

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

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5 Running head: spatial replicates estimate climate effects

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12 **Abstract**

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

29

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

32 INTRODUCTION

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

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

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

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

60 Here, we are not advocating a “space-for-time substitution”, but simply to prioritize spatial
61 versus temporal replication. Space-for-time substitution studies use spatial gradients that differ
62 dramatically in climate to infer temporal links between climate and population dynamics (Blois et al.,
63 2013). Here, we are instead advocating to replicate sampling across populations that occur in similar
64 climates, and to use this spatial data as a *replicate* of the same temporal process. This
65 recommendation relies on the assumption that in similar environments, plant populations should
66 respond similarly to climate anomalies. For example, the effect of hot or cold years on the growth
67 rate of populations all located at the upper elevational limit of a species’ range should be similar in
68 sign and magnitude (Kleinhesselink & Adler, 2018; Morley et al., 2017). There are already many
69 studies that sample populations across species’ ranges in order to capture different climates (e.g.
70 Doak & Morris, 2010; Kleinhesselink & Adler, 2018; Merow et al., 2014; Sheth & Angert, 2018).
71 However, to our knowledge, no plant population study has yet prioritized spatial replication across
72 sites with similar climatic conditions to study climate-demography relationships.

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

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

87 **METHODS**

88 *Spatial correlation in climate*

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

103 For each of these five reference locations, we calculated the correlation between its 35
104 annual temperature and precipitation anomalies, and the same anomalies observed at the other
105 3252 locations. We plotted the correlation between climatic anomalies versus the distance from the
106 reference location. We produced heatmaps showing the correlation of the climatic anomalies with
107 the reference locations.

108

109 *Range of climates sampled with different sampling designs*

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

$$114 \quad \mathbf{X} \sim \text{Normal}(0,1), \quad (1a)$$

$$115 \quad \text{Range}_x = \frac{\text{Max}(X) - \text{Min}(X)}{2}, \quad (1b)$$

116 where \mathbf{X} is a vector of climate anomalies at the site. The length of \mathbf{X} is n , which is the temporal
117 replication of the study. The standard deviation in Eq. 1a is one, reflecting that we are simulating a
118 series of anomalies. To obtain Range_x , the expected range of \mathbf{X} values (Eq. 1b), we simulated Eq. 1a
119 1000 times across n values ranging from two to 30 in increments of one. We calculated the mean of
120 Range_x across these 1000 replicate simulations.

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

$$123 \quad \mathbf{X} \sim \text{MVN}(\mathbf{0}, \begin{bmatrix} 1 & \rho \\ \rho & 1 \end{bmatrix}), \quad (2)$$

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

128

129 *Statistical power for climate-demography relationship with different sampling designs*

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

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

$$134 \quad \mathbf{X} \sim \text{Normal}(0,1), \quad (3a)$$

$$135 \quad \hat{Y}_i = \beta_0 + \beta_1 X_i, \quad (3b)$$

$$136 \quad Y_i \sim \text{Normal}(\hat{Y}_i, \varepsilon), \quad (3a)$$

137 where \mathbf{X} is a vector of size n of normally distributed climatic anomalies, \hat{Y}_i is the average prediction of
138 the model, β_0 the intercept of the linear model, β_1 is the slope, and Y_i represents the natural
139 logarithm of a population growth rate at year i . We used a log population growth rate because we
140 have synthetic estimates of climatic effects on this variable (Compagnoni et al., 2021), because this
141 variable is the central focus of demographic theory (Caswell, 2001; Lewontin & Cohen, 1969; Sibly &
142 Hone, 2002), and because log population growth rate is normally distributed, facilitating simulations
143 and their interpretation by the reader. We simulated the process in Eq. 3 1000 times, assuming
144 study durations, n , of 20, and 30 years. For this and subsequent simulations we used a β_1 value of
145 0.05, and a ε value of 0.15. Our choice of β_1 reflects the effect size of precipitation anomalies on log
146 population growth rate that we estimated across 162 plant populations (Compagnoni et al., 2021).
147 The choice of our ε reflects the median standard deviation of the log population growth rate
148 estimated on the same 162 populations.

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

$$151 \quad \mathbf{X} \sim \text{MVN}(\mathbf{0}, \begin{bmatrix} 1 & \rho \\ \rho & 1 \end{bmatrix}), \quad (4a)$$

$$152 \quad \hat{Y}_{ip} = \beta_0 + \beta_1 X_{ip}, \quad (4b)$$

$$153 \quad Y_{ip} \sim \text{Normal}(\hat{Y}_{ip}, \varepsilon), \quad (4c)$$

154 where ρ is the correlation between the climatic anomalies of two sites, and subscript p refers to each
155 site. We simulated the process described in Eq. 4 1000 times using study durations, n , of three and
156 five years, correlations ρ of 0.95 and 0.5, 0, and -0.5 and a number of spatial replicates of two, 10,
157 20, 30, 40, and 50. When the number of spatial replicates exceeded two, we divided the populations
158 in two subsets, and assigned each subset to one of the two series of climatic anomalies simulated by
159 Eq. 4a. For example, when spatial replicates were 50, we subdivided these replicates in two groups
160 of 25 replicates. Note that replicates within each group experienced identical climate. We used low
161 values for n to reflect that the median length of demographic studies of plants is four years
162 (Salguero-Gómez et al., 2015). This sampling effort likely reflects the length of many PhD programs.
163 We calculated power as the proportion of the 1000 simulations for which β_1 had a p-value below
164 0.05. We performed a power analysis not because we expect investigators to perform null
165 hypothesis tests relying on p-values. Rather, our power analysis is a simple, intuitive way to quantify
166 how the uncertainty of model estimates is influenced by the sampling design.

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

176
$$\beta_{1g} \sim \text{Normal}(\mu = 0.05, \sigma), \quad (5)$$

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

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

182 **RESULTS**

183 *Spatial correlation in climate*

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

192

193 *Range of climates sampled with different sampling designs*

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

199

200 *Statistical power for climate-demography relationship with different sampling designs*

201 Our power analysis indicates that spatial replication greatly increases the power to detect a
202 relationship between climate and population growth rate (Fig. 3). The statistical power of very long
203 time series for a single site is comparable to that of datasets with high spatial replication. This holds
204 even when the climate of the spatial replicates has a high correlation (e.g. correlation 0.95, Fig. 3).
205 20 and 25 temporal replicates with one spatial replicate provides a statistical power of about 30 and

206 40%, respectively. These two statistical powers are reached by just three temporal replicates with,
207 respectively, 10 and 20 spatial replicates experiencing highly correlated climate (0.5, 0.95). Still
208 assuming high climatic correlations, statistical power exceeds 40% when the temporal replication
209 increases to five years. Lower climatic correlation between populations slightly increases statistical
210 power: going from a climatic correlation of 0.95 to zero can increase power by over 10% when
211 temporal replicates are three (Fig. 3).

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

215 **DISCUSSION**

216 Until recently, understanding the response of plant species to temporal climatic gradients has relied
217 on either long-term monitoring efforts, which are extremely rare (Salguero-Gómez et al., 2015,
218 2016), or on responses of plant populations to spatial climate gradients ("space-for-time
219 substitutions", Blois et al., 2013), which are affected by several confounding factors (Damgaard,
220 2019). Fortunately, our power analysis shows that we can propel our understanding of species
221 responses to climate using spatial replicates that come from sites with similar climate (i.e., similar
222 long-term average climates). Moreover, dividing spatial replicates by large distances (e.g. 100 Km)
223 ensures climates are not perfectly correlated. Such imperfect correlation allows for sampling a larger
224 range of climates sampled in a shorter timeframe, further compounding gains in statistical power.
225 We believe this finding could foster progress in global climate change vulnerability assessments,
226 near-term demographic forecasts, and ecological understanding in general. Based on our results, we
227 provide suggestions on sampling designs leveraging spatial replication.

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

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

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

247 Spatial replicates are particularly suited to address two mechanisms that could confound
248 climate-demography relationship: species interactions, and microsite variation. First, species
249 interactions mediated by conspecific and heterospecific densities are known to be a key component
250 of population and community dynamics (Chesson, 2000). As a consequence, a growing body of
251 research emphasizes the role of the indirect effects of climate mediated through heterospecific
252 abundances (Adler et al., 2012; Gilman et al., 2010; Suttle et al., 2007). Understanding these effects
253 relies on estimates of conspecific and heterospecific densities which, however, are hard to perform:
254 conspecific effects are attenuated by observation error, which leads to “regression dilution” (Detto
255 et al., 2019; Knape & de Valpine, 2011). However, regression dilution is weaker as the range of
256 densities increases. In the short term, variation in conspecific densities is likely to be much greater
257 across space than time. Spatial replicates are therefore ideal to capture a wide range of conspecific
258 and heterospecific densities. The result is that spatial replication facilitates the estimation of
259 conspecific and heterospecific effects which can be used to project the effect of indirect climatic
260 effects. Second, climate effects on populations should be modulated by soil conditions (Lindell et al.,
261 2022; Nicolè et al., 2011). Reaching a general understanding on this subject could be achieved by
262 stratifying spatial replicates by soil type, and fitting hierarchical models on the resulting data.

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

265 However, even when sites are separated by relatively large distances, factors other than climate
266 (e.g. outbreaks of natural enemies) could result in spatially autocorrelated vital rates. Therefore, it is
267 prudent for investigators to plan on estimating the spatial autocorrelation among spatial replicates.
268 A previous study suggests that to estimate spatial autocorrelation, replicates should be disposed at
269 random through the landscape, rather than according to regular sampling designs (Fortin et al.,
270 1989). If detected, explicit modeling of spatial autocorrelation within linear models can increase
271 statistical power and decrease parameter uncertainty (Zuur et al., 2009).

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

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

286 While our manuscript has focused on plants, the benefits of spatial replication extends also
287 to animals with short dispersal distances. Just like in plants, the quantification of climate sensitivity
288 in animals suffers from important geographic and taxonomic biases (Paniw et al., 2021). Moreover,
289 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 lanceolata* around the world (Villemas 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

315 Integrative Biodiveristy Research (iDiv), which is funded by the German Research Foundation (FZT-
316 118-202548816).

317

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

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478 **FIGURE LEGENDS**

479

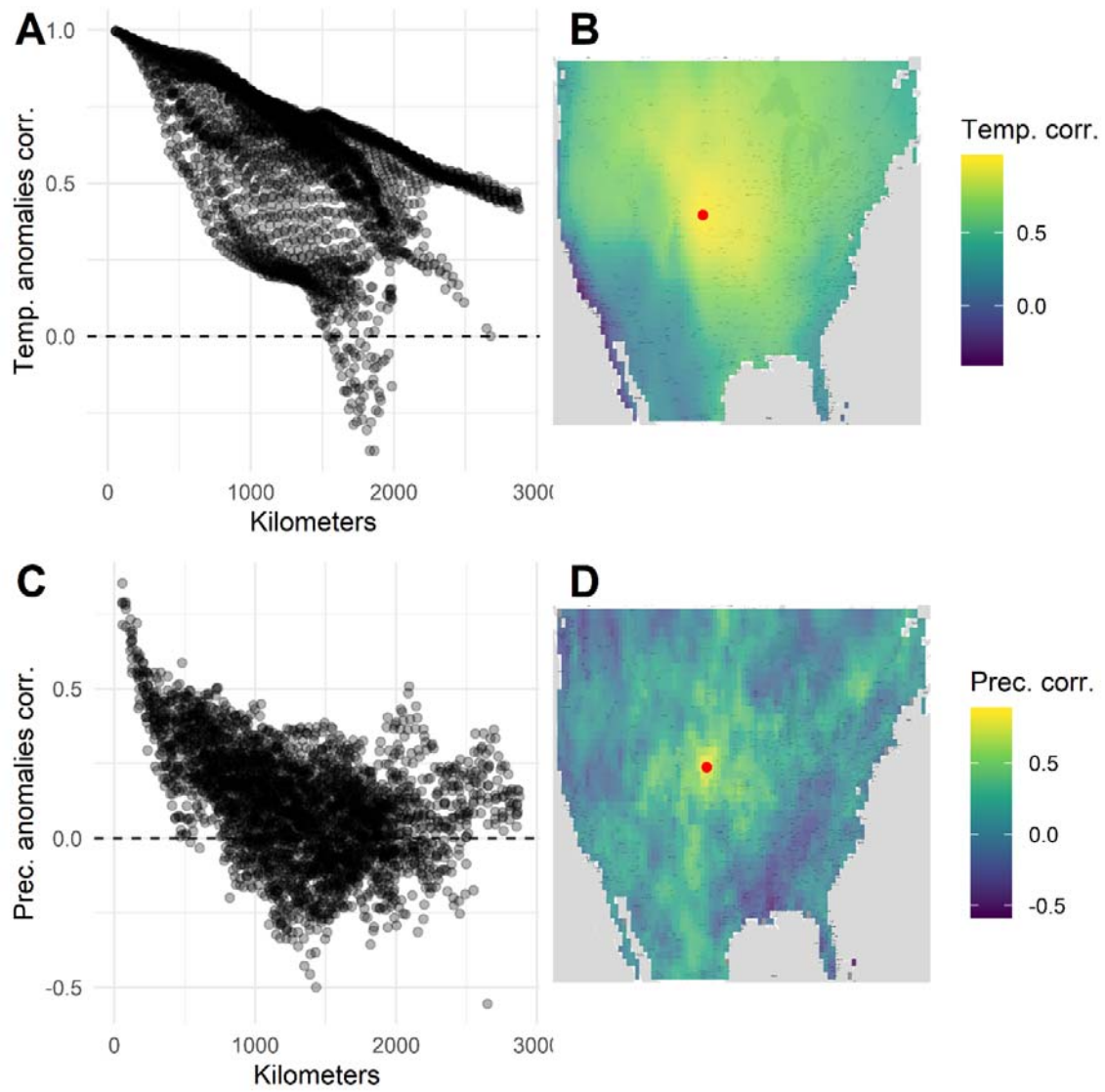
480 **Figure 1.** The correlation between temperature and precipitation anomalies decays slowly with
481 distance. The left column shows how temperature (A) and precipitation (C) anomalies change with
482 distance from a reference location located in the middle of the great plains. The right column shows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

485

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

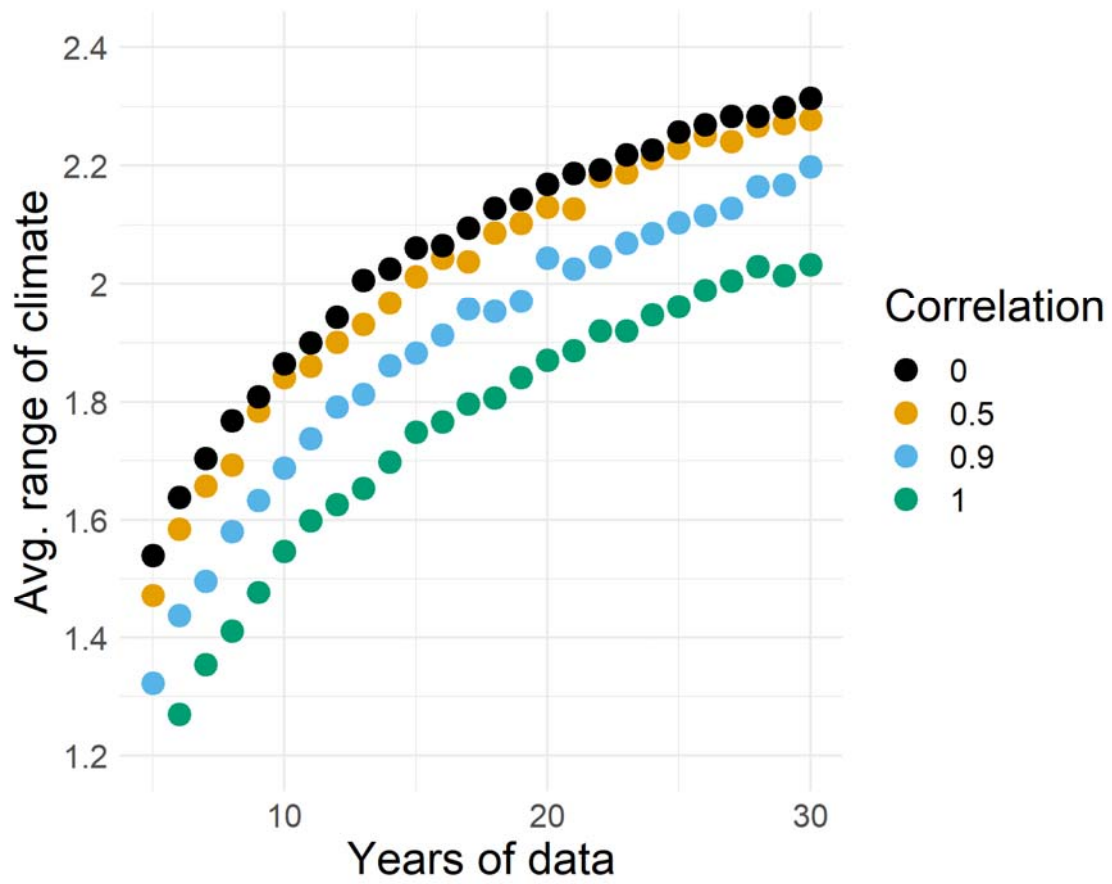
491

492 **Figure 3.** Spatial replication provides a statistical power similar, or higher, to temporal replication.
493 Plot showing statistical power on the y-axis against spatial replication on the x-axis. Symbols show
494 temporal replication which goes from three (triangles), five (circles), 20 (square), and 30 (cross). The
495 color of symbols refers to the correlation among spatial replicates. This correlation is one for the
496 simulations with a single spatial replicate. The dashed horizontal line highlights a statistical power of
497 80%.



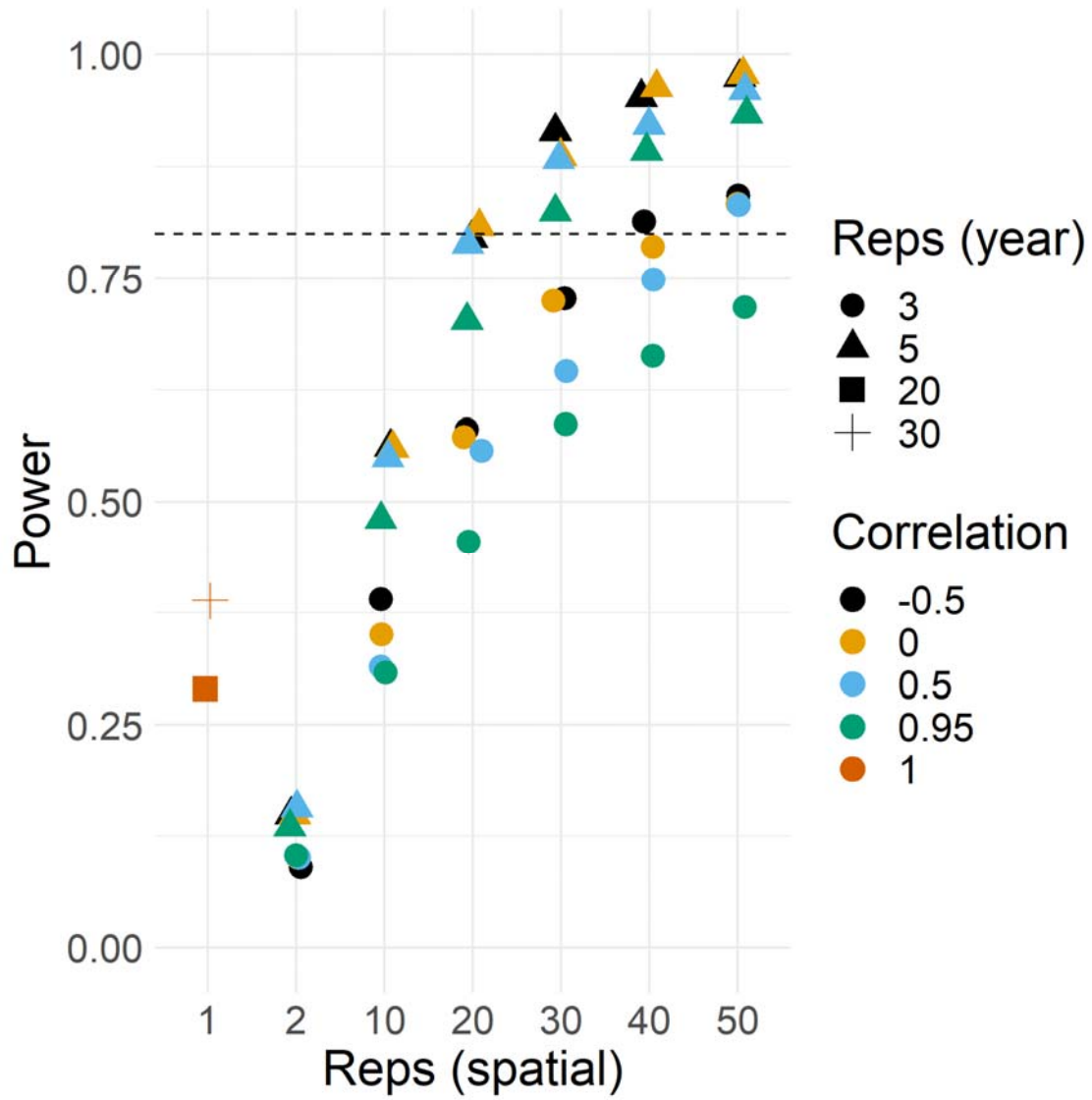
498

499 **Figure 1.**



500

501 **Figure 2.**



502

503 Figure 3.