Spatial replication can best advance our understanding of population responses to climate

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Running head: climate effects on populations

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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, the field of ecological forecasting has experienced substantial theoretical and applied growth (Grevstad et al., 2022; Harris et al., 2018; Hartman et al., 2020). These forecasts on population dynamics are necessary to assess species extinction risk (Mace et al., 2008) and predict range shifts (Schurr et al., 2012). However, forecasting the effects of climate on populations remains elusive. This plausibly occurs because 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 sufficiently wide range of climatic conditions and to increase statistical power.

We have important knowledge gaps in population ecology that cannot wait 20-25 years to be filled. Our recent synthesis showed 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.

We propose 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 by increasing the range of climates that can be sampled across a short period of time, and 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 from each other that the correlation of yearly climatic anomalies among them is low.

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 *replicates* of the same temporal process. This recommendation relies on the assumption that in similar environments, plant populations should respond similarly to climate anomalies. This assumption has so far motivated much research on the demography across species ranges (Kleinhesselink & Adler, 2018; Morley et al., 2017; Sheth & Angert, 2018). However, to our knowledge, no study on climate-demography relationships has yet prioritized spatial replication across sites with similar climatic conditions.

In this manuscript, we show the opportunities of spatial replication in climate-demography studies through data analysis and simulation. First, we assess how far apart populations must be from each other to attenuate temporal correlations in climate using gridded climatic data from the conterminous USA. Second, we consider how sampling design can maximize the range of climates captured during a study. To do so, we estimate how the range of climates sampled depends on the climate correlations among the 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 in the strength of spatial correlations in climate between populations. In this simulation, we also address cases in which populations respond differently to climate. Based on these results, we make recommendations for new demographic research.

METHODS

Spatial correlation in climate

To understand how spatial correlation in climate depends on the distance between sites, we estimate the spatial correlation of annual climate in the conterminous United States of America (USA), a large and climatically heterogeneous section of terrestrial environments. We downloaded monthly temperature and precipitation data for the conterminous USA from the CHELSA database (Karger et al., 2017, 2018). CHELSA data is accurate on varied topographic terrain, and gridded climatic data generally correlates strongly with weather station data (Behnke et al., 2016). We downloaded data between 1979 and 2013 following a regular grid of 0.5 degrees, for a total of 3253 locations. For each location, we calculated annual temperature means, annual precipitation sums, and computed their standardized yearly anomalies (z-scores, henceforth "anomalies"). We analyzed the correlation of temperature and precipitation anomalies using five reference locations. We picked these locations subjectively, locating them in the Southwestern coast, Northwestern coast, Northeastern Coast, Southeastern coast, and in the center of the USA.

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. Moreover, 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 depending on temporal replication, spatial replication, and the spatial correlation of climatic

anomalies. We estimated the range of climatic anomalies sampled at two sites using a multivariate normal (MVN) distribution:

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

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

where **X** is an *n* by 2 matrix of climate anomalies at two separate sites, *n* is the temporal replication of the study, ρ represents the correlation between the climatic anomalies of the two sites. The parameters of the MVN distribution show **0** for the means, and diagonal elements of 1 for the variance to simulate a series of anomalies. When simulating the climate at a single site, we needed a single series of climate anomalies, so we substituted Eq. (1a) with X ~ N(0,1). 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, and across a series of ρ values of 0, 0.5, 0.95, and one. We calculated the mean of $\mathbf{Range_X}$ across these 1000 replicate simulations.

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. Starting from a case with two separate sites,

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

$$\hat{Y}_{is} = \beta_0 + \beta_1 X_{is}, \qquad (2b)$$

$$Y_{is} \sim Normal(\hat{Y}_{is}, \varepsilon) \qquad (2c)$$

where ***X*** is an *n* by 2 matrix of normally distributed climatic anomalies, *n* refers to temporal replicates, $\hat{Y}_{is}$ is the average prediction of the model referred to site *s* and year *i*, β_0 the intercept of

the linear model, β_1 is the slope, and Y_{is} represents the observed log population growth rate. Y_i is a log population growth rate because we have synthetic estimates of climatic effects on this variable (Compagnoni et al., 2021), because it is the central focus of demographic theory (Caswell, 2001; Lewontin & Cohen, 1969; Sibly & Hone, 2002), and because it is normally distributed, facilitating simulations and their interpretation. For this and subsequent simulations we used a β_1 value of 0.05, and a ε value of 0.15 to reflect empirical estimates from 162 plant populations (Compagnoni et al., 2021). We simulated the process described in Eq. 2 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. 2. For example, when spatial replicates were 50, we subdivided these replicates in two groups of 25 replicates, each group experiencing 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.

As an alternative, we also simulated assuming a single population, using study durations of 20 and 30 years. This simulation was meant to represent the handful of single site, long-term studies found in the literature (Chu et al., 2016). In these simulations, we substituted Eq. 2a with $X \sim N(0,1)$. We calculated power as the proportion of the 1000 simulations for which β_1 had a p-value below 0.05. This power analysis is a straightforward 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. 2b, were the same for each population. In the Appendix, we address the sensitivity of our power estimates to spatial variation in β_1.

RESULTS

Spatial correlation in climate

In the conterminous USA 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). In the conterminous USA, the distance to reach a correlation of 0.5 is approximately at least 100 Km for both precipitation (Fig. S1) and temperature (Fig. S2).

Range of climates sampled with different sampling designs

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 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 (Fig. S5).

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. 2). The statistical power of very long time series for a single site is comparable to that of datasets with high spatial replication. One site sampled for 20 and 25 times provides a statistical power of about 30 and 40%, respectively. These two statistical powers are reached in just three temporal samples with, respectively, 10 and 20 spatial replicates experiencing medium to highly correlated climate (0.5, 0.95); 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. 2).

Assuming variation in the effect of climate on demography (represented by β_1 values) did not noticeably affect statistical power (Fig. S6). Statistical power remained unchanged, reflecting that the average β_1 is still 0.05.

DISCUSSION

Until recently, understanding the response of plant species to climatic variation has relied on either long-term monitoring efforts, which are 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 long-term average climates.

We argue that using numerous spatial replicates in studies of demographic responses to climate is an opportunity that should be exploited urgently by conservation scientists. Our power analysis suggests that large spatial replication allows obtaining estimates of climate effects in as little as three years. This short temporal horizon would allow early career researchers or distributed networks to study the effects of climatic variability on populations. Such abundance of investigators would enable covering the taxonomic, geographic, and life-history biases present in current data (e.g. Compagnoni et al., 2021). The result would propel species vulnerability assessments which, while ideally focused on population-level data (Mace et al., 2008), must often rely on distribution data instead (BGCI, 2021).

In a context of global change, we suggest new studies focusing on sites with similar climate located at the leading or rear edge of species ranges. These locations have climate conditions in which contractions and expansions are occurring, and thus offer an opportunity to understand range limits and forecasting future ranges of species (Ehrlén & Morris, 2015; Parmesan, 2006). However, to date, studies of this kind are missing from the literature.

We believe that the assumptions of our power analysis are likely to hold, as they reflect current ecological understanding. First, the assumption that populations experiencing the same average climate respond similarly to climate variation is well supported in the literature (Kleinhesselink & Adler, 2018; Morley et al., 2017). Moreover, our power analysis is robust to

relaxing this assumption (Fig. S6). Second, the assumption that residual variance (represented by ε in Eq. 2c) is constant across replicates also reflects the current literature. Specifically, the literature finds that the variability of population growth rates should become larger only at range edges (Csergő et al., 2017; Sexton et al., 2009). Third, so long as the spatial replicates are sufficiently spaced, they should meet the assumption of statistical independence (e.g., separated by dispersal). In principle, statistical independence might not hold in response to large-scale drivers such as herbivores with large foraging ranges, or epidemic outbreaks. For this reason, we recommend testing for the presence of spatial autocorrelation in the residuals (see below).

To increase ecological inference, we suggest that researchers explicitly consider the covariates that might mediate demographic responses to climate, such as soil conditions (Lindell et al., 2022; Nicolè et al., 2011) and competitors (Alexander et al., 2015), and examine the roles of these covariates in statistical analyses. We further suggest that spatial replicates should be chosen randomly, as this facilitates our ability to detect spatial autocorrelations that might occur due to unexpected, large-scale processes such as epidemics (Fortin et al., 1989). Testing for spatial autocorrelation is important, because its presence indicates that the spatial replicates are not fully independent. Finally, while distributing sites by 100 Km might be possible for a distributed network of researchers, this may be prohibitively expensive or logistically difficult for a doctoral researcher. We suggest that given the relatively small effect of climate correlation on statistical power, that smaller spacing between populations might be reasonable and advantageous.

The spatially replicated sampling we propose here is a practical solution to estimate climate-demography relationships and rapidly fill important knowledge gaps in the field of population ecology. However, monitoring 20 or more populations simultaneously is a large task for a single researcher. Such spatial replication might become more feasible with modern methods, such as unmanned aerial vehicles (Bogdan et al., 2021), and through collaborative research networks (e.g. Villellas et al., 2021). We believe that the sampling choices we advocate in this article will contribute

to the maturation of population ecology and its links to conservation science, functional ecology, and macro-ecology.

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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.

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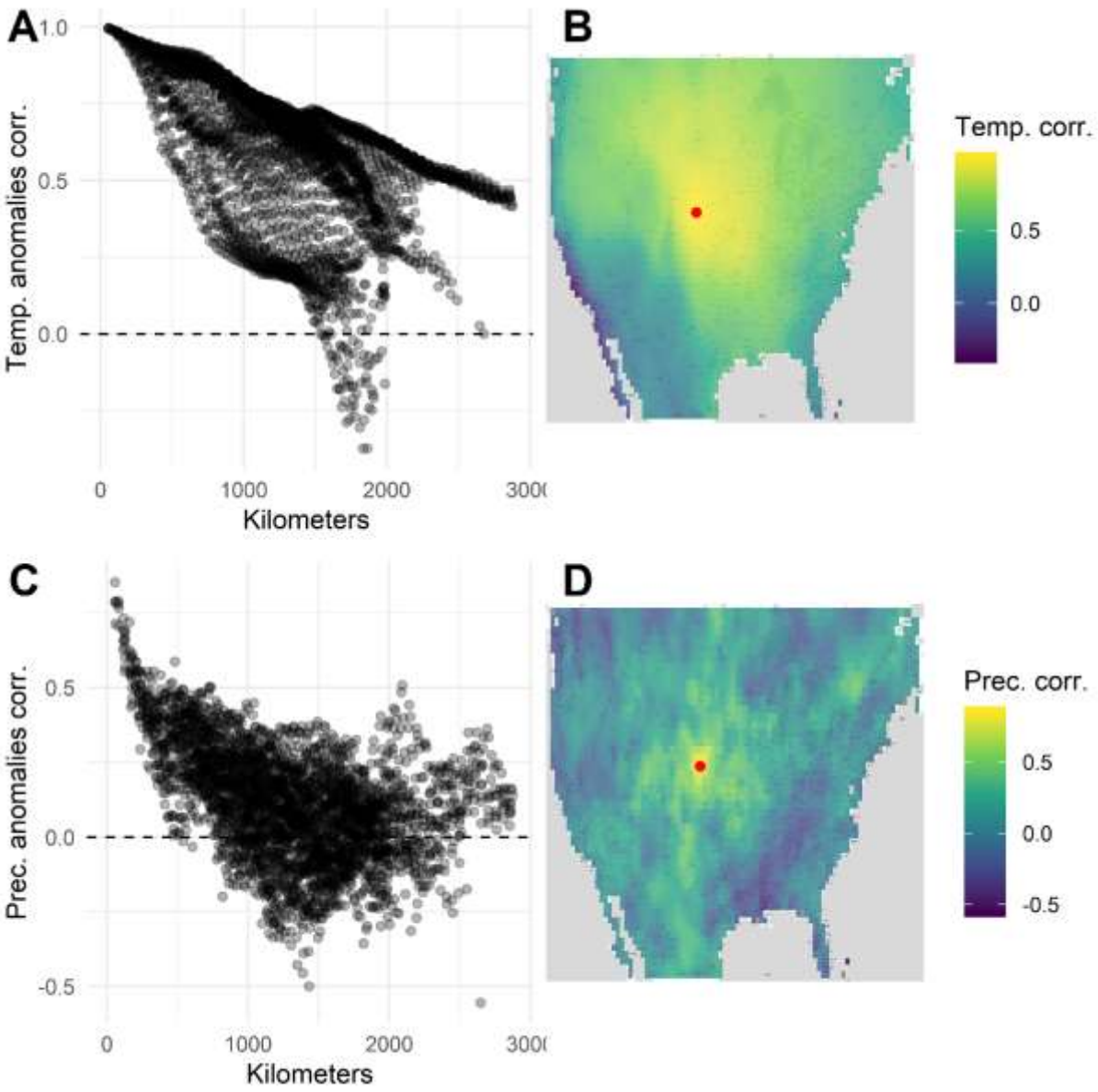
FIGURE LEGENDS

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. 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
B
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Temp. anomalies corr.
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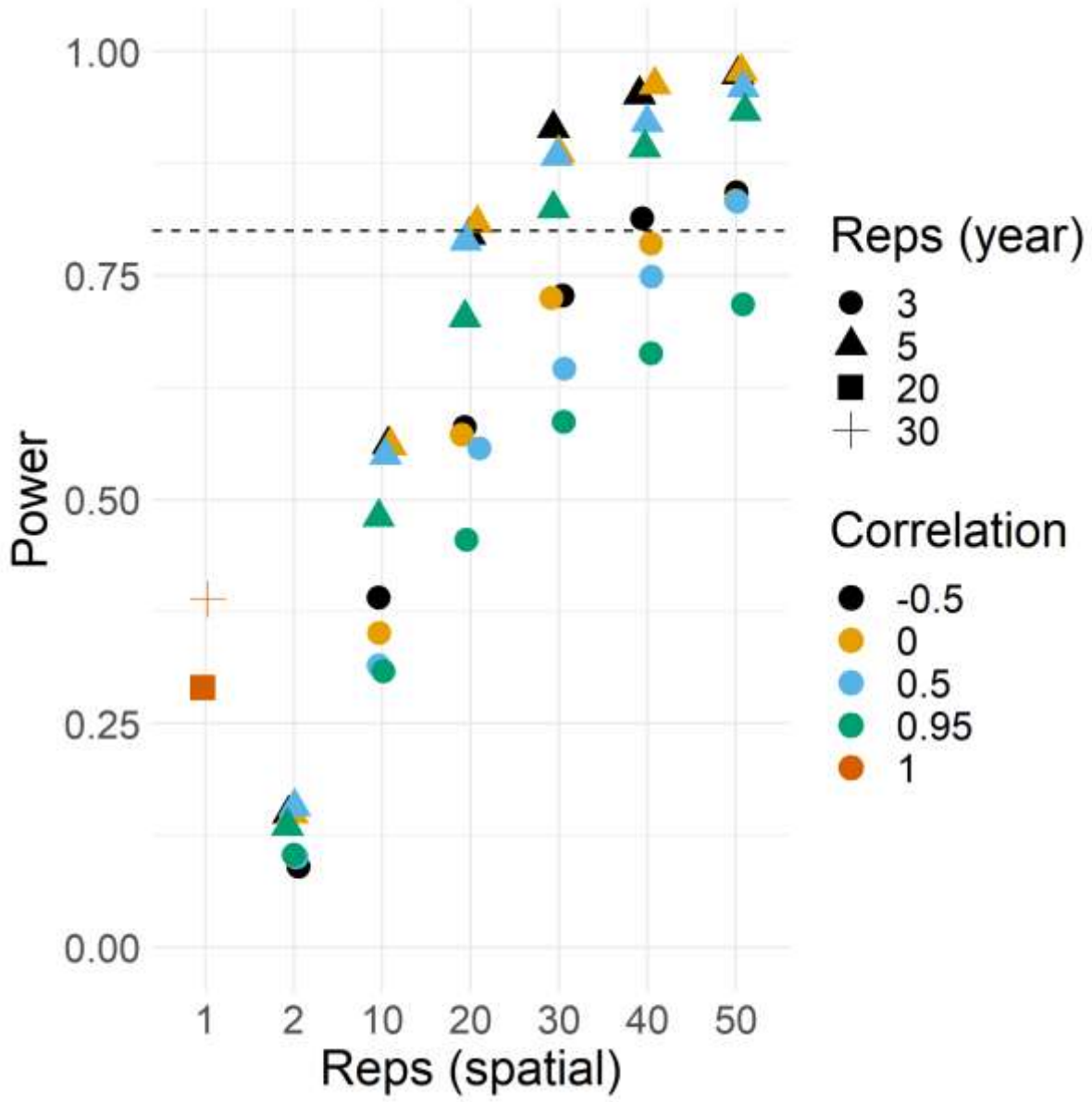
Figure 1.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Power
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Reps (spatial)
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3
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Correlation
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Figure 2.