

1 Title: Extrapolating demography with climate, proximity and phylogeny: approach with  
2 caution

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25 refining ideas and interpretations.

## ABSTRACT

Plant population responses are key to understanding the effects of threats such as climate change and invasions. However, we lack demographic data for most species, and the data we have are often geographically aggregated. We determined to what extent existing data can be extrapolated to predict population performance across larger sets of species and spatial areas. We used 550 matrix models, across 210 species, sourced from the COMPADRE Plant Matrix Database, to model how climate, geographic proximity and phylogeny predicted population performance. Models including only geographic proximity and phylogeny explained 5-40% of the variation in four key metrics of population performance. However, there was poor extrapolation between species and extrapolation was limited to geographic scales smaller than those at which landscape scale threats typically occur. Thus, demographic information should only be extrapolated with caution. Capturing demography at scales relevant to landscape level threats will require more geographically extensive sampling.

# INTRODUCTION

Global threats to biodiversity such as climate change, invasive species and land conversion for agriculture affect multiple species at regional and global scales (McGeoch *et al.*, 2010; Hartmann *et al.*, 2013). Invasion and extinction are fundamentally demographic processes, regulated by the vital rates of the population (e.g. survival, growth, reproduction). Consequently, we are pressed to understand and predict how demography responds to environmental conditions across multiple taxa worldwide (Sutherland *et al.*, 2013). Historically, developing such a predictive framework has proven difficult. Even describing demographic patterns across species and regions is challenging due to the lack of both detailed demographic data for multiple species at large geographic scales, and high resolution comparative approaches (but see Blomberg & Garland 2002, Buckley *et al.* 2010, Salguero-Gómez *et al.* 2016). Another challenge is that we often do not understand the underlying factors that drive population responses to environmental gradients (Ehrlén & Morris, 2015). Further, determining the response of every population of every species is impractical. Consequently, we frequently generalize important aspects of population ecology, such as life history strategy (Silvertown *et al.*, 1996; Salguero-Gómez *et al.*, 2016) and invasiveness (Ramula *et al.*, 2008), from a handful of well studied species and populations to wider areas and other species.

Even though demographic studies have been carried out on thousands of species, most of those species have only been studied in a few locations. It is common to then assume that those studies adequately capture the demographic performance of a species across an entire region (Burns *et al.*, 2010; Crone *et al.*, 2011; Salguero-Gómez *et al.*, 2016). However, it is currently unknown how close, both geographically and phylogenetically, populations or species must be before demographic performance can be extrapolated among them. Likewise, it remains unknown which aspects of demographic performance (e.g. population growth rate, recovery from perturbations) are most transferable across populations.

Matrix population models (Caswell, 2001) provide an ideal means to test how transfer-  
able population performance metrics are across a wide suite of regions, life histories and  
taxa within the plant kingdom. To date, matrix population models have been developed  
for over 1,300 plant species (R. Salguero-Gómez, unpubl. data), (Salguero-Gómez *et al.*,  
2015). Matrix population models are typically constructed from field measurements and  
summarise life histories ranging from simple to complex in a standard format (Caswell,  
2001). This allows the direct comparison of ecologically and biologically meaningful de-  
mographic metrics across populations, species and years (Silvertown *et al.*, 1993; Caswell,  
2001; Salguero-Gómez & de Kroon, 2010). These metrics include population growth rate  
(Tuljapurkar & Orzack, 1980; Caswell, 2001), the underlying impacts of demographic  
processes (i.e. vital rates of survival, growth and reproduction) on population perfor-  
mance (de Kroon *et al.*, 1986; Caswell, 2001), or the ability of populations to recover from  
perturbations (Stott *et al.*, 2010).

We focused on the generalisability of four demographic metrics across species and popu-  
lations: the asymptotic population growth rate ( $\lambda$ ), its variation over time, elasticities of  
 $\lambda$  to demographic processes, and damping ratio ( $\rho$ ). Previous comparative studies have  
found that populations of the same species tend to have similar values for  $\lambda$  (Doak &  
Morris, 2010; Vilellas *et al.*, 2015), although other work has shown significant differences  
among populations of the same species (Silvertown *et al.*, 1996). Comparative studies have  
found that phylogenetic relationships above the species level do not predict  $\lambda$  (Buckley  
*et al.*, 2010; Burns *et al.*, 2010). Environment has been found to explain some variation in  
 $\lambda$  (Buckley *et al.*, 2010). However, the effect of any one environmental variable on  $\lambda$  may  
be reduced as multiple environmental factors can affect  $\lambda$ . In addition, stable populations  
can be maintained across environmental gradients by increasing some vital rates to offset  
decreases in others (Doak & Morris, 2010; Vilellas *et al.*, 2015). Temporal variation of  
population growth rates is expected to increase with increasing environmental constraints  
due to limitations on vital rates (Gerst *et al.*, 2011). Less evidence exists on how geo-  
graphic proximity and phylogeny predict elasticities and damping ratio. However, plant

growth form affects which vital rates are most important for population growth (Enright *et al.*, 1995; Franco & Silvertown, 2004; Salguero-Gómez *et al.*, 2016). Further, we expect that in general species which are closely related are more likely to have the same growth form, although there are exceptions (Mack, 2003; Salguero-Gómez *et al.*, 2016). Thus, we expect that the elasticity structure of a population will be predicted by its close relatives. Higher damping ratios (index of the rate that populations return to an equilibrium after disturbance) are expected to be advantageous in more frequently disturbed environments (Stott *et al.*, 2011). Supporting this conjecture, sensitivities of  $\lambda$  to vital rates (closely related to elasticities) have been shown to have a high phylogenetic signal (Burns *et al.*, 2010). Because disturbance frequency can be spatially correlated (Fox *et al.*, 2008; Premoli & Kitzberger, 2005), we expect the damping ratio to be predicted by geographically near populations.

Here we examine how transferable these four demographic metrics are across space and phylogeny. We also estimate how far, on average, these demographic measures can be extrapolated. Using the largest dataset of geo-located demographic models currently available, we show that while demographic metrics are predictable to some extent using neighbouring populations and related species, caution must be used in extrapolating demographic data.

## MATERIALS AND METHODS

We tested the cross-population, cross-species generalisability of four different aspects of population performance using matrix population models (matrix models, hereafter) from the COMPADRE Plant Matrix Database (COMPADRE henceforth; Salguero-Gómez *et al.* 2015). This version of COMPADRE (obtained 24th October 2014) is included in Appendix 1, Supporting Information. The current version of COMPADRE Plant Matrix database is available at <http://www.compadre-db.org/Data/Compadre>.

We used a set of selection criteria to choose matrix models from the 5,672 obtained from COMPADRE to allow fair comparisons and to ensure the same set of predictor variables were available for each matrix model. Briefly, matrix models had to (i) be parameterised with at least three years of data to enable assessment of temporal variability, (ii) have GPS coordinates in COMPADRE reported to at least arc minute precision so that the location of each population could be matched up with climatic variables, (iii) have a dimension of at least  $3 \times 3$  to appropriately account for individual heterogeneity (Salguero-Gómez *et al.*, 2016), (iv) be based on field data that had not been purposefully manipulated so as to examine demographic performance under unmanipulated conditions (to reduce variability unrelated to natural environmental gradients), and (v) be from 'herbaceous perennial' 'tree', 'palm', 'shrub' and 'succulent' species. We did not include annuals as their matrix models are based on a shorter temporal reference (i.e. months, seasons) than perennials, where matrix models are built on annual transitions. Further details on matrix model selection are described in Appendix 2. These criteria resulted in 550 matrix models for our analysis, covering 210 plant species from 156 genera and 66 families (Table S1, Appendix 2), with populations from tropical regions to the high latitudes (Figure 1a).

The demographic data are confounded in three different ways. First, some matrix models were built with data from almost the same geographic location and those populations are likely to experience similar environmental conditions (Figure 1c). Secondly, some species have closer phylogenetic relationships to others, thus, any demographic signatures that may be due to phylogenetic constraints must be separated from those that are due to environmental filtering (Blomberg & Garland, 2002). Further, populations of the same species tended to be at similar geographic locations. Of the 112 species in our dataset that were represented by more than one population, over half (70) had a maximum distance between populations  $\leq 2$  km, and all but five had a maximum distance between populations  $\leq 100$  km (Figure 1c). Finally, most (92% of species) of the matrix models for a given species come from a single study. Thus, geographic location, phylogeny and methodological differences between studies are all confounded to some extent, necessitating careful

modelling of the data and cautious interpretation of results.

## Metrics of demographic performance

We test the transferability of four fundamental metrics of short- and long-term population performance: asymptotic population growth rate,  $\lambda$ , its coefficient of variation through time,  $CV(\lambda)$ , the damping ratio,  $\rho$ , and a composite axis of matrix element elasticities, the Stasis-Progression Gradient (hereafter SPG).

The population growth rate,  $\lambda$ , is an index of how a population is projected to grow ( $\lambda > 1$ ) or decline ( $\lambda < 1$ ) in the long-term, if the abiotic conditions under which the population was studied do not change (Caswell, 2001).  $\lambda$  is one of the most widely used demographic metrics when assessing population performance and extinction risk (Tuljapourkar & Orzack, 1980; Caswell, 2001; Ramula *et al.*, 2008; Buckley *et al.*, 2010; Crone *et al.*, 2011). The coefficient of variation in  $\lambda$  indicates how much population performance varies interannually. Greater  $CV(\lambda)$  is expected to increase local extinction risk (Lande & Orzack, 1988; Fieberg & Ellner, 2001). Note that  $CV(\lambda)$  does not, in general, inform on the realized temporal variation in population growth rate, because populations are unlikely to be at their stable stage distribution over the entire measurement period (Williams *et al.*, 2011).

The damping ratio,  $\rho$ , is an index of the rate that a population converges to its stable age or stage distribution after it has been perturbed (Stott *et al.*, 2011), and it has important implications for conservation (Koons *et al.*, 2005; Stott *et al.*, 2011). Values of  $\lambda$  and  $\rho$  for each matrix model were calculated with the 'popbio' R package (Stubben & Milligan, 2007).

Matrix element elasticities of  $\lambda$  are the proportional changes in  $\lambda$  caused by small propor-



tional changes in corresponding matrix elements (Caswell, 2001). Elasticities indicate the relative importance of the demographic transitions of stasis, progression and retrogression, as well as the *per capita* contributions from sexual reproduction, to  $\lambda$  (de Kroon *et al.*, 1986). After the population growth rate, elasticities are the most commonly used demographic metric in plant population studies (Franco & Silvertown, 2004; Ramula *et al.*, 2008). This is especially true in conservation and invasion biology where stages and demographic processes with the highest elasticities are typically targeted for conservation across wider areas and similar species (Silvertown *et al.*, 1996; Shea & Kelly, 1998; Ramula *et al.*, 2008).

In order to compare matrix element elasticities of  $\lambda$  across populations and species, we classified each matrix element as belonging to the process of reproduction (both asexual and sexual), progression, stasis or retrogression (Silvertown *et al.*, 1993), producing a vector of four elasticities. Because these four elasticities must add up to one (de Kroon *et al.*, 1986), a higher value for one necessitates a lower value for the others. To overcome this limitation, we used Principal Components Analysis (PCA) to reduce the four elasticities to a single axis, PC1, which accounted for 59% of the variance. We term this axis the Stasis-Progression Gradient, SPG. At high SPG scores elasticities of  $\lambda$  to stasis transitions are large (loading 0.65), and elasticities of  $\lambda$  to reproduction and progression transitions are small (loadings -0.48 and -0.56 respectively). The opposite applies to populations with low SPG scores (see Appendix 3, Table S1 for loadings and variance explained by each axis).

Values of  $\lambda_n$ ,  $\rho_n$  and  $\text{SPG}_n$  are derived from  $\mathbf{M}_n$ , the  $n^{\text{th}}$  mean matrix model in our dataset, where each element is the arithmetic mean of the transition rate over the study period.  $\text{CV}(\lambda)_n$  was calculated from several individual matrix models (between 3 and 51), each built using data for a single annual transition. Of the 550 matrix models in our dataset, 306 reported matrix models for each year separately allowing us to calculate coefficient of variation in  $\lambda$  across years.

## Predictors of demographic performance

We explained variation in these four demographic metrics of population performance using climate, demographic performance at neighbouring locations, and performance in related species, along with matrix model and species level attributes. The location of each matrix model is given by GPS coordinates recorded in COMPADRE, which are sourced from publications or through personal communication with the authors (R. Salguero-Gómez, unpubl. data). GPS locations were used to calculate the distance between data collection sites and to extract 16 climatic variables from the BioClim database (bio\_1, bio\_3 - bio\_9, bio\_12 - bio\_19; [www.worldclim.org/bioclim](http://www.worldclim.org/bioclim)) along with an Aridity index from CGIAR-CSI (<http://www.csi.cgiar.org>). These variables cover different aspects of the mean and seasonal variability of temperature and precipitation, for more details see Table S3, Appendix 4. Climate predictors were extracted from raster files with 30 arc-second resolution. For each location we averaged each climatic variable over a 2km buffer zone to reduce the effect of uncertainty in study location.

Because the eight temperature variables (Table S3, Appendix 4) were highly correlated with each other we created one composite temperature variable using a Principal Component Analysis (PCA) with the `prcomp` function of the 'stats' R library (R Core Team, 2013). The first PC axis, which we refer to as PC\_temp, explains 71% of the variance in temperature variables and represents a gradient from cooler seasonably variable temperate climates to hot, non-seasonal tropical climates (see Appendix 3 for more details). The Aridity Index (AI) is positively correlated with all the other precipitation variables in BioClim (Appendix 4, Table S4), except for precipitation seasonality (bio\_15; Figure S1d, Appendix 3). Thus, we selected Aridity Index and bio\_15 to describe precipitation at each location. We log-transformed AI because we expect small absolute differences in water availability have larger effects on population vital rates when water is a limiting factor (i.e. arid areas) (Levine *et al.*, 2008).

224 We measured phylogenetic relatedness,  $t_{i,n}$ , as millions of years since the last common an-  
225 cestor of species described by matrix models  $\mathbf{M}_i$  and  $\mathbf{M}_n$ . We used the phylogeny supplied  
226 with COMPADRE (Appendix S5; Salguero-Gómez *et al.* 2015). Phylogenetic relatedness  
227 was calculated with the 'cophenetic' function from the 'stats' R package (R Core Team,  
228 2013). We measured the geographic distance,  $d_{i,n}$ , as the shortest great arc distance be-  
229 tween the locations of matrix models  $\mathbf{M}_i$  and  $\mathbf{M}_n$ , using the 'Ellipsoidal.Distance' function  
230 in the 'GEOmap' R package (Lees, 2015).

231 To test if life history traits or matrix model attributes were correlated with demographic  
232 performance we used matrix dimension, species' growth form and mean life expectancy as  
233 predictors. Growth form and mean life expectancy have life history trade-off implications  
234 that may be reflected in the demographic metrics we test (Silvertown *et al.*, 1993; Enright  
235 *et al.*, 1995; Salguero-Gómez & Plotkin, 2010; Stott *et al.*, 2011). Matrix dimension has  
236 also been shown to affect the calculation of demographic metrics like  $\rho$  and elasticities (En-  
237 right *et al.*, 1995; Salguero-Gómez & Plotkin, 2010; Stott *et al.*, 2010). The 'GrowthType'  
238 variable retrieved from COMPADRE was used to classify species as either herbaceous or  
239 non-herbaceous (trees, palms, shrubs, succulents), as non-herbaceous growth forms apart  
240 from trees did not have a large enough sample size to fit them individually. At the pop-  
241 ulation level, the fundamental matrix method was used to derive mean life expectancy  
242 conditional on having germinated, from each mean matrix (Caswell, 2001, pp. 120). We  
243 used the matrix dimension extracted from COMPADRE. See Table S5, Appendix 4 for  
244 the list of predictors.

245 The predictor and response variables in the statistical models occur at three hierarchical  
246 levels, as shown in Box 1. Briefly, phylogeny, matrix dimension and growth type are  
247 defined at the species level; the four demographic metrics, geographic location, mean  
248 life expectancy and the environmental variables are defined at the matrix model level;  
249 finally variation in population growth rate over time is based on population matrix models  
250 constructed with data from annual transitions.

## Statistical analyses

We predicted transformed demographic metrics ( $\ln(\lambda_n)$ ,  $\ln(\text{CV}(\lambda)_n + 1)$ ,  $\ln(\rho_n)$ ,  $\text{SPG}_n$ ) using a spatially and phylogenetically lagged, linear model (Ward & Gleditsch, 2008). We transformed the demographic metrics to improve their error distributions and model fitting. Parameters were estimated in a Bayesian framework using MCMC sampler JAGS 3.4.0-1. Models were fit in R (R Core Team, 2013) using the 'R2jags' interface. The specific details of the MCMC sampling changes slightly from model to model but in general we use three chains of 100,000 samples each, thinned to take every 100<sup>th</sup> sample, with a burn in of 50,000 samples (Appendix 1).

We define our model as

$$Y_n \sim N(\mu_n, \sigma_a) \quad (1a)$$

$$\mu_n = \beta_0 + \boldsymbol{\beta}\mathbf{X}_n + \theta_p\Phi_n + \theta_g\Psi_n \quad (1b)$$

where  $Y_n$  is the predicted value for one of the transformed demographic metrics for matrix model  $n$ , drawn from a normal distribution with a standard deviation of  $\sigma_a \sim \text{Gamma}(0.0001, 0.0001)$  and a mean of  $\mu_n$ . The parameter  $\beta_0$  is the intercept and  $\boldsymbol{\beta}$  is a column vector of slopes. Each slope corresponds to an effect size of one of the aforementioned predictors or their interactions.

$$\boldsymbol{\beta} = \begin{pmatrix} \beta_1 \\ \beta_2 \\ \vdots \\ \beta_K \end{pmatrix}$$

with  $K$  being the total number of climatic and species-level predictors in the model. There are six main effect predictors (matrix dimension, growth type, mean life expectancy, PC\_temp, Aridity Index, precipitation seasonality), including two-way interactions be-

273 tween the main effects resulted in  $K = 18$ . Each slope in  $\beta$ , and the intercept  $\beta_0$ , were  
 274 drawn from wide prior distributions,  $\beta_k \sim N(0, 0.0001)$ , where  $N(\cdot)$  is a normal distribu-  
 275 tion.  $\mathbf{X}$  is a  $K \times J$  matrix of  $K$  species-level and climatic predictors, and their interactions,  
 276 for all  $J$  matrix models.

277 To capture the effect of phylogeny and geographic location, we included a phylogenetic  
 278 predictor term  $\theta_p \Phi_n$ , and a geographic predictor term  $\theta_g \Psi_n$ , respectively (Eq. 2). The  
 279 terms  $\theta_p \Phi_n$  and  $\theta_g \Psi_n$  predict the value of  $Y_n$  as a weighted average of matrix model  $n$ 's  
 280 relatives or neighbours respectively.

$$281 \quad \Phi_n = \frac{\sum_{\forall i \neq n} Y_i \exp[-\phi t_{i,n}]}{\sum_{\forall i \neq n} \exp[-\phi t_{i,n}]} \quad (2a)$$

$$282 \quad \Psi_n = \frac{\sum_{\forall i \neq n} Y_i \exp[-\psi d_{i,n}]}{\sum_{\forall i \neq n} \exp[-\psi d_{i,n}]} \quad (2b)$$

284 where  $\phi \sim \text{Unif}(0, 1)$  (see Appendix 1 for minor modifications to these limits) modulates  
 285 how phylogenetically close *vs.* distant relatives contribute to predicting  $Y_n$ . Similarly  
 286  $\psi \sim \text{Unif}(0, 1)$  controls how geographically near *vs.* distant neighbours contribute to pre-  
 287 dicting  $Y_n$ . When  $\phi$  or  $\psi$  are 0, all populations contribute equally to the prediction of  $Y_n$   
 288 regardless of distance, either phylogenetic or geographic; as  $\phi$  or  $\psi$  increase, more closely  
 289 related species, or geographically closer locations, have a greater contribution to the pre-  
 290 diction of  $Y_n$ . The term  $t_{i,n}$  is the phylogenetic distance between species represented by  
 291 matrix models  $i$  and  $n$ .  $d_{i,n}$  is the geographic distance between the locations of matrix  
 292 models  $i$  and  $n$ .  $\theta_p \sim N(0, 0.0001)$  and  $\theta_g \sim N(0, 0.0001)$  are coefficients that scale the  
 293 phylogenetic and geographic predictions. Any explanatory power from the geographic  
 294 and phylogenetic predictor terms is a result of spatial auto-correlation in both measured  
 295 and unmeasured environmental variables and phylogenetically conserved functional traits,  
 296 rather than distance *per se*. If demographic attributes are random with respect to spa-  
 297 tially auto-correlated environmental factors, or are not phylogenetically constrained, the

298 phylogenetic and geographic and predictor terms ( $\Phi$ , and  $\Psi$  respectively) will explain  
299 none of the variance in the four demographic metrics tested.

300 Study, species and location are all to some extent confounded, due to many populations  
301 of the same species being from the same study and similar geographic locations. To test  
302 the effect this had on the performance of our models, we also tested models where the  
303 spatial and phylogenetic predictor terms were based on a reduced, but less confounded set  
304 of neighbours and relatives. We ran models where  $Y_i$  in the geographic and phylogenetic  
305 prediction terms (Eq. 2) were only based on matrix models from different locations (that  
306 is, where  $d_{i,n} \neq 0$ ) or which were based on a different species (*i.e.* where  $t_{i,n} \neq 0$ ). We  
307 call these 'no\_self' models. In addition, we tested five combinations of predictors so that  
308 the explanatory power of simplified models could be tested. This led to eight different  
309 modifications of the general model (Eq. 1), detailed in Table 1. These model versions  
310 were used to predict the four demographic metrics outlined above, resulting in a total of  
311 32 separate models.

312 Since geographic location was used to define our climatic predictors, those predictors  
313 were geographically and phylogenetically correlated. Thus, we carefully examined the  
314 simplification of the general model in Eq. 1. Models that contained environmental and  
315 species level predictors (*i.e.* 'main\_int' and 'main', see Table 1 for model names) also  
316 had to include the geographic and phylogenetic predictor terms based on all populations  
317 (as opposed to the 'no\_self' geographic and phylogenetic predictor term). When running  
318 'no\_self' models containing environmental and species-level predictors we could not know  
319 if any significantly non-zero coefficients in  $\beta$  represented a real effect, or if that predictor  
320 was simply acting as a poor proxy for geographic location. This raises the general point  
321 that these are phenomenological models which find patterns in the data, patterns which  
322 are likely to be caused by multiple related processes acting simultaneously.

## RESULTS

None of the environmental, species- or matrix model level variables had a significant effect on the demographic metrics tested ( $\lambda$ ,  $CV(\lambda)$ ,  $\rho$ , and SPG) over and above the effect of the geographic and phylogenetic predictor terms. All of the credible intervals on the coefficients in  $\beta$ , Eq. 1 encompass 0. This is further illustrated by Figure 2, where the full model containing all the predictors did not explain much more variance in any of the demographic metrics than the model that only contained the prediction terms based on geographic and phylogenetic distance (phygeo-allpops). For this reason we do not report results for the 'main' model as it produced the same results as the 'main\_int' and 'phygeo-all\_pops' models. The 'phygeo' also had the lowest (or equal lowest) DIC values (Figure 2), suggesting that having both geographic and phylogenetic predictor terms was a good trade-off between parsimony and explanatory power. Overall, models including only predictor terms based on phylogenetic or geographic distance had  $R^2$  values between 20% and 65% depending of the demographic metric (Figure 2). This explanatory power suggests that some environmental and species level factors had important effects on population performance. See diagnostic plots in Appendix 1 for full breakdown of credible intervals and model performance (Appendix\_1\_analysis\_pipeline/Appendix\_1\_model\_code\_and\_plotting /pre-run\_model\_output).

The best models had  $R^2$  values around 65%, however care must be taken not to overinterpret the predictive power of these models. In models where the geographic and phylogenetic prediction terms were fit using all populations the effect of species, local environment and study methodology are confounded. To test how much of an effect this had on the explanatory power of our models we fitted 'no\_self' models (Table 1). Even after these self predictions were removed several of the 'no\_self' models still explained 20-40% of variation in the metrics of demographic performance (Figure 2).

Our models explained more variation in some metrics of population performance than

others; with relatively high explanatory power for a matrix model's position on the SPG continuum and damping ratio ( $\rho$ ), and lower explanatory power for asymptotic population growth rate ( $\lambda$ ) and its temporal variation. The best models explained around 65% of the variation in SPG and damping ratio ('main\_int', 'main' and 'phygeo-all\_pops' density distributions 2) and only 25-45% of variation in  $CV(\lambda)$  and  $\lambda$ . The 'no\_self' models explained between 12-25% of the variation in SPG, 40% of the variation in damping ratio, 5% of the variation population growth rate ( $\lambda$ ), and 15-25% of variation in  $CV(\lambda)$  (Figure 2).

For all demographic metrics, except  $\rho$ , the spatial term explained more variation than the phylogenetic term (Figure 2). The 'no\_self' models with only a spatial term explain almost as much variation as models with both a geographic and phylogenetic prediction term (phygeo-no\_self in Figure 2). In contrast 'no\_self' models with only a phylogenetic term typically had an  $R^2$  about half that of the model including both spatial and phylogenetic terms. Thus, both the spatial and phylogenetic terms are explaining much of the same variance in the response, with the spatial term explaining some variance not explained by phylogenetic term.

To examine the way predictive support drops off with geographic and phylogenetic distance, we plotted the negative exponential decay models that underpin the geographic and phylogenetic prediction terms (Eq. 2). Here we present decay curves for the 'phygeo-no\_self' model (Table 1), since this model had the lowest DIC of the 'no\_self' models. Results were similar across different models, although uncertainty around the decay curves varies greatly between models (Appendix 5). For models predicting population growth rates ( $\lambda$ ) and SPG virtually all predictive support came from locations that were within 15 km of the target location (Figure 3a,c). Predictive support for  $CV(\lambda)$  and damping ratio ( $\rho$ ) came from locations within 35 km (Figure 3b,d). Predictive support based on phylogeny came from species that diverged <100 mya for SPG, < 20 mya for  $CV(\lambda)$  and < 10 mya for  $\lambda$  and  $\rho$  (Figure 3).



## DISCUSSION

Important aspects of plant population performance, data which are time-consuming and expensive to collect for each population, can be inferred from nearby locations and, to a lesser extent, from related species. Even after removing predictions from the same location or the same species, we can still explain 25%-40% of the variation in damping ratio, elasticities and temporal variation in population growth rate. However, our results also suggest that there are important limits to generalising population performance across geographic locations and between species.

It is common practice in demography, applied ecology and conservation to measure the demography of a species in a few locations and then apply that understanding to the species over a much wider region (Shea & Kelly, 1998; Doak *et al.*, 2005; Crone *et al.*, 2011; Sæther *et al.*, 2005; Salguero-Gómez *et al.*, 2016). In contrast, we often expect considerable geographic variation in demographic performance of populations within species (e.g., Jongejans & de Kroon 2005, Merow *et al.* 2014). In our dataset, species and geographic location are too confounded to directly test how transferable demographic information is within species because most populations of the same species were geographically close to each other. However, in our analysis using a dataset of unprecedented size in comparative plant demography, closely related species were much weaker predictors of population performance than geographically close populations. The explanatory power of the geographic predictor term suggests that something about the mid to small-scale environment is predictive of demography, specifically elasticities of population growth rate, damping ratio and temporal variation in population growth rate. Mid- to small-scale environmental variables will likely include many local drivers beyond climate, such as soil, anthropogenic impacts (Cole *et al.*, 2014), disturbances and biotic interactions (Silvertown *et al.*, 1996; Thuiller *et al.*, 2014). It is this mid to small-scale signal that is often lost with global comparisons (Salguero-Gómez *et al.*, 2016).

Borrowing information across closely related species may be more useful for some aspects of demography than others (Blomberg & Garland, 2002). The phylogenetic term unambiguously explained around 10% of the variance in damping ratio over and above the variance explained by the geographic predictor term, much more than the other three demographic metrics. In the case of the damping ratio, only species that diverged  $< 10$  mya provided good support for predicting the damping ratio of another species. In our dataset 38 genera were represented by two or more species; of these eight had at least one species pair that diverged  $< 15$  mya, and three had species that diverged from each other  $< 10$  mya. This suggests that, in our dataset at least, it is uncommon for species in the same genus to have diverged recently enough to help explain variation in each others damping ratio.

Why we were able to explain so much variation in damping ratio remains an open question. It has been suggested that damping ratio is strongly influenced by a limited set of traits and life history strategies (e.g. resprouting) that help plant populations recover from, or take advantage of, disturbances (Pausas & Lavorel, 2003; Clarke *et al.*, 2010). In contrast the other three demographic metrics are strongly influenced by multiple environmental and biotic factors (Silvertown *et al.*, 1996), each of which will introduce noise into the prediction. Further, populations at their stable stage distribution can show up to a 16-fold difference in population growth rate compared to those that have been perturbed (Williams *et al.*, 2011). Given this large difference in population performance, it is likely that traits and demographic strategies which affect the time taken to return to the stable stage distribution (measured by damping ratio) are under strong selective pressure (Lamont & Downes, 2011), resulting in a high phylogenetic signal (Blomberg & Garland, 2002). In addition, variability in environmental conditions are spatially correlated (Fox *et al.*, 2008; Premoli & Kitzberger, 2005), and thus we might expect disturbance driven demography to be more spatially predictable.

An important caveat to our analysis is that most species were represented in our dataset

by a single location - although we used the most extensive database of plant demography available (Salguero-Gómez *et al.*, 2015). This means that the decay curves are averages across many different species and habitats, and could be different for any given species or location (Diez *et al.*, 2014). Geographic location and phylogeny are confounded to some extent in our dataset and some of the signal in the geographic decay curves may be due to phylogenetic signal. We can however see that the geographic predictor term in our analysis does explain variation in the demographic metrics that cannot be explained by the phylogenetic term. Our analysis did not show which environmental and species level variables are driving the explanatory power of the geographic and phylogenetic predictor terms. Even those variables we included as predictors were highly spatially auto-correlated, and so could have contributed to the explanatory power of the geographic predictor term. The effect of climatic variables that vary at scales smaller than the accuracy of study locations (e.g. soil properties) will be impossible to test using comparative methods. Likewise, we could not say much about the effect of growth type, aside from herbaceous perennials, due to the small sample size of trees, palms and succulents. To get an understanding of the drivers of demography across space and species, and whether the same drivers are common between species and locations, we need to sample multiple species, at multiple locations, at different scales.

Despite these caveats, our dataset covered a large number of species and environments and the general results are clear: we can generalise from individual demographic studies. However, even with the largest geo-located dataset of demographic studies available we can only justify extrapolating important aspects of demography at limited scales, especially compared to the scales that threats such as species invasions and climate change occur at. Thus, the initial assumption should be that any demographic results we obtain are applicable to the population they were measured for and those in the immediate environment. This does not mean that we will never be able to extrapolate demographic results, but more spatially extensive sampling is needed to understand how population performance changes between species and in response to environmental drivers.

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## SUPPORTING INFORMATION

Appendix 1: Statistical analysis and plotting scripts

Appendix 2: Selection criteria applied to COMPADRE Plant Matrix Database

Appendix 3: PCA loadings and variance explained by each axis

Appendix 4: Environmental variables and predictors used in the analysis

Appendix 5: Phylogenetic and geographic decay curves for all models and demographic metrics

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**Table 1.** Statistical models used to predict the four demographic metrics, population growth rate, its temporal variation, damping ratio and the composite elasticities, Stasis Progression Gradient (SPG). Because the environmental and species level predictors (matrix dimension, growth type, mean life expectancy, first principal component of the temperature variables (PC\_temp), Aridity Index, precipitation seasonality) are spatially autocorrelated the 'main\_int' and 'main' models were only fit using geographic and phylogenetic predictor terms based on all 550 matrix models in our dataset.

model name	environmental and species level predictors	phylogenetic predictor	geographic predictor
main_int	All six main effects and 2-way interactions, giving 18 terms	Based on all populations	
main	Only the six main effects	Based on all populations	
phygeo-all_pops	Not included	Based on all populations	
phygeo-no_self	Not included	Based only on populations that were not of the same species	Based only on populations that were not in the same location
phy-all_pops	Not included	Based on all populations	Not included
phy-no_self	Not included	Based only on populations that were not of the same species	Not included
geo-all_pops	Not included	Not included	Based on all populations
geo-no_self	Not included	Not included	Based only on populations that were not in the same location

**Box 1.** We use statistical models to explain variation in four demographic metrics (response variables) using environmental and species level predictors, along with neighboring populations and related species. Response and predictor variables in our statistical models are defined at three hierarchical levels:

### Species

#### Predictors defined at the species level

- Phylogeny is defined at the species level, and thus the phylogenetic predictor term,  $\Phi$ , is defined at the species level.
- Growth type

### Matrix model

Each species is represented by one or more matrix models

#### Responses defined at the matrix model level

- Pop. growth rate,  $\lambda$
- Coefficient of variation in  $\lambda$  across time,  $CV(\lambda)$
- Damping ratio,  $\rho$
- Stasis progression gradient, SPG

#### Predictors defined at the matrix model level

- Geographic location is defined for each matrix model, and thus the geographic predictor term,  $\Psi$ , is defined at the matrix model level.
- Mean life expectancy
- Matrix dimension
- Aridity index
- Precip. seasonality
- Temperature

### Transitions

Each matrix model is based on transition rates from at least 3 years (two observed transitions)

The response variable  $CV(\lambda)$  is based on population growth rates calculated from each annual transition matrix

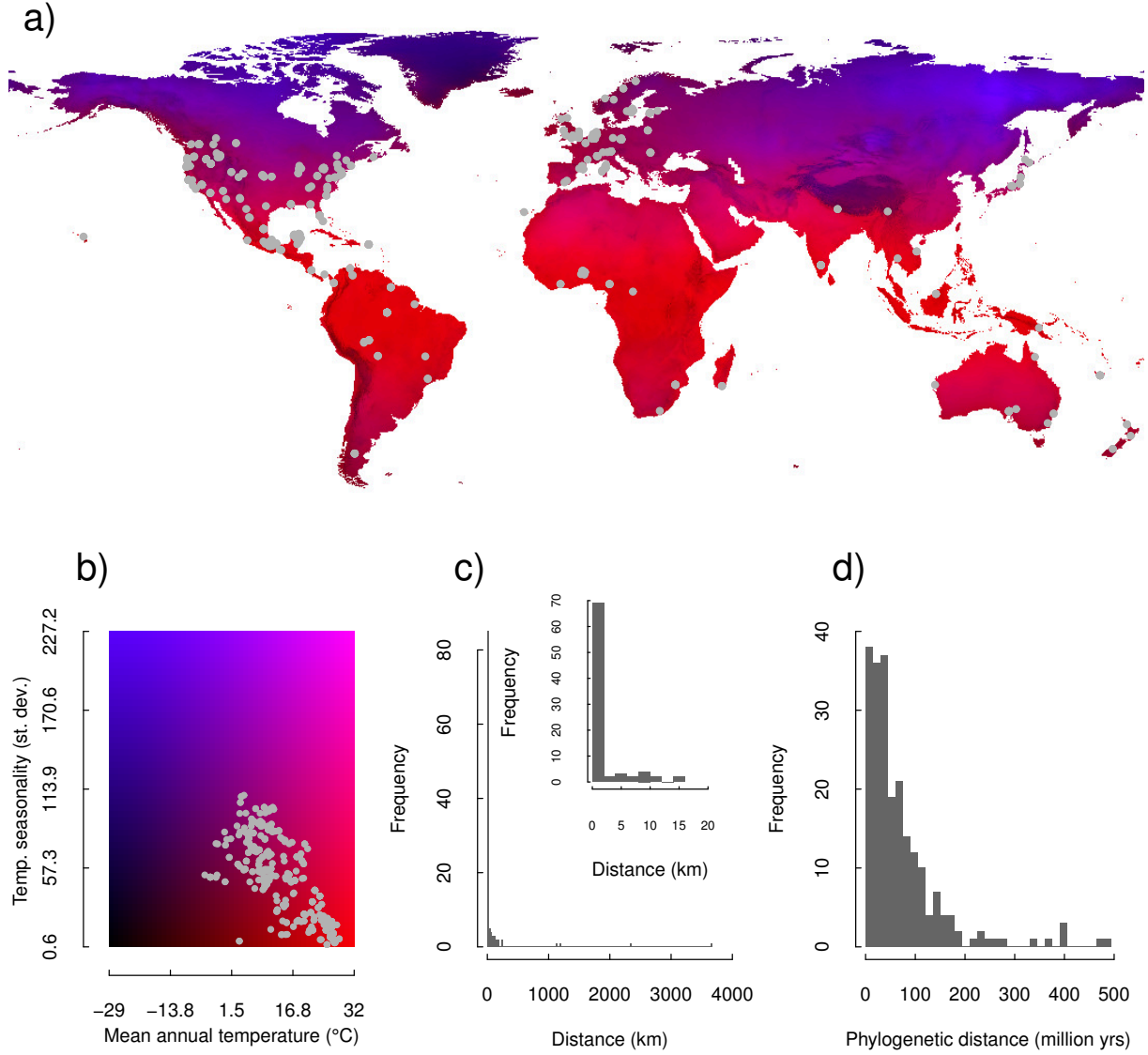
**Figure 1.** Locations of the 550 populations used in the analysis plotted on, a) world map coloured with mean annual temperature ( $^{\circ}\text{C}$ ) and temperature seasonality (standard deviation over year). Redder areas are warm and non-seasonal (i.e. tropics), blue areas are cold and seasonal, purple areas are warm and seasonal (continental temperate), and dark areas are cold and non-seasonal. b) Populations plotted on to this temperature environmental space. c) Frequency distribution of maximum between-population distance within each of the 112 species (out of 210 total), that were represented by more than one population in our dataset. Bins are 25km wide in larger plot and 2km wide in the inset. d) Phylogenetic distance (in millions of years since last common ancestor) between each of the 210 species in the dataset and the closest relative to that species in the dataset. Bins are 15 million years wide.

**Figure 2** We use geographically and phylogenetically lagged statistical models to explain the variance in four key demographic metrics. We use  $R^2$  to quantify explanatory power, higher values indicate more variance explained. Median  $R^2$  (points) and 95% (solid lines) quantiles were taken across 1,500 MCMC samples. Deviance Information Criteria (DIC) is an index of model performance penalized by the number of parameters. Lower DIC numbers indicate more parsimonious models that performed well relative to the other models tested. Note that DIC cannot be compared between metrics, or between 'all\_pops' and 'no\_self' models for the same metric. Colour indicates the model structure. See Table 1 for definitions of 'main\_int', 'phygeo', 'geo' and 'phy' models, and the difference between models with spatial and phylogenetic prediction terms based 'all\_pops' and 'no\_self' predictions.

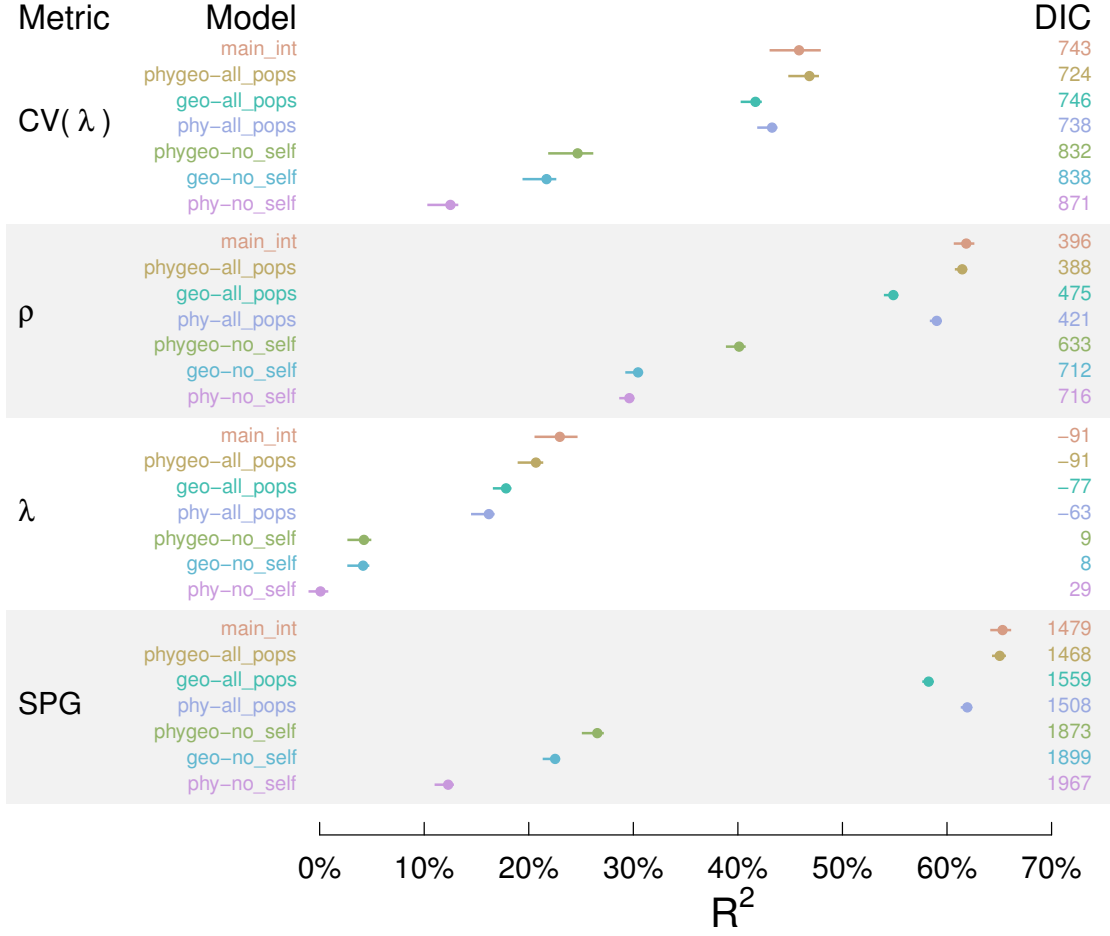
**Figure 3.** Decay curves are the basis of the geographic and phylogenetic predictor terms, and show how quickly predictive support from neighbouring locations or other species declines with distance (either geographic or phylogenetic). Decay curves for geographic (a-d) and phylogenetic (e-h) predictive terms for each metric, population growth rate ( $\lambda$ ), its temporal variation ( $\text{CV}(\lambda)$ ), Stasis Progression Gradient (SPG) and damping ratio

690 ( $\rho$ ). The model presented here, phygeo-no\_self, has no fixed effects, and predictions were  
691 based on geographic locations and species that were different to that being predicted  
692 for. Lines show the curve produced by the estimated decay parameter for each of the  
693 1,500 MCMC samples. Grey lines depict the average curve. Average decay curves for  
694 other models are generally similar, although the uncertainty around decay curve can vary  
695 greatly between different models for the same measure. Decay plots for all other models  
696 can be found in Appendix 5.

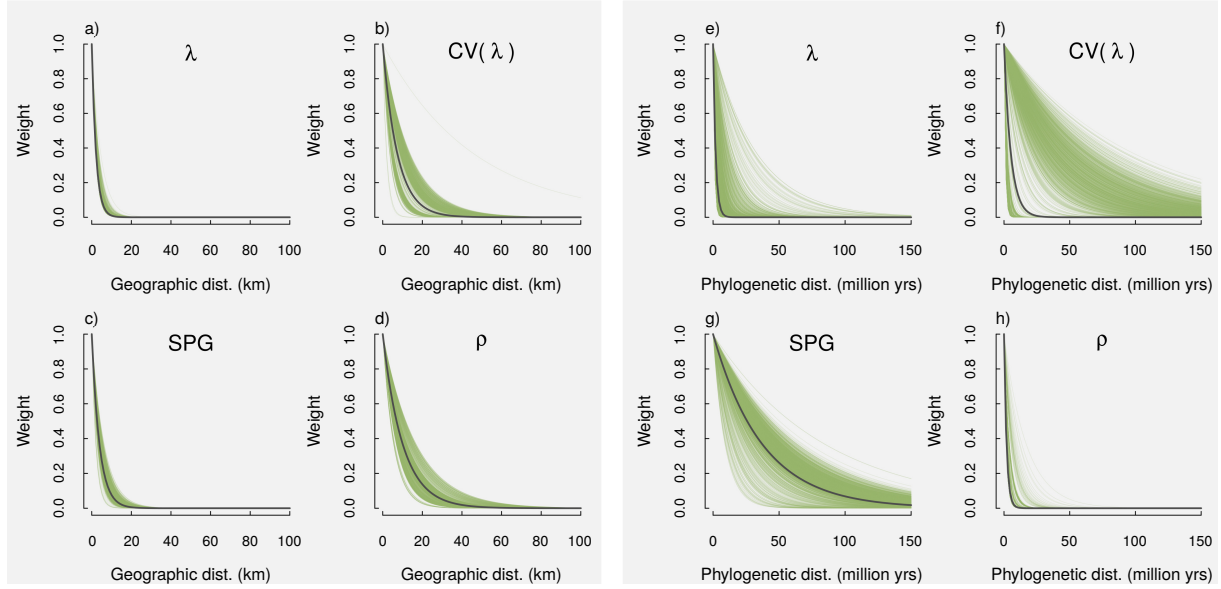




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