

ARTICLE

Effects of range and niche position on the population dynamics of a tropical plant

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Abstract

The center-periphery hypothesis predicts a decline in population performance toward the periphery of a species' range, reflecting an alteration of environmental conditions at range periphery. However, the rare demographic tests of this hypothesis failed to disentangle the role of geography from that of ecological niche and are biased toward temperate regions. We hypothesized that, because species are expected to experience optimal abiotic conditions at their climatic niche center, (1) central populations will have better demographic growth, survival, and fertility than peripheral populations. As a result, (2) central populations are expected to have higher growth rates than peripheral populations. Peripheral populations are expected to decline, thus limiting species range expansion beyond these boundaries. Because peripheral populations are expected to be in harsh environmental conditions, (3) population growth rate will be more sensitive to perturbation of survival-growth rather than fertility in peripheral populations. Finally, we hypothesized that (4) soils properties will drive the variations in population growth rates for narrowly distributed species for which small scale ecological factors could outweigh landscape level drivers. To test these hypotheses, we studied the demography of *Thunbergia atcorensis* (Acanthaceae), a range-limited herb in West Africa. We collected three years of demographic data to parameterize an integral projection model (IPM) and estimated population level demographic statistics. Demographic vital rates and population growth rates did not change significantly with distance from geographic or climatic center, contrary to predictions. However, populations at the center of the geographic range were demographically more resilient to perturbation than those at the periphery. Soil nitrogen was the main driver of population growth rate variation. The relative influence of survival-growth on population growth rates exceeded that of fertility at the geographic range center while we observed the opposite pattern for climatic niche. Our study highlights the importance of local scale processes in shaping the dynamics and distribution of range-limited species. Our findings also suggest that the distinction between geographic distribution and climatic niche is important for a robust demographic test of the center-periphery hypothesis.

KEYWORDS

abundance center model, center-periphery hypothesis, elasticity, integral projection model, plant demography, population dynamics, species range limitation

INTRODUCTION

Understanding the mechanisms driving species range limitation has long captured the interest of ecologists (Darwin, 1859) and remains a highly debated topic (Dallas et al., 2020; Sutherland et al., 2013). In the context of climate change and increasing anthropogenic influence, understanding the distribution of range-limited species, which are more prone to extinction than wide-spread species, has direct implications for their conservation. The center-periphery hypothesis predicts that species abundance is higher at the center of their geographic distribution and decreases toward the edge (Brown, 1984). This distribution pattern is often explained by the expectation that the most favorable ecological conditions (biotic and abiotic) exist at the center of distribution. However, the geographic center of distribution does not necessarily coincide with species' optimal climatic conditions (Moutouama & Gaoue, 2022a). Therefore, species are not always expected to be most abundant at the center of their range, and this limits the generalization of the center-periphery hypothesis (Dallas et al., 2017; Pironon et al., 2017).

The climatic center or niche centroid represents the optimal conditions for a species only if the species' response to the environmental conditions is Gaussian (or Gaussian-like), unimodal with symmetrical tails, for all the variables that define the species' niche (Samis & Eckert, 2007; but Waldo et al., 2019). However, non-Gaussian responses and niche truncation due to geographic constraints, heterogeneous population dynamics (Louthan et al., 2015; Sagarin et al., 2006), and sampling biases (Eckert et al., 2008; Sagarin & Gaines, 2002) are commonly reported and this challenges the notion that the climatic center represents the optimal conditions for the species. When species environmental response departs from such Gaussian-like distribution, the relationship between abundance (or any fitness trait) and distance to niche centroid weakens, indicating that the niche optimum may not be at the centroid (Dallas et al., 2020).

Previous tests of the center-periphery hypothesis examined how population parameters such as abundance (Dallas et al., 2017; Osorio-Olvera et al., 2020) or demographic vital rates (e.g., reproduction, survival, and growth) (Abeli et al., 2014; Gerst et al., 2011; Samis & Eckert, 2007) vary across species ranges. However, using only population abundance or vital rates as metrics of population responses limits our understanding of the

mechanisms underlying species range limitation (Sagarin et al., 2006). Population abundance provides only a snapshot of population status that may not correlate with long-term population dynamics. Population size or abundance varies across space and time, suggesting that tests of the center-periphery hypothesis might yield different results depending on the temporal or spatial scales at which the study is conducted. Moreover, because there is a trade-off between demographic vital rates (e.g., growth, survival, fecundity), using only one vital rate as a response variable to test range limitation can be misleading given that these vital rates respond differently to environmental stochasticity (Merow et al., 2017; Pironon et al., 2018). For example, freezing conditions reduce the survival rate of *Lathyrus venus* (Fabaceae) but increase fruit production (Greiser et al., 2020). In *Prenanthis roanensis* populations, abundance did not change from center to periphery, but peripheral populations had lower growth rates than central populations (Aikens & Roach, 2014). Thus, using a more reliable metric like population growth rate, estimated across several years and which integrate vital rates, to capture the demographic response to spatio-temporal environmental changes can enhance our mechanistic understanding of range limitation (Louthan et al., 2015).

Demographic tests of the center-periphery hypothesis are rare but increasing. Previous studies showed that central populations have higher growth rates than peripheral populations, which may explain range limitation for some plant species. For example, central populations of *Mimulus lewisii* (Angert, 2006) and *Ulex galli* (Stokes et al., 2004) have higher growth rates than peripheral populations. However, in these studies, the assignment of populations to range center and periphery was categorical (i.e., isolated populations were considered as peripheral) but, in reality, populations exist along a continuum from center to periphery. Moreover, geographically central populations are not necessarily ecologically or climatically central (Yakimowski & Eckert, 2007). Therefore, studying how population dynamics vary from center to periphery using continuous predictors such as distances from geographic and climatic centers can provide a more rigorous test of the center-periphery hypothesis (Pironon et al., 2017; Sagarin et al., 2006).

Nevertheless, using demographic models to test the center-periphery hypothesis must go beyond comparing vital rates and population growth rates. Understanding how central versus peripheral populations respond

differently to perturbation of vital rates (elasticity analysis) can be used to tailor sustainable management strategies. Elasticity analyses show that, at the edge of their ranges, the populations dynamics of long-lived perennials species are more elastic to adult survival than to fertility (Svensson et al., 1993). Empirical studies also have showed that population dynamics tend to be more elastic to survival in sites with harsh environmental conditions, expected in peripheral populations, suggesting that investment in survival can buffer species against fast extinction (Gaoue et al., 2011). However, demographic trade-offs may contribute to high population growth rate in peripheral populations in two ways. First, low survival rate at the periphery could be compensated by a high investment in fertility resulting in high population growth rate at the periphery, particularly for short-lived species which are demographically more sensitive to reproductive investment (Aikens & Roach, 2014). Second, peripheral populations may recover faster than central populations by compensating low reproduction with high survival that can lead to rapid population growth in long-lived species (Salguero-Gómez et al., 2016).

Furthermore, using sensitivity analysis to investigate how selective pressures change from species distribution center to periphery can help explore whether demographic trait values in peripheral populations are more likely to be favored or selected for by natural selection. Although rarely tested, central populations, which are predicted to have high densities, are relatively resistant to quick directional evolutionary change (Brown, 1984). In contrast, if peripheral populations are spatially isolated enough to experience low gene flow, they can experience directional selection and strong local adaptation (Bontrager et al., 2021). Population growth rate is a measure of mean fitness, fundamentally linking ecology and evolution (Metcalf & Pavard, 2007). Thus, phenotypic traits that increase population fitness will more likely be favored by natural selection. One way of estimating the selection gradient is to estimate the slope of the relation between population fitness with respect to population trait values (Caswell, 2019). Because sensitivity analysis measures the rate of change of population fitness with respect to a given life history trait, it estimates natural selection pressure on life history traits (Caswell, 2006; Stearns, 1992).

Processes driving the center-periphery variation in population demography can be scale-dependent. While most tests of the center-periphery hypothesis are conducted at a macroscale, local scale heterogeneity in ecological conditions can outweigh the effects of large scale factors (Soberón & Nakamura, 2009). For example, microclimatic variation in riparian forests can outweigh the influence of macro-scale climatic variation (Baker, 1989), and local soil properties can directly influence riparian plants'

population dynamics (Frye & Quinn, 1979). Such ecological heterogeneity is more likely in tropical regions (Townsend et al., 2008). However, most tests of the center-periphery hypothesis are biased toward temperate regions (Eckert et al., 2008), limiting our ability to generalize the predictions of this theoretical framework. Relative to temperate regions, tropical regions often have older soils (Aerts & Chapin, 1999), higher plant nitrogen-to-phosphorus ratios (Hou et al., 2018; Yuan et al., 2011), and lower soil phosphorus concentration (Aerts & Chapin, 1999). Thus, incorporating microscale factors such as soil quality in the test of the center-periphery hypothesis can contribute new insights into our understanding of species range limitation.

In this study, we used *Thunbergia atacorensis* (Acanthaceae), an endemic and range-limited tropical herb in West Africa, to investigate the drivers of vital rates and variation in population growth rate from geographic and climatic center to periphery. We combined field observations and mathematical modeling to provide four independent tests of the center-periphery hypothesis using vital rates, population growth rate, selection gradients, and population recovery time to perturbation. We addressed the following hypotheses: (1) central populations will have higher demographic growth, survival, and fecundity rates than peripheral populations because ecological conditions, particularly soil quality, are expected to be optimal in central populations. As a result, (2) central populations are expected to have higher growth rates and faster recovery from perturbation than peripheral populations which are expected to show declining trends, limiting species range expansion beyond these boundaries. We also hypothesized that, because ecological conditions are expected to be less optimal toward the periphery, (3) population growth rate will be most sensitive to perturbation of survival-growth rather than fertility in peripheral than central populations. Finally, we hypothesized that (4) soil properties will drive population dynamics given the narrow distribution of the study species.

MATERIALS AND METHODS

Study system

T. atacorensis (Akoègninou Lisowski & Sinsin) is a perennial herb endemic to the Atacora mountain chain (1°00'–2°00' E and 10°40'–11°28' N) and the Sobapkerou mountain chain (2°9' N–9°8' E) in West-Africa (Akoègninou et al., 2006). Annual rainfall in these mountains varies from 1200 to 1350 mm with an average temperature of 28°C (Sinsin & Kampmann, 2010). The species occurs in gallery forests (Akoègninou et al., 2006). We used the information from Fandohan et al. (2005),

which described the distribution of *T. atacorensis* in West-Africa, to identify 12 known populations across Benin. Reproductive individuals flower from June to early September and set seed 2 weeks after flowering.

Demographic data

In August 2019, we located the 12 known populations of *T. atacorensis* previously identified (Fandohan et al., 2015) across the entire range of species in West Africa (Figure 1). During the second year of demographic data collection in 2020, one of the populations was heavily disturbed by road

construction and this population was removed from the final analysis. From August 2019 to August 2021, we monitored all the remaining 11 populations of *T. atacorensis* using 52 sampled plots. In each population, we randomly established five 25 m² permanent plots and tagged each individual *T. atacorensis* plant in the plots. For a few populations that were too small to establish five 25 m² plots, we used a minimum of three plots (Appendix S1: Table S1). In August of each year, we collected demographic data on the tagged plants, including basal diameter, number of flowers, number of fruits, and survival status (dead or alive). We identified new seedlings that emerged at the censuses of August 2020 and 2021.

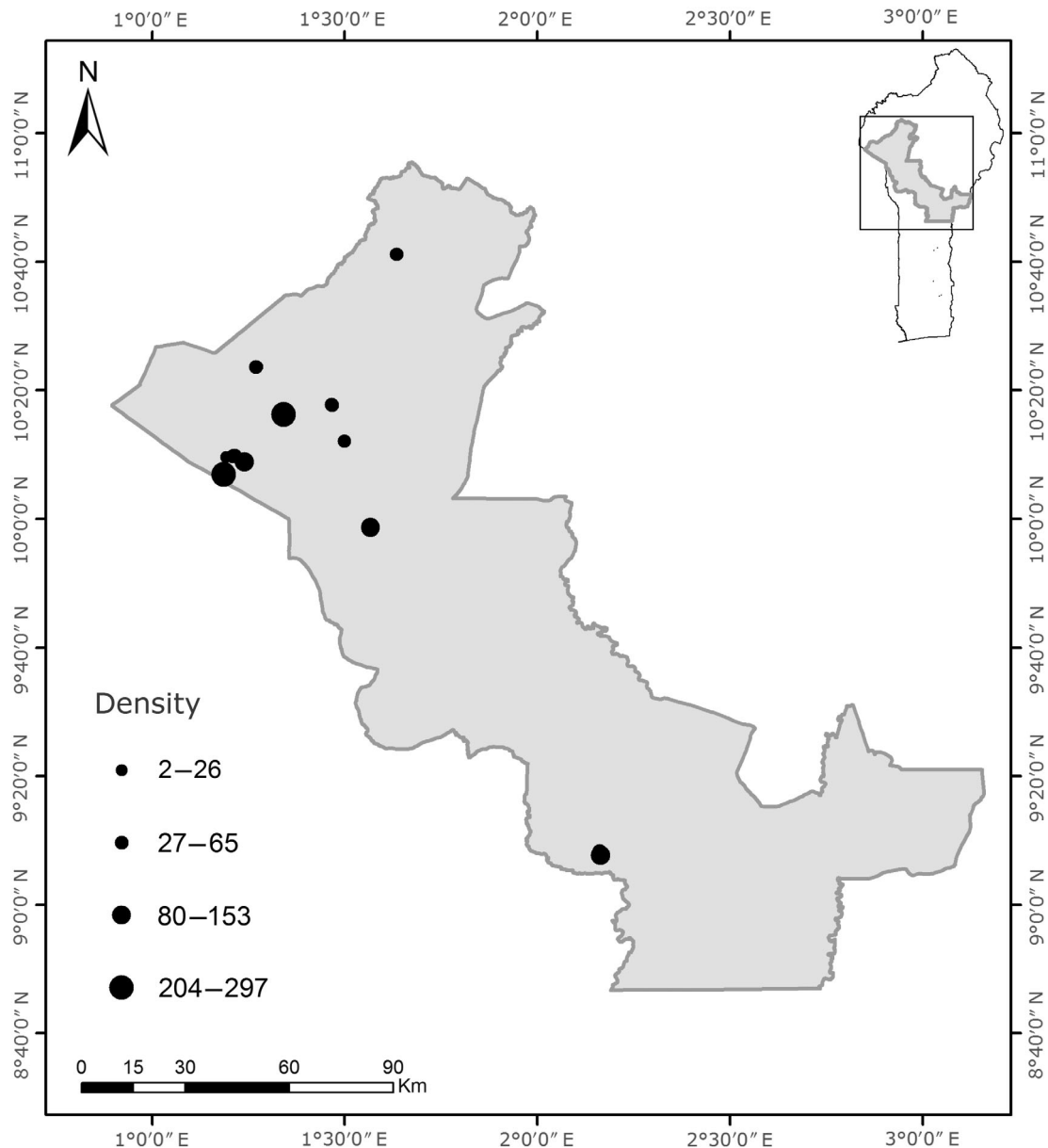


FIGURE 1 Distribution of 12 *Thunbergia atacorensis* populations in Benin. The gray square in the insert represents the study area in Benin (West Africa). The black dots represent sampled populations. The size of each dot is proportional to population density (plants/25 m²).

We used the total number of fruits produced in 2019 and 2020 to estimate the probability of seeds germinating (p_g) and establishing within a year (p_e) as the ratio of the number of seedlings at $t+1$ over the number of seeds at t . The basal diameter was used as a metric of plant size and a predictor of vital rates (survival, growth and fertility) because size is often a better predictor of demographic rates than age (Silvertown, 1993).

Estimating distances from geographic range center and from climatic niche centroid

In this study, we sought to disentangle the influence of distance from geographic range center versus distance from climatic niche centroid on demographic vital rates and population dynamics. We investigated the vital rates-distance relationship by measuring the distance from all the populations to the geographic center or the niche centroid. The geographic center was identified as the center point of a convex hull around all the 12 sampled populations (Dallas et al., 2017). The geographic distance emphasizes the location of the population relative to the central populations. The geographic gradient captured here is not only the general latitudinal gradient but also specific to the distribution of our study species.

The distance from climatic niche centroid was measured as a Mahalanobis distance (Calenge et al., 2008; Etherington, 2019). To calculate the Mahalanobis distance (Osorio-Olvera et al., 2020), we used 1101 presence points of *T. atacorensis* within the 12 populations and split these occurrences into training (80%) and testing (20%) to build a minimum volume ellipsoid model. The minimum ellipsoid represents the Hutchinson's hypervolume model describing species fundamental niche. To build the minimum ellipsoid we retrieved, for these occurrence records, solar radiation data along with annual mean temperature, annual precipitation, and precipitation seasonality from WorldClim2 (Fick & Hijmans, 2017), at a spatial resolution of 30 s. Previous studies showed that these climatic variables are important predictor of the distribution of our study species (Fandohan et al., 2015). Next, the environmental data for each occurrence point was utilized to estimate of the minimum volume ellipsoid and its centroid using the package "ntbox" (Luis Osorio-Olvera et al., 2020). We used 10,000 points as background to calculate the approximate area under curve (AUC) ratio which measured the ability of models to predict the presence of the species (Luis Osorio-Olvera et al., 2020). The AUC ranges from 0 to 1 and higher AUCs indicate better model performance in predicting

the presences. The ellipsoid model describing our study species climatic niche had high value AUC of 0.95, an omission rate (OR) ≤ 0.02 , a significant value of partial receiver operating characteristics (ROC) ($p < 0.01$). This suggests a good ability of the model to predict the niche of the species (Appendix S1: Table S2). Finally, we used the Mahalanobis function in the package *stats* to calculate the distance from climatic niche centroid of the minimum volume ellipsoid (Bolar, 2019). Thus, the climatic distance captures how temperature and rainfall change over space thereby capturing climatic gradient for the most species-relevant parameters. We projected the climatic niche (Figure 2a) into geographic space (Appendix S1: Figure S1) and found no significant correlation ($R = -0.05$, $p = 0.88$, Appendix S1: Figure S2) between the distances from climatic niche centroid and from geographic center (Figure 2b), suggesting a mismatch between the climatic niche and the geographic range.

Soil properties

In each *T. atacorensis* plot, we collected 20 g of composite soil samples by mixing soil collected from the center and the four corners of each plot at the sampling depth of 7 in. We collected a total of 52 soil samples which were analyzed for macronutrients (nitrogen, potassium, phosphorus, sulfur, and magnesium), micronutrients (iron and zinc), and soil pH at the Soil, Water and Plant Testing Laboratory at Colorado State University (CO, USA). We also measured soil moisture in each plot using a EXTECH MO750 soil moisture meter (Extech, Boston, MA, USA).

Fitting size-dependent demographic models

We used general linear mixed-effects models (GLMMs) to fit size-dependent vital rate regressions for the probability of survival, probability of flowering, and the mean number of fruits per plant. In each of the GLMM, we included population as a random effect to address pseudo-replication due to the spatial structure of the data. We modeled the size-dependent probabilities of survival $s(x)$ (Equation 1) and of flowering, $f_f(x)$ (Equation 2) using GLMMs with a binomial error distribution and a logit link function with the package *lme4* in R (Bates et al., 2015):

$$s(x) = \frac{\exp(a + bx)}{1 + \exp(a + bx)} \quad (1)$$

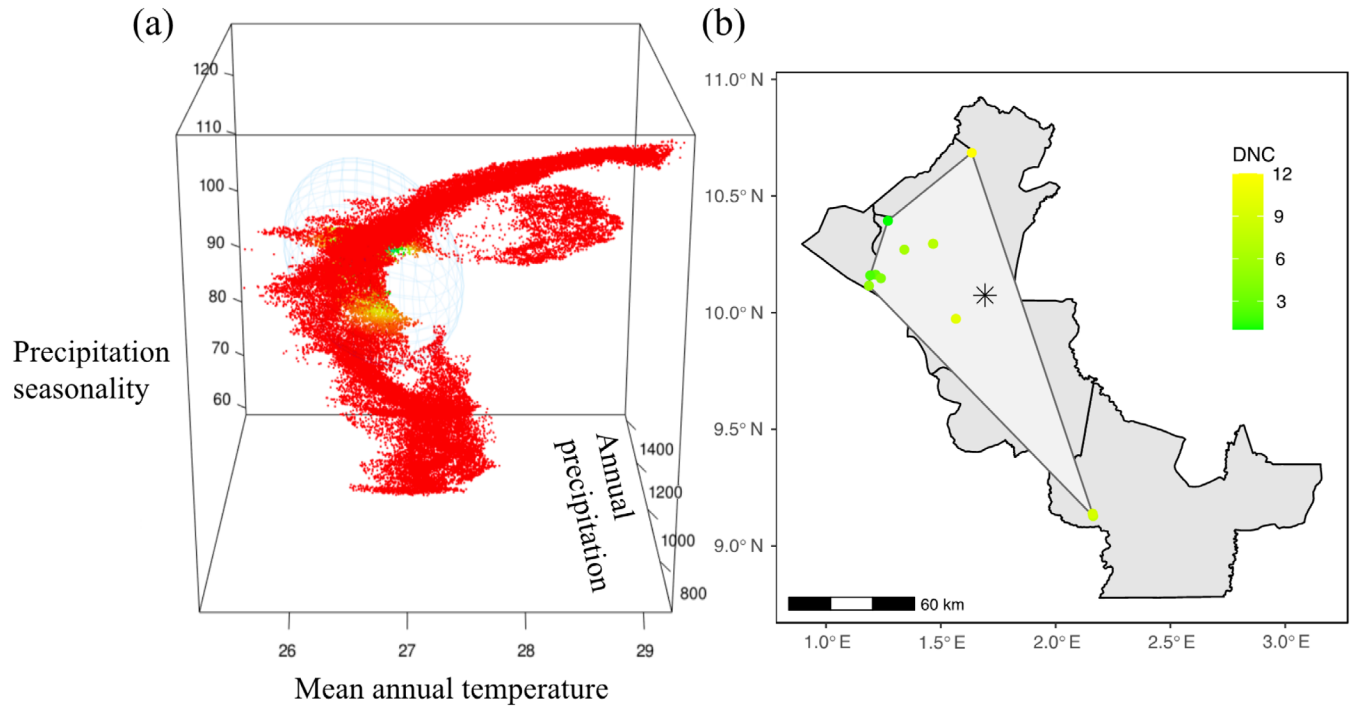


FIGURE 2 (a) Minimum volume ellipsoid defined by the standardized values of three variables: mean annual temperature ($^{\circ}\text{C} \times 10$), the annual precipitation (mm), precipitation seasonality (mm). Blue ellipsoid represents a hypothetical fundamental niche built with presence records of the species. The colors represent distances to the niche centroid (DNC), starting from green color (populations near to niche centroid), yellow (populations inside the niche but not close as the one near the niche centroid), and red (populations outside of the niche). (b) Geographic range with a convex hull polygon. The start in is the center of a convex hull polygon. The dots in color represent each population and they DNC.

$$f_f(x) = \frac{\exp(a + bx)}{1 + \exp(a + bx)} \quad (2)$$

$$g(y, x) = d\text{norm}(\mu, \sigma) \quad (4)$$

$$\mu = a + bx \quad (5)$$

$$\sigma^2 = \phi \exp(-\gamma \hat{y}) \quad (6)$$

The size-dependent mean fruit production per plant, $f_n(x)$, was modeled using zero-inflated negative binomial model with the package *glmmTMB* (Brooks et al., 2017):

$$f_n(x) = \exp(a + bx). \quad (3)$$

The size-dependent growth, $g(y, x)$, (Equation 4) was modeled using a normal error distribution with a mean μ and a standard deviation σ (Equations 5 and 6). Because the variance was heterogeneous ($p < 0.05$, Fligner test), we used generalized least squares (*gls*) function in the package *nlme* to model the variance σ^2 as function of fitted values \hat{y} (Equation 6) (Pinheiro et al., 2021). We used the Akaike Information Criterion (AIC) (Crawley, 2012) to compare two models of size-dependent variance: as an exponential function of size and as a power function of size (Appendix S1: Table S3). We used the exponential variance function which had the smallest AIC for and (Equation 6).

In Equations (1), (2), (3), and (5), the parameter a represents the intercept of the model and b represents the slope of the relationship between the size (x) at time t and vital rates, respectively the probability of survival to time $t + 1$, $s(x)$, probability of flowering $f_f(x)$, the fruit number $f_n(x)$, and the probability of growth, μ . In Equation (6), γ represents the size-dependent variance and ϕ is the residual variance.

Our first test of the center-periphery hypothesis investigated how median demographic vital rates varied across the geographic distribution (with distance from geographic center) and the climatic niche (with distance from niche centroid). We first calculated the median plant size for each population to estimate the median demographic vital rates (survival, growth, and fecundity) for each population. We preferred the median over the mean because most of the plant size distributions were

skewed (Appendix S1: Figure S3). To obtain the median vital rates (survival, growth, fertility) for each population, we evaluated Equations (1)–(3) using the appropriate population-specific median plant size x , and the slopes and intercepts previously estimated from the GLMMs. We then used a general linear model to test the effect of distance from climatic niche centroid and distance from geographic range center on the median demographic vital rates. All the statistical analyses were performed in R 3.6.2 (R Core Team, 2019).

Integral projection model

Our second test of the center-periphery hypothesis examined how the long-term population growth rate λ varied across the geographic distribution range and the climatic niche gradient. To estimate each population growth rate λ , we used the demographic data to parameterize an IPM (Equation 7) (Easterling et al., 2000) of the form:

$$n(y, t + 1) = \int_L^U K(y, x)n(x, t)dx \quad (7)$$

where, the vector $n(y, t + 1)$ represents the number of individuals of size y at time $t + 1$ and the vector $n(x, t)$ represents the number of individuals of size x at time t . L and U represent the minimum and the maximum plant size respectively. The kernel K is the nonnegative surface of all demographic transitions (i.e., survival, growth, and fecundity) of individual plants from size x at time t to size y at time $t + 1$. The kernel K which is composed of the survival-growth function $p(y, x)$ and the fertility function $f(y, x)$, such that $K(y, x) = p(y, x) + f(y, x)$. The survival-growth function $p(y, x)$ represents the probability that individuals of size x survive $s(x)$ and grows $g(y, x)$ to size y : $p(y, x) = s(x)g(y, x)$. The fertility function is the product of the size dependent survival function $s(x)$, the flowering function $f_f(x)$, the fruit production function $f_n(x)$, seed germination probability (p_g), the probability of establishing for new seedlings (p_e), and the size distribution of new seedlings $f_d(y)$ (Equation 8):

$$f(y, x) = s(x)f_f(x)f_n(x)p_gp_e f_d(y) \quad (8)$$

The probability of germination and establishment p_gp_e was calculated as the ratio of the number of new seedlings in year $t + 1$ over the number of seeds in year t . The kernel K was integrated numerically over all possible plant sizes $[L, U]$, using the mid-point rule (Ellner & Rees, 2006). The result is a high-dimensional matrix with

mathematical properties similar to matrix projection models. The dominant eigenvalue of this high-dimensional matrix represents the long-term population growth rate λ , which we calculated using the package *popbio* in R (Stubben & Milligan, 2007). Thus, populations with $\lambda > 1$ are projected to grow while those with $\lambda < 1$ are projected to decline. We built IPMs for each of the 11 *T. atacorensis* populations and determined their long-term population growth rates. We used general linear models to test the effect of the distance from geographic center, distance from climatic niche centroid, and soil properties on the long-term population growth rate.

Perturbation analysis and demographic recovery

Our third test of the center-periphery hypothesis investigated how the sensitivity (Equation 9) of the long-term population growth rate λ , $S(y, x)$, varied across the geographic distribution and the climatic niche gradient. Sensitivity analysis measures how a small variation in vital rates influences population growth rate. Because population growth rate is a measure of population fitness, we used the sensitivity analysis to examine the eco-evolutionary implications of the variation in sensitivity from center periphery of species range of climatic niche. If a variation in a vital rate reduces population fitness, there will be a selection on that vital rate proportional to the change in fitness (Caswell & Salguero-Gómez, 2013). Moreover, for a given population, if a slight increase in reproduction increases population fitness, individuals with higher reproduction rate will be selected for. Thus, sensitivity analysis was used to measure the strength of directional selection.

For direct management implications, we used elasticity analysis (Equations 10 and 11) to investigate the relative importance of perturbing each IPM demographic functions (survival-growth or fertility) on the long-term population growth rate and how it varies from central to peripheral populations. We evaluated the elasticities of the long-term population growth rate to perturbation of survival-growth (Equation 10), $e_p(y, x)$, and fertility, $e_f(y, x)$ (Equation 11) for each *T. atacorensis* population:

$$S(y, x) = \frac{v(y)w(x)}{\langle v, w \rangle} \quad (9)$$

$$e_p(y, x) = \frac{p(y, x)S(y, x)}{\lambda} \quad (10)$$

$$e_f(y, x) = \frac{f(y, x)S(y, x)}{\lambda} \quad (11)$$

where $w(x)$ is the stable size distribution and $v(y)$ is the size-dependent reproductive values. Elasticity analysis estimates the proportional change in population growth rate for a proportional change in a vital rate (de Kroon et al., 1986). We used a general linear model to test how the elasticities of λ to perturbation of survival-growth or fertility changed with distance from geographic range center and distance from climatic niche centroid.

Our fourth test of the center-periphery hypothesis was to investigate how populations' time to recovery from perturbation (measured by the damping ratio) varies across the geographic distribution range and the climatic niche gradient. We calculated the damping ratio, ρ (Equation 12), a dimensionless metric of how fast transient dynamics decay following a disturbance, regardless of the population structure.

$$\rho = \frac{\|\lambda_2\|}{\lambda}, \quad (12)$$

where λ is the dominant eigenvalue, λ_2 is the subdominant eigenvalue of the high-dimensional matrix. The damping ratio, ρ , varies between zero and one. The closer the damping ratio is the one, the faster the population will converge to stability, and the lower the recovery time after perturbation (Haridas & Tuljapurkar, 2007). We used a general linear model to test how this metric of demographic resilience varied from distance to geographic range center or climatic niche centroid.

RESULTS

Demographic vital rates variation from center to periphery

Our first test of the center-periphery hypothesis was to understand how median demographic vital rates varied across the geographic distribution range. We found that the median probability of flowering ($\beta = 0.060 \pm 0.012$, $p = 0.001$, Figure 3) and growth ($\beta = 0.246 \pm 0.084$, $p = 0.018$, Figure 3) significantly increased with distance from the geographic center, suggesting faster growth and more frequent flowering in peripheral than central populations. However, such advantage in flowering probability did not translate into higher fecundity in peripheral population (Figure 3). We found no significant relationship between distance from geographic center and the median fruit production ($\beta = -0.351 \pm 1.750$, $p = 0.842$, Figure 3) and probability of survival ($\beta = 0.129 \pm 0.121$, $p = 0.317$, Figure 3). Surprisingly, climatic distance had no significant effect on demographic vital rates suggesting that the effect of geography is most likely driven by

non-climatic factors. We found no significant relationship between distance from climatic niche centroid and the probability of flowering ($\beta = -0.012 \pm 0.013$, $p = 0.361$, Figure 3), median fruit production ($\beta = -0.582 \pm 0.976$, $p = 0.566$, Figure 3), median growth rate ($\beta = 0.036 \pm 0.067$, $p = 0.607$, Figure 3), or the probability of survival ($\beta = -0.020 \pm 0.074$, $p = 0.794$, Figure 3).

Population growth rates and soil properties

Nearly 73% of *T. atacorensis* populations were declining across its range with a mean log population growth rate of -0.37 ± 0.45 . Our second test of the center-periphery hypothesis examined how long-term population growth rates varied across the geographic range and the climatic niche gradient. Consistent with the results on median demographic rates, we found no significant variation in population growth rates with climatic distance ($\beta = -0.031 \pm 0.133$, $p = 0.822$, Figure 4) but also with geographic distance ($\beta = 0.327 \pm 0.211$, $p = 0.156$, Figure 4). However, population growth rates significantly decreased with soil nitrogen ($\beta = -0.423 \pm 0.120$, $p = 0.006$, Figure 4). In contrast, we found no variation in population growth rates with soil phosphorus ($\beta = -0.509 \pm 0.559$, $p = 0.386$, Figure 4), soil potassium ($\beta = -0.2785 \pm 0.2094$, $p = 0.216$), soil salinity ($\beta = -0.1955 \pm 0.3696$, $p = 0.61$), soil manganese ($\beta = 0.001 \pm 0.198$, $p = 0.996$), soil iron ($\beta = 0.012 \pm 0.192$, $p = 0.948$), soil copper ($\beta = 0.012 \pm 0.192$, $p = 0.948$), soil zinc ($\beta = -0.267 \pm 0.146$, $p = 0.101$), and soil moisture ($\beta = -0.406 \pm 0.40$, $p = 0.337$).

Elasticity and sensitivity analyses and recovery time from center to periphery

Our third test of the center-periphery hypothesis investigated how the sensitivity of the long-term population growth rate λ varied across the geographic distribution and the climatic niche gradient. Our result showed that the sensitivity of λ to perturbation of survival-growth was not significantly associated with climatic distance ($\beta = 0.016 \pm 0.073$, $p = 0.829$, Figure 5) or geographic distance ($\beta = 0.130 \pm 0.119$, $p = 0.301$, Figure 5). Similarly, sensitivity of λ to perturbation of fecundity was not significantly correlated with climatic distance ($\beta = 0.00 \pm 0.046$, $p = 0.998$, Figure 5) or geographic distance ($\beta = 0.047 \pm 0.078$, $p = 0.560$, Figure 5). The non-significant variation of the sensitivity of population fitness to change in vital rates from center to periphery suggest no difference in selective pressure from center to periphery.

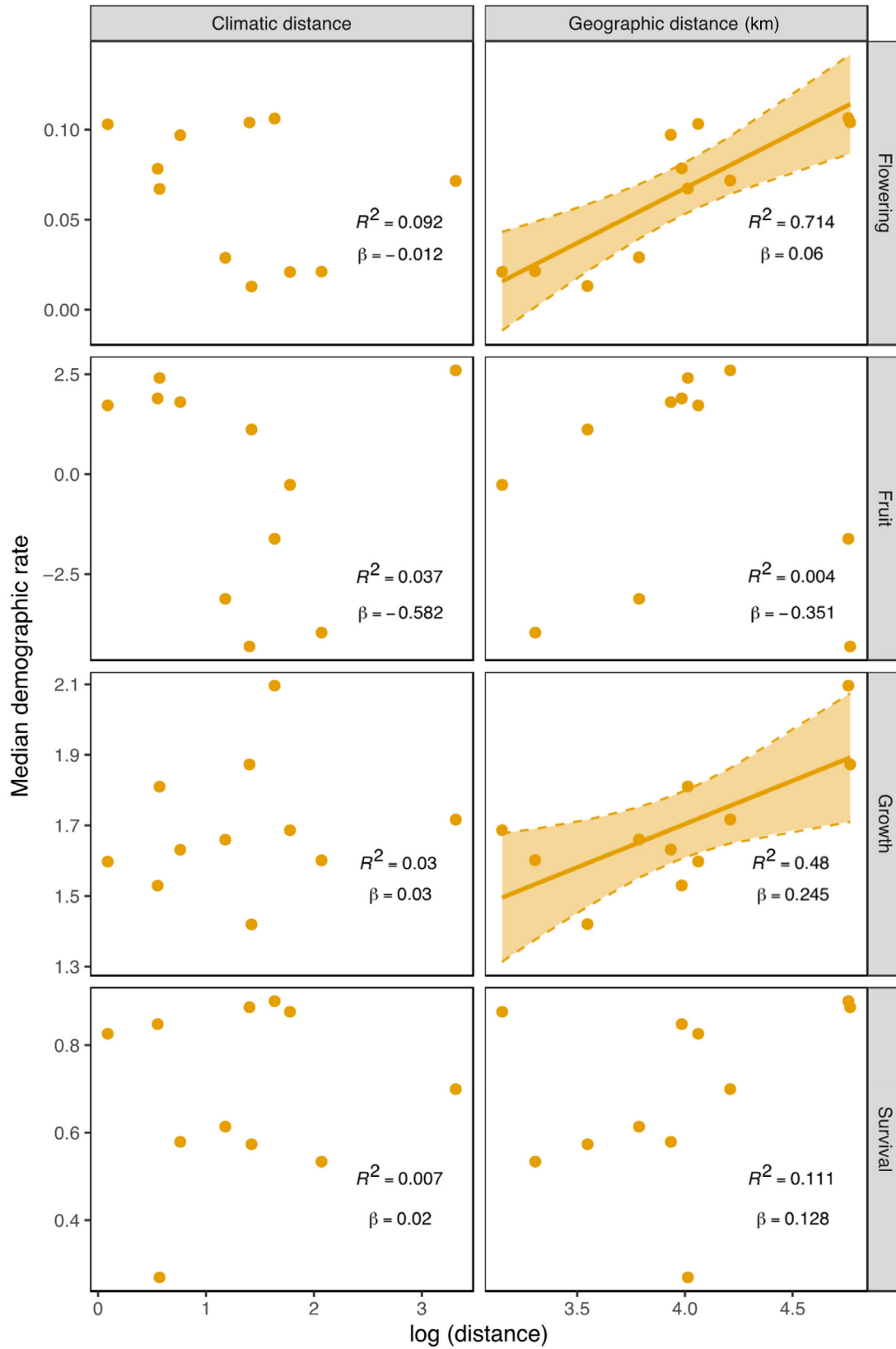


FIGURE 3 Vital rates (growth, survival, flowering, fruit production) as function of distances as geographic distance in km (log scale) from species range center and climatic distance from niche centroid, unitless (log scale). Points correspond to each population vital rate as function of median size. The solid line is the fitted line from a linear model with $p < 0.05$, and orange shadings shows 95% confidence interval around fitted line. β represents the slope of the of the relationship between vital rates and distance from climatic/geographic center. R^2 represents the proportion of variance for vital rates explained by the distance from climatic/geographic center.

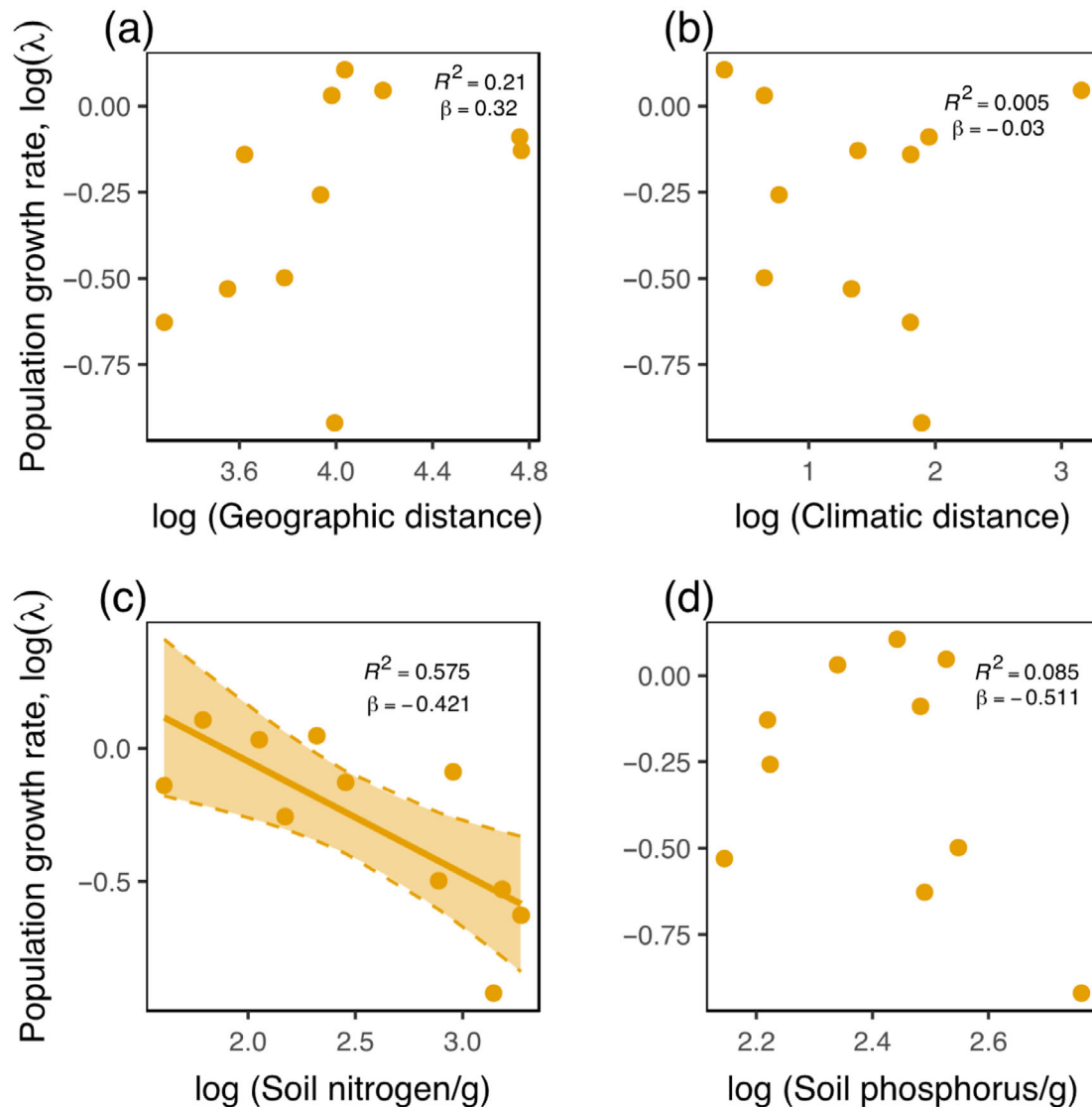


FIGURE 4 Population growth rate as function of distance as geographic distance from species range center in km (log scale) (a) and climatic distance from niche centroid unitless (log scale) (b), nitrogen in g (log scale) (c) and phosphorus in soil originally in gram (log scale) (d). The solid line is the fitted line from a linear model $p < 0.05$, and orange shadings shows 95% confidence interval around fitted line. β represents the slope of the of the relationship between population growth rate and distance from climatic/geographic center, soil nitrogen and soil phosphor. R^2 represents the proportion of variance for population growth rate explained by each predictors: the distance from climatic/geographic center, soil nitrogen and soil phosphorus.

Furthermore, we found slightly higher elasticity values for larger individuals (individuals reaching sizes near 7.4 mm, Appendix S1: Figure S4). However, the elasticity of λ to perturbation of vital rates was similar in central and peripheral populations (Appendix S1: Figure S5), suggesting that proportional changes in survival-growth or fertility of individuals had no effect on population growth rate of *T. atacorensis*.

Our fourth test of the center-periphery hypothesis investigated how population time to recovery, measured using the damping ratio, varies across the geographic distribution range and the climatic niche gradient. We found that populations' time to recovery declined with

geographic distance ($\beta = -0.201 \pm 0.069$, $p = 0.017$, Figure 6), suggesting that central populations are demographically more resilient to perturbation than peripheral populations. However, the damping ratio did not vary with climatic distance ($\beta = -0.051 \pm 0.053$, $p = 0.356$, Figure 6).

DISCUSSION

The center-periphery hypothesis predicts that vital rates and population growth rates will decrease with distance from climatic niche centroid or geographic range center as climatic conditions become less optimal toward the range

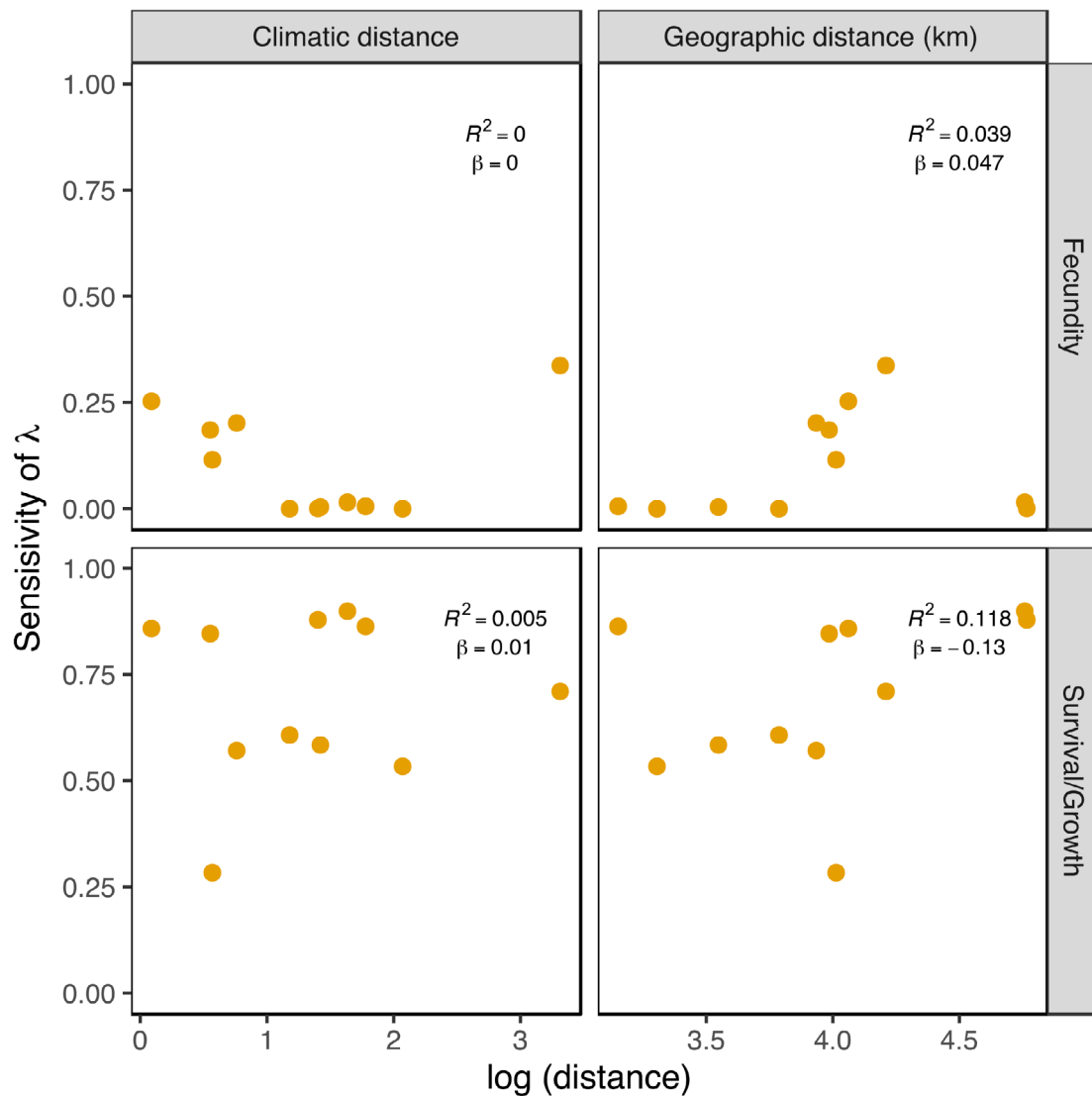


FIGURE 5 Sensitivity of vital rates (selection gradient) of each population as function of distance as geographic distance from species range center in km (log scale) and climatic distance from niche center unitless (log scale). β represents the slope of the relationship between elasticity and distance from climatic/geographic center. R^2 represents the proportion of variance for elasticity explained by the distance from climatic/geographic center. The plotted values are the sum of the elasticities of fertility (upper panel) terms and growth/survival terms (lower panel). For a single population, the value in the upper panel and the value in the lower panel are sum to 1.

periphery. We provided four independent tests of the center-periphery hypothesis using demographic vital rates, population growth rates, selection gradients, and population recovery time to perturbation. We found no support for this hypothesis using vital rates, population dynamics, and selection gradients when we used climatic distance as the predictor. However, the median probabilities of flowering and growth increased with distance from geographic range center. Such an increase in vital rates was not strong enough to significantly influence the center-periphery variation in population growth rates. Soil nitrogen was the main driver of population growth rates, which were most sensitive to perturbation of plant’s survival-growth. Moreover, the sensitivity of population growth rate to vital rate

changes did not vary significantly with climatic or geographic distances. Nevertheless, geographically peripheral populations were demographically less resilient to perturbation than central populations.

Distances from climatic niche centroid and from geographic center were not correlated, suggesting a mismatch between the climatic niche and geographic distribution (Martínez-Meyer et al., 2013; Pagel et al., 2020). Previous studies on the center-periphery hypothesis rely on the assumption of the “Eltonian noise hypothesis,” that biotic interactions are irrelevant to predict species distribution at coarse grained resolution and large scales (Soberón & Nakamura, 2009). Such biotic factors were not included in our climatic niche model. This is one

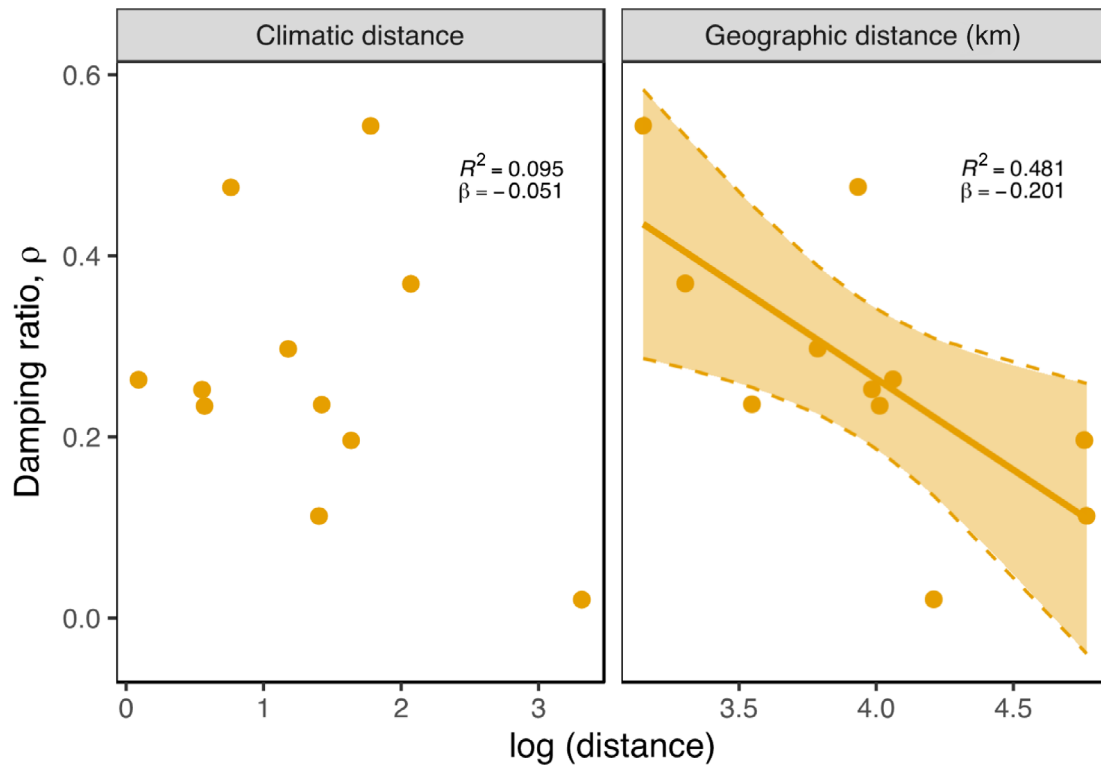


FIGURE 6 Damping ratio, ρ as function of distance as geographic distance from species range center in km (log scale) and climatic distance from niche center unitless (log scale). Points correspond to each population damping ratio. The solid line is the fitted line from a linear model with $p < 0.05$, and orange shadings show the 95% confidence interval around the fitted line. β represents the slope of the relationship between damping ratio and distance from climatic/geographic center. R^2 represents the proportion of variance for damping ratio explained by the distance from climatic/geographic center.

limitation of our study because biotic factors could limit the presence of the species even in suitable areas. Further, our climatic niche model was built under the environmental equilibrium assumption that individuals can disperse freely and be present in all abiotically suitable sites, while being absent from all unsuitable ones. Several studies show that dispersal limitation can restrict species ranges. Thus, the absence of the species from climatically suitable areas could be a result of dispersal limitation (Pulliam, 2000; Schurr et al., 2012). However, we do not have sufficient data on the dispersal ability of *T. atacorensis* to test the dispersal limitation hypothesis.

We found no support for the hypothesis that central populations have higher vital rates (growth, survival, and fecundity) than peripheral populations. Previous studies found higher vital rates at the geographic range periphery (Angert, 2006; Gerst et al., 2011) due to local adaptation in peripheral populations or more suitable microhabitats at the periphery (Angert and Schemske 2005; Angert et al., 2008; Lee et al., 2009). Consistent with this trend, but contrary to expectation, we found higher growth and flowering probability in peripheral populations. These surprising results could be explained by the fact that some peripheral populations of *Thunbergia* occur on the most

suitable areas (Appendix S1: Figure S1). Further studies on local adaptation using a reciprocal transplantation across the range of *T. atacorensis* populations could help clarify the mechanisms behind such center-periphery variation in vital rates. From our analysis of damping ratio, we found that geographically central populations of *T. atacorensis* had high demographic resilience to perturbation suggesting that they recover faster following perturbation than the geographically peripheral populations. This fast recovery to perturbation could drive demographic compensation (Capdevila et al., 2020). However, we did not test demographic compensation in our study species.

We hypothesized that population growth rates would decrease with increasing distance from geographic center and climatic niche centroid. However, we found no significant variation in population growth rates across geographic range and climatic niche. These findings indicated that differences in median vital rates between central and peripheral populations failed to translate into significantly higher population growth rate in peripheral populations. In contrast, previous studies showed that population growth rates decrease toward the periphery and that geographic range limits often coincide with niche boundaries (Hargreaves et al., 2014; Lee-Yaw et al., 2016). In addition,

this result contrasts with the postulate that peripheral populations are maladapted (Kirkpatrick & Barton, 1997) and may explain why the population growth rates did not decrease toward the periphery. The absence of decreasing population growth rate toward range periphery is not surprising given the greater relative importance of survival-growth to population fitness than fertility which is a typical trait of long-lived species. Consistent with our findings on population growth rates, our previous study on the same system showed no significant variation in population abundance between range center and periphery (Moutouama & Gaoue, 2022a). These convergent results of two different metrics (e.g., population abundance and population growth rate) must not be interpreted as if population abundance could be used as a surrogate measure of population growth rate. Nevertheless, the demographic analysis conducted in this study provides further insights into species' ecological and evolutionary response to distribution gradients.

We postulated that population growth rates would be more sensitive to perturbation of survival-growth than fertility in peripheral populations. However, despite spatial variations in the mean selective pressure and elasticity, these variations were not linearly associated with geographic or climatic distances, suggesting similar selective pressure from center to periphery. This result contrasts with previous findings that natural selection will most likely act more at the periphery than at the center of species geographic range (Antonovics, 1976; Lesica & Allendorf, 1995). Spatial population genetic studies on *T. atacorensis* can directly assess the variation of selective pressure and strength of genetic differentiation between peripheral and central populations to confirm the pattern observed here.

Further, long-lived species tend to invest more in survival than in reproduction (Silvertown, 1993). Therefore, it is expected that *T. atacorensis* population dynamics are more elastic to survival-growth than fecundity across the range. Conservation actions should target strategies that increase species survival and growth rather than fecundity. Although the elasticity of population growth rates to perturbation in demographic rates did not change significantly from center to periphery, conservation strategies should be nuanced between central and peripheral populations (Channell, 2004; Haak et al., 2010). Our analysis also showed that central populations were more resilient to perturbation than peripheral populations indicating potential difference in response time after conservation actions take place. As global warming will impact vulnerable species disproportionately (Brook et al., 2008), peripheral populations will likely be more affected than central populations.

Consistent with our results, previous studies demonstrate that an increase of nitrogen in soil can significantly increase plant species probability of extinction (Gotelli & Ellison, 2002). In our study system, high soil nitrogen

concentration was associated with high herbivory (Moutouama & Gaoue, 2022b), suggesting that the negative effect of soil nitrogen on population dynamics could be due to excessive herbivory. The detrimental effects of nitrogen could be also explained by its saturation in the soil and a resulting decrease in nitrogen retention in the soil (Heil & Diemont, 1983). However, the effect soil heterogeneity on population dynamics should be interpreted with caution. Soil properties were measured at the plot level rather than at the individual plant level. If soil variation at the plot level is smaller than at the individual level, then the real demographic effects of soil properties would be underestimated in our model. In addition, because we only demonstrated association between soil properties and population growth rates, manipulative experiments are needed to establish causal influence of soil heterogeneity on population dynamics.

CONCLUSION

Ecological conditions at the periphery of the species' distribution range tend to be more stressful than those experienced by central populations. These stressful conditions may favor a decrease in population performance and thereby limit species range expansion. Overall, our study provided evidence that demographic vital rates, population growth rate, and its sensitivity to perturbation of vital rates vary irrespective of geographic or climatic gradient. Our study also revealed that central populations recover faster after perturbation than peripheral populations across the geographic range. The mismatch observed between geographic distribution and climatic niche potentially masks the effects of biotic drivers and abiotic factors such as soil quality which are not directly included in the geographic or climatic distances used as predictors in our study. Most tests of the center-periphery hypothesis used species abundance or genetic diversity as response variable but rarely estimated demographic traits or population dynamics. More demographic tests of the center-periphery hypothesis are necessary to conduct meta-analyses and provide more robust conclusions.

AUTHOR CONTRIBUTIONS

Jacob K. Moutouama and Orou G. Gaoue conceived of the study and developed the models, Jacob K. Moutouama collected the data, performed the analyses, and lead the writing of the manuscript with editorial assistance from Orou G. Gaoue.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Data (Moutouama & Gaoue, 2023) are available in figshare at <https://doi.org/10.6084/m9.figshare.21648074>. WorldClim2 data were downloaded from <https://www.worldclim.org/data/worldclim21.html> by downloading the 30 s monthly climate data for “bioclimatic variables” and “solar radiation.”

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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