.ecolsys.110308.120317

Sheth, S. N., & Angert, A. L. (2018). Demographic compensation does not rescue populations at a trailing range edge. *Proceedings of the National Academy of Sciences*, *115*(10), 2413–2418. https://doi.org/10.1073/pnas.1715899115

Sibly, R. M., & Hone, J. (2002). Population growth rate and its determinants: An overview. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *357*(1425), 1153–1170. https://doi.org/10.1098/rstb.2002.1117

Sletvold, N., Dahlgren, J. P., Øien, D.-I., Moen, A., & Ehrlén, J. (2013). Climate warming alters effects of management on population viability of threatened species: Results from a 30-year

experimental study on a rare orchid. *Global Change Biology*, *19*(9), 2729–2738. https://doi.org/10.1111/gcb.12167

Suttle, K. B., Thomsen, M. A., & Power, M. E. (2007). Species Interactions Reverse Grassland Responses to Changing Climate. *Science*, *315*(5812), 640–642. https://doi.org/10.1126/science.1136401

Teller, B. J., Adler, P. B., Edwards, C. B., Hooker, G., & Ellner, S. P. (2016). Linking demography with drivers: Climate and competition. *Methods in Ecology and Evolution*, *7*(2), 171–183. https://doi.org/10.1111/2041-210X.12486

Tenhumberg, B., Crone, E. E., Ramula, S., & Tyre, A. J. (2018). Time-lagged effects of weather on plant demography: Drought and Astragalus scaphoides. *Ecology*, *99*(4), 915–925. https://doi.org/10.1002/ecy.2163

Thorne, J. H., Viers, J. H., Price, J., & Stoms, D. M. (2009). Spatial Patterns of Endemic Plants in California. *Natural Areas Journal*, *29*(4), 344–366. https://doi.org/10.3375/043.029.0402

Tye, M., Dahlgren, J. P., Øien, D.-I., Moen, A., & Sletvold, N. (2018). Demographic responses to climate variation depend on spatial- and life history-differentiation at multiple scales. *Biological Conservation*, *228*, 62–69. https://doi.org/10.1016/j.biocon.2018.10.005

Urban, M. C., Bocedi, G., Hendry, A. P., Mihoub, J.-B., Peer, G., Singer, A., Bridle, J. R., Crozier, L. G., De Meester, L., Godsoe, W., Gonzalez, A., Hellmann, J. J., Holt, R. D., Huth, A., Johst, K., Krug, C. B., Leadley, P. W., Palmer, S. C. F., Pantel, J. H., … Travis, J. M. J. (2016). Improving the forecast for biodiversity under climate change. *Science*, *353*(6304), aad8466–aad8466. https://doi.org/10.1126/science.aad8466

Villellas, J., Ehrlén, J., Crone, E. E., Csergő, A. M., Garcia, M. B., Laine, A., Roach, D. A., Salguero-Gómez, R., Wardle, G. M., Childs, D. Z., Elderd, B. D., Finn, A., Munné-Bosch, S., Bachelot, B., Bódis, J., Bucharova, A., Caruso, C. M., Catford, J. A., Coghill, M., … Buckley, Y. M. (2021). Phenotypic plasticity masks range-wide genetic differentiation for vegetative but

not reproductive traits in a short-lived plant. *Ecology Letters*, *24*(11), 2378–2393. https://doi.org/10.1111/ele.13858

Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed Effects Models and Extensions in Ecology with R*. Springer Science & Business Media.

FIGURE LEGENDS

Figure 1. The correlation between temperature and precipitation anomalies decays slowly with distance. The left column shows how temperature (A) and precipitation (C) anomalies change with distance from a reference location located in the middle of the great plains. The right column shows heatmaps of correlations in temperature (B) and precipitation (D) anomalies between the reference location (red point) and the remaining points for which we sampled climatic data.

Figure 2. The lower temporal correlation between two climatic anomalies allows to sample a larger absolute range of anomalies. Bivariate plot representing the range of climate anomalies sampled (y-axis) at two hypothetical sites, as a function of years sampled (x-axis). The color of dots shows the correlation of climate anomalies at these two hypothetical sites. A correlation of one implies that the two sites experience identical climatic anomalies each year.

Figure 3. Spatial replication provides a statistical power similar, or higher, to temporal replication. Plot showing statistical power on the y-axis against spatial replication on the x-axis. Symbols show temporal replication which goes from three (triangles), five (circles), 20 (square), and 30 (cross). The color of symbols refers to the correlation among spatial replicates. This correlation is one for the simulations with a single spatial replicate. The dashes horizontal line highlights a statistical power of 80%.

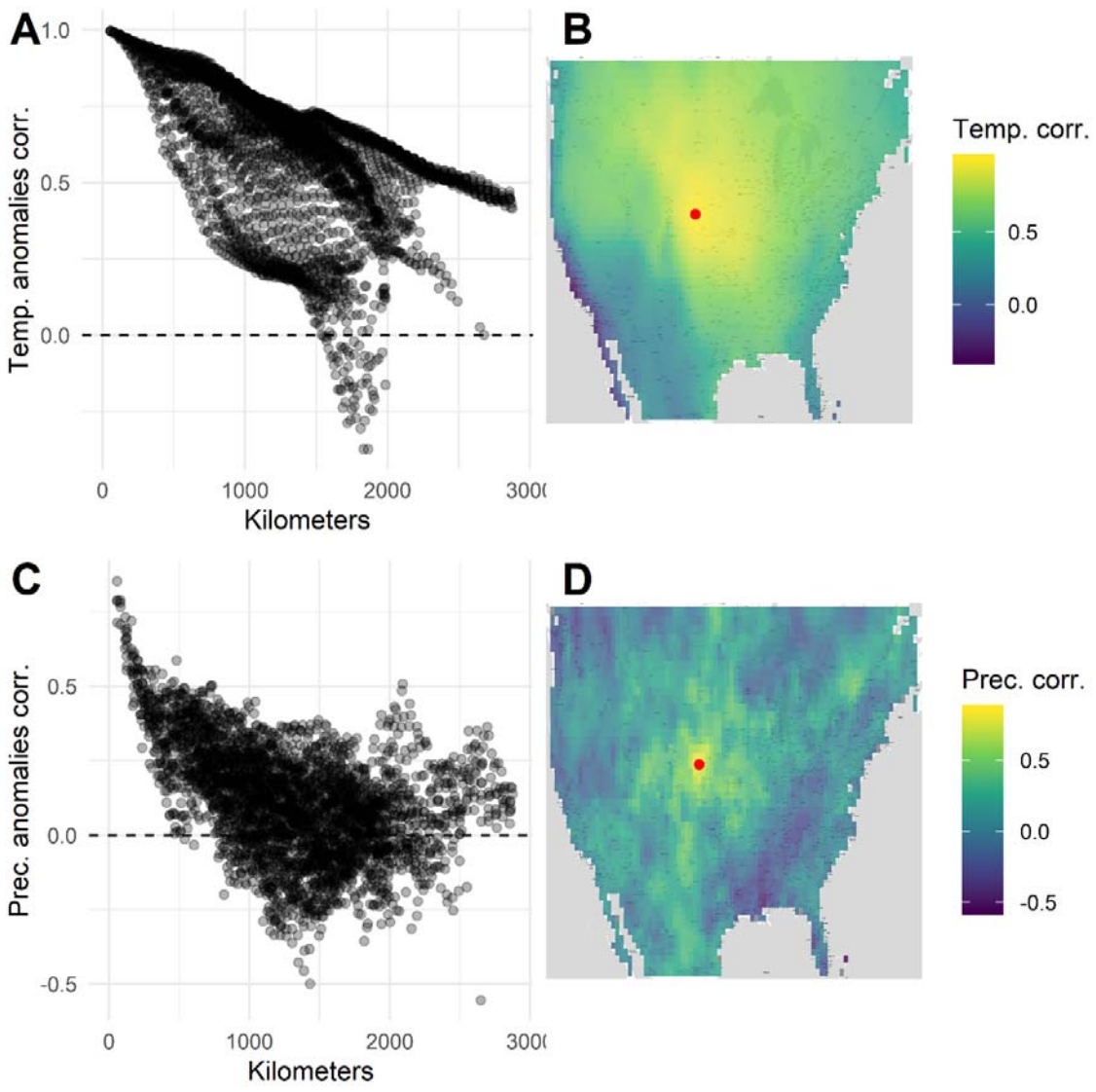
A
1.0
0.5
0.0
Temp. anomalies corr.
0
1000
2000
Kilometers
B
Temp. corr.
0.5
0.0
C
0.5
0.0
-0.5
Prec. anomalies corr.
0
1000
2000
Kilometers
D
Prec. corr.
0.5
0.0
-0.5

Figure 1.

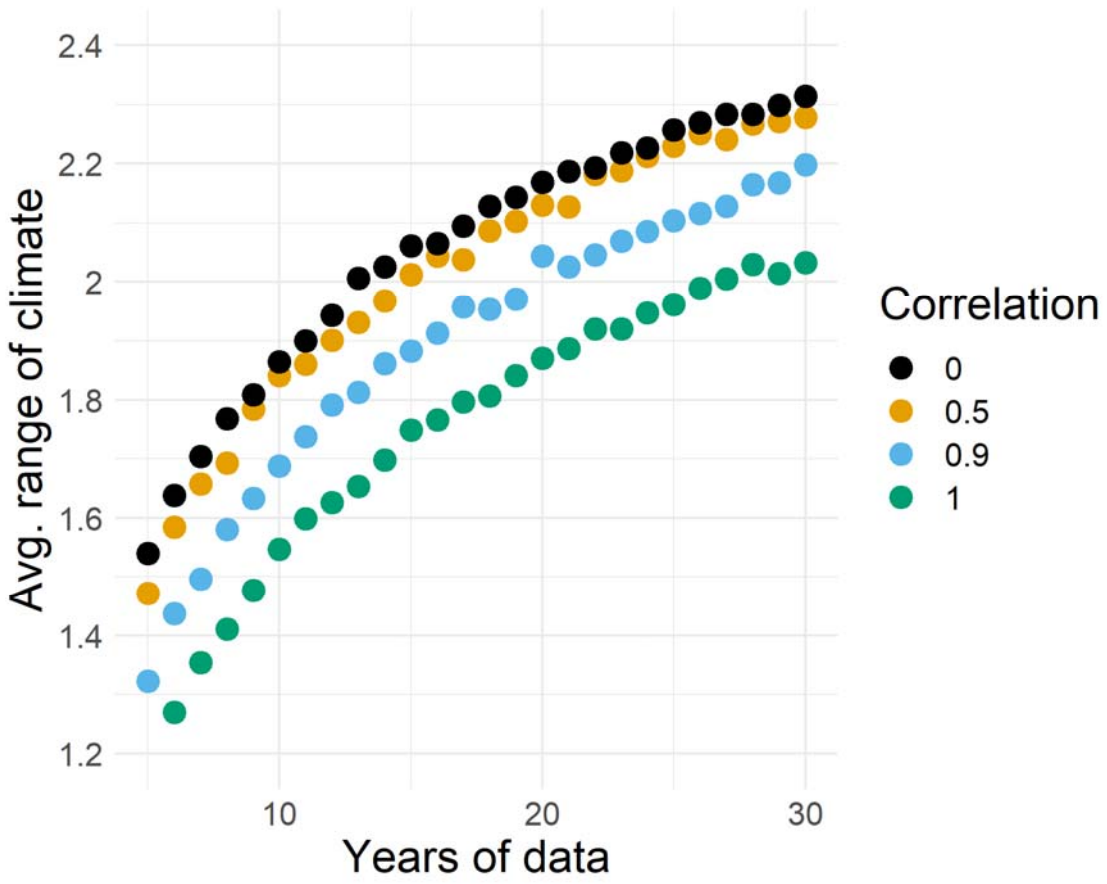
2.4
2.2
2
1.8
1.6
1.4
1.2
Avg. range of climate
10
20
30
Years of data
Correlation
0
0.5
0.9
1

Figure 2.

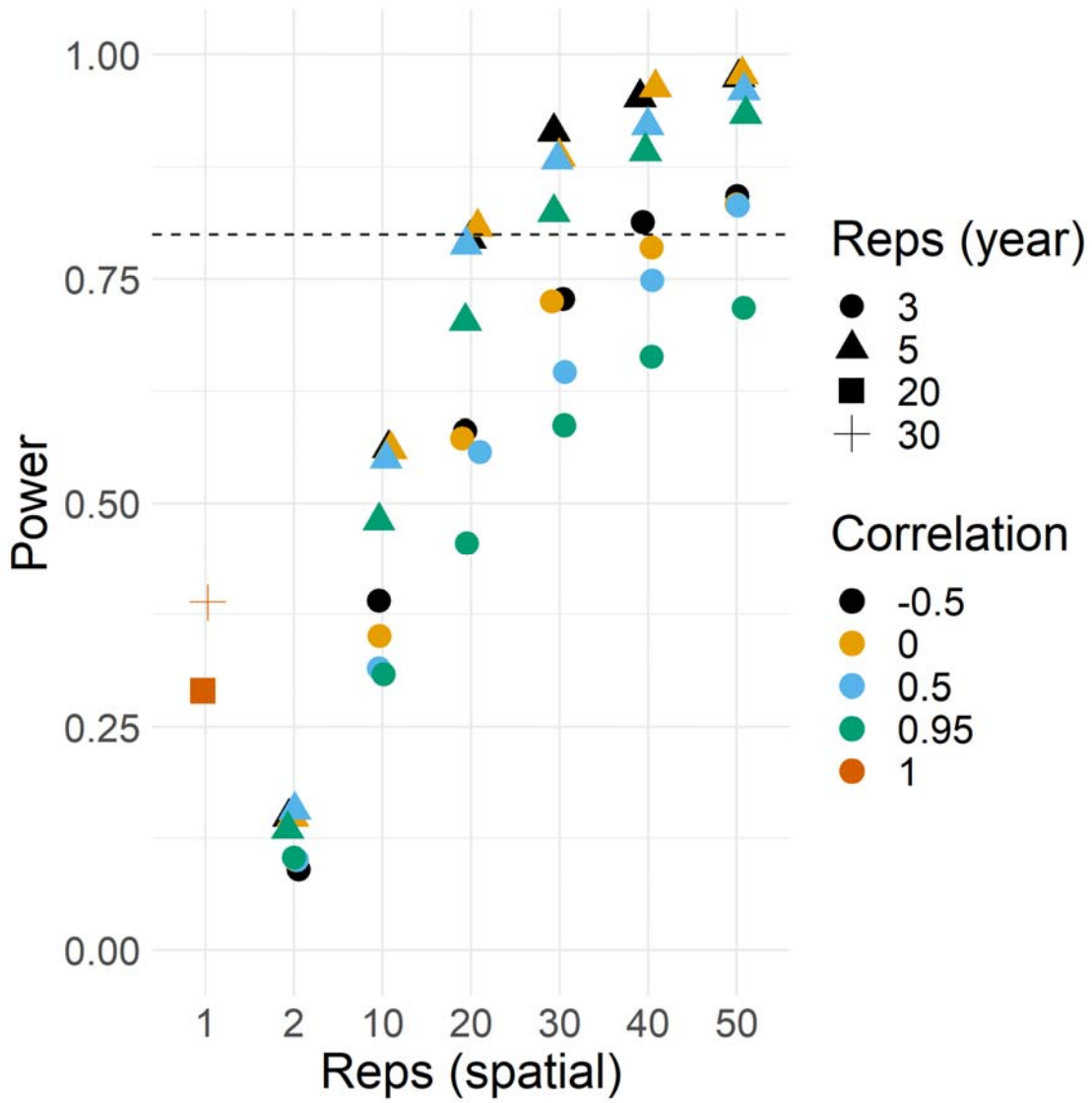
1.00
0.75
0.50
0.25
0.00
Power
1
2
10
20
30
40
50
Reps (spatial)
Reps (year)
3
5
20
30
Correlation
-0.5
0
0.5
0.95
1

Figure 3.