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ORIGINAL ARTICLE

Determinants of resource use in lizard assemblages from the semiarid Caatinga, Brazil

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Abstract

Nonsessile animals could partition the use of resources in different axes, reducing the effects of competition and allowing coexistence. Here, we investigated the spatial and trophic niche dimensions in four lizard assemblages in the Neotropical semiarid Caatinga to investigate the determinants of resource use and the extent to which lizards partition their niches. We sampled each lizard assemblage once, for 10 days, in the dry season of 2017 and 2018. In two lizard assemblages, we detected nonrandom niche overlap patterns that were higher or lower than expected by chance. The high niche overlap patterns suggest that either there is intense current competition for available microhabitats or an abundance of microhabitats. The lower niche overlap may be influenced by the presence of species adapted to sandy habitats (psammophilous), suggesting that spatial partitioning detected has historical basis, which is supported by the pPCA results and by the lack of patterns in the realized niche distribution of species across niche space. We detected trophic niche partitioning in three lizard assemblages. In one assemblage, we discovered random spatial and trophic niche overlap patterns, revealing that competition is not a determining factor in the structure of that assemblage. In fact, phylogenetic effects were predominantly the main determinants of resource use in the four studied lizard assemblages. Arid and semiarid habitats cover about one third of land surface of the world. Comparisons between our findings and those from other regions of the world may aid identify general trends in the lizard ecology of dry environments.

KEYWORDS
assemblage structure, competition, ecological niche, historical structure, niche partitioning, phylogenetic basis, semiarid region

1 | INTRODUCTION

Whether by phylogenetic inertia or phenotypic plasticity, nonsessile animals could partition the use of resources in different axes, such as temporal, spatial, and trophic niche dimensions of the ecological niche, reducing the effects of competition and allowing species coexistence (Chesson, 2000; Levine & HilleRisLambers, 2009; Pianka et al., 2017). Niche overlap represents the use of a common resource by two or more species (Colwell & Futuyma, 1971), and nonrandom patterns in niche overlap have traditionally been considered

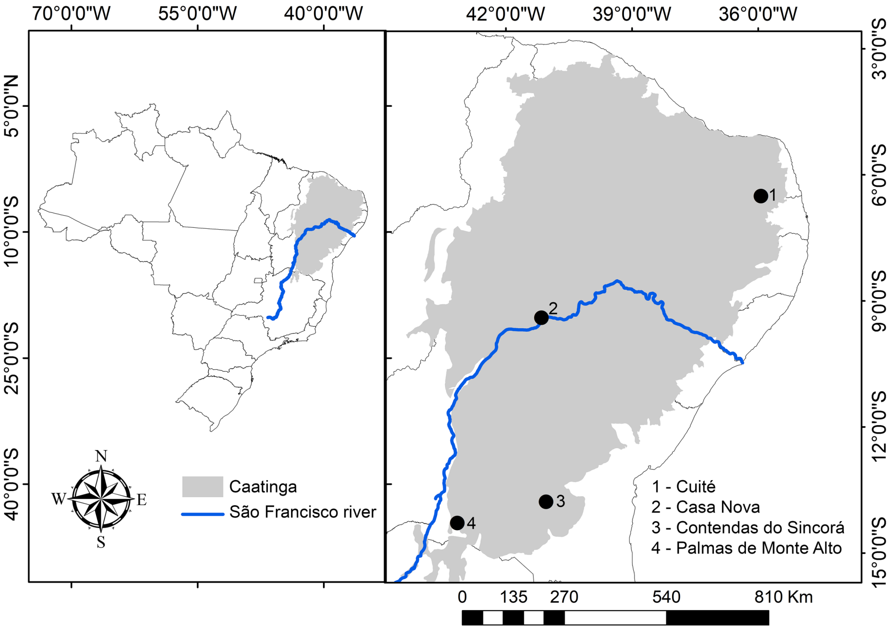


FIGURE 1 Map showing the sites of the lizard assemblages studied in the Brazilian Caatinga, a Neotropical semiarid region. Distance between points: 1–2: 660 km straight line; 1–3: 980 km; 1–4: 1160 km; 2–3: 480 km; 2–4: 570 km; 3–4: 220 km.

evidence of competition (Gotelli & Graves, 1996). For example, nonrandom niche overlap patterns lower than expected by chance (niche partitioning) may be considered evidence of interspecific competition playing an important role in structuring the assemblage (Connell, 1980; Pianka, 1973; Schoener, 1974) or may be the result of a phylogenetic basis in which lizard functional traits (e.g., foraging mode, physiological tolerances, and food preferences) are linked to niche segregation, as reflected by their ancestral taxa (Brooks & McLennan, 1993; Goodman et al., 2008; Losos, 1996). Alternatively, nonrandom niche overlap patterns higher than expected by chance may reflect intense current competition for any available resource or abundance of resources with no detectable competition in the present (Glasser & Price, 1988; Gotelli & Graves, 1996; Schoener, 1983).

Historical factors (such as evolutionary history and phylogenetic inertia) can be responsible alone or coupled with ecological factors (such as prey availability and biotic interactions) to determine the structure of assemblages (HilleRisLambers et al., 2012; Vitt et al., 2003; Vitt & Pianka, 2005). A biotic assemblage is a generic group of phylogenetically related species that inhabit the same location, such as lizards, frogs, and birds (Stroud et al., 2015). Studies carried out at different scales and in environments with extremely different conditions have confirmed that historical factors influence portions of the structure of lizard assemblages, limiting the biology of a species due to past adaptations in their evolutionary history (Gonçalves-Sousa et al., 2019; Pianka, 1973; Vitt et al., 1999, 2003; Vitt & Pianka, 2005). The influence of historical effects on lizards may be readily detected in cases where there is conservatism in functional characteristics that are related to their shared evolutionary histories (Mesquita et al., 2007, 2016; Vitt & Pianka, 2005).

The ecological niche of a species is multidimensional and dynamic, responding to spatiotemporal changes in abiotic conditions, biotic interactions, and resources availability (Pianka et al., 2017). Several studies carried out in different environments of the Neotropical region have detected nonrandom patterns of spatial (microhabitat use) and/or trophic (prey consumption) niche overlap. In this region, niche partitioning in lizard assemblages was found from forested, such as in the Amazon rainforest (Vitt et al., 1999; Vitt & Zani, 1996), to open environments, such as in the semiarid steppic savanna (Caatinga) (Gonçalves-Sousa et al., 2019; Vitt, 1995). On the contrary, spatial niche partitioning was not detected whereas partitioning in the trophic niche was detected in some lizard assemblages from the Brazilian savanna (Cerrado) (Gainsbury & Colli, 2003; Werneck et al., 2009). Hence, the set of biotic interactions, functional complementarity, and abiotic characteristics of each site has led to different patterns of lizard assemblage assembly and structure.

Here, we investigated the spatial and trophic niche dimensions of four lizard assemblages in Caatinga habitats from the Brazilian Neotropical semiarid region. For each studied lizard assemblage, we quantified the spatial and trophic niche breadth and overlap to (I) examine the extent to which Caatinga lizards share space and food resources, (II) test the hypothesis that lizards from the semiarid Caatinga partition their niches to reduce the effects of biotic interactions, such as competition, and (III) test the hypothesis that in this semiarid environment, ecological factors, such as microhabitats and food availability, are better predictors than phylogeny for partitioning these ecological niche dimensions.

2 | METHODS

2.1 | Studied area

We investigated four lizard assemblages in the semiarid region of northeastern Brazil. The Brazilian semiarid region has approximately 1,128,697 km^2 (13.3% of the Brazilian territory; SUDENE, 2018). This region is distinguished by the irregularity and unpredictability of the rains, which occur in a brief season, with an average annual rainfall of 773 mm^3 (Andrade et al., 2017). The study area is divided into two regions of roughly similar size by the São Francisco river, where both are mainly covered by vegetation of Caatinga (steppic savanna).

The four lizard assemblages studied are in areas of shrubby Caatinga vegetation (Figure 1). Two lizard assemblages are located in the northern region of the São Francisco river, in the municipalities of Casa Nova, Bahia state (9°24'S 41° 09' W; 400 m altitude; 516 mm^3 annual precipitation), and Cuité, Paraíba state (6° 30' S; 35° 56' W; 470 m; 556 mm^3); and two assemblages are located to the south, in the municipality of Contendas do Sincorá (13° 50' S; 41° 03 W; 356 m; 613 mm^3), and in the surroundings of the Serra dos Montes State Park, municipality of Palmas de Monte Alto (14° 17' S; 43° 04' W; 574 m; 792 mm^3), both in the Bahia state.

Despite the distance between the areas, the vegetation structure is similar in all four areas surveyed, shrubby Caatinga composed of deciduous and thorny plants. The soils of Casa Nova are sandy, influenced by Paleo quaternary dunes on the banks of the São Francisco River, the most important river of the Brazilian semiarid region. The São Francisco river is an important historical factor for lizard assemblage structure at regional scale (Gonçalves-Sousa et al., 2022; Recoder & Rodrigues, 2020). The north of the São Francisco River represents the most severe subregion of the Brazilian semiarid region. The water deficit associated with the environmental deterioration caused by anthropogenic pressures has resulted in extensive centers of desertification (Vieira et al., 2015), resulting in increased temperature, decreased humidity, and alteration of the habitat structure used by the lizards. On the contrary, the higher humidity levels of the subregion to the south of this river allow longer duration of temporary water bodies, sustaining a milder environment and greater heterogeneity of habitats (Queiroz et al., 2017) and, consequently, less annual fluctuation of food resources than in the northern region (McCluney et al., 2012; Pinheiro et al., 2002).

2.2 | Data collection

We sampled each lizard assemblage once, for 10 days, in the dry season of 2017 and 2018. In each assemblage, we collected up to 30 lizards per species through active search, manually, and with rubber bands. Each collector performed active search for 6 h during the day and 4 h at night, totaling 300 h of sampling effort in each area.

In the field, we categorized the microhabitats used by lizards at the time that it was first sighted. These categories correspond to bromelia, fallen trunk, leaf litter, open ground, piles of small woody debris, rock, termite nest, tree branch, tree trunk, and soil between vegetation.

In the laboratory, we removed the stomachs of all individuals collected and analyzed them under a stereomicroscopy to identify prey items to the lowest possible taxonomic level (usually Order). We measured the length and width of the most intact items found in the stomachs (maximum three per prey category) with a digital caliper (±0.01 mm). Then, we estimated their volumes using the ellipsoid formula: $V = \frac{4}{3}\pi\left(\frac{L}{2}\right)\left(\frac{W}{2}\right)^2$, where V = volume, L = length and W = width.

Lizards collected were euthanized with hydrochloride lidocaine, fixed in 10% formaldehyde, preserved in 70% alcohol, and deposited in the Herpetological Collection of the Universidade Regional do Cariri. We collected the lizards under permission of Instituto Chico Mendes de Conservação da Biodiversidade-ICMBio (permit number 29613–1), and its use procedure was approved by the Comitê de Experimentação e Uso de Animais da Universidade Regional do Cariri (00260/2016.1).

2.3 | Sampling effort

To evaluate our sample effort, we considered lizard microhabitat use records of each sampling site as the lizard abundance of that site to develop rarefaction curves and to estimate the taxonomic diversity by using two nonparametric abundance-based estimators (Chao1 and ACE) in the vegan R package (Oksanen et al., 2018). We used the Jaccard distance index in the vegan R package, which is appropriate for estimating differences in composition between two sample sets, to assess dissimilarities in lizard species composition between pairwise assemblages.

2.4 | Ecological niche

We used the spaa R package (Zhang, 2016) to estimate the spatial and trophic niche breadth (B) for each species and the niche overlap between the pairs of species from each assemblage. To estimate the niche breadth, we selected the "Levins" method, which results in B values that can vary from 1 (exclusive use of a single category of microhabitat or prey, specialist habit) to n (equal use of all categories, generalist habit). For the niche overlap, we used the "Pianka" method, which results in values ranging from 0 (without overlapping) to 1 (total overlap in the use of resources).

We used null models to test whether the extent to which mean niche overlap observed in the spatial and trophic niche differs from that expected by chance in the EcosimR R package (Gotelli et al., 2015). We obtained these models by randomizing 1000 times (pseudocommunities) the original data matrix. We configured the null models with the "pianka" metric and RA2 algorithm. The RA2 algorithm replaces the frequency of microhabitat use and the prey volume in the original matrix with a uniform randomization between zero and one, retaining the zero structure of the matrix (Winemiller & Pianka, 1990), which is essential to verify the existence of niche partition.

To assess the overlapping patterns between unified niche dimensions of each lizard assemblage, we used the method proposed by Geange et al. (2011). For this analysis, the microhabitat and food use matrix must contain the same species. Thus, we removed species from the microhabitat matrix when they were observed in the field but not collected, or if all individuals collected had empty stomachs.

We used the appropriate modeling technique to estimate the overlap between the pairs of species for each niche dimension in each lizard assemblage studied. We then performed null models (1000 permutations of the original matrix) to assess the realized niche distribution of all species of each assemblage across the hyperdimensional niche space.

2.5 | Historical and ecological effects

We performed phylogenetic principal components analysis—pPCA (Jombart et al., 2010) to verify the influence of historical (phylogeny) and ecological factors on the spatial and trophic niche dimensions. For each analysis, we used a matrix with branch lengths from the phylogenetic tree of Tonini et al. (2016), and a matrix with quantitative spatial (relative frequency of microhabitat use) or trophic (relative frequency of food volume) of species of the assemblage. We used this analysis to detect the presence of global or local phylogenetic structure. These structures are indicated by the global and local phylogenetic component axis generated by the pPCA, where large positive eigenvalues indicate strong phylogenetic inertia in the conservation of ecological features and large negative eigenvalues indicate ecological convergence, resulting in niche drift close to the terminal branches (Jombart et al., 2010). We performed this analysis using the Adephylo R package (Jombart & Dray, 2013), using only individuals identified at the species level.

3 | RESULTS

3.1 | Species richness and composition

The lizard richness was 13 species per assemblage in average, ranging from nine in Contendas do Sincorá to 16 species in Casa Nova. The four assemblages totaled 27 species from nine families, of which Teiidae (six spp.), Gymnophthalmidae (five spp.), and Tropiduridae (five spp.) were the most speciose families (Table 1). The most abundant species (all sites pooled) were *Tropidurus hispidus* (n = 190), *Ameivula pyrrhogularis* (n = 169), *Tropidurus semitaeniatus* (n = 99), and *Phyllopezus pollicaris* (n = 92) (Table 1).

The rarefaction curves approached the asymptote in all sites, except Palmas de Monte Alto (Figure 2). In all sites, the Chao1 and ACE estimated the average richness of one to two species more than that found by us, suggesting that our sampling in the four sites was satisfactory. Lizard assemblages showed a dissimilarity in the species composition of about 60%, except for Palmas de Monte Alto, which presented the highest values of dissimilarity (Table 2).

3.2 | Spatial niche dimension

Tropidurus hispidus was one of the most generalist species in the use of microhabitat in all areas, followed by *Ameivula* sp1. in the sandy dunes of Casa Nova, *A. pyrrhogularis* in Contendas do Sincorá, *Gymnodactylus geckoides* in Cuité, and *P. pollicaris* in Palmas de Monte Alto (Table S1).

The highest spatial niche overlap occurred between geckos in Casa Nova: *Hemidactylus agrius* versus (vs) both *Hemidactylus brasilianus* (0.99) and *Lygodactylus klugei* (1.00), and *H. brasilianus* vs *L. klugei* (0.99); and in Contendas do Sincorá: *Hemidactylus mabouia* vs *H. brasilianus* (0.97). In Cuité, the highest spatial niche overlap occurred between *Acratosaura mentalis* vs both *Coleodactylus meridionalis* (1.00) and *Vanzosaura multiscutata* (1.00), *C. meridionalis* vs *V. multiscutata* (1.00), *Phyllopezus periosus* vs both *P. pollicaris* (0.92) and *T. semitaeniatus* (1.00); and *P. pollicaris* vs *T. semitaeniatus* (0.92). In Palmas de Monte Alto, the highest overlap occurred between *P. pollicaris* vs *Tropidurus cocorobensis* (0.92; Table S2).

Pseudocommunity analyses revealed nonrandom patterns in the use of microhabitat (spatial niche) lower than expected by chance in Casa Nova ($\bar{\mathbf{x}}\phi_{\text{observed}} = 0.206$; $\bar{\mathbf{x}}\phi_{\text{expected}} = 0.247$; $p = .019$) and higher than expected by chance in Cuité ($\bar{\mathbf{x}}\phi_{\text{observed}} = 0.312$; $\bar{\mathbf{x}}\phi_{\text{expected}} = 0.263$; $p = .042$). The assemblages of Contendas do Sincorá ($\bar{\mathbf{x}}\phi_{\text{observed}} = 0.250$; $\bar{\mathbf{x}}\phi_{\text{expected}} = 0.284$; $p = .215$) and Palmas de Monte Alto ($\bar{\mathbf{x}}\phi_{\text{observed}} = 0.263$; $\bar{\mathbf{x}}\phi_{\text{expected}} = 0.267$; $p = .436$) did not differ significantly from the expected by chance.

3.3 | Trophic niche dimension

Lizard diet was mainly composed of arthropods, but also included plant material and lizards. The trophic niche breadth based on prey volume ranged from 1.00 (*Brasiliscincus heathi* in Casa Nova) to 6.38 (*T. semitaeniatus* in Cuité; Table S3).

In Casa Nova, the highest trophic niche overlaps occurred between the tropidurids *Eurolophosaurus divaricatus* and *T. semitaeniatus* (0.99), between the geckos *G. geckoides* and *L. klugei* (0.89) and between *B. heathi* and *H. agrius* (0.89); in Contendas do Sincorá, the highest trophic niche overlap occurred between the congeners *H. agrius* and *H. mabouia*; in Cuité, it occurred between *B. heathi* and *G. geckoides* (0.95), while in Palmas de Monte Alto, it occurred between *Ameivula nigrigula* and *T. hispidus*, and between *C. meridionalis* and *G. geckoides* (Table S2).

Pseudocommunity analyses based on the prey volume revealed nonrandom patterns of trophic niche overlap lower than expected by chance in Casa Nova ($\bar{\mathbf{x}}\phi_{\text{observed}} = 0.268$; $\bar{\mathbf{x}}\phi_{\text{expected}} = 0.379$; $p = .002$), Contendas do Sincorá ($\bar{\mathbf{x}}\phi_{\text{observed}} = 0.231$; $\bar{\mathbf{x}}\phi_{\text{expected}} = 0.399$; $p < .001$) and Cuité ($\bar{\mathbf{x}}\phi_{\text{observed}} = 0.187$; $\bar{\mathbf{x}}\phi_{\text{expected}} = 0.267$; $p < .001$). Similar to spatial niche, the trophic niche of the lizards of Palmas de Monte Alto did not differ from that expected by chance ($\bar{\mathbf{x}}\phi_{\text{observed}} = 0.402$; $\bar{\mathbf{x}}\phi_{\text{expected}} = 0.369$; $p = .813$).

TABLE 1 Composition of the four lizard assemblages in Caatinga habitats of the Neotropical semiarid region.

Taxa	Casa Nova	Contendas do Sincorá	Cuité	Palmas de Monte Alto	Total
Gekkonidae					
Hemidactylus agrius	4/4	-	-	-	4/4
Hemidactylus brasilianus	8/9	3/3	9/12	10/9	30/31
Hemidactylus mabouia	-	5/5	-	-	5/5
Lygodactylus klugei	15/5	10 /8	18/14	-	43/27
Gymnophthalmidae					
Acratosaura mentalis	-	-	3/3	-	3/3
Calyptommatus leiolepis	12/-	-	-	-	12/-
Nothobachia ablephara	5/8	-	-	-	5/8
Procellosaurinus tetradactylus	2/-	-	-	-	2/-
Vanzosaura multiscutata	-	-	8/6	1/-	9/6
Iguanidae					
Iguana iguana	-	-	-	2/-	2/-
Mabuyidae					
Brasiliscincus heathi	5/2	-	9/5	-	14/7
Phyllodactylidae					
Gymnodactylus geckoides	11/6	-	11/20	10/13	32/39
Phyllopezus periosus	-	-	19/17	-	19/17
Phyllopezus pollicaris	32/16	16/11	16/16	28/18	92/61
Polychrotidae					
Polychrus acutirostris	-	-	1/-	1/-	2/-
Sphaerodactylidae					
Coleodactylus meridionalis	-	-	11/8	12/17	23/25
Teiidae					
Ameiva ameiva	-	-	-	2/-	2/-
Ameivula nigrigula	-	-	-	42/13	42/13
Ameivula pyrrhogularis	31/10	77/18	61/17	-	169/45
Ameivula sp1.	40/-	-	-	-	40/-
Ameivula sp2.	5/-	-	-	-	5/-
Salvator merianae	1/-	1/-	-	2/-	4/-
Tropiduridae					
Eurolophosaurus divaricatus	25/8	-	-	-	25/8
Tropidurus cocorobensis	-	-	-	9/16	9/16
Tropidurus hispidus	25/11	54/9	28/14	83/5	190/39
Tropidurus pinima	-	39/11	-	31/7	65/18
Tropidurus semitaeniatus	55/9	-	39/17	-	99/26
Species richness	16	9	13	13	27

Note: The values represent the frequency of individuals that we recorded for the use of microhabitats/the number of specimens collected and used for diet analysis.

3.4 | Overlap across niche dimensions

The lizard realized niche distribution across niche space showed significant clusters across niche space in the assemblages from Contendas do Sincorá and Palmas de Monte Alto; significant evenness in Cuité; and lack of patterns in Casa Nova (Table 3).

3.5 | Historical and ecological effects

The pPCA revealed greater phylogenetic (historical) influence on the spatial niche in the assemblages of Casa Nova, Contendas do Sincorá, and Cuité (Figure 3). Although ecological factors have a greater influence on the spatial niche of lizards in Palmas de Monte

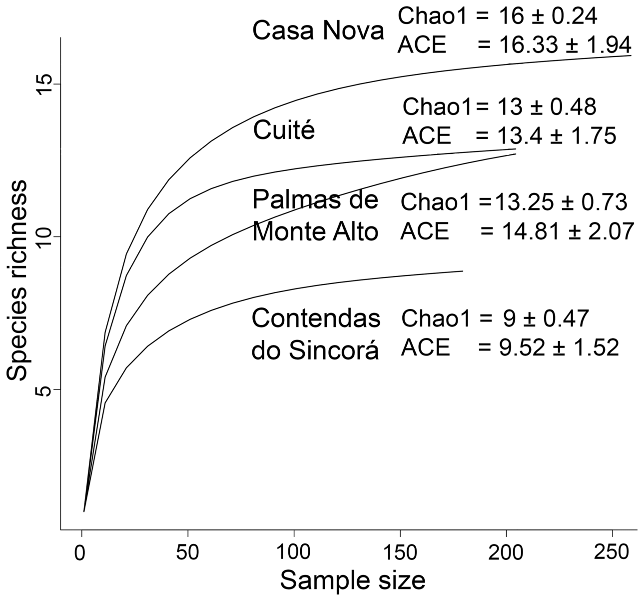


FIGURE 2 Rarefaction curves and richness estimators based on abundance (Chao1 and ACE) of the four lizard assemblages studied in Caatinga habitats of the Neotropical semiarid region.

TABLE 2 Comparison of similarity in species composition of four lizard assemblages studied in Neotropical semiarid Caatinga habitats.

	Casa Nova	Contendas do Sincorá	Cuité	Palmas de Monte Alto
Casa Nova	0			
Contendas do Sincorá	0.61	0		
Cuité	0.62	0.63	0	
Palmas de Monte Alto	0.79	0.71	0.63	0

Note: Dissimilarity between assemblages was calculated based on the Jaccard distance index. Values range from 0 (equal in species composition) to 1 (totally different species composition).

TABLE 3 Measures of the evenness vs. clustering of four lizard assemblages across niche space incorporating spatial (based on microhabitat use) and trophic (based on diet) niche dimensions.

Lizard assemblages	Test	*p*-overall
Casa Nova	Evenness	.795
	Clustering	.205
Contendas do Sincorá	Evenness	.994
	Clustering	.006
Cuité	Evenness	
	Clustering	1
Palmas de Monte Alto	Evenness	.978
	Clustering	.022

Note: Clustering vs. evenness distribution on niche space is measured by the average coefficient of heterogeneity over the two niche dimensions analyzed.

Alto, based on the similar size of the eigenvalues we can conclude that phylogeny acts together with ecological factors to determine the use of microhabitats carefully observing the eigenvalues we can conclude that phylogeny acts together with ecological factors to determine the use of microhabitats (Figure 3).

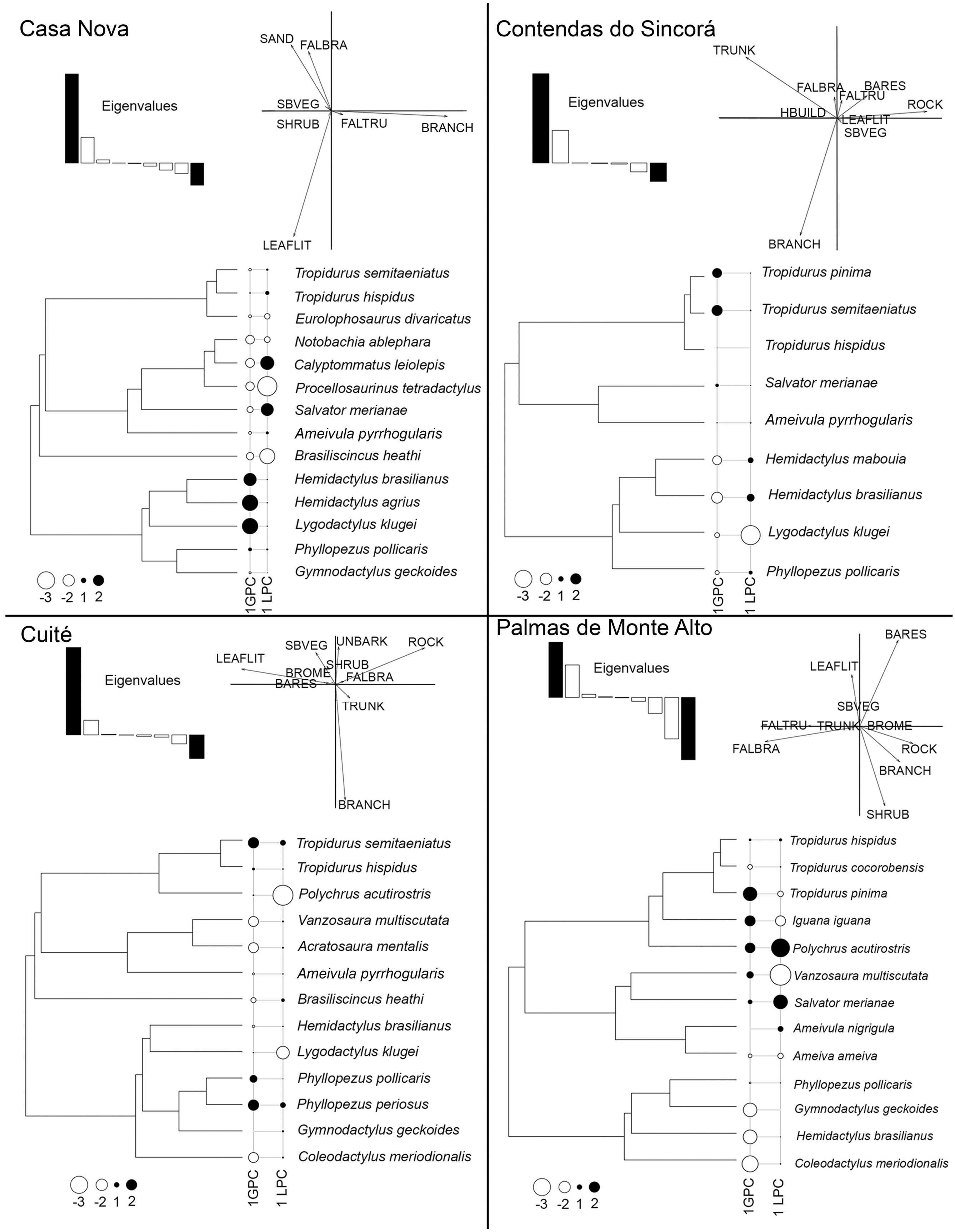
The pPCA revealed greater phylogenetic than ecological influence on the trophic niche in the assemblages of Casa Nova, Contendas do Sincorá, and Palmas de Monte Alto (Figure 4). On the contrary, ecological factors had a greater influence on the trophic niche of Cuité (Figure 4).

4 | DISCUSSION

4.1 | Species richness and composition

In this study, we found 27 out of 51(53%) lizard species reported from Caatinga habitats (Gonçalves-Sousa et al., 2022). The most abundant species were common in the four assemblages studied and correspond to four of the five species with the largest distribution in the Caatinga (Gonçalves-Sousa et al., 2022). These four species are either generalists in the use of microhabitat (*T. hispidus* and *A. pyrrhogularis*) or use very abundant microhabitats, such as rock outcrops (*P. pollicaris* and *T. semitaeniatus*). Except in Palmas de Monte Alto, the studied assemblages presented about 60% dissimilarity in their composition. Curiously, considering species composition, Palmas de Monte Alto is more similar to Cuité, which is the further assemblage (63% dissimilar; ~1160 km straight line), compared with the nearest (Contendas do Sincorá; 71% dissimilar; ~220 km). We found the most dissimilarity between Palmas de Monte Alto and Casa Nova (79%; ~620 km). These assemblages are located on opposite sides of the São Francisco River, which represents an important historical factor structuring beta diversity of lizards on a regional scale (Gonçalves-Sousa et al., 2022; Recoder & Rodrigues, 2020). Furthermore, the occurrence of endemic species in Casa Nova, due to the presence of several psammophilous species in the sandy dune habitats of the São Francisco

FIGURE 3 Phylogenetic principal component analyses for lizard microhabitat use in four sites of Caatinga habitat in Brazil. Eigenvalue bar plots correspond to global (left) and local (right) principal components. Microhabitats categories close to 0 on both X and Y axes were omitted. The lower panels show trees built for the lizard assemblage that incorporates the first global (black circles, positive scores) and local (white circles, negative scores) principal components. Circle size is proportional to score value. BARES = bare soil; BRANCH = tree branch; BROME = bromeliads; FALBRA = piles of woody debris; FALTRU = fallen trunk; HBUILD = human building; LEAFLIT = leaf litter; ROCK = rock; SBVEG = soil between vegetation; TERMIT = termite nest; TRUNK = tree trunk; UNBARK = under tree bark. 1GPC = first global principal components; 1LPC = first local principal components.


Casa Nova
Eigenvalues
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FALBRA
SBVEG
SHRUB
FALTRU
BRANCH
LEAFLIT
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Tropidurus hispidus
Eurolophosaurus divaricatus
Notobachia ablephara
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Procellosaurinus tetradactylus
Salvator merianae
Ameivula pyrrhogularis
Brasiliscincus heathi
Hemidactylus brasilianus
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Ameiva ameiva
Phyllopezus pollicaris
Gymnodactylus geckoides
Hemidactylus brasilianus
Coleodactylus meriodionalis
-3 -2 1 2
1GPC
1 LPC

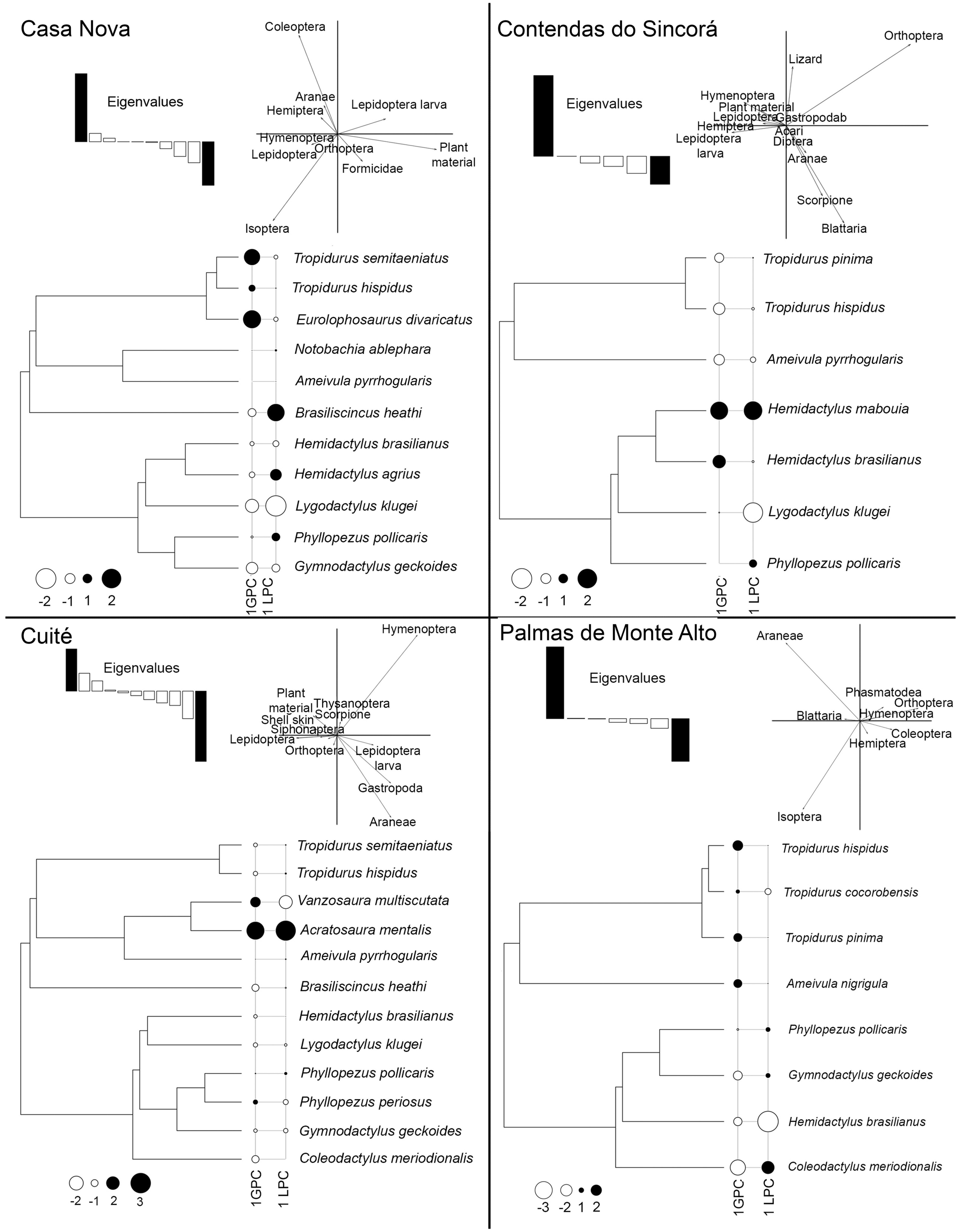

FIGURE 4 Phylogenetic principal component analyses for lizard diet in four sites of Caatinga habitat in Brazil. Eigenvalue bar plots correspond to global (left) and local (right) principal components. Prey categories close to 0 on both X and Y axes were omitted. The lower panels show trees built for the lizard assemblage that incorporates the first global (black circles, positive scores) and local (white circles, negative scores) principal components. Circle size is proportional to score value.

River, such as the gymnophthalmids *Calyptommatus leiolepis* and *Procellosaurinus tetradactylus* and the tropidurid *Eurolophosaurus divaricatus* (Recoder & Rodrigues, 2020; Rodrigues, 1996), leads to such dissimilarity.

4.2 | Spatial niche dimension

Although the spatial niche breadth has changed between the four sites, the lizards maintained its preferred habitats. This result suggests that phylogenetic conservation effects in the spatial dimension of the niche are stronger than environmental factors in influencing the life history of lizards, as two of the assemblages studied are located in the hottest and driest area of the semiarid region of northeastern Brazil, and two are in the milder area of this region. This is also supported by the results of pPCA, which showed that phylogenetic effects are stronger predictors of microhabitat use and diet of lizards from Caatinga habitats.

We detected nonrandom spatial niches that were higher and smaller than expected by chance in Cuité and Casa Nova, respectively. The high spatial niche overlap detected in Cuité suggests either that current intense competition for available microhabitats or that some microhabitats categories are abundant, supporting their exploitation by a larger number of species (Glasser & Price, 1988; Schoener, 1983). Studies assessing the Caatinga habitat heterogeneity are needed to understand whether lizard assemblages presenting nonrandom niche overlap higher than expected by chance reflect intense current competition or abundance of microhabitats. The lack of niche partitioning or high niche overlap in Contendas do Sincorá and Palmas de Monte Alto suggests that microhabitats are not limiting and that competition does not play an important role on the spatial structure of these assemblages.

Contrary to our expectations, we found niche partitioning in the spatial niche only in the assemblage of Casa Nova. Partitioning in some niche dimension is traditionally considered evidence of competition occurred in the past (Connell, 1980; Rabosky et al., 2011; Schoener, 1974), but it also may be the result of preexisting phylogenetic differences in the niche during the assemblage assembly (Brooks & McLennan, 1993; Goodman et al., 2008; Losos, 1996). The presence of several species adapted to the sandy dunes habitats of the São Francisco River suggests that this spatial partitioning has historical basis, which is strongly supported by the pPCA results, and also by the absence of significant patterns in the distribution of species across niche space. Spatial niche partitioning is a common pattern in lizard assemblages (e. g. deserts from Africa; Luiselli, 2008a; Pianka, 1973) and Australia (Pianka, 1973), and it was also observed in other Caatinga areas (Gonçalves-Sousa et al., 2019; Vitt, 1995). However, we did not detect spatial niche partitioning in three of the assemblages analyzed, similar to that found in Cerrado habitats (Gainsbury & Colli, 2003; Mesquita, Colli, et al., 2006; Mesquita, Costa, & Colli, 2006).

4.3 | Trophic niche dimension

We detected trophic niche partitioning in the assemblages of Casa Nova, Contendas do Sincorá, and Cuité. These findings suggest that trophic niche divergence among the lizards that compose these assemblages may have been caused by competition in the past. Evidence of competition in the past may be detected when phylogenetically related species are functionally different (Brooks & McLennan, 1993; Losos, 1996). Competition may have excluded species that were functionally very similar, if one of them did not diverge in at least one niche dimension (Chesson, 2000; Connell, 1980; HilleRisLambers et al., 2012). Alternatively, these niche partitioning could be due to conserved traits of species (e.g., foraging mode, physiological tolerances, and food preferences) present at the time of assemblage colonization (Brooks & McLennan, 1993, Goodman et al., 2008, Losos, 1996). Whatever the scenario, competition drives assemblage structure in conjunction with historical and abiotic factors (such as temperature and water availability) (HilleRisLambers et al., 2012; Kraft et al., 2007).

Similar to the spatial niche overlap, the trophic niche overlap in Palmas de Monte Alto did not differ from what was expected by chance. This result supports that competition does not represent a determining factor for the structure of this assemblage. Furthermore, the random overlap in the spatial and trophic niche dimensions may reflect greater availability and less seasonal fluctuation of resources, as consequence of the greater water availability in the subregion south of the São Francisco river (Andrade et al., 2017; Queiroz et al., 2017). In a global analysis, only 20% of the lizard assemblages evaluated showed trophic niche partitioning (Luiselli, 2008b). By contrast, studies of Neotropical lizard assemblages have consistently found partitioning in this niche dimension (Gonçalves-Sousa et al., 2019; Vitt, 1995; Vitt et al., 1999; Vitt & Zani, 1996; Werneck et al., 2009).

Contendas do Sincorá was the poorest assemblage, and the absence of spatial niche partitioning suggests that lizards may be expanding the spatial niche breadth to use available microhabitats (Gonçalves-Sousa et al., 2022; Pianka, 2011). Both complementarity and niche expansion are closely related to interspecific competition, acting in opposite directions, but not mutually exclusive. Niche breadth expansion increases the levels of overlap in the use of resources, while niche complementarity decreases the overlap of one niche dimension that is highly overlapping in another, thus allowing the coexistence of species (Huey, 1979; Pianka, 2011; Schoener, 1974).

We found clustered distribution across niche space of lizards in the assemblages of Contendas do Sincorá and Palmas de Monte Alto, and these results seem to have different origins. Although this clustering pattern may have occurred due to the expansion of the niche breadth in Contendas do Sincorá, it appears to originate from greater availability of resources in Casa Nova. Both these localities are in the region south of the São Francisco River and present milder environments than the localities of the other two studied taxocenoses. Both assemblages are in the region south of the São Francisco River and present milder environments than the areas of the other two studied lizard assemblages.

When there is no partitioning of a niche dimension between pairs of species, potential negative effects from competition in one niche dimension may be counterbalanced by partitioning in another (Huey, 1979; Schoener, 1974). The trophic niche partitioning and high spatial niche overlap in Cuité suggests the occurrence of niche complementarity. Furthermore, also seems that lizards are expanding their niche breadths in these assemblages. In Cuité, lizards appear to have eaten prey out of their food preferences, but abundant in the microhabitats they use, which is consistent when considering the greater number of prey categories (27) ingested by the lizards of this assemblage. The trophic niche partitioning found in Cuité may be influenced by the high number of prey categories identified. Overall, these findings can be supported by the evenness distribution of the realized niche across niche space by the lizards of Cuité, which suggests that lizards use available resources opportunistically.

Contrary to what is expected for tropidurids, which are generally generalists in the use of food resources (Alcantara et al., 2018; Gonçalves-Sousa et al., 2019; Rocha & Siqueira, 2008), *T. hispidus* from Cuité, *E. divaricatus*, and *T. semitaeniatus* from Casa Nova had a low trophic niche breadth, and their diet was strongly influenced by the high consumption of plant material (leaves, flowers, and seeds). In Brazil, omnivory in *Tropidurus* was recorded in *T. hispidus*, *T. jaguaribanus*, and *T. semitaeniatus* in Caatinga habitats (Alcantara et al., 2018; Gonçalves-Sousa et al., 2019; Ribeiro & Freire, 2011; Vitt, 1995); *T. hispidus* and *T. montanus* in Rupestrian Fields (Van Sluys et al., 2004); *T. torquatus*, *T. itambere*, *T. oreadicus*, and *T. spinulosus* in Cerrado (Colli et al., 1992; Faria & Araujo, 2004; Werneck et al., 2009); *T. oreadicus* in Canga ferruginous habitats (Rocha & Siqueira, 2008); *T. torquatus* and *T. hygomi* in coastal areas (Siqueira et al., 2010) and islands (Carvalho et al., 2007; Rocha et al., 2002). Although omnivorous lizards avoid leaf consumption due to the presence of salts (Sokol, 1967) and other components that are difficult to digest (cellulose and hemicellulose) or even indigestible (lignina; Zimmerman & Tracy, 1989), the consumption of plants may represent an important source of nutrients and water, especially in the dry season, when the availability of arthropods is lower (McCluney et al., 2012; McCluney & Sabo, 2009; Pinheiro et al., 2002). Besides, the plant consumption may also facilitate the elimination of intestinal parasites and aid in the digestion of exoskeletons (McCluney et al., 2012, McCluney & Sabo, 2009, Pinheiro et al., 2002).

4.4 | Historical and ecological effects

Historical effects were predominantly the major determinants for the use of resources in the studied assemblages. This historical structure highlights strong phylogenetic inertia in the conservation of the functional traits of Caatinga lizards. Recognizably, the effects of historical factors are stronger over phylogenetically more diverse lizard assemblages (Vitt et al., 1999, 2003). These results are supported by the presence of phylogenetic signal in 88% (7 of 8) of the functional traits and by the phylogenetic and functional overdispersion of the Caatinga lizard assemblages (Gonçalves-Sousa et al., 2022). Results obtained by sampling biotic assemblages in natural environments reflect current consequences of the interaction of historical and ecological effects that have led to ecological differences between species (Vitt et al., 1999). Ultimately, the morphology, physiology, and foraging mode are potential determinants of the competition levels and coexistence patterns of the Caatinga lizards (Goodman et al., 2008; Vitt et al., 2003; Vitt & Pianka, 2005).

5 | CONCLUDING REMARKS

In general, we found high species dissimilarity between the studied areas and we showed that the four grouped areas shelter about 53% of the species known to inhabit areas of Caatinga vegetation (which covers about 845,000 km^2) (Gonçalves-Sousa et al., 2022) and 33% of all lizard species that occur in the semiarid region of Northeast Brazil (1,128,697 km^2) (Dubeux et al., 2022; Mesquita et al., 2017). These findings underline the substantial conservation value of these four areas and the need to consider studies related to the ecological niche of ectothermic animals with low dispersion, such as lizards, in the development of management plans and strategies for land use and occupation. Currently, more than half of the Caatinga areas have been deforested, and it is known that the intensification of land use and consequent degradation of natural habitats negatively affects species richness and number of functional groups (Berriozabal-Islas et al., 2017; Flynn et al., 2009). In addition to the irreparable loss of species, changes in habitats lead to patterns of distribution of functional traits and overdispersed evolutionary histories (Gonçalves-Sousa et al., 2022). Arid and semiarid habitats cover about one third of land surface of the world (Wickens, 1998). Thus, making comparisons between our findings and those from other regions of the world may aid in identifying general trends in the lizard ecology of dry environments. Besides, understanding how different species in arid and semiarid environments use the available resources and how assemblages are structured as a result of this use may contribute to creation of predictive models on how the global warming, the decrease in humidity in altered habitats, and, consequently, the increase in aridity will affect the life histories of lizards from other regions of the world.

AUTHOR CONTRIBUTION

JGGS and RWA conceived and designed the study. JGGS, LAC, and RWA collected the data. JGGS, LAC, and DOM examined and analyzed the data. JGGS led the manuscript writing, and all co-authors contributed to editing the drafts.

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CONFLICT OF INTEREST

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.msbcc2g24.

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