

Unravelling distribution patterns of Neotropical lianas: an analysis of endemism of tribe Bignonieae (Bignoniaceae)

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Received 17 November 2020; revised 21 June 2021; accepted for publication 19 September 2021

Areas of endemism characterize geographical regions by their unique biotas, providing the basis for studies on the ecological and historical drivers of these biologically distinct units. Tribe Bignonieae (Bignoniaceae) are a highly diverse clade of lianas distributed throughout the Neotropics, representing an excellent model for studying the drivers of species diversity and distribution patterns in this region. We used a dataset representing 98% of the diversity of Bignonieae and 21 170 unique locality records to perform an analysis of endemism using NDM/VNDM. We recovered areas of endemism distributed across the Neotropics, including a higher number of areas at coarser spatial scales. Although overlapping and nested patterns of endemism were common and the spatial congruence with the individual units of previous regionalization schemes was low, the patterns of endemism recovered were in general agreement with those documented for other taxa. Our findings are generally consistent with key Neotropical biogeographical hypotheses. These results highlight the importance of studying detailed distribution patterns of selected taxa for an improved understanding of Neotropical biogeography.

ADDITIONAL KEYWORDS: analysis of endemism – areas of endemism – Bignonieae – lianas – NDM/VNDM – Neotropical flora – Neotropical biogeography.

INTRODUCTION

A key component of biogeographical analyses is discovering and documenting areas of endemism (Escalante, 2009). Delimiting these areas allows the ecological and historical drivers of endemism (Anderson, 1994; Weeks, Claramunt & Cracraft, 2016) to be explored, contributing important information for conservation (Myers *et al.*, 2000). An area of endemism can be defined as a location where at least two species that occur nowhere else exhibit a non-random arrangement of extensive sympatry among their geographical ranges (Morrone, 1994; Platnick, 1991; Szumik & Goloboff, 2004). The search for these patterns involves a two-step approach of discovery

and explanation. Among the methods to discover areas of endemism, analysis of endemism uses a combinatorial approach in which the congruence and fit among multiple species ranges and a possible area of endemism is calculated and optimized (Szumik & Goloboff, 2004). The optimality criterion and the spatially explicit approach have shown that overlapping patterns of endemism are common (Szumik, Pereyra & Casagrande, 2018) and that the inherent properties and biases of the occurrence data may result in multiple optimal areas with slight variation in species composition (Aagesen, Szumik & Goloboff, 2013; Casagrande & Goloboff, 2019). This variation and overlap may result in a variety of areas of endemism, and the thorough description and analysis of their conforming species is a prerequisite for inferring the possible drivers of distribution.

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A first step to sort potential hypotheses is to situate the area of endemism in the context of the biogeographical knowledge of the study region. This can be achieved by comparing and finding spatial agreements between the area and the constituent units of a biogeographical regionalization scheme. The underlying assumption is that regionalization schemes can serve as comparative frameworks to distinguish shared from unique patterns and to inform hypotheses about distributional drivers. This methodological assumption has deep historical roots (Wallace, 1894) that underly regionalization efforts (Morrone, 2018), and it is generally applied by depicting a map to visually inspect the similarity between the areas discovered and the units of a biogeographical regionalization scheme (e.g. Ferretti, González & Pérez-Miles, 2014; Ribeiro *et al.*, 2014; Klassa & Santos, 2015; Noguera-Urbano & Escalante, 2015; Gomes-da-Silva, Amorim & Forzza, 2017). Regionalizations can be based on different criteria such as species composition similarity (Kreft & Jetz, 2010), beta-diversity (Holt *et al.*, 2013), species composition and habitat similarity (Udvardy, 1975; Olson *et al.*, 2001), presence-absence patterns in network analyses (Vilhena & Antonelli, 2015; Edler *et al.*, 2016) and endemism (Escalante, 2009; Morrone, 1994, 2018). To ensure that comparisons between areas of endemism and the units of regionalization are valid, the regionalization scheme must correspond to major patterns of endemism. Although methods to compare categorical maps quantitatively are available for complete biogeographical regionalization schemes (Edler *et al.*, 2016) and vegetation maps (Nowosad & Stepinski, 2018), quantitative assessments of the similarity between areas and specific regionalization units are rare. The documentation and formulation of areas of endemism would greatly benefit from objective measures of similarity.

Comparisons of areas of endemism and regionalization schemes can help advance the understanding of biogeographical patterns and processes in the Neotropics. The Neotropics has been divided by different regionalization schemes based on distribution data from animals (Kreft & Jetz, 2010; Rueda, Rodríguez & Hawkins, 2013), plants (Gentry, 1982; Takhtajan, 1986; Fiaschi & Pirani, 2009) and a variety of taxa (Udvardy, 1975; Cabrera & Willink, 1980; Morrone, 2017). Boundaries and biogeographical units of some of these schemes have been associated with possible drivers such as contemporary climate for Wallace's zoogeographical boundaries (Ficetola, Mazel & Thuiller, 2017), correspondence of morphoclimatic domains to the phytogeographical regions of South America (Prance, 1982; Ab'Sáber, 2003) and Neotropical geological events during the Cretaceous (Morrone, 2014a). Furthermore, taxon-specific

distribution patterns are often associated with possible drivers. For example, patterns of endemism and diversity of plants have been attributed to species geographical origins. Laurasian floristic components seem to be concentrated in highlands (e.g. the Andes), whereas Gondwanan elements seem to predominate in the lowlands (Gentry, 1982). In turn, differences in plant habit associated with these distribution patterns show that trees and lianas display Amazon-centred distributions, whereas epiphytes, understory shrubs and palms display Andean-centred distributions (the 'Gentry pattern' *sensu* Antonelli & Sanmartín, 2011). Observing these common distribution patterns among species with similar sets of shared traits may help frame ecological hypotheses about the drivers behind these patterns (e.g. Swenson & Weiser, 2010; Violle *et al.*, 2014). By comparing areas of endemism to regionalization schemes and searching for patterns in species traits among endemic species, it would be possible to shed light on the biogeography of selected lineages (Fine & Lohmann, 2018).

Bignonieae (Bignoniaceae) are the most diverse clade of lianas in the Neotropics (Lohmann, 2004, 2006; Lohmann & Taylor, 2014), including 20 genera and 393 species (Lohmann & Taylor, 2014; Fonseca & Lohmann, 2019) distributed throughout the American continental platform (between 39°N and 35°S), including the Antilles (Lohmann, 2006). These plants occur in a great variety of habitats, from the Caatinga and dry savannas to humid rain forests and montane vegetation, occurring in most Neotropical biogeographical subdivisions (Gentry, 1983; Lohmann *et al.*, 2013). They are centred in south-eastern Brazil and the Amazon Basin (Meyer, Diniz-Filho & Lohmann, 2018), representing an excellent model to frame questions about distributional drivers in this region. The patterns of endemism of Bignonieae were described by Gentry (1979, 1992), the most prolific collector of these lianas, as centred in five main regions: (1) Central America and Western South America, encompassing south-eastern Venezuela and extending through the Andes to northern Venezuela; (2) Lowland Amazonia, from the westernmost limit of the Amazon Basin in Peru and Ecuador, extending to the Amazon mouth in the east; (3) Guayana region, encompassing the Guyana lowlands and the tepuis, a subset of Amazonia; (4) Coastal Brazil, comprising the eastern Atlantic coast of Brazil; and (5) Brazilian dry areas, including the Caatinga and Cerrado, extending south-west to the Chaco in northern Argentina. Although the limits between some of these regions can be sharp (e.g. north and south of the Orinoco river, Amazonian and Andean lowlands), other limits seem diffuse, containing taxa that occur in more than one area (e.g. Brazilian dry areas, Coastal Brazil and

Amazonia). Gentry's analyses were qualitative, and no quantitative assessment of areas of endemism in Bignoniaceae has ever been conducted to date. It remains unclear whether patterns of endemism in Bignoniaceae agree with (1) Gentry's phytogeographical regions, (2) other biogeographical regionalization schemes and/or (3) areas of endemism identified for other taxa. It is also unknown whether all endemic species with the same patterns of endemism share a common set of traits that might point to underlying ecological processes.

Here, we conduct an analysis of endemism (Szumik *et al.*, 2002; Szumik & Goloboff, 2004) for Bignoniaceae and explore the biogeographical implications of these patterns by assessing the similarity of areas of endemism with previous regionalization schemes of the Neotropics. More specifically, we evaluate whether areas of endemism of Bignoniaceae agree with phytogeographical regions proposed by Gentry (1982, 1990) and whether they display the shared patterns of the multi-taxon regionalization scheme of Morrone (2014b). To aid this comparison, we formalize a quantification of spatial congruence between areas of endemism and selected biogeographical units. We also explore the spatial configuration of areas of endemism and the characteristics of the endemic species in these patterns to make inferences about potential drivers.

MATERIAL AND METHODS

DISTRIBUTION DATABASE

The database for Bignoniaceae contains 28 763 records and encompasses 386 out of 393 described species, representing 98% of the known species diversity of Bignoniaceae (Lohmann & Taylor, 2014). The specimen records were originally downloaded from the TROPICOS database at the Missouri Botanical Garden (<http://legacy.tropicos.org/SpecimenSearch.aspx>) and subsequently supplemented with records from the herbarium of the University of São Paulo (SPF) (acronym follows Thiers, 2021) to increase species diversity and alleviate sampling for species with fewer than five records. The taxonomic identity of each herbarium specimen was confirmed by LGL, except for *Adenocalymma* Mart. ex Meisn. emend. L.G.Lohmann for which confirmation was jointly done by LGL and Luiz Henrique Fonseca (SPF). Species identifications follow the classification of Lohmann & Taylor (2014), including subsequent updates for *Adenocalymma* (Fonseca & Lohmann, 2019), *Bignonia* L. (Zuntini *et al.*, 2015a, b), *Dolichandra* Cham. emend. L.G.Lohmann (Fonseca *et al.*, 2017), *Martinella* Baill. (Kataoka & Lohmann, 2021), *Pachyptera* DC. ex Meisn. (Francisco & Lohmann, 2019), *Tanaecium* Sw. emend. L.G.Lohmann (Frazão & Lohmann, 2018), *Tynanthus*

Miers. (Medeiros & Lohmann, 2015) and *Xylophragma* Sprague (Kaehler & Lohmann, 2020). Geographical locality descriptions were revised using regional maps and gazetteers (Getty Thesaurus of Geographic Names Online, <http://www.getty.edu/research/tools/vocabularies/tgn/>). Recurrent issues affecting the quality of geographical information in biodiversity databases (i.e. points in the sea, zero coordinates, occurrences at centroids of main cities, around research institutions, geographical outliers) were checked and corrected whenever possible (Zizka *et al.*, 2019). New georeferences were assigned following the best practices to interpret point locality descriptions (Chapman & Wieckzoreck, 2006) and using Google Earth (<https://earth.google.com/web/>). Duplicated specimens from a single species collected in the same locality were excluded from the database resulting in a dataset of 21 170 records. For a detailed description of the database and analysis of its spatial biases, see Narváez-Gómez, Guedes & Lohmann (2021).

ANALYSIS OF ENDEMISM

The analysis of endemism is a grid-based spatial analysis of patterns of endemism (Szumik *et al.*, 2002; Szumik & Goloboff, 2004). This criterion is implemented in the software NDM/VNDM v.3.1 (Goloboff, 2004), which can use point occurrence data and range maps to generalize species distributions into presence-absence matrices. NDM/VNDM generates candidate areas of endemism algorithmically and assesses the spatial fit between the areas and the distribution of the individual species. The endemism index (EI) measures this spatial fit by applying a series of rules that count the number of grid cells that lie outside and inside the candidate area, while assessing how homogeneous the distribution of the individual species in this area is. The minimum number of species allowed per candidate area is two, and the optimization procedure retains the areas with the higher EI. Therefore, a higher number of species scoring in the area and a higher spatial fit of their distributions lead to higher EI and stronger support for the candidate area as an area of endemism.

Multiple equally optimal candidate areas with minor differences in species composition can be obtained, reflecting the ambiguity inherent to empirical distributional data. These areas can be summarized using consensus techniques in which similarity thresholds of species composition allow aggregating similar areas (Aagesen *et al.*, 2013). Two rules may be applied while controlling for the rigour of comparisons among areas. The loose consensus rule merges candidate areas sharing a percentage of their scoring species with any other candidate area; the tight consensus rule merges candidate areas sharing a percentage of their scoring species with every candidate area in the

consensus. While the loose rule can identify gradients of endemic species at coarser spatial scales, the tight rule can identify patterns with higher congruent sets of species at finer scales (Aagesen *et al.*, 2013). To use higher values of similarity in both rules increases the resulting consensus areas because slight differences in species composition decrease similarity among patterns, thus separating areas and approaching the number of individual candidate areas in the analysis. After the consensus rule is applied, some species can still support more than one pattern, making these species ambiguous evidence of patterns of endemism. Therefore, intermediate thresholds of similarity produce a better compromise between the aggregation of candidate areas, the number of consensus areas presented, and a better representation of ambiguous evidence.

PARAMETER SET FOR THE ENDEMICITY ANALYSIS

Presence-absence matrix

We conducted three analyses of endemism using the default parameters of NDM/VNDM v.3.1 at three spatial scales by creating presence-absence data matrices with grid sizes of $1^\circ \times 1^\circ$, $2^\circ \times 2^\circ$ and $3^\circ \times 3^\circ$. To alleviate possible sampling issues and assist the identification of patterns, we used the fill radius option. Because the fill radius is defined as a percentage of the cell width, a different radius was selected for each grid size, proportionally decreasing it by half of the fill percentage assumed for the immediate broader scale following Casagrande, Roig-Juñent & Szumik (2009). Thus, the larger the grid size, the smaller the radius (i.e. 1° : fill 40%, assumed 80%; 2° : fill 20%, assumed 40%; 3° : fill 10%, assumed 20%). Species with disjunct distributions were excluded from the automatic filling procedure and filled manually with minimum convex polygons (see Supporting Information, Appendix S1). Manual cleaning of grid cells around continental borders was avoided to guarantee reproducibility of areas obtained at continental margins.

To consider higher taxa in the analyses (Szumik & Goloboff, 2015), individual species were aggregated per genera following the current generic classification of Bignoniaceae (Lohmann & Taylor, 2014) and recent adjustments in the circumscription of *Adenocalymma* (Fonseca & Lohmann, 2019). Likewise, we used clades of a supertree assembled in TNT 1.5 (Goloboff & Catalano, 2016) from phylogenetic hypotheses available for the tribe (Lohmann, 2006; Zuntini, 2014; Fonseca & Lohmann, 2015; Medeiros & Lohmann, 2015) (see Supporting Information, Appendix S1). VNDM-NDM automatically generates clade distributions as the union of distribution of constituent species, counting the endemism score from the clade if higher than the

sum of scores for the constituent species and vice-versa (see Szumik & Goloboff, 2015 for details).

Consensus areas

We applied the loose consensus rule with a similarity cut-off of 40% to all analyses. To assess the effect of spatial scale on patterns of endemism, we compared species composition among consensus areas across spatial scales by considering areas with similar geographical locations across the three analyses. We identified overlapping and nested patterns and the species supporting more than one consensus area. To distinguish the regions with the highest number of overlapping areas of endemism, we counted the number of overlapping areas per 1° cells across the geographic extent of Bignoniaceae by rasterizing all consensus areas and adding the resulting layers using the raster package (Hijmans, 2020) of the R scripted language (R Core Team, 2020). To better visualize regions with a similar number of overlapping consensus areas, we grouped the 1° grid cells with a similar number of overlapping areas and successively increased the range of overlapping areas per cell allowed in the group. This visualization scheme allowed us to observe patterns of overlap by identifying areas where the greater and lower overlap are centred. Although this visualization provides a broad view of all patterns found in the analyses, some areas at different spatial scales might represent the same pattern but with slight differences in species composition that ultimately depend on the data quality and its representation using different grid sizes.

Spatial congruence between patterns of endemism and regionalization schemes

We compared consensus areas against Gentry's phytogeographical proposal (1979, 1982) and Morrone's (2014b) hierarchical classification of the Neotropics. Ideally, areas should be compared based on species fit. However, in the absence of hard data about species supporting the regionalization schemes of Gentry and Morrone, only a purely spatial criterion is possible. Similar approaches have compared categorical vegetation maps and assessed similarity and association between complete regionalizations (Hargrove, Hoffman & Hessburg, 2006; Edler *et al.*, 2016; Nowosad & Stepinski, 2018), but not for individual patterns of endemism against the units of a regionalization.

Inspired by those approaches, we calculated spatial agreement between polygons of the consensus areas and selected biogeographical units proposed in regionalization schemes. More specifically, we calculated spatial agreement between polygons of

the consensus areas and selected the biogeographical units proposed in regionalization schemes. Because polygons can have different shapes and sizes that make the assessment of one-to-one spatial matching challenging, we characterized the spatial agreement using two complementary measures as follows: (1) uniformity of the consensus area (U_c), which measures the proportion of the consensus area covered by a biogeographical unit; and (2) uniformity of the biogeographical unit (U_b), which measures the proportion of the biogeographical unit covered by the consensus area. To measure the spatial congruence (Sc) between the consensus area and the biogeographical unit, we used the average between U_c and U_b .

When the spatial match between a consensus area and a biogeographical unit is perfect, the values of U_c , U_b and Sc equal 100%. However, in cases where any of the areas are nested (e.g. consensus area inside reference area or vice-versa), one of the uniformity values equals 100%, with the other being close to 0%. In this case, the corresponding spatial congruence approaches 50% (depending on size and shape). To calculate U_c , U_b and Sc , we used the shapefiles of the Neotropical Region by Löwenberg-Neto (2014) and georeferenced the map of phytogeographical regions of Gentry (1982) using Georeferencer GDAL plug-in 3.1.9 of QGIS v.2.1.8. All comparisons and figures were scripted in R (R Core Team, 2020) using the *sf* (Pebesma, 2018) and *tidyverse* set of packages (Wickham, 2019) (scripts available at https://github.com/jupanago/RCode_BignonAoE).

Exploring traits of endemic species

The joint appearance of common distribution patterns and shared sets of species traits may indicate possible shared distributional drivers. We conducted an exploratory analysis of species traits and looked for commonalities among species with shared patterns. We examined the elevational range of all endemic species to identify whether patterns occurred mainly in a particular elevational belt and whether the species scoring to more than one consensus area occurred preferentially in one elevational belt. We obtained elevation data from the Bignoniaceae database. In the case of species without information about elevation range, digital elevation models were extracted using concurrence points (Narváez-Gómez *et al.*, 2021). Sister species pairs were identified in the phylogenetic trees for Bignoniaceae available to date (Lohmann, 2006; Kaehler, Michelangeli & Lohmann, 2012, 2019; Zuntini, 2014; Medeiros & Lohmann, 2015; Firetti *et al.*, 2017; Fonseca & Lohmann, 2018, 2019; Thode & Lohmann, 2019; Supporting Information, Appendix S1) and used as the basis for examining identified species pairs that

contributed to the EI of particular areas of endemism. We classified the areas with sister species pairs as 'disjunct' and 'nested'. Using a morphological character matrix with information on pollination syndromes and vegetative traits related to herbivory (i.e. presence or absence of domatia, glands at the prophylls of the axillary glands, nectar-robber protection), we searched for areas that shared the same set of traits. Naming conventions used for consensus areas are: (1) letters referring to the approximate geographical sector where the area is located; and (2) number identifying the area. Thus, area AM-1 refers to 'Consensus Area 1 in the Amazonia sector'.

RESULTS

AREAS OF ENDEMISM FOR BIGNONIEAE

Three independent analyses of endemism were conducted considering three spatial scales. Overall, we obtained 70 consensus areas, summarizing 494 individual patterns of endemism that were composed by 286 of the 386 species of Bignoniaceae considered in the analyses (Table 1; Fig. 1; see Supporting Information, Appendix S2). In general, consensus areas were formed by three to 103 species, with most areas ranging from three to 14 species and only two areas having c. 100 species each (Table 2). Five higher taxa also contributed to the EI of consensus areas but only at the spatial scale of three degrees (i.e. the genera *Amphilophium* Kunth emend L.G.Lohmann, *Cuspidaria* DC. and *Pachyptera* and the clades GRP-15 and GRP-1; Table 2, a list of all the genera comprising each clade is available in the Supporting Information, Appendix S1). The values of the EI followed a trend in which consensus areas with fewer species showed higher total values relative to the total number of scoring species in the pattern (Table 2). Twenty-one consensus areas were composed of exclusive sets of species, and 49 consensus areas shared between one and four species. Eighty-nine species contributed to the EI of more than one consensus area.

In general, the effect of a larger spatial scale was to increase the number of species, individual patterns and consensus areas while covering a wider geographical region (Fig. 1F). A comparison across the analyses showed that consensus areas found at broader spatial scales tended to include the species of the consensus areas found at finer spatial scales. Patterns of species compositional changes across scales consisted of a complete or incomplete inclusion of species in the broader consensus areas and the emergence of new combinations of species at the broader spatial scales (see Supporting Information, Appendices S1 and S3).

Table 1. Summarized results of the analysis of endemism. Spatial scale: the grid size in degrees. Individual areas: the number of individual sets recovered in each search. Scoring: the total number of scoring species contributing to the endemism index of individual areas. Higher taxa: the number of higher taxa groups contributing to the endemism index of individual areas. Consensus areas: the number of consensus areas per analysis obtained under the loose rule at 40% cut-off of similarity. Shared species: the number of species supporting more than one pattern of endemism. Consensus areas with shared species: the number of consensus areas that share one or more species

Spatial scale	Individual areas	Species	Higher taxa	Consensus areas	Shared species	Consensus areas with shared species
1	16	39	0	10	5	6
2	159	166	0	28	33	17
3	319	277	5	32	54	26

The consensus areas represent areas of endemism discovered consistently over the same wide geographic sectors across all the analyses of endemism (Table 2, Fig. 1A–E). The spatial configuration of areas of endemism in these sectors exhibited extensive degrees of overlap and nested patterns which were more numerous at the scale of three degrees. Species that supported different areas of endemism were observed mainly among the nested patterns and, in some cases, corresponded to species located in a particular elevation belt (Supporting Information, Appendix S3). When all the spatial scales were considered together, and the geographic space was divided into one-degree cells, the number of overlapping areas per cell varied and showed higher values in Amazonia and Eastern South America, with some cells recording up to 20 overlapping areas of endemism (Fig. 2A). Patterns of overlap were revealed by grouping cells with the same range of overlapping patterns and increasing the number of overlapping patterns considered in each group step by step (Fig. 2B). This decomposition of overlapping patterns showed that the regions encompassed by the Amazon, the Central Atlantic Forest in Eastern South America, the Dry and Open Vegetation Diagonal and Mesoamerica could be broadly delimited by the number of overlapping areas of endemism of Bignoniaceae.

SPATIAL CONGRUENCE OF AREAS OF ENDEMISM AND BIOGEOGRAPHICAL REGIONALIZATION SCHEMES

Overall, the spatial congruence among areas of endemism of Bignoniaceae and the units of the biogeographical regionalization schemes proposed by Gentry (1982) and Morrone (2014b) was low (Fig. 2C). At each spatial scale, the areas of endemism overlapped with several biogeographical units and covered the areas in different degrees. However, 15 areas of endemism at the spatial scales of two and three degrees showed spatial congruence values > 66%. Nine of these areas were located and centred in the geographical sector of Amazonia, and their congruence

values ranged between 67 and 83% for Gentry's and Morrone's biogeographical units (AM_3-15; Table 2, Fig. 1B). Two areas of endemism showed spatial congruence between 80 and 82% with the Neotropical Region as a whole (i.e. NEO_1 and SA_1; Fig. 1A), with one of those two areas covering a region equivalent to Tropical South America (i.e. SA_1). Similarly, other areas showed congruence values between 67 and 70% for the biogeographical units of Parana Dominion, Chacoan Subregion, the Cerrado and Associated Dry Areas (i.e. THDD_5 and THDD_2; Fig. 1C), and the Guiana Province and Guiana Lowlands (i.e. GU_7 and GU_6; Fig. 1D). The other two areas of endemism resembled the Mesoamerican Dominion and the Pacific dominion (MESO_1 and NWSA_1, Fig. 1E), although with lower congruence values. In general, despite the lower spatial congruence among most comparisons among areas of endemism and biogeographical units, many areas of endemism showed patterns that were similar to those of other Neotropical taxa (Table 2).

DISTRIBUTION OF SISTER SPECIES PAIRS AMONG AREAS OF ENDEMISM

Only 33 out of the 83 sister species pairs for Bignoniaceae examined contributed to the EI of the areas of endemism (Table 3, Fig. 3A). Sister species pairs belonged to ten genera, among which *Adenocalymma* showed the highest number, and *Mansoa* DC. and *Tanaecium* showed the lowest (Table 3). Most of the sister species pairs were distributed among overlapping and nested areas of endemism, whereas the number of species pairs in disjunct patterns and inside the same area of endemism was the same (Table 3). Areas of endemism located in different geographical sectors can be represented as connected by species pairs (Fig. 3A). These connections were more numerous among local patterns of endemism in the broad sectors of Amazonia and Eastern South America than in other sectors. Central Amazonia was connected to Western Amazonia, Eastern Amazonia and the Guiana Shield by two species pairs in each case. Similarly, different numbers

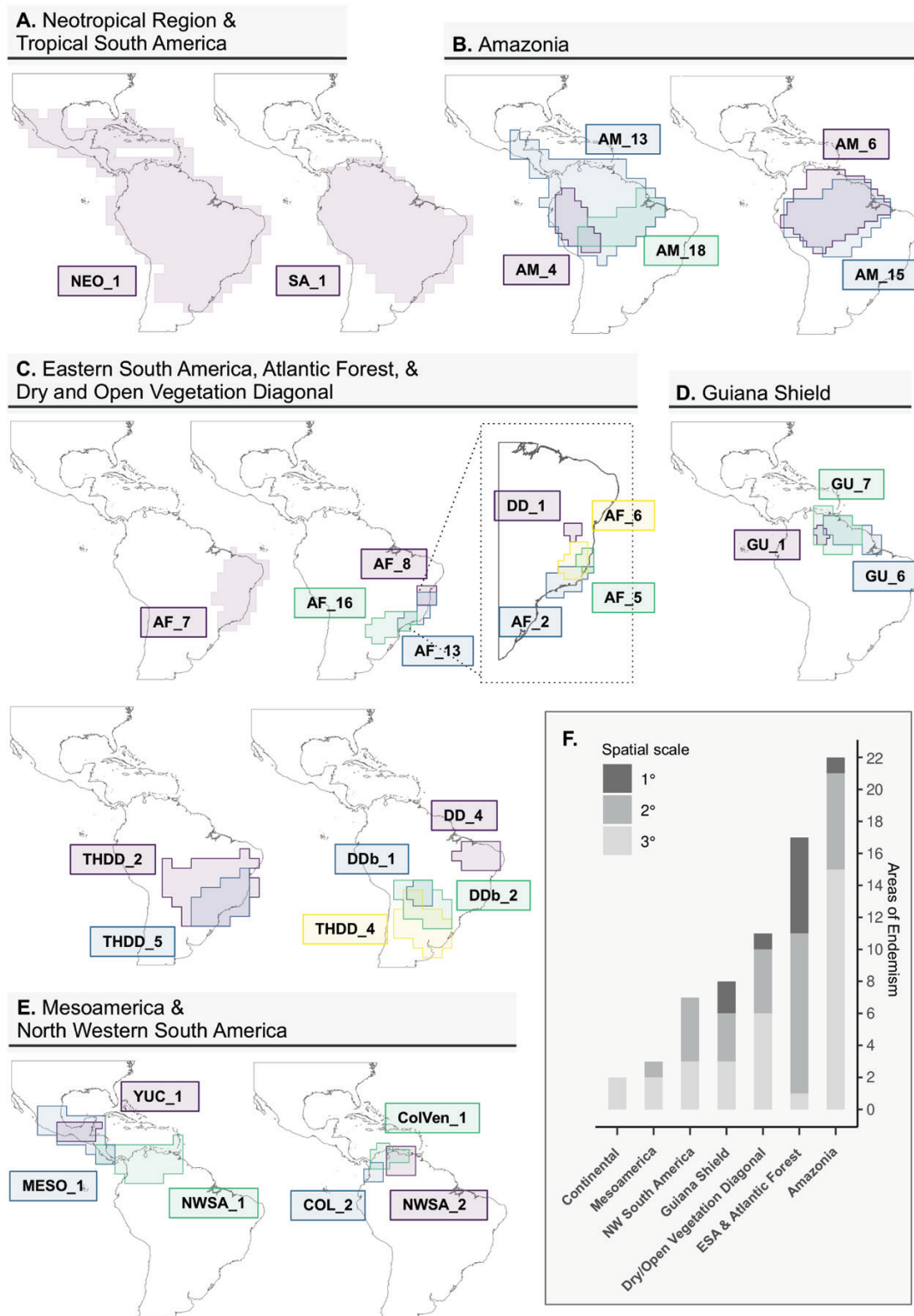


Figure 1. A selection of the diversity of Areas of endemism of the tribe Bignoniaceae in the Neotropics, and the geographical sectors over which they were clustered. A, Continental-scale patterns: Neotropical Region and Tropical South America. B, Amazonia (AM). C, Eastern South America: Atlantic Forest, and Dry and Open Vegetation Diagonal. D, Guiana Shield. E, Mesoamerica and North-western South America. F, Number of areas of endemism per geographic sector and spatial scale. For the complete set of 70 areas of endemism, please refer to the [Supporting Information, Appendix S3](#).

Table 2. Areas of endemism of tribe Bignonieae (Bignoniaceae) in the Neotropics. Geographical sectors: the geographical sectors over which areas are clustered and overlap. Area of endemism: consensus of the individual areas found at the default analysis from one to three degrees. Higher taxa: the number of individual areas formed by genera and clades in the consensus area. Individual areas: the number of individual areas summarized in the consensus area. Endemic species: the number of scoring species in the consensus area. Minimum and maximum EI scores: the endemicity index range that individual areas showed in the consensus area. Other taxa: the individual taxa for which similar patterns of endemism have been documented previously, including areas defined by different methods. A detailed description of the endemicity analysis is provided in the [Supporting Information, Appendix S2](#)

Geographical sector	Area of endemism	Spatial scale	Endemic species	Higher taxa	Individual areas	Minimum EI score	Maximum EI score	Similar patterns of endemism published for other taxa
Continental scale: Neotropical Region	NEO_1	3	2	3	7	2.64	2.89	Mammals (Noguera-Urbano & Escalante, 2017)
Continental scale: Tropical South America	SA_1	3	1	2	1	2.587	2.837	Hemiptera (Ferrari <i>et al.</i> , 2010); fish (Albert & Reis, 2011)
Central America: Mesoamerica	YUC_1	2	3	0	3	2.157	2.407	Gymnosperms (Contreras-Medina <i>et al.</i> , 2007); mammals (Noguera-Urbano & Escalante, 2015); mammals (Escalante <i>et al.</i> , 2009); Hemiptera (Ferrari <i>et al.</i> , 2010)
North-Western South America	MESO_1	3	5	0	3	2.098	2.348	Tabanomorpha (Klassa & Santos, 2015); Capparaceae (Mercado Gómez & Escalante, 2019)
	MESO_2	3	5	0	1	3.14	3.39	
	NWSA_1	3	20	0	23	2.115	4.962	
	NWSA_2	3	4	0	1	2.399	2.649	
	Col_1	2	5	0	1	3.068	3.318	Mammals (Noguera-Urbano & Escalante, 2015); Capparaceae (Mercado Gómez & Escalante, 2019)
	Col_2	2	3	0	1	2.176	2.426	
	Col_3	3	4	0	1	2.328	2.578	
	ColVen_1	2	5	0	2	2.108	2.858	
	ColVen_2	2	4	0	2	2.143	2.393	Mammals (Noguera-Urbano & Escalante, 2015); oryzomyne rodents (Prado <i>et al.</i> , 2015)

Table 2. Continued

Geographical sector	Area of endemism	Spatial scale	Endemic species	Higher taxa	Individual areas	Minimum EI score	Maximum EI score	Similar patterns of endemism published for other taxa
Guiana Shield	GU_1	1	3	0	1	2.017	2.267	Mammals (Noguera-Urbano & Escalante, 2015); birds (Oliveira <i>et al.</i> , 2017); birds (Cracraft, 1985); Hymenoptera (Camargo & Pedro, 2003)
	GU_2	1	4	0	2	2.204	2.454	Plants (Prance, 1973, 1982)
	GU_3	2	4	0	3	2.119	2.369	Mammals (Noguera-Urbano & Escalante, 2015); oryzomyne rodents (Prado <i>et al.</i> , 2015); plants (Prance, 1973, 1982); birds (Cracraft, 1985); Hymenoptera (Camargo & Pedro, 2003)
	GU_4	2	6	0	3	3.392	3.892	Mammals (Noguera-Urbano & Escalante, 2015); birds (Cracraft, 1985)
	GU_5	2	6	0	2	2.174	3.424	Mammals (Noguera-Urbano & Escalante, 2015); birds (Cracraft, 1985; Oliveira <i>et al.</i> , 2017); Hymenoptera (Camargo & Pedro, 2003)
Amazonia	GU_6	3	6	0	3	2.429	2.679	Oryzomyne rodents (Prado <i>et al.</i> , 2015)
	GU_7	3	18	0	12	2.015	4.298	Hymenoptera (Camargo & Pedro, 2003)
	GU_8	3	7	0	2	3.429	4.429	Plants (Prance, 1973, 1982); birds (Cracraft, 1985); fish (Hubert & Renno, 2006)
	AM_1	1	3	0	1	2.473	2.723	Birds (Oliveira <i>et al.</i> , 2017)
	AM_2	2	7	0	7	2.27	3.02	
	AM_3	2	4	0	2	2.395	3.145	
	AM_4	2	3	0	1	2.354	2.604	Fish (Hubert & Renno, 2006); Hemiptera (Ferrari <i>et al.</i> , 2010); palms (Alvez-Valles <i>et al.</i> , 2018)
	AM_5	2	3	0	1	2.532	2.782	Fish (Hubert & Renno, 2006); Hemiptera (Ferrari <i>et al.</i> , 2010); palms (Alvez-Valles <i>et al.</i> , 2018)
	AM_6	2	3	0	1	2.337	2.587	
	AM_7	2	3	0	1	2.1	2.35	Birds (Oliveira <i>et al.</i> , 2017)
	AM_8	3	17	0	39	2.311	6.013	Tabanomorpha (Klassa & Santos, 2015)
	AM_9	3	13	0	17	2.321	4.077	Tabanomorpha (Klassa & Santos, 2015); fish (Hubert & Renno, 2006)

Table 2. Continued

Geographical sector	Area of endemism	Spatial scale	Endemic species	Higher taxa	Individual areas	Minimum EI score	Maximum EI score	Similar patterns of endemism published for other taxa
Eastern South America, Atlantic Forest, & Dry and Open Vegetation Diagonal	AM_10	3	11	0	9	2.144	3.144	
	AM_11	3	6	0	6	2.024	3.024	Palms (Alvez-Valles <i>et al.</i> , 2018)
	AM_12	3	5	0	2	2.742	3.242	Oryzomys rodents (Prado <i>et al.</i> , 2015)
	AM_13	3	7	1	13	2.372	3.372	
	AM_14	3	7	0	5	2.237	2.987	
	AM_15	3	4	0	2	2.16	2.41	Palms (Alvez-Valles <i>et al.</i> , 2018)
	AM_16	3	14	0	6	2.336	5.83	
	AM_17	3	4	0	1	2.249	2.499	
	AM_18	3	3	0	1	2.021	2.271	
	AM_19	3	5	0	1	3.78	4.03	Fish (Hubert & Renno, 2006); Hemiptera (Ferrari <i>et al.</i> , 2010)
	AM_20	3	4	0	1	2.638	2.888	
	AM_21	3	3	0	1	2.063	2.313	
	AM_22	3	7	0	1	4.573	4.823	
	DD_1	1	3	0	1	2.388	2.638	Birds (Silva, Sousa & Castelletti, 2004); orchid bees (Garraffoni Moura & Lourenço, 2017); Capparaceae (Mercado Gómez & Escalante, 2019)
	DD_2	2	6	0	3	2.249	3.249	
	DD_3	2	4	0	1	2.737	2.987	Birds (Silva <i>et al.</i> , 2004)
	DD_4	3	14	0	6	3.339	6.291	
	DDb_1	2	4	0	1	2.246	2.496	Mammals (Costa <i>et al.</i> , 2000; Nogueira-Urbano & Escalante, 2015); Capparaceae (Mercado Gómez & Escalante, 2019)
	DDb_2	3	7	0	5	2.3	2.55	Primates (Goldani <i>et al.</i> , 2006)
	AF_1	1	9	0	3	3.789	4.289	Plants (Prance, 1973, 1982); harvestmen (Pinto-da-Rocha, da Silva & Bragagnolo, 2005); Galipeinae (Rutaceae) (Colli-Silva & Pirani, 2019)
	AF_2	1	7	0	4	3.025	3.275	Galipeinae (Rutaceae) (Colli-Silva & Pirani, 2019)

Table 2. Continued

Geographical sector	Area of endemism	Spatial scale	Endemic species	Higher taxa	Individual areas	Minimum EI score	Maximum EI score	Similar patterns of endemism published for other taxa
AF_3		1	4	0	1	2.615	2.865	<i>Piper</i> (Piperaceae) (Quijano-Abril <i>et al.</i> , 2006); several taxa (Sigrist & Carvalho, 2008); plants (Prance, 1973, 1982) Muscidae (Löwenberg-Neto & De Carvalho, 2009); harvestmen (Pinto-da-Rocha <i>et al.</i> , 2005); plants (Menini Neto <i>et al.</i> , 2016); Galipeinae (Rutaceae) (Colli-Silva & Pirani, 2019)
AF_4		1	5	0	1	3.282	3.532	Several taxa (Sigrist & Carvalho, 2008); plants (Prance, 1973, 1982; Menini Neto <i>et al.</i> , 2016); harvestmen (Pinto- da-Rocha <i>et al.</i> , 2005); Galipeinae (Rutaceae) (Colli-Silva & Pirani, 2019)
AF_5		1	5	0	1	3.035	3.285	Several taxa (Sigrist & Carvalho, 2008); plants (Prance, 1973, 1982); har- vestmen (Pinto-da-Rocha <i>et al.</i> , 2005); Galipeinae (Rutaceae) (Colli-Silva & Pirani, 2019)
AF_6		1	3	0	1	2.021	2.271	Plants (Prance, 1973, 1982); har- vestmen (Pinto-da-Rocha <i>et al.</i> , 2005); Pitcairniaceae (Bromeliaceae) (Gomes-da-Silva <i>et al.</i> , 2017); Galipeinae (Rutaceae) (Colli-Silva & Pirani, 2019)
AF_7		2	86	0	110	2.081	11.806	Capparaceae (Mercado Gómez & Escalante, 2019)
AF_8		2	4	0	2	2.024	2.274	Diptera (Amorim & Santos, 2017); Galipeinae (Rutaceae) (Colli-Silva & Pirani, 2019)
AF_9		2	6	0	3	2.865	3.115	Galipeinae (Rutaceae) (Colli-Silva & Pirani, 2019)
AF_10		2	3	0	1	2.328	2.578	Galipeinae (Rutaceae) (Colli-Silva & Pirani, 2019)
AF_11		2	4	0	2	2.184	2.684	
AF_12		2	5	0	1	3.506	3.756	
AF_13		2	6	0	1	4.116	4.366	Galipeinae (Rutaceae) (Colli-Silva & Pirani, 2019)
AF_14		2	3	0	1	2.67	2.92	

Table 2. Continued

Geographical sector	Area of endemism	Spatial scale	Endemic species	Higher taxa	Individual areas	Minimum EI score	Maximum EI score	Similar patterns of endemism published for other taxa
	AF_15	2	3	0	1	2.121	2.371	Mammals (Noguera-Urbano & Escalante, 2015); Hemiptera (Ferrari <i>et al.</i> , 2010); orchid bees (Garraffoni <i>et al.</i> , 2017); Galipeinae (Rutaceae) (Colli-Silva & Pirani, 2019)
	AF_16	2	3	0	1	2.506	2.756	Mammals (Noguera-Urbano & Escalante, 2015); oryzomyne rodents (Prado <i>et al.</i> , 2015); several taxa (Sigrist & Carvalho, 2008); Muscidae (Löwenberg-Neto & De Carvalho, 2009); primates (Goldani <i>et al.</i> , 2006)
	ESA_1	3	103	0	119	2.181	20.77	Oryzomyne rodents (Prado <i>et al.</i> , 2015); plants (Prance, 1973, 1982); primates (Goldani <i>et al.</i> , 2006); Hemiptera (Ferrari <i>et al.</i> , 2010)
	THDD_1	2	3	0	1	2.376	2.626	
	THDD_2	3	16	0	26	2.074	4.559	
	THDD_3	3	7	0	2	2.989	4.239	Hemiptera (Ferrari <i>et al.</i> , 2010)
	THDD_4	3	3	0	1	2.068	2.318	
	THDD_5	3	4	0	1	2.863	3.113	Oryzomyne rodents (Prado <i>et al.</i> , 2015); several taxa (Sigrist & Carvalho, 2008); Hemiptera (Ferrari <i>et al.</i> , 2010)

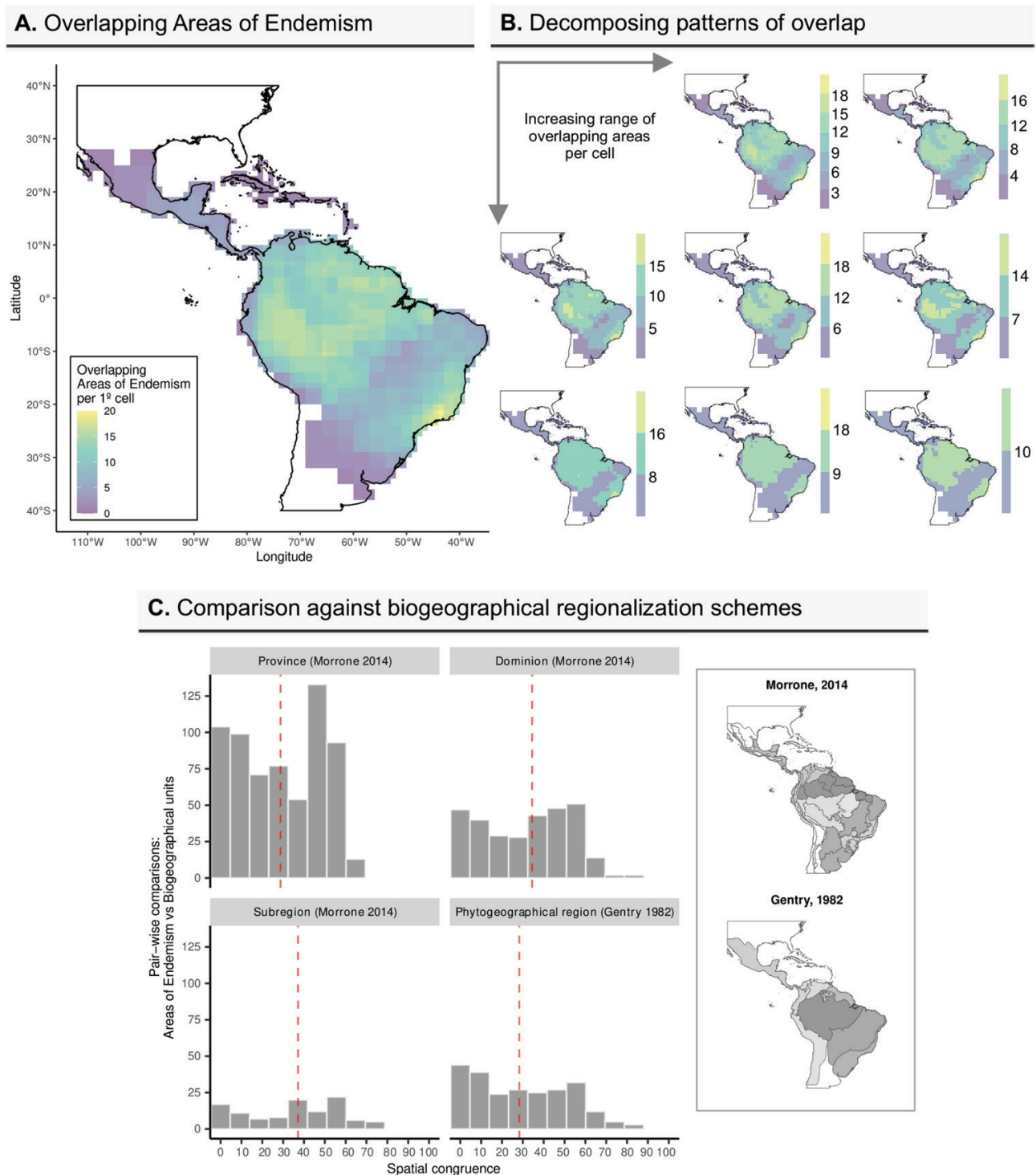


Figure 2. The biogeographical scenario of Bignoniaceae. A, Number of overlapping areas of endemism per 1° cells. Note the high number of areas of endemism per cell in the Amazonia and the Atlantic Forest in contrast to the Mesoamerica, North-western South America and the Dry and Open Vegetation Diagonal. B, Decomposition of patterns of overlapping consensus areas, each map presents the cells with the same range of overlapping areas per cell grouped by distinctive colours. Note how different patterns emerge across the continent, and how the regions of the Amazon and the Atlantic Forest are defined at the greatest range of cells considered (fewer than ten and more than ten areas of endemism per cell). This shows a biogeographical scenario where biogeographical regions are defined not only by local sets of endemic species, but also by

Table 3. Number of sister species pairs per genus and the spatial configuration of areas of endemism in which they occur. Definitions of 'Nested', 'Overlapped' and 'Disjunct' area based on counting the number of rows of cells in overlap following Szumik *et al.* (2019). 'Same' indicates the species pair occur in the same area

Genera	Sister species pairs	Spatial configuration of areas of endemism			
		Disjunct	Nested	Overlapped	Same
<i>Adenocalymma</i>	9	0	5	3	1
<i>Amphilophium</i>	4	1	2	0	1
<i>Anemopaegma</i>	4	1	1	1	1
<i>Fridericia</i>	4	1	1	1	1
<i>Cuspidaria</i>	3	1	0	2	0
<i>Lundia</i>	3	0	1	0	2
<i>Bignonia</i>	2	2	0	0	0
<i>Tynanthus</i>	2	0	0	1	1
<i>Mansoa</i>	1	0	0	1	0
<i>Tanaecium</i>	1	1	0	0	0
TOTAL	33	7	10	9	7

of species pairs connecting the Central Atlantic Forest with either the South Atlantic Forest and other areas located to the north in the Dry and Open Vegetation Diagonal were found. Five sister species pairs also connected the Amazonian and Eastern South America sectors, four of which among areas located in Central and Western Amazonian and in the Dry and Open Vegetation Diagonal (Fig. 3A, Supporting Information, Appendix S3). There were fewer connections among Mesoamerica, North-western South America and the southernmost areas of endemism in the Dry and Open Vegetation Diagonal.

COMMON TRAITS OF ENDEMIC SPECIES

All endemic species of 17 out of 70 areas of endemism showed at least one exclusive morphological trait related to pollination or herbivory (Fig. 3B, Supporting Information, Appendix S1). The floral type *Anemopaegma* and the pollination by large to medium-size bees were the two exclusive trait states that characterized most endemic species among these areas. The presence of nectar-robber protection,

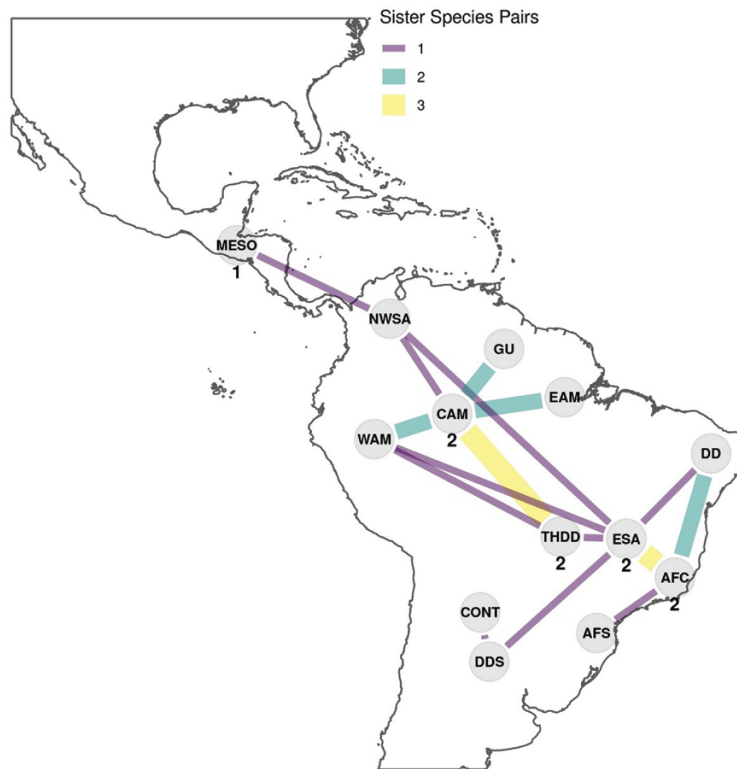
domatia and glands at the prophylls of the axillary buds was also common. Only six areas were formed by species characterized by two to three of these morphological traits, whereas 11 areas included species with only one of these traits. These areas were mainly located over the Eastern South America sector (ten areas), followed by North-western South America (four areas) and Amazonia (ten areas).

DISCUSSION

Our analysis of endemism of Bignonieae recovered 70 areas of endemism across three spatial scales and throughout the Neotropics (Fig. 1A–F, Table 2). Bignonieae supported the Neotropical Region (NEO_1, Fig. 1A) and Tropical South America (SA_1, Fig. 1A) as areas of endemism in agreement with previous studies focused on mammals (Noguera-Urbano & Escalante, 2017) and freshwater fish (Albert & Reis, 2011). According to our results, areas of endemism of Bignonieae are clustered over seven geographical sectors across the Neotropics, namely: Amazonia,

many overlapping areas of endemism that extend beyond the limits of these regions. This visualization indicates how overlap can be integrated into the definition of broad biogeographical patterns. C, Spatial congruence values for comparisons among areas of endemism and the units of the biogeographical regionalization schemes from the phytogeographical regions of Gentry (1982) and the Neotropical Region of Morrone (2014b). The dashed red line depicts the median value for congruence in each regionalization scheme. Note that most of the comparisons showed congruence values < 80%. Dominions and phytogeographical regions showed similar congruence values. Many provinces obtained congruence values of c. 50% because they are nested into broader consensus areas. Similarly, congruence values of c. 50% are observed for subregions because smaller consensus areas got nested into these same areas. Overall, the degree of spatial congruence between consensus areas and the biogeographical schemes of Gentry (1982) and Morrone (2014b) is low, therefore the patterns of endemism of Bignonieae are different from those described for the taxa included in these regionalization schemes.

A. Distribution of sister species pairs among areas of endemism



B. Areas of endemism with exclusive trait states

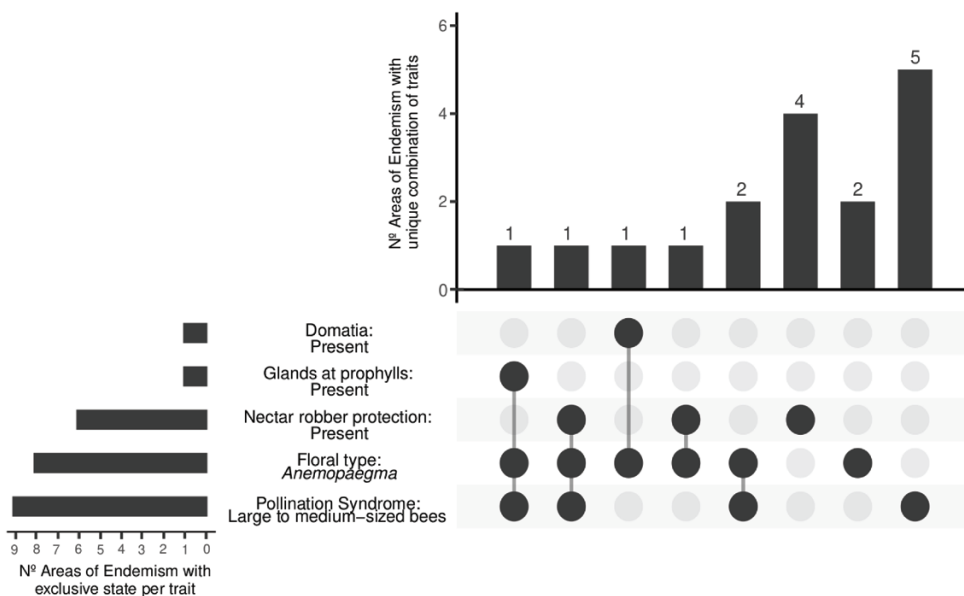


Figure 3. Exploration of endemic species composition. A, Distribution of sister species pairs among areas of endemism. Each geographical sector from Figure 1 is represented by an acronym: MESO (Mesoamerica); NWSA (North-western South America);

Eastern South America, Atlantic Forest, Dry and Open Vegetation Diagonal, Guiana Shield, Mesoamerica and North-western South America (Table 2; Fig. 1B–E). This clustering is generally consistent with the distribution of centres of endemism of many taxa on which different regionalization schemes of the Neotropics have been based (Udvardy, 1975; Cabrera and Willink, 1980; Gentry, 1982; Kreft & Jetz, 2010; Morrone 2017; Myers *et al.*, 2000).

However, the spatial arrangement of areas of endemism of Bignoniaceae reveals a complex scenario of overlapping and nested distribution patterns (Fig. 2A, B). When cells with the same range of number of overlapping areas are grouped, the Amazonian region *sensu lato* (Gentry, 1982; ter Steege *et al.*, 2006; Fiaschi & Pirani, 2009) and the Central Corridor of the Atlantic Forest *sensu lato* (Joly *et al.*, 1999; Oliveira & Fontes, 2000; Fiaschi & Pirani, 2009) were defined by the overlap of more than ten but fewer than 20 areas of endemism of Bignoniaceae (Fig. 2B), whereas regions such as the Dry and Open Vegetation Diagonal (Gentry, 1982; Werneck, 2011), North-western South America (Gentry, 1982) and Mesoamerica (Montaño-Arias *et al.*, 2018) also emerge but are less clearly defined with a lower range of overlapping areas per cell (Fig. 2B). The high degree of overlap among areas of endemism of Bignoniaceae seems to agree with two shared distribution patterns of plants in Amazonia and the Atlantic Forest. In Amazonia, the basin centred co-distribution of narrow and wide-range species described by the Amazon-centred distribution of Gentry (1982, 1992) can cause a high degree of overlap between local groups of spatially congruent species (Fig. 1B, and Supporting Information). In the South-Eastern South America sector, the absence of discrete boundaries between the Cerrado and the Atlantic Forest phytogeographic domains (Fiaschi & Pirani, 2009) (Fig. 1C) that are caused by the interspersed enclaves of humid and seasonally dry vegetation formations may allow the expansion of the distribution of species from one domain into the other (Prado & Gibbs, 1993; Oliveira & Fontes, 2000; Oliveira-Filho, Jarenkow & Rodal, 2006; Cardoso & Paganucci, 2008). Groups of

spatially congruent species penetrating the Cerrado or the Atlantic Forest might produce sufficient spatial congruence to define overlapping areas of endemism across this sector (Fig. 1C). Overlapping patterns are common in nature and occur around ecotones between biomes (Van Rensburg, Levin & Kark, 2009) and in transition zones between biogeographical regions (Ferro & Morrone, 2014). Accordingly, other studies have used overlapping areas of endemism to identify biogeographical transition zones (Noguera-Urbano & Escalante, 2017) and define areas of endemism across spatial scales (Martínez-Hernández *et al.*, 2015; Mercado Gómez & Escalante, 2019). Adding to such interpretations of overlapping patterns, Bignoniaceae show us that overlap among areas of endemism (1) is conspicuous in the Neotropics, (2) can encompass vast geographical sectors and (3) might reveal known biogeographical patterns when observed across scales.

In general, the geographical clusters of areas of endemism identified here are congruent with the distribution of species richness of Bignoniaceae (Meyer *et al.*, 2018). The greatest number of areas of endemism are located over its main centres of diversity, the Amazon Basin and the Atlantic Forest, with 22 and 17 areas each, respectively (Fig. 1B, C, F; Table 2). In studies like ours, with a focus on unravelling the areas of endemism of a given plant lineage, the coincidence between species richness and the highest number of areas of endemism can be expected because the chance of finding an area of endemism increases with a growing number of species co-occurring in a particular area. In studies where narrow-range size is required to define areas of endemism (Beard, Chapman & Gioia, 2000; Crisp *et al.*, 2001; Kessler *et al.*, 2001; Hobohm, 2003), it is necessary to deal with the uneven distribution of groups of narrow-range species and the dominance of the richness spatial distribution by widespread and common species (Jetz & Rahbek, 2002; Lennon *et al.*, 2004; Kreft, Sommer & Barthlott, 2006), which may cause a lack of correlation between centres of endemism and diversity (Ceballos & Brown, 1995; Hobohm, 2003; Lamoreux *et al.*, 2006). Using a multi-grid size analysis, VNDM/NDM may allow both the

GU, Guiana Shield; WAM, Western Amazonia; CAM, Central Amazonia; EAM, Eastern Amazonia; ESA, Eastern South America; THDD, the patterns from ESA that expand across the Dry and Open Vegetation Diagonal; DD, local patterns in the northern sector of the Dry and Open Vegetation Diagonal; ADC, Central Atlantic Forest; AFS, South Atlantic Forest; DDS, local patterns in the southern sector of the Dry and Open Vegetation Diagonal; CONT, continental-size patterns like Tropical South America. The nodes represent each one of these sectors, and the lines indicate a sister species pair connecting two sectors. Numbers below the nodes indicate the number of sister species pairs in that sector. Note that the number of species pairs is greater within Amazonia and Eastern South America sectors. B, Exploration of species morphological traits related to species interactions with ants and pollinators using UpSetR diagrams (Conway, Lex & Gehlenborg, 2017). The bars on the left indicate the number of areas of endemism with the specified trait. The bars on the top show the number of areas with the specified combination of traits indicated in the central dot and lines panel. Note that the most frequent attributes were the *Anemopaegma* floral type and the pollination by medium-sized to large bees. Only 17 areas include species with at least one exclusive attribute.

discovery of congruence among narrow-range species and the formation of broad-scale patterns by species with wider ranges. The relevance of this approach is demonstrated by the discovery of a variety of areas of endemism that go from smaller areas in the Atlantic Forest (i.e. AF_5, Fig. 1C) to continental sizes, such as the Neotropical Region (NEO_1, SA_1, and AM-13, Fig. 1A, B). These areas resulted from the support of wide-range species together with the geographical range of genera and clades (Table 2).

This scale dependency of areas of endemism is further illustrated by the results in the Atlantic Forest and Amazonia sectors, both of which obtained the highest numbers of areas of endemism with grid sizes of 1° and 3°, respectively (Fig. 1F). This result could be explained by the combined effect of two factors: species range properties and sampling. The properties of species ranges may vary, producing areas of endemism with different sizes and shapes. Species of Bignoniaceae tend to have wider and more widespread ranges in the Amazon, but narrower and localized ranges in the Atlantic Forest (Lohmann *et al.*, 2013; Meyer *et al.*, 2018). This observation matches the high level of narrow-ranged species and endemism found in the Atlantic Forest (Werneck *et al.*, 2011; Menini *et al.*, 2016). Sampling effort can also have an effect given that collection effort is much higher in the Atlantic Forest than in the Amazon (Sousa-Baena, García & Peterson, 2014; Narváez-Gómez *et al.*, 2021). Using larger grid sizes and fills in VNDM/NDM, sampling differences are mitigated, allowing the discovery of areas in densely and loosely sampled regions (Szumik *et al.* 2004).

Other multi-scale studies using a selected lineage with continental distribution in the Neotropics (oryzomyine rodents, Prado *et al.*, 2015) have questioned whether datasets of taxa with low diversity and low levels of sympatry may prevent the identification of known areas of endemism. The highest number of areas of endemism at a broad spatial scale was identified in the Amazon, where Bignoniaceae is centred (Meyer *et al.*, 2018), despite the fact that this region houses the highest sampling gaps (Narváez-Gómez *et al.*, 2021). None of these areas recovered previously recognized areas of endemism in the Amazon (see below). This result shows how the discovery of areas of endemism depends on the interaction of sampling coverage, species range properties and spatial scale (Szumik *et al.*, 2004; Casagrande *et al.*, 2019). Our findings also indicated that areas from different spatial scales might share species or show new species combinations. The best way to integrate these multi-scale patterns remains to be determined. Our results reinforce the need to include different spatial scales in the study of patterns of endemism and other biogeographical patterns (Levin, 1992; Peterson & Watson, 1998;

Whittaker, Willis & Field, 2001; Morrone & Escalante, 2002; Laffan & Crisp, 2003; Casagrande *et al.*, 2009; Cabral, Valente & Hartig, 2016; Daru *et al.*, 2020).

Geographical clusters of areas of endemism seem to be consistent with the historical biogeography of Bignoniaceae. In this tribe, species diversification has been geographically structured since its origin in Eastern South America during the Eocene (c. 54 Mya), with further colonization and diversification events in Lowland Amazonia, Central America, North-western South America and the Dry and Open Vegetation Diagonal of South America (Lohmann *et al.*, 2013). This consistency is also reflected by the distribution of the 33 sister species pairs that support some areas of endemism, with higher numbers of species pairs concentrated in Amazonia and Eastern South America sectors and by the biogeographic connections suggested among areas of endemism (Fig. 3A). The spatial configuration of areas supported by sister species showed that more sister species supported nested and overlapping patterns than disjunct areas of endemism. These findings support the idea that areas of endemism are not necessarily defined exclusively by groups of sister species and clades (Harold & Mooi, 1994; Szumik *et al.*, 2018).

Although an agreement exists between the biogeographical history of Bignoniaceae and the areas of endemism reported here, the spatial congruence between these areas and the units of the regionalization schemes of Gentry (1982) and Morrone (2014b) was generally low (Fig. 2C). The highest spatial congruence was found between areas of endemism and the larger biogeographical units dividing the Amazonian geographic sector (i.e. dominions and subregions), whereas the lowest spatial congruence was dominant in comparisons against the smaller biogeographical units (i.e. provinces) (Fig. 2C). The low spatial congruence may be due to the particularities of the biogeographical history of Bignoniaceae, which may have led these species to deviate from patterns observed in other taxa. Alternatively, limitations in the synthetic and approximated nature of boundaries in regionalization schemes or caveats in our approach to quantify spatial congruence may have also led to those differences. In particular, the angular shape of grids involved low degrees of mismatch at the borders of polygons describing the biogeographical units reducing the final spatial congruence. This case is exemplified by the area of endemism MESO_1 and the Mesoamerican Dominion (Fig. 1E), highlighting the need to develop more precise means to assess congruence among areas of endemism and biogeographical regionalization schemes. The increasing amount of occurrence data in public data repositories (e.g. GBIF) allows for additional studies of areas of endemism (Table 2) demanding the development of new approaches to

facilitate appropriate comparison and synthesis across studies.

The areas of endemism of Bignoniaceae support Gentry's Amazonian centred patterns for trees and lianas of endemic plant families of the Neotropics (Gentry, 1990, 1992). This pattern was expected given that members of Bignoniaceae are important components of canopy structure in Amazonian rainforests (Gentry, 1979; Lohmann & Taylor, 2014; Meyer *et al.*, 2019). However, there were disagreements within Amazonian Provinces (Morrone, 2014b). Only some of the areas of endemism documented from the North-western block (i.e. Imeri, Napó and Inambari, except for Guiana) and none of the South-eastern block (i.e. Rondônia, Tapajós, Xingú and Belém; Haffer, 1969; Prance, 1982; Cracraft, 1985; Silva & Oren, 1996; Bates, Hackett & Cracraft, 1998; Ron, 2000; Racheli & Racheli, 2004; Fiaschi & Pirani, 2009; Lynch Alfaro *et al.*, 2015) were recovered in our analyses. Instead, we recovered groups of nested and overlapping areas defining three sectors with diffuse limits in the Amazon Basin: (1) Western Amazonia (i.e. areas AM_2, 4, 5, 9, 19 and 20, Table 2, Supporting Information, Appendix S3); (2) Central Amazonia (i.e. areas AM_1, 7, 16, 17 and 21, Table 2) and (3) South-eastern Amazonia, (i.e. AM_18 and 22, Table 2). In turn, three overlapping groups of areas of endemism were identified in the Guiana Shield sector in agreement with the (1) Eastern (i.e. areas GU_2, GU_4 and GU_8) and (2) Central (i.e. GU_1, GU_5 and GU_3, Table 2, Supporting Information, Appendix S3.) provinces and the Guiana region (i.e. areas GU_7 and GU_6). These areas provide a more detailed description of the Amazonian patterns of Bignoniaceae that are similar to the areas of endemism and patterns of distribution recovered for other plant groups (Huber, 1988; ter Steege *et al.*, 2000; Alveiz-Valles *et al.*, 2018), fish (Hubert & Renno, 2006), birds (Oliveira, Vasconcelos & Santos, 2017) and Hemiptera (Ferrari *et al.*, 2010) (Table 2). These areas imply that internal divisions of Amazonia might be more complex than previously suggested by the regionalization schemes examined here.

In this context, a plausible hypothesis is that the Amazonian rivers may not have represented a strong driver of plant endemism patterns as they did for vertebrates (Wallace, 2009; Gascon *et al.*, 2000; Albert & Reis, 2011). Indeed, recent studies have shown that young and narrow rivers such as the Rio Branco probably did not represent an important barrier to gene flow in various plant clades (Nazareno, Dick & Lohmann, 2019a; Nazareno *et al.*, 2021), with only large and older rivers like the Rio Negro representing putative gene-flow barriers for plants (Nazareno, Dick & Lohmann, 2017, 2019b). Understanding the relative contribution of various processes forming areas of endemism requires additional studies and analyses

of the abiotic drivers of distribution like climate and topography in the various areas of endemism.

Although areas of endemism also showed low spatial congruence with the biogeographical units of previous regionalization schemes in the Eastern South America sector, the areas recovered here agree with the centres of endemism separated by the Doce river in the northern and southern portions of the Atlantic Rainforest (Fig. 1C, Table 2) (Cracraft, 1985; Costa *et al.*, 2000; Santos *et al.*, 2007; Sigrist & Carvalho, 2008, 2009). Although some areas occur over the Central Corridor of the Atlantic Forest (i.e. AF_13 and 15) and the centres of endemism of the Rio de Janeiro and Espírito Santo (i.e. areas AF_1, 3, 4, 5, 6 and 9), other areas are located over the Serra do Mar (i.e. areas AF_12, AF_14 and AF_16). Climate-driven habitat changes and diversification in these centres of endemism have been linked to global climatic oscillations since the Last Glacial Maximum, with northern centres of endemism associated with climatic stability, and the southern centres of endemism with the current climate (Carnaval & Moritz, 2008; Carnaval *et al.*, 2014). Further studies using environmental niche modelling to test whether climatic responses have similar spatial dynamics (Waltari & Guralnick, 2009; Linder *et al.*, 2013) are needed in Bignoniaceae to further evaluate the driving causal factors of the areas of endemism recovered here.

Species of Bignoniaceae show widespread distributions across the dry and open vegetation biogeographical regions of Eastern South America (Gentry 1979). The areas of endemism of Bignoniaceae were also wide in this area, showing little spatial congruence with the phytogeographical domains currently accepted in this region (i.e. Caatinga, Cerrado and Chaco; Fiaschi & Pirani, 2009; Werneck, 2011) (Fig. 1C). Instead, four groups of overlapping areas were identified in (1) North-eastern Brazil (i.e. AF_7, 8, 10 and 11; DD_2 and 4; ESA_1); (2) Bahia centre of endemism within the Chapada Diamantina (i.e. DD_1 and 3); (3) South-eastern Brazil (i.e. THDD_1, 2, 3 and 5; DDb_2); and (4) across the grand Chaco and Pampas (i.e. THDD_4). These patterns are wide enough to encompass several phytogeographical domains, expanding from the Atlantic Forest into open vegetation biomes, reaching the Amazon from the north or the south and even touching the southern Andes. These patterns are similar to those described for plants and other taxa that have responded to the contraction and expansion of humid rainforests across the open vegetation biomes during the Pleistocene (Rizzini, 1963; Oliveira-Filho & Ratter, 1995; Costa, 2003; Oliveira-Filho, Jarenkow & Rodal, 2006; Batalha-Filho *et al.*, 2013). Likewise, these patterns are also consistent with the reciprocal contraction and expansion of tropical dry forests that caused

the current location of islands of a previously wider Seasonal Dry Tropical Forest across the Caatinga, Cerrado and Chaco (Prado & Gibbs, 1993; Werneck, 2011). Previous studies suggest that Bignoniaceae are an excellent model for studying the climate-driven contraction and expansion of species distributions on these forest types because of their high dispersal capacity and broad distribution (Gentry, 1979, 1990).

In previous biogeographical studies of Bignoniaceae (Gentry, 1979, 1990) and Bignoniaceae (Lohmann *et al.*, 2013), Central America and North-western South America were treated as unique biogeographical units because individual species tend to be broadly distributed across these areas. However, our findings showed that groups of areas of endemism of Bignoniaceae differentiate both sectors (Fig. 1E). The biotic differentiation of these regions is observed by the areas MESO_1 and NWSA_1, both of which partially overlap in Costa Rica (Fig. 1E). In Central America, areas of endemism for Bignoniaceae are located around the Yucatan peninsula (i.e. YUC_1), extending southward to Costa Rica (i.e. MESO_2) and covering the complete Mesoamerican Dominion (i.e. MESO_1). In North-western South America, they are located over the Northern Andes of Colombia and Venezuela (i.e. ColVen_1 and 2; Col_1, 2, and 3) and the savannas of Venezuela that broadly correspond to the Orinoco Basin (i.e. NWSA_2). North-western South America and Central America have a characteristic biota, resulting from *in situ* diversification and biotic interchanges between Neotropical and Nearctic biotas mediated by the uplift of the Andes and the Isthmus of Panama (Antonelli & Sanmartín, 2011; Bacon *et al.*, 2015; Hughes *et al.*, 2013; Villaseñor *et al.*, 2020). More in-depth studies of the structural integrity of areas of endemism and the characteristics of endemic species are needed to identify the drivers of the patterns of endemism recovered here.

Although not a single evolutionary or ecological mechanism can explain how taxa become endemic to particular areas (Hovenkamp, 1997; Hobohm, 2014), it is generally accepted that endemism results from the contingency of past events and subsequent ecological processes determining the boundaries of species distributions and speciation (Anderson, 1994; Cracraft, 1994; Crother & Murray, 2011; Linder *et al.*, 2013; Noguera-Urbano, 2016; Weeks *et al.*, 2016). Clues about possible processes behind areas of endemism might be found in the ecology of Bignoniaceae. The coincidence between centres of diversity and endemism might suggest that just like richness, endemism could be correlated to evapotranspiration (Meyer *et al.*, 2018) and canopy height (Meyer *et al.*, 2019). The high number of overlapping and nested patterns in these centres suggests that different groups of species share particular abiotic preferences.

The community structure of Bignoniaceae has been associated with specialization to abiotic conditions (Alcantara *et al.*, 2014; Gentry, 1992), suggesting that the spatial patterns described by the areas of endemism might have resulted from this association. The role of specialization is promising given the lack of niche conservatism in some genera (Medeiros, Guisan & Lohmann, 2015) and the correspondence between distribution patterns and continental climatic regimes (Gentry, 1990). The association between the distribution of lianas and endemism patterns with climate is supported by the fact that precipitation and seasonality can regulate liana abundance and diversity (Schnitzer, 2005; Parolari *et al.*, 2019). Associations between climate and centres of endemism across many taxa (Harrison & Noss, 2017; Zuloaga, Currie & Kerr, 2019) provide further support to the possible role of climate for the establishment of areas of endemism of this tribe. Further exploration of the climatic environment of the areas of endemism and the niche occupied by the endemic species can help us recover additional dimensions of this association in Bignoniaceae.

Even though a previous study did not find a role of pollinators for the Bignoniaceae community assembly (Alcantara *et al.*, 2014), we recovered some areas of endemism, especially in the Eastern South America sector, in which species possessed open-mouthed flowers pollinated by medium- to large-sized bees exclusively (i.e. *Anemopaegma* type, Fig. 3B). It would be interesting to study the patterns of endemism of Bignoniaceae pollinators and test for spatial congruence between those pollinators and Bignoniaceae.

CONCLUSIONS

In this study, we described the areas of endemism of Bignoniaceae in the Neotropics and compared those areas to biogeographical regionalization schemes and patterns recovered for other taxa. The drivers of the areas of endemism recovered here remain to be determined. The wide geographical extent of our analyses, combined with the high number of patterns across the Neotropics and the high number of species studied prevented us from testing any of the possible drivers suggested here by comparing to regionalizations and areas of endemism of other taxa. Although a calibrated phylogenetic tree is available for Bignoniaceae (Lohmann *et al.*, 2013), not all endemic species of Bignoniaceae were sampled in this study, preventing a detailed understanding of the drivers behind the patterns recovered.

The high numbers of overlapping areas of endemism of Bignoniaceae recovered using explicit spatial methods (Szumik *et al.*, 2018) highlight the importance of

such patterns in biogeographical syntheses (Ferro & Morrone, 2014). Overall, our findings illustrate: (1) multiple transitions among areas of endemism from different geographical sectors in the Neotropics, (2) biogeographic regions defined by both local sets of endemic species and the overlap of areas of endemism that extend beyond the proposed geographical boundaries for these regions and (3) the difficulty to define discrete limits between biogeographic patterns. The decomposition of patterns of overlap is a possible path towards using the overlap and multi-scale analyses of endemism in regionalization schemes based on endemism (Escalante, 2009). However, it is important to keep in mind that different spatial scales imply differences in sampling issues (Casagrande & Goloboff, 2019). This approach acknowledges the blurring effect that overlapping distributions have in biogeographical analyses. Integrating distribution overlap into biogeographical analyses is key to biogeographical syntheses derived from analyses of endemism. Making the results from the analyses of endemism available in a portable format with enriched metadata and defining protocols with methodological standards (e.g. DaSilva Pinto-da-Rocha & Desouza, 2015) would facilitate reproducible ways to integrate patterns derived from different taxa.

ACKNOWLEDGEMENTS

We thank Drs Thaís Guedes, Silvio Nihei and André Carvalho for comments on earlier versions of this manuscript, Drs Andrea Sánchez-Tápia and Leila Meyer for assistance with R programming language. We thank Dr David Coomes for hosting JPNG in the Forest Ecology and Conservation Group at the Department of Plant Sciences of the University of Cambridge, UK. We also thank Dr Andrea Manrique-Rincón for assistance with figures, and colleagues from Lohmann's lab group at the University of São Paulo for insightful conversations about the distribution and biology of tribe Bignonieae.

FUNDING

We also thank the following funding sources: Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for a Ph.D. fellowship to JPNG (Finance Code 001); Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) for a Thematic Project (2018/23899-2) and a collaborative FAPESP/NSF/NASA grant 'Assembly and evolution of the Amazonian biota and its environment' to LGL (2012/50260-6); the Conselho Nacional de

Desenvolvimento Científico e Tecnológico (CNPq) for a Pq-1B grant to LGL (310871/2017-4); and, the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) for a grant to CS (PUE 0070).

CONFLICT OF INTEREST

The authors and co-authors declare no conflict of interest in the production of this research.

DATA AVAILABILITY STATEMENT

Data outputs from NDM/VNDM are available as **Supporting Information**. The Bignonieae distribution database will be available once other research projects under development are finished at Dr Lohmann's Laboratory. All R scripts are available from https://github.com/jupanago/RCode_BignonAoE.

AUTHORS' CONTRIBUTIONS

JPNG, CS, PG and LGL planned the study. LGL compiled the trait dataset and led the compilation of the georeferenced locality dataset. JPNG performed all analyses, produced the figures and tables assisted by LGL. JPNG led the writing with contribution from all authors. All authors contributed to the interpretation and discussion of the results and approved the final version of the manuscript.

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SUPPORTING INFORMATION

Additional Supporting Information can be found in the online version of this article at the publisher's web-site:

Table S1.1. Species with probable disjunct distribution whose ranges were filled manually in NDM/VNDM.

Table S1.2. Higher taxa represented by genera and clades. The areas of the genera were estimated from the aggregation of species individual areas. The areas of the clades were estimated using a supertree concatenated in TNT v.1.5 from the phylogenetic trees available for the tribe Bignonieae. The area of clades was estimated by aggregating the areas of species and genera.

Table S1.2. List of sister species pairs supporting areas of endemism and the spatial configuration of these areas. When a species support areas recovered at different scales, the spatial configuration is evaluated only with those areas occurring at the same spatial scale. Definitions of 'Nested', 'Overlapped' and 'Disjunct' area based on counting the number of rows of cells in overlap following Szumik *et al.* (2019). 'Same' indicates the species pairs that occur in the same area.

Table S1.3. Correspondences among areas of endemism in different spatial scales. **Geographic sector:** geographical region. **Spatial scale:** grid size at which the area was recovered. **Class:** Class of effect of spatial scale in species composition from finer to coarser spatial scale. Classes are divided into four categories as follows: (i) Identical: The areas are composed by the same species across scales; (ii) Completely nested: Complete inclusion of the species from a pattern into the other; (iii) Nested but incomplete: A pattern is included into the other but some new species area added (+) or lost (-) at the coarser spatial scale; and, (iv) Nested but reverse: The species from a pattern at the coarser scale are a subset of the species defining a pattern at the finer scale. Changes in species composition across scales may imply that some species may contribute to the support of many different patterns across scales (Figure S1.2).

Table S1.4. Endemic species with exclusive sets of morphological traits and states.

Figure S3.1. Complete set of areas of endemism of Bignonieae obtained for three analyses performed using grids with sizes of 1°, 2° and 3°. Areas are listed considering the sectors in which they are located, so the results from the three independent analyses are shown mixed here. Please refer to the [Appendix S2](#) to access the list of areas, species and the detailed description of the NDM/VNDM analyses.

Figure S3.2. Visualization of intersections among areas of endemism from different spatial scales and located in the same geographic sector: A, Amazonia and Guiana Shield; B, North-western South America; C, Eastern South America, Atlantic Forest and Dry and Open Vegetation Diagonal and D, Mesoamerica. The Neotropical and Tropical South America areas of endemism did not share any species or higher taxa in common. These are Upset diagrams (Gehlenborg, 2019), which are useful to represent intersections among more than three sets at once. Bars on the left show the number of species per area; bars on top show the number of species shared by the areas of endemism indicated by points and lines in the bottom central panel. Areas of endemism are listed with the spatial scale at which they were recovered; these areas are indicated between parenthesis. Note that the effect of grids may not change species composition or may add new species to the patterns across scales. The Upset diagrams show all the possible intersections between areas of endemism revealing how some species may contribute to many different patterns.

Figure S3.3. A sample of areas of endemism that share supporting species and the altitudinal profile of all the endemics in each area. A, map of consensus areas on the left; B, a boxplot of elevation for each endemic species on the top-right position and C, a table with the range of endemism index values that the shared species had in each area. Box plot colours indicate to what area species belong to (yellow and purple) and what species are shared (red). The dashed lines indicate the altitudinal belt lower boundaries: Lowlands and Lower Mountain Forest (750 m a.s.l.), Upper Mountain Forest (1800 m a.s.l.), Subalpine Forests (3600 m a.s.l.) and Snowy Highlands (4500 m a.s.l.) (Prance, 1989; Frahm & Gardstein, 1991). Note that some areas of endemism are a subset of the other and its conforming endemic species profiles are similar (1). In other cases, despite similar altitudinal profiles only some species areas are shared (2 and 3). Shared species can also occur between areas of endemism with endemic species occurring at very similar altitudinal belts (4).

Figure S3.4. Sister species that contributed to the endemism index of the Areas of Endemism of Bignonieae. The following are the areas of endemism among which the 33 sister species pairs of Bignonieae are distributed. Each pattern shows the location of areas of endemism and the possible corresponding cladogenetic event implied by the species pair. In red, the category of spatial configuration of the areas of endemism in which the sister species pair occur. Summarized in Table S1.3.