

Ecomorphometric structure of Restinga da Marambaia lizard community, Rio de Janeiro, southeastern Brazil

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ABSTRACT. In restinga areas of Marambaia, Rio de Janeiro, we recorded nine species of lizards, grouped in four families. The morphometric analysis suggested an invasion-structured pattern, with two distinct groups of species in the community: the “ground-runners”, composed of animals with robust bodies and long limbs, represented by *Tropidurus torquatus* (Wied, 1820), *Ameiva ameiva* (Linnaeus, 1758), *Liolaemus lutzae* Mertens, 1938, *Cnemidophorus littoralis* Rocha, Araujo, Vrcibradic & Costa, 2000 and *Tupinambis merianae* (Duméril & Bibron, 1839); and the “hiders”, composed of small-bodied animals with short limbs, represented by *Hemidactylus mabouia* (Moreau de Jonnès, 1818), *Gymnodactylus darwinii* (Gray, 1845), *Mabuya agilis* (Raddi, 1823) and *M. macrorhyncha* Hoge, 1947. The morphological relationships within the restinga lizard community reflect the influence of the habitat physical structure: bromeliad availability and other refugia, used by the “hiders”, and the distribution of open areas, used by the “ground-runners”. Our results also indicate that the restingas hold “ecomorphological spaces” (vacant niches) available for occupation by additional lizard species.

KEY WORDS. Atlantic Forest; community structure; morphometry; vacant niche.

RESUMO. **Estrutura ecomorfométrica da comunidade de lagartos da Restinga da Marambaia, Rio de Janeiro, sudeste do Brasil.** Em áreas de restinga da Marambaia, Rio de Janeiro, foram registradas nove espécies de lagartos, pertencentes a quatro famílias. A análise morfométrica sugeriu um padrão de estruturação por invasão, com dois grupos distintos de espécies compondo a comunidade: os “corredores de chão”, formado pelos animais de corpo mais robusto e membros mais longos, representados por *Tropidurus torquatus* (Wied, 1820), *Ameiva ameiva* (Linnaeus, 1758), *Liolaemus lutzae* Mertens, 1938, *Cnemidophorus littoralis* Rocha, Araujo, Vrcibradic & Costa, 2000 e *Tupinambis merianae* (Duméril & Bibron, 1839); e os “escondedores”, reunindo lagartos de menor tamanho e membros mais curtos, representados por *Hemidactylus mabouia* (Moreau de Jonnès, 1818), *Gymnodactylus darwinii* (Gray, 1845), *Mabuya agilis* (Raddi, 1823) e *M. macrorhyncha* Hoge, 1947. As relações morfométricas dentro da comunidade de lagartos de restinga da Marambaia espelham a influência da estrutura física do habitat (habitat estrutural): a disponibilidade de bromélias e de outros locais para esconder, importantes para os lagartos “escondedores”, assim como a distribuição de áreas abertas para os “corredores de chão”. Nossos resultados também indicam que as restingas apresentam “espaços ecomorfológicos” disponíveis (níchos vagos) para ocupação por espécies adicionais de lagartos.

PALAVRAS-CHAVE. Estrutura de comunidades; Floresta Atlântica; morfometria; nicho vago.

Morphology of animal species can be used to describe and compare communities, based on the premise that adaptations of organisms reflect their ecological relationships. If environment imposes constraints on the adaptation of organisms and these are expressed simultaneously in their morphology and ecology, then morphological comparisons of sets of coexisting species should also have predictable ecological properties (KARR & JAMES 1975). In the ecomorphological approach, the “morphological space” is mapped closely into ecological space (RICKLEFS & TRAVIS 1980). There are some classical examples of

studies of vertebrate communities demonstrating this assumption: HESPENHEIDE (1971, 1973), CODY & MOONEY (1978), and RICKLEFS & TRAVIS (1980), working with birds; FINDLEY (1973, 1976) with bats, and RICKLEFS *et al.* (1981) and IRSCHICK *et al.* (1997), studying lizards.

Correlations among habitat structure, ecology and morphology of coexisting lizard species are well documented in MOERMOND (1979a, b, 1986), POUNDS (1988), and IRSCHICK & LOSOS (1999). Relative leg lengths are strongly correlated with habitat use and head lengths correlated with prey size (PIANKA 1969,

PIANKA & PARKER 1972, PIANKA & PIANKA 1976). However, despite suggestions that space usage is a stronger factor (more than food usage) in determining the structure of lizard communities (RICKLEFS *et al.* 1981, ARAÚJO 1991), this question remains unsatisfactorily tested. Most of the studies on lizard community-ecology in Brazil have been conducted in open habitats of the southeastern coast (restinga vegetation, ARAÚJO 1984, 1991), Cerrado (VITT 1991, BRANDÃO & ARAÚJO 1998, 2001, COLLI *et al.* 2002) and Caatinga dry woods (VANZOLINI 1976, VITT 1995). Most of these works dealt with general aspects of space, food and time usage by lizards, only a few were dedicated to the study of ecomorphology (ARAÚJO 1991, TEIXEIRA-FILHO *et al.* 2001, RIBAS *et al.* 2004, PINTO & ÁVILA-PIRES 2004).

Coastal restingas are Brazilian habitats easily accessible for this sort of study because of the type of formation and the abundance and easiness of surveying lizards (ARAÚJO 1984, 1991). This open xeromorphic habitat covers the recent Quaternary sand-dunes of the coast (LACERDA *et al.* 1984) and is characterized by landscapes dominated by scrubs, cacti, bromeliads, and grass patches, with extended areas of exposed sand. Considering its recent history (SUGUIÓ & TESSLER 1984, FLEXOR *et al.* 1984, MUEHE 1984, RONCARATI & MENEZES 2005), we expected an invasion-structured pattern (RUMMEL & ROUGHGARDEN 1983) to be present in the lizard communities of restingas: high morphological overlap to use some good resources and low species packing. In order to evaluate this hypothesis, we investigated the morphological attributes of the restinga lizard assemblage of Marambaia, and compare our results to another restinga area of Southeastern Brazil.

MATERIAL AND METHODS

The present work was conducted in Marambaia, located in Sepetiba Bay, Mangaratiba, Rio de Janeiro State (between 23°04'51"S-44°00'39"W and 23°03'48"S-43°33'96"W). Marambaia is physically partitioned in two distinct geographical areas, the Marambaia paleo-island and the contiguous Restinga da Marambaia (Fig. 1). The restinga area is composed of a 40 km sand bar, deposited along the last 5100 years (RONCARATI & MENEZES 2005). The paleo-island has its highest peak reaching 640m and holds beaches with restinga vegetation, rocky shoreline, small mangrove patches and Atlantic Forest, with high habitat heterogeneity (CONDE *et al.* 2005, MENEZES & ARAÚJO 2005).

Lizard sampling took place between July 2003 and July 2005. Lizards were observed along trails, collected and fixed with 10% formalin, to obtain morphometric data, following the protocol presented by ARAÚJO (1991). Nine measurements of the lizards collected were taken using a digital caliper (± 0.05 mm): snout-vent length, arm length, hand length, leg length, foot length, head length, head width, head height and jaw length. For this study, only the lizards that occur in restingas were considered. 120 specimens collected are housed in the Coleção Herpetológica do Laboratório de Herpetologia da Universidade Federal Rural do Rio de Janeiro (CH-UFRJ), and a list of the vouchers is presented in appendix I.

Lizard measurements were log transformed and ordinated with Principal Components Analysis (PCA, using the covariance matrix, PIELOU 1984), following RICKLEFS *et al.* (1981). The identification of ecomorphological groups of lizard species were confirmed using Discriminant Analysis. In order to evaluate the morphological affinities of each lizard species, a Cluster Analysis (Ward's method) was performed using the mean of the scores of the first and second principal components for each species (centroid) generated by PCA. All statistical analysis were performed using SYSTAT 11.0, except by the Cluster Analysis, executed using PAST.

RESULTS AND DISCUSSION

Of the 12 lizard species known to occur in Marambaia (CARVALHO *et al.* 2007), nine were encountered during our surveys in the restingas: *Ameiva ameiva* (Linnaeus, 1758) ($n = 6$), *Cnemidophorus littoralis* Rocha, Araújo, Vrcibradic & Costa, 2000 ($n = 5$), *Gymnodactylus darwini* (Gray, 1845) ($n = 7$), *Hemidactylus mabouia* (Moreau de Jonnès, 1818) ($n = 6$), *Liolaemus lutzae* Mertens, 1938 ($n = 6$), *Mabuya agilis* (Raddi, 1823) ($n = 4$), *Mabuya macrorhyncha* Hoge, 1947 ($n = 4$), *Tupinambis merianae* (Duméril & Bibron, 1839) ($n = 1$), and *Tropidurus torquatus* (Wied, 1820) ($n = 81$). Table I presents the measurements of the lizards collected. The most common species was *T. torquatus*, easily observed in the restingas, as in other habitats of Marambaia. *Mabuya agilis* was recorded in the restingas and forest habitats, while *M. macrorhyncha* was only found in the restingas. *Cnemidophorus littoralis* was encountered only in the restinga scrubs, and *L. lutzae* only in the fields of the dunes facing the open sea. Surprisingly, *A. ameiva* was observed in the forest gaps and in the restinga boundaries, but not in the restinga scrubs, or in the restinga beach dunes of Marambaia. This teiid is commonly encountered in the scrub habitat of others restingas (ARAÚJO 1991, FREIRE 1996, TEIXEIRA 2001, ROCHA *et al.* 2004). In addition to being found in the restingas, *G. darwini* was recorded in the forests also, as was the other gekkonid in our study, *H. mabouia*.

The hypothesis of an invasion-structured pattern (RUMMEL & ROUGHGARDEN 1983), with high morphological overlap among species, and low levels of species packing, was confirmed. The morphometric analysis distinguished two lizard groups (Discriminant Analysis, Wilks' lambda = 0.139; df = 3, 116; p = 0.000; PCA plots; Figs 2 and 3, Tab. II). The first group included *T. torquatus*, *A. ameiva*, *L. lutzae*, *C. littoralis*, and *T. merianae*. The second group included *H. mabouia*, *G. darwini*, *M. agilis*, and *M. macrorhyncha*. To classify these ecomorphological groups of lizards, we modified the nomenclature proposed by ARAÚJO (1991). The group formed by robust lizards with long extremities (*T. torquatus*, *A. ameiva*, *L. lutzae*, *C. littoralis*, and *T. merianae*) was named "ground-runners", and the other group, composed of small and slender lizard species, with short limbs, was denominated "hiders" (*H. mabouia*, *G. darwini*, *M. agilis*, and *M. macrorhyncha*).

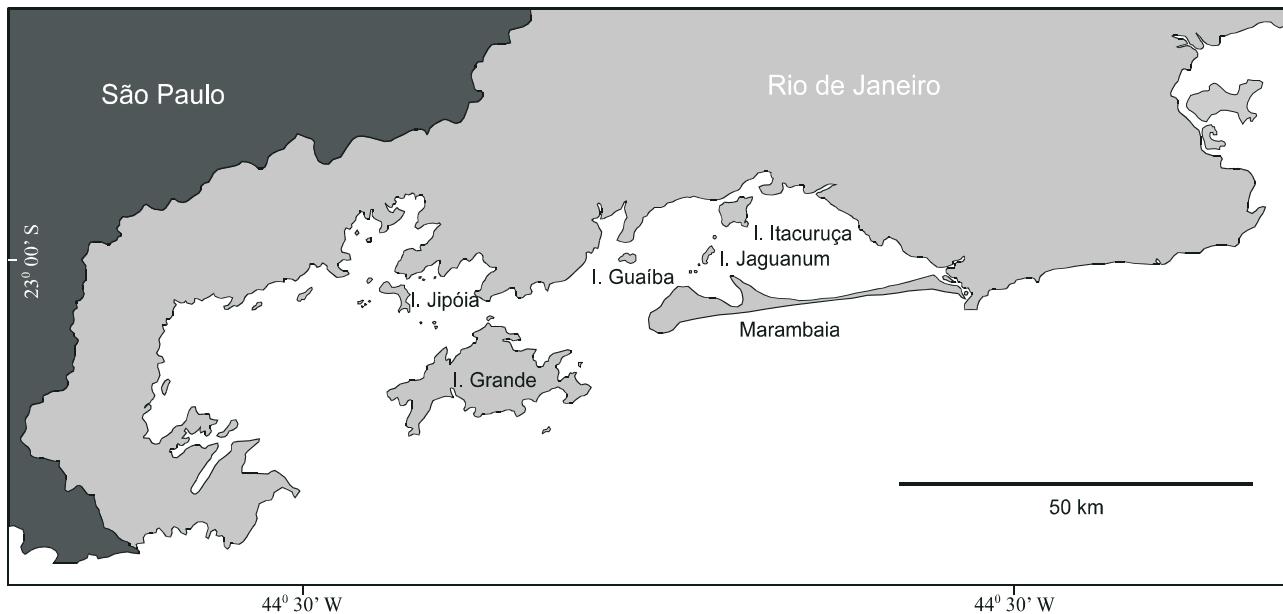
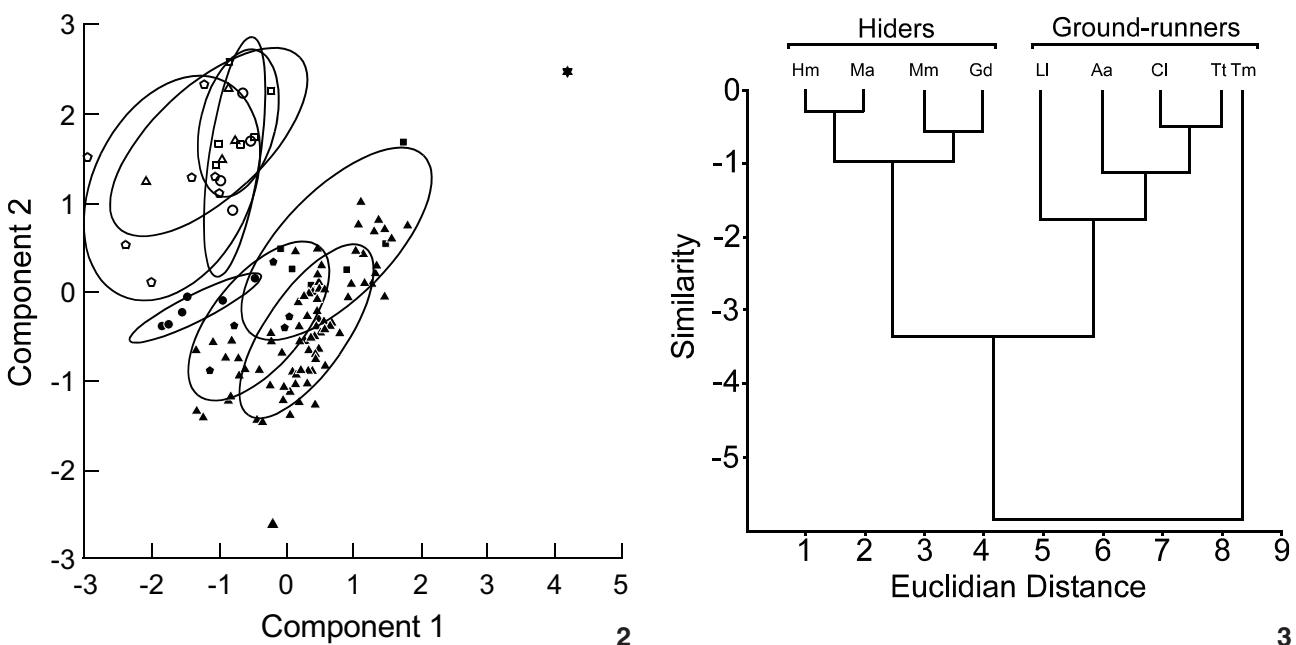


Figure 1. Map of the southern portion of the State of Rio de Janeiro, with the location of Marambaia and other nearby islands and coastal areas.



Figures 2-3. (2) Scatterplot of the first and second principal components generated by the morphometric analysis of the lizards of Marambaia. (■) *Ameiva ameiva*, (▲) *Cnemidophorus littoralis*, (○) *Gymnodactylus darwini*, (□) *Hemidactylus mabouia*, (●) *Liolaemus lutzae*, (○) *Mabuya agilis*, (△) *M. macrorhyncha*, (★) *Tupinambis merianae*, (▲) *Tropidurus torquatus*. (3) Euclidian distances and morphometric similarity levels for the lizard species of Marambaia. Cophenetic correlation coefficient = 0.92 (clustering by Ward's method). (Aa) *Ameiva ameiva*, (CI) *Cnemidophorus littoralis*, (Gd) *Gymnodactylus darwini*, (Hm) *Hemidactylus mabouia*, (LI) *Liolaemus lutzae*, (Ma) *Mabuya agilis*, (Mm) *M. macrorhyncha*, (Tm) *Tupinambis merianae*, (Tt) *Tropidurus torquatus*.

Table I. Measurements (mean ± standard deviation, in mm) of the lizards of restinga areas of Marambaia. (SVL) Snout-vent length, (ARM) arm length, (HND) hand length, (LEG) leg length, (FOO) foot length, (HDL) head width, (HDW) head height, (HDH) head width, (JAW) jaw length.

Species	n	SVL	ARM	HND	LEG	FOO	HDL	HDW	HDH	JAW
<i>Anneiva ameiva</i>	6	85.08 ± 25.50	14.92 ± 4.01	12.68 ± 3.99	26.75 ± 6.94	31.68 ± 9.12	25.35 ± 7.51	13.01 ± 3.50	10.16 ± 3.40	19.72 ± 5.80
<i>Cnemidophorus littoralis</i>	5	52.83 ± 10.81	10.07 ± 2.85	8.62 ± 1.64	16.71 ± 3.36	20.17 ± 3.65	16.09 ± 2.85	7.58 ± 1.23	6.30 ± 1.28	12.55 ± 2.43
<i>Gymnodactylus darwini</i>	7	38.21 ± 12.76	6.42 ± 1.99	4.80 ± 1.64	8.89 ± 3.05	7.17 ± 2.41	11.89 ± 3.01	6.91 ± 1.83	4.30 ± 1.36	9.05 ± 2.29
<i>Hemidactylus mabouia</i>	6	55.01 ± 9.20	11.27 ± 1.75	5.92 ± 1.02	15.51 ± 2.18	8.27 ± 1.57	17.12 ± 2.03	10.53 ± 1.44	5.78 ± 1.21	12.67 ± 1.95
<i>Liolemaus lutzae</i>	6	37.34 ± 8.72	6.90 ± 1.44	6.39 ± 1.70	10.16 ± 2.46	11.86 ± 2.61	11.28 ± 2.25	7.16 ± 1.50	4.70 ± 1.04	8.64 ± 1.59
<i>Mabuya agilis</i>	4	72.29 ± 7.21	10.35 ± 0.86	6.15 ± 0.89	13.31 ± 1.60	10.03 ± 0.40	14.47 ± 1.49	8.92 ± 0.77	6.06 ± 0.73	9.94 ± 1.49
<i>Mabuya macrorhyncha</i>	4	57.95 ± 13.70	7.86 ± 2.23	6.02 ± 1.44	9.88 ± 2.49	9.24 ± 1.83	14.72 ± 1.79	8.17 ± 1.57	5.06 ± 1.37	10.77 ± 2.85
<i>Tupinambis merianae</i>	1	265.0	57.00	44.00	86.00	95.00	84.00	55.00	31.25	63.76
<i>Tropidurus torquatus</i>	81	61.64 ± 14.97	16.82 ± 4.80	12.45 ± 2.80	25.05 ± 7.07	21.55 ± 4.60	18.67 ± 4.52	12.47 ± 3.84	8.01 ± 2.60	14.17 ± 3.96

The morphometric assemblage resulting from the present investigation is congruent with that reported by ARAÚJO (1991) for the lizard community of restinga de Maricá (also in the State of Rio de Janeiro). The morphometric relationships observed for both lizard communities suggest that phylogeny partially explains ecological relationships: the group of hider lizards includes only scleroglossian species, while ground-runners included both scleroglossan and iguanian lizard species (i.e., both major clades of Lacertilia; VITT *et al.* 2003).

The sum of the principal component values (Tab. II) suggest that the variables associated with space usage (limb measurements) are as important in explaining the total variance as variables associated with diet (i.e., head measurements). However, the highest score value pertains to a variable relating to the use of space (foot length), indicating that habitat structure is the most important factor clustering the two groups of lizards identified in our study. The availability and distribution of bromeliads, as well as the distribution of other refugia, are important to the "hiders", whereas open areas between scrubs are important to "ground-runners". Similar results were found by RICKLEFS *et al.* (1981), studying lizard communities of deserts in three continents (North America, Africa and Australia), who applied the same protocol to the lizards collected by PIANKA (1973, 1975).

Considering that the ecomorphological groups of lizards of Marambaia present distinct strategies for escaping predation – run to the scrubs ("ground-runners") and hide inside bromeliads and other refugia ("hiders") – our results also suggest that predation may be another important ecological factor structuring lizard communities of restings. However, a test of this hypothesis requires experimental analyses that are beyond the scope of the present study.

Gymnophthalmids and polychrotids, extensively sympatric in different localities of the Cerrado (VITT 1991, BRANDÃO & ARAÚJO 1998, 2001, COLLI *et al.* 2002) and Caatinga (VITT 1995, BORGES-NOJOSA & CARAMASCHI 2003), are absent in the southeastern Brazilian restings. The absence of small gymnophthalmids in the litter cannot be explained by the absence of litter, which is present in restings. The same reasoning applies to the absence of arboreal polychrotids and leiosaurids, because trees are common in restings also. The explanation for these vacant ecomorphometrical spaces seems to relate to the nonexistence of lizard species in the Atlantic-Forest stock capable of colonizing restinga scrubs, which are drier and hotter than the humid forest more to the interior of the continent.

FREIRE (1996) pointed out the influence of the Caatinga lizard fauna on the composition of two restinga lizard communities of northeastern Brazil, inhabited by a common gymnophthalmid species of open areas, *Micrablepharus maximiliani* (Reinhardt & Luetken, 1862). The Atlantic Forest arboreal lizards, *Anolis fuscoauratus* D'Orbigny, 1837, *A. ortonii* Cope, 1868, and *Enyalius bibronii* Boulenger, 1885, occur in the northeastern restings, but associated with dry forests, not with the scrub habitats. In addition, even in Marambaia, species of Gymnoph-

Table II. Eigenvalues (EVL), eigenvectors (EVT) and explained variance (%) generated by the Principal Component Analysis (covariance matrix), using the log transformed measurements of the lizards of Marambaia.

	Component 1		Component 2		Component 3	
	EVL	EVT	EVL	EVT	EVL	EVT
Snout-vent length	0.130	0.286	0.047	0.415	0.001	0.014
Arm length	0.167	0.366	-0.021	-0.186	-0.048	-0.603
Hand length	0.160	0.352	-0.038	-0.332	-0.009	0.109
Leg length	0.186	0.408	-0.030	-0.265	-0.027	-0.333
Foot length	0.179	0.394	-0.052	-0.459	0.049	0.619
Head length	0.123	0.270	0.037	0.328	0.010	0.119
Head width	0.137	0.300	0.029	0.250	-0.017	-0.210
Head height	0.141	0.310	0.027	0.240	0.009	0.109
Jaw length	0.128	0.281	0.048	0.417	0.019	0.244
Explained Variance	87.931		5.542		2.706	

thalmidae, Leiosauridae and Polychrotidae use the forested habitats next to the restinga scrubs, but not the scrubs themselves (CARVALHO *et al.* 2007), what reinforce the hypothesis of non-saturated lizard communities in southeastern coastal areas be determinated by physiological constraints of the stock of species present in the Atlantic Forest.

The existence of community saturation in nature is contested by evidence that community structuring mechanisms may be related to extrinsic biogeographical events, rather than intrinsic local processes (CORNELL & LAWTON 1992). Some authors present evidence for random structure of the natural communities (RICKLEFS & TRAVIS 1980, RICKLEFS *et al.* 1981, GILPIN & DIAMOND 1984, SIMBERLOFF 1984). Others contested this with evidence that evolution has indeed produced nonrandom assemblages of interacting species (GATZ 1979, SCHOENER 1984). Nevertheless, restinga vegetation is extremely dynamic – in a few decades, the grassfields of the beaches can be replaced by scrub patches, after which the shrubs can grow and fuse to form a dry forest, leading to a humid forest, connected to the mainland (LACERDA *et al.* 1984) – and the spatial heterogeneity due to the ecological succession permits space niche partitioning among the lizard species (ARAÚJO 1984, 1991). However, the existence of vacant niches (marked by the absence of semifossorial and arboreal lizards) is evident in the southeastern Brazilian restingas; the existence of empty ecomorphological spaces in the analysis reinforces this idea.

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Appendix. List of the lizards collected in Marambaia, Mangaratiba, Rio de Janeiro, Brazil. The specimens are housed in the Coleção Herpetológica, Laboratório de Herpetologia, Universidade Federal Rural do Rio de Janeiro (RU).

Species	Collection number
<i>Ameiva ameiva</i>	RU 715, RU 716, RU 717, RU 718, RU 719, RU 720
<i>Cnemidophorus littoralis</i>	RU 721, RU 722, RU 723, RU 724, RU 725
<i>Gymnodactylus darwini</i>	RU 734, RU 742, RU 746, RU 893, RU 902, RU 944, RU 983
<i>Hemidactylus mabouia</i>	RU 735, RU 726, RU 727, RU 899, RU 900
<i>Liolaemus lutzae</i>	RU 736, RU 737, RU 738, RU 739, RU 740, RU 741
<i>Mabuya agilis</i>	RU 728, RU 729, RU 730, RU 731
<i>Mabuya macrorhyncha</i>	RU 731, RU 733, RU 744, RU 904
<i>Tropidurus torquatus</i>	RU 641, RU 642, RU 643, RU 644, RU 645, RU 646, RU 647, RU 648, RU 649, RU 650, RU 651, RU 652, RU 653, RU 654, RU 655, RU 656, RU 657, RU 658, RU 659, RU 660, RU 661, RU 662, RU 663, RU 664, RU 665, RU 666, RU 667, RU 668, RU 669, RU 670, RU 671, RU 672, RU 673, RU 674, RU 675, RU 676, RU 677, RU 678, RU 679, RU 680, RU 681, RU 682, RU 683, RU 684, RU 685, RU 686, RU 687, RU 688, RU 689, RU 690, RU 691, RU 692, RU 693, RU 694, RU 695, RU 696, RU 697, RU 698, RU 699, RU 700, RU 701, RU 702, RU 703, RU 704, RU 705, RU 706, RU 707, RU 708, RU 709, RU 710, RU 711, RU 712, RU 713, RU 714, RU 743
<i>Tupinambis merianae</i>	RU 747

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