



Spider (*Arachnida-Araneae*) diversity in an amazonian altitudinal gradient: are the patterns congruent with mid-domain and rapoport effect predictions?

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Abstract: The Mid-Domain Effect (MDE) and the Rapoport (RE) effect are two biogeographical theories that make predictions about biogeographic patterns. MDE predicts higher richness in the central portions of a gradient if it is within a bounded domain. RE predicts a positive relation between altitude and species range size along an altitudinal gradient. Our aim was to document the distribution of spider species richness along an altitudinal gradient in the Brazilian Amazon, and to test the influence of MDE and RE on the diversity patterns. Our study was conducted at the Pico da Neblina (Amazonas state, Brazil), and we sampled spiders at six different altitudes using two methods: nocturnal hand sampling and a beating tray. We obtained 3,140 adult spiders from 39 families, sorted to 529 species/morphospecies. Richness declined continuously with an altitude increase, but the fit with the MDE richness estimates was very weak and was not significant. Range size was not related to altitude, i. e., no RE. Finally, the abundance distribution within each species range varied more specifically, which prevented the occurrence of a RE at the community level. The influence of MDE was extremely low, a consequence of our community characteristics, formed mostly by small range size species. Short and medium range species were located at all altitudes, preventing a significant relation between range size and altitude. The distribution of abundance within a species range varied specifically and do not support a RE hypothesis.

Keywords: *Arachnology, geometric constraints, mountain ecology, environmental gradients, biodiversity, Amazon.*

Diversidade de aranhas (*arachnida-Araneae*) em um gradiente altitudinal na amazônia. seriam os padrões congruentes com o esperado pelo efeito do domínio central e pelo efeito rapoport?

Resumo: O Efeito do Domínio Central (MDE) e o Efeito Rapoport (ER) são duas teorias biogeografias que fazem previsões sobre a distribuição da diversidade ao longo de gradientes. O MDE prevê maior riqueza nas porções centrais de um gradiente, se este estiver dentro de um domínio fechado. O ER prevê uma relação positiva entre altitude e tamanho da distribuição ao longo do gradiente altitudinal. Nosso objetivo foi o de registrar a distribuição de uma comunidade de aranhas ao longo de um gradiente altitudinal na Amazônia Brasileira, e testar se há uma influência do EDC e do ER sobre os padrões de diversidade da comunidade. Nosso estudo foi feito no Parque Nacional do Pico da Neblina (AM, Brasil), e nós amostramos aranhas em seis altitudes diferentes. Nós coletamos 3.140 exemplares adultos de 39 famílias, que foram divididos em 529 espécies/morfoespécies. A riqueza declinou com o aumento de altitude, mas o padrão não mostrou ajuste com as previsões feitas pelo EDC. O tamanho da distribuição altitudinal também não esteve relacionado ao previsto pelo ER. Por fim, a distribuição de abundância ao longo da distribuição altitudinal das espécies variou de maneira específica, o que impediu a ocorrência de um ER nos padrões da comunidade. A influência do EDC sobre os padrões observados foi baixíssima, uma consequência de características de nossa comunidade, já que esta é formada por espécies com pequena distribuição altitudinal. Espécies de distribuição altitudinal médias e grandes ocorreram em todas as partes do gradiente o que impediu

a ocorrência de um ER. Por fim, o ER também não foi observado na distribuição de abundância das espécies ao longo do gradiente, já que essa variou de maneira específica.

Palavras-chave: *Aracnologia, restrições geométricas, ecologia de montanhas, gradientes ambientais, biodiversidade, Amazônia.*

Introduction

Altitudinal gradients have always attracted the attention of scientists, from eighteenth and nineteenth century naturalists to modern ecologists and biogeographers. Partially relegated for a certain period (Lomolino 2001), the study of altitudinal gradients has been experiencing a recovery of interest, especially during the last decade, with richness patterns being increasingly well documented, for a larger range of taxa and environments (e.g., McCain 2005, 2009a, 2010, Dunn et al. 2006, Grau et al. 2007, Liew et al., 2010, Scheibler et al. 2014, Transpurger et al. 2017, Thormann et al. 2018). Richness usually decreases with altitude, either monotonically, or after low altitude plateau of high richness, but it may also present a unimodal pattern, peaking at mid altitudes, which is frequently observed (Rahbek 2005, McCain 2009a, Dong et al. 2017).

In the last decade, two new biogeographical theories became a recurring subject for empirical studies on altitudinal gradients, the mid-domain effect (MDE) (Colwell & Lees 2000a) and Rapoport's rule (RE) (Stevens 1989). MDE represented a new and original approach to explain peaks of species richness at mid altitudes (or latitude, or any other gradient). Colwell & Lees (2000a) demonstrated through simulations that the reshuffling of species range inside a domain delimited by hard boundaries (*i. e.*, limits from which no species can expand its range) results in a larger overlap of species ranges around the center of the domain, producing a richness distribution pattern very similar to those observed in some empirical studies. This process was also referred to as the effect of geometric constraints in the placement of species ranges on a bounded domain.

By explaining observed patterns while dispensing the influence of any ecological or environmental gradients, the MDE aroused a lot of interest and has been the subject of a thorough scrutiny (Colwell et al. 2005, Romdal et al. 2005, Zapata et al. 2005, Storch et al. 2006, Letten et al. 2013, Pan et al. 2016). Criticisms range from the methodologies employed to test it to its assumptions (Laurie & Silander 2002, Zapata et al. 2003, Hawkins et al. 2005, Currie & Kerr 2008), but other studies still advocate its validity as an explanatory hypothesis for certain gradients in species richness (Carranza et al. 2008, Grytnes et al. 2008, VanDerWal et al. 2008), although maybe restricted to some limited situations (Dunn et al. 2007).

Rapoport's rule is a positive relation between range size and latitude and was proposed as an explanation for latitudinal gradients of species richness (Stevens 1989). It was hypothesized that species from higher latitude have broader environmental tolerance, due to greater climatic variation, and thus could expand their range at lower latitudes, increasing the local richness at these latitudes. But the opposite would not be possible, due to the narrow environmental tolerance of species from lower latitudes. Stevens (1989) also proposed that the large range expansion observed for high latitude species would happen through a rescue effect (Brown & Kodric-Brown 1977), *i. e.* the maintenance

of populations at unsuitable places through a continuous migration of individuals from source populations located at places with more adequate conditions for its existence.

Rapoport's rule was later extended to altitudinal and bathymetric gradients (Stevens 1992, 1996), and also raised an intense debate on its validity, causes and consequences. Although the support to the role of Rapoport's rule as a driver of species richness gradient is very weak (Rohde 1996, Colwell & Lees 2000, Willig et al. 2003, Bhattarai & Vetaas 2006), the positive association between range size and latitude/altitude/depth was actually detected in several studies (Stevens 1992, Fleishman et al. 1998, Fortes & Absalão 2004, Brehm et al. 2007, Chettri et al. 2010). Nonetheless, since a considerable number of studies failed to observe this relation, the rule was called into question, which led Blackburn & Gaston (1996) state that the humbler term "effect" would be more appropriate to describe this phenomenon.

The Rapoport rescue effect has been much less investigated, although it was proposed as the mechanism responsible for the Rapoport effect (Stevens 1989). The only study that directly tried to verify Steven's prediction, by investigating the relative abundance of species at each altitude, revealed a pattern opposite to what could be expected by the theory. Large ranged species were more abundant at lower altitudes and expanded their range upwards (Almeida-Neto et al. 2006), which the authors called the "alternative rescue effect".

Information about spiders along altitudinal gradients is scarce. Most of the few studies about spiders along altitudinal gradients are from temperate localities, usually for a subset (guilds or families) of the spider community (Otto & Svensson 1982, Bosmans et al. 1986, Olson 1994, Russel-Smith & Stork 1994, Chatzaki et al. 2005), and most reported a mid-altitudinal richness peak. Only Chatzaki et al. (2005) tested, and supported a Rapoport effect, in a study on the family Gnaphosidae at Cretan mountains, but Otto & Svensson (1982) also reported larger altitudinal ranges for species from higher altitudes.

Given the large literature available on species richness patterns on altitudinal gradients, spiders are clearly underrepresented, if we consider their high diversity (> 49,000 species – World Spider Catalog, 2021) and ecological importance as a top invertebrate predator (Coddington et al. 1991). Our focal group is understory and forest floor spiders.

In this study, we investigated a spider community along an altitudinal gradient in Brazilian Amazonia. Our study area - Pico da Neblina (AM - Brazil) is the highest mountain in Brazil, and is renowned for its botanical diversity and endemism levels (Berry & Riina 2005), while its fauna is less known (see Willard et al. 1991 and McDiarmid & Donnelly 2005). Moreover, it is located in a remote area still mainly covered by forest at a very large scale, which guarantees an unusual conservation level even at lower altitudes, rarely observed in studies on altitudinal gradients (Nogués-Bravo et al. 2008).

Our objectives are: 1 - to record the pattern of spider species distribution along the altitudinal gradient at the Pico da Neblina and

to assess the relation of this pattern with altitude and with MDE predictions, 2 - to test for the occurrence of a Rapoport effect, 3 - to investigate the existence of a rescue effect, and 4 - contribute to the knowledge of spider diversity in tropical mountains, expecting high diversity and endemism.

Material and Methods

1. Study area

The study was carried out at the Pico da Neblina (00°48'07" N e 66°00'40" W) (Figure 1), the highest Brazilian mountain with 2,994 m.a.s.l. (IBGE, 2004). Located in the municipality of São Gabriel da Cachoeira, north of the Amazonas state, Brazil, the study sites belongs to the Pico da Neblina National Park, with 2,260,344 ha, and also overlapped with the Yanomami Indigenous Land. The Pico da Neblina lies within a mountainous region that represents the boundary between Brazil and Venezuela (RADAM, 1978). It is also one of the southern components of the Guayana Region, a region of very old geological origin (mostly Precambrian rocks) famous for its sandstone mountains with vertical cliffs and table tops, the tepuis (Steyermark, 1986), as well as for its diverse and endemic biota (Rull, 2005). Although the Pico da Neblina is also formed by sandstone rocks and harbours extensive high altitude plateaus (2,000 to 2,400 m), it does not present the typical tepui shape.

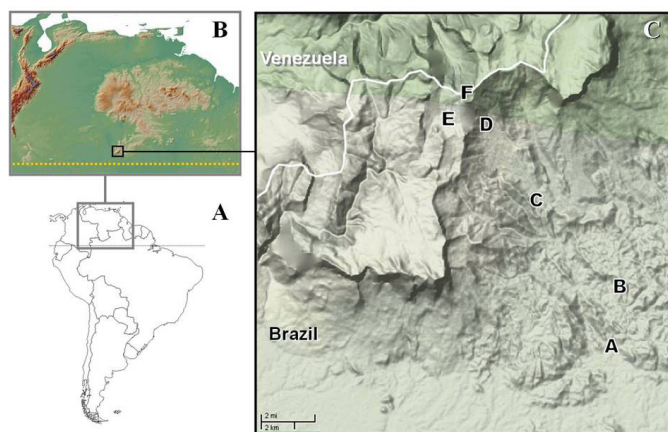


Figure 1. Study area.. A) South America; B) Northern South America (rectangle of map A enlarged). The mountain range at the left of the map represents the northern part of the Andes, and the mountainous region in the center of the map is the Guayana Shield, showing the study area in its southern part. The dotted yellow line represents the equator; C) Closer view of the study area (rectangle of map B enlarged), the Pico da Neblina. Letters represent the altitudes sampled: A - 100 m, B - 400 m, C - 860 m, D - 1,550 m, E - 2,000 m, F - 2,400 m.

According to a division proposed for the Guayana region, the study area can be divided in three main physiographic units according to the temperature and altitude. Lowlands, up to 500 m and macrothermic climate ($> 24^{\circ}\text{C}$ annual average); uplands, from 500 to 1,500 m and submesothermic climate ($18^{\circ} - 24^{\circ}\text{C}$); and highlands, from 1,500 to 2,994, with mesothermic ($12^{\circ} - 18^{\circ}\text{C}$) and submicrothermic climate ($8^{\circ} - 12^{\circ}\text{C}$) (Huber 1995, Nogués & Rull 2007). At the Pico da Neblina, the annual average rainfall in the lowlands is 3,000 mm/year, without a dry season, and the humidity is about 85-90% (RADAMBRASIL 1978). Rainfall increases with altitude until around 1800 m, being gradually

replaced by a constant mist, and the average humidity reaches almost 100% (RADAMBRASIL 1978).

Vegetation in the lowlands is composed by a tall, evergreen forest. Uplands are covered by montane forests, which present decreasing biomass and tree size, especially when declivity is accentuated, leading to shallower soils (Pires & Prance 1985). In the highlands, forests are replaced by more open types of vegetation like high altitude scrublands and broad leaf meadows, which grow on organic peat soils and on rocky substrates. At the Neblina, forests formation occurs up almost to 2,000 m, and their high altitude formations stand out for their diversity and endemism (Berry & Riina 2005). Species from the families Bromeliaceae, Rapateaceae and Theaceae are among the most characteristics elements of this flora. Detailed information on the geology and vegetation of the region can be found at Berry et al. (1995) and Berry & Riina (2005).

2. Sampling and identification

Spiders were collected with two traditional methods in spider inventories (Coddington et al., 1991): beating tray and manual active search. In the first method the understory vegetation was sampled through the beating of leaves, branches, vines and other parts of the vegetation with a stick, while holding a 1 m^2 tray under it. The spiders falling in the tray were collected, and the sampling unit consisted of 20 of those beating events, in different plants, randomly located along a 30 m long transect.

In the second method spiders from the forest floor and from the understory were directly collected with the help of tweezers and/or plastic vials. The sampling unit represents one hour of search within an approximate area of 300 m^2 ($30 \times 10\text{ m}$).

The first method was employed during the day, from 08.00 h to 11.00 h, and the second at night from 19.30 h to 23.00 h. All spiders collected with both methods were immediately preserved in 70% ethanol.

Sampling was carried out by three collectors at six altitudes, 100, 400, 860, 1,550, 2,000 and 2,400 m. At each altitude we investigated three sites, about 100 m apart from each other. In each of those three sites, the three collectors sampled gathered three samples with the beating tray technique, during the morning, and three samples by manual active search during the night, totaling nine samples of each method by site. This correspond to a total sampling effort of 54 samples by altitude (27 of each method) 324 samples (162 of each method) for the whole gradient. We also measured the temperature at each sampling site, at the beginning and at the end of nocturnal sampled. The sampling expedition occurred from 22 September to 13 October 2007, period considered as dry season locally.

Only adult spiders were identified. Specimens were sorted into morphospecies usually by the first author and then identified until the lowest taxonomic level by specialists. Voucher specimens were deposited at the collection of the Instituto Nacional de Pesquisas da Amazônia (INPA), at Manaus (AM), and duplicates were deposited at the Instituto Butantan (IBSP), São Paulo (SP) and at the Museu Paraense Emílio Goeldi (MPEG), Belém (PA).

3. Richness measures

The species richness for each altitude was calculated as the total number of species collected in the three sites at each altitude, pooling data from both sampling methods. We interpolated richness estimates

in all analysis, for all taxonomic levels. Interpolation assumes that a species occurs in all altitudes between its maximum and minimum altitudinal record, and represents a common procedure in studies on species richness on altitudinal gradients (Stevens 1992, Sanders 2002, Almeida-Neto et al. 2006, Bhattarai & Veetas 2006, Grau et al. 2007). It is based on the assumption that the sampling of biological communities is usually incomplete, which is certain for a community of tropical arthropods (Coddington et al. 2009), and that altitudinal ranges are continuous. So we believe that the increase in richness provided by the interpolation represents a realistic contribution to our data, although it may enhance or even create mid-altitude peaks (Grytnes & Vetaas 2002).

We also compare interpolated richness with other richness measures calculated for each altitude: observed richness, rarefied richness (coverage-based rarefaction) and the exponential of Shannon-Wiener index, or numbers equivalents (D). D was selected as a measure of diversity because it take into account the relative abundance of species. Its use over raw diversity indices has been recommended for allowing a more intuitive interpretation (Jost 2006), as it possess the doubling propriety (Hill 1973), *i. e.* if two equal sized, completely distinct communities with a diversity $D = X$ are combined, their diversity will be $D = 2X$.

To calculate the rarefied richness we used a coverage-based rarefaction (Chao & Jost 2012). This technique compares communities not by equaling all of them to the lowest abundance recorded, as is done in individual-based rarefaction, but by the same level of inventory completeness. This is calculated based on the proportion of species that are still missing, which is calculated according to richness estimatives. This technique also compares the richness of different communities by extrapolation, when necessary, and it also allow us to produce rarefaction curves with richness estimators and 95% confidence intervals.

Shannon-Wiener index values were obtained with the software Paleontological Statistical (PAST, Hammer et al. 2001), and their exponential in a excel sheet. The rarefaction analyzes were performed in R Cran Project software 4.0.5 (2021), using packages vegan (Oksanen et al. 2020), iNEXT (Hsieh et al. 2020) e ggplot2 (Wickham, 2016).

4. Geometric constraints

The software RangeModel (Colwell 2006) was used to estimate the spiders communities richness along a dimensional gradient under the assumption of geometric constraints. The gradient is represented by all the altitudes sampled, and the lower and highest altitudes represent the limits of the domain, with no range can extend beyond. This null model places the empirical altitudinal ranges of each species randomly along the gradient, without replacement, and richness at each sampling site is counted. This procedure was repeated 1,000 times, without replacement, and the mean estimated richness and its 95% confidence intervals were calculated.

Species recorded in just one altitude represent a problem, since their range is restricted to a single point, the altitude in which it was recorded. This decreases drastically the chance of those species being recorded during the randomization process, leading to an underestimation of richness. A simple solution is to expand the altitudinal range of the species upslope and downslope (Bhattarai & Veetas 2006, Brehm et al. 2007), usually to half the distance from the nearest sampling site. In our study, however, the distance between our sampling sites was too uneven to allow this procedure.

To overcome this problem, we used the discrete domain model, developed by Dunn et al. (2006) available at RangeModel. In the discrete model the domain is divided into discrete, ordered sampling points, and each empirical species range encompasses the distance from the first to the last sampling point where that species was recorded. Additional information required is the 'fill', which is the number of sites at which each species was actually recorded. To perform the analysis, we just filled the gaps in the fill input data to represent complete interpolation. The discrete model may be less realistic, since different distances among sampling sites are artificially standardized. Moreover, probably in order to avoid this situation, it was recommended for use with datasets gathered at evenly or approximately evenly sampling sites (Dunn et al. 2006, Colwell 2008). However, by this approach we were able to obtain simulations without missing any record and, more important, we believe that we maintained the main principle of geometric constraints models, which is to randomize observed ranges along a bounded domain.

5. Analyses

We analyzed the variation in interpolated species richness along the gradient through an ordinary least squares (OLS) multiple regression with mean richness estimates predicted by a MDE simulation and altitude as explanatory variables. We used the AICc (small sample corrected Akaike Information Criterion) to select the best model. We used altitude as an environmental variable because it is usually strongly correlated with other environmental factors, as temperature and vegetation type (Dunn et al. 2007), and could be used as a surrogate for environmental variation along the gradient (Bateman et al. 2010). The temperature measured at our sampling sites was indeed closely related to altitude ($R^2 = 0.99$, $p < 0.001$). We tested this relationship for richness at the species, genus and family level. Geometric constraints are stronger on large ranged taxa (Colwell & Lees 2000, Dunn et al. 2006), so we expect that MDE predictions will present a better fit with increasingly higher taxonomic levels, since the range of the analyzed taxa will greatly increase, especially at the family level. We analyzed the residuals of the regression through Moran's I correlogram to assess the occurrence of spatial autocorrelation, but no significant trend was found, which allowed us to keep our analysis design with OLS regression (Diniz-Filho et al. 2003). The analysis was performed with Spatial Analysis Macroecology (SAM) software (Rangel et al. 2010).

Rapoport effect was investigated with an OLS regression between recorded range size and the altitudinal midpoint of each species. We calculated the range as the difference between upper and lower altitudinal limits, and the midpoint was the average altitude between the range extremities, *i. e.*, a geometric midpoint. We added 200 m to each ranges, since otherwise species recorded at just one altitude would have an altitudinal range of 0, which is not very realistic. However, this approximation does not have any influence in the analyses, unlike what is observed in the geometric constraints simulations for this study. We also tested the Rapoport effect for a subset of the community based on a minimum abundance criterion. Most species from our dataset are rare, represented by just a few individuals. They thus have a large probability of being recorded in just one altitude, but this may be simply due to undersampling rather than a genuine narrow distribution. Thus, we removed all species represented by just one or two individuals to perform another OLS regression between range size and midpoint for the species represented by at least three individuals (243 species or 46% of total richness), an arbitrary criterion. This allows us to keep in the analysis species

present in just one altitude, but whose distribution is more reliable due to the larger number of individuals.

We investigated the occurrence of a rescue effect by the following procedure. First we calculated the weighted average midpoint (WAM) (Almeida-Neto et al. 2006) for each species. The WAM is obtained by multiplying the number of individuals present at each altitude by the corresponding altitude, summing up those products from all altitudes and dividing it by the total abundance of the species. Assuming that a species attains its maximum abundance in optimal environmental conditions (Whitaker 1967, Brown 1984) the WAM can represent more accurately the actual altitudinal preference of a species than the midpoint. Then we checked the relation between the midpoint and the WAM through an OLS regression with the midpoint as independent variable. We inspected the graph and considered that any species placed outside of the 95% CI of its WAM presented a significant rescue effect, *i. e.*, its WAM presented a significant deviation from its midpoint. We included only species with large ranges (defined here as those present in at least four altitudes), since both Rapoport and Alternative rescue effect are attributed to large range species.

Finally, we present the RSFD (range size frequency distribution) and the altitudinal range profile of the community. We produced the RSFD by plotting the range size of each species, ordered by range size. In the altitudinal range profile, species are represented by their range and WAM and are ordered by their WAM in an increasing manner. Due to the large number of species, we divided the altitudinal range profile in three groups, according to the range size: short (present at just one altitude), medium (two to three altitudes), and large (four to six altitudes).

Results

1. Richness patterns and sampling completeness

We obtained a total of 3,140 adult spiders, which were sorted to 529 morphospecies, representing 196 genera and 39 families. A complete list is presented in Nogueira et al. (2014).

The species richness of spiders decreased with increasing altitude. The decrease was monotonic and was observed for all four richness and diversity measures employed (Table 1). While the observed and rarefied richness and D showed a more or less gradual decline, the interpolation greatly increased the number of species of the second altitude (400 m), which became only slightly lower than the richness of the first altitude

(Figure 2). The remaining richness measures declined monotonically. Abundance also decreased along the gradient but the decline was not monotonic. Notably, the second altitude presented a relatively low number of individuals. Nonetheless, abundance remained quite high until the fourth altitude (1,550 m), and then presented a steep decrease, although remaining similar between the two highest altitudes.

The rarefied richness values indicate a monotonic decline in richness (Figure 3), but the rarefaction curves also allow us to evaluate the diversity pattern of the community. It is possible to see that the two first altitudes, the most species-rich, possess a very similar diversity pattern, and there is an overlap of those two altitudes confidence interval.

Richness declines more in the two following altitudes, but the fifth altitude, at 2,000 m, presents a considerable diversity, and its confidence intervals overlap with the interval from the altitude below, at 1,550. Even though the richness obtained at 2,000 is much lower than that of the preceding altitude, the slope of the curve indicates that this is more due to the low spider abundance at this altitude. The last altitude sampled presented a much smaller richness, and the value and shape of the rarefaction curve, beginning to stabilize, show that it represents a much less diverse community.

Richness at higher taxonomic levels presented a similar pattern to that observed for species, with decreasing richness along the gradient, but there is an inversion between the two first altitudes, and a slightly higher number of genera and families is found at 400 m than at 100 m. This is an effect of interpolation, which had already greatly increased species richness at the second altitude, although not enough to overcome richness at 100 m. It indicates that the broader distribution of genus and families along the gradient, based on a increasingly higher number of individuals enhance the possibility of interpolation, in addition to reduce the differences in richness along the gradient, which make the decrease in richness less steep than that observed for specific level.

2. Richness predictors – MDE and altitude

The variation of spider species richness across the gradient (Figure 4) was negatively related to altitude, and the contribution of MDE to the observed pattern was negligible (Table 2). The Altitude model was able to explain 97.9% of the variation, with the lowest AICc. The MDE model had an extremely weak and non-significant fit with spider species richness. Altitude was also selected as the best model for genera and family richness, but the explained variation decrease with increasing taxonomic level, although remaining quite large (Table 2).

Table 1. Abundance and richness by altitude. For species we present the observed richness (S obs), interpolated richness (S int), numbers equivalents (D) and rarefied richness (Raref). For genera and families we present observed and interpolated richness.

Altitude	N	Genera			Families				
		S obs	S int	D	Raref	S obs	S int	S obs	S int
100	687	225	224	142.74	377.1	116	116	30	30
400	591	194	223	98.59	302.7	107	125	29	32
860	713	171	185	82.02	271.3	87	96	25	28
1550	597	115	120	61.68	197,1	71	79	23	25
2000	295	69	71	26.31	115,9	45	49	17	18
2400	257	24	24	6.10	34.1	22	22	11	11
Total	3140	528				196		39	

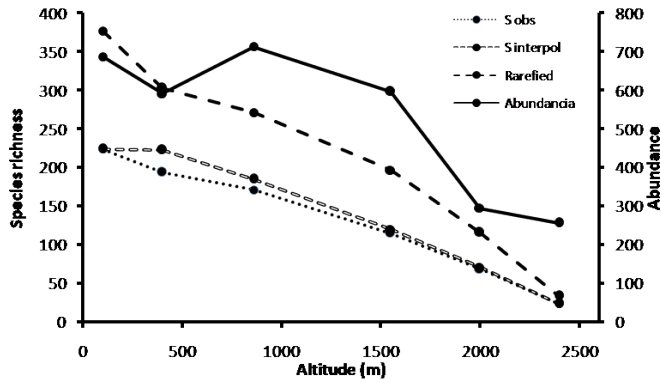


Figure 2. Abundance, observed, interpolated and rarefied species richness of spiders along the gradient of altitude at the Pico da Neblina.

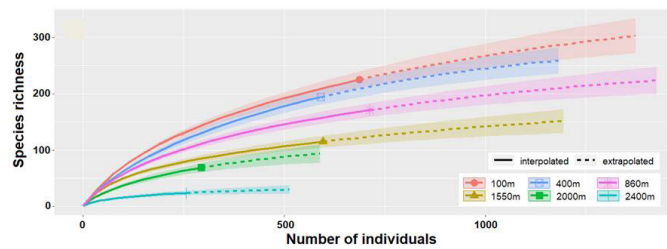


Figure 3. Rarefaction curves of spider species richness for six altitudes sampled at the Pico da Neblina. The full line represents the interpolated richness and the dotted line the richness calculated by extrapolation. The colored band surrounding the richness lines represents 95% confidence intervals.

3. RSFD and Rapoport effect

Most of the species (63%) had small ranges, occurring in just one altitude (Figure 5), while only 25 species, 5% of the total, had large ranges, encompassing at least half of the domain. The decrease in species number with increasing altitude for the three range sizes is visible in the range profile (Figure 5). Small range species peaked at the first altitude (100 m), and maintained a relatively high number of species until the fourth altitude (1,550 m). With increasing range size it is possible to see that the richness of mid altitude sites is largely determined by species from low altitudes. There is little overlap between species from the upper half of the gradient and those from the much more diverse lower part.

The test of the Rapoport effect showed that range size was not related to altitude ($R^2 = 0.003$, $p = 0.189$). The largest range species are situated at the center of the domain, and they decrease towards the gradient edges. The relation between range size and altitude performed for the 243 species represented by at least three individuals were also very weak and not significant ($R^2 < 0.001$, $p = 0.666$).

4. Abundance distribution along the range

The WAM and the midpoint presented a significant positive relation ($R^2 = 0.473$, $p < 0.001$). The WAM of almost half (12) of the 25 large range species presented a significant deviation from its midpoint. Among them, seven had a WAM smaller than the midpoint (upwards range expansion) and five had a WAM larger than the midpoint (downwards range expansion).

Discussion

The results revealed that spider species richness declined monotonically along the altitudinal gradient at the Pico da Neblina. The estimated richness

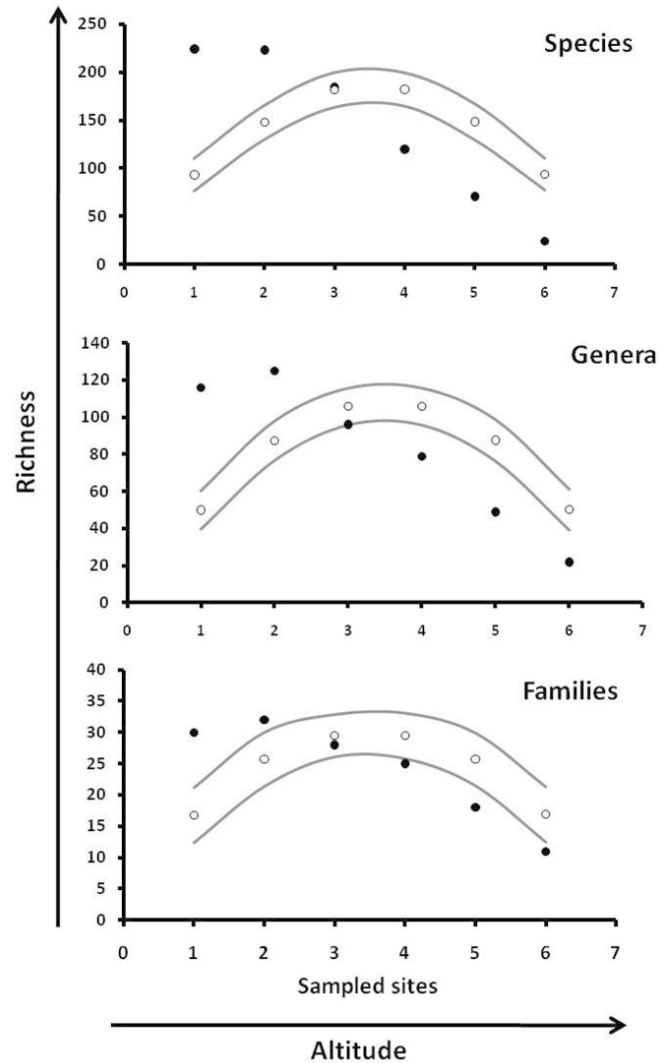


Figure 4. Observed richness (closed circles) and mean richness estimated by the MDE (open circles) based on 1000 randomization, with 95% confidence intervals (grey lines). Data include all the spiders sampled at Pico da Neblina.

values produced by the coverage-based rarefaction reveal some interesting patterns. The values calculated to the first two altitudes predicts a community composed by hundreds of species, a richness similar to that obtained in other spider inventories from lowland Amazonian terra-firme forests (Dias & Bonaldo 2012, Bonaldo & Dias 2010, Höfer & Brescovit 2001).

The rarefaction/extrapolation curves also helped to highlight the relative high diversity recorded at the 5th altitude, at 2,000 m. Even though the richness obtained at this altitude is much lower than that of the preceding altitude, the slope of the curve indicates that this is more due to the low spider abundance. So, during the transition from montane forest to high-altitude open habitats, the abundance of the community presented a larger decrease than the diversity itself. Only at the highest altitude sampled the richness really dropped, and since the curve shows signs of stabilization the number of species still to be detected is probably not very large.

The negative relation with altitude and the lack of any apparent influence of the MDE on the richness patterns points that the species distribution along the gradient is not explained by random processes, and the lower altitudes represent a more favorable environment for most species, resulting in higher richness and abundance.

Spiders richness in an altitudinal gradient

Table 2. Results of the multiple regression performed among spider richness and three explanatory models, altitude, richness estimated by the MDE simulations, and Altitude + MDE. We present the Akaike Information criterion (AICc), Delta AICc, coefficient of determination and probability in F test for the three models to the specific, generic and familiar level. Models are ordered according to the AICc.

	Model	AICc	Delta AICc	R ²	p
Species	Altitude	63,676		0.979	< 0.001
	MDE + Altitude	80.318	16.642	0.998	< 0.001
	MDE	86.847	23.171	0.022	0.777
Genus	Altitude	61.148		0.941	0.001
	MDE	77.811	16.664	0.05	0.669
Family	MDE + Altitude	84.061	22.913	0.982	0.002
	Altitude	46.069		0.883	0.005
	MDE	58.176	12.107	0.117	0.507
	MDE + Altitude	62.588	16.52	0.988	1

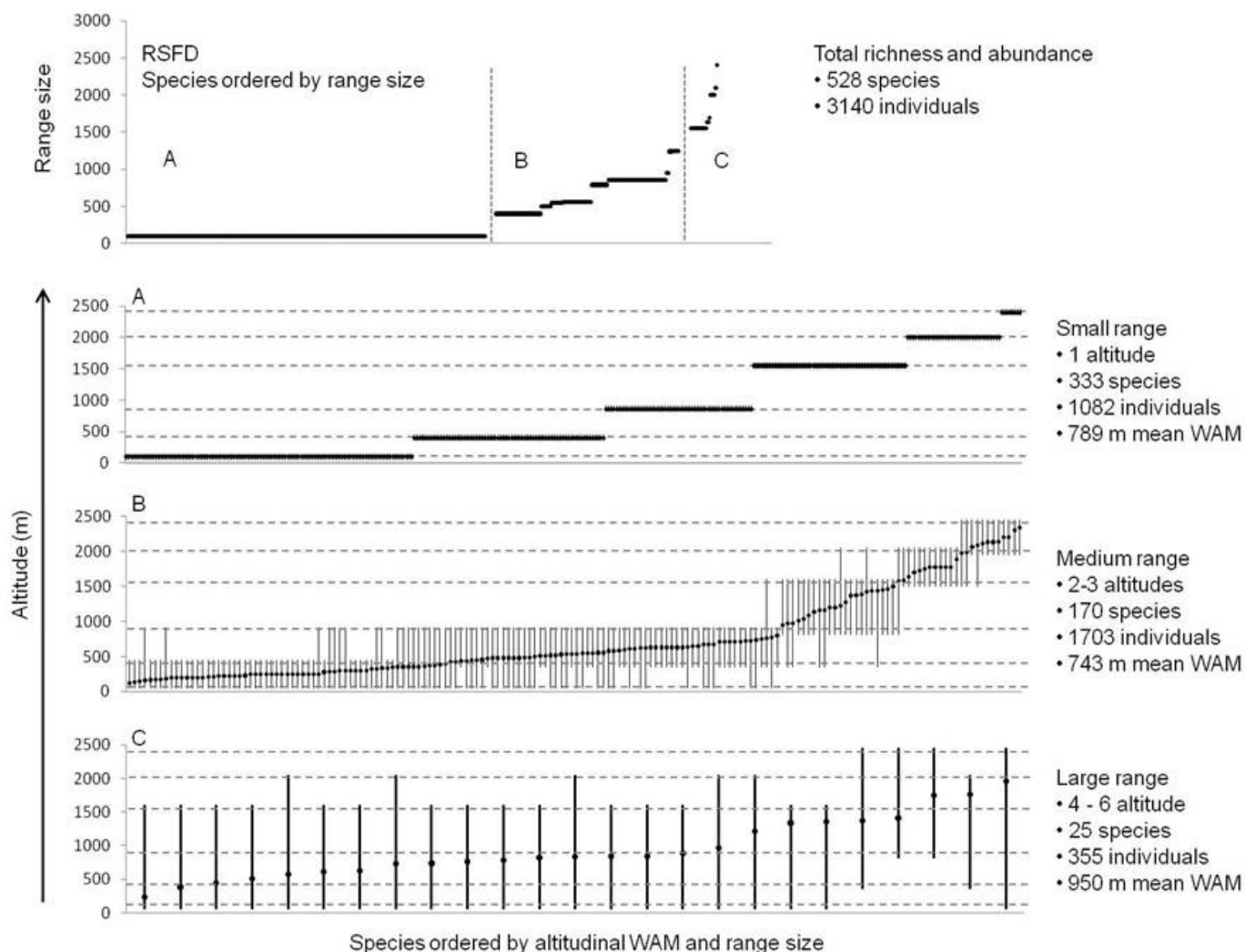


Figure 5. Range size frequency distribution (RSFD) of the spider community sampled at Pico da Neblina, and range profile of the species for three range size categories. Species in the RSFD graphic are represented by points and are ordered by increasing range size. Ranges are represented by vertical bars in graphs A, B and C, and their WAMs (weighted average midpoints) are represented by closed circles. Species are ordered according to the values of their WAMs and then by range size. Dotted lines at graphs A, B and C represent the six altitudes sampled.

1. Spider species richness at altitudinal gradients

Our results differ from most information available on spiders at altitudinal gradients (Olson 1994, Bosmans et al. 1986, Olson 1994, Chatzaki et al. 2005). However, differences in important factors, as sampling design, climate or target group demand a cautious approach when comparing the results. Some studies were performed on tropical mountains, but focused only on a subset of the community, like orb-weavers (Ferreira-Ojeda & Flórez-D. 2007) or canopy spiders (Russell-Smith & Stork 1994), or, in one case, on the fauna of an irrigated rice ecosystem (Sebastian et al. 2005). Moreover, they were not designed *a priori* to investigate altitudinal trends in a detailed manner, sampling as few as three altitudes or presenting very unbalanced designs, biased towards low altitude sites. As a consequence the high variability observed in the results, reporting a richness peak from the lowest, mid and even highest altitudes sampled, may be difficult to interpret.

More detailed studies reported a richness peak at mid-altitude sites. Some of them focused on litter-dwelling spider (Otto & Svensson 1982, McCoy 1990, Olson 1994) and this pattern was suggested to be an indirect consequence of optimal environmental conditions at those altitudes for herbivorous arthropods (Olson 1994), since precipitation often peaks at mid-altitudes (McCain 2007). Mid-altitude richness peak are also characteristics of studies from temperate localities (Otto & Svensson 1982, Bosmans et al. 1986, Chatzaki et al. 2005) which may indicate a different and more tolerant response of the temperate fauna to the decrease in temperature than that of the tropical fauna from our study, or to be a reflex of the greater environmental zonation at tropical mountains (Wiens & Graham, 2005, Ghalambor, 2006, McCain, 2009b). Additionally, the lower richness at lower altitudes may also be a consequence of human disturbance (McCoy 1990, Chatzaki et al. 2005), a problem already highlighted in others studies (Wolda 1987, Sanders 2002, McCain 2009a). Finally, mid-altitude richness peak could, of course, be due to geometric constraints, but this seems unlikely, as is exposed above.

2. Geometric constraints and richness predictors

The accumulation of information in the literature and its organization in recent reviews has challenged the importance of geometric constraints as a driver of richness patterns. Performance of MDE models as richness predictors has proven poor in several situations for several taxa (reviews in McCain 2007a, b, 2009a, Currie & Kerr 2008), and seems to be restricted to certain situations. Basically, the importance of geometric constraints increases at biome and regional levels (Jetz & Rahbek, 2001, Bellwood et al. 2005, Dunn et al. 2007, but see Rangel & Diniz-Filho 2005) and for large ranged species (Colwell et al. 2004, Dunn et al. 2007, VanDerWal et al. 2008).

Moreover, altitudinal gradients possess some characteristics that may make them inadequate to test MDE predictions. First, altitude is more closely related to area and temperature than latitude (Dunn et al. 2007). Moreover, environmental changes along altitudinal gradients are notoriously steep, exhibiting drastic changes over relatively small spatial scales, which may reduce average range size and, as a consequence, the influence of geometric constraints (Colwell et al. 2009). Finally, and more important, the very essence of geometric constraints theories, a domain delimited by hard boundaries, may be very questionable for altitudinal gradients. Lower limits of altitudinal domains, unless

located at the sea border or small islands, actually lack any evident geographic barrier.

Mountains from arid localities present a sharp climatic transition from dry lowlands to more humid places at mountain slopes, which may represent an environmental barrier at the base of the gradient. However, in mountains from humid, tropical localities, as the Pico da Neblina, the base is covered by the very same lowland forest that surrounds the gradient (in our case in a very large scale), what was termed as a “soft” (and ineffective) barrier (Colwell & Hurtt 1994). Moreover, while simulations clearly show that richness effectively decrease at the border of domains delimited by hard boundaries (Colwell & Hurtt 1994, Grytnes & Vetaas 2002, Rangel & Diniz-Filho 2005), models assuming soft boundaries at the gradient base with an underlying decreasing richness trend generates a pattern of monotonic decrease very similar to that observed in our study (Colwell & Hurtt 1994 – hybrid model, Grytnes & Vetaas 2002 – model III).

The application and effectiveness of the assumption of hard boundaries had already been scrutinized in several aspects (Laurie & Silander 2002, Zapata et al. 2005), but critics didn't include the asymmetry of boundaries in altitude gradients, although this characteristic was already highlighted when geometric constraints models were presented (Colwell & Hurtt 1994). Curiously, it hasn't been much taken into account since then and is not usually mentioned as one of the causes of poor performance of MDE models when richness decreases along the gradient (Almeida-Neto et al. 2006, Sanders et al. 2007, Liew et al. 2010, McCain 2010, but see Chettri et al. 2010). Given the above exposed, the lack of fit of MDE with our data, obtained from a small range community species (average range represents only 15% of domain size) on an altitudinal gradient on a local scale seems perfectly logical, and geometric constraints can be discarded as a meaningful driver of species richness pattern for our community.

Richness at higher taxonomic levels presented a small, low altitude, unimodal richness peak, due to interpolation. It indicates that the broader distribution of genus and families along the gradient, based on an increasingly higher number of individuals enhances the possibility of interpolation, in addition to reducing the differences in richness along the gradient, which makes the decrease in richness less steep than that observed for species level.

Concerning geometric constraints, it is possible to see in Figure 4 a gradual approach to the MDE prediction as taxonomic levels increase, although the relation remains small and not significant. This is a consequence of the great increase in range size (mean average range size in relation to domain size: genus – 29.1%, family – 55.1%) but it is also a final evidence of the lack of influence of geometric constraints on our richness patterns, given the already mentioned positive relation between range size and fit to MDE predictions. This is an unequivocal evidence of the influence of some strong environmental or historical gradient on our community.

Actually, our data indicates an intimate relation with temperature, an environmental factor that continuously declines with altitude (McCain 2007b, and references therein). The importance of climatic factors has obviously already been explored in numerous studies and its influence on altitudinal gradients was synthesized in the climate model proposed by McCain (2007b). Based on water availability and temperature, it predicts richness peaks at mid-altitudes in mountains located at arid environments and decreasing richness at mountains from

wet environments, which was corroborated by our study. Temperature was also exerted the most positive influence on ant species richness (Sanders et al. 2007).

Our richness patterns results are from the combined influence of several factors, and some hypothesis offer theoretic support for these, for example species-area relationship (SAR). One of the oldest patterns reported by ecologists (Hawkins 2001), SAR predicts a positive relation between area size and richness (Rosenzweig 1995), and has often been used as an explanatory factor with several positive results. However, recent studies failed to find significant area effects for several taxa at altitudinal gradients (Fu et al. 2006, Kluge et al. 2006, McCain 2007a, 2009a 2010, Beck & Chey 2008), and SAR also seems to have a larger influence on richness patterns at regional rather than at local scales (Lomolino 2001, McCain 2005, Romdal & Grytnes 2007). This suggests that an eventual bias in our data due to area effects is probably not very important.

3. Rapoport effect, rescue effect and RSFD

Our data didn't support a Rapoport effect, as range size was not related to altitude. The triangular pattern of our data is a product of the geometric constraints on range size (Colwell & Hurr 1994). As range size increases it has fewer possibilities of location and is constrained to have its midpoint near the center of the domain. This pattern will necessarily arise whenever large ranges encompass the whole domain. As a consequence, a RE may only be possible in the absence (or occurrence in a proportionally very small number) of short or/and medium range species at higher and even mid altitudes, or when ranges are small in relation to the domain, which reduces the geometric restrictions on their location.

Evidence of RE at altitudinal gradient is variable. As observed in relation to its application on the latitudinal gradient (Gaston et al. 1998, Ribas & Schoereder 2006), a considerable number of studies failed to find a significant positive relation between range size and altitude (Vetaas & Grytnes 2002, Grau et al. 2007, Liews et al. 2010), which reinforces the impression that it is not a general pattern. Other works, in contrast, presents evidences in its support (Fleishman et al. 1998, Sanders 2002, McCain 2009a), including the only study that verified its occurrence for spiders, more precisely, for ground dwelling spiders of the family Gnaphosidae in Cretan mountain ranges (Chatzaki et al. 2005). The authors attributed the results to the high environmental tolerance of this family, as several species, most of them from lowlands, occupied a large portion of the gradient. At the Pico da Neblina, on the other hand, most of the spiders had small ranges. This may reflect intrinsic differences between communities from tropical and temperate environments (although it is observed that Gnaphosidae seems particularly tolerant) and also may offer evidence of higher biological zonation on tropical mountains than on temperate ones. This would lead to narrower altitudinal ranges for tropical species, an old theory (Janzen 1967) that has recently received empirical support (Ghalambour et al. 2006, McCain 2009b).

The only study that assessed Rapoport effect for tropical arachnids investigated the altitudinal distribution of harvestman (Opiliones) from mountains of the Brazilian Atlantic coastal forest (Almeida-Neto et al. 2006), with positive results. Most of the large range species were from low altitudes, but, as their range encompassed most of the domain they also presented most of the highest midpoints, which produced the positive relation between

range size and altitude. At the Pico da Neblina, most of the large range species were also present at low altitudes (only four of the 25 large ranged species were not recorded at the first altitude), but an important number of short and medium range species were recorded at all altitudes, preventing a Rapoport effect. Logically, the different result may reflect differences in the biology of spiders and harvestman, such as dispersal capacity, notoriously poor for the latter group (Mestre & Pinto-da-Rocha 2004, Pinto-da-Rocha et al. 2005), among many other factors that vary between the studies. But we can further hypothesized that the lower height of mountains sampled at the Atlantic Forests (gradient extent of 950 m, against 2,400 m for the Pico da Neblina) allowed a proportionally larger range expansion from lowland species as well as preventing, with few exceptions, the existence of high altitude specialists (Almeida-Neto et al. 2006).

Although almost half of the large range species presented an important range expansion based on the form of individual abundance patterns, interpreted as an evidence of rescue effect, the number of species expanding their range downwards and upwards was similar. This suggests a more specific variation in the response of species to the environmental changes along the altitudinal gradient, instead of a rescue effect at the community level, as predicted by both rescue hypotheses. This result contrasts with those observed for harvestman of the Atlantic forest (Almeida-Neto et al. 2006) and Gnaphosidae from Crete (Chatzaki et al. 2005). In both cases results signaled a predominant upwards range expansion (alternative rescue effect), which may be a consequence of the fact that most of these communities were formed by lowland species, as mentioned above.

There were no important downwards range expansions either, as expected by a Rapoport rescue effect. Nonetheless, daily temperature variations at high altitude tropical sites can be comparable to seasonal temperature variations at higher latitudes (Ghalambour et al. 2006, McCain 2009b), characterizing the environmental conditions theoretically responsible for the occurrence of Rapoport rescue effect as well as Rapoport effect itself. In our case, a characteristic of our study area may have prevented the occurrence of these phenomena. Forest formations that occupy the gradient up until around 1,800 m are abruptly replaced by open formations from 2,000 m, representing a very different kind of environment. This may lead to a higher degree of specialization of the spider fauna from these habitats (2,000 and 2,400 m), as they may be thus unable to expand their range significantly to lower, forested altitudes. An evidence of this is that most of the species with medium and large range present at the high altitude sites are more abundant at lower altitudes. If true, it may offer evidence that broader thermal tolerance does not necessarily leads to a broad environmental tolerance in a more general way. Instead, broader climatic tolerance could have evolved at the cost of competitive ability to face species from lower altitudes (Ghalambour et al. 2006), or it could represent just another requirement to the specialization for these high altitude formations.

Although our data supported neither Rapoport effect nor a strong rescue effect, positive results observed in other studies and the evidence that high altitude environments demands a broad thermal tolerances indicates that theories based on rescue effects should be tested more often, as they may clarify the mechanisms responsible for RE. We suggest that the calculation of the weighted altitudinal midpoint (WAM) (Almeida-Neto et al. 2006) may represent a useful and easily accessible tool for this purpose, as abundance data can be easily obtained in studies based on sampling at different altitudes.

Conclusions

Our study represents the most complete spider inventory performed along an altitudinal gradient on a tropical mountain. Richness declined monotonically with increasing altitude, suggesting a strong positive relation with temperature, while the influence of geometric constraints was extremely low. We claim that our results seem in accordance with the current state of knowledge on richness patterns along altitudinal gradients, and the poor performance of MDE models is a consequence of the inadequacy of altitudinal gradients (at least at humid tropical sites) to test geometric constraints hypothesis, which also seem to be supported by the literature. Our data didn't corroborate a RE either. Actually, most of the species with large ranges were mainly located from low to mid altitudes, but any significant relation between range size and altitude was prevented by the fact that medium and small range species, the vast majority of our community, occurred in all altitudes. Finally, we couldn't observe any strong rescue effect at the community level, which means that the direction of range expansion varied more specifically, and was not related to range size or altitude. By focusing on an important albeit little studied group, our study represents a contribution to the knowledge of species richness distribution along altitudinal gradient, which is important to test the universality of the models proposed to predict and explain richness patterns observed in mountains.

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Authors Contributions

André do Amaral Nogueira: lead the sampling trip, material identification, data analysis and writing.

Antonio D. Brescovit: helped in the identification of the material and provided resources and facilities to help this process.

Gilmar Perbiche-Neves: helped with submission and reviewing process.

Eduardo Martins Venticinque: conceptualized the study and assisted the first author in all the steps of the study, as well as providing financial and logistical resources.

Conflict of interest

The authors declare no conflict of interest

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