Vegetation structure as the main source of variability in scorpion assemblages at small spatial scales and further considerations for the conservation of Caatinga landscapes

Stênio Ítalo Araújo Foerster¹,², André Felipe de Araújo Lira³, Cauê Guion de Almeida⁴

¹ Department of Zoology, Institute of Ecology and Earth Sciences, University of Tartu, Tartu, Estonia
² Universidade Federal de Pernambuco (Departamento de Genética), Avenida da Engenharia, s/n, Cidade Universitária, CEP 50740-580, Recife, Brazil
³ Universidade Federal Rural de Pernambuco (Departamento de Morfologia e Fisiologia Animal), Rua Dom Manoel de Medeiros, s/n, Dois Irmãos, CEP 52171-900, Recife, Brazil
⁴ Universidade Federal Rural de Pernambuco, Unidade Acadêmica de Serra Talhada, Avenida Gregório Ferraz Nogueira, s/n, José Tomé de Souza Ramos, CEP 56909-535, Serra Talhada, Brazil

Corresponding author: Stênio Ítalo Araújo Foerster (stenio.foerster@ut.ee)

Abstract
Even at the local scale, environmental changes due to anthropogenic actions represent a source of disturbance in terrestrial ecosystems, forcing species to respond according to their ecological plasticity. Thus, stenotopic species and those with low-dispersal ability will likely be negatively affected by landscape modifications that reduce environmental complexity. In this study, we identify and quantify the effects of biotic and abiotic factors related to habitat complexity on the variation in scorpion assemblages in terms of both species’ richness, abundance and composition across 18 transects covering Caatinga landscapes with different levels of degradation. Using ultraviolet flashlights, we sampled 269 scorpions, belonging to six species and two families. The results showed contrasting patterns of species richness and abundance that depend on the level of habitat complexity. More specifically, we reported that scorpion species richness could be predicted by the number of trees, while the coefficient...
of variation of the diameter at breast height of trees (cvDBH) is a predictor of scorpion abundance. These findings suggest that vegetation structure is deterministic for the maintenance of scorpion assemblages in Caatinga landscapes. In addition, the cvDBH and tree number may explain 39% and 40% of the variability observed amongst scorpion assemblages in terms of richness difference and species composition, respectively. This study provides insights concerning the development of conservation strategies, clarifying the role of habitat complexity for the preservation of low-dispersal animals in neglected environments, such as those within the Caatinga domain.

**Keywords**
Biodiversity, environmental changes, habitat complexity, macroecology, SDTF

**Introduction**

Species composition derives from a combination of environmental factors and historical events attributed to a given area (Philippi et al. 1998), which can act synergistically to promote the establishment of different species in a community (Moura et al. 2016). As the response of species to environmental conditions may diverge according to their ecological requirements, the variation in species composition can be a sensitive tool to assess relevant environmental changes (Philippi et al. 1998; Pardini et al. 2009; Lira et al. 2019a, b). As a logical consequence, the variation in environmental factors can also be used to predict species interactions and community changes (Dunson and Travis 1991; Gilman et al. 2010). Furthermore, understanding the reciprocal processes of how different species interact with their environment is the main challenge and the central task in community ecology (Bühning-Gaese 1997; Sutherland et al. 2013). Clarification of the mechanisms that shape communities is thus essential to assess the functionalities of the ecosystems (Schneiders et al. 2012; Hou et al. 2013).

Our ability to determine the impact of environmental factors on species composition varies depending upon spatial scale. For instance, if ecological inferences are examined at small spatial scales, we expect that dispersal limitations would have a minor effect (if any) over the variation in species composition. In this scenario, individuals could have access to the resources available within a given area, meaning that space would act as proxy for dispersal limitation (Delatorre et al. 2015). This assumption is particularly true if we assume a background of undisturbed environments, especially those that share the same history of landscape composition. In contrast, it is plausible to presume that unstable or disturbed environments can experience significant changes in species assemblages, even at small spatial scales, especially if unequal sources of environmental variation (e.g. topography, land use, habitat fragmentation) are expected to occur within these landscapes (Filgueiras et al. 2019; Lira et al. 2019a, b). In addition, variation in assemblage composition can also be related to the ecological plasticity of their species, wherein dispersion over disturbed environments and habitat requirements may play a key role in the spatial distribution of the species (Cavender-Bares and Wilczek 2003; Fischer and
Vegetation structure as the main source of variability in scorpion assemblages (Lindenmayer 2007). Thus, species with low-dispersal ability, such as scorpions, are suitable for using as a model to infer the effects of environmental constraints of variation in species assemblages (Polis 1993; Husemann et al. 2012; Nime et al. 2014; Lira et al. 2019b), even at small spatial scales (Nime et al. 2013; Foord et al. 2015; Dionisio-da-Silva et al. 2018). Nevertheless, the knowledge regarding scorpion ecology in South America is scarce, especially those from open vegetation formations, such as the Chaco (Nime et al. 2014) and the Caatinga (Porto et al. 2014). These biomes harbour a relatively-high scorpion species richness (e.g. Acosta 1995a, b; Porto et al. 2014; Lira et al. 2018). The scorpion fauna from the Caatinga domain, for example, contains at least 33 described species (Porto et al. 2014; Esposito et al. 2017; Lira et al. 2017; Santos-da-Silva et al. 2017). However, few studies addressing the community ecology of Caatinga scorpions have been published (Araújo et al. 2010; Carmo et al. 2013; Lira et al. 2018, 2020).

In this study, we aimed to measure and disentangle community parameters (species composition, α-diversity and β-diversity components) of scorpion assemblages in Caatinga environments at small spatial scales. First, we explored the potential responses of scorpion assemblages to environmental features related to habitat complexity, identifying and testing the predictors of species richness and abundance, as well as the environmental sources of similarity in species composition. Second, we explored and disentangled the patterns of β-diversity to reveal the relative contribution of species replacement and richness, as well as their environmental determinants. Third, we quantified the local contributions to the estimated β-diversity across areas of Caatinga with different levels of degradation and tested their potential association with species richness to investigate if ecological uniqueness (sensu Legendre and De Cáceres 2013) is related to an increase or decrease in species richness in Caatinga landscapes.

Material and methods

Data sampling

Fieldwork was conducted in three areas of Caatinga vegetation with different levels of degradation in the Municipality of Serra Talhada (07°58’53.32"S, 38°17’21.21"W), State of Pernambuco, Brazil. The Parque Estadual Mata da Pimenteira (Pimenteira, 07°54’0.25"S, 38°18’0.58"W) is the most preserved area we sampled in terms of vegetation diversity (Suppl. material 1: Fig. S1), comprising a high number of woody species, such as Anadenanthera colubrina (Vell.) Brenan, Mimosa tenuiflora (Willd.) Poir and Croton sp. (Farias et al. 2016). In addition, the high diversity of vertebrates and invertebrates in the Pimenteira area is an indicator of its environmental quality (Santos et al. 2013). The second area is the Pollinator Trail (07°56’59.40"S, 38°18’0.76"W), located near the campus of the Unidade Acadêmica de Serra Talhada (UAST), which is less preserved than the Pimenteira area regarding woody plants. The vegetation in this area is mainly composed of herbaceous
plants (Suppl. material 1: Fig. S2), such as \textit{Tridax procumbens} \textit{L.}, \textit{Crotalaria incana} \textit{L.} and \textit{Alternanthera} \textit{sp.}, whereas the woody flora is sparse and mainly represented by \textit{Mimosa} \textit{sp.}, \textit{Croton} \textit{sp.} and \textit{A. colubrina}. Both herbaceous and woody plants are distributed in separated patches. Agricultural experiments, such as bean and corn cultivation, are frequently implemented around the Pollinator Trail as part of the curricular activities of the courses offered at the UAST campus. Saco Road (07°57′2.83″S, 38°17′40.09″W) is the third area, comprising the most homogeneous landscape (Suppl. material 1: Fig. S3), with vegetation cover mainly composed by herbaceous plants, such as \textit{Sida galheirensis} \textit{Ulbr.} and \textit{Waltheria} \textit{sp.}, without arboREAL or shrubby species. Livestock activities and the presence of a dirt road represent the most important sources of degradation at Saco Road, but this area is not considered an urban environment due to the lack of human habitations nearby. In each area, six straight-line transects of 30 m × 10 m were established (100 m apart).

All transects were sampled in March 2015 and September 2016 for five consecutive days each month (2–6 Mar 2015 / 1–5 Sep 2016). Scorpions were collected at night, by three collectors who randomly walked each transect for 1 h using ultraviolet flashlights to detect scorpions because they glow a bright cyan-green under ultraviolet light (Gaffin et al. 2012). At night, a thermo-hygrometer was used to measure the mean temperature and the mean relative humidity of the soil within each transect, based on three individual measurements performed at each 10 m along the centre of each transect. These variables were measured in both campaigns (March and September) and pooled for the computation of the overall mean values of temperature and relative humidity of the soil. Structural elements, including the amount of debris, number of trees and their diameter at breast height (DBH) were recorded during the day. For the amount of debris, we refer to the sum of the number of rocks (≥ 10 cm long), fallen logs (diameter ≥ 15 cm) and sticks (≥ 20 cm long) falling underneath a straight line (30 m long) extended along the centre of each transect. Trees that touched the reference line were counted and their DBH were measured. The structural elements cited above were counted in both campaigns and pooled for the computation of the overall mean values of the amount of debris observed in each transect. All environmental variables were recorded by the same collector (SIAF). Scorpions were identified according to Lourenço (2002) and Esposito et al. (2017). Voucher specimens are deposited in the Arachnological collection at the Universidade Federal de Pernambuco – Recife, Brazil (curator: Dr. Débora Almeida).

Data analysis

Sampling efficiency was estimated separately for each area (Pimenteira, Pollinator Trail and Saco Road) using rarefaction/extrapolation curves, based on the estimator of species richness described in Chao et al. (2014) and implemented in ‘iNEXT’ R package (Hsieh et al. 2020; R Core Team 2020). Considering that habitat heterogeneity can be represented by a quantitative estimation of structural elements present in a given area (McCoy and Bell 1991; Carvalho and Barros 2017), we therefore used the amount of debris (rocks, fallen logs and sticks), the number of trees and the coefficient
of variation of their DBH (cvDBH) as environmental proxies to represent habitat complexity in each transect. The cvDBH of the trees were obtained using the ‘raster’ R package (Hijmans 2020). Thereafter, the ‘usdm’ R package (Naimi et al. 2014) was used to compute the variance inflation factor (VIF) for all variables, confirming the absence of multicollinearity problems (VIF ≤ 5.82) according to the criteria proposed by O’Brien (2007). Responses of both species richness and abundance to habitat complexity were then modelled using generalised linear mixed-effects models (GLMMs) to account for the nested structure of our sampling design, which was included as a random term (Zuur et al. 2009). GLMMs were constructed using the ‘lme4’ package (Bates et al. 2015) in the R environment and fitted with a Poisson error structure after a prior square root transformation of the environmental variables to reduce asymmetries due to extreme values (Zuur et al. 2009). Models were initially fitted with all environmental variables and then simplified to contain only significant (p < 0.05) variables. The simplification procedure consisted of simply dropping non-significant predictors in decreasing order of significance (i.e. removing the variable with the largest p value after each instance where the model was fitted) until only significant variables remained (Zuur et al. 2009). After that, irregularities related to model overfitting were analysed using the χ² test of “goodness of fit” implemented in the ‘aods3’ R package (Lesnoff and Lancelot 2018). Correlation structures within the dataset were analysed using a principal component analysis (PCA) with prior standardisation (mean = 0, unit variance = 1) of input variables. In addition, similarity patterns in species composition amongst scorpion assemblages were graphically analysed using an UPGMA cluster constructed from a dissimilarity matrix of species composition, based on the quantitative form the Podani-family of the Sørensen dissimilarity index (Legendre 2014), estimated in the ‘adespatial’ R package (Dray et al. 2019).

The relative contribution of species replacement and richness difference to the overall β-diversity were accessed using the ‘adespatial’ R package taking the community matrix (sites × species) as input and applying the quantitative form of the Podani-family decomposition of Sørensen dissimilarity (Legendre 2014). This decomposition method was chosen because it returns Euclidean matrices of richness difference that are suitable for ordination methods (Legendre 2014) and required for the downstream analysis used in this study. Moreover, the Euclidean propriety can also be approximated for the species replacement matrix after a square root transformation (Legendre 2014; Borcard et al. 2018). Yet, the response of species composition to the habitat complexity proxy variables was modelled using a redundancy analysis (RDA) after a logarithmic transformation (Anderson et al. 2006) of the community matrix and the standardisation of environmental variables. Similarly, the influence of habitat complexity on both species’ replacement and richness difference (β-diversity terms) were measured using a series of distance-based redundancy analysis (dbRDA) as proposed by McArdle and Anderson (2001) and applying a Lingoes correction to avoid negative eigenvalues (Legendre and Anderson 1999); the species replacement matrix was square-rooted prior to dbRDA (Legendre 2014). For all constraining ordinations (RDA and dbRDA), we fitted full models containing all environmental variables and then applied a
forward selection to retain only significant \((p < 0.05)\) variables to the final models (Borcard et al. 2018). Statistical significance and explanatory power of these models were accessed using, respectively, permutation tests (1000 permutations) and the unbiased coefficient of determination \((R^2_{adj})\), proposed by Peres-Neto et al. (2006), both implemented in the ‘vegan’ R package (Oksanen et al. 2019). Finally, the local contributions to β-diversity (LCBD) were first quantified for each transect using the ‘adespatial’ R package and applying the Hellinger transformation to the community matrix and then regressed against the species richness observed in each transect using a simple Pearson correlation test implemented in the ‘stats’ R package (R Core Team 2020).

**Results**

A total of 269 scorpions were collected, comprising six species: *Bothriurus asper* Pocock, 1893, *Bothriurus rochai* Mello-Leitão, 1932, *Jaguarj ir agamemnon* (C.L. Koch, 1839), *Jaguarj ir rochae* (Borelli, 1910), *Physoctonus debilis* (C.L. Koch, 1841) and *Tityus stigmurus* (Thorell, 1876). The most abundant species were *J. rochae* \((n = 91)\), *P. debilis* \((n = 84)\) and *B. rochai* \((n = 73)\). All species were present in Pimenteira, of which, *J. agamemnon* and *T. stigmurus* occurred only in this location (Table 1). In terms of species richness, the sampling strategy and effort applied to collect scorpions delivered a satisfactory coverage of the assemblages present in the three areas (Fig. 1). The correlation structures amongst species abundance and environmental predictors revealed that the most abundant species (e.g. *J. rochae*, *B. rochai* and *P. debilis*) were mainly correlated with environmental features related to the vegetation structure, while climatic factors (temperature and relative humidity of the soil) correlated with low-abundance species, such as *B. asper*, *J. agamemnon* and *T. stigmurus* (Fig. 2A). Overall, environmental variables related to vegetation structure contributed more to the first two axis of the PCA than those variables related to climatic conditions (Suppl. material 1: Table S1). Additionally, Saco Road and Pollinator Trail were the

| Table 1. Species composition and absolute number of scorpion species collected at Pimenteira, Pollinator Trail and Saco Road (Pernambuco, Brazil). Specimens were collected in March 2015 and September 2016, during the rainy (R) and dry (D) season, respectively. The sample effort resulted in the collection of 269 specimens. |
|---|---|---|---|---|---|---|---|---|---|
| Species | Pimenteira |  |  | Pullinator Trail |  |  | Saco Road |  |  |
|  | D | R | Total | D | R | Total | D | R | Total |
| *Bothriurus asper* Pocock, 1893 | 1 | 3 | 4 | 2 | 2 | 4 | 2 | 3 | 5 |
| *Bothriurus rochai* Mello-Leitão, 1932 | 14 | 39 | 53 | 1 | 2 | 3 | 8 | 9 | 17 |
| *Jaguarj ir agamemnon* (C.L. Koch, 1839) | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Jaguarj ir rochae* (Borelli, 1910) | 19 | 44 | 63 | 7 | 12 | 19 | 5 | 4 | 9 |
| *Physoctonus debilis* (C.L. Koch, 1841) | 64 | 4 | 68 | 14 | 2 | 16 | 0 | 0 | 0 |
| *Tityus stigmurus* (Thorell, 1876) | 4 | 2 | 6 | 0 | 0 | 0 | 0 | 0 | 0 |
| Total | 104 | 92 | 196 | 24 | 18 | 42 | 15 | 16 | 31 |
most similar in terms of species composition and climatic characteristics (Fig. 2A) – a pattern also recovered when species composition was analysed separately (Fig. 2B).

Generalised linear mixed-effects models detected significant responses of scorpion assemblages to the vegetation structure observed in each transect: the number of trees had a positive effect upon species richness (estimate ± SE = 0.23 ± 0.1; \( z = 2.34; p = 0.02 \), Fig. 3A), whereas scorpion abundance could be predicted by the cvDBH of trees (estimate ± SE = 0.08 ± 0.03; \( z = 2.33; p = 0.02 \), Fig. 3B). Environmental predictors related to vegetation structure were markedly different amongst sampling localities, with Pimenteira being the most heterogeneous environment in terms of number and DBH of trees (Fig. 3C, D). No overfitting was detected during the modelling of species richness (\( \chi^2_{(15)} = 5.48, p = 0.99 \)) or species abundance (\( \chi^2_{(15)} = 21.38, p = 0.12 \)).

The decomposition of the total β-diversity (\( \beta_{total} = 0.30 \)) computed for the entire region (i.e. pooling the data from all sampling localities) revealed the large contribution of richness difference (80%) over species replacement amongst transects (20%). Species replacement could be explained only by temperature (dbRDA: \( F_{(1)} = 1.53, p = 0.01; R^2_{adj} = 0.03 \)). Pimenteira was the most variable site in terms of soil temperature differences (Fig. 3E). Variation in species richness were explained only by the number of trees amongst transects (dbRDA: \( F_{(1)} = 12.02, p < 0.01; R^2_{adj} = 0.39 \)). However, variation in the cvDBH of trees explained 40% of the species

Figure 1. Species rarefaction/extrapolation curves showing the sampling efficiency of scorpions collected at Pimenteira, Saco Road and the Pollinator Trail (Pernambuco, Brazil). Solid lines represent the species richness observed from the number of individuals collected in each site, while the dashed line is a prediction (extrapolation) of the species richness if the sampling effort were multiplied by two. Grey shades around the estimated sampling curves correspond to their 95% confidence interval.
Table 2. Absolute number of species and individuals collected from scorpion assemblages sampled at Pimenteira, Pollinator Trail and Saco Road (Pernambuco, Brazil). Scorpions were collected across 18 straight-line transects of 30 m × 10 m (six transects in each area). Geographical coordinates (longitude, latitude) were provided for each transect, as well as their local contributions to β-diversity (LCBD).

<table>
<thead>
<tr>
<th>Transect</th>
<th>Site</th>
<th>Longitude and Latitude</th>
<th>Number of species</th>
<th>Number of individuals</th>
<th>LCBD</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Pimenteira</td>
<td>-7.9065, -38.3002</td>
<td>3</td>
<td>36</td>
<td>0.0290</td>
</tr>
<tr>
<td>2</td>
<td>Pimenteira</td>
<td>-7.9054, -38.3003</td>
<td>3</td>
<td>40</td>
<td>0.0165</td>
</tr>
<tr>
<td>3</td>
<td>Pimenteira</td>
<td>-7.9045, -38.3004</td>
<td>3</td>
<td>26</td>
<td>0.0178</td>
</tr>
<tr>
<td>4</td>
<td>Pimenteira</td>
<td>-7.9035, -38.3005</td>
<td>5</td>
<td>34</td>
<td>0.0142</td>
</tr>
<tr>
<td>5</td>
<td>Pimenteira</td>
<td>-7.9027, -38.3008</td>
<td>6</td>
<td>36</td>
<td>0.0204</td>
</tr>
<tr>
<td>6</td>
<td>Pimenteira</td>
<td>-7.9016, -38.3010</td>
<td>6</td>
<td>24</td>
<td>0.0210</td>
</tr>
<tr>
<td>7</td>
<td>Pollinator Trail</td>
<td>-7.9566, -38.2981</td>
<td>2</td>
<td>6</td>
<td>0.0669</td>
</tr>
<tr>
<td>8</td>
<td>Pollinator Trail</td>
<td>-7.9558, -38.2986</td>
<td>2</td>
<td>8</td>
<td>0.0750</td>
</tr>
<tr>
<td>9</td>
<td>Pollinator Trail</td>
<td>-7.9550, -38.2992</td>
<td>4</td>
<td>13</td>
<td>0.0149</td>
</tr>
<tr>
<td>10</td>
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<td>-7.9542, -38.2997</td>
<td>3</td>
<td>7</td>
<td>0.0670</td>
</tr>
<tr>
<td>11</td>
<td>Pollinator Trail</td>
<td>-7.9534, -38.3002</td>
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<td>4</td>
<td>0.0133</td>
</tr>
<tr>
<td>12</td>
<td>Pollinator Trail</td>
<td>-7.9526, -38.3070</td>
<td>2</td>
<td>4</td>
<td>0.0635</td>
</tr>
<tr>
<td>13</td>
<td>Saco Road</td>
<td>-7.9510, -38.2934</td>
<td>1</td>
<td>1</td>
<td>0.1569</td>
</tr>
<tr>
<td>14</td>
<td>Saco Road</td>
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<td>2</td>
<td>0.1094</td>
</tr>
<tr>
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<td>4</td>
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<td>3</td>
<td>9</td>
<td>0.0516</td>
</tr>
<tr>
<td>18</td>
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<td>-7.9497, -38.2980</td>
<td>2</td>
<td>6</td>
<td>0.1478</td>
</tr>
</tbody>
</table>

Figure 2. Correlation structures amongst species abundance and environmental predictors measured at Pimenteira, Saco Road and the Pollinator Trail (Pernambuco, Brazil), as summarised by two PCA axes that account for 70.1% of the total variation within the dataset (A). Environmental predictors are temperature (temp), relative humidity of the soil (ur), amount of debris (debr), number of trees (trees) and the coefficient of variation of their diameter at breast height (cvDBH); species abbreviation can be interpreted from Table 1. UPGMA topology depicting the similarity pattern amongst transects (tips) of each sampling locality (point symbols) obtained from the computation of quantitative Sørensen’s dissimilarity index (B).
composition amongst transects (RDA: $F_{(1)} = 12.5, p < 0.01; R^2_{adj} = 0.40$). Finally, the degree of ecological uniqueness, measured for the species composition observed in each transect, ranged from 0.10 to 0.16 (Table 2), being negatively correlated with species richness ($r = -0.71, t_{(16)} = -4.08, p < 0.01$, Fig. 3F).
Discussion

In this study, we assessed the effects of environmental structure on scorpion diversity patterns in 18 linear transects covering the three Caatinga areas with different levels of environmental degradation and, thus, habitat complexity. Overall, our results indicated that heterogeneous areas of Caatinga typically support more scorpion species. These results corroborate previous assumptions that scorpion assemblages are sensitive to habitat structure, with complex habitats containing a greater number of species than monotonous landscapes (e.g. Smith 1995; Druce et al. 2007; Foord et al. 2015; Lira et al. 2016). Moreover, we disentangled the effects of habitat complexity and revealed that, amongst the environmental variables considered in this study, vegetation structure was deterministic for the modulation of scorpion assemblages in terms of both α-diversity (species richness and abundance) and β-diversity (species composition and richness difference). In theory, vegetation structure may increase environmental complexity by providing a set of suitable microhabitats (Reid and Hochuli 2007; Morales et al. 2008; Habel et al. 2018). In such circumstances, species richness is expected to increase and this may, in part, be explained by the reduced exposure to predation due to the presence of more physical barriers as the complexity of the environments increases (Keiser et al. 2018; Lichtenstein et al. 2019). This seems to be the case observed in Pimenteira and the Pollinator Trail, in which habitat complexity, mediated by local vegetation structure (Fig. 3C, D), allows the occurrence of ground-dwelling dominant species, such as B. rochai and J. rochae (Carmo et al. 2013; Lira et al. 2018) and also the niche specialist species P. debilis, found only on tree trunks of woody plants. Consequently, these findings have important implications for the development of conservation strategies. Current trends in anthropogenic land use will both reduce habitat complexity, leading to a potential reduction in levels of α and β diversities in arthropod assemblages, as demonstrated here and in previous studies (Ribeiro et al. 2015; Ribeiro-Neto et al. 2016; Lira et al. 2019b). This is especially important in Caatinga environments because the exploitation of woody vegetation is a common subsistence activity practised by local people in Brazilian semi-arid regions (Silva et al. 2018).

Vegetation structure may also be involved in the maintenance of arthropod assemblages, not only by its direct and additive effects upon the availability of physical microhabitats, but also by establishing a microclimate favourable to the occurrence of a plethora of species (Leal et al. 2016; Mata et al. 2017). In the case of scorpions, previous studies have demonstrated that the variation in species richness and composition may follow climatic clines (Lira et al. 2019b), even at small spatial scales (Foord et al. 2015). Accordingly, our results indicated that scorpion assemblages are responsive to temperature variations in terms of species replacement. This suggests that climatic features play a relevant role in the maintenance of species variability amongst scorpion assemblages, which is in accordance with previous studies that investigate the effects of climatic variation on scorpion assemblages at local and regional scales (e.g. Araújo et al. 2010; Lira et al. 2018). This finding could also explain why sites with similar vegetation structure and thus climatic conditions,
Vegetation structure as the main source of variability in scorpion assemblages are expected to harbour similar scorpion assemblages in term of species composition (Fig. 2A, B). This assumption, however, should be confirmed by future studies addressing the potential effects of microclimatic conditions on the structuring of scorpion assemblages in Caatinga landscapes. Ideally, such studies should be temporally broad, to encompass entire climatic trends (e.g. precipitation seasonality) present in Caatinga environments (Silva et al. 2018). Nevertheless, we reiterate that ineffective efforts to preserve the native vegetation in Caatinga landscapes may lead to a reduction in the species pool of arthropod assemblages mediated by the reduction of physical microhabitats and the homogenisation of their climatic conditions. A similar mechanism was adopted to explain the reduction of species richness in other taxa, such as ants (Arnan et al. 2018) and dung beetles (Liberal et al. 2011).

The variation in species composition observed in our study may be a product of the spatial dispersal capabilities of scorpions (Polis et al. 1985; Bryson Jr et al. 2016), combined with the ecological plasticity inherent to each species (Prendini 2001). Thus, the assembly of scorpion communities would be modulated by the trade-off between the degree of anthropogenic disturbance observed in each area (Pimenteira, Saco Road and the Pollinator Trail) and the ecological traits of scorpion species, especially those related to dispersion and resource exploitation (e.g. microhabitat use). These assumptions could explain the negative relationship between species richness and LCBD observed here (Fig. 3F), corroborating the idea that changes in species composition amongst scorpion assemblages may be linked to the environmental degradation mediated by human activities related to land use (Lira et al. 2016, 2019b). Interestingly, the high contribution of the richness difference component (80%) to overall β-diversity, reported in our study, is an indicator that dispersal limitation may not be an important source of species variation amongst scorpion assemblages at small spatial scales. Instead, this pattern of β-diversity would likely be produced by a combination of both biological interactions and environmental filters (Legendre et al. 2005; Legendre 2014). This implies that conservation strategies should ideally be broad in terms of habitat coverage and size, in order to ensure the sustainability of local biodiversity throughout potential ecological corridors (Legendre et al. 2005). We advocate that such recommendations can be useful to support decision-makers during the development of new policies addressing the conservation of Caatinga landscapes, giving special weight for the preservation of the remnants of native vegetation, alongside improvement of current policies aiming to create sustainable management of natural resources in the Brazilian semi-arid regions.

**Conclusions**

The present study corroborates the assumption that changes in species composition amongst scorpion assemblages may be mediated by anthropogenic land use (e.g. roads and farming). Moreover, human-related land use modifies species composition and promotes reductions in abundance and species diversity in scorpion assemblages of Caatinga and Atlantic Rainforest environments, as already reported.
by previous studies (Lira et al. 2016, 2019b; Dionisio-da-Silva et al. 2018). In this sense, the combination of high rates of unsustainable exploration for natural resources in Caatinga (Santos et al. 2014; Silva et al. 2018), the poor knowledge of its fauna, particularly for scorpions (Porto et al. 2014) and other arthropods (Bravo and Calor 2014) and negligence imposed by the political authorities of Brazil represent a threat to Brazilian biodiversity.

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Vegetation structure as the main source of variability in scorpion assemblages


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**Supplementary material 1**

**Table S1; Figures S1–S3**

Authors: Stênio Ítalo Araújo Foerster, André Felipe de Araújo Lira, Cauê Guion de Almeida

Data type: table and figures

Explanation note: **Table S1.** Numerical output of the principal component analysis (PCA), showing the percentual contribution of each variables for the first two axis (PC1 and PC2) of the PCA. **Figure S1.** General composition of microhabitat structure representing the Parque Estadual Mata da Pimenteira, located in the municipality of Serra Talhada, state of Pernambuco, northeastern Brazil. **Figure S2.** General composition of microhabitat structure representing the Pollinator Trail, located in the municipality of Serra Talhada, state of Pernambuco, northeastern Brazil. **Figure S3.** General composition of microhabitat structure representing the Saco Road, located in the municipality of Serra Talhada, state of Pernambuco, northeastern Brazil.

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