



ECOSYSTEMS

The role of spatial heterogeneity in diversity of squamate reptiles in the Atlantic Forest highlands of southeastern Brazil

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Abstract: Spatial heterogeneity of vegetation is considered to be one of the most important factors that can influence species richness in a region and, therefore, an important driver for species diversity. Here, we investigate how squamate diversity varies throughout a heterogeneous area in southeastern Atlantic Forest. Our sampling site corresponded to a mosaic of forest and open fields in Curucutu nucleus, Serra do Mar State Park, São Paulo State, Southeastern Brazil. Species diversity varied throughout the mosaic in terms of species composition and relative abundance, with some species being clearly associated with a particular physiognomy. However, a decrease is observed in species richness in forest, after the rarefaction method is applied, showing that when the abundance effect is excluded, only species composition differed between physiognomies. On the other hand, both space and environmental heterogeneity were associated with diversity and distribution of squamates. Our results emphasize the importance of environmental heterogeneity, as well as the influence of the spatial location of the sample units, in structuring squamate diversity in a highland assemblage from the Atlantic Forest.

Key words: Atlantic forest, biodiversity, heterogeneity, distribution, squamata.

INTRODUCTION

Spatial heterogeneity of vegetation is considered to be one of the most important factors that can influence species richness in a region, and many studies have found a positive relationship between these two aspects (*see review by Tews et al. 2004*). Apparently, heterogeneity would have a positive effect on richness by allowing more species to coexist when compared to more homogeneous environments (Pianka 1966, Cardoso et al. 1989), also influencing the way species are distributed in the environment (Tews et al. 2004). Furthermore, spatial heterogeneity of vegetation is seen as an important factor on distribution and diversity of squamate (Garda et al. 2013, Dias & Rocha 2014, Lewin et al. 2016).

Snakes and lizards belong to order Squamata and are closely related, configuring a monophyletic group (Apesteguía & Zaher 2006, Caldwell et al. 2015). These organisms are good models for the study of community structure, especially regarding diversity and distribution among particular environments, once these animals share available resources in environment (*e.g.* habitat, diet), that are used in diversified ways (Nogueira et al. 2005, Hartmann & Marques 2005, Luiselli 2006). Moreover, in some cases, spatial distribution is associated with particular habitats or microhabitats, and habitat requirements are often responses to phylogenetic constraints (Martins et al. 2001).

The Atlantic Forest, one of the most diverse and threatened biomes, currently has about

12% of its original coverage formally protected (Fundação SOS Mata Atlântica 2019). Still, Serra do Mar, a mountain range located in southeastern Brazil, is one of the five centers of endemism (da Silva & Casteleti 2003) of this biome, houses about 36% of the original vegetation, and constitutes one of the largest and best-connected fragments (Ribeiro et al. 2009). This mountain range presents high environmental heterogeneity, along its altitudinal and latitudinal variation (Secretaria de Estado do Meio Ambiente 2006). This heterogeneity is composed not only by forested and shrubby physiognomies (“restingas”), but also by open fields, that, in some areas, date back about 30,000 years (Usteri 1911, Garcia & Pirani 2005, Secretaria de Estado do Meio Ambiente 2006).

Herein we explore the diversity of squamate in a heterogeneous area (a mosaic of physiognomies) in southeastern Atlantic Forest, including one of the last remnants of the enclave of open fields (Usteri 1911, Garcia & Pirani 2005). Our aims were to investigate how the diversity and distribution of squamate vary in a heterogeneous environment and if it is correlated with geographic location of sampling units, or type of physiognomy.

MATERIALS AND METHODS

Taxon and study area

Among squamate, we sampled only snakes and lizards. Amphisbaenians were not included in our analyses in view of their restrict fossorial habits and difficulties to sample (Vanzolini 1991, Kearney 2003).

Our sampling area was a heterogeneous area of Atlantic Forest within the Curucutu nucleus (CTU) of Serra do Mar State Park (Figure 1). The CTU is located in an area between the coast and highlands in eastern São Paulo State, in southeastern Brazil (23°59'9" S, 46°44'35" W).

It is a mosaic of physiognomies including cloud forests and open fields of vegetation. This last one, is a natural physiognomy was historically common in highland areas of southeastern Brazil - its presence dates back to almost 30,000 years in the region - (Usteri 1911, Garcia & Pirani 2005, Pessenda et al. 2009). The highland cloud forests that intersperse with open fields are characterized by its small size, twisted appearance, high canopy overlap, with frequent presence of epiphytic and soil bromeliads (Garcia & Pirani 2005). On the other hand, the open areas can be “cleared”, presenting isolated grasses and shrubs, turning into “dirty fields”, near to cloud forest (Garcia & Pirani 2005). The mosaic formed by these two physiognomies was the place chosen for our sampling. The elevation of the CTU varies from 700 to 870 m asl, and it experiences one of the highest amounts of rainfall in this range of Atlantic forest (annual average between 1.600 mm to 2.200 mm; and temperature varying seasonally from 12°C to 28°C, average), with the frequent formation of mist in fields and forests (Monteiro 1973, Batista 2017).

Sampling strategy

We carried out field sampling over 31 months, between February of 2015 and August of 2017, with 25 months of regular sampling (six continuous days/month – June of 2015 to June of 2016, and September of 2016 to August of 2017) and six months of irregular sampling (three continuous days/month – February to May of 2015 and July and August of 2016). We used the following methods: (1) pitfalls traps with drift fences (PT; Campbell & Christman 1982); (2) funnel traps (FT; Fitch 1987); (3) time-constrained searches (TCS; Martins & Oliveira 1999); and (4) accidental encounters (AE; Campbell & Christman 1982).

Our pitfall traps included 12 lines of five 100-L buckets and drift fences (1-meter high

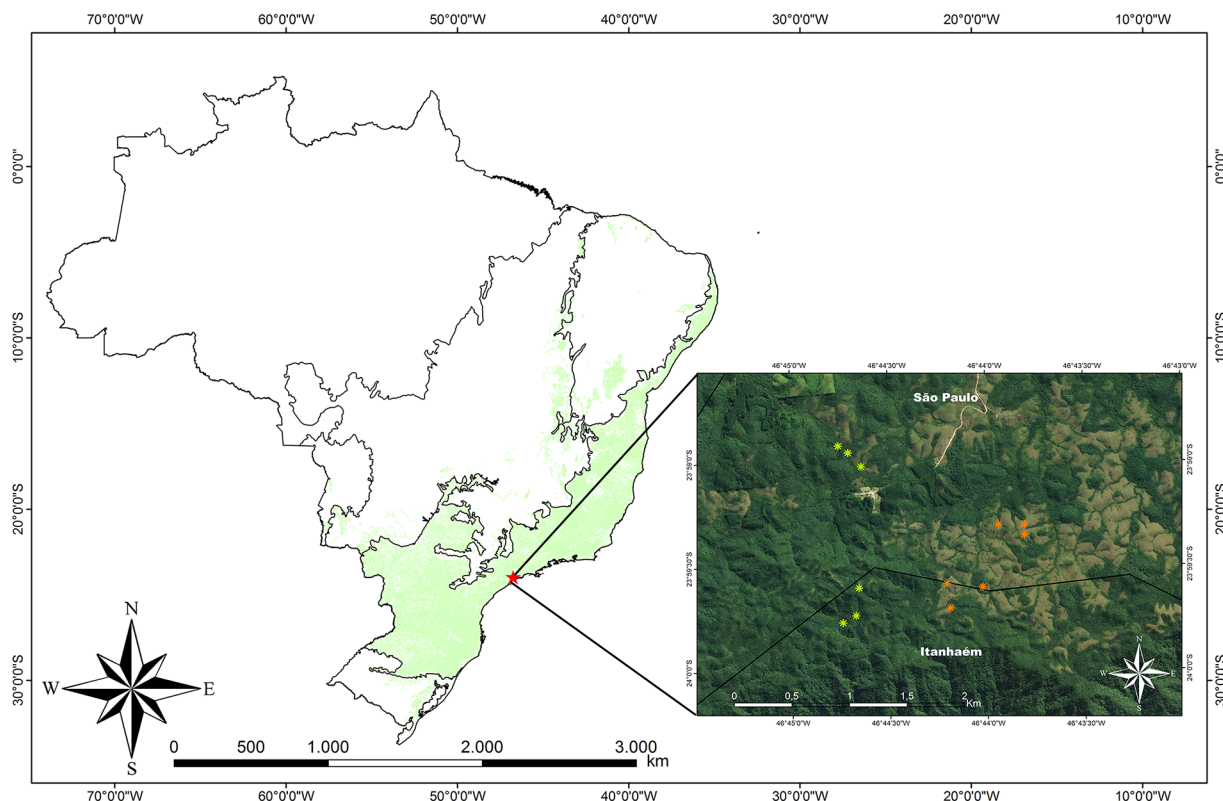


Figure 1. Location of the sampled area. Remnants of Atlantic Forest are in green. Red star represents the location of Curucutu nucleus. The mosaic open fields and cloud forest physiognomies of Curucutu nucleus, and the distribution of sample units, are shown in the detail to the right.

and 40-meters long), with spacing of 10m between each bucket. Six lines were installed in each physiognomy. We installed two funnel traps along the drift fence of each pitfall trap line for a total of 24 funnels with 12 in each physiognomy. Lines of pitfalls and funnel traps were arranged in two sets spaced 500-m apart within each physiognomy. The choice of pitfall traps was based on ease of access, observing a minimum distance of 100m from the opposite physiognomy.

Time-constrained searches were performed along 12 transects of about 200 m each, six in each physiognomy (cloud forest and field). The choice of transects was made according to the same criteria for the choice of pit falls location. Transects were grouped into two sets in each physiognomy, distant at least 500 m from each.

On each sampling day, four researchers sampled, in pairs, each physiognomy simultaneously. Visual time-constrained search was carried at the transects chosen out for about two hours, between 19h and 21h. This interval was chosen based on literature (e.g. Sazima & Haddad 1992, Trevine et al. 2014).

We considered individuals sighted and/or collected during the sampling inside the CTU. All four methods were applied for the 25 months of regular sampling, whereas only TCS and AE were applied during irregular sampling. In accordance to the authorizations granted (ICMBio; Permit number 44913-3; COTEC; Permit number 260108 – 006.928/2014; CEUAIB n. 5283280415), up to 10 individuals of each species ($n = 98$) were collected, euthanized (according to Conceia 2018), and deposited in the Herpetological collection

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Analyses

We implemented Sanders rarefaction (Sanders 1968) to compare species richness and dominance between forest and open fields. Since the number of species recorded is related to the number of individuals sampled, and the number of individuals recorded in each physiognomy differed (Melo et al. 2003), the rarefaction method allowed us to compare richness and dominance for the same sampling size (number of individuals), which in our case was $n = 27$ (smaller number registered in one of physiognomies). Analyses were performed in EcoSim 7.0 (Gotelli & Entsminger 2016). We also performed a contingency analysis using the Kolmogorov test for two samples to verify if the species abundance patterns differed between the two physiognomies (Zar 2010).

In order to explore the effects of physiognomy and geographic location of each sampling unit on species composition and abundance of snakes and lizards, we performed a Mantel test with two dissimilarity matrices. The first matrix was calculated by applying the Bray Curtis index, considering records of abundance of species from all methods (PT, FT, TSC and AE). For this, we considered each PT/FT point as a sample unit ($n = 12$), and included all specimens recorded by TCS and AE inside a 100 m radius from PT/FT points (Figure 2 and Table I). Individuals found outside this radius were excluded from these analyses. The second matrix corresponded to Euclidean distances among coordinates of each sample unit. We also implemented nonmetric multidimensional scaling (NMDS) to ordinate our sample units in two dimensions using the Bray-Curtis dissimilarity coefficient, because

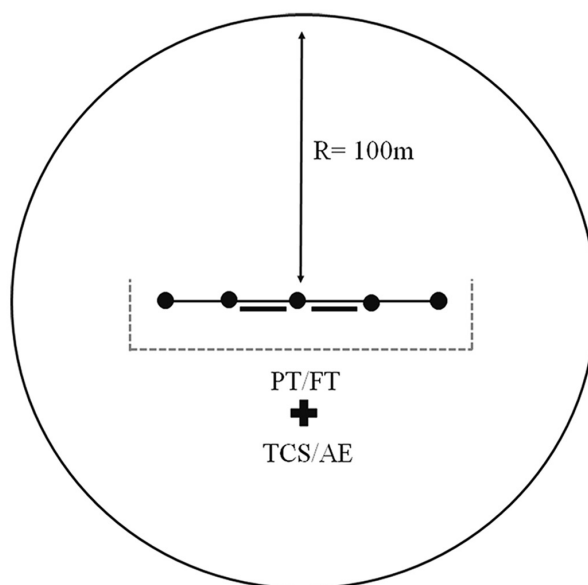


Figure 2. Diagram showing the spatial conformation of our sample units.

of the quantitative nature of our data (Gotelli & Ellison 2004). To highlight the distribution along the Atlantic Forest and other biomes, we classified the species by geographic distribution (species restricted to the Atlantic Forest = AF and species broadly distributed in Brazil, with records outside of the Atlantic Forest Domain = BR). All analyses described above, with the exception of rarefaction, were conducted using the Vegan Package (Oksanen et al. 2017) in R software (R Core Team 2016).

RESULTS

Fourteen snakes and seven lizard species were recorded (Table I). Two distribution patterns were identified from the species composition of squamate of CTU: (1) species restricted to the Atlantic Forest (southeastern, northeastern and/or southern Brazil) (AF); and (2) species broadly distributed in Brazil, with records outside of the Atlantic Forest Domain (BR) (Marques et al. 2019, Uetz et al. 2019). Almost three times more individuals were recorded from forest than open fields (Table I).

Table I. Squamate reptile composition of Curucutu nucleus, sampling method, distribution (according to Guedes et al. 2018), and abundance in forest and open fields individuals collected in sampling units and used Mantel test they are bold; see details on text. Method: PT: Pitfalls traps with drift fences, FT: Funnel traps, TCS: Time-constrained searches, AE: accidental encounters. Geographic distribution: AF: species restricted to the Atlantic Forest (southeastern, northeastern and/or southern Brazil), BR: species broadly distributed in Brazil, with records outside of the Atlantic Forest Domain.

Family/ Species	Method	Distribution	Forests	Open Fields
Anguidae				
<i>Ophiodes fragilis</i> (Raddi, 1826)	PT	BR		1
Gymnophthalmidae				
<i>Cercosaura quadrilineata</i> Boettger, 1876	PT, TCS	AF		5
<i>Cercosaura schreibersii</i> (Wiegmann, 1834)	AE	BR	1	
<i>Colobodactylus taunayii</i> Amaral, 1933	PT, FT	AF	18	6
<i>Placosoma glabellum</i> (Peters, 1870)	PT, FT	AF	8	
Leiosauridae				
<i>Enyalius iheringii</i> Boulenger, 1885	PT, FT, TCS, AE	AF	18	1
Teiidae				
<i>Salvator merianae</i> (Dumeril & Bibron, 1839)	FT, AE	BR	1	1
Colubridae				
<i>Chironius bicarinatus</i> (Wied-Neuwied, 1820)	PT, FT, AE	BR	1	2
<i>Chironius exoletus</i> (Linnaeus, 1758)	FT, AE	BR	2	1
Dipsadidae				
<i>Dipsas alternans</i> (Fischer, 1885)	AE	AF	1	
<i>Echinanthera amoena</i> (Jan, 1863)	AE	AF	1	
<i>Taeniophallus bilineatus</i> (Fischer, 1885)	FT, AE	AF	1	
<i>Taeniophallus persimilis</i> (Cope, 1869)	PT, TSC, AE	AF	2	
<i>Erythrolamprus aesculapii</i> (Linnaeus, 1758)	AE	BR	4	
<i>Erythrolamprus miliaris</i> (Linnaeus, 1758)	PT, FT, AE	BR	3	2
<i>Philodryas patagoniensis</i> (Girard, 1858)	FT, TCS, AE	BR		6
<i>Taeniophallus affinis</i> (Günther, 1858)	PT	BR	1	
<i>Xenodon neuwiedii</i> (Günther, 1863)	FT, AE	BR	3	
Elapidae				
<i>Micrurus corallinus</i> (Merrem, 1820)	PT, AE	BR	3	
Viperidae				
<i>Bothrops jararaca</i> (Wied-Neuwied, 1824)	PT, TCS, AE	BR	6	2
<i>Bothrops jararacussu</i> Lacerda, 1884	AE	BR	1	
Total number of individuals			75	27

Species diversity differed between physiognomies when considering species composition, richness and absolute abundance (Table I). Ten species were recorded in open fields, whereas 19 species were recorded in forest (Table II). Furthermore, relative abundance of species differ significantly between physiognomies (Kolmogorov test; $D = 0.44$, $p = 0.05$) (Figure 3).

However, the rarefaction method estimated from eight to 13 species in forest for a sampling of $n = 27$ individuals (95% confidence interval, average = 10.3), showing that when the abundance effect is excluded, only species composition differed between physiognomies. *Philodryas patagoniensis* and *Colobodactylus taunayii* were equally dominant in open fields (each representing 22.2 % of total number of individuals), whereas *C. taunayii* and *Enyalius iheringii* were dominant in the forests (24.7 % each). When rarefied to 27 individuals, dominance in forest did not differ from that of open fields (18 to 40%, 95% confidence interval; average = 28.6; Table II).

Mantel tests showed a positive correlation between dissimilarity of species abundance and geographic location of our sampling units ($r = 0.59$, $p < 0.05$). NMDS analysis showed stabilization in a three-dimensional solution (k

= 3), with a good ordination pattern with Stress = 0.07, since stress values below 0.1 correspond to a reliable ordination (Clarke 1993). Samples from open fields and forest did not overlap in the ordination space of first two dimensions of NMDS, with some species being more associated with one physiognomy than the other (Figure 4).

DISCUSSION

The way as assemblages are structured can be influenced by historical and/or ecological factors, including environmental heterogeneity (Cadle & Greene 1993, Levin 2000). Here, we find a squamate assemblage correlated with environmental heterogeneity and geographical location of the sample units. Thus, we argue that not only the physiognomies mosaic configuration found in our study area is a determining factor in the diversity, but also the spatial conformation of the sample units, that is, their geographical location along this area.

We recorded 21 species for the physiognomies sampled in CTU. Most species are common and relatively abundant in Atlantic Forest and some have wide geographic distributions, including other biomes (see Guedes et al. 2018). May (1975)

Table II. Diversity of squamate reptiles distributed in the studied physiognomies (open fields and forest) in Curucutu nucleus.

RAREFACTION	PHYSIOGNOMY	
	OPEN FIELDS	FOREST
Number of individuals	27	75
Observed richness	10	19
Estimated richness ($n = 27$)	-	10.3 (8-13)
Dominant species	<i>P. patagoniensis</i> / <i>C. taunayii</i>	<i>C. taunayii</i>
Observed dominance ($n = 73$)	22.2%	24.7%
Estimated dominance ($n = 27$)	-	28.6% (18 - 40%)

suggested that patterns of relative abundance are among the best measures of diversity, while Magurran (2004) proposed that richness and dominance of the most abundant species are among most comprehensive way to compare species diversity. After rarefaction considering the same number of sampled individuals ($n = 27$), the diversity of the two physiognomies had similar richness and dominance and differed only in species composition. This is expected, because the number of species found is directly

related to the number of individuals sampled (Melo et al. 2003). Furthermore, the affinity of some species to particular habitats probably drove this difference (Luiselli 2006).

The ordination obtained by NMDS revealed a structured distribution between the physiognomies, since there are more species associated with one physiognomy than species occurring in both. Thus, the conformation of this mosaic (*i.e.* its environmental heterogeneity) should also influence the distribution of

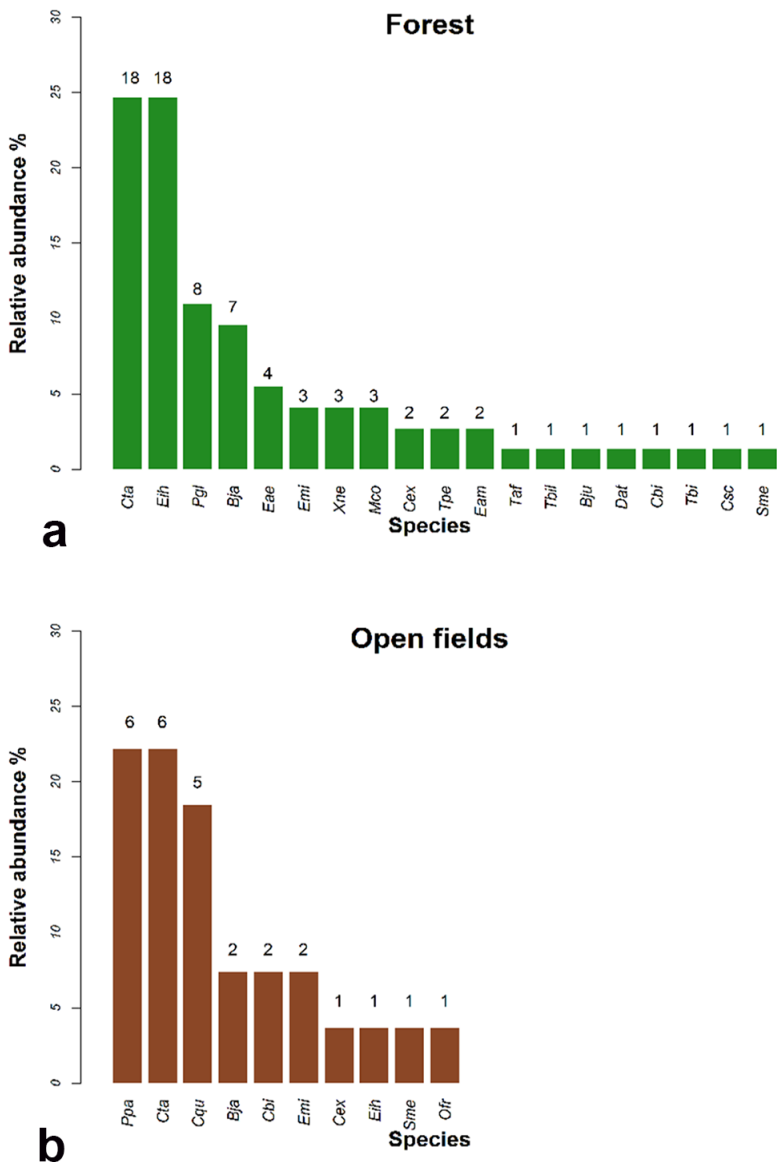


Figure 3. Relative abundance (%) of species sampled in forest (a) and open field (b) physiognomies. Absolute values for each species are shown above each bar. Bja (*Bothrops jararaca*); Bju (*Bothrops jararacussu*); Cbi (*Chironius bicarinatus*); Cex (*Chironius exoletus*); Cta (*Colobodactylus taunayii*); Csc (*Cercosaura schreibersii*); Cqu (*Cercosaura quadrilineata*); Dat (*Dipsas alternans*); Eae (*Erythrolamprus aesculapii*); Eih (*Enyalius iheringii*); Emi (*Erythrolamprus miliaris*); Eam (*Echianthera amoena*); Mco (*Micrurus corallinus*); Ofr (*Ophiodes fragilis*); Ppa (*Philodryas patagoniensis*); Pgl (*Placosoma glabellum*); Taf (*Taeniophallus affinis*); Tbi (*Taeniophallus bilineatus*); Tpe (*Taeniophallus persimilis*); Sme (*Salvator merianae*); Xne (*Xenodon newwiedii*).

squamate (see Martins et al. 2001, Garda et al. 2013). However, it must be considered that some species sampled here constitute samples from one or two records.

Studies in Amazon have found squamate assemblages responding to environmental heterogeneity in a variety of ways. The diversity of lizards of an Amazonian community seems to be strongly influenced by the microhabitat structure, although the abundance of species responds more local factors, spatially structuring their variation (Garda et al. 2013). Similarly, a study on “restinga” of Atlantic Forest, from northeastern Brazil, point aspects of vegetation as determinants of lizard richness and abundance (Dias & Rocha 2014). In fact, the vegetation structure (i.e. vegetation height and form, or presence of open areas spots) is indicated as a factor driving squamate diversity,

in diverse tropical forest environments (e.g. Pianka 1966, Garden et al. 2007), as well as for other ectothermic animals (e.g. Cardoso et al. 1989, Keller et al. 2009).

Historically, open fields, such as those of the present study, were more widely distributed in south and southeast from Brazil (Usteri 1911, Behling 2002, Garcia & Pirani 2005, Pessenda et al. 2009). Thus, their reduction may have had an insularization effect, resulting in the loss of species in open fields. However, these fields also seem to influence the structure of this community, since the NMDS ordination revealed two groups of samples according to physiognomy. *Philodryas patagoniensis* is a species highly associated to open areas in the biomes where it occurs (Sazima & Haddad 1992, Hartmann & Marques 2005), and its occurrence in other open fields areas of the

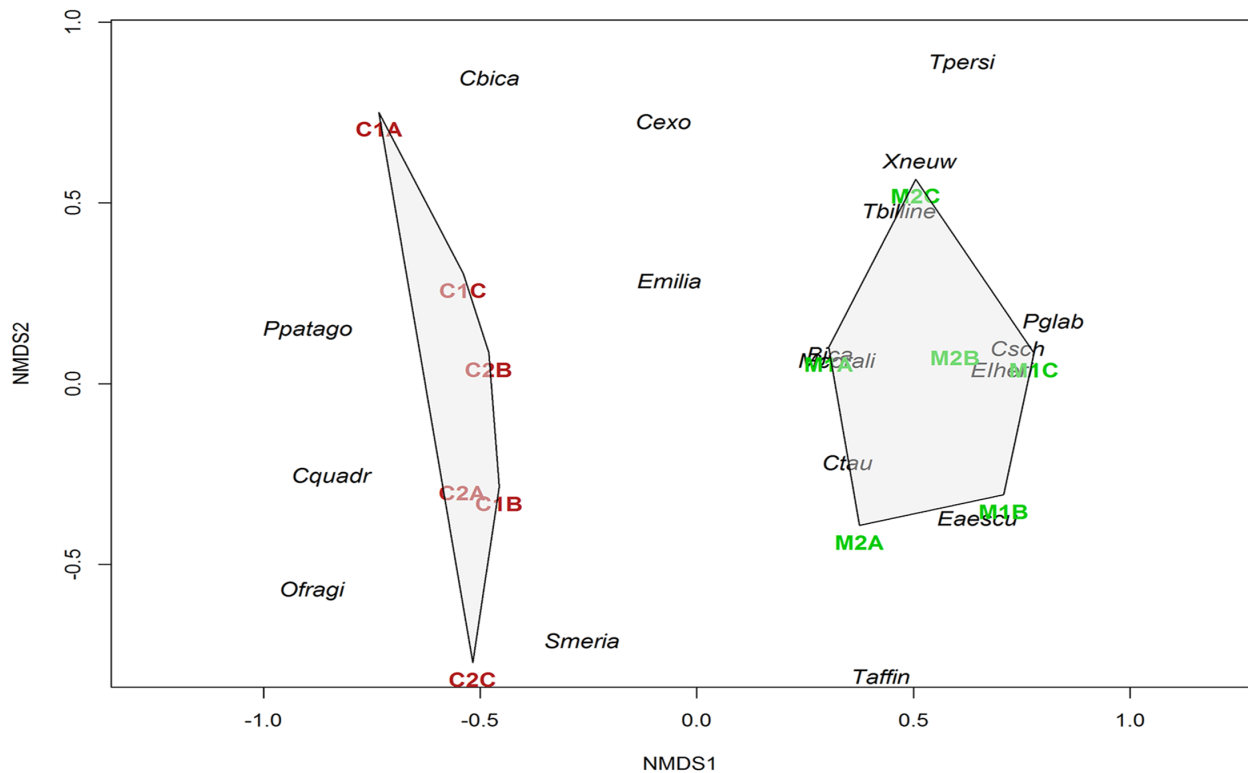


Figure 4. Ordination of nonmetric multidimensional scaling (NMDS; Stress = 0.07) for the squamate reptiles distributed in two physiognomies in the Curucutu nucleus. Sampling units of open fields in brown, and sampling units of forest in green, grouped by gray polygons.

Atlantic Forest, next to the CTU is also reported (Marques et al. 2009). Apparently, these open fields inside Atlantic forest can be function as refuges for this species, since these areas were widely distributed and connected with current savannas of the Cerrado (Behling 2002).

Our results evidence a clear influence of environmental heterogeneity in structuring squamate assemblages from the highlands of the Atlantic Forest. Thus, in the mosaic of physiognomies of the sampled area, environmental heterogeneity and spatial location were both important in structuring squamate assemblages, as previously observed for squamate reptiles (e.g. Marques et al. 2009, Garda et al. 2013, Dias & Rocha 2014) and other animal groups (see Tews et al. 2004). Although open fields have been reduced to small spots in the Atlantic Forest as whole, these open areas increase the local squamate diversity in such mosaics of forests and natural open fields.

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SFB and OAVM conceived the ideas and designed the methods; SFB collected the data; SFB and RJS analyzed the data; OAVM and RJS provided the funding. The original draft of the manuscript was written by SFB. All authors considerably improved the manuscript, contributed critically to the drafts, and approved the final version.

