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Diversity and habitat use of snakes from the coastal Atlantic rainforest in northeastern Bahia, Brazil

Ricardo Marques[1,2,4], Dennis Rödder[3,4], Mirco Solé[4] & Moacir Santos Tinôco[2,5]

[1] Universidade Federal da Paraíba, Cidade Universitária. Rua José Dionísio da Silva, s/n, 58059-900, João Pessoa, PB, Brasil

[2] Universidade Católica do Salvador, SPPG-MPPA – Centro de Ecologia e Conservação Ambiental – ECOA. Avenida Prof. Pinto de Aguiar, 2589. CEP 41740-090. Pituaçu, Salvador, BA, Brazil

[3] Zoological Research Museum Alexander Koenig, Department of Herpetology, Adenauerallee 160, 53113 Bonn, Germany

[4] Universidade Estadual de Santa Cruz, Programa de Pós-Graduação em Zoologia. Rodovia Jorge Amado, km 16. CEP 45662-900. Ilhéus, BA, Brazil

[5] University of Kent at Canterbury; DICE – Durrell Institute of Conservation and Ecology; School of Anthropology and Conservation. Marlowe Building, Kent, CT2 7NZ, UK

Corresponding author: Ricardo Marques, e-mail: rcdmarquess@gmail.com

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Abstract. The north coast of Bahia comprises a 220 km long region within the Atlantic rainforest ecoregion. Studies focusing on snake communities are still scarce in this part of the state of Bahia. In this study, we assess snake diversity at nine locations, including habitat use and activity patterns. The sites were surveyed for three years, and four museum collections were visited to compile additional data. We obtained information on 50 species from 774 specimens. While the snake fauna at Instituto da Mata contained the greatest richness with 15 observed species, the snake fauna at Imbassaí exhibited the greatest snake diversity due to a lower dominance. The estimated species richness of the region might be as many as 55 species. Snakes occurred mainly in the restinga ecosystem (N = 27), followed by ombrophilous forest (N = 25), and consisted mainly of terrestrial species. The restinga dry forest is home to most species, however some are restricted to habitats in other vegetation types related to their biology. The snake assemblage on the north coast of Bahia is similar to others in the Atlantic rainforest and Caatinga domain in northeastern Brazil.

Key words. Mata de São João, restinga, ombrophilous forest, Caatinga, snake habits.

Introduction

Studying the spatial distribution of organisms in geographic space helps to understand how species diversity is structured, as it moves along the space-time continuum if there is an alternation between environments (Vitt & Caldwell 2009). The geographical distribution of a species is strictly related to habitat selection, its trophic niche and the organisms' evolutionary lineage capability to colonize a given area (Morris 1987, Wiens 1989). Thus, organisms can be endemic to a specific ecoregion or present in different ecosystems, but not in others.

The Atlantic forest domain holds a large portion of biodiversity in the Brazilian territory (Laurance 2008, Metzger 2009). The ecoregion is threatened due to urbanisation and agricultural expansion, which threatens forested ecosystems, mangroves and coastal sand dunes or restinga (IBGE 2000, Pinto & Brito 2005, Tabarelli et al. 2005, Laurance 2008, Ribeiro et al. 2009).

The restinga is a recent coastal ecosystem dating from the Quaternary. Marine ingressions and regressions resulted in the deposition of marine sediment that created the great plains and sand dunes known today (Leão & Dominguez 2000, Tessler & Goya 2005, Souza et al. 2008). The biotic colonisation of this environment is strongly influenced by nearby ecoregions, with shared species pools within the Cerrado, the Caatinga, and the Atlantic Forest in northeastern Brazil (Freire 1990, Oliveira et al. 2005). Additionally, it contains endangered and endemic biocenoses (Cerqueira 2000, Queiroz 2007, Dias & Rocha 2014).

A few studies dealing with the restinga snake communities of Brazil have been previously undertaken, e.g., for the restinga of Jurubatiba in the State of Rio de Janeiro (Rocha et al. 2004), that of Juréia in São Paulo (Marques & Sazima 2004), in Linhares, Espírito Santo (Rocha 1998), in Lençóis Maranhenses National Park in the State of Maranhão (Miranda et al. 2012), and that of the north coast of Bahia (Marques et al. 2011, Dias & Rocha 2014). In spite of these contributions, a greater focus on the ecology and habitat use of snakes in the restinga ecosystems is needed, considering the scarce or non-existent knowledge of its role in this environment (Rocha 2000, Rocha & Van Sluys 2007). This study aims at providing information about the diversity of different sites and habitat use in ecosystems and vegetation types on the north coast of Bahia.

Material and methods

Study area

Our study was conducted on the north coast of Bahia, covering 16 municipalities with a maximum distance of 60 km from the coastline: Lauro de Freitas, Simões Filho, Camaçari, Dias D'Ávila, Mata de São João, Itanagra, Acajutiba, Cardeal da Silva, Pojuca, Catu, Rio Real, Araçás, Entre Rios, Esplanada, Conde and Jandaíra (Fig. 1). The annual mean temperature and humidity in this region are around 25°C and 83%, respectively, receiving an annual average precipitation of 1,900 mm (IBGE 2002, SIDE 2013). The whole region holds dense ombrophilous forests and

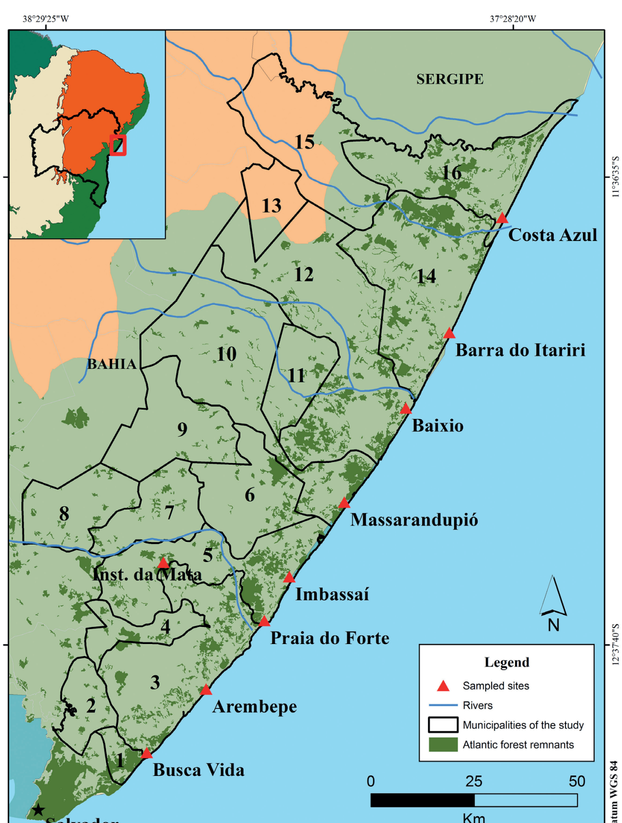

Figure 1. Municipalities on the north coast of Bahia: 1 – Lauro de Freitas; 2 – Simões Filho; 3 – Camaçari; 4 – Dias D'Ávila; 5 – Mata de São João; 6 – Itanagra; 7 – Pojuca; 8 – Catu; 9 – Araçás; 10 – Entre Rios; 11 – Cardeal da Silva; 12 – Esplanada; 13 – Acajutiba; 14 – Conde; 15 – Rio Real; 16 – Jandaíra. Triangles show the surveyed sites.

seasonal semideciduous forest in its inner portion, which contains Cerrado enclaves. The Caatinga domain also influences the northern municipalities. The coastline is composed of sand dunes or restinga ecosystem (SIDE 2013). The restinga vegetation is highly heterogeneous, increasing its vegetal structure from coastline to inland. Four different vegetation habitat types are found:

The beach vegetation habitat is composed of invasive coconut trees, herbaceous and small shrub vegetation on sandy soil. The flood plains or wetlands present clumps of herbaceous vegetation (Cyperaceae) and low subshrub vegetation, usually bathed by a river or lake (Menezes et al. 2009). These water bodies can vary in level and dry out during the dry season. The shrub vegetation habitat is mainly composed of large bushes (*Clusia* spp.) with an abundance of bromeliads. The bushes are isolated by the sandy soil, which often reaches high temperatures unless shaded by ground-covering vegetation. Only within the restinga dry forest does vegetation become arboreal, reaching a canopy height of 10–14 metres. This creates a shaded environment with a constant ground cover of leaf litter (Fig. 2) (Menezes et al. 2009, Silva & Menezes 2012).

The restinga ecosystem was sampled at eight sites: Busca Vida (-12.8619 S, -38.2708 W), Arembepe (-12.7236 S, -38.1416 W), Praia do Forte (-12.5748 S, -38.0147 W), Imbassaí (-12.4791 S, -37.9602 W), Massarandupió (-12.3172 S, -37.8404 W), Baixio (-12.1123 S, -37.7062 W), Barra do Itariri (-11.9478 S, -37.6113 W), and Costa Azul (-12,0000 S, -37.4960 W). As we also searched for species from forested environments, the site of Instituto da Mata (-12.4500 S, -38.2345 W) was included to increase species composition. It is located 20 km from the coastline and composed of dense ombrophilous forest.

Sampling design

We conducted fieldwork on each site every two months, totalling 18 field surveys. The eight sites within restinga habitats were surveyed from June of 2010 to August to 2013. Instituto da Mata was surveyed from December of 2010 to October of 2013. We sampled each site for one day, totalling 162 non-consecutive fieldwork days. Only daytime surveys were conducted until June of 2012, from 06:00 to 18:00 h. Fieldwork beyond this included nighttime surveys from 19:00 through 21:00 h at Busca Vida, Instituto da Mata, Baixio, and Barra do Itariri. Fieldwork was conducted under ICMBio permit No. 23355-2 - 04/2016.

We sampled the snakes using Visual Encounter Surveys (VES), incidental encounters, dead specimens found by locals, carcasses, and exuviae. We performed the VES along four transects of 500 m each established simultaneously and covering each vegetation type. Two researchers sampled snakes for two hours. Animals detected before or after the VES were included as incidental encounters. Carcasses and exuviae were considered only when they could be identified to species level. The total sample effort was 3,024 h (2,592 h daytime and 432 h nighttime).

We obtained, when available, additional data on species distribution and habitat use within the region from the scientific collections of the Universidade Estadual de Santa Cruz – UESC, Universidade Federal da Bahia – UFBA, Universidade Estadual de Feira de Santana – UEFS, and the Universidade Católica do Salvador – UCSAL.

Analyses

The estimated species richness was calculated only on the basis of species obtained during fieldwork, considering each survey as a sample. Additional species from museums were not included in the analyses. We used the non-parametric estimator Chao 1 based on the total observed

Figure 2. Restinga vegetation habitat types: (A) beach; (B) wetland; (C) shrub; (D) restinga dry forest.

richness and rare species with only one or two specimens. The rarefaction curve was calculated with 1,000 randomisations from the species obtained during fieldwork using the software EstimateS 9.5 (Colwell et al. 2012). To assess the diversity of each site, we used Simpson's index based on dominance and weighted on species abundance, considering each survey as a sample and using the software Past 3.0 (Hammer et al. 2001).

To compare the snake community of the north coast of Bahia with assemblages at other localities, we used the Coefficient of Biogeographic Resemblance (hereafter CBR). It is calculated according to the formula

$$2C/A + B,$$

where C is the number of species common to two areas, and A and B are the numbers of species from the first and second area (Duellman 1990). We compared the faunal compositions per site of this study to those of nine other sites reported in the literature. Four of these studies were performed within the Atlantic rainforest domain in forested or coastal environments; north coast of Bahia, Bahia (this study); in the south of Bahia State (Argôlo 2004); on the Rio Tinto, Paraíba (França et al. 2012); at Viçosa, Minas Gerais (Costa et al. 2010); and in the restinga of Linhares, Espírito Santo (Rocha 1998). Five others were performed in open habitats from Caatinga and Cerrado domains. Both domains also occur in the state of Bahia: São Gonçalo do Amarante, Ceará (Borges-Leite et al. 2014); Parque Estadual do Jalapão, Tocantins (Vitt et al. 2005); Planalto da Ibiapaba, Ceará (Loebmann & Haddad 2010); Parque Nacional dos Lençóis Maranhenses, Maranhão (Miranda et al. 2012); and upper Tocantins River, Goiás (Moreira et al. 2009).

Results and discussion

Diversity

We obtained 774 specimens (194 specimens during field surveys and 580 examined in collections) representing 50 snake species, with Dipsadidae (51% spp.) being the best represented family. Among the sampled localities, we recorded the highest species richness at the Instituto da Mata (15 spp.). However, the diversity at this site was not the highest recorded, probably because of the high frequency of *Helicops angulatus*. Imbassaí and Praia do Forte presented similar abundance values for each recorded species, resulting in the highest diversity (0.88 and 0.86, respectively). Barra do Itariri presented the lowest incidence due to the predominance of *Chironius flavolineatus*, which was responsible for 57.89% of the records. For restinga habitats, Imbassaí (13 spp.), Baixio (10 spp.), and Busca Vida (8 spp.) were the localities with highest species richness values (Table 1), while species richness at the other localities varied between 6 and 7 taxa. The low numbers at each site may be a result of the low density of snakes and the difficulty in sampling them; a common problem in ecological studies involving snakes (Sawaya et al. 2008).

Table 1. Observed richness (Sa), number of individuals (N), total richness (St), Simpson index (D), and dominance (d) at the nine sites of our study: BV – Busca Vida; AR – Arembepe; PF – Praia do Forte; IM – Imbassaí; IsM – Instituto da Mata; MA – Massarandupió; BA – Baixio; BI – Barra do Itariri; CA – Costa Azul.

	BV	AR	PF	IM	IsM	MA	BA	BI	CA
Sa	8	6	7	13	15	6	10	6	7
N	16	10	10	31	34	12	19	38	18
St	10	10	19	23	16	10	10	6	9
D	0.82	0.8	0.86	0.88	0.85	0.69	0.83	0.67	0.82
d	0.17	0.2	0.14	0.11	0.14	0.3	0.16	0.32	0.17

Using the complete dataset, the Chao 1 estimator suggests up to 55 species may occur within the region. Although our sampling was intense, the rarefaction curve did not reach stability (Fig. 3), suggesting that it was not possible to cover all species. Since more sample effort was applied to open-vegetation habitats of restinga, the detection rate of species adapted to densely vegetated environments was probably limited. In addition, we observed a predominance of terrestrial species, but some of them were likely under-sampled. Species with a secretive ecology or cryptic colorations make detecting them difficult, however, they are easily sampled using drift fences and pitfall traps (Fisher & Rochester 2012). It is worth mentioning that for this analysis, only the collected species were used. Therefore the inclusion of 18 species from museum collections could increase the estimate of species present in the area.

Habitat use

Among the recorded species, 27 are from the restinga ecosystem. Based on inventories of different restinga ecosystems (Marques et al. 2011, Miranda et al. 2012, Dias & Rocha 2014), five of these species represent new records for this habitat, i.e., *H. leopardinus, Clelia plumbea, Oxyrhopus petolarius, Pseudoboa nigra,* and *Erythrolamprus almadensis.* Another 20 species were recorded only at sites

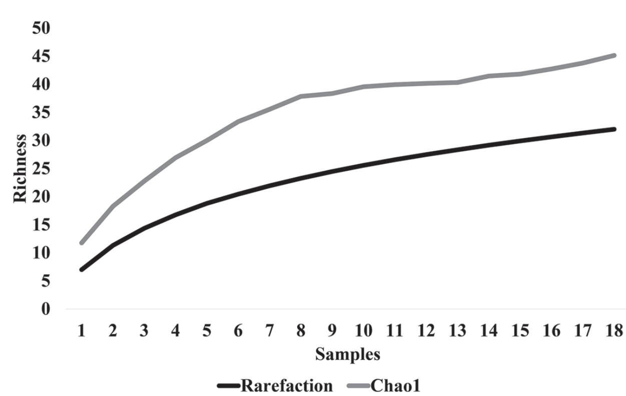

Figure 3. Rarefaction curve and Chao 1 richness estimates on the basis of specimens from 18 samples (45.13 ± 10.17).

where ombrophilous forest is predominant and two from the relictual Cerrado enclaves.

The biotic composition of the restinga in northeastern Brazil is influenced not only by the predominance of Atlantic Forest, but also by the dominance of Cerrado and Caatinga (Freire 1990). These dry and open habitat ecoregions expanded and retracted their boundaries due to climatic fluctuations through geological time, reaching coastal areas of northeastern Brazil (Ab'Saber 1977, Pennington et al. 2006) where elements of both still remain. The environments and vegetated habitats where snakes were found are specified in Table 2. We observed that species were shared between the Instituto da Mata and Imbassaí, both in the municipality of Mata de São João (e.g., *Bothrops leucurus*, *Taeniophallus occipitalis*, *Micrurus ibiboboca*, *Philodryas olfersii herbeus*, *Xenodon merremii*). We suppose that the forested ecosystem within which the Instituto da Mata is located serves as a source of a number of forest-adapted species and supplies the forested environments of the restinga.

Terrestriality is predominant among the snakes found on the north coast of Bahia, being to the lifestyle of 28 species within the study area. We also observed terrestriality in species that live in aquatic environments (e.g., *E. taeniogaster*) and semi-arboreal habitats, such as *B. constrictor* and *C. flavolineatus*. Only the genus *Micrurus* was considered cryptozoic, while *Amerotyphlops brongersmianus* is fossorial. *Chironius exoletus* and *Oxybelis aeneus* presented a semi-arboreal lifestyle, and *Eunectes murinus* and *Helicops* spp. have aquatic habits. Even though *Leptophis ahaetulla liocercus, Corallus hortulanus*, *Imantodes cenchoa*, *P. olfersii herbeus, Spilotes sulphureus sulphureus*, and *Siphlophis compressus* have arboreal habits (Argôlo 2004, Marques & Sazima 2004), only *L. ahaetulla liocercus* was recorded in arboreal strata. The remaining species were recorded at ground level in the ombrophilous forest fragment with the exceptions of *S. sulphureus sulphureus* in the restinga and *P. olfersii herbeus* in both habitats. The sampled open-habitat structure in the restinga is a determinant of the predominance of terrestrial species since open environments do not offer consolidated vertical strata. Inventories in other restinga environments also show that most of the detected squamate species were those with terrestrial habits (see Rocha 1998, Rocha 2000, Dias & Rocha 2014), whereas in the forest environment of Estação Ecológica Juréia-Itatins (Marques & Sazima 2004), half of the snake species are arboreal.

The vegetation type with the greatest abundance observed was the restinga dry forest (28 spp.), followed by shrub vegetation (23 spp.) and wetland (17 spp.). On the beach, where vegetation is scant, we obtained only seven species. Santos et al. (2012) inventoried a coastal environment with low heterogeneity and observed a low richness of 13 species. It is possible that this type of vegetation does not provide enough habitat heterogeneity either resources to support a great number of species. Individual fitness and foraging performance are intrinsically related to habitat selection (Huey 1991).

Species with aquatic lifestyles, like *E. murinus* (N = 3) and *H. leopardinus* (N = 1), were found only in habitats of wetland vegetation. Amphibians are common in this habitat, and snakes specialising in this type of prey were also predominant (*C. flavolineatus* [N = 6], and *Leptodeira annulata* [N = 3]) (Pinto et al. 2008). In restinga dry forest, species with arboreal or semi-arboreal habits, such as *B. constrictor* (N = 8), *C. flavolineatus* (N = 8), or fossorial species that use leaf litter as microhabitat such as *M. ibiboboca* (N = 8) and *A. brongersmianus* (N = 1), are predominant. Evolutionary adaptations in morphology and natural history directly result in the habitat selection of snakes (Vitt & Caldwell 2009). Snakes with cryptic colour patterns tend to be terrestrial and show a camouflage coloration intended to avoid predation and facilitate prey capture (Hartmann & Marques 2005). Arboreal snakes tend to have slender bodies, long tails, and reduced weight (Pizzatto et al. 2007), as seen here in *C. hortulanus, C. flavolineatus*, *L. ahaetulla liocercus*, *Oxybelis aeneus*, *P. olfersii herbeus*, *S. sulphureus sulphureus*, and *S. compressus*.

Some of the snakes found in the restinga ecosystem are common and recurrent in this environment, such as *B. constrictor, O. aeneus, O. trigeminus, P. olfersii,* and *P. patagoniensis* (Rocha 1998, Rocha et al. 2004, Marques et al. 2011, Miranda et al. 2012, Dias & Rocha 2014, this study). These species are common in open environments and are dietary generalists (Vanzolini et al. 1980, Hartmann & Marques 2005, Alencar et al. 2012). Generalist snakes have a high plasticity in exploiting ecological resources (Segura et al. 2007), facilitating their occurrence in restinga habitats as long as it includes herbaceous and scrubby parts.

Populations of *Crotalus durissus cascavella* have been recorded from open, dry or semi-arid areas with seasonal rain, which are traits usually attributed to Caatinga (McCranie 1993, Campbell & Lamar 2004). Here we sampled the species in restinga, but voucher specimens were from localities with original forested habitats. The deforestation and fragmentation of the Atlantic Forest results in the creation of artificial open areas, increasing the distribution of this species in these originally forested habitats (Bastos et al. 2005). Such facts could explain the record of the species in ombrophilous forest on the north coast of Bahia.

Lachesis muta is a typical element of old rainforests with an annual precipitation of more than 2,000 mm. It is occasionally recorded in dry, secondary forests or in recently deforested areas close to conserved areas (Campbell & Lamar 2004). In this study, the species was sampled on a farm on the north coast of Bahia with forest patches of secondary and dry forests, but also with a strong influence of agriculture (Side 2013), thus providing a record in atypical habitat.

Of all the species, *B. leucurus*, *O. trigeminus*, and *C. flavolineatus* are those with the widest ranges of habitats in the region. These species are well adapted to natural, urban, and disturbed environments, facilitating their colonisation and wide distribution in the area (Sawaya et al. 2008, Lira-da-Silva et al. 2009, Alencar et al. 2012).

Table 2. List of snake species found on the north coast of Bahia. Table entries include abundance (N), relative frequency of each species (f%), environments (1 – restinga, 2 – ombrophile forest, 3 – Cerrado enclave), habitat (be – beach, fl – flooded plain, sv – shrub vegetation, rf – restinga dry forest, fr – ombrophilous forest fragment, pa – pasture, at – anthropogenic environments), and habit (see Martins & Oliveira 1998 for habit descriptions: F – fossorial, C – cryptozoic, AQ – aquatic, T – terrestrial, SA – sub-arboreal, and A – arboreal). Other legends: * extracted from Dias & Rocha (2014); ** exotic species.

Species	N	f%	Environment	Habitat	Habit
Typhlopidae					
Amerotyphlops brongersmianus (Vanzolini, 1976)	7	0.9	1,2	rf	F
Boidae					
Boa constrictor constrictor Linnaeus, 1758	23	2.9	1,2	be,fl,sv,rf,at	SA,T
Corallus hortulanus (Linnaeus, 1758)	1	0.12	2	fr	A
Epicrates assisi Machado, 1945	1	0.12	3	–	T
Eunectes murinus (Linnaeus, 1758)	5	0.64	1,2	fl	AQ
Colubridae					
Chironius bicarinatus (Wied, 1820)*	–	–	1	–	SA
Chironius carinatus (Linnaeus, 1758)	2	0.25	2	fr	T
Chironius exoletus (Linnaeus, 1758)	14	1.8	1,2	fl,rf	SA
Chironius flavolineatus (Jan, 1863)	38	4.9	1,2	be,fl,sv,rf,at	SA
Drymarchon corais corais (Boie, 1827)	2	0.25	2	fr	A
Drymoluber dichrous (Peters, 1863)	4	0.51	2	fr	T
Leptophis ahaetulla liocercus (Wied, 1824)	4	0.51	2	fr	A
Mastigodryas bifossatus (Raddi, 1820)	4	0.51	2	fr	T
Oxybelis aeneus (Wagler, 1824)	11	1.42	1,2	fl,sv	SA
Pantherophis guttatus (Linnaeus, 1766)**	1	0.12	2	fr	T
Spilotes pullatus pullatus (Linnaeus, 1758)	9	1.16	1,2	fl,sv	SA
Spilotes sulphureus sulphureus (Wagler, 1824)	1	0.12	1	fl,rf	A
Tantilla melanocephala (Linnaeus, 1758)	11	1.42	1,2	sv,rf	T
Dipsadidae					
Sibynomorphus neuwiedi (Ihering, 1911)	15	1.93	2	fr	T
Clelia plumbea (Wied, 1820)	3	0.38	–	–	T
Erythrolamprus aesculapiii venustissimus Wied, 1821	1	0.12	1,2	fr,pa,fl	T
Erythrolamprus almadensis (Wagler, 1824)	19	2.45	2	fr	T
Erythrolamprus miliaris merremi (Wied, 1821)	3	0.38	2	fr	AQ,T
Erythrolamprus poecilogyrus schotti (Schlegel, 1837)	21	2.71	1,2	fr,fl	T
Erythrolamprus taeniogaster (Jan, 1863)	13	1.67	2	fr	AQ,T
Erythrolamprus viridis viridis (Günther, 1862)	1	0.12	2	fr	T
Erythrolamprus reginae semilineatus (Wagler, 1824)	9	1.16	1,2	fr,fl,sv	T
Helicops angulatus (Linnaeus, 1758)	21	2.71	1,2	fr,fl	AQ
Helicops leopardinus (Schlegel, 1837)	15	1.93	2	fr	AQ
Imantodes cenchoa cenchoa (Linnaeus, 1758)	2	0.25	1,2	fl,rf,at	A
Leptodeira annulata annulata (Linnaeus, 1758)	26	3.35	1,2	pa	SA
Oxyrhopus petolarius digitalis Reuss, 1834	5	0.64	1,2	be,fl,sv,rf,pa	T
Oxyrhopus trigeminus Duméril, Bibron & Duméril, 1854	55	7.1	1,2	be,fl,sv,rf	T
Philodryas nattereri Steindachner, 1870	49	6.33	1,2	be,fl,sv,rf	SA,T
Philodryas olfersii herbeus Wied, 1825	22	2.84	1,2	be,fl,sv,rf	A
Philodryas patagoniensis (Girard, 1858)	32	4.13	1,2	sv,rf,at	T
Phimophis guerini (Duméril, Bibron & Duméril, 1854)	4	0.51	1,2	fr	T
Pseudoboa nigra (Duméril, Bibron & Duméril, 1854)	7	0.9	2	pa,at	T
Siphlophis compressus (Daudin, 1803)	1	0.12	2	fr	A
Taeniophallus occipitalis (Jan, 1863)	9	1.16	1,2	fr,be,rf	T
Thamnodynastes pallidus (Linnaeus, 1758)	1	0.12	2	fr	T

Species	N	f%	Environment	Habitat	Habit
Xenodon rabdocephalus rabdocephalus (Wied, 1824)	2	0.25	2	–	T
Xenodon merremii (Wagler, 1824)	24	3.1	1,2	fr,sv	T
Elapidae					
Micrurus corallinus (Merrem, 1820)	1	0.12	2	–	C
Micrurus ibiboboca (Merrem, 1820)	97	12.53	1,2	fr,pa,sv,rf,at	C
Viperidae					
Bothrops erythromelas Amaral, 1923	2	0.26	2	–	T
Bothrops leucurus Wagler, 1824	156	20.15	1,2	fr,pa,be,fl,sv,rf,pa	T
Bothrops lutzi (Miranda-Ribeiro, 1915)	3	0.38	3	–	T
Crotalus durissus cascavella Wagler, 1824	16	2.06	1,2	fr,sv,rf,at	T
Lachesis muta rhombeata Wied-Neuwied, 1824	1	0.12	2	fr	T

Coefficient of Biogeographic Resemblance

Similarities of restinga sites to others varied from 0.46 to 0.70 except between Busca Vida and Praia do Forte with 0.26 (Table 3). The highest resemblance between sites on the north coast of Bahia was between Imbassaí and Praia do Forte, which are separated by 15 km. Of the 27 species recorded for the restinga in the region, we sampled half of them in Imbassaí. Some species were only recorded once at a few sites, decreasing the number of species in common and therefore influencing the CBR result. Busca Vida is the southernmost site and if compared to the others, we see the likeness decreasing from 0.57 to 0.40 on the northern site. This suggests that snake composition changes slightly over the whole restinga expanse. Though the region is also sectioned by three main rivers: Pojuca river between Arembepe and Praia do Forte, Inhambupe river between Baixio and Barra do Itariri, and Itapicuru river which separates Costa Azul from the remaining sites, it is unlikely these small rivers limits species distribution since few squamate studies have shown even larger rivers do not serve as barriers (Ávila-Pires et al. 2009, Geurgas & Rodrigues 2010, Souza et al. 2013). As expected, the similarity of Instituto da Mata to any other restinga site was very low, varying between 0.24 and zero. The species composition at the Instituto da Mata, even though its being only 20 km distant from Praia do Forte, is quite different. This is likely a result of differences in habitat structure, resulting in the presence of species that are specifically adapted to this habitat and therefore found only at this site. This reinforces our assumption that the forested habitats of the region can further enhance the species composition on the north coast of Bahia.

Among the compared localities, we listed a total of 145 species including subspecies as estimated based on their distribution. *Pantherophis guttatus* was not included in this analysis since it is an allochthonous species. The north coast of Bahia is especially similar to the assemblages of the Atlantic Forest and the Caatinga in northeastern Brazil (Table 4). The assemblage at Rio Tinto, Paraíba, showed the highest CBR (0.66) and it is 615 km distant. The upper Tocantins River in Goiás, at a distance of 1,080 km, presented

Table 3. Assemblage similarities among the sample sites on the north coast of Bahia. Bold figures indicate the local richness, underlined numbers are the species in common, and the Coefficient of Biogeographic Resemblance is given in italics. Abbreviations are: BV – Busca Vida; AR – Arembepe; PF – Praia do Forte; IM – Imbassaí; IsM – Instituto da Mata; MA – Massarandupió; BA – Baixio; BI – Barra do Itariri; and CA – Costa Azul.

	BV	AR	PF	IM	ISM	MA	BA	BI	CA
BV	**8**	4	2	6	2	4	4	3	3
AR	*0.57*	**6**	4	4	2	3	4	3	3
PF	*0.26*	*0.61*	**7**	7	2	3	4	4	2
IM	*0.57*	*0.42*	*0.7*	**13**	3	6	6	4	3
IsM	*0.17*	*0.19*	*0.18*	*0.21*	**15**	0	3	1	2
MA	*0.57*	*0.50*	*0.46*	*0.63*	*0.00*	**6**	4	2	2
BA	*0.44*	*0.50*	*0.47*	*0.52*	*0.24*	*0.50*	**10**	4	3
BI	*0.42*	*0.50*	*0.61*	*0.42*	*0.09*	*0.33*	*0.50*	**6**	3
CA	*0.40*	*0.46*	*0.28*	*0.30*	*0.18*	*0.30*	*0.35*	*0.46*	**7**

Table 4. Assemblage similarities with other regions. Bold figures are the local richness, underlined figures are the species in common, and italic numbers are the Coefficient of Biogeographic Resemblance. Abbreviations are: NCB – North coast of Bahia; SBR – south Bahia region; RIT – Rio Tinto; VIC – Viçosa; RLI – restinga of Linhares; PLM – Lençóis Maranhenses National Park; IBP – Ibiapaba Plateau; SGA – São Gonçalo do Amarante; JSP – Jalapão State Park; UTR – upper Tocantins River.

	NCB	SBR	RIT	VIC	RLI	PLM	IBP	SGA	JSP	UTR
NCB	**49**	36	30	14	13	18	22	15	20	10
SBR	*0.65*	**61**	24	16	15	13	19	12	15	9
RIT	*0.66*	*0.47*	**42**	12	9	15	25	14	18	9
VIC	*0.34*	*0.34*	*0.32*	**34**	5	5	8	5	9	3
RLI	*0.39*	*0.38*	*0.30*	*0.19*	**18**	4	10	4	5	1
PLM	*0.49*	*0.31*	*0.45*	*0.17*	*0.19*	**24**	14	15	17	6
IBP	*0.46*	*0.36*	*0.57*	*0.2*	*0.31*	*0.4*	**46**	14	13	6
SGA	*0.43*	*0.29*	*0.44*	*0.18*	*0.21*	*0.67*	*0.42*	**21**	11	8
JSP	*0.42*	*0.28*	0.41	*0.23*	*0.16*	*0.49*	*0.28*	*0.33*	**46**	13
UTR	*0.27*	*0.21*	*0.26*	*0.1*	*0.05*	*0.24*	*0.17*	*0.34*	*0.36*	**26**

the lowest CBR when compared to the north coast of Bahia (0.27), whilst its largest score was recorded at Jalapão State Park (0.36). Another three areas are relevant when compared to the north coast of Bahia: the southern region of Bahia (0.65), at a distance of approximately 300 km, which is likely due to the dominance of Atlantic Forest biomes, and two distant localities, both within the Caatinga domain, the Ibiapaba Plateau in Ceará (0.46; 1,000 km) and the Lençóis Maranhenses National Park (0.49; 1,180 km). Rio Tinto and the southern region of Bahia presented similar CBR scores and the closest species composition compared to our study area. Although Rio Tinto is farther from the north coast of Bahia, its CBR was slightly higher containing a great number of species often recorded to open habitats (e.g. *E. assisi*, *C. flavolineatus*, *H. angulatus*, *P. nattereri*, *P. patagoniensis*, *P. guerini*) whilst the southern region of Bahia presented more species with preferable arboreal habits and forested habitats (e.g. *C. hortulanus*, *C. carinatus*, *C. bicarinatus*, *M. bifossatus*, *L. muta*).

Comparisons between snake communities are complicated due to different sampling methods, varying efforts and studied environments (Martins & Oliveira 1998). However, among the four areas with the highest similarity (Argôlo 2004, Loebmann & Haddad 2010, França et al. 2012, this study), 13 species are present in the four communities: *A. brongersmianus, B. constrictor, C. hortulanus, Drymarchon corais, Drymoluber dichrous, L. ahaetulla, O. aeneus, S. sulphureus, Spilotes pullatus, E. taeniogaster, P. olfersii, P. nigra,* and *T. occipitalis*. The snake fauna of Bahia's northern coastal restinga is mostly composed of widespread species of high plasticity concerning diet and habitats. *Philodryas nattereri*, which is more abundant on the north coast of Bahia, appears mainly in assemblages inhabiting open environments, but also in the wooded environments of Caatinga (Vitt et al. 2005, Loebmann & Haddad 2010, França et al. 2012, Miranda et al. 2012, França & Braz 2013).

Cadle & Greene (1993) described the biogeography of Neotropical snakes and suggested that an increase in latitude reduces the incidence of Colubrinae and Dipsadinae, while it increases the incidence of Xenodontinae. Herein, Colubrinae and Dipsadinae represent 23.5 and 5.8% of the richness, respectively, while Xenodontinae are represented by 45%. This biogeographic pattern has been observed in other studies as well (Bernarde & Abe 2006, Sawaya et al. 2008, Barbo et al. 2011).

Conclusions

In this study, we provide novel insights into the biogeography and natural history of snake communities in restinga habitats, expanding upon previous information (Rocha 1998, Rocha et al. 2004, Marques et al. 2011, Miranda et al. 2012, Dias & Rocha 2014). Some species seem to be restricted to specific vegetation types. While most wetlands next to rivers and restinga forests are areas of permanent protection, the bush vegetation is commonly not protected even though it may harbour the greatest species richness. This fact should be acknowledged in selection processes of priority areas for conservation, but in particular so during the licensing processes for residential estate and hotel/resort development projects, which are responsible for major losses of habitat of these and other elements of the herpetofauna in the region (Tinôco et al. 2008, Tinôco 2011).

The predominance of terrestrial species in the region is strongly influenced by the habitat structure, but may also be a result of the extensive sample effort in restinga habitats. This scenario might change with an increase of sampling effort in forest remnants within the region, as we have recorded six arboreal species in the region, four of which were found within ombrophilous fragments. Its composition is considered similar to other assemblages of the Atlantic Forest and of Caatinga. The region is expansive, holding many different habitats and snake diversity is still not well studied in the majority of municipalities. Therefore, more studies of the ecology and assemblage structures are recommended to improve our understanding them.

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