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Lizard assemblage from a sand dune habitat from southeastern Brazil: a niche overlap analysis

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ABSTRACT

Communities are structured by interactions of historical and ecological factors, which influence the use of different resources in time and space. We acquired data on time of activity, microhabitat use and diet of a lizard assemblage from a sand dune habitat in a coastal area, southeastern Brazil (Restinga de Jurubatiba). We analyzed the data of niche overlap among species in these three axes (temporal, spatial and trophic) using null models. We found a significant overlap within the trophic niche, whereas the overlap for the other axes did not differ from the expected. Based on this result, we discuss the factors acting on the structure of the local lizard community.

Key words: null models, communities, sand dune habitat, lizards, Brazil.

INTRODUCTION

The structuring of communities is modeled by interactions of both historical and ecological factors (e.g., Araújo 1994, Vitt 1995). Ecological factors comprise mainly interactions between sympatric species and their relationships with the local environment, which ultimately may result in the segregation of basic resources used by species (e.g., food, microhabitat and time of activity; Pianka 1973, Schoener 1974, Toft 1985, Araújo 1994). Differences on how sympatric species use available resources may be influenced by the community itself (ecological factors), and/or may reflect a historical divergence (historical factors) (Vitt et al. 1999, Vitt and Pianka 2005). Even the availability of a given resource may vary in time and space, according to consumers and behavioral divergences (Winemiller and Pianka 1990). Also, temporal differences in activity and in microhabitat used influence the resource acquisition (Winemiller and Pianka 1990). A methodology to interpret its structure evaluates the overlap of different niche axes from species in a community, and involves the construction of random null models (pseudo-communities or null models) based on real data

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(Gotelli and Graves 1996). This methodology was proposed during the 1970's (Sale 1974) and since then, has been used in many studies (e.g., Winemiller and Pianka 1990, Gainsbury and Colli 2003).

Most ecological studies on the structure of lizard assemblages have been carried out in deserts and mostly in temperate areas (e.g., Pianka 1986, Winemiller and Pianka 1990, Vitt 1995). Nevertheless, comparative ecological studies on lizard assemblages in tropical cis-Andean South America have increased considerably in number over the last decades, encompassing different habitats such as Amazonian Rainforest (Rand and Humphrey 1968, Magnusson et al. 1985, Duellman 1987, Martins 1991, Vitt and Zani 1996, 1998), Amazonian savanna (Vitt and Carvalho 1995, Mesquita et al. 2006a), Brazilian Cerrado (Vitt 1991, Mesquita et al. 2006b), and dry Caatinga from northeastern Brazil (Vitt 1995, Rocha and Rodrigues 2005). Both qualitative and quantitative studies are scarce for lizard assemblages occurring within the Atlantic Rainforest domain and, with a few exceptions (e.g., Sazima and Haddad 1992, Freire 1996, Carvalho et al. 2007), most information came from the comparative studies of Araújo (1984, 1991) on the lizard assemblage of Barra de Maricá, southeastern Brazil. Additionally, some studies have been done on individual lizard species from that assemblage (e.g., Rocha 1998, 2008, Teixeira-Filho et al. 1995, Rocha and Vrcibradic 1996, 1999, Vrcibradic and Rocha 1996), and in other similar sites in southeastern and southern Brazil (e.g., Bergallo and Rocha 1993, 1994, Verrastro and Krause 1994, Vrcibradic and Rocha 1996, Verrastro and Bujes 1998, Teixeira and Giovanelli 1999, Hatano et al. 2001, Siqueira et al. 2013). However, information on interactions among species comprising these communities is still limited.

In this study we present basic ecological data on sympatric lizard species from a coastal area in the Atlantic Rainforest domain (Restinga de Jurubatiba). Our purpose was to assess the interspecific overlap in temporal, spatial and trophic axes, to analyze a possible influence on the structure of the lizard assemblage.

MATERIALS AND METHODS

STUDY AREA

We carried out the study in the Parque Nacional da Restinga de Jurubatiba, situated between 22º and 22º 23' S and between 41º 15' and 41º45'W (Figure 1). The area spans three municipalities (Macaé, Carapebus and Quissamã) in northeastern Rio de Janeiro state. Jurubatiba is part of a continuous sand dunes complex extending through ca. 6,000 km² of coastal plains (Araújo and Henriques 1984) in Southeastern Brazil. Rainfall is seasonal and varies from 1,100 to 1,300 mm annually; monthly average ranges from 41 mm during winter (June to September) to 189 mm in summer (December to March; Araújo et al. 1998). Monthly average temperature varies from 29.7 ºC in January to 20 ºC in July; annual temperature averages 22.6 ºC (Henriques et al. 1986).

Open coastal sand dune habitats are inserted in the Atlantic Rainforest biome domain. Their main features include the change of vegetation zones as the distance from seashore increases (see Araújo and Henriques 1984): i) beach vegetation, comprised mainly by herbaceous halophilous species; ii) shrubby vegetation; iii) arbustive-arboreal vegetation; iv) closed vegetation, composed mainly by arboreal trees with liana species; and v) "restinga" forest, characterized by trees of reduced height compared to those in the ombrophilous forest. A comprehensive description of the vegetation in the area can be found in Araújo et al. (1998). The current configuration of sand-dune habitats is relatively recent due to marine regressions and transgressions (see Martin et al. 1996, 2003, Cerqueira 2000). In these coastal habitats, lizards are usually in high densities (Rocha and Bergallo 1997). Lizard assemblages in those areas are typically structured by "invasion" (see

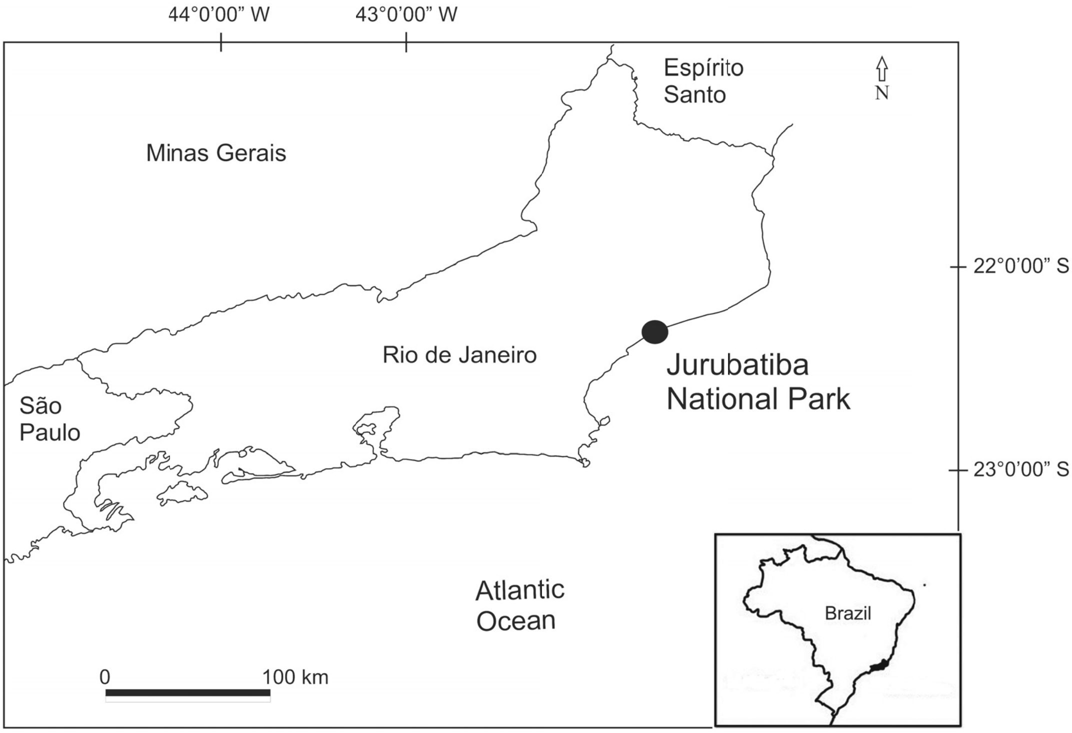

Figure 1 - Location of the Jurubatiba National Park, Rio de Janeiro state, southeastern Brazil.

Rummel and Roughgarden 1983), and most species are characteristic from the Atlantic Rainforest or from open habitats in general (Araújo 1984, 1994). Endemism is rare (Rodrigues 1990).

We conducted the study adjacent to the Cabiúnas lagoon (22º16'S, 41º41'W), which corresponds to the sub-area that Henriques et al. (1986) designated as "open *Clusia* formation". There, the arbustive-arboreal vegetation is dominated by species of Clusiaceae, Myrtaceae, Erythroxylaceae and Burseraceae, with abundant bromeliads and cacti, and a high density of the dwarf sand palm ("guriri"), *Alagoptera arenaria* (Arecaceae) (Araújo et al. 1998).

FIELD DATA COLLECTION AND ANALYZES

We conducted field work in March 1999, although we also included data from lizards collected on earlier fieldwork in the area (i.e., April 1997, and January, September, October and December 1998). We restricted the study entirely to the months of wet season (October-April) in order to minimize possible effects of seasonality in our results. Data included both visual observation and specimen collection for diet analysis. We undertook visual observations during activity transects in areas different from those where we collected the lizards, but similar in phytophysiognomy. Our transects consisted of a precisely demarcated path (evidenced by a trail in the sand and bright orange tapes tied to the vegetation and spaced 10 m from one another). We made daily observations from 0600 to 1900 during three days (2-4 March 1999). A pair of researchers walked in transects during an average of 30 minutes each hour. All lizards seen were recorded and categorized according to species, microhabitat used at first sighted, and whether they were exposed to sun, shade or active under cloudy weather. Lizard taxonomy followed Pyron et al. (2013).

We classified microhabitat types in eight categories: (1) open sand, at the edge of bushes;

(2) open sand, standing more than 20 cm away from the border of bushes; (3) on leaf-litter; (4) on tree trunks or branches; (5) inside shrubs; (6) bromeliad; (7) cactus; (8) dwarf palm. To non-frequent species (i.e., *Mabuya* spp., *Tupinambis merianae* and *Hemidactylus mabouia*), we combined data on activity periods and microhabitat use gathered along transects (for *Mabuya* and *Hemidactylus*) or observed on other occasions (for *T. merianae*). Thus, data on microhabitat use were taken from all lizards collected plus those observed in activity transects during the hourly period of highest activity for each species (in order to avoid pseudoreplication of data).

We performed collections using air-pressure rifles, rubber bands, nooses, and glue traps. We placed the glue traps randomly on the leaf-litter near bromeliads and on bromeliad leaves, at the edge and inside bushes. All collected lizards were transferred to a plastic bag and euthanized with diethyl ether, method usually permitted at the time. For each specimen collected, we recorded the time of capture, type of microhabitat, and perch height (in cm, for lizards perched above ground). We weighted the collected lizards in the field using Pesola© dynamometers, individually identified and placed on ice.

In laboratory, we measured the lizards using digital calipers (snout-vent length, SVL, to the nearest 0.1 mm) before preservation in 10% formalin. Later we examined stomachs and their contents under stereomicroscope. Animal prey was identified to Order (Hymenopteran insects were further subdivided in ants, non-ants) and plant matter was classified according to structure (i.e., leaf, flower or fruit). We measured length and width of each food item (excluding miscellaneous fragments) with digital calipers (to the nearest 0.1 mm), and estimated their individual volumes with a modified version of the ovoid-spheroid formula (Dunham 1983): Prey size distributions were log-transformed (ln) to fit normal distribution. Using prey measures, we obtained the importance index (Ix) (see Gadsden and Palacios-Orona 1997, Powell et al. 1990) for each prey category per lizard species. The index is calculated by the sum of the proportions for number, volume and frequency of each item, divided by three. We conducted this study under permission of Instituto Brasileiro do Meio Ambiente e Recursos Naturais Renováveis (IBAMA, authorization number 096/99-DIFAS).

We analyzed the niche overlap of four species, regarding three niche axes (time, space and trophic): *Tropidurus torquatus* (Wied, 1820), *Cnemidophorus littoralis* Rocha, Araújo, Vrcibradic & Costa, 2000, *Mabuya agilis* (Raddi, 1823) and *M. macrorhyncha* Hoge, 1947. These species were selected due to their probable similar use of the habitat (*T. torquatus* and *C. littoralis* using the border of vegetation; and *M. agilis* and *M. macrorhyncha* using the inner portion of vegetation) (G.R. Winck, unpublished data). We tested the overlapping probability along each axis by null models (1,000 iterations or pseudocommunities) using the software EcoSim (Gotelli and Entsminger 2004), through estimations of the MacArthur and Levins' index modified by Pianka (1973) (ϕ). We used randomization algorithm numbers two and three (RA2 and RA3). RA2 relaxes the niche breadth and retains the zero states of resources (i.e., effectively not used), whereas the RA3 retains the resource use, while retaining the niche breadth of species (Gotelli and Graves 1996). Contrary to R2, R3 algorithm reshuffles the resources that were not used in nature by one species, assuming the hypothesis that these resources might be used in the absence of interspecific competition (Gotelli and Graves 1996). Luiselli (2008) suggested RA2 algorithm as the one that more often uncovers structure in trophic axis in lizard assemblages, whereas Winemiller and Pianka (1990) suggested RA3 as the most suitable for lizards in general. As our aim comprises different niche axis (not just the trophic one), we opted to use both algorithms. Also, most lizard species may be considered as diet generalist (Luiselli 2008), and that also seems to be the case in our assemblage. For temporal analysis, we used a matrix containing the relative frequency of species in each period sampled. For spatial analysis, we utilized the frequency of use of each microhabitat category. For trophic analysis, we used a matrix containing the importance index (Ix) of each prey category by species. Prey categories with an Ix lower than 5% in the diet of all lizards were excluded (following Gainsbury and Colli 2003).

In order to graphically display the niche relations among species based on the three niche axes, we calculated a unified index:; where "T" is the number of niche axes and $NO_{i,j,t}$ is the result of the estimated pairwise niche overlap (Geange et al. 2011). NO_{ij} varies from zero (both distributions are dissimilar) to one (distributions coincide). We constructed a distance matrix for unified pairwise niche overlap using d_{ij} = 1- NO_{ij}, and performed a non-metric multidimensional scaling (NMDS) for visualization (Geange et al. 2011).

RESULTS

We recorded seven lizard species in the restinga of Jurubatiba: *Tropidurus torquatus* (Tropiduridae), *Cnemidophorus littoralis* and *Tupinambis merianae* (Duméril & Bibron, 1839) (Teiidae), *Mabuya agilis* and *M. macrorhyncha* (Scincidae), *Hemidactylus mabouia* (Moreau de Jonnès, 1818) (Gekkonidae), and *Gymnodactylus darwini* (Gray, 1845) (Phyllodactylidae). We are aware of the existence of *Ameiva ameiva* in the area, however, the species apparently has a low local abundance and we were not able to record it during the study. *Tupinambis merianae* was only observed, but not collected. *Gymnodactylus darwini* was collected only in glue traps set in the interior of shrubs and no individuals were observed during activity transects; thus no activity data was gathered for it. Only four specimens of *H. mabouia* were found during fieldwork. Therefore, we excluded these three species from niche overlap analyzes due to their low abundance.

For the temporal analysis, we used data on *Tropidurus torquatus* (N = 698), *C. littoralis* (N = 57), *M. macrorhyncha* (N = 11), and *M. agilis* (N = 11). Temporal niche overlap varied from ϕ = 0.095, for *C. littoralis* and *M. agilis*, to ϕ = 0.688 for *T. torquatus* and *M. macrorhyncha* (Table I). Mean observed index for both algorithms did not differ from the expected by chance (R2: $\phi_{obs} = 0.42$, $\phi_{exp} = 0.42$, $p_{obs} \leq p_{exp} = 0.49$, $p_{obs} \geq p_{exp} = 0.5$; R3: $\phi_{obs} = 0.42$, $\phi_{exp} = 0.39$, $p_{obs} \leq p_{exp} = 0.68$, $p_{obs} \geq p_{exp} = 0.32$; Figure 2a, b). Variance was low and similar for both algorithms: var(R2, R3) = 0.004.

TABLE I

Observed overlap indices for time of activity (temporal axis), microhabitat use (spatial axis), and diet (trophic axis) for four lizard species, in Jurubatiba National Park, Rio de Janeiro State, Brazil. TT = *Tropidurus torquatus*; CL = *Cnemidophorus littoralis*; MA = *Mabuya agilis*; MM = *M. macrorhyncha*. NO_{ij} = estimated pairwise niche overlap considering all niche axes. Numbers in bold represent the highest and the lowest overlaps.

Temporal axis				
Species	TT	CL	MA	MM
TT	1	0.53	**0.69**	0.59
CL		1	0.38	**0.09**
MA			1	0.23
MM				1
Spatial axis				
Species	TT	CL	MA	MM
TT	1	**0.99**	0.14	0.45
CL		1	**0.13**	0.42
MA			1	0.33
MM				1
Trophic axis				
Species	TT	CL	MA	MM
TT	1	0.76	0.29	0.7
CL		1	**0.18**	**0.93**
MA			1	0.39
MM				1
Mean niche overlap (NO_{ij})				
Species	TT	CL	MA	MM
TT	0	0.44	0.89	0.57
CL		0	>1	0.69
MA			0	>1
MM				0

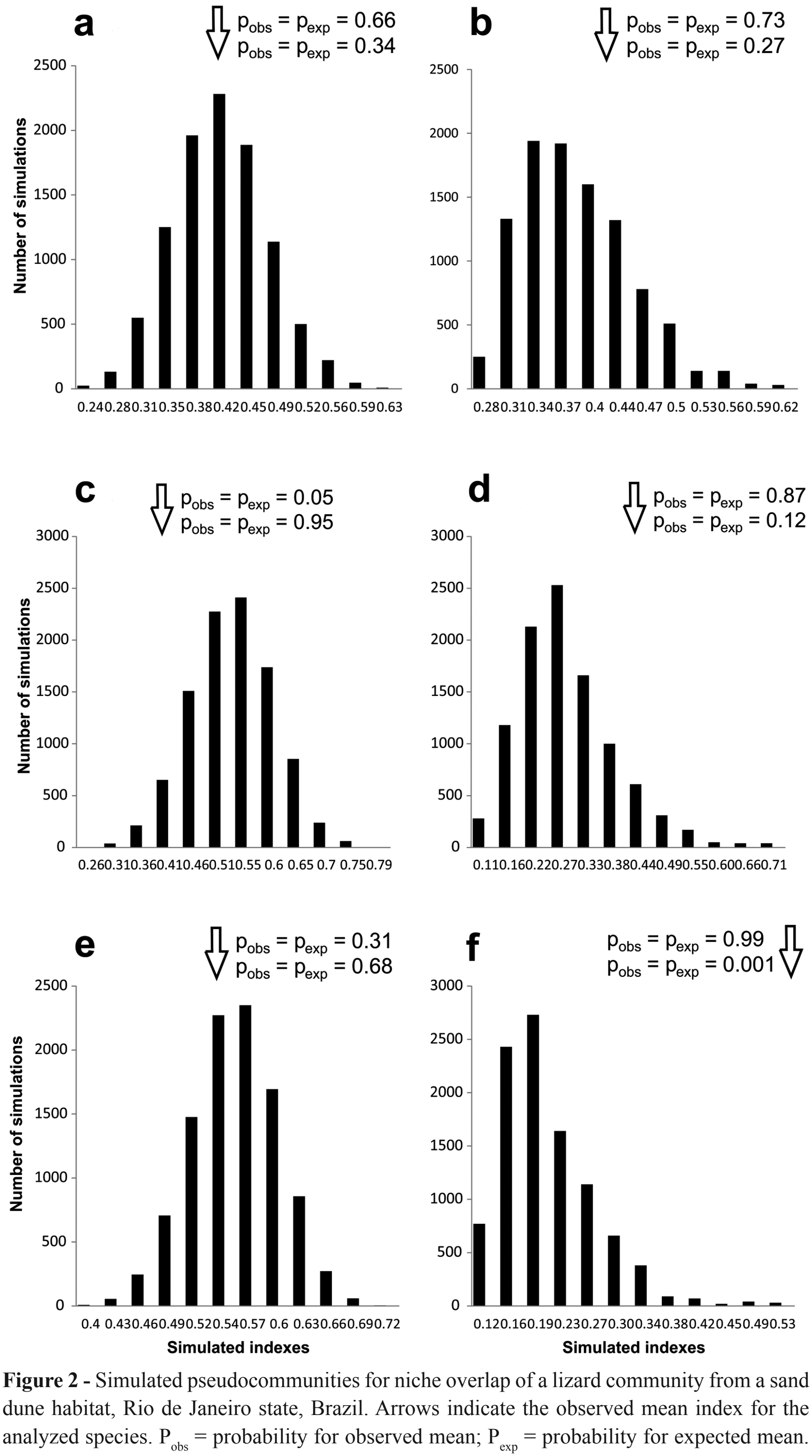

Figure 2 - Simulated pseudocommunities for niche overlap of a lizard community from a sand dune habitat, Rio de Janeiro state, Brazil. Arrows indicate the observed mean index for the analyzed species. P_{obs} = probability for observed mean; P_{exp} = probability for expected mean. Left column comprises simulations performed through RA2 algorithm, whereas right column using RA3 algorithm. **a, b** = temporal axis; **c, d** = spatial axis; **e, f** = trophic axis.

In order to evaluate the overlap on spatial niche (microhabitat use), we used data on *T. torquatus* (N = 805), *C. littoralis* (N = 92), *M. macrorhyncha* (N = 55), and *M. agilis* (N = 11). Spatial niche overlap varied from ϕ = 0.13, for *C. littoralis* and *M. macrorhyncha*, to ϕ = 0.99 for *T. torquatus* and *C. littoralis* (Table I). Mean observed index was significantly lower from the expected by chance using R2 (ϕ_{obs}=0.41, ϕ_{exp} = 0.54, $p_{obs} \leq p_{exp}$ = 0.05, $p_{obs} \geq p_{exp}$ = 0.95; Figure 2c); whereas no significant difference was found when using R3 (ϕ_{exp} = 0.29, $p_{obs} \leq p_{exp}$ = 0.87, $p_{obs} \geq p_{exp}$ = 0.12; Figure 2d). The variance of simulated indices was low for both algorithms: var(R2) = 0.006 and var(R3) = 0.01.

For the trophic analysis, we used data from *T. torquatus* (N = 58), *C. littoralis* (N = 22), *M. macrorhyncha* (N = 40), and *M. agilis* (N = 8) (Table I). The trophic niche overlap varied from ϕ = 0.18, for *C. littoralis* and *M. macrorhyncha* to ϕ = 0.93, for *C. littoralis* and *M. agilis*. The mean observed index using R2 did not differ from chance (ϕ_{obs}=0.54, ϕ_{exp}=0.57, $p_{obs} \leq p_{exp}$ = 0.31, $p_{obs} \geq p_{exp}$ = 0.68; Figure 2e), whereas it was significantly higher than the expected using R3 (ϕ_{exp} = 0.21, $p_{obs} \leq p_{exp}$ = 0.99, $p_{obs} \geq p_{exp}$ = 0.004; Figure 2f). Variance of simulated indices was low for both algorithms: var(R2) = 0.002 and var(R3) = 0.004.

Jointly analyzing the three niche axes, there was no grouping among the lizard species (Fig. 3; final configuration stress = 0.001, RSQ = 0.28). Pairwise mean niche overlap (NO_{ij}) shows the shortest distance between *T. torquatus* and *C. littoralis*, and the greater distances between the latter and *M. agilis* and between both *Mabuya* species (Table I).

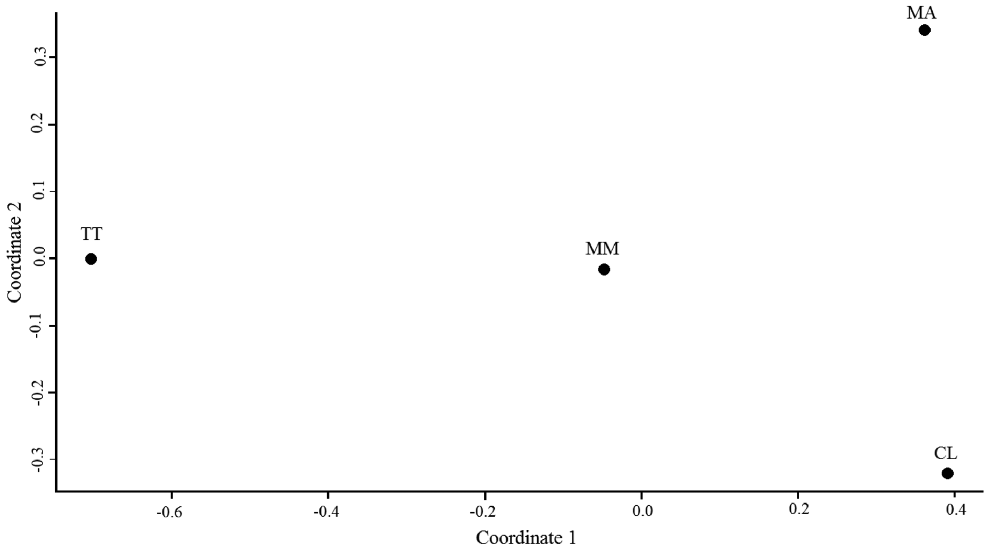

Figure 3 - Non-metric multidimensional scaling analysis showing statistical placing of each species, considering all three niche axis (temporal, space and trophic). TT = *Tropidurus torquatus*; CL = *Cnemidophorus litorallis*; MA = *Mabuya agilis*; MM = *Mabuya macrorhyncha.* Final configuration stress = 0.001; RSQ = 0.28.

DISCUSSION

The species composition and structure of the lizard assemblage of Jurubatiba is quite similar as that of Barra de Maricá, except for the absence of the Liolaemid *Liolaemus lutzae* and low abundance of the teiid *Ameiva ameiva* (Hatano et al. 2001). Although the former was expected to be absent, since Jurubatiba lies outside its range (see Rocha 1986, Rocha et al. 2009), the low abundance of the latter was not expected. *Ameiva ameiva* is widely distributed in many habitats throughout South America (Vitt and Colli 1994), and usually is present in sand dune habitats along the Brazilian coast, where it is relatively abundant (Araújo 1994, Freire 1996, Rocha and Bergallo 1997). Rocha and Bergallo (1997), recorded *A. ameiva* in all of the nine sand dune sites they surveyed along *ca*. 1200 km of Brazilian coast, between latitudes 17º and 23º S. They noted, however, that population densities of this teiid varied considerably among areas depending of the structural habitat of each sand dune habitat. This may explain the comparatively very low density at the particular site (open *Clusia* formation) where this study was done. The phyllodactylid *G. darwini* was only sampled in glue traps. Its secretive habits and behavior make it difficult to detect in the field. This phyllodactylid occur in more shaded conditions in the innermost portions of shrubs (it was caught only in glue traps set at those places), combined with its cryptic coloration, low movement rate and reclusive habits. Thus, we believe that the low number of records of *G. darwini* in Jurubatiba may be an artifact of sub-sampling.

Regarding the niche overlap along the three axes, our data highlights the importance of the trophic axis in structuring the local lizard assemblage, under the assumption of niche breadth retaining (RA3 simulations). For the four species analyzed, it is probable that their coexistence is currently viable due to divergences in times of activity and use of space. The significant overlap in trophic axis may indicate some degree of resources partitioning and, therefore, the absence of competition (Pianka 1986, Gotelli and Graves 1996), or even a strong competition that did not lead to a divergence on the use of this particular type of resource until the present (Gotelli and Graves 1996). We believe that both scenarios may be possible as result of the relatively recent conformation of sand dune habitats (Pleistocene; see Martin et al. 1996, Cerqueira 2000), and due to the lack of data on when these environments were colonized by the lizard species that currently constitute the local community. Since Jurubatiba became isolated from other sand dune habitats (Rocha et al. 2007), and is currently highly impacted by human actions (Rocha et al. 2003, 2007), we believe that new colonization by other species (both lizards and their preys) is hardly possible. Therefore, an isolated community comprised mainly by active/mixed foragers may not be induced to diverge in trophic axis, if the resources remain stable. At the same time, lizards presenting a generalist and/or opportunistic diet seem to be the rule in communities worldwide (Luiselli 2008).

The knowledge on how lizard communities are structured is important especially for recent habitats where anthropogenic actions also stress the interaction among species, besides historical and ecological factors. The apparently constant result of trophic axis being the most important niche element was also found here. However, we believe that possible intraspecific variations on prey items could highlight hinder relations or even disregard the trophic axis influence found in more general studies concerning niche relations, such as the present.

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RESUMO

As comunidades são estruturadas por uma interação de fatores históricos e ecológicos que influenciam o uso de diferentes recursos no tempo e no espaço. Coletamos dados sobre tempo de atividade, o uso de micro-habitat e dieta de uma assembleia de lagartos de um habitat de restinga na costa do Sudeste do Brasil (Restinga de Jurubatiba). Os dados foram analisados em relação à sobreposição de nicho entre as espécies ao longo de três eixos (temporais, espaciais e tróficos), utilizando modelos nulos. Encontramos uma sobreposição significativa no nicho trófico, enquanto que a sobreposição para os outros eixos não diferiu do esperado. Com base neste resultado, discutimos os fatores que atuam sobre a estruturação da comunidade local de lagartos.

Palavras-chave: modelos nulos, comunidades, restinga, lagartos, Brasil.

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