



The striking endemism pattern of the species-richest snake genus *Atractus* (Dipsadidae: Serpentes) highlights the hidden diversity in the Andes

Andrés D. Pomar-Gómez¹, Paulo Cordeiro¹, Thaís B. Guedes^{2,3}, Paulo Passos^{1,*}

Abstract. The distribution of the highly diversified and species-rich snake genus *Atractus* was assessed in search for endemism areas. The dataset of 6000 museum specimens was used to run an Endemicity Analyses in order to identify areas of biogeographic relevance for the genus *Atractus*. By using distinct methodological approaches and modifying the size and shape of grid cells we obtained a better adjustment to each species range, taking into account species distributed along the Andean and Atlantic Forest mountain ranges or certain vegetation constraints. Three scales of endemism were observed: micro endemic areas, represented by three different regions; intermediate sized endemic areas, represented by nine different regions; and macro-endemic areas, represented by four different provinces. Although most assessed regions corroborate well-defined biogeographic units according to the scientific literature, some, mainly located in the Colombian Andes, are not regularly considered in biogeographic syntheses carried out for vertebrates. Methodological approaches, along with a well curated database and taxonomic accuracy, may significantly influence the recovery of endemism areas, mainly considering mountain topography and local niche structure. The results present herein highlight the relevance of three Colombian Cordilleras, in order to completely understand Neotropical biota patterns of distribution. It is important to note that a well-resolved taxonomy represents both the framework and the first step toward a comprehensive biographical synthesis reducing Wallacean shortfalls in biodiversity.

Keywords: Amazonia, Andes, areas of endemism, Atlantic Forest, Chaco, Guiana Shield, NDM/VNDM, Pantepui.

Introduction

Organisms show non-random distributions patterns as a result of many historical events but, in final instances, these patterns reflect the dispersion limits of each species into certain niche parameter ranges (Wiens, 2011). Areas of Endemism represent biogeographical regions where at least two species present distribution range overlapping (Morrone, 1994; Ebach, 2017). These areas can be interpreted as the result of the intersection between historical and

environmental factors, leading to distributional concordance for two or more species under the same or very similar influence of these factors (Szumik et al., 2002). Endemism areas are fundamental units in many broad-scale ecological and evolutionary studies (Crisp et al., 2009; Edler et al., 2017) and provide an essential tool for conservation planning (Whittaker et al., 2005; Peixoto et al., 2020). However, since different taxa exhibit distinct patterns of diversity, distribution and evolutionary history, these areas are not trivial to identify (Edler et al., 2017).

South America, as part of the Neotropical region, is noteworthy for its biodiversity and has been a preferred target for biogeographical research. A long and complex history of studies attempting to detect areas of biogeographical relevance (e.g., Rapoport, 1968; Sánchez Osés and Pérez-Hernández, 1998; Morrone, 2014) is noted, with diverse schemes proposed for the last 150 years (see Morrone, 2014). Most of

1 - Departamento de Vertebrados, Museu Nacional, Universidade Federal do Rio de Janeiro, Quinta da Boa Vista, São Cristóvão, Rio de Janeiro, 20940-040 Rio de Janeiro, Brasil

2 - Centro de Estudos Superiores de Caxias, Universidade Estadual do Maranhão, Programa de Pós-graduação em Biodiversidade, Ambiente e Saúde, Caxias, 65064-380, Maranhão, Brasil

3 - Department of Biological and Environmental Sciences and Gothenburg Global Biodiversity Center, University of Gothenburg, Box 461, 405 30 Göteborg, Sweden

*Corresponding author; e-mail: atractus@gmail.com

these schemes have been considered the baseline for many studies aiming at understanding the evolutionary history of biotas and their areas (e.g., Lohmann et al., 2013). However, although regionalisation proposal schemes are of crucial relevance for evolutionary studies, conflicting delimitations in the proposed schemes are still present (Morrone, 2014), as well as a lack of biogeographical units in complex topography regions, such as mountain ranges (Hazzi et al., 2018; Guedes et al., 2020; Peixoto et al., 2020).

Non-avian reptiles represent about one third of the total diversity of the extant vertebrates, comprising over 11 000 currently recognised species, of which more than one third (ca. 3800) are snakes (Uetz, Freed and Hošek, 2019). However, most models explaining the distribution and endemicity of vertebrate taxa are best studied and understood for mammals and birds (Roll et al., 2017), both presenting lower species richness compared to reptiles (Uetz, Freed and Hošek, 2020). The genus *Atractus* comprises about 150 currently recognised species of cryptozoic snakes distributed from Panama to Argentina (Passos et al., 2018). The natural history data in the group is very scarce but it is known that all species are oviparous, active mainly during the day and twilight, and feed on earthworms (Martins and Oliveira, 1999; Passos et al., 2019a). Despite being the most extant snake genus, several *Atractus* species are still known from small series with relatively restricted distributions and an apparently high level of local endemism (Passos et al., 2019a, b). *Atractus* comprises a monophyletic group (Graziotin et al., 2012; Arteaga et al., 2017; Melo-Sampaio et al., 2019; Murphy et al., 2019) with a complex taxonomic history due to its significant population polymorphism and geographic variability (Passos et al., 2017; Menezes-Pelayo and Passos, 2019). The renewed interest in *Atractus* systematics indicated that the group diversity still remain in a flux state, with frequent taxonomic changes (Passos, Prudente and Lynch, 2016), which directly reflect their distribution patterns

(Guedes et al., 2018; Passos et al., 2018, 2019a, b; Melo-Sampaio et al., 2019).

In this context, the aim of the present study is to use the speciose genus *Atractus* throughout its distribution in South America (i) to identify areas of biogeographic relevance (Endemism Areas); (ii) to test the effect of different grid sizes and shapes to detect areas of endemism of this clade of snakes; and (iii) to examine how congruent the detected areas are to those previously reported, for distinct groups of organisms in the Neotropics.

Material and methods

Study area

The study area evaluated herein includes almost all South America, ranging from Panamá to Argentina (between 13°N and 40°S latitude and between 84°E and 34°W longitude), which represents the total area of distribution for all species allocated in the genus *Atractus* (Passos et al., 2018, 2019a, b). The ecosystems and habitats of the species in this area are well known as presenting a high species diversity (Morrone, 2014), with *Atractus* records being reported from the sea level to approximately 4500 m above sea level (Passos et al., 2010).

Data sources

The data used herein was mostly based on a personal dataset from PP derived, mainly, from the taxonomic revision of the genus *Atractus* (Passos, 2008), and also considering several subsequent publications (Passos et al., 2019a and references therein). A total of 125 valid *Atractus* species were selected, excluding junior synonymies still listed in some sources (e.g., Natera, Esqueda and Castelaín, 2015), which have not yet been formally synonymized (P. Passos, unpubl. data). The same rationale was applied with respect to new species awaiting formal description based on unpublished manuscripts, as well as papers under review that are in the process of being published. The database used herein total about 6000 personally verified specimens (supplementary table S1). Some species were only represented by one or few individuals (usually the type-series), in contrast to species with a higher number of samples available in collections (about 1000 individuals). This huge imbalance concerning sample size among species is due to the fact that some species are extremely scarce in collections, because of distinct reasons and causations (see Passos, Prudente and Lynch, 2016).

As most historical records were not georeferenced in the field through the use of GPS devices, the point-radius (P-R) method described by Wieczorek, Guo and Hijmans (2004) was applied, in order to refine locations. This methodology considers an appreciable error for each point based on

the size of the generated circle, taking into account a fraction of the decimal units (e.g., 1 km: $1/1 = 1$ km; 1.5 km: $1/2 = 0.5$ km; 1.75 km: $3/4 = 0.25$ km; etc.). In cases of higher values, the error will be calculated by multiplying the free decimal number for 0.5 (i.e., 140 km: $10 * 0.5 = 5$ km; 100 km: $100 * 0.5 = 50$ km). Given the variability of the data collected throughout South America and scale-related variations, the same error calculation for all records was not possible. In certain cases, many individuals were registered at the same point, but without providing major references about the specific area. Thus, they were randomly distributed among the P-R area for a given geographic reference. This methodology was carried out using the Google Earth Pro software, version 7.3.1.4507 (© 2018 Google Inc.). When the specimen was too old and a given toponymy was not available, South American Gazetteers were consulted. The Notepad++ software was used to generate a major list of all species (supplementary table S1), followed by Endemicity Analyses implemented in NDM/VNDM software, version 3.0 (Szumik et al., 2002; Szumik and Goloboff, 2004).

Endemicity analyses

The Endemicity Analyses were implemented through two connected software's (NDM and VNDM) that work together. NDM is the basic search engine while VNDM allow the visual inspection of the insertion of data, the diagnostic of the analyses and download the results via shapefile. Thus, because of this we mention the software as NDM/VNDM along the text. The input of NDM/VNDM software (Szumik et al., 2002; Szumik and Goloboff, 2004) to recover endemism areas is based on a binary matrix (presence and absence). The NDM/VNDM draw a cartographic grids (editable by chosen degrees or kilometres) superimposed to an area (South America) and the distribution data of a given organisms (*Atractus*), and searches for congruencies among species distribution of as many taxa as possible, considering the support of at least two different species (Aagesen, Szumik and Goloboff, 2013), following the definition of Area of Endemism in accordance with Platnick (1991) and Morrone (1994). The method also allows to give special weights depending of some characteristics concerning species distribution, the recognition of different shaped and sized areas, and possible occurrence areas of a given species, based on their known or assumed distribution (Szumik and Goloboff, 2004). In contrast to other methods that require the exclusive and strict overlap of two or more species to recognise an endemism area, NDM/VNDM flexibilize such restriction, counting points for the endemism area by adjusting species. The method provides a score that can increase if the species is present in all grids from the endemism area or decrease if is outside the area (Szumik et al., 2002; Szumik and Goloboff, 2004). By following the definition adopted here, minimum score to recognize an Area of Endemism is 2 (i.e., two species) in which the overlaps must be extensive along the given grids. Considering that species with larger distributions are not too significant for the formula (Szumik et al., 2002; Szumik and Goloboff, 2004), generating noise and obfuscating the recognition of

the areas of endemism, a total of 14 species were eliminated. Thus, a total of 111 species with moderate to small distribution ranges were considered in all analyses, taking into account grid size resolution, grid shape resolution and Atlantic Rainforest resolution.

Grid size resolution: The dataset was analysed considering three distinct grid cell sizes (one, three and five degrees grid cells) superimposed onto the study area. For each analysis, only the grid-cell sizes were variables. The origin of the grid was -83.391 and 13.582 . The input matrixes to run each grid size resolution analyses on NDM/VNDM are available in the supplementary fig. S1). We consider endemism areas as those with score higher than two (i.e., two endemic species; supplementary fig. S1). After performing the Endemicity Analysis, we also searched for consensus areas by a strict consensus of which area cutoff was of 75%, as this value represents a more restrictive aggregation pattern without being completely restrictive (Aagesen, Szumik and Goloboff, 2013), allowing the unification of similar areas presenting only a few different species.

Grid shape resolution: The effect of grid shape on the endemic areas was also assessed, by using a rectangle. The origin of the grid was the same as before and details on the input matrix to run each grid shape resolution analyses are also available in the supplementary fig. S1. Only grid shape varied among the analyses. We initially applied $1^\circ \times 3^\circ$, followed by $3^\circ \times 1^\circ$ to analyse the same database (supplementary table S1) used for grid size. Subsequently, the strict consensus at 75% similarity was applied. After observing the modified shape effect, the shape relationship was modified to improve the described area, generating $1/2$, $3^\circ \times 6^\circ$ grids, followed by $6^\circ \times 3^\circ$ (see supplementary fig. S1). Finally, the strict consensus at 75% similarity was applied to the latter.

The special case of the Atlantic Rainforest: After observing the Atlantic Rainforest and Chaco, we noticed that *Atractus pantostictus* distributed throughout the Brazilian Cerrado ecoregion blurred the distribution pattern for Atlantic Rainforest species, mixing both ecoregions into one endemism area. The distribution pattern observed for *A. pantostictus* is probably derived from a recent expansion of the Cerrado species into Atlantic Rainforest limits, due to Atlantic Rainforest fragmentation (see Passos et al., 2010). To solve this problem, the analyses for the Atlantic Rainforest region were repeated using 13 species previously described for the area, excluding *A. pantostictus*, maintaining only those occurring strictly along forest habitat remnants, and using the same grid size and shape resolution described previously (supplementary fig. S1). This was possible due to the fact that the species in this area will not suffer any influence of distantly distributed species (Szumik et al., 2002; Szumik and Goloboff, 2004; Aagesen, Szumik and Goloboff, 2013). The results for this region in both cases (supplementary fig. S1) are displayed, but *A. pantostictus* from the Atlantic Forest is excluded from the final maps, as a non-informative and putative outsider and invasive element (supplementary fig. S1).

In total we run 14 analyses, being three using squares format of the grid ($1^\circ \times 1^\circ$, $3^\circ \times 3^\circ$, $5^\circ \times 5^\circ$) and four using rectangle format of the grid ($1^\circ \times 3^\circ$, $3^\circ \times 1^\circ$, $3^\circ \times$

$6^\circ \times 6^\circ \times 3^\circ$) for the whole South America and seven for the special case of The Atlantic Forest ($1^\circ \times 1^\circ$, $3^\circ \times 3^\circ$, $5^\circ \times 5^\circ$, $1^\circ \times 3^\circ$, $3^\circ \times 1^\circ$, $3^\circ \times 6^\circ$, $6^\circ \times 3^\circ$). Different endemism areas were determined based on the use of different grid size and shape resolutions (Casagranda, Roig-Juñent and Szumik, 2009). Micro endemic areas (MEA) were defined as those recovered by using one-degree grid cells, endemic areas (EA), as those recovered by using three-degree grid cells, and macro endemic areas (MAEA), as those detected by using five-degree grid cells. All maps showing the areas of endemism were drawn using the QGIS 2.18.16 software (QGis Development Team, 2016).

Results

Grid size resolution

The one-degree grid cells led to determination of seven endemic areas (S2AB) before the consensus, all located along the Andes between Colombia, Ecuador and Venezuela. The same seven areas were maintained after the strict consensus application, indicating that differences between the areas are higher than 25% of the species. For the three degrees grid cells, we recovered nine endemic areas before the consensus, this time indicating endemic tree spots, mostly along the Andes, as well as one spot located in the Pantepui province and one in the Atlantic Rainforest (supplementary fig. S1C). After the strict consensus, seven endemic areas were maintained, identifying areas located in the Andes and along the west coast of Ecuador and Colombia, in the Chocoan province. The five-degree grid cells determined 14 endemic areas (supplementary fig. S1D), seven in the Andes, three in the Atlantic Rainforest and four in the Pantepui province. After the strict consensus, 13 consensus areas were maintained, aggregating areas all in the Guiana Shield, indicating one probable endemism area for the Pantepui province.

Grid shape resolution

The $1^\circ \times 3^\circ$ grid shape resulted in 11 endemism areas (supplementary fig. S1E) for the genus *Atractus* revealing areas in the Colombia, Ecuador and Venezuela Andes. The consensus analyses maintained nine of these areas.

The $3^\circ \times 1^\circ$ analyses identified six endemic areas (supplementary fig. S1F). This grid shape allowed the identification of areas presenting elongated corological geographic distribution shapes, such as the Andes mountain ranges, as well as the Chocoan province lowlands, located at the Colombia and Ecuador Pacific coasts. While a 1° scale is small and displays only micro-endemic areas, also elongated, the modified $3^\circ \times 6^\circ$ grid found seven endemic areas (supplementary fig. S1G), four in the Andes, two in the Atlantic Forest and one at Pantepui. The consensus area recovered the same seven areas. The $6^\circ \times 3^\circ$ grid recovered 13 endemic areas (supplementary fig. S1H), nine restricted to the Colombia, Ecuador and Venezuela Andes, two located in the Guianas region and two in the Atlantic Forest, one located in the south, uniting the Atlantic Rainforest to the east side of the Chaco region. The consensus analyses generated nine endemic areas.

Delimitation of endemism areas

In general, three micro endemic areas (MEA; table 1, fig. 1) were recovered by using one degree grid cells: the first (MEA1) is located on the Huaca massif and southern Chocó rainforest, supported by ten species; the second area (MEA2) found along the Cauca and Magdalena drainages, supported by eight species and the third micro endemic area (MEA3), corresponding to the northeast portion of the Andes and western portion of the Merida mountain range, supported six species. The second micro-endemic area (MEA2) was a mixture of River Valleys caused by the distribution of species present in elevated mountain areas nearby generated by pixel limits, considering the natural Andes curvature. Furthermore, three species were located in the northern portion of the Central Cordillera distributed throughout lower altitudes, uniting the upper pixels for both River Valleys. Nonetheless, it is understood that these species do not transpose the Central Cordillera slopes. Because of these

Table 1. Endemism areas and endemic species of *Atractus* detected by NDM/VNDM in the present study, and their congruence with from previous studies (references).

Endemism areas	Endemic species of <i>Atractus</i> supporting the area	References
MEA1 – Ecuadorian Andes (sp. 10)	<i>A. dunni</i> , <i>A. gigas</i> , <i>A. typhon</i> , <i>A. paucidens</i> , <i>A. resplendens</i> , <i>A. dubosi</i> , <i>A. gaigeae</i> , <i>A. modestus</i> , <i>A. occipitoalbus</i> , <i>A. orcesi</i>	Morrone, 2015; Prado et al., 2015; Hazzi et al., 2018; Rangel et al., 2018
MEA2 – Colombian Andes (sp. 8)	<i>A. melanogaster</i> , <i>A. nicefori</i> , <i>A. werneri</i> , <i>A. sp3</i> , <i>A. obtusirostris</i> , <i>A. lasallei</i> , <i>A. nasutus</i> , <i>A. sanguineus</i>	Morrone, 2015; Prado et al., 2015; Hazzi et al., 2018; Rangel et al., 2018
MEA3 – Col-Venezuela Andes (sp. 6)	<i>A. erythromelas</i> , <i>A. indistinctus</i> , <i>A. pamplonensis</i> , <i>A. taphorni</i> , <i>A. ventrimaculatus</i> , <i>A. emigdioi</i>	Morrone, 2015; Prado et al., 2015; Hazzi et al., 2018; Rangel et al., 2018
EA1 – Ecu-Col-Andes (sp. 9)	<i>A. duboisii</i> , <i>A. gaigeae</i> , <i>A. multicinctus</i> , <i>A. lehmanni</i> , <i>A. occipitoalbus</i> , <i>A. melas</i> , <i>A. orcesi</i> , <i>A. atlas</i> , <i>A. iridescens</i>	Morrone, 2015; Prado et al., 2015; Hazzi et al., 2018; Rangel et al., 2018
EA2 – Ecu-Col Andes-Choco (sp. 12)	<i>A. clarki</i> , <i>A. melanogaster</i> , <i>A. obesus</i> , <i>A. crassicaudatus</i> , <i>A. melas</i> , <i>A. orcesi</i> , <i>A. iridescens</i> , <i>A. multicinctus</i> , <i>A. punctiventris</i> , <i>A. lehmanni</i> , <i>A. nicefori</i> , <i>A. werneri</i>	Morrone, 2015; Prado et al., 2015; Hazzi et al., 2018; Rangel et al., 2018
EA3 – NE Andes-Merida (sp. 7)	<i>A. erythromelas</i> , <i>A. pamplonensis</i> , <i>A. indistinctus</i> , <i>A. lancinii</i> , <i>A. taphorni</i> , <i>A. ventrimaculatus</i> , <i>A. matthewi</i>	Morrone, 2015; Prado et al., 2015; Hazzi et al., 2018; Rangel et al., 2018
EA4 – Guiana Shield (sp. 3)	<i>A. badius</i> , <i>A. flamigerus</i> , <i>A. zidoki</i>	Rull et al., 2019
EA5 – Guiana Shield (sp. 4)	<i>A. alphonsehoegei</i> , <i>A. badius</i> , <i>A. flammigerus</i> , <i>A. zidoki</i>	Rull et al., 2019
EA6 – Atlantic Forest (sp. 5)	<i>A. francoi</i> , <i>A. reticulatus</i> , <i>A. serranus</i> , <i>A. trihedrurus</i> , <i>A. zebrinus</i>	Costa et al., 2000; Silva et al., 2004; DaSilva et al., 2015; Moura et al., 2016
EA7 – central Atlantic F. (sp. 4)	<i>A. francoi</i> , <i>A. serranus</i> , <i>A. trihedrurus</i> , <i>A. zebrinus</i>	Costa et al., 2000; Silva et al., 2004; DaSilva et al., 2015; Moura et al., 2016
EA8 – NE Chaco-S Atl. Forest (sp. 3)	<i>A. paraguayensis</i> , <i>A. reticulatus</i> , <i>A. thalesdelemai</i>	Costa et al., 2000; Silva et al., 2004; DaSilva et al., 2015; Moura et al., 2016
EA9 – Atl. Forest-Chaco (sp. 3)	<i>A. paraguayensis</i> , <i>A. reticulatus</i> , <i>A. zebrinus</i>	Costa et al., 2000; Silva et al., 2004; DaSilva et al., 2015; Moura et al., 2016
MAEA1 – North Andes (sp. 14)	<i>A. obesus</i> , <i>A. iridencens</i> , <i>A. punctiventris</i> , <i>A. fuliginosus</i> , <i>A. lehmanni</i> , <i>A. duboisii</i> , <i>A. gaigae</i> , <i>A. melas</i> , <i>A. modestus</i> , <i>A. multicinctus</i> , <i>A. occipitoalbus</i> , <i>A. orcesi</i> , <i>A. resplesdens</i> , <i>A. typhon</i>	Morrone, 2015; Prado et al., 2015; Hazzi et al., 2018; Rangel et al., 2018
MAEA2 – Guiana Shield (sp. 5)	<i>A. alphonsehoegei</i> , <i>A. badius</i> , <i>A. flamigerus</i> , <i>A. zidoki</i> , <i>A. tartarus</i>	Rull et al., 2019
MAEA3 – Atlantic Forest-Chaco (sp. 6)	<i>A. trihedrurus</i> , <i>A. zebrinus</i> , <i>A. reticulatus</i> , <i>A. thalesdelemai</i> , <i>A. paraguayensis</i> , <i>A. serranus</i>	Costa et al., 2000; Silva et al., 2004; DaSilva et al., 2015; Moura et al., 2016
MAEA4 – Gui Shield-Midel Amazon (sp. 4)	<i>A. franciscopaivai</i> , <i>A. insipidus</i> , <i>A. riveroi</i> , <i>A. trilineatus</i>	Rull et al., 2019

methodological caveats, we established a minimal polygon (fig. 2) to better visualise the areas of endemism for each drainage, without ignoring the Central Cordillera mountain range. On

the other hand, the micro endemic areas found in this study indicate three hotspots associated to the Andean mountain ranges (MEA1-3; fig. 1), and the regions associated to Andean

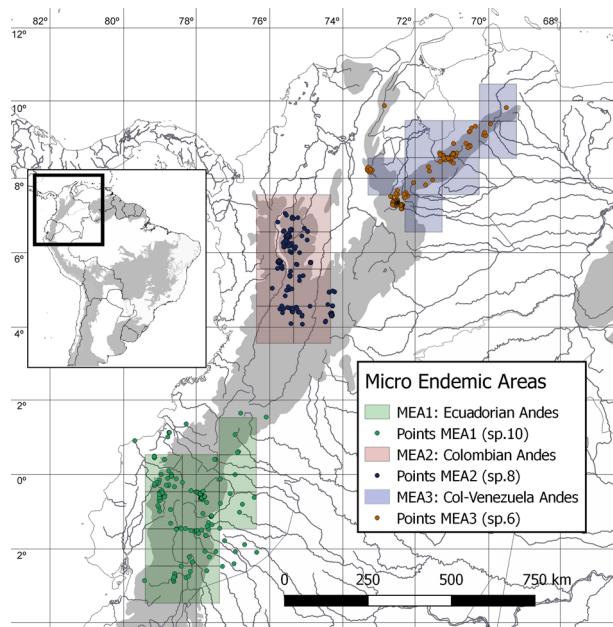


Figure 1. Micro Endemic Areas (MEA) generated after strict consensus using $1^\circ \times 1^\circ$ grid size. Abbreviations: MEA1 Ecuadorian Andes (comprising 10 spp.); MEA2 Colombian Andes (comprising 8 spp.); and MEA3 Colombia-Venezuela Andes (Merida) (comprising 6 spp.).

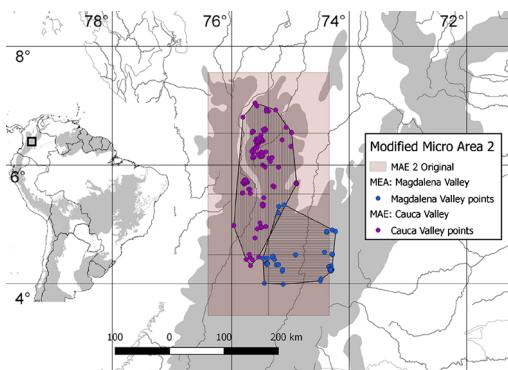


Figure 2. Modified Micro Endemic Areas (MEA) 2 for better visualization of two trans-Andean Valleys, adjusting the geographical distribution according to natural barriers. Abbreviations: MEA2 Colombian Andes (comprising 8 spp.), MEA Magdalena Valley (comprising 3 spp.); and MEA Cauca Valley (comprising 5 spp.).

River Valleys are also noted as extremely relevant (MEA Magdalena Valley and MEA Cauca Valley; fig. 2).

We identified nine endemism areas (EA; table 1, fig. 3) using three degree grid cell resolution, while some of them also recovered differentially with grid cell shape resolutions of

1° , 3° and 6° . The first endemism area (EA1; fig. 3A) in the Andes extended along the mountain ranges from southern portions of Colombian mountain ranges, Ecuador, until northern Peru, supported by nine species. The second endemism area (EA2; fig. 3B) was located in the Andes from the middle Ecuador to the end of the central Cordillera in Colombia and western Cordillera of Colombia and Merida Mountain range on the frontier of Colombia and Venezuela, supported by 12 species. The third endemism area (EA3; fig. 3C), supported by seven species, is comprised by the northern portion of Colombia and Venezuela from the Darien Cordillera, Sierra Nevada de Santa Marta north portion of Merida Mountain range. The fourth endemism area (EA4; fig. 3B), supported three species and is located in the Guiana region between northeast Brazil, Guyana, Surinam, and French Guyana. The fifth endemism area (EA5; fig. 3A), supported by four species, includes the Guiana region and northeastern portion of Brazil, but extends to the end of the Amazonas River until northern region of the

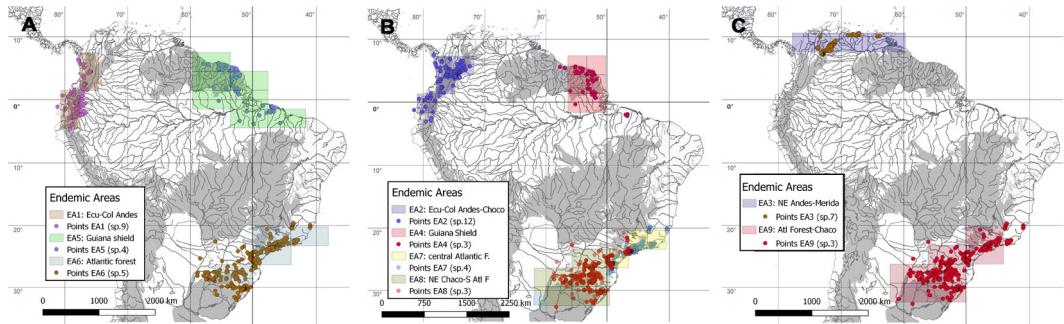


Figure 3. Intermediate Endemic Areas (EA) generated after strict consensus using $3^\circ \times 3^\circ$ grid size compared to the grid with 3° and 6° , in different locations and scales. A) EA1 = Endemic areas 1 (Ecuador-Colombia Andes, comprising 9 spp.); EA5 = Endemic areas 5 (Guiana Shield-East Amazonas, comprising 5 spp.); and EA6 = Endemic areas 6 (Atlantic Forest, comprising 5 spp.); B) Endemic areas 2 = EA2 (Andes and Chocó Ecuador-Colombia, comprising 12 spp.); Endemic areas 4 = EA4 (Guiana Shield, comprising 3 spp.); Endemic areas 7 = EA7 (Atlantic Forest, comprising 4 spp.); and Endemic areas 8 = EA8 (NE Chaco region and Atlantic Forest, comprising 3 spp.); C) Endemic areas 3 = EA3 (NE Andes, Merida and Cordillera Oriental in the Colombia-Venezuela border, comprising 7 spp.); and 9 (Atlantic Forest-Chaco transition region, comprising 3 spp.).

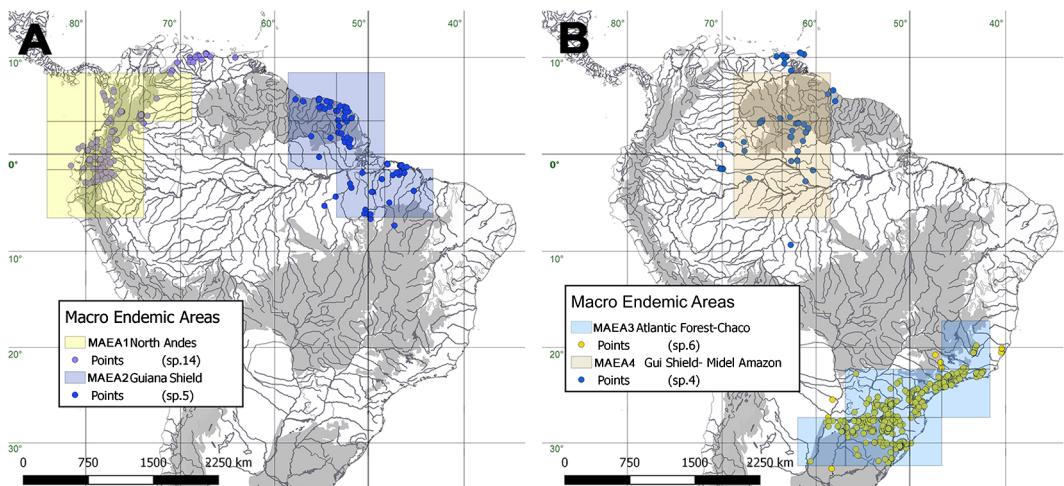


Figure 4. Macro Endemic Areas (MAEA) generated after strict consensus using $5^\circ \times 5^\circ$. Abbreviations: (a) Macro endemic areas 1 = MAEA1 (North Andes, comprising 14 spp.) and Macro endemic areas 2 = MAEA2 (Guiana Shield, comprising 5 spp.); and (b) Macro endemic areas 3 = MAEA3 (Atlantic Forest-Chaco transition region, comprising 6 spp.); and Macro endemic areas 4 = MAEA4 (West Guiana Shield-Central Amazonas, comprising 4 spp.).

state of Piauí. The sixth endemism area (EA6; fig. 3A) supported by five species, encompasses the Brazilian Atlantic Forest from the south of Bahia to the north of Rio Grande do Sul States. The seventh endemism area (EA7; fig. 3B), supported by four species, is located in the middle of the Brazilian Atlantic Forest from Espírito Santo to the frontier between Paraná and Santa Catarina States. The eighth endemism area

(EA8; fig. 3B), supported by three species, comprises the south of the Atlantic Forest, until the Chaco, located between the northern Argentina and eastern Paraguay. The ninth endemism area (EA9; fig. 3C), with three species, is found in the eastern Chaco to last southern portion of the Atlantic Forest, from Paraná, to northeastern Argentina, Uruguay and eastern Paraguay.

Four macro endemic areas (MAEA; table 1, fig. 4) were identified, all recovered by the $5^\circ \times$

5° pixel. The first area (MAEA1; fig. 4A) is located in the northern portion of the Andes and the Darien Cordillera, supported by the congruence among the distribution of 14 species. The second area (MAEA2; fig. 4A) is located in the northeastern portion of Brazil and the Guianas Shield, supported by five species. The third area (MAEA3; fig. 4B) is located in the Atlantic Rainforest in Brazil, northern Argentina and Paraguay, supported by six species. The fourth area (MAEA4; fig. 4B) is located in Pantepui in northern Brazil, Venezuela and Guyana, sharing four species.

Discussion

Grid size and shape resolutions

When applying grid sizes $1^\circ \times 1^\circ$, $1^\circ \times 3^\circ$ and $3^\circ \times 1^\circ$ numerous endemism areas were detected (in order: seven, 11, and six; supplementary fig. S1). Some of these overlapped, supported by four to six species (table 1). However, the use of these small grids was shown to be efficient to detect most endemism areas established in the Ecuadorian, Colombian and Venezuelan Andes. The shape and size of some areas of endemism may make them difficult to identify if only a single grid scheme is used. The use of several grid sizes and shapes is known to increase the probability to identify endemism areas, and this approach can be especially effective where steep and rugged terrain leads to very small areas (the case of the Andes) (Szumik et al., 2012). The use of intermediate and large grids ($3^\circ \times 3^\circ$, $5^\circ \times 5^\circ$, $3^\circ \times 6^\circ$, $6^\circ \times 3^\circ$; supplementary fig. S1) was useful to find numerous endemism areas in different regions throughout South America, supported by three to 14 species (table 1). One known objection against small grid cells is that they lead to overlapping of different distribution patterns in a given region (Szumik et al., 2012). Larger grids are also limited, as they do not consider natural barriers, especially in the Andes Mountains

where they recovered only a unique coarse pattern. Grid shape allowed for the differentiation of one area related to the south Atlantic Forest portion not recovered by the square grid shape, also recognised for its high biodiversity, located in north-eastern Chaco.

The approach of using small, intermediate and large grids (of two distinct shapes) reflected in the hierarchical levels of the identified endemism areas. The four micro endemic areas (MEA) recovered in the northern Andes (figs 1-2), represent taxa presenting a very restricted distribution along only one side of the Andes mountain range (see Passos and Lynch, 2011). The three distinct mountain ranges and river valleys present different topography gradients, precipitation and temperature regimes, resulting in a variety of soil and vegetation types at each Andean slope (Szumik et al., 2012; Morrone, 2014). Moreover, altitudinal oviparous reptile limits along the Andes are also noted (Doody, 2011; Lara-Reséndiz et al., 2014; Castillo et al., 2015), resulting in each mountain range ridge acting as an effective barrier to transversal dispersion, due to the environmental constraints of oviparous reptiles. Intermediate size also recovered areas of endemism (EA) (fig. 3), and this is probably the most accurate grid size to represent *Atractus* endemism, since it recovered the highest number of endemism areas (nine), representing some also identified by small and/or large size grid cells. In addition, macro areas were also obtained (fig. 4), displaying major biogeographic provinces located in the Neotropics (Morrone, 2014), with a considerable number of identified areas.

Endemism areas

In general, the methodological approach applied herein for the genus *Atractus* allowed the recovery of endemism areas along the Andes, Atlantic Rainforest and Pantepui that represent well-known biogeographic units known to harbour a high level of biodiversity and endemism in the Neotropical region, including major groups of plants and animals (Prado et

al., 2015; Moura et al., 2016; Hazzi et al., 2018; Rangel et al., 2018 Rull et al., 2019; Guedes et al., 2020).

Regarding the Andean region, the unprecedented and remarkable distribution pattern found herein verified the most significant hotspot for the *Atractus* genus on the northern portion of the Colombian Andes (cf. Passos et al., 2009; Menezes-Pelayo and Passos, 2019). Despite recent comprehensive biogeographic studies for Neotropical snakes (Guedes et al., 2018) and global tetrapods (Roll et al., 2017), this region has not been previously reported as a significant species rich area. Although both studies were performed based of datasets derived from the examination of scientific collections, increased by clean databases available in public repositories, the Colombian Andes remain a poorly inventoried region. Systematised explorations on the northern Andes are very recent and have already generated a more extensive understanding of this region's biodiversity (Hugo et al., 2017). To complicate matters, several snake groups with a complex taxonomic history and high species diversity distributed throughout the northern Colombian Andes (such as *Atractus*) have only recently been studied on the basis of integrative approaches (e.g., Torres-Carvajal et al., 2015). Consequently, three possible, not mutually exclusive, causations may explain the lack of snake hotspots in the northern Colombian Andes, as follows: (i) the evident gap of databases housed in public repositories may be the result of a lack of collections due to logistic difficulties of country inventories (see Passos, Prudente and Lynch, 2016); (ii) this pattern represent a knowledge gap, derived from the misidentification of records available at online databases (Jenkins et al., 2015, Maldonado et al., 2015; Tingley, Meiri and Chapple, 2016); (iii) most Neotropical squamate groups comprising a high number of species in the Andes or trans-Andean regions still await comprehensive taxonomic revisions.

Conversely, recent studies have corroborated the importance of the northern Andes as a highly relevant hotspot for mammals and birds and have classified the area as a biographical cradle (Prado et al., 2015; Hazzi et al., 2018; Rangel et al., 2018). Prado et al. (2015) found endemism areas largely coherent with the micro endemic areas reported herein, as well as areas recovered by Rangel et al. (2018). This repeated pattern suggests a certain level of phylogenetic allopatric breaks along the northern Central Colombian Cordillera to the Eastern Cordillera plus the Merida Cordillera, in Venezuela (Hazzi et al., 2018; Rangel et al., 2018). Similarly, most intermediate to macro endemic areas recovered by Prado et al. (2015) for the northern Andes, Guiana shield, Atlantic Rainforest and Chaco region were largely congruent with the present results (figs 3-4). Therefore, all the aforementioned areas are strongly indicated as endemic to plants, birds and mammals (Rangel et al., 2018) and, therefore, a possible knowledge gap for other snake groups.

Contrary to the refined results for the Andes, the Atlantic Rainforest results did not corroborate certain biogeographical regions previously reported for snakes, birds, mammals, butterflies and harvestmen (Costa et al., 2000; Silva et al., 2004; DaSilva et al., 2015; Moura et al., 2016). Moura et al. (2016) understand that inventory data for the Atlantic Rainforest are spatially discontinuous, hampering the identification of biogeographical units. Nevertheless, without performing any additional methodology to fill the sampling gaps, an area that joins the southern Atlantic Rainforest with the northeastern Chaco was identified, demonstrating this area as of biogeographical importance due to the presence of *A. francoi*, *A. serranus*, *A. trihedrurus* and *A. zebrinus*, in one recovered area set, and *A. paraguayensis*, *A. reticulatus* and *A. thalesdelemai*, in the other. In addition, areas with different mixtures of these species were also observed (see supplementary fig. S1). Additionally, 14 *Atractus* species were present in five out of six biogeographical subregions found

for Atlantic Rainforest snakes (Moura et al., 2016). Although no endemism area was identified in both the Cerrado and Caatinga in the present study, *Atractus* species were relevant to detect areas of biogeographical importance in both biomes. In the Cerrado, *Atractus spinalis* supported the biogeographical unit called the Espinhaço Mountain Range (Azevedo et al., 2016). In the Caatinga, *A. maculatus* supported a biogeographical area located in the transition between the Atlantic Rainforest and Caatinga, in northeastern Brazil, and *A. ronnie* supported the Ibiapaba-Araripe plateau complex (Guedes et al., 2014).

Conclusions and future research prospects

The identification of endemism areas as provided herein is a first step towards interpreting evolutionary process that require additional ecology, distribution, phylogeny, palaeoclimatological and palaeogeographical data to explain the diversification history of a certain taxa or region. Exploring different grid cells sizes and shapes, along with a well-curated database, allowed us to overcome a significant challenge and recover endemism areas using cryptozoic snakes as a model. Three micro endemic areas, nine moderate and four macro endemic areas in the Neotropical region were identified for *Atractus* along the Andes, Atlantic Rainforest and Pantepui recovering patterns and improving previous syntheses (Hoorn et al., 2010; Roll et al., 2017; Guedes et al., 2018). This approach using *Atractus* snakes, recovered relevant areas for conservation and biogeography and should encourage similar applications to other major animal or plant groups. Overall, there is still a need to improve faunal inventories in the northern Andes, as samples are still elusive for several groups (mainly for taxa presenting secretive lifestyles). At the same time, it is mandatory to better sampling complex groups in order to refine species hypotheses by integrating distinct lines of evidence (Padial et al., 2010). It is important to note that a well-resolved taxonomy represents both the framework and the first

step toward a comprehensive biogeographical synthesis that usually lead to better knowledge concerning biodiversity and the implementation of efficient conservation strategies.

Acknowledgements. APG thanks the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior by MSc fellowship. Financial support for PP was provided by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (Grants 306227/2015-0, 439375/2016-9, 302611/2018-5 and 309560/2018-7) and the Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (Grant E-26/202.737/2018). TBG thanks the State University of Maranhão for a Senior Researcher fellowship.

Supplementary material. Supplementary material is available online at:
<https://doi.org/10.6084/m9.figshare.13573466>

References

- Aagesen, L., Szumik, C., Goloboff, P. (2013): Consensus in the search for areas of endemism. *J. Biogeogr.* **40**: 2011-2016.
- Ab'Sáber, A. (1977): Os domínios morfoclimáticos da América do Sul. Primeira aproximação. *Geomorfologia* **52**: 1-21.
- Azevedo, J.A.R., Valdujo, P.H., Nogueira, C.C. (2016): Biogeography of anurans and squamates in the Cerrado hotspot: coincident endemism patterns in the richest and most impacted savanna on the globe. *J. Biogeogr.* **43**: 2454-2464.
- Casagranda, M.D., Roig-Juñent, S., Szumik, C. (2009): Endemismo a diferentes escalas espaciales: un ejemplo con Carabidae (Coleoptera: Insecta) de América del Sur Austral. *Rev. Chil. Hist. Nat.* **82**: 17-42.
- Casagranda, M.D., Taher, L., Szumik, C. (2012): Endemicity analysis, parsimony and biotic elements: a formal comparison using hypothetical distributions. *Cladistics* **28**: 645-654.
- Castillo, N., Villavicencio, H.J., Acosta, J.C., Marinero, J. (2015): Temperatura corporal de campo y actividad temporal de las lagartijas *Liolemus vallecurensis* y *Liolemus ruibali* en clima riguroso de los Andes centrales de Argentina. *Multequina* **24**: 19-31.
- Costa, L.P., Leite, Y.L.R., da Fonseca, G.A.B., da Fonseca, M.T. (2000): Biogeography for South American forest mammals: endemism and diversity in the Atlantic Forest. *Biotropica* **32**: 872-881.
- Crisp, M.D., Arroyo, M.T.K., Cook, L.G., Gandolfo, M.A., Jordan, G.J., McGlone, M.S., Weston, P.H., Westoby, M., Wilf, P., Linder, H.P. (2009): Phylogenetic biome conservatism on a global scale. *Nature* **458**: 754-756.

- Da Silva, M.B., Pinto-da-Rocha, R., DeSouza, A.M. (2015): A protocol for the delimitation of areas of endemismo and the historical regionalization of the Brazilian Atlantic Rain Forest using harvestmen distribution data. *Cladistics* **31**: 692-705.
- Doody, J.S. (2011): Environmentally cued hatching in reptiles. *Integr. Comp. Biol.* **51**: 49-61.
- Eback, M.C. (2017): Reinvention of Australasian Biogeography: Reform, Revolt and Rebellion. CSIRO Publisher, Clayton South.
- Edler, D., Guedes, T.B., Zizka, A., Rosvall, M., Antonelli, A. (2017): Infomap bioregions: interactive mapping of biogeographical regions from species distributions. *Syst. Biol.* **66**: 197-204.
- Graziotin, F.G., Zaher, H., Murphy, R.W., Scrocchi, G., Benavides, M.A., Zhang, Y., Bonatto, S.L. (2012): Molecular phylogeny of the new world Dipsadidae (Serpentes: Colubroidea): a reappraisal. *Cladistics* **28**: 437-459.
- Guedes, T., Sawaya, R., Zizka, A., Laffan, S., Faurby, S., Pyron, R.A., Bérnilds, R.S., Jansen, M., Passos, P., Prudente, A.L.C., Cisneros-Heredia, D.F., Braz, H.B., Nogueira, C.C., Antonelli, A. (2018): Patterns, biases and prospects in the distribution and diversity of Neotropical snakes. *Global Ecol. Biogeogr.* **27**: 14-21.
- Guedes, T.B., Sawaya, R., Nogueira, C.C. (2014): Biogeography, vicariance and conservation of snakes of the neglected and endangered Caatinga region, north-eastern Brazil. *J. Biogeogr.* **41**: 919-931.
- Guedes, T.B., Azevedo, J.A.R., Bacon, C.D., Provete, D.B., Antonelli, A. (2020): Diversity, endemismo, and evolutionary history of montane biotas outside the Andean Region. In: *Neotropical Diversification: Patterns and Process*, p. 299-328. Rull, V., Carnaval, A.C., Eds, Springer, Cham.
- Hazzi, N.A., Moreno, J.S., Ortiz-Movilav, C., Palacio, R.D. (2018): Biogeographic regions and events of isolation and diversification of the endemic biota of the Tropical Andes. *P. Nat. Acad. Sci. USA* **31** (115): 7985-7990.
- Hoorn, C., Wesselingh, F.P., Steege, H., Bermudez, M.A., Mora, A., Sevink, J., Sanmartín, I., Sanchez-Meseguer, A., Anderson, C.L., Figueiredo, J.P., Jaramillo, C., Riff, D., Negri, F.R., Hooghiemstra, H., Lundberg, J., Stadler, T., Särkinen, T., Antonelli, A. (2010): Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. *Science* **330**: 927-931.
- Hugo, W., Hobert, D., Köljalg, U., Tuama, É.O., Saarenmaa, H. (2017): Global infrastructures for biodiversity data and services. In: *The GEO Handbook on Biodiversity Observation Networks*, p. 259-291. Walters, M., Scholes, R.J., Eds, Springer, Cham.
- Jenkins, C., Alves, M., Uezu, A., Vale, M. (2015): Patterns of vertebrate diversity and protection in Brazil. *PlosOne* **10** (12): e0145064.
- Lara-Reséndiz, R.A., Larraín-Barrios, B.C., Vega-Pérez, A.H.D., Méndez-De la Cruz, F.R. (2014): Calidad térmica a través de un gradiente altitudinal para una comunidad de lagartijas en la Sierra del Ajusco y el Pedregal de San Ángel, México. *Rev. Mex. Biodivers.* **85**: 885-897.
- Lohmann, L.G., Bell, C.D., Calió, M.F., Winkworth, R.C. (2013): Pattern and timing of biogeographical history in the Neotropical tribe Bignoniae (Bignoniaceae). *Bot. J. Linn. Soc.* **171**: 154-170.
- Maldonado, C., Molina, C., Zizka, A., Persson, C., Taylor, C.M., Albán, J., Chilquillo, E., Rønsted, N., Antonelli, A. (2015): Estimating species diversity and distribution in the era of big data: to what extent can we trust public databases. *Global Ecol. Biogeogr.* **24**: 973-984.
- Martins, M., Oliveira, M.E. (1999): Natural history of snakes in forest of the Manaus region, central Amazonia, Brazil. *Herpetol. Nat. Hist.* **6**: 78-150.
- Melo-Sampaio, P.R., Passos, P., Fouquet, A., Prudente, A.L.C., Torres-Carvajal, O. (2019): Systematic review of *Atractus schach* (Serpentes: Dipsadidae) species complex from the Guiana Shield with description of three new species. *Syst. Biodivers.* **3**: 207-229.
- Meneses-Pelayo, E., Passos, P. (2019): New polychromatic species of *Atractus* (Serpentes: Dipsadidae) from the eastern portion of the Colombian Andes. *Copeia* **107**: 250-262.
- Morrone, J. (1994): On the identification of areas of endemism. *Syst. Biol.* **43** (3): 438-441.
- Morrone, J. (2014): Biogeographical regionalization of the Neotropical region. *Zootaxa* **3782** (1): 1-110.
- Moura, M.R., Argôlo, A.J., Costa, H.C. (2016): Historical and contemporary correlates of snake biogeographical subregions in the Atlantic Forest. *J. Biogeogr.* **44**: 640-650.
- Murphy, J.C., Salvi, D., Braswell, A.L., Jowers, M.J. (2019): Phylogenetic position and biogeography of three-lined snakes (*Atractus trilineatus*: Squamata, Dipsadidae). *Herpetologica* **73** (3): 247-253.
- Natera, M.M., Esqueda, L.F.G., Castelaín, M.F. (2015): *Atlas Serpientes de Venezuela: Una Visión Actual de su Diversidad*. Published by the authors, Santiago.
- Padial, J., Miralles, A., De la Riva, I., Vences, M. (2010): The integrative future of taxonomy. *Front. Zool.* **7** (16): 1-14.
- Passos, P. (2008): Revisão Taxonômica do Gênero *Atractus* Wagler, 1828 (Serpentes: Colubridae: Dipsadinae). Unpublished PhD Thesis, Universidade Federal do Rio de Janeiro, Rio de Janeiro.
- Passos, P., Lynch, J.D., "2010" (2011): Revision of *Atractus* (Serpentes: Dipsadidae) from middle and upper Magdalena drainage of Colombia. *Herpetol. Monogr.* **24**: 149-173.
- Passos, P., Prudente, A.L.C., Lynch, J.D. (2016): Redescription of *Atractus punctiventris* and description of two new *Atractus* (Serpentes: Dipsadidae) from Brazilian Amazonia. *Herpetol. Monogr.* **30**: 1-20.
- Passos, P., Arredondo, J.C., Fernandes, R., Lynch, J.D. (2009): Three new *Atractus* (Serpentes: Dipsadidae) from the Andes of Colombia. *Copeia* **2009**: 425-436.
- Passos, P., Fernandes, R., Bérnilds, R., Moura-Leite, J.C. (2010): Taxonomic revision of the Brazilian Atlantic forest *Atractus* (Reptilia: Serpentes: Dipsadidae). *Zootaxa* **2364**: 1-63.

- Passos, P., Ramos, L.O., Fouquet, A., Prudente, A.L.C. (2017): Taxonomy, morphology, and distribution of *Atractus flammigerous* Boie, 1827 (Serpentes: Dipsadidae). *Herpetologica* **74** (4): 349-363.
- Passos, P., Prudente, A.L.C., Ramos, L.O., Caicedo-Portilla, J.R., Lynch, J.D. (2018): Species delimitations in the *Atractus collaris* (Serpentes: Dipsadidae). *Zootaxa* **4392** (3): 491-520.
- Passos, P., Azevedo, J.A.R., Nogueira, C.C., Fernandes, R., Sawaya, R.J. (2019a): An integrated approach to delimit species in the puzzling *Atractus emmeli* complex (Serpentes: Dipsadidae). *Herpetol. Monogr.* **33**.
- Passos, P., Scanferla, A., Melo-Sampaio, P.R., Brito, J., Almendariz, A. (2019b): A Giant on the ground: another large-bodied *Atractus* (Serpentes: Dipsadinae) from Ecuadorian Andes, with comments on the dietary specializations of the goo-eaters snakes. *An. Acad. Bras. Cienc.* **91** (1): e20170976.
- Peixoto, M.A., Guedes, T.B., Silva, E.T., Feio, R.N., Romano, P.S. (2020): Biogeographic tools help to assess the effectiveness of protected areas for the conservation of anurans in the Mantiqueira mountain range, southeastern Brazil. *J. Nat. Conserv.* **54**: 125799.
- Platnick, N.I. (1991): On areas of endemism. *Aust. Syst. Bot.* **4**: 9-11.
- Prado, J.R., Brennand, P.G.G., Godoy, L.P., Libardi, G.S., Abreu-Júnior, E.F., Roth, P.R.O., Chiquito, E.A., Percequillo, A.R. (2015): Species richness and areas of endemism of oryzomysine rodents (Cricetidae, Sigmodontinae) in South America: an NDM/VNDM approach. *J. Biogeogr.* **42**: 540-551.
- QGIS Development Team (2016): Quantum GIS Geographic Information System. Version 2.18.16. <http://qgisbrasil.org/blog/2016/10/28/lancamento-do-qgis-versao-2-18-las-palmas/>.
- Rangel, T.F., Edwards, N.R., Holden, P.B., Diniz-Filho, J.A.F., Gosling, W.D., Coelho, M.T.P., Cassemiro, F.A.S., Rahbek, C., Colwell, R.K. (2018): Modeling the ecology and evolution of biodiversity: biogeographical cradles, museums and graves. *Science* **361**: eaar5452.
- Rapoport, E.H. (1968): Algunos problemas biogeográficos del Nuevo Mundo con especial referencia a la región Neotropical. In: *Biologie de l'Amérique Australe*, p. 55-110. Delamare Debouteville, C., Rapoport, E.H., Eds, CNRS, Paris.
- Roll, U., Feldman, A., Novosolov, M., Allison, A., Bauer, A.M., Bernard, R., Böhm, M., Castro-Herrera, F., Chirio, L., Collen, B., Colli, G.R., Dabool, L., Das, I., Doan, T.M., Grismer, L.L., Hoogmoed, M., Itescu, Y., Kraus, F., LeBreton, M., Lewin, A., Martins, M., Maza, E., Meirte, D., Nagy, Z.T., Nogueira, C.C., Pauwels, S.G., Pinchera-Danoso, D., Powney, G.D., Sindaco, R., Tallowin, O.J.S., Torres-Carvajal, O., Trape, J.-F., Vidan, E., Uetz, P., Wagner, P., Wang, Y., Orme, C.D.L., Grenyer, R., Meiri, S. (2017): The global distribution of tetrapods reveals a need for targeted reptile conservation. *Nat. Ecol. Conserv.* **1** (11): 1677-1682.
- Rull, V., Huber, O., Vegas-Vilarrúbia, T., Señaris, C. (2019): Definition and characterization of the Pantepui biogeographical province. In: *Biodiversity of Pantepui: the Pristine "Lost World" of the Neotropical Guiana Highlands*, p. 3-32. Rull, V., Vegas-Vilarrúbia, T., Huber, O., Señaris, C., Eds, Academic Press, London.
- Sánchez Osés, C., Pérez-Hernández, R. (1998): Revisión histórica de las subdivisiones biogeográficas de la región Neotropical, con especial énfasis en Suramérica. *Montalbán* **31**: 169-210.
- Silva, J.M.C., Sousa, M.C., Castelletti, C.H.M. (2004): Areas of endemism for passerine birds in the Atlantic Forest, South America. *Global Ecol. Biogeogr.* **13**: 85-92.
- Szumik, C., Cuezzo, F., Goloboff, P., Chalup, A. (2002): An optimality criterion to determinate areas of endemism. *Syst. Biol.* **51** (5): 806-816.
- Szumik, C., Goloboff, P. (2004): Areas of endemism: an improved optimality criterion. *Syst. Biol.* **53** (6): 968-977.
- Tingley, R., Meiri, S., Chapple, D. (2016): Addressing knowledge gaps in reptile conservation. *Biol. Conserv.* **204**: 1-5.
- Torres-Carvajal, O., Echevarría, L.Y., Vanegas, P.J., Chavez, G., Camper, J.D. (2015): Description and phylogeny of three new species of *Synophis* (Colubridae, Dipsadinae) from the tropical Andes in Ecuador and Peru. *ZooKeys* **546**: 153-179.
- Uetz, P., Freed, P., Hošek, J., Eds (2020): The reptile database, <http://www.reptile-database.org>, accessed [April 20 2020].
- Whittaker, R.J., Araújo, M.B., Jepson, P., Ladle, R.J., Watson, J.E.M., Willis, K.J. (2005): Conservation biogeography: assessment and prospect. *Divers. Distrib.* **11**: 3-23.
- Wieczorek, J.R., Guo, Q., Hijmans, R.J. (2004): The point-radius method for georeferencing point localities and calculating associated uncertainty. *Int. J. Geogr. Inf. Sci.* **18**: 745-767.
- Wiens, J.J. (2011): The niche, biogeography and species interactions. *Philos. T. Roy. Soc. B* **366** (1576): 2336-2350.

*Submitted: May 10, 2020. Final revision received: October 12, 2020. Accepted: January 4, 2021.
Associate Editor: Salvador Carranza.*