

Soil nitrogen mediates the effect of climatic distance on herbivory rates in a tropical herb

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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.

KEYWORDS

abiotic drivers, center-periphery hypothesis, ecological interaction, growth defense trade-off

1 | 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 & 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 (M. A. Parker & 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

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conservation biology for two reasons. First, it is important to know whether 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 yield mixed results. For example, herbivory intensity did not vary from center to periphery for *Daphne laureola* (Castilla et al., 2013a) and *Ficus sp* (Sam et al., 2020). 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 & 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 & 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 & Coley, 2011). Therefore, herbivory rate is expected to be higher at the climatic center than at the periphery (Castilla et al., 2013b; 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 & Tilman, 1993) or less severe under abiotic stresses (Callaway & 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). Because the species is range-limited and suffers from high rates of insect herbivory, *T. atacorensis* is 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 soil nutrients and light consistent with the resource availability hypothesis (Coley et al., 1985; Endara & 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 1).

2 | METHODS

2.1 | Study system

Thunbergia atacorensis (Akoègninou Lisowski & Sinsin) is a perennial herb that belongs to the *Acanthaceae* family (Figure 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 Sobakperou mountain chain is in the center of Benin (2°9' N - 9°8' E). Data on the natural history of species are lacking. However, our field observations revealed two insect herbivores feeding on *T. atacorensis*: a generalist, *Philopona aburiensis* Bryant (Col.: Chrysomelidae) (Figure 2f) and the specialist (Figure 2e), the larvae of *Filodes costivitalis* Guenée (Lep.:

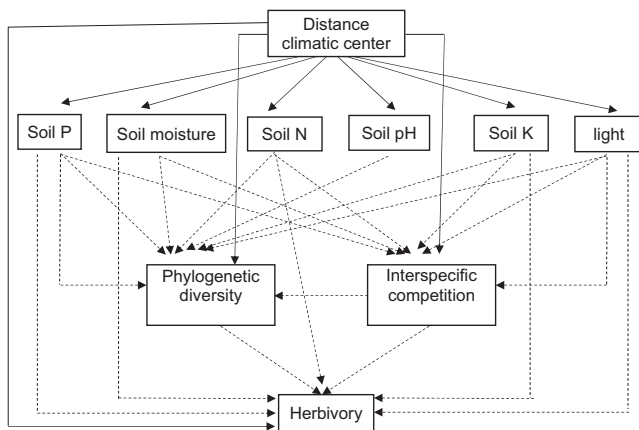


FIGURE 1 Conceptual framework. Main predictions of the distance from the center (geographic and climatic) direct and indirect positive and negative effects on herbivory in *Thunbergia atacorensis* populations. Dash arrows denote positive effects; solid arrows denote negative effects. Soil N is the extractable soil nitrogen; Soil P is the extractable soil phosphorus; Soil K is the extractable soil potassium; pH is soil pH

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).

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 (Appendix S1; Table S1).

2.2 | 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 costivitalis* feeds on leaves margins while *Philopona aburiensis* feeds on the lamina (Figure 2b and c). 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 whether 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 CI-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 & 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 is the total number of species per plot and A is plot area.

2.3 | 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*, and *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 & Qian, 2019) on 238 angiosperms species belonging to 52 families to generate a species-level phylogenetic tree (see Appendix S1, Figure S1). 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).

2.4 | 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

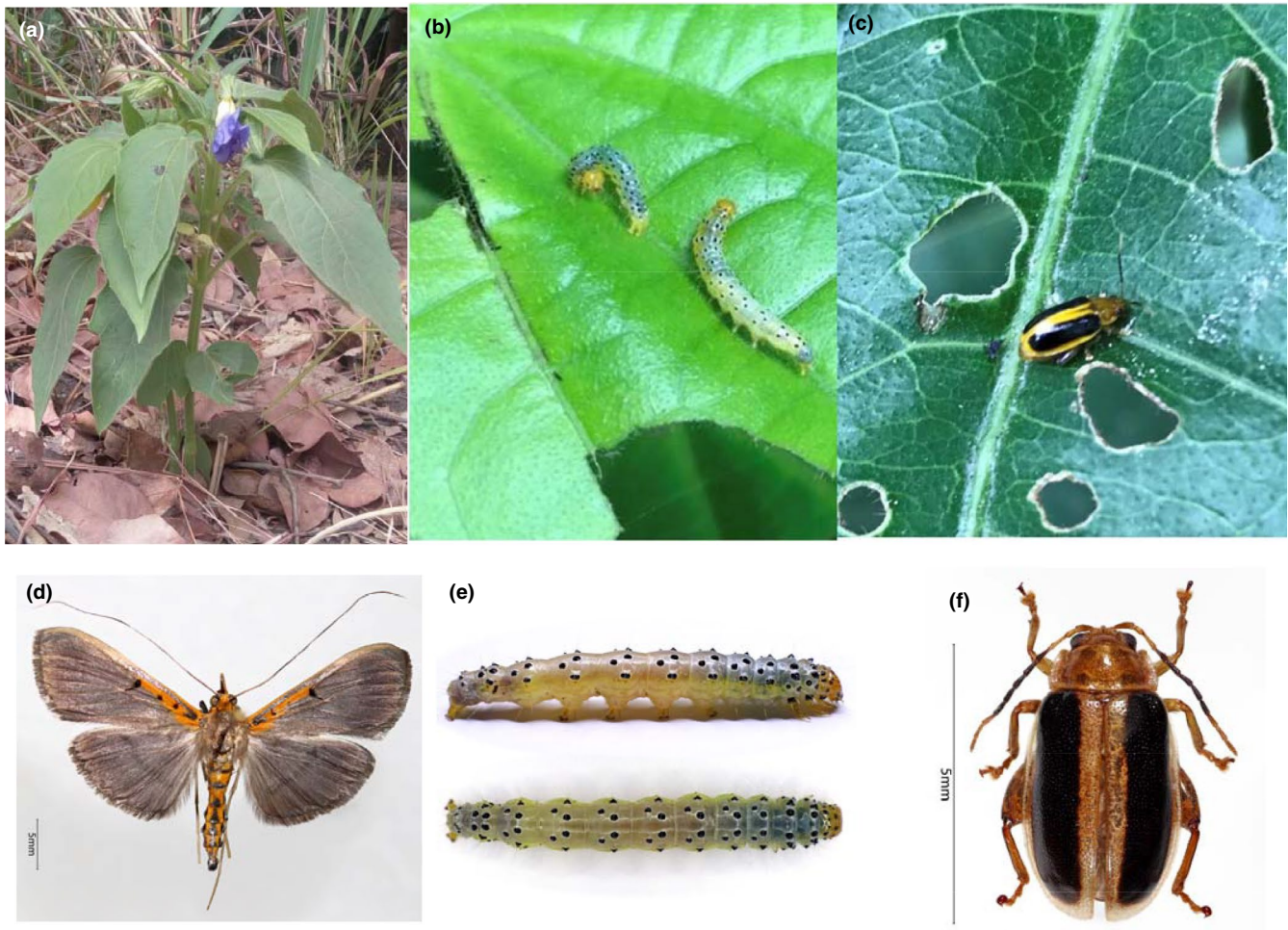


FIGURE 2 (a) *Thunbergia atacorensis* adult plant showing a characteristic purple flower in one of our study sites in Benin (West Africa). The species is found in gallery forest along the Atacora mountain and Soubakperou mountains where it suffers distinct leaf herbivory by (b) specialist *Filodes costivitalis* (leaf margin herbivory) and generalist (c) *Philopona aburiensis* (herbivory as leaf spots). (d) Adult individuals of *Filodes costivitalis* 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

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).

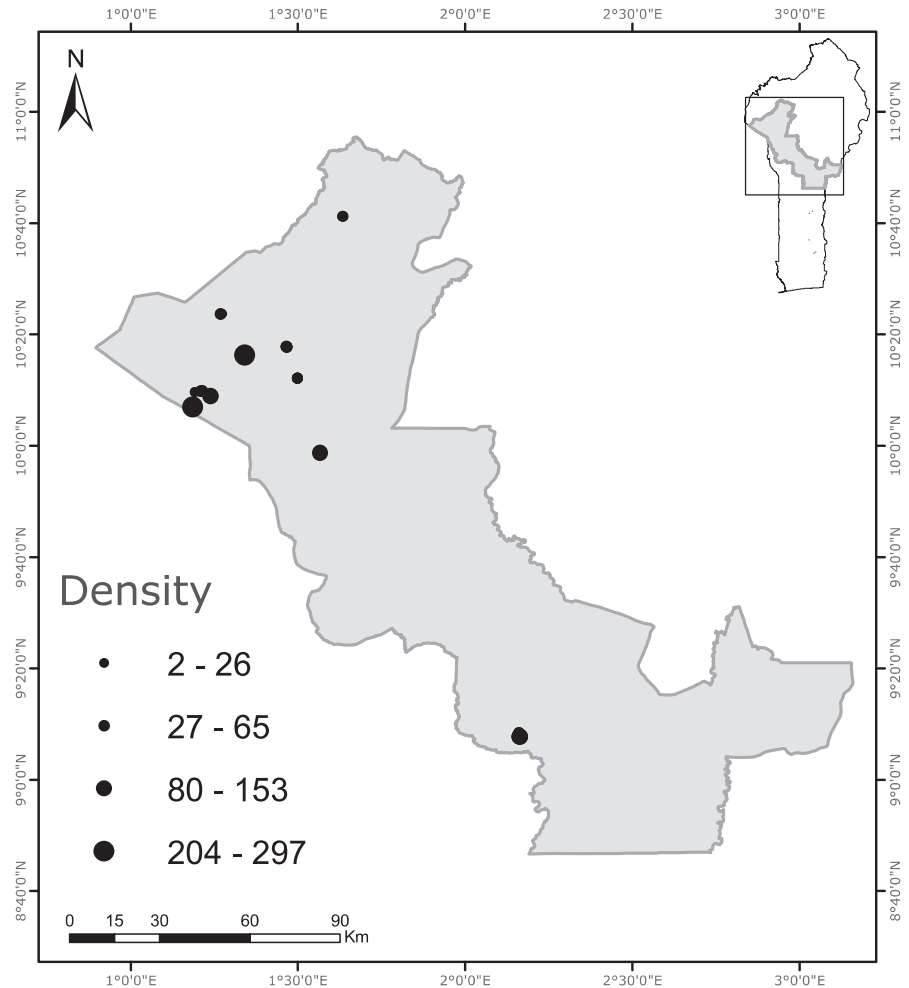
To calculate the Mahalanobis distance, we split *T. atacorensis* occurrence points into training (80% of points) and testing (20%) for the ellipsoid model. We retrieved for these occurrence points four bioclimatic variables (annual mean temperature, annual precipitation, solar radiation, and precipitation 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 & 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, Lira-Noriega, et al., 2020). Finally, we used the function *mahalanobis* in the package *stats* to calculate the mahalanobis distance.

2.5 | 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

FIGURE 3 Distribution of 12 *Thunbergia atacorensis* populations in Benin. The gray square in the insert represents the study area in Benin (West Africa). The black dots represent sampled populations. The size of each dot is proportional to population density (plants/25 m²)



study, we particularly tested the effect of phylogenetic species diversity variation and distance from geographic or climatic center on herbivory rate of *Thunbergia 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 (Appendix S1, Figure S2) 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 this analysis are available online (Moutouama & Gaoue, 2022).

3 | RESULTS

3.1 | Variation in herbivory rate, abiotic, phylogenetic diversity, and competition with distance from climatic center

Extractable soil nitrogen decreased significantly from climatic center to periphery ($\beta = -0.37$; 95%CI: -0.73 to -0.01) and herbivory rate increased significantly with increasing soil nitrogen concentration ($\beta = 0.2$; 95%CI: 0.01 to 0.39 ; Figures 4, 5a), 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 4, Table S3). In contrast, extractable soil phosphorus decreased from climatic center to periphery (Figure 4, Appendix S1, Table S3). We found no significant direct effects of climatic distance on herbivory rate (Figure 4, Appendix S1, Table S3) or interspecific competition

and no significant effect of phylogenetic diversity on herbivory rate (Figure 4, Appendix S1, Table S3). 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; Figures 4, 5b).

3.2 | 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 costivitalis* relative to the generalist *Philopona aburiensis* ($\beta = 0.43 \pm 0.06$, $Z = 7.01$, $p < .0001$; Figure 6). We found no significant change in extractable soil nitrogen, phosphorus, pH, soil moisture, and light with distance from geographic center (Appendix S1, Table S2). Extractable soil

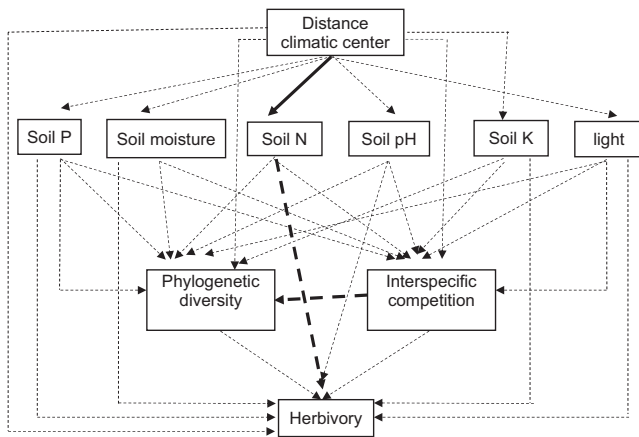


FIGURE 4 Structural equation model showing the direct and the indirect drivers of herbivory in *Thunbergia atacorensis* populations. Dash arrows represent non-significant effect. Solid arrows denote negative effects; solid arrows denote negative effects. The bold arrow represents significant relationship. 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

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 (Appendix S1, Table S2).

4 | 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, and flavonoids (Chan & Lim, 2006; Sultana & 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 & Kursar, 1996). In these peripheral populations, soil nitrogen availability is perhaps

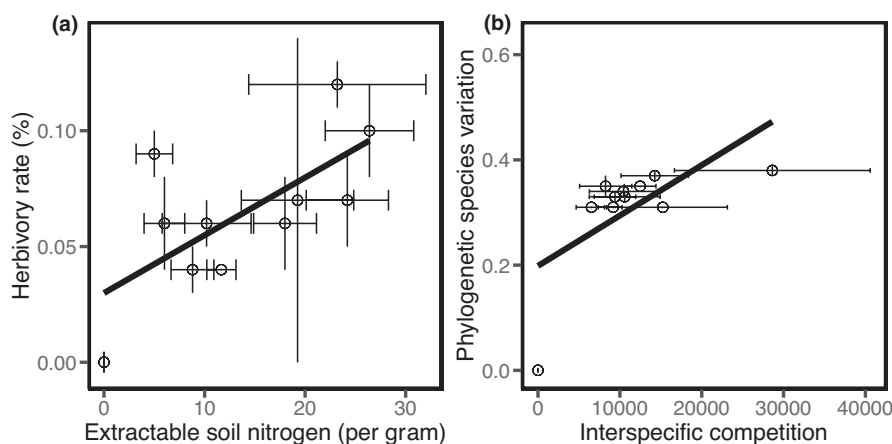


FIGURE 5 (a) Effects of extractable soil nitrogen on herbivory rates, (b) interspecific competition on phylogenetic species variation

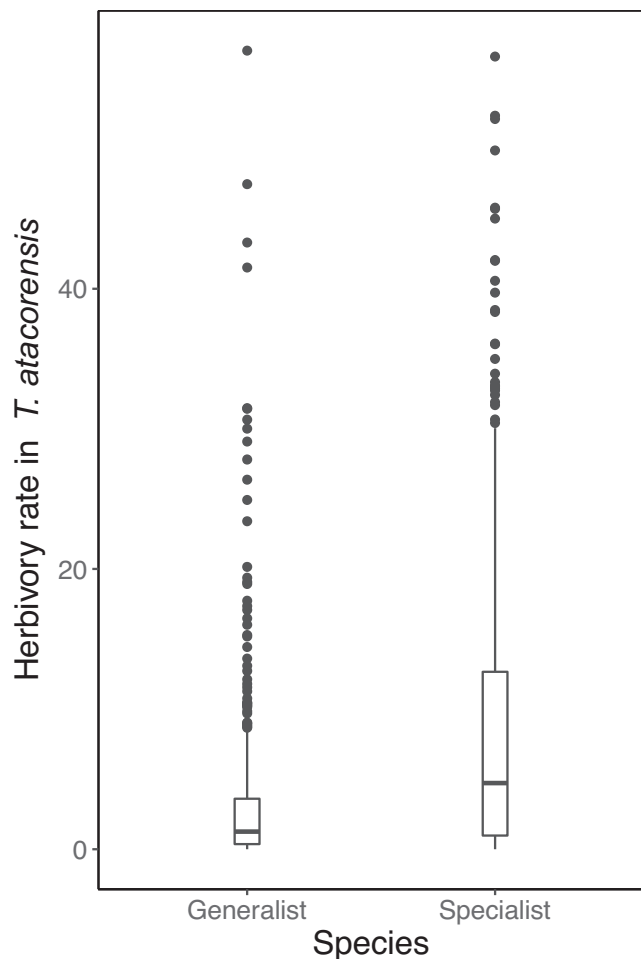


FIGURE 6 Herbivory rate by (a) specialist *Filodes costivitalis* was significantly greater than that of the (b) generalist *Philopona aburiensis* across the 12 populations of *T. atacorensis* ($\beta = 0.43 \pm 0.06$, $Z = 07.01$, $p < .0001$)

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 observations*). However, manipulative experiments and further demographic studies are needed to establish how soil nitrogen-mediated herbivory rates can alter *Thunbergia* spatially explicit dynamics.

Higher rate of herbivory is expected in phylogenetically clustered communities (J. D. 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, 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 costivitalis* 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 competitiveness exclude smaller neighbors. Thus, soils nutrient-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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CONFLICT OF INTEREST

The authors declare no competing interests.

AUTHOR 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.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are open available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.kpr4xh61> (Moutouama & Gaoue, 2022).

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