Ecological drivers of range limitation in species

A Dissertation Presented for the
Doctor of Philosophy
Degree
The University of Tennessee, Knoxville

Jacob K. Moutouama
December 2022

DEDICATION

To my father, older sister, and older brother, who never saw this adventure.

ACKNOWLEDGEMENTS

I would first like to thank my advisor Orou Gaoue, who has provided tremendous guidance in preparing me for a career in research. I would also like to acknowledge my committee members, Stephanie Kivlin, Laura Russo, Charles Kwit, and James Fordyce, generous support, advice, and conversation throughout my Ph.D. I would like to thank the Bailey Kivlin Sweitzer (BKS) Lab for inviting me to their lab meeting during my time at Knoxville. I am grateful to Lalasia Bialic Murphy and Robert McElderry for their advice and motivation throughout my Ph.D.

Secondly, I want to thank the institutions that have provided funds through grants and awards to collect data or publish my research. I want to thank particularly the Department of Ecology and Evolutionary Biology at University of Tennessee Knoxville, the Herbarium of University of Tennessee at Knoxville, the British Ecological Society, the Society for Conservation Biology, the Association for Tropical and Biological Conservation, the Ecological Society of America, the National Institute for Mathematical and Biological Synthesis, the Nation Socio-Environment Synthesis Center, the Lewis Clark Research foundation, the Rufford Small Grant foundation, the Organization of Tropical Studies, the Scholarly Activity and Research Incentive Funds (SARIF) and the Center for Global Engagement.

Thirdly, I want to think Kim G. Mortega, Kevin Wallace and Johannes Penner for everything I learned from them during my Tropical Biology course at Kirindy (Madagascar).

Finally, I am grateful to my family and friends who supported me during my Ph.D.

ABSTRACT

Understanding the ecological and evolutionary drivers of species range limitation is a central debate in evolutionary ecology with direct implications for conservation ecology. This is important because such understanding provides insights into the mechanistic drivers of species adaptation or extinction in peripheral populations where species are often exposed to severe and stochastic biotic and abiotic stressors. The center-periphery hypothesis (CPH) posits that species performance decreases toward range periphery, a potential mechanism to explain range limitation. However, after several decades of testing the center-periphery hypothesis, we still lack general support for this hypothesis. In my dissertation, I combined meta-analysis, field observation, and modeling to gain general understanding of the drivers of range limitation. First, I ask whether there is general support for the center-periphery hypothesis. To address this question, I conducted a meta-analysis on studies that tested the CPH. I found that only genetic diversity decreased from center to periphery. Population dynamics and population abundance did not decrease from center to periphery. This lack of support of the CPH was explained by high heterogeneity in effect size due to species kingdom, pollination type, and methods used to test the CPH. This works also revealed that most tests of the CPH are only conducted in temperate regions. This motivated me to use a tropical herb, *Thunbergia atacorensis*, as a study system to test the role of soil heterogeneity, and altitude on the variation of herbivory, population abundance and population dynamics between central and peripheral populations. I found that there was no change in plant density, herbivory rate and population dynamics from niche centroid to periphery. Instead, soil nutrients were the primary drivers of population abundance, herbivory rate and population growth rate in *Thunbergia* populations. While intuitive, the CPH is not common across taxa and the mixed support for the CPH indicates that range limitation is not a direct result of alteration of conditions toward the periphery but rather the result of the combined influences of biotic and abiotic factors on population performance across the range.

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INTRODUCTION

Understanding the mechanisms underpinning species range limits is a fundamental question in ecology (Sutherland et al., 2013). Theory suggests several processes by which range limits arise including resource availability, natural enemies, unstable population dynamics, and insufficient genetic variability (Gaston, 2009; Sexton et al., 2009). The challenge is to identify, empirically, in each context the exact process driving range limitation and how that process causes range limitation. As a result, there are major gaps between theoretical predictions and empirical test of range limitation. Accurately predicting range limits empirically could serve as ground to understand the conditions by which populations can adapt or fail to adapt to novel environmental conditions. Such understanding can provide insights into the response (extinction or adaptation) of species to climate change, particularly at the periphery where environmental conditions are often harsh for species.

The interest in the ecology of range limits dates to the 19th century. Darwin (1859) discussed "the effect of environment on limiting the geographical range of species" and concluded that some species were progressively getting scarcer and scarcer and finally disappearing along geographical gradients. Brown (1984) observed that, in general, species abundance tends to decrease from center to periphery of the range due to alterations in environmental conditions at range periphery. This tendency of a species to decline in abundance toward its geographic distribution edge is referred to as the abundance center distribution (Sagarin and Gaines, 2002) or abundance niche centroid (Yañez et al., 2020). The center-periphery hypothesis (CPH) is an extension of the abundance center distribution to other measures of population performance such as vital rate, population growth rate and genetic diversity. As population performance depends on population size (abundance), the center-periphery hypothesis predicts that species performance in terms of abundance, genetic diversity, or population growth rate decreases toward the periphery, which may drive range limitation (Pironon et al., 2017). Over the last decade, the test of the center-periphery hypothesis received increasing attention from ecologists, prompted by the need to perfectly predict species' response to

climate change at the edge of their distribution (Dallas et al., 2017a; Osorio-Olvera et al., 2020). This renewed interest has been enhanced by the development of extensive online databases compiling species occurrences, environmental variables, and robust machine learning algorithms. However, after more than 35 years of research on CPH, we still lack a general support for the center-periphery hypothesis or even any consensus on whether this is a valid biogeographical debate (Eckert et al., 2008; Hargreaves et al., 2014; Sagarin and Gaines, 2002).

Decades of tests on the center-periphery hypothesis showed mixed results for several reasons. First, the expectation of the center-periphery hypothesis relies on several assumptions including an equilibrium between range and niche limits, the absence of dispersal limitation, and equilibrium population density within each population across the range (Dallas et al., 2020). The equilibrium population density is the value at which the number of individuals in a given population does not change and will return to the initial population size after disturbance (Wolda, 1989). However, these assumptions may not hold in several ecological contexts. Previous studies showed that environmental gradients and geographic gradients could be different such that environmental optima do not coincide with geographic center (Aikens and Roach, 2014; Pironon et al., 2015). Further, individual performance patterns might not always be determined by the spatial distribution of physiological stress and local conditions. For instance, dispersal can be an essential factor driving species density. Dispersal limitation could prevent species from being present in suitable parts of the niche and thereby influence the support for the center periphery hypothesis (Bridle et al., 2010). Finally, studies showed that population density equilibrium itself, spatially or temporally, is not constant (Wolda, 1989). Therefore, temporal variation in abundance or density is likely to introduce bias to snapshot estimates of spatial trends in abundance across the range.

Second, the periphery and center concept has not been clearly defined in the literature. Most studies consider as peripheral only populations that are distinctly isolated along the species geographical distribution (Castilla et al., 2011). One group of studies considers the periphery as the part of the range at which the interpolated local abundance value reaches fifty percent of the maximum abundance value (Root, 1988). Another

group of studies considers peripheral populations as those found in the region located within half the distance to the edge of a species' geographical range from central point (Channell and Lomolino, 2000). Species range is often considered as its ecological niche in space. The ecological niche is considered here as Hutchinson *n*-dimensional hypervolume (Hutchinson, 1957). The common assumption for most studies is that at least one of the niche axes, corresponding to a fundamental environmental driver, should be limited or missing in peripheral populations, otherwise the species would have been able to extend its range beyond the observed boundaries (Martínez-Meyer et al., 2013). Thus, species range periphery is often defined as the least suitable part of the ecological niche, and this often represents non suitable habitats. Rather than classifying the range into center and periphery, some authors use distance from range center or periphery. For example, Blackburn et al. (1999) used the average distance to all unoccupied local area and average distance to all occupied local areas as metrics of the population's departure from range limits. Dallas et al. (2017a) used the distance from niche center (e.g. euclidean and mahanalobis distance) and geographic from range center. Olivera et al. (2020) used the mahalanobis distance and suggested that distance might be the best one because it takes into account the covariance between variables.

To gain insights into species range limits, it is critical to address the methodological and conceptual limitations of existing studies on the center-periphery hypothesis. Specifically, it is critical to analyze how the methods utilized to calculate the distance from species range center or niche centroid affect the likelihood of finding support for the center-periphery hypothesis. It is also important to gain a mechanistic understanding of the role of species' life history and functional traits in shaping species response from center to periphery. Moreover, because range limitations could arise from a combined effect of abiotic and biotic factors, it is critical to analyze how biotic drivers such as pollination type, and plant herbivory mediates the center-periphery dynamics. Furthermore, population density, as a static measure of population performance, is not sufficient to understand the temporal dynamics of species from center to periphery (Aikens and Roach, 2014). Therefore, an increasing number of studies use population vital rates and population growth rates to test the center-periphery hypothesis (Dallas and

Santini, 2020; Pagel et al., 2020). Existing studies also use population genetics to illustrate how genetic diversity decreases (or not) from central to peripheral populations (Bontrager and Angert, 2019; Case and Taper, 2000; Kennedy et al., 2020). However, we still lack a comprehensive synthesis of the variation of genetic diversity across species range. Several attempts at synthesizing the literature on the center-periphery hypothesis used vote count approach which ignores the between-study variation in precision and the influence of phylogenetic relatedness between study species on the generality of the conclusions.

In this dissertation, I combined field observation, modelling, and meta-analytical approaches to investigate how biotic and abiotic drivers shape the range limits of tropical species while synthesizing the literature to provide a global test of the center-periphery hypothesis. Because most tests of the center-periphery hypothesis focused on temperate region thus limiting our ability to generalize to tropical regions, I chose to use a tropical perennial herb, *Thunbergia atacorensis* Akoègn. & Lisowki, as the study species for my field observation. The study species is confined to Benin in West-Africa and is subject to herbivory. The combination of these characteristics makes the species a good tropical system to test the center-periphery hypothesis. I organized the dissertation in four results chapters including revisiting the global test of the center-periphery hypothesis using phylogenetic meta-analysis (Chapter 1), an integral projection modeling of population dynamics response variation between center periphery (Chapter 2), and two chapters studying the mechanistic role of micro-scale soil heterogeneity (Chapter 3) and insect herbivory (Chapter 4) on the performance of species between central and peripheral populations. To account for some of the weaknesses of previous studies, I used distance from geographic center and distance from climatic niche centroid rather than the commonly used approach of designating some populations as central and others as peripheral.

In chapter one, I tested for the global support for the center periphery hypothesis. I developed a meta-analysis in which I controlled for phylogenetic relatedness of taxa for which previous studies tested the hypothesis. I tested whether species kingdom, pollination type, longevity and the methods utilized to estimate the distance from range

center explained the lack of support for the center-periphery hypothesis. I found no support for a decrease in species abundance or population growth rate toward the periphery. However, genetic diversity did decrease from center to periphery. The lack of support was due to difference in response across animals and plants range. We also noticed that the method utilized to estimate the distance from range center could affect the likelihood of finding support for the center-periphery hypothesis. For plant species, the type of pollination (out and cross) could affect the support for the center-periphery hypothesis.

In chapter two, I used a field study to test if population density decreased from center to periphery and investigated what may explain patterns in species abundance in *T. atacorensis* populations. Most of the studies testing the center-periphery hypothesis are biased toward temperate regions and often test the effects of only one environmental driver. I used abiotic, biotic and functional traits to develop a structural equation model to understand the mechanisms driving the variation in abundance for the study species. I found that species abundance did not decrease from center to periphery. Instead, altitude mediated by soil properties was the main driver of species abundance.

In chapter three, I investigated whether herbivory rate in *Thunbergia atacorensis* increased towards the edge of the species range, thereby limiting the species distribution. I also investigated the factors that may drive such an increase in herbivory rate. Most studies assume that high levels of herbivory at the periphery mainly drive species range limitation. However, some species are tolerant to herbivory, and, for these species, high levels of herbivory do not necessarily have a negative impact on population dynamics. I developed a Bayesian structural equation model to test the relative role of abiotic and biotic factors including how phylogeny diversity can reduce herbivory rate consistent with the theory of biotic resistance. This work revealed that high herbivory rate did not drive species range limitation in Thunbergia populations.

In the last chapter, I studied if the long-term population growth rate decreased at the periphery so that peripheral populations may be unable to expand beyond their range limits. I used three years of demographic data collected on *T. atacorensis* to develop an integral projection model allowing the estimation of population growth rate from center

to periphery. This study illustrated that range limitation does not necessarily arise from decreasing population growth rate from center to periphery.

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CHAPTER 1: THE CENTER-PERIPHERY HYPOTHESIS REVISITED: A META-ANALYSIS.

A version of this chapter is to be submitted by Jacob Moutouama and Orou Gaoue as a manuscript to *Nature communications*:

Moutouama, J.K. and Gaoue. The center-periphery revised: a meta-analysis.

Authors contributions: JKM and OGG conceived the study and developed the models, JKM collected the data, performed the analyses, and led the writing of the manuscript with editorial assistance from OGG.

Abstract

A long-standing biogeographical hypothesis of species range distributions, the center-periphery hypothesis, sets up the expectation that species will have higher abundance, demographic performance, and genetic diversity at the center of their range distributions and decreasing performance at their range edges. This emergent pattern is thought to be driven by divergent biotic interactions and diminishing habitat quality from central populations to range edges. Yet empirical support for the CPH is mixed and the moderating effects that underpin these divergent patterns remain unclear. Using the most comprehensive list of plant and animal CPH studies to date on species abundances, population growth rates, and genetic diversity from the center to the periphery of species range, we conducted a meta-analysis. We also quantified the moderating effects of species kingdom, the method utilized to estimate the distance from niche/geographic center, longevity and pollination mode, which are known to have strong effects on species meta-population dynamics and genetic diversity. We find strong support for declining species genetic diversity from center to periphery populations. Interestingly, we found no consistent differences in population growth rate and species abundances across species range distributions. This lack of support was driven by high heterogeneity in the effect size among studies due to different method used to estimate the distance from niche/geographic center to species kingdom and the pollination mode. Our results reveals that the CPH is an exception rather than a general rule. Conservation value of populations is not necessarily related to their geographic position.

Introduction

The recent debate over the center-periphery hypothesis has been quite polarized. At one extreme, some studies suggest that species are most abundant (Brown, 1984; Osorio-Olvera et al., 2020), demographically more performant and genetically more diverse in the center of their distribution range. At the other extreme, some studies suggest no consistent distance-abundance (Dallas et al., 2017a; Dallas and Santini, 2020), distance-demography or distance-genetic relationships (Duncan et al., 2015) from range center to range periphery. The strength of each pole's arguments raises an important question. Are species more abundant, demographically more performant, and genetically more diverse at the center of their distribution? Answering this question could help to predict the ecological and evolutionary consequences of range shift in response to climate change or human-mediated habitat destruction on focal species (Louthan et al., 2015), and therefore allow for practical conservation actions to be more easily planned and directed for mitigation (Rehm et al., 2015).

Several studies have reviewed the center-periphery hypothesis (Dallas et al., 2020; Gaston, 2009; Sexton et al., 2009). For example, Sagarin et al. (2002) found that only 39% of relevant studies supported the center-periphery hypothesis. Similarly, Pironon et al. (2017) revealed that 51% of studies showed a significant difference in abundance between center and periphery of their range, 47% of studies supported higher genetic variation at the center than at the periphery of their range, and 55% of studies showed no significant difference in demographic performance between central and peripheral populations. However, these studies used a vote-counting approach and lacked effect sizes. Vote counting yields a binary response to the question: "Does the study support the center-periphery hypothesis?" Two problems arise when using a vote counting. Firstly, problems occur when statistical significance is used to define 'supporting" and "non supporting" studies because the number of significant outcomes has little or no relationship with the magnitude of an effect. Secondly, vote counting takes no account of the differential weights given to each study, which does not account for the fact that individual studies frequently have different sample sizes. Finally, these reviews

did not control for residuals being potentially non-independent due to phylogenetic relatedness of the taxa investigated (Pironon et al., 2017). Thus, general support for the CPH remains unclear. Moreover, the mechanisms explaining variability among studies are unknown.

Several factors are likely to explain observed variability among studies. Species' kingdom could explain variability in outcomes when testing the center periphery hypothesis. In general, animal species are more likely to support the center-periphery hypothesis than plant species (Pironon et al., 2017; Svensson, 1992). Competition for resources among animals promotes long-distance dispersal to new potentially suitable habitats (Nathan, 2006), with highly vagile individuals frequently observed outside of their range (Holmes and Wilson, 1998). Although these new habitats may not meet the requirements for species to establish populations, they may broaden the range of ecological conditions encountered by the species in nature, exposing individuals to harsher conditions at range margins (Pagel et al., 2020). As a result, source-sink dynamics would be more common and spatially structured in highly vagile animals than in plants.

Another factor that could explain the variability in studies testing the center-periphery hypothesis is the method utilized by authors to calculate the distance from the range center. Some studies measured the distance from the geographical range center or edge, while others measure the distance from climatic niche centroid (Euclidean or mahanalobis distance). Different measures of distance from geographic or climatic center may produce drastically different results. Some studies suggest the niche centroid distance is a the more accurate method to test the center periphery hypothesis because it accounts for the environmental conditions across a species range distribution when identifying center and periphery populations (Martínez-Meyer et al., 2013; Osorio-Olvera et al., 2020). Even though the estimation of species niche often relies on models assuming that species are in equilibrium with the environment, the estimation of distance from niche centroid reflects more the variability of ecological conditions than the distance from geographic center. Within studies promoting the distance from niche centroid, some studies recommended the mahanalobis distance as best metric of distance

from niche centroid because it takes into account the covariance between climatic axes (Osorio-Olvera et al., 2020; Soberón et al., 2018).

Differences in pollination mode (cross pollination vs. self-pollination) from center to periphery could be another source of variability among studies testing the center-periphery hypothesis for plant species. Cross pollination requires pollen transfer from plant to plant by external vectors such as wind or water or mutualistic relationships with animals that transport pollen. In cross-pollinated plants, pollen quantity could increase plant reproductive success and increase population growth rate (Ashman et al., 2004). For some species, the availability of pollen decreases from range center to range periphery, which may explain range limitation for these species (Chalcoff et al., 2012; Moeller et al., 2012). However, some species may be able to shift from outcross pollination to self-pollination at the periphery and thereby expand their range (Herlihy and Eckert, 2007, 2005). Depending on pollination type, one could have support or not for the center-periphery hypothesis. Because cross pollinated plants rely on pollination services and these pollination services may decrease toward the periphery, cross-pollinated plants are more likely to support the center-periphery hypothesis than self-pollinated species.

Species' longevity may result in differences in species abundance, population dynamics, and genetic diversity from center to periphery. Lifespan has an important relationship with fitness, whereby long-lived species for which survival is a determinant factor in population response over the long-term drive demographic buffering (Morris and Doak, 2004). Unlike long-lived species, short-lived species, for which reproduction contributes greatly to population dynamics, are expected to show increasing fluctuations in population size with increased environmental variation (McDonald et al., 2017). Species range periphery is often characterized by variable and unstable environmental conditions (Volis and Kark, 1994). Therefore, short-lived species are more likely to decline in performance at the periphery while long live species will remain constant toward the edge.

In this study, we conducted a meta-analysis on studies testing the CPH. We focused on studies using population abundance, population growth rate and population genetics, which are the most used response variables to test the CPH. We addressed the

following questions: (1) What is the magnitude of the cumulative effect size across studies for CPH support, and is it significantly different from zero? (2) Is this magnitude consistent across studies, given random sampling variation, or is there heterogeneity among study outcomes? (3) To what extent can heterogeneity among studies be explained by hypothesized moderators that characterize study outcomes? (4) Do closely related species have a similar effect size?

Materials and methods

Literature search

We searched for suitable studies by examining the bibliographies of previous reviews on the center-periphery hypothesis (Eckert et al., 2008; Pironon et al., 2017; Sagarin and Gaines, 2002; Sexton et al., 2009). In addition, studies were identified by searching the online database Web of Science, set with restrictions on the field of ecology on 28 May 2020 for papers with the following terms: ('cent*' or 'core') AND ('marg*' or 'peripher*' or 'edge' or 'limit*') AND (plant* or animal*). We obtained 9894 articles. To be integrated in the final data set, studies had to meet the following criteria: (1) they related to variation in population density, population growth rate or genetic diversity (expected heterozygosity) from the center to the periphery, (2) central and peripheral mean, standard deviation or Pearson correlation and sample size values of population abundances, population genetics and population growth rate were either explicitly reported or could be inferred from tables or figures using Webdigitize (Rohatgi, 2021). We used 17 species for studies using population growth rate, 53 species for studies using genetic diversity, and 3819 species for studies using abundance data as the response variable to test the CPH (Figure 1.1).

Moderating factors

We identified three independent variables (moderators) as potential sources of effect size variation among studies. We predicted that the kingdom of the species (animal vs. plant), pollination mode (out-crossed vs. self-pollinated species), type of distance used to test the CPH (geographic distance, euclidean distance or mahanalobis distance) and species longevity would explain the heterogeneity among species. We retrieved the

pollination mode for plant species from TRY data base (Kattge et al., 2019) and species longevity for animal species from AnAge (https://genomics.senescence.info).

Statistical analysis

To estimate the grand mean effect size across studies, we performed a multilevel random-effects model including species and author as random effects using the package metafor (Viechtbauer, 2010). Phylogeny was included in the model testing the variation of population growth rate from center to periphery using a variance-covariance matrix, assuming that traits evolve via Brownian motion. We incorporate the phylogeny for these studies because only plant species were utilized to test how population growth rate decreases from center to periphery. We did not include the phylogeny for studies testing abundance and genetic diversity from center to periphery because these studies included animal and plants. For all analyses, we used two effect size; the Hedges's *d* (Hedges et al., 1999) and Fisher's Z-transformed-r, Zr (Hedges et al., 1999) in the package metafor (Viechtbauer, 2010)**.** We preferred the Hedges's *d* because it is most appropriate for small sample sizes (Rosenberg et al., 1997). We used the Hedges's *d* for studies using population growth rate and genetic diversity (expected heterozygosity) as response variables. Similarly, we used the package metafor (Viechtbauer, 2010) to calculate the Fisher's Z-transformed-r, Zr (Hedges et al., 1999) as the effect size for studies using population abundance as the response variable. We preferred the Fisher's Z-transformed-r because the studies testing the CPH using abundance data had only the correlation coefficient.

We estimated the percentage of heterogeneity among studies testing the center periphery hypothesis using the I^2 statistic, where 25%, 50% and 75% respectively represent low, moderate, and high heterogeneity (Higgins et al., 2003). A significant I^2 suggests that the variance among effect sizes was greater than expected by sampling error and implied that other explanatory variables (i.e., moderators) could explain such variation. To determine which moderator explained the heterogeneity in the effect sizes, we conducted a mixed effect model using the function rma.mv in metafor (Viechtbauer, 2010). We included the phylogeny for pollination mode and for species longevity

because these moderators were only related respectively to plants and animals. We scaled species longevity to facilitate model convergence. All the statistics were performed in R 4.1.3 (R Core Team et al., 2019).

Inference from meta-analyses can be biased by studies that are outliers. We explored the publication bias using funnel plot. Further, we tested whether funnel plot was asymmetric with regression tests (Sterne & Egger, 2006) using regtest function in metafor (Viechtbauer, 2010). To test whether closely related species have a similar effect size due to shared phylogenetic history, we first submitted the list of species to the National Center for Biotechnology Information Company (NCBI) to produce a topographically correct tree species levels using tazise (Chamberlain et al., 2020). Then, we combined the phylogenetic tree and each species' effect size to detect phylogenetic signals in taxa used to test the center periphery hypothesis. We used Blombergs's K and Pagel's λ to test for a phylogenetical signal (Revell, 2012). Blombergs's K was estimated from a null model where there was a random evolution of traits. $K < 1$ implied closely related species are less alike than a random null model, whereas $K > 1$ suggested the opposite (Blomberg et al., 2003). $\lambda \cong 0$ showed a low correlation and weak phylogenetic signal. Similarly, $\lambda \cong 1$ suggested a high correlation and strong phylogenetic signal (Pagel, 1999). Finally, we estimated the statistical significance of phylogenetic signals from a randomization test and likelihood ratio test for K and λ, respectively (Münkemüller et al., 2012).

Results

Cumulative effect size

We failed to find a significant difference between the grand mean effect size and zero for studies using population growth rate as a response variable (Figure 1.2a), suggesting that for population growth rate, central populations are not significantly different from peripheral populations. Similarly, the grand mean effect size of species abundance was not significantly different from zero, implying that species abundances at the center of the range are not different from those at the periphery (Figure 1.2c). However, the grand mean effect size differed significantly from zero for studies using

plant genetic diversity as the response variable (Figure 1.2b): studies conducted on genetic diversity provide support for the CPH.

Heterogeneity and Moderators

Heterogeneity was moderate for all effect size ($I^2 > 65\%$). The kingdom of the species did not explain a significant part of the variation among studies testing the CPH with genetic diversity as a response variable (Figure 1.3a). However, we detected a significant positive influence of plant species on the mean effect size when studies used plant abundance as a response variable to test the CPH (Figure 1.3b), suggesting that studies using plant abundance from center to periphery are more likely to find support for the center periphery hypothesis.

When studies used the geographic distance to test the CPH, we found a significant positive effect of geographic distance on the mean effect size when the studies used species abundance (Figure 1.3c), suggesting that studies using geographic distance to test the CPH are more likely to find support for the CPH. In contrast, the Euclidean distance and mahanalobis distance have a negative influence on the mean effect size, suggesting that studies using these two metrics of distance from range center are more likely to find high abundance at the periphery than at the center (Figure 1.3c).

Further, we found no significant influence of pollination mode (out-crossed vs. self-pollinated) on the mean effect size for studies using population growth rate and population genetic diversity as response variable (Figure 1.4a and 1.4b). However, we found a significant positive influence of self-pollination on the mean effect size for studies using abundance as response variable (Figure 1.4c). We detected no significant influence of species longevity on the mean effect size for studies using population abundance as response variable (Figure 1.4d).

Publication bias and phylogeny signal.

Funnel plots showed no evidence of publication bias (Figure 1.5). Egger's regression test revealed no evidence of publication bias for studies using population growth rate ($z=0.39$, $p=0.69$), genetic diversity ($z=0.51$, $p=0.60$) and abundance ($z=1.50$, $p=0.13$) to test the CPH. We found no phylogenetic signal in studies using population

growth rate and genetic diversity as response variables to test the center-periphery hypothesis (all K<1, Table 1.1; Figure 1.6). Similarly, there was no phylogenetic signal in studies testing the relationship between geographic/euclidean distance and species abundance (Table 1.1, Figure. 1.7 a,b,c,d). However, when using abundance as response variable and mahanalobis distance as a predictor, closely related species resembled each other in effect size less than expected under the Brownian motion model of trait evolution (Table 1.1, Figure 1.7 e).

Discussion

Our meta-analysis found support for the CPH for studies using genetic diversity. We did not detect a relationship between species population growth rates or species abundance and distance from geographic center. These findings are in agreement with previous studies that suggested no relationship between species abundance or population growth rate and distance from geography or climatic center (Dallas et al., 2017b; Pironon et al., 2017). We failed to find support for the CPH for species abundance and population growth rate probably because studies often consider a small fraction of environmental conditions of the species and thus only a portion of the full response of species to climatic or geographic is sampled (Sagarin and Gaines, 2002). Moreover, the use of population abundance has been challenged because there is a tight link between abundance and the suitability of ecological conditions (Sagarin et al., 2006). This mainly because species abundance could be driven by micro-scale factors that lead to a clumped distribution of species (Gaston, 2009). In addition, population abundance varies across space and time, suggesting that tests of the CPH at different time or spatial scales might yield different results for a given species.

Demographic compensation at the periphery of the species range, whereby decreases in some vital rates are counterbalanced by increases in others across time or space (Sheth and Angert, 2018), could explain why the population growth rate was not higher at the center than at the periphery. Even though population abundance did not decrease from center to periphery, genetic diversity did decrease from center to periphery. Thus, small effective population size at the periphery could not explain the

lower genetic diversity at the periphery (Pironon et al., 2017). Instead, stochastic events such as drift, inbreeding, founder effects, and directional selection in peripheral populations may have led to low genetic diversity (Gaston, 2009).

We also found that studies on plant species are more likely to find support for the CPH than studies on animal species. This result contrasts with a recent review showing that the CPH was supported for animals, but not for plants (Pironon et al., 2017). The authors suggested microenvironmental factors (Chapin et al., 1987) could be more important for sessile organism abundance, leading to a weak support for CPH in plants. Conversely, individual metabolism and resource availability could be more important for vagile animal abundance, leading to high geographical dependency in species population dynamics. Micro-environmental factors tend to not be, or be less, correlated with geography, while metabolism and resource availability are strongly correlated to climate. The methodological approach we used in our study could help explain divergent results from previous studies. While previous syntheses performed a chi-square test (Pironon et al., 2017) on count data of studies supporting or not supporting the CPH for animals and plants, we used more a robust model to test if the magnitude of variation of population abundance, genetic diversity and population growth rate was significantly different from 0.

Contrary to expectation, we found that studies using geographic distance to test the CPH found more support than studies using euclidean and mahanalobis distance. The positive influence of geography on the support for CPH may mask the effect of spatial scale on the likelihood of finding support for the CPH. Previous studies showed that large scale studies, or studies including more than 50% of the geographic range, tended to support the CPH (Pironon et al., 2017; Sagarin et al., 2006). Most of the data included in our metanalysis are from studies conducted on a large scale, which may explain why we found support for the CPH when using distance from the geography center. In addition, most studies testing the CPH using the euclidean and the mahanalobis rely on models that often estimate the species' niche. A lack of support for the CPH is more likely to occur for strongly seasonal, temporarily unpredictable, or spatially patchy environments because estimating the niche is more challenging for species living in these types of

environments. Also, models estimating the species' niche often assume species are in equilibrium with the environment. However, this assumption biases the estimation of species' realized niche and may explain why we don't have support for the center-periphery hypothesis.

We found no relationship between species longevity and the likelihood of finding support for the center-periphery hypothesis. This result could be explained by the biotic interactions of the species (generalist vs. specialist). Generalist species use a variety of food resources and can thrive in a variety of environmental conditions, while specialists require a specific food and can only live where that food resource is available (Nordén et al., 2013; Segura et al., 2007). Therefore, generalist species could have higher population performance at the periphery because they may be able to adjust to suboptimal food sources, and this may bias the support of the center-periphery hypothesis (Gaston, 2003). However, this explanation should be taken with caution because we did not have information on the ranges of food consumed by each species to infer if the species is a generalist or a specialist.

Under Brownian Motion, we found that closely related species do not respond similarly to distance whether the distance was estimated as distance from range center or climatic niche centroid. As Pagel's λ usually outperforms Blomberg's K in identifying phylogenetic signals and K is appropriate for models with changing evolutionary rates (Münkemüller et al., 2012), we used λ values to evaluate phylogenetic signals in each effect size. The similarity of phylogenetic patterns based on Blomberg's K and Pagel's λ values reinforced our interpretation of the λ results. Overall, the effect size was not phylogenetically conservative, consistent with a previous study showing no phylogenetic signals in studies testing the center-periphery hypothesis (Dallas et al., 2017a). This result also implies that a species response across the range is not driven by internal factors such as the species genetics but rather external factors (e.g., abiotic factors).

Conclusions

Using the most comprehensive list of plant and animal testing the CPH to date, we characterized the relative change in population abundances, population growth rates, and

genetic diversity from the center to the periphery of species range distributions. We also investigated the drivers of such a change in population abundances, population growth rates, and genetic diversity from the center to the periphery of species range distributions. We found that only genetic diversity decreases from the center to periphery. In addition, we found that plant species are more likely to have a higher abundance at the center than at the periphery. In contrast, animal species do not have a higher abundance at the center than at the periphery. We also found methodological bias as a determinant of non-support for the center-periphery hypothesis. When using the distance from the geographic center, we found support, whereases when using the niche center (euclidean and the mahanalobis distance), we did not find support for the center-periphery hypothesis. Within the plants, the self-pollinated species tend to find support for the center-periphery hypothesis than out-cross-pollinated. Further, using the range position as a proxy of conservation value could be misleading for efficient conservation strategies.

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Appendix A

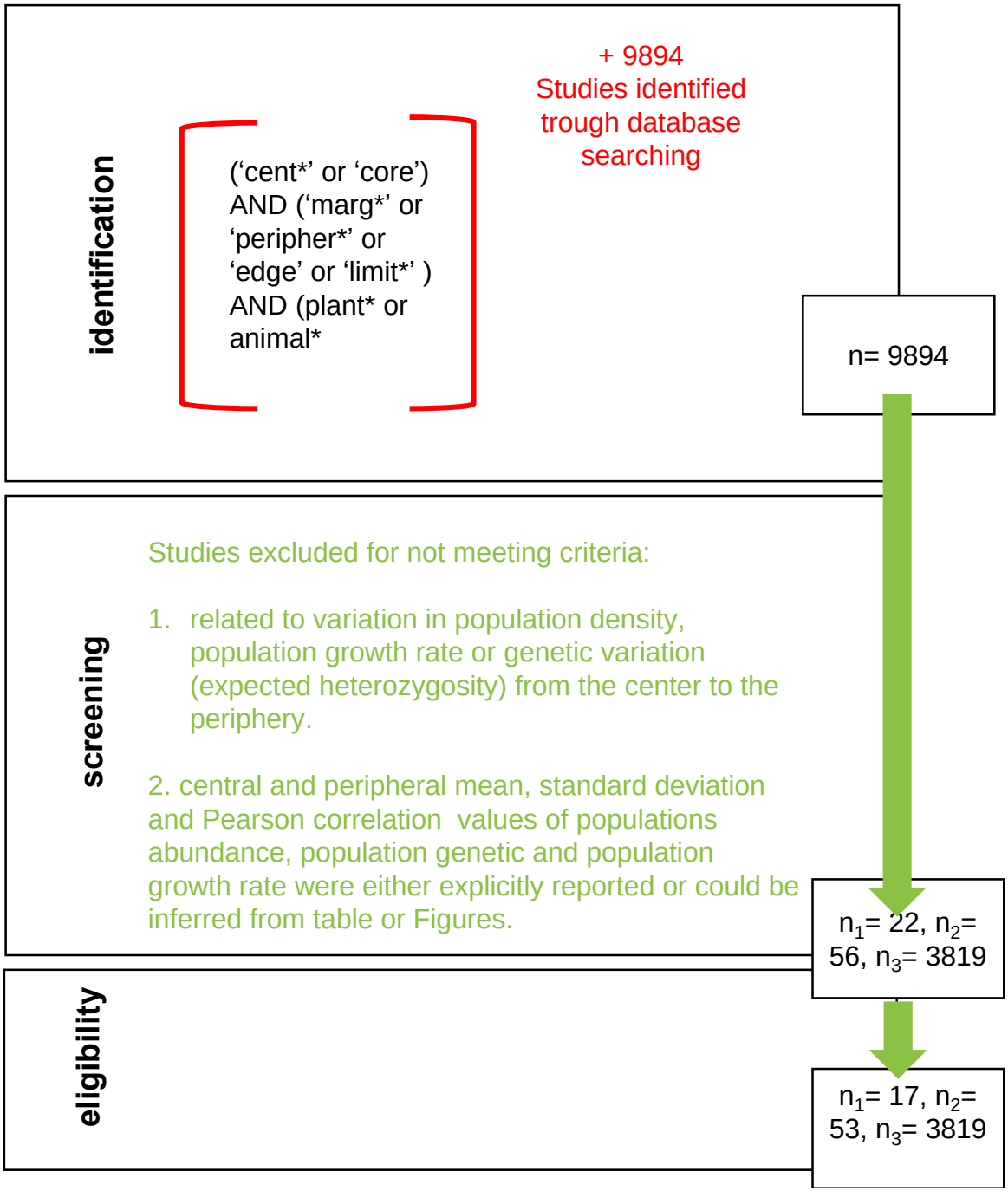

Figure 1.1 : Flowchart showing selection process for studies using population growth rate as response in the meta-analysis.

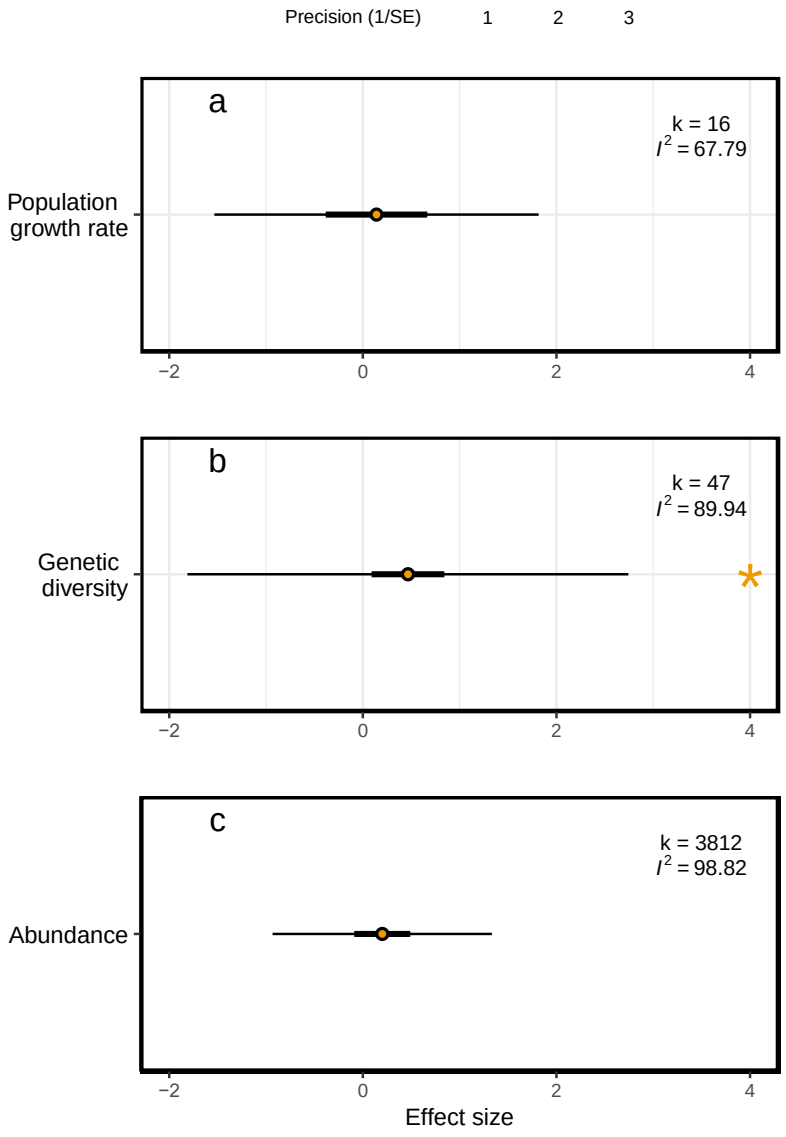

Figure 1.2 : Grand mean effect for studies using a) population growth rate, b) genetic diversity and abundance as response variable when testing the center-periphery hypothesis. 95% confidence intervals (95% CIs are depicted in heavy black lines (and partially hidden by the mean data points, depicted by a circle symbol), prediction intervals in thin black lines. The size of each data point is proportional to the precision of the study (1/SE (Standard Error)). k is number of effect sizes per group. An asterisk indicates that 95% CIs do not span zero. The dashed vertical reference line indicates the point on the x-axis where the effect size equals zero (no effect). A positive effect size indicates a support for the center-periphery hypothesis.

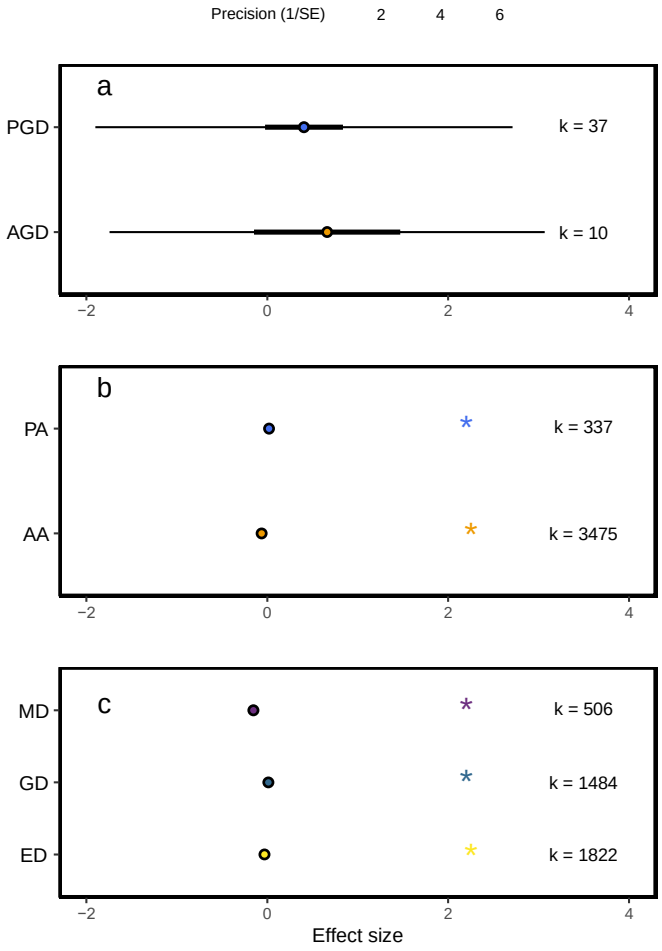

Figure 1.3 : The effect of Kingdom on the mean effect size for a) genetic diversity and b) population abundance. PGD stands for plant genetic diversity and AGD stands for Animal genetic diversity. c) The effect of type of distance on the mean effect size. MD stands for mahanalobis distance, GD for geographic distance and ED for euclidean distance. 95% confidence intervals (95% CIs) are depicted in heavy black lines (often hidden by the mean data point, depicted by a circle symbol), and prediction intervals are in thin black lines. The size of each data point is proportional to the precision of the study (1/SE (Standard Error)). k = number of effect sizes per group. An asterisk indicates that 95% CIs do not overlap 0.

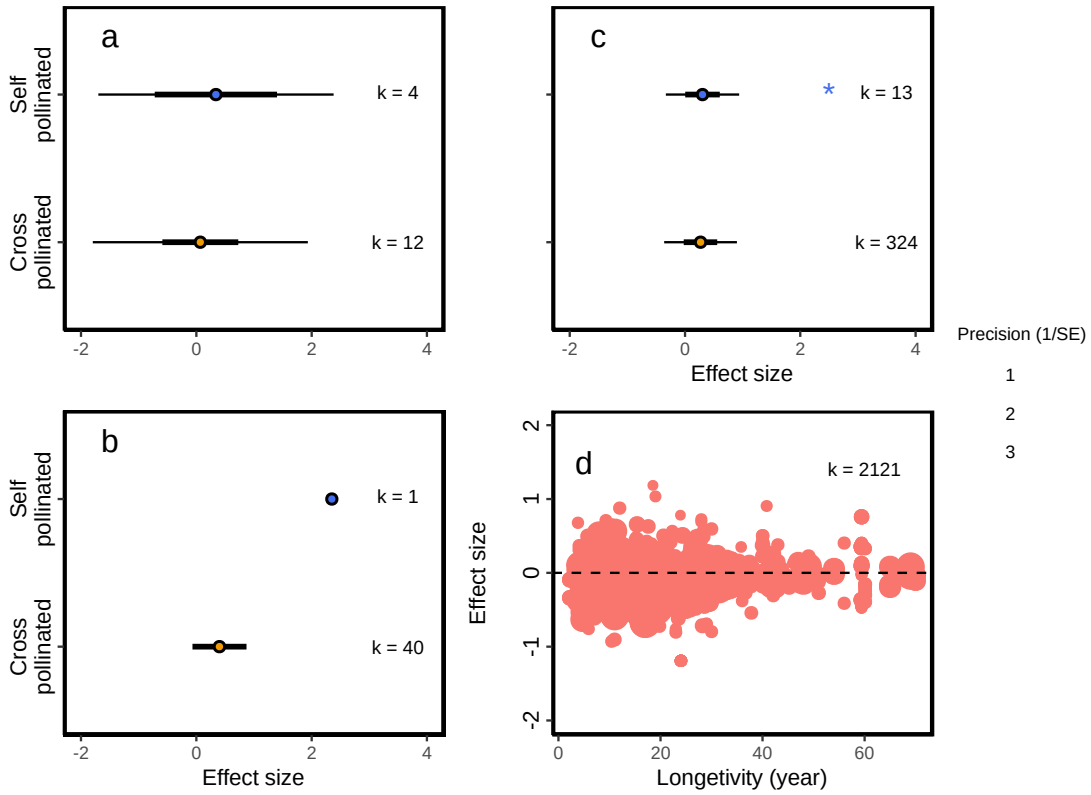

Figure 1.4 : The effect of pollination mode (out-crossed vs. self-pollinated) on the mean effect size for a) population growth rate, b) genetic diversity and c) population abundance. d) The effect of longevity on the mean effect size. 95% confidence intervals (95% CIs) are depicted in heavy black lines (often hidden by the mean data represented by a circle symbol), prediction intervals in thin black lines. The size of each data point is proportional to the precision of the study (1/SE (Standard Error)). k = number of effect sizes per group. An asterisk indicates that 95% CIs do not overlap 0.

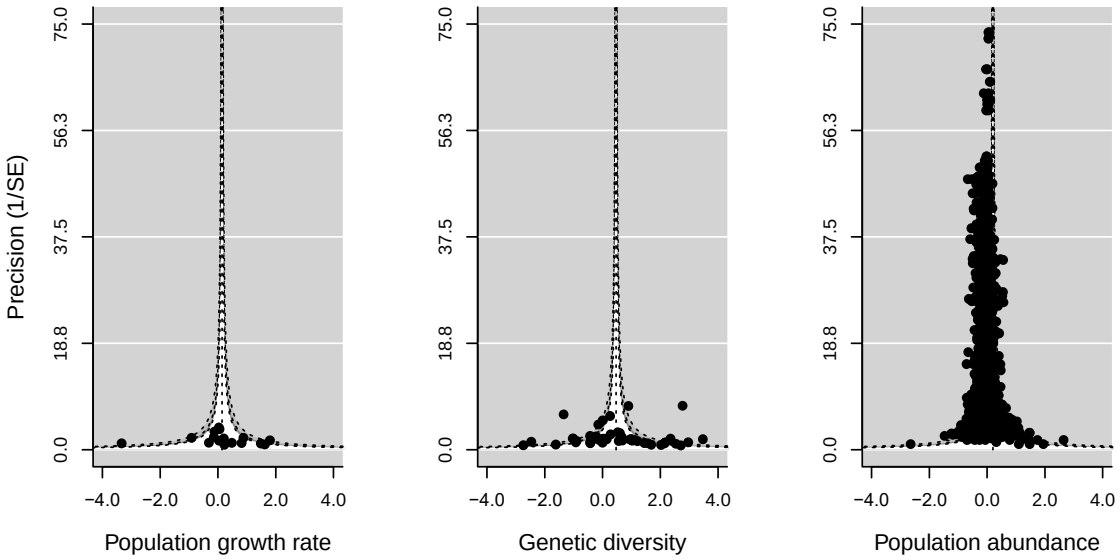

Figure 1.5 : A weighted (1/SE) plot (Funnel plot) showing publication bias in studies testing the CPH. More precise studies (those with higher 1/SE (Standard Error)) are located at the top of the plot, and less precise studies are located at the bottom.

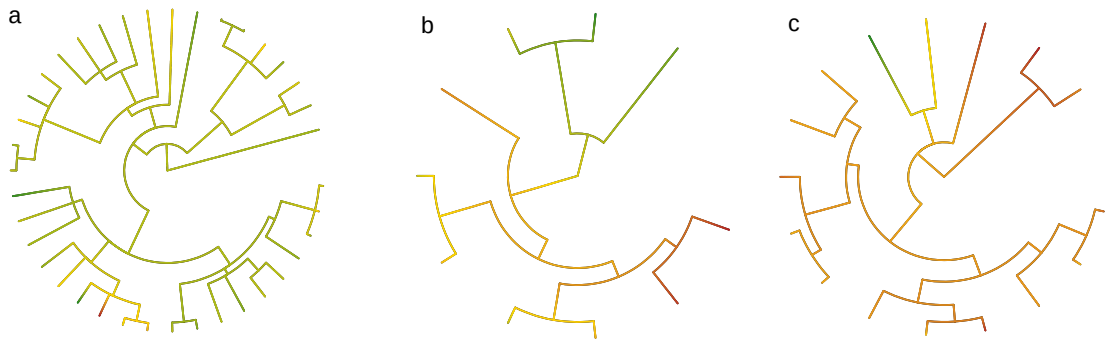

Figure 1.6 : Clustering patterns of species used to test the center-periphery hypothesis along the phylogeny: (a) plant population growth rate with geographic distance, (b) plant genetic diversity with geographic distance, and (c) animal genetic diversity with geographic distance. A green color indicates a negative effect size, a yellow color indicates zero effect size and red indicates a positive effect size.

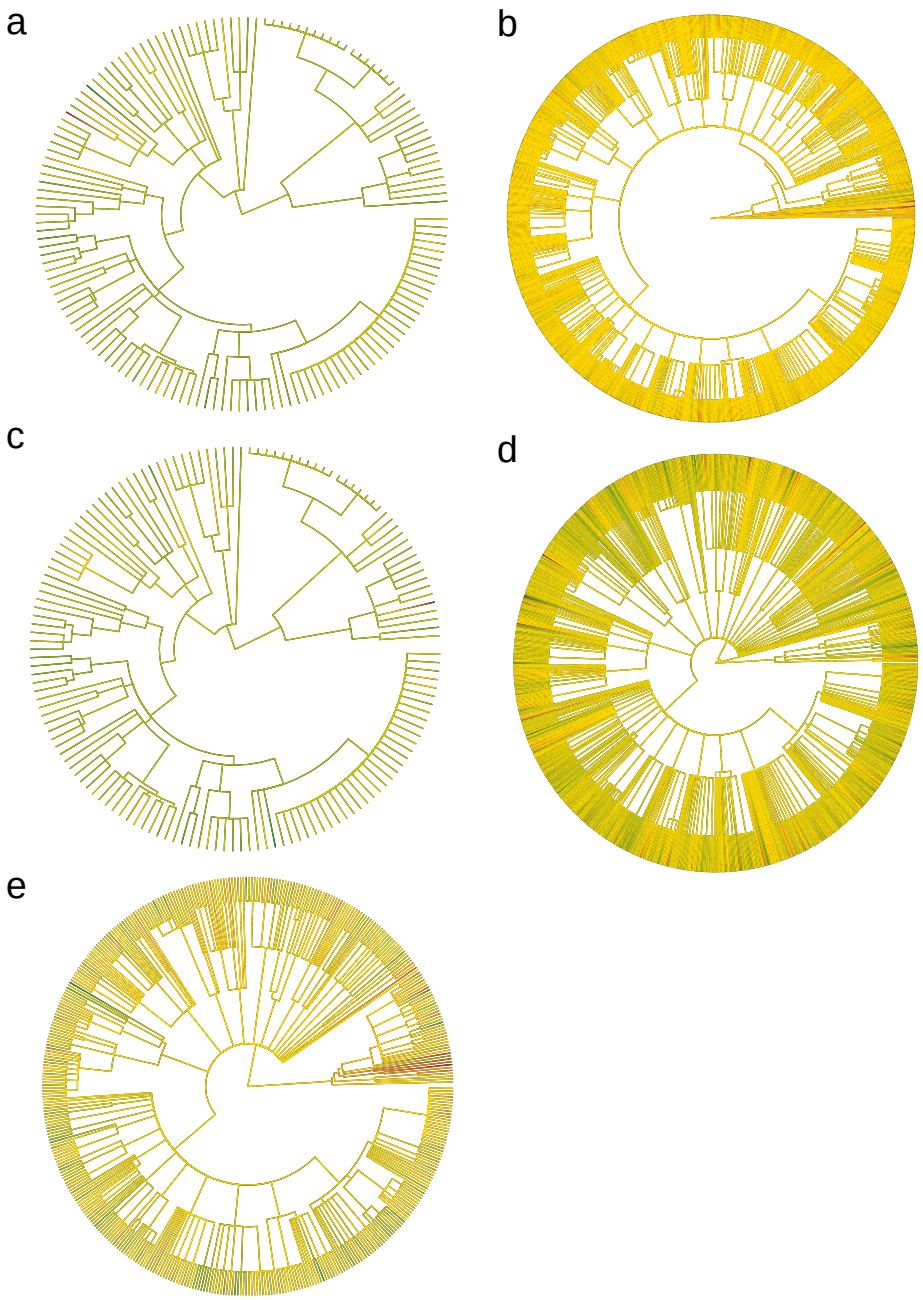

Figure 1.7 : Clustering patterns of species used to test the center-periphery hypothesis along the phylogeny: (a) plant abundance with geographic distance, (b) animal abundance with geographic distance, (c) plant abundance with Euclidean distance, (d) animal abundance with Euclidean distance, (e) animal abundance with mahanalobis distance. A green color indicates a negative effect size, a yellow color indicates zero effect size and red indicates a positive effect size.

Table 1.1: Phylogenetic signal in studies testing the center-periphery hypothesis. Variables indicate the dependent and explanatory variables used to test the center-periphery hypothesis. For each column, the value of the Blomberg K and the and the Pagel's λ and the level of significance of the phylogenetic test.

Variables	**Kingdom**	**Blomberg K**	**Pagel's λ**
Population growth rate vs Geographic distance	Plant	0.475, P=0.16	0.745, P=0.27
Genetic diversity vs Geographic distance	Plant	0.198, P= 0.413	0, P= 1
	Animal	0.785, P=0.046	0.741, P=0.168
Abundance vs Geographic distance	Plant	0.225, P=0.107	0, P=1
	Animal	0.312, P= 0.002	0.122, P= 0.116
Abundance vs Euclidian distance	Plant	0.178, P= 0.41	0, P=1
	Animal	0.277, P=0.365	0, P=1
Abundance vs Mahanalobis distance	Animal	0.298, P= 0.001	0.160, P= 0.000

CHAPTER 2: ALTITUDE-MEDIATED SOIL PROPERTIES, NOT GEOGRAPHY OR CLIMATIC DISTANCE, EXPLAIN THE DISTRIBUTION OF A TROPICAL ENDEMIC HERB

A version of this chapter was originally published by Jacob Moutouama and Orou Gaoue:

Moutouama, J.K. and Gaoue, O.G. (2022). Altitude-mediated soil properties, not geography or climatic distance, explain the distribution of a tropical endemic herb. *Ecology and Evolution*, 12: e8572, 1-10

Authors contributions: JKM and OGG conceived the study and developed the models, JKM collected the data, performed the analyses, and lead the writing of the manuscript with editorial assistance from OGG.

Abstract

Understanding the ecological processes that govern species' range margins is a fundamental question in ecology with practical implications in conservation biology. The centre-periphery hypothesis predicts that organisms have higher abundance at the centre of their geographic range. However, most tests of this hypothesis often used raster data, assuming that climatic conditions are consistent across one square km. This assumption is not always justified, particularly for mountainous species for which climatic conditions can vary widely across a small spatial scale. Previous studies rarely evenly sample occurrence data across the species' distribution. In this study, we sampled an endemic perennial herb, *Thunbergia atacorensis* (Acanthanceae), throughout its range in West-Africa using 54 plots and collected data on (a)biotic variables, the species density, leaf mass per area, and basal diameter. We built a structural equation model to test the direct and indirect effects of distance from geographic and climatic niche centres, and altitude on *Thunbergia* density as mediated by abiotic and biotic factors, population demographic structure, and individual size. Contrary to the prediction of the centre-periphery hypothesis, we found no significant effect of distance from geographic or climatic niche centres on plant density. This indicates that even the climatic centre does not necessarily have optimal ecological conditions. In contrast, plant density varied with altitudinal gradient, but this was mediated by the effect of soil nitrogen and potassium which had positive effect on plant size. Surprisingly, we found no direct or mediating effect of interspecific competition on plant density. Altogether, our results highlight the role of geography, climatic and ecological mismatch in predicting species distribution. Our study

highlights that where altitudinal gradient is strong local scale heterogeneity in abiotic factors can play important role in shaping species range limits.

Introduction

Understanding the evolutionary and ecological processes that govern species range margins is a central goal in ecology (Sutherland *et al.* 2013). The centre-periphery hypothesis (CPH) predicts that species are most abundant at the centre of their distribution, and decline in abundance toward the edge of their distribution (Brown 1984). One assumption underlying the CPH is that the centre of the geographical range coincides with preferred habitats of the species, where ecological conditions are optimal compared to the edge, where conditions are less suitable (Parsons 1991). This is particularly true when the species' response curve along environmental gradients is unimodal and symmetrical in their tails for all the variables determining the niche (Yañez *et al.* 2020). Such ecologically optimal conditions will favour higher population density either directly via improved growth, survival, and/or fertility (Greiser *et al.* 2020) or indirectly via gene flow (Kirkpatrick & Barton 1997). Recent studies show that a mismatch between geographic and ecological niches is more likely among species that are poorly dispersed or organisms that are resilient and can persist in poor habitats (Schurr *et al.* 2012; Pagel *et al.* 2020).

Two decades ago, Sagarin & Gaines (2002) showed that 61% of studies that empirically or theoretically tested the centre-periphery hypothesis failed to find support for this hypothesis. However, the authors cautioned that only two of the studies included in their analysis sampled the entire species' range, and in most studies range edges were "severely under-sampled." Moreover, most studies used only the geographic distance from range centre, which itself does not explain the range of climatic conditions across the species distribution area. With the increase popularity of ecological niche modelling, it is now possible to identify species preferred sites (most suitable areas across the range). Therefore, one could use both the ecological and the geographic marginality gradient to test the centre-periphery hypothesis. Studies that have done this found that species are often more abundant at more suitable sites (Weber *et al.* 2017), and that species

abundance is associated with the ecological, rather than the geographic gradient (Yañez-Arenas *et al.* 2012; Martínez-Meyer *et al.* 2013).

A recent review by Dallas et al. (2017) used data across taxa to show no change in abundance with distance from their geographic range or climatic niche centre. Another synthesis reports that only 51% of studies showed decreased abundance from geographic centre to periphery (Pironon *et al.* 2017). These authors suggested that the lack of support for the CPH is due to the lack of overlap between geographic and climatic ranges. Given such inconsistent patterns in the centre-periphery distribution, a process-based approach is necessary to examine the variation of not just species abundance but also demography to improve our understanding of the mechanism behind range limitation (Sexton *et al.* 2009). This includes investigating the centre-periphery variation in functional traits, population demographic structures and dynamics (Angert 2009; Pironon *et al.* 2015; Treurnicht *et al.* 2020).

Functional traits determine the response of organisms to environmental drivers. These traits are good predictors of species abundance (Li *et al.* 2021). For example, in grassland communities, plant height and leaf mass per area can explain variation in species abundance (Lisner *et al.* 2021). In tropical forests, studies have shown that maximum plant height and leaf area were positively correlated with species abundance (Yan *et al.* 2013). Species traits could therefore determine whether species are most abundant at the centre of their distribution. For instance, in North American bird populations, body mass, migratory status, and habitats affected the abundance centre-relationship (Luis Osorio-Olvera *et al.* 2020). However, few studies have investigated how functional traits can mediate the centre-periphery distribution of species abundance (but see Treurnitcht *et al.* 2020).

Population demographic structures can vary across species distribution range from centre to periphery (Gerst *et al.* 2011). Skewness measures the asymmetry of the population demographic structure, indicating if the population is dominated by young or mature individuals. Skewness of the trait distribution can be used to understand environmental-trait relationships (Wool 1980). For example, the distribution of species traits is expected to be symmetrical in suitable conditions, and asymmetrical in stressful

environmental conditions (Fraser 1977). Similarly, in central populations where more suitable ecological conditions are expected, one may expect symmetric (skewness = 0) population size distribution. Peripheral populations with less ideal environmental conditions are expected to have more skewed population structures.

Species interactions can shape their range limits (Louthan *et al.* 2015; Stanton-Geddes *et al.* 2016; Nottebrock *et al.* 2017). Due to species-specific energy costs and gains in response to environmental conditions competition can have more impact at the edge than at the centre, thereby preventing species expansion beyond range limits (Hall *et al.* 1992). Further, competition can synergistically interact with abiotic factors to decrease population density at the edge of a species' range (Pulliam 2000; Vergeer & Kunin 2013). However, most studies investigating the centre-periphery hypothesis focused on either abiotic or biotic factors, rarely studying the synergistic effects of both drivers. This ultimately limits our mechanistic understanding of the relative roles of abiotic and biotic factors in shaping species ranges. This limitation has implications for both the conservation of rare species and control of invasive species. Even when abiotic factors are included in estimating the climatic niche, the predictor variables used are often rasters collected from Worldclim (See Dallas et al. (Dallas *et al.* 2017) and Osorio-Olvera et al. (2020). These rasters are derived from monthly temperature and precipitation variables at 1km by 1km or larger scale, with the assumption that abiotic factors are homogenous across the $1km^2$. This assumption is rarely true in mountainous areas where abiotic conditions often vary at a smaller scale (Egli & Poulenard 2016). Such microscale ecological changes can outweigh the macroclimatic influence on species distribution. It is therefore important to test the centre-periphery variation in species abundance not just considering geographic position or climatic niche variation but also altitudinal gradient particularly for species that occur in mountainous habitats.

In this study, we tested the predictions of the centre-periphery hypothesis by evaluating population density and distance from the centre of the geographic range and the climatic niche. We collected biotic and abiotic variables including, altitude, species' density, leaf mass per area, individual size in 54 plots in 12 populations of an endemic perennial herb in West Africa, *Thunbergia atacorensis* (Acanthanceae), monitored

throughout its entire range. We predict that plant density will be shaped by climatic and altitudinal gradients that affect plant functional traits and population structure. We used structural equation modelling (Shipley 2000; Grace *et al.* 2010) to examine how variation in soil properties, light availability, and interspecific competition can mediate the effects of altitude, geography and climatic gradients on plant size, functional traits, population demographic structure and ultimately plant density from range centre to periphery.

Methods

Study system

We tested the centre-periphery hypothesis using *Thunbergia atacorensis* (Acanthaceae), a range-limited perennial herb endemic to West Africa, one of the least studied regions of the tropics. *Thunbergia atacorensis* (Akoègninou Lisowski & Sinsin) is an endemic herb that can reach up to 80 cm in height and is found in gallery forests (Figure 2.1) along the Atacora mountain chain (Akoègninou *et al.* 2006) and the Sobakperou mountain in Benin (Fandohan et al. 2015). *Thunbergia atacorensis* reproduces both sexually (Akoègninou *et al.* 2006) and asexually (Asseh *et al.* 2017). The species produces flowers and fruits from February to April and September to November (Akoègninou *et al.* 2006).

We identified and studied all 12 known populations of *Thunbergia atacorensis* to test the centre-periphery hypothesis (Figure 2.2). These populations were geographically isolated into two disjoint subgroups, ten populations were located in the Atacora mountains (1°00’ - 2°00’ E and 10°40’ - 11°28’ N) in northwest Benin and two populations in the Sobakperou mountains (2°9’ N -9°8' E) in central Benin. Across these regions, the annual rainfall varies from 1200 to 1350mm and the annual temperature is 28° C (Sinsin & Kampmann 2010). We established a total of 54 permanent plots in these populations. At each population, we randomly established five 5 m x 5 m permanent plots for demographic studies and to estimate plant density. Because three of the populations were small, we installed a minimum of two plots instead of five (Table 2.1).

Plant density, functional traits, competition, and abiotic factors

In each plot, we estimated *T. atacorensis* density by counting the number of individual plants per plot. For each plant, we measured the basal stem diameter (using a digital calliper) as a metric of size, leaf chlorophyll content and estimated leaf mass per area. On each plant, we used a Konica Minolta SPAD-502Plus Chlorophyll Meter to measure chlorophyll content from three leaves randomly chosen and averaged the values. These three leaves were collected to estimate their area using 'LeafByte' (Getman-Pickering *et al.* 2019) and later oven-dried to measure their dry mass. We estimated the leaf mass per area (LMA) as the ratio of leaf dry mass to leaf area. We calculated the skewness of *T. atacorensis* basal diameter distribution for each population, using the R package *'*e1071*'* (Meyer *et al.* 2019).

To account for abiotic conditions, we measured plot-level light as the photosynthetic active radiation (PAR) using a Cl-110 Plant Canopy Imager (CID Bio-Science Inc., Camas, WA, USA). In each plot, we also measured soil moisture using a Extech MO750 soil moisture meter (Extech, Boston, MA, USA). We then collected 20g of composite soil samples per plot by mixing soil collected at seven inches depth from the centre and the four corners of each plot. In total, we collected 54 soil samples, which were analysed for macronutrients (nitrogen, potassium, phosphorus, sulphur, and magnesium), micronutrients (Iron, Zinc), and pH by the Soil, Water & Plant Testing Laboratory at Colorado State University (CO, USA). To reduce the number of soil variable to consider in our analysis, we performed a principal component analysis (PCA) on soil macronutrients and micronutrients variables using the package 'FactoMineR' (Le *et al.* 2008). The PCA summarized soil variables into five principal components, each representing a unique weighted combination of variables. We used the first two principal components (PC) which explained >50% of observed soil variation (Figure 2.3) as metric of soil fertility. The first PC captures increasing concentrations of nitrogen, potassium and the second PC captures increasing pH and phosphorus concentrations.

To measure interspecific competition for each plot, we recorded every single plant species found in the plot and measured the maximum height for each species and estimate each species percent cover. We calculated the space resource utilization (SRU), a proxy

of species competitive ability for light (Zhang *et al.* 2015), as SRU= $\sum_i^n H_i C_i A$, where H_i is the average maximum height of species i, C_i represents the percent cover of species i in a plot, n the total number of species per plot and A is the plot area.

Estimation of the distance from the geographic center and climatic center

We identified the geographic centre of *T. atacorensis* by first projecting the geographic coordinates of the twelve populations of *T. atacorensis* on a map, using the packages '*sp'* (Pebesma & Bivand 2020) and '*rgdal'* (Hijmans 2019) in *R* (R Core Team 2019). Then, we determined the convex polygon formed by all the 12 populations with the *geosphere* package (Hijmans 2019). The geographic centre was estimated as the centroid of this convex polygon using the function *centroid* in '*geosphere'*. Finally, we estimated the geographic distance of each *T. atacorensis* population from the centroid of the convex polygon.

In addition to the geographic centre, we identified the climatic niche centre and estimated the distance of each population to this centre. Unlike the geographic distance, the "climatic distance" measures how far the climatic conditions of a given population is from the optimum climatic conditions of the species. The further the distance, the worst climatic conditions the population is expected to experience. We estimated the climatic distance as a Mahalanobis distance (Osorio-Olvera *et al.* 2020). We preferred the Mahalanobis distance because it takes into account the covariance among variables and therefore corrects the problem of scale and correlation inherent in most other methods used to estimate the climatic distance (Farber & Kadmon 2003; Calenge *et al.* 2008; Etherington 2019). To estimate the Mahalanobis distance, we used the following steps. First, we built a minimum volume ellipsoid model. We combined occurrences data of *Thunbergia atacorensis* with non-correlated bioclimatic variables. Specifically, we used 80% of *T. atacorensis* occurrence points to calibrate the ellipsoid model, 20% to test the ellipsoid model, and eight non-correlated bioclimatic variables. The bioclimatic variables were annual mean temperature, mean diurnal range, isothermality, temperature seasonality, maximum temperature of warmest month, annual precipitation, precipitation of driest month, precipitation of warmest quarter. These bioclimatic variables were

derived from spatial interpolation of monthly average temperature (maximum and minimum) and precipitation (total) throughout 1970-2000 for the study region (Fick & Hijmans 2017) and had a spatial resolution of 30 arc-second. Second, we estimated the centroid of the minimum volume ellipsoid model using the package "*ntbox*" (Luis Osorio-Olvera *et al.* 2020). Finally, we used the *mahalanobis* function in the package '*stats'* to calculate the Mahalanobis distance from the centroid of the minimum volume ellipsoid to each plot (Bolar 2019).

Data analysis

We developed structural equation models (SEM) to test the centre-periphery hypothesis and the mediating role of processes related to soil, competition, and altitude (Lefcheck 2016). Structural equation modelling is a robust statistical modelling technique that fits network of hypotheses to data (Grace et al. 2010, Shipley 2000). We developed two meta-models for our SEM: one using the geographic distance and the other climatic distance (Figure 2.4) as the main predictor of *T. atacorensis* density. For each meta-model, we tested the direct and indirect effects of altitude and distances on plant density and population structure skewness as mediated by abiotic factors, including soil fertility, soil moisture, and light exposure. We also tested for the mediating role of biotic factors (interspecific competition) and functional traits like leaf mass-per-area, basal diameter, and chlorophyll content. We built structural equation models using the package 'piecewiseSEM' (Lefcheck 2016) that incorporates linear mixed-effect models with our study populations as random effects (Bates *et al.* 2015). We used the *d-separation* test to evaluate whether any non-hypothesized, independent relationships were significant and whether including a missing path could improve the model (Shipley 2013). We reported the conditional variance explained (R^2) for each response variable included in our final SEM. The conditional R^2 explains the proportion of variance explained by both fixed and random factors in the mixed effect models (Nakagawa & Schielzeth 2013). We log-transformed plant density and standardized all quantitative predictors to a mean of 0 and a variance of 1, to compare the path coefficients. All analyses were performed in R 3.6.2 (R Core Team 2019).

Results

We found no significant direct effects of geographic distance (β = 0.146 ± 0.176, *p = 0.430*, R^2 = 0.59, Figure 2.5) or climatic distance *(*β = -0.002 ± 0.001, *p* = 0.848, R^2 = 0.53, Figure 2.6) on *T. atacorensis* density. As expected, plant size was positively affected by leaf chlorophyll content (Figure 2.5, Figure 2.6). Similarly, to plant density, the skewness of population structure was not significantly affected by climatic distance (β = -0.012 ± 0.008, *p* = 0.16, R^2 = 0.24, Figure 2.5) or geographical distance (β = -0.244 ± 0.134, *p* = 0.05, R^2 = 0.27, Figure 2.5). We found no direct effect of interspecific competition on population density (β = - 0.031 ± 0.1139, *p = 0.789*, R^2 = 0.27, Figure 2.5). Soil pH and P increased with climatic distance (β = - 0.054 ± 0.09, *p = 0.033*, R^2 = 0.62, Figure 2.6).

Surprisingly, we found no mediating effect of interspecific competition on population density, skewness, and basal diameter (Table 2.2). Similarly, except for soil N and P, we found no mediating effect of geographic/climatic distance on other abiotic factors (soil moisture, pH, P, and light) or functional traits (LMA, Chlorophyll content) (Figure 2.5, Figure 2.6). In contrast, *T. atacorensis* density increased with soil N and K (β = 0.371 ± 0.082, *p* = 0.038, R^2 = 0.53, Figure 2.6, 2.7d) and soil N and K increased with altitude (β = 0.391 ± 0.302, *p*= 0.011, R^2 = 0.61, Figure 2.6, 2.7b). In addition, we found an indirect positive effect of altitude on plant size (basal diameter) mediated by the positive effect of soil N and K (Figure 2.6, 2.7b, c). Overall, the structural equation model that included climatic distance and altitude had better fit (AIC = 187.58) than the one that included geographic distance (AIC = 192.69). Including or removing the two isolated Sobakperou mountain populations from our models did not change our results (Table 2.3, Table 2.4).

Discussion

No support for the centre-periphery hypothesis

Most tests of the centre-periphery hypothesis considered the geographical gradient as the main driver of the spatial variation of plant density. In this study, we used the geographic and climatic gradient and collected empirical data to advance our understanding of the ecological and evolutionary drivers of range limitation in endemic

species. Using a tropical study system from a region where the centre-periphery hypothesis has rarely been tested, we found no support for the centre-periphery hypothesis using the geographic or climatic distance. These results add to increasing evidence that geographic or climatic distances by themselves do not influence species abundance. Particularly, Dallas et *al.* (2017) used a range of species including plants and animals to show that there was no significant variation in abundance across their geographic range and climatic niche. The authors suggested that species abundance could be driven by unmeasured factors such as biotic and abiotic factors, which may explain the failure to detect a significant decline in density from center to periphery. In our study, we measured several additional (a)biotic variables but still did not find support for the centre-periphery hypothesis. This lack of support for the centre-periphery hypothesis could also be due to mismatches between geographic distribution and the ecological niche as reported elsewhere (Pagel *et al.* 2020). Other possible causes include niche truncation caused by the lack of similar conditions in central and peripheral range due to geographic constraints (Papuga *et al.* 2018; Yañez *et al.* 2020), stabilizing selection at the periphery (Devictor *et al.* 2010) or dispersal limitation (Willi & Van Buskirk 2019).

Previous studies showed that competition can synergistically interact with abiotic conditions to decrease population density at range's edge (Pulliam 2000; Vergeer & Kunin 2013). However, we found no mediating effect of most abiotic or biotic factors on the relationship between distance from climatic centre and population density. Several mechanisms could explain such patterns. Environmental conditions at the centre of climatic and geographic range may not be the most favourable to the species. Similarly, interspecific competition may be weaker at the centre of the range than at periphery limiting its interactive influence. For example, we found that soil nitrogen and potassium increased with climatic distance but with no consequence on the spatial variation of interspecific competition. Beside competition, other potential biotic interactions such as herbivory or pollination which we did not measure in this study may be the drivers of the observed distribution of *T. atacorensis* populations.

Soil nutrients as an important driver of range limitation

Altitude had no direct influence on plant density and size. However, we found a strong direct positive effect of soil nutrients on plant density. Several studies showed that plant density decreases with altitude due to temperature variation and metabolic limitations at higher elevations (Angert 2006; Souza *et al.* 2018). Instead of temperature gradient, for *T. atacorensis*, soil macronutrients variation along elevational gradient drives plant density. Particularly in tropical soils, phosphorus is a limiting factor (Camenzind *et al.* 2018; Hou *et al.* 2020). For instance, soil phosphorus decreased with altitude, and this can slow plant growth at higher elevations (Coomes & Allen 2007). However, in our study, *T. atacorensis* individuals were larger at higher elevations due to high soil nitrogen and potassium concentrations but in low density. Such trade-offs between large individual size and low density at higher elevations could be due to stronger intraspecific competition at higher elevations.

Overall, we found no support for the centre-periphery hypothesis that predicts that species density will decrease from centre to the periphery of its range. Variation in soil properties along the elevation gradient drove the spatial distribution of our study species. Our finding that peripheral populations, with suboptimal climate, have similar population density suggests that for mountainous species in heterogenous landscapes, local ecological processes are stronger drivers of species distribution than macro scale climatic factors.

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Appendix B

Figure 2.1: A *Thunbergia atacorensis* adult plant showing a characteristic purple flower in one of our study sites in Benin (West Africa). The species is found in gallery forest along the Atacora mountain chain.

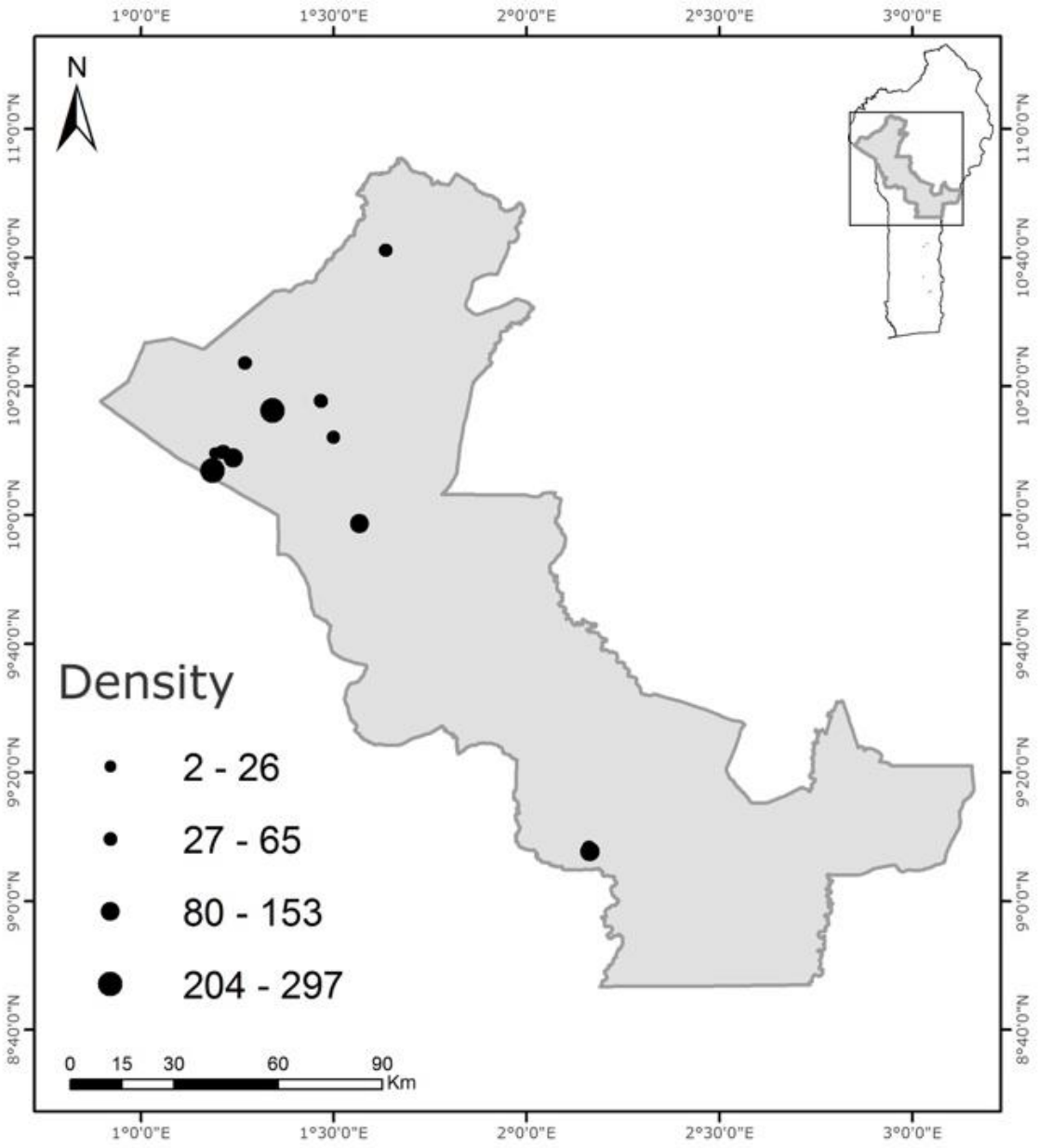

Figure 2.2 : Distribution of 12 *Thunbergia atacorensis* populations in Benin. The grey square in the insert represents the study area in Benin (West Africa). The black dots represent sampled populations. The size of each dot is proportional to population density (individuals/25 m^2).

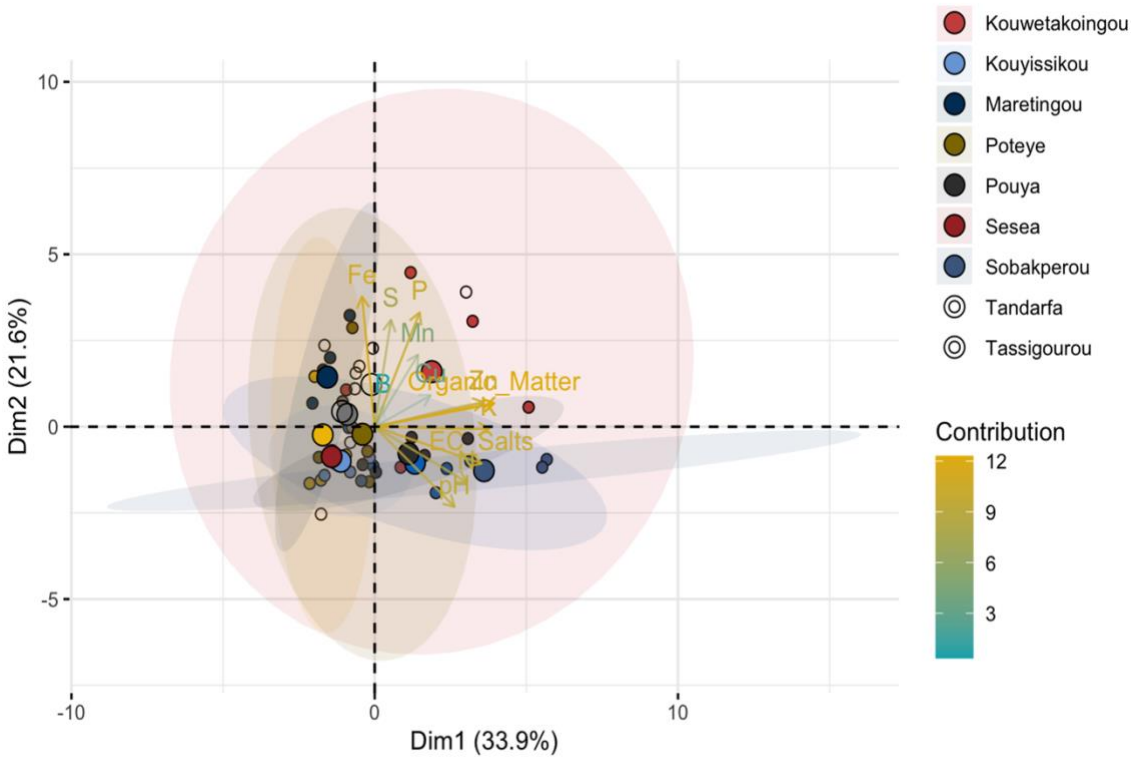

Figure 2.3: Principal component analysis of soil fertility data. Here the two first components explain more than 54% of variability of soil fertility. Nitrogen and Potassuim are more associated with the first component and and the pH and Phosphorus are more associated with the second component.

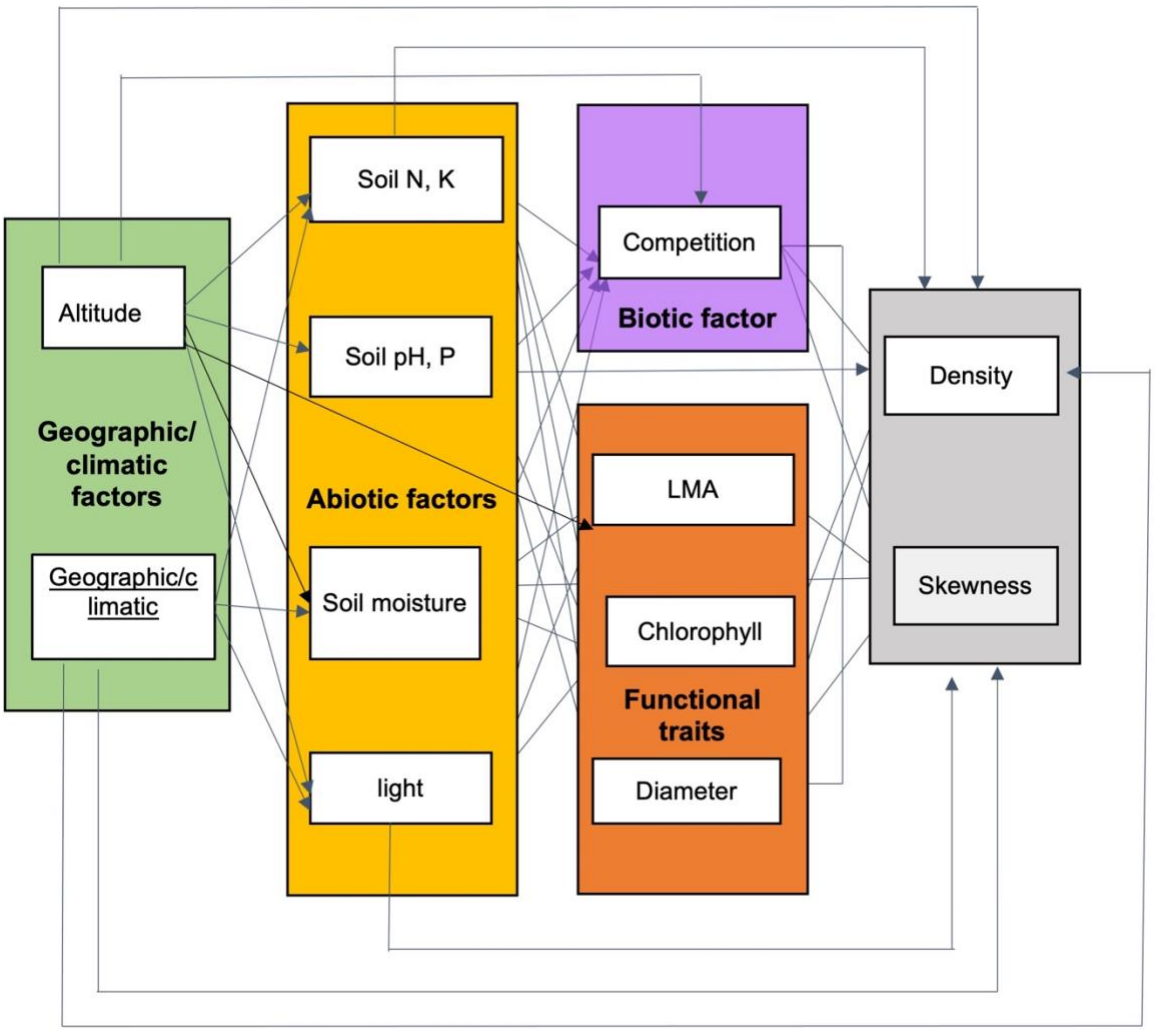

Figure 2.4: Conceptual framework. The diagram demonstrates the relationship between main predictions of the direct and indirect effects of distance from the center (geographic and climatic) and altitude on *Thunbergia atacorensis* population density, as well as population skewness mediated by abiotic and biotic factors. The line with one arrow illustrates a uni-directional relationship, while the solid line with double arrow depicts a bi-directional relationship. Soil (N, K) represents mainly the effect of Nitrogen and Potassium in soil while Soil (N, K) represent the effect of Phosphorus and pH. Skewness represents the measure of asymmetry of basal diameter per population. Density is the abundance of *Thunbergia atacorensis* per 25 m^2.

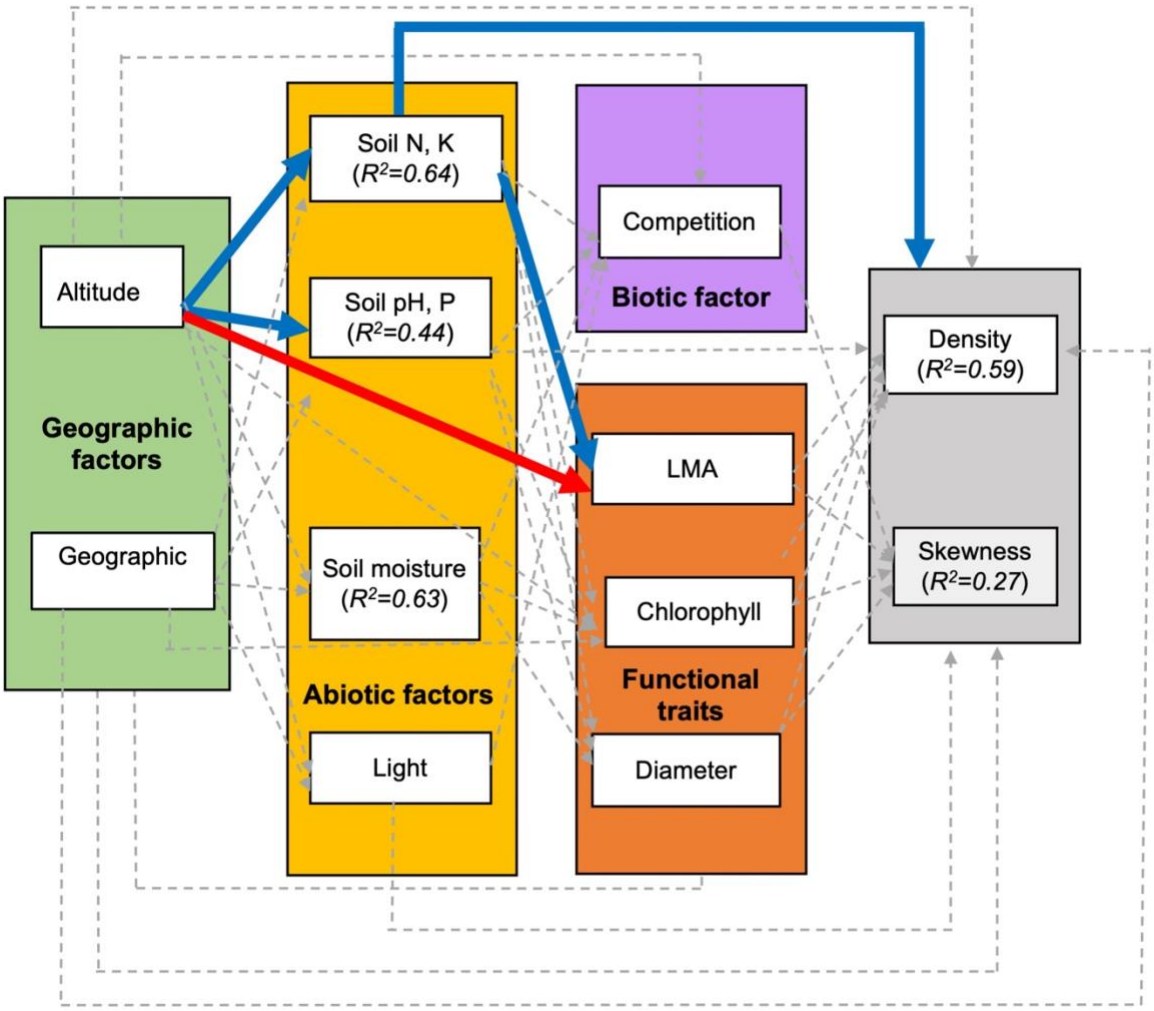

Figure 2.5: Structural equation model showing how the distance from the geographic center and altitude drives *T. atacorensis* population density and population structure. Dashed arrow shows non-significant correlation, blue arrow means positive correlation and red arrow show negative correlations. R^2 represent the conditional coefficients of determination for each linear mixed effect. Soil N, K represent the first component of the PCA of soil fertility while soil pH, P represent the second component.

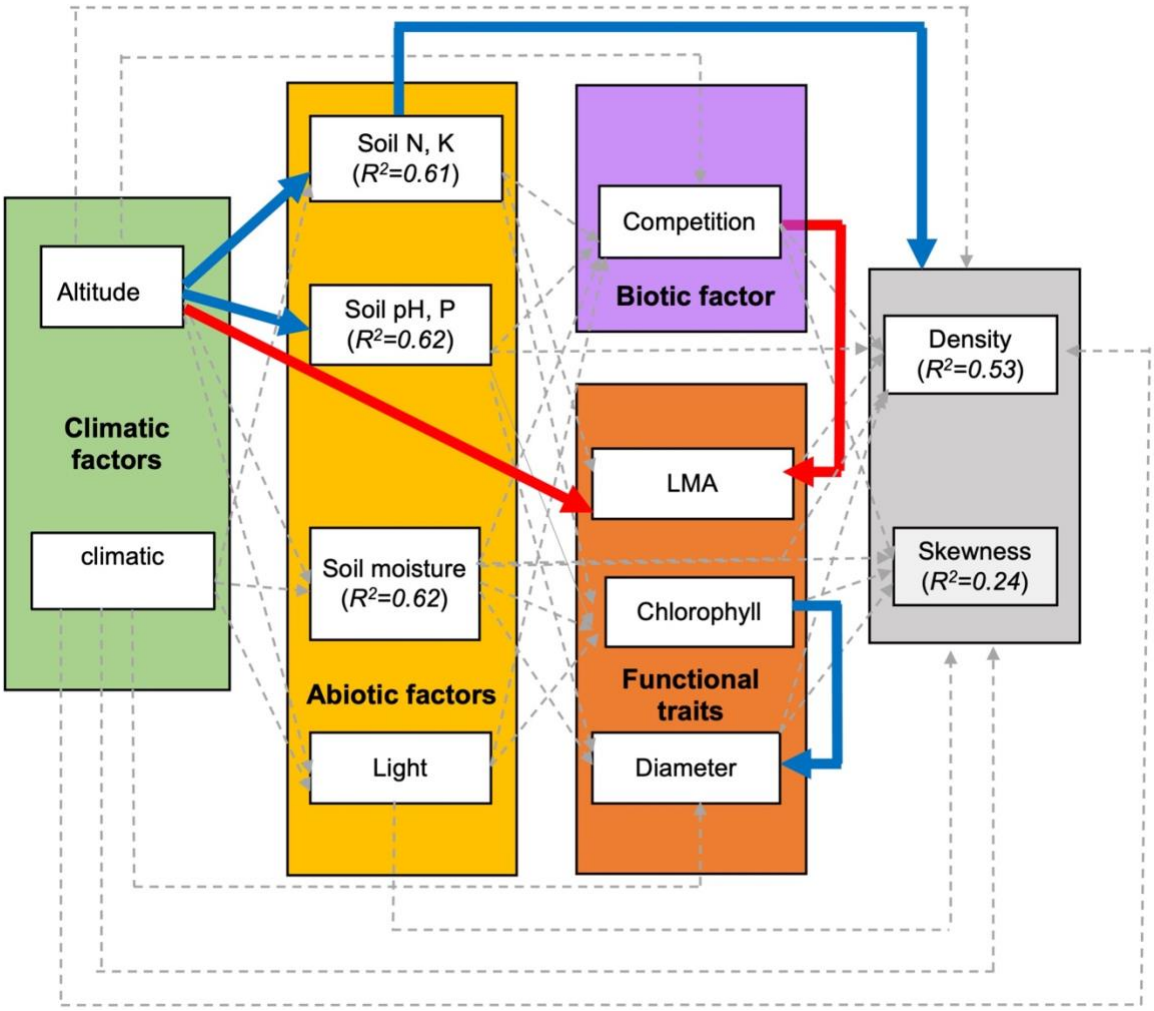

Figure 2.6: Structural equation model showing how the distance from the centroid of climatic niche and altitude affects *T. atacorensis* population density and population structure. Dashed arrow shows non-significant correlation, blue arrow means positive correlation and red arrow show negative correlations. R^2 represents the conditional coefficients of determination for each linear mixed effect. Soil N, K represent the first component of the PCA of soil fertility while soil pH, P represent the second component.

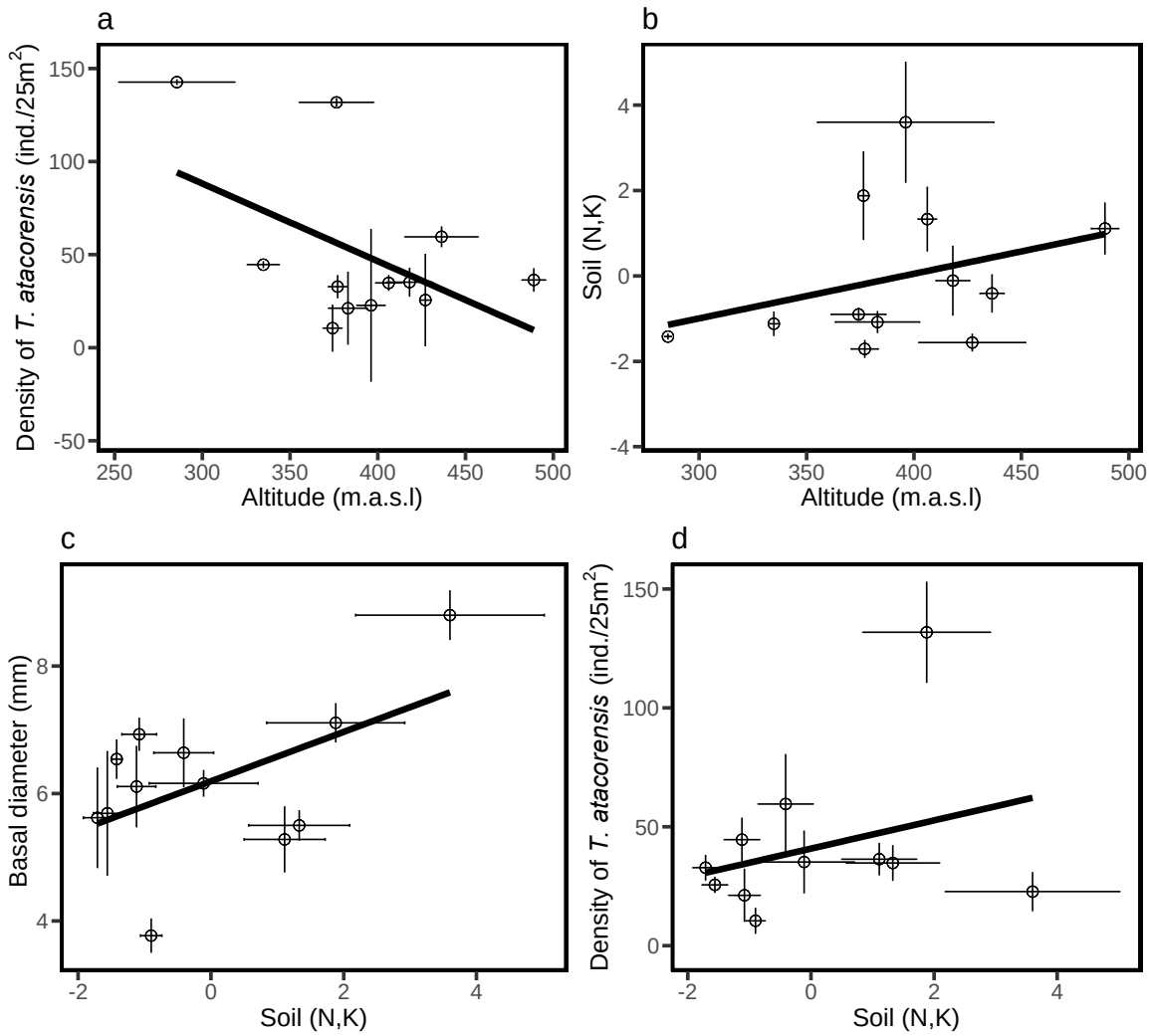

Figure 2.7: Relationship between a) altitude and density per plot, b) altitude and soil fertility (N, K), c) soil fertility and basal diameter, d) density and soil fertility (N, K). All these relationships are significant ($p<0.05$).

Table 2.1: Occurrence records for populations sampled and the number of plots installed per population.

Longitude	Latitude	Population	Number of plots installed
1.34105	10.270279	Poteye	5
1.466705	10.294874	Pouya	5
1.499549	10.201108	Kouaterna	5
1.634746	10.68536	Tandarfa	5
1.269294	10.393611	Marétingou	5
1.209394	10.162479	Koubirgou	5
1.239261	10.146821	kouyissikou	5
1.192084	10.159625	Kougnangou	2
1.186998	10.1157	Kouwetacoingou	5
1.566943	9.977977	Tassigourou	5
2.160704	9.138537	Sobakperou	4
2.163432	9.127444	Sesea	3

Table 2.2: The relationship between the distance from climatic center and altitude on population abundance and population skewness with the 10 Northern populations. PCA 1 is the first component of the principal component analysis and capture mainly the effect of Nitrogen and Potassium in soil while PCA 2 is the second component of the principal component analysis and represent the effect of Phosphorus and pH in soil. LMA is leaf mass per area. PAR is Photosynthetic active radiation. SRU is space resource utilization which is a proxy of inter specific competition. The "*" represents the level of significance of the relationship.

Response	**Predictor**	**Estimate**	**SE**	**DF**	**Critical Value**	**P**	**Std Estimate**
PCA1	Geographic Distance	0.1187	0.3372	35	0.3521	0.7269	0.0697
PCA1	Altitude	0.4194	0.3377	35	1.2421	0.2225	0.2415
PCA2	Geographic Distance	0.1102	0.3519	35	0.3132	0.756	0.0662
PCA2	Altitude	0.9487	0.3525	35	2.691	0.0108	0.5582*
LMA	PCA1	0.1838	0.071	29	2.5882	0.0149	0.3139 *
LMA	Geographic Distance	0.0029	0.1847	29	0.0154	0.9878	0.0029
LMA	PCA2	0.109	0.0703	29	1.5509	0.1318	0.1822
LMA	SRU	-0.1246	0.0906	29	-1.375	0.1797	-0.1236
LMA	PAR	0.0471	0.1167	29	0.4036	0.6895	0.0468
LMA	Altitude	-0.4425	0.2099	29	-2.1086	0.0437	-0.4351*
LMA	Soil moisture	-0.0271	0.1237	29	-0.2193	0.828	-0.0272
Chlorophyll	PCA1	0.0466	0.0984	29	0.4736	0.6393	0.08
Chlorophyll	Geographic Distance	-0.0832	0.1971	29	-0.422	0.6762	-0.0838
Chlorophyll	PCA2	-0.0341	0.0949	29	-0.3587	0.7224	-0.0572
Chlorophyll	SRU	0.032	0.1356	29	0.2361	0.815	0.0319
Chlorophyll	PAR	0.2365	0.1572	29	1.5044	0.1433	0.2362
Chlorophyll	Altitude	-0.436	0.212	29	-2.0568	0.0488	-0.4308*
Chlorophyll	Soil moisture	0.0164	0.1696	29	0.0969	0.9234	0.0166
PAR	Geographic Distance	0.0632	0.2032	34	0.3109	0.7578	0.0638
PAR	Altitude	0	0.2098	34	0.0001	0.9999	0
Soil moisture	Geographic Distance	0.3317	0.199	34	1.6664	0.1048	0.3311
Soil moisture	Altitude	0.14	0.199	34	0.7035	0.4865	0.137

Table 2.2 Continued

Response	Predictor	Estimate	SE	DF	Critical Value	P	Std Estimate
Soil moisture	SRU	0.044	0.1294	34	0.34	0.7359	0.0435
SRU	PAR	0.0999	0.1779	28	0.5615	0.5789	0.1001
SRU	Geographic Distance	0.0554	0.1705	28	0.3249	0.7477	0.056
SRU	Altitude	0.067	0.2086	28	0.3214	0.7503	0.0664
SRU	PCA1	0.0062	0.1051	28	0.0586	0.9537	0.0106
SRU	PCA2	0.0753	0.1029	28	0.7322	0.4701	0.1268
SRU	Chlorophyll	0.1057	0.1822	28	0.5801	0.5665	0.106
SRU	LMA	-0.1341	0.1747	28	-0.7673	0.4493	-0.1351
SRU	Soil moisture	0.1243	0.1906	28	0.6521	0.5196	0.1258
diameter	PAR	0.0676	0.1314	26	0.514	0.6116	0.0713
diameter	Geographic Distance	0.3218	0.1277	26	2.5189	0.0183	0.3430 *
diameter	Altitude	0.0845	0.1584	26	0.5336	0.5982	0.0883
diameter	PCA1	0.126	0.08	26	1.5751	0.1273	0.2287
diameter	PCA2	0.0532	0.0756	26	0.7041	0.4876	0.0944
diameter	SRU	-0.0878	0.1199	26	-0.7324	0.4705	-0.0926
diameter	Chlorophyll	0.5735	0.1467	26	3.9089	0.0006	0.606***
diameter	LMA	-0.0528	0.1328	26	-0.3976	0.6942	-0.0561
diameter	density	0.0495	0.1687	26	0.2932	0.7717	0.0465
diameter	Soil moisture	-0.1271	0.1475	26	-0.8617	0.3967	-0.1357
density	PAR	-0.0813	0.1379	25	-0.5896	0.5607	-0.0915
density	Geographic Distance	-0.0461	0.1722	25	-0.2679	0.791	-0.0523
density	Altitude	-0.2325	0.2013	25	-1.1546	0.2592	-0.2586
density	PCA1	0.1002	0.088	25	1.1381	0.2659	0.1936
density	PCA2	-0.017	0.0802	25	-0.2118	0.834	-0.0321
density	SRU	-0.0308	0.1139	25	-0.2704	0.7891	-0.0346
density	Chlorophyll	0.2408	0.1626	25	1.4814	0.151	0.2712
density	LMA	-0.2103	0.1612	25	-1.3045	0.2039	-0.2379
density	diameter	0.008	0.1634	25	0.0489	0.9614	0.0085
density	Soil moisture	0.3156	0.1451	25	2.1748	0.0393	0.3588*
density	skewness	0.0792	0.1259	25	0.6289	0.5351	0.0888

Table 2.2 Continued

Response	**Predictor**	**Estimate**	**SE**	**DF**	**Critical Value**	**P**	**Std Estimate**
density	skewness	0.0792	0.1259	25	0.6289	0.5351	0.0888
skewness	PAR	0.163	0.1618	26	1.0076	0.3229	0.1634
skewness	Geographic Distance	-0.242	0.1674	26	-1.4461	0.1601	-0.2449
skewness	Altitude	-0.0146	0.1891	26	-0.0773	0.939	-0.0145
skewness	PCA1	-0.0044	0.0988	26	-0.0447	0.9647	-0.0076
skewness	PCA2	-0.0249	0.0942	26	-0.2648	0.7932	-0.042
skewness	SRU	0.0703	0.1495	26	0.4706	0.6419	0.0704
skewness	Chlorophyll	-0.226	0.2063	26	-1.0955	0.2833	-0.2268
skewness	LMA	0.0713	0.1594	26	0.4472	0.6584	0.0719
skewness	diameter	-0.2655	0.209	26	-1.2704	0.2152	-0.252
skewness	Soil moisture	-0.2569	0.1745	26	-1.4717	0.1531	-0.2604

Table 2.3: The relationship between the distance from the geographical center and altitude on population abundance and population skewness. The "*" represents the level of significance of the relationship.

Response	Predictor	Estimate	SE	DF	Critical Value	P	Std Estimate
PCA1	Geographic Distance	0.8557	0.3084	40	2.7748	0.0084	0.4057**
PCA1	Altitude	0.883	0.2822	40	3.1292	0.0033	0.4069**
PCA2	Geographic Distance	0.3781	0.2831	40	1.3356	0.1892	0.2343
PCA2	Altitude	0.73	0.266	40	2.7441	0.009	0.4397**
LMA	PCA1	0.1011	0.0748	30	1.3515	0.1866	0.2139
LMA	Geographic Distance	0.1744	0.1661	30	1.0502	0.302	0.1749
LMA	PCA2	-0.0078	0.075	30	-0.1035	0.9183	-0.0126
LMA	SRU	-0.1085	0.0977	30	-1.1102	0.2757	-0.1108
LMA	PAR	0.2849	0.1114	30	2.5581	0.0158	0.2908*
LMA	Altitude	-0.2769	0.1819	30	-1.5223	0.1384	-0.2698
LMA	Soil moisture	-0.1692	0.138	30	-1.2259	0.2298	-0.1618
Chlorophyll	PCA1	0.0759	0.0848	34	0.8949	0.3771	0.1651
Chlorophyll	Geographic Distance	-0.3903	0.1751	34	-2.2292	0.0325	-0.4023*
Chlorophyll	PCA2	-0.004	0.0882	34	-0.0448	0.9645	-0.0066
Chlorophyll	SRU	0.1418	0.1253	34	1.1316	0.2657	0.1489
Chlorophyll	PAR	0.1848	0.1348	34	1.371	0.1794	0.194
Chlorophyll	Altitude	-0.5078	0.1909	34	-2.6605	0.0118	-0.5088*
Chlorophyll	Soil moisture	-0.0958	0.1534	34	-0.6245	0.5365	-0.0942
PAR	Geographic Distance	-0.0705	0.1753	39	-0.4023	0.6896	-0.0693
PAR	Altitude	0.0861	0.1726	39	0.4987	0.6208	0.0821
Soil moisture	Geographic Distance	-0.0845	0.1811	39	-0.4667	0.6433	-0.0886
Soil moisture	Altitude	-0.2879	0.1639	39	-1.7567	0.0868	-0.2933
Soil moisture	SRU	-0.0009	0.1142	39	-0.0079	0.9938	-0.001
SRU	PAR	-0.0392	0.1761	29	-0.2229	0.8252	-0.0392
SRU	Geographic Distance	0.1802	0.1927	29	0.935	0.3575	0.1769
SRU	Altitude	-0.1125	0.2322	29	-0.4843	0.6318	-0.1073

Table 2.3 Continued

Response	Predictor	Estimate	SE	DF	Critical Value	P	Std Estimate
SRU	PCA2	0.0917	0.1073	29	0.8542	0.4	0.1452
SRU	Chlorophyll	0.1802	0.1881	29	0.958	0.346	0.1716
SRU	LMA	-0.1823	0.1909	29	-0.9548	0.3476	-0.1785
SRU	Soil moisture	0.2998	0.2188	29	1.37	0.1812	0.2807
diameter	PAR	0.1135	0.1187	27	0.956	0.3475	0.1332
diameter	Geographic Distance	0.4316	0.1319	27	3.2716	0.0029	0.4976**
diameter	Altitude	-0.0537	0.1714	27	-0.3133	0.7565	-0.0602
diameter	PCA1	0.1256	0.0692	27	1.816	0.0805	0.3055
diameter	PCA2	0.0053	0.0725	27	0.0729	0.9424	0.0098
diameter	SRU	-0.1438	0.1066	27	-1.3495	0.1884	-0.1689
diameter	Chlorophyll	0.4356	0.129	27	3.3778	0.0022	0.4871**
diameter	LMA	-0.0977	0.1309	27	-0.7463	0.4619	-0.1123
diameter	density	-0.1678	0.1512	27	-1.1094	0.277	-0.1684
diameter	Soil moisture	0.0973	0.1565	27	0.6217	0.5393	0.107
density	PAR	-0.0367	0.1279	26	-0.2868	0.7765	-0.0429
density	Geographic Distance	-0.085	0.1782	26	-0.4769	0.6374	-0.0976
density	Altitude	-0.3908	0.1903	26	-2.0542	0.0501	-0.4363
density	PCA1	0.0485	0.0791	26	0.6138	0.5446	0.1176
density	PCA2	0.001	0.0767	26	0.013	0.9897	0.0018
density	SRU	0.0057	0.1047	26	0.0542	0.9572	0.0066
density	Chlorophyll	0.0962	0.1485	26	0.6475	0.523	0.1071
density	LMA	-0.0956	0.16	26	-0.5978	0.5551	-0.1096
density	diameter	-0.1047	0.1597	26	-0.6559	0.5177	-0.1043
density	Soil moisture	0.3447	0.1468	26	2.3474	0.0268	0.3776*
density	skewness	0.0024	0.1221	26	0.0199	0.9843	0.0027
skewness	PAR	0.1795	0.1583	27	1.1338	0.2669	0.1864
skewness	Geographic Distance	-0.0649	0.1999	27	-0.3246	0.748	-0.0662
skewness	Altitude	-0.0206	0.2108	27	-0.0979	0.9227	-0.0205
skewness	PCA1	-0.0316	0.0942	27	-0.3353	0.74	-0.068

Table 2.3 Continued

Response	Predictor	Estimate	SE	DF	Critical Value	P	Std Estimate
skewness	PCA2	0.043	0.0953	27	0.4507	0.6558	0.0707
skewness	SRU	-0.0098	0.1416	27	-0.0694	0.9452	-0.0102
skewness	Chlorophyll	-0.335	0.186	27	-1.801	0.0829	-0.3313
skewness	LMA	0.2251	0.1765	27	1.275	0.2132	0.2289
skewness	diameter	-0.3771	0.2105	27	-1.7914	0.0844	-0.3336
skewness	Soil moisture	-0.1737	0.1938	27	-0.8963	0.378	-0.1689

Table 2.4: The relationship between the distance from the climatic center and altitude on population abundance and population skewness. The "*" represents the level of significance of the relationship

Response	**Predictor**	**Estimate**	**SE**	**D**	**Critical Value**	**P**	**Std Estimate**
PCA1	Climatic Distance	0.0121	0.0149	40	0.8149	0.4199	0.4014**
PCA1	Altitude	0.8711	0.3163	40	2.7539	0.0088	0.4014**
PCA2	Climatic Distance	-0.0006	0.0126	40	-0.0483	0.9617	-0.0089
PCA2	Altitude	0.626	0.2698	40	2.32	0.0255	0.3771*
LMA	PCA1	0.1327	0.0696	30	1.907	0.0661	0.2806
LMA	Climatic Distance	0.0008	0.007	30	0.108	0.9147	0.0179
LMA	PCA2	0.0057	0.075	30	0.0755	0.9403	0.0092
LMA	SRU	-0.1198	0.0987	30	-1.2147	0.234	-0.1224
LMA	PAR	0.2801	0.1129	30	2.4805	0.019	0.286*
LMA	Altitude	-0.3191	0.1897	30	-1.6826	0.1028	-0.311
LMA	Soil moisture	-0.1959	0.1425	30	-1.3748	0.1794	-0.1874
Chlorophyll	PCA1	0.0063	0.0835	34	0.0755	0.9403	0.0137
Chlorophyll	Climatic Distance	0.0003	0.0078	34	0.0426	0.9662	0.0081
Chlorophyll	PCA2	-0.0388	0.0921	34	-0.4209	0.6765	-0.0645
Chlorophyll	SRU	0.1441	0.1309	34	1.1009	0.2787	0.1514
Chlorophyll	PAR	0.169	0.1426	34	1.1849	0.2443	0.1774
Chlorophyll	Altitude	-0.3299	0.1937	34	-1.7027	0.0978	-0.3305
Chlorophyll	Soil moisture	-0.0588	0.1641	34	-0.3583	0.7223	-0.0578
PAR	Climatic Distance	0.0038	0.0077	39	0.4934	0.6245	0.0877

Table 2.4 Continued

Response	Predictor	Estimate	SE	D	Critical Value	P	Std Estimate
PAR	Altitude	0.1255	0.1688	39	0.7438	0.465	0.1198
Soilmoisture	Climatic Distance	0.011	0.0079	40	1.4003	0.1691	0.2737
Soil moisture	Altitude	-0.2125	0.1673	40	-1.27	0.2114	-0.2166
SRU	PAR	-0.0355	0.182	29	-0.1951	0.8467	-0.0355
SRU	Climatic Distance	-0.0044	0.0078	29	-0.5609	0.5792	-0.1019
SRU	Altitude	-0.2453	0.2269	29	-1.0812	0.2885	-0.234
SRU	PCA1	-0.0468	0.1012	29	-0.4621	0.6475	-0.0969
SRU	PCA2	0.1203	0.1101	29	1.0929	0.2834	0.1905
SRU	Chlorophyll	0.1095	0.1796	29	0.61	0.5466	0.1043
SRU	LMA	-0.1797	0.2029	29	-0.8857	0.3831	-0.1759
SRU	Soil moisture	0.2791	0.227	29	1.2292	0.2289	0.2613
diameter	PAR	0.1333	0.1367	27	0.9752	0.3381	0.1565
diameter	Climatic Distance	0.0041	0.0065	27	0.6244	0.5376	0.1105
diameter	Altitude	-0.2019	0.2	27	-1.0095	0.3217	-0.2262
diameter	PCA1	0.2019	0.0768	27	2.6279	0.014	0.4909*
diameter	PCA2	-0.0037	0.083	27	-0.0441	0.9652	-0.0068
diameter	SRU	-0.0979	0.1169	27	-0.8376	0.4096	-0.115
diameter	Chlorophyll	0.3258	0.1336	27	2.438	0.0216	0.3643*
diameter	LMA	-0.0412	0.1605	27	-0.2565	0.7995	-0.0473

Table 2.4 Continued

Response	Predictor	Estimate	SE	D	Critical Value	P	Std Estimate
diameter	density	-0.1662	0.1823	27	-0.9117	0.37	-0.1668
diameter	Soil moisture	0.0255	0.1827	27	0.1394	0.8902	0.028
density	PAR	-0.0383	0.1235	27	-0.31	0.759	-0.0448
density	Climatic Distance	-0.006	0.0061	27	-0.9845	0.3336	-0.1618
density	Altitude	-0.437	0.1733	27	-2.521	0.0179	-0.4878*
density	PCA1	0.0409	0.0748	27	0.5464	0.5893	0.099
density	PCA2	0.0111	0.0741	27	0.15	0.8819	0.0206
density	SRU	-0.0021	0.1042	27	-0.0201	0.9841	-0.0025
density	Chlorophyll	0.1369	0.1256	27	1.0901	0.2853	0.1525
density	LMA	-0.106	0.1477	27	-0.7182	0.4788	-0.1215
density	diameter	-0.1309	0.144	27	-0.9088	0.3715	-0.1304
density	Soil moisture	0.3759	0.1482	27	2.5358	0.0173	0.4118*
skewness	PAR	0.1633	0.144	27	1.1337	0.2669	0.1695
skewness	Climatic Distance	-0.0128	0.0058	27	-2.2067	0.036	-0.308*
skewness	Altitude	-0.0528	0.1722	27	-0.3069	0.7612	-0.0524
skewness	PCA1	-0.0733	0.0869	27	-0.844	0.4061	-0.1577
skewness	PCA2	0.064	0.0884	27	0.7239	0.4753	0.1053
skewness	SRU	-0.0283	0.1305	27	-0.2172	0.8297	-0.0294
skewness	Chlorophyll	-0.3419	0.1537	27	-2.2245	0.0347	-0.3382*
skewness	LMA	0.2105	0.1514	27	1.3899	0.1759	0.2141

Table 2.4 Continued

Response	**Predictor**	**Estimate**	**SE**	**D**	**Critical Value**	**P**	**Std Estimate**
skewness	diameter	-0.3548	0.177	27	-2.0044	0.0551	-0.3139
skewness	Soil moisture	-0.0658	0.1885	27	-0.3488	0.7299	-0.064

CHAPTER 3: SOIL NITROGEN MEDIATES THE EFFECT OF CLIMATIC DISTANCE ON HERBIVORY RATES IN A TROPICAL HERB

A version of this chapter was originally published by Jacob Moutouama and Orou Gaoue

Moutouama, J.K. and Gaoue, O.G. (2022). Soil nitrogen mediates the effect of climatic distance on herbivory rates in a tropical herb. *Biotropica*, 54: 3, 682-690. https://doi.org/10.1111/btp.13082

Authors contributions: JKM and OGG conceived the study and developed the models, JKM collected the data, performed the analyses, and lead the writing of the manuscript with editorial assistance from OGG.

Abstract

The center-periphery hypothesis predicts that species are most abundant at the center of their distribution range. Differential herbivory rates between center and periphery populations can explain this variation in species abundance. However, if the geographic center of a species distribution coincides with its ecological optimum, the resource availability hypothesis predicts higher herbivory rates and tolerances at the center compared to the periphery. Biogeographical studies on herbivory have treated these two mechanisms separately, limiting our mechanistic understanding of the role of herbivory in shaping species range limits. We analyzed the role of resource availability on herbivory variation from center to periphery using data collected across the distribution of *Thunberbia atacorensis,* a range-limited species of West Africa. We used two types of distances: geographic distance (the distance from each plot to the geographic center of all populations) and climatic distance (the distance from each plot to the preferendum of the species). We found no increase in herbivory toward the periphery of the climatic and geographic ranges. However, herbivory rates increased with soil nitrogen. Soil nitrogen decreased from the center to the periphery of the climatic range. Phylogenetic diversity and competition from surrounding plants did not affect herbivory rates. Our study provides insights into how nutrient limitation can shape species center-periphery distribution by altering spatial variation in herbivory rates.

Introduction

Over the past decades, ecologists increasingly recognized the role of biotic factors in shaping species distribution (Louthan et al., 2015; Lynn et al., 2021; Maron and Crone,

2006). Differential rates of herbivory can mediate the effect of abiotic factors on plant survival across space (Lau et al., 2008) and thereby limit plant distribution. Moreover, the occurrence of a plant species can limit the range of another, not through interspecific competition but through increased herbivore intensity (Parker and Root, 1981). However, the circumstances under which biotic factors (e.g., insect herbivores) limit or control densities of a host species remain equivocal, particularly for tropical Africa. Gaining an in-depth understanding of the response of range-limited plant species to herbivory can provide valuable insights into conservation biology for two reasons. First, it is important to know if herbivory is a threat to range-limited plant species, particularly in areas with intensive restoration and conservation efforts. Second, changes in the abundance of endemic plant species due to herbivory can affect the dynamics of many interacting species, like specialist herbivores.

Existing studies on the effect of herbivory from center to periphery populations yield mixed results. For example, herbivory intensity did not vary from center to periphery for *Daphne laureola* (Castilla et al., 2013) and *Ficus sp* (Sam et al., 2020). Fagan et al., (Fagan et al., 2005) found that central populations experienced more intense herbivory than peripheral populations. In contrast, herbivory was higher at the periphery than at the center for *Poa alapina*, *Festuca brachyphylla*, and *Elymus scribneri* (Lynn et al., 2021). Further, studies showing high herbivory at the periphery often conclude that such a pattern may explain range limitation. However, high herbivory rates do not necessarily translate into negative impacts on species distribution. This is particularly true for herbivory tolerant species (Anderson et al., 1995; Fornoni, 2011; Rosenthal and Kotanen, 1994). Moreover, most studies testing the effect of herbivory from center to periphery often assume that the geographic center corresponds the climatic range center (Herrero et al., 2012; Scheidel and Bruelheide, 1999). However, this assumption may be wrong given that geographically marginal populations are not necessarily ecologically marginal (Pironon et al., 2015; Soberón et al., 2018).

Considering the climatic range, peripheral populations are expected to have more stressful environments due to poor abiotic conditions (e.g., soil nutrients, light, and water) compared to central populations (Brown, 1984). In contrast, geographic range

centers are not expected to have more significant resources than the peripheries (Pironon et al., 2017). The resource availability hypothesis predicts that fast-growing plants, which characterize nutrient-rich environments, invest less in herbivory defenses (Coley et al., 1985; Endara and Coley, 2011). Therefore, herbivory rate is expected to be higher at the climatic center than at the periphery (Castilla et al., 2013; Lewis et al., 2006). However, few studies tested the effect of resource availability on the variation of herbivory from center to periphery.

At climatic range edges, abiotic stress can reduce the species competitive ability and increase their vulnerability to herbivory (Agrawal et al., 2006). Variation in plants' competitive ability with changing environmental conditions may ultimately limit their investment in defense. In this case, competition mediates the relationship between available resources and herbivory (Donaldson et al., 2006). Given that competition is expected to be more (Wilson and Tilman, 1993) or less severe under abiotic stresses (Callaway and Walker, 1997), peripheral populations may have high or low competition levels. If competition is stronger at the periphery, substantial investment in competition response would reduce the investment in defense and lead to higher herbivory at the periphery.

Besides abiotic factors, herbivory can be affected by species diversity. Phylogenetic diversity decreases species-specific levels of herbivory via negative density dependence mechanisms (Cavender-Bares et al., 2009; Paine et al., 2012). However, this relationship depends on the degree of herbivores specialization (specialist or generalist). For example, the effect of a specialist insect herbivore on a focal plant is predicted to increase with the plant density, regardless of the phylogenetic distance between the focal species and its neighboring species (Castagneyrol et al., 2014). Conversely, the effect of a generalist herbivore on a focal plant species is lower when neighboring species are more phylogenetically distant from the focal species. However, the effect of phylogenetic diversity on herbivory rate from center to periphery has been rarely investigated.

In this study, we integrated several hypotheses and investigated the synergistic effects of the above mechanisms on the herbivory rate of a tropical perennial herb from the center to the periphery of its geographic and climatic range. Our study focused on

Thunbergia atacorensis and its interactions with insect herbivores in West Africa. *T. atacorensis* has a restricted range and is endemic to the west African Atacora and Sobakperou mountain chains (Fandohan et al., 2015)(Fandohan et al., 2015). The species has. Because the species is range-limited and suffers from high rates of herbivory from two main known native insect herbivores makes *T. atacorensis* an interesting model system to explore the geographic variation of the underlying mechanisms of herbivory.

We hypothesized that abiotic factors (soil nutrients and light) decrease with distance from climatic center consistent with the center-periphery hypothesis (Brown, 1984; Pironon et al., 2017) and that herbivory rates increase with an increase sol nutrients and light consistent with the resource availability hypothesis (Coley et al., 1985; Endara and Coley, 2011). Furthermore, because species that invest more to compete tend to invest less in defense, we hypothesized that herbivory rates will increase with increasing competition intensity (Agrawal et al., 2006). Finally, species diversity decreases with an increase in species competition. We tested this network of hypotheses using structural equation models (Lefcheck, 2016) which provides possibilities of uncovering indirect or mediating effect of abiotic drivers on plant response to herbivory (Figure 3.1).

Methods

Study system

Thunbergia atacorensis (Akoègninou Lisowski & Sinsin) is a perennial herb that belongs to the *Acanthaceae* family (Figure 3.2a). The plant can reach up to 80 centimeters in height and is found in gallery forests along the Atacora (Akoègninou et al., 2006) and Sobakperou mountain chains in Benin, West Africa (Fandohan et al., 2015). The Atacora mountain chain (1°00’ - 2°00’ E and 10°40’ - 11°28’ N) is in the Northwest of Benin, and the Sobapkerou mountain chain is in the center of Benin (2°9’ N -9°8' E). Data on the natural history of species is lacking. However, our field observations revealed two insect herbivores feeding on *T. atacorensis*: a generalist, *Philopona aburiensis* Bryant (Col.: Chrysomelidae) (Figure 3.2f) and the specialist (Figure 3.2e), the larvae of *Filodes costivitralis* Guenée (Lep.: Crambidae) (Figure 2d) (Bippus, 2019).

For this study we selected all the 12 known occurrence sites of *Thunbergia atacorensis* (Fandohan et al., 2015) along the Atacora and the Sobapkerou mountains (Figure 3.3).

In each *Thunbergia* population, we randomly established five 5 m x 5 m permanent plots to collect demographic data, soil data and estimate insect herbivory rates, interspecific competition among surrounding species. We used a minimum of two plots for three populations that were too small for five 5 m x 5 m plots to be established (Table 3.1).

Measuring herbivory rate, abiotic factors, and interspecific competition

In each population and plot, we measured herbivory rate in August 2019 for each *Thunbergia* plant by randomly sampling and photographing three leaves, which were later analyzed to estimate the proportion eaten using *LeafByte* (Getman-Pickering et al., 2019). We aggregated values across all individual *Thunbergia* found in the plot across size classes to obtain plot level herbivory rates. Two different insect herbivores feed on *Thunbergia* leaves. Each herbivore species has a distinctive pattern of herbivory. Specialist herbivore *Filodes costivitralis* feeds on leaves margins while *Philopona aburiensis* feeds on the lamina (Figure 3.2 b and Figure 3.2c). We estimated the rate of herbivory for each insect species at the plot level and compared them across populations. We developed a generalized mixed-effect model with a beta error structure, using the package glmmTMB (Brooks et al., 2017), to test if the rate of herbivory was significantly different between insect species. To understand the patterns of total herbivory rate from center to periphery, we measured the additive effect of both insect herbivores.

In each plot, we measured understory light availability as the photosynthetic active radiation (PAR) using a Cl-110 Plant Canopy Imager (CID Bio-Science Inc., Camas, WA, USA) and soil moisture using Extech MO750 soil moisture meter (Extech, Boston, MA, USA). We incorporated light in the analysis because plant competition to sunlight can affect herbivory rate (Kurashige and Agrawal, 2005). We collected 20g composite soil samples per plot by mixing soil taken at 7cm depth in the four corners and the center of each plot. These soil samples were sent to the Soil, Water & Plant Testing Laboratory at Colorado State University (CO, USA) for analysis extractable nitrogen,

phosphorus, and potassium. We conducted a complete survey and identified all plant species within each plot. For each species, we measured the maximum height and the percent biomass cover (C_i). In addition, we estimated plot level interspecific species competition of surrounding species by calculating space resource utilization (SRU) (Zhang et al., 2019): SRU=$\sum_i^n H_i C_i A$, where H_i is the average maximum height of species *i*, C_i represents the percent cover of species *i* in the plot, *n* the total number of species per plot and *A* is plot area.

Phylogenetic species variation

To test the effect of phylogenetic diversity on herbivory rate from center to periphery, we estimated the phylogenetic species variation which is the degree of relatedness among groups (Helmus et al., 2007) within the community (Webb, 2000). First, we standardized taxonomy among plots using The Plant List (http://www.theplantlist.org) via the R package *Taxonstand* (Cayuela et al., 2019). Second, we used the most recent and largest dated phylogeny for seed plants, GenBank taxa with a backbone (GBOTB) (Smith & Brown, 2018), as the backbone of our phylogeny. Only four plant species did not have correspondence species in GBOTB (*Aspilia kotschyi, Aspilia rudis, Adenodolichos paniculatus, Aspilia helianthoides*). We deleted these species from our final species list. Third, we used the options *nodes.info.1* and scenario 3 of function *phylo.maker* in the package *V.PhyloMaker* (Jin and Qian, 2019) on 238 angiosperms species belonging to 52 families to generate a species-level phylogenetic tree (Figure 3.4). Further, we created community data which represents the species density per plot. We used the function *match.phylo.comm* in the package *picante* to match the previously built phylogeny tree with the community data (Kembel et al., 2020). Finally, we used the same package to estimate the Phylogenetic species variation (PSV) in R (R Core Team, 2019). A PSV of 1 represents the maximum phylogenetic variability (Helmus et al., 2007).

Estimation of the distance from the geographic and climatic center

To estimate the distance from the geographic center of *Thunbergia atacorensis*, we calculated the distance from each population to the center of a convex polygon formed by

all 12 populations using the package *geosphere* (Hijmans, 2019). We assumed that the geographic center is not necessarily the point that is ecologically or climatically most suitable for the study species. Consequently, we estimated the distance from niche centroid or climatic center as a mahalanobis distance (Osorio-Olvera et al., 2020). The mahalanobis distance represents the distance between every population and the point with the most suitable conditions. Estimating this distance allowed us to link herbivory rate with geographic and climatic distances, biotic (interspecific competition), and abiotic factors (soil nutrients, light).

To calculate the Mahanalobis distance, we split *T. atacorensis* occurrence points into training (80% of points) and testing (20%) for the ellipsoid model. We retrieved for these occurrence points four bioclimatic variables (annual mean temperature, annual precipitation, solar radiation, and precipitation seasonality) from WorldClim2, at a spatial resolution of 30 arc second, to characterize the niche of *T. atacorensis* as a minimum volume ellipsoid. We selected these four variables because they were not correlated among each other and previously identified as the best predictors of *T. atacorensis* distribution (Adomou, 2005; Fandohan et al., 2015). These four bioclimatic variables were derived from spatial interpolation of monthly average temperature (maximum and minimum) and precipitation (total) throughout 1970-2000 (Fick and Hijmans, 2017). We fitted the minimum volume ellipsoid with 99% of calibration occurrences of the species, with 6% as omission criteria and 10,000 as background. We selected the best of three candidate models using the package *stringr* (Wickham, 2019). We used the best model to estimate the niche centroid using the package *ntbox* (Luis Osorio-Olvera et al., 2020). Finally, we used the function *mahalanobis* in the package *stats* to calculate the mahalanobis distance.

Bayesian structural equation modeling

We developed structural equation models (SEM) (Lefcheck, 2016) to investigate the mechanisms driving the variation in *Thunbergia* herbivory rates (for both insects) across its geographic and climatic ranges. SEM is a statistical method that can test causation or mediation between variables (Shipley, 2009). Mediation occurs when the

relationship between two variables depends on a third one. In this study, we particularly tested the effect of phylogenetic species diversity variation and distance from geographic or climatic center on herbivory rate of *Thunberger atacorensis* individuals as mediated by interspecific competition (SRU) and abiotic factors. Because some of our dependent variables have non-normal residuals, we used a piecewise SEM which allows the inclusion of variables with non-normal residuals (Lefcheck, 2016). We especially used a beta distribution for the herbivory rate, which is the main response variable, then linearized and standardized predictors including soil fertility, soil moisture, light exposure, interspecific competition (SRU) and phylogenetic diversity. This improved model fit and facilitated interpretation of the outputs and the comparison of path coefficients (Lefcheck, 2016).

To estimate the path coefficients of the SEM, we used a Bayesian modeling framework. We used the package *brms* to run each model linking predictors to each endogenous variable with 2 chains and non-informative prior, 10,000 iterations and a warm-up of 1000 (Bürkner, 2017). We used the trace plot to visually evaluate chains mixing (Figure 3.5) and the Gelman-Rubin criterion to check model convergence. The closer this factor is to 1, the better the convergence of our chains. We used the leave-one-out cross-validation (loo) (Vehtari et al., 2017). We consider that a relation is significant if the 95% credible interval did not include zero. Finally, we reported the Bayesian coefficients of determination for each path included in our final piecewise SEM. All analyses were performed under R 3.2 (R Core Team, 2019) and the data used to perform these analysis are available online (Moutouama and Gaoue, 2022).

Results

Variation in herbivory rate, abiotic, phylogenetic diversity, and competition with distance from climatic enter

Extractable soil nitrogen decreased significantly from climatic center to periphery (β = -0.37; 95%CI: -0.73 to -0.01) and herbivory rate increased significantly with increasing soil nitrogen concentration (β = 0.2; 95%CI: 0.01 to 0.39; Figure 3.6, 3.7a), which suggested a mediating role of soil nitrogen in the variation of herbivory rate. We

found no significant variation in other soil properties (soil pH, soil potassium) and light from climatic center to periphery (Figure 3.6, Table 3.2). In contrast, extractable soil phosphorus decreased from climatic center to periphery (Figure 3.6, Table 3.2). We found no significant direct effects of climatic distance on herbivory rate (Figure 3.6, Table 3.2) or interspecific competition and no significant effect of phylogenetic diversity on herbivory rate (Figure 3.6, Table 3.2). However, phylogenetic diversity was positively associated with interspecific competition, suggesting that most diverse communities faced higher competitive effect ($\beta = 0.3$; 95%CI: 0.01 to 0.59; Figure 3.6, 3.7b).

Variation in herbivory rate, abiotic, phylogenetic diversity, and competition with distance geographic from center

Across all *Thunbergia atacorensis* populations, herbivory was mostly due to the larvae of the specialist herbivore *Filodes costivitralis* relative to the generalist *Philopona aburiensis* ($\beta = 0.43 \pm 0.06$, $Z = 7.01$, $P < 0.0001$; Figure 3.8). We found no significant change in extractable soil nitrogen, phosphorus, pH, soil moisture and light with distance from geographic center (Table 3.3). Extractable soil potassium increased significantly with geographic distance ($\beta = 0.41$; 95%CI: 0.10 to 0.72). However, phylogenetic diversity and interspecific competition had no significant effect on herbivory rates in the model testing the effect of geographic center on herbivory rate (Table 3.3).

Discussion

Contrary to predictions, our study shows that herbivory rate in *T. atacorensis* was not significantly affected by geographic or climatic distance. We hypothesized that environmental stress would increase with climatic and geographic distance with less nutrient availability away from the distribution centers. Consequently, herbivory rate was expected to be higher in central than peripheral populations due to higher tolerance to herbivory given the availability of resources at the center (Coley et al., 1985; Stamp, 2003). Our results suggest that climatic distance indirectly influences herbivory rates through the mediating effect of soil nitrogen which decreased toward the periphery and herbivory rates in *T. atacorensis* decreased as a result. Nitrogen is a vital element for plant growth due to its role in photosynthesis (Kirkby, 1981) and in the synthesis of

certain classes of secondary compounds (Richardson et al., 1999). For a perennial herb such as *T. atacorensis*, soil nitrogen will be assimilated by the plant and with direct impact on plant biomass increase (Blue et al., 2011) which will facilitate the replacement of biomass loss to insect herbivory (Wallace et al., 1985). A high soil nitrogen availability can also lead to plant luxury nitrogen consumption with a subsequent increase in the risk of insect herbivory (Behmer, 2009; Tripler et al., 2002).

Thunbergia sp. is rich in secondary compounds such as phenolic, tannins, flavonoids (Chan and Lim, 2006; Sultana and Chatterjee, 2015). These compounds are known for their crucial role in anti-herbivory defense (Bazzaz et al., 1987; Coley, 1983). The lower rate of herbivory observed in low nitrogen soils in peripheral populations of *T. atacorensis* can also be due to a stronger chemical and physical defense (e.g., leaves toughness or trichomes) in these nutrient-poor sites with higher cost of biomass loss (Coley and Kursar, 1996). In these peripheral populations, soil nitrogen availability is perhaps not sufficient to compensate such biomass loss. Such a high level of herbivory may explain range limitation in *Thunbergia* populations, given that we observed florivory in most populations that can suppress fertility (JK Moutouama, *personal observation*s). However, manipulative experiments and further demographic studies are needed to establish how soil nitrogen mediated herbivory rates can alter *Thunbergia* spatially explicit dynamics.

Higher rates of herbivory are expected in phylogenetically clustered communities (Parker et al., 2012). Clearly, more phylogenetically similar host plant species are more likely to share similar functional traits involved in host recognition and exploitation (Wiens et al., 2010) and are therefore more prone to share common herbivores (Weiblen et al., 2006). Focal plant species may also be chemically well defended in phylogenetically diverse communities due to the diversity of competitive strategies they experience (Agrawal et al., 2012). In contrast to this prediction, the herbivory rate in *T. atacorensis* was not affected by phylogenetic diversity. Such lack of significant effect of plant diversity on herbivory rate is often attributed to the role of herbivore specialization. When herbivory is dominated by generalist herbivore, one would expect limited effect of

diversity. However, in our study system, *T. atacorensis* suffers more herbivory from the specialist *Filodes costivitralis* than from the generalist *Philopona aburiensis*.

Contrary to previous studies on competitive exclusion (Cavender-Bares et al., 2009; Paine et al., 2012), species competition increased with phylogenetic species variation. This is perhaps due to the confounding influence of other mechanisms which could also influence phylogenetic species variation or competition. In our study, our measure of competition index captures light rather than nutrient competition where larger plants can shade, and competitivity exclude smaller neighbors. Thus, soils nutrients-based competition may respond to the variation in phylogenetic diversity in a different way. Perhaps in our study system, current soil nutrient availability is sufficient enough for species to partition their niches and coexist rather than compete vigorously (Adler et al., 2007; Chesson, 2000).

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Appendix C

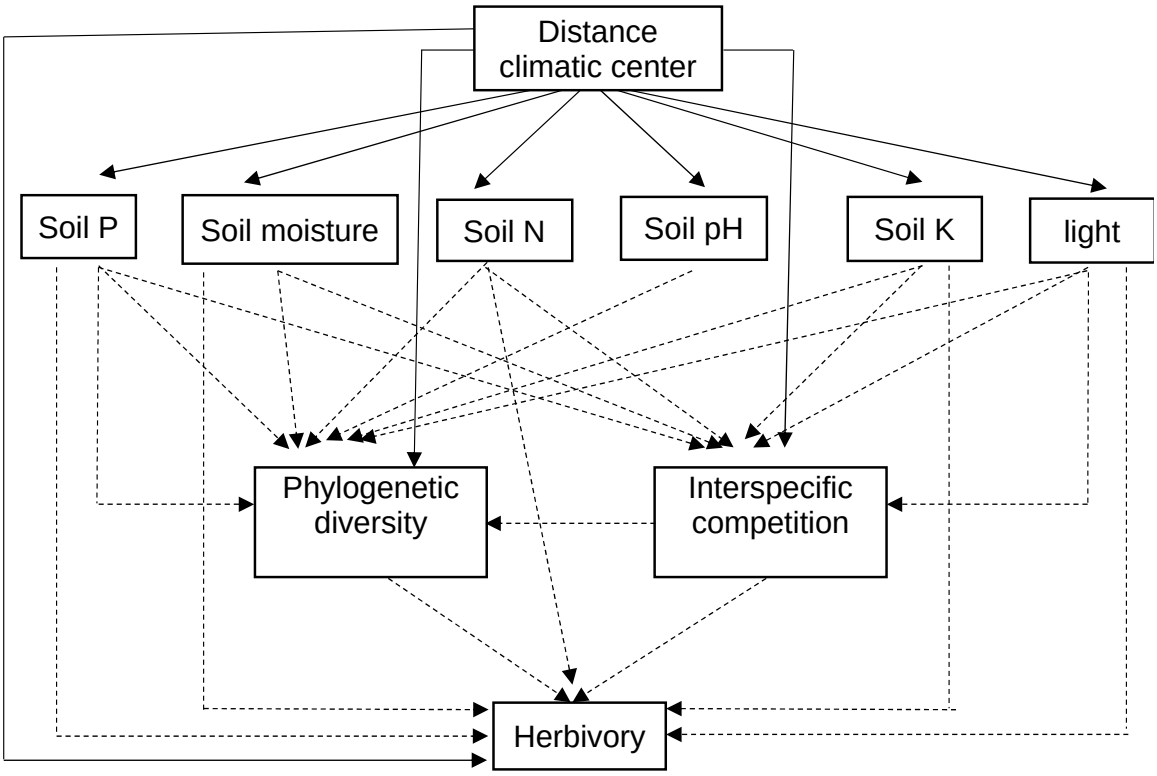

Figure 3.1: Conceptual framework. Main predictions of the distance from the center (geographic and climatic) direct and indirect positive and negative effects on herbivory in *Thunbergia atacorensis* populations. Dashed arrows denote positive effects, solid arrows denote negative effects. Soil N is the extractable soil nitrogen, Soil P is the extractable soil phosphorus.

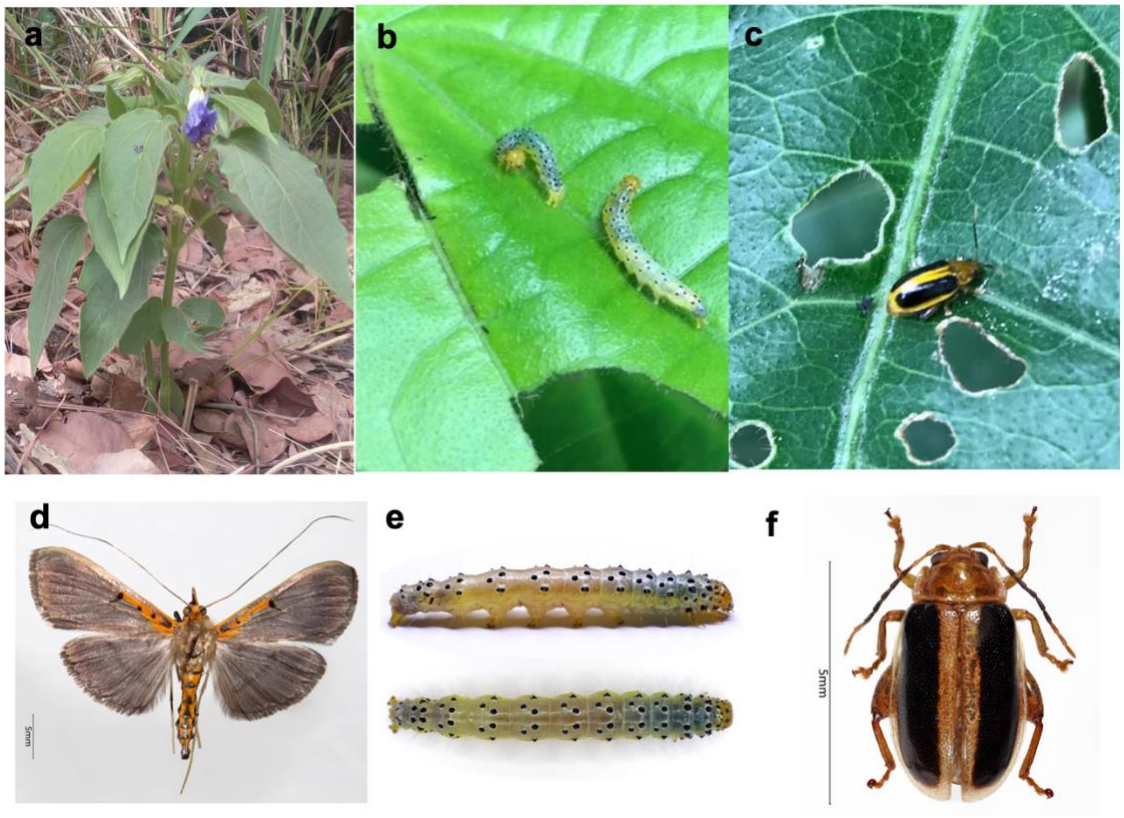

Figure 3.2: (a) A *Thunbergia atacorensis* adult plant showing a characteristics purple flower in one of our study sites in Benin (West Africa). The species is found in gallery forest along the Atacora mountain and Soubakperou mountains where it suffers distinct leaf herbivory by (b) specialist *Filodes costivitralis* (leaf margin herbivory) and generalist (c) *Philopona aburiensis* (herbivory as leaf spots). (d) Adult individuals of *Filodes costivitralis* lay the eggs on *Thunbergia* which develop into (e) larvae that feed on *Thunbergia* plants. (f) Generalist *Philopona aburiensis* Bryant feed not only on *Thunbergia* but other plant species.

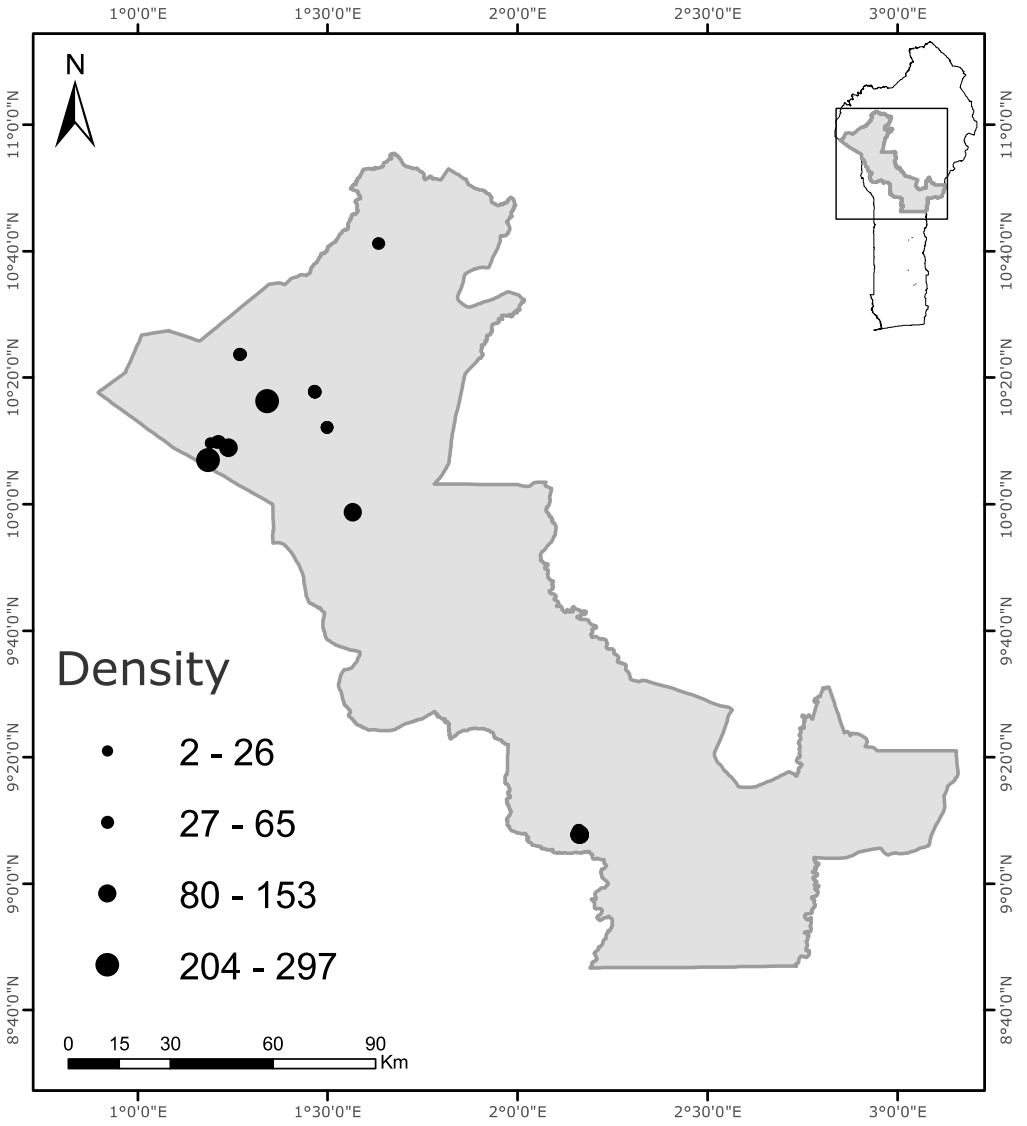

Figure 3.3: Distribution of 12 *Thunbergia atacorensis* populations in Benin. The grey square in the insert represents the study area in Benin (West Africa). The black dots represent sampled populations. The size of each dot is proportional to population density (plants/25 m^2).

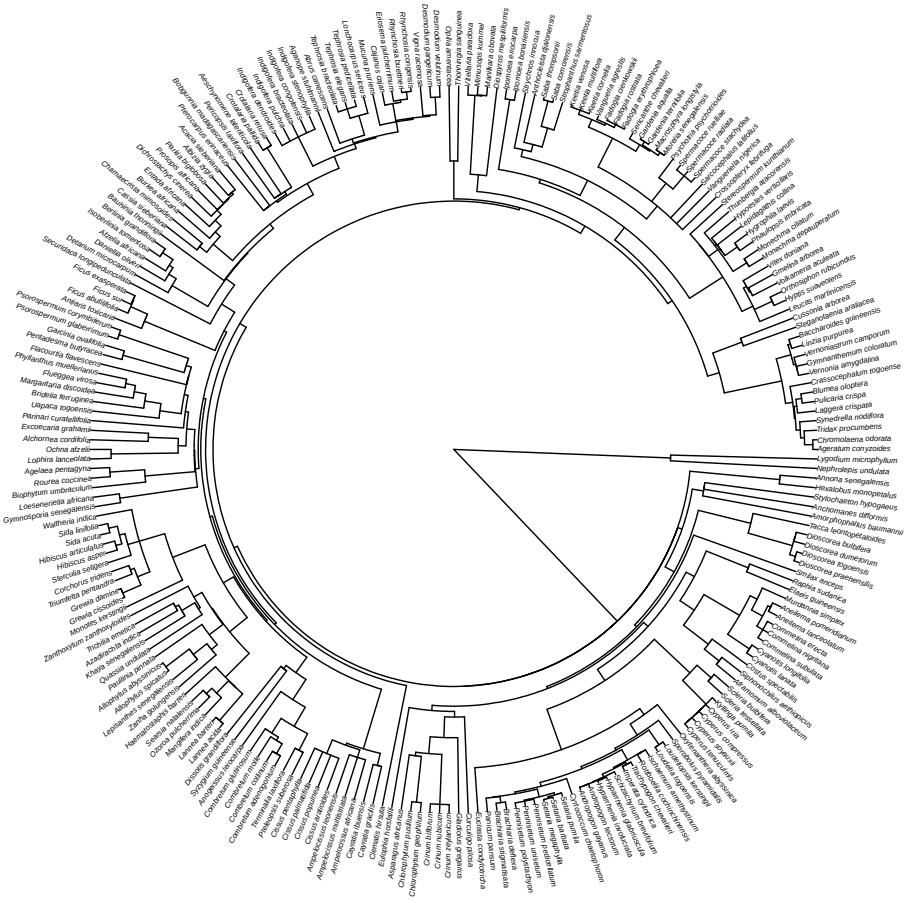

Figure 3.4: Phylogenetic tree of the neighbor plants of *Thunbergia atacorensis*

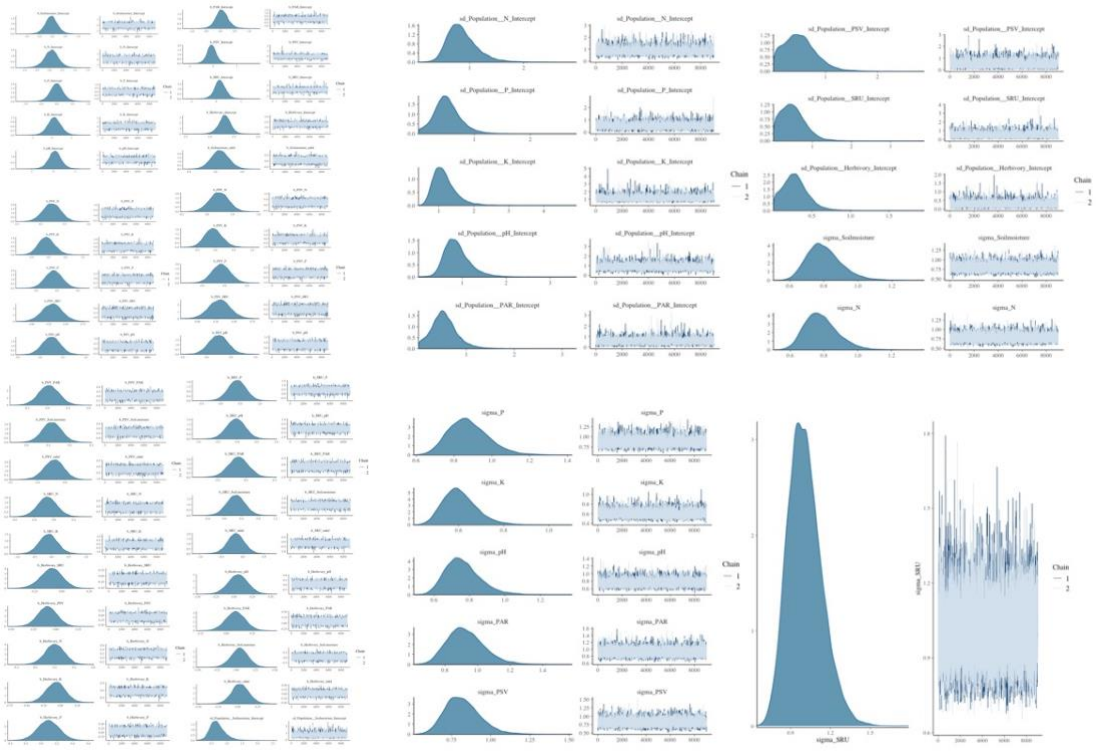

Figure 3.5: Trace and density plots assessing mixing of a chain for the structural equation model (distance from climatic center).

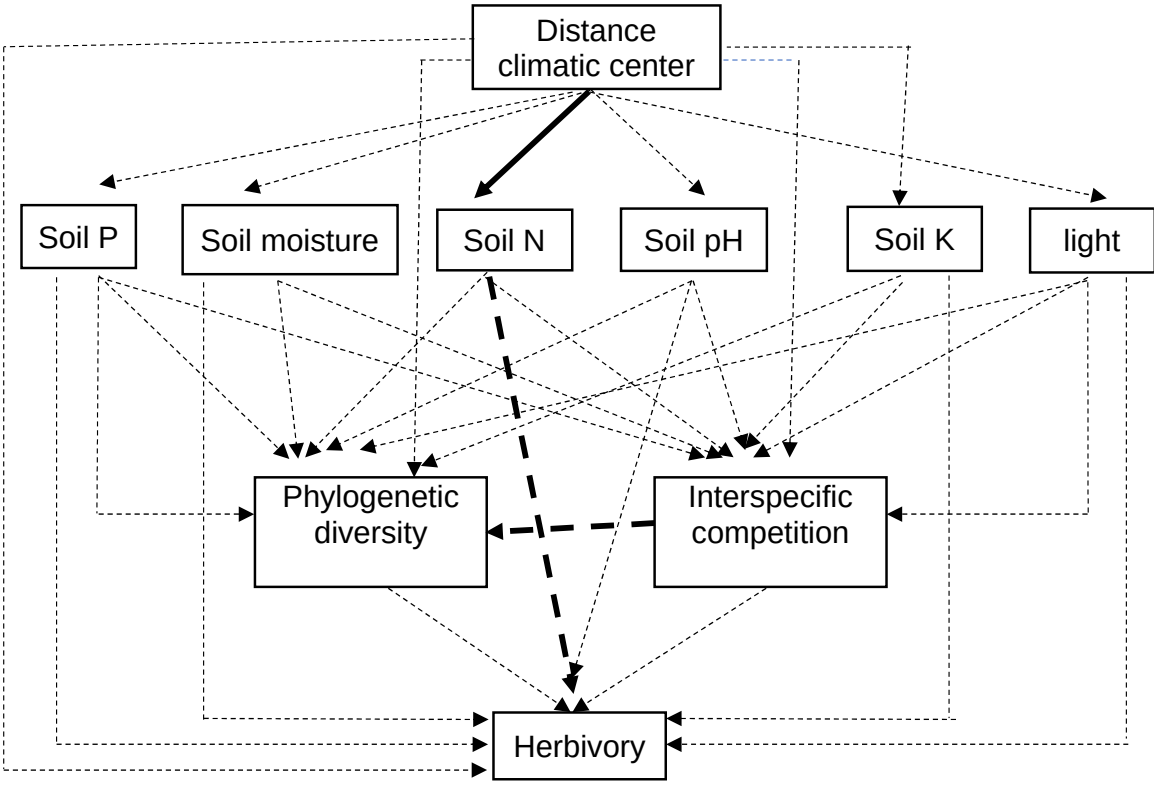

Figure 3.6: Structural equation model showing the direct and the indirect drivers of herbivory in *Thunbergia atacorensis* populations. Dashed arrows represent a non-significant effect. Solid arrows denote negative effects. The bold arrow represents a significant relationship. Soil N is the extractable soil nitrogen, Soil P is the extractable soil phosphorus, Soil K is the extractable soil potassium, pH is soil pH.

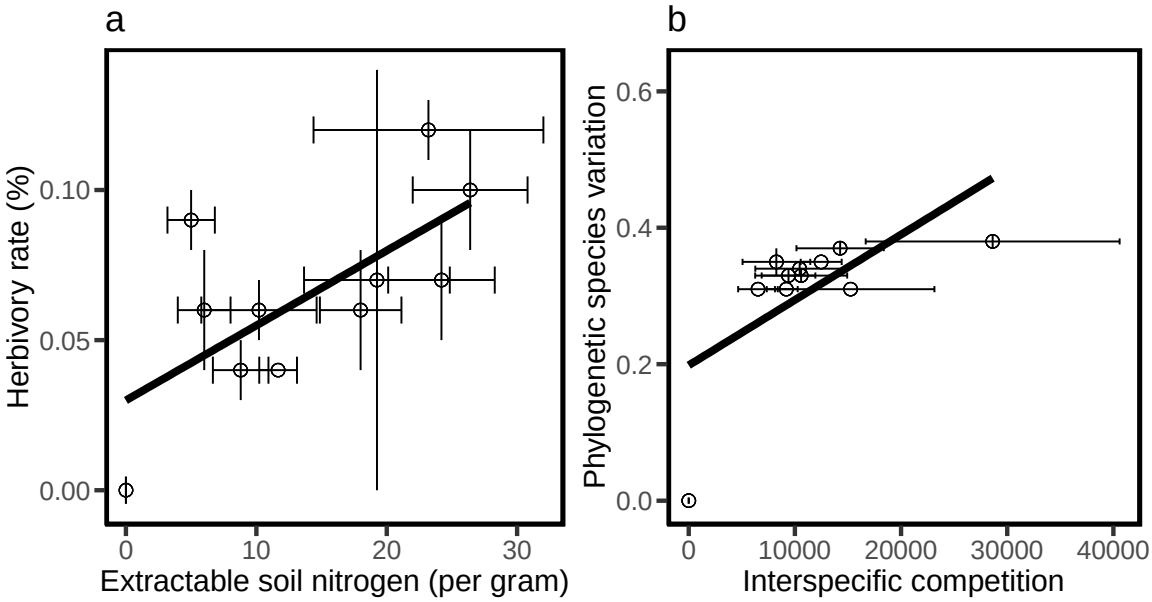

Figure 3.7: (a) Effects of extractable soil nitrogen on herbivory rates, (b) interspecific competition on phylogenetic species variation.

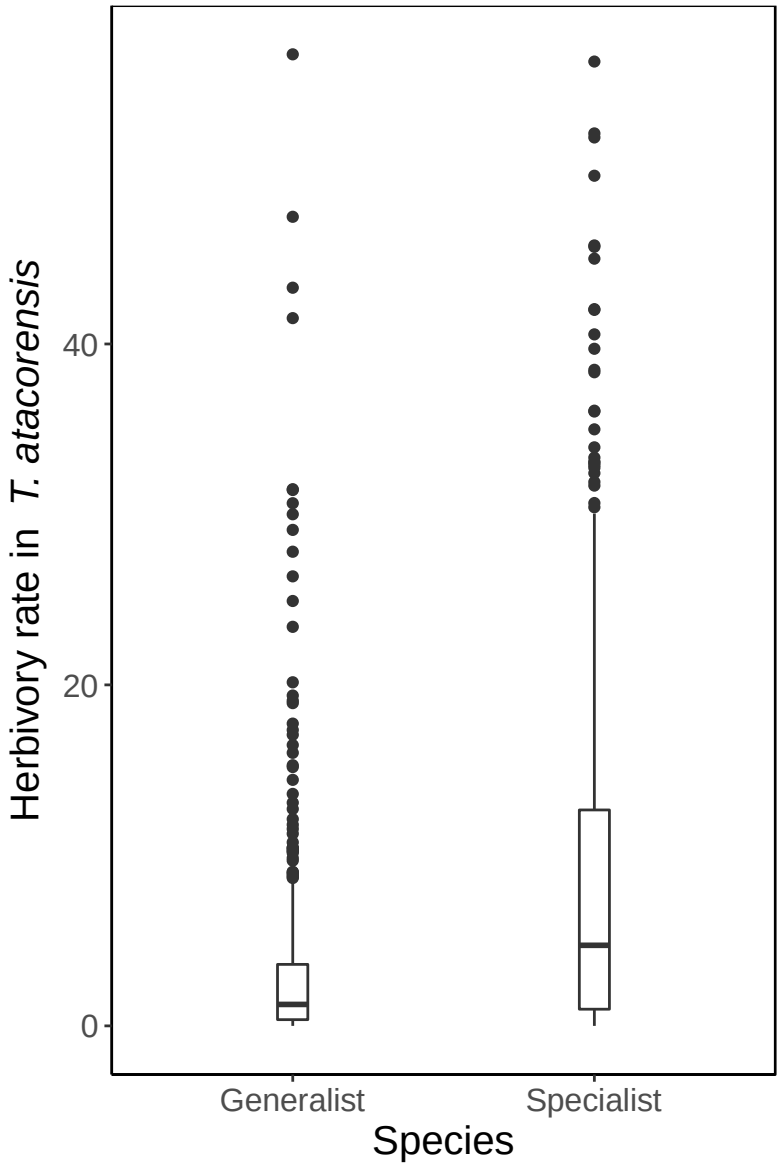

Figure 3.8: Herbivory rate by (a) specialist *Filodes costivitralis* was significantly greater than that of the (b) generalist *Philopona aburiensis* across the 12 populations of *T. atacorensis* ($\beta = 0.43 \pm 0.06$, Z = 07.01, P <0.0001).

Table 3.1: Occurrence records for populations sampled and the number of plots installed per population.

Longitude	Latitude	Population	Number of plots installed
1.34105	10.270279	Poteye	5
1.466705	10.294874	Pouya	5
1.499549	10.201108	Kouaterna	5
1.634746	10.68536	Tandarfa	5
1.269294	10.393611	Marétingou	5
1.209394	10.162479	Koubirgou	5
1.239261	10.146821	kouyissikou	5
1.192084	10.159625	Kougnangou	2
1.186998	10.1157	Kouwetacoingou	5
1.566943	9.977977	Tassigourou	5
2.160704	9.138537	Sobakperou	4
2.163432	9.127444	Sesea	3

Table 3.2: The relationship between the distance from climatic center on herbivory rate mediated by interspecific competition, abiotic factors and phylogenetic diversity. N is extractable soil nitrogen, P is extractable soil phosphorus, K is extractable soil potassium, pH is soil pH. PSV is phylogenic species variation. PAR is Photosynthetic active radiation. SRU is space resource utilization which is a proxy of inter specific competition. The bold rows represent significant relationships.

	Estimate	**Est.Error**	**Lower 95%CI**	**Upper 95%CI**	**Rhat**	**Bulk_ESS**	**Tail_ESS**
Intercepts							
Soil moisture	-0.05	0.25	-0.54	0.46	1.00	12106.00	11673.00
N	0.07	0.29	-0.52	0.64	1.00	10597.00	11381.00
P	-0.01	0.21	-0.42	0.42	1.00	16050.00	13305.00
K	0.12	0.36	-0.59	0.84	1.00	7392.00	9926.00
pH	0.07	0.30	-0.54	0.67	1.00	8925.00	9481.00
PAR	0.05	0.23	-0.40	0.51	1.00	15073.00	11795.00
PSV	-0.07	0.22	-0.51	0.36	1.00	13518.00	10748.00
SRU	0.15	0.23	-0.31	0.61	1.00	16239.00	11712.00
Herbivory	-2.68	0.13	-2.95	-2.43	1.00	15504.00	11707.00
Effects of distance from climatic center on abiotic factors							
Soil moisture	0.08	0.17	-0.24	0.41	1.00	23034	13818
N	**-0.37**	**0.18**	**-0.73**	**-0.01**	**1.00**	**15449**	**13494**
P	0.25	0.16	-0.07	0.58	1.00	25695	14541
K	-0.21	0.15	-0.50	0.10	1.00	23252	13162
pH	-0.11	0.17	-0.46	0.23	1.00	17857	13642
PAR	-0.04	0.17	-0.39	0.30	1.00	21594	14297
Effects of abiotic factors and abiotic factors on PSV							
N	0.23	0.19	-0.14	0.59	1	9804	12421
K	-0.06	0.24	-0.52	0.44	1	12043	11490
P	-0.08	0.2	-0.48	0.32	1	13774	13431
SRU	**0.3**	**0.15**	**0.01**	**0.59**	**1**	**11031**	**13493**
pH	0.24	0.2	-0.15	0.64	1	20978	13729
PAR	0.02	0.15	-0.27	0.31	1	24763	14396
Soil moisture	-0.33	0.18	-0.68	0.03	1	23209	13824
Distance center	-0.21	0.18	-0.57	0.14	1	14330	12829
Effects of abiotic factors and abiotic factors on interspecific competition							
N	-0.14	0.2	-0.53	0.26	1	25732	14306
K	-0.1	0.27	-0.62	0.44	1	16755	13686

Table 3.2 Continued

	Estimate	Est.Error	Lower 95%CI	Upper 95%CI	Rhat	Bulk_ESS	Tail_ESS
Effects of abiotic factors and abiotic factors on interspecific competition							
P	0.41	0.23	-0.05	0.87	1	14648	14030
pH	-0.04	0.24	-0.51	0.43	1	19041	14567
PAR	-0.14	0.18	-0.49	0.21	1	22776	14970
Soil moisture	0.27	0.22	-0.16	0.69	1	20831	13928
Distance center	-0.16	0.2	-0.56	0.23	1	20314	13653
Effects of abiotic factors and abiotic factors on Herbivory							
SRU	-0.1	0.1	-0.3	0.09	1	23973	13973
PSV	-0.09	0.11	-0.3	0.11	1	20571	14557
N	**0.2**	**0.1**	**0.01**	**0.39**	**1**	**22282**	**13995**
K	-0.07	0.14	-0.34	0.2	1	15743	13827
P	0.09	0.14	-0.18	0.36	1	11461	13028
pH	0.05	0.13	-0.21	0.31	1	17540	13835
PAR	0.09	0.09	-0.1	0.27	1	21008	15032
Soil moisture	0.04	0.11	-0.18	0.26	1	24201	14697
Distance center	0.03	0.11	-0.18	0.25	1	15206	14038

Table 3.3: The relationship between the distance from geographic center on herbivory rate mediated by interspecific competition, abiotic factors and phylogenetic diversity. N is extractable soil nitrogen, P is extractable soil phosphorus, K is extractable soil potassium, pH is soil pH. PSV is phylogenic species variation. PAR is Photosynthetic active radiation. SRU is space resource utilization which is a proxy of inter specific competition. The bold rows represent significance relationship.

	Estimate	**Est.Error**	**Lower 95%CI**	**Upper 95%CI**	**Rhat**	**Bulk_ESS**	**Tail_ESS**
Intercepts							
Soil moisture	-0.04	0.26	-0.56	0.48	1.00	7060.00	9442.00
N	0.06	0.27	-0.48	0.60	1.00	6862.00	9911.00
P	0.00	0.23	-0.46	0.47	1.00	9463.00	10170.00
K	0.07	0.31	-0.54	0.68	1.00	4483.00	7217.00
pH	0.04	0.28	-0.53	0.61	1.00	5235.00	8491.00
PAR	0.05	0.23	-0.40	0.54	1.00	9087.00	10334.00
PSV	-0.09	0.21	-0.52	0.34	1.00	10746.00	8745.00
SRU	0.14	0.23	-0.32	0.60	1.00	11777.00	9039.00
Herbivory	-2.69	0.11	-2.92	-2.47	1.00	12147.00	10847.00
Effects of distance from climatic center on abiotic factors							
Soil moisture	-0.05	0.18	-0.42	0.31	1.00	11370	13238
N	0.01	0.19	-0.36	0.38	1.00	13166	13740
P	0.01	0.18	-0.35	0.37	1.00	13571	13023
K	**0.41**	**0.16**	**0.10**	**0.72**	**1.00**	**12410**	**14034**
pH	0.26	0.18	-0.09	0.61	1.00	12840	13794
PAR	-0.10	0.19	-0.48	0.25	1.00	11770	12553
Effects of abiotic factors and abiotic factors on PSV							
N	0.26	0.19	-0.12	0.64	1	7209	12422
K	0.03	0.28	-0.51	0.6	1	6510	10914
P	-0.18	0.2	-0.57	0.21	1	9718	13060
SRU	0.33	0.15	0.03	0.63	1	8709	12373
pH	0.22	0.2	-0.18	0.61	1	14414	13803
PAR	0.05	0.15	-0.25	0.35	1	16288	13284
Soil moisture	-0.37	0.19	-0.74	-0.01	1	14828	14152
Distance center	-0.08	0.2	-0.49	0.29	1	9647	10850
Effects of abiotic factors and abiotic factors on interspecific competition							
N	-0.06	0.2	-0.47	0.34	1	14935	13289
K	-0.15	0.32	-0.78	0.5	1	7671	11006

Table 3.3 Continued

	Estimate	**Est.Error**	**Lower 95%CI**	**Upper 95%CI**	**Rhat**	**Bulk_ESS**	**Tail_ESS**
Effects of abiotic factors and abiotic factors on interspecific competition							
P	0.38	0.22	-0.05	0.82	1	12443	13082
pH	-0.06	0.24	-0.53	0.41	1	13216	12974
PAR	-0.12	0.18	-0.47	0.23	1	19124	13823
Soil moisture	0.26	0.22	-0.18	0.69	1	13021	13503
Distance center	0.12	0.25	-0.43	0.58	1	6763	7475
Effects of abiotic factors and abiotic factors on Herbivory							
SRU	-0.11	0.1	-0.31	0.08	1	20101	13914
PSV	-0.13	0.1	-0.32	0.07	1	16267	13431
N	0.16	0.1	-0.03	0.36	1	17121	14134
K	0.01	0.15	-0.28	0.3	1	10398	11837
P	0.09	0.12	-0.16	0.34	1	10227	12082
pH	0.07	0.13	-0.19	0.32	1	12421	13379
PAR	0.09	0.09	-0.09	0.26	1	20700	13938
Soil moisture	0.03	0.11	-0.19	0.24	1	15779	13885
Distance center	-0.16	0.12	-0.39	0.08	1	13119	11500

CHAPTER 4: EFFECTS OF RANGE AND NICHE POSITION ON POPULATION DYNAMICS OF A TROPICAL PLANT

A version of this chapter was originally submitted by Jacob Moutouama and Orou Gaoue:

Moutouama, J.K. and Gaoue, O.G. (2023). Effects of range and niche position on population dynamics of a tropical plant. *Ecology*

Authors contributions: JKM and OGG conceived the study and developed the models, JKM collected the data, performed the analyses, and lead the writing of the manuscript with editorial assistance from OGG.

Abstract

The center-periphery hypothesis (CPH) predicts a decline in population performance toward the periphery of species range, reflecting a spatially explicit environmental variation. 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, (i) central populations will have better demographic growth, survival, and fertility than peripheral populations. As a result, (ii) central populations are expected to have higher growth rates than peripheral populations. Peripheral populations are expected to decline in population dynamics, limiting species range expansion beyond these boundaries. Because peripheral populations are expected to be in harsh environmental conditions, (iii) population dynamics will be more sensitive to perturbation of survival-growth rather than fertility in peripheral populations. Finally, we hypothesized that (iv) soils properties will drive population dynamics for narrowly distributed plant species for which small scale factors variation could influence ecology more than landscape level drivers. To test these hypotheses, we studied the demography of *Thunbergia atacorensis* (Acanthaceae), a range-limited herb in West Africa. We collected 3 years of demographic data to parametrize an integral projection model. Demographic vital rates and population growth rates did not decrease significantly with distance from geographic or climatic center contrary to CPH predictions. However, populations at the center of the geographic range were demographically more resilient to perturbation than those at periphery. Soil nitrogen

was the main driver of population dynamics. The relative influence of survival-growth on population growth rates exceeded that of fecundity 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 and suggest that explicitly considering the disconnect between geography and niche axes is important when testing the CPH.

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 anthropogenic disturbance, 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 most favorable ecological conditions (biotic and abiotic) will prevail at the center of the distribution, as opposed to the harsh conditions at the periphery. However, the geographic center of distribution does not necessarily coincide with species' optimal climatic conditions (Moutouama and Gaoue, 2022a). Species are not, therefore, expected to always 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 and Eckert 2007; but Waldock 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 and Gaines, 2002) are commonly reported which challenges this fundamental notion. 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 vital rates (e.g. reproduction, survival and growth) (Abeli et al., 2014; Gerst et al., 2011; Samis and Eckert, 2007) vary across species range. Using only population abundance or vital rate as a metric of population response limits our understanding of the mechanisms underlying species range limitation (Sagarin et al., 2006). Static measures such as population abundance provide only a snapshot of population condition 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 at different period or spatial scale might yield different results for a given species. Moreover, because there is a trade-off between demographic vital rates (e.g., growth, survival, fecundity), using only one vital rate as a metric to test range limitation can lead to suboptimal conclusions 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 *Lathyrys venus* (Fabaceae) but increase the number of fruits produced (Greiser et al., 2020). In *Prenanthus roanensis* populations, individual abundance did not change from center to periphery, while peripheral populations showed a lower population growth rate than central populations (Aikens and Roach, 2014). Thus, using a more reliable metric like population growth rate, estimated across several years to capture the demographic response to spatiotemporal environmental changes, can enhance our understanding of range limitation (Louthan et al., 2015).

Demographic tests of the center-periphery hypothesis are rare but increasing. Existing studies show that central populations have higher population growth rates than peripheral populations, which may explain range limitation for some species. For example, central populations of *Mimulus lewisii* have higher population growth rates than peripheral populations (Angert, 2006) . Similarly, Stokes et al. (2004) showed that *Ulex galli* has higher population growth rates at the center than at the periphery. However, in

these studies the identification of central and peripheral populations was dichotomous with isolated populations considered as peripheral populations. Moreover, geographically central populations are not necessarily ecologically or climatically central (Yakimowski and Eckert, 2007). Therefore, studying variations of population dynamics from center to periphery using continuous variable (distance from geographic and climatic center) can provide a more appropriate test of the center-periphery hypothesis (Pironon et al., 2017; Sagarin et al., 2006).

Using demographic analysis to test the center-periphery should go beyond comparing the vital rates and population dynamics. Understanding how central versus peripheral populations respond differently to perturbation of vital rates (elasticity analysis) can be used to tailor management strategies that account for the context dependency in conservation response. In addition, investigating how the selective pressure (sensitivity analysis) varies between center-periphery and the evolutionary demographic implications of this are seldom appreciated. Previous studies show that peripheral populations may experience strong selective pressure that can lead to strong adaptive potential (Casazza et al., 2021; Morente-López et al., 2021). 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 show 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. First, weak relative importance of survival vital rates at the periphery could be outweighed by a significant relative importance of fertility, resulting in high population growth rates at the periphery, particularly for short-lived species (Aikens and Roach, 2014). Second, peripheral populations may recover faster than central populations by compensating low reproduction with high survival, thereby driving high population dynamics (Salguero-Gómez et al., 2016). Furthermore, since sensitivity of population growth rate gives the eventual rate at which offspring within a certain phenotype will increase, it can be considered to measure the fitness for that

phenotype (Benton and Grant, 1999). From an evolutionary perspective, sensitivity analysis has been used to understand how variation in vital rate affects the likelihood of a given phenotype to increase across the range (Caswell, 2019; Caswell and Salguero-Gómez, 2013).

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 and Nakamura, 2009). For example, the microclimate variation in riparian forests can be more pronounced than its macroclimate variation (Baker, 1989), and local level soil properties influence riparian plants' population dynamics (Frye and 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' soils, tropical soils often have older soils (Aerts and Chapin, 1999)higher plant nitrogen-to-phosphorus ratios (Hou et al., 2018; Yuan et al., 2011), and lower soil phosphorus concentrations (Aerts and 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 the case study of *Thunbergia atacorensis* (Acanthaceae), an endemic and range-limited tropical herb in West Africa, to investigate the drivers of vital rates and population dynamics variation from the center to the periphery of species' distribution range. We combined field observations and mathematical modelling to provide four independent tests of the center-periphery hypothesis using demographic response, population dynamics, selection gradient 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 best in central populations. As a result, (2) central populations are expected to have higher growth rates, 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 worsen toward the periphery, (3) population dynamics 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 and the microscale factors variation across the species distribution range.

Materials and methods

Study system

Thunbergia 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). We used the national flora inventory (Akoègninou et al., 2006) and gallery forest vegetation assessment (Natta, 2003) to collect the presence-absence data of the species in 2015. The goal of that study was to understand the distribution of *Thunbergia atacorensis* in West-Africa (Fandohan et al., 2015). We used the information gather in that study to identify 12 known populations across the country. The annual rainfall in these mountains ranges from 1200 to 1350 mm, and the average temperature is 28 °C (Sinsin and Kampmann, 2010). The species is found in gallery forests (Akoègninou et al., 2006). Reproductive individuals flower from June to early September and set seed two weeks after flowering.

Demographic data

In August 2019, we located the 12 known populations of *Thunbergia atacorensis* previously identified (Fandohan et al., 2015) across the entire range of species in West Africa (Figure 4.1). During the second year of demographic data collection, one of the populations was heavily disturbed by road construction. We removed this population 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 25m^2 permanent plots and tagged each individual *T.*

atacorensis plant in the plots. In August of each year, we collected demographic data on the tagged individuals, including plant's basal diameter, number of flowers, number of fruits, and survival status (dead or alive). We identified the new seedlings at the censuses of August 2020 and 2021 and 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 better than age when predicting plant growth, seed production, and survival (Silvertown, 1993). For a few populations that were too small to establish five 25m^2 plots, we used a minimum of 3 plots (Table 4.1).

Estimating distance from geographic range center and distance from climatic niche centroid

In this study, we seek 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 considered as reference. The geographic gradient that is captured here is not only the general latitudinal gradient but one that is more 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 Mahanalobis distance (Osorio-Olvera et al., 2020), we first record 1101 presence points of the species within the 12 populations identified. Then we split these occurrence points into training (80%) and testing (20%) for to build a minimum volume ellipsoid model. The minimum ellipsoid represents the Hutchinson's hypervolume model describing the fundamental niche of a species. 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 and Hijmans, 2017), at a spatial

resolution of 30s. We preferred these variables because previous studies showed that these variables were important for the distribution of the species (Fandohan et al., 2015). Second, 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). More specifically, we used 10000 points as background to calculate the approximate Area Under Curve (AUC) ratio which inform about the ability of model to predict the presence of the species (Luis Osorio-Olvera et al., 2020). The higher the AUC, the better the performance of the model at predicting the presence of the species. When the AUC is equal to one the model perfectly the predict the presence of the species. 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 distances capture exactly how temperature and rainfall change over space thereby capturing climatic gradient but only for climate parameters that are important for the study species.

We projected niche for environmental space (Figure 4.2a) into geographic space and then compared the correlation between distance from niche centroid to geographic centroid (Figure 4.2b). The ellipsoid model describing the climatic niche of the species had an omission rate (OR) ≤0.02, a significant value of partial Receiver Operating Characteristics ROC ($p < 0.01$) and the high value of Area Under Curve (0.95), suggesting a good ability of the model to predict the niche of the species (Table 4.2). There was no correlation between distance from climatic niche centroid and distance from geographic center (R= - 0.05, p=0.88, Figure 4.3), suggesting a mismatch between the climatic niche and the geographic range.

Soil properties

In *Thunbergia atacorensis* populations, we collected 20g of composite soil samples in each plot by mixing soil collected from the center and the four corners of each plot. Each soil sample was collected at seven inches of depth. We collected a total of 52 soil samples, which were analyzed for macronutrients (nitrogen, potassium, phosphorus, Sulphur, 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 using a Extech MO750 soil moisture meter (Extech, Boston, MA, USA).

Fitting size-dependent demographic models

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

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

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

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

$$f_n(x) = exp(a + bx) \quad \text{eqn 3}$$

The size-dependent growth, $g(y, x)$, (eqn 4) was modelled using a normal error distribution with a mean μ and a standard deviation σ (eqn 5, 6). Because the variance was heterogeneous ($p < 0.05$, Fligner test), we used generalized least squares (*gls*) function in the *nlme* package to model the variance σ^2 as function of fitted values $\hat{y}$ (eqn 6) (Pinheiro et al., 2021). We used the Akaike Information Criterion (AIC) (Crawley, 2012) to compare two models of variance: variance as an exponential function of size and variance as a power function of size (Table 4.3). We found greater support for and used the exponential variance function which had the smallest AIC (eqn 6).

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

$$\mu = a + bx \quad \text{eqn 5}$$

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

In eqn1, 2, 3, and 5, *a* represents the intercept of the model and *b* represents the slope of respectively the relationship between the size (x) at time *t* and the probability of survival $s(x)$, probability of flowering $f_f(x)$, the fruit number $f_n(x)$, and the probability of growth, μ.

Our first test of the center periphery hypothesis was to investigate how median demographic vital rates varied across the geographic distribution range (with distance from geographic center) and the climatic niche (distance from niche centroid). We first calculated the median plant size for each population and used it 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 (Figure 4.4). To obtain the median vital rates (survival, growth, fertility) for each population, we evaluated eqns 1— 3 using the appropriate population-specific median size x, and the slopes and the 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 was to investigate 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 parametrize an integral projection model (eqn 7) (Easterling et al., 2000) of the form:

$$n(y, t+1) = \int_L^U K(y,x)n(x,t)dx \qquad \text{eqn 7}$$

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 respectively the minimum and the maximum size. 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 $K(y,y) = p(y,x) + f(y,x)$. 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 $f_d(y)$ (eqn 8):

$$f(y,x) = s(x)f_f(x)f_n(x)p_g p_e f_d(y) \qquad \text{eqn 8}$$

The probability of germination and establishment $p_g p_e$ was calculated as the ratio of the number of new seedlings in year $t+1$ over the number of fruits in year t. The kernel *K* was integrated numerically over all possible plant sizes Ω, using the mid-point rule (Ellner and Rees, 2006). The result is a high-dimensional matrix, which has 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 and Milligan, 2007). Thus, populations with λ >1 are projected to grow while those with λ < 1 are projected to decline. We built IPM for each of the 11 *T. atacorensis* populations and determined their λ. We used general linear models to test the effect of the distance from geographic center, distance from climatic niche centroid and soil properties on population dynamics.

Perturbation analysis and demographic recovery

Our third test of the center-periphery hypothesis was to investigate how the sensitivity (eqn 9) of the long-term population growth rate λ varied across the geographic distribution range and the climatic niche gradient. This allowed us to analyze how the relative importance of various demographic vital rates to the persistence of the populations changed from center to periphery. If a variation in a vital rate drives a change in population growth rate (fitness), there will be a selection on that vital rate that is proportional to the change in fitness (Caswell and Salguero-Gómez, 2013). Thus, sensitivity analysis was used to measure of the selection gradient. A sensitivity to a specific trait greater than 0 suggests that selection favors an increase in that trait (Caswell, 2019).

For a direct management implication of prospective analysis, we investigated the relative influence of perturbing each demographic functions (survival-growth or fertility) on the long-term population growth rate from center to periphery, using elasticity analysis (eqn 10, and 11) and regression analysis. We evaluated the elasticities of the long-term population growth rate to perturbation of survival-growth (eqn 10) and fertility (eqn 11) for each *T. atacorensis* populations:

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

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

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

where $w(x)$ is the stable size distribution and $v(y)$ 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 and of 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 varies across the geographic distribution range and the climatic niche gradient. We calculated the damping ratio, ρ (eqn 12), a dimensionless metric of how fast transient dynamics decays following a disturbance, regardless of the population structure.

$$\rho = \frac{\|\lambda_2\|}{\lambda}, \quad \text{eqn 12}$$

where λ is the dominant eigenvalue, λ_2 is the largest subdominant eigenvalue of the high-dimensional matrix. The damping ratio, ρ varies between 0 and 1. When the damping ratio is closer to 1, the faster the population converges, and the lower the time of recovery after perturbation (Haridas and Tuljapurkar, 2007). We used a general linear model to test how this metric of demographic resilience vary from distance from geographic range center or climatic niche centroid.

Results

Demographic vital rates variation from center to periphery

The median probability of flowering and median growth rate significantly increased with distance from geographic centroid ($\beta = 0.060 \pm 0.012$, $p = 0.001$, Figure 4.5; $\beta = 0.246 \pm 0.084$, $p = 0.018$, Figure 4.5) suggesting faster growth and more frequent flowering in peripheral than central populations. However, such an advantage in flowering probability did not translate into better fecundity in peripheral population (Figure 4.5). 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 4.5) and probability of survival ($\beta = 0.129 \pm 0.121$, $p = 0.317$, Figure 4.5). Surprisingly climate distance had no significant effect on demography, 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 4.5), median fruit production ($\beta = -0.582 \pm 0.976$, $p = 0.566$, Figure 4.5), median growth rate ($\beta = 0.036 \pm 0.067$, $p = 0.607$, Figure 4.5) and the probability of survival ($\beta = -0.020 \pm 0.074$, $p = 0.794$, Figure 4.5).

Population growth rates and soil properties

Nearly 73 percent of *T. atacorensis* populations were declining across its distribution range with a mean log population growth rate declining rate of -0.37 ± 0.45. Consistent with the demographic trends, we found no significant variation of population growth rates with climatic ($\beta = -0.031 \pm 0.133$, $p = 0.822$, Figure 4.6) and geographic distances ($\beta = 0.327 \pm 0.211$, $p = 0.156$, Figure 4.6). However, population growth rate significantly decreased with soil nitrogen ($\beta = -0.423 \pm 0.120$, $p = 0.006$, Figure 4.6). In contrast, population growth rate did not vary with soil phosphorus ($\beta = -0.509 \pm 0.559$, $p = 0.386$, Figure 4.6), 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, sensitivity, and recovery time from center to periphery

Across the species' range, population dynamics were more elastic and more sensitive to perturbation of the survival or growth of large individuals than of their fecundity (Figure 4.7, Figure 4.8; Figure 4.9). The elasticity to perturbation of survival-growth was not significantly associated with climatic distance ($\beta = 0.020 \pm 0.055$, $p = 0.696$, Figure 4.7) or geographic distance ($\beta = -0.047 \pm 0.086$, $p = 0.592$, Figure 4.7). Similarly, elasticity to perturbation of fecundity was not significantly associated with climatic distance ($\beta = -0.020 \pm 0.050$, $p = 0.696$, Figure 4.7) or geographic distance ($\beta = 0.0478 \pm 0.087$, $p = 0.593$, Figure 4.7).

The damping ratio, a measure of population recovery from perturbation, declined with geographic distance ($\beta = -0.201 \pm 0.069$, $p = 0.017$, Figure 4.10), suggesting that geographically central populations are demographically more resilient than peripheral populations. However, damping ratio did not vary with climatic distance ($\beta = -0.051 \pm 0.053$, $p = 0.356$, Figure 4.10).

Discussion

The center periphery hypothesis predicts that vital rates and population growth rates will decrease from climatic niche or geographic range centroid as climatic conditions worsen toward range periphery. We found no support for this hypothesis. We found that the median probability of flowering and growth rates increased with distance from geographic range centroid. However, this increase in vital rates was not significant enough to drive population growth rate. Geographically peripheral populations were demographically less resilient to perturbation than central populations. Across the climatic niche, the vital rates did not vary. As a result, population growth rates did not vary from center to periphery. Soil nitrogen was the main driver of population dynamics, and populations were more sensitive to perturbation of survival-growth across the range. However, this sensitivity did not vary significantly from climatic niche or geographic range centroid.

Distance from climatic niche centroid and distance from geographic centroid were not correlated, consistent with other studies that found a mismatch between the climatic niche and geographic distribution (Martínez-Meyer et al., 2013; Pagel et al., 2020). Research on the center periphery hypothesis relies on the assumption of the "Etonian noise," which is when biotic interactions are irrelevant to predict species distributions at coarse grained resolution and large scales (Soberón and Nakamura, 2009). However, we did not include several biotic factors in our climatic niche model that could limit the presence of the species even in suitable areas. Further, our climatic niche model was built under the environmental equilibrium assumption, which states that individuals can disperse freely and be present in all abiotically suitable conditions, while being absent from all unsuitable ones. However, many studies show that species can be limited by dispersal ability. Thus, the absence of the species from areas suitable to its climatic niche could indicate a dispersal limitation (Pulliam, 2000; Schurr et al., 2012). However, we do not have sufficient information on the dispersal ability of *Thunbergia* to test that hypothesis.

We found no support for our hypothesis suggesting that central populations will have higher demographic 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 et al., 2008; Angert and Schemske, 2005; 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 are perhaps due to the fact that some peripheral populations of *Thunbergia* occupy the most suitable area (Figure 4.11). Further studies should investigate local adaptation using a reciprocal transplant across and beyond the range of *Thunbergia atacorensis* populations to understand the mechanism behind such center-periphery variation in vital rates. From our analysis of damping ratios, we found that geographically central populations of *Thunbergia* had high demographic resilience to perturbation which suggests 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 dynamics would decrease with increasing distance from geographic center or niche centroid. However, we found similar population dynamics across geographic range and climatic niche indicating that differential median demography between central and peripheral populations failed to significantly increase population growth rate in peripheral population above that of central populations. This result contrasts with previous studies supporting that population growth rate decreases at the periphery and that geographic range limits often coincide with niche limits (Hargreaves et al., 2014; Lee-Yaw et al., 2016). This result is not surprising given the importance of survival-growth to population fitness than fertility which is a typical characteristic of long-lived species. In *Thunbergia*, there is a life history trade-off noted in populations across the geographic range in which the fitness benefit demonstrated by the increased probability of flowering and growth rate is balanced against a constant probability of survival and probability of fruit production (Figure 4.12; Figure 4.13). Such a trade-off could explain why we found similar population fitness across the distribution range (Stearns, 1989). Biotic factors such as competition and herbivory may reduce growth rate in populations living in environments near the climatic niche centroid (Yañez et al., 2020). Smaller population sizes at the periphery can reduce population performance and adaptability and decrease reproduction and survival rates (Abeli et al., 2014). Here, similarly to population growth rates, a previous study on the same system found that population abundance remained similar from center to periphery (Moutouama and Gaoue, 2022a). This convergence in results using static measure of population size and population dynamics must not be interpreted as a proof that classical test of center-periphery hypothesis using species abundance is enough to draw strong conclusions. The demographic analysis conducted in this study provides further insights into the ecological and evolutionary response of species to distribution gradients.

We postulated that population dynamics would be most sensitive to perturbation of survival-growth rather than fertility in peripheral populations. However, we did not find any variation in sensitivity or elasticity values across the range indicating no spatial

change in selective pressure or the relative importance of demographic processes. Long-lived species tend to invest more in survival than in reproduction (Silvertown, 1993). Therefore, it is not surprising that *Thunbergia* population dynamics is more sensitive to survival-growth than fecundity across the range. These results have implications in terms of conservation and evolutionary ecology. The non-variability of elasticity across the range implies that central populations are valuable as peripheral populations from a conservation standpoint. Conservations' actions should target strategies that increase species survival and growth rather than a fecundity. Natural selection is a process that investigates the consequences for the fitness of varying the phenotypic traits that influence demographic parameters (Caswell, 2019). Directional selection occurs when one phenotype of individuals in the population has high fitness (i.e., survive better and produce more offspring) than the others (Kingsolver and Diamond, 2011). The sensitivities of population growth rates (here selection gradients) were all positive and did not decrease from center to periphery, suggesting that across the range, individuals with higher reproduction rate or higher survival rate do not have better fitness than individuals with small sizes. This result contrast with the postulate that peripheral populations are maladapted (Kirkpatrick and Barton, 1997). Further genetic analysis of *Thunbergia atacorensis* populations can evaluate the selection pressure and strength of genetic differentiation between peripheral and central populations.

Soil nitrogen was the main driver of population dynamics. This result is consistent with a previous studies demonstrating that an increase of nitrogen in soil can significantly increase the probability of a plant's extinction (Gotelli and Ellison, 2002). In *Thunbergia* populations, high soil nitrogen concentration was associated with high herbivory (Moutouama and Gaoue, 2022b) suggesting that the negative effect of soil nitrogen on population dynamics could be mediated by 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 and Diemont, 1983). However, the soil's effects on populations dynamics should be interpreted with caution. Soil characteristics were measured at a plot level rather than at an individual level. If variation at plot level is smaller than variation at individual level, then the real effects of soil in the system are

underestimated in our model. We also investigated the correlation between soil properties and population growth rate rather than showing causations. Therefore, experimental manipulations are needed to corroborate the causal relationship.

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Appendix D

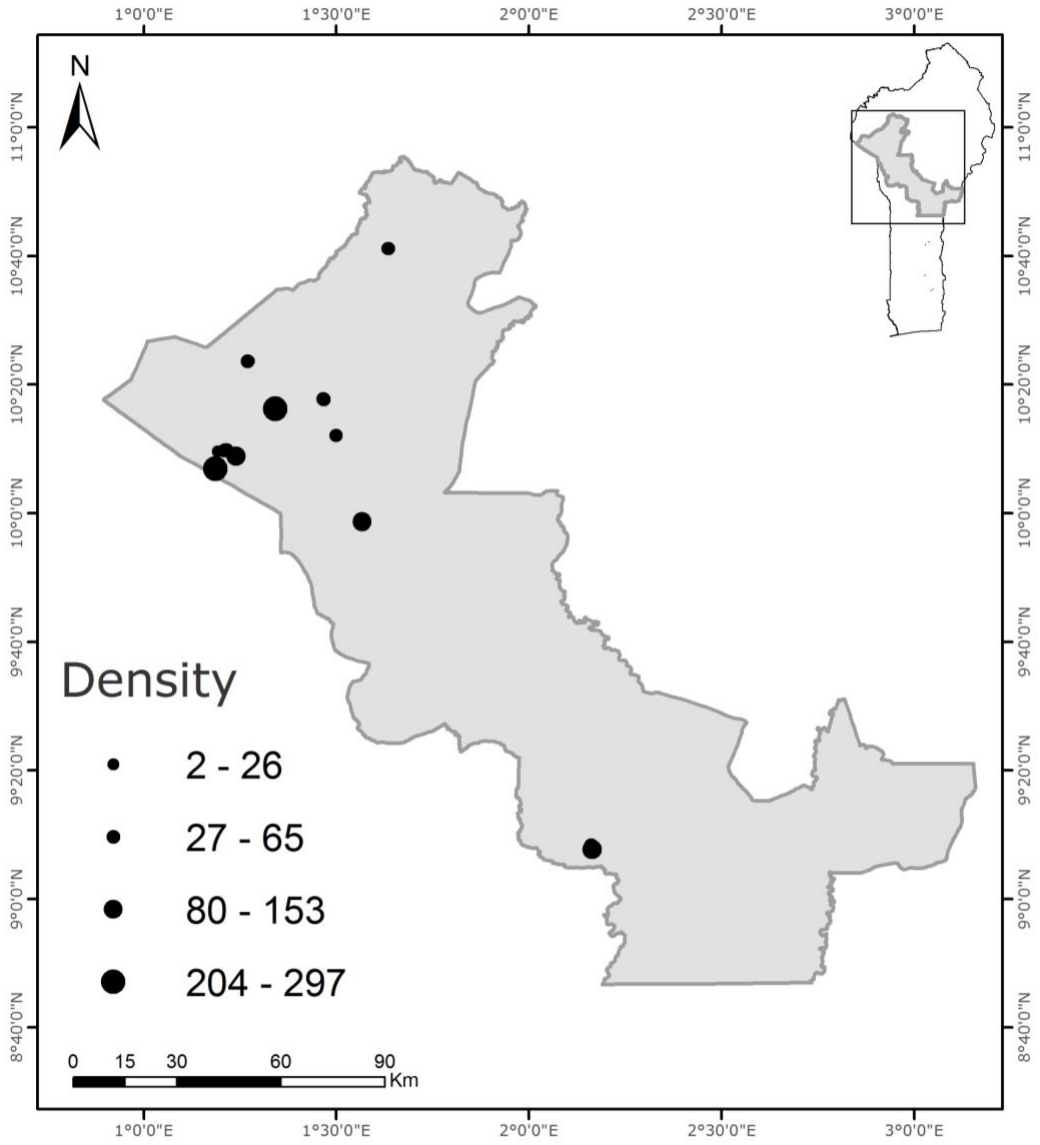

Figure 4.1: Distribution of 12 *Thunbergia atacorensis* populations in Benin. The grey square in the insert represents the study area in Benin (West Africa). The black dots represent sampled populations. The size of each dot is proportional to population density (plants/25 m^2).

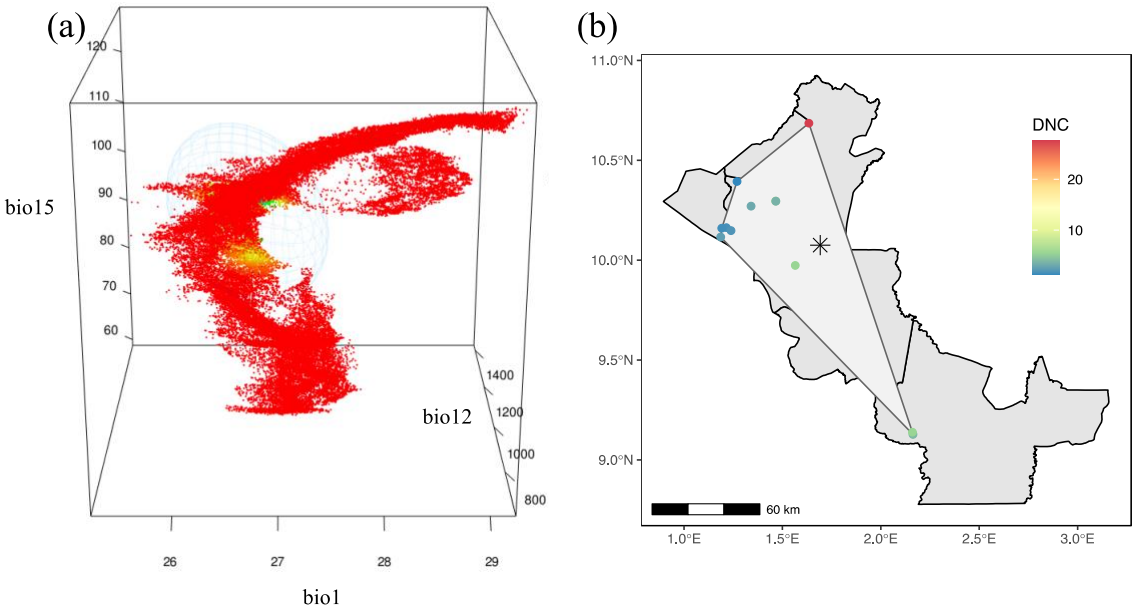

Figure 4.2: a) Minimum volume ellipsoid defined by three variables: bio 1 which is the mean annual temperature, bio 12 which is the annual precipitation, bio 15 which is precipitation seasonality. Blue ellipsoid: hypothetical fundamental niche built with presence records of the species, b) Geographic 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 distance from niche centroid. DNC represents the distance from niche centroid.

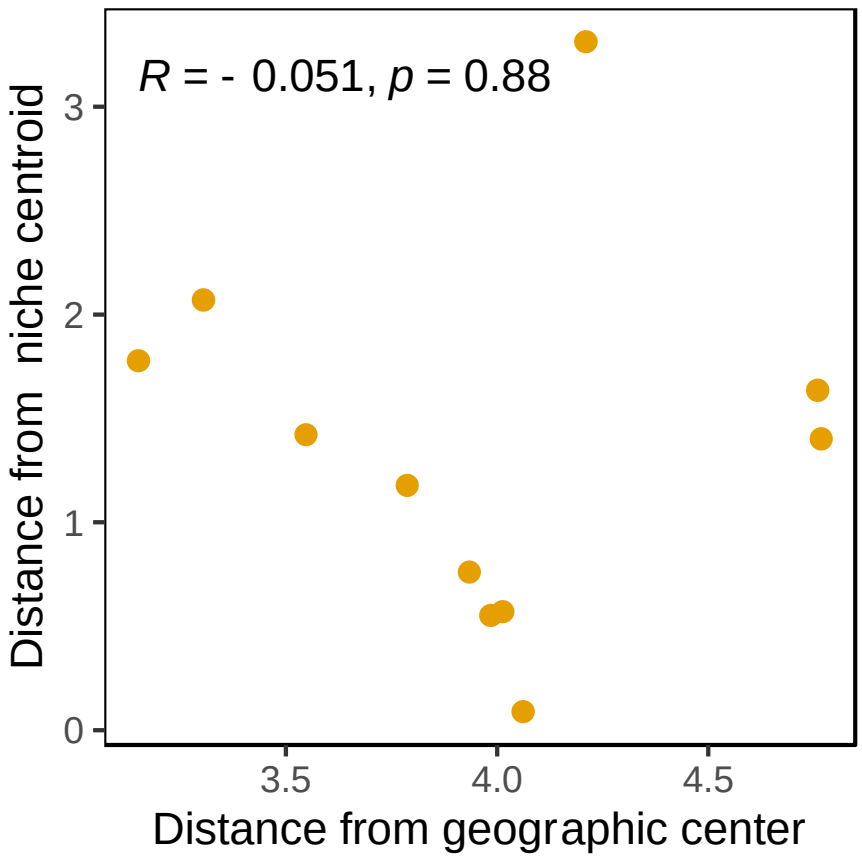

Figure 4.3: Correlation between distance from geographic center and niche centroid. R represents the Pearson correlation; p represents the significance of the correlation regression.

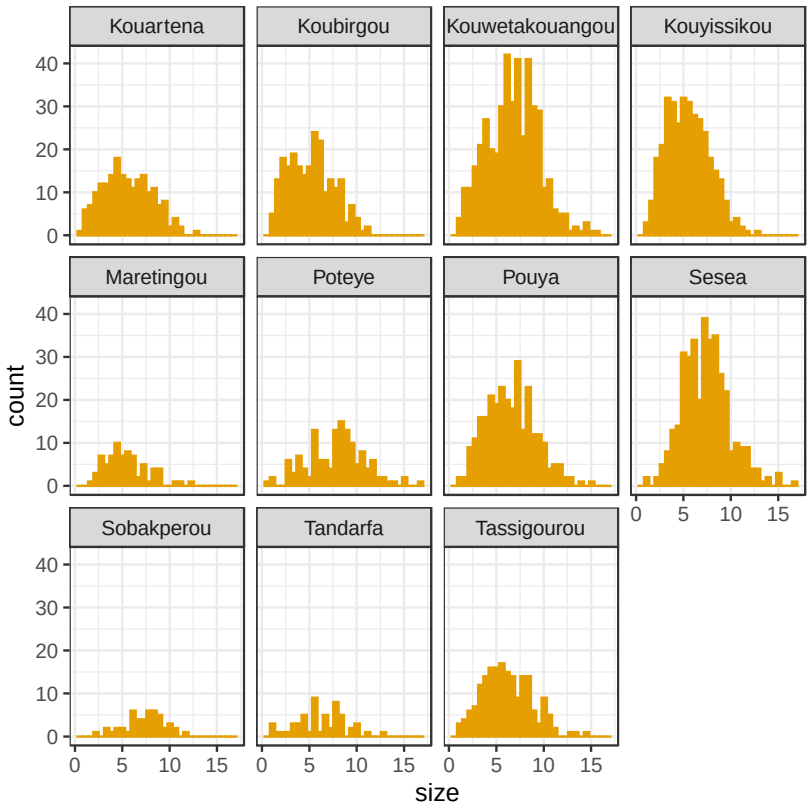

Figure 4.4: Size structure of each population. Most populations size structure is skewed.

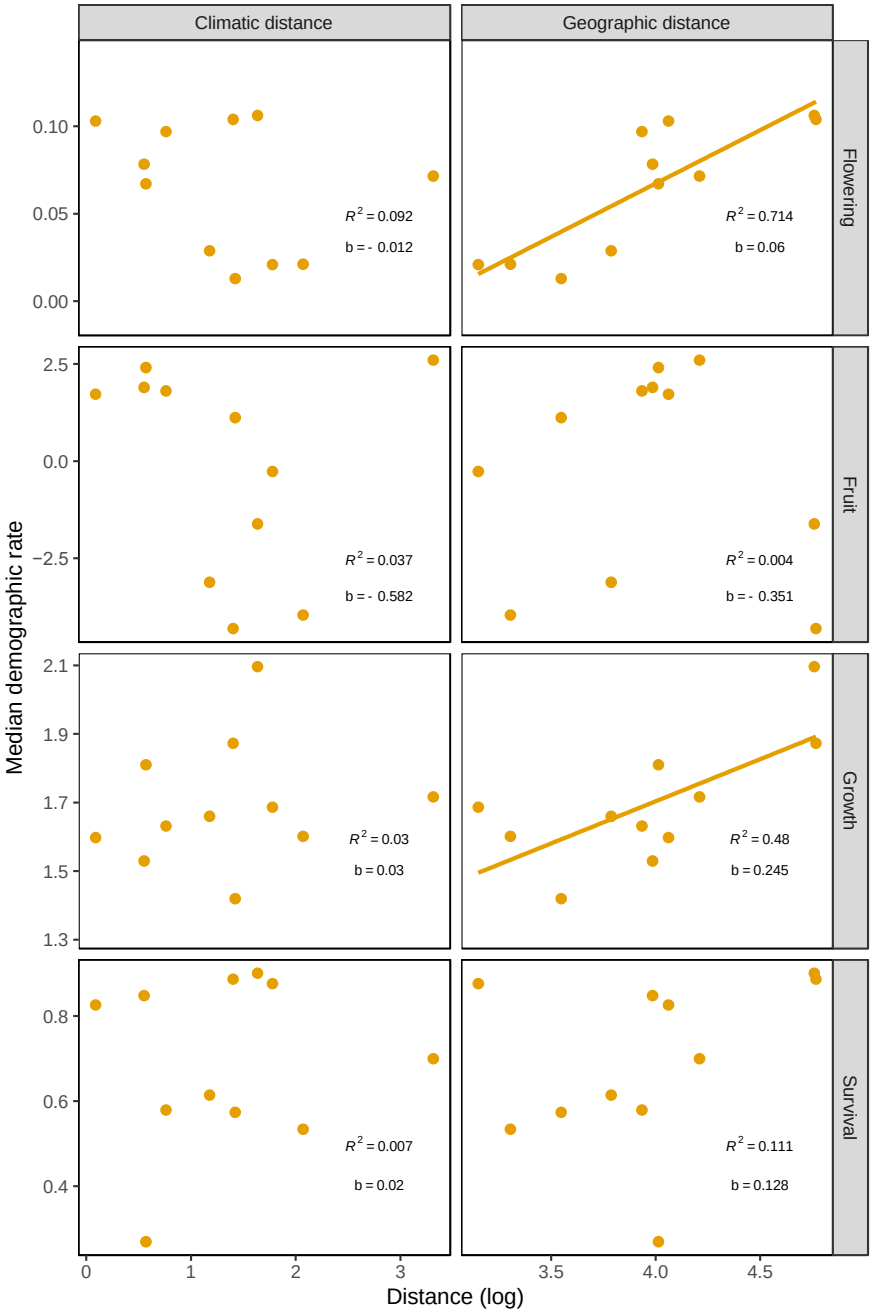

Figure 4.5: Vital rates (growth, survival, flowering, fruit production) as function of distance as geographic distance from species range center and climatic distance from niche center. Points correspond to each population vital rate as function of median size. The solid line is the fitted line from 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.

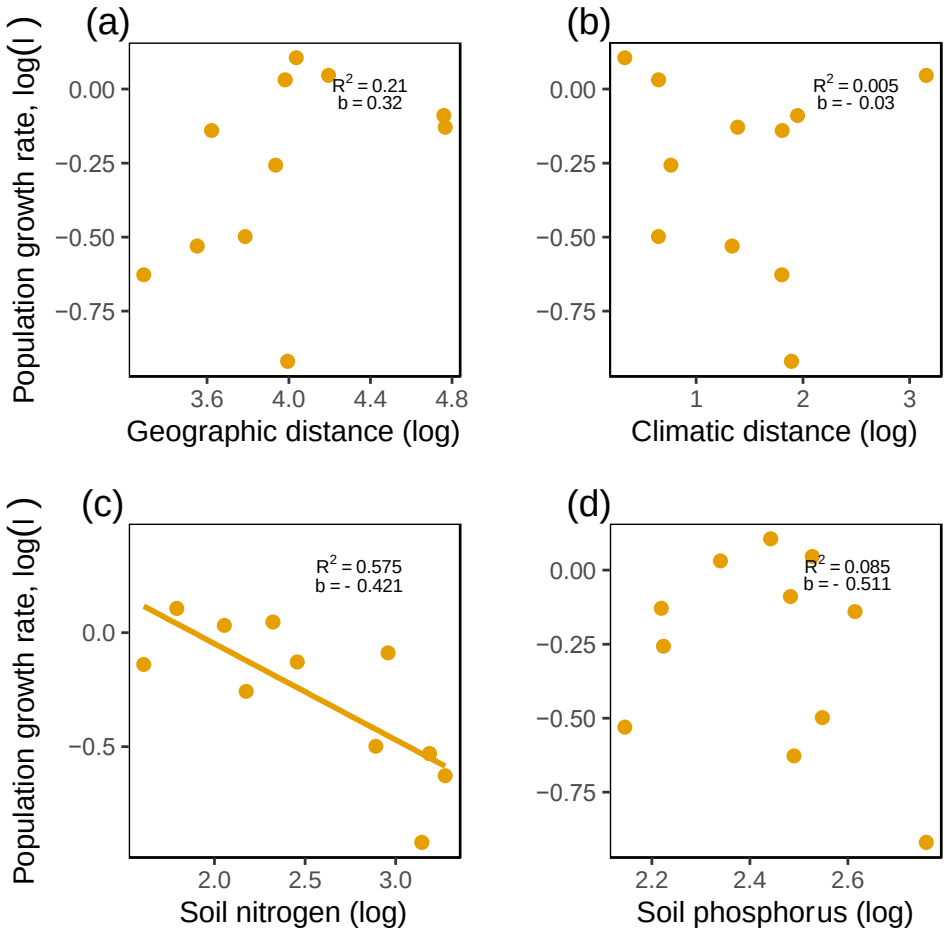

Figure 4.6: Population growth rate as function of distance as geographic distance from species range center (b) and climatic distance from niche center (b), nitrogen (c) and phosphorus in soil (d). The solid line is the fitted line from a non-linear model $P < 0.05$, and orange shadings shows 95% confidence interval around fitted line. β represents the slope of the of the relationship between population growth rate and distance from climatic/geographic center. R^2 represents the proportion of variance for population growth rate explained by the distance from climatic/geographic center.

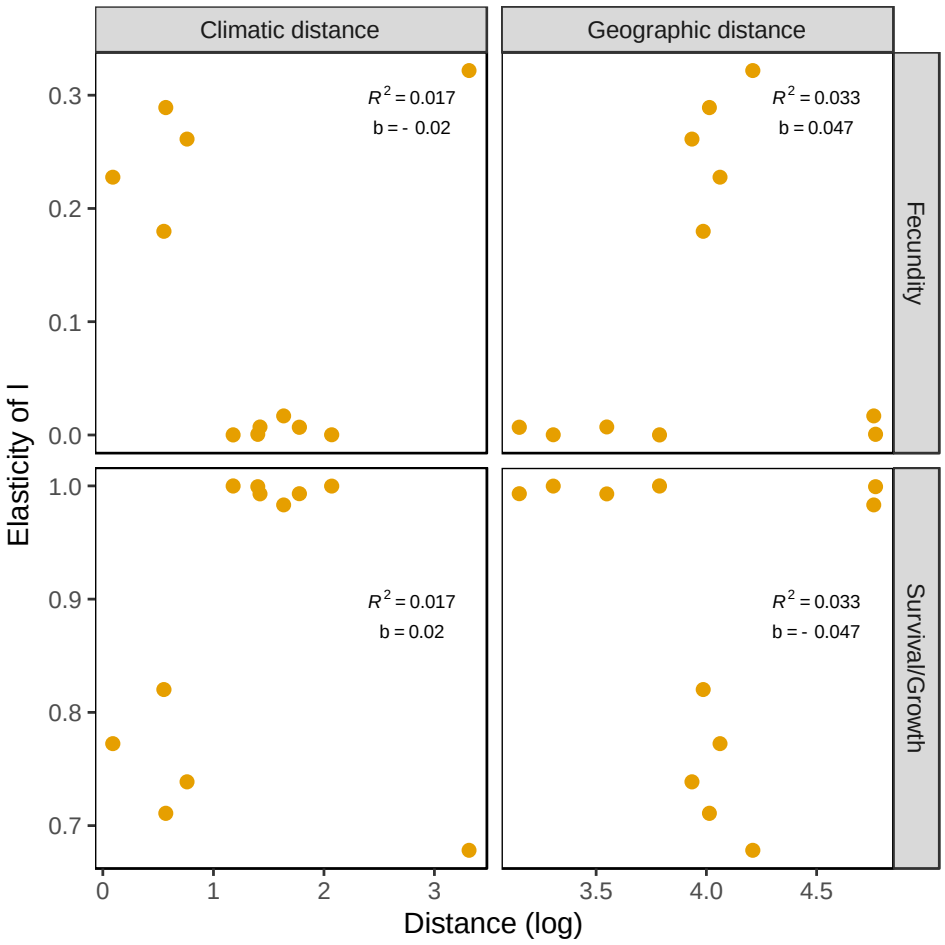

Figure 4.7: Relative influence of vital rates (survival-growth and fertility) of each population as function of distance as geographic distance from species range center and climatic distance from niche center. β represents the slope of the of the relationship between elasticity and distance from climatic/geographic 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 (upper panel). For a single population, the value in the upper panel and the value in the lower panel are sum to 1.

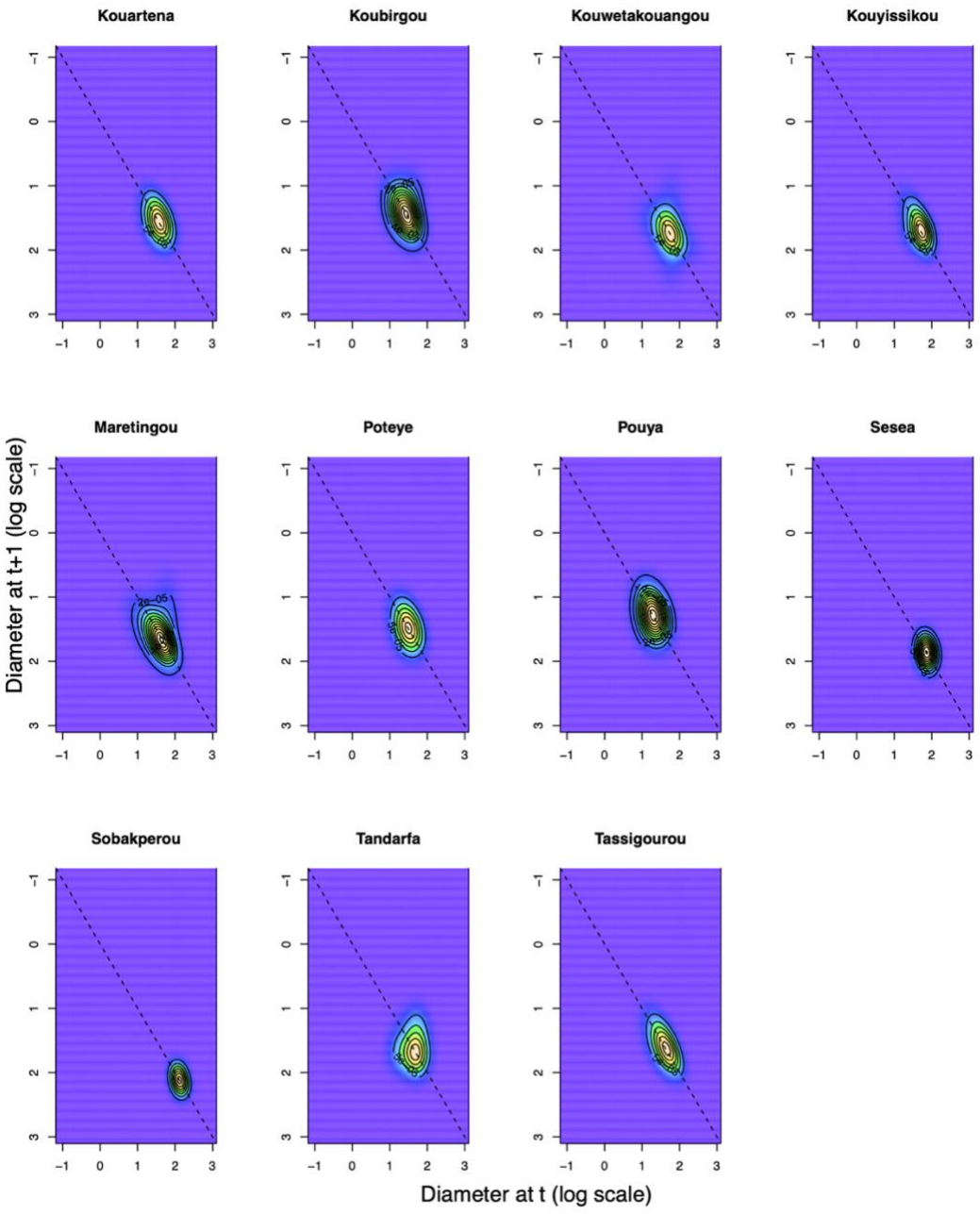

Figure 4.8: Relative influence of vital rates (survival-growth and fertility) of each population.

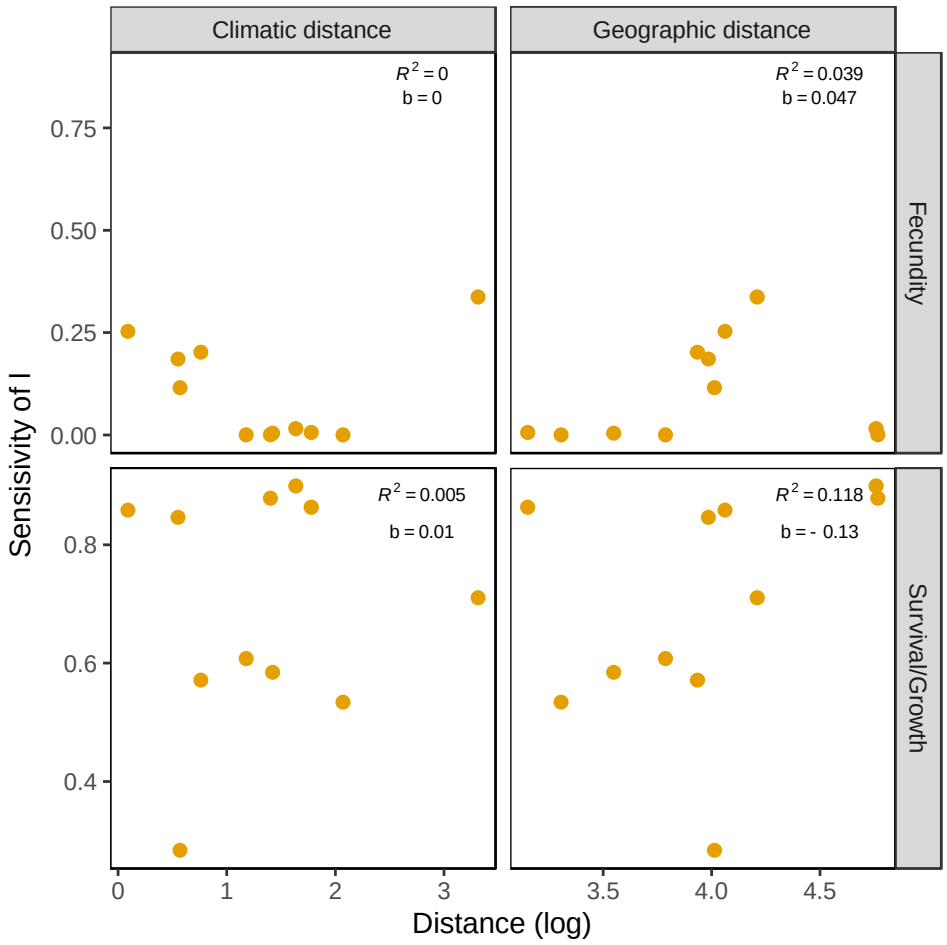

Figure 4.9 :Variation of sensitivity (selection gradient) from center to periphery.

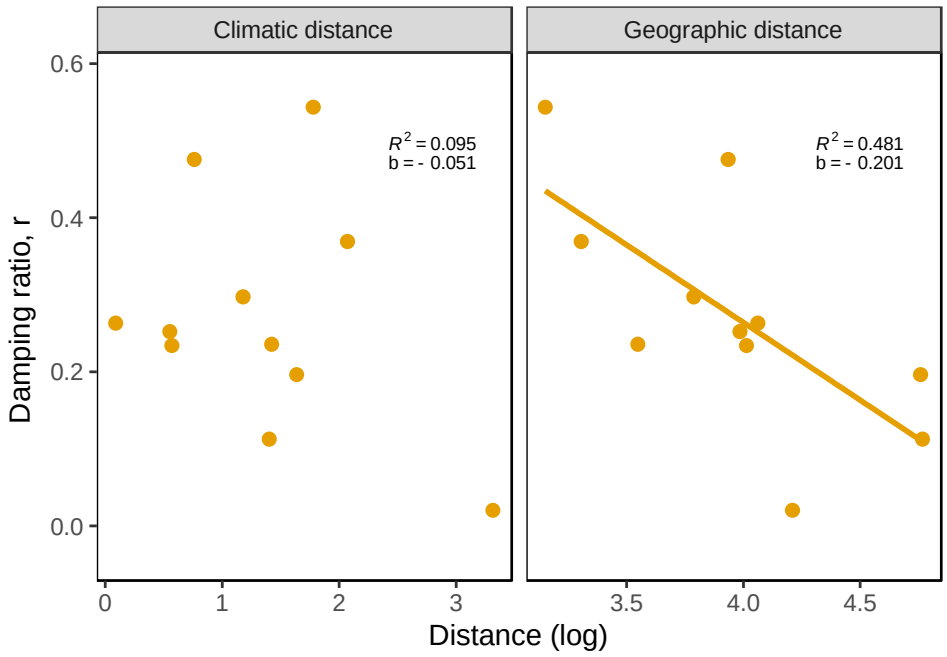

Figure 4.10: Damping ratio, ρ as function of distance as geographic distance from species range center and climatic distance from niche center. Points correspond to each population damping ratio. The solid line is the fitted line from a linear model with P < 0.05, and orange shadings shows 95% confidence interval around fitted line. β represents the slope of the 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.

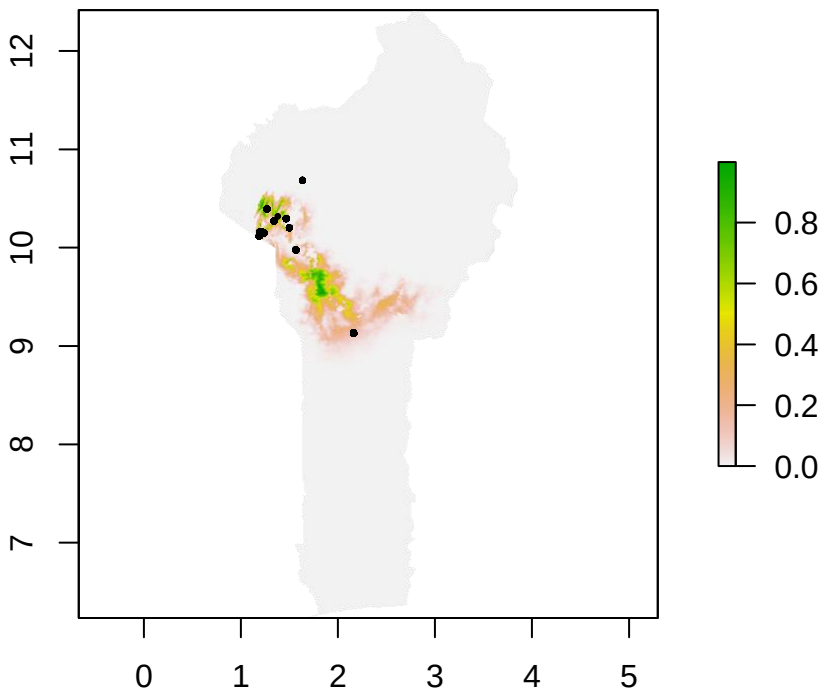

Figure 4.11: Map of suitable area of the species. The scale at the right represents the probability of occurrence of *Thunbergia atacorensis* in Benin from low (grey) to high (green).

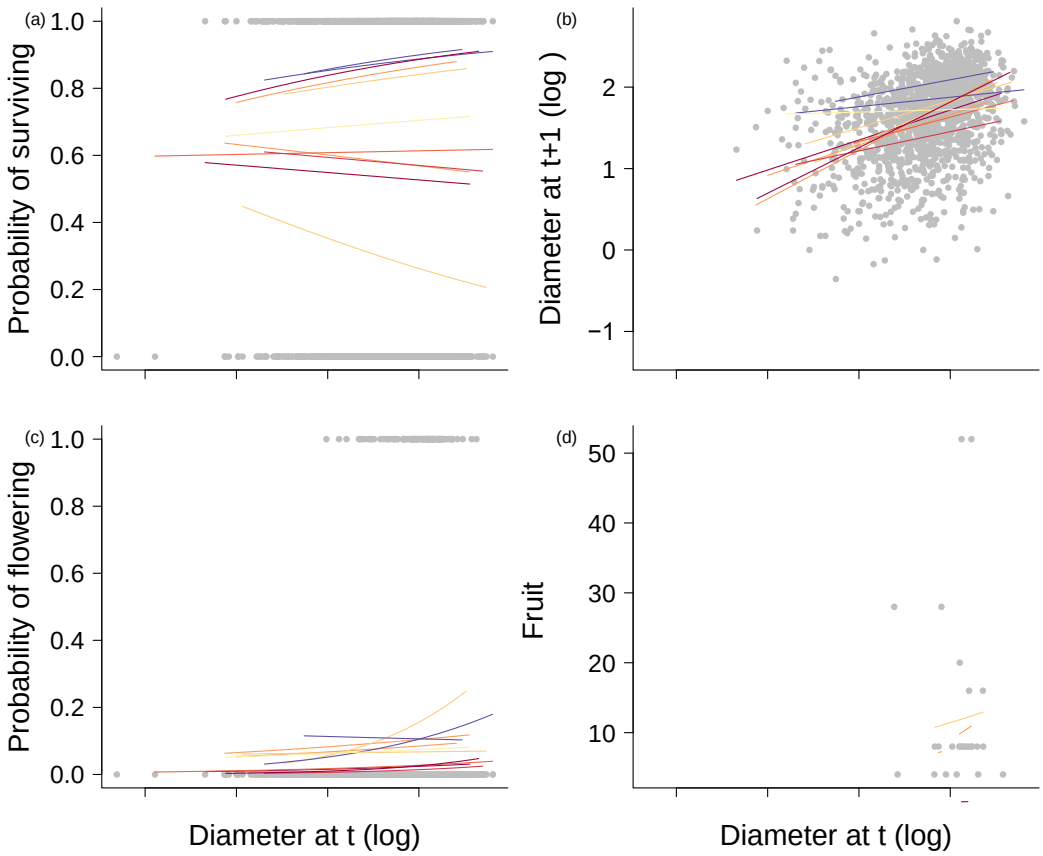

Figure 4.12: Vital rates as a function of size. Gray points represent observed values across all populations, and colored lines represent model predictions based on distance from geographic center. Each color represent a unique population.

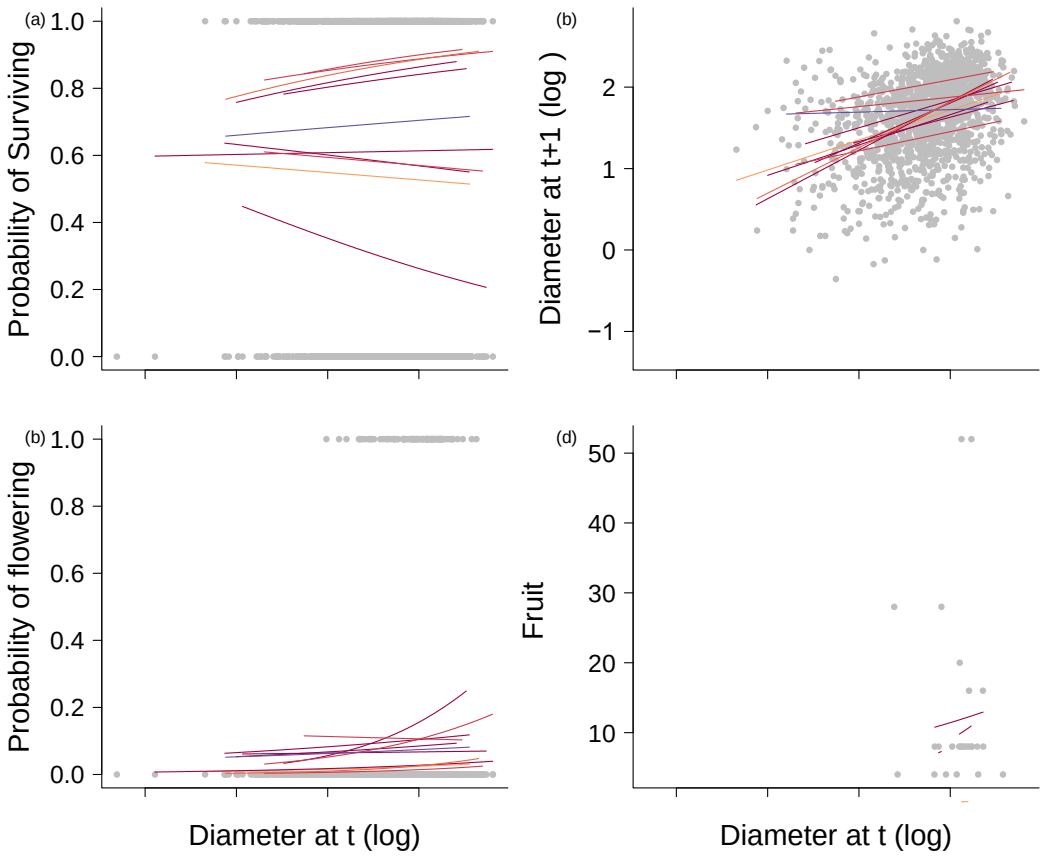

Figure 4.13: Vital rates as a function of size. Gray points represent observed values across all populations, and colored lines represent model predictions based on distance from the niche centroid.

Table 4.1: Occurrence records for populations sampled and the number of plots installed per population. For each year, we provided the sample size. For example, from 2020, we could not collect demographic data in Kougnangou because road construction disturbed that population.

Longitude	**Latitude**	**Population**	**Number of plots in 2019**	**Number of plots 2020**	**Number of plots 2021**
1.34105	10.270279	Poteye	5	5	5
1.466705	10.294874	Pouya	5	5	5
1.499549	10.201108	Kouaterna	5	5	5
1.634746	10.68536	Tandarfa	5	5	5
1.269294	10.393611	Marétingou	5	5	5
1.209394	10.162479	Koubirgou	5	5	5
1.239261	10.146821	kouyissikou	5	5	5
1.192084	10.159625	Kougnangou	2	**0**	**0**
1.186998	10.1157	Kouwetacoingou	5	5	5
1.566943	9.977977	Tassigourou	5	5	5
2.160704	9.138537	Sobakperou	4	4	4
2.163432	9.127444	Sesea	3	3	3

Table 4.2: List of the best minimum-volume ellipsoid models for *Thunbergia atacorensis* using the model calibration and selection protocol implemented in the ntbox r package.

model **variables** **(bios)**	**OR train**	**OR test**	**p-value pROC**	**AUC**
1,12,15	0.0284	0.0227	0.000	0.952

Table 4.3: Model comparison between generalized least squares (gls) models. “g1” is the model with variance as a linear function of size, “g2” is the model with variance as a power function of size and “g3”is the model with variance as an exponential function of size. The exponential variance function “g2” had the smallest AIC.

Model	**df**	**AIC**	**BIC**	**logLik**	**Test**	**L.Ratio**	**p-value**
g1	25	1916.302	2049.149	-933.1508			
g2	26	1884.785	2022.946	-916.3923	g1 vs. g2	33.51699	<.0001
g3	26	1886.148	2024.309	-917.0738			

CONCLUSION

Range limits of species are often imposed by physical barriers or alteration in abiotic or biotic conditions at the periphery of species (Gaston, 2003). The center-periphery hypothesis is one of the hypotheses used to understand range limitation. Because peripheral populations could be subject to extinction or adaption, the center-periphery hypothesis has direct consequences on evolutionary ecology (Hardie and Hutchings, 2010) and conservation biology (Yakimowski and Eckert, 2007). In this dissertation, I combined field data, modeling, and meta-analysis to test the center-periphery hypothesis. To provide a general test of the center-periphery hypothesis, I conducted a global meta-analysis using data from existing studies. I also tested the center-periphery hypothesis using a study system from one of the least studied areas in the world for this hypothesis. As study model, I used a perennial tropical herb, *Thunbergia atacorensis*, endemic to the northeastern region of Benin in West Africa. I used two different metrics of distance from the range center. The first metric was the distance from the geographic range center, which expresses the geographic gradient. In contrast, the second metric was the distance from the niche centroid, representing the climatic gradient and reflecting the variation of ecological conditions from the niche centroid to the niche periphery. These are standard methods to estimate the distance from the range center. The goal was to disentangle the effect of the geographic gradient from the climatic gradient. Specifically, (i) I explored how generalizable is the center-periphery hypothesis and what are the potential drivers of variation in studies testing the center-periphery hypothesis, (ii) I investigated the drivers of a tropical species abundance from center to periphery (iii) I studied how biotic drivers (e.g., herbivory rate) of species abundance varies from center to periphery, and (iv) I studied population dynamics from center to periphery. I summarize below the main results and contributions from my dissertation and outline some future directions.

Synthesis

First, I developed a meta-analysis to test for the global support for the center-periphery using the most exhaustive list of studies testing the center-periphery hypothesis. I found that in general, genetic diversity decreases from center to periphery.

However, population abundance and population growth rate do not change from center to periphery. This lack of support was explained mainly by high variability between studies due to pollination type, species kingdom, species longevity and the method utilized to estimate distance from range center. Our study contributed to the current debate on the center-periphery hypothesis and demonstrated that the center-periphery hypothesis is not common across all taxa. Depending on the taxa, the methods utilized to estimate the distance from the niche/geographic center, and the pollination mode (out-crossed vs. self-pollinated), one might find support or not for center-periphery hypothesis.

Second, I tested whether population abundance/density decreases from center to periphery as a consequence of poor abiotic environmental conditions and increased biotic stressors in peripheral populations. This hypothesis is often tested in temperate regions where climatic conditions contrast with tropical ones. I developed a structural equation model and used field data from a tropical perennial herb to demonstrate no decrease in species density from center to periphery contrary to predictions from the center-periphery hypothesis. This lack of support for the center-periphery hypothesis was mainly due to similar abiotic and biotic conditions and species functional traits between central and peripheral populations. Population density was particularly affected by altitude mediated by soil nutrients. Thus, alteration in climatic conditions at the edge does not explain range limitation in a tropical species.

Third, I examined one of the drivers of the center-periphery variation. I tested the pattern of variation in herbivory rate from range center to the periphery. I also tested the mediating role of inter-specific competition, soil nutrients and phylogenetic diversity on the variation of herbivory rate with distance from range center. Previous studies showed that a high herbivory rate at the periphery was a potential driver of species range limitation. I used Bayesian structural equation models to demonstrate that, contrary to predictions, herbivory rate was not higher at the periphery. I found no mediating role of phylogenetic diversity and interspecific competition on the relationship between distance from range center and herbivory rate. Instead, herbivory rate increased with nitrogen in soil, consistent with the resource availability hypothesis. This study shows that high biotic stressors at the periphery do not explain range limitation in a tropical species.

Finally, beyond the classical approach of testing the center-periphery hypothesis using plant density as the response variable, I developed an integral projection model to estimate population growth rates as a more synthetic response variable. I found that despite high resilience to environmental disturbance, vital rates (survival, reproduction, and growth rate) did not change toward range periphery. As a result, I found no variation in population growth rate from center to periphery. This result is consistent with our finding that population density did not change toward the edge. However, this similar trend between population growth rate and abundance does not imply that population abundance could be used as a surrogate to population growth rate. Using population density in lieu of population growth rate could be misleading, particularly for conservation decisions. In our study, the population growth rate decreased with an increase in soil nitrogen. That direct role of soil nitrogen in driving population growth rates is consistent with our result that high herbivory rate is associated with high soil nitrogen. Altogether, I showed that variation in population dynamics from center to periphery does not explain range limitation in a tropical species.

Future directions

Modeling nature has several limitations due to the assumptions made to simplify the complexity of the interactions between organisms and their environment. The structure of range limits is very complex and is often a result of synergistic mechanisms such as historical processes occurring during post-glacial expansion, long-distance dispersal events, biotic and abiotic drivers, and landscape heterogeneity. Here, the model I developed to describe the species' niche did not account for biotic factors, dispersal events, and historical processes occurring during post-glacial expansion. This is mainly because such methods do not exist yet. Incorporating these factors in the estimation of the species niche will profoundly improve the assessment of species niche and provide better insights into species range limitation (Dallas et al., 2020).

Most methods utilized to estimate the distance from niche centroid do not incorporate species dispersal. The dispersal mode (long distance vs. short distance) could affect the likelihood of finding support for the center-periphery hypothesis (Pagel et al., 2020). Dispersal is particularly important for species living in gallery forests. For these

species, it is possible that water-borne seed dispersal downstream provides a mechanism for unidirectional long-distance distribution among central and peripheral populations. A flux of migrants downriver would explain the high density and population growth rate at the periphery and thereby influence the support of the center-periphery hypothesis (Sheth and Angert, 2018). Both genetic tests (Bontrager and Angert, 2019) and reciprocal transplant experiments (Angert et al., 2008; Lee-Yaw et al., 2016) could aid in confirming or rejecting this hypothesis.

One could expand on the relationship between herbivory and range limitation. One way of doing that would be to estimate the cost of defense from center to periphery and understand how the cost of defense affects population growth rate across the range. A common garden experiment could allow the estimation of such a cost of defense for each range position. Then, by simulating a range of variation of cost of defense as a covariate in an integral projection model, one could understand how high cost of defense reduces or increases population growth rates.

Finally, this dissertation focused only on negative ecological interactions such as inter-specific competition and herbivory rate from center to periphery. However, positive ecological interactions such as mutualism could explain range limitation. While studies showed how negative ecological interaction could limit species range (Lynn et al., 2021; Miller et al., 2009), we know little about what can happen with positive ecological interactions. For example, interactions with the fungal community could explain range limitation (Bennett and Cahill, 2016). Estimating hyphae length in each population and root colonization rate for each individual will allow us to study if the low colonization rate (less mutualism) at the periphery explains range limitation. Incorporating positive interaction in our models will add novel perspectives to our understanding of range limitations.

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VITA

Jacob Moutouama was born and raised in Benin, West Africa, where he received his B.S and M.S in Forestry. After two gap years spent taking Tropical Biology Association courses, African mathematical school courses, and an internship at the National Forestry office in Benin, he joined the Department of Ecology and Evolutionary Biology at The University of Tennessee at Knoxville for his doctoral studies. He graduated with a Doctor of Philosophy in Fall 2022.