



Lizard assemblages on sandy coastal plains in southeastern Brazil: An analysis of occurrence and composition, and the role of habitat structure

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Abstract: Data on the structure of lizard communities in the different biomes and ecosystems of Brazil are still limited. In this study, we related the species richness, abundance and the spatial occurrence of lizards to the structure of the vegetation found on the coast of the state of Espírito Santo, southeastern Brazil, to determine whether habitat influences the structure of lizard communities. We conducted fieldwork in 2012, 2013 and 2014, collecting data in standardized samples. We analyze whether variables of vegetation structure influenced species richness and abundance, using Generalized Linear Models (GLMs). We recorded 12 lizard species from eight families. In general, species richness and abundance were similar among sites. Locally, we recorded the highest species richness in shrubby vegetation, open *Clusia* vegetation, and the restinga forest zone. Bromeliads explained the occurrence of teiids, although there was no systematic relationship between species richness and vegetation structure. Our results provide important insights into the characteristics of the lizard communities found on sandy coastal plains and contribute to the conservation of these species in these ecosystems.

Key words: community ecology, community structure, mesohabitat, Squamata.

INTRODUCTION

In Ecology, understanding how species composition, abundance and their interactions are organized is a fundamental issue (Sutherland et al. 2013). On geographical scale, physical barriers, local extinctions and recolonizations (Hanski 1994), as well as the dispersal capacity of species (Pulliam 2000) are fundamental to the formation

of assemblages and their spatial and temporal variation (Mouquet and Loreau 2003). Furthermore, historical factors may also combine to influence the spatial and temporal variation found in communities (Nekola and White 1999). On regional and local scales, assemblage composition is fundamental to ecosystems dynamics and functioning (e.g. Wedin and Tilman 1990), and plays a fundamental role in the stability, resilience and invasiveness of these systems (e.g. Tilman 1999).

Brazilian sandy coastal plain ecosystems harbor a considerable diversity of lizard species,

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compared with the Atlantic Rainforest *sensu stricto* (e.g. Rocha et al. 2003). These coastal plains were formed during the Holocene from fluvial sediments deposited over the past 6.5 thousand years (Suguio and Tessler 1984) and the phytophysiognomy of their vegetation is usually related by local topography, and may vary from herbaceous vegetation and grasses to trees of up to five meters in height (Pereira 1990). Lizard assemblages vary among sites, but typically comprise both endemic and wide-ranging species (Rocha et al. 2005, Dias and Rocha 2014), despite their varying habitat requirements (e.g. Rocha and Bergallo 1997, Vitt et al. 2007, Dias and Rocha 2014). The variation in the composition of the lizard communities among Brazilian sandy coastal plains has been evaluated in relation to habitat structure and temporal changes (e.g. Rocha and Bergallo 1997, Dias and Rocha 2014). These studies also found some degree of turnover among sites and suggested that habitat structure influenced part of the variation observed in the composition of the lizard species.

In the present study, then, we evaluated the structure of lizard assemblages in five remnants of the sandy coastal plain of southeastern Brazil. Our principal hypothesis is that these lizard communities are structured primarily by local habitat factors. Specifically, we aimed to analyze (1) the difference in species richness and abundance among lizard assemblages; (2) the difference in habitat structure among sites; (3) the extent to which lizard assemblages vary among mesohabitats and sites; and (4) whether there is a relationship between species richness and abundance and vegetation structure.

MATERIALS AND METHODS

We analyzed lizard species richness and community composition in remnants of five sandy coastal plains in southeastern Brazil, in the state of Espírito Santo. The sites were (datum WGS84): Praia das

Neves (PN) (21°13'S, 40°57'W), Paulo Cesar Vinha State Park (PCVSP) (20°36'S, 40°25'W), Comboios Biological Reserve (CBR) (19°40'S, 39°53'W), Conceição da Barra Environmental Protection Area (CBEPA) (18°37'S, 39°44'W), and Itaúnas State Park (ISP) (18°24'S, 39°42'W) (Figure 1). The structure of the vegetation on the sandy coastal plains varies according to the distance from the seashore, creating distinct mesohabitats (vegetation zones) (Pereira 1990). For the purposes of our study, we considered four zones: (i) beach vegetation, comprising herbaceous vegetation near the sea; (ii) shrubby vegetation, composed of low-lying bushes, cacti, and bromeliads; (iii) open *Clusia* zone, comprising taller bushes, with arboreal plants (*Clusia* spp.) grouped in widely-spaced clusters, with high densities of bromeliads, and (iv) restinga forest, composed of a continuous canopy of relatively short trees, in comparison with typical rainforest (e.g. Araújo and Henriques 1984, Bastazini et al. 2007, Oliveira et al. 2017).

We collected data at each site during two periods in the rainy season (from November to March) and two periods in the dry season (from May to July) in 2012, 2013 and 2014/1. At each site, we conducted 15 one-hour transects by visual search (Campbell and Christman 1982) in each mesohabitat (a total of 60 hours at each site). Transects were at least 50 m apart, whenever possible, and parallel to the beach line. We minimized the pseudo-replication of individuals by establishing this distance between transects, as well as alternating the sites sampled during the study, with an interval of at least three months between samples. As we did not use mark-recapture methods during this study, it is possible that some individuals were visualized more than once, although, as we did not estimate population size, but only the abundance of individuals at the time of the sample, this was not considered to be problematic. We standardized sampling effort from 0800 a.m. to 0100 p.m., the period of peak activity of most lizard species (Araújo 1984, Hatano et al.

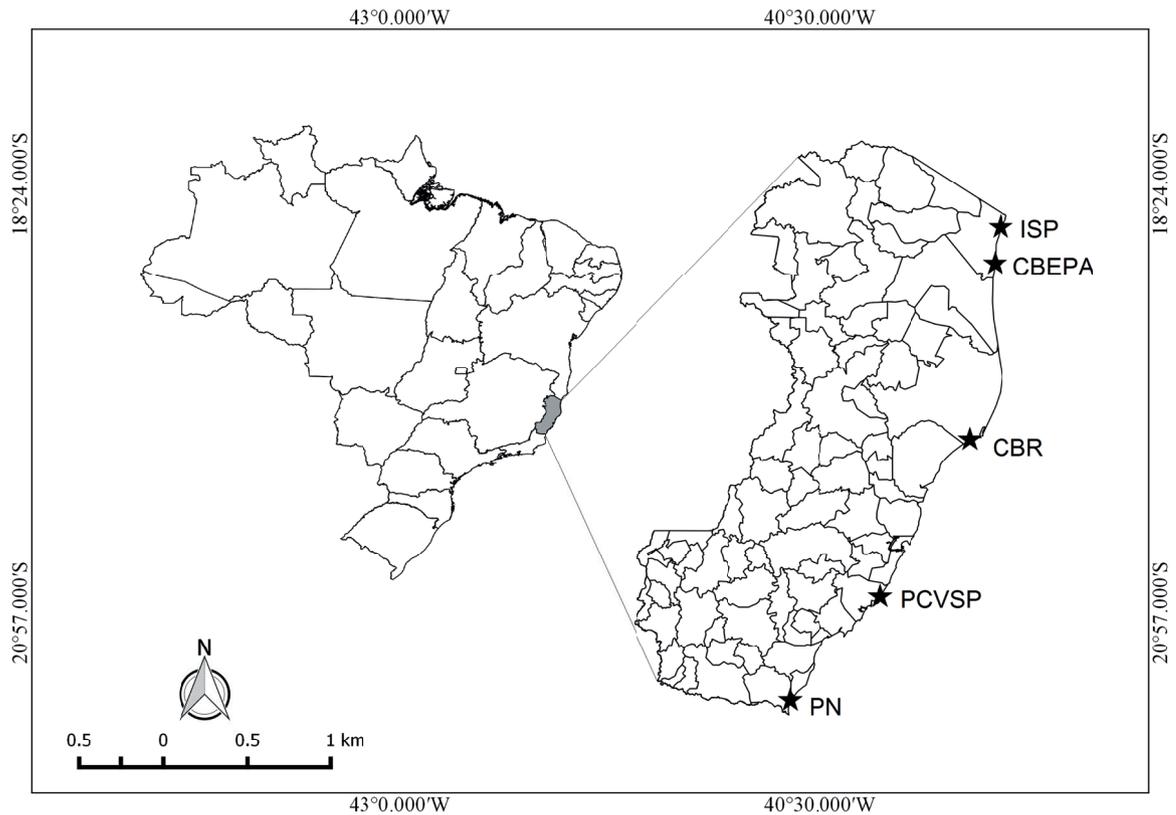


Figure 1 - Geographic location of sandy coastal plains remnants studied throughout the state of Espírito Santo, Southeastern Brazil. ISP: Itaúnas State Park; CBEP: Conceição da Barra Environmental Protection Area; CBR: Comboios Biological Reserve; PCVSP: Paulo Cesar Vinha State Park; PN: Praia das Neves.

2001). We collect one individual of each species, at each site, as voucher specimens (Sisbio License No. 28276). These specimens were euthanized with intravenous anesthetic, fixed in 10% formalin, and preserved in 70% alcohol. The voucher specimens are deposited in the Herpetological Collection of the National Museum in Rio de Janeiro (MNRJ).

We estimated the vegetation structure at each site through a measure of heterogeneity among sample units (transects) to evaluate the effects of habitat on the structuring of the lizard assemblages. At each site, we established 20 circular plots of 2 m in diameter in each mesohabitat type, arranged in a straight line, 20 meters apart. In each plot, we recorded: (1) the height of the vegetation (measuring the tallest and the shortest plants); (2) the distance to the nearest shrub; (3) the stem diameter of the

central plant; (4) the presence/absence and the number of cacti and bromeliads; (5) depth of the leaf litter at the central point of the plot, measured with a manual calliper; and (6) percentage canopy and ground cover, measured using a 50 cm x 50 cm square with 100 cells of 25 cm² (Freitas et al. 2002). We measured the vegetation structure in 2013. We characterized each mesohabitat for analysis based on the mean values recorded for each variable in the 20 plots.

We tested all data for homoscedasticity of variance and calculated the species accumulation curves for each site through data permutation (1000 iterations), based on the cumulative number of species recorded (S) as a function of sampling effort (n). To evaluate the similarity in abundance and richness among sites, we used the ANOSIM

(One-Way Similarity Analysis) permutation test on the Bray-Curtis measure (Clarke 1993) with 999 iterations. We estimated total species richness through a Bootstrap Index (Magurran 2011).

We used Generalized Linear Models (GLMs) with a Poisson distribution and log-link function (Poisson regression) to analyze whether variables of vegetation structure influenced lizard species richness and abundance. We selected variables through a stepwise regression (both backward and forward selection), using a null model (all species and no variables) for comparison, and Akaike's information criterion (AIC; Burnham and Anderson 2004) for the selection of the model for each group (lizard clades or families: all species, teiids, scincids, gekkonids, and tropidurids). We excluded *Ophiodes* sp., *S. merianae*, *L. lutzae* and *K. calcarata* from this analysis due to the low numbers of records ($N = 1, 1, 2$ and 2 , respectively).

To evaluate the similarity of the vegetation structure among sites, we ran a cluster analysis using the Jaccard index with simple linkage (Magurran 2011). The accumulation curve was generated in EstimateS® 8.0 (Colwell 2005). We used PAST 2.17 (Hammer et al. 2001) to calculate the Jaccard indices. The ANOSIM and GLM were run in R 3.2 (Rstudio Team 2015).

RESULTS

We recorded 1529 lizards during the study, representing 12 species in eight families (Table I). The most species rich families were the Teiidae and Mabuyidae with three species each. *Tropidurus torquatus* was the species with the highest abundance, accounting for 58% of the records ($N_{\log_2} = 9.78$, Figure 2). *Salvator merianae*, *Liolaemus lutzae*, *Kentropyx calcarata*, *Polychrus marmoratus* and *Ophiodes* cf. *striatus* were the least abundance species (Table I, Figure 2). Four species (*T. torquatus*, *Ameiva ameiva*, *B. agilis* and *P. macrorhyncha*) were recorded at all study sites,

whereas three species were registered at only one site (*L. lutzae* at Praia das Neves, *P. marmoratus* at Paulo Cesar Vinha State Park, and *K. calcarata* at Itaúnas State Park) (Table I).

Species richness did not vary significantly among sites (ANOSIM, $R = -0.083$; $P = 0.6$). The highest lizard abundance was recorded at Conceição da Barra Environmental Protection Area ($N_{\log_2} = 8.79$), and the lowest, at Itaúnas State Park ($N_{\log_2} = 7.31$) (Table I). However, abundance did not vary significantly among sites (ANOSIM: $R = -0.038$; $p = 0.573$). Two of the species recorded in this study (*Liolaemus lutzae* and *Ameivula nativo*) are endemic to sandy coastal plain ecosystems and have a restricted geographic distribution. *Hemidactylus mabouia*, an exotic gecko species from Africa was recorded at three of the five study sites.

The cumulative species curves did not reach the asymptote (Figure 3). The greatest similarities in the composition of the assemblages were recorded between Paulo Cesar Vinha State Park and Comboios Biological Reserve, and between the APA Conceição da Barra and Itaúnas State Park. Praia das Neves had the lowest similarity with all sites (Figure 4). Lizard species richness did not vary significantly among mesohabitats within the same site (ANOSIM; $R = 0.440$; $P = 1$), although abundance was greatest in the shrubby vegetation and open *Clusia* zones (Tables II and III). We observed *T. torquatus* and *H. mabouia* in all mesohabitats, while *Ophiodes* cf. *striatus*, *S. merianae*, *K. calcarata* and *P. marmoratus* were restricted to forest, and *L. lutzae* to the beach vegetation zone.

The vegetation structure did not vary significantly among sites (see Table SI - Supplementary Material for the Mantel scores). The model that best fit the abundance of all studied species included five variables: distance to the nearest bush, the number of cacti, number of bromeliads, leaf litter depth, and canopy cover

TABLE I
Species and their specific abundances of lizards sampled in five sandy coastal plains remnants on the coast of the state of Espírito Santo, southeastern Brazil.

| TAXA | Sandy coastal plains | | | | | Total |
|--|----------------------|-------|-------|-----|-----|-------|
| | PN | PCVSP | CBEPA | CBR | ISP | |
| Squamata | | | | | | |
| Diploglossidae Cope, 1864 | | | | | | |
| <i>Ophiodes cf. striatus</i> | – | – | 1 | – | – | 1 |
| Tropiduridae Bell in Darwin, 1843 | | | | | | |
| <i>Tropidurus torquatus</i> (Wied, 1820) | 258 | 178 | 225 | 125 | 95 | 881 |
| Gekkonidae Gray, 1825 | | | | | | |
| <i>Hemidactylus mabouia</i> (Moreau de Jonnés, 1818) | 15 | – | 29 | – | 1 | 45 |
| Teiidae Merrem, 1820 | | | | | | |
| <i>Ameiva ameiva</i> (Linnaeus, 1758) | 36 | 27 | 47 | 41 | 24 | 175 |
| <i>Ameivula nativo</i> (Rocha, Bergallo & Peccinini-Seale, 1997) | – | 123 | 84 | 73 | 12 | 292 |
| <i>Kentropyx calcarata</i> Spix, 1825 | – | – | – | – | 2 | 2 |
| <i>Salvator merianae</i> (Duméril & Bibron, 1839) | 1 | – | – | – | 1 | 2 |
| Liolaemidae Frost & Etheridge, 1989 | | | | | | |
| <i>Liolaemus lutzae</i> Mertens, 1938 | 2 | – | – | – | – | 2 |
| Phyllodactylidae Gamble, Bauer, Greenbaum & Jackman, 2008 | | | | | | |
| <i>Gymnodactylus darwini</i> (Gray, 1845) | 2 | 1 | – | 6 | – | 9 |
| Mabuyidae Mittleman, 1952 | | | | | | |
| <i>Brasiliscincus agilis</i> (Raddi, 1823) | 15 | 8 | 13 | 17 | 22 | 75 |
| <i>Psychosaura macrorhyncha</i> (Hoge, 1947) | 8 | 6 | 4 | 13 | 12 | 43 |
| Polychrotidae Fitzinger, 1843 | | | | | | |
| <i>Polychrus marmoratus</i> (Linnaeus, 1758) | – | 3 | – | – | – | 3 |
| Total richness | 8 | 7 | 6 | 6 | 8 | |
| Abundance | 327 | 336 | 442 | 265 | 159 | 1529 |

PN = Praia das Neves; PCVSP = Paulo Cesar Vinha State Park; CBEPA = Conceição da Barra Environmental Protection Area; CBR = Comboios Biological Reserve; ISP = Itaúnas State Park.

($R^2 = 0.62$; $F(5,14) = 4.56$; $P = 0.01$, $DF = 5$ and 14 ; $AIC = 225.17$; see Supplementary Material for scores), with bromeliads and leaf litter being the most important variables ($P = 0.004$ and 0.03 , respectively). The best model for the Teiidae included the bromeliads, leaf litter depth, and canopy cover ($R^2 = 0.4$; $F(3,16) = 3.6$; $P = 0.036$; $DF = 3$ and 16 ; $AIC = 191.62$), with bromeliads being significant ($P = 0.009$), and the others marginally

significant ($P = 0.08$ and 0.087). For Scincidae, the best fit model was marginally significant, and included the shortest plant height, the diameter of the tallest plant, the distance between bushes, the number of cacti and bromeliads, leaf litter depth, and canopy cover ($R^2 = 0.59$; $F(7,12) = 2.47$; $P = 0.08$; $DF = 7$ and 12 ; $AIC = 142$). Number of cacti and bromeliads were significant ($P = 0.03$ and 0.04 , respectively), other three variables were marginally

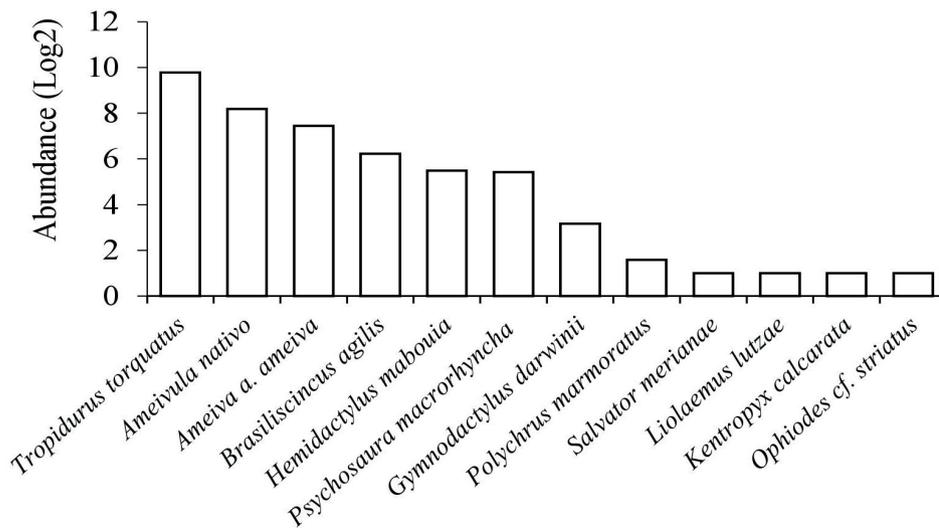


Figure 2 - Total abundance (log₂) of lizards recorded at: Itaúnas State Park; Conceição da Barra Environmental Protection Area; Comboios Biological Reserve; Paulo Cesar Vinha State Park and Praia das Neves. Species are ranked from highest to lowest abundance.

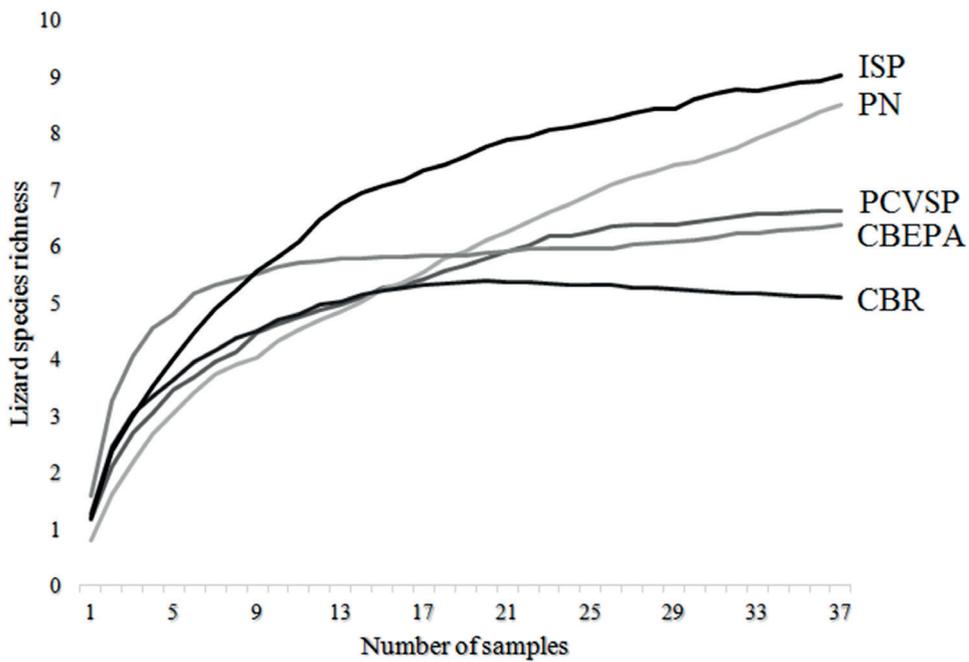


Figure 3 - Species richness curves estimated for lizards for the studied sandy coastal plains in Espírito Santo state, Brazil. ISP: Itaúnas State Park; CBEP: Conceição da Barra Environmental Protection Area; CBR: Comboios Biological Reserve; PCVSP: Paulo Cesar Vinha State Park; PN: Praia das Neves.

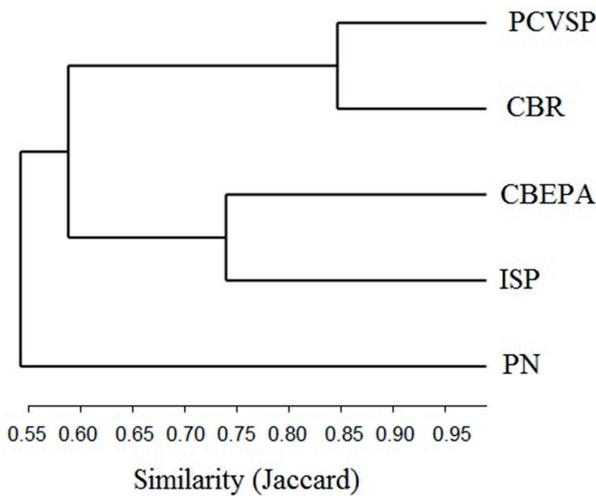


Figure 4 - Cluster analysis (Jaccard) related to the lizard species richness in the five sampled sandy coastal plains remnants on the coast of Espírito Santo state, Brazil. ISP: Itaúnas State Park; CBEPA: Conceição da Barra Environmental Protection Area; CBR: Comboios Biological Reserve; PCVSP: Paulo Cesar Vinha State Park; PN: Praia das Neves.

significant (distance between bushes $P = 0.06$; leaf litter depth $P = 0.07$; canopy cover $P = 0.09$). Plant height ($P = 0.14$) and the diameter of the tallest plant ($P = 0.11$) did not present significant p-values. The best model for the gekkonid clade (*H. mabouia* + *G. darwini*) was not statistically significant, and included the diameter of the tallest plant, and canopy and ground cover ($R^2 = 0.28$; $F(3,16) = 2.1$; $P = 0.14$; $DF = 3$ and 16 ; $AIC = 136$), although ground cover was significant ($P = 0.05$). The best model for *T. torquatus* (Tropiduridae) included the distance between bushes, the number of cacti and bromeliads, leaf litter depth, and canopy cover ($R^2 = 0.65$; $F(5,14) = 5.15$; $P = 0.007$; $DF = 5$ and 14 ; $AIC = 201$; Table SII), and canopy cover was the only variable that was non-significant ($P = 0.16$). The best model for *P. marmoratus* (Iguanidae) included plant height (shortest and tallest), the diameter of the tallest plant, leaf litter depth, and canopy cover ($R^2 = 0.71$; $F(5,14) = 6.7$; $P = 0.002$; $DF = 5$ and 14 ; $AIC = 29.25$; Table SII). Significant values were obtained only for plant height ($P = 0.0002$) and leaf litter depth ($P = 0.005$).

DISCUSSION

The lizard species richness recorded in the present study was relatively high in comparison with similar studies based on a Rapid Assessment Program (RAP) approach (Rocha et al. 2014). Our study periods were longer and sampling effort was more intense, however, which contributed to the registration of four additional species, *O. cf. striatus*, *S. merianae*, *L. lutzae* and *P. marmoratus*. While at least two of these species (*S. merianae* and *P. marmoratus*) are relatively common on Brazilian sandy coastal plains (Castro and Silva-Soares 2016), our results highlight the importance of longer sampling periods to ensure a reliable record of the composition of lizard communities. In fact, our accumulation curves revealed that our sampling effort was essential to the analysis of the assemblages (see Figure 3), even though this analysis indicated that we did not record the total number of species known to occur in the coastal ecosystems of Espírito Santo (e.g., *Eubleopis gaudichaudii*, *Iguana iguana*, *Dactyloa punctata*, and *Strobilurus torquatus*: Castro and Silva-Soares 2016, Oliveira and Castro 2017).

As expected, we recorded some widely-distributed species (e.g., *T. torquatus*, *A. ameiva*, *B. agilis*, and *P. macrorhyncha*), which were found at all sites, and three (*L. lutzae*, *P. marmoratus* and *K. calcarata*) that were restricted to a single site. The record of *L. lutzae* is the result of an experimental introduction at Praia das Neves (Soares and Araújo 2008). This species is endemic to the coast of Rio de Janeiro state, between Marambaia and Cabo Frio (Rocha et al. 2009). At Praia das Neves, *L. lutzae* is associated with the halophilic-psamophilic vegetation in the vegetation zone, the same type of habitat inhabited by its natural populations in Rio de Janeiro (Rocha 1991, Rocha et al. 2009). *Polychrus marmoratus* is common in forested environments, and is widely distributed in the Amazon and Atlantic Forests (e.g., Ávila-Pires 1995, Castro

and Silva-Soares 2016). *Kentropyx calcarata* is also widely-distributed in the Amazon and Atlantic Forests (e.g., Ávila-Pires 1995, Sousa and Freire 2008), although Linhares, in the Rio Doce basin of Espírito Santo represents the southern limit of its range (Rocha 1998, Rocha et al. 2014).

We found no significant variation in the abundance of species among sites. As expected, only a few of the species (*T. torquatus*, *A. nativo* and *A. ameiva*) dominated lizard abundance, while most other species are rare. This is a typical pattern in most ecological communities (e.g. Gaston and Blackburn 2000). In the specific case of lizard communities on sandy coastal plains, Rocha and Bergallo (1997) suggested that this pattern is probably related to the structure of these environments, and their exposure to high levels of solar radiation, which favors the occurrence of heliophilous organisms, such as lizards.

Species richness did not vary significantly among mesohabitats, although the lowest richness and abundance were recorded in the beach vegetation zone. By contrast, abundance was highest in the shrubby vegetation and open

Clusia zones (see Table II). The occurrence and distribution of lizard species typically reflect their ecological requirements and capacity for the exploitation of resources. In the present case, the herbaceous, shrubby or arboreal vegetation (Rocha and Bergallo 1997), and the occurrence and density of cacti and/or bromeliads are crucial as sites for thermoregulation (Vrcibradic and Rocha 2002). Some microhabitats are also fundamental for foraging and shelter (Rocha and Vrcibradic 1998). These factors determine the most favorable sites in each mesohabitat, according to the ecophysiology and behavior of each species. These factors are important determinants of the spatial structure of animal communities worldwide (e.g. Tilman 1999, Cottenie 2005, Ackerly et al. 2006).

Habitat structure is known to determine the variation in the composition of the communities of sandy coastal ecosystems (e.g. Rocha and Bergallo 1997), and our results indicate an association of specific taxa with specific mesohabitats and microhabitats. While the variables tested did not explain the composition of the communities, bromeliads were the most important microhabitats.

TABLE II

Abundance of each lizard species using the different mesohabitats at: Praia das Neves, Paulo Cesar Vinha State Park, Conceição da Barra Environmental Protection Area, Comboios Biological Reserve and Itaúnas State Park.

| Lizard species | Beach zone | Shrubby zone | Open <i>Clusia</i> | Forest |
|---------------------------------|------------|--------------|--------------------|--------|
| <i>Ophiodes cf. striatus</i> | 0 | 0 | 0 | 1 |
| <i>Tropidurus torquatus</i> | 9 | 207 | 663 | 2 |
| <i>Hemidactylus mabouia</i> | 2 | 21 | 14 | 8 |
| <i>Ameiva ameiva</i> | 1 | 37 | 137 | 0 |
| <i>Ameivula nativo</i> | 3 | 97 | 192 | 0 |
| <i>Salvator merianae</i> | 0 | 0 | 0 | 1 |
| <i>Liolaemus lutzae</i> | 2 | 0 | 0 | 0 |
| <i>Kentropyx calcarata</i> | 0 | 0 | 0 | 2 |
| <i>Gymnodactylus darwini</i> | 0 | 0 | 1 | 2 |
| <i>Brasiliscincus agilis</i> | 0 | 51 | 24 | 0 |
| <i>Psychosaura macrorhyncha</i> | 0 | 29 | 14 | 0 |
| <i>Polychrus marmoratus</i> | 0 | 0 | 0 | 3 |

TABLE III
Mesohabitats used by lizard species in sampled sandy coastal plains of Espírito Santo state.

| TAXON | Sandy coastal plain | | | | |
|--|---------------------|----------|----------|----------|-------|
| | PN | PCVSP | CBEPA | CBR | ISP |
| Squamata | | | | | |
| Diploglossidae Cope, 1864 | - | - | RF | - | - |
| <i>Ophiodes cf. striatus</i> | | | | | |
| Family Tropiduridae Bell in Darwin, 1843 | | | | | |
| <i>Tropidurus torquatus</i> (Wied, 1820) | BV/SV/OC/RF | BV/SV/OC | BV/SV/OC | BV/SV/OC | BV/OC |
| Family Gekkonidae Gray, 1825 | | | | | |
| <i>Hemidactylus mabouia</i> (Moreau de Jonnés, 1818) | BC/SV | - | OC | - | OC |
| Family Teiidae Merrem, 1820 | | | | | |
| <i>Ameiva ameiva ameiva</i> (Linnaeus, 1758) | BV/OC | OC | BV/SV/OC | BV/OC | BV/OC |
| <i>Ameivula nativo</i> (Rocha, Bergallo & Peccinini-Seale, 1997) | - | BV/OC | BV/SV/OC | SV/OC | SV/OC |
| <i>Sabvator merianae</i> Duméril & Bibron, 1839 | OC | - | - | - | RF |
| Family Liolaemidae Frost & Etheridge, 1989 | | | | | |
| <i>Liolaemus lutzae</i> Mertens, 1938 | BV | - | - | - | - |
| Family Phyllodactylidae Gamble, Bauer, Greenbaum & Jackman, 2008 | | | | | |
| <i>Gymnodactylus darwini</i> (Gray, 1845) | RF | RF | - | OC | - |
| Family Mabuyidae Mittleman, 1952 | | | | | |
| <i>Brasiliscincus agilis</i> (Raddi, 1823) | SV/OC | OC | SV/OC | OC | SV/OC |
| <i>Psychosaura macrorhyncha</i> (Hoge, 1947) | SV/OC | OC | SV/OC | OC | SV/OC |
| <i>Kentropyx calcarata</i> Spix, 1825 | - | - | - | - | RF |
| Family Polychrotidae Fitzinger, 1843 | | | | | |
| <i>Polychrus marmoratus</i> (Linnaeus, 1758) | - | RF | - | - | - |

PN = Praia das Neves; PCVSP = Paulo Cesar Vinha State Park; CBEPA = Conceição da Barra Environmental Protection Area; CBR = Comboios Biological Reserve; ISP = Itanhas State Park; BV = beach vegetation zone; SV = Shrubby vegetation zone; OC = open *Clusia* zone and RF = restinga forest.

This association is probably at least partly associated with causal factors such as the habitats in which these species forage and the principal concentrations of bromeliads. In general, teiid lizards, such as *Ameivula nativo*, move through the habitat, foraging actively at the edge of the vegetation or in the bushes, while *Ameiva ameiva* tends to forage actively in denser shrubby vegetation (Araújo 1984, Rocha and Bergallo 1997). Shrubby vegetation on sandy coastal plains tends to have an abundance of bromeliads, and this habitat provides cover from predators, especially those for the juveniles (*A. ameiva*) and the smaller-bodied adults (*A. nativo*). The leaf litter found under bromeliads also harbors an abundant fauna of invertebrates and small vertebrates, providing potential prey for these lizards (Araújo 1984). This association is clearest, for example, in open *Clusia* mesohabitats, which has the greatest diversity and density of bromeliads in the coastal restinga (Rocha-Pessoa et al. 2008), and in our study, the greatest abundance of lizards. It thus seems likely that bromeliads represent important microhabitats for the structuring of the lizard communities on the sandy coastal plains, in particular teiids.

In our study, while the vegetation structure did not vary significantly among sites, bromeliads were the variable most closely associated with species richness and abundance. The strong association between the species composition and habitat structure indicates that local environmental factors have a major influence on the composition of communities (Parris 2004). Over geological time, the successive transgressions and regressions of sea levels determined the topography and vegetation structure of these sandy coastal plains (see Cerqueira 2000, Rocha et al. 2003), which may have been fundamental to processes such as speciation and extinctions, and in particular the formation of species assemblage (see Losos 1994). In this context, evolutionary and historical processes, combined with local ecological factors,

have determined the present structure of the lizard communities found on these sandy coastal plains.

We found that the different lizard assemblages on the sandy coastal plains of Espírito Santo state are similar in their structure (species richness and composition), with their variations reflecting differences in the local environment. These findings have important implications for the conservation of these lizard assemblages, at different scales. The occurrence of species in different mesohabitats reinforces the importance of integrated conservation measures that prioritize the management of the different mesohabitats found within the ecosystem. Otherwise, the selective suppression of specific portions (mesohabitats) of the coastal plain would have an immediate impact on the structure of the local lizard assemblages.

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SUPPLEMENTARY MATERIAL

Table SI - Mantel values for comparisons between pairs of restingas in relation to the habitat structure.

Table SII - Best models results relating lizard abundance and habitat structure.