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Factors shaping a lizard community structure in a semiarid region of north-eastern Brazil

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ABSTRACT

We assessed the roles of historical and recent factors on the structure of a Neotropical lizard community from Serra da Capivara, in the semiarid Caatinga of north-eastern Brazil. We found no phylogenetic structure in community composition. Spatial niche overlap was high for most species pairwise comparisons. Null model analyses indicated that mean spatial and trophic niche overlaps did not differ, while mean morphological niche overlap was significantly lower than expected by chance, indicating a community structured along the morphological niche axis but not along the trophic nor spatial niche axes. We suggest that the lack of spatial niche segregation and species association may be related to current environmental conditions, such as habitat homogeneity and climatic variables. Morphological and dietary niches were influenced by historical factors, with phylogeny accounting for most of the variation in our data. Most of the variation is accounted for by the divergence of basal lineages (Gekkota/Scincomorpha/Iguania). These segregations influence behaviour and foraging modes of the given clades. Finally, these results are quite like those found for lizard communities in Seasonal Tropical Dry Forests (STDFs) and Cerrado savannahs, which can be a starting point to discuss the relationship between these formations to Caatinga domain.

1. Introduction

Community structure can be defined as the non-random use of resources by species in an ecological community (Strong et al., 1979). Under this definition, in a structured community mean niche overlap among species should be smaller than expected by chance (Case, 1983). The competitive exclusion principle posits that two species that compete for the same limiting resource cannot coexist indefinitely (Hardin, 1960). Therefore, limited ecological similarity through resource partitioning among syntopic species should minimize interspecific competition and favour their long-term coexistence (MacArthur and Levins, 1967).

Resource partitioning can arise from two basic mechanisms (Connell, 1980). First, from ecological interactions among coexisting species during the process of community assembly, such that their overlap along relevant niche dimensions is minimized, e.g., ecological character displacement. In this situation, species traits and patterns of resource use will tend to diverge from the condition present in their ancestors through trait evolution and niche shifts. Second, community structure can originate when species are drawn from the available pool according to their pre-existing traits, in a way to minimize niche overlap and interspecific competition, e.g., ecological assortment. Here, species traits and patterns of resource use will tend to resemble the condition present in their ancestors through trait and niche conservatism (Wiens and Graham, 2005). The contrasting patterns of trait evolution *vs.* conservatism between these two mechanisms can be assessed by evaluating the phylogenetic signal on traits, as more related species tend to resemble each other more than expected by chance (Münkemüller et al.,

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2012).

The burgeoning field of community phylogenetics uses patterns of phylogenetic dispersion among co-occurring species to make inferences about the mechanisms that influence community assembly (Cavender-Bares et al., 2012). This approach considers that, when traits are phylogenetically conserved, habitat filtering results in phylogenetically clustered communities, whereas biotic interactions—most notably competition—results in phylogenetically overdispersed communities (Webb et al., 2002). Recent studies, however, have raised concerns about our ability to infer assembly mechanisms based solely on phylogenetic dispersion patterns (Gerhold et al., 2015) and indicated that more powerful approaches can arise by combining both trait evolution and phylogenetic data in community assembly research. Therefore, to unravel the processes that operated during community assembly, one needs to integrate patterns of species traits and niche overlap with knowledge of species phylogenetic relationships and trait evolution.

Studies on lizard communities have contributed a great deal to the development of community ecology (Pianka and Vitt, 2003). This has been particularly true for lizard communities from arid regions, where lizard diversity is highest (Roll et al., 2017), and islands, which are taxonomically simpler and more amenable to experimental approaches (Losos, 2009). Lizard species typically partition environmental resources along three fundamental niche dimensions: time, space and food (Pianka, 1973). Resource partitioning among lizards seems to increase with environmental complexity at varying spatial scales (Garda et al., 2013) and with the number of species in the community (Mesquita et al., 2006a, 2006b). Both recent (e.g., niche differentiation) and historical (e.g., niche conservatism) processes influence patterns of resource partitioning and community assembly among lizard species. Overall, lizard diets and diel activity seem to be more evolutionarily conserved than patterns of habitat use (Rabosky et al., 2011). For instance, iguanian lizards tend to feed more often on hymenopterans and beetles than non-iguanian lizards (Vitt and Pianka, 2005) and geckos are the sole primarily nocturnal lizard clade (Pianka and Vitt, 2003). As such, trophic niche segregation seems to be more pervasive than spatial niche segregation among phylogenetically diverse lizard communities (Werneck et al., 2009).

The Caatinga is the largest and most biologically diverse seasonally dry tropical forest of the New World (Silva et al., 2017). Previous studies in the Caatinga documented patterns of resource use and overlap among lizard species (Andrade et al., 2013; Vitt, 1995), and recently mechanisms of community assembly using null models and phylogenetic comparative analysis tools (Gonçalves-Sousa et al., 2019, 2022). Here, we integrate patterns of niche overlap, trait evolution and phylogenetic relationships to investigate the structure and assembly of a Caatinga lizard community at the dense Caatinga in Parque Nacional da Serra da Capivara, north-eastern Brazil. Caatinga is a semiarid ecoregion with unpredictable rainfall patterns, making local species persistence possibly dependant on specific phenotypic traits adapted to survive in these conditions. Likewise, local species pools in arid and semiarid regions could also present phenotypic attraction and, therefore, a phylogenetically clustered pattern (Webb et al., 2002). However, there is evidence for the opposite, i.e. phylogenetic overdispersion in lizard communities in Australian deserts and in Caatinga itself (Gonçalves-Sousa et al., 2022; Rabosky et al., 2011).

Here, we tested if the local lizard community presented a phylogenetic structure distinct from what is expected at random given the larger regional species pool (is it phylogenetically clustered or overdispersed?). Subsequently, we tested if species morphological, spatial (microhabitat use) and trophic niches were clustered or evenly distributed by using null models. Lastly, we investigated the role of historical and ecological processes shaping the evolution of morphological traits, of habitat use and diet of the local lizard assemblage.

2. Material and methods

2.1. Study site

The Parque Nacional (PARNA) da Serra da Capivara covers approximately 92,000 ha of the municipalities of Canto do Buriti, Coronel José Dias, São João do Piauí and São Raimundo Nonato, in Piauí state, Brazil (Fig. 1), and is located in the Caatinga dry forests of north-eastern Brazil. The climate is semiarid, *Bs* in Köppen's classification, characterized by high mean annual temperature (>26.5 C) and low (<800 mm/year), seasonal (3–5 months) and erratic precipitation. The vegetation is xeric, thorny and deciduous, including trees, bushes, and cactuses, and ranges from open areas to dense forests (Silva et al., 2017). The landscape in PARNA da Serra da Capivara includes high rock outcrops covered by cactuses and shrubs, dense Caatinga areas on top of plateaus, and canyons, locally known as "boqueirões," covered by semideciduous forests with high canopy (Lemos, 2004). Herein, we provide a detailed description of the lizard assemblage from "dense Caatinga" areas, which cover most of the Serra da Capivara. We did not consider the "Boqueirões" nor the rocky outcrops.

2.2. Sampling methods

We sampled lizards with pitfall, funnel, and glue traps. Pitfall traps were organized in arrays consisting of four 30 l plastic buckets, buried to ground-level in a Y-shape, with one bucket at the centre and three at the ends, and interconnected by three 5 m–long and 50 cm–high drift fences built with plastic tarp. Along each fence, we placed two funnel traps (one on each side of the fence), totalling 6 funnel traps per array. Each funnel trap consisted of a 42 cm–long and 25 cm–diameter, torpedo-shaped minnow trap, with vinyl-dipped steel mesh construction. We also placed four glue traps next to each trap array, in different microhabitats (two on the ground and two on the vegetation, or across fallen branches). Pitfall trap arrays were placed at every 20 m, along two linear transects, ca. 1600 m apart, one with 18 arrays and the other with 19 arrays. Traps were checked at least once a day for 30 days. We also performed haphazard searches collecting specimens by hand with four collectors for at least 8 h each day, 5 h during the day and 3 h at night, which allowed us to maximize our sample size, totalling 960 h. Specimens were euthanized with lidocaine, fixed in 10% formalin and preserved in a 70% ethanol. Collection permits were issued by the appropriate agencies to AAG (SISBIO # 33402-1) and TBC (SISBIO # 29550-2). All specimens were deposited at Coleção Herpetológica da Universidade Federal da Paraíba (CHUFPB). The following analyses were conducted using the whole species dataset, except when stated otherwise (see results). However, for the sake of bias reduction, we performed the niche overlap and phylogenetic structure on each dataset using only individuals captured on the trap arrays (excluding *P. pollicaris*, *S. merianae* and *I. iguana* from the analyses). For morphological niche, we included animals from other collecting methods (e.g., haphazard searches) to increase sample size. We also performed all analyses without the rare species to check if any significant changes in our results occurred.

2.3. Morphometric data

We collected eight morphometric variables from each specimen using an electronic calliper (0.01 mm precision): snout-vent length (SVL), tail length (TL), body width (BW), body height (BH), head width (HW), head height (HH), head length (HL), hind-limb length (HIL) and forelimb length (FOL). We log-transformed (base 10) all morphometric variables to improve their distributions prior to analyses. To partition the total morphometric variation between size and shape, we defined body size as an isometric size variable (Rohlf and Bookstein, 1987) following the procedure described by Somers (1986). We calculated an isometric eigenvector, defined a priori with values equal to $p^{-0.5}$, where

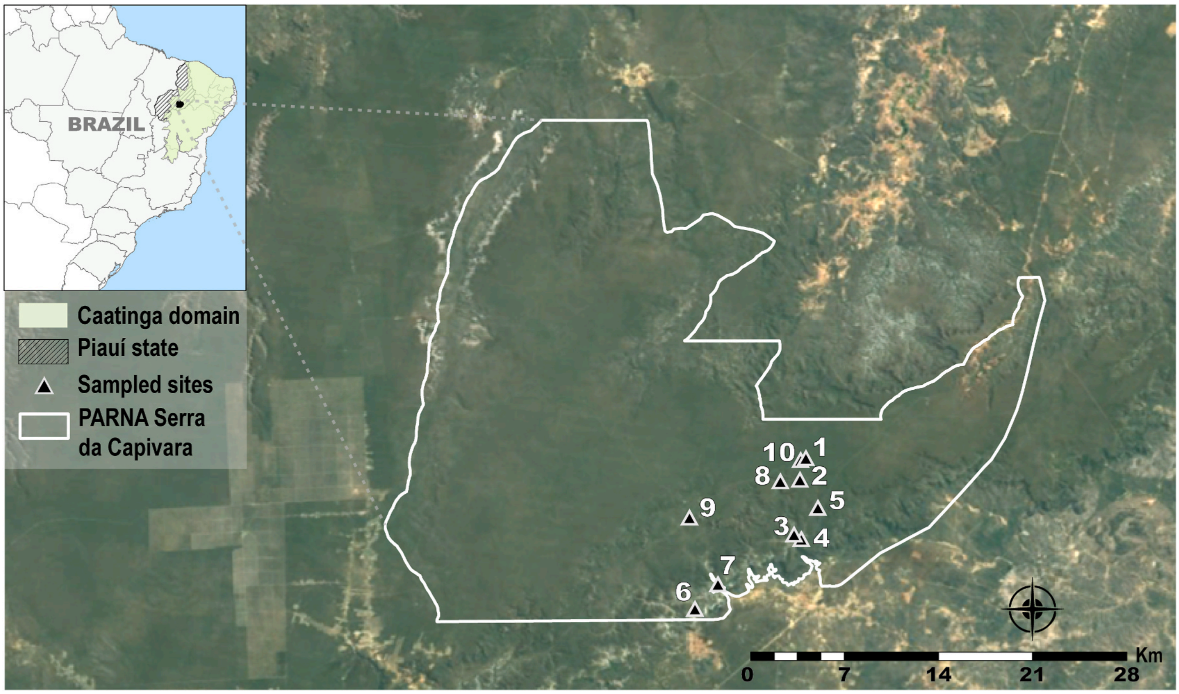

Fig. 1. Schematic map showing the study site location and the ten sampled points. Points 1 and 2 refer to the pitfall trap array trails, while points 3–10 were sampled using haphazard searches.

p is the number of variables (Jolicoeur, 1963). Next, we obtained scores from this eigenvector, hereafter called body size (BS), by post-multiplying the *n* by *p* matrix of log-transformed data, where *n* is the number of observations, by the *p* by 1 isometric eigenvector. To remove the effects of body size from the log-transformed variables, we used Burnaby's method (Burnaby, 1966), where our n x p matrix of log-transformed variables is multiplied by a symmetric matrix, defined as $L = I_p - V(V^TV)^{-1}V^T$, where Ip is a p x p identity matrix, V is an isometric size eigenvector, and V^T is the transpose of matrix V (Rohlf and Bookstein, 1987). Hereafter, morphometric variables refer to size-adjusted variables representing body shape variation. We analysed morphometric variables twice, once considering all species and once considering only those with a sample size larger than five. We used five specimens as a threshold for comparative purposes, which allows accounting for rare species (e.g., Werneck et al. 2009).

2.4. Microhabitat data

In each trap array, we measured the following microhabitat variables within 6 m from the central bucket: (1) exposed soil percentage, (2) bush ground cover percentage, (3) canopy cover percentage, (4) number of trees, (5) number of fallen logs, (6) number of termite nests, (7) number of trees per quadrat, (8) number of bushes, (9) nearest tree distance and (10) nearest tree circumference. We defined as trees all woody plants with at least 10 cm in circumference at breast height and 120 cm tall. We also used the 10 cm in circumference as a lower threshold for fallen logs. We measured variables 1, 2 and 3 using a 50 × 50 cm square frame divided into 25 smaller squares of 10 × 10 cm (Vitt et al., 2007). To generate a percentage value, were counted squares that were filled with more than 50% of a given variable. We randomly placed the square frame three times around each array and obtained a mean value that was used in subsequent analyses. Additionally, for variables 7 and 8, we placed a stick measuring 1 m at the centre of the square frame and spun it 360°; each time it hit a stem, we counted that plant.

2.5. Diet data

We performed diet analysis by direct observation of prey items in lizard stomachs. We dissected all collected specimens and removed their stomachs for analysis under a stereomicroscope. We identified and categorized prey to the taxonomic level of order, except Formicidae (ants), and other prey that were placed in artificial categories, such as insect larvae and plant material. For each prey category, we calculated absolute and relative occurrence, number, and volume (mm^3). To calculate volume, we measured width and length from each intact prey using an electronic calliper (0.01 mm) and then applied the following ellipsoid formula:

$$V = \frac{4}{3}\pi\left(\frac{l}{2}\right) \times \left(\frac{w}{2}\right)^2,$$

where *l* is the prey length, and *w* is the prey width. Using prey volume data, we calculated the niche breadth (*B*) for each specimen and species, using the inverse of Simpson's index:

$$B = \frac{1}{\sum_{i=1}^{n} p_i^2},$$

where *p* is the volumetric proportion of prey category *i* and *n* is the total number of categories.

2.6. Community phylogenetic structure

To test for phylogenetic community structure, we first built a tree depicting the phylogenetic relationships among 62 lizard species we recorded at 9 Caatinga sites (Appendix, Fig. S1) by pruning the Squamate phylogeny of Pyron et al. (2013). Because some species present in our community were absent from this phylogeny, we used their putative closest relatives to represent them in the subsequent analyses (see Gonçalves-Sousa et al., 2022): *Enyalius bibronii* replaced *Enyalius bilineatus*, *Stenocercus squarrosus* replaced *Stenocercus caducus*, and *Glaucomastyx venetacauda* replaced *Cnemidophorus lemniscatus*. Because the genus *Glaucomastyx* is, in fact, more closely related to *Ameivula* than to *Cnemidophorus lemniscatus*, this substitution could potentially overestimate the divergences among *Ameivula* and *Glaucomastyx*. Small changes among these more closely related tips are unlikely to cause significant changes in the analyses and results. Indeed, most evolutionary change in the Squamate tree of life took place at deeper nodes, not at the tips (Vitt and Pianka, 2005). We consider this phylogenetic tree as representing the regional pool of species. Next, we calculated phylogenetic diversity (PD), mean phylogenetic distance (MPD), and mean nearest taxon distance (MNTD) (Webb et al., 2002) for the PARNA da Serra da Capivara lizard community. To test for non-random patterns of phylogenetic community structure, we compared the observed values of PD, MPD, MNTD with a null distribution of each metric generated by shuffling taxon labels on the regional phylogeny 10,000 times (Rabosky et al., 2011). These analyses were implemented in R package PhyloMeasures (Tsirogiannis and Sandel, 2016).

2.7. Niche overlap

We regarded morphometric, microhabitat and diet data as axes of a multidimensional niche space, hereafter referred as morphological, spatial, and trophic niches, respectively. Because these axes are described by continuous (e.g., body size), discrete (e.g., number of termite nests) or data in proportions (e.g., canopy cover), we used appropriate transformations and density estimation techniques to produce unified measures of morphological, spatial, and trophic niche overlap. This approach, first suggested by Slobodchikoff and Schulz (1980) and later developed by Geange et al. (2011), uses a combination of mixture models (for discrete data) and kernel density estimation (for continuous data) to approximate the observed distribution of each niche axis and produce directly comparable niche overlap measures ranging from 0 (no overlap) to 1 (complete overlap). Next, we created separate composite niche overlap measures for morphological, spatial, and trophic niches. To assess differences in niche overlap between pairs of species, we used null models (Gotelli and Graves, 1996) by permutating species labels over all species (1000 iterations). We used the coefficient of heterogeneity to evaluate how species are distributed across each niche axis:

$$\eta = \frac{s^2}{\bar{x}(1-\bar{x})}$$

where s^2 is variance and $\bar{x}$ is the mean of the $i(i-1)/2$ values of niche overlap among i species in the community (Geange et al., 2011). When species are evenly spaced across niche space, η will be near 0; conversely, when species are clustered across niche space, η will be near 1. For each niche axis, we calculated values of η across 1000 permutations of species labels to determine if lizard species are randomly (observed η not significantly different from null expectation), clustered (observed η significantly greater than null expectation) or evenly spaced (observed η significantly smaller than null expectation). We implemented niche overlap analyses in R (R Core Team, 2019) using a modified version of the script provided by Geange et al. (2011).

2.8. Phylogenetic autocorrelation in morphological, spatial, and trophic niches

We used a phylogenetic principal component analysis (pPCA) to assess the presence of phylogenetic structure in the morphometric, microhabitat and diet data of PARNA Serra da Capivara lizard community. The pPCA is a multivariate method that summarize a set of biological traits into a few synthetic variables (principal components) maximizing the product of the variance of the scores and their phylogenetic autocorrelation, as measured by Moran's I (Jombart et al., 2010). Phylogenetic autocorrelation among trait values reflects their non-independence given a phylogenetic tree, such that positive autocorrelation arises when closely related taxa tend to be more similar than expected by chance, whereas negative autocorrelation arises when closely related taxa tend to be less similar than expected by chance (Webb et al., 2002). These contrasting patterns are referred to as global *vs.* local phylogenetic structures, respectively, and represent phylogenetic signal due to close-to-the-root, historical influences, which can be interpreted as the result of niche conservatism, *vs.* more recent, close-to-the-tips divergence interpreted as ecological interactions (biotic or abiotic) leading to convergence or character displacement (Jombart et al., 2010). In the pPCA, the largest eigenvalues principal components (referred as global PCs) represent large variances and strong, positive phylogenetic autocorrelation (historical structures, role of evolutionary factors), whereas the lowest eigenvalues principal components (referred as local PCs) represent large variances and strong, negative autocorrelation (contemporary structures, role of local factors). The computation of the amount of variance and phylogenetic autocorrelation, as well as the loadings associated with each principal component allows identifying which lineages and taxa are involved with global and local structures. For each data set (morphometric, microhabitat and diet), we recovered the global PC and the local PC which explained the higher amount of variation. We used the same phylogenetic tree as described above (Fig. 2) and implemented the pPCA with the R package ADEPHYLO (Jombart et al., 2010).

We conducted all statistical analysis using R (R Core Team, 2019) and used a 5% significance threshold for hypotheses testing. Throughout the text, sample parameters are represented as $\bar{x} \pm$ SD.

3. Results

3.1. Sampled species

We collected 515 individuals of 15 lizard species from eight different families: Phyllodactylidae (*Phyllopezus pollicaris*), Gekkonidae (*Lygodactylus klugei* and *Hemidactylus brasilianus*), Scincidae (*Copeoglossum nigropunctatum*), Teiidae (*Ameiva ameiva*, *Ameivula ocellifera*, *Glaucomastix venetacauda* and *Salvator merianae*), Gymnophthalmidae (*Colobosaura modesta*, *Micrablepharus maximiliani* and *Procellosaurinus erythrocercus*), Leiosauridae (*Enyalius bibronii*), Iguanidae (*Iguana iguana*) and Tropiduridae (*Stenocercus squarrosus* and *Tropidurus hispidus*). For more information about sampling effort, see methods section, and Cavalcanti et al. (2014).

Our analyses without rare species produced results that did not differ substantially from those we found using the complete dataset. Therefore, all results presented in the following sections are based on the complete data (except for the exclusion of species not captured in trap arrays; see Sampling Methods in the "Methods" section). For morphological niche, we included animals from other collecting methods (e.g., haphazard searches) to increase sample size.

3.2. Community phylogenetic structure

The analyses of phylogenetic community structure indicated a lack of phylogenetic structure based on PD (observed = 1407.62; p-value = 0.513), MPD (observed = 276.60; p-value = 0.836) or MNTD (observed = 121.33; p-value = 0.345).

3.3. Niche overlap

Based on morphometric data, niche overlap was highest between *Ameivula ocellifera* and *Glaucomastix venetacauda* (overlap = 0.702, Table 1A), but lowest between *Enyalius bibronii* vs. *Colobosaura modesta* and *Micrablepharus maximiliani* (overlap = 0.222, Table 1A). Except for the overlap between *Ameiva ameiva* and *Ameivula ocellifera*, and *Enyalius bibronii* and *Stenocercus squarrosus*, all other overlap values indicated non-random morphological niche differences between species (Table 1A). The calculated niches of the 12 lizard species displayed

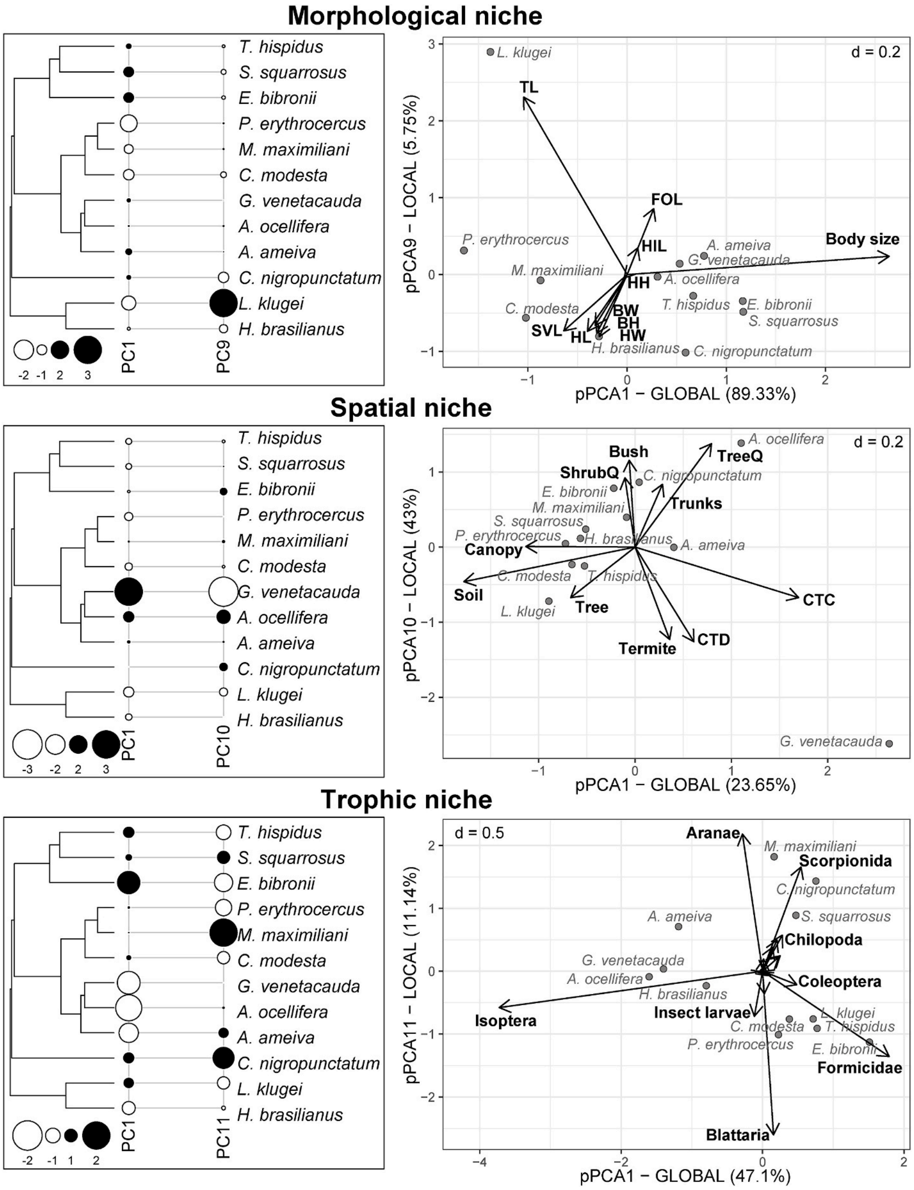

Fig. 2. Phylogenetic trees (on the left) and scatterplots from phylogenetic principal component analysis (pPCA) from Parque Nacional (PARNA) Serra da Capivara lizard assemblage divided in morphological, spatial, and trophic niches. The canonical axes eigenvalues on phylogenetic trees are represent by black (positive autocorrelation) and white (negative autocorrelation) circles, from local (Local PC) and global (Global PC) principal components respectively. Phylogeny was adapted from Pyron et al. (2013). In pPCA scatterplot panels, traits (morphological, microhabitat, and diet) and species loadings were standardized to allow coupled visualization (traits in black, species in grey). Acronyms for morphological variables are **SVL**: snout-vent length, **TL**: tail length, **BW**: body width, **BH**: body height, **HW**: head width, **HH**: head height, **HL**: head length, **HLL**: hind-limb length and **FOL**: forelimb length. Codes for microhabitat variables are **Soil**: exposed soil percentage, **Bush**: bush ground cover percentage, **Canopy**: canopy cover percentage; **Tree**: number of trees, **Trunks**: number of fallen logs, **Termite**: number of termite nests; **TreeQ**: number of trees per quadrat, **ShrubQ**: number of shrubs per quadrat; **CTD**: closest tree distance and **CTC**: closest tree circumference. Names from standardized loadings from prey categories below ±0.48 were excluded from diet pPCA scatterplot to facilitate interpretation.

significant differentiation in all axes but tail length and head length; overall, species were evenly distributed across morphological niche space (Table 1B).

Microhabitat niche overlap was highest between *Hemidactylus brasilianus* and *Tropidurus hispidus* (overlap = 0.867, Table 2A), and lowest between *Ameivula ocellifera* and *Glaucomastix venetacauda* (overlap = 0.422, Table 2A). *Ameivula ocellifera* had the most distinct spatial niche, which differed from *Colobosaura modesta*, *Micrablepharus maximiliani*, *Procellosaurinus erythrocercus* and *Tropidurus hispidus* (Table 2A). The calculated niches of the 12 lizard species displayed significant differentiation only in relation to fallen logs and, overall, species were randomly distributed across spatial niche space (Table 2B).

Based on diet composition data, niche overlap was highest between *Glaucomastix venetacauda* and *Procellosaurinus erythrocercus* (overlap = 0.671, Table 3A), but lowest between *Ameiva ameiva* and *Tropidurus hispidus* (overlap = 0.274, Table 3A). *Tropidurus hispidus* had the most distinct niche, which differed from *Ameiva ameiva*, *Ameivula ocellifera*, *Glaucomastix venetacauda*, *Hemidactylus brasilianus, Lygodactylus klugei* and *Micrablepharus maximiliani* and *Procellosaurinus erythrocercus* (Table 3A). The calculated niches of the 12 species displayed significant clustering in terms of the consumption of Coleoptera, Hemiptera, Hymenoptera and Scorpionida, and significant differentiation in the consumption of Diptera, Formicidae, and Orthoptera; overall, species were randomly distributed across trophic niche space (Table 3B).

Table 1

A - Unified analysis of morphometric niche overlap between 12 species of lizards (N = 466) from Parque Nacional (PARNA) da Serra da Capivara, Piauí, Brazil. Niche overlap was based on nine continuous morphometric variables. Values below diagonal indicate *P*-values of null model tests and statistically significant niche overlap values are indicated in bold. Aa: *Ameiva ameiva* (N = 16), Ao: *Ameivula ocellifera* (N = 35), Gv: *Glaucomastix venetacauda* (N = 20), Cm: *Colobosaura modesta* (N = 7), Eb: *Enyalius bibronii* (N = 6), Hb: *Hemidactylus brasilianus* (N = 28), Lk: *Lygodactylus klugei* (N = 14), Cn: *Copeoglossum nigropunctatum* (N = 6), Mm: *Micrablepharus maximiliani* (N = 102), Pe: *Procellosaurinus erythrocercus* (N = 91), Ss: *Stenocercus squarrosus* (N = 5), Th: *Tropidurus hispidus* (N = 136). **B** - Results of null model tests for species evenness or clustering across niche space based on nine continuous morphometric variables. Size: isometric body size; and size-adjusted values of SVL: snout-vent length, TL: tail length, BW: body width, BH: body height, HW: head width, HH: head height, HL: head length, HLL: hind-limb length and FOL: forelimb length; Overall: average coefficient of heterogeneity over the nine morphometric variables. Numbers represent *P*-values of null model tests, with statistically significant evenly spaced or clustered distributions indicated in bold ($P < 0.05$).

A - Morphometric niche overlap values

	Aa	Ao	Gv	Cm	Eb	Hb	Lk	Cn	Mm	Pe	Ss	Th
Aa		0.761 (0.084)	**0.686** (0.120)	**0.291** (0.267)	**0.479** (0.288)	**0.462** (0.283)	**0.344** (0.257)	**0.348** (0.243)	**0.330** (0.269)	**0.404** (0.320)	**0.343** (0.280)	**0.475** (0.257)
Ao	0.078		**0.702** (0.111)	**0.349** (0.265)	**0.408** (0.221)	**0.498** (0.277)	**0.333** (0.239)	**0.410** (0.258)	**0.372** (0.247)	**0.420** (0.295)	**0.324** (0.243)	**0.504** (0.243)
Gv	**0.007**	**0.004**		**0.291** (0.291)	**0.345** (0.257)	**0.430** (0.287)	**0.273** (0.226)	**0.350** (0.276)	**0.298** (0.265)	**0.356** (0.315)	**0.289** (0.277)	**0.438** (0.280)
Cm	**<0.001**	**<0.001**	**<0.001**		**0.222** (0.303)	**0.421** (0.270)	**0.376** (0.251)	**0.356** (0.285)	**0.524** (0.211)	**0.530** (0.142)	**0.206** (0.238)	**0.322** (0.331)
Eb	**0.003**	**0.001**	**<0.001**	**<0.001**		**0.263** (0.265)	**0.227** (0.248)	**0.299** (0.250)	**0.222** (0.308)	**0.248** (0.266)	0.496 (0.262)	**0.525** (0.270)
Hb	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**		**0.280** (0.172)	**0.333** (0.221)	**0.372** (0.319)	**0.353** (0.235)	**0.310** (0.288)	**0.381** (0.289)
Lk	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**		**0.231** (0.203)	**0.399** (0.221)	**0.500** (0.258)	**0.259** (0.265)	**0.287** (0.230)
Cn	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.001**	**<0.001**	**<0.001**		**0.471** (0.285)	**0.398** (0.268)	**0.332** (0.222)	**0.448** (0.259)
Mm	**<0.001**	**<0.001**	**<0.001**	**0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**		**0.610** (0.248)	**0.302** (0.317)	**0.334** (0.315)
Pe	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**		**0.291** (0.275)	**0.324** (0.256)
Ss	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.103	**<0.001**	**<0.001**	**0.003**	**<0.001**	**<0.001**		**0.512** (0.290)
Th	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.004**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.027**	

B- Overall null model tests for species evenness or clustering across morphometric niche space

	Size	SVL	TL	BW	BH	HW	HH	HL	HLL	FOL	Overall
Clustering	0.997	0.994	0.937	0.979	0.989	0.872	0.999	0.917	0.989	0.965	>0.999
Evenness	**0.003**	**0.006**	0.063	**0.021**	**0.011**	**0.128**	**0.001**	0.083	**0.011**	**0.035**	**< 0.001**

3.4. Phylogenetic autocorrelation in morphological, spatial, and trophic niches

Based on the morphological niche, the global PC (highest phylogenetic autocorrelation; positive eigenvalue) accounted for 89.32 % of the total variation (Fig. 2, Morphological niche). Conversely, the local PC (lowest phylogenetic autocorrelation, negative eigenvalue) accounted for 5.75 % of the total variation (Fig. 2, Morphological niche). Considering the global PC (highest variation explained), axis loadings of morphological niche were contrasts between a set of morphometric variables containing isometric body size, hind-limb length, and forelimb length (larger lizards with longer limbs) against tail length, snout-vent length, and head length (longer lizards with both longer heads and tails).

Based on microhabitat data, the global PC (highest phylogenetic autocorrelation; positive eigenvalue) accounted for 23.65 % of the total variation (Fig. 2, Spatial niche). Conversely, the local PC (lowest phylogenetic autocorrelation, negative eigenvalue) accounted for 43.03 % of the total variation (Fig. 2, Spatial niche). Considering the local PC (highest variation explained), axis loadings of spatial niche were contrasts between a set of microhabitat variables containing bush ground cover percentage, number of trees per quadrat and nearest tree distance (large and patched trees with bush covered soil), against canopy cover percentage, number of trees and exposed soil percentage (dense arboreal patches). These results suggest a higher influence of contemporary factors on the partitioning of spatial niche among species, while evolutionary factors seem to play a lesser role on the structure of microhabitat resource usage.

Based on diet composition data, the global PC (highest phylogenetic autocorrelation; positive eigenvalue) accounted for 47.10 % of the total variation (Fig. 2, Trophic niche). Conversely, the local PC (lowest phylogenetic autocorrelation, negative eigenvalue) accounted for 11.14 % of the total variation (Fig. 2, Trophic niche). Considering the global PC (highest variation explained), axis loadings of trophic niche were contrasts between a set of dietary variables containing Formicidae, Scorpionida, and Coleoptera against Isoptera and Aranae (termites and spiders). These results suggest a higher influence of evolutionary factors on the partitioning of trophic niche among species, while contemporary factors seem to play a lesser role on the structure of dietary resource usage.

4. Discussion

We detected no phylogenetic structure in the lizard community from Serra da Capivara, which implies that no ecological forces, such as habitat filtering, drove the community composition to a clustered pattern (Webb et al., 2002). In this phylogenetic scenario, the role of ecological interactions can be determinant on the composition and niche structure of the lizard community. The niche overlap analysis indicated that the lizard community from Serra da Capivara is structured along morphometric niches, with low niche overlap among species, while spatial and trophic niches lacked an overall structure. However, most ecological traits showed a strong phylogenetic basis (especially morphometric and trophic niches). These findings are similar to other studies examining seasonal and/or arid regions on South America (Mesquita et al., 2006a, 2006b; Werneck et al., 2009) and Australia

Table 2
A - Unified analysis of spatial (microhabitat) niche overlap between 12 species of lizards (N = 370) from Parque Nacional (PARNA) da Serra da Capivara, Piauí, Brazil based on ten microhabitat variables. Values above diagonal indicate mean (standard deviation); values below diagonal indicate *P*-values of null model tests. Statistically significant niche overlap values are indicated in bold. Aa: *Ameiva ameiva* (N = 12), Ao: *Ameivula ocellifera* (N = 6), Cm: *Colobosaura modesta* (N = 10), Cn: *Copeoglossum nigropunctatum* (N = 5), Eb: *Enyalius bibronii* (N = 4), Gv: *Glaucomastix venetacauda* (N = 2), Hb: *Hemidactylus brasilianus* (N = 24), Lk: *Lygodactylus klugei* (N = 6), Mm: *Micrablepharus maximiliani* (N = 104), Pe: *Procellosaurinus erythrocercus* (N = 97), Ss: *Stenocercus squarrosus* (N = 4), Th: *Tropidurus hispidus* (N = 96). **B** - Results of null model tests for species evenness or clustering across niche space based on the ten microhabitat variables, Soil: exposed soil percentage, Bush: bush ground cover percentage, Canopy: canopy cover percentage (proportion data, bounds at 0 and 1), Tree: number of trees, Trunks: number of fallen logs, Termite: number of termite nests (count data); TreeQ: number of trees per quadrat, ShrubQ: number of shrubs per quadrat, CTD: closest tree distance and CTC: closest tree circumference (continuous data), Overall: average coefficient of heterogeneity over the ten microhabitat variables. Numbers represent *P*-values of null model tests, with statistically significant evenly spaced or clustered distributions indicated in bold ($P < 0.05$).

A – Microhabitat niche overlap values

	Aa	Ao	Cm	Cn	Eb	Gv	Hb	Lk	Mm	Pe	Ss	Th
Aa		**0.529 (0.264)**	0.678 (0.195)	0.628 (0.111)	0.724 (0.124)	0.570 (0.214)	0.744 (0.136)	0.639 (0.091)	0.778 (0.135)	0.729 (0.147)	0.704 (0.123)	0.774 (0.152)
Ao	**0.015**		**0.508 (0.273)**	0.619 (0.243)	0.557 (0.265)	0.422 (0.257)	0.541 (0.210)	0.561 (0.231)	**0.605 (0.223)**	**0.575 (0.238)**	0.565 (0.293)	**0.573 (0.225)**
Cm	0.113	**0.01**		0.620 (0.203)	0.641 (0.217)	0.526 (0.260)	0.691 (0.184)	0.594 (0.180)	0.719 (0.198)	**0.703 (0.203)**	0.577 (0.208)	0.748 (0.197)
Cn	0.254	0.457	0.266		0.670 (0.167)	0.522 (0.225)	0.705 (0.103)	0.626 (0.156)	0.762 (0.111)	0.709 (0.131)	0.635 (0.191)	0.742 (0.121)
Eb	0.856	0.215	0.425	0.825		0.466 (0.168)	0.665 (0.156)	0.645 (0.167)	0.739 (0.126)	0.684 (0.155)	0.635 (0.137)	0.693 (0.156)
Gv	0.678	0.144	0.462	0.587	0.338		0.534 (0.176)	0.513 (0.211)	0.548 (0.184)	0.540 (0.198)	0.551 (0.193)	0.570 (0.193)
Hb	0.172	**0.011**	0.061	0.561	0.412	0.402		0.722 (0.087)	0.821 (0.082)	0.826 (0.070)	0.711 (0.149)	0.867 (0.074)
Lk	0.175	0.139	0.086	0.471	0.629	0.479	0.513		0.712 (0.112)	0.734 (0.098)	0.673 (0.147)	0.714 (0.089)
Mm	0.195	**0.028**	0.051	0.821	0.855	0.419	0.108	0.322		**0.855 (0.057)**	0.698 (0.166)	**0.849 (0.074)**
Pe	**0.029**	**0.012**	**0.026**	0.464	0.44	0.379	0.16	0.477	**0.002**		0.700 (0.181)	0.859 (0.066)
Ss	0.769	0.257	0.145	0.701	0.714	0.735	0.728	0.773	0.552	0.57		0.709 (0.162)
Th	0.181	**0.01**	0.144	0.708	0.513	0.555	0.671	0.335	**0.001**	**0.003**	0.644	

B - Overall null model tests for species evenness or clustering across microhabitat niche space

	Soil	Bush	Canopy	Trees	Trunks	Termite	TreeQ	ShrubQ	CTD	CTC	Overall
Clustering	0.484	0.455	0.269	0.035	0.972	0.691	0.327	0.118	0.629	0.623	0.534
Evenness	0.516	0.545	0.731	0.965	**0.028**	0.309	0.673	0.882	0.371	0.377	0.466

(Rabosky et al., 2011), where trophic and morphological niches were largely predicted by phylogeny, while the spatial niche was more related to contemporary factors not related to interspecific relations, but to local resource abundance.

We observed an overall significant partitioning across the morphometric space among species, indicating assemblage structure. In addition, most morphometric variables presented a niche differentiation pattern. These segregations among body forms were mirrored among lizard families. Teiids and gymnophthalmids present streamlined, cylindrical, and uniform long bodies and heads, whereas iguanians have more robust bodies and longer limbs and claws (Pianka and Vitt, 2003), as corroborated by our pPCA results (association of iguanians with both hind-limb and forelimb lengths). These structural differences have strong implications for natural history and ecological characteristics such as foraging mode, which is generally sit-and-wait in Iguania and actively foraging in Teiioidea. For Gymnophthalmidae, small body sizes, elongated body shapes, elongated head shapes and a tendency toward limb reduction are typical in the family. This allows them to access specific niches (e.g., leaf litter) and consequently to have cryptozoic and fossorial habits (Pianka and Vitt, 2003). Furthermore, these ecological characteristics together with dietary patterns seem to be closely associated with the cranial morphology of gymnophthalmids (Barros et al., 2011). For gekkotans, we can highlight smaller limbs, longer heads, flattened bodies, of which longer heads, and smaller limbs were also significant (pPCA results presented negative correlations with limb lengths and positive correlations with head lengths on the global axis), like what was reported by Pianka and Vitt (2003). All these differences group geckos as a guild with access to specific niches, such as vertical microhabitats (from trees to rocky outcrops). Based on this and on the variation explained in our pPCA analysis, we suggest that the morphometric structure of the PARNA Serra da Capivara lizard community is a pool of species with very intrinsic morphometric characteristics, basically predicted by their evolutionary histories. The results we found are similar to other studies on Neotropical lizard communities, with phylogeny being a determinant factor for the morphometric structure of those communities (Mesquita et al., 2006a, 2006b). Moreover, high body size variation among co-existing taxa can be an important predictor of coexisting species within lizard communities (Mesquita et al., 2006b). This can be also an explanation for the PARNA Serra da Capivara lizard community composition, since we found a large variation among species body sizes (Appendix Table S1).

The community was not structured based on the overall spatial niche. Except for the number of logs, no other variable presented a significant pattern of niche differentiation. This contrasts with previous studies addressing lizard communities from Neotropical rainforests and savannas, where associations between species and microhabitat variables are explained by a significant phylogenetic influence (Garda et al., 2013; Vitt et al., 2007). Although niche conservatism is shown in many biological communities (Losos, 2008) and is well documented for the spatial niche in lizards (Schulte et al., 2012; Vitt et al., 2003), microhabitat use by the PARNA Serra da Capivara lizard community does not seem to be influenced by these factors, unlike previous reports for lizard communities in other Caatinga areas (Andrade et al., 2013; Vitt, 1995). Nevertheless, Neotropical savannas and seasonally dry tropical forest

Table 3

A - Unified analysis of trophic niche overlap between 12 species of lizards (N = 224) from Parque Nacional (PARNA) da Serra da Capivara, Piauí, Brazil, based on the percentage volume of nineteen prey categories. Values above diagonal indicate mean (standard deviation); values below diagonal indicate *P*-values of null model tests. Species pairs occupying statistically different niches are indicated in bold. Aa: *Ameiva ameiva* (N = 5), Ao: *Ameivula ocellifera* (N = 26), Cm: *Colobosaura modesta* (N = 4), Cn: *Copeoglossum nigropunctatum* (N = 3), Eb: *Enyalius bibronii* (N = 5), Gv: *Glaucomastix venetacauda* (N = 14), Hb: *Hemidactylus brasilianus* (N = 9), Lk: *Lygodactylus klugei* (N = 6), Mm: *Micrablepharus maximiliani* (N = 26), Pe: *Procellosaurinus erythrocercus* (N = 15), Ss: *Stenocercus squarrosus* (N = 3), Th: *Tropidurus hispidus* (N = 107). **B** - Results of null model tests for species evenness or clustering across niche space based on nineteen prey categories, Ac: Acari, Ar: Aranae, Bl: Blattaria, Ch: Chilopoda, Co: Coleoptera, Dl: Diplopoda, Dp: Diptera, Fo: Formicidae, Ga: Gastropoda, He: Hemiptera, Hy: Hymenoptera, Il: insect larvae, Id: Isopoda, It: Isoptera, Or: Orthoptera, Ps: Pseudoescorpiones, Sc: Scorpionida, So: Solifuga and Ve: vegetable remains. Overall: average coefficient of heterogeneity over the nineteen prey categories. Numbers represent *P*-values of null model tests, with statistically significant evenly spaced or clustered distributions indicated in bold ($P < 0.05$).

A – Trophic niche overlap values

	Aa	Ao	Cm	Cn	Eb	Gv	Hb	Lk	Mm	Pe	Ss	Th
Aa		0.548 (0.161)	0.627 (0.106)	0.643 (0.104)	**0.623 (0.145)**	0.601 (0.149)	0.633 (0.129)	0.655 (0.097)	0.558 (0.145)	0.622 (0.109)	0.620 (0.084)	**0.274 (0.147)**
Ao	0.789		0.498 (0.128)	0.529 (0.184)	0.497 (0.201)	0.659 (0.178)	0.593 (0.175)	0.541 (0.166)	0.639 (0.227)	0.620 (0.185)	0.515 (0.141)	**0.409 (0.214)**
Cm	0.666	0.474		0.612 (0.090)	0.604 (0.132)	0.542 (0.124)	0.573 (0.099)	0.618 (0.121)	0.534 (0.108)	0.579 (0.082)	0.623 (0.121)	0.311 (0.170)
Cn	0.688	0.921	0.645		0.618 (0.159)	0.569 (0.180)	0.592 (0.109)	0.630 (0.095)	0.535 (0.124)	0.605 (0.116)	0.627 (0.101)	0.278 (0.152)
Eb	**0.01**	0.224	0.312	0.18		**0.540 (0.192)**	**0.575 (0.145)**	0.638 (0.130)	0.497 (0.138)	0.577 (0.143)	0.612 (0.098)	0.313 (0.201)
Gv	0.607	0.865	0.252	0.69	**0.025**		0.624 (0.165)	0.584 (0.160)	0.616 (0.178)	0.671 (0.189)	0.546 (0.138)	**0.351 (0.175)**
Hb	0.412	0.675	0.223	0.359	**0.002**	0.292		0.633 (0.122)	0.609 (0.139)	0.640 (0.114)	0.588 (0.100)	**0.332 (0.156)**
Lk	0.343	0.51	0.619	0.593	0.118	0.168	0.235		0.565 (0.126)	0.641 (0.106)	0.618 (0.098)	**0.304 (0.183)**
Mm	0.88	0.406	0.855	0.952	0.236	0.487	0.818	0.776		0.643 (0.157)	0.545 (0.115)	**0.378 (0.186)**
Pe	0.917	0.475	0.838	0.99	0.385	0.729	0.637	0.921	0.726		0.584 (0.092)	**0.333 (0.180)**
Ss	0.207	0.832	0.814	0.221	0.133	0.351	0.3	0.313	0.972	0.905		0.313 (0.192)
Th	**0.006**	**<0.001**	0.152	0.063	0.18	**0.003**	**0.012**	**0.023**	**<0.001**	**0.001**	0.449	

B - Overall null model tests for species evenness or clustering across trophic niche space

	Ac	Ar	Bl	Ch	Co	Dl	Dp	Fo	Ga	He	Hy	Il	Id	It	Or	Ps	Sc	So	Ve	Overall
Clustering	0.519	0.677	0.546	0.636	**0.017**	0.843	0.975	0.982	0.439	**0.002**	<0.001	0.077	0.355	0.157	0.530	0.614	**0.017**	0.803	0.319	0.772
Evenness	0.423	0.323	0.454	0.340	0.983	0.157	0.025	**0.018**	0.561	0.995	1.000	0.899	0.645	0.826	**< 0.001**	0.385	0.983	0.197	0.662	0.228

lizard communities are similar to the PARNA Serra da Capivara lizard community (Mesquita et al., 2006b; Werneck et al., 2009), with both lacking structure in spatial niche and with historical factors unable to predict the patterns observed. This indicates that these communities are likely young, but with resource abundance driving community structure instead of competition.

Because the Caatinga expanded relatively recently (late Quaternary) when compared to other Neotropical formations, and its original distribution was drastically reduced (Silva, 2011), we can speculate that lizards in Serra da Capivara have been coexisting for short periods of time when compared with other Neotropical environments. This short time likely did not allow species divergences among ecological characteristics and promoted the observed lack of ecological and historical structure. Nevertheless, the effects of phylogeny in defining ecological traits at Serra da Capivara lizard community could be masked, because major taxa are underrepresented (e.g., some families, such as Leiosauridae and Scincidae, are present by a single species each), a bias also reported for other Neotropical lizard communities (Garda et al., 2013; Mesquita et al., 2006b). In contrast, the role of contemporary factors presented by pPCA results suggests local influence in spatial niche segregation. But, the relatively homogenous habitat structure of the studied area could drive species to a more convergent pattern, despite the morphometric structure indicated below. Another explanation for the observed pattern is the age of community formation. Older taxa are, theoretically, less influenced by competition than taxa those that recently began to share the same habitat; the chance of coevolution and consequently historical community structure increases with the time during which species interact (Losos, 1996).

Finally, there is also a chance that the collecting period may have influenced the resource use pattern and microhabitat availability for lizard species. When the sampling was conducted, the Caatinga region was suffering the most severe drought within the last three decades, and in our study site there was a lack of effective rainfall for nearly a year. Because the Caatinga is a vegetational formation that presents foliar deciduousness, the drought may have affected local microhabitat conditions, influencing species coexistence. Lizard richness and diversity may be lower during the dry season in Caatinga (Andrade et al., 2013), and other resources, such as food, are directly influenced by drought. This seasonality in resources can directly affect lizard niche breadth in these communities. In many tropical regions, including the Caatinga, prey abundances reduce sharply during the dry season causing species to increase foraging effort, expanding habitat use and hence niche overlap among species (Griffiths and Christian, 1996).

The lizard community from PARNA Serra da Capivara was not structured based on the trophic niche. Yet at least three prey categories presented a common pattern of niche differentiation among species (Formicidae, Diptera and Orthoptera, Table 3B). This contrasts with forested regions, like Amazonia and Dry forests, where communities are commonly structured based on diet (Vitt et al., 1999; Werneck et al., 2009), but is similar to Neotropical savannas (Mesquita et al., 2006a, 2006b). This can be explained by low niche segregation between species and/or the existence of intrinsic factors (e.g., phylogenetic heritage) defining species ecological characteristics (Losos, 1996). It is important to highlight that these two theories are not exclusive. Our results suggest a lack of community structure, but a high influence of phylogenetic factors defining diet niche structure (based on pPCA results). Most of the phylogenetic influence was observed in Teiidae and Tropiduridae. Classical ecological studies underscored a main ecological divergence among squamates, relating it to the basal Squamata divergence between Iguania and Scleroglossa recovered in previous phylogenies (Vitt and Pianka, 2005). Scleroglossans were believed to have evolved and developed physiological and morphological characteristics that allowed a shift in their ecological habits, such as mandibular prey capture, chemosensory system, and active foraging mode (for autarchoglossans). Iguanians, conversely, were thought to not have undergone such changes and retained most of the ancestral characteristics (lingual prey capture, visual discrimination and sit-and-wait foraging mode) (Vitt and Pianka, 2005). However, such basal phylogenetic distinction between Iguania and Scleroglossa was not supported by subsequent hypotheses (Burbrink et al., 2020). Recent studies have provided different interpretations for the divergence on dietary aspects of squamates based on these new phylogenetic hypotheses. For instance, the high ingestion of Hymenoptera (especially ants) by iguanian lizards may be more related to the timing of ant diversification, which matches Iguania diversification time (Sites et al., 2011). Such differences between taxa are very useful to explain differences among dietary patterns that we observed in our study. Teiids (previously considered scleroglossans) ingested mostly prey lacking chemical defences and presenting high energetic rates and low accessibility, such as isopterans, spiders, larvae, and crickets. Iguanians usually eat prey with chemical defences, such as hymenopterans (including ants) and beetles (Vitt and Pianka, 2005). In addition, teiid diets have been shown to be significantly influenced by phylogenetic relationships in a previous global analysis (Vitt and Pianka, 2005).

Despite the large amount of variation explained by historical effects, many closely related species from PARNA Serra da Capivara lizard community presented moderate to low trophic niche overlaps. Also, we did not find significant phylogenetic effects in many pairs of sister species, so contemporary factors (e.g., interactions) may be acting to maintain these relationships, which can be determinant for the structure of lizard communities (e.g., absence of roaches in the diet of *Micrablepharus maximiliani*, while being very abundant in the diet of two other gymnophthalmids: *Colobosaura modesta* and *Procellosaurinus erythrocercus*). Finally, at a broader scale, our findings are somehow similar to those found in other arid areas across the globe, especially in deserts (Rabosky et al., 2011). Many assemblages of these regions (both Australia and North America) exemplify how phylogenetic relatedness may account for diet similarity. Moreover, trophic niche segregation occurs between phylogenetic distant species rather than among closely related ones, suggesting highly conserved dietary preferences (niche conservatism Rabosky et al., 2011), which is corroborated by the results from pPCA.

We conclude that ecological interactions, local resource availability and evolutionary history are responsible for the community structure in PARNA Serra da Capivara, with local factors (local resource availability) predicting the lack of spatial niche structure while a strong phylogenetic basis predicts both morphometric and dietary niche structures. The first study with lizard communities in the Caatinga evidenced the presence of community structure based on microhabitat and dietary axis promoted by historical factors (Vitt, 1995), like suggested by our pPCA result based on diet composition. Interestingly, the patterns found in PARNA Serra da Capivara are also similar to STDFs enclaves within the Cerrado (Mesquita et al., 2006a, 2006b; Werneck et al., 2009). Evidence supports previous connections among Caatinga and other STDFs, suggesting a shared history among these areas, with the Caatinga region harbouring the largest fragment of STDF (Prado, 2003). Although these results from two local communities are quite preliminary, we can observe congruence in the behaviour and structure of lizard communities in the Caatinga, Cerrado and other STDFs when considering the relationships among these environments. Hence, the present study partially corroborates the pioneer study on the structure of lizard communities in the Caatinga (Vitt, 1995) and many other studies in Neotropical open formations, such as Caatinga, Cerrado and STDF enclaves. We also present further information regarding similarities between lizard communities from three open formations. Although observations between these communities are preliminary, they open a pathway for further comparative studies. Finally, we provide further data on how lizard community niche structure in the Caatinga can be similar to other arid areas, such as Australian and North American deserts.

CRediT authorship contribution statement

Lucas Barbosa de Queiroga Cavalcanti: Methodology, Formal analysis, Data curation, Writing – original draft, Investigation, Writing – review & editing, Visualization. **Adrian Antonio Garda:** Conceptualization, Methodology, Writing – review & editing, Resources, Supervision, Project administration, Funding acquisition. **Taís Borges Costa:** Data curation, Methodology, Investigation. **Anaïs Savaugere:** Data curation, Methodology, Investigation. **Giselle Pessoa:** Data curation, Methodology, Investigation. **Guarino Rinaldi Colli:** Conceptualization, Methodology, Software, Formal analysis, Writing – review & editing, Resources, Supervision, Project administration, Funding acquisition. **Marília Bruzzi Lion:** Methodology, Software, Formal analysis, Writing – review & editing, Visualization. **Daniel Oliveira Mesquita:** Conceptualization, Methodology, Software, Formal analysis, Writing – review & editing, Resources, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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