Squamata (Reptilia) from four sites in southern Amazonia, with a biogeographic analysis of Amazonian lizards

Squamata (Reptilia) de quatro localidades da Amazônia meridional, com uma análise biogeográfica dos lagartos amazônicos

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Abstract: We studied the squamate fauna from four sites in southern Amazonia of Brazil. We also summarized data on lizard faunas for nine other well-studied areas in Amazonia to make pairwise comparisons among sites. The Biogeographic Similarity Coefficient for each pair of sites was calculated and plotted against the geographic distance between the sites. A Parsimony Analysis of Endemicity was performed comparing all sites. A total of 114 species has been recorded in the four studied sites, of which 45 are lizards, three amphisbaenians, and 66 snakes. The two sites between the Xingu and Madeira rivers were the poorest in number of species, those in western Amazonia, between the Madeira and Juruá Rivers, were the richest. Biogeographic analyses corroborated the existence of a well-defined separation between a western and an eastern lizard fauna. The western fauna contains two groups, which occupy respectively the areas of endemism known as Napo (west) and Inambari (southwest). Relationships among these western localities varied, except between the two northernmost localities, Iquitos and Santa Cecilia, which grouped together in all five area cladograms obtained. No variation existed in the area cladogram between eastern Amazonia sites. The easternmost localities grouped with Guianan localities, and they all grouped with localities more to the west, south of the Amazon River.

Keywords: Herpetofauna. Amazonia. Species composition. Biodiversity. Biogeography. PAE.

Resumo: Estuda-se a fauna de répteis Squamata de quatro localidades da Amazônia meridional brasileira, comparando-as entre si e, com relação aos lagartos, com outras nove áreas bem amostradas de toda a Amazônia. O Coeficiente de Similaridade Biogeográfico para cada par de localidades é calculado e analisada sua correlação com a distância entre as localidades. Uma Análise Parcimoniosa de Endemismos (PAE) é realizada, comparando todas as áreas. Um total de 114 espécies foi registrado nas quatro localidades de estudo, representando 45 espécies de lagartos, três de anfisbenas e 66 de ofídios. As duas localidades entre os rios Xingu e Madeira foram as mais pobres em número de espécies; as localidades mais a oeste, entre o Madeira e o Purus, as mais ricas. As análises biogeográficas corroboram a existência de uma separação bem definida entre uma fauna de lagartos ocidental e uma oriental. A fauna ocidental contém dois grupos, os quais ocupam, respectivamente, as áreas de endemismo conhecidas como Napo (a oeste) e Inambari (a sudoeste). A relação entre as localidades estudadas da Amazônia ocidental variou, exceto pelas duas áreas mais ao norte, Iquitos e Santa Cecilia, que se agruparam nos cinco cladogramas de área obtidos. Na parte oriental, a relação entre as áreas se mostrou constante, com as duas localidades mais a leste, ao sul do rio Amazonas, agrupando-se com as localidades da região das Guianas, e, após, às localidades mais a oeste, ao sul do Amazonas.

Palavras-chave: Herpetofauna. Amazônia. Composição de espécies. Biodiversidade. Biogeografia. PAE.

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INTRODUCTION

During the last few decades a large effort has been made to understand the high biodiversity observed in the Amazonian region. The idea of a long period of stability has been substituted by one of a dynamic history, with pronounced changes in vegetation cover (Haffer, 1969, 1982), changes in river courses (Salo *et al.*, 1986), tectonic events in upper Amazonia (Räsänen, 1993), and more recently the recognition that tectonic events have been more frequent than previously thought, even in Central and Lower Amazonia (Rossetti *et al.*, 2005; Rossetti & Valeriano, 2007). An important part of this discussion is to understand how the Amazonian fauna is distributed and how areas with different faunal composition relate to each other. For some of the better studied groups, especially birds and primates, the large Amazon tributaries seem to be barriers (primary or secondary). However, a broader pattern has been observed for reptiles, with a western fauna subdivided into a western and a southwestern group, a Guianan fauna with a weaker east-west division, and a few endemic elements in southeast Amazonia (Avila-Pires, 1995; for Guianas also Hoogmoed, 1973, 1979). The strongest biogeographic signal, for both reptiles and primates, seems to be an east-west dichotomy (e.g., Avila-Pires, 1995; Silva Jr. & Sites Jr., 1995; Silva & Oren, 1996; Duellman, 1999; Ron, 2000), with the Madeira and Negro Rivers having the greatest impact in dividing the faunas (Hoogmoed, 1979; Ayres & Clutton-Brock, 1992; Haffer, 1992), as already pointed out by Wallace (1852) while studying the distribution of monkeys in Amazonia. Avila-Pires (1995) has shown that for lizards known distributions south of the Amazon pointed to a transitional zone between the Purus and Tapajós Rivers, rather than a single limit for all species. However, deficiency of sampling in Amazonia hindered better analyses. Between 1995 and 1998 a series of expeditions were made, covering four sites along an approximate east-west transect in southern Amazonia, in the states of Pará, Amazonas, Rondônia and Acre, Brazil. Each of these sites has been extensively surveyed for Squamate reptiles, especially lizards, providing a good opportunity to compare faunas along this east-west transect. These new data are added to a biogeographic analysis comparing different sites in Amazonia, including localities north of the Amazon, and in the eastern and western extremes of Amazonia.

MATERIALS AND METHODS

Four Amazonian sites south of the Amazonas/Solimões (hereafter referred to as 'Amazon') river have been studied, all in Brazil (in bold the names used throughout the text to refer to each one). From east to west they are: (1) Pará: Agropecuária Treviso, c. 101 km S and 18 km E of Santarém, close to **Curuá-Una** River, 3° 9' S - 54° 50' W; (2) Rondônia: Parque Estadual **Guajará-Mirim**, 10° 19' S - 64° 33' W; (3) Amazonas: rio **Ituxi**: Fazenda Scheffer, 8° 20' S - 65° 43' W; (4) Acre: rio **Juruá**, 5 km N of Porto Walter, 8° 16' S - 72° 47' W (Figure 1).

All localities are covered by tropical rain forest. With the exception of Ituxi, terra firme forest dominated; Ituxi consisted of a mix of varzea and terra firme forest. Part of the forest studied in Curuá-Una had been selectively logged eight years before our survey, but forest structure was very close to that of a primary forest. Guajará-Mirim was the least disturbed, including reduced hunting pressure due to its protected status as a state park (Avila-Pires & Vitt, 1998; Caldwell & Araújo, 2005; Vitt & Avila-Pires, 1998; Vitt *et al*., 1997, 1998). The herpetofauna of all sites was actively surveyed for about three months, always in the rainy season (December to April), by a team of 4–6 persons. Collected specimens have been deposited at the Museu Paraense Emílio Goeldi (MPEG), at the Sam Noble Oklahoma Museum of Natural History (OMNH), and a smaller part at the Instituto Nacional de Pesquisas da Amazônia (INPA).

Lizard faunas from these sites were compared to those of the following localities (use in text indicated in bold font): (1) **Belém**, Pará, Brazil, based on Avila-Pires (1995) and the collection of Museu Paraense Emílio Goeldi. (2) Estação Científica Ferreira Penna, Floresta Nacional de

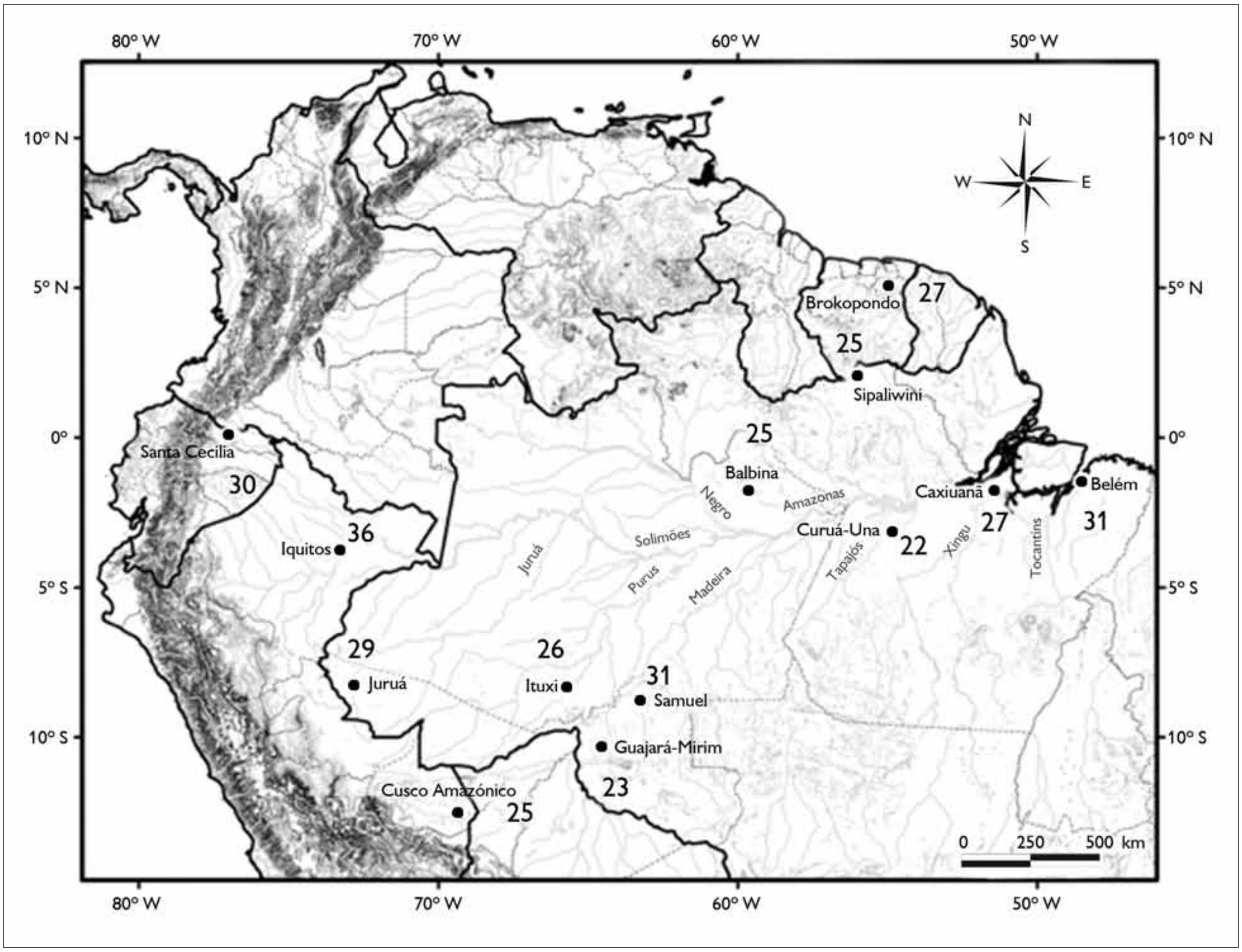


Figure 1. Map of northern South America showing studied localities (Curuá-Una, Guajará-Mirim, Ituxi, and Juruá, all in Brazil), and localities added for biogeographic analyses (Belém, Caxiuanã, Balbina, and Samuel, in Brazil; Sipaliwini and Brokopondo, in Suriname; Cusco Amazónico and Iquitos, in Peru, and Santa Cecilia, Ecuador). Number of lizard species in each area is also shown. For more details about localities see text.

Caxiuanã, Pará, Brazil (1° 42' S - 51° 31' W). This site has been surveyed intermittently since 1992 (Avila-Pires & Hoogmoed, 1997; Bernardi *et al.*, 2002), and recently more thoroughly, using pitfall traps (M. C. Santos Costa, pers. comm.), with specimens deposited in MPEG. (3) **Balbina**, c. 90 km northeast of Manaus, in the state of Amazonas, Brazil, and (4) **Samuel**, c. 36 km east or Porto Velho, state of Rondônia, Brazil. Both localities have been surveyed before and during the flooding of these areas due to the construction of a hydroelectric dam; data from Silva Jr. & Sites Jr. (1995). (5) Forested areas surrounding **Sipaliwini** savanna, westward to the Kutari River headwaters; and (6) between the Suriname River and Brown's Mountain, **Brokopondo** District. Both localities in Suriname, based on data from Hoogmoed (1973). (7) **Cusco Amazónico**, Peru, based on Duellman (2005). (8) **Iquitos** region, Peru, based on Dixon & Soini (1986). (9) **Santa Cecilia**, Ecuador, based on Duellman (1978, 1987). Only forest species have been considered in all analyses (therefore no *Cnemidophorus* spp. or *Tropidurus* spp. were considered). *Hemidactylus mabouia*, when present, was not included, because it clearly represents a recent introduction in Amazonia.

In order to compare species composition in terms of geographic distribution, we classified species into seven categories – 'Widespread', when occurring in most of Amazonia (endemic or not to the region; species as *Pseudogonatodes guianensis* and *Bachia flavescens*, even though missing in some parts, were also included in this category); 'Guianan', if restricted to the Guianan region (all area north of the Amazon and east of the Negro river, as defined by Hoogmoed, 1979) or predominantly in this region (as *Arthrosaura kockii* and *Tretioscincus agilis*, that occur south of the Amazon only east of the Xingu river); 'Eastern', when present both north and south of the Amazon, but absent from the western part; 'Southern', if only known south of the Amazon, but throughout a large part of it (*Enyalius leechii* is the only species in this category); 'Southeastern', referring to two species (*Stenocercus dumerilii* and *Colobosaura modesta*), which in Amazonia occur only east of the Tocantins river; 'Western', when present in western Amazonia (Colombia, Ecuador, Peru, and western part of Brazilian Amazonia – but not necessarily in the entire area), but absent from most of the eastern part; and 'Southwestern', with main occurrence in this part of Amazonia (mainly Peru, Bolivia, and southwestern part of Brazilian Amazonia). These definitions were designed to be specifically broad, since the aim is to understand the relationship between areas. Based on this classification, pie graphs showing the proportion of each group per site have been plotted in a map. Distribution data were mainly based on Avila-Pires (1995, 2005), Duellman (1990, 2005), and Hoogmoed (1979), updated to take into consideration the new collections here reported and other material in the herpetological collection of Museu Paraense Emílio Goeldi. Classification of each species is shown in Appendix.

Additionally, species composition has been compared using the Biogeographic Similarity Coefficient, used by Duellman (1990; as a replacement of the name Faunal Resemblance Factor previously in use for the same coefficient), and equivalent to $2C/(N_1 + N_2)$, where N_1 = number of species in locality 1, N_2 = number of species in locality 2, and C = number of species common to both localities. Correlation between these coefficients and the linear geographic distances between localities was calculated to determine the proportion of variation among localities that can be attributed to distance alone.

A Parsimony Analysis of Endemicity (PAE; Rosen, 1985; Rosen & Smith, 1988) was performed to construct an area cladogram on the basis of presence of taxa. By using the same algorithms used for phylogenetic trees and the establishment of an outgroup where absence of species is considered primitive, only presence of species is used to establish area relationships. This is a more meaningful analysis than taking into consideration both presence and absence of species, because it is difficult to ascertain with confidence if the absence is real or represents missing data. PAE was performed with Winclada/Nona (respectively Nixon, 2002 and Goloboff, s/d, choosing heuristic analysis, with 100 replications). For this analysis taxa present in only one area or in all areas have not been considered, because they are uninformative regarding relationships between areas. Subspecies were not considered, except for *Anolis nitens*, for which strong evidences indicate that they should be considered distinct species (Glor *et al*., 2001). As a consequence, 46 taxa have been considered informative.

RESULTS

Considering all four sites together, a total of 114 Squamate reptiles were registered, of which 45 (39.5%) were lizards, three (2.6%) amphisbaenians, and 66 (57.9%) snakes (Table 1). When each area is considered separately, Guajará-Mirim is the richest, with 62 species (54.4%) of the total, and Juruá is the poorest, with 50 species (43.9% of the total). Snakes and amphisbaenians, however, are probably undersampled. When only lizards are compared, Juruá is the richest area (29 species) and Curuá-Una the poorest (22 species). Among the other Amazonian sites included in this study for comparison, numbers of snake and amphisbaenian species are available for Caxiuanã, Balbina, Samuel, Cusco Amazônico, Iquitos and Santa Cecilia. These groups together

Table 1. Squamate species recorded in the four studied areas. Totals and percentages by locality and group are given at the end.

Continue

	Curuá-Una	Guajará-Mirim	Ituxi	Juruá	All Areas
Enyalioides laticeps (Guichenot, 1855)	-	-	X	X	
Enyalioides palpebralis (Boulenger, 1883)	-	-	-	X	
Iguana iguana (Linnaeus, 1758)	-	-	X	-	
Anolis fuscoauratus D'Orbigny, 1837	X	X	X	X	
Anolis nitens (Wagler, 1830)	-	-	X	X	
Anolis ortonii Cope, 1868	X	-	X	X	
Anolis punctatus Daudin, 1802	X	X	X	X	
Anolis trachyderma Cope, 1876	X	-	-	X	
Anolis transversalis Duméril, 1851	-	X	X	X	
Enyalius leechii (Boulenger, 1885)	X	-	-	-	
Polychrus marmoratus (Linnaeus, 1758)	X	-	-	-	
Plica plica (Linnaeus, 1758)	X	X	X	X	
Plica umbra (Linnaeus, 1758)	X	X	X	X	
Stenocercus roseiventris D'Orbigny, 1837	-	-	-	X	
Uranoscodon superciliosus (Linnaeus, 1758)	X	X	X	-	
Coleodactylus amazonicus (Andersson, 1918)	X	X	X	-	
Gonatodes hasemani Griffin, 1917	-	X	X	X	
Gonatodes humeralis (Guichenot, 1855)	X	X	-	X	
Pseudogonatodes guianensis Parker, 1935	-	-	-	X	
Thecadactylus rapicauda (Houttuyn, 1782)	X	X	X	X	
Alopoglossus angulatus (Linnaeus, 1758)	-	X	X	X	
Alopoglossus atriventris Duellman, 1973	-	-	X	X	
Arthrosaura reticulata (O'Shaughnessy, 1881)	X	X	X	-	
Bachia gr. *dorbignyi* (Duméril & Bibron, 1839)	-	X	-	X	
Bachia flavescens (Bonnaterre, 1789)	X	-	-	-	
Cercosaura argulus Peters, 1863	-	X	-	X	
Cercosaura eigenmanni (Griffin, 1917)	-	X	X	-	
Cercosaura ocellata Wagler, 1830	X	-	X	X	
Cercosaura oshaughnessyi (Boulenger, 1885)	-	-	-	X	
Iphisa elegans Gray, 1851	X	X	-	X	
Leposoma osvaldoi Avila-Pires, 1995	-	X	-	-	
Leposoma percarinatum (Müller, 1923)	X	X	-	-	
Neusticurus ecpleopus Cope, 1876*	X	-	-	X	
Neusticurus juruazensis Avila-Pires & Vitt, 1998*	-	-	-	X	
Ptychoglossus brevifrontalis Boulenger, 1912	-	-	X	X	
Ameiva ameiva (Linnaeus, 1758)	X	X	X	X	

Continue

	Curuá-Una	Guajará-Mirim	Ituxi	Juruá	All Areas
Cnemidophorus lemniscatus (Linnaeus, 1758)	X	-	-	-	
Kentropyx altamazonica Cope, 1876	-	X	X	-	
Kentropyx calcarata Spix, 1825	X	X	-	-	
Kentropyx pelviceps Cope, 1868	-	-	X	X	
Tupinambis longilineus Avila-Pires, 1995	-	-	X	-	
Tupinambis teguixin (Linnaeus, 1758)	-	X	X	X	
Mabuya bistriata (Spix, 1825)	-	-	X	-	
Mabuya nigropunctata (Spix, 1825)	X	X	X	X	
Amphisbaena alba Linnaeus, 1758	-	-	X	-	
Amphisbaena cunhai Hoogmoed & Avila-Pires, 1991	-	-	X	-	
Amphisbaena fuliginosa Linnaeus, 1758	-	-	X	X	
Typhlophis squamosus (Schlegel, 1839)	X	-	-	-	
Leptotyphlops macrolepis (Peters, 1857)	X	-	-	-	
Typhlops reticulates (Linnaeus, 1758)	X	-	X	-	
Anilius scytale (Linnaeus, 1758)	X	-	-	-	
Boa constrictor Linnaeus, 1758	-	-	X	X	
Corallus caninus (Linnaeus, 1758)	X	X	-	-	
Corallus hortulanus (Linnaeus, 1758)	X	X	X	X	
Epicrates cenchria (Linnaeus, 1758)	X	X	-	X	
Atractus major Boulenger, 1894	-	X	-	X	
Atractus latifrons Günther, 1868	-	X	-	-	
Atractus snethlageae Cunha & Nascimento, 1983	X	X	-	-	
Chironius exoletus (Linnaeus, 1758)	-	-	X	-	
Chironius fuscus (Linnaeus, 1758)	X	X	X	X	
Chironius multiventris Schmidt & Walker, 1942	-	X	X	-	
Chironius scurrulus (Wagler, 1824)	X	X	X	-	
Clelia clelia (Daudin, 1803)	-	X	X	X	
Dendrophidion dendrophis (Schlegel, 1837)	X	X	-	X	
Dipsas catesbyi (Sentzen, 1796)	X	X	X	-	
Dipsas indica Laurenti, 1768	X	X	-	-	
Dipsas pavonina Schlegel, 1837	X	-	-	-	
Dipsas variegata Duméril, Bibron & Duméril, 1854	-	X	-	-	
Drepanoides anomalus (Jan, 1863)	-	X	X	-	
Drymarchon corais (F. Boie, 1827)	-	-	-	X	
Drymoluber dichrous (Peters, 1863)	X	X	X	X	
Erythrolamprus aesculapii (Linnaues, 1766)	-	-	X	-	
Helicops angulatus (Linnaeus, 1758)	X	X	X	X	

Continue

	Curuá-Una	Guajará-Mirim	Ituxi	Juruá	All Areas
Helicops hagmanni Roux, 1910	-	X	-	-	
Imantodes cenchoa (Linnaeus, 1758)	X	X	X	X	
Imantodes lentiferus Cope, 1894	-	X	X	-	
Leptodeira annulata (Linnaeus, 1758)	X	X	X	-	
Leptophis ahaetulla (Linnaeus, 1758)	-	-	X	X	
Liophis reginae (Linnaeus, 1758)	-	X	X	X	
Liophis typhlus (Linnaeus, 1758)	-	X	X	-	
Mastigodryas boddaerti (Sentzen, 1796)	X	-	-	-	
Oxyrhopus formosus (Wied, 1820)	-	X	X	X	
Oxyrhopus petola (Linnaeus, 1758)	-	X	-	X	
Oxyrhopus trigeminus Duméril, Bibron & Duméril, 1854	X	-	-	-	
Philodryas viridissimus (Linnaeus, 1758)	-	X	X	-	
Pseudoboa coronata Schneider, 1801	X	-	-	-	
Pseustes poecilonotus (Günther, 1858)	X	X	-	-	
Pseustes sulphureus (Wagler, 1824)	-	-	X	-	
Rhinobothryum lentiginosum Scopoli, 1785	X	X	-	-	
Siphlophis cervinus (Laurenti, 1768)	-	X	-	-	
Siphlophis compressus (Daudin, 1803)	-	X	-	-	
Spilotes pullatus (Linnaeus, 1758)	-	-	X	-	
Taeniophallus brevirostris (Peters, 1863)	X	-	-	X	
Taeniophallus occipitalis (Jan, 1863)	-	-	X	-	
Tantilla melanocephala (Linnaeus, 1758)	-	X	-	-	
Xenodon rhabdocephalus (Wied, 1824)	-	-	X	-	
Xenopholis scalaris (Wucherer, 1861)	X	X	X	-	
Xenoxybelis argenteus (Daudin, 1803)	X	X	-	X	
Xenoxybelis boulengeri (Procter, 1923)	-	-	X	-	
Mircrurus albicinctus Amaral, 1926	-	X	-	-	
Micrurus hemprichii (Jan, 1885)	-	-	X	-	
Micrurus langsdorffi (Wagler, 1824)	-	-	X	-	
Micrurus lemniscatus (Linnaeus, 1758)	X	X	-	-	
Micrurus spixii (Wagler, 1824)	-	-	X	-	
Mircurus surinamensis (Cuvier, 1817)	-	X	-	X	
Bothriopsis bilineata (Wied, 1825)	X	X	-	-	
Bothiropsis taeniata (Wagler, 1824)	X	X	X	-	
Bothrops atrox (Linnaeus, 1758)	X	X	X	X	
Lachesis muta (Linnaeus, 1758)	-	-	-	X	

Conclusion

	Curuá-Una	Guajará-Mirim	Ituxi	Juruá	All Areas
Total	**52**	**62**	**61**	**50**	**114**
Lizards	22	23	26	29	45
Amphisbaenians	0	0	3	1	3
Snakes	30	39	32	20	66
% lizards	42.3	37.1	42.6	58.0	39.5
% amphisbaenians	0.0	0.0	4.9	2.0	2.6
% snakes	57.7	62.9	52.5	40.0	57.9

* These two species have been reallocated to a new genus, *Potamites*, by Doan & Castoe (2005), but we prefer to wait a more thorough taxonomic study on the genus *Neusticurus* before accepting such changes.

represent between 1.8 to three times the number of lizards in each locality, while in the four studied sites this proportion ranges between 0.7 to 1.7 (Table 2), reinforcing the idea that several species of snakes (and some amphisbaenians) are still to be expected in the four areas studied.

Considering only lizards, two areas, Curuá-Una and Guajará-Mirim, have a lower number of species (respectively 22 and 23), with the other two, Ituxi and Juruá, containing respectively 26 and 29 species, a number closer to that also found in other areas (Table 2). Since Curuá-Una had been subjected to selective logging before our studies in the area, we cannot rule out that this low number is a consequence of disturbance. Guajará-Mirim, however, is a protected area, thus disturbance is less likely an explanation for its low number of species, even though the history of the area previous to protection is not known (see also below). When the additional Amazonian sites are included in the comparison, lowest values in lizard species are found in the more central Amazonian sites, except for Samuel, and in Cusco Amazónico, in the extreme southwest corner of Amazonia (Figure 1). Although part of these differences may be due to deficiency of collecting, central Amazonian sites may well have less species than peripheral ones, since species restricted to the west do not reach sites progressively further east, those from the extreme east are similarly absent from more central sites and, for the localities south of the Amazon, Guianan species are absent (Figure 2). The larger number of species in Samuel, when compared to Ituxi and Guajará-Mirim, either could be because of sampling a more heterogeneous area, or due to better sampling as a result of the complete flooding of a large area – a question that at present remains open.

Table 2. Proportion of number of snake and amphisbaenian species in relation to number of lizard species in each of the areas included for comparison and in the four studied areas.

	Number of species		
	Snakes + amphisbaenians	Lizards	Proportion
Caxiuanã	61	27	2,3
Balbina	72	25	2,9
Samuel	95	32	3,0
Cusco Amazónico	52	25	2,1
Iquitos	90	36	2,5
Santa Cecilia	54	30	1,8
Curuá-Una	30	22	1,4
Guajará-Mirim	39	23	1,7
Ituxi	35	26	1,3
Juruá	21	29	0,7

Regarding species composition in each site (Figure 2), Ituxi, Guarajá-Mirim, Samuel, Curuá-Una and Belém are more mixed than remaining sites, where species from two or three categories are present. In the case of Belém, this is due to a mainly Guianan species (*Arthrosaura kockii*) and two species (*Stenocercus dumerilii* and *Colobosaura modesta*)

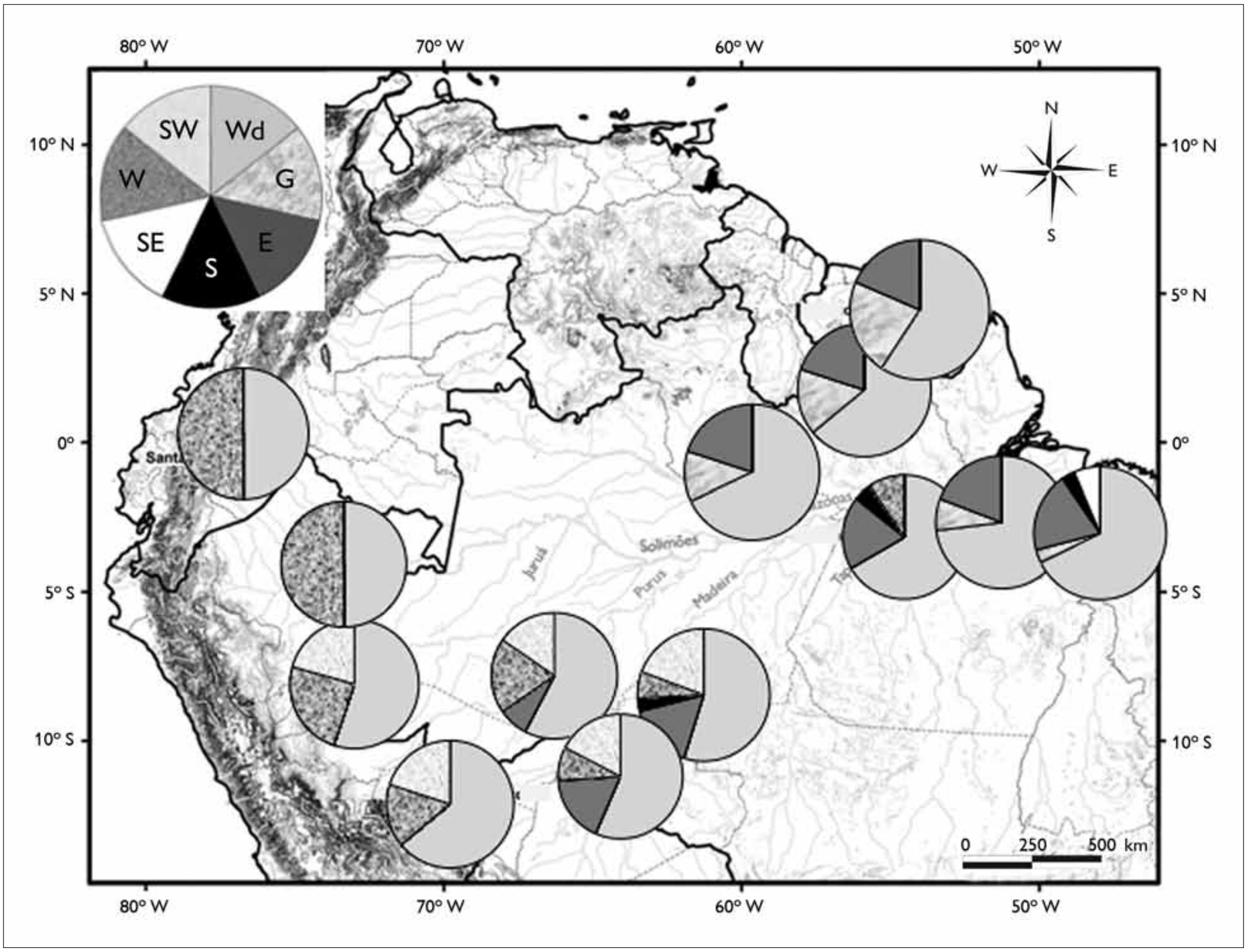


Figure 2. Distribution of species in relation to geographic composition, for each site. Legend for geographic categories appears in the upper left corner. For category definitions see text, and for site names see Figure1.

restricted to this easternmost part of Amazonia. Curuá-Una contains two species, *Anolis trachyderma* and *Neusticurus ecpleopus*, which are distributed mainly in the western part of Amazonia. Guajará-Mirim and Samuel, east of the Madeira River, and Ituxi, west of the Madeira River, present a mixture of eastern, western, and southwestern elements. They represent therefore composite areas.

Biogeographic Similarity Coefficients (BSC) between the studied sites, based solely on lizards, are presented in Table 3, while correlation between BSC and geographic distance is shown in Figure 3. Distance explains about 47% of the variation observed among sites. Rondonian localities (Guajará-Mirim and Samuel) are less similar than expected by distance alone (BSC distinctly below the 99% confidence interval of the regression line) in relation to western localities in Peru (Cusco Amazónico, Iquitos) and Ecuador (Santa Cecilia), but not in Brazil (Ituxi, Juruá). Balbina, in Brazilian Guiana, is also more different than expected by distance alone in relation to all western localities (Ituxi and Juruá included), while differences between these localities and Sipaliwini and Brokopondo, in Suriname, could be in large part explained by distance. Curuá-Una, in central Amazonia south of the Amazon, and Cusco Amazónico, in southern Peru, are also less similar

Table 3. Total number of lizard species per site (in bold, diagonal line), number of species in common (above diagonal line), and Coefficient of Biological Similarity (below diagonal line) between each pair of sites. Details about localities are given in the text.

	BEL	CAX	CUR	BAL	SAM	GJM	ITU	JUR	SIP	BRO	CA	IQU	SC
Belém	**28**	22	16	19	22	15	14	13	18	21	13	14	12
Caxiuanã	0.80	**27**	17	19	20	16	16	14	21	22	13	15	12
Curuá-Una	0.64	0.69	**22**	15	17	14	12	13	15	16	10	14	13
Balbina	0,72	0,73	0,64	**25**	17	14	12	11	19	19	11	14	11
Samuel	0,75	0,69	0,64	0,61	**31**	21	20	18	17	18	16	16	13
Guajará-Mirim	0.59	0.64	0.62	0,58	0,78	**23**	16	15	14	15	13	13	11
Ituxi	0.52	0.60	0.50	0,47	0,70	0.65	**26**	18	14	13	16	19	14
Juruá	0.46	0.50	0.51	0,41	0,60	0.58	0.65	**29**	12	12	19	21	19
Sipaliwini	0.68	0.81	0.64	0,76	0,61	0.58	0.55	0.44	**25**	22	13	14	11
Brokopondo	0.76	0.81	0.65	0,73	0,62	0.60	0.49	0.43	0.85	**27**	11	13	10
Cusco Amazónico	0,49	0,50	0,43	0,44	0,57	0,54	0,63	0,70	0,52	0,42	**25**	18	15
Iquitos	0.44	0.48	0.56	0,46	0,48	0.44	0.61	0.65	0.46	0.41	0,59	**36**	27
Santa Cecilia	0.41	0.42	0.50	0,40	0,43	0.42	0.50	0.64	0.40	0.35	0,55	0.82	**30**

than expected when distance is taken into consideration. Conversely, eastern Amazonian localities (Belém, Caxiuanã) are more similar than expected by distance alone in relation to Guianan localities (Balbina, Sipaliwini, Brokopondo), as well as among Guianan localities. These localities (eastern Amazonia and Guianan) are also more similar than expected in relation to Rondonian localities.

Parsimony Analysis of Endemicity resulted in five most parsimonious trees, with 117 steps and consistency index of 44 (Figure 4 and Appendix). In all five trees an east-west dichotomy is evident, with an eastern group formed by ((Guajará-Mirim – Samuel) (Curuá-Una (Balbina (Sipaliwini – Brokopondo) (Caxiuanã-Belém)))). This whole group is linked by the presence of *Leposoma percarinatum* and *Kentropyx calcarata*. The relationship between the western sites varies, except for a sister relationship between Iquitos and Santa Cecilia, but *Kentropyx pelviceps* is common to all of them. Ituxi groups in one case with the eastern sites (linked to them by the presence of *Uranoscodon superciliosus* and *Coleodactylus amazonicus*), in all other cases with the western sites. Even though Guajará-Mirim and Samuel, both in Rondônia, appear always linked to the eastern group, they share a number of species with the western sites (which are absent from eastern sites), e.g. *Enyalioides laticeps*, *Anolis transversalis*, *Bachia* gr. *dorbignyi*. Cusco Amazónico and Samuel have in common *Polychrus liogaster*; Cusco Amazónico, Ituxi, Guajará-Mirim and Samuel *Cercosaura eigenmanni*; and these sites plus Juruá have in common *Gonatodes hasemani*.

DISCUSSION

Our results point to a deficiency in snake data for our four studied sites, which was to be expected. Duellman (1978, 2005) already showed that long-term surveys are needed for representative sampling of snakes. Sampling of lizards, on the contrary, seems to be reasonably complete as a result of our three-month surveys.

Regarding the distribution of lizards, all analyses point to a main east-west dichotomy in Amazonia, while relationships within each of these groups are less clearly defined. For most vertebrates a distinct western fauna is evident, usually also with a distinction between a western and a southwestern group, while eastern Amazonian areas may appear either as a distinct group (e.g., in lizards

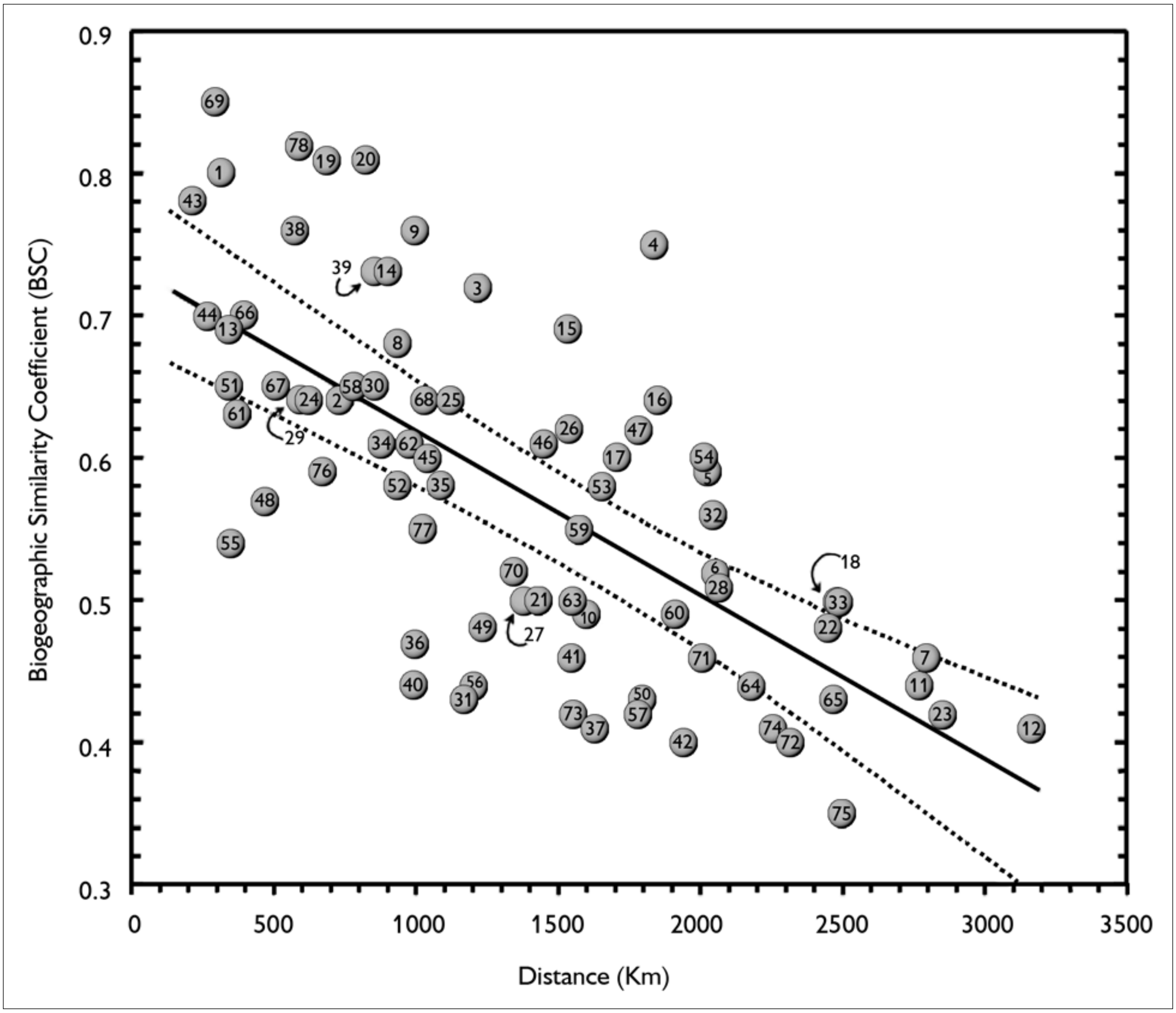
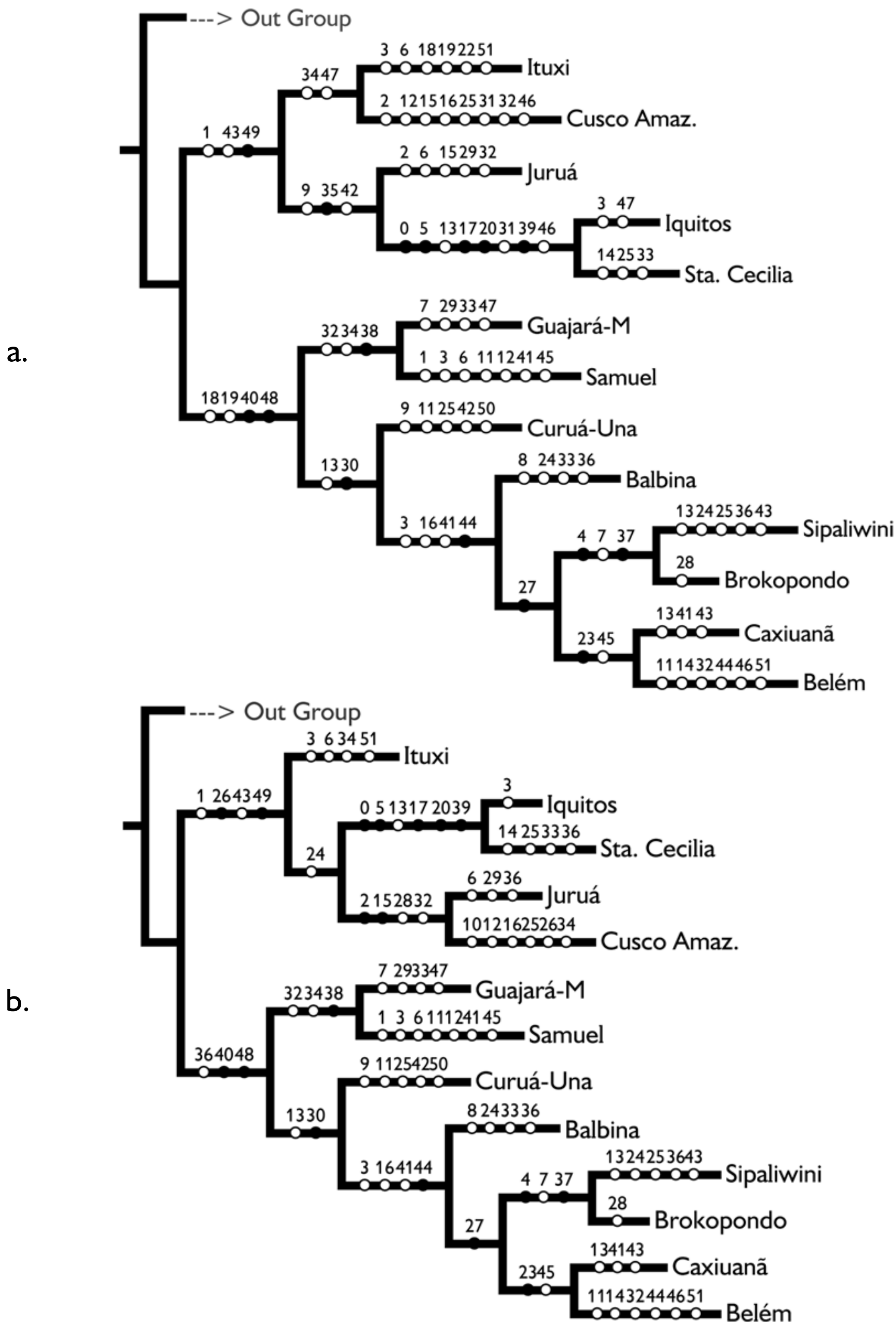
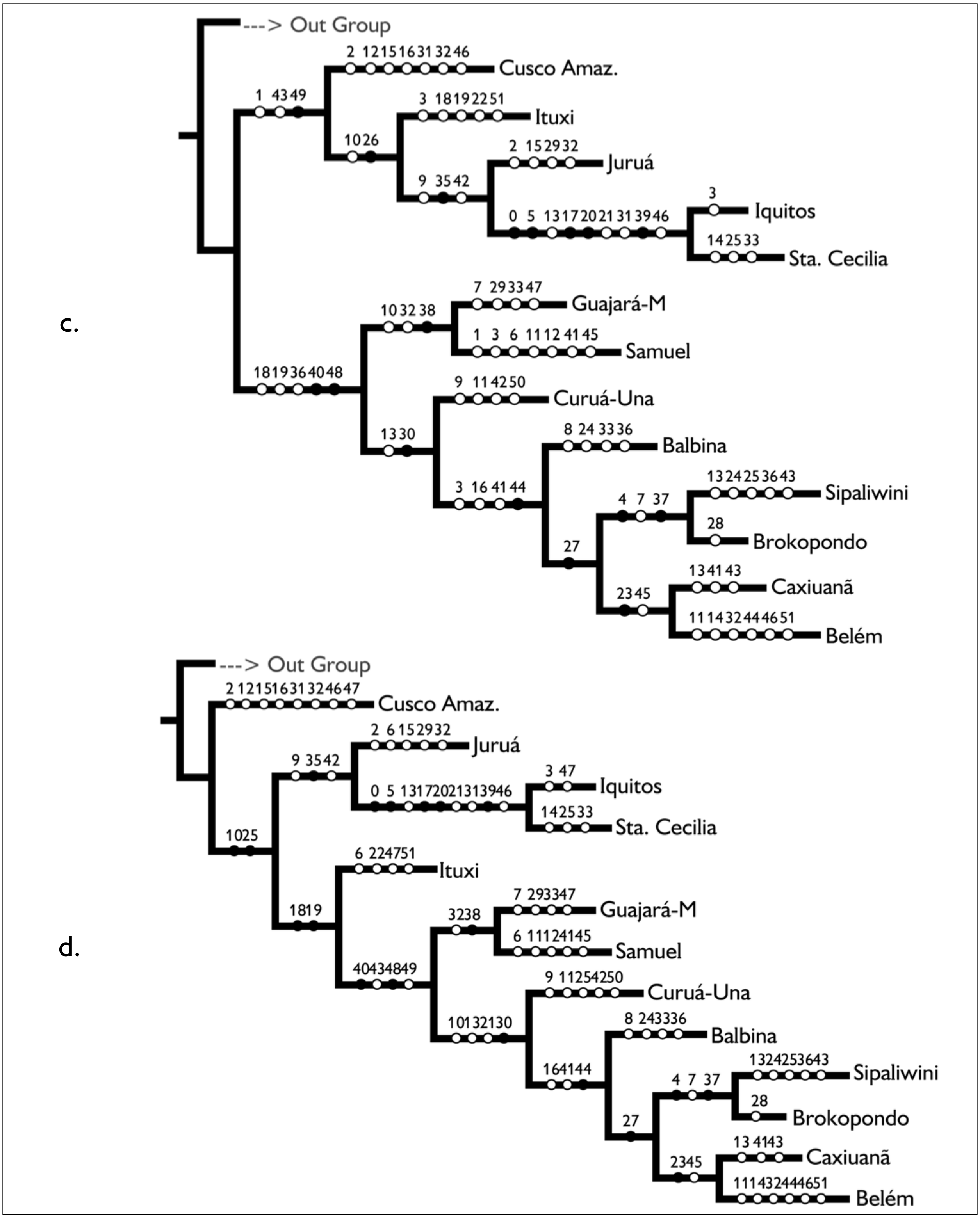


Figure 3. Correlation between Biogeographic Similarity Coefficient (BSC) and geographic distance (in kilometers) between pairs of sites. Regression line and 99% confidence interval lines are shown (BSC = 0.7333 – 0.0001 *Distance; $r^2 = 0.4682$). Numbers correspond to the following pairs of sites: 1. Belém – Caxiuanã, 2. Belém – Curuá-Una, 3. Belém – Balbina, 4. Belém – Samuel, 5. Belém – Guajará-Mirim, 6. Belém – Ituxi, 7. Belém – Juruá, 8. Belém – Sipaliwini, 9. Belém – Brokopondo, 10. Belém – Cusco Amazónico, 11. Belém – Iquitos, 12. Belém – Santa Cecilia, 13. Caxiuanã – Curuá-Una, 14. Caxiuanã – Balbina, 15. Caxiuanã – Samuel, 16. Caxiuanã – Guajará-Mirim, 17. Caxiuanã – Ituxi, 18. Caxiuanã – Juruá, 19. Caxiuanã – Sipaliwini, 20. Caxiuanã – Brokopondo, 21. Caxiuanã – Cusco Amazónico, 22. Caxiuanã – Iquitos, 23. Caxiuanã – Santa Cecilia, 24. Curuá-Una – Balbina, 25. Curuá-Una – Samuel, 26. Curuá-Una – Guajará-Mirim, 27. Curuá-Una – Ituxi, 28. Curuá-Una – Juruá, 29. Curuá-Una – Sipaliwini, 30. Curuá-Una – Brokopondo, 31. Curuá-Una – Cusco Amazónico, 32. Curuá-Una – Iquitos, 33. Curuá-Una – Santa Cecilia, 34. Balbina – Samuel, 35. Balbina – Guajará-Mirim, 36. Balbina – Ituxi, 37. Balbina – Juruá, 38. Balbina – Sipaliwini, 39. Balbina – Brokopondo, 40. Balbina – Cusco Amazónico, 41. Balbina – Iquitos, 42. Balbina – Santa Cecilia, 43. Samuel – Guajará-Mirim, 44. Samuel – Ituxi, 45. Samuel – Juruá, 46. Samuel – Sipaliwini, 47. Samuel – Brokopondo, 48. Samuel – Cusco Amazónico, 49. Samuel – Iquitos, 50. Samuel – Santa Cecilia, 51. Guajará-Mirim – Ituxi, 52. Guajará-Mirim – Juruá, 53. Guajará-Mirim – Sipaliwini, 54. Guajará-Mirim – Brokopondo, 55. Guajará-Mirim – Cusco Amazónico, 56. Guajará-Mirim – Iquitos, 57. Guajará-Mirim – Santa Cecilia, 58. Ituxi – Juruá, 59. Ituxi – Sipaliwini, 60. Ituxi – Brokopondo, 61. Ituxi – Cusco Amazónico, 62. Ituxi – Iquitos, 63. Ituxi – Santa Cecilia, 64. Juruá – Sipaliwini, 65. Juruá – Brokopondo, 66. Juruá – Cusco Amazónico, 67. Juruá – Iquitos, 68. Juruá – Santa Cecilia, 69. Sipaliwini – Brokopondo, 70. Sipaliwini – Cusco Amazónico, 71. Sipaliwini – Iquitos, 72. Sipaliwini – Santa Cecilia, 73. Brokopondo – Cusco Amazónico, 74. Brokopondo – Iquitos, 75. Brokopondo – Santa Cecilia, 76. Cusco Amazónico – Iquitos, 77. Cusco Amazónico – Santa Cecilia, 78. Iquitos – Santa Cecilia.


a.
---> Out Group
Ituxi
Cusco Amaz.
Juruá
Iquitos
Sta. Cecilia
Guajará-M
Samuel
Curuá-Una
Balbina
Sipaliwini
Brokopondo
Caxiuanã
Belém
b.
---> Out Group
Ituxi
Iquitos
Sta. Cecilia
Juruá
Cusco Amaz.
Guajará-M
Samuel
Curuá-Una
Balbina
Sipaliwini
Brokopondo
Caxiuanã
Belém


c.
---> Out Group
Cusco Amaz.
Ituxi
Juruá
Iquitos
Sta. Cecilia
Guajará-M
Samuel
Curuá-Una
Balbina
Sipaliwini
Brokopondo
Caxiuanã
Belém
d.
---> Out Group
Cusco Amaz.
Juruá
Iquitos
Sta. Cecilia
Ituxi
Guajará-M
Samuel
Curuá-Una
Balbina
Sipaliwini
Brokopondo
Caxiuanã
Belém

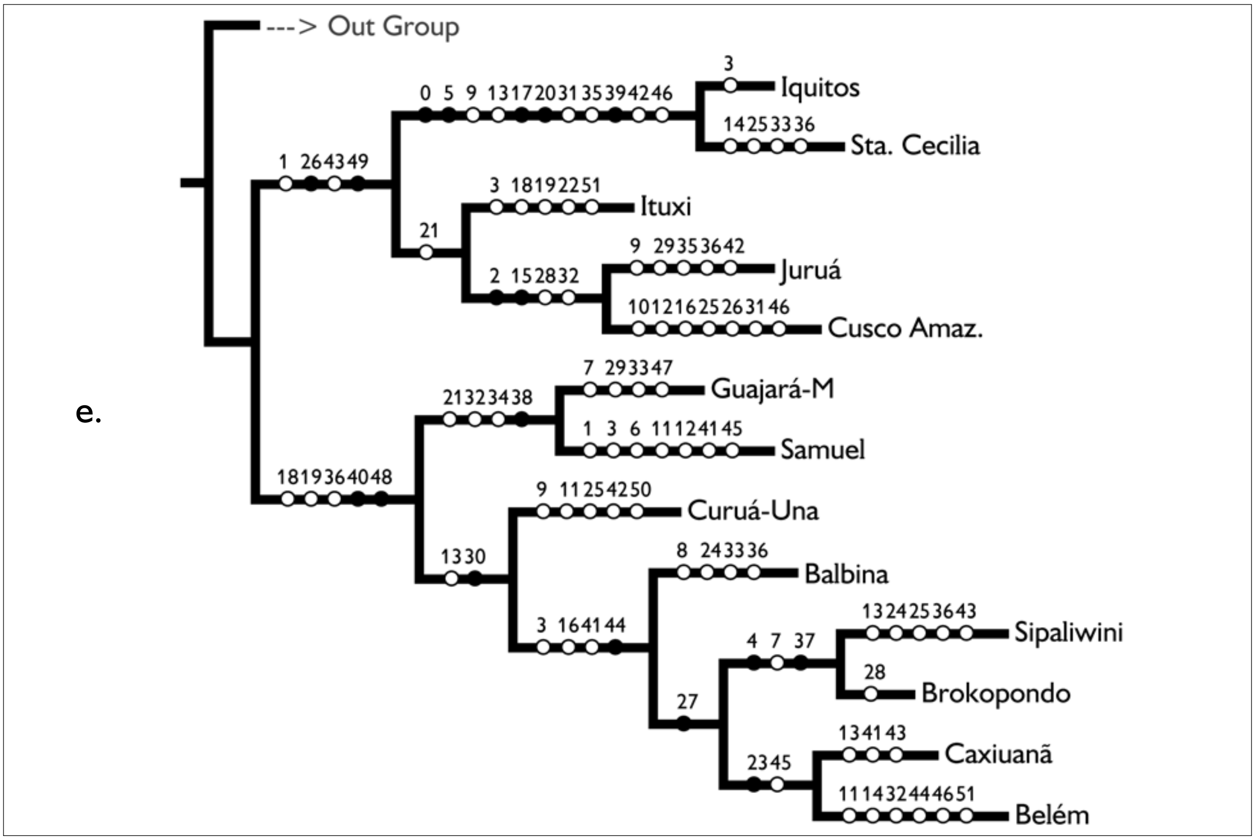


Figure 4. Most parsimonious area cladograms (a-e) obtained through a Parsimony Analysis of Endemicity comparing lizard fauna of 13 Amazonian sites (length = 117, consistency index = 44, retention index = 55). Numbers in each branch correspond to taxa: 0 - *Enyalioides cofanorum*. 1 - *Enyalioides laticeps*. 2 - *Enyalioides palpebralis*. 3 - *Iguana iguana*. 4 - *Anolis nitens chrysolepis*. 5 - *Anolis nitens scypheus*. 6 - *Anolis nitens tandai*. 7 - *Anolis ortonii*. 8 - *Anolis punctatus*. 9 - *Anolis trachyderma*. 10 - *Anolis transversalis*. 11 - *Enyalius leechii*. 12 - *Polychrus liogaster*. 13 - *Polychrus marmoratus*. 14 - *Plica plica*. 15 - *Stenocercus roseiventris*. 16 - *Uracentron azureum*. 17 - *Uracentron flaviceps*. 18 - *Uranoscodon superciliosus*. 19 - *Coleodactylus amazonicus*. 20 - *Gonatodes concinnatus*. 21 - *Gonatodes hasemani*. 22 - *Gonatodes humeralis*. 23 - *Lepidoblepharis heyerorum*. 24 - *Pseudogonatodes guianensis*. 25 - *Alopoglossus angulatus*. 26 - *Alopoglossus atriventris*. 27 - *Arthrosaura kockii*. 28 - *Arthrosaura reticulata*. 29 - *Bachia* gr. *dorbignyi*. 30 - *Bachia flavescens*. 31 - *Bachia trisanale*. 32 - *Cercosaura argulus*. 33 - *Cercosaura ocellata*. 34 - *Cercosaura eigenmanni*. 35 - *Cercosaura ochaughnessyi*. 36 - *Iphisa elegans*. 37 - *Leposoma guianense*. 38 - *Leposoma osvaldoi*. 39 - *Leposoma parietale*. 40 - *Leposoma percarinatum*. 41 - *Neusticurus bicarinatus*. 42 - *Neusticurus ecpleopus*. 43 - *Ptychoglossus brevifrontalis*. 44 - *Tretioscincus agilis*. 45 - *Crocodilurus amazonicus*. 46 - *Dracaena guianensis*. 47 - *Kentropyx altamazonica*. 48 - *Kentropyx calcarata*. 49 - *Kentropyx pelviceps*. 50 - *Tupinambis teguixin*. 51 - *Mabuya bistriata*.

– Ron, 2000; Silva Jr. & Sites Jr., 1995 –, and partially in snakes – Silva Jr. & Sites Jr., 1995), or as progressively more basal areas (e.g., amphibians and primates – Ron, 2000). Avila-Pires (1995), analyzing the lizard fauna of Rondônia as a whole, found a dubious relationship of this region with eastern or western faunas. In the present study, the two sites in Rondônia grouped with the eastern sites, even though they also contain species that have a western or southwestern distribution.

Relationships between eastern areas are more variable, with eastern areas south of the Amazon more related to each other than to Guiana (e.g., in snakes and lizards according to Silva Jr. & Sites Jr., 1995), or easternmost areas south of the Amazon more similar to Guiana than to areas further west, especially Rondônia (e.g., lizards according to Ron, 2000, and this study). Ayres & Clutton-Brock (1992) found that primate faunas on opposite sides of the Amazon became more similar closer to the river's mouth. Silva (1995), analyzing patterns of distribution of the avifauna associated with cerrado vegetation, concluded that one of the main corridors linking savannas north and south of the Amazon could have been along the Atlantic coast, a possibility also raised by Avila-Pires (1995) in relation to *Tropidurus hispidus*. Part of the similarity between Guiana and the easternmost fauna south of the Amazon could be therefore a result of migration across the lower Amazon River.

A number of areas of endemism have been recognized in Amazonia, initially for birds (e.g., Haffer, 1978, 1985; Cracraft, 1985), later on also for primates (e.g., Silva & Oren, 1996), and partially for other groups (Ron, 2000; Silva *et al*., 2005). When we look at lizard distribution, western and southwestern groups correspond to the Napo and Inambari areas of endemism. Guiana as a whole is considered an area of endemism, also recognizable for lizards. For the other areas of endemism (Imeri, in northwestern Amazonia, and Rondônia, Tapajós, Xingu and Belém, in southeastern Amazonia – Silva *et al*., 2005), there is little or no evidence for lizards. A single species, *Gonatodes tapajonicus*, is known from only one locality in the Tapajós area of endemism, and another species, *Stenocercus dumerilii*, is restricted to the Belém area of endemism. Moreover, the Tocantins River forms the eastern limit of the distribution of *Plica plica*, and the Xingu River the western limit (south of the Amazon) of *Arthrosaura kockii*, *Colobosaura modesta*, and *Tretioscincus agilis*, indicating a barrier effect of these rivers for at least a few species.

The Madeira River is considered the main barrier between the eastern and western faunas. Its importance as a faunal divisor, together with the Negro and Amazon Rivers, was already recognized by Wallace (1852), and has been since confirmed by several other studies (Silva *et al*., 2005). Data on lizards by Avila-Pires (1995) corroborated the importance of the Madeira River in this aspect, even though she observed that species limits occurred variably between the Purus and Tapajós Rivers. Of the five area cladograms we obtained in the PAE analysis, four showed a division between the sites west and east of the Madeira River, while one showed the Ituxi site, in the interfluvium Madeira-Purus, as basal to the group containing all eastern sites. Looking at the Biogeographic Similarity Coefficient, differences in the lizard fauna in Guajará-Mirim and Samuel, east of the Madeira River, and Ituxi and Juruá, west of it, could be explained by distance, with no evidence of a faunal barrier between these sites (while between Rondonian sites and those in Peru and Ecuador distance alone could not explain the low BSC). As Rondônia lies in the upper Madeira River basin, one may suppose that, even if the river forms a barrier, this would not be as effective upstream as downstream. However, Aleixo (2004) found that for birds of the *Xiphorhynchus elegans* group, populations of *X. e. elegans* (Pelzeln, 1868) from the western bank of the lower Madeira River were more similar to other populations to the east, while upriver the Madeira River separated two clades of this group, *X. e. elegans* and *X. e. juruanus* (Ihering, 1904). Undoubtedly this is a complex region, where distinct faunas coalesce. It is plausible that a barrier existed formerly around the area of the Madeira River, the river acting as a secondary, but partial barrier. The Madeira River is a "white-water" river, thus relatively slow flowing and meandering, which facilitates river crossing, even if it is a large river (by far the largest southern tributary of the Amazon). Thus both historical and present conditions would explain the large dissimilarity of faunas on the two sides of the river, while at the same time several species are presently found that have clearly crossed the river.

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APPENDIX. Lizard data used for PAE analysis comparing 13 Amazonian sites and geographic classification (GC) used in pie graphs. '0' represents absence, '1' presence. Species with occurrence in all sites or in only one site (shaded rows below) were excluded, and an outgroup with no species present was added to the analysis. CUR = Curuá-Una, GJM = Guajará-Mirim, ITU = Ituxi, JUR = Juruá, CAX = Caxiuanã, BEL = Belém, BAL = Balbina, SAM = Samuel, CA = Cusco Amazónico, IQUI = Iquitos, SC = Santa Cecilia, SIP = Sipaliwini, BRO = Brokopondo. GC: E = Eastern (species), G = Guianan, S = Southern, SE = Southeastern, SW = Southwestern, W = Western, Wd = Widespread. For details about localities and GC definitions see text.

Continue

Taxa	Sites													GC
	CUR	GJM	ITU	JUR	CAX	BEL	BAL	SAM	CA	IQUI	SC	SIP	BRO	
Enyalioides cofanorum Duellman, 1973	0	0	0	0	0	0	0	0	0	1	1	0	0	W
Enyalioides laticeps (Guichenot, 1855)	0	0	1	1	0	0	0	1	1	1	1	0	0	W
Enyalioides palpebralis (Boulenger, 1883)	0	0	0	1	0	0	0	0	1	0	0	0	0	SW
Iguana iguana (Linnaeus, 1758)	0	0	1	0	1	1	1	1	0	1	0	1	1	Wd
Anolis bombiceps Cope, 1876	0	0	0	0	0	0	0	0	0	1	0	0	0	W
Anolis fuscoauratus D'Orbigny, 1837	1	1	1	1	1	1	1	1	1	1	1	1	1	Wd
Anolis nitens chrysolepis Duméril, Bibron & Duméril, 1837	0	0	0	0	0	0	0	0	0	0	0	1	1	G
Anolis nitens nitens (Wagler, 1830)	0	0	0	0	0	0	1	0	0	0	0	0	0	G
Anolis nitens scypheus Cope, 1864	0	0	0	0	0	0	0	0	0	1	1	0	0	W
Anolis nitens tandai Avila-Pires, 1995	0	0	1	1	0	0	0	1	0	0	0	0	0	SW
Anolis ortonii Cope, 1868	1	0	1	1	1	1	1	1	1	1	1	0	0	Wd
Anolis philopunctatus Rodrigues, 1988	0	0	0	0	0	0	1	0	0	0	0	0	0	G
Anolis punctatus Daudin, 1802	1	1	1	1	1	1	0	1	1	1	1	1	1	Wd
Anolis trachyderma Cope, 1876	1	0	0	1	0	0	0	0	0	1	1	0	0	W
Anolis transversalis Duméril, 1851	0	1	1	1	0	0	0	1	0	1	1	0	0	W
Enyalius leechii (Boulenger, 1885)	1	0	0	0	0	1	0	1	0	0	0	0	0	S
Polychrus liogaster Boulenger, 1908	0	0	0	0	0	0	0	1	1	0	0	0	0	SW
Polychrus marmoratus (Linnaeus, 1758)	1	0	0	0	0	1	1	0	0	1	1	0	1	Wd
Plica plica (Linnaeus, 1758)	1	1	1	1	1	0	1	1	1	1	0	1	1	Wd
Plica umbra (Linnaeus, 1758)	1	1	1	1	1	1	1	1	1	1	1	1	1	Wd
Stenocercus dumerilii Steindachner, 1867	0	0	0	0	0	1	0	0	0	0	0	0	0	SE
Stenocercus fimbriatus Avila-Pires, 1995	0	0	0	0	0	0	0	0	0	1	0	0	0	W
Stenocercus roseiventris D'Orbigny, 1837	0	0	0	1	0	0	0	0	1	0	0	0	0	SW
Uracentron azureum (Linnaeus, 1758)	0	0	0	0	1	1	1	0	1	0	0	1	1	Wd
Uracentron flaviceps (Guichenot, 1855)	0	0	0	0	0	0	0	0	0	1	1	0	0	W
Uranoscodon superciliosus (Linnaeus, 1758)	1	1	1	0	1	1	1	1	0	0	0	1	1	E
Coleodactylus amazonicus (Andersson, 1918)	1	1	1	0	1	1	1	1	0	0	0	1	1	E
Gonatodes annularis Boulenger, 1887	0	0	0	0	0	0	0	0	0	0	0	0	1	G

Continue

Taxa	Sites													GC
	CUR	GJM	ITU	JUR	CAX	BEL	BAL	SAM	CA	IQUI	SC	SIP	BRO	
Gonatodes concinnatus (O'Shaughnessy, 1881)	0	0	0	0	0	0	0	0	0	1	1	0	0	W
Gonatodes hasemani Griffin, 1917	0	1	1	1	0	0	0	1	1	0	0	0	0	SW
Gonatodes humeralis (Guichenot, 1855)	1	1	0	1	1	1	1	1	1	1	1	1	1	Wd
Lepidoblepharis festae Peracca, 1897	0	0	0	0	0	0	0	0	0	1	0	0	0	W
Lepidoblepharis heyerorum Vanzolini, 1978	0	0	0	0	1	1	0	0	0	0	0	0	0	E
Pseudogonatodes guianensis Parker, 1935	0	0	0	1	0	0	1	0	1	1	1	1	0	Wd
Thecadactylus rapicauda (Houttuyn, 1782)	1	1	1	1	1	1	1	1	1	1	1	1	1	Wd
Alopoglossus angulatus (Linnaeus, 1758)	0	1	1	1	1	1	1	1	0	1	0	0	1	Wd
Alopoglossus atriventris Duellman, 1973	0	0	1	1	0	0	0	0	0	1	1	0	0	W
Alopoglossus copii Boulenger, 1885	0	0	0	0	0	0	0	0	0	0	1	0	0	W
Arthrosaura kockii (Lidth de Jeude, 1904)	0	0	0	0	1	1	0	0	0	0	0	1	1	G
Arthrosaura reticulate (O'Shaughnessy, 1881)	1	1	1	0	1	1	1	1	0	1	1	1	0	Wd
Bachia gr. *dorbignyi* (Duméril & Bibron, 1839)	0	1	0	1	0	0	0	0	0	0	0	0	0	SW
Bachia flavescens (Bonnaterre, 1789)	1	0	0	0	1	1	1	0	0	0	0	1	1	Wd
Bachia trisanale (Cope, 1868)	0	0	0	0	0	0	0	0	1	1	1	0	0	W
Cercosaura argulus Peters, 1863	0	1	0	1	0	1	0	1	1	0	?	0	0	Wd
Cercosaura eigenmanni (Griffin, 1917)	0	1	1	0	0	0	0	1	1	0	0	0	0	SE
Cercosaura manicatus O'Shaughnessy, 1881	0	0	0	0	0	0	0	0	0	0	1	0	0	Wd
Cercosaura ocellata Wagler, 1830	1	0	1	1	1	1	0	1	1	1	0	1	1	G
Cercosaura oshaughnessyi (Boulenger, 1885)	0	0	0	1	0	0	0	0	0	1	1	0	0	SW
Cercosaura schreibersii Wiegmann, 1834	0	0	0	0	0	0	0	1	0	0	0	0	0	W
Colobosaura modesta (Reinhardt & Lütken, 1862)	0	0	0	0	0	1	0	0	0	0	0	0	0	E
Iphisa elegans Gray, 1851	1	1	0	1	1	1	0	1	0	0	1	0	1	G
Leposoma guianense Ruibal, 1952	0	0	0	0	0	0	0	0	0	0	0	1	1	E
Leposoma osvaldoi Avila-Pires, 1995	0	1	0	0	0	0	0	1	0	0	0	0	0	W
Leposoma parietale (Cope, 1885)	0	0	0	0	0	0	0	0	0	1	1	0	0	SW
Leposoma percarinatum (Müller, 1923)	1	1	0	0	1	1	1	1	0	0	0	1	1	G
Leposoma sp.	0	0	0	0	0	0	1	0	0	0	0	0	0	SW
Neusticurus bicarinatus (Linnaeus, 1758)	0	0	0	0	0	1	1	1	0	0	0	1	1	Wd
Neusticurus ecpleopus Cope, 1876	1	0	0	1	0	0	0	0	0	1	1	0	0	SW
Neusticurus juruazensis Avila-Pires & Vitt, 1998	0	0	0	1	0	0	0	0	0	0	0	0	0	W
Neusticurus rudis Boulenger, 1900	0	0	0	0	0	0	0	0	0	0	0	0	1	W

Conclusion

Taxa	Sites													GC
	CUR	GJM	ITU	JUR	CAX	BEL	BAL	SAM	CA	IQUI	SC	SIP	BRO	
Ptychoglossus brevifrontalis Boulenger, 1912	0	0	1	1	1	0	0	0	1	1	1	1	0	Wd
Tretioscincus agilis Ruthven, 1916	0	0	0	0	1	0	1	0	0	0	0	1	1	G
Ameiva ameiva (Linnaeus, 1758)	1	1	1	1	1	1	1	1	1	1	1	1	1	Wd
Crocodilurus amazonicus Spix, 1825	0	0	0	0	1	1	0	1	0	0	0	0	0	Wd
Dracaena guianensis Daudin, 1802	0	0	0	0	0	1	0	0	1	1	1	0	0	Wd
Kentropyx altamazonica Cope, 1876	0	1	1	0	0	0	0	0	1	1	0	0	0	W
Kentropyx calcarata Spix, 1825	1	1	0	0	1	1	1	1	0	0	0	1	1	E
Kentropyx pelviceps Cope, 1868	0	0	1	1	0	0	0	0	1	1	1	0	0	W
Tupinambis longilineus Avila-Pires, 1995	0	0	1	0	0	0	0	0	0	0	0	0	0	SW
Tupinambis teguixin (Linnaeus, 1758)	0	1	1	1	1	1	1	1	1	1	1	1	1	Wd
Mabuya bistriata (Spix, 1825)	0	0	1	0	0	1	0	0	0	0	0	0	0	Wd
Mabuya nigropunctata (Spix, 1825)	1	1	1	1	1	1	1	1	1	1	1	1	1	Wd