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DISENTANGLING DIVERSITY PATTERNS IN CUBAN SCORPIONS (ARACHNIDA: SCORPIONES)

Desenredando los patrones de diversidad de los escorpiones cubanos (Arachnida: Scorpiones)

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ABSTRACT

The assembly of communities is often viewed as a process involving the dispersal of species from a regional pool. An oceanic island provides a unique opportunity to test such a hypothesis and many others related to the patterns and processes behind biodiversity. Our aim was to investigate the patterns of scorpion diversity in the Cuban archipelago, using biotic and abiotic variables and their interactions as explanatory features. We use biotic and abiotic variables related to vegetation, climate and topography characterize the landscape of the Cuban archipelago. In this way, we analyze the patterns of beta diversity of the scorpions, verifying the effects of the variables alone and together. Scorpion fauna of the Cuban archipelago comprises 61 species, grouped into nine genera and two families: Buthidae and Diplocentridae. The interplay between biotic and abiotic variables explained scorpion species composition, especially when spatial predictors were considered. Climatic and spatial predictors affected scorpion beta diversity in terms of richness difference. These patterns are discussed emphasizing the role of biotic and abiotic environmental features and their interactions on the mechanisms of scorpion biodiversity generation and maintenance in Cuban archipelago.

Keywords: species distribution, beta diversity, landscape ecology, island biogeography, Greater Antilles.

RESUMEN

El ensamblaje de comunidades se considera a menudo como un proceso que implica la dispersión de especies procedentes de una fuente regional. Una isla oceánica brinda una oportunidad única para probar tal hipótesis y muchas otras relacionadas con los patrones y procesos detrás de la biodiversidad. Nuestro objetivo fue investigar los patrones de diversidad de los escorpiones en el archipiélago cubano, utilizando variables bióticas y abióticas y sus

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interacciones como características explicativas. Se utilizaron variables bióticas y abióticas relacionadas con la vegetación, el clima y la topografía que caracterizan el paisaje del archipiélago cubano. De esta forma, se analizaron los patrones de diversidad beta de los escorpiones, verificando los efectos de las variables solas y juntas. La fauna de escorpiones del archipiélago cubano comprende 61 especies, agrupadas en nueve géneros y dos familias: Buthidae y Diplocentridae. La interacción entre las variables bióticas y abióticas explicó la composición de las especies, especialmente cuando se consideraron predictores espaciales. Los predictores climáticos y espaciales afectaron la diversidad beta en términos de diferencia de riqueza. Estos patrones se discuten enfatizando el papel de las características ambientales bióticas y abióticas y sus interacciones en los mecanismos de generación y mantenimiento de la biodiversidad de los escorpiones en el archipiélago cubano.

Palabras clave: distribución de especies, diversidad beta, ecología del paisaje, biogeografía insular, Antillas Mayores.

INTRODUCTION

Biological diversity is modulated by several processes that contribute to the addition or removal of species across time and space, which may include speciation, dispersion, and extinction events (Ricklefs, 2004). Most of these processes are associated with biotic (*e.g*., land cover and vegetation structure) or abiotic (*e.g*., climate and topography) features (Moura *et al*., 2016; Fergnani & Ruggiero, 2017; Alves *et al*., 2018). Biotic and abiotic factors are naturally related to each other. Climate, for instance, can affect species richness indirectly via its effect on vegetation structure and dynamics (Stein *et al*., 2014). In turn, climate and vegetation can be a product of topographic heterogeneity, leading to an additional source of variability that affects the patterns of species diversity (Ruggiero & Hawkins, 2008; Stein *et al*., 2014). Frequently, previous studies have tried to explain species diversity using only abiotic factors (*e.g.*, Vasconcelos *et al.*, 2010; Nemésio & Vasconcelos, 2013; Valdujo *et al*., 2013), giving a little attention to the potential effects of biotic counterparts (Qian *et al*., 2009; Jiménez-Valverde *et al*., 2010; Carvalho *et al*., 2011).

Therefore, it is important to study the unique and shared contributions of abiotic and biotic factors to biodiversity patterns (Ray-Mukherjee *et al*., 2014). These factors do not necessarily drive species diversity in similar ways; instead, their importance depends on the group and taxonomic level studied, as well as the spatial scale and biogeographical history of the contextualized region (Belmaker & Jetz, 2011; Rodriguez-Artigas *et al*., 2016). Understanding their relative contribution is therefore crucial to improve our knowledge of the effect of global climate and land use changes on biodiversity (Jetz *et al*., 2007; Hof *et al*., 2011). In addition, the natural dynamics of diversity patterns have been represented more efficiently by beta diversity (dβ) measurements because it describes the species variation between habitats and interacts directly with species richness gradients, which are influenced by environmental aspects at both the local and regional scales (Soininen *et al*., 2018).

Landscape-scale studies on oceanic islands have a major advantage over comparable studies on continental systems (Irl *et al*., 2015; Rominger *et al*., 2016; Liu *et al*., 2018). The presence of a large share of species that have evolved *in situ* allows the inference of general drivers of speciation from spatial patterns of diversity (Irl *et al*., 2015; Mittelbach & Schemske, 2015). Thus, spatial distribution within a given oceanic island can provide valuable insights regarding drivers of biodiversity patterns at the landscape scale, depicting important implications for conservation (Richardson & Whittaker, 2010; Socolar *et al*., 2016).

In island systems, competition for resources drives ecological niche divergence (Schluter, 2000; Losos, 2010). Moreover, the competing species increases, ecological opportunity (niche availability) decreases, and the pace of diversification slows (Sepkoski, 1978; Schluter, 2000; Mahler *et al*., 2010). Therefore, bigger islands tend to have more ecomorphs, suggesting that the degree of niche filling depends on the environmental properties of the island (*e.g*., area and habitat diversity) (MacArthur & Wilson, 1967; Mahler *et al*., 2013). For example, the Cuban archipelago that comprises an important part of the Caribbean Islands hotspot (Myers *et al*., 2000; Mittermeier *et al*., 2005), exhibiting a significant taxa diversity and endemism rate in the region (Borroto-Páez & Mancina, 2017; Denis *et al*., 2018). These patterns are results of a complex geological history that produced sequences of isolations and reconnection along thousand years generating the emergence of groups with strong adaptive radiation (Iturralde-Vinent & MacPhee, 1999; Hedges, 2006; Denis *et al*., 2018).

Animals with low vagility, long life cycles, and microhabitat specialization, such as scorpions, offer a good model for studying the patterns and processes of biological diversity (*e,g*., Foord *et al*., 2015; Esposito & Prendini, 2019; Foerster *et al*., 2019; Lira *et al*., 2019a). These arachnids possess high environmental requirements that are not distributed randomly throughout the landscape (Polis, 1990). Previous studies provide evidences that assemblages of these arachnids are driven by several environmental factors, which includes temperature, precipitation, vegetation structure, as well as by the complex interaction among these factors (e.g., Warburg & Ben-Horin, 1981; Prendini, 2005; Foord *et al*., 2015). For example, Lira *et al.* (2021a) detected that vegetation cover (biotic variable) is a key factor to scorpion diversity in a Brazilian Atlantic Rainforest. In addition, vegetation structure also plays a role to maintenance of scorpion assemblage on Seasonal Dry Tropical Forest (Foerster *et al*., 2020; Lira *et al*., 2021b). At the regional scale, Lira *et al.* (2019a) investigated the effect of the bioclimatic gradient between wet and dry forests on scorpion assemblages in Brazil and found that temperature and precipitation (abiotic variables) were the major explanatory factors of scorpion richness and dβ, which increased toward the dry forest gradient. Finally, topographic factors, such as elevation may exert influence on scorpion species distribution ranges (Prendini & Bird, 2008; Campón *et al*., 2014). Thus, the sensitivity of these animals at different scales makes them a good model for studies that focus on analyzing diversity patterns.

OBJECTIVES

- Considering the higher vegetation and topography complexity of Cuban archipelago, our aim was determining large–scale patterns from beta diversity of Cuban scorpions, using the association and interaction between abiotic (climatic and topographic measures) and biotic (vegetation complexity) factors.

MATERIALS AND METHODS

Study area

The Cuban archipelago (23°18’ N – 80°54’W) is composed by the main island of Cuba, the Isla de la Juventud (previously Isle of Pines) who is the second-largest Cuban island and almost 4000 other smaller insular territories. Around the Cuban main island (Isle of Cuba), there are four groups of keys and smaller islands: in the northwest, De los Colorados archipelago; in the middle north, Sabana-Camagüey archipelago, also known as Jardines del Rey; in the southwest, Canarreos archipelago; and in the southeast, Jardines de la Reina archipelago.

Approximately one-fourth of the Cuban territory is mountainous, with four principal orographic systems: in the west, Guaniguanico (comprising Sierra de los Órganos and Sierra del Rosario); in the central southern region, Guamuhaya, sometimes called Escambray (comprising Alturas de Trinidad and Banao); in the southeastern region, Sierra Maestra (comprising Sierra Maestra *s.s.* and Sierra de La Gran Piedra); and Nipe-Sagua-Baracoa in the northeastern region. The highest elevation, Pico Turquino (1974 m a.s.l.), is located in Sierra Maestra, where several summits are over 1400 m a.s.l, with the western and central regions having elevations lower than 1200 m a.s.l. (González-Alonso & Armas, 2007).

For most plants and animals, the eastern region of Cuba (provinces of Guantánamo, Santiago de Cuba, Holguín, and Granma) is the most biodiverse, likely because of its geological and ecological complexity and arid ecosystems; however, this region also has the largest and most well–preserved tropical rainforests (González-Alonso & Armas, 2007).

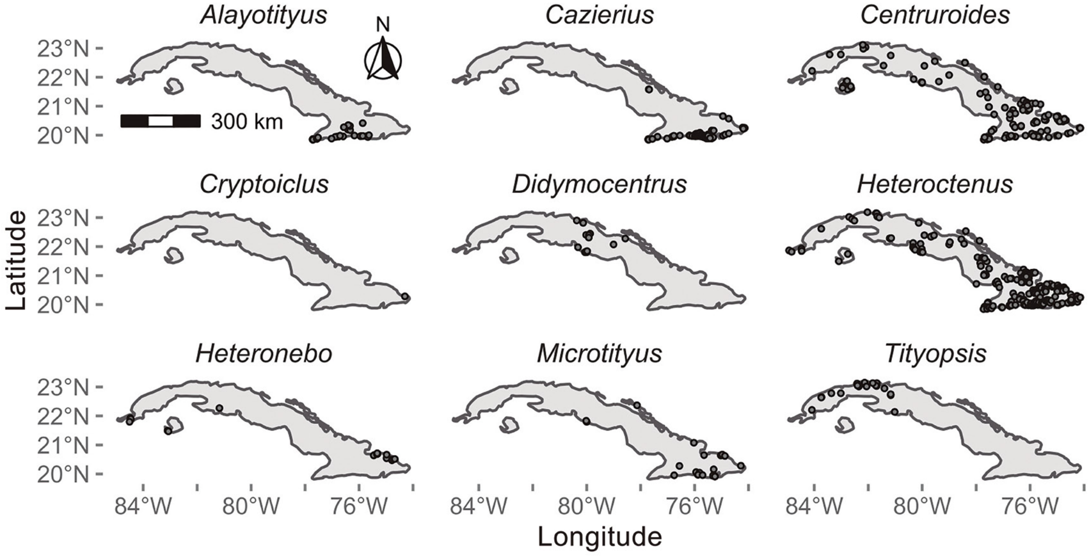

Figure 1. Geographical distribution of scorpion genera over the Cuban archipelago.

Species data

To achieve a representability that was close to the real scenario for the occurrence areas of the Cuban scorpion species, we used data obtained from the following two sources: the arachnological collection of the Institute of Ecology and Systematics, Havana, Cuba and previous literature records (Appendix I). All occurrences were inspected carefully to detect and correct any problems associated with taxonomic misidentification, duplication, and geographically discordant localities. The data set used in this study comprises 57 scorpion species (excluding four introduced species), which are grouped into nine genera and two families: Buthidae C. L. Koch, 1837 and Diplocentridae Karsch, 1880 (Appendix I).

Buthids scorpions are represented by five genera and 42 species, while diplocentrids were represented by 15 species grouped into four genera (Appendix I). Diplocentrid scorpions were represented by genera *Cazierus* Francke, 1978, *Cryptoiclus* Teruel & Kovarik, 2012, *Didymocentrus* Kraepelin, 1905, and *Heteronebo* Pocock, 1899, with *Cryptoiclus* being monotypic and *Cazierus* being more specious (Appendix I). In addition, the records of exotic species found in the Cuban archipelago were excluded from our analysis: *Isometrus maculatus* (DeGeer, 1778), *Centruroides gracilis* (Latreille, 1804), *Centruroides edwardsii* (Gervais, 1843) and *Centruroides margaritatus* (Gervais, 1841). We established a spatial grid with cell size of 25 × 25 km, cropping it according to a shapefile of the Cuban archipelago. This cell size was chosen to adequately capture the environmental features from the raster layers (*e.g*., minimizing the proportion of missing data), taking into account the low–dispersal capabilities of scorpions (Bryson Jr *et al*., 2016) and also their specificity in terms of microhabitat use (Prendini, 2001). We annotated the scorpion species for each grid cell, and for those cells, we extracted a set of environmental predictors (Table I) using the 'raster' package (Hijmans, 2019) in the R environment (R Core Team, 2020). To simplify the procedures adopted in this study, we interpreted each grid cell containing scorpion occurrence as an individual biological assemblage.

Table I. Environmental predictors used in the analysis of the present study to explain the diversity patterns in scorpions on the Cuban archipelago

Variable	Predictor class	Description	Raster source
Land cover diversity	Vegetation Complexity	Expressed as the entropy level (Shannon's index) computed for the land cover classes within each grid cell.	Latham *et al*. (2014)
Canopy standard deviation	Vegetation Complexity	Average standard deviation of canopy height (in meters) measured within each grid cell.	Simard *et al*. (2011)
Canopy range	Vegetation Complexity	Average amplitude of canopy height (in meters) measured within each grid cell.	Simard *et al*. (2011)
Annual mean temperature	Climatic	Average annual mean temperature (°C) calculated for each grid cell.	Brown *et al*. (2018)
Temperature annual range	Climatic	Average annual temperature (°C) range observed per grid cell.	Brown *et al*. (2018)
Annual precipitation	Climatic	Mean annual precipitation range (mm/year) observed per grid cell.	Brown *et al*. (2018)
Precipitation range	Climatic	Mean difference between the precipitation of the wettest quarter and the precipitation observed on the driest quarter (mm/year).	Brown *et al*. (2018)
Elevation range	Topography	Average amplitude of elevation per grid cell, given in meters.	USGS (1996)
Elevation (coefficient of variation)	Topography	Average value of coefficient of variation calculated for each grid cell (meter).	USGS (1996)

Environmental predictors

We split the list of environmental predictors into three matrices that included variables related to 1) vegetation complexity, 2) climatic features, and 3) topographic constraints (Table I). Vegetation variables were generated from raster layers provided by the Global Land Cover–SHARE database (Latham *et al*., 2014), and the 3D Global Vegetation Map database (Simard *et al*., 2011). Similarly, we used the bioclimatic raster files from Paleoclim (Brown *et al*., 2018), and those from the GTOPO30 project (USGS, 1996) to generate the variables related to climate and topography, respectively. All raster files were downloaded at a pixel resolution of 30 arc-sec and resampled in the 'raster' R package to assure their equality in terms of spatial extent and map projection (EPSG:4326). Vegetation complexity was represented by vegetation structure metrics (*e.g.*, the standard deviation and range interval of the canopy height) and also by the land cover diversity within each grid cell containing scorpion occurrences (Table I). In turn, land cover diversity was expressed by the Shannon's entropy index calculated from the land cover classes sampled within each grid cell, using the 'vegan' R package (Oksanen *et al*., 2019). The remaining variables related to climate and topography (Table I) were computed using simple statistic metrics (*e.g*., mean, range interval, coefficient of variation) implemented in base packages of the R software.

Data analysis

We first determined the total dβ (βtotal) among scorpion assemblages distributed over the Cuban archipelago, and then decomposed this metric to obtain the relative contribution of species replacement and richness difference–the two components of the total dβ (*sensu* Legendre, 2014). Both procedures were conducted in the 'adespatial' R package (Dray *et al*., 2018), taking the assemblage matrix (grid cells × scorpion species) as input and applying the Podani-family of Sørensen dissimilarity index (Legendre, 2014). This family of dissimilarity decomposition was chosen because it produces Euclidean matrices of richness difference that is suitable for constrained ordination methods (Legendre, 2014) required for the subsequent analyzes present in this study. In addition, the species replacement matrix resulted from this procedure can also present Euclidean behavior after a simple square root transformation (Legendre, 2014; Borcard *et al*., 2018).

Stochastic processes, such as dispersion, may have a relevant role in the structuring of biological assemblages (Padial *et al*., 2014) especially in low-dispersal taxa (Heino, 2013). Therefore, we included a set of orthogonal spatial predictors in the downstream analysis to account for potential effects of stochastic process over the pattern of β-diversity presented by scorpion assemblages. Spatial predictors were generated using Distance-Based Moran's Eigenvector Maps (dbMEM: Borcard and Legendre, 2002; Borcard *et al*., 2004; Dray *et al*., 2006). Following the procedures described in Moura *et al*. (2016), we used the 'adespatial' R package to perform the dbMEM analysis, recovering all spatial descriptors with positive spatial autocorrelation structure, which are compatible for constrained ordination methods (Borcard & Legendre, 2002). After that, we applied a variation partitioning analysis to measure the unique and shared effects of environmental and spatial predictors on the variability of 1) assemblage dissimilarity, 2) species replacement, and 3) richness difference among scorpion assemblages. To access the statistical significance of combined fractions in explaining the variability in the response matrices, we used a series of distance–based redundancy analysis (dbRDA: McArdle & Anderson, 2001) followed by permutation tests (1,000 permutations), both implemented in the 'vegan' R package. The isolated contribution of each predictor class (Table I), as well as the variability in the response matrices explained solely by spatial predictors, were tested using partial-dbRDA and the same permutation tests mentioned above. In both cases (dbRDA and partial-dbRDA) we applied the Lingoes correction to avoid the generation of negative eigenvalues during the modeling processes (Legendre and Anderson, 1999). We quantify the relative contribution of shared and non-shared explained fractions using the adjusted coefficient of determination (R^2adj) proposed by Peres-Neto *et al*. (2006). Prior to variation partitioning, all environmental predictors were log(x+1) transformed and checked for collinearity problems using variance inflation factor (VIF) obtained in the 'usdm' R package (Naimi, 2015). We assume a VIF less than 10 as an indicator of negligible collinearity effects during the modeling processes (Zuur *et al*., 2009).

RESULTS

Buthidae species showed a widespread distribution in the Cuban archipelago, species from *Heteroctenus* Pocock, 1893 and *Centruroides* Marx, 1890 genera were found in practically all Cuban territory. In contrast, some buthid genera such as *Tityopsis* Armas, 1974 and *Alayotityus* showed a more restricted distribution and were found on the western and eastern sides of the Cuban archipelago, respectively (Fig. 1). Diplocentrid scorpions are also found throughout the Cuban territory. However, their genera exhibited a clumped distribution pattern, representatives from *Cazierus* and *Cryptoiclus* genus were restricted to eastern side of the Cuban archipelago (Fig. 1). Species richness ranged from one to nine species per grid cell, with a slightly increase in the observed number of species towards the southern region of the Cuban archipelago (Fig. 2).

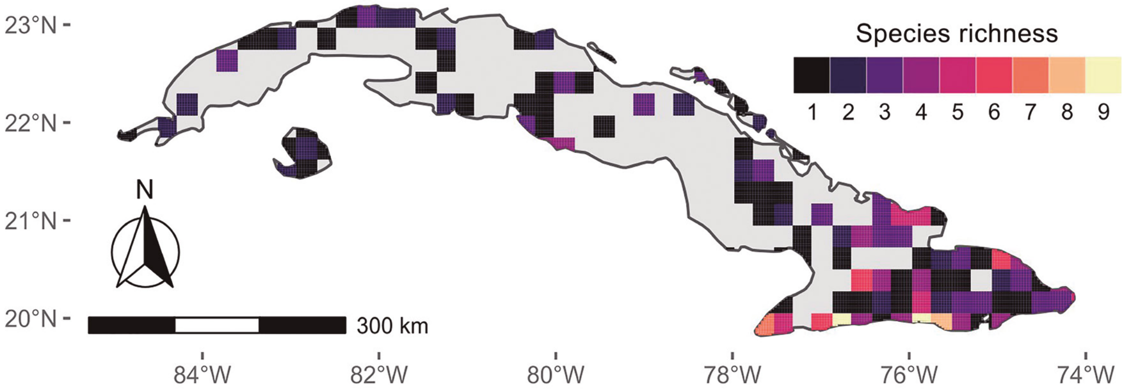

Figure 2. Spatial distribution of scorpion richness over the Cuban archipelago. Species richness is given as the number of scorpion species counted per grid cell at 25 × 25 km pixel resolution.

Species replacement accounted for 56 % of the total β-diversity estimated from scorpion assemblages (βtotal = 0.358), while the remaining 44 % was attributed to the richness difference component. The average dissimilarity observed among scorpion assemblages was estimated in 0.716 ± 0.305 (mean ± standard deviation), whereas the mean levels of species replacement and richness difference were quite similar (Fig. 3).

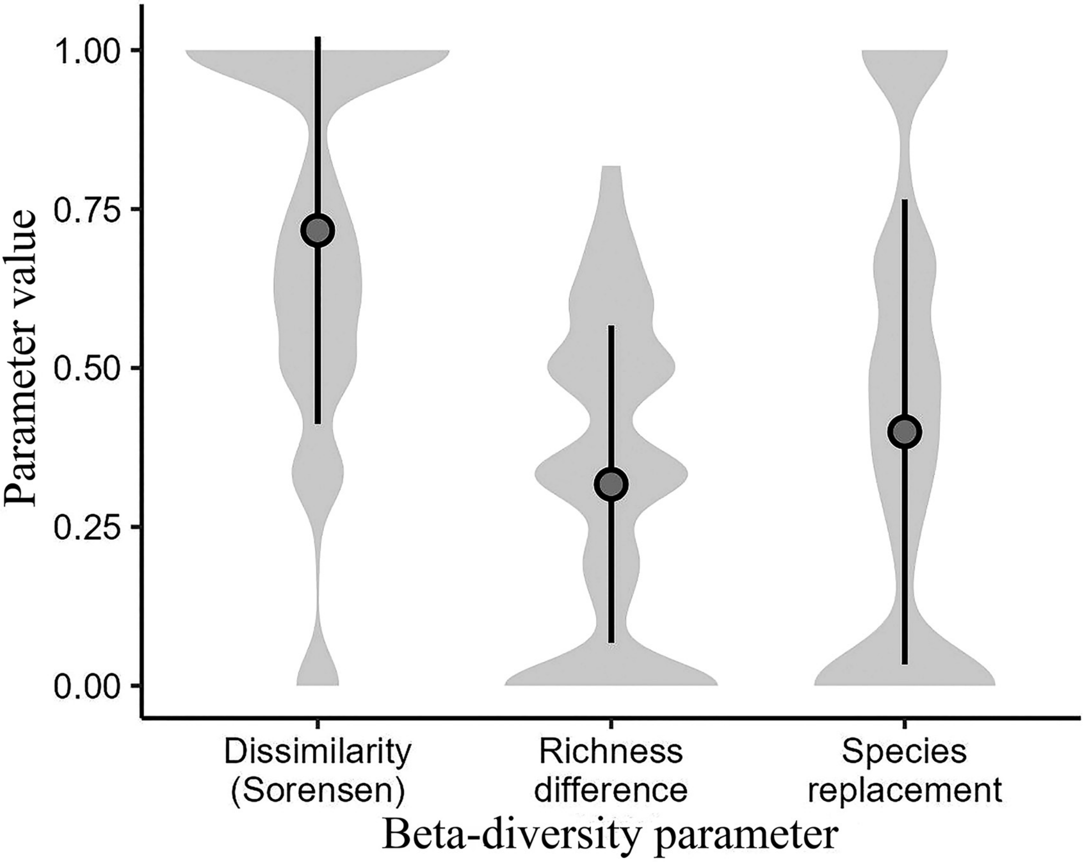

Figure 3. Graphical summary of β-diversity parameters (Sørensen dissimilarity, richness difference, and species replacement) observed for the scorpion assemblages of Cuban archipelago. Mean values and standard deviation are illustrated by dots and vertical bars, respectively, while the distributional structures of each β-diversity parameter are represented by grey shades.

Together, the set of environmental and spatial predictors explained 7 % of the dissimilarity observed among scorpion assemblages (Table II). This dissimilarity could be better explained when environmental and spatial predictors were combined, although the percentual contribution resulting from these combinations were relatively low (2–7 %, Table II). Individually, the dissimilarity among scorpion assemblages could be explained only by spatial predictors (R^2adj = 0.047, $p < 0.05$, Table II). Different combinations of environmental and spatial predictors explained only 0.1 % to 0.4 % in the levels of species replacement present among scorpion assemblages (Table II). Levels of richness difference among scorpion assemblages could not be explained solely by vegetation complexity, although isolated effects were detected for climate, spatial structure and topography (Table II). In addition, 10–28 % of the variation in richness difference could be attributed to the mixed effects between environmental and spatial predictors (Table II). Environmental variables did not present collinearity problems (VIF < 4.18).

Table II. Statistical summary from the variation partitioning analysis of assemblage dissimilarity, species replacement, and richness difference observed among scorpion assemblages in the Cuban archipelago

Predictor class		Assemblage dissimilarity		Species replacement		Richness difference	
	d.f.	F	R^2adj	F	R^2adj	F	R^2adj
Individual effects							
VEG	3	1.145	0.005	1.016	0.001	0.915	0.000
CLI	4	1.096	0.004	0.979	0.000	5.245	**0.155**
TOP	2	0.882	0.000	0.979	0.000	3.135	**0.0399**
SPA	30	1.177	**0.047**	1.007	0.002	1.744	**0.153**
Shared effects							
CLI + VEG	7	1.424	**0.025**	1.016	**0.001**	2.854	**0.102**
CLI + TOP	6	1.360	**0.019**	1.005	<0.001	3.650	**0.122**
CLI + SPA	34	1.248	**0.069**	1.013	**0.004**	1.552	**0.141**
VEG + TOP	5	1.459	**0.020**	1.007	<0.001	3.819	**0.110**
VEG + SPA	33	1.256	**0.070**	1.014	**0.004**	1.395	0.103
TOP + SPA	32	1.212	**0.056**	1.009	**0.002**	1.600	**0.144**
CLI + VEG + TOP	9	1.320	**0.025**	1.009	0.001	2.833	**0.126**
CLI + VEG + SPA	37	1.248	**0.074**	1.010	**0.003**	1.971	**0.240**
CLI + TOP + SPA	36	**1.225**	0.066	1.007	0.002	2.244	**0.282**
VEG + TOP + SPA	35	1.234	**0.067**	1.012	**0.004**	1.464	0.125
All	39	1.226	**0.072**	1.008	**0.003**	2.135	**0.280**
Residuals	0	-	0.928	-	0.997	-	0.720

Environmental features were grouped into three classes representing vegetation complexity (VEG), climatic features (CLI) and topography (TOP). Spatial predictors were included as a fourth class of independent variables (SPA). The relative amount of variance explained by each predictor class is given by the unbiased coefficient of determination (R^2adj), in which statistically significant values ($P < 0.05$) are presented in bold.

DISCUSSION

This study assessed the isolated and combined contributions of vegetation, climatic and topographic variables regarding the diversity pattern of scorpion assemblages in the Cuban archipelago. We found vegetation, climatic, and spatial predictors combined influences in scorpion species composition and dβ pattern. These synergisms between biotic and abiotic variables in scorpion composition have also been described in previous studies (Due and Polis, 1986; Prendini, 2001; Foord *et al*., 2015; Lira *et al*., 2019a). Our results favor the rationale of a filter compounded by the interplay between biotic (*e.g.*, vegetation complexity) and abiotic (*e.g.*, climate and topography) components that determine which scorpion species successfully colonize and coexist at a local site.

Scorpions belong to an arthropod predator group with low dispersion capacity and their ecological requirements are likely to have a prominent role in the spatial arrangement of their assemblages (Dionisio-da-Silva *et al*., 2018; Foerster *et al*., 2019; Lira *et al*., 2021). For example, Lira *et al*. (2019a) found that 36 % of scorpion species composition along a 712 km dry–wet bioclimatic gradient was explained by spatial predictors. In scorpion species of a Brazilian montane forest fragments, 51 % of composition variability was influenced by spatial predictors (Foerster *et al*., 2019). Therefore, the scorpion bionomical properties could be a potential source of variation on the size and composition of scorpion assemblages along the Cuban archipelago. Cuban scorpion fauna is composed by eurytopic species (*e.g.*, *Centruroides* spp.) (Teruel & Kovařík, 2012) and by stenotopic species (*e.g.*, *Tityopsis* spp.) considered as forest scorpions (Teruel & Rodríguez-Cabrera, 2020). In this way, scorpion species with limited vagility and lower ecological plasticity may be restricted to small territorial extensions in archipelagos as Cuba. Such interpretations are supported by the effect of spatial distance on the species composition, in which scorpion assemblages in the eastern portion are quite different from those distributed on the western side of the Cuban archipelago (see Fig. 1).

In the Cuban archipelago, the dβ of scorpions was explained in similar way by the species replacement component and richness difference. We found a synergism between species richness differences with biotic and abiotic variables. These results indicate that interactions between biotic and abiotic variables act as species filter, allowing the establishment of natural communities according to their environmental requirements. Thus, our finding suggests that the assembly of diversity patterns among scorpion assemblages in the Cuban archipelago may be the result of interplay between ecology and evolution. Besides, the interactions between scorpion intrinsic features, (limited vagility and microhabitat specificity) and the high geological and vegetation complexity of the Cuban archipelago may explain a high number of scorpion species and the dβ pattern. Lira *et al*. (2019a, 2021) argue that landscape structure changes such vegetation cover may act as a complex filter, limiting the dispersion of the majority of the scorpion species in Brazilian Atlantic Forest and Caatinga. For example, forest specialists' scorpions are unable to colonize the open forested areas neighboring their forest remnant (Lira *et al*., 2019b; Lira *et al*., 2020). Therefore, the larger contribution of species replacement to the overall scorpion dβ found in our study indicates that the mechanism behind the assembly of scorpion assemblages in the Cuban archipelago is likely related to the high environmental heterogeneity, as well as the historical and independent colonization events that are intrinsically associated to the biogeographical history of the Cuban archipelago (Crews & Esposito, 2020).

CONCLUSIONS

In summary, we found that scorpion species composition and richness differences in the Cuban archipelago depend on biotic and abiotic variables, such vegetation and topography. Our results also indicate that the variables explained a relevant fraction of the scorpion community assembly together rather than individually. Thus, a good practice for future studies focusing on the scorpion community assembly would be to consider both types of variables and analyze them together and separately.

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Appendix 1. List of non-exotic scorpion species present in the Cuban archipelago. Data compiled from the Arachnological Collection of the Institute of Ecology and Systematics (Havana, Cuba) and also from the scientific literature

Scorpion species	Sources
Buthidae	
Alayotityus delacruzi Armas, 1973	Armas 1973
Alayotityus feti Teruel, 2004	Teruel 2004
Alayotityus granma Armas, 1984	Armas 1984
Alayotityus juraguaensis Armas, 1973	Armas 1973
Alayotityus lapidocola Teruel, 2002	Teruel 2002, 2004
Alayotityus nanus Armas, 1973	Armas 1973; Teruel 2002
Alayotityus pallidus Teruel, 2002	Teruel 2002, 2004
Alayotityus sierramaestrae Armas, 1973	Armas 1973
Centruroides anchorellus Armas, 1976	Teruel 2019
Centruroides arctimanus (Armas, 1976)	Armas 1976a
Centruroides baracoae Armas, 1976	Armas 1976a; Teruel 2000
Centruroides galano Teruel, 2001	Teruel 2001b
Centruroides guanensis Franganillo, 1930	Teruel 2017
Centruroides melanodactylus Teruel, 2001	Teruel 2001b
Centruroides navarroi Teruel, 2001	Teruel 2001b
Centruroides nigropunctatus Teruel, 2006	Teruel 2006c
Centruroides polito Teruel, 2007	Teruel 2007
Centruroides robertoi Armas, 1976	Armas 1976a
Centruroides spectatus Teruel, 2006	Teruel 2006c
Centruroides stockwelli Teruel, 2001	Teruel 2001b
Heteroctenus aridicola Teruel & Armas, 2012	Teruel and Armas 2012a
Heteroctenus garridoi (Armas, 1974)	Teruel 2006b; Teruel and Armas 2012a
Heteroctenus gibarae (Teruel, 2006)	Teruel 2006b; Teruel and Armas 2012a
Heteroctenus granulimanus (Teruel, 2006)	Teruel 2006b; Teruel and Armas 2012a
Heteroctenus junceus (Herbst, 1800)	Teruel and Armas 2012b
Heteroctenus melloleitaoi (Teruel & Armas, 2006)	Teruel and Armas 2006b; 2012a
Microtityus difficilis Teruel & Armas, 2006	Teruel and Armas 2006c
Microtityus farleyi Teruel, 2000	Institute of Ecology and Systematics, Havana
Microtityus flavescens Teruel, 2001	Institute of Ecology and Systematics, Havana
Microtityus fundorai Armas, 1974	Teruel 2001a
Microtityus guantanamo Armas, 1984	Institute of Ecology and Systematics, Havana
Microtityus jaumei Armas, 1974	Institute of Ecology and Systematics, Havana
Microtityus kovariki Teruel & Infante, 2007	Teruel and Infante 2007
Microtityus pusillus Teruel & Kovarik, 2012	Institute of Ecology and Systematics, Havana
Microtityus trinitensis Armas, 1974	Teruel 2001a; Teruel and Rodríguez 2014

Appendix 1. Continuation

Scorpion species	Sources
Microtityus vulcanicus Teruel, 2019	Institute of Ecology and Systematics, Havana
Tityopsis canizaresorum Teruel & Rodríguez-Cabrera, 2020	Teruel and Rodríguez-Cabrera, 2020
Tityopsis inaequalis (Armas, 1974)	Teruel and Rodríguez-Cabrera, 2020
Tityopsis inexpectata (Moreno, 1940)	Teruel and Rodríguez-Cabrera, 2020
Tityopsis mulata Teruel & Rodríguez-Cabrera, 2020	Teruel and Rodríguez-Cabrera, 2020
Tityopsis pumila Teruel & Rodríguez-Cabrera, 2020	Teruel and Rodríguez-Cabrera, 2020
Tityopsis sheylae Teruel & Rodríguez-Cabrera, 2020	Teruel and Rodríguez-Cabrera, 2020
Diplocentridae	
Cazierius asper Teruel, 2006	Teruel and Cala-Riquelme 2006; Teruel 2006a
Cazierius chryseus Teruel & Armas, 2006	Teruel and Armas 2006a
Cazierius granulosus Teruel, 2013	Teruel 2013
Cazierius gundlachii (Karsch, 1880)	Teruel and Cala-Riquelme 2006; Teruel 2006a
Cazierius paradoxos Teruel & Díaz, 2004	Teruel and Díaz 2004; Teruel 2006a
Cazierius parvus Armas, 1984	Teruel and Cala-Riquelme 2006; Teruel 2006a
Cazierius torrei (Moreno, 1938)	Teruel and Armas 2006a
Cryptoiclus rodriguezi Teruel & Kovarik, 2013	Teruel and Kovarik 2013
Didymocentrus armasi Teruel & Rodriguez, 2008	Teruel and Rodríguez 2008
Didymocentrus jaumei Armas, 1976	Teruel and Rodríguez 2008
Didymocentrus sanfelipensis Armas, 1976	Teruel and Rodríguez 2008
Didymocentrus trinitarius (Franganillo, 1930)	Teruel and Rodríguez 2008
Heteronebo bermudezi (Moreno, 1938)	Armas 1976b, 1984
Heteronebo morenoi (Armas, 1973)	Armas 1976b, 1984
Heteronebo nibujon Armas, 1984	Teruel and Díaz 2004

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