Chapter 7
Latitudinal Trends in Scorpion Assemblages of Brazilian Atlantic Forest: Do the Rapoport's and Bergmann's Rules Apply?

André F. A. Lira, Alessandra R. S. Andrade, and Stênio I. A. Foerster

7.1 Effects of Latitudinal Gradients in Biodiversity

Considering that species are not evenly distributed across space (Stevens et al. 2013), researchers have attempted to describe and understand broad scale patterns of biodiversity that characterize the world's biota (Darwin 1859; Wallace 1878; LaManna et al. 2017). Few species possess a widespread distribution across habitats, while most species are adapted to a limited range of environmental conditions, referred to as the ecological niche (Peterson 2011). Although niche breadths are generally thought to vary positively with latitude (e.g., Sunday et al. 2011; Papacostas and Freestone 2016; Sexton et al. 2017), a better comprehension of such geographic patterns in species diversity is mandatory for ecological studies with conservation backgrounds (Gaston 2000; Whittaker et al. 2005). In such a context, one of the best-known patterns of species distribution is the latitudinal gradient expressed by an overall increase in species diversity toward the equator (e.g., Brown 2014; Fine 2015; Roll et al. 2017). This geographical trend has been reported for several taxa, including birds, mammals, reptiles, arthropods, and mollusks (Willig et al. 2003; Hillebrand 2004; Kinlock et al. 2018). However, others such as parasitic species and

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A. F. A. Lira (✉)
Programa de Pós-Graduação em Biociência Animal, Universidade Federal Rural de Pernambuco, Recife, Brazil

A. R. S. Andrade
Centro de Ciências Agrárias, Ambientais e Biológicas, Universidade Federal do Recôncavo da Bahia, Cruz das Almas, Brazil

S. I. A. Foerster
Department of Zoology, Institute of Ecology and Earth Sciences, University of Tartu, Tartu, Estonia
e-mail: stenio.foerster@ut.ee

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taxa with narrow latitudinal ranges may show a positive or non-significant relationship with latitude (Visser et al. 2014; Timms et al. 2016; Brocklehurst et al. 2017).

Different hypotheses have been formulated to explain the effect of latitudinal gradient in biodiversity (reviewed in Pontarp et al. 2019), these hypotheses can be divided into three main categories: (i) ecological limits, (ii) diversification rates, and (iii) time for species accumulation (Mittelbach et al. 2007). In the first, competition for limited resources is a key factor that limits the number of species co-occurring in the same locality (e.g., Mittelbach et al. 2007; Rabosky 2009), and the niche conservatism is often evoked to explain the differential dispersal rates across latitudes (Wiens et al. 2010). In the diversification rate hypothesis, variation in speciation or extinction rates, which may occur faster in the tropics than temperate regions, exert an important role (Allen and Gillooly 2006; Weir and Schluter 2007). Finally, in the third category, historical colonization rates assume an unbalanced diversity dynamic, implying that regions that were colonized first are expected to harbor long periods of diversification, resulting in high levels of species richness (Stephens and Wiens 2003).

Interestingly, the processes behind latitudinal diversity gradients are still under debate (e.g., Fine 2015; Lomolino et al. 2016; Willig and Presley 2018). Several factors may explain the lack of consensus on the relative importance of the processes that generate and maintain such gradients in biodiversity (e.g., Latham and Ricklefs 1993; Willig et al. 2003; Weiser et al. 2017). It is well known, for example, that biodiversity gradients are expected to be driven by spatial ranges in species distribution (e.g., Cardillo et al. 2005; Mittelbach et al. 2007) and the taxonomic resolution (Weiser et al. 2007; Kreft and Jetz 2007). In some cases, latitudinal patterns in species richness are not generally attributed to latitude per se, but to the variation in bioclimatic conditions across latitudinal ranges. In this way, the macroecological approach evokes a set of biotic and abiotic covariables to explain the described patterns of biodiversity (e.g., Currie et al. 2004; Kaspari et al. 2004). For this, explanations for the latitudinal gradient of diversity make implicit assumption that these covariables of latitude are not taxon scale-dependent. For example, the area of a continent or the temperature of a habitat is independent of the taxonomic rank of the focal taxon (Weiser et al. 2018). Therefore, variation in species richness along geographical gradients may help us to understand the evolutionary history of organisms through the interplay between ecological adaptability and dispersal capabilities (Albuquerque et al. 2011; Silveira et al. 2019).

7.2 Rapoport and Bergmann Rules

Species' ecological traits and their tolerance to environmental factors act as a complex interplay constraining their dispersion and thus, determining their geographical ranges (Gaston 2003). In their monograph study, Rapoport (1975) found that latitude correlates with species distribution ranges. This author found that the range size of species was positively correlated with latitude, with smaller ranges for species occurring closer to the equator. Since the description of Rapoport's rule, many studies have tested Rapoport effects in different taxa (e.g., Liu et al. 2020; Murphy et al. 2020; Pie et al. 2021). Ruggiero and Werenkraut (2007) demonstrated that Rapoport's rule was applied particularly for the large, continental landmasses of the Northern Hemisphere and less so in other geographic regions. Applications of Rapoport rule in tropical regions and the Southern Hemisphere appear to be less well defined (Rohde 1996). Many studies in these regions support the existence of complex regional patterns, providing only partial support for Rapoport's rule (e.g., Fortes and Absalão 2004; Pintor et al. 2015; Núñez-Flores et al. 2019).

In addition, species range size is fundamental for understanding of many life sciences disciplines, such as ecology, biogeography, and conservation, and has received significant research attention throughout the decades (e.g., Jablonski and Roy 2003; Böhm et al. 2017). For example, through the determination of drivers of range size we can measure the level of extinction risk of species. Large-ranged species generally possess a large environmental tolerance (Jablonski and Roy 2003) and lower extinction risk than small-ranged species that exhibits a higher environmental specificity, which may result in elevated extinction risks (Purvis et al. 2000; Lee and Jetz 2010; Böhm et al. 2017). Thus, understanding the drivers of range size in species can provide valuable information about appropriate conservation actions for range-restricted species. Therefore, studies at macro-scale are particularly important for testing the universality of latitudinal Rapoport's rule, principally in the Southern Hemisphere.

Furthermore, to richness and range size, latitudinal gradient may affect the ecological traits of species with many of these traits being influenced by body size (Peters and Wassenberg 1983; Smith and Lyons 2013). Body size mediates several aspects of an animal's life history, such as life span, clutch size and growth rate, and its variability across spatial gradients is a prominent topic in biogeography and ecology (Brown et al. 2004; Peters and Wassenberg 1983; Smith and Lyons 2013). The most known ecogeographical rule is the Bergmann's rule (BR), which predicts that closely related endothermic vertebrates increase in body size toward cold environments (Bergmann 1847; Blackburn et al. 1999). The mechanism proposed to explain this pattern toward colder sites is that heat generation capacity increases with body volume, whereas heat loss increases with surface area in endotherms (Blackburn et al. 1999). However, there is increasing evidence pointing that this mechanism is not universal (Blackburn et al. 1999; Meiri 2011). For ectotherm animals, on the other hand, there are comparatively few studies addressing whether variation in body size can be properly represented by latitudinal trends (Blanckenhorn and Demont 2004), with more evidences suggesting mixed indirect effects of latitude on body size variation in arthropods, as an example (Chown and Gaston 2010; Entling et al. 2010; Tseng et al. 2018). For these animals, previous studies have demonstrated that either an increase, or decrease in body size may associate to colder climates, as expected by Bergmann's rule and the so-called converse BR, respectively (Shelomi 2012; ; Scriven et al. 2016). The application of BR to ectotherms is justified by the dependence of environmental temperatures required for these animals to thermoregulatory activities. This implies that thermoregulation in larger ectotherms is expected to be less efficient in cooler climates because they absorb heat more slowly than the smaller ones (Aragon and Fitze 2014). In contrast, the converse BR posits that colder sites limit the time available for foraging and growth, resulting in smaller organisms (Mousseau 1997; Blanckenhorn and Demont 2004). Therefore, these mixed results in the application of BR to ectotherms has been hotly debated, because both geographical patterns have been found (Chown and Gaston 2010).

7.3 Scorpions as Organism Model in Ecological Studies

Scorpions constitute one of the oldest groups of terrestrial arthropods, with their first records dated to the Silurian (Kjelleswig-Waering 1986; Jeram 1998; Dunlop 2010). Due to the long evolutionary period and low modification in the basic *bauplan*, these animals are considered living fossils (Polis 1990). Corresponding to the fifth highest order of Arachnida in terms of species richness, scorpions are currently represented by about 2600 species (Brazil and Porto 2011; Rein 2021), with a total estimated diversity of around 7000 species (Coddington and Colwell 2001). In general, these arachnids present a wide spectrum of ecological requirements, being distributed in a plethora of habitats (e.g., tropical forests, dry forests, mountain tops, deserts, caves, and urban centers) across almost all landmasses (Polis 1990; Lourenço 2015). Scorpion richness seems to be maximized in arid and semiarid environments, with local assemblages being usually represented by an average of 5–6 species (Polis 1990, 1993; Porto et al. 2014), although neotropical forests can eventually harbor a comparable number of species at local scales (Lourenço 1994; Brito and Borges 2015). Despite their wide distribution, scorpions cannot be considered as ecologically generalist, as the vast majority of species have specific requirements regarding habitat and microhabitat (Polis 1990).

Several evidences suggest that scorpion assemblages are, in part, driven by environmental temperature, precipitation, type of substrate (e.g., soil hardness, litter quantity), vegetation structure, as well as by the complex interaction among these factors (Warburg and Ben-Horin 1981; Prendini 2005; Foord et al. 2015; Lira et al. 2019a, 2021a). In some cases, the responses of scorpion assemblages to the environmental variation may be detected even at very small spatial scales (Raz et al. 2009; Foerster et al. 2020). For example, a strong correlation of species composition with climate variation was described by Foord et al. (2015) when investigating the effect of the altitudinal gradient on a mountain system in South Africa. Species of the genus *Hottentotta* Birulla, 1908 and *Parabuthus* Pocock, 1890 were absent in areas where rainfall was above 600 mm. Similar results were described by Prendini (2005) when investigating the scorpion assemblage along a longitudinal gradient in the southern region of Africa, finding that species of *Afroisometrus* Kovarik, 1997, *Lychas* C. L. Koch, 1845, *Cheloctonus* Pocock, 1892, *Pseudolychas* Kraepelin, 1911 and *Opistacanthus* Peters, 1861 were restricted to areas with high rainfall such as montane forests. In a recent study, Lira et al. (2019a) investigated the effects of bioclimatic variables across a longitudinal gradient on Brazilian scorpions. These authors found that variables associated with precipitation and temperature had a strong effect on scorpion distribution.

On a local scale, even within the habitat, scorpions are not randomly distributed within the environment. Different substrates exert different selective pressures on scorpions, resulting in microhabitat-specialist species (Polis 1990; Prendini 2001). In a study carried out in a humid forest enclave in northeastern Brazil, no niche overlap was detected between the three scorpion species (*Tityus brazilae* Lourenço and Eickstedt 1984; *T. neglectus* Mello-Leitão 1932 and *T. pusillus* Pocock 1893) that co-occur in the area with each one collected exclusively in specific microhabitats (Lira and DeSouza 2014). Similarly, when analyzing the use of microhabitat in Colombian species from a dry forest fragment, Álvarez et al. (2013) described that *Opisthacanthus elatus* (Gervais 1844) and *T. tayrona* Lourenço 1991 preferentially use fallen objects (trunks and stones) while *T. ashtenes* Pocock 1893 and *Ananteris columbiana* Lourenço 1991 were frequently found in vegetation and litter, respectively. Such specificity in microhabitat selectivity can be observed even in species that coexist on the same substrate. Lira et al. (2013, 2018) investigating the use of microhabitat in Atlantic Forest scorpions, found a vertical stratification in two litter species, with *T. pusillus* colonizing the upper layers, while *Ananteris mauryi* Lourenço 1982 uses the lower layers of the litter. Due to environmental requirements, whether regional (climate variation) or local (microhabitat specificity), scorpions are responsive to habitat modification. Smith (1995) studying the effect of habitat fragmentation in Australia, reported that larger fragments support higher abundance and richness of scorpions than smaller fragments. Similar results with higher scorpion richness observed in larger fragments have been described for a hyper-fragmented Brazilian Atlantic Forest landscape (Lira et al. 2016). These authors suggested that larger fragments have a greater number of microhabitats available in relation to smaller ones, thus supporting a greater diversity of these arachnids. In a study conducted on locations with different usage histories in the Caatinga, Foerster et al. (2020) corroborates the idea that environmental complexity is crucial for the maintenance of local species pool. In this work, the authors found more species in areas that presented greater environmental complexity than in monotonous landscapes. Therefore, the sensitivity of scorpion species to environmental variations at different scales (regional or local) make these animals good candidates for environmental bioindicators. Polis (1990) argues that scorpions meet a series of criteria that frame them as bioindicators, such as being easily sampled, classified and stored. In addition, Gerlach et al. (2013) point out that these arachnids have a high potential as bioindicators, and may even be used as flagship species, due to their charisma. However, the authors emphasize that the low diversity and abundance in many areas can act as a limiting factor for their potential use as bioindicators. Within this context, scorpions have been used as models for ecological studies that address environmental changes, especially in Neotropics (e.g., Nime et al. 2014; Lira et al. 2020, 2021a).

7.4 The Brazilian Atlantic Forest

As the second largest rainforest biome on the American continent, the Brazilian Atlantic Forest is one of the 36 global hotspots in biodiversity conservation (Conservation International 2009). The exuberant biodiversity contained in Brazilian Atlantic Forest has been continuously threatened by habitat loss and fragmentation due to anthropogenic activities (Laurance 2009; Haddad et al. 2015). Such human activities were (and still are) one of the major drivers affecting the current spatial configuration of the Atlantic Forest, represented today by small islands of vegetation inserted in a matrix of areas converted to the human settlements (Ribeiro et al. 2009; Joly et al. 2014; Haddad et al. 2015; Rezende et al. 2018). These factors, together with other threats to the biome (e.g., hunting and illegal logging), have led to the extinction of numerous species (Marini and Garcia 2005), compromising regions where important centers of endemism are located. Nowadays, the estimated fraction of original vegetation cover in the Atlantic Forest is estimated in only 28%, which includes native forest and non-forest formations (Rezende et al. 2018). Those original formations are extremely important to assure ecological corridors aimed to improve the connectivity among Atlantic Forest patches (i.e., fragments) within the landscape, preventing populations from deleterious effects of genetic isolation and improving their capacity to remain viable over time (Rezende et al. 2018).

High levels of endemism in the Brazilian Atlantic Forest were detected for several taxa, such as bees (Garraffoni et al. 2017), harvestmen (DaSilva et al. 2015), birds (Marini and Garcia 2005; Carvalho et al. 2021), and anuran (Vasconcelos et al. 2014). Different hypotheses have been formulated to explain the causes of the high diversity and endemism in the Atlantic Forest. For example, tectonic activities, marine introgressions, Pleistocene refuges (Martins 2011), and environmental gradients shaped the distribution of lineages in this biome. In the latter case, environmental gradients along the same biome would favor speciation (Silva and Casteleti 2003) and would limit the distribution of species in time and space.

The Atlantic Forest has a wide geographic distribution extending along the entire Atlantic coast of Brazil (Galindo-Leal and Câmara 2003) originally ranged between latitudes 6° S and 30° S and covered approximately 1.1 million km^2. It is characterized by strong environmental gradients, seasonality (Ribeiro et al. 2009), and complex topography. Their latitudinal gradient reveals a biome with a vegetational complex, described below, and climate heterogeneity (Fiaschi and Pirani 2009; Oliveira-Filho et al. 2015). Some researchers have demonstrated the role of climate on floristic differentiation, along altitudinal gradients and between geographic regions in the biome (Oliveira-Filho and Fontes 2000; Joly et al. 2012; Eisenlohr et al. 2013). Temperature and precipitation, for example, varies in a north–south gradient (Oliveira-Filho and Fontes 2000), where the decreasing temperatures toward higher latitudes and altitudes along the coast (Oliveira-Filho et al. 2015) which influence several species. In addition to historical factors, these climatic variations contribute to the high turnover of species in the biome (Condit et al. 2002; Silva et al. 2014; Nogueira et al. 2019).

This complex biome is composed of three forest types influenced by rainfall regime: the Dense Rainforest, the Mixed Rainforest, and the Seasonal Forest (Oliveira-Filho and Fontes 2000). The Dense Rain forests (or ombrophilous forest) are located on the Atlantic coast and are distributed in lowlands (generally the climate is hot and wet) and slopes (climate cold and wetter) from northeastern to southern Brazil (Oliveira-Filho and Fontes 2000), where rainfall is increased by oceanic winds and mountain ranges, especially in the south (Cancello et al. 2014). Associated with the vegetation in lowlands it presents the "*restinga*," characterized by drier climate and sand soil (Marques et al. 2011). Mixed Rain forests, also known as Araucaria forests because of the presence of the conifer *Araucaria angustifolia* (Bertol.) Kuntze, constitute the main forest type on the highland plateau in southern Brazil. The mixed rain forest is characterized by tropical and sub-tropical humid climates without pronounced dry periods. Seasonal forests are characterized by two distinct seasons with marked seasonality (summer with intense rainfalls and winter with low temperatures and scarce precipitation) and extends across the plateau (usually 600 m elevation) in the center and southeastern interior of Brazil (Oliveira-Filho and Fontes 2000) and are influenced by Cerrado biome.

Several mountain ranges and cliffs compose the Atlantic Forest landscape along the latitudinal gradient. Originally, more than 80% of their area occurred at elevations from 200 to 1200 m (Tabarelli et al. 2010). In some high altitudes can be observed an increase in precipitation and humidity (Camara 2003). For example, in southeastern Brazil, the remnants located in "Serra do Mar" and "Serra da Mantiqueira" stand out where the occurrence of orographic rains provides greater humidity in these forests (Por 1992). Due to variations in altitude, we found in Atlantic Forest differences in the phytophysiognomy along its extension that, in addition to lowland forests, montane, and submontane forests. Differences in species composition in relation to the latitudinal gradient in the Atlantic Forest, which are influenced by climate and historical factors, have been the subject of several studies (e.g., Almeida-Neto et al. 2006; Martins et al. 2015; Nogueira et al. 2019; Shimabukuro and Trivinho-Strixino 2021). In this context, this chapter is intended to provide insights into the scorpion assemblages in a latitudinal gradient at Brazilian Atlantic Forest through application of Rapoport effect and Bergmann rule.

7.5 Case Study: Scorpion Assemblage Along Latitudinal Gradient in Brazilian Atlantic Forest

In order to investigate the applicability of Rapoport and Bergman's rules on scorpion assemblages along the latitudinal gradient in the Brazilian Atlantic Forest, we first georeferenced scorpion occurrence data were primarily extracted from public repositories, notably the Global Biodiversity Information Facility (GBIF 2021) and the SpeciesLink platform (CRIA 2021). All georeferenced data available for the order Scorpiones until 18 September 2021 were downloaded from both repositories.

Additional information on scorpion occurrence in Atlantic Forest was also added from scientific literature (Galiano and Maury 1979; Lourenço 2002, 2005; Yamaguti and Pinto-da-Rocha 2003; Lourenço and Giupponi 2004; Dias et al. 2006; Santos et al. 2006; Giupponi et al. 2009; Quintela et al. 2014; Lira et al. 2021a). Combined datasets resulted in a raw amount of 66,976 occurrences, of which, 2429 occurrences were used in downstream analyses as a result of the data cleaning process. This consisted in the exclusion of taxa that were not identified to Linnean species names, as well as those occurrences that fell outside the boundaries of a spatial grid of 0.5° × 0.5° pixel resolution, intersecting the spatial extent of the Brazilian Atlantic forest (Fig. 7.1). The spatial grid was drawn on QGis 3.18 (QGIS Development Team 2021) using a shapefile of the Brazilian Atlantic Forest provided by the MapBiomas project (MaPBiomas Project 2021) as a reference for the delineation of its spatial extent. Spatial operations (i.e., overlapping the spatial grid over the Atlantic Forest boundaries and scorpion occurrences) were performed in the R environment (R Core Team 2021) using the 'sf' (Pebesma 2018) and 'dplyr' (Wickham et al. 2021) packages and assuming the SIRGAS 2000 (EPSG: 4674) map

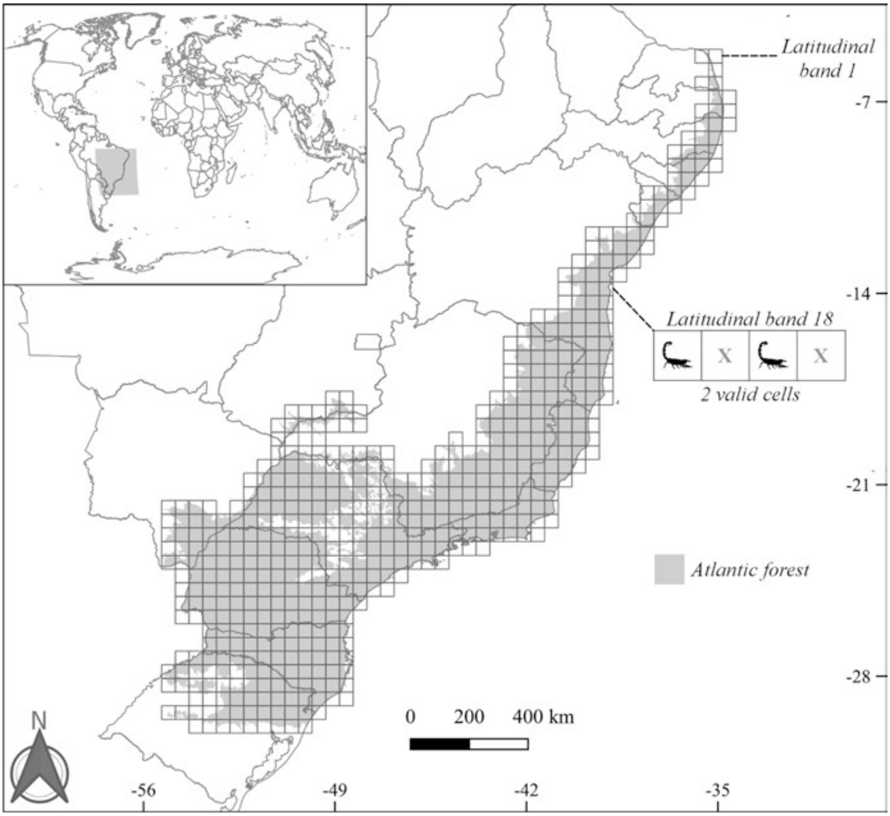

Fig. 7.1 Scheme of grid division applied in each scorpion species from Brazilian Atlantic Forest

projection. Species with dubious distributions within the Atlantic Forest were also excluded from the dataset based on our expertise about their ecological requirements and scientific information from the literature when available. Based on such criteria, the following species were removed from the dataset: *Bothriurus rochai* Mello-Leitão 1932, *Jaguajir rochae* (Borelli 1910), *Physoctonus debilis* (C. L. Koch 1840) – both typical species of Caatinga forests (Foerster et al. 2019; Lira et al. 2020); *Tityus obscurus* (Gervais 1843), *T. metuendus* Pocock 1897, *T. raquelae* Lourenço 1988 – Amazonian species (Martins et al. 2021); *Ananteris franckei* Lourenço 1982 and *B. araguayae* Vellard 1934 commonly found in montane forests of northeastern Brazil and Cerrado formations, respectively (Lourenço 2002; Foerster et al. 2019). The list of scorpion species of the Brazilian Atlantic Forest recovered in this study is presented in Appendix 7.1.

After this, the geographic range of each species was initially calculated as the latitudinal distance (in kilometers) between the northernmost and the southernmost location that each species was found (Lear et al. 2017). To this end, species with a single occurrence (singletons) were excluded from the dataset (Appendix 7.1). As described in the previous section, an average geographic species range per latitudinal band was obtained from the computation of a mean value of the geographic ranges of the species present in each latitudinal band. The average geographic species range per latitudinal band was then adjusted by the number of valid grid cells in each band (thereafter referred to as “latitudinal species range”). Species richness per latitudinal band was obtained by summing the number of species present in each latitudinal band (i.e., latitudinal species richness). The latitudinal species range, latitudinal species richness, and the absolute latitude of each latitudinal band were correlated in a pairwise scheme through the Spearman’s rank correlation coefficient with Holm’s adjustment of *p*-values. Statistical analyses (i.e., mean arithmetic adjustments and Spearman’s rank correlations) were performed in R using the ‘correlation’, dplyr, and ‘base’ (R Core Team 2021) packages.

A second dataset containing the carapace length of scorpion species listed in Appendix 7.1 was assembled based on direct specimen measurements and additional data from the literature. Previous studies have demonstrated that carapace length is a reliable proxy of body size in scorpions (e.g., Outeda-Jorge et al. 2009; Lira et al. 2021b). Moreover, the use of a single corporal structure (carapace) to represent body size in these animals is expected to minimize the error inherent to the measurement process, especially if compared to a more complex metric of body size, such as the total length. This is because total length can be obtained by both measuring the specimen at once – usually a straight line ranging from the anterior tip of the carapace to the distal tip of the telson – or by summing the length of its body parts separately. For the information extracted from the literature, the most recent publications were prioritized (Appendix 7.1) and an average carapace length was calculated when this metric was available for more than one specimen and sex, allowing the incorporation of a potential sexual dimorphism in this character.

To test the presence of latitudinal trends in body size of scorpion species distributed along the Atlantic Forest, the grid cells containing scorpion occurrences were initially identified. After that, those grid cells were consistently grouped according to the latitudinal position of their centroids, resulting in latitudinal bands across the Atlantic Forest (Fig. 7.1). All the species found in each of the latitudinal bands were translated to its measurements of body size, allowing the calculation of an average body size per latitudinal band (c.f. de Menezes et al. 2018). To account for the inevitable difference in the number of grid cells per latitudinal band (Fig. 7.1), the average body size calculated for each latitudinal band was adjusted by the number of valid grid cells (i.e., cells with scorpion occurrence) through the mean arithmetic approach:

$$\frac{\sum_{i=1}^{n} VCi \times BSi}{\sum_{i=1}^{n} VCi} = wBS$$

where, *w*BS corresponds to the mean body size per latitudinal band weighted by the number of valid grid cells in that band (thereafter referred as to "latitudinal body size"); VC*i* is the number of valid grid cells in the latitudinal band *i*; and BS*i* is the mean body size calculated for the latitudinal band *i*. The latitudinal body size was then correlated to the absolute latitude of each latitudinal band through the Spearman's rank correlation coefficient (ρ), thus, avoiding any assumptions about the shape of the relationship between these two variables or the potential noise due to the presence of skewed data (McDonald 2014; de Menezes et al. 2018). *P*-values for Spearman's correlation were adjusted using Holm's correction as implemented in the 'correlation' R package (Makowski et al. 2020).

We found a total of 28 species belonging to seven genera and two families (Bothriuridae and Buthidae) for the Atlantic Forest (Appendix 7.1, Fig. 7.2). Buthid scorpions are represented by four genera and 21 species, while bothriurids were represented by eight species grouped into three genera. Buthidae species show a widespread distribution in the Brazilian Atlantic Forest, species from *Tityus* C. L. Koch 1836 genera were found in practically all latitudinal gradient (Fig. 7.3). In contrast, other buthid genera such as *Zabius* Thorell 1893 showed a more limited distribution being found on the southern side of the latitudinal gradient, respectively (Fig. 7.3). Bothriurids scorpions were represented by genera *Bothriurus* Peters 1861, *Thestylus* Simon 1880, and *Urophonius* Pocock 1893, with *Urophonius* represented by one species and *Bothriurus* being more specious with four species. Scorpions from this family are also found throughout the latitudinal gradient (Fig. 7.3).

Species with the highest number of occurrences were also the widest distributed ones in terms of number of occupied grid cells (Fig. 7.4). In terms of genera, *Tityus*, *Bothriurus*, and *Ananteris* Thorell 1891 were the most abundant in number of occurrences, and together with genus *Isometrus* Ehrenberg 1828 presented the wider latitudinal ranges within the Atlantic Forest (Fig. 7.3). The latitudinal range of the scorpion species used to test the Rapoport's effect in Atlantic Forest ranged from 85.25 to 2625.46 km (Fig. 7.5). Although the largest latitudinal ranges were reported to the genera *Isometrus*, *Tityus*, *Bothriurus*, and *Ananteris* (Fig. 7.3), there was a considerable variation in the latitudinal range sizes among species within these

Fig. 7.2 Representatives of scorpion species found in Brazilian Atlantic Forest. (**a**) *Bothriurus asper* Pocock 1893, (**b**) *Thestylus aurantiurus* Yamaguti and Pinto-da-Rocha 2003, (**c**) *Ananteris mauryi* Lourenço 1982, (**d**) *Tityus adrianoi* Lourenço 2003, (**e**) *Tityus bahiensis* (Perty 1833), (**f**) *Tityus brazilae* Lourenço and Eickstedt 1984, (**g**) *Tityus neglectus* Mello-Leitão 1932 and (**h**) *Tityus pusillus* Pocock 1893. (Photos A, B and G by Dr. Leonardo Carvalho, C, F and H by Dr. Adriano DeSouza and D and E by Dr. Pedro Martins)

genera (Fig. 7.5), except for *Isometrus*, represented here by a single species *I. maculatus* (DeGeer 1778). Latitudinal species range increased toward the equator, as evidenced by the positive correlation ($\rho = 0.390$, $p = 0.016$) found between absolute latitude and latitudinal species range. Yet, there was also a strong positive correlation between the latitudinal species range and the latitudinal species richness ($\rho = 0.787$, $p < 0.001$). To a lesser extent, the latitudinal species richness was positively correlated to the absolute latitude ($\rho = 0.339$, $p = 0.023$), increasing toward the equator. At family level, buthid scorpions from the Atlantic Forest were the most variable in terms of body size (carapace length) than bothriurid species. Most of 50% of Atlantic Forest scorpion assemblage body size was composed by large-mid species (Fig. 7.6). *Tityus* species being overall larger than the species from the other genera in this environment (Fig. 7.6). Nevertheless, body size in Atlantic Forest scorpions was notably conserved among congeneric species (Fig. 7.6) and no latitudinal trends in this trait could be detected, as indicated by the Spearman rank correlation coefficient ($\rho = 0.227$, $p = 0.130$).

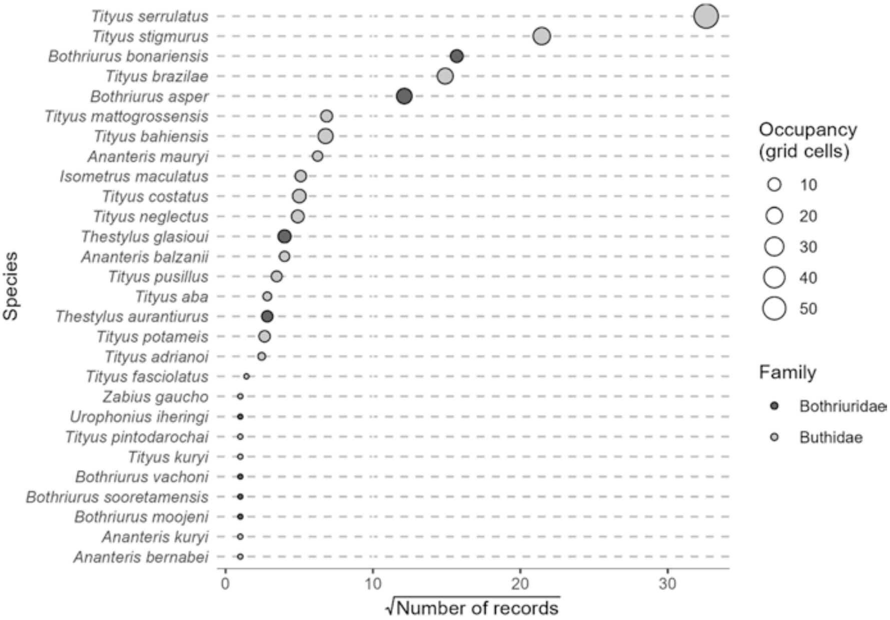

Fig. 7.3 Occupancy in grid cell in Brazilian Atlantic Forest by scorpion species

Our study was a first attempt to help in understanding the patterns behind scorpion diversity in an Atlantic Forest. The scorpions recorded from this biome belong to either Buthidae (70%) or Bothriuridae (30%), the two most diverse scorpion families in the Brazilian fauna (Lourenço 2002). Considering the higher degradation level of this biome (e.g., Ribeiro et al. 2009; Haddad et al. 2015), the Brazilian Atlantic Forest exhibited a greater number of species, corresponding to 20% of the Brazilian scorpion fauna. Most of this fauna is composed of forest-specialist scorpions, such as *T. brazilae*, *T. pusillus*, and *A. mauryi* (Porto et al. 2018; Lira et al. 2020). However, species considered typical of other biomes can occur in ecotonal regions with characteristics of the Atlantic Forest, such as the species *T. fasciolatus*, considered typical of the Cerrado (Savana-like vegetation: Lourenço 2002). We also found records of *I. maculatus*, an Indo-Malayan species, possibly introduced in several coastal regions of the world through ships (Kovařík 2003). In addition, Atlantic Forest scorpion fauna is composed also by species adapted to disturbed environments, such *T. serrulatus* and *T. stigmurus*, considered as synanthropic because of their intimate relationship with urban areas (Amado et al. 2021).

We found that scorpion diversity can be explained by the latitudinal gradient along the Brazilian Atlantic Forest with species richness increasing toward the equator. Although there have been no previous studies on the influence of latitudinal gradient on Atlantic Forest scorpion diversity, studies with other organisms, such as termites (Cancello et al. 2014) and epiphytic lichens (Menezes et al. 2018), indicate effects of latitudinal gradient on species richness similar to those found in this study. In contrast, studies with other animals such as harvestmen (Nogueira et al. 2019), bats (Stevens 2013), and leaf litter ants (Silva and Brandão 2014) described an

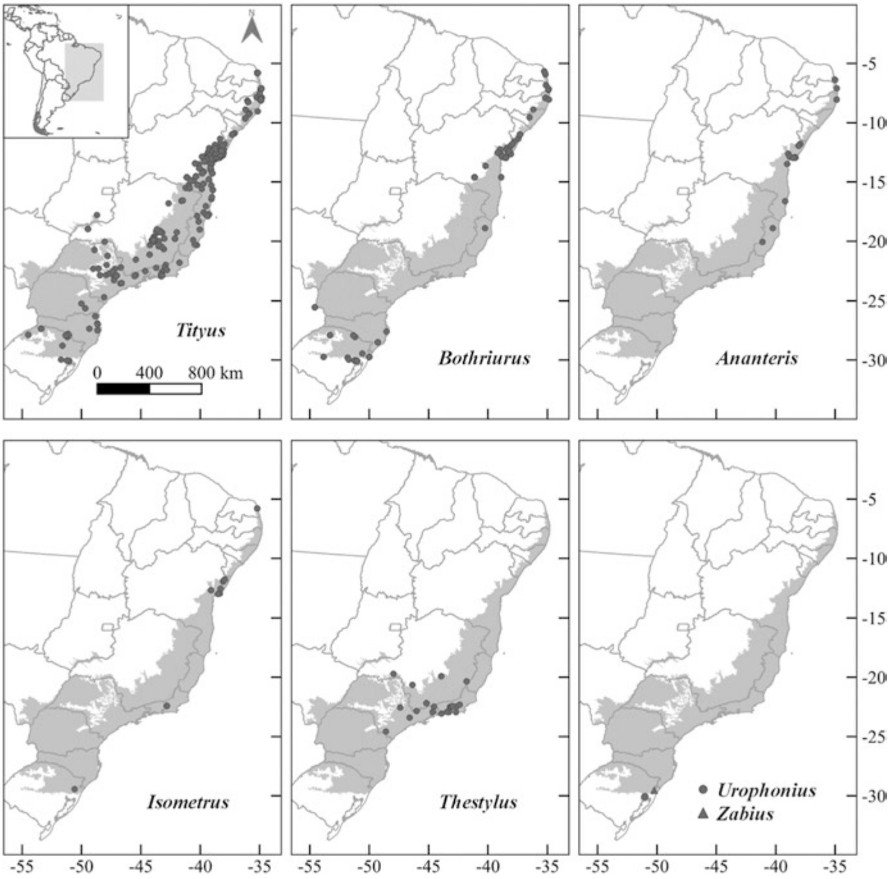

Fig. 7.4 Distribution records of scorpion genus along Brazilian Atlantic Forest

opposite pattern with species richness increasing toward the southern portion of Atlantic Forest. In latitudinal gradients we found a clinal variation in climatic factors, mainly temperature and precipitation, that are the major predictors of floristic structure (Prata et al. 2018). Habitat complexity generated by vegetation structure in a determined area, influencing the habitat structure and providing keystone structure (Tews et al. 2004). Therefore, habitats with greater microhabitat availability are associated with a high species richness once scorpion assemblages are composed of niche specialists, due to aggressive behavior between scorpion heterospecifics (Polis 1990; Lira et al. 2013, 2018). Alternatively, another possible and non-exclusive explanation for the increase in the scorpion species richness toward the equator is related to the species range size. In contrast to the proposed by Rapoport rule, our results pointed up an increase in range size toward the equator. Therefore, the higher species richness found on the north portion of Atlantic Forest may be an artificial artifact resulting from the overlapping distribution of species with a large range size.

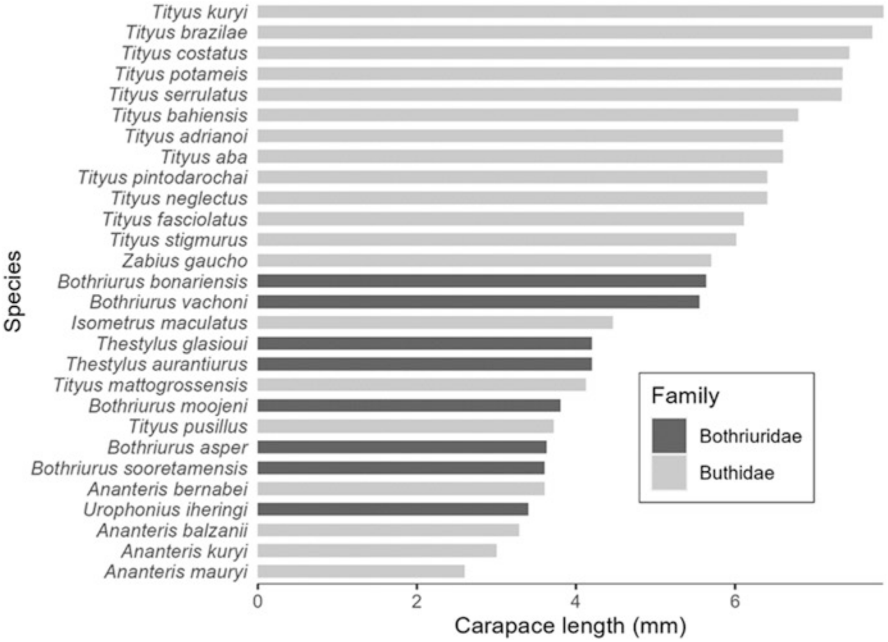

Fig. 7.5 Body size (in mm) of scorpion species from Brazilian Atlantic Forest

Scorpion species range in Atlantic Forest may be related to two main factors: (1) biological traits of these arachnids and (2) historical biome formation. In the first, scorpions are considered invertebrates with poor dispersal capacity (Polis et al. 1985) and dependent on forested habitats (Dionisio et al. 2018; Lira et al. 2019b). For example, Lira et al. (2019b) investigated the scorpion fauna in Atlantic Forest remnants and in their neighboring cropland. These authors found that scorpion species are unable to colonize the croplands being restricted to forested remnants. Although some scorpions may be found in disturbed environments such as urban areas (Brazil et al. 2009; Bertani et al. 2018), these species are exceptions and the majority of Atlantic Forest scorpions are forest-dwelling species (Lira et al. 2021a). In the second main factor, the historical process of Atlantic Forest formation was marked by successive forest reduction during climatic fluctuations and global cooling since the Pliocene or late Miocene (Holbourn et al. 2014; Ravelo et al. 2004). According to Carnaval et al. (2014), the northern portion of Atlantic Forest exhibited a more stable climate. In this way, larger mesic refugia were formed when compared to southern and southeastern portions. This complex process led to the proposal to delimit 12 areas of endemism for the biome, corresponding to two areas in the northern region and ten in the southern region (DaSilva et al. 2015). Therefore, these two main factors may have acted synergistically for the range size pattern found for Atlantic Forest scorpions. Contrary to our expectations, we found any

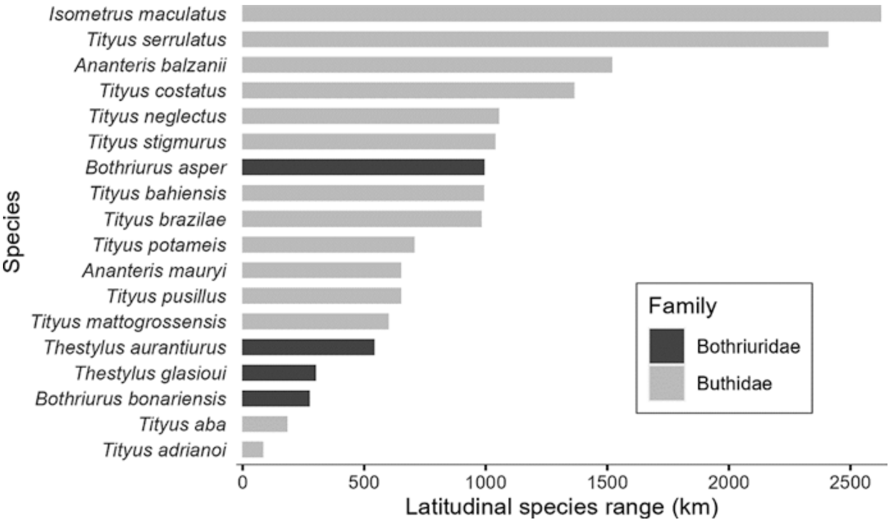

Fig. 7.6 Latitudinal range of each scorpion species from Brazilian Atlantic Forest

effect of latitude on scorpion body size. In addition, the body size of these arachnids seems to be conserved within genus and also within the subgenera (*Tityus* and *Archeotityus*) that subdivide the genus *Tityus* (Lourenço 2006) found in Atlantic Forest. Therefore, in Atlantic Forest, scorpions may be a result of a synergistic interaction encompassing both ancestry and environmental constraints, which, in many cases, may lead to the emergence of ecomorphotypes (Polis 1990; Prendini 2001; Koch et al. 2017).

In summary, this chapter provides a first insight of diversity patterns from Atlantic Forest scorpions. Overall, we found the three main results: (1) the species richness of these arachnids increases toward the equator as postulated in latitudinal diversity gradient hypothesis; (2) species range size follows an inverse that was proposed in the Rapoport rule with range size increasing toward equator; and (3) no latitudinal effects was detected on scorpion body size. These findings may reflect that scorpion natural history traits and historical processes of Atlantic Forest exerts a key role on diversity patterns of these arachnids along a latitudinal gradient in Brazilian Atlantic Forest. However, these findings may be interpreted with some caution as new collection expeditions and taxonomic revisions in progress may alter knowledge about the diversity of Atlantic Forest scorpions.

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Appendix 7.1

Scorpion species listed to the Brazilian Atlantic Forest. The occupancy refers to the number of 0.5° × 0.5° grid cells in which the species were present. "Rapoport" column states if the species were used to test the Rapoport's Effect in the Brazilian Atlantic Forest; all species listed below were used to test the adequacy of Bergmann's rule to the scorpion assemblages in the Brazilian Atlantic Forest. Bergmann's reference states the source of the carapace length was obtained.

Species	Records	Occupancy	Rapoport	Bergmann's reference
Bothriuridae				
Bothriurus asper Pocock, 1893	147	18	yes	Lira et al. (2021a, b)
Bothriurus bonariensis (C.L. Koch 1842)	246	10	yes	Olivero et al. (2012)
Bothriurus moojeni Mello-Leitao, 1945	1	1	No	San Martin (1967)
Bothriurus sooretamensis San Martín, 1966	1	1	No	San Martin (1966)
Bothriurus vachoni San Martín, 1968	1	1	No	San Martin (1968)
Thestylus aurantiurus Yamaguti & Pinto-da-Rocha, 2003	8	7	yes	Yamaguti and Pinto-da-Rocha (2003)
Thestylus glasioui Bertkau, 1880	16	11	yes	Yamaguti and Pinto-da-Rocha (2003)
Urophonius iheringi Pocock, 1893	1	1	No	Pocock (1893)
Buthidae				
Ananteris balzanii Thorell, 1891	16	5	yes	Outeda-Jorge et al. (2009)
Ananteris bernabei Giupponi, Vasconcelos & Lourenço, 2009	1	1	No	Giupponi et al. (2009)
Ananteris kuryi Giupponi, Vasconcelos & Lourenço, 2009	1	1	No	Giupponi et al. (2009)
Ananteris mauryi Lourenço, 1982	39	5	Yes	Lira et al. (2021a, b)
Isometrus maculatus (DeGeer, 1778)	26	7	Yes	Sulakhe et al. (2020)
Tityus aba Candido, Lucas, de Souza, Diaz & Lira-da-Silva, 2005	8	3	Yes	Candido et al. (2005)
Tityus adrianoi Lourenço, 2003	6	2	yes	Lourenço (2003)
Tityus bahiensis (Perty, 1833)	46	16	yes	Outeda-Jorge et al. (2009)
Tityus brazilae Lourenço & Eickstedt, 1984	222	19	yes	Lira et al. (2021a, b)
Tityus costatus (Karsch, 1879)	25	12	yes	Outeda-Jorge et al. (2009)
Tityus fasciolatus Pessôa, 1935	2	1	no	Lourenço (1980)
Tityus kuryi Lourenço, 1997	1	1	no	Outeda-Jorge et al. (2009)

(continued)

Species	Records	Occupancy	Rapoport	Bergmann's reference
Tityus mattogrossensis Borelli, 1901	47	8	yes	Outeda-Jorge et al. (2009)
Tityus neglectus Mello-Leitao, 1932	24	10	yes	Lira et al. (2021a, b)
Tityus pintodarochai Lourenço, 2005	1	1	no	Lourenço (2005)
Tityus potameis Lourenço & Leao Giupponi, 2004	7	7	yes	Lourenço and Giupponi (2004)
Tityus pusillus Pocock, 1893	12	6	yes	Lira et al. (2021a, b)
Tityus serrulatus Lutz & Mello, 1922	1063	58	yes	Outeda-Jorge et al. (2009)
Tityus stigmurus (Thorell, 1876)	460	24	yes	Lira et al. (2021a, b)
Zabius gaucho Acosta, Candido, Buckup & Brescovit, 2008	1	1	no	Acosta et al. (2008)

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