ARTICLE

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Biotic rather than abiotic factors influence ground-dwelling mygalomorph spider assemblages along an altitudinal gradient in the Brazilian semi-arid domain

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Abstract. The species richness of organisms associated with altitudinal gradients tends to decline with increasing altitude, however, this pattern is not observed in mygalomorph. The present study tests the hypothesis that the richness and abundance of ground-dwelling mygalomorph spiders will be positively correlated with the increase in altitude, as well as will be influenced by variation of potential prey along an altitudinal gradient in the Brazilian semi-arid domain. Sampling took place during August 2020 to August 2021, through pitfall traps, totaling 50 traps/area/month. A total of 125 adult individuals belonging to 10 morphospecies were collected along the altitudinal gradient. Theraphosidae was the richest family in morphospecies, the most abundant mygalomorph was *Neodiplotele caucaia* Gonzalez-Filho, Lucas & Brescovit, 2015, *Guyruita* sp., and *Diplura sanguinea* (F.O. Pickard-Cambridge, 1896). Our results shows that mygalomorph abundance and species richness were affected by potential prey availability and not by altitude *per se*. Therefore, our results shows that the biotic (*e.g.,* availability of potential preys) and no abiotic (*e.g.,* elevation) may have a key factor to the mygalomorph spider assemblage modulation along an altitudinal gradient. The study opens precedents for further investigations on the distribution patterns of mygalomorph spiders in the Brazilian semiarid region.

Keywords. Araneae; Brejos de altitude; Tarantula; Edaphic arthropods; Caatinga.

INTRODUCTION

The distribution of species is defined by biotic and abiotic patterns as a function of gradients, such as altitude, latitude or depth (Brown & Lomolino, 1998; Rahbek, 1995; Lomolino, 2001). Overall, species richness tends to decline as altitude increases (Rahbek, 1995), differing as a function of taxa (Owen, 1990) and localities (Almeida-Neto *et al.,* 2006). For example, Salomão *et al.* (2023) found a decline in dung beetle species towards higher elevation in an Amazon table-top mountain. However, according to previous studies, peak of species richness in Intermediate altitudes followed by their decline appears to be the most common pattern (Rahbek, 1995, Almeida-Neto *et al.,* 2006). Recently, this pattern was found for edaphic spider assemblages from Brazilian semi-arid region (Azevedo *et al.,* 2024).

For semi-arid areas, it is observed that factors such as high evapotranspiration, intense solar radiation, low rainfall and seasonal water availability are constant (Reyes-López *et al.,* 2003; Barrow & Par, 2008). In this scenario, however, the 'Brejos de Altitude' appear in areas inserted in Brazilian semi-arid region at altitudes above 500 m and are associated with a greater volume of rainfall (Prado, 2003; Leal *et al.,* 2005), presenting flora and fauna different from those existing in the surrounding semi-arid region (Werneck, 2011). In these areas, an increase in species richness, density and activity in the rainy season is observed, especially for insect communities (Vasconcellos *et al.,* 2007, 2010). Predatory arthropods, such as spiders and scorpi-

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ons, also respond to increased rainfall because there is an increase in the amount of prey available (Araújo *et al.,* 2010; Carvalho *et al.,* 2015; Lira *et al.,* 2018; Wise, 1993).

Spiders are directly influenced by abiotic factors such as rainfall and soil moisture (Langlands *et al.,* 2006), relative humidity and temperature (Cardoso *et al.,* 2007; Mineo *et al.,* 2010), as well as prey availability, which influences their foraging activity (Romero & Vasconcellos-Neto, 2003; Carvalho *et al.,* 2015). According to Malumbres-Olarte *et al.* (2018) spider assemblages associated with altitudinal gradients respond directly to changes in abiotic and biotic factors. Despite this, for mygalomorph spiders, the diversity patterns in altitudinal gradients diverge, with several individuals of some species recorded at higher elevation (Ferretti *et al.,* 2018; Perafán *et al.,* 2020; Kaderka *et al.,* 2021). The infraorder Mygalomorphae comprises 16 families and more than 3,000 species distributed in 298 genera (Pérez-Miles, 2020; World Spider Catalog, 2022). Representatives of this infraorder generally occur in tropical and subtropical regions (Foelix, 2011; Ferretti *et al.,* 2012; Pérez-Miles, 2020). In addition, some groups are endemic to Neotropical region, such as members of the subfamily Theraphosinae (Miglio *et al.,* 2013), representing about half of the known mygalomorph species (Pérez-Miles, 2020).

The present study aimed to document species richness and abundance of ground-dwelling mygalomorph spiders along an altitudinal gradient in Brazilian semi-arid domain. Specific objectives of this study were to: (1) assess whether the abundance, richness and diversity of ground-dwelling mygalomorph spiders varies along the altitudinal gradient and (2) to evaluate the influence of the abundance of potential prey in the abundance, richness and diversity of spider species. Our hypotheses are that, as altitude increases, the abundance, richness and diversity of ground-dwelling mygalomorph spider species also increases. Regarding the effect of available potential prey, our hypothesis is that there is a positive correlation between the abundance, richness, diversity of ground-dwelling mygalomorph spiders.

MATERIAL AND METHODS

Study area

The 'Maciço do Baturité' is one of the 'Brejos de Altitude' in the state of Ceará, Brazil (Moura-Fé, 2018). High rainfall is observed, with an average of 1,500 mm per year, with the occurrence of a rainy season corresponding to the period from December to March and a dry season in April to November, respectively (SEMACE, 2010). The predominant type of vegetation in the 'Maciço de Baturité' is the Atlantic Forest, whose flora is composed of 92 families, whose composition changes along the altitudinal strata, with a predominance of thorny deciduous vegetation in the lower part, which is gradually replaced by forest vegetation (Oliveira & Araújo, 2007).

We delimited five different areas according to their elevation in the "Maciço de Baturité": two areas with Caatinga and Transition Forest vegetation respectively in the municipalities of Redenção (04°14′23,2″S, 38°45′55,4″W; 04°13′51,7″S, 38°49′33,5″W); one area in humid forest vegetation in the municipality of Pacoti (04°13′45,5″S, 38°53′27,9″W); and two areas with humid forest vegetation in the municipality of Guaramiranga (04°15′50,2″S, 38°54′56,9″W; 04°12′50,9″S, 38°57′59,0″W). The areas displaying the following altimetry: 374, 600, 700, 845 and 1,114 meters of altitude respectively.

Ground dwelling mygalomorph sampling

The fieldwork took place during the period from August 2020 to August 2021, making a monthly collection in each of the five research areas. At each area, sampling was performed using pitfall traps for terrestrial invertebrates, where each trap remained operational for 7 days/month, and each set of 5 traps arranged in a cross formed a sampling unit and a pitfall battery traps (Carvalho, 2015). In total, 10 batteries of pitfall traps were installed at each point of the altitudinal gradient, totaling 50 square meters of sampled area/altitudinal band. The batteries were installed in a linear fashion, with a minimum spacing of 10 m between each battery, thus avoiding spatial pseudo-replication (Hullbert, 1984).

Each pitfall trap consisted of a plastic container (10 × 15 cm deep), buried at ground level, in which 400 mL of supersaturated saline solution (1 kg of table salt per liter of water) was placed, in addition to drops of detergent to break the surface tension of water (Carvalho, 2015). Above each pitfall trap, an improvised roof made of styrofoam was installed, fixed with wood sticks, thus avoiding excessive sunlight under the pitfall traps, as well as helping to reduce the miscellaneous materials that eventually fall into the pitfall traps, such as leaves and animals that fall from nearby vegetation above the traps (Ferretti *et al.,* 2012; Carvalho, 2015).

Abundance of potential prey

The abundance of potential preys observed corresponds to edaphic entomofauna individuals that fell into pitfall traps concomitantly with spiders, given that insects are among the main prey of mygalomorph spiders (Foelix, 2011; Hénaut & Machkour-M'Rabet, 2020). Of all the insects observed, only the abundance of insects of the following orders was used: Blattodea, Coleoptera, Dermaptera, Hemiptera, Hymenoptera, Isoptera, Orthoptera, Phasmatodea. We also consider caterpillars and beetle larvae recorded in pitfall traps. The sorting of insects in taxonomic resolution of order was performed using the identification key for insect order (Triplehorn *et al.,* 2005).

Statistical Analysis

Firstly, we calculate the diversity using the 1D Hill numbers that corresponds to exponential of Shannon entropy, which considers the relative abundance of dominant species. The 1D was calculated through hillR package (Chao & Shen, 2004). The relationships between mygalomorph spider assemblage and biotic (*e.g.,* potential prey availability) and abiotic (*e.g.,* altitude) variables were performed through generalized linear models (GLMs). We used morphospecies richness, abundance and diversity as response variables and the biotic and abiotic variables as predictors in our GLMs. We used Poisson distribution for abundance and Binomial negative for morphospecies richness and diversity. The assumptions of normality of the residuals were visually analyzed with normal q-q plots and outliers were evaluated through Cooks distance. These analyses were performed through MASS package (Venables & Ripley, 2002). All analyses were performed by in R software (R Core Team, 2020).

RESULTS

A total of 137 individuals of ground-dwelling mygalomorph spiders of these 92% (n = 127) were adults. Were collected 10 morphospecies of ground-dwelling mygalomorphs along the altitudinal gradient in 'Maciço do Baturité' (Table 1). The family with the highest morphospecies richness was Theraphosidae with 5 morphospecies. The most abundant morphospecies were *Neodiplothele caucaia* Gonzalez-Filho, Lucas & Brescovit, 2015 (51 individuals), *Guyruita* sp. (18 individuals) and *Diplura sanguinea* (F.O. Pickard-Cambridge, 1896) (17 individuals) (Table 1). Among the observed species, only *N. caucaia* and *Kochiana* sp. occurred in all altitudinal extracts of the analyzed gradient. *Hapalopus* sp. and *Tmesiphantes nordestinus* Fabiano-da-Silva, Guadanucci & DaSilva, 2019 (Therasphosidae) occurred only in a single altitudinal extract, being represented by a single individual each species. While, *D. sanguinea* occurred only in the last portion of the altitudinal gradient.

Table 1. Ground-dwelling mygalomorph spiders collected along the altitudinal gradient established in Maciço do Baturité, Ceará state, Brazil.

Taxon	Altitude (m)					Total
	374	600	700	855	1,114	
Actinopodidae						
Actinopus gr. *nattereri*	—	1	—	—	3	**4**
Barychelidae						
Neodiplotele caucaia (Gonzalez-Filho *et al.,* 2015)	13	7	7	5	19	**51**
Neodiplotele sp.	—	1	1	—	5	**7**
Cyrtaucheniidae						
Fufius sp.	2	3	—	—	—	**5**
Dipluridae						
Diplura sanguinea (F.O. Pickard-Cambridge, 1896)	—	—	—	—	17	**17**
Theraphosidae						
Guyruita sp.	1	—	—	—	17	**18**
Hapalopus sp.	1	—	—	—	—	**1**
Kochiana sp.	3	1	2	1	2	**9**
Tmesiphantes nordestinus (Fabiano-da-Silva *et al.,* 2019)	—	3	—	—	1	**4**
Tmesiphantes guayarus (Fabiano-da-Silva *et al.,* 2019)	2	—	4	—	3	**9**
Abundance	**22**	**16**	**14**	**6**	**67**	**125**
Richness	**6**	**6**	**4**	**2**	**8**	**10**

The number of morphospecies varied between 2 and 8, with the highest altitude (1,114 m) presenting 8 morphospecies (Table 1). The richness of morphospecies was influenced by the availability of potential prey ($z = 3.77$, $p < 0.01$, $R^2 = 0.22$, Fig. 1) but not by altitude ($z = 0.21$, $p = 0.82$). In terms of abundance, a variation from 6 to 67 adult individuals was found, with the largest quantity collected at an elevation of 1,114 m and the smallest at 855 m. Ground dwelling mygalomorph abundance was positively related to the availability of potential prey ($z = 7.37$, $p < 0.01$, $R^2 = 0.30$, Fig. 2) and was not related to altitude ($z = 0.46$, $p = 0.64$). Morphospecies diversity was similar among altitudinal bands not being affected by altitude ($z = 0.42$, $p = 0.67$) or availability of potential prey ($z = 1.67$, $p = 0.09$). *Neodiplothele caucaia* was dominant in all altitudinal bands, except in 1,114 m where *D. sanguinea* was dominant (Fig. 3).

DISCUSSION AND CONCLUSION

In the present study, we assessed the effects of biotic (abundance of potential preys) and abiotic (elevation) in mygalomorph spiders richness, abundance and diveristy along an altitudinal gradient. Our study provides two key results. First, our result confirms our hypothesis that the abundance of individuals and the species richness of mygalomorph spiders are positively correlated with prey availability. Second, contrary to our hypothesis, abun-

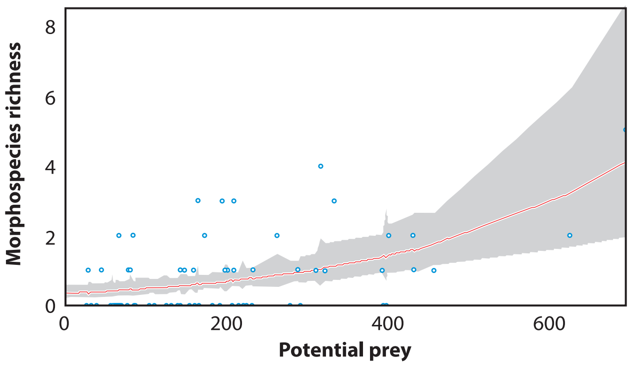

Figure 1. Relationship between ground-dwelling mygalomorph spider abundance and availability of potential prey along an altitudinal gradient in Baturité Massif, Brasil.

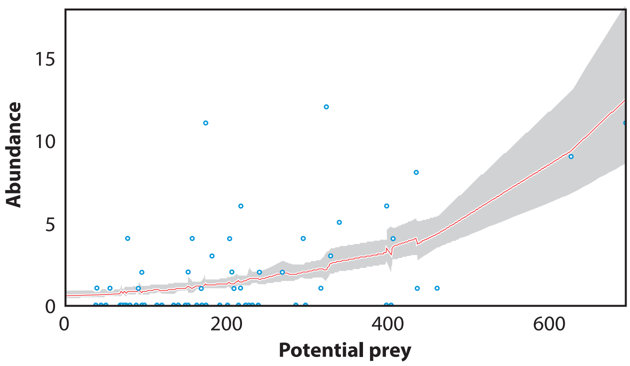

Figure 2. Relationship between ground-dwelling mygalomorph spider morphospecies richness and availability of potential prey along an altitudinal gradient in Baturité Massif, Brasil.

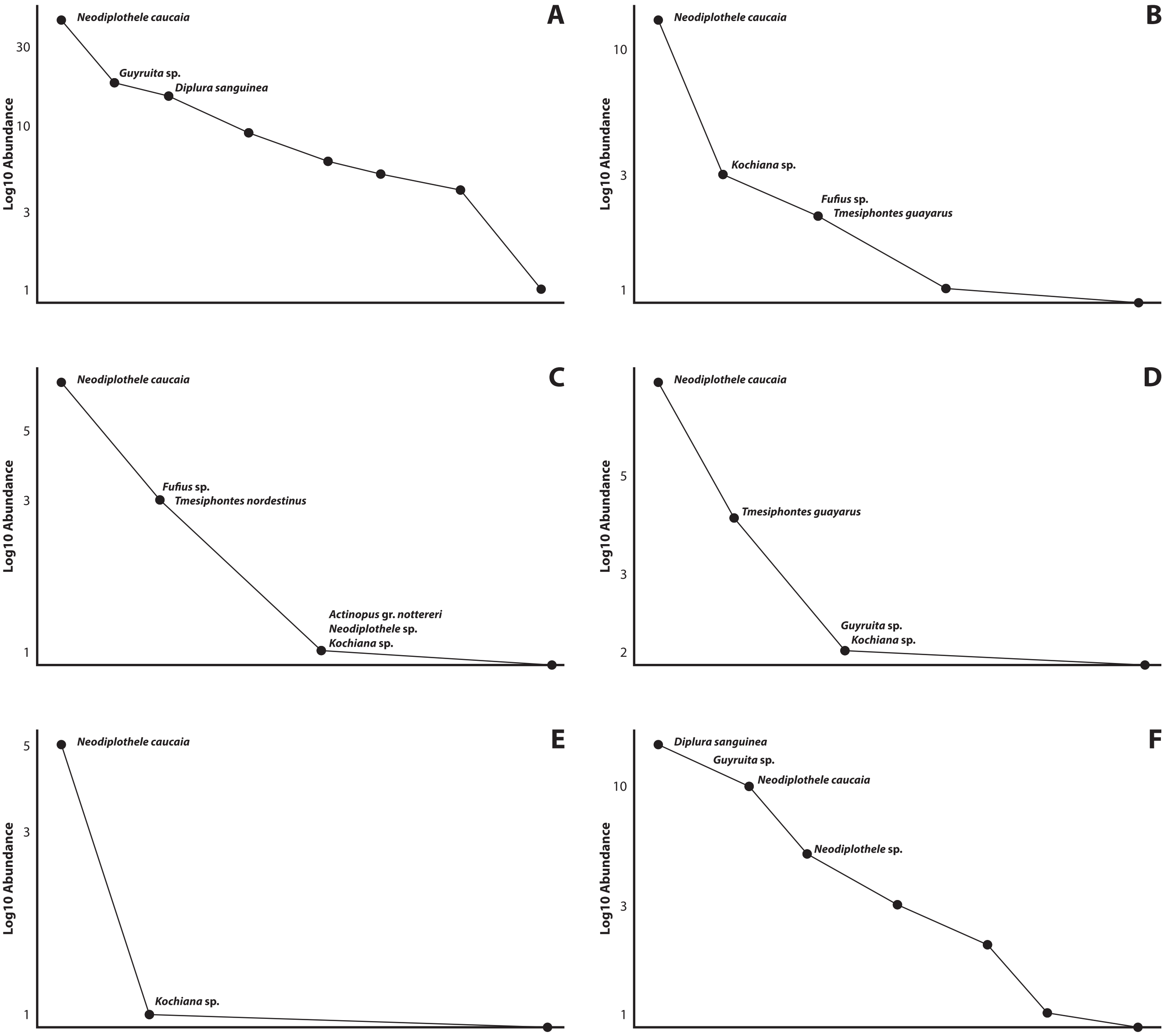

Figure 3. Rank-abundance curves of ground-dwelling mygalomorph spider morphospecies sampled along an altitudinal gradient in Baturité Massif, Brasil. (A) Entire gradient, (B) 374 m, (C) 600 m, (D) 700 m, (E) 855 m and (F) 1,114 m.

dance of individuals, species richness and diversity of spiders are not correlated with elevation. Studies related to the effects of altitudinal gradients in spider assemblages are scarce, and often not directed to the study of the effects of altitudinal gradients *per se* (Nogueira *et al.,* 2021; Azevedo *et al.,* 2024). This scarcity of scientific literature permeates deficits such as Linean, Wallacean, Huntchinsonian (Hortal *et al.,* 2015), associated with sampling bias, and geographic distribution in altitude gradients (Lomolino, 2001).

The species richness observed for Theraphosidae (5 species) reflects the current state of knowledge of the group, given that it is the richest family in mygalomorph spiders group, comprising more than 1,000 species distributed in tropical and subtropical regions (Pérez-Miles, 2020, World Spider Catalog, 2022). We must take into account that the size of the pitfall traps used in the field may not be appropriate for collecting species from large genera, for example, the genres *Acanthoscurria* and *Lasiodora* of the family Theraphosidae. Spiders of these genre are relatively large that may be in the study area, but may not have been collected due to the size of the traps, so it is possible that the species richness of the site was undersampled. For the state of Ceará, 24 species of mygalomorph spiders are observed, of which the family Theraphosidae is represented by 13 morphospecies (Moura-Neto *et al.,* 2021). Mygalomorph spider species richness and abundance were positively influenced by potential prey availability. A growing body of research suggests that the abundance of animal populations, ranging from herbivores to top predators, is constrained by food availability, which is, in turn, influenced by meteorological conditions (White, 2008). In spiders, on the one hand, similar results were obtained in the same ecosystem, semi-arid Caatinga vegetation, Brazil, where the total invertebrate abundance has a direct influence on spider richness and abundance (Carvalho *et al.,* 2015). In temperate regions, the same positive correlation between prey availability and spider community richness and abundance was also recorded (Halaj *et al.,* 1998;

Spears & MacMahon, 2012). Probably, in our study area, the initiation of the rainy season within Atlantic Forest ecosystems provides optimal environmental circumstances for the proliferation of numerous organisms, particularly insects. The resurgence of plant growth during this period is directly correlated with an increase in insect reproductive activity and population density (Carvalho *et al.,* 2015). This pattern of positive correlation between prey availability and predator abundance was also observed in other group like scorpions, where the abundance of different orders of hexapods was positively correlated with precipitation and with increased activity of scorpion species, also in semi-arid Caatinga ecosystem (Araújo *et al.,* 2010). On the other hand, in the endangered tarantulas, *Brachypelma klaasi* and *B. vagans* (Araneae: Theraphosidae) in Mexico, it has been recorded that the availability of prey is almost unimportant when compared to soil quality or physical conditions such as temperature and humidity for burrow location (Yáñez & Floater, 2000; M'rabet *et al.,* 2007). Unfortunately, there are few studies that evaluate the importance of prey availability specifically in the Mygalomorphae group, which makes it difficult to have a general pattern. Therefore, more future studies are needed to evaluate the effect of prey together with environmental variables.

In our study, contrary to our hypotheses, we did not record any correlation between elevation and abundance, species richness and diversity of mygalomorph spiders. Although the majority of tarantula species are distributed below 1,600 meters, three genres (*Bistriopelma, Hapalotremus,* and *Antikuna*) have been documented at extraordinary altitudes of 4,000-4,700 meters in the Peruvian Andes (Kaderka, 2015; Ferretti *et al.,* 2018; Kaderka *et al.,* 2021). These genera represent the highest elevation records for theraphosid spiders. This association between mygalomorph spiders and their habitats would still allow the occurrence of these arachnids in specific altitudinal ranges associated with altitudinal gradients (Ferretti *et al.,* 2018; Kaderka *et al.,* 2021). For example, we found that *N. caucaia* was the mygalomorph spider dominant in all elevational bands, except in higher sample site that was dominated by *D. sanguinea. Neodiplothele caucaia* shows a wider distribution in Brazilian dry region, such as Caatinga and Cerrado (Gonzalez-Filho *et al.,* 2015), similar environmental conditions found in lower bands of our elevational gradient. However, *D. sanguinea* is found only in rainforests, being widespread in Amazon Forest and may be found in higher elevation in Ceará state (Brescovit *et al.,* 2021). Therefore, considering the species-specific traits and that the availability of microhabitats for ground-dwelling mygalomorphs is limited, this may influence the absence of altitude influence on the spider assemblage in the studied landscape, however this needs to be tested in future work.

Thus, the present work allows us to infer those biotic factors as availability of potential preys is more important that altitude *per se* for ground-dwelling mygalomorph spiders assemblages along an elevational gradient in the Brejo de Altitude existing in the Baturité Massif. An increase in availability of potential preys was determinant for mygalomorph abundance and morphospecies richness. This increase in resources may be related to the reproductive period, since many species reproduce when there is a greater supply of food. However, despite the information obtained, the study opens precedents for further investigations in order to fill the knowledge gaps associated with the distribution patterns of Mygalomorphae spiders in the Brejos de Altitude and Caatinga Domain.

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SUPPLEMENTARY MATERIAL

SS1. Temporal variation of males and females of adult edaphic Mygalomorphae spiders along the altitude gradient established in Maciço do Baturité, Ceará. Males individuals are cited as normal font, female individual was represented in bold font and highlighted as gray.

Species	2020								2021					Total
	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	
Actinopodidade														
Actinopus gr. *nattereri* sp. nov.1						3	1							**4**
Barychelidae														
Neodiplothele caucaia Gonzalez-Filho, Lucas & Brescovit, 2015				1	4		24	14	4	4				**51**
Neodiplothele sp. nov.1	1	2	1	1						2				**7**
Cyrtaucheniidae														
Fufius sp. nov.1		4					1							**5**
Dipluridae														
Diplura sanguinea (F.O. Pickard-Cambridge, 1896)	7	8										2		**17**
Theraphosidae														
Guyruita sp. nov.1		2		2	6	1	6	1						**18**
Hapalopus sp.1									**1**					**1**
Kochiana sp. nov.1							2	7						**9**
Tmesiphantes guayarus Fabiano-da-Silva, Guadanucci & DaSilva, 2019					1	6	1	1						**9**
Tmesiphantes nordestinus Fabiano-da-Silva, Guadanucci & DaSilva, 2019				1			2	1						**4**
Abundance	**8**	**16**	**1**	**5**	**11**	**10**	**37**	**24**	**5**	**6**	**0**	**2**	**0**	**125**
Richness	**2**	**4**	**1**	**4**	**3**	**3**	**7**	**5**	**2**	**2**	**0**	**1**	**0**	