

## INTERRELATIONS BETWEEN ENVIRONMENTAL HETEROGENEITY, COMPETITION, AND PHYLOGENY IN THE STRUCTURE OF A LIZARD ASSEMBLAGE IN A HYPOXEROPHILIC CAATINGA AREA OF BRAZIL

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**Abstract.**—The dynamics of a lizard assemblage are influenced by both stochastic and deterministic factors. Structure within the assemblage can result from contemporary factors and differences in evolutionary history among lineages. The objective of this study was to analyze the spatial and trophic structure of a lizard assemblage in Serra dos Macacos, Sergipe, Brazil, and its relationship with historical and ecological factors. We collected data between March and September 2019 during four 14-d-long campaigns using pitfalls, glue traps, and an active search to capture lizards. We recorded information on the substrates occupied by lizards, collected individuals, and we removed their digestive tracts for dietary analysis. We measured the structural characteristics of the microhabitats around the pitfalls and we related these to the abundance of captured species. The results showed that the assembly was structured only with respect to the trophic niche, with most species showing preferences for certain features related to vegetation cover, probably reflecting inherent differences in thermoregulation, as well as spatial heterogeneity itself. We recorded 16 lizard species belonging to 10 families, and phylogenetic analysis revealed a greater contribution of the historical component, although phylogeny alone did not significantly explain the variation. Therefore, it is important to consider the ecological and historical factors when interpreting the results. Serra dos Macacos is a hypoxerophytic Caatinga formation with perennial vegetation strata, and there is an association between spatial heterogeneity and the saurofauna. Thus, forest suppression and habitat loss may negatively affect the diversity of these animals.

**Key Words.**—community ecology; diet; ecological factors; historical factors; niche; space use; Squamata

**Resumo.**—A dinâmica de um taxocenose de lagartos é influenciada por fatores estocásticos e determinísticos. A estrutura da comunidade pode resultar de fatores contemporâneos e de diferenças na história evolutiva das linhagens. O objetivo deste estudo foi analisar a estrutura espacial e trófica de uma taxocenose de lagartos na Serra dos Macacos, Sergipe, Brasil, e sua relação com fatores históricos e ecológicos. Coletamos dados entre março e setembro de 2019, durante quatro campanhas de 14 dias de duração, utilizando armadilhas de queda, armadilhas de cola e busca ativa. Registramos informações sobre os substratos ocupados pelos lagartos, coletamos indivíduos e removemos seus tratos digestivos para análise da dieta. Medimos as características estruturais dos microhabitats em torno das armadilhas e as relacionamos com a abundância de espécies capturadas. Os resultados mostraram que a taxocenose esteve estruturada apenas no nicho trófico, com a maioria das espécies mostrando preferências por certas características relacionadas à cobertura vegetal, provavelmente refletindo diferenças inerentes à termoregulação, bem como a própria heterogeneidade espacial. Foram registradas 16 espécies de lagartos pertencentes a 10 famílias, e a análise filogenética revelou uma maior contribuição do componente histórico, embora a filogenia por si só não tenha explicado significativamente a variação. Portanto, é importante considerar os fatores ecológicos e históricos na interpretação dos resultados. A Serra dos Macacos é uma formação de Caatinga hipoxerófito com estratos de vegetação perene, e há uma associação entre a heterogeneidade espacial e a saurofauna. Assim, a

**supressão florestal e a perda de habitat podem afetar negativamente a diversidade desses animais.**

*Palavras Chave.*—ecologia de comunidades; dieta; fatores ecológicos; fatores históricos; nicho; uso do espaço; Squamata

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**INTRODUCTION**

A community is a group of organisms with multiple species that coexist in space and time (Vellend 2010). Identifying and studying their patterns (e.g., diversity, abundance, and species composition) as well as the processes underlying these patterns have been a main interest in ecology (McGill et al. 2006; Weber et al. 2018; Catford et al. 2022). Owing to their complex and dynamic nature, however, it is extremely difficult to study communities. Therefore, scientists usually work with subsets of organisms with defined affinities (e.g., guilds and assemblages) to identify patterns of interactions between them (Pianka 1973; Fauth et al. 1996).

An assemblage of phylogenetically close organisms is structured when the species and their ecological traits are arranged non-randomly and can be tested using null models (Winemiller and Pianka 1990; Gotelli 2000). In modern coexistence theory, two mechanisms (equalizers and stabilizers) are responsible for maintaining and structuring assemblages; they involve both stochastic and deterministic elements that can operate at different scales in space and time (Chesson 2000; Hubbell 2005; Mohd 2022). From a deterministic perspective, the structure can be a result of contemporary (ecological) factors, and also a reflection of evolutionary history among the lineages that comprise the assemblages (Webb et al. 2002; Rabosky et al. 2011; Gonçalves-Sousa et al. 2019). To understand key elements, therefore, it is important to consider both historical (phylogeny) and ecological factors when interpreting the results, because analyzing them separately can lead to biased conclusions (Mesquita et al. 2007; Winck et al. 2016; Gonçalves-Sousa et al. 2022).

In recent decades, improvements in phylogenetic comparative methods have revealed the influence of historical aspects on the organization of lizard assemblages; indeed, evolutionary divergence among clades implies different ways of resource acquisition and utilization (Cooper 1995; Vitt et al. 2003; Mesquita et al. 2016). Thus, the closest lineages are assumed to share ecomorphological traits acquired through competitive and selective pressures that have occurred in the past (Connell 1980; Losos 1996; Vitt and Pianka 2005). It is thought that niche conservatism

and phylogenetic inertia have significantly influenced the composition and organization of present-day assemblages (Pyron and Burbrink 2014; Albuquerque et al. 2018). Additionally, other historical factors related to biogeography, such as spatial distribution, a regional pool of species, and their relation to local richness and composition, may contribute to assemblage structure (Chase and Myers 2011; Weber et al. 2018; Pavón-Vázquez et al. 2022).

Recent studies suggest that ecological patterns exhibit global convergence and are typically influenced by characteristics such as diet, activity, habitat, and metabolism, indicating the existence of functional groups of lizards (Pianka et al. 2017; Vidan et al. 2019). In turn, ecological patterns related to habits, such as the terrestrial, nocturnal, or ambush foraging mode are strongly constrained by phylogeny, and the most widespread and species-rich families have multiple functional groups, thus contributing to the high incidence of niche convergence (Pelegrin et al. 2021). When examining global dietary patterns, there are correlations between feeding habits, periods of activity, and life history (Pianka et al. 2017). For example, myrmecophagy is an important specialization that is phylogenetically concentrated in Iguania and has only recently evolved in Lacertoidea, with higher ingestion in lizards with smaller home ranges and lower ingestion in lizards with extensive home ranges (Cavalcanti et al. 2023a). In Brazil, Mesquita et al. (2006a) observed similarities in diet, microhabitat use, and activity time among more closely related species in a Cerrado lizard assemblage. In turn, Albuquerque et al. (2018) found signs of niche fidelity in diet, microhabitat, body temperature, and clutch size in three populations of Neotropical Lava Lizards (*Tropidurus hispidus*) and Spix's Whiptails (*Ameivula ocellifera*) distributed in different biomes in northeastern Brazil.

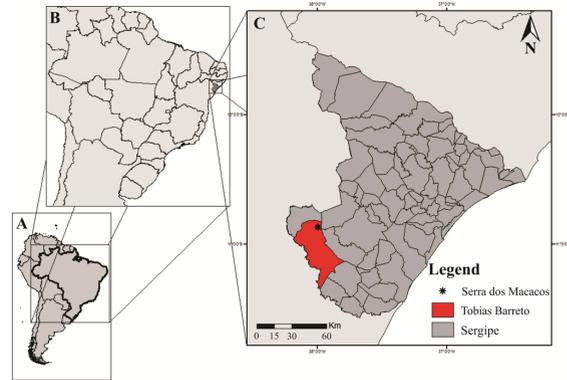
Regarding ecological factors, competition is traditionally recognized as the most important force in the organization of assemblages (Pianka 1973; Schoener 1977; Gotelli and McCabe 2002). Thus, we assume the existence of a similarity limit between sympatric species and that ecologically similar species diverge on at least one of the niche axes (trophic, spatial, or temporal). In the absence

of mechanisms to equalize fitness differences, species generally occur in allopatry (Pianka 1973; Chesson 2000; Faria and Araújo 2004). Despite the emphasis on competition, other ecological factors, such as predation, parasitism, seasonality, and habitat heterogeneity can influence an assemblage (Chesson 2000; Brito et al. 2014; Passos et al. 2016; Barros et al. 2022).

Diet, microhabitat use, thermoregulation, and life history of lizards can be strongly influenced by environmental, physical, and climatic aspects (Brandt and Navas 2011; Dell et al. 2014; Albuquerque et al. 2018). At the physical level, more heterogeneous habitats have more available resources that can support more species than more homogeneous and/or degraded environments (Ricklefs and Miller 1999; Luiselli et al. 2022). In addition, structural variables that influence light, temperature, and humidity can directly affect the fitness of organisms and, consequently, determine the occurrence or non-occurrence of a species (Dias and Rocha 2014; Arenas-Moreno et al. 2021; Žagar et al. 2023).

Several authors have discussed the effect of seasonality on lizard ecology (Huey and Pianka 1977; Maia-Carneiro et al. 2012; Passos et al. 2016). In highly seasonal environments such as the Brazilian Caatinga, characterized by high temperatures, a prolonged dry season, and scarce and irregular rainfall (Prado 2005; Albuquerque et al. 2012), some species alter their diet and avoid breeding during dry periods in response to the low availability of trophic resources (James and Shine 1985; Albuquerque et al. 2018). As ectothermic organisms, lizards can also restrict their daily activity due to high temperatures in warmer seasons, a choice that affects their foraging activity (Huey and Pianka 1977; Winck et al. 2011; Maia-Carneiro et al. 2012).

Over the last few decades, studies on lizard assemblages have been conducted in several habitats in the Neotropical region (e.g., Vitt 1995; Vitt and Zani 1998; Winck et al. 2016; Souza et al. 2021); however, only a few studies have investigated the real influence of historical and ecological factors on these groupings (e.g., Werneck et al. 2009; Gonçalves-Sousa et al. 2019; Gonçalves-Sousa et al. 2022; Cavalcanti et al. 2023b). Some authors suggest that historical factors have a greater influence on the trophic axis than on the spatial axis (Gainsbury and Colli 2003; Werneck et al. 2009; Cavalcanti et al. 2023b). In contrast, a recent study conducted in the Caatinga indicated that ecological factors have a greater influence on both spatial and trophic



**FIGURE 1.** Map showing the location of Serra dos Macacos, Tobias Barreto, Sergipe, Brazil. Map A is South America, map B is Brazil, and map C is Sergipe with Tobias Barreto shown in red.

niche structures (Gonçalves-Sousa et al. 2019). It is possible to conclude that ecological and historical factors (individually or together) act in distinct ways on assemblage structures, culminating in different patterns among localities. To study the possible causes of lizard assemblage in a tropical environment, we analyzed the trophic and spatial structure of a lizard community in an area of hypoxerophilous Caatinga in the northeast region of Brazil. We expected that: (1) the structural characteristics of the habitat influence the abundance of lizards; (2) the assemblage is structured in at least one of the investigated niche dimensions (spatial or trophic), given the irregularity of the environmental conditions observed in the Caatinga and the oscillations in the availability of resources; and (3) ecological factors exert a greater influence on the assemblage because of the water irregularities and severity of some abiotic parameters typical of the Caatinga

## MATERIALS AND METHODS

**Study site.**—We conducted this study at Serra dos Macacos (10°52′52″S, 37°59′12″W), which is approximately 360 km<sup>2</sup> in area at an elevation of 600 m, in the Tobias Barreto municipality, Sergipe State, Brazil (Fig. 1). The mountain is located in the central-southern part of Sergipe, where the predominant vegetation type is the hypoxerophilous Caatinga, characterized by larger trees and forest physiognomies (Arboreal Caatinga or Dry Forest; Instituto Brasileiro de Geografia e Estatística [IBGE] 2011; Fernandes et al. 2015). The climate is hot and semi-arid, with annual temperature and precipitation averages of approximately 28° C and 780 mm, respectively (Nimer 1989; IBGE 2011). Serra dos Macacos

presents strong seasonality: May to July show the highest rainfall rates, while October to December show the lowest rainfall (<http://www.semarh.se.gov.br/meteorologia>). The peak of Serra dos Macacos is the headwater of the Macacos stream, which is part of the Rio Real watershed. The riparian forest on the rocky banks along the stream presents substantial semideciduous arboreal vegetation, favoring the formation of a dense understory associated with large terrestrial bromeliads and epiphytes (Soares et al. 2018)

**Data collection.**—We conducted the fieldwork between March and September 2019, in four campaigns each lasting 14 d, totaling 56 d of sampling. We selected three sample sites: (1) Site A (10°52'48.83"S, 37°59'15.43"W) refers to a forest area on the mountain slope, on the margins of the stream, with large arboreal vegetation, leaf litter, rocky outcroppings, and walls; (2) Site B (10°52'41.76"S, 37°59'24.65"W) was a tree-shrub area without leaf litter formation and with grazing by goats; (3) Site C (10°52'39.16"S, 38°0'36.81"W) was a mosaic area of large tree vegetation with leaf litter, interspersed with open areas due to logging activity on-site.

We used three sampling methods to maximize the amount of information and the number of species we could collect: (1) Active Search (Blomberg and Shine 2004) - A three-person team spent 3 h/d systematically searching for lizards in their preferred microhabitats. The team collected lizards by hand and using rubber bands and nooses. They evenly distributed the search time across morning, afternoon, and early evening shifts; (2) Pitfall traps (Blomberg and Shine 2004) - We installed 30 sets of traps (stations) consisting of four 30-L buckets buried in the ground and connected by 5-m plastic drift fences arranged in a Y pattern. We evenly distributed these traps among the sampling sites (10 sets in each area) across a wide range of environments. We checked and cleaned the traps twice a day during the sampling period to prevent the lizards from dying or eating other animals. We sealed the buckets with lids between the campaigns to avoid unnecessary capture; (3) Glue traps (Bauer and Sadler 1992) - We deployed six strips of glue traps (about 5 × 35 cm) in the vicinity of each pitfall trap. We placed three on elevated substrates (tree trunks, branches, and tall rocks) and three on lower substrates (fallen logs and smaller rocks). We monitored these traps twice a day and extracted captured specimens using cotton swabs pre-saturated with mineral oil.

For each lizard observed or captured during active searches, we recorded species, date, and microhabitat used during the first sighting. We categorized microhabitats into shrub, cactus, human construction, rock, leaf litter, open ground, vine, tree trunk, and fallen log and used their frequencies in the pseudocommunity and phylogenetic analyses. Upon reaching the number of individuals determined by the collection license (SISBIO n° 66720), we recorded the surplus specimens, marked them with water-based correction fluid (non-toxic), and released them into the environment to avoid pseudoreplication of the abundance data with the pitfalls. We pooled the data obtained from the three sites for all analyses. We euthanized the collected individuals by injecting high doses of anesthetic (lidocaine 2%), fixed them in 10% formalin, and preserved them in 70% alcohol for further analysis. After analysis, we registered the specimens and incorporated them into the Coleção Herpetológica da Universidade Federal de Sergipe (CHUFS).

**Habitat descriptors.**—To establish a correlation between lizard abundance and microhabitats, we recorded structural parameters within a 6-m radius of the central bucket of each pitfall array at the end of each campaign: (1) the number of bromeliads (NBro); (2) the number of cacti (Ncac); (3) the number of holes in the ground (NHG) with a diameter greater than 5 cm; (4) the number of fallen logs (NFL) with a minimum circumference of 5 cm and a length of 1 m; (5) the distance (DTCB) of the closest tree to the central bucket with a minimum breast height circumference (CTCB) of 5 cm; (6) the percentage of exposed soil (%OG) or litter (%LL) in three random 50 × 50 cm quadrants; (7) the distance from the random points described in (6) (DTRP) to the closest tree with at least a 5-cm circumference at breast height (CTRP); and (8) the number of stems (Nste) of all vegetation at least 0.2 cm in circumference and over 25 cm in height in a 1-m radius area at the same random locations as in parameter 6. To measure the parameters DTRP, CTRP, %OG, %LL, and Nste, we used a 50 × 50 cm frame quadrat with a 5 × 5 cm grid. A blindfolded person positioned in the center of the trap randomly threw the quadrat three times after rotating around its axis a few times. We used the average of the three measurements to obtain a single measurement for each parameter for each set per campaign. We adapted this protocol from a study by Garda et al. (2012b).

**Data analysis.**—To analyze the relationship between lizard abundance and environmental variables, we considered only species with more than three specimens captured in the pitfalls and glue traps. For this purpose, we built two matrices: one composed of the sum of the abundance data from all campaigns at each station and the other containing the averages of the measured environmental variables. To standardize the variables of different scales, we converted those whose values corresponded to a linear measure (cm; DTCB, CTCB, DTRP, and CTRP) into log+1, whereas we converted percentage values (%OG and %LL) to the arc sine of its square root (Zar 1999). To test for this association, we performed a Canonical Correlation Analysis (CCA) using the vegan package (Oksanen et al. 2022) in the R software (R Development Core Team 2022). This is a restricted ordination focused on identifying and quantifying the association between two datasets (e.g., species and environmental variables) through their linear relationship in the same sample sites (Silva et al. 2022).

For diet analysis, in the laboratory we removed the entire digestive tract from the collected specimens and analyzed it under a stereoscopic microscope. We identified and quantified the food items to the order level by using a specialized bibliography (Triplehorn and Jonnson 2011). We classified ants and termites down to family (Formicidae) and suborder (Isoptera) levels, respectively. We measured the length and width of the intact items by using a digital caliper with an accuracy of 0.01 mm.

We estimated the prey volume (V) by using the ellipsoid volume formula (Magnusson et al. 2003):

$$V = \frac{(\pi * l * w^2)}{6}$$

where l is the length and w is the width of food items. To determine the relative contribution of each prey category to the diet of the species, we calculated the Importance Value Index (IVI) by using the following equation (Acosta 1982):

$$IVI = \frac{F\% + N\% + V\%}{3}$$

where F%, N%, and V% correspond to the relative frequency, abundance, and volume, respectively, of each prey type consumed by the species.

We calculated food and spatial niche breadths (Ba) for each lizard species by using the standardized version of Levin's index (Hurlbert 1978):

$$B_a = \frac{\left(1 / \sum_{i=1}^n p_i^2\right) - 1}{n - 1}$$

where p is the proportion of the prey or substrate category used and i and n correspond to the number of prey or substrate categories. The value of Ba varied from 0 (exclusive use of one type of food or spatial resource) to 1 (homogeneous use of all types of resources).

We calculated the trophic niche and spatial overlap ( $\emptyset$ ) between species by using the symmetric overlap index (Pianka 1973), where the symbols are the same as above, but j and k represent the pair of species being compared.

$$\emptyset_{jk} = \frac{\sum_{n=1} P_{ij} P_{ik}}{\sqrt{\sum_{i=1}^n P_{ij}^2 \sum_{i=1}^n P_{ik}^2}}$$

We checked the possible interrelationships between the trophic and spatial niches of the lizards and whether they were complementary with a partial Mantel test, from the crossing of both generated overlap matrices (trophic and spatial niche), by using the vegan package (Oksanen et al. 2022) in the R software (R Development Core Team 2022).

To examine the presence of trophic and/or spatial structures in the assemblage, we used the EcoSim niche overlap module (Gotelli and Entsminger 2010). Specifically, we built a matrix in which the rows corresponding to the species and resource categories (spatial or trophic) arranged in the columns. We reformulated the matrix based on the 30,000 randomizations (pseudocommunities) expected in the absence of a structure. Based on the comparison between the observed and simulated overlap averages, it was possible to infer whether the assemblage was structured; in other words, if the observed mean was lower than the simulated mean, adopting a significance of 5%, then we considered the assemblage to be structured. In EcoSim, we selected the options Pianka Niche Overlap Index and Randomization Algorithm 2, which correspond to the zero retained state and relaxed niche width settings. Following the method by Werneck et al. (2009) and Caldas et al. (2019), we ran the analyses twice, once considering all species in the assemblage and once excluding species with fewer than four individuals, to assess whether rare species had a significant effect on the results. For trophic overlap analysis, we used the volume of prey consumed. In addition, we

selected the resource status option and entered the electivity values (sum of the raw volume values of each prey item for the entire assemblage). Thus, if structuring is observed, then the diet is not a random sample of electivity but rather an indication of greater specialization in resource use.

To evaluate the contribution of the historical component to assemblage organization, we employed a phylogenetic Principal Component Analysis (pPCA), considering the same species evaluated in the pseudocommunity analyses. It also allowed us to understand the extent to which the observed patterns can be attributed to the influence of ecological factors. This multivariate analysis tests the dependence of a given trait along specific phylogenetic lineages through autocorrelation (Gittleman and Kot 1990; Jombart et al. 2010). For this purpose, we assembled two matrices, X and W. In matrix X, we inserted the ecological variables collected in the field, that is, the diet data (the IVI for each category consumed by the species) and substrate use (the frequency of use for each substrate category) of the lizards. We chose to use the IVI to construct the diet matrix because it covers a larger number of taxa, as seen in the study by Gonçalves-Sousa et al. (2019). Matrix W corresponds to a phylogenetic matrix of the species and their respective phylogenetic distances based on the Squamata phylogeny by Pyron et al. (2013). We replaced the absent species in this phylogeny: the Naked-toed Gecko (*Gymnodactylus geckoides*); Brazilian Galliwasp (*Diploglossus lessonae*); *Enyalius bibronii* (no common name); and Striped Lava Lizard (*Tropidurus semitaeniatus*) with the closest taxa present: Peraiba Gecko (*Phyllopezus periosus*); Puerto Rican Galliwasp (*Diploglossus pleii*); Two-lined Fathead Anole (*Enyalius bilineatus*); and Reinhardt's lava lizard (*Tropidurus hygomi*). In a previous study that used the same analysis (Caldas et al. 2019), we found that this approach should not significantly affect the results, given that major evolutionary changes usually occur in the most basal branches of the lizard phylogenetic tree (Simões and Pyron 2021). Higher autocorrelation values indicate that closely related lineages show similar resource use, while lower values indicate divergence among the same taxa; that is, positive eigenvalues indicate historical effects and negative eigenvalues indicate ecological effects (Jombart et al. 2010).

To assess whether historical factors alone explain the niche differences present in the assemblage, we performed a partial Mantel test by crossing overlap data and phylogenetic distances of the assemblage

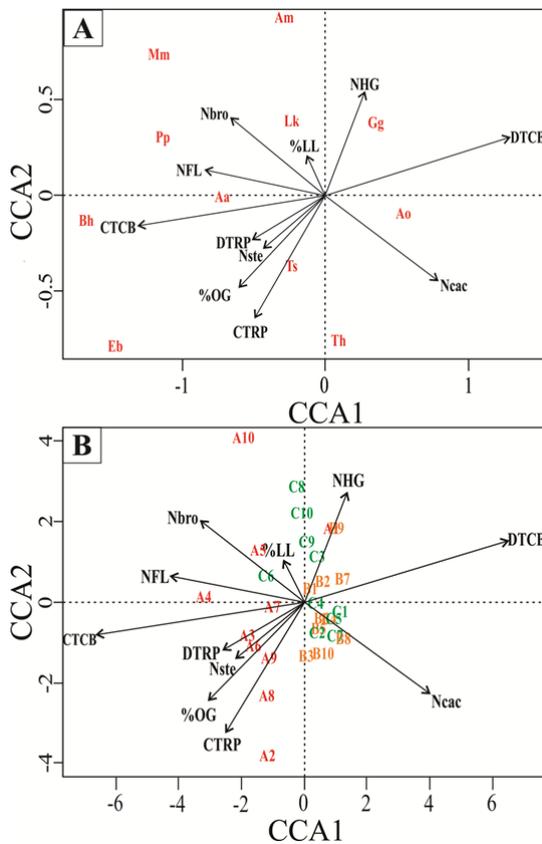
for both spatial and trophic niches. We performed a pPCA by using ade4 (Dray et al. 2018), adephylo (Jombart et al. 2017), and ape (Paradis et al. 2019) packages in R for Windows (R Development Core Team 2022). For the partial Mantel test, we used the vegan package (Oksanen et al. 2022). We adopted a significance level of 5% for all analyses.

## RESULTS

**Richness and species composition.**—We recorded 491 lizards (pitfalls = 189, glue traps = 45, active search = 257) belonging to 16 species and 10 families (Supplemental Information Table S1). The nomenclature we adopted is in accordance with Sociedade Brasileira de Herpetologia (Guedes et al. 2023). Regarding relative abundance, three species accounted for more than 60% of the total records: *T. semitaeniatus* (26.2%), *T. hispidus* (21.6%), and *A. ocellifera* (14.7%).

**Species × habitat structure.**—The abundance of lizards and the structural characteristics of the habitat were significantly associated ( $F_{11,234} = 1.86$ ,  $P < 0.01$ ). We generated a biplot, and the main canonical axes (CCA1 and CCA2) accounted for 31% of the variation in the data. In the first axis, responsible for 20.17% of this variation (Table 1), only *A. ocellifera*, *G. geckoides*, and *T. hispidus* correlated with the distance of the nearest tree to the central bucket, the number of holes in the ground, and the number of cacti. Conversely, eight species were associated with sites with trees of larger circumference and sparser distribution, with fallen logs, and with bromeliads (Fig. 2; Table 1). On the CCA2 axis, which accounted for 10.83% of variation (Table 1), two gymnophthalmids, two phyllodactylids, one teiid, and one geckonid were mainly associated with the distance of the nearest tree to the central bucket, leaf litter, the abundance of bromeliads, and the number holes in the ground. In contrast, *A. ocellifera*, the Brazilian Mabuya (*Brasiliscincus heathi*), *E. bibronii*, *T. hispidus*, and *T. semitaeniatus* were associated with sparser and larger trees, a high cacti abundance, and open ground (Fig 2; Table 1).

**Spatial niche.**—Spatial niche breadths ranged from 0 to 0.37, with the lowest values for the Brazilian Bush Anole (*Polychrus acutirostris*), Argentine Black and White Tegu (*Salvator merianae*), and *T. semitaeniatus* (Table 2). We observed the largest breadths for the Brazilian Gecko (*Phyllopezus*



**FIGURE 2.** The matrix of the structural measures of the microhabitat with the matrix of the abundance of (A) lizard species and (B) and pitfalls arrays for the first two axes of the Canonical Correlation Analysis (CCA). Structural measures are Nbro = number of bromeliads, Ncaac = number of cacti, NHG = number of holes in the ground, NFL = number of fallen trunks, DTTCB = distance from the nearest tree to the central bucket, CTCB = circumference of the nearest tree to the central bucket, DTRP = distance from the nearest tree in a random point, CTRP = circumference of the closest tree to a random point, %OG = percentage of open ground, %LL = percentage of ground covered by leaf litter, and Nste = number of stems. Lizard species are Am = *A. mentalis*, Aa = *A. ameiva*, Ao = *A. ocellifera*, Bh = *B. heathi*, Cm = *C. meridionalis*, Dl = *D. lessonae*, Eb = *E. bibronii*, Gg = *G. geckoides*, Hb = *H. brasiliensis*, Lk = *L. klugei*, Mm = *M. maximiliani*, Pp = *P. pollicaris*, Sm = *S. merianae*, Th = *T. hispidus*, Ts = *T. semitaeniatus*. See Table 2 for common names of species. In subgraph B, pitfall sites are A1–10 = pitfalls of sampling site A (arboreal forest, red), B1–10 = pitfalls of sampling site B (grazed forest, yellow), and C1–10 = pitfalls of sampling site C (logged forest, green).

*pollicaris*, *T. hispidus*, and *B. heathi* (Table 2). The Giant Ameiva (*A. ameiva*; 57.1%, n = 7), *A. ocellifera* (90.9%, n = 33), and *S. merianae* (100%, n = 2) along with *G. geckoides* (75.0%, n = 4) had open ground as the main category. Species that used rock as the primary substrate included *T. hispidus* (46.3%, n = 82), *T. semitaeniatus* (93.0%, n = 100), and *P. pollicaris* (42.9%, n = 14). The typical arboreal species, Kluge’s Dwarf Gecko (*Lygodactylus klugei*;

**TABLE 1.** Results of the first two axes of CCA using the structural variables of microhabitats and the sample size of lizard species recorded in Serra dos Macacos, Tobias Barreto/Sergipe, Brazil.

Variable	CCA1	CCA2
<b>Species</b>		
Giant Ameiva ( <i>Ameiva ameiva</i> )	-0.723	0.013
Amaral’s Colobosaura ( <i>Acratosaura mentalis</i> )	-0.283	0.953
Spix’s Whiptail ( <i>Ameivula ocellifera</i> )	0.554	-0.070
Brazilian Mabuya ( <i>Brasiliscincus heathi</i> )	-1.668	-0.127
<i>Enyalius bibronii</i> (no common name)	-1.473	-0.787
Naked-toed Gecko ( <i>Gymnodactylus geckoides</i> )	0.357	0.385
Kluge’s Dwarf Gecko ( <i>Lygodactylus klugei</i> )	-0.233	0.400
Maximilian’s Blue-tailed Microteiid ( <i>Micrablepharus maximiliani</i> )	-1.164	0.742
Brazilian Gecko ( <i>Phyllolopezus pollicaris</i> )	-1.136	0.300
Neotropical Lava Lizard ( <i>Tropidurus hispidus</i> )	0.092	-0.753
Striped Lava Lizard ( <i>Tropidurus semitaeniatus</i> )	-0.236	-0.362
<b>Structural microhabitat variables</b>		
Number of bromeliads	-0.396	0.243
Number of Cactaceae	0.477	-0.272
Number of holes in the ground	0.164	0.327
Number of fallen logs	-0.509	0.078
Distance from nearest tree to central bucket	0.779	0.184
Circumference of tree closest to central bucket	-0.794	-0.097
Distance from nearest tree to artifact 1	-0.308	-0.141
Circumference of the nearest tree to artifact 1	-0.296	-0.388
Percentage of open ground	-0.365	-0.292
Percentage of ground covered by leaf litter	-0.078	0.123
Number of stems close to artifact 1	-0.261	-0.166
Explained Variation	20.17%	10.83%
Cumulative Variation	20.17%	31.00%

85.7%, n = 7) and *P. acutirostris* (100%, n = 1), almost exclusively used tree trunks. Spatial overlap values ranged from 0 to 1, with *A. ocellifera* and *S. merianae* being the species pair with maximum overlap, followed by *L. klugei* and *P. acutirostris* ( $\Phi M = 0.99$ ), and *G. geckoides* with *A. ocellifera* and *S. merianae* ( $\Phi M = 0.95$ ). Conversely, there was no degree of sharing between arboreal (*L. klugei* and *P. acutirostris*) and terrestrial (*A. ameiva*, *A. ocellifera*, *S. merianae* and *G. geckoides*) species (Table 3).

We found a lack of spatial structure in the assemblage: the mean overlap was higher than expected if random ( $\Phi_{obs} = 0.39$ ;  $\Phi_{esp} = 0.37$ ;  $P > 0.05$ ), even disregarding less frequent species (n ≤ 4;  $\Phi_{obs} = 0.70$ ;  $\Phi_{esp} = 0.46$ ;  $P > 0.05$ ). Finally, the pPCA results indicated a greater phylogenetic influence on

**TABLE 2.** Niche breadths (Ba) of lizards from Serra dos Macacos, Tobias Barreto, Sergipe, Brazil. Acronyms are BaS = spatial niche breadth, BaF = food niche breadth, and n = sample size.

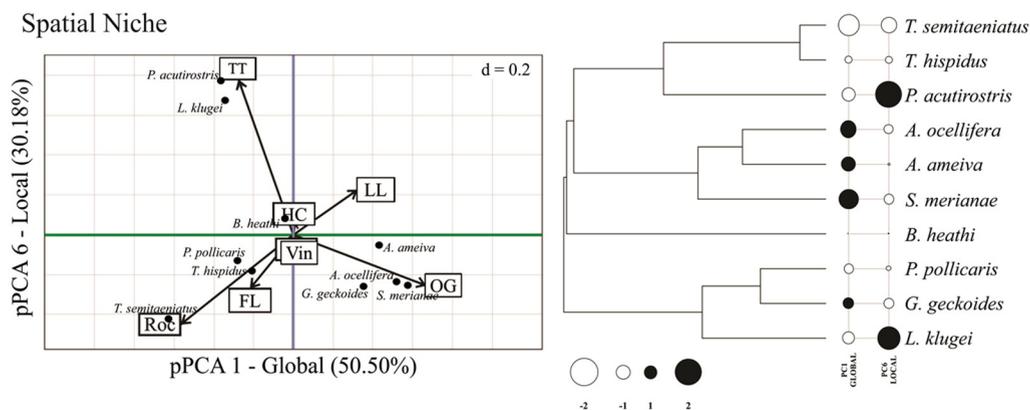
Species	$B_{aS}$ (n)	$B_{aF}$ (n)
Amaral's Colobosaura ( <i>Acratosaura mentalis</i> )	--	0.07 (17)
Giant Ameiva ( <i>Ameiva ameiva</i> )	0.12 (7)	0.25 (13)
Spix's Whiptail ( <i>Ameivula ocellifera</i> )	0.03 (33)	0.07 (38)
Brazilian Mabuya ( <i>Brasiliscincus heathi</i> )	0.25 (3)	0.01 (10)
Meridian Gecko ( <i>Coleodactylus meridionalis</i> )	--	0.04 (2)
Brazilian Galliwasp ( <i>Diploglossus lessonae</i> )	--	0.05 (1)
<i>Enyalius bibronii</i>	--	0.04 (8)
Naked-toed Gecko ( <i>Gymnodactylus geckoides</i> )	0.08 (4)	0.03 (37)
Amaral's Brazilian Gecko ( <i>Hemidactylus brasilianus</i> )	--	0.00 (1)
Kluge's Dwarf Gecko ( <i>Lygodactylus klugei</i> )	0.04 (7)	0.24 (35)
Maximilian's Blue-tailed Microteiid ( <i>Micrablepharus maximiliani</i> )	--	0.10 (7)
Brazilian Gecko ( <i>P. pollicaris</i> )	0.37 (14)	0.29 (10)
Brazilian Bush Anole ( <i>Polychrus acutirostris</i> )	0.00 (1)	0.02 (1)
Argentine Black and White Tegu ( <i>Salvator merianae</i> )	0.00 (2)	0.12 (2)
Neotropical Lava Lizard ( <i>Tropidurus hispidus</i> )	0.27 (82)	0.06 (33)
Striped Lava Lizard ( <i>Tropidurus semitaeniatus</i> )	0.02 (100)	0.11 (35)

spatial resource usage in the studied assemblage. Both components (historical and ecological) together explained approximately 80% of the variation in the data ( $H = 50.50\%$ ,  $E = 30.18\%$ ; Fig. 3). The teiids (*A. ocellifera*, *A. ameiva*, and *S. merianae*), along with *G. geckoides*, had positive eigenvalues in the global component (history); this axis mainly included the open ground and leaf litter categories. On the other

hand, members of Iguania (*P. acutirostris*, *T. hispidus*, and *T. semitaeniatus*) and Gekkota (*L. klugei* and *P. pollicaris*) presented negative eigenvalues, with rock, tree trunks, and fallen log as the most significant categories on this axis. Regarding the local components (ecological), *P. acutirostris* and *L. klugei* showed positive eigenvalues, with tree trunks being the most expressive substrates on this axis. The

**TABLE 3.** Spatial (left diagonal) and food (right diagonal) niche overlap values of lizards from Serra dos Macacos, Tobias Barreto, Sergipe, Brazil. Species are Am = *Acratosaura mentalis*, Aa = *Ameiva ameiva*, Ao = *Ameivula ocellifera*, Bh = *Brasiliscincus heathi*, Eb = *Enyalius bibronii*, Gg = *Gymnodactylus geckoides*, Lk = *Lygodactylus klugei*, Pp = *Phyllorhynchus pollicaris*, Pa = *Polychrus acutirostris*, Sm = *Salvator merianae*, Th = *Tropidurus hispidus*, Ts = *Tropidurus semitaeniatus*. See Table 2 for common names of species.

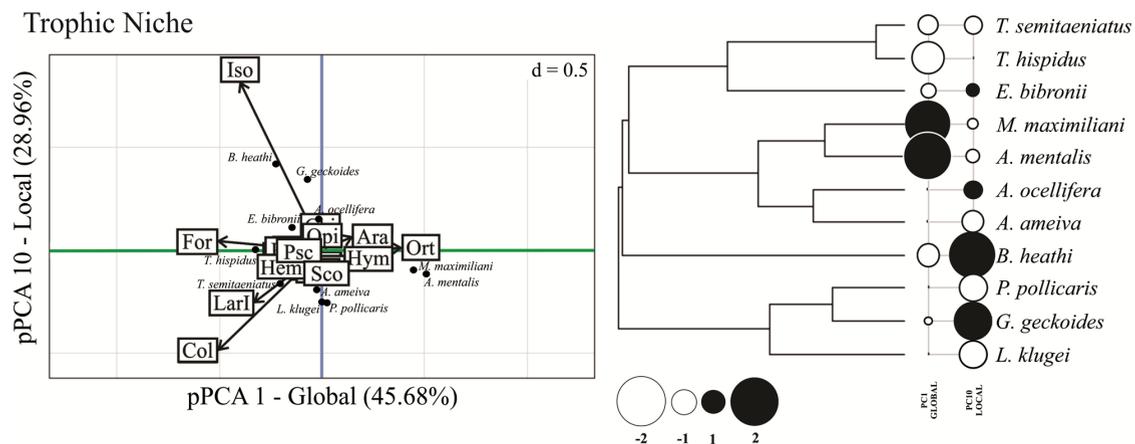
	Aa	Ao	Bh	Eb	Gg	Lk	Pp	Pa	Sm	Th	Ts
Am	0.20	0.28	0.15	0.04	0.02	0.01	0.03	--	--	0.19	0.31
Aa		0.47	0.04	0.10	0.01	0.01	0.35	--	--	0.13	0.08
Ao	0.84		0.18	0.14	0.02	0.01	0.25	--	--	0.11	0.12
Bh	0.46	0.58		0.11	0.07	0.02	0.11	--	--	0.32	0.14
Eb	--	--	--		0.01	0.00	0.08	--	--	0.09	0.02
Gg	0.76	0.95	0.73	--		0.28	0.02	--	--	0.17	0.03
Lk	0.00	0.00	0.57	--	0.00		0.06	--	--	0.07	0.21
Pp	0.23	0.31	0.33	--	0.27	0.28		--	--	0.33	0.21
Pa	0.00	0.00	0.58	--	0.00	0.99	0.28		--	--	--
Sm	0.80	1.00	0.58	--	0.95	0.00	0.28	0.00		--	--
Th	0.46	0.53	0.49	--	0.51	0.23	0.90	0.24	0.50		0.18
Ts	0.02	0.05	0.04	--	0.03	0.02	0.86	0.02	0.02	0.84	



**FIGURE 3.** Phylogenetic tree (on the right) and scatter plot of the phylogenetic Principal Component Analysis (pPCA) for the spatial niche data of lizards from Serra dos Macacos, Tobias Barreto, Sergipe, Brazil. The eigenvalues of the canonical axes in the phylogenetic tree are represented by black circles (positive autocorrelation) and white circles (negative autocorrelation) of the first global component (PC1) and the first local component (PC6). The acronyms Shr = shrub, Cac = cacti; HC = human constructions, Roc = rock, LL = leaf litter, OG = open ground, Vin = vines, TT = upright tree trunk, and FL = fallen tree trunk.

**TABLE 4.** Importance Value Index (IVI) of prey categories consumed by lizards in Serra dos Macacos, Tobias Barreto, Sergipe, Brazil. Prey categories (left vertical column) are: Aca = Acari, Ara = Araneae, Bla = Blattodea, Chi = Chilopoda, Col = Coleoptera, Dipl = Diplopoda, Dipt = Diptera, For = Formicidae, Gas = Gastropoda, Hem = Hemiptera, Hym = Hymenoptera, Iso = Isoptera, Lac = Lacertilia, LarI = insect Larva, Lep = Lepidoptera, PMat = plant material, Opi = Opiliones, Ort = Orthoptera, Pha = Phasmatodea, Psc = Pseudoscorpiones, and Sco = Scorpions. Lizard species (top line) are: Am = *A. mentalis*, Aa = *A. ameiva*, Ao = *A. ocellifera*, Bh = *B. heathi*, Eb = *E. bibronii*, Gg = *G. geckoides*, Lk = *L. klugei*, Pp = *P. pollicaris*, Pa = *P. acutirostris*, Sm = *S. merianae*, Th = *T. hispidus*, Ts = *T. semitaeniatus*. See Table 2 for common names of species. The three highest IVI values for the species are highlighted in bold.

Prey	Am	Aa	Ao	Bh	Cm	Dl	Eb	Gg	Hb	Lk	Mm	Pp	Pa	Sm	Th	Ts
Aca	--	3.4	1.0	--	--	--	--	1.0	--	7.8	--	--	--	32.1	3.1	1.0
Ara	<b>9.2</b>	11.0	<b>23.0</b>	7.3	--	--	14.8	6.4	<b>66.7</b>	7.6	<b>15.9</b>	9.8	--	--	9.4	5.3
Ave	--	--	--	--	--	--	--	--	--	--	--	--	--	17.9	--	--
Bla	--	12.3	3.9	--	<b>45.0</b>	--	4.4	5.5	--	3.5	--	4.7	34.6	--	5.6	1.0
Chi	--	--	1.9	--	--	--	--	4.7	--	--	--	--	--	--	2.1	--
Col	--	<b>41.4</b>	15.4	<b>23.6</b>	--	<b>50.0</b>	<b>32.0</b>	3.3	--	<b>25.4</b>	--	<b>31.1</b>	<b>93.6</b>	17.9	<b>40.0</b>	<b>34.6</b>
Dipl	--	2.9	--	--	--	--	--	--	--	--	--	--	--	--	3.2	--
Dipt	--	3.4	--	3.5	<b>71.7</b>	--	4.4	2.0	--	2.5	--	--	--	--	3.1	6.4
For	--	17.5	<b>19.3</b>	7.0	--	--	<b>20.3</b>	<b>20.5</b>	--	--	--	<b>14.8</b>	--	<b>39.3</b>	<b>41.9</b>	<b>43.5</b>
Gas	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1.1	--
Hem	--	2.9	2.9	7.0	--	--	4.4	--	--	2.9	--	9.3	--	--	6.9	3.0
Hym	<b>24.4</b>	6.0	12.6	11.5	--	--	--	2.1	--	<b>17.0</b>	<b>15.9</b>	7.3	--	--	19.4	<b>20.7</b>
Iso	--	18.2	<b>41.6</b>	<b>81.8</b>	--	--	<b>47.6</b>	<b>58.2</b>	--	11.3	--	6.0	--	19.0	<b>43.9</b>	18.7
Lac	--	--	--	--	--	--	--	--	--	--	--	--	--	<b>51.2</b>	--	1.0
LarI	6.9	13.1	11.5	<b>15.1</b>	--	--	13.2	<b>12.9</b>	--	<b>42.3</b>	--	<b>19.5</b>	--	<b>38.1</b>	27.8	20.5
Lep	--	--	1.0	--	--	--	6.1	--	--	--	--	--	--	--	3.1	--
PMat	--	7.7	1.8	--	--	--	--	5.4	--	1.9	4.8	6.7	33.3	16.7	9.1	4.8
Opi	--	--	--	--	--	--	--	1.1	--	--	--	--	--	--	--	--
Ort	<b>49.7</b>	<b>21.2</b>	6.6	--	--	--	15.4	7.4	--	--	<b>15.9</b>	10.7	<b>37.2</b>	17.9	12.6	5.8
Pha	--	--	--	--	--	--	14.6	--	--	--	--	--	34.6	--	1.0	--
Psc	--	--	--	--	--	--	--	1.1	--	2.6	--	--	--	--	--	--
Sco	--	<b>18.5</b>	8.6	--	--	<b>83.3</b>	6.0	--	--	--	--	--	--	--	--	3.2



**FIGURE 4.** Phylogenetic tree (on the right) and scatter plot of the phylogenetic Principal Component Analysis (pPCA) for the trophic niche data of lizards from Serra dos Macacos, Tobias Barreto, Sergipe, Brazil. The eigenvalues of the canonical axes in the phylogenetic tree are represented by black circles (positive autocorrelation) and white circles (negative autocorrelation), of the first global component (PCI) and the first local component (PCI10). In the pPCA scatter plot, the IVI matrix data has been standardized ( $IVI \times 0.01$ ) to allow for a coupled visualization. Food items are Aca = Acari, Ara = Araneae, Bla = Blattodea, Chi = Chilopoda, Col = Coleoptera, Dipl = Diplopoda, Dipt = Diptera, For = Formicidae, Gas = Gastropoda, Hem = Hemiptera, Hym = Hymenoptera, Iso = Isoptera, Lac = Lacertilia, Larl = Insect Larva, Lep = Lepidoptera, PMat = Plant Material, Opi = Opiliones, Ort = Orthoptera, Pha = Phasmatodea, Psc = Pseudoscorpiones, Sco = Scorpiones.

other species had negative eigenvalues, represented mainly by rocks, fallen logs, and open ground (Fig. 3). Phylogeny was not significantly correlated with spatial niche ( $r = -0.204$ ,  $P = 0.898$ ).

**Trophic niche.**—We analyzed 250 stomachs, counting 4,210 food items distributed into 22 categories (empty stomachs:  $n = 10$ ; advanced digestion:  $n = 20$ ). The most frequent prey items, regardless of the ingesting species, were Coleoptera ( $F = 15.97\%$ ), Formicidae ( $F = 15.04\%$ ), and Isoptera ( $F = 14.73\%$ ), while the most abundant were Isoptera ( $N = 53.60\%$ ), Formicidae ( $N = 26.92\%$ ), and Coleoptera ( $N = 6.41\%$ ). The most volumetrically representative categories were Coleoptera ( $V = 30.25\%$ ), insect larvae ( $V = 21.30\%$ ), and Lacertilia ( $V = 13.58\%$ ; Supplemental Information Table S2). Concerning the IVI, Isoptera was the most important category for *A. ocellifera*, *B. heathi*, *E. bibronii*, *G. geckoides*, and *T. hispidus*, while Coleoptera and Formicidae were among the most important categories for *E. bibronii*, *P. pollicaris*, *T. hispidus*, and *T. semitaeniatus* (Table 4).

We observed the largest niche breadths for *P. pollicaris*, *A. ameiva*, and *L. klugei*, and the smallest for Amaral's Brazilian Gecko (*Hemidactylus brasiliensis*), *B. heathi*, and *P. acutirostris* (Table 2). We recorded low overlaps in food resource sharing: *A. ameiva* and *A. ocellifera* showed the highest degree of sharing, followed by *A. ameiva* and *P. pollicaris*, *P.*

*pollicaris*, and *T. hispidus* (Table 3). Spatial niches were not significantly related to trophic niches ( $r = 0.206$ ,  $P = 0.137$ ).

The assemblage was structured based on the trophic niche, both with ( $\Phi_{obs} = 0.10$ ;  $\Phi_{esp} = 0.30$ ;  $P < 0.001$ ) and without ( $n \geq 4$ ;  $\Phi_{obs} = 0.13$ ;  $\Phi_{esp} = 0.50$ ;  $P < 0.001$ ) the less frequent species. Although rare species did not exert a significant influence on our results, we still disregarded those with  $n \leq 4$  because of a better fit in the pPCA (Mesquita et al. 2006a). The pPCA results indicated a greater contribution of the historical components compared with the ecological components, and together they explained more than 70% of the variation in the data ( $H = 45.68$ ,  $E = 28.96$ ; Fig. 4). The ecological component was most prominent in Teiidae (*A. ocellifera* and *A. ameiva*), Gekkota (*P. pollicaris*, *G. geckoides* and *L. klugei*), and *B. heathi*. Among these, *A. ocellifera*, *B. heathi*, and *G. geckoides* showed positive eigenvalues and this axis mainly included Isoptera, while *A. ameiva*, *P. pollicaris* and *L. klugei* had negative eigenvalues, the axis that mainly included beetles and insect larvae. Conversely, the historical component was prominent in Iguania (*E. bibronii*, *T. hispidus*, and *T. semitaeniatus*) and Gymnophthalmidae (*A. mentalis* and *M. maximiliani*). Iguania lizards had negative eigenvalues, and Coleoptera, Formicidae, and Isoptera were the main representatives of this axis. Finally, *A. mentalis* and *M. maximiliani* showed positive eigenvalues for the global component,

which was represented by Orthoptera, Araneae, and Hymenoptera (Fig. 4). Phylogeny was not significantly correlated with trophic niche ( $r = 0.127$ ,  $P = 0.148$ ).

## DISCUSSION

**Species × habitat structure.**—We found significant correlations between lizard abundances and certain habitat characteristics, a pattern observed in other assemblages (Garda et al. 2012b; Dias and Rocha 2014; Flores et al. 2023). The first axis (CCA1) represented the differences between the pitfalls placed in areas with more forest cover, sparser and larger trees, and a greater number of bromeliads and fallen logs, in contrast to pitfalls placed in modified areas, farther from trees, and with a greater abundance of cacti and holes in the ground. On the other hand, the CCA2 axis represented more specific variations found in the microhabitats, including the gradient from sites with leaf litter, bromeliads, fallen logs, and holes in the ground to sites with open ground, a greater number of cacti, and/or larger trees. Based on our results, there are indications that species preferences for certain characteristics related to the level of vegetation cover may reflect the temperature differences inherent in thermoregulation, as well as the level of spatial heterogeneity.

Among the species that were more associated with open and/or human-disturbed areas, the abundance of the small lizard *G. geckoides* was correlated to the number of holes in the ground and more weakly to leaf litter, which can be explained by the availability of shelter against the high temperatures of site B (the absence of leaf litter and little canopy cover) and possible predators (Gaudenti et al. 2021). *Ameivula ocellifera* was correlated with the abundance of cacti, which were associated with more open areas (B and C), where we captured all specimens used in the analysis. We expected this relationship because the terrestrial habit and heliophilic behavior of this lizard, as well as its predominance in open formations, have been well described in the literature (Mesquita and Colli 2003; Dias and Rocha 2007; Machado et al. 2016). Finally, although *T. hispidus* did not show an expressive preference for more preserved or human-disturbed areas, it was associated with sites with a higher vertical stratification. This result reinforces the plastic and habitat-generalist character of the species, which can occupy forested, open, and human-disturbed areas (Santana et al. 2014; Andrade 2019).

*Acratosaura mentalis* and *M. maximiliani* were associated with more humid microhabitats, with bromeliads and leaf litter. Access to these spatial resources is very conservative for the Gymnophthalmidae family, which is composed of small lizards that constantly seek refuge and avoid high temperatures (Vanzolini et al. 1980; Delfim and Freire 2007; Oliveira and Pessanha 2013). The general abundance data support this inference, because neither species occurred in site B, which lacked leaf litter.

*Phyllopezus pollicaris* and *L. klugei* belong to the Gekkota clade, which comprises several predominantly arboreal taxa capable of occupying different stratifications in the environment (Vitt et al. 2003). We confirmed this association based on the presence of these species in areas with high forest cover; however, we observed distinct ecological adjustments between the two. *Phyllopezus pollicaris* preferred habitats with more bromeliads and fallen logs, which can be used as perches, shelters, or thermoregulation substrates (Rodrigues 1987). In contrast, *L. klugei* did not exhibit a strong relationship with tree diameter or spacing. The small size of this species probably allows for the use of trees of various sizes, some of which are unsuitable for larger arboreal species (Galdino et al. 2011), such as *E. bibronii*, which is strongly related to larger trees. Species of the genus *Enyalius* are typically arboreal or semiarboreal (Rodrigues et al. 2014). In addition, the small size of *L. klugei* implies limited mobility, which explains the minimal relationship between this species and the distance between trees.

It has been well documented in the literature that *A. ameiva* can be found in open areas, forest edges, and more preserved environments (Sales et al. 2011b). The low correlation of this species with CCA2 variables may be related to its plasticity in environments with different spatial characteristics. Additionally, although the traps indicated a greater association between *A. ameiva* and conserved areas, the records of the active search revealed a relatively uniform presence among sampling sites, supporting the previously mentioned pattern. *Brasiliscincus heathi* was predominant in forested environments, with lower direct insolation rates. Despite its heliophilic habit, this lizard has a smaller body temperature range than teiids and tropidurids (Vitt 1995; Ribeiro et al. 2019), that is, it can thermoregulate more efficiently in shadier habitats.

Although *T. semitaeniatus* has widely understood saxicolous habits (Gomes et al. 2015), this was not

evident because of the positioning of the pitfalls, given the difficulty of burying them near rocky slabs and walls. Thus, our results imply that we collected the specimens during the movement between their usual microhabitats (rocky outcrops), resulting in the absence of a correlation between *T. semitaeniatus* and the environmental variables measured. The records obtained by the active search corroborated the traditional pattern. Additionally, Andrade-Lima et al. (2022) suggested that, despite its high fidelity to this substrate, *T. semitaeniatus* may increase its movement rate in response to low food availability. Finally, the relatively low explanatory power of the main canonical axes of the analysis may be due to methodological issues related to scale and sampling. Open formations such as the Caatinga have greater horizontal heterogeneity, making the detection of these patterns at the local scale more difficult compared with continuously forested environments, whose habitats vary more vertically (Garda et al. 2012b).

**Spatial niche.**—When analyzing the use of microhabitats, we noticed that the majority of species exhibited specialist behavior. The saxicolous *T. semitaeniatus*, the arboreal *L. klugei* and *P. acutirostris* maintained high fidelity to their respective substrates (Vitt and Lacher 1981; Galdino et al. 2011; Caldas et al. 2015). The similarity in the use of the same resources in different environments by these species or congeners (Simbotwe 1983; Nogueira et al. 2005; Pelegrin et al. 2017) suggests a strong influence of historical factors on their spatial niche. Among those species more closely associated with the ground, we observed *S. merianae* and *A. ocellifera* in open ground without leaf litter cover, and the latter was also related to open areas with higher insolation rates (Teixeira-filho et al. 1995; Mesquita and Colli 2003; Albuquerque et al. 2018). In contrast, *A. ameiva*, a species widely distributed in the Brazilian biomes (e.g., Caatinga, Mata Atlântica, Restinga, and Cerrado), similarly occupied soils with and without leaf litter, seen both in forested and open areas, demonstrating a certain plasticity in this aspect (Werneck and Colli 2006; Sales et al. 2011b; Benício et al. 2019).

We mainly observed *G. geckoides* on open ground, in contrast to other studies, where it was primarily associated with leaf litter, rocks, and fallen logs (Vitt 1995; Muniz et al. 2016; Oitaven et al. 2022). Among the species that use substrates more broadly, *T. hispidus* is recognized as a habitat generalist: it

has been recorded in a wide variety of microhabitats in natural or even human-disturbed environments (Gomes et al. 2015; Machado et al. 2016; Albuquerque et al. 2018). Despite its wide niche breadth, we also primarily observed the nocturnal lizard *P. pollicaris* on rocks, probably using the accumulated heat in this substrate to satisfy its thermal requirements, as well as to find shelter from potential predators (Recoder et al. 2012; Ferreira et al. 2014; Condez et al. 2021).

Although most species showed low niche breadths, we observed high overlap rates among some, suggesting the influence of niche conservatism on the selection of the same substrate categories by certain lineages. According to Pianka (1973), sympatric species that use the same spectrum of resources available along one of the niche axes, in this case the spatial axis, tend to diverge in at least one of the other two axes (temporal and trophic). Although there was no significant complementarity between the trophic and spatial niches in the overall aspect of assemblage, by observing some ecological and morphological elements known to the taxa, we can infer that regardless of the high overlap observed, some species do not effectively compete for the same resources. A good example is *L. klugei* and *P. acutirostris*, which almost entirely overlap with the use of trees as perches; however, the discrepancy between their body sizes and shapes may allow the differential use of spatial and trophic resources (Carvalho and Araújo 2007; Pelegrin et al. 2017). The same can be said regarding the overlap we observed between *G. geckoides* and other terrestrial lizards (*A. ameiva*, *A. ocellifera*, and *S. merianae*). Despite the high overlap between *P. pollicaris*, *T. hispidus*, and *T. semitaeniatus*, they were temporally segregated, as *P. pollicaris* has nocturnal habits and the other two are diurnal (Recoder et al. 2012; Ferreira et al. 2014; Gomes et al. 2015).

Similarly to other studies in the Neotropics, including in the Caatinga, we found no signs of spatial structure (Machado et al. 2016; Winck et al. 2016; Gonçalves-Sousa et al. 2022). This suggests that space is not a limiting resource for lizards at Serra dos Macacos and that competition is not a relevant force in substrate selection (Mesquita et al. 2006a,b). Some of these authors have related the lack of structuring to the bias imposed by the scarcity of microhabitat data for some taxa because of the difficulty in recording the habits of some cryptic, discrete-moving, and/or less abundant species (Mesquita et al. 2006a,b; Werneck et al. 2009). It is important, however, to highlight the influence of

environmental heterogeneity demonstrated by the CCA. Although the species showed high overlap in substrate use, they were segregated at the habitat level. Thus, there was not necessarily an intensification in the use of certain resources in the same locality, as they would be available in other areas.

The pPCA revealed a greater contribution of historical components to the spatial niche, although phylogeny alone did not explain the variation we found. The main indication of phylogenetic influence is the relationship between microhabitat use and foraging strategies (Huey and Pianka 1981; Brito et al. 2014; Rodda 2020). In our study, all species that had the ground as their main substrate (except for *G. geckoides*) were active foragers, whereas the other taxa (sit-and-wait foragers) used vertical substrates such as rocks, tree trunks, and fallen logs (Vitt et al. 2003). Thus, substrate selection would be mediated by the availability of historically preferred dietary resources (Vitt et al. 1999; Werneck et al. 2009; Lanna et al. 2022). Furthermore, the similarities in space use of this assemblage with those in other regions and biomes point to a certain degree of spatial niche conservatism (Losos 1996).

**Trophic niche.**—The dietary compositions of some species were similar to those previously reported for other populations distributed throughout the Neotropical region (Vitt et al. 1999; Mesquita et al. 2006a; Vilanova-Júnior et al. 2016; Gonçalves-Sousa et al. 2019). The low variation in diet among assemblages exposed to different scenarios suggests a strong influence of phylogeny (Vitt et al. 2003; Vitt and Pianka 2005). For example, *A. ameiva* maintains a varied consumption pattern of prey in different biomes, indicating that its trophic plasticity has been conserved (Vitt et al. 1999; Mesquita et al. 2006a; Sales et al. 2011a; Vilanova-Júnior et al. 2016; Gonçalves-Sousa et al. 2019). The degree of importance of each of these categories in *A. ameiva* populations, however, is subject to ecological factors, such as resource availability and/or competition (Sales et al. 2011a). Additionally, the divergence between our results and those of other studies regarding the main diet components of Isoptera and Isopoda in the Meridian Gecko (*Coleodactylus meridionalis*; Silva et al. 2015), and plant material in *P. acutirostris* (Garda et al. 2012a) and *S. merianae* (Kiefer and Sazima 2002) may be due to the low number of specimens we collected.

Sit-and-wait foragers tend to be less selective in their prey choice and, consequently, have a larger

niche width than active foragers (Bergallo and Rocha 1994; Vitt and Caldwell 2014). Among the more generalist species of Serra dos Macacos, *P. pollicaris* and *L. klugei* fit this pattern well. In contrast, the other sit-and-wait lizards showed considerably smaller niche widths, and the active forager *A. ameiva* had the second-largest niche width of the assemblage. These findings suggest that ecological factors (e.g., resource availability and/or competition) may contribute to the expansion or reduction of the niches of species (Mesquita et al. 2007; Caldas et al. 2019).

Contrary to our observations for the spatial niche, the assemblage showed low trophic overlap. The pair of species with the greatest similarity in diet composition was *A. ameiva* and *A. ocellifera*; however, they differed considerably in the most important prey categories. Thus, pseudocommunity analysis detected structure for the trophic niche. In other words, competition is a relevant factor in prey selection, and this segregation over time is likely necessary to maintain the lizard richness of Serra dos Macacos (Werneck et al. 2009; Gonçalves-Sousa et al. 2019; Gonçalves-Sousa et al. 2022). Researchers have reported similar results in other areas of the Caatinga and in other environments where seasonality has a great impact on the abundance and availability of arthropods (Winemiller and Pianka 1990; James 1991; Gonçalves-Sousa et al. 2019).

We also found a higher influence of historical components compared with ecological ones, reinforcing the importance of phylogeny in the diet composition of lizards (Vitt and Pianka 2005; Lanna et al. 2022). As indicated by the pseudocommunity analysis, however, contemporaneous factors showed a significant effect on the assemblage, and some clades were more influenced by them. We detected signs of niche conservatism in Iguania lizards (*E. bibronii*, *T. hispidus*, and *T. semitaeniatus*) with respect to the ingestion of ants and beetles. Similar results have been reported in the literature (Kolodiuk et al. 2010; Gomes et al. 2015; Ferreira et al. 2017), and this relationship is attributed to the evolutionary origin of this group, linked to the diversification of the major ant lineages and, to a minor degree, Coleoptera (Vitt and Pianka 2005; Sites-Junior et al. 2011; Cavalcanti et al. 2023a). The members of Gymnophthalmidae (*A. mentalis* and *M. maximiliani*), on the other hand, ingested mainly Orthoptera, Araneae, and Hymenoptera. The importance of phylogeny in the diet of these taxa is reinforced by other studies in the Cerrado, where orthoptera and spiders are among the main items consumed by *M. maximiliani*

(Mesquita et al. 2006a; Werneck et al. 2009; Vechio et al. 2014), or when Orthoptera is a relevant item in the diet of *Micrablepharus atticolus* (Vieira et al. 2000). In contrast, other clades (Teiidae, Mabuyidae, Phyllodactylidae, and Gekkonidae) were more prominently influenced by local components. Most closely related species diverged in diet composition, whereas *A. ocellifera* and *G. geckoides* had positive eigenvalues (represented mainly by termites), and their respective relatives *A. ameiva* and *P. pollicaris* had negative eigenvalues (the latter represented by beetles and insect larvae).

**Conclusion.**—Our results demonstrate that lizard lineages may respond differently to environmental pressures, reinforcing the importance of considering both factors (ecological and phylogenetic) to interpret the determinants of assemblage organization. Additionally, the data have direct implications for the conservation and management of Serra dos Macacos, as lizards are usually abundant and represent a significant portion of vertebrate diversity in tropical environments, especially in semi-arid regimes such as the Caatinga. We found that even an aspect such as the trophic niche, which is normally conservative, can be influenced by local factors that are crucial in competitive interactions and resource sharing. We also observed that the similarity in microhabitat use may reflect their high availability as habitats vary, meaning that horizontal heterogeneity would allow the use of similar resources along a vegetation gradient. As a formation of hypoxerophilous Caatinga, Serra dos Macacos represents an enclave of humid forest (Moro et al. 2024), with the presence of springs and watercourses that maintain the perennial status of certain portions of the vegetation stratum. Thus, as there is an association between spatial heterogeneity and the lizard assemblage, and that forest suppression and habitat loss directly affect lizard diversity. Furthermore, there have been very few studies evaluating the interrelationship between spatial heterogeneity, competition, and phylogeny, and our work is important in this regard. Therefore, the development of integrative methods to measure the action of these effects at the local scale and their use in different assemblages is fundamental to elucidate the patterns that emerge from the complex synergy between historical and ecological factors. This approach would facilitate the generalization and formulation of more consistent theories at larger scales.

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