Desvendando padrões de endemismo e sua relação com o clima na região Neotropical: Um estudo de caso com a tribo Bignonieae (Bignoniaceae)

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Juan Pablo Narváez-Gómez











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Orientadora: Dra. Lúcia G. Lohmann

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¡Cuán innumerables son los caminos por los cuales puede ir nuestra vida! Innumerables son los senderos que desde el instante presente conducen al futuro... Cierto es que no puedes escoger entre ellos, que el pasado fija tu camino venidero; pero cierto es también que tú ignoras cual será esa tu senda.

Fernando González Ochoa
Pensamientos de un viejo, 1916.

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Table of Contents

Resumo

Bignonieae (Bignoniaceae) é um clado de lianas distribuído por toda a região Neotropical e um componente importante de florestas úmidas. A história biogeografica deste clado está profundamente associada aos principais eventos que moldaram as paisagens Neotropicais. O clima aparenta ter tido um papel importante na distribuição das espécies tanto em escala ampla quanto local neste clado de plantas. Esta tese visa ampliar esse conhecimento através da definição de áreas de endemismo da tribo e investigar sua relação com o clima através de três objetivos centrais. Em primeiro lugar, avaliamos qual é o estado do conhecimento da distribuição das espécies de Bignonieae, através de uma análise de viés espacial e da qualidade do banco de dados de distribuição de Bignonieae mais completo até o momento. Em segundo lugar, realizamos uma análise de endemicidade para descobrir quais são as áreas de endemismo de Bignonieae e explorar o efeito da escala espacial e possíveis ambiguidades na formação destes padrões. Também analisamos a congruência espacial das áreas de endemismo com diferentes esquemas de regionalização biogeográfica. Terceiro, exploramos a relação dessas áreas com o clima por meio de uma análise do nicho climático Grinnelliano das espécies endêmicas usando técnicas de ordenação. Descobrimos que (i) mais esforços de coleta são necessários em toda a região Neotropical para aumentar a representação de novas localidades, especialmente na floresta amazônica que apesar de ser o principal centro de diversidade do grupo é a região menos amostrada. As áreas com melhor amostragem foram encontradas espalhadas pela América Central, pela Amazônia Peruana e Boliviana e ao redor de algumas cidades brasileiras. Descobrimos que (ii) as áreas de endemismo estão distribuídas por toda a região Neotropical, são mais numerosas em escalas espaciais mais abrangentes e se sobrepõem extensivamente em setores geográficos específicos aonde apresentam baixos níveis de ambiguidade. A congruência espacial entre as áreas de endemismo e as unidades biogeográficas da região Neotropical foi baixa de uma forma geral, embora os padrões de endemismo encontrados são semelhantes aos de outros taxa. Finalmente, descobrimos que (iii) diferenças de nicho entre as espécies endêmicas pertencentes a diferentes áreas de endemismo não têm relação com as áreas de endemismo nas quais as espécies pertencem, mas refletem a heterogeneidade climática dessas áreas. Nenhum processo ecológico comum foi encontrado entre as espécies da mesma área. Os nossos achados corroboram a hipótese de que a correlação entre o endemismo e o clima contemporâneo se deve principalmente à auto-correlação espacial entre o clima e geografia. Esta tese destaca a importância do uso de bancos de dados de distribuição bem curados para explorar padrões de distribuição de espécies e suas causas.

Palavras chave: Bignonieae, região Neotropical, viés espacial, esforço de coleta, distribuição de espécies, áreas de endemismo, nicho climático.

Abstract

Bignonieae (Bignoniaceae) is a clade of neotropical lianas distributed throughout the Neotropics and an important component of rainforests. The biogeographical history of this clade is deeply connected to the main events that shaped the Neotropical landscapes. Climate has been suggested as an important factor shaping species distributions at broad and local scales in this plant clade. This thesis aims to expand this knowledge by defining the areas of endemism of this tribe and investigating their relationship with climate through three main objectives. First, we evaluate what is the state of the knowledge of Bignonieae species distributions by analyzing the spatial biases and the completeness of survey efforts of the most complete distribution database of Bignonieae available so far. Second, we perform an analysis of endemicity to discover areas of endemism of Bignonieae and explore the effect of spatial scale and possible ambiguity for the establishment of these patterns. We also analyze the spatial congruence of the areas of endemism to regionalization schemes. Third, we explore the relationship of these areas of endemism with climate through an analysis of the Grinnellian climatic niche of endemic species using ordination techniques. We found that (i) more collection effort is needed across the Neotropics to increase the representation of new localities, in particular in the Amazon rainforest that despite being the main center of diversity for this groups is also the most under-sampled region. The best sampled areas were scattered across Central America, the Peruvian and Bolivian Amazon, and around some Brazilian cities. We found that (ii) areas of endemism are distributed across the Neotropics, are more numerous at coarser spatial scales, and overlap extensively over specific geographic sectors where they have low levels of ambiguity. The spatial congruence between areas of endemism and the biogeographical units of the Neotropical region was generally low, though they exhibit patterns that are similar to other taxa. Finally, we found that (iii) niche differences among endemic species belonging to different areas of endemism are not associated with the area of endemism to which they belong but reflect the climatic heterogeneity of these areas. No common ecological processes were found among species of the same area. Our findings corroborate the hypothesis that the correlation between endemism and contemporary climate is due to the spatial autocorrelation between climate and geography. This thesis highlights the importance of using well curated distributional databases to explore species distribution patterns and their causes.

Keywords: Bignonieae, Neotropics, completeness, spatial biases, species distributions, areas of endemism, climatic niche.

Introduction

Biogeography documents the distribution of species and their traits and examines the role of environment and evolutionary history on species distributions (Morrone, 2009; Soberón, 2010; Violle et al., 2014). The broad spatial and temporal scales encompassed have justified a pragmatic disciplinary subdivision. On the one hand, ecological biogeography aims to explain distributions at local spatial scales and short time spans emphasizing the role of environmental factors, biotic interactions, and dispersion (Hengeveld, 1993; Peterson et al., 2011). On the other hand, historical biogeography aims to explain distributions at broad spatial scales and long timespans, stressing the role of past geologic and climatic events over species vicariance, dispersal, and extinction (Crisci et al., 2003). This subdivision makes biogeography a diverse research field that is conceived as a problem-solving process where different questions are addressed and complementary methods applied in a step-by-step fashion (Morrone, 2009). The intricate web of causal relationships among ecological processes and Earth's history contingent events contribute for the formation of species distribution patterns, making the subdivision artificial. Promising lines of research have been proposed to address integrative questions (Donoghue & Moore, 2003; Crisci et al., 2006; Wiens, 2011; Cabral & Kreft, 2012).

Addressing questions about the spatial dimension is the first step of many biogeographical approaches. A thorough documentation of species arrangements in geographic space precedes the inference of explanations and predictions (Pequet, 1994; Vuilleumier, 1999; Crisci et al., 2006). Association with environmental variables (Hengeveld, 1992), hypotheses testing procedures (Ball, 1975; Crisp et al., 2011), and the elaboration of explanatory narratives (Andersson, 1996; Morrone, 2009) are used to join the crucial pieces of evidence and reveal the most likely common cause (or causes) of the observed distribution patterns by choosing the most coherent explanation among competing alternative hypotheses (Cleland, 2001, 2002, 2013). Given that data about species distributions, biology, and evolutionary history are scarce (Hortal et al., 2015), the first duty of the biogeographer is to gather high-quality data, including raw species distribution point localities, which represent the basis for all biogeographical studies (Ball-Damerow et al., 2019). The second duty is to relate distribution patterns to patterns of environmental variation and the available biogeographical knowledge in order to investigate potential drivers of such patterns (Crisci et al., 2006). Finding commonalities with other organisms and associations with environmental variables can guide the exploration and inference of relevant explanatory hypotheses for the common causes underlying the patterns observed (Cleland, 2013).

The quality of point locality data is essential to document species distributions and infer biogeographical processes (Jackson, 2012; Ball-Damerow et al., 2019). The Wallacean shortfall, i.e., the lack of precise information about geographical distributions (Hortal et al., 2015), is pervasive across biological databases obtained from natural history museums (Meyer et al., 2016; Daru et al., 2018). Issues such as the inherent uncertainty in estimating species distributions (Rondinini et al., 2006; Rocchini et al., 2011), biases in sampling design (Moerman & Estabrook, 2006; Hortal et al., 2007), and erroneous species identifications (Newbold, 2010; Pyke & Ehrlich, 2010) increase the severity of this knowledge gap. There is an urgent need to close this gap in the most diverse regions of the world such as the Neotropics, where species richness is the highest but sampling is still low (Gentry, 1982; Barthlott et al., 2005; Oliveira et al., 2016; Raven et al., 2020). Assessing collection biases and explicitly reporting the knowns and unknowns of distribution databases is crucial to properly fine-tune the scope of biogeographical analyses and secure the effectiveness of conservation measures (Grand et al., 2007; Ladle & Hortal, 2013; Lobo et al., 2018).

Endemism is affected by the Wallacean shortfall, directly impacting biogeographical processes and conservation efforts (Noguera-Urbano, 2017). Patterns of endemism, or areas of endemism, refer to distribution patterns formed by at least two species occurring nowhere and exhibiting an arrangement of extensive sympatry among their geographical ranges (Platnick, 1991; Morrone, 1994; Szumik et al., 2002). The causes behind those patterns have been a major focus of biogeography since the establishment of this discipline (Nelson, 1978). For instance, these patterns can result from multiple factors such as the accumulation of narrow-ranging species (i.e., centers of endemism) (Peterson & Watson, 1998; Linder, 2001; Laffan & Crisp, 2003), habitat loss (i.e., hotspots) (Myers et al., 2000), the phylogenetic origin of co-occurring species (i.e. neo- and paleo-endemisms) (Cowling & Holmes, 1992), or the history of biotas (Anderson, 1994; Cracraft, 1994; Weeks et al., 2016). The geographical patterns of speciation (Cracraft, 1994), the ecology of species range dynamics (Anderson, 1994), and the coincidence of collection hotspots within an areas of endemism (Nelson et al., 1990) are common themes in the endemism literature. The inclusion of a temporal dimension into studies of this nature have indicated that areas of endemism are dynamic (Nihei, 2008) and caused by multiple consecutive events (Noguera-Urbano, 2016), complicating the association of a unique set of causes to those areas.

The availability of point locality data from natural history museums and climatic datasets have advanced the study of climate as a driver of endemism at ecological and evolutionary timescales (Harrison & Noss, 2017; Zuloaga et al., 2019). Climatic data has been further used to assist the definition of areas of endemism and to analyze their temporal dimension (Escalante et al., 2013; Linder et al., 2013; Gámez et al., 2014). These approaches rely on a correspondence between species ranges and their ecological niches (Sexton et al., 2009; Peterson et al., 2011; Wiens, 2011). The ecological niche was derived from studies of community assembly and is a useful concept to study broad scale biogeographical patterns (Peterson et al., 2011). By focusing on non-interactive variables such as climate or other landscape features that allow the survival of species populations, the Grinellian niche has allowed us to improve our understanding about the interplay between species environmental requirements, their mobility, and species interactions (Soberón, 2007). Some applications of the ecological niche concept have allowed the study of processes relevant to the formation of areas of endemism such as habitat tracking (range dynamics) under climate change (Graham et al., 2010; Guisan et al., 2014; Stigall, 2014), and geographical patterns of speciation in relation to climate (Anacker & Strauss, 2014; Cardillo & L. Warren, 2016; Li et al., 2018).

Among the correlative methods available to study species environmental niches (Elith & Leathwick, 2009; Peterson et al., 2011; Franklin, 2013), ordination methods are useful to represent and characterize the climatic niche directly from species occurrence data (Austin, 1985; Janekovi & Novak, 2012). By reducing the multi-dimensionality and summarizing the variability of environmental bioclimatic variables, ordination methods provide a means to explore and visualize patterns of variation in the niche properties and their association with species distributions (Thuiller et al., 2005; Broennimann et al., 2006; Guisan et al., 2014). By creating a unique abstract space in which species are located in accordance to their ecological properties and climatic tolerance, ordination techniques provide a means to fairly compare species and study their differences and similarities. Properties such as niche breadth and position in the multivariate space can reveal species climatic preferences and their distribution within the climatic space (Jackson & Overpeck, 2000; Devictor et al., 2010; Sánchez-Tapia et al., 2018). Relative properties such as niche overlap quantify the similarity among species niches and can measure how likely can ecological processes lead to niche conservatism or niche divergence (Rödder & Engler, 2011; Broennimann et al., 2012). Using ordination techniques to explore areas of endemism could help reveal common patterns of variation in the niche properties of endemic species that can put us in the way to uncover common ecological processes related to climate operating and contributing to the formation or maintenance of areas of endemism.

The relationship between plant distribution and climatic regimes has been well documented (Stephenson, 1990; O'Brien, 1998; Coutinho, 2006), with many plant groups exhibiting clear patterns of latitudinal variation in richness and habits in relation to climate (Qian & Ricklefs, 2007; Hawkins et al., 2011; Chen et al., 2015; Mateo et al., 2016). Patterns of niche conservation and evolution in climatic space are important to understand how plants have expanded their ranges and colonized areas with different environments (Crisp et al., 2009; Donoghue & Edwards, 2014). More specifically, the evolution of novel phenological and anatomical cold-resistant traits have allowed angiosperms to colonize temperate regions with different environments (Zanne et al., 2018) and to conserve their climatic niches (Donoghue, 2008; Fisher-Reid et al., 2012; Quintero & Wiens, 2013). Studying the niche of endemic species that define the areas of endemism themselves allow us to identify shared patterns of variation in the climatic space. It further allows us to explore whether the recovered patterns represent fingerprints of common ecological process.

This thesis aims to use tribe Bignonieae (Bignoniaceae), one of the best studied Neotropical plant clades (Lagomarsino & Frost, 2020) to study endemism patterns and explore their relationship with climate using the ecological niche as represented by ordination techniques. Multiple aspects of Bignonieae have been intensively studied, including its taxonomy (e.g., Lohmann & Taylor, 2014; Zuntini et al. 2015a, b; Medeiros & Lohmann 2015; Fonseca et al. 2017; Frazão & Lohmann 2019; Fonseca & Lohmann 2019; Kaehler and Lohmann 2019), biogeography (e.g., Lohmann et al., 2013; Thode et al. 2019; Francisco & Lohmann 2020), and biology (e.g., Firetti-Leggieri et al. 2012; Sousa-Baena et al. 2014; Meyer et al. 2019). Climate seems to represent an important driver of Bignonieae species distribution (Gentry, 1983; Alcantara et al., 2014).

Bignonieae is monophyletic (Lohmann, 2006) and includes all the lianas and half of the current species diversity of the Bignoniaceae (Lamiales, Asterids I) (APG IV, Chase et al., 2016). The tribe includes 386 species grouped in 20 genera (Lohmann & Taylor, 2014; Fonseca & Lohmann, 2019), and is characterized by the following morphological features (Lohmann & Taylor, 2014): (i) a lianescent or rarely shrubby habit; (ii) wood with phloem wedges produced by a discontinuous vascular cambium; (iii) opposite-compound leaves with the terminal leaflet generally modified into a multifid, trifid, or single tendril; (iv) prophylls of the axillary buds with variable morphologies; (v) showy, sympetalous, and pentamerous flowers; (vi) tetramerous and didynamous androecium containing one staminode; (vii) gynoecium with a superior bilocular carpel with axial placentation, elongated style and bilamellated stigma, usually surrounded by a basal and conspicuous nectar disk; and, (viii) septicidal capsule with seeds with reduced endosperm.

The distribution of Bignonieae extends from 35°S to 39°N across the continental platform of America, including the Antilles in the Caribbean Sea. The tribe occurs in all Brazilian phytogeographical domains, the northern Andes and Central America, with a single species reaching south-eastern North America (Lohmann et al., 2013). Species can be narrowly or broadly distributed, and centered in the Amazon basin and the Brazilian Atlantic Forest (Meyer et al., 2018). No areas of endemism have been recovered for Bignonieae to date. However, Bignoniaceae distribution patterns are thought to be congruent with centers of endemism described for other Neotropical plant groups and correlated with continental climatic regimes (Gentry, 1982, 1992). The biogeographical history of Bignonieae includes diversification across the Neotropics punctuated by frequent distribution shifts from areas with contrasting environments from rainforests to savannas and vice-versa (Lohmann et al., 2013). Species diversity patterns are correlated with evapotranspiration (Meyer et al., 2018), with abiotic specialization having had a key role in local Bignonieae community assemblage (Alcantara et al., 2014). The fact that these liana communities are not phylogenetically clustered (i.e., are composed by species from different clades), with several species showing wide geographic ranges, suggest that Bignonieae species distribution patterns are not limited by their dispersal abilities, with species being able to track their climatic preferences. Indeed, their winged seeds seem to have been adaptively optimized to fly long distances in horizontal wind layers, leading to high dispersal capacity (Rochelle, 2013). Furthermore, a lack of climatic niche conservatism has been recovered for the Bignonieae genus Tynanthus (Medeiros et al., 2015). Altogether, these observations suggest that climatic niche evolution and lability in Bignonieae may represent an important driver of species distribution in this group.

Objective and thesis organization

This thesis aims to address three key questions: (i) What do we know about Bignonieae species distribution, and what are our knowledge gaps? (ii) Where are the areas of endemism of Bignonieae, and how do these areas relate to the Neotropical biogeographical context? and (iii) Can we consider climate as a driving factor of areas of endemism in Bignonieae? For this purpose, the thesis is divided into three chapters, each one structured as an independent research paper.

Chapter one is entitled "*Recovering the drivers of sampling bias in Bignonieae (Bignoniaceae) and identifying priority areas for new survey efforts.*" In this chapter, we describe and assess the quality of the Bignonieae distribution database that is used as basis for the subsequent chapters. We analyze geographical biases in species collection effort and evaluate the completeness of survey effort in order to propose new surveys that will increase the knowledge of species distributions and alleviate the Wallacean Shortfall.

Chapter two is entitled "*Unraveling distribution patterns of neotropical lianas: An analysis of endemicity of the tribe Bignonieae (Bignoniaceae).*" In this chapter, we present the areas of endemism of Bignonieae as discovered by an analysis of endemicity at three spatial scales. We investigate the ambiguity in the definition of these patterns when using an optimality criterion and develop a strategy to objectively compare areas of endemism against regionalization schemes. We propose relevant hypothesis about the drivers of these areas.

Chapter three is entitled "*Do shared distribution patterns entail common causes? A case study of the Grinnellian climatic niche and areas of endemism using neotropical lianas (Bignonieae, Bignoniaceae).*" In this chapter, we explore the climatic niche of the endemic species and test the hypothesis that endemic species have been affected by common ecological processes involving the contemporary climate.

Each chapter follows the guidelines of selected scientific journals.

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CHAPTER 1.

Recovering the drivers of sampling bias in Bignonieae (Bignoniaceae) and identifying priority areas for new survey efforts

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Recovering the drivers of sampling bias in Bignonieae (Bignoniaceae) and identifying priority areas for new survey efforts

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Abstract

Identifying knowledge gaps and the potential biases and limitations of biological databases is essential for biogeographical research, as well as to efficiently plan biodiversity surveys and conservation efforts. Here we describe the taxonomic, temporal, and spatial coverage of the largest database of the Neotropical tribe Bignonieae (Bignoniaceae). We also assess the level of database completeness and propose new survey areas to fill knowledge gaps and optimize sampling coverage. The Bignonieae Database includes 28,763 records representing 98% of the known species. The database covers 72% of the Neotropical region and represents data collected during the past 204 years. The tribe is a conspicuous component of lowlands, with most species showing narrow range sizes. The Amazon rainforest is the most under-sampled region and the area with the lowest sampling rate. On the other hand, the best sampled areas are scattered across Central America, the Peruvian and Bolivian Amazon, and selected Brazilian cities. Sampling rate across the geographical extent of Bignonieae was best predicted by the distance from cities. More collection effort is needed across the Neotropics to increase the representation of new localities, especially in the Amazon, where Bignonieae is centered. New surveys are urgently needed to maximize new species discoveries and to effectively design conservation plans that maximize biodiversity-rich regions facing increased threat.

Keywords: Botanical inventories, herbarium data, lianas, Neotropics, Wallacean shortfall, occurrence data.

Declarations

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Conflict of interest: Nothing to declare.

Availability of data and material: Additional information supporting all results presented in this paper are available in Supporting Information section.

Code availability: Scripts used here are available on <https://github.com/jupanago/RCode_BignonieaDatabase>.

Authors' contribution: JPNG, TBG, LGL planned the study. LGL led the compilation of the distribution dataset with input from JPNG. JPNG performed all analyses, produced the figures and tables assisted by TBG and 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 this manuscript.

Introduction

Biological databases are key resources to improve our understanding of biodiversity distribution patterns and diversification (Meyer et al. 2015). Current biodiversity threats expedited the digitization of specimens deposited in natural history museums around the world, allowing for the increased inclusion of distribution data in several macroecological and biogeographical studies (Soberón and Peterson 2004). Correlations among occurrence data and biotic and/or abiotic factors have allowed us to test hypotheses about the drivers of species distribution patterns and diversification (Pyke and Ehrlich 2010; Peterson et al. 2011; Wiens 2011), as well as to implement efficient strategies for biodiversity management and conservation (Soberón and Peterson 2009). Despite the recent efforts and the easy access to biodiversity information, data quality remains a concern (Guralnick et al. 2007). Issues such as spatial and temporal biases in sampling effort, poor georeferencing quality, and taxonomic errors can drastically affect the results of spatial analyses and their respective biological inferences (Newbold 2010; Daru et al. 2018). Therefore, understanding inherent biases of biodiversity databases allow us to evaluate the limitations of our data and the significance of our conclusions.

Biases in collection effort result from logistic limitations and opportunistic collection efforts, causing species occurrences to be clustered in space and time (Hortal et al. 2015). This aggregation and patchiness of species records is determined by the accessibility to remote areas, the relative biological importance of some regions (i.e., protected or high endemism richness areas), and the detectability of species given their phenology and biology, among others (Meyer et al. 2015). The richness peak around rivers and roads (Zizka et al. 2020) and the inflation of richness values around well-collected areas has been documented across taxa (e.g., Meyer et al. 2015; Guedes et al. 2018). Moreover, socioeconomic factors of research institutions and the costs and challenges involved in sampling remote places also increase the patchiness of records across and within species ranges (Meyer et al. 2015, 2016a). Indeed, most biodiversity databases include an imbalanced sampling of the species ranges to a certain degree.

Biases can also emerge from the very process of assembling databases, including the lack of metadata documenting the assembly process, and the quality of the information contained in the database. Low quality of biodiversity databases might arise from different types of errors, such as mechanic errors (e.g., typos, empty fields, mixed specimen information), geo-referencing mistakes (e.g., wrong specimen localities, high geographical uncertainty, lack of geo-referencing metadata), and/or taxonomic errors (e.g., lack of taxonomic information, specimen misidentification, outdated classifications) (Maldonado et al. 2015). These mistakes lead to false estimations of the habitats and environments occupied by each species, leading to erroneous inferences about species traits and their associated landscapes (Hortal et al. 2015). Accounting for these uncertainties and associated errors is critical for precise and accurate understanding of species distribution patterns and their underlying process (Meyer et al. 2016b).

Several analyses can address biases in biodiversity databases (Walther and Moore 2005). For example, by determining the spatial distribution of collection density from a database and associating this data with factors such as the distance from populated places and roads, we can estimate the biases produced by collection activity (Kadmon et al. 2004; Pautasso and McKinney 2007). By determining the completeness of individual biodiversity databases, we are able to identify localities with: (i) unknown survey efforts, caused by a lack of documentation of the sampling effort; (ii) unknown absences, caused by a lack of data on species absences; and (iii) unknown recurrences, caused by the exclusion of duplicate records of a single species from an individual location (Lobo et al. 2018). This information allows us to drawn ignorance maps in which well-collected and poor-sampled areas can be identified (Lobo et al. 2018).

Sampling biases are especially problematic in tropical regions of the world, where species diversity is the highest (Prance et al. 2000; Kier et al. 2005; Raven et al. 2020). For example, the Neotropical region houses three of the world centers of plant diversity (i.e., Costa Rica-Chocó, Tropical Eastern Andes, and Atlantic Brazil) but remains as one of the least known regions floristically (Gentry 1982; Barthlott et al. 2005). Amazonia continues as one of the most under-collected biomes with collecting efforts focused on the most populous regions, along roads, and rivers (Nelson et al. 1990; Hopkins 2007). Likewise, higher levels of richness and endemism in the Atlantic Forest are correlated with the location of major museums and herbaria, illustrating past collecting preferences and decisions. On the other hand, collection effort in the Cerrado seems to have been more homogeneous (Bridgewater et al. 2004), while knowledge gaps in the Caatinga are more severe (Santos et al. 2011; Moro et al. 2014). Similar patterns have been recovered for other neotropical countries such as Mexico (Bojórquez-Tapia et al. 1995), Colombia (Arbeláez-Cortés 2013), Peru (Rodríguez and Young 2009), Ecuador (Engemann et al. 2015), and Guyana (Funk et al. 2005). Given that spatial bias in sampling effort is so pervasive across the Neotropics, detailed analyses of the biases and uncertainties of Neotropical databases are greatly needed.

Bignonieae (Bignoniaceae) is a monophyletic tribe, broadly distributed throughout the Neotropics, including the Antilles (Lohmann and Taylor 2014). Taxonomic studies of this group conducted by one of us (LGL) during the past 30 years have led to the compilation of a comprehensive database with ca. 30.000 occurrence points of examined specimens. Previous versions of the Bignonieae database were used to evaluate potential correlations between range size and detectability (Sheth et al. 2008), as well as to estimate biases in range size estimation (Sheth et al. 2012). While detectability and range size are not correlated in this group (Sheth et al. 2008), the greater the area of occupancy of individual species, the lower the spatial bias (Sheth et al. 2012). Other studies have used the Bignonieae database to investigate species richness and the relationship with species traits and the environment (Meyer et al. 2018, 2019, 2020). Despite that, the biases of the Bignonieae database have not been addressed. Here, we conduct a thorough analysis of the Bignonieae database, including an assessment of its level of completeness. We further explore its spatial, temporal, and taxonomic coverage, as well as propose new survey areas and taxa to fill knowledge gaps and optimize coverage.

Methods

Database assembly

The compilation of the Bignonieae database followed several stages. First, Bignonieae occurrence data was downloaded from the TROPICOS database at the Missouri Botanical Garden. The species identification of each sample was then verified by L.G. Lohmann (LGL). Geographic coordinates where extracted from herbarium specimens whenever available and verified to confirm that the coordinates really belonged to the described location. Whenever coordinates were not included in the specimen label, the most specific locality was identified and its coordinate determined using regional maps and online gazetteers, especially the “Getty Thesaurus of Geographic Names Online” (http://www.getty.edu/research/tools/vocabularies/tgn/). This led to a database with 30,277 geo-referenced entries, including 26,660 unique records (88.06%) and 3,617 (11.94%) duplicate records or records with limited information for geo-referencing. After exclusion of those records, the database included 26,660 records. For species with less than five records, we searched for additional specimens at the Herbarium of the Universidade de São Paulo (SPF, Brazil), which led to the inclusion of 504 additional geo-referenced records and a total of 27,164 entries. The occurrence records of each species were then mapped and verified by a Bignonieae expert (LGL), who updated taxonomic identifications following the most recent and comprehensive classification for the tribe (Lohmann and Taylor 2014). For groups for which new species had been described or for which subsequent taxonomic updates were available, the most recent treatments were followed instead, namely: *Adenocalymma* (Fonseca and Lohmann 2019), Bignonia (Zuntini et al. 2015a, b), *Dolichandra* (Fonseca et al. 2017), *Pachyptera* (Francisco and Lohmann 2019), *Tanaecium* (Frazão and Lohmann 2018), *Tynanthus* (Medeiros and Lohmann 2015), and *Xylophragma* (Kaehler and Lohmann 2019). For *Adenocalymma*, species distribution ranges were verified by LGL and Luiz Henrique Fonseca (Universidade de São Paulo) simultaneously adding 1,599 new localities. The coordinates of the additional specimens of *Adenocalymma* were obtained using specimen labels. Coordinates for specimens without this information were obtained using coordinates of the gazetteers, localities obtained thought Google Earth (https://earth.google.com/web/), or using the centroids of municipalities. The final Bignonieae database includes 28,763 records, representing all 20 genera currently recognized and 386 species of the tribe Bignonieae (Lohmann and Taylor 2014; Fonseca and Lohmann 2019). Details about the Bignonieae database are provided in Fig. S1.2, see Online Resource 1 in Electronic Supplementary Material.

To detect potential problems in geographic coordinates of the Bignonieae database, we used the function clean_coordinates() from the package CoordinateCleaner (Zizka et al. 2020) implemented in R (R Core Team, 2020). All records flagged as problematic were mapped and verified using the locality descriptions available in Google Earth (https://www.google.com/earth/); new coordinates were assigned whenever necessary.

Temporal, taxonomic, and spatial coverage

We described all the information contained in the Bignonieae database in detail. Taxonomic coverage was represented as the number of records per genus, with unique and duplicated localities (i.e., records for the same species occurring in the same locality but collected by different collectors at different times) being accounted for. The temporal coverage of Bignonieae database was measured as the number of collected specimens per collection date per year and month across the complete temporal span covered. The most representative collectors were identified by counting the total number of collections per collector in the Bignonieae database. To asses the most representative herbaria, we counted the number of duplicated specimens deposited at each herbarium registered within the Bignonieae database. This estimate allowed us to measure the proportion of the database available from a particular herbarium. We cross-checked each herbarium acronym against the Index Herbariorum (Thiers 2019), and excluded herbaria not included in the Index. A list containing the number of records per herbarium can be found in Online Resource 1.

We accessed the spatial coverage of the Bignonieae Database by superimposing the records to different geographic operational units (one degree lat/long cells, administrative areas, biogeographical regions sensu Morrone 2014, and ecoregions sensu Olson et al. 2001). Range size and the altitudinal profile of each species was estimated as described below.

Range size profile. We used the function CalcRange available in the speciesgeocodeR R package (Töpel et al. 2017) to calculate the range of each species thorough convex hull. We defined species range size categories by using the kmean clustering technique available in the stats package of the R programming language (R Core Team 2020). This cluster analysis technique partitions a set of observations of range sizes into k groups, where membership to the k group is determined by the shortest distance to the group mean range size value. It applies an iterative and heuristic algorithm that sets an arbitrary number of cluster centroids around which observations are grouped together based on the minimum mean distance to centroids. In a second step, this algorithm recalculates the centroid value from the observations in the group; this procedure is repeated 100 times. We assigned the number of centroids and clusters to classify the species range size in four categories, as follows: narrow, medium-narrow, medium-wide, and wide. We divided the medium category into two (i.e., medium-barrow and medium-wide) because the amplitude of the wide cluster and the variance of range sizes included was high when only three categories were used (i.e., narrow, medium, wide). Species with less than three unique locality records were manually assigned to an additional category named “micro.”

Altitudinal range profile. An elevational database was created by cross checking the Bignonieae database with elevation data obtained from the U.S. Geological Survey’s EROS Data Center (https://www.usgs.gov/centers/eros) and Google Earth Pro 7.3 (https://earth.google.com/web/). This procedure included four steps: (i) the GTOPO30 global digital elevation model was downloaded from the USGS service in raster format from different global zones encompassing the Neotropics and using the geographical extension of Bignonieae as proxy; (ii) all layers were merged into a unique raster file using QGIS 2.18.16 (QGIS Development Team 2018); (iii) elevation values for all point records in the occurrence database were obtained using the extract function from the raster package in R; and, (iv) outliers were identified using boxplots for each species and compared with the elevation data already available from locality descriptions in the occurrence database (when these values were different we opted to keep the value from the collector). New geo-references were provided only when points were erroneously georeferenced (see last paragraph of the database assembly section). The same procedure was applied to maximum and minimum elevation values for each one of the 386 species. Some altitudinal outliers remained even after cleaning the elevation data and were interpreted to reflect sampling biases.

Spatial biases and database completeness

We used the sampbias R package (Zizka et al. 2020) to assess the effect of accessibility over the geographic biases of the Bignonieae database. This method calculates the expected change in the sampling rates of the individual records as a function of the distance from rivers, airports, and populated places. It describes observed sampling rate as a Poisson process, and models the expected species records as exponentially decaying from these geographic features using a Bayesian statistical framework. As different biasing factors might be correlated (e.g., cities, airports), it estimates the joint effect of all factors. This method operates under the assumption that species are distributed across the entire study region, and calculates not only how strong the biases are, but also identifies unexplored places. The bias effect is then interpreted as the proportion of records missed in each cell as a function of distance to geographical features. If the biases are strong, a fast decaying sampling intensity is expected from the specific type of geographic bias factor under examination. Unexplored and under-collected places are identified as those with the lowest bias effect and no observed records, reflecting the difficulty to access the region. This analysis was run using a spatial scale of one degree, with a buffer of two, using the sampbias default gazetteer.

We used the R package KnownBR (Lobo et al. 2018) to analyze the geographical distribution of survey completeness and identify places with the highest and lowest knowledge of Bignonieae diversity. This analysis estimates species accumulation curves for each geographic unit under examination and estimates the survey coverage intrinsic to the database. To achieve this, the analysis assumes that the distributional database is the most comprehensive possible and uses the number of records and species to calculate species accumulation curves for each geographical unit included in the analysis. Under the assumption of infinite survey, these curves are fitted to theoretical functions with asymptotic behavior to predict how many species would be expected in each geographic unit (Lobo et al. 2018). The percentage of observed against expected records defines the completeness of the database, representing a surrogate of the survey effort and knowledge contained in the database. The final slope of the accumulation curve tells the amount of effort necessary to complete the survey within a particular geographic unit. The values of slope, completeness, and ratio of records per species indicate the quality of the survey conducted in each geographic unit. Lower values of slope, greater values of completeness, and higher observed-expected species ratios define the best surveyed areas.

We applied this method to the Bignonieae database to assess the quality of the geographic information and how well the species diversity is known for each 1 degree cell in which species occurrences are recorded across the whole geographic extent of the tribe. This analysis was implemented using a format A matrix of species occurrences for cell sizes of 60 minutes (1 degree), a ratio between records and species of 1 (R/S), and applying the exact estimator of Ugland et al. (2003) to obtain the species accumulation curves and estimate sampling completeness. Although, higher ratios of species records are preferable, we used an R/S = 1 because the point occurrence density is low across the geographic extend of the tribe. This R/S ratio allowed us to discriminate between cells with higher completeness and lower slopes from cells with lower completeness and higher slopes. We also calculated the quality of the survey effort in each cell using the function SurveyQ of the “KnownBR” package (Lobo et al. 2018). This function uses the completeness, final slope of the species accumulation curves, and the R/S ratio to identify localities with high and low sampling effort in order to help decide future survey efforts (Lobo et al. 2018). We used the default definitions for well (slope < 0.02, completeness > 90%, and R/S ratio > 15) and poor (slope > 0.3, completeness < 50%, and R/S ratio < 3) sampled localities.

Identifying priority areas for new survey efforts

To produce an ignorance map, we combined the bias effect data with the quality survey assessment to identify: (i) areas with the lowest sampling rates and expected records conditional to accessibility, and (ii) areas with the poorest survey effort conditional to the Bignonieae database quality. For this purpose, we reclassified the raster layers coming from sampling bias and completeness analyses and joined the reclassified raster layers with the cells lacking records across the geographical extent of the tribe. We assigned values to each of these layers, as follows: (i) cells with no occurrence data were coded as 1; (ii) cells with poor surveyed areas were assigned a value of 3; and (iii) cells with the lowest sampling rates were coded with a value of 5. A categorical map of the unknowns for each cell in the geographical extent of the tribe was produced by summing the three different layers. Within this map, six types of cells were recovered: (i) cells without any records, (ii) cells fairly surveyed, (iii) cells poorly surveyed, (iv) cells with the lowest sampling rates, (v) cells without any records but modeled as the lowest sampling rate cells, and (vi) cells poorly surveyed but modeled as the lowest sampling rate cells. Cells without any records and poorly surveyed cells cannot be included in “KnowBR” because this software only operates with cells where at least one occurrence is recorded. Through this approach we were able to identify priority areas for new survey efforts despite the intrinsic geographic biases of the Bignonieae database that resulted from accessibility limitations and poor surveys.

Results

Temporal, taxonomic, and spatial coverage

The Bignonieae database comprises 386 species representing all 20 Bignonieae genera currently recognized. Overall, it includes 28,763 records of which 21,170 are unique localities (same unique combination of XCOOR and YCOOR), while 7,593 correspond to collections made for the same species at the same locality at different times (Online Resource 1). Within the Bignonieae database, five genera are more representative accounting for 16,230 (64.36%) records: *Fridericia* (5,201 records representing 59 spp.), *Bignonia* (4,117 records representing 30 spp.), *Adenocalymma* (3,803 records representing 72 spp.), *Amphilophium* (3,109 records representing 46 spp.), and *Tanaecium* (2,282 records representing 21 spp.) (Fig. 1a). Together, these five genera encompass 207 out the 386 sampled species, representing 53.63% of the overall species diversity in the database. In contrast, *Callichlamys*, *Manaosella*, and *Perianthomega*, the three monospecific genera of Bignonieae, showed the lowest number of records, i.e., 448, 56, and 26 records, respectively. In total, 304 species have more than 10 records each, 60 species have less than 10 records, and 22 species have less than three records.

Out of the 28,763 records, 19,399 (67.5%) include information about the herbaria where duplicates are deposited (Fig. 1b). Overall, 196 different herbaria located in 39 countries are represented. While 89.8% of the 19,399 samples are deposited in herbaria based in the USA, especially MO (88.7%), NY (6.9%), F (4.9%), and US (4%), 14.7% of all samples are deposited in Brazilian herbaria, especially SPF (3.4%) and RB (2%). The other samples are deposited in other Latin American countries (17.9%), especially Colombia (3.2%), Paraguay (2.8%), and Bolivia (2.7%), as well as European Countries (9.8%), especially the UK (1.9%), the Netherlands (1.7%), and Sweden (1.5%). These percentages represent the proportion of the specimens deposited at each herbarium; most specimens have duplicates deposited at various herbaria (Online Resource 1).

Specimens were collected between 1816 and 2015, with 11.33% (3,260 specimens) collected before 1950, 68.80% (19,788 specimens) collected between 1950 and 2000, and 3.58% (1,031 specimens) collected after 2000 (Fig. 1c). The remaining 16.26% (4,684 specimens) do not include information about collection date. The distribution of records by month shows that specimens were collected throughout the year, with a minor decrease in collections from August to December, which correspond to the cooler and drier months in the Tropics (Fig. 1d). The highest peak of collection activity throughout the complete temporal span of the database coincide with the active years of A.H. Gentry, E. Zardini, G. Hatschbach, and J.A. Steyermark. However, a monthly tendency was not identified among the 12 most productive collectors (Online Resource 1). Overall, the temporal coverage of the database seems to follow a peak of collection activity during the 80’s to 90’s, with a mild tendency to higher collection activity during the summer.

The geographic extent of Bignonieae currently covered by the occurrence database encompasses the continental platform of America between 39°N and 35°S of latitude, and the Antillean Islands in the Caribbean sea (Fig. 1e). This tribe encompasses the whole Neotropical region, extending some degrees further into north America, where Bignonia capreolata occurs. When administrative areas were examined, Brazil presented the highest number of records, species, and endemic taxa (Fig. 1f-h), doubling the numbers of Venezuela, Peru, Bolivia, and Colombia altogether. Likewise, the less inclusive biogeographical units of the regionalization scheme of the Neotropical region showed the lowest counts of records, species, and endemic taxa (Fig. S2.1-2, see Online Resource 2 in Electronic Supplementary Material). Namely, Bignonieae occurred predominantly in the Brazilian and Chacoan subregions, with the latter showing the highest number of endemic species (Online Resource 2). The tribe also occurred in both the South American and Mexican transition zones. However, while one endemic species was found in the Mexican transition zone, no endemic species were recovered in the South American transition zone. Similarly, the three dominions with highest numbers of records were the Pacific, the Boreal Brazilian, and the Paraná dominions, respectively; the three dominions with the highest number of endemics were the Paraná, the Brazilian, and the Pacific dominions (Online Resource 2). Few provinces included endemic species, with the highest number of endemics being located in the Atlantic Forest, followed by the Caatinga and Paraná provinces (Online Resource 2). Ecoregions showed a similar pattern. However, given that ecoregions show a smaller number of subdivisions, the number of endemics recovered in this region was smaller (Online Resource 2). In sum, when considering the spatial coverage of different geographical units, the number of endemic species decreased at smaller and less inclusive spatial subdivisions.

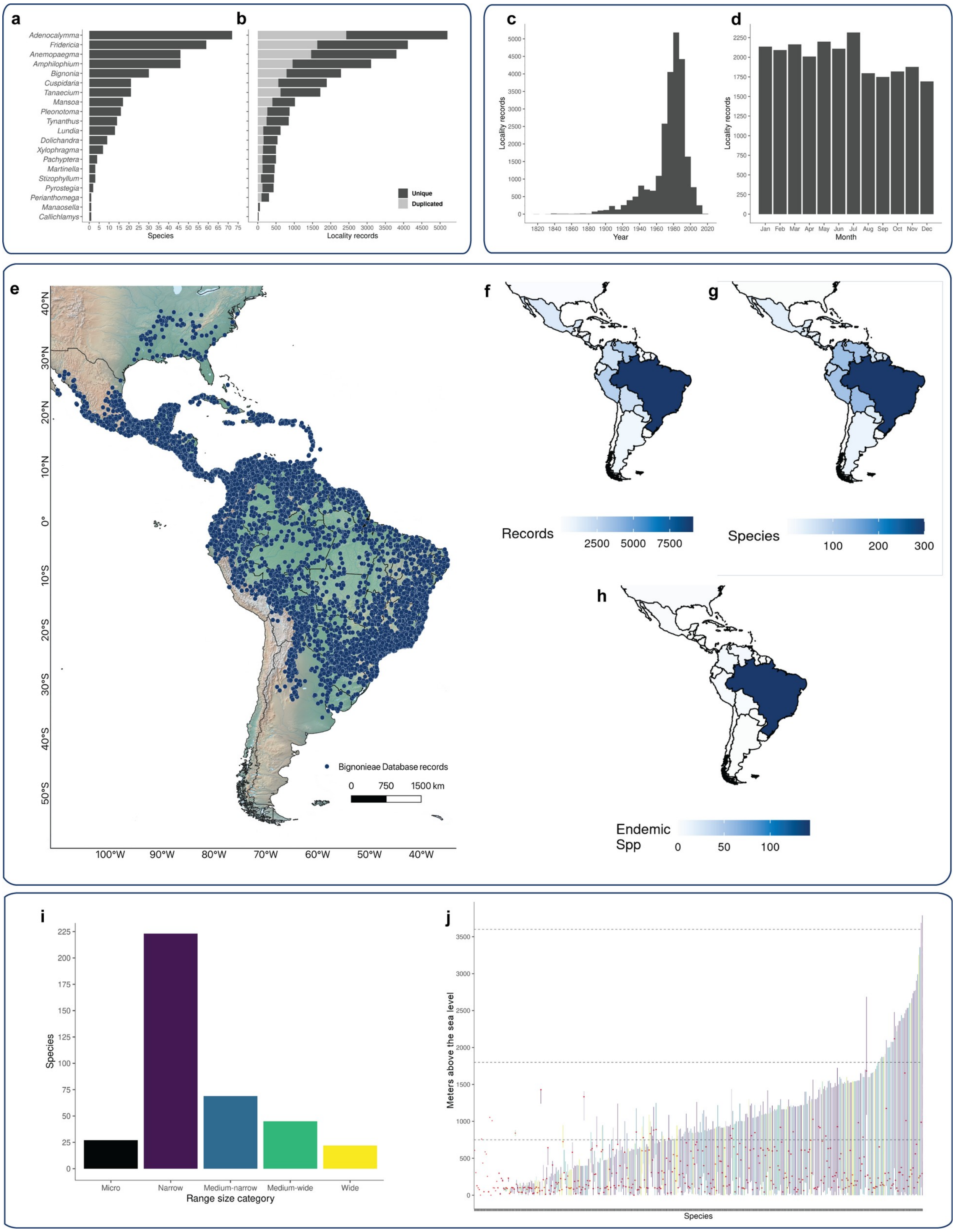

Fig. 1 Taxonomic, temporal, and spatial coverage of the Bignonieae database in the Neotropical region: a-b) Number of unique and duplicated records per genus; c-d) Number of specimens sampled throughout months and years (1816-2015); e) Geographical extension of the Bignonieae database; f) Number of species in each range size class; g) Altitudinal range profile of specimens included in the Bignonieae database, with each line representing the linear altitudinal range between the minimum and maximum elevation values per species; red dots indicate that the median value is located within the range, while dashed horizontal lines show the limits of the boundaries of lowlands (750 m.a.s.l.), montane (1800 m.a.s.l.), and paramo (4500 m.a.s.l.) altitudinal zones

Range size. Most species showed narrow range sizes (Online Resource 2). When range size variation was broken into categories using a K-means clustering with four centers, the following species numbers per categories were recovered: (i) 223 species with narrow range sizes (i.e., below 1.361.662 km2) (ii) 69 species with medium-narrow range sizes (i.e., between 1.410.303 km2 and 4.357.140 km2); (iii) 45 species with medium-wide range sizes (i.e., between 4.653.741 km2 and 7.731.285 km2); and (iv) 22 species with widespread range sizes (i.e., between 11.425.411 km2 and 18.642.351 km2) (Table 1). Area calculations were not possible for the 22 species with less than three locality records classified under the “micro” range size category.

Table 1. Definition of range size categories in square kilometers from Kmeans clustering showing the number of species per class, centroids, quantiles, minimum and maximum values.

Size class	**Species**	**Centroid**	**Min**	**1st Q**	**2ndQ**	**3rd Q**	**Max**
Narrow	223	358428.5	0	58218	192842	592229.5	1361662
Medium-narrow	69	2435854.7	1410303	2226514	2226514	3031349	4357140
Medium-wide	45	6694466.1	4653741	6186717	6186717	7731285	10400739
Wide	22	15763456.5	11425411	12511736	13543922	18642351.8	26349177

Altitudinal range. The altitudinal profile of the Bignonieae database shows that the tribe is conspicuous in the lowlands, although a relatively high number of species show wide altitudinal ranges due to a few outliers (Fig. 1j). No genera occupy a preferred altitudinal belt (Online Resource 2). While 137 species are restricted to lowlands (less than 750 m.a.s.l.) and seven species are restricted to mountains, 239 species are found in both of these altitudinal belts. In general, species with smaller altitudinal ranges also show fewer occurrence points and restricted ranges. On the other hand, species with wider altitudinal ranges are also widespread and show a higher number of occurrence points. Although outliers were checked and wrong geo-references were addressed, some outliers remained, displacing upward the altitudinal range of these species. Given that the taxonomic identity of all specimens was carefully verified by a Bignonieae expert (LGL), these outliers are assumed to represent correct occurrences of the species geographic distributions.

Quality of georeferenced occurrence points

We gathered georeferenced occurrence points from two sources: coordinates recovered from specimen labels and coordinates assigned from the interpretation of locality descriptions. In the Bigninieae database, 1,114 records (3%) were flagged as possible geographic errors, which is an excellent indication of the uninterrupted database curation. The main issue in this assessment was the presence of records close to capitals and country centroids, where 562 records were flagged as problematic. These records were maintained as such, because the species associated with those records were shown to truly occur nearby capitals and country centroids. The second potential source of geographic errors were 509 records falling in the sea. A detailed evaluation of those records indicated that most of these records were located near the coastal shores and were not encompassed by the reference polygon used in the CoordinateCleaner package (Zizka et al. 2020). In addition, several records from the Antillean islands were also located within the sea, which is due to the fact that geometry of the islands displace the centroid out of their territories, or due to points laying in the middle of rivers. All of these records were georeferenced using the locality description in order to correct for these kinds of mistakes. Part of these records were also identified by verifying the altitudinal range profile of each species with altitude values of 0 m.a.s.l. The third potential source of geographic errors was associated with 65 records classified as species range outliers. These outliers were also assumed to represent correct occurrences because they were checked in previous stages of data curation and were shown to fall within the geographic distribution of the associated species. The fourth potential source of error corresponded to records located over administrative area centroids that were either georeferenced with imprecise locality descriptions or using natural reserve centroids. In all of these cases the original coordinates were conserved. The last two issues, the presence of zero coordinates and records located near biodiversity institutions, were not problematic because the species ranges were shown to encompass these locations. An inspection for duplicated records identified 7,576 records. However, these records corresponded to different collections made at different times, by different collectors, and those records were maintained. In sum, the assessment of geo-reference quality allowed us to verify the high quality of the Bignonieae database.

Sampling biases and accessibility

A map of the database at 1 degree grid cells of spatial resolution showed that although the spatial coverage of the Neotropics is high, with 72% of the total number of cells showing at least one record, most cells showed less than 50 records (Fig. 2a). The Amazon was under-collected with huge gaps inside the biome and adjacent areas next to the Cerrado, the Savannas of Colombia, and Peru. The great Chaco was also shown to be under-collected despite a good spatial coverage in surrounding areas. Some centers with a high number of occurrence records (i.e., more than 200 records per grid cell) were identified within and around the following locations: (i) San Jose (Costa Rica); (ii) Barro Colorado Island (Panama); (iii) Iquitos, Manu, and Madre de Dios National Parks (Peru); (iv) Natural Reserves Madidi and Noel Kemp, and Santa Cruz (Bolivia), (v) Asunción (Paraguay), and (vi) Manaus, Belém, São Paulo, Rio de Janeiro, Brasilia, and Belo Horizonte (Brazil), among others. Species richness was high in just few cells scattered inside and around Amazonia, the south-eastern Brazil, and Central America (Fig. 2b). The highest richness per cell was 65 species; these same cells also included the highest occurrence records count per cell. Most grid cells included less than 20 species.

The distance from cities was the main predictor of sampling rate across the geographical extent of Bignonieae, followed by a moderate effect of rivers and airports, and a negligible effect of roads (Fig. 2c-d). This means that the number of expected records rapidly decreased with distance from cities, while records decreased in a steady fashion with distance from roads. A projection of bias effect in geographical space shows that cities dominate over the other biasing factors (Online Resource 2). Areas with lower and zero sampling rates were sparse inside the Amazon region surrounded by areas with slightly higher bias effect values. These zero bias effect areas correspond to remote places, where sampling rate is zero. Other regions such as south-eastern Brazil and northern Andes are highly biased towards cities despite the high number of collections and species.

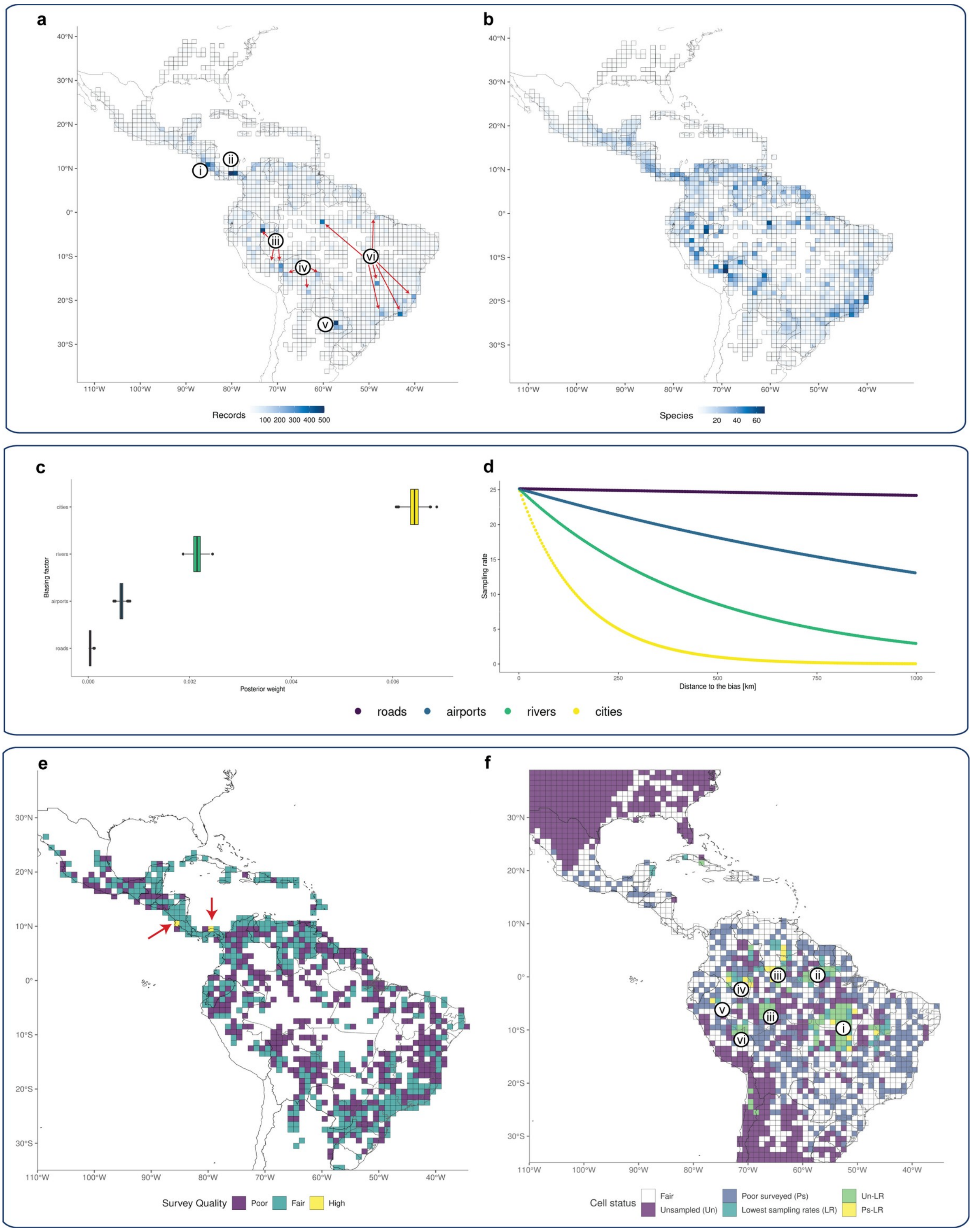

Fig. 2 Spatial bias and ignorance maps of the Bignonieae database throughout the Neotropical region. a-b) Number of occurrence records and species (richness) by one degree grid cell. The centers with more than 200 records per grid cell are indicated by red arrows per country (i) Costa Rica, (ii) Panamá, (iii) Perú, (iv) Bolivia, (v) Paraguay, and (vi) Brazil. c) Posterior weight of each category of biasing factors. d) Change in sampling rate with distance for each biasing factor, showing the distance to cities as the strongest biasing factor. e) Geographical projection of sampling effort showing Well, Fair, and Poor surveys per geographical unit, highlighting the highest quality surveys in Costa Rica and Panama. f) Map of ignorance on the knowledge of species richness and distribution of Bignonieae. Areas with the highest collection priority located within the Amazon basin: (i) Brazilian states of Mato Grosso and Pará; (ii) northern Pará; (iii) northern and southern portions of the Amazonas state; (iv) Colombian Amazon; (v) northern Perú; and, (vi) region between Acre and Perú

Completeness of survey efforts

The species accumulation curves and the completeness of each geographical unit showed a moderate number of cells with lower values of slope, and a lower number of cells with higher completeness, suggesting that the sampling effort has been heterogeneous. Lower values of slope (Online Resource 2) indicate that a higher number of records are necessary to discover new species either because the diversity is well-sampled or because there is a high prevalence of rare species in a particular geographic unit. In other words, no matter how intensive the collection effort is, no new species are likely to be recorded. These units with lower values of slope are relatively sparse across the Neotropics but are common in Central America, the Antillean Islands, and south-eastern Brazil. Cells with completeness values higher than 80% are scarce, although a few are located in Central America and the Antilles, while others are dispersed across South America, with a slightly higher concentration in South-eastern Brazil, Paraguay, and northern Argentina (Online Resource 2). Intermediate values of completeness (i.e., around 50%) and completeness values below 30% are more numerous and well distributed across the geographic extent of the tribe, indicating that additional survey efforts are needed across the whole geographical extent of the tribe (Online Resource 2).

Survey effort quality showed that higher collection efforts are still needed in order to accurately represent the species diversity of the tribe Bignonieae in the Neotropics (Fig. 2e-f, Online Resource 2). The relationship between completeness, the ratio between records and species (R/S), and the final slope of the species accumulation curves varied across localities. While the best surveyed localities were characterized by high completeness values, low final slopes, and high number of records relative to the number of species (R/S), the worse surveyed localities were characterized by low completeness, low slopes, and low R/S ratio values (Online Resource 2). Only two cells showed high quality surveys in contrast to 390 cells with fair quality sampling, and 397 with poor sampling (Online Resource 2). The two high quality surveyed cells were located in Costa Rica and Panama. In sum, despite the high quality of the Bignonieae database, additional survey efforts are still needed throughout the geographical extent of tribe Bignonieae (Fig. 2E-f).

Priority areas for future surveys

The Amazon is the most under-sampled region throughout the Neotropics, as well as the area with the lowest sampling rate, which is due to accessibility biases (Fig. 2e). The areas with highest collection priority in the Amazon are: (i) an area located in the Brazilian states of Mato Grosso and Pará, next to the transition zone between the Cerrado and the Amazon; (ii) an area located in northern Pará, next to Suriname and Guiana; (iii) two areas within the state of Amazonas, one in the northern portion, close to Venezuela, and another in the southern portion of the state; (iv) the Colombian Amazon; (v) northern Perú; and, (vi) an area between the state of Acre and Perú (Fig. 2f). Similarly, an area located over the states of Maranhão, Tocantis, Piauí, and Bahia in the Brazilian Cerrado is also under-collected (Fig. 2e-f). Poor surveyed areas are also scattered across the whole geographical extent of the tribe and should be considered as secondary priorities when planning new expeditions (Fig. 2e-f, Online Resource 2). This contrasts with Central America and south-eastern Brazil, which are the regions were sampling has been most intensive.

Discussion

Identifying knowledge gaps and biases in biodiversity databases is fundamental to appropriately frame research questions and understand the scope of conclusions. The Wallacean shortfall (i.e., the lack in the knowledge about species distributions) derives mainly from the strong relationship between geographic information and the collecting effort done by researchers to gather species distribution data, which has the undesirable consequence of aggregating records in space and time (Hortal et al. 2015). The Bignonieae database includes samples collected by many different botanists over the course of ca. 65 years, mainly between 1950 to 2015. The taxonomic, spatial, and temporal coverages of this database are wide, encompassing most species known, across the whole geographical extent. Knowledge gaps were identified, especially in Amazonia, which is still incompletely surveyed for these lianas although the tribe is centered in this region (Meyer et al. 2018). The completeness assessment and the ignorance maps produced here will help increase the efficiency of future Bignonieae sampling.

Coverage of the Bignonieae database

The Bignonieae database is among the best available datasets for the study of plant diversity and distribution in the Neotropics (Hopkins 2007). This dataset built from specimens deposited at the Missouri Botanical Garden, where Alwyn Gentry, the most prolific collector of the Bignoniaceae worked and deposited his samples. The next most representative herbaria in this database are the New York Botanical Garden (NY, 1,333 records), the Field Museum of Natural History (F, 953 records), the Smithsonian Institution (US, 780 records), and the herbarium of the University of São Paulo (SPF, 666 records). Our database includes a lower number of Bignonieae vouchers from South American herbaria, even though this is where most of the Bignonieae diversity is located. This unbalanced distribution of collections needs to be further explored in order to determine whether this is a bias of the Bignonieae database or whether it reflects past legacies and the distribution of biodiversity collections between north and south (Gaston and May 1992; Peterson et al. 2015).

An effort to increase the taxonomic and geographic knowledge of Bignonieae has been conducted by one of us (LGL) in collaboration with her graduate students and postdocs. Together, they published several synopses, taxonomic revisions, and monographs in the last decade (e.g., Kaehler 2011; Zuntini 2014; Medeiros and Lohmann 2015; Fonseca et al. 2017; Francisco and Lohmann 2018; Kataoka 2018; Fonseca and Lohmann 2019; Frazão and Lohmann 2019; Kaehler and Lohmann 2019). Those taxonomic treatments have contributed important pieces of information about the taxonomy and distribution of various Bignonieae taxa. The classifications adopted in the Bignonieae database follow those treatments. Despite that, the specimens collected by these botanists are still being curated and have not yet been included in the current database. The Species Link (http://www.splink.org.br) alone lists more than 2,600 Bignoniaceae records collected by these botanists, namely by L.G. Lohmann (744 specimens), A.R. Zuntini (482), L.H. Fonseca (320), A.F. Nunes (249), A. Nogueira (236), F. Firetti (229), M. Kaeheler (202), M.R. Pace (176), R.S. Ribeiro (98), J.N. Francisco (69), M.F. Calió (48), E.Y. Kataoka (24), and M. Beyer (5). These records might help improve some of the sampling gaps and should be incorporated into the Bignonieae database once this data has been fully curated. Likewise, specimens deposited in other Latin American herbaria should be further studied, geo-referenced, and catalogued. The importance of regional herbaria cannot be underestimated (see Colombo et al. 2016). While the Bignonieae database would certainly benefit from more intensive studies of specimens deposited in botanical institution across the Neotropics, there is also a clear need for continued botanical exploration throughout Latin America, especially in the regions with the lowest collection efforts.

The database temporal sampling seems to be relatively homogeneous throughout the year, with a mild increase in sampling effort during the summer months (Fig. 1d). This suggests that biases on detectability by phenology might not be severe in this database, corroborating earlier findings (Sheth et al. 2012). However, further phenological studies of Bignonieae are still needed. Although the taxonomic coverage of the database includes all twenty genera of Bignonieae recognized to date (Lohmann and Taylor 2014; Fonseca and Lohmann 2019), the number of unique records is high for each genus. Furthermore, the proportion of duplicated localities is also significant (Fig. 1a-b). Further efforts to explore new regions are necessary so that different localities are added to known species ranges. Additional sampling would also increase the probability of finding new species across the geographical extent of the tribe.

The geographic coverage of the Bignonieae dataset is high, with records being reported from all Neotropical countries and geographical units identified by various biogeographical classification schemes (e.g., Olson et al. 2001; Morrone 2014) (Fig. 1e). The number of occurrences, species, and endemic species decreases with geographical unit size, suggesting that Bignonieae species geographical ranges tend to be wider. Most species appear to have narrow range sizes, with the mean range size within this category being around 358.439 km2 (Fig. 1i). Range size categories were defined based on the Bignonieae database, with narrow range sizes being seven times that of narrow endemics for other groups of organisms (i.e., 50.000 km2). Placing range sizes into categories helps us understand the variability of predefined operational geographic units. Further studies about patterns of species co-occurrence are needed to better describe and understand several distribution patterns in Bignonieae, especially regionalization proposals, patterns of endemism, phylogenetic and endemism diversity measures (Guedes et al. 2018). Information about patterns of species co-occurrence are also needed to understand better how geological and climatic predictors are associated to the origin and diversification of the tribe.

The Bignonieae database supports the observation that this tribe constitutes a conspicuous lowland plant clade (Gentry 1979; Lohmann and Taylor 2014). It also shows that a high proportion of species reach mountain regions (Fig. 2f), although high altitude records correspond to geographical outliers. The amplitude of the geographical range is positively correlated to the number of records, suggesting that a higher collection effort is needed to increase the knowledge of the altitudinal range of the species of this tribe. Reviewing altitude data allowed us to identify several erroneous geo-referenced localities that were subsequently corrected.

Georeferencing quality

The high quality of the geographic data contained in the Bignonieae database is due to several rounds of georeferencing work conducted during the course of more than 20 years. More specifically, the history of georeferencing behind this database has undergone four main stages. The first stage was conducted by LGL between 2003-2004 and involved the extraction of geographic coordinates from herbarium specimens whenever available and verifying that those coordinates really belonged to the described location. Whenever coordinates were not included in the specimen label, coordinates were obtained using regional maps and online gazetteers, especially the "Getty Thesaurus of Geographic Names Online" (http://www.getty.edu/research/tools/vocabularies/tgn/). The second stage used ArcMap 9.1 to detect geographical outliers, corroborate the presence of records in verbatim administrative areas, and assess the correspondence between coordinates and locality descriptions (see Sheth et al. 2008). The third stage checked for geographical outliers and taxonomic identity by visual inspection of species occurrence points and a rough estimation of the species ranges. At this stage, outliers were checked for taxonomic identity and new geo-references were assigned by taxonomic experts whenever necessary (see Meyer et al. 2018). The fourth stage, conducted here, implemented automatic georeferencing quality assessment in R, and manual solutions to flag potential errors by checking individual problematic records in Google Earth. Together, these four georeferencing stages substantially increased the database quality. Despite that, additional work is still needed, especially in what concerns the quantification of the geographic uncertainty radius (Wieczorek et al. 2004). Further additions of data from other Bignonieae experts will certainly increase the quality of this database.

Geographic biases and survey completeness

The spatial coverage of Bignonieae database throughout the Neotropics was substantial at the spatial resolution of one degree of grid cell size. The cells with the highest occurrence record numbers and species richness are not necessarily coincident (Fig. 2a-b). Records were mainly biased toward cities and secondarily towards rivers (Fig. Fc-d). This pattern of aggregation of occurrence records around populated places and routes that guarantee accessibility to the surveyed regions has been documented in several taxa in the Neotropics, especially plants (Nelson et al. 1990; Kadmon et al. 2004; Pautasso and McKinney 2007; Vale and Jenkins 2012; Oliveira et al. 2016; Guedes et al. 2018). Cities are the centers of botanical institutions from which expeditions are generally undertaken and the entrance to remote and unexplored places. The Bignonieae database clearly reflects this general pattern. South-eastern Brazil is not only one of its centers of diversity, but also one of the most intensively sampled regions, likely reflecting the high number of research centers and universities located in this region (Sousa-Baena et al. 2014).

The Amazon sensu lato (including the Guiana region) corresponds to the center of diversity of the tribe (Meyer et al. 2018). Despite that, it is by far the most under-sampled region for Bignonieae, with vast areas showing the lowest sampling rates, and often not a single collection record (Fig. 2f). For this region the effect of rivers has clearly biased collection efforts, with collections concentrated along rivers. The Amazon is one of the most remote and under-sampled

Neotropical areas for many taxa (Milliken et al. 2010; Guedes et al. 2018). Knowledge from occurrence databases obtained from herbaria are insufficient to account for species diversity and distribution in this region, calling for additional botanical expeditions (Hopkins 2019). Increasing sampling efforts in the Amazon have become even more urgent in recent years given the high deforestation rates, which are eliminating many species-rich yet under-sampled regions (Stropp et al. 2020).

In order to identify priority locations for new survey efforts, we analyzed the survey completeness of one degree cells across the Neotropics, in locations where Bignonieae species have been recorded (Fig. 2f). For this analysis, we considered the Bignonieae database as the most exhaustive compilation of information available for this tribe to date. Our analyses indicate that new species discoveries are likely to emerge from a high number of locations, while fewer places seem to represent well the diversity of Bignonieae species. Databases in which a large group of species are only known from a few geographical units, while widespread species dominate the records in cells in vast areas across the whole geographical extent are common among plants (Tobler et al. 2007).

Priority areas for new survey efforts

To properly identify priority collection areas, we classified cells as poor, fair, and high-quality surveys (Fig. 2e). Half the sites where Bignonieae is known to occur were classified as poor quality indicating that revisiting those locations can increase the number of species reported. Lots of these cells are within Amazonia, highlighting how important it is to intensify sampling efforts in this region. Although only two cells located in the Neotropics (i.e., around Barro Colorado Island in Panama and Guanacaste in Costa Rica) were classified as high quality surveys, a lot of cells with fair quality surveys were also recovered across the Neotropics, a pattern that has been recovered for other groups (Sousa-Baena et al. 2014; Pelayo-Villamil et al. 2018; La Sorte and Somveille 2020).

Our ignorance map compiled from cells without records, poorly surveyed cells, and cells with lowest sampling rates suggested priority areas for new survey efforts (Fig. 2f). According to this analysis, the Amazon and the Cerrado in eastern Brazil appeared as the first sampling priority. Given that Amazonia is the center of diversity of the tribe, it offers the best chance not only to expand the geographical knowledge of species ranges but also to discover new species. Sites with poor quality surveys within the Amazon represent a second priority given the low completeness of sampling in these regions. Those findings corroborate the recommendations of other studies that have indicated the need to focus sampling efforts in remote and under-sampled areas, while also revisiting accessible but under-sampled areas, and sampling highly threatened regions (Hopkins 2019; Stropp et al. 2020).

Conclusion

Well-curated distribution databases are crucial to address conservation issues and provide reliable answers to biogeographical questions. Obtaining raw point locality data is a demanding, costly, and endless task, although it is one with high returns. When compared to other kinds of distribution representation techniques such as range polygons, raw point locality data provide a better perspective of what is known and unknown about species geographical ranges (Rocchini et al. 2011; Maldonado et al. 2015; Guedes et al. 2018). The Bignonieae database is well curated, covering its taxonomic diversity, and presenting accurate geographical data. However, our analyzes have shown that there is still room for improvement. Additional collection efforts are greatly needed across the Neotropics in order to encompass new localities. In particular, the knowledge gap in the Amazon region is substantial, contrasting with the fact that this region represents the main center of species diversity of Bignonieae. Further survey efforts will not only tackle the Wallacean shortfall in this group of lianas but could certainly increase the rate of new species discoveries. The current deforestation pressures in the Amazon (Stropp et al. 2020) is threatening the diversity of Bignonieae, increasing the relevance of this region for conservation efforts. Accelerating the assembly of higher-quality distribution databases for multiple taxa in the Neotropics is urgently needed if we want to effectively design conservation plans for its most diverse regions.

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Appendix 1

Recovering the drivers of sampling bias in Bignonieae (Bignoniaceae) and identifying priority areas for new survey efforts

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Online Resource 1 – Bignonieae Database

Supplementary material of the temporal and taxonomic coverage.

Table S1. Number of records of specimens of the Bignonieae database that are kept at herbaria in different countriesN.

Country	Records	% over the total of records in the database (28,763 records)	% records with information about herbaria (19,399 records)
U.S.A.	17,428	60.592	89.84
Brazil	2,849	9.905	14.686
Colombia	612	2.128	3.155
Paraguay	549	1.909	2.83
Bolivia	526	1.829	2.711
Venezuela	468	1.627	2.412
Mexico	369	1.283	1.902
U.K.	359	1.248	1.851
Netherlands	335	1.165	1.727
Denmark	299	1.04	1.541
Sweden	296	1.029	1.526
Germany	280	0.973	1.443
Switzerland	264	0.918	1.361
Costa Rica	256	0.89	1.32
Argentina	252	0.876	1.299
France	139	0.483	0.717
French Guiana	121	0.421	0.624
Panama	85	0.296	0.438
Ecuador	76	0.264	0.392
Peru	72	0.25	0.371
Spain	70	0.243	0.361
Belgium	40	0.139	0.206
Dominican Republic	29	0.101	0.149
Austria	27	0.094	0.139
Cuba	26	0.09	0.134
Italy	24	0.083	0.124
Jamaica	19	0.066	0.098
El Salvador	16	0.056	0.082
Puerto Rico	15	0.052	0.077
Russia	15	0.052	0.077
Honduras	11	0.038	0.057
Suriname	11	0.038	0.057
Nicaragua	4	0.014	0.021
Madagascar	3	0.01	0.015
Canada	2	0.007	0.01
China	2	0.007	0.01
Finland	1	0.003	0.005
India	1	0.003	0.005
Lithuania	1	0.003	0.005
Unknown	**9487**	**32.983**	Non applicable

*Unknown records correspond to those for which no herbarium information is available.

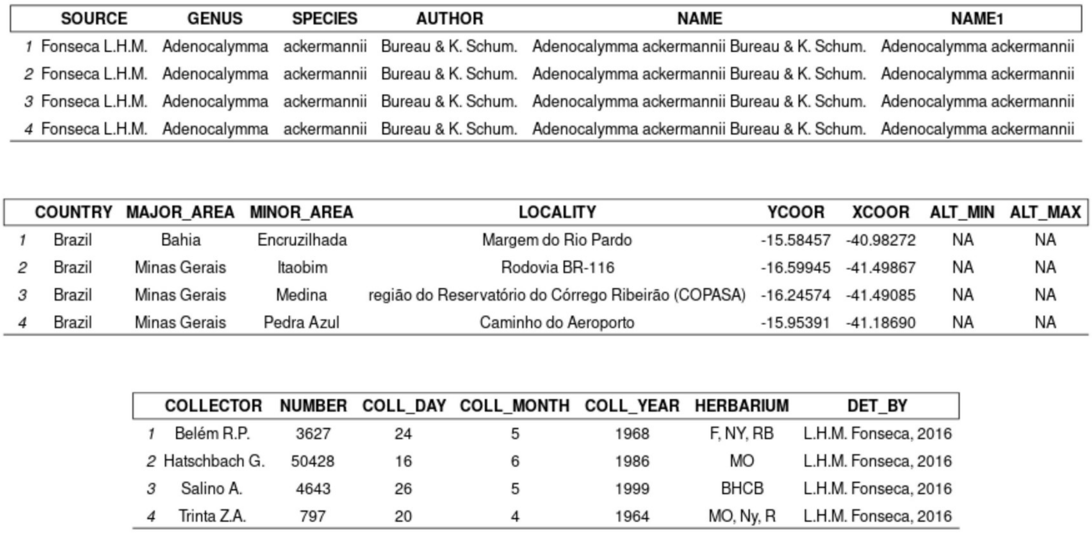
Table S2. Number of records of specimens included in the Bignonieae database per herbarium.

Herbaria	Records	% over the total of records in the database (28763 records)	% records with information about herbaria (19399 records)	Organization	Country
MO	17,220	59.869	88.767	Missouri Botanical Garden	U.S.A.
NY	1,333	4.634	6.871	The New York Botanical Garden	U.S.A.
F	953	3.313	4.913	Field Museum of Natural History	U.S.A.
US	780	2.712	4.021	Smithsonian Institution	U.S.A.
SPF	666	2.315	3.433	Universidade de São Paulo	Brazil
COL	474	1.648	2.443	Universidad Nacional de Colombia	Colombia
VEN	428	1.488	2.206	Universidad Central de Venezuela	Venezuela
RB	397	1.38	2.046	Jardim Botânico do Rio de Janeiro	Brazil
USZ	387	1.345	1.995	Museo de Historia Natural Noel Kempff Mercado -- Universidad Autónoma Gabriel René Moreno	Bolivia
HRCB	269	0.935	1.387	Universidade Estadual Paulista	Brazil
MBM	264	0.918	1.361	Museu Botânico Municipal	Brazil
MEXU	261	0.907	1.345	Universidad Nacional Autónoma de México	Mexico
G	258	0.897	1.33	Conservatoire et Jardin botaniques de la Ville de Genève	Switzerland
S	248	0.862	1.278	Swedish Museum of Natural History	Sweden
MICH	241	0.838	1.242	University of Michigan	U.S.A.
GH	235	0.817	1.211	Harvard University	U.S.A.
FCQ	231	0.803	1.191	Universidad Nacional de Asunción	Paraguay
CR	229	0.796	1.18	Museo Nacional de Costa Rica	Costa Rica
UB	222	0.772	1.144	Universidade de Brasília	Brazil
K	220	0.765	1.134	Royal Botanic Gardens	U.K.
U	220	0.765	1.134	Naturalis	Netherlands
CTES	201	0.699	1.036	Instituto de Botánica del Nordeste	Argentina
SP	199	0.692	1.026	Instituto de Botânica	Brazil
M	197	0.685	1.016	Botanische Staatssammlung München	Germany
PY	186	0.647	0.959	Centro de Estudios y Colecciones Biológicas para la Conservación	Paraguay
AAU	180	0.626	0.928	Aarhus University	Denmark
BM	138	0.48	0.711	The Natural History Museum	U.K.
LPB	138	0.48	0.711	Herbario Nacional de Bolivia, Universidad Mayor de San Andrés	Bolivia
P	137	0.476	0.706	Muséum National d'Histoire Naturelle	France
R	135	0.469	0.696	Museu Nacional	Brazil
AS	132	0.459	0.68	Jardín Botánico	Paraguay
UEC	128	0.445	0.66	Universidade Estadual de Campinas	Brazil
BHCB	127	0.442	0.655	Universidade Federal de Minas Gerais	Brazil
TEXLL	126	0.438	0.65	University of Texas (TEX) and Lundell (LL) herbaria	U.S.A.
CAY	121	0.421	0.624	Institut de Recherche pour le Developpement (IRD)	French Guiana
C	120	0.417	0.619	University of Copenhagen	Denmark
CEPEC	119	0.414	0.613	CEPEC, CEPLAC	Brazil
L	114	0.396	0.588	Naturalis	Netherlands
A	113	0.393	0.583	Harvard University	U.S.A.
WIS	103	0.358	0.531	University of Wisconsin	U.S.A.
ESA	95	0.33	0.49	Universidade de São Paulo	Brazil
VIC	89	0.309	0.459	Universidade Federal de Viçosa	Brazil
JBGP	86	0.299	0.443	Jardín Botánico de Cartagena “Guillermo Piñeres”	Colombia
MV	84	0.292	0.433	Unknown	Unknown
HB	79	0.275	0.407	Herbarium Bradeanum	Brazil
B	78	0.271	0.402	Botanischer Garten und Botanisches Museum Berlin-Dahlem, Zentraleinrichtung der Freien Universität Berlin	Germany
MG	78	0.271	0.402	Museu Paraense Emílio Goeldi	Brazil

IAN	71	0.247	0.366	Embrapa Amazônia Oriental, Ministry of Agriculture	Brazil
SCZ	71	0.247	0.366	Smithsonian Tropical Research Institute	Panama
MA	70	0.243	0.361	Real Jardín Botánico	Spain
XAL	68	0.236	0.351	Instituto de Ecología, A.C.	Mexico
HUEFS	58	0.202	0.299	Universidade Estadual de Feira de Santana	Brazil
DS	53	0.184	0.273	California Academy of Sciences	U.S.A.
MBML	53	0.184	0.273	Museu de Biologia Mello Leitão	Brazil
TEX	45	0.156	0.232	University of Texas at Austin	U.S.A.
CAS	43	0.149	0.222	California Academy of Sciences	U.S.A.
USM	41	0.143	0.211	Universidad Nacional Mayor de San Marcos	Peru
BR	40	0.139	0.206	Botanic Garden Meise	Belgium
INPA	38	0.132	0.196	Instituto Nacional de Pesquisas da Amazônia	Brazil
ENCB	36	0.125	0.186	Instituto Politécnico Nacional	Mexico
QCNE	36	0.125	0.186	Museo Ecuatoriano de Ciencias Naturales del Instituto Nacional de Biodiversidad	Ecuador
PA	34	0.118	0.175	Universidade Federal do Oeste do Pará	Brazil
GB	33	0.115	0.17	University of Gothenburg	Sweden
LP	33	0.115	0.17	Museo de La Plata	Argentina
ARAR	31	0.108	0.16	Unknown	Unknown
JBSD	29	0.101	0.149	Jardín Botánico Nacional Dr. Rafael M. Moscoso	Dominican Republic
W	27	0.094	0.139	Naturhistorisches Museum Wien	Austria
HAC	26	0.09	0.134	Instituto de Ecología y Sistemática	Cuba
UPS	26	0.09	0.134	Museum of Evolution	Sweden
FI	23	0.08	0.119	Natural History Museum	Italy
PORT	23	0.08	0.119	BioCentro-UNELLEZ	Venezuela
QCA	23	0.08	0.119	Pontificia Universidad Católica del Ecuador	Ecuador
CM	20	0.07	0.103	Carnegie Museum of Natural History	U.S.A.
HUA	18	0.063	0.093	Universidad de Antioquia	Colombia
FUEL	17	0.059	0.088	Universidade Estadual de Londrina	Brazil
LAGU	16	0.056	0.082	Asociación Jardín Botánico La Laguna, Urbanización Plan de La Laguna	El Salvador
AMAZ	15	0.052	0.077	Universidad Nacional de la Amazónia Peruana	Peru
CHAPA	15	0.052	0.077	Colegio de Postgraduados	Mexico
CUVC	15	0.052	0.077	Universidad del Valle	Colombia
LE	15	0.052	0.077	Komarov Botanical Institute of RAS	Russia
MER	15	0.052	0.077	Universidad de Los Andes	Venezuela
USJ	15	0.052	0.077	Universidad de Costa Rica	Costa Rica
VALE	15	0.052	0.077	VALE	Brazil
CH	14	0.049	0.072	El Colegio de la Frontera Sur	Mexico
INB	14	0.049	0.072	Instituto Nacional de Biodiversidad	Costa Rica
PMA	14	0.049	0.072	Universidad de Panamá	Panama
GUA	13	0.045	0.067	DIVEA, DEP, FEEMA	Brazil
MEDEL	13	0.045	0.067	Universidad Nacional de Colombia - Sede de Medellín	Colombia
SI	13	0.045	0.067	Instituto de Botánica Darwinion	Argentina
TRUJ	13	0.045	0.067	Universidad Nacional de La Libertad-Trujillo	Peru
SEL	12	0.042	0.062	Marie Selby Botanical Gardens	U.S.A.
SPSF	12	0.042	0.062	Instituto Florestal	Brazil
UCWI	12	0.042	0.062	University of the West Indies, Mona	Jamaica
UPR	12	0.042	0.062	Botanical Garden of the University of Puerto Rico	Puerto Rico
BBS	11	0.038	0.057	University of Suriname	Suriname
CVRD	11	0.038	0.057	Reserva Natural da Vale, Meio Ambiente	Brazil
IPA	11	0.038	0.057	Empresa Pernambucana de Pesquisa Agropecuária, IPA	Brazil
JAUM	11	0.038	0.057	Jardín Botánico Joaquín Antonio Uribe	Colombia
BOLV	9	0.031	0.046	Centro de Biodiversidad y Genetica-UMSS	Bolivia
GOET	9	0.031	0.046	Universität Göttingen	Germany

GUAY	9	0.031	0.046	Universidad de Guayaquil	Ecuador
MAD	9	0.031	0.046	Forest Products Laboratory	U.S.A.
MCNS	9	0.031	0.046	Museo de Ciencias Naturales de Salta	Argentina
EAP	7	0.024	0.036	Escuela Agrícola Panamericana	Honduras
G-DC	7	0.024	0.036	Geneva Herbarium – De Candolle's Prodromus	Switzerland
IJ	7	0.024	0.036	Natural History Museum of Jamaica (NHMJ)	Jamaica
UFACPZ	7	0.024	0.036	Universidade Federal do Acre/Parque Zoobotânico	Brazil
WAG	7	0.024	0.036	Naturalis	Netherlands
FTG	6	0.021	0.031	Fairchild Tropical Botanic Garden	U.S.A.
QAME	6	0.021	0.031	Dirección Nacional Forestal, Ministerio de Agricultura y Ganadería	Ecuador
HJ	5	0.017	0.026	Universidade Federal de Jataí	Brazil
HUESB	5	0.017	0.026	Universidade Estadual do Sudoeste da Bahia-Campus de Jequié	Brazil
UEL	5	0.017	0.026	Universidade Estadual de Londrina	Brazil
EAC	4	0.014	0.021	Universidade Federal do Ceará	Brazil
GA	4	0.014	0.021	University of Georgia	U.S.A.
MJC	4	0.014	0.021	Unknown	Unknown
MSC	4	0.014	0.021	Michigan State University	U.S.A.
MY	4	0.014	0.021	Universidad Central de Venezuela	Venezuela
RPSC	4	0.014	0.021	Río Palenque Science Center	Ecuador
TEFH	4	0.014	0.021	Universidad Nacional Autónoma de Honduras	Honduras
UCR	4	0.014	0.021	University of California	U.S.A.
UJAT	4	0.014	0.021	Universidad Juárez Autónoma de Tabasco	Mexico
CABI	3	0.01	0.015	CABI Bioscience UK Centre	U.K.
CESJ	3	0.01	0.015	Universidade Federal de Juiz de Fora	Brazil
CPFCN	3	0.01	0.015	Unknown	Brazil
ECON	3	0.01	0.015	Harvard University	U.S.A.
HBG	3	0.01	0.015	Biozentrum Klein-Flottbek, Universität Hamburg	Germany
TAN	3	0.01	0.015	Parc de Tsimbazaza	Madagascar
TEPB	3	0.01	0.015	Universidade Federal do Piauí	Brazil
UC	3	0.01	0.015	University of California	U.S.A.
UPRRP	3	0.01	0.015	University of Puerto Rico	Puerto Rico
ALCB	2	0.007	0.01	Universidade Federal da Bahia, Campus Universitário de Ondina	Brazil
BOLFOR	2	0.007	0.01	Unknown	Bolivia
COAH	2	0.007	0.01	Instituto Amazónico de Investigaciones Científicas SINCHI	Colombia
E	2	0.007	0.01	Royal Botanic Garden Edinburgh	U.K.
FMB	2	0.007	0.01	Instituto de Investigación de Recursos Biológicos Alexander von Humboldt	Colombia
HNMN	2	0.007	0.01	Universidad Centroamericana	Nicaragua
HRB	2	0.007	0.01	IBGE	Brazil
HST	2	0.007	0.01	Herbário Sérgio Tavares - Universidade Federal Rural de Pernambuco	Brazil
ITIC	2	0.007	0.01	Universidad de El Salvador	El Salvador
LIV	2	0.007	0.01	World Museum Liverpool	U.K.
MUT	2	0.007	0.01	Eberhard Karls Universität Tübingen	Germany
PERD	2	0.007	0.01	Herbário do Parque Estadual do Rio Doce - Parque Estadual do Rio Doce, Instituto Estadual de Florestas Marliéria	Brazil
SCNLS	2	0.007	0.01	Unknown	Peru
UCLA	2	0.007	0.01	EEB Herbarium - University of California	U.S.A.
VALLE	2	0.007	0.01	Universidad Nacional de Colombia	Colombia
WCS	2	0.007	0.01	The Wildlife Conservation Society	U.S.A.
AMES	1	0.003	0.005	Harvard University	U.S.A.
BHMB	1	0.003	0.005	Unknown	Unknown
BHMH	1	0.003	0.005	Universidade Federal de Minas Gerais	Brazil
BI	1	0.003	0.005	Museo Orto Botanico, Università degli Studi di Bari.	Italy
CBB	1	0.003	0.005	Universidade Estadual de Londrina	Brazil
CBR	1	0.003	0.005	Unknown	Unknown

CEN	1	0.003	0.005	EMBRAPA Recursos Geneticos e Biotecnologia - CENARGEN	Brazil
CGE	1	0.003	0.005	Cambridge University	U.K.
CHOCO	1	0.003	0.005	Universidad Tecnológica del Chocó	Colombia
CLEMS	1	0.003	0.005	Clemson University	U.S.A.
CO	1	0.003	0.005	Muséum National d'Histoire Naturelle	France
CORD	1	0.003	0.005	IMBIV-Museo Botánico	Argentina
CUZ	1	0.003	0.005	Universidad Nacional San Antonio Abad del Cusco	Peru
CVG	1	0.003	0.005	Unknown	Unknown
DUKE	1	0.003	0.005	Duke University	U.S.A.
ENAG	1	0.003	0.005	Universidad Nacional Agraría	Nicaragua
FLAS	1	0.003	0.005	Florida Museum of Natural History	U.S.A.
FLOR	1	0.003	0.005	Universidade Federal de Santa Catarina	Brazil
FURB	1	0.003	0.005	Universidade Regional de Blumenau	Brazil
H	1	0.003	0.005	University of Helsinki	Finland
HAS	1	0.003	0.005	Fundação Zoobotânica do Rio Grande do Sul	Brazil
HEPH	1	0.003	0.005	Jardim Botânico de Brasília	Brazil
HT	1	0.003	0.005	Herbario Tropical S.A.S.	Colombia
HUEMG	1	0.003	0.005	Universidade do Estado de Minas Gerais	Brazil
HUFU	1	0.003	0.005	Universidade Federal de Uberlândia	Brazil
HULE	1	0.003	0.005	Universidad Nacional Autónoma de Nicaragua	Nicaragua
HUT	1	0.003	0.005	Universidad Nacional de La Libertad-Trujillo	Peru
IBGE	1	0.003	0.005	Reserva Ecológica do IBGE	Brazil
ICN	1	0.003	0.005	Universidade Federal do Rio Grande do Sul	Brazil
JBB	1	0.003	0.005	Jardín Botánico José Celestino Mutis	Colombia
KU	1	0.003	0.005	Kwangsi University	People's Republic of China
LA	1	0.003	0.005	University of California, Los Angeles	U.S.A.
LAM	1	0.003	0.005	Natural History Museum of Los Angeles County	U.S.A.
LPM	1	0.003	0.005	Living Prairie Museum	Canada
MSU	1	0.003	0.005	Herbarium of the Michigan State University	U.S.A.
N	1	0.003	0.005	Nanjing University	People's Republic of China
PACA	1	0.003	0.005	Instituto Anchietano de Pesquisas/UNISINOS	Brazil
PAN	1	0.003	0.005	Panjab University	India
PAR	1	0.003	0.005	Museo de Ciencias Naturales y Antropológicas Prof. Antonio Serrano	Argentina
RVH	1	0.003	0.005	Unknown	Unknown
SMU	1	0.003	0.005	Southern Methodist University	U.S.A.
STR	1	0.003	0.005	Institut de Botanique	France
UBC	1	0.003	0.005	University of British Columbia	Canada
UFG	1	0.003	0.005	Universidade Federal de Goiás	Brazil
UFMT	1	0.003	0.005	Universidade Federal de Mato Grosso	Brazil
UPCB	1	0.003	0.005	Universidade Federal do Paraná	Brazil
VI	1	0.003	0.005	Gotlands Fornsal	Sweden
WI	1	0.003	0.005	Vilnius University	Lithuania



	SOURCE	GENUS	SPECIES	AUTHOR	NAME	NAME1
1	Fonseca L.H.M.	Adenocalymma	ackermannii	Bureau & K. Schum.	Adenocalymma ackermannii Bureau & K. Schum.	Adenocalymma ackermannii
2	Fonseca L.H.M.	Adenocalymma	ackermannii	Bureau & K. Schum.	Adenocalymma ackermannii Bureau & K. Schum.	Adenocalymma ackermannii
3	Fonseca L.H.M.	Adenocalymma	ackermannii	Bureau & K. Schum.	Adenocalymma ackermannii Bureau & K. Schum.	Adenocalymma ackermannii
4	Fonseca L.H.M.	Adenocalymma	ackermannii	Bureau & K. Schum.	Adenocalymma ackermannii Bureau & K. Schum.	Adenocalymma ackermannii

	COUNTRY	MAJOR_AREA	MINOR_AREA	LOCALITY	YCOOR	XCOOR	ALT_MIN	ALT_MAX
1	Brazil	Bahia	Encruzilhada	Margem do Rio Pardo	-15.58457	-40.98272	NA	NA
2	Brazil	Minas Gerais	Itaobim	Rodovia BR-116	-16.59945	-41.49867	NA	NA
3	Brazil	Minas Gerais	Medina	região do Reservatório do Córrego Ribeirão (COPASA)	-16.24574	-41.49085	NA	NA
4	Brazil	Minas Gerais	Pedra Azul	Caminho do Aeroporto	-15.95391	-41.18690	NA	NA

	COLLECTOR	NUMBER	COLL_DAY	COLL_MONTH	COLL_YEAR	HERBARIUM	DET_BY
1	Belém R.P.	3627	24	5	1968	F, NY, RB	L.H.M. Fonseca, 2016
2	Hatschbach G.	50428	16	6	1986	MO	L.H.M. Fonseca, 2016
3	Salino A.	4643	26	5	1999	BHCB	L.H.M. Fonseca, 2016
4	Trinta Z.A.	797	20	4	1964	MO, Ny, R	L.H.M. Fonseca, 2016

Fig. S1. The Bignonieae database contains a total of 28,763 records and the data are organized in 16 fields: (i) Genus, (ii) Species, (iii) Author, (iv) Collector, (v) Collector Number, (vi) Collection Day, (vii) Collection Month, (viii) Collection Year, (ix) Herbaria (i.e., herbaria where duplicates are deposited), (x) Det By, (xi) Y Coordinate, (xii) X Coordinate, (xiii) Country, (xiv) Major Area (i.e., State or Department), (xv) Minor Area (i.e., City), and (xvi) Locality (i.e., detailed description of the locality).

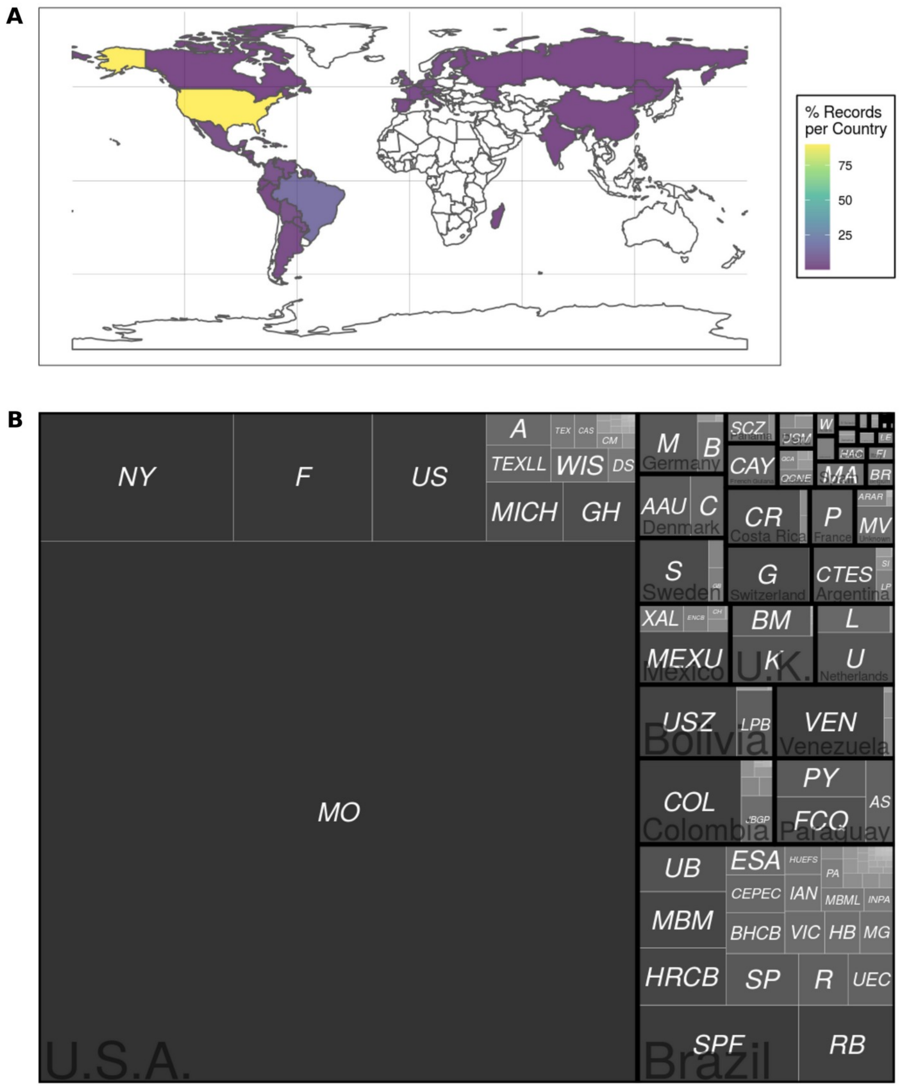


Fig. S2. Countries and herbaria where the Bignonieae specimens and the respective duplicates are deposited. A. Percentage of Bignonieae samples stored in international herbaria per country. B. Proportion of specimens and their duplicates held at different herbaria. The size of the square is proportional to the number of specimens deposited in each herbarium, highlighting the Missouri Botanical Garden Herbarium (MO) as the most relevant source of information for Bignonieae, where 59.86% of the overall samples of Bignonieae included in the database are deposited. Black subdivisions group herbaria from different countries.

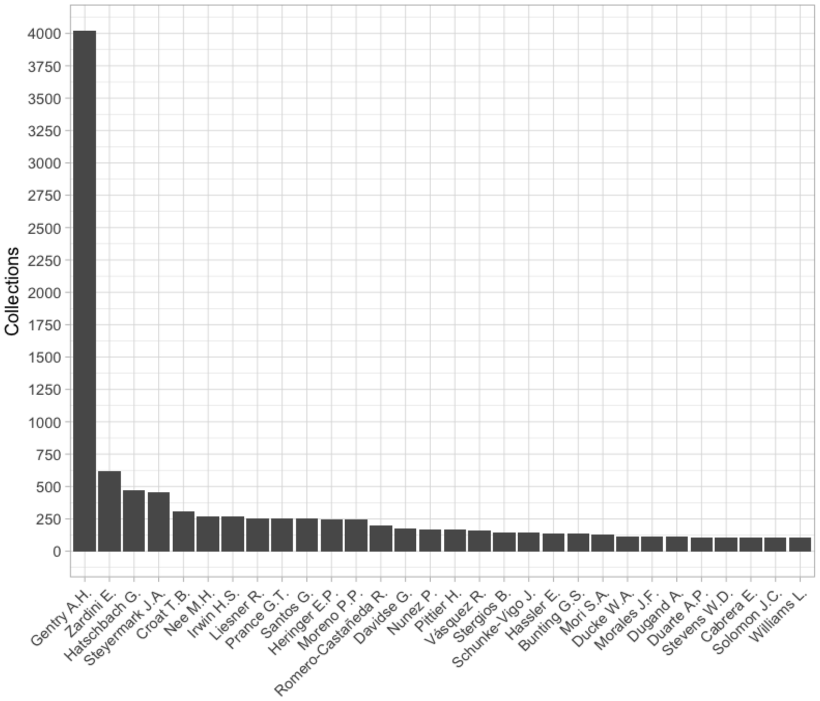


Fig. S3. Graph showing the most prominent collectors of Bignonieae (up to 100 records). The Bignonieae database includes specimens collected by 3,116 collectors of which the ten most prolific collectors account for 35% of the collected records: (1) Alwyn H. Gentry (MO) collected most Bignonieae samples, accounting for 4,021 (14%) of all specimens; (2) Elza Zardini with 617 records (2.1%) of all samples; and, (3) Gert Hatshbach 471 records (1.6%) of all samples.

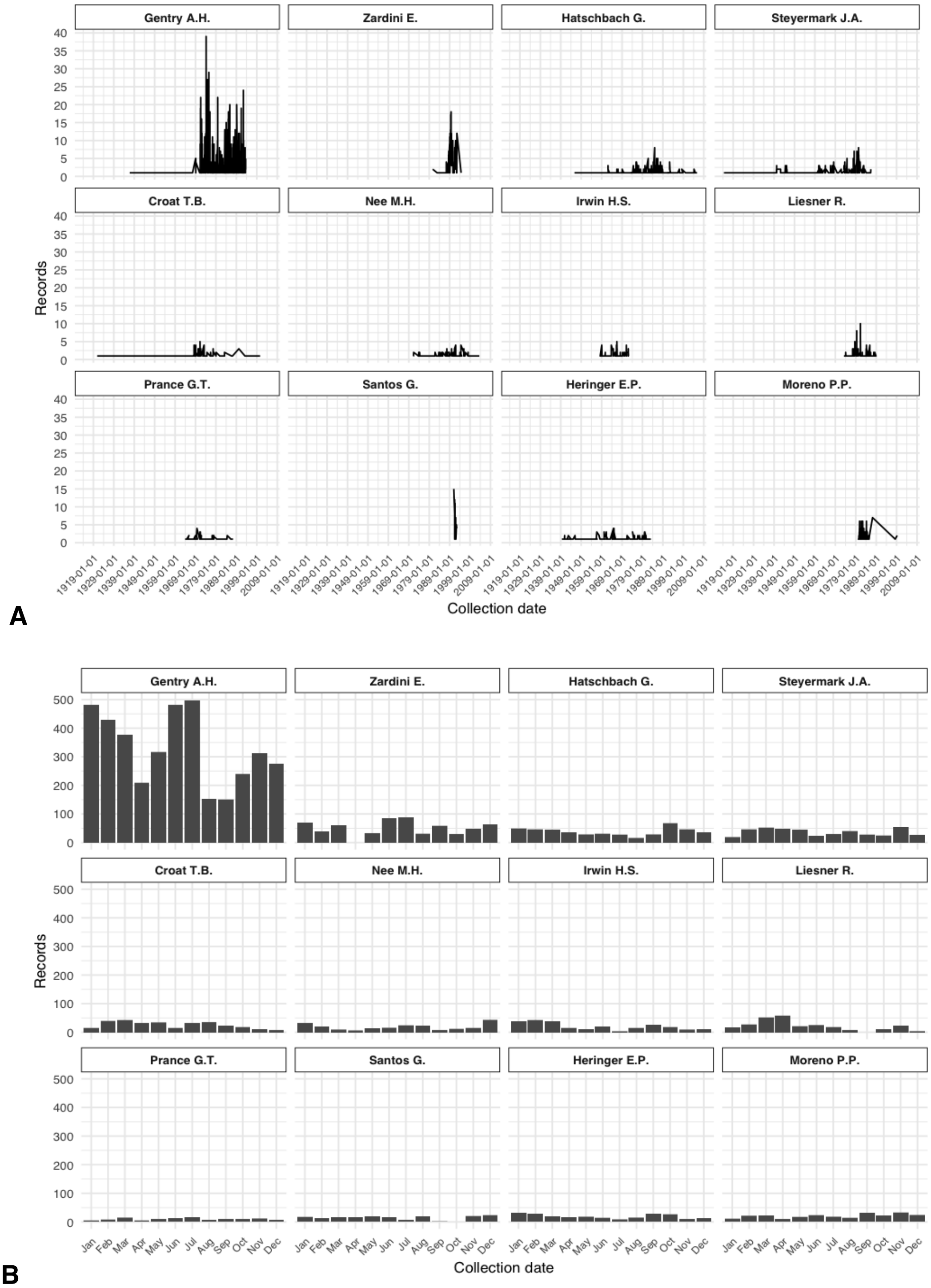


Fig. S4. Temporal coverage of collecting effort for the 12 most productive collectors by year (A) and month (B).

Appendix 2.

Recovering the drivers of sampling bias in Bignonieae (Bignoniaceae) and identifying priority areas for new survey efforts

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Online Resource 2 – Sampling Bias in Bignonieae Database

Supplementary material of the spatial coverage, sampling bias analysis, and completeness.

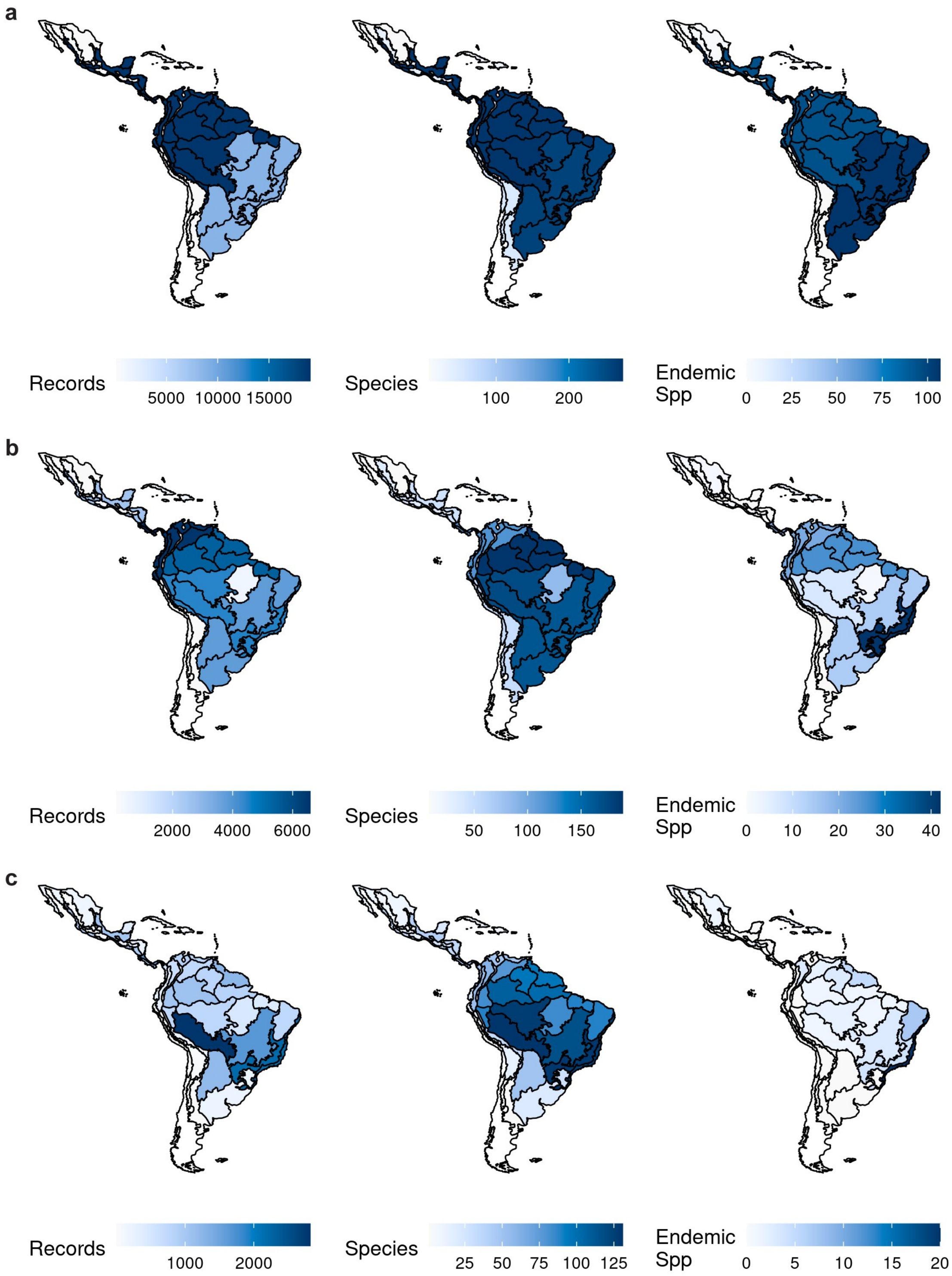

Fig. S1. Number of records within the Bignonieae database per (a) Subregion, (b) Dominion, and (c) Province; biogeographical subdivisions follow Morrone (2014).

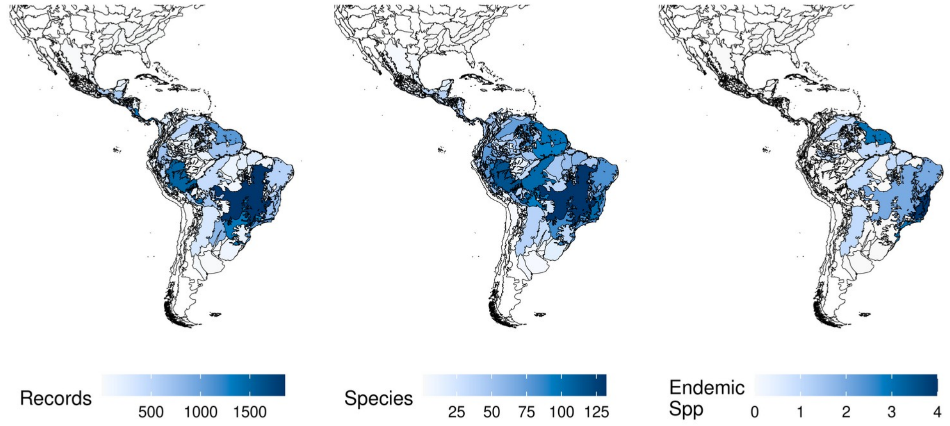

Fig. S2. Number of records within the Bignonieae database per ecoregion sensu Olson et al. (2001). Only ecoregions with more than 50 records are shown.

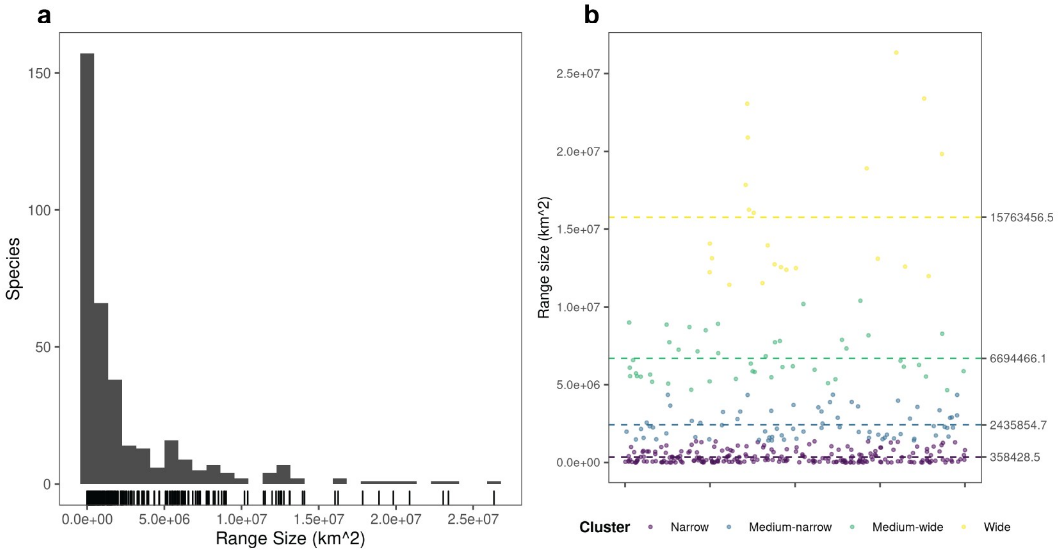

Fig. S3. Kmeans clustering for species range size categories: A) Bignonieae range size distribution, B) Scatter plot of species range size. Each dot represents a species range size. Colors identify range size categories as follows: Purple = narrow, blue = medium-narrow, green = medium-wide, and, yellow = wide. The centroid of each cluster is shown at the right axis and depicted by dashed lines.

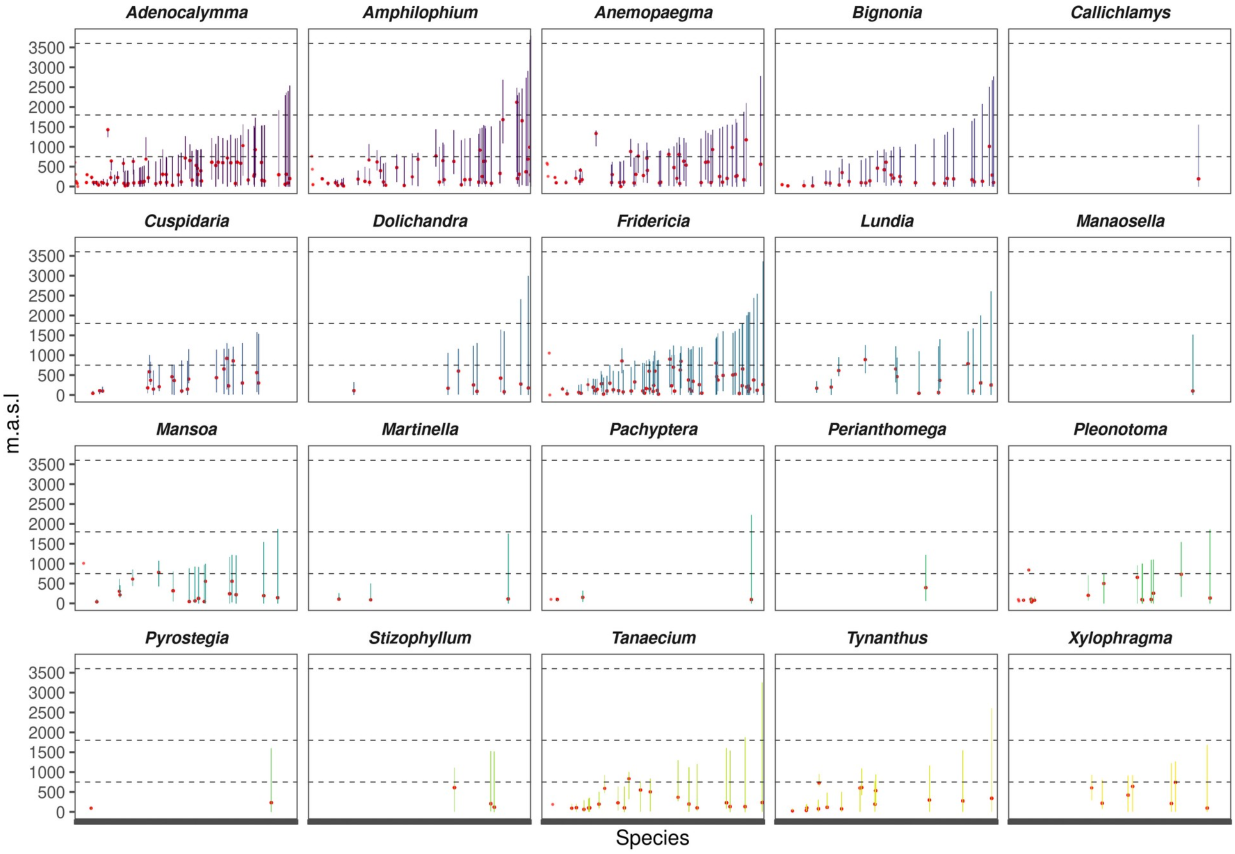

Fig. S4. Altitudinal range profile of specimens included in the Bignonieae database discriminated by genera. Each line represents the linear altitudinal range between the minimum and maximum elevation values for a given species. Red dots indicate where the median value is located along the range. Dashed horizontal lines show the limits of the boundaries of lowlands (750 m.a.s.l.), montane (1800 m.a.s.l.), and paramo (4500 m.a.s.l.) altitudinal zones.

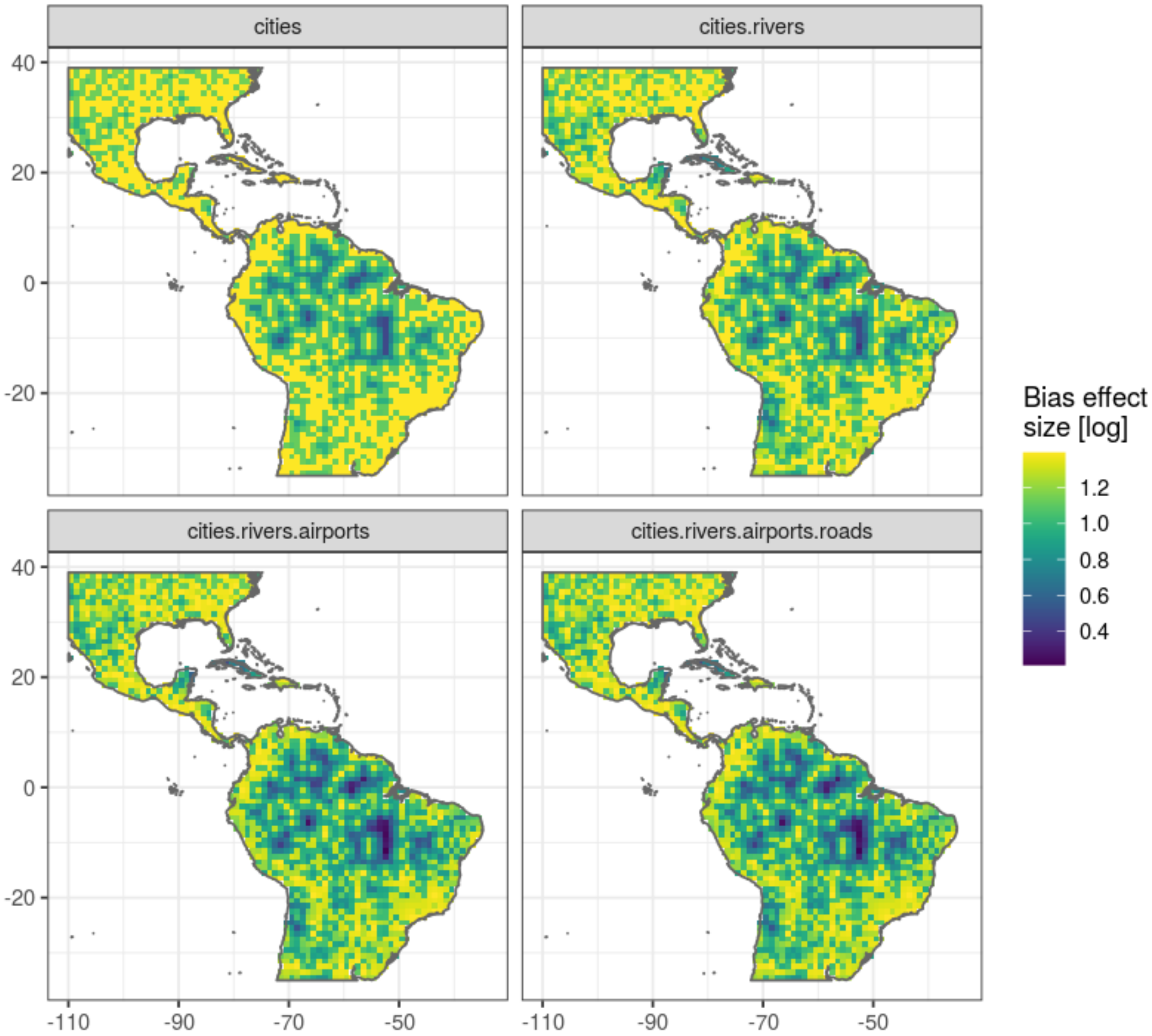

Fig. S5. Map showing the bias effect in logarithmic scale across the geographical extent of the Bignonieae database showing the relative contribution of cities, rivers, airports, and roads. The higher the bias effect, the steeper the change in sampling rate. Note the low bias effect in some regions of the Amazon.

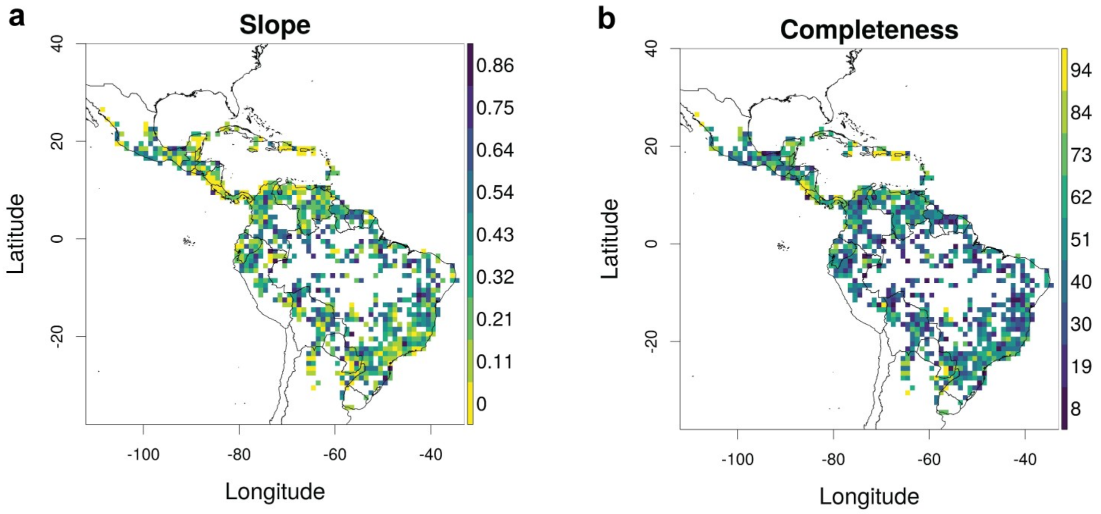

Fig. S6. Survey completeness analysis of the Bignonieae database at the spatial scale of one degree. A. The slope of the species accumulation curves per geographical unit. B. The completeness value representing the percentage of observed versus expected species records under the exact estimator of Ugant et al. (2003).

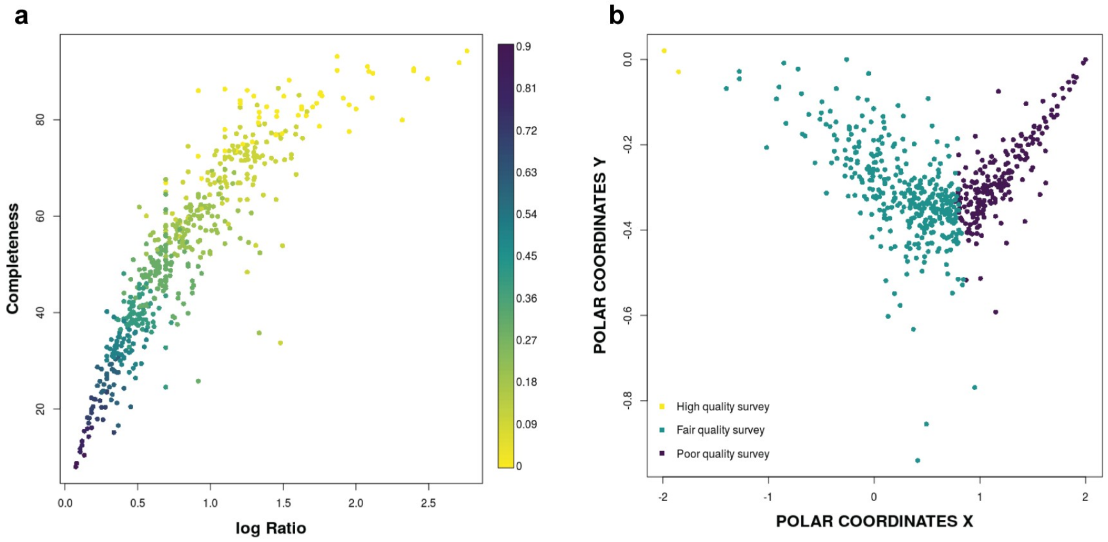

Fig. S7. Survey quality analysis of the Bignonieae database at the spatial scale of one degree. a. Ratio between species records and species richness. Colour scale depicts the slope. Note that with the Bignonieae database a R/S = 1 discriminates between well-sampled (yellow cloud of points at the upper-left corner), moderate, and poorly sample grid cells (point cloud at the middle and lower-left corner). b. Polar coordinates representation of well to poorly sampled cells. Note that only two cells have well-sampled surveys conditional to the quality of the database.

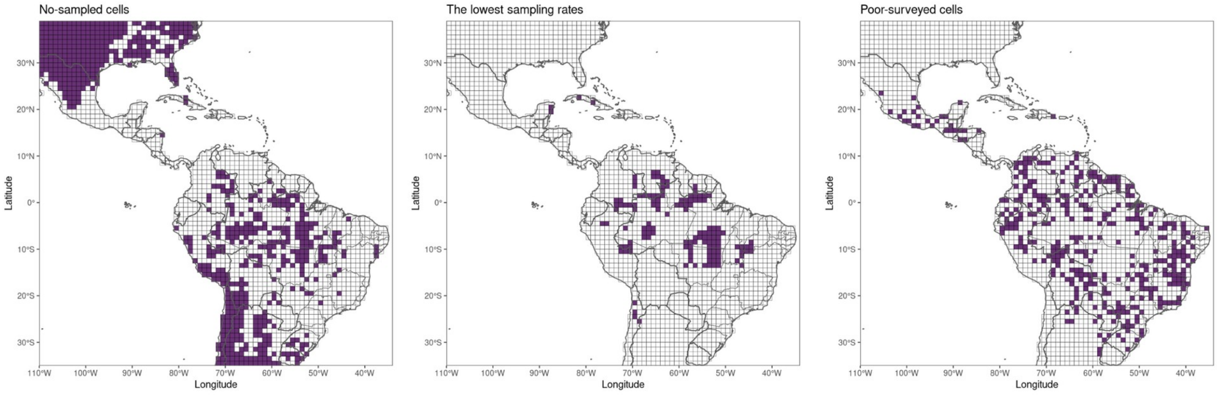

Fig. S8. Maps indicating the layers containing the cells with no records (left), poorly surveyed localities (middle), and localities with the lowest sampling rates used to make the ignorance map (right).

CHAPTER 2.

Unraveling distribution patterns of neotropical lianas: An analysis of endemicity of the tribe Bignonieae (Bignoniaceae)

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Unraveling distribution patterns of Neotropical lianas: An analysis of endemicity of tribe Bignonieae (Bignoniaceae)

Running Title: Areas of endemism of Bignonieae

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Data availability statement

Data outputs from NDM/VNDM are available as Supporting Information. The Bignonieae distribution database will available once other research projects under development are finished at Dr. Lohmann's Lab.

All R scripts area available from <https://github.com/jupanago/RCode_BignonieaeAoE>

Abstract

Aim

We explore the potential of neotropical lianas to discover areas of endemism and assess the effect of spatial scale. We investigate how species can contribute to different areas of endemism causing ambiguity in the definition of these patterns when using an optimality criterion. We infer relevant hypotheses to explain areas of endemism by comparing those hypotheses against the biogeographical units of different Neotropical regionalization schemes.

Location

The Neotropics between 39°N and 35°S.

Taxon

The plant tribe Bignonieae (Bignoniaceae).

Methods

We used a dataset containing 21,152 unique locality records and 98% of the species diversity of Bignonieae. We performed an analysis of endemicity at three spatial scales using the software VDNM-NDM. Analyses were performed to verify the ambiguity of species membership to areas of endemism and the distribution of higher taxa. A measure of spatial congruence between areas of endemism and specific biogeographical units is proposed to assist the inference of hypotheses.

Results

We found that areas of endemism of Bignonieae distributed across the Neotropics are more numerous at coarser spatial scales and clustered over specific geographic sectors. Overlapping and nested patterns of endemism are common, while the number of ambiguous species is low but persistent across spatial scales and analyses. The spatial congruence among areas of endemism and the biogeographical units of the Neotropical region is generally low. Similar patterns of endemism have been documented for other taxa.

Main conclusions

Spatial explicit criteria in quantitative biogeography indicate that the discovery of areas of endemism requires detailed information on species distributions. Overlapping patterns, nested patterns, and ambiguities are common. By thoroughly describing the areas of endemism of Bignonieae, we reveal their potential links to important historical events and climate in the Neotropics.

Keywords: Areas of endemism, Bignonieae, Neotropical Flora, analysis of endemicity, ambiguity, NDM/VNDM

Introduction

Areas of endemism are used to document shared distribution patterns, representing a key component of biogeography (Escalante et al., 2009). These areas allow us to explore the processes and historical events responsible for species confinement to particular regions (Anderson, 1994; Weeks, Claramunt, & Cracraft, 2016),, contributing important information for conservation (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000). Areas of endemism are defined as the pattern of distribution in which 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 can be broadly described as a two-step approach of discovery and explanation. Among the methods to discover areas of endemism, the analysis of endemicity uses a combinatorial approach in which the congruence and fit of multiple species ranges to a possible area of endemism is calculated and optimized (Szumik & Goloboff, 2004). The optimality criterion and the spatial explicit approach reveal that multiple optimal areas with slight variation in species composition are possible, indicating that ambiguity needs to be carefully addressed. Although consensus techniques (Aagesen, Szumik, & Goloboff, 2013) and improved sampling design (Casagranda & Goloboff, 2019) can help to represent and alleviate ambiguity, a few species may contribute to the definition of different areas of endemism. These ambiguous species complicate the search for the causes of overlapping and nested patterns because areas of endemism with shared species are not mutually exclusive and non-independent from the perspective of statistical tests, preventing associations with explanatory variables and clear decisions about group differences. Documenting these species can be helpful not only to better understand how a specific distribution database supports the areas found but also to decide how to better investigate the causes of the patterns in posterior analyses.

A first step to analyze the causes of an area of endemism is to locate the pattern of endemism in the context of the biogeographical knowledge of the study region. This step allows us to identify which hypotheses best explain the distribution patterns given the space encompassed by an area of endemism. This strategy is based on the premise that biogeographical regionalization schemes are comparative frameworks that synthesize the shared distribution patterns across many taxa and assist the inference of the causes of these distributions (Wallace, 1894). The visual inspection of the similarities between the discovered areas and the units of a biogeographical regionalization scheme (e.g. Ferretti, González, & Pérez–Miles, 2014; Gomes-da-Silva, Amorim, & Forzza, 2017; Klassa & Santos, 2015; Noguera-Urbano & Escalante, 2015; Ribeiro et al., 2014) should consider that regionalization schemes imply an agreement with major areas of endemism (Escalante, 2009; Morrone, 1994, 2018). However, using regionalization schemes based on different criteria such as species similarities (Kreft & Jetz, 2010), beta-diversity (Holt et al., 2013), ecological properties (Olson et al., 2001; Udvardy, 1975), and presence-absence patterns in network analyses (Edler, Guedes, Zizka, Rosvall, & Antonelli, 2016; Vilhena & Antonelli, 2015) may entail comparisons among units that are not directly comparable. Although quantitative approaches have been applied to compare categorical maps of different kinds of regionalization schemes (Edler et al., 2016; Nowosad & Stepinski, 2018), no quantitative approach allows for comparisons of individual areas of endemism to specific biogeographical units.

Comparing individual 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 distributional data that comes from animals (Kreft & Jetz, 2010; Rueda, Rodríguez, & Hawkins, 2013), plants (Fiaschi & Pirani, 2009; Gentry, 1982; Takhtajan, 1986), or a variety of taxa (Cabrera & Willink, 1980; Morrone, 2017; Udvardy, 1975). Moreover, the boundaries and biogeographical units of some of these schemes have been associated to possible diversity drivers such as contemporary climate in the case of Wallace's zoogeographical boundaries (Ficetola, Mazel, & Thuiller, 2017), past geological events during the Cretaceous in the case of the Neotropics (Morrone, 2014b), and general similarity to morphoclimatic domains in the case of the phytogeographical regions of South America (Prance, 1989; Ab'Sáber, 2003). Furthermore, taxon-specific patterns of distribution have been studied and associated to their causes. For example, patterns of endemism and diversity of plants have been attributed to species geographical origins. While Laurasian floristic components seem to be concentrated in highlands (e.g., Andes), Gondwanan elements seem to predominate in the lowlands (Gentry, 1982). In turn, differences in plant habit associated with these distribution patterns are also recognized showing that trees and lianas display Amazon-centered distributions, while epiphytes, understory shrubs, and palmettos display Andean-centered distributions (the "Gentry pattern" sensu Antonelli & Sanmartín, 2011). All of these conceptual and empirical advances allow for comparisons of regionalization schemes and areas of endemism of individual taxa, enabling us to unravel the biogeographical history of selected lineages (Fine & Lohmann, 2018).

The tribe Bignonieae (Bignoniaceae) constitutes the most diverse clade of lianas in the Neotropics (Lohmann, 2004, 2006; Lohmann & Taylor, 2014). This clade includes 20 genera and 393 species (Lohmann & Taylor, 2014; Fonseca & Lohmann, 2019) and is distributed throughout the American continental platform (between 39ºN to 35ºS), including the Antilles (Lohmann, 2006). These plants occur in a great variety of habitats, from caatingas and dry savannas to humid rain forests and montane vegetation, being found in almost all Neotropical biogeographical subdivisions (Gentry, 1983; Lohmann, Bell, Calió, & Winkworth, 2013). The tribe is centered in southeastern Brazil and in the Amazon basin (Meyer, Diniz-Filho, & Lohmann, 2018), representing an excellent model to frame questions about distribution drivers in this region (Chapter 1). Patterns of endemism of the plant family Bignoniaceae are thought to be centered in five main regions (Gentry, 1979, 1992): (1) **Central America** and **Western South America**, encompassing southeastern Venezuela and extending through the Andes down 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 southwest to the Chaco in northern Argentina. While the limits between these regions could be sharp between some of these areas (e.g., north and south of the Orinoco river, Amazonian and Andean lowlands), other limits could be diffuse, containing taxa that occur in more than one area (e.g., Brazilian dry areas, Coastal Brazil, and Amazonia). However, no quantitative assessment of areas of endemism has ever been conducted for Bignonieae and it remains unclear whether Bignonieae patterns of endemism are coincident with: (1) Gentry's regions, (2) other biogeographical regionalization schemes, and (3) areas of endemism identified for other taxa.

Here, we conduct an analysis of endemicity (Szumik, Cuezzo, Goloboff, & Chalup, 2002; Szumik & Goloboff, 2004) of tribe Bignonieae (Bignoniaceae) in the Neotropics. We further compare the areas identified to the units of previous regionalization schemes as a means to consider hypotheses about their underlying causes. In particular, we evaluate whether the areas of endemism of Bignonieae are coincident with the phytogeographical regions proposed by Gentry (1982, 1990), and whether the areas identified display the shared patterns of the regionalization scheme based on multiple taxa proposed by Morrone (2014a). To aid this comparison, we propose a quantification of spatial congruence between areas of endemism and specific biogeographical units. We also explore the ambiguity in overlapping and nested patterns in which we explore the number of ambiguous species remaining in consensus areas after modifying the NDM/VNDM search parameters to save areas with higher minimum index of endemicity per species and higher percentage of unique species in overlapping patterns. A list of ambiguous species in overlapping areas is provided.

Materials and methods

Distribution database

We used a georeferenced point locality dataset that contains 28,764 records representing 21,170 unique localities across the entire geographical extent of tribe Bignonieae (Lohmann unpubl. data). The database contains the 20 genera accepted under the most recent taxonomic treatments of the tribe and contains 386 out of the 393 species recognized (Lohmann & Taylor, 2014; Fonseca & Lohmann, 2019). For details about the database, including spatial biases refer to Chapter 1.

Analysis of endemicity

The analysis of endemicity is a spatial analysis that allows the discovery of patterns of endemism at different spatial scales (Szumik et al., 2002; Szumik & Goloboff, 2004). This grid-based method is implemented in the software NDM/VNDM 3.1 (Goloboff, 2004), which generalizes species distribution areas from point occurrence data and range maps into a presence-absence matrix. Spatial congruence between species is assessed by using a candidate area that is generated in an algorithmic fashion. An index of endemicity (IE) is calculated as the spatial match between grid-cells from each species distribution area with the grid-cells of the candidate area. This approach counts the numbers of grid-cells of the species that lie outside or inside the candidate area by applying a series of rules that ponder how homogeneously the species distribution fits the area. The minimum number of species per candidate is set at two and the optimization procedure retains the candidate areas with greater overall index of endemicity. Therefore, higher numbers of scoring species in the candidate area, and higher spatial fit of their distributions, lead to higher endemicity scores and stronger support for the candidate area as an area of endemism.

Multiple equally optimal candidate areas with few differences in species composition can be obtained reflecting the ambiguity inherent to the distributional data. These areas can be summarized using consensus techniques in which similarity thresholds of species composition are used to aggregate areas into a consensus (Aagesen et al., 2013). Two rules may be applied while controlling for the rigor of comparisons among areas. The loose consensus rule merges the candidate areas that share a percentage of their scoring species with any of the other candidate areas. In turn, the tight consensus rule merges the candidate areas that share a percentage of their scoring species with every and all of the other candidate areas 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. Higher values of similarity in both rules increase the number of consensus areas that approach the number of individual candidate areas in the analysis. This is due to the fact that the ambiguity of species membership to candidate areas is less tolerated in the consensus. Therefore, intermediate thresholds of similarity allow for a better compromise between the aggregation of candidate areas, the number of consensus presented, and the ambiguity of the distributional data.

Parameters set for the endemicity analysis

Two types of search parameters can be modified in an analysis of endemicity. The first includes the factors that weight the contribution of observed records and the inferred presences to the overall index of endemicity. These parameters were implemented using default settings in NDM/VNDM. The species index of endemicity (IE) ranges from 0 to 1, with increasing values indicating that species ranges increasingly match a candidate area. Sometimes overlapping patterns of endemism might share species because their fit is not perfect for any of them. Under this situation, the index of endemicity of a species can be lower and the evidence the species provides for the areas of endemism becomes ambiguous. The second type of parameter is used to circumscribe the heuristic exploration of cell configurations and filter the areas to be saved. Two parameters can help to assess how ambiguous species might impact the total number of endemic species within a particular pattern, the size of the area, and its shape. The minimum index of endemicity per species can be tuned to save areas composed by species with lower or higher spatial fit. Increasing its value allow us to save areas with higher spatial congruence from which ambiguous species with lower fit are excluded. Similarly, it is possible to define a minimum percentage threshold of unique species per pattern in cases of overlap. The higher the percentage, the greater the number of unique species that a pattern must have to be saved during the search, even at lower IE values. Looking at the number of ambiguous species and the areas conserved after modifying these parameters allows for a better characterization of how the discovered patterns are supported by the data. Ambiguous species can be appropriately managed in posterior analyses of the underlying causes of the patterns of endemism. In order to account for these aspects, we conducted two different analyses modifying the minimum index of endemicity per species and the minimum percentage of unique species in overlapping patterns. The Default analysis (D) conserved the default parameters of NDM/VNDM, while the Strict analysis (S) assumed a minimum index of endemicity of 0.66 and minimum percentage of unique species in overlapping patterns of 40% (Table 1). In the case of no ambiguity in species endemism patterns, the areas of endemism obtained through the Strict analysis are similar to those obtained through the Default analysis.

Presence-absence matrix

We created presence-absence data matrices at three spatial scales using grid sizes of 1° × 1°, 2° × 2°, and 3° × 3° in the software NDM/VNDM 3.1. Because the fill radius is defined as a percentage of the cell width, different radii were selected as grid size changed. The radius was proportionally diminished by half of the value of the fill percentage that was assumed for the immediate broader scale (Table 1) (as in Casagranda, Roig-Juñent, & Szumik, 2009). Thus, the larger the grid size, the smaller the radius. Species with disjunct distributions were excluded from the automatic filling procedure and filled manually following the logic of a minimum convex polygon (see Appendix S1 in Supporting Information). Manual cleaning of grid-cells around the borders of the South American continent was avoided to guarantee reproducibility of areas obtained at continental margins.

Table 1. NDM/VNDM search strategies. Values for the search parameters of NDM/VNDM 3.1 that were used for exploring the patterns of endemism of Bignonieae. All searches were repeated 100 times with random seed value of 10. *Analysis*: label identifying each analysis in the text. *Scale*: grid cell size in degrees. *Min_IE*: minimum endemicity score per species in individual areas. *Min_Spp*: minimum number of species per set to define a pattern of endemism. *%overlap*: percentage of unique species to keep overlapping sets. *R_fill*: filling radius for observed records. *R_assum*: filling radius for assumed records.; *Consensus rule*: consensus technique used to summarize the results.

Analysis	Scale	Min_IE	Min_Spp	%overlap	R_fill	R_assum	Consensus rule
D	1	Default	2	Default	40	80	Loose 40%
	2	Default	2	Default	20	40	Loose 40%
	3	Default	2	Default	10	20	Loose 40%
S	1	0.66	2	40	40	80	Loose 40%
	2	0.66	2	40	20	40	Loose 40%
	3	0.66	2	40	10	20	Loose 40%

To consider the distribution area of higher taxa in the analyses (Szumik & Goloboff, 2015), individual species were aggregated per genera following the current generic classification of Bignonieae (Lohmann & Taylor, 2014). Likewise, we used the clades from a super-tree assembled with some of the phylogenetic hypotheses available for the tribe (Lohmann, 2006; Zuntini, 2014; Fonseca & Lohmann, 2015; Medeiros & Lohmann, 2015) (see Appendix S1) in TNT 1.5 (Goloboff & Catalano, 2016). VNDNM-NDM automatically generates distributions of clades as the union of the distribution of the constituent species. It then counts the endemicity score from the clade when this is higher than the score for the constituent species and vice-versa (see Szumik & Goloboff 2015 for details).

Consensus areas

The loose consensus rule with cutoff of similarity equal to 40% was applied to all analyses. To assess the particular effect of the Default and Strict analyses, we compared consensus areas belonging to the same spatial scale and with similar geographical locations between the two analyses. We called these areas as Equivalent Consensus Areas across analyses and assessed their species composition and size. To assess the effect of spatial scale on patterns of endemism, we compared the species composition among consensus areas of the Default Analysis that had similar geographical locations in the Neotropics within each spatial scale. Species shared among consensus areas were dubbed Ambiguous Species. We attempted to determine to which areas the species could belong to using auxiliary information from endemic species elevation data. The expectation was to detect whether ambiguous species could belong to patterns whose scoring species occurred predominantly at a specific altitudinal belt.

Spatial congruence between patterns of endemism and regionalization schemes

We compared consensus areas against Gentry's phytogeographical proposal (1979, 1982) and the hierarchical classification of the Neotropical region proposed by Morrone (2014a). Ideally, areas should be compared on the basis of species fit. However, in the absence of data about the species supporting the regionalization schemes, a purely spatial criterion is acceptable. Similar approaches are used to compare vegetation categorical maps and to assess the similarity and associations between complete regionalizations (Edler et al., 2016; Hargrove, Hoffman, & Hessburg, 2006; Nowosad & Stepinski, 2018) but not for individual patterns of endemism against the units of a regionalization.

Inspired on these approaches, we proposed to calculate the spatial coincidence between the polygons of both the consensus areas and the specific biogeographical units of the regionalization schemes. Given that these polygons can have different shapes and sizes, the spatial correspondence between the polygons was characterized by two complementary measures: (i) Uniformity of the Consensus area (Uc), corresponding to the proportion of the consensus area that is covered by a biogeographical unit, and (ii) Uniformity of the Biogeographical Unit (Ub), corresponding to the proportion of the biogeographical unit that is covered by the consensus area. The average between these two variables informs us about the spatial congruence (Sc) between the consensus area and the biogeographical region.

Every time the spatial match between a consensus area and a biogeographical unit is perfect, the values of Uc, Ub, and Sc are equal to 100%. However, in cases where both of these areas are nested (e.g., the consensus area is inside the biogeographical area or vice-versa), one of the uniformity values is equal to 100%, while the other is closer to 0%; the corresponding spatial congruence is closer to 50% depending on their size and shape. To calculate Uc, Ub, and Sc, we used the shapefile of the Neotropical region by Löwenberg-Neto (2014) and georeferenced the map of the phytogeographical regions depicted in Gentry (1982) using the Georeferencer GDAL plugging 3.1.9. of QGIS 2.1.8. All comparisons and figures were prepared using language R (R Core Team, 2019). All scripts are available upon request.

Consensus areas discussed follow the Default analysis as a reference, unless indicated otherwise. The following naming conventions are used for the consensus areas: (i) names of consensus areas begin with "D" when presenting results derived from the Default analysis, and begin with "S" when presenting results derived from the Strict analysis; (ii) numbers between 1, 2, or 3 indicate the spatial scale to which the area belongs, (iii) numbers are followed by the initials "CA" (i.e., Consensus Areas) and the number of the corresponding internal NDM code of that consensus area (numbers that are reproducible by using the same random seed and search were used). For example, the area D2CA1 refers to 'Default analysis at 2 degrees, Consensus Area 1.'

Results

Effect of default and strict analyses over patterns of endemism

Six analyses of endemicity were conducted considering two sets of different parameter values and three spatial scales (Table 2, Fig. 1). Increasing the values of the parameters *minimum score of endemicity (IE) per species* and *minimum percentage of unique species per overlap* decreased the number of individual areas, scoring species, and consensus areas from the Default (D) to the Strict (S) analyses (Table 2). The reduction of the number of consensus areas was smaller with an increase of one area in S at the scale of three degrees (Table 2). Only a subset of the species provided support to the patterns found in both analyses. The list of scoring species of S was a subset of the total scoring species in D. The number of endemic species in consensus areas followed the same tendency in both D and S, with most of the areas consisting of 3 to 10 species, and only six areas consisting of 20 to 102 species throughout scales. The range of the IE of consensus areas showed similar mean values between analyses, although the variation around the mean was lower for S (Fig. 1). These differences in the range of IE were caused by the lower number of species in some of the consensus areas in S, while the narrower variation in IE were related to excluding species with a spatial fit lower than 0.66. The main effect of modifying these parameters was the loss of numerous scoring species that were endemic to a particular consensus area despite their lower spatial fit.

The number of shared species remaining from D to S showed that the ambiguity in species membership to patterns of endemism in Bignonieae is low but persistent (Table 3, Fig. 2). Overall the number of shared species between overlapping consensus areas increased with spatial scale but was reduced from D to S (Table 2). Still, new cases of ambiguous species that appeared in S were not previously observed in D (Fig. 2). The reduction in the percentage of ambiguous species was lower than the percentage of scoring species lost from the analyses (Table 3). For example, although the ambiguity in D was completely reduced in S exclusively, at the scale of one degree, the percentage of species lost from D to S was 41%, and similar values were observed at the other spatial scales (Table 3). Therefore, the strategy proposed to explore the ambiguity in species membership by using stricter values of the *minimum score of endemicity (IE) per species* and *minimum percentage of unique species per overlap* revealed low levels of ambiguity in Bignonieae. However, given that this strategy reduced the total number of endemic species per pattern, we do not recommend it to reduce ambiguity.

The effect of these parameters in the percentage of retained species and grid number among equivalent consensus areas varied (Fig. 3). We identified four kinds of effects: (i) consensus areas that were identical in D and S; (ii) consensus areas from D that were completely lost at S; (iii) consensus areas in S that were composed exclusively of a subset of the species from an area in D; and (iv) consensus areas in S that were composed of a subset of species from an area in D plus other species added only in S (Table 4). The latter kind of mixed subset resulted from NDM/VNDM identifying patterns from the species that remained after the species with lower fit and ambiguous taxa were excluded. In this way, the changes from D to S reflected the degree of spatial fit among endemic species and patterns of endemism. For example, while some areas with relatively high IE values only lost few species and grid cells (D2CA1-S2CA2, Fig. 3), other large areas in D composed by numerous species and showing a wide range of values of IE were decomposed into smaller subsets of fitter species in S (i.e., D2CA0 was decomposed into S2CA0, S2CA1, S2CA4, and S2CA5 among others, Fig. 3). These consensus areas in D represent patterns of endemism distributed in a gradient-like manner, and their fragmentation into smaller areas in S showed the relatively more congruent sets of endemic species it contained.

Because of all these changes and the high number of non-ambiguous species lost from D to S, we focus our discussion on the areas found in D. We use these areas to present the effects of spatial scale on species composition of the consensus areas and to characterize the patterns of endemism of tribe Bignonieae.

Table 2. Summary of the results. *Analysis*: Labels indicating the set of parameters used in each search as defined in the text; D and S stand for Default and Strict analyses, respectively. *Spatial Scale*: Grid size in degrees. *Individual Areas*: Number of individual sets recovered in each search. *Scoring Species*: Total number of scoring species contributing to the index of endemicity of individual areas. *Groups:* Number of higher taxa groups contributing to the index of endemicity of individual areas. *Consensus areas*: Number of consensus areas per analysis obtained under the loose rule at 40% cutoff of similarity. *Consensus Areas with ambiguous species*: Number of consensus areas that share species. *Ambiguous species*: Number of species for which evidence of membership to a pattern of endemism is ambiguous because they support different patterns.

Analysis	Spatial Scale	Individual Areas	Scoring Species	Groups	Consensus Areas	Consensus Areas with ambiguous species	Ambiguous species
D	1	15	39	0	10	5	3
D	2	160	166	0	28	17	29
D	3	325	281	5	34	28	61
S	1	8	23	0	7	0	0
S	2	65	103	0	22	8	11
S	3	203	187	5	35	23	41

Table 3. Percentage of ambiguous species among consensus areas. *Spatial scale*: Grid sizes of one, two, and three degrees. *Percentage of ambiguous species*: Proportion of shared species in the Default (D) analysis as a measure of the ambiguity. *Percentage of solved ambiguity*: Proportion of species that stopped being ambiguous after the Strict (S) analysis. *Percentage of unsolved ambiguity:* Proportion of ambiguous species that were still ambiguous after the S analysis. *Percentage of lost species*: Proportion of species lost from D to S as a consequence of modifying the minimum IE and the minimum percentage of unique species in overlap. *Percentage of ambiguous species in S*: Total ambiguity that includes new species not identified as ambiguous in analysis D. Note that the percentage of lost species is high when compared to the percentage of solved ambiguity. The cost of modifying these parameters together is high because the percentage of lost species is higher than the percentage of solved ambiguity.

Spatial Scale	% of Ambiguous Species in D – Ambiguity D	% of Solved Ambiguity	% of Unsolved Ambiguity	% of Lost Species	% of Ambiguous Species in S – Ambiguity S
1	7.692	7.692	0	41.03	0
2	17.47	12.048	5.422	37.95	10.68
3	21.708	9.964	11.744	27.76	20.2

Table 4. Effect over pairs of equivalent consensus areas at each spatial scale. *Identical*: The consensus area has the same species composition in D and S. *Lost*: The consensus area from D was not recovered in S. *Subset from D*: The consensus area in S consists of a subset of species from D. *Mixed subset*: The consensus area in S consists of a subset of species from D and few additional species scoring only at S. The same area from D can be equivalent to several areas in S. Only one consensus area is unique to S.

Spatial scale	Identical	Lost	Subset from D	Mixed subset
1	2	3	5	0
2	6	8	16	10
3	3	8	31	21

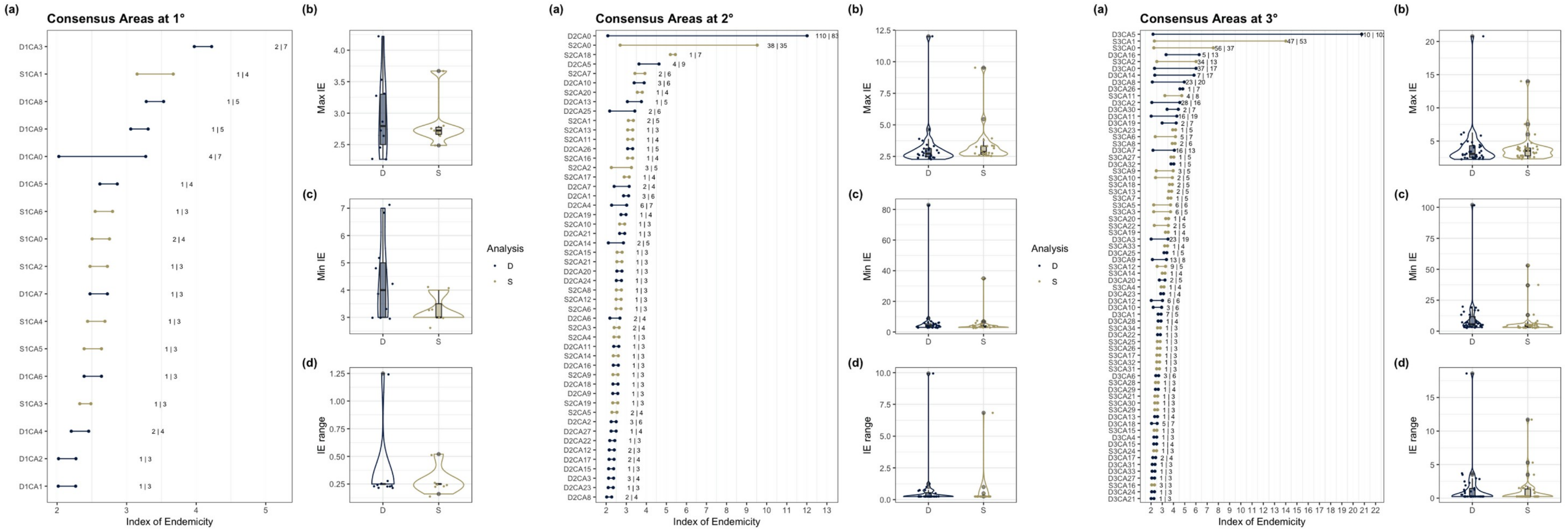


Figure 1. Index of endemicity (IE) for consensus areas of Default (D) and Strict (S) Analyses at grid sizes of one, two, and three degrees. (a) Range of endemicity scores for all consensus areas. (b) Distribution of the maximum endemicity score per consensus area.; (c) Distribution of the minimum endemicity score per consensus area; and (d) Distribution of the range of endemicity scores per consensus area. The numbers in black indicate the number of individual areas in the consensus separated by a slash of the number of species in the consensus. Note the similarity among IE values of consensus areas across both analyses across all spatial scales. The main difference between D and S was the generally lower range of variation of IE among consensus areas in S.

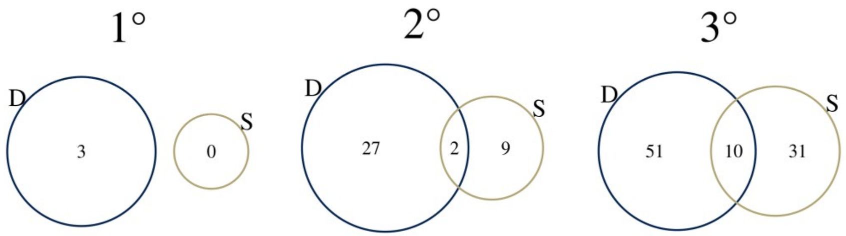


Figure 2. Number of shared species among consensus areas in the Default (D) and Strict (S) analyses across scales. The Venn Diagrams show the total number of ambiguous species shared between the D and S analyses. The intersection shows the number of ambiguous species identified in D that remained at S. The number in S correspond to ambiguous species not found in D. The number of species from D that stop being ambiguous at S was 3 at one degree, 20 at two degrees, and 28 at three degrees. At three degrees, 23 of the ambiguous species in D were lost at S because lower spatial fit. Ambiguity could not be eliminated using higher values of minimum IE and percentage of unique species per overlap (Table 3).

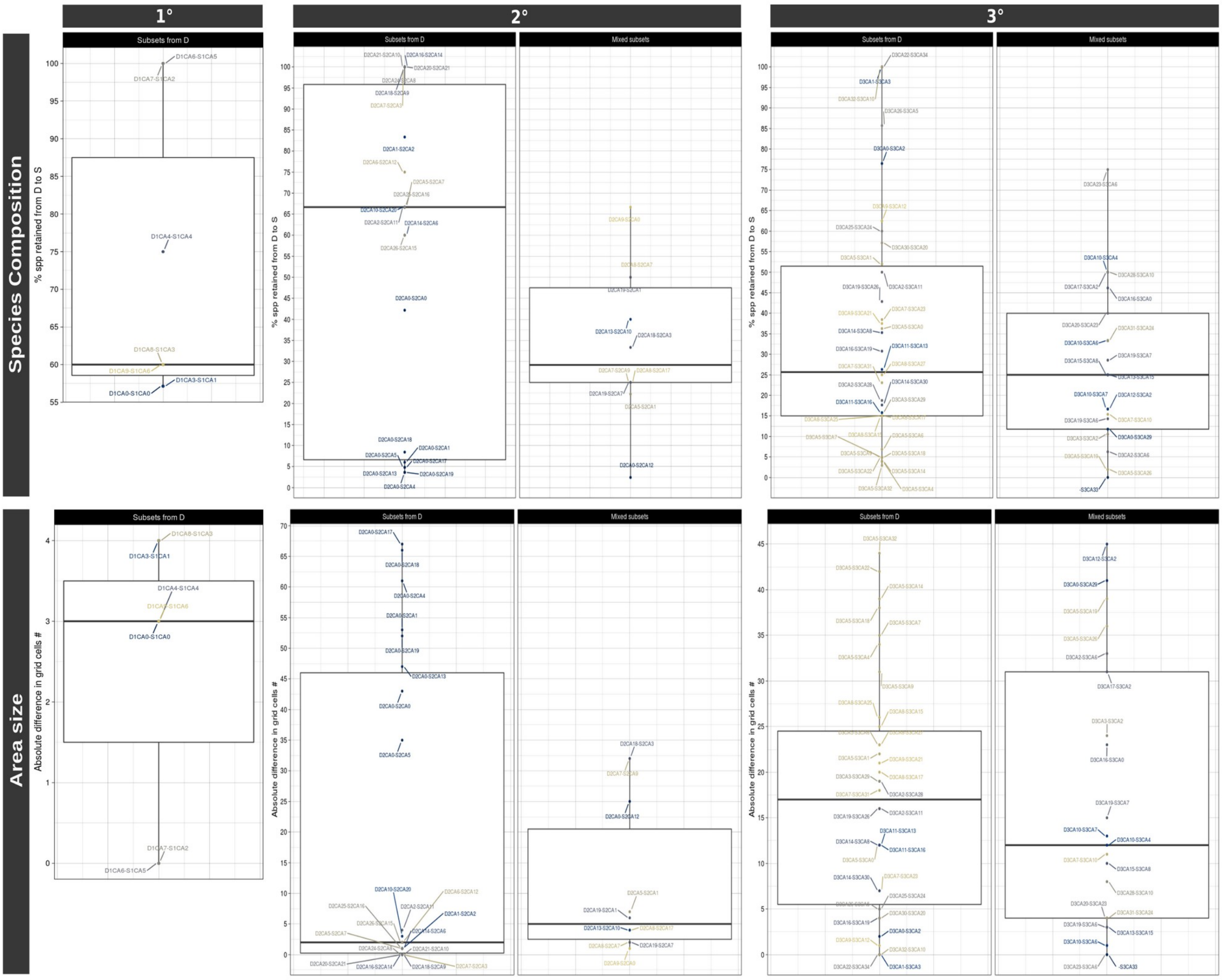


Figure 3. Comparison of equivalent consensus areas between the Default (D) and Strict (S) analyses at the spatial scales of one, two, and three degrees. Species composition between equivalent consensus areas is presented as the percentage of species retained from D to S. Consensus area sizes differences are presented as the absolute difference in grid cells. The higher the percentage of retained species the more similar the areas in D and S. The higher the absolute difference in grid cell the more drastic the change in consensus area size from D to S. Equivalent consensus areas are depicted as a name duet separated by a dash ("D2CA0-S2CA0"), and the same color indicates that the same area from D is compared to several areas from S. While some areas in S were subsets from areas in D (Subsets from D), other areas in S were subsets from areas in D but included additional new endemic species (Mixed subsets). The number of cases of these Mixed Subsets increased with spatial scale, while none was obtained at the scale of one degree. In total, 19 areas from D showed no equivalent areas in S: 3 at one degree, 8 at two degrees, and 8 at three degrees.

Areas of endemism of tribe Bignonieae (Bignoniaceae)

For the Default analysis we obtained 72 consensus areas (Table 5; Fig. 4; see Appendix S2 in Supporting information). From the 386 species of Bignonieae examined here, 289 (74.87%) species scored to individual areas, 90 (23.32%) species were ambiguous, and 97 (25.13%) species did not score to any pattern (Table 2, Appendix S2). The representation of species from different genera increased with spatial scale, with 10 genera being represented at one degree, 16 genera at two degrees, and 18 at three degrees (Fig. 5). The monotypic genera *Callichlamys* and

Manaosella did not score for any of the consensus areas, and all consensus areas contained at least two species from different genera. The distribution areas of supra-specific taxa (*Amphilophium, Cuspidaria,* and *Pachyptera)* and clades (phylogroups GRP-15 and GRP-1) contributed to the IE score of patterns of endemism only at the scale of three degrees (see Appendix S1). These results suggest that most of the patterns of endemism in Bignonieae are broad scale patterns formed by species with relatively wide distributions and spread in a gradient-like configuration across wide geographical regions.

A comparison of all consensus areas across spatial scales showed how patterns obtained with smaller grid sizes were nested into patterns at bigger grid sizes (see Appendix S3 in Supporting information). In total, we identified 25 cases of complete nested patterns in which endemic species from an area at a finer spatial scale were completely included in areas at larger spatial scales. Likewise, we identified 31 cases of incomplete nested patterns in which areas at larger scales only include a subset of the endemic species that formed the pattern at the finer scale. Only one area was the same at every spatial scale (i.e., D2CA4-D3CA26; Fig. 4B). Two cases of reverse nested patterns were identified, with areas at the scale of three degrees being included in areas at the scale of two degrees composed by a higher number of endemic species (i.e., D2A0-D3CA4 and D2CA11-D3CA2; Fig. 4C). These results showed the scale dependency of patterns of endemism and how their endemic species are progressively integrated into broader patterns.

Overall, the areas of endemism of Bignonieae were clustered on specific geographical sectors across the Neotropics that broadly corresponded to Central America, Northwestern South America, Amazon basin, Guiana shield, and Eastern South America (Fig. 4). Several areas of endemism were larger and extended across these sectors, creating numerous overlapping patterns (Fig. 6). Many nested and overlapping areas with ambiguous species were also identified within these geographical sectors (Table 6). Among the nested patterns with ambiguous species, some of the smaller areas were formed by species predominantly occupying a specific altitudinal belt, with the broader nested pattern being formed by species from many different elevations (see Appendix S3). The species shared by these patterns were located precisely at the specific altitudinal belt of the smaller area. For example, there were two of these cases in Eastern South America, the first over the Chapada Diamantina and adjacent regions in Northeastern Brazil (i.e., between D2CA0 and the areas D2CA5, D2CA19, and D2CA8; Fig. 4C, Fig. S2), and the second over the Serra do Mar and Serra da Mantiqueira mountain ranges and across the Atlantic Forest central corridor (i.e., between D2CA0 and D2CA1; Fig. 4C, Fig. S2). Likewise, one case was identified in Central America (i.e., between D3CA25 and the areas D3CA31 and D3CA33; Fig. 4A, Fig. S2), and another in the Amazon basin (i.e., between D3CA15 and the areas D3CA3 and D3CA14; Fig. 4B, Fig. S2). The remaining cases of ambiguity did not show any particular tendency regarding the elevation of endemic species.

Table 5. Areas of endemism of tribe Bignonieae (Bignoniaceae) in the Neotropics. Geographic sectors: The geographic sectors over which areas are clustered and overlap. Consensus areas: Consensus of the individual areas found at the Default analysis from one to three degrees. If the name is followed by an asterisk (*), then the area is also formed by the areas of higher taxa. Size: Number of cells per area. Individual Areas: Number of individual areas summarized in the consensus area. Species: Number of scoring species in the consensus area. The number in parenthesis indicates the number of supra-specific taxa in the consensus area. Minimum and Maximum Scores: they Endemicity score range that individual areas showed in the consensus area. Other Taxa: Individual taxa for which similar patterns of endemism have been documented previously, including areas defined by different methods.

Geographic sectors	Consensus Area	Size	Individual Areas	Species	Minimum Score	Maximum Score	Other Taxa
Central America Centered	D2CA12	18	2	3	2.15245	2.40245	Gymnosperms (Contreras-Medina et al., 2007); Mammals (Noguera-Urbano & Escalante, 2015); Mammals (Escalante et al., 2009); Hemiptera (Ferrari et al., 2010)
	D3CA25	16	1	5	3.15538	3.40538	
	D3CA31	15	1	3	2.10795	2.35795	Gymnosperms (Contreras-Medina et al. 2007); Mammals (Noguera-Urbano & Escalante, 2015); Hymenoptera (Camargo & Pedro, 2003)
	D3CA33	24	1	3	2.09763	2.34763	Hemiptera (Ferrari et al., 2010)
Northern South America centered	D2CA14	17	2	5	2.10821	2.85821	Mammals (Noguera-Urbano & Escalante, 2015); Oryzomyne rodents (do Prado et al., 2015)
	D2CA17	11	2	4	2.14286	2.39286	Mammals (Noguera-Urbano & Escalante, 2015; Oryzomyne rodents (do Prado et al., 2015)
	D2CA22	8	1	3	2.17647	2.42647	Mammals (Noguera-Urbano & Escalante, 2015); Oryzomyne rodents (do Prado et al., 2015)
	D2CA26	7	1	5	3.06823	3.31823	
	D3CA8	30	23	20	2.11548	4.96222	Tabanomorpha (Klassa & Santos, 2015)
	D3CA13	8	1	4	2.32813	2.57813	Mammals (Noguera-Urbano & Escalante, 2015)
	D3CA29	9	1	4	2.39855	2.64855	Mammals (Noguera-Urbano & Escalante, 2015)
Guiana Shield Centered	D1CA1	20	1	3	2.01663	2.26663	Mammals (Noguera-Urbano & Escalante, 2015); Birds (Oliveira et al., 2017); Birds (Cracraft, 1985); Hymenoptera (Camargo & Pedro, 2003)
	D1CA4	17	2	4	2.20357	2.45357	Plants (Prance, 1973, 1982)
	D2CA3	13	3	4	2.11923	2.36923	Mammals (Noguera-Urbano & Escalante, 2015); Oryzomyne rodents (do Prado et al., 2015); Plants (Prance, 1973, 1982); Birds (Cracraft, 1985); Hymenoptera (Camargo & Pedro, 2003)
	D2CA10	8	3	6	3.39208	3.89208	Mammals (Noguera-Urbano & Escalante, 2015); Birds (Cracraft, 1985)

	D2CA25	9	2	6	2.17406	3.42406	Mammals (Noguera-Urbano & Escalante, 2015); Birds (Oliveira et al., 2017) Birds (Cracraft, 1985); Hymenoptera (Camargo & Pedro, 2003)
	D3CA6	15	3	6	2.42947	2.67947	Oryzomyne rodents (do Prado et al., 2015)
	D3CA11	19	16	19	2.01481	4.29814	Hymenoptera (Camargo & Pedro, 2003)
	D3CA30	8	2	7	3.42857	4.42857	Plants (Prance, 1973, 1982); Birds (Cracraft, 1985); Fishes (Hubert & Renno, 2006)
Amazon Basin Centered	D1CA7	7	1	3	2.47321	2.72321	Birds (Oliveira et al., 2017)
	D2CA4	28	6	7	2.27019	3.02019	
	D2CA7	167	2	4	2.39523	3.14523	
	D2CA16	44	1	3	2.35441	2.60441	Fishes (Hubert & Renno, 2006); Hemiptera (Ferrari et al., 2010); Plants (Alvez-Valles et al., 2018)
	D2CA18	135	1	3	2.33658	2.58658	
	D2CA20	57	1	3	2.53234	2.78234	Fishes (Hubert & Renno, 2006); Hemiptera (Ferrari et al., 2010); Plants (Alvez-Valles et al., 2018)
	D2CA23	5	1	3	2.1	2.35	Birds (Oliveira et al., 2017)
	D3CA0	88	37	17	2.3109	6.01263	Tabanomorpha (Klassa & Santos, 2015)
	D3CA3	66	23	19	2.0124	3.5124	
	D3CA7	38	16	13	2.17574	4.07727	Tabanomorpha (Klassa & Santos, 2015); Fishes (Hubert & Renno, 2006)
	D3CA9*	108	13	7(1)	2.12217	3.37217	
	D3CA12	45	6	6	2.02172	3.02172	Plants (Alvez-Valles et al., 2018)
	D3CA14	19	7	17	2.33636	5.83034	
	D3CA15	17	1	4	2.24906	2.49906	
	D3CA17	59	2	4	2.15983	2.40983	Plants (Alvez-Valles et al., 2018)
	D3CA20	27	2	5	2.74221	3.24221	Oryzomyne rodents (do Prado et al., 2015)
	D3CA21	29	1	3	2.01193	2.26193	
	D3CA24	8	1	3	2.06250	2.31250	
	D3CA26	12	1	7	4.57343	4.82343	
	D3CA28	19	1	4	2.63827	2.88827	

	D3CA32	27	1	5	3.78037	4.03037	Fishes (Hubert & Renno, 2006); Hemiptera (Ferrari et al., 2010)
Eastern South America centered	D1CA0	28	4	7	2.02476	3.27476	
	D1CA2	23	1	3	2.02069	2.27069	Plants (Prance, 1973, 1982); Harvestmen (Pinto-da-Rocha et al., 2005)
	D1CA3	22	2	7	3.97262	4.22262	Plants (Prance, 1973, 1982); Harvestmen (Pinto-da-Rocha et al., 2005)
	D1CA5	9	1	4	2.61537	2.86537	Several taxa (Sigrist & Carvalho, 2008); Plants (Prance, 1973, 1982) Muscidae (Löwenberg-Neto & De Carvalho, 2009); Harvestmen (Pinto-da-Rocha et al., 2005); Plants (Menini Neto et al., 2016)
	D1CA6	7	1	3	2.38839	2.63839	Aves (Silva et al., 2004); Orchid bees (Garraffoni et al., 2017)
	D1CA8	11	1	5	3.28178	3.53178	Several taxa (Sigrist & Carvalho, 2008); Plants (Prance, 1973, 1982); Harvestmen (Pinto-da-Rocha et al., 2005); Plants (Menini Neto et al., 2016)
	D1CA9	9	1	5	3.05918	3.30918	Several taxa (Sigrist & Carvalho, 2008); Plants (Prance, 1973, 1982); Harvestmen (Pinto-da-Rocha et al., 2005)
	D2CA0	72	110	83	2.08138	12.01492	
	D2CA1	19	3	6	2.86547	3.11547	Diptera (Amorim & Santos, 2017)
	D2CA2	14	3	6	2.2487	2.4987	
	D2CA5	12	4	9	3.6317	4.6317	Birds (Silva et al., 2004)
	D2CA6	49	2	4	2.18409	2.68409	
	D2CA8	9	2	4	2.02446	2.27446	
	D2CA9	28	1	3	2.32805	2.57805	
	D2CA11	71	1	3	2.37622	2.62622	Oryzomyne rodents (do Prado et al., 2015); Plants (Prance, 1973, 1982); Primates (Goldani et al., 2006); Hemiptera (Ferrari et al., 2010)
	D2CA13	13	1	5	3.05566	3.75566	
	D2CA15	29	1	3	2.12116	2.37116	Mammals (Noguera-Urbano & Escalante, 2015); Hemiptera (Ferrari et al., 2010); Orchid bees (Garraffoni et al., 2017)
	D2CA19	13	1	4	2.73744	2.98744	Birds (Silva et al., 2004)
	D2CA21	9	1	3	2.66959	2.91959	
	D2CA24	26	1	3	2.50599	2.7599	Mammals (Noguera-Urbano & Escalante, 2015); Oryzomyne rodents (do Prado et al., 2015); Several taxa (Sigrist & Carvalho, 2008); Muscidae (Löwenberg-Neto & De Carvalho, 2009); Primates (Goldani et al., 2006)
	D2CA27	14	1	4	2.24574	2.49574	Mammals (Noguera-Urbano & Escalante, 2015); Mammals (Costa et al., 2000)

	D3CA2	58	28	16	2.07361	4.55947	
	D3CA4	24	1	3	2.25928	2.50928	Primates (Goldani et al., 2006)
	D3CA5	48	110	102	2.1814	20.76971	
	D3CA10	26	3	6	2.19583	2.94583	Hemiptera (Ferrari et al., 2010)
	D3CA16	13	5	13	3.33889	6.29142	
	D3CA18	22	5	7	2.04987	2.54987	Primates (Goldani et al., 2006)
	D3CA19	28	2	7	2.98892	4.23892	Hemiptera (Ferrari et al., 2010)
	D3CA23	25	1	4	2.8632	3.1132	Oryzomyne rodents (do Prado et al., 2015); Several taxa (Sigrist & Carvalho, 2008); Hemiptera (Ferrari et al., 2010)
	D3CA27	27	1	3	2.06841	2.31841	
Continental Patterns	D3CA22*	150	1	2(1)	2.58829	2.83289	Hemiptera (Ferrari et al., 2010)
	D3CA1*	237	7	2(3)	2.63879	2.8979	Mammals (Noguera-Urbano and Escalante, 2017)

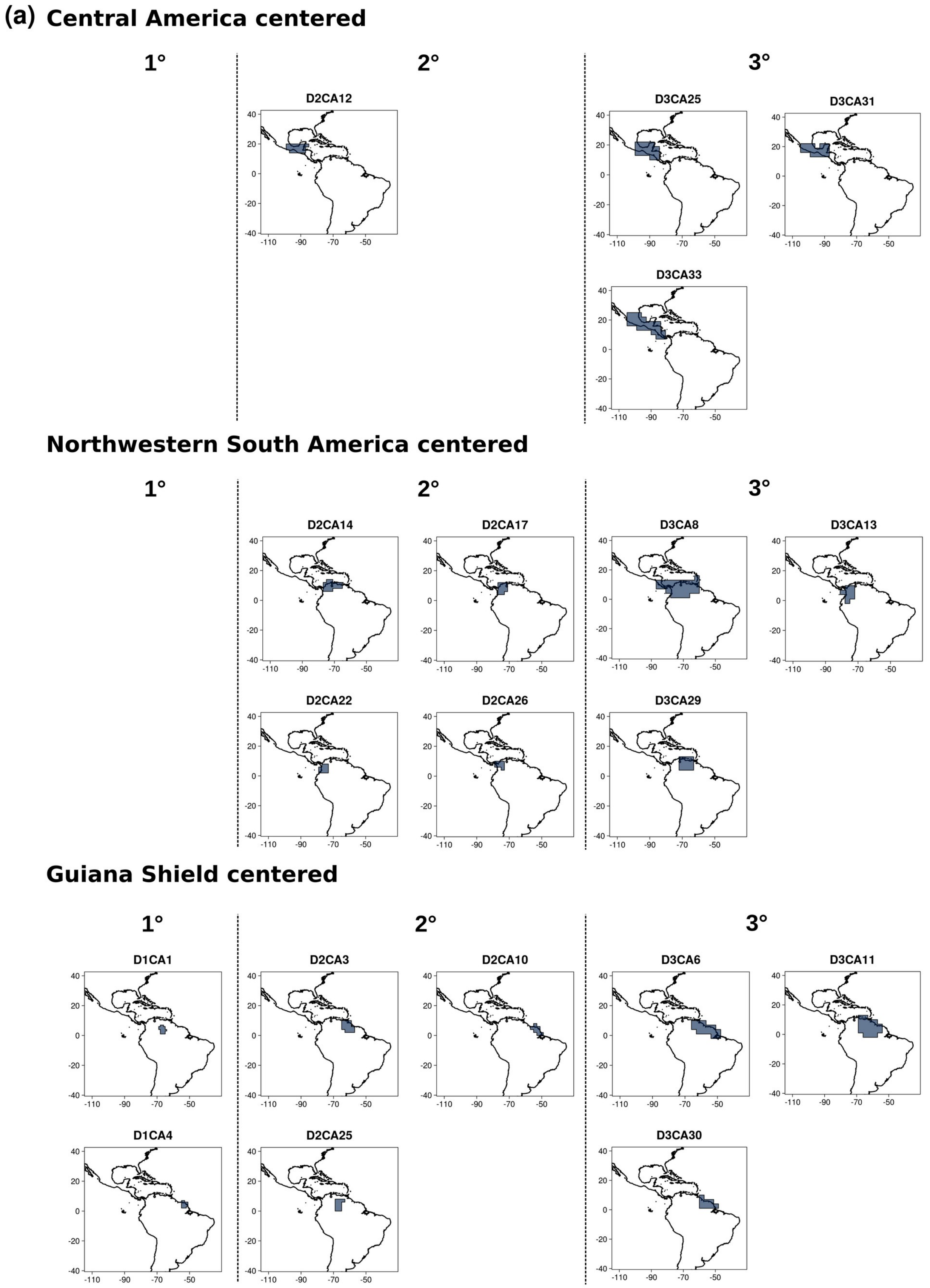
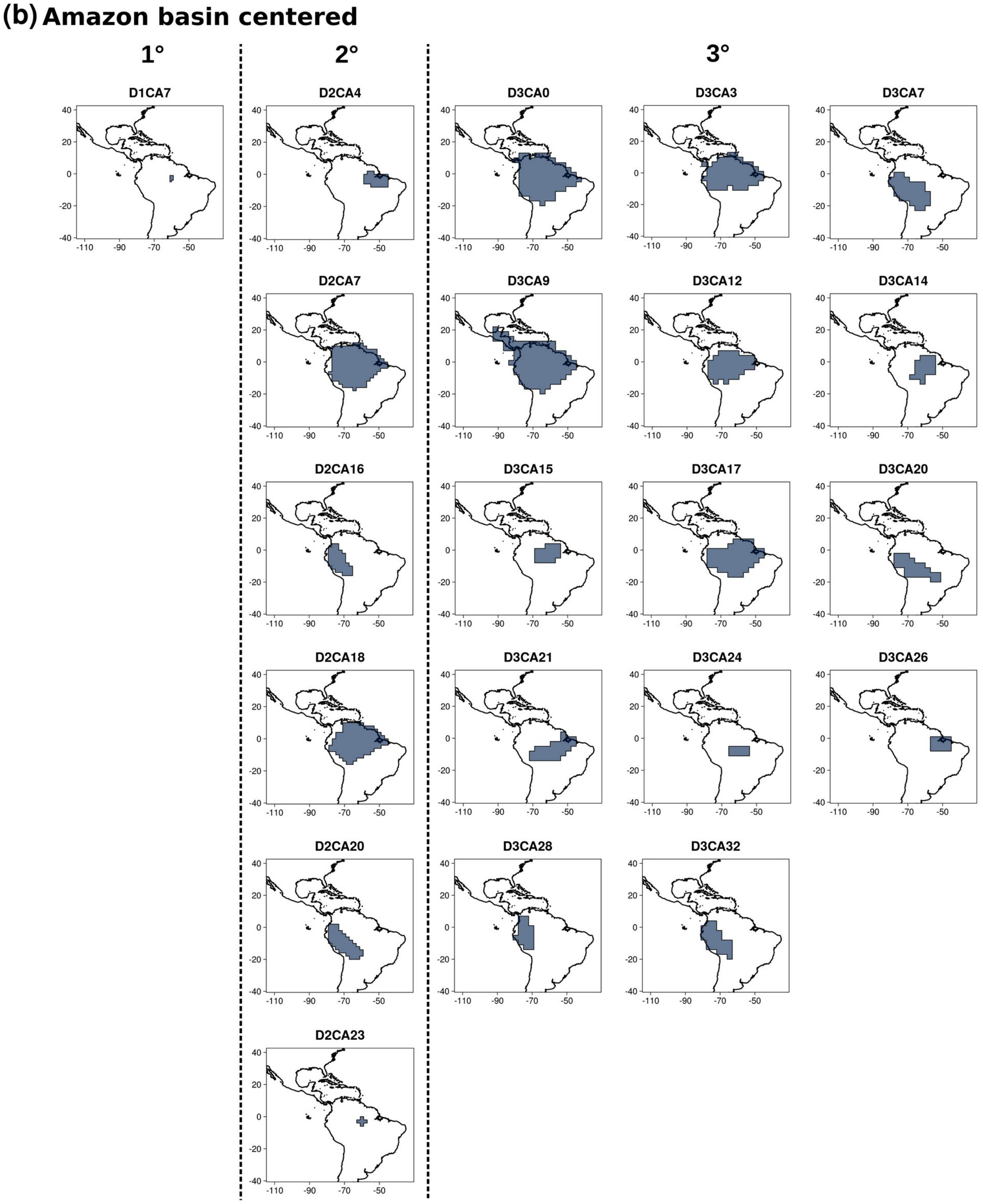


Figure 4. Areas of endemism of tribe Bignonieae (Bignoniaceae) at the spatial scale of one, two, and three degrees obtained using NDM/VNDM. (a) Consensus Areas located over Central America, Northwestern South America, and Guiana Shield. (b) Consensus areas located over the Amazon basin. (c) Consensus areas located over Eastern South America and Continental scale patterns. Note that most of the patterns were found at two and three degrees. See Appendix S2 in Supporting information for the detailed information of consensus areas.



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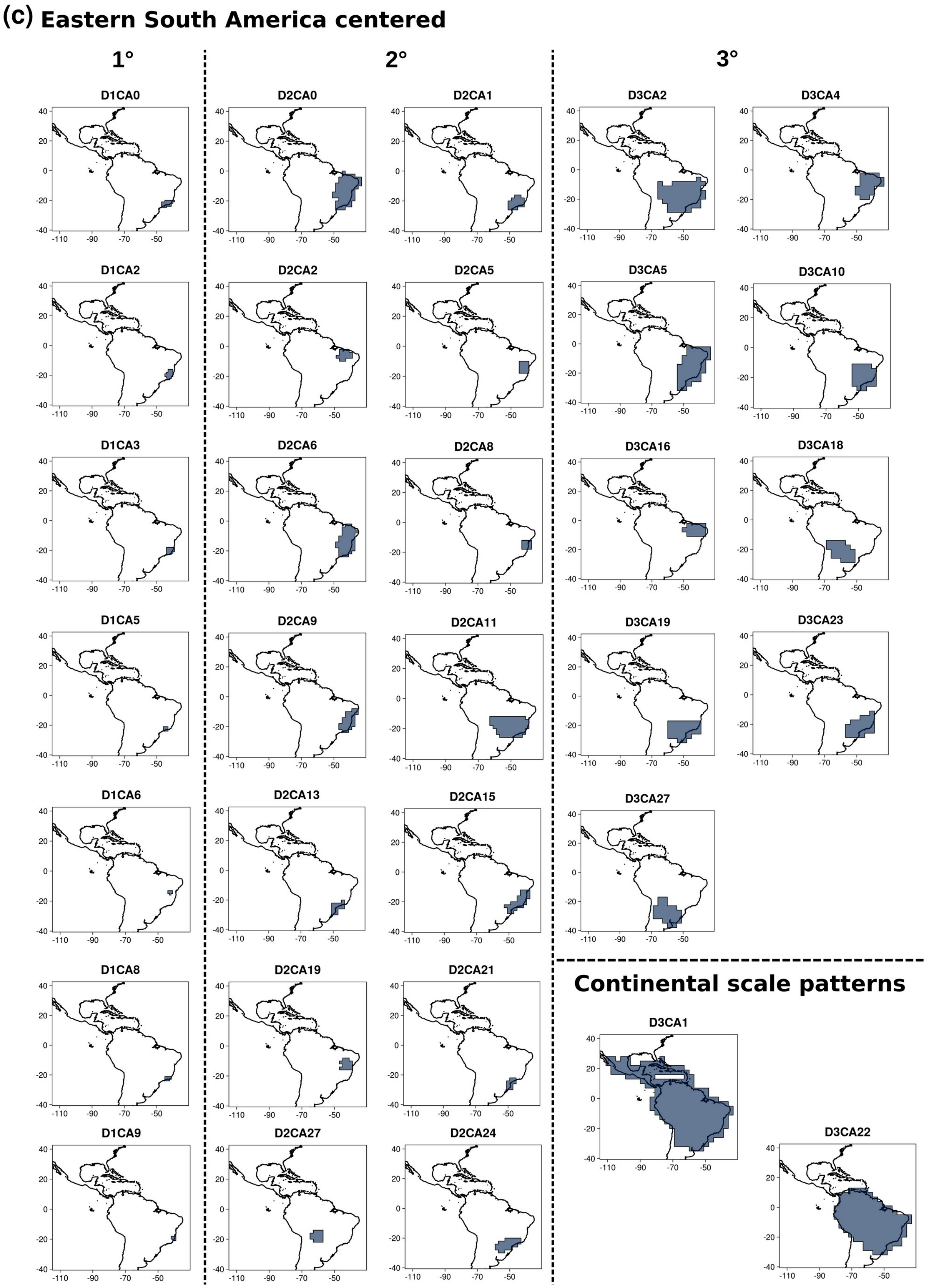

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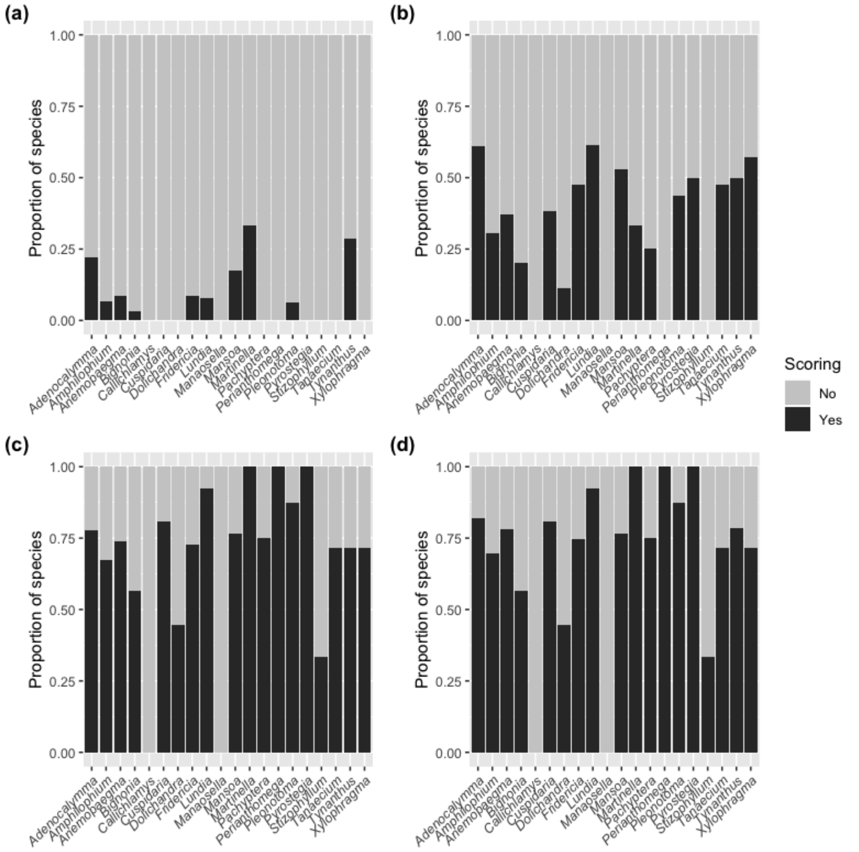

Figure 5. Proportion of scoring species per genera at different spatial scales in the Default Analysis. The proportion of species was computed individually for each spatial scale without counting the number of species implied by the inclusion of higher taxa. Note that the number of species taking part in the analysis increase with increasing scale as does the number of genera. Not all genera contribute equally to the discovery of patterns of endemicity at every spatial scale, with the monotypic genera *Manaosella* and *Callichlamys* not taking part in any pattern. (a) Proportion of scoring species at one degree. (b) Proportion of scoring species at two degrees. (c) Proportion of scoring species at three degrees. (d) Proportion of scoring species in the Default Analysis as a whole. These bar plots reflect the fact that the majority of species of Bignonieae possess very wide geographical extents of occurrence.

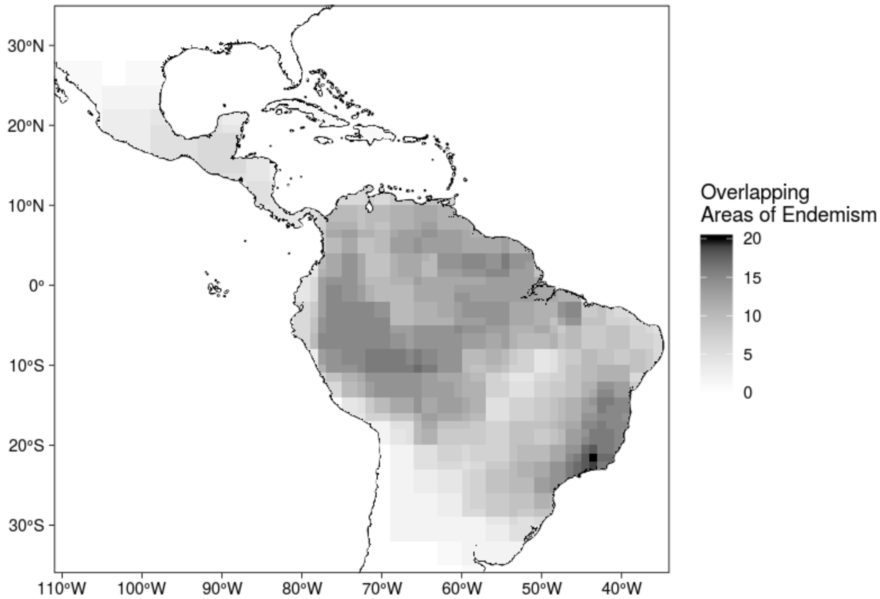

Figure 6. Map of all areas of endemism of Bignonieae showing the high degree of spatial overlap. The darker the color scale, the higher the number of consensus areas overlapping. Geographic space was divided in pixels of one degree size.

Table 6. Groups of consensus areas with ambiguous species that are clustered in specific geographic sectors. Geographic sector: Sector where the consensus areas are grouped. Consensus areas: Consensus areas sharing species. Asterisk (*) denotes the overlapping or nested areas from different altitudinal belts. Geographical pattern: Spatial configuration of the consensus areas, which can be: a. Perfectly nested: One of the consensus area is completely included in the other; b. Nested with edge effect: Smaller consensus areas is completely included in another bigger area but one of its lines of cells lays outside and adjacent: c. Overlapping: Consensus areas overlap by at least two lines of cells but conserved also at least two lines of cells outside of their intersection zone (following terminology of Szumik et al., 2018). Ambiguous species: List of species shared by the group of consensus areas.

Geographic sector	Consensus areas	Geographical pattern	Ambiguous species
Central America centered	D3CA25, D3CA33 *	Nested with edge effect	*Bignonia potosina*
	D3CA25, D3CA31 *	Overlapping	*Fridericia floribunda*
	D3CA33, D3CA31	Nested with edge effect	*Fridericia viscida*
Northwestern South America Centered	D2CA17, D2CA22	Nested with edge effect	*Tanaecium exitiosum*
	D2CA14, D2CA17	Nested with edge effect	*Adenocalymma magdalenense*
	D2CA26, D2CA17	Nested with edge effect	*Bignonia neouliginosa, Pachyptera aromatica*
Guiana Shield Centered	D3CA11, D3CA30, D3CA6	Overlapping Perfectly nested	*Fridericia oligantha*
	D3CA11, D3CA6	Overlapping	*Amphilophium porphyrotrichum, Bignonia microcalyx, Fridericia oligantha, Pleonotoma echitidea*
	D3CA30, D3CA6	Perfectly nested	*Amphilophium parkeri, Fridericia oligantha*
	D3CA11, D3CA14	Overlapping	*Anemopaegma ionanthum, Cuspidaria monophylla*
	D3CA11, D3CA3	Nested with edge effect	*Anemopaegma robustum*
	D3CA11, D3CA29	Nested with edge effect	*Fridericia carichanensis*
	D3CA8, D3CA13	Nested with edge effect	*Adenocalymma dugandii, Amphilophium chocoense, Anemopaegma santaritense*
	D3CA8, D3CA29	Perfectly nested	*Amphilophium steyermarkii, Anemopaegma villosum*
Amazon Basin Centered	D2CA7, D2CA18	Perfectly nested	*Tanaecium bilabiatum*
	D3CA3, D3CA0, D3CA12	Nested with edge effect	*Amphilophium granulosum, Fridericia prancei*
	D3CA3, D3CA0	Nested with edge effect	*Adenocalymma schomburgkii, Amphilophium granulosum, Anemopaegma paraense, Fridericia nigrescens, Fridericia prancei, Pleonotoma clematis*
	D3CA3, D3CA12	Nested with edge effect	*Amphilophium granulosum, Fridericia prancei, Pleonotoma jasminifolia*
	D3CA3, D3CA14, D3CA15 *	Nested with edge effect Perfectly nested	*Cuspidaria subincana*
	D3CA3, D3CA14	Nested with edge	*Anemopaegma ionanthum, Cuspidaria subincana*

		effect	
	D3CA3, D3CA15	Perfectly nested	*Anemopaegma foetidum, Cuspidaria subincana*
	D3CA14, D3CA15	Nested with edge effect	*Adenocalymma adenophorum, Amphilophium lohmanniae, Cuspidaria subincana*
	D3CA14, D3CA24	Nested with edge effect	*Adenocalymma cidii, Amphilophium laeve*
	D3CA0, D3C17	Perfectly nested	*Adenocalymma impressum, Fridericia tuberculata*
	D3CA3, D3CA9	Perfectly nested	*Dolichandra steyermarkii*
	D3CA7, D3CA20	Overlapping	*Fridericia arthrerion, Pleonotoma pavettiflora, Tanaecium xanthophyllum*
	D3CA7, D3CA32	Nested with edge effect	*Fridericia pearcei, Lundia spruceana*
	D3CA32, D3CA28	Nested with edge effect	*Bignonia bracteomana, Tanaecium affine*
Eastern South America Centered	D1CA2, D1CA3	Nested with edge effect	*Adenocalymma sessile*
	D1CA0, D1CA5, D1CA8	Nested with edge effect Perfectly nested	*Adenocalymma bullatum, Bignonia costata*
	D2CA0, D2CA5, D2CA19 *	Nested with edge effect Perfectly nested	*Adenocalymma dichilum, Lundia gardneri*
	D2CA0, D2CA5 *	Perfectly nested	*Adenocalymma ackermannii, Adenocalymma dichilum, Adenocalymma hypostictum, Lundia gardneri, Xylophragma harleyi*
	D2CA0, D2CA19 *	Perfectly nested	*Adenocalymma dichilum, Lundia gardneri, Mansoa hirsuta*
	D2CA5, D2CA19 *	Nested with edge effect	*Adenocalymma dichilum, Amphilophium blanchetii, Lundia gardneri*
	D2CA0, D2CA5, D2CA8 *	Nested with edge effect Perfectly nested	*Adenocalymma ackermannii, Adenocalymma hypostictum*
	D2CA0, D2CA8	Perfectly nested	*Adenocalymma ackermannii, Adenocalymma hypostictum, Martinella insignis*
	D2CA0, D2CA1 *	Nested with edge effect	*Adenocalymma bullatum, Fridericia formosa, Lundia obliqua, Tynanthus fasciculatus*
	D2CA0, D2CA2 *	Nested with edge effect	*Adenocalymma subspicatum, Lundia gardneri*
	D2CA0, D2CA6	Perfectly nested	*Adenocalymma divaricatum, Fridericia erubescens, Pleonotoma pavettiflora*
	D2CA0, D2CA9	Perfectly nested	*Anemopaegma citrinum, Cuspidaria lachnaea*
	D2CA0, D2CA13	Overlapping	*Amphilophium bracteatum, Amphilophium dolichoides*
	D2CA0, D2CA15	Overlapping	*Dolichandra unguiculata*
	D2CA13, D2CA21	Perfectly nested	*Adenocalymma dusenii, Adenocalymma*

		hatschbachii
D3CA5, D3CA2, D3CA19, D3CA10, D3CA23	Overlapping Nested with edge effect	*Fridericia samydoides*
D3CA2, D3CA19, D3CA23	Nested with edge effect Perfectly nested	*Cuspidaria convoluta, Fridericia samydoides*
D3CA5, D3CA10	Nested with edge effect	*Cuspidaria pulchella, Fridericia samydoides, Lundia virginalis, Pleonotoma tetraquetra, Xylophragma myrianthum*
D3CA5, D3CA19	Overlapping	*Adenocalymma paulistarum, Fridericia samydoides, Tynanthus micranthus*
D3CA5, D3CA23	Nested with edge effect	*Fridericia samydoides, Mansoa glaziovii, Tynanthus cognatus*
D3CA5, D3CA16	Nested with edge effect	*Anemopaegma foetidum, Cuspidaria subincana*
D3CA5, D3CA4	Perfectly nested	*Adenocalymma divaricatum, Adenocalymma scabriusculum, Fridericia dispar*

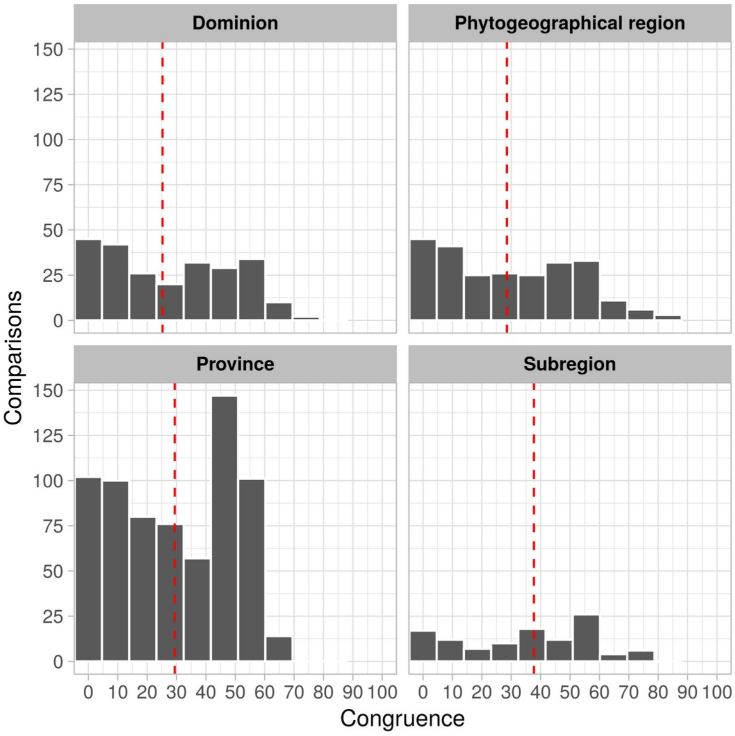

Figure 7. Spatial congruence values for comparisons among consensus areas and the units of the biogeographical regionalization schemes from the phytogeographical regions of Gentry (1982) and the Neotropical Region of Morrone (2014). The dashed red line depicts the median value for congruence in each regionalization scheme. Note that most of the comparisons showed congruence values smaller than 80%. Dominions and phytogeographical regions showed similar congruence values. Many provinces obtained congruence values around 50% because they are nested into broader consensus areas. Similarly, congruence values around 50% are observed for Subregions because smaller consensus areas got nested into them. Overall, the degree of spatial congruence between consensus areas and the biogeographical schemes of Gentry (1982) and Morrone (2014) is low, therefore the patterns of endemism of Bignonieae are different from those described for the taxa included in these regionalization schemes.

Spatial congruence of consensus areas and biogeographical regionalization schemes

In general, patterns of endemism of Bignonieae showed low percentages of spatial congruence when compared against the units of the biogeographical regionalization schemes proposed by Gentry (1982) and Morrone (2014) for the Neotropics (Fig. 7). The low spatial congruence resulted from consensus areas that overlapped among several biogeographical units but covering them in different degrees at every spatial scale of analysis (Fig. 8). In other words, most areas of endemism of Bignonieae differ from the distribution patterns synthesized in these biogeographical schemes. The biogeographical units of these schemes are composed by a mixture of endemic Bignonieae species that belong to different areas of endemism.

Few areas of endemism showed higher values of spatial congruence with some biogeographical units. The most notorious case was the whole Neotropics which showed 80% of congruence (i.e., D3CA1; Fig. 4C). In the case of Gentry's (1982) phytogeographical regions, values between 70% and 83.4% of congruence were obtained for consensus areas compared against Amazonia (i.e., D2CA7, D2CA18, D3CA0, D3CA3, D3CA9, D3CA12, and D3CA17; Fig. 4B) and the Guiana Subregion (i.e., D3CA6; Fig. 4A). In the case of Morrone's (2014) regionalization scheme, values of spatial congruence varied according to the inclusiveness level of the biogeographical unit. At the subregional level, values between 70% and 78.5% of spatial congruence were obtained for six consensus areas compared against the Brazilian subregion (i.e., D2CA7, D2CA18, D3CA0, D3CA3, D3CA9, and D3CA12; Fig. 4B). At the Dominion level, the highest spatial congruence was 72% for a consensus area compared against the South Brazilian dominion (i.e., D3CA7; Fig. 4B). At the Province level, the highest spatial congruence was 68% for an area that was compared to the Guianan Lowlands province (i.e., D3CA30 in Fig. 4A). All the mentioned cases correspond to Amazon basin centered patterns (Fig. 4B).

Despite the general lack of spatial congruence among areas of endemism and most of the biogeographical units, areas of endemism recovered for other Neotropical taxa are similar to those reported here. For example, similarities are recovered with other plants (Prance, 1973) and harvestmen Pinto-da-Rocha, Silva, & Bragagnolo, 2005) in the Atlantic Forest of Eastern South America; birds (Silva, Sousa, & Castellteti, 2004) and primates (Goldani, Carvalho, & Bicca-Marques, 2006) in the Cerrado; and, rodents (J. R. Prado et al., 2015) and hemiptera (Ferrari, Paladini, Schwertner, & Grazia, 2010) in the Amazon basin (Table 5). These shared patterns suggest that the areas of endemism found here are not necessarily unique to Bignonieae suggesting common distribution drivers.

Figure 8 (Next page). Biogeographical region uniformity for the proposals of (a) Gentry (1982), and (b) Subregions, (c) Dominions, and (d) Provinces of Morrone (2014). The biogeographical region uniformity (Ub) refers to the proportion of the area of the biogeographical unit covered by a consensus area. It is one of the components of the Spatial Congruence calculated to assess spatial similarity among areas of endemism and biogeographical units. It allows to see the degree of overlap between the unit and multiple areas of endemism. Consensus areas are shown in the y axis and biogeographical regions in the x axis. Central panels separate each spatial scale and show the Ub as a percentage in color scale. Lighter colors indicate the biogeographical region is extensively covered by a specified consensus area in the x axis. Darker colors indicate that a small fraction of the biogeographical region is covered by the consensus area. Consensus areas depicted at the bottom intersected only one biogeographical unit while those at the top intersected the maximum number of biogeographical units possible. This figure illustrates the dominance of wider consensus areas over consensus areas with smaller sizes, and the scarce number of consensus areas that intersect with a single biogeographical region. →

Figure 8a (Continued)

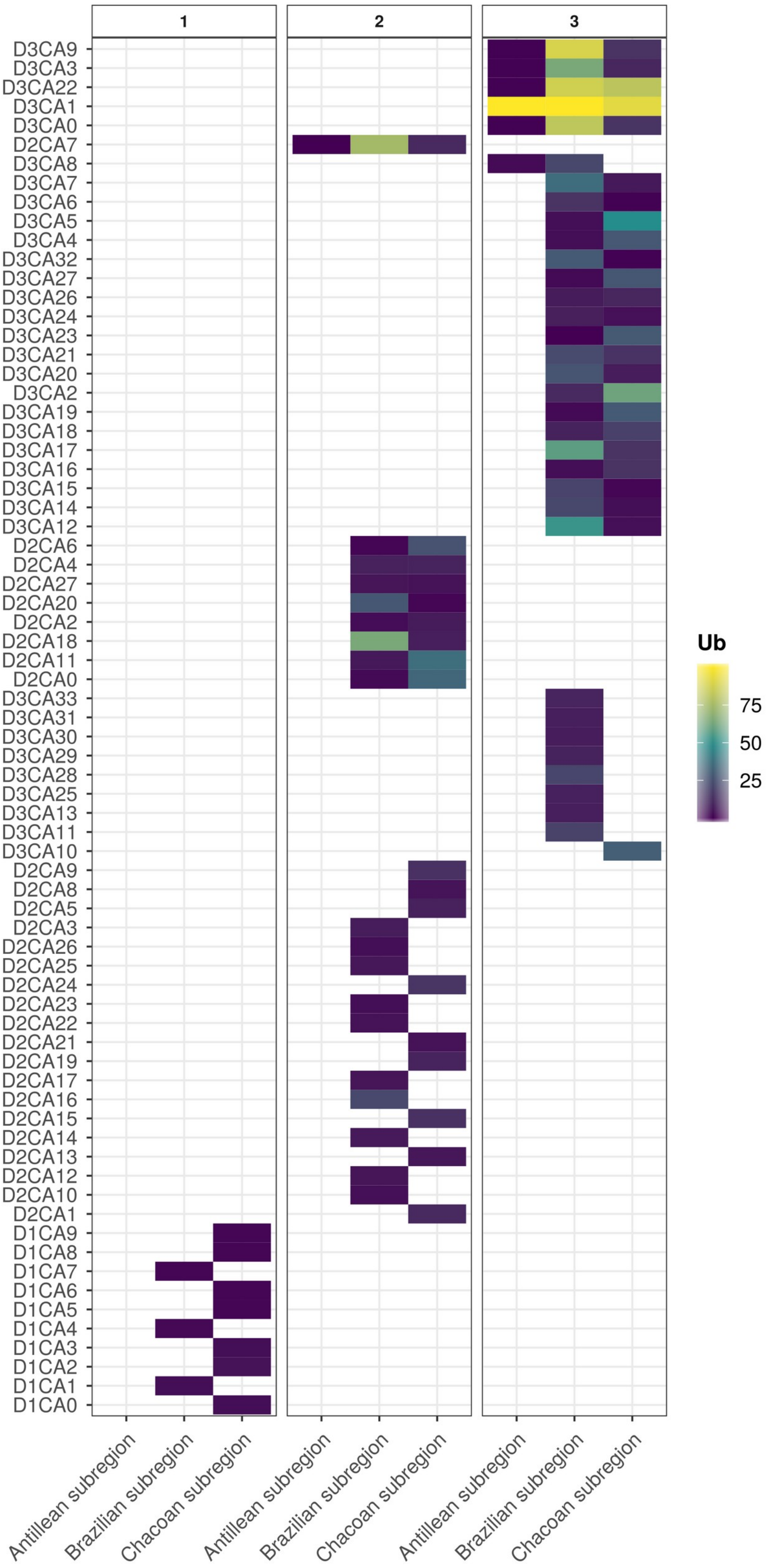

Figure 8(b) (Continued)

Figure 8c (Continued)

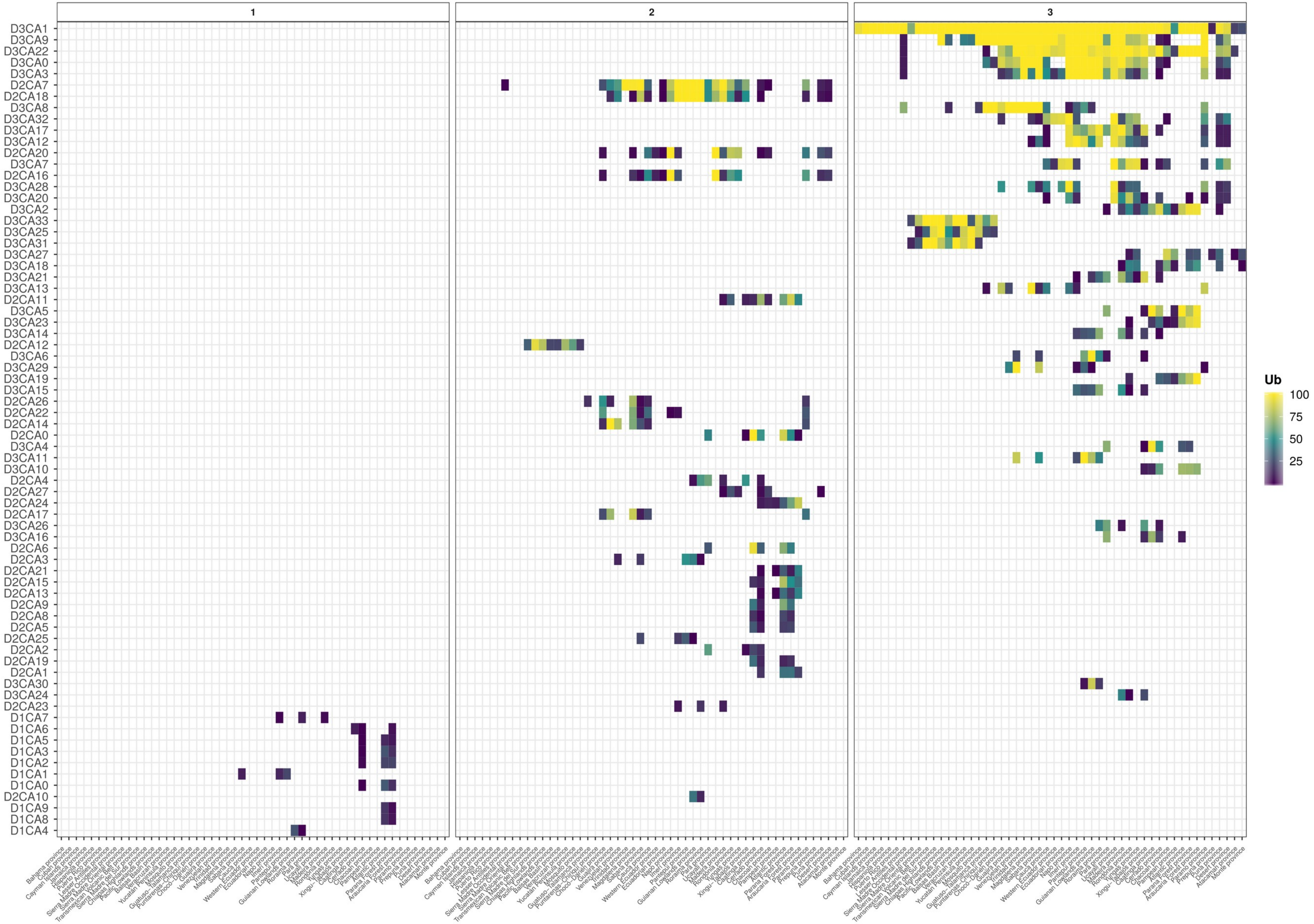

Figure 8d (Continued)

Discussion

We found that areas of endemism of tribe Bignonieae (Bignoniaceae) were more numerous at regional spatial scales and clustered in geographic sectors with many overlapping and nested patterns, some of which showed low levels of ambiguity. Although the spatial congruence with biogeographical units was low, areas of endemism were similar to patterns found for other taxa.

The number of Bignonieae areas of endemism and species composition varied with different grid sizes in VNDM, indicating that Bignonieae areas of endemism are scale dependent (Fig. 3). While larger grid sizes might be masking the effect of the sparse sampling of species ranges and defining coarse biogeographical patterns, the identification of broad patterns of endemism might also be related to the high number of wide-ranging species of Bignonieae (Lohmann et al., 2013; Meyer et al., 2018). These wide-ranging species might help explain why Bignonieae areas of endemism were also defined by the contribution of the distributional areas of higher taxa. A similar scale dependence of areas of endemism has been observed for different taxa (Casagranda et al., 2009; J. R. Prado et al., 2015; Szumik & Goloboff, 2015). Our findings show that areas from different spatial scales can be nested within each other, suggesting that the same endemic species are contributing to different areas. As patterns and processes are scale dependent in ecology and biogeography (Levin, 1992; Whittaker, Willis, & Field, 2001) exploring different grid sizes in NDM/VNDM can help isolate different patterns, characterize how these patterns interact across scales, and understand how processes acting at different spatial scales impact endemism (Daru, Farooq, Antonelli, & Faurby, 2020). The scale dependency of patterns is not only associated with methodological decisions about grain size (Peterson & Watson, 1998) but also with ecological and biogeographical processes that operate at different scales (Cabral, Valente, & Hartig, 2016), highlighting the importance of studying areas of endemism at different spatial scales (Laffan & Crisp, 2003; Morrone & Escalante, 2002).

Geographical clusters of areas of endemism were congruent with the distribution of the potential richness of Bignonieae, with a higher number of areas grouped over its two main centers of diversity: the Amazon basin and the Atlantic Forest of Eastern South America (Meyer et al., 2018). Although centers of diversity and endemism are not necessarily correlated for many taxa (Ceballos & Brown, 1995; Hobohm, 2003; Lamoreux et al., 2006), the coincidence found here is explained by the explicit spatial criterion of NDM/VNDM that discovers a pattern each time sufficient spatial fit exists among several species. In general, the low correlation between patterns of diversity and endemism is attributed to the interplay of using centers of endemism defined as the concentration of narrow-ranging species, and accounting for the higher contribution of wide-ranging species to richness patterns (Beard, Chapman, & Gioia, 2000; Crisp, Laffan, Linder, & Monro, 2001; Hobohm, 2003; Kessler, Herzog, Fjeldså, & Bach, 2001). Narrow-ranging species are unevenly distributed in geographical space, while widespread and common species dominate the spatial distribution of richness (Jetz & Rahbek, 2002; Kreft, Sommer, & Barthlott, 2006; Lennon, Koleff, Greenwood, & Gaston, 2004). As NDM/VNDM define endemism independently of range size, many areas of endemism were found in the centers of diversity of Bignonieae because many species with high spatial congruence to different areas were found within these centers. Apart from this methodological difference in how endemism is defined, the match or mismatch between centers of diversity and endemism can result from the particular history and biology of the taxa under study (Lamoreux et al., 2006; Ochoa-Ochoa, Campbell, & Flores-Villela, 2014).

Although there is not a unique evolutionary or ecological mechanism that explains how taxa become endemic to individual areas (Hobohm, 2014; Hovenkamp, 1997), it is generally accepted that endemism results from the contingency of past events and the modification of ongoing ecological processes that determine the boundaries of species distributions and speciation (Anderson, 1994; Cracraft, 1994; Crother & Murray, 2011; Linder, Antonelli, Humphreys, Pirie, & Wüest, 2013; Noguera-Urbano, 2016; Weeks et al., 2016). From the theoretical perspective that privileges vicariance and allopatric speciation (Harold & Mooi, 1994; Morrone, 1994), areas of endemism must not overlap and must be formed by groups of sister taxa. In agreement with other studies that tested this assumption and showed that overlapping patterns of endemism are common (Szumik, Pereyra, & Casagranda, 2018), we showed here that the areas of endemism of Bignonieae overlap substantially with many nested patterns (Figs. 4 and 6). Overlapping patterns are common in nature and can be observed around ecotones between biomes (Van Rensburg, Levin, & Kark, 2009) and in transition zones between biogeographical regions (Sandoval & Ferro, 2014). However, areas of endemism of Bignonieae were clustered and nested within specific and broad geographic sectors, with low ambiguity (Table 6, Fig. 4).

Some clues about the processes that might have caused these clustering and overlapping patterns can be inferred from the ecology and biogeography of Bignonieae. From an ecological standpoint, the coincidence between centers of diversity and endemism might suggest that just like richness, endemism could be correlated with evapotranspiration (Meyer et al., 2018) and canopy height (Meyer et al., 2019). The high number of overlapping and nested patterns in these centers would suggest specialization into the specific conditions that characterized the space encompassed by the pattern. The community structure of Bignonieae has been associated with specialization to abiotic conditions (Alcantara, Ree, Martins, & Lohmann, 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 of lianas' distribution and endemism patterns with climate is supported by the fact that precipitation and seasonality can regulate liana abundance and diversity (Parolari et al., 2019; Schnitzer, 2005). Associations between climate and centers of endemism across many taxa (Harrison & Noss, 2017; Zuloaga, Currie, & Kerr, 2019) provide further support to the possible role that climate might have in the formation of the 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 Bignonieae.

From a historical biogeography standpoint, the cluster of overlapping areas of endemism is consistent with the diversification patterns and geographical spread of Bignonieae in the Neotropics (Lohmann et al., 2013). Bignonieae dates back to the Eocene (ca. 54 Mya) and evolved concomitantly with main geological and climatic events shaping the neotropical landscape (Antonelli & Sanmartín, 2011; Bacon et al., 2015; Hoorn & Wesselingh, 2010; Hughes, Pennington, & Antonelli, 2013; Pennington et al., 2004; Werneck, 2011). Diversification in this group was a geographically structured process with a likely origin in Eastern South America and further colonization and diversification events in Lowland Amazonia, Central America, Northwestern South America, and the open vegetation dry diagonal of South America (Lohmann et al., 2013). The detailed distribution patterns described by the areas of endemism could represent responses of specific sets of species to particular historical events. The events suggested by these patterns could be different from those used to explain the common distribution patterns synthesized by the units of different regionalization schemes (Figs. 7 and 8). In order to understand finer-scale patterns, we discuss the areas of endemism of Bignonieae within geographical sectors (Fig. 4A-C).

Amazon basin centered patterns

Bignonieae is an important component of the Amazon rainforest (Gentry, 1979; Lohmann & Taylor, 2014). It is not surprising that many of its areas of endemism support the existence of Gentry's Amazonian centered patterns for trees and lianas (Gentry, 1990, 1992) (Fig. 4B). Although the highest values of spatial congruence between areas of endemism and biogeographical units were obtained here at the subregional level (Fig. 8), areas were highly discordant within less inclusive units such as dominions and provinces (Figs. 4B, 8). Traditionally, eight areas of endemism in the Amazon are accepted for multiple taxa: Guiana, Imeri, Napó, and Inambari forming a northwestern block of areas; and Rondônia, Tapajós, Xingú, and Belém forming a southeastern block (Bates, Hackett, & Cracraft, 1998; Cracraft, 1985; Da Silva & Oren, 1996; Fiaschi & Pirani, 2009; Haffer, 1969; Lynch Alfaro et al., 2015; Prance, 1982; Racheli & Racheli, 2004; Ron, 2000). In contrast, areas of endemism in Bignonieae formed three groups of overlapping areas: (i) Western Amazonia (i.e., areas D2CA4, D2CA16, D2CA20, D3CA7, D3CA16, D3CA28, and D3CA32); (ii) Central Amazonia (i.e., areas D1CA7, D2CA23, D3CA14, D3CA15, and D3CA24); and (iii) South Eastern Amazonia, (i.e., D3CA21, and D3CA26), all of which were coincident with areas found for other individual taxa (Table 5).

The traditional areas of endemism of Amazonian lowlands are thought to have resulted from two main processes: climate-driven transformation of the landscape that changed the distribution of forests and savannas, and the fragmentation of the forest by the formation of the Amazon drainage system (Gascon et al., 2000; Rull & Carnaval, 2020; Wallace, 1852). The main implication of this result is that the Amazon river system fragmented the biota and confined groups of endemic species into the interfluvial regions. Our findings suggest that species of Bignonieae have responded differently to the formation of the Amazon drainage system and the evolution of the Amazonian landscape. The fact that most Bignonieae species are wind or water dispersed may have weakened the barrier effect of rivers, with various Bignonieae species distribution limits being less affected by rivers (Lohmann & Taylor, 2014). Our patterns seem to be consistent with the observation that the Amazon biome has experimented a climatic dipole causing a wetter western Amazonia and drier Eastern Amazonia climatic regimes in the past (Cheng et al., 2013). In other words, the areas of endemism over western Amazonia might be composed of species with higher affinities with wet and stable conditions than the areas in southeastern Amazonia. Further studies are needed to address this question.

Eastern South America centered patterns

The Atlantic Forest of Eastern Brazil is characterized by multiple centers of endemism and a major biogeographical transition zone between Northern and Southern biotas separated by the

Doce river (Costa, Leite, Fonseca, & Fonseca, 2000; Cracraft, 1985; Santos, Cavalcanti, Da Silva, & Tabarelli, 2007; Sigrist & Carvalho, 2008, 2009). Despite the low spatial congruence within this region as a whole (Fig. 8), the areas of endemism of Bignonieae are aggregated over these centers of endemism (Fig. 4C, Table 5). While some areas are located over the central corridor of the Atlantic Forest and the centers of endemism of Rio de Janeiro and Espirito Santo (i.e., areas D1CA2, D1CA3, D1CA5, D1CA8, D1CA9, and D2CA1), other areas are located over the Serra do Mar center of endemism (i.e., areas D2CA13, D2CA21, and D2CA24). Climatic-driven habitat changes and diversification of different taxa in these centers of endemism have been associated to global climatic oscillations since the last glacial maximum, with the Northern centers of endemism being associated to climatic stability, and the Southern centers of endemism associated to the current climate (Carnaval & Moritz, 2008; Carnaval et al., 2014). Further studies using environmental niche modeling aiming to test whether climatic responses showed the same spatial dynamics are needed to further evaluate the driving causal factors of endemism in Bignonieae in this region (Linder et al., 2013; Waltari & Guralnick, 2009).

Species of the Bignoniaceae are known to have widespread distributions across the open vegetation biogeographical regions of Eastern South America (Gentry 1979). The areas of endemism of Bignonieae were also wide in this area and showed little spatial congruence with the phytogeographical domains currently accepted in this region (i.e., Caatinga, Cerrado, and Chaco; Fiaschi & Pirani, 2009; Werneck, 2011) (Fig. 4C and 8). Instead, four groups of overlapping areas were identified in (i) Northeastern Brazil (i.e., D2CA0, D2CA2, D2CA5, D2CA6, D2CA8, D2CA9, D2CA19, D3CA4, D3CA5, and D3CA16); (ii) Bahia center of endemism within the Chapada Diamantina (i.e., D1CA6, D2CA19 and D2CA19); (iii) Southeastern Brazil (i.e., D2CA11, D3CA2, D3CA10, D3CA18, D3CA19, and D3CA23); and (iv) Across the grand Chaco (i.e., D3CA27). The main attribute of these patterns is that they are wide enough to encompass several of the phytogeographical domains, expanding from the Atlantic Forest into the open vegetation biomes, reaching the Amazon through 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 (Batalha-Filho, Fjeldså, Fabre, & Miyaki, 2013; Costa, 2003; Oliveira-Filho, Jarenkow, & Rodal, 2006; Oliveira-Filho & Ratter, 1995; Rizzini, 1963), as well as 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 (D. E. Prado & Gibbs, 1993; Werneck, 2011). Previous studies suggested that Bignonieae is an excellent model for studying the climate-driven contraction and expansion of species distribution on these forest types because of their high dispersal capacity and broad distribution (Gentry, 1979, 1990).

Guiana Shield centered patterns

The Guayana region is a well characterized biogeographical region over the Guiana Shield in northern South America (Huber, 1988; Mori et al., 2017; Rull, 2010; Ter Steege et al., 2000), with a complex biogeographical history linked to Quaternary climate-driven species migration between the highlands and the lowlands around the Tepuis (Rull & Carnaval, 2020). Species of Bignonieae occur predominantly in the lowlands, with species from the Guiana Subregion being treated as part of Lowland Amazonia (Gentry, 1979). However, our results suggest that Bignonieae has several overlapping areas of endemism in this region. Endemic species of Bignonieae occur below 1500 m.a.s.l, coinciding with the Eastern (i.e., areas D1CA4, D2CA10, and D3CA30, Fig. 4A) and Central (i.e. D1CA1, D2CA25, and D2CA3) provinces, as well as the Guiana region as a whole (i.e., areas D3CA11 and D3CA6). Most of these areas coincide with patterns found for other taxa (Table 5).

Northwestern South America and Central America centered patterns

Northwestern South America and Central America have a characteristic biota that has resulted from *in situ* diversification and biotic interchanges between Neotropical and Neartic biotas mediated by the uplift of the Andes and the Panama Isthmus (Antonelli & Sanmartín, 2011; Bacon et al., 2015; Hughes et al., 2013; Villaseñor, Ortiz, Delgadillo-Moya, & Juárez, 2020). Based on Bignoniaceae distribution patterns, these two regions were treated as a single unit (Gentry, 1979). However, our findings highlight groups of areas of endemism of Bignonieae in both regions (Fig. 4A) some of which overlap with Costa Rica and coincide with the Pacific and Mesoamerican dominions of Morrone (2014a) (i.e., areas D3CA33 and D3CA8). In Central America, Bignonieae areas of endemism are located over the Yucatan peninsula (i.e., areas D2CA12, D3CA25, and D3CA31), while in Northwestern South America they are located over the Northern Andes of Colombia (i.e., areas D2CA14, D2CA17, D2CA22, D2CA26, and D3CA13) and the savannas of Venezuela (i.e., area D3CA29). The same patterns have been recovered for other taxa (Table 5).

CONCLUSIONS

In this study we unravel the areas of endemism of Bignonieae and compare those areas to other biogeographical regionalization schemes and patterns recovered for other taxa. Given that patterns of endemism result from multiple factors that act over species distributions at different time frames (Crisci, Sala, Katinas, & Posadas, 2006; Donoghue & Moore, 2003; Hunn & Upchurch, 2001; Nihei, 2008), the plausibility of these hypotheses depends on information about the age of past geological events, the age of taxa, and the age of shared distribution patterns. Past climatic changes and contemporary climate are both important to understand current patterns of endemism. Though a calibrated phylogenetic tree is available for tribe Bignonieae (Lohmann et al., 2013), not all endemic species have been sampled, preventing a detailed understanding of the causal factors behind the endemism patterns recovered in this group. This study paved the way for future studies on the biogeographical processes behind endemism by recovering sets of species that are relevant while investigating distribution hypotheses across the Neotropics.

Data availability statement

Data outputs from NDM/VNDM are available as Supporting Information. The Bignonieae distribution database will available once other research projects under development are finished at Dr. Lohmann's Lab.

All R scripts area available from <https://github.com/jupanago/RCode_BignonieaeAoE>

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Appendix 1

Unraveling distribution patterns of Neotropical lianas: An analysis of endemicity of tribe Bignonieae (Bignoniaceae)

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Supporting information – Appendix S1

Tables for species with disjunct distributions and higher taxa included in the analysis of endemicity of Bignonieaee (Bignoniaceae)

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

Disjunct Species
Adenocalymma albiflorum
Adenocalymma flaviflorum
Adenocalymma validum
Amphilophium falcatum
Amphilophium rodriguesii
Anemopaegma brevipes
Anemopaegma floridum
Anemopaegma patelliforme
Bignonia campanulata
Bignonia decora
Bignonia prieurii
Cuspidaria lachnaea
Fridericia cinerea
Fridericia platyphylla
Lundia corymbifera
Manaosella cordifolia

Table S1.2. Higher taxa represented by genera and phylogroups. The areas of the genera were estimated from the aggregation of species individual areas. The areas of the phylogroups 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.

NDM GRPCode	**Genera & Phylogroups**
GRP-0	*Adenocalymma*
GRP-1	*Adenocalymma + Amphilophium + Anemopaegma + Bignonia + Callichlamys + Cuspidaria + Dolichandra + Fridericia + Lundia + Manaosella + Mansoa + Martinella + Pachyptera + Pleonotoma + Pyrostegia + Stizophyllum + Tanaecium + Tynanthus + Xylophragma*
GRP-2	*Amphilophium*
GRP-3	*Amphilophium + Anemopaegma + Bignonia + Mansoa + Pyrostegia*
GRP-4	*Amphilophium + Anemopaegma + Bignonia + Dolichandra + Mansoa + Pyrostegia*
GRP-5	*Amphilophium + Anemopaegma + Bignonia + Callichlamys + Cuspidaria + Dolichandra + Fridericia + Lundia + Mansoa + Martinella + Pachyptera + Pyrostegia + Tanaecium + Tynanthus + Xylophragma*
GRP-6	*Amphilophium + Anemopaegma + Bignonia + Callichlamys + Cuspidaria + Dolichandra + Fridericia + Lundia + Manaosella + Mansoa + Martinella + Pachyptera + Pleonotoma + Pyrostegia + Tanaecium + Tynanthus + Xylophragma*
GRP-7	*Amphilophium + Anemopaegma + Bignonia + Callichlamys + Cuspidaria + Dolichandra + Fridericia + Lundia + Manaosella + Mansoa + Martinella + Pachyptera + Pleonotoma + Pyrostegia + Stizophyllum + Tanaecium + Tynanthus + Xylophragma*
GRP-8	*Anemopaegma*
GRP-9	*Anemopaegma + Pyrostegia*
GRP-10	*Anemopaegma + Mansoa + Pyrostegia*
GRP-11	*Anemopaegma + Bignonia + Mansoa + Pyrostegia*
GRP-12	*Bignonia*
GRP-13	*Callichlamys + Cuspidaria + Fridericia + Lundia + Martinella + Pachyptera + Tanaecium + Tynanthus + Xylophragma*
GRP-14	*Cuspidaria*

GRP-15	*Cuspidaria + Fridericia + Lundia + Tynanthus + Xylophragma*
GRP-16	*Cuspidaria + Fridericia + Lundia + Tanaecium + Tynanthus + Xylophragma*
GRP-17	*Cuspidaria + Fridericia + Lundia + Pachyptera + Tanaecium + Tynanthus + Xylophragma*
GRP-18	*Cuspidaria + Fridericia + Lundia + Martinella + Pachyptera + Tanaecium + Tynanthus + Xylophragma*
GRP-19	*Dolichandra*
GRP-20	*Fridericia*
GRP-21	*Fridericia + Xylophragma*
GRP-22	*Lundia*
GRP-23	*Manaosella + Pleonotoma*
GRP-24	*Mansoa*
GRP-25	*Martinella*
GRP-26	*Pachyptera*
GRP-27	*Pleonotoma*
GRP-28	*Pyrostegia*
GRP-29	*Stizophyllum*
GRP-30	*Tanaecium*
GRP-31	*Tynanthus*
GRP-32	*Xylophragma*

Appendix 2

Unraveling distribution patterns of Neotropical lianas: An analysis of endemicity of tribe Bignonieae (Bignoniaceae)

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Supporting information: Appendix S2

Detailed information about the consensus areas obtained in the Default and Strict analyses at three spatial scales. This information was taken form the text output file given by NDM/VNDM.

Table S2.1. Summary of the consensus areas at 40% of cutoff of similarity with the loose rule for the Default Analysis at one degree.

Spatial Scale	Analysis	Consensus Area	Size	Individual Areas	Species	Minimum Score
1	D	CA 0	28	4	7	2.02476
1	D	CA 1	20	1	3	2.01663
1	D	CA 2	23	1	3	2.02069
1	D	CA 3	22	2	7	3.97262
1	D	CA 4	17	2	4	2.20357
1	D	CA 5	9	1	4	2.61537
1	D	CA 6	7	1	3	2.38839
1	D	CA 7	7	1	3	2.47321
1	D	CA 8	11	1	5	3.28178
1	D	CA 9	9	1	5	3.05918

Table S2.2. Species per consensus area at 40% cutoff of similarity under the loose rule in the Default Analysis at one degree of grid. In red, the three species with ambiguous membership to consensus areas. Minimum score: species minimum index score in the individual areas aggregated in the consensus area. Maximum score: species maximum index score in the individual areas aggregated in the consensus area.

Consensus Area	Species	Minimum score	Maximum score
CA 0	*Adenocalymma bullatum**	0	0.725
	Adenocalymma grandifolium	0.547	0.821
	Adenocalymma trifoliatum	0.438	0.792
	*Bignonia costata**	0	0.738
	Fridericia leucopogon	0	0.787
	Lundia damazioi	0	0.692
	Tynanthus fasciculatus	0	0.453
CA 1	*Amphilophium monophyllum*	0.694	0.694
	Anemopaegma salicifolium	0.702	0.702
	Pleonotoma exserta	0.62	0.62
CA 2	*Adenocalymma aurantiacum*	0.563	0.563
	*Adenocalymma sessile**	0.718	0.718
	Mansoa minensis	0.739	0.739
CA 3	*Adenocalymma cinereum*	0.732	0.784
	Adenocalymma macrophyllum	0.804	0.895
	Adenocalymma salmoneum	0.777	0.932
	*Adenocalymma sessile**	0.553	0.565
	Adenocalymma subsessilifolium	0	0.683
	Anemopaegma setilobum	0	0.861
	Fridericia trachyphylla	0	0.578
CA 4	*Adenocalymma album*	0.65	0.933
	Adenocalymma saulense	0.683	0.768
	Anemopaegma granvillei	0	0.786

	Tynanthus sastrei	0	0.821
CA 5	*Adenocalymma bullatum**	0.62	0.62
	Adenocalymma ubatubense	0.625	0.625
	Anemopaegma pachyphyllum	0.778	0.778
	*Bignonia costata**	0.593	0.593
CA 6	*Amphilophium perbracteatum*	0.821	0.821
	Mansoa ivanii	0.781	0.781
	Mansoa longicalyx	0.786	0.786
CA 7	*Adenocalymma molle*	0.844	0.844
	Amphilophium reticulatum	0.786	0.786
	Tynanthus densiflorus	0.844	0.844
CA 8	*Adenocalymma bullatum**	0.567	0.567
	*Bignonia costata**	0.581	0.581
	Fridericia elegans	0.771	0.771
	Fridericia subexserta	0.682	0.682
	Fridericia subverticillata	0.682	0.682
CA 9	*Adenocalymma apetiolatum*	0.778	0.778
	Adenocalymma hirtum	0.389	0.389
	Adenocalymma lineare	0.778	0.778
	Martinella insignis	0.337	0.337
	Tynanthus espiritosantensis	0.778	0.778

Table S2.3. Summary of the consensus areas at 40% of cutoff of similarity with the loose rule for the Default Analysis at two degrees.

Spatial Scale	Analysis	Consensus Area	Size	Individual Areas	Species	Minimum Score	Maximum Score
2	D	CA 0	72	110	83	2.08138	12.01492
2	D	CA 1	19	3	6	2.86547	3.11547
2	D	CA 2	14	3	6	2.2487	2.4987
2	D	CA 3	13	3	4	2.11923	2.36923
2	D	CA 4	28	6	7	2.27019	3.02019
2	D	CA 5	12	4	9	3.6317	4.6317
2	D	CA 6	49	2	4	2.18409	2.68409
2	D	CA 7	167	2	4	2.39523	3.14523
2	D	CA 8	9	2	4	2.02446	2.27446
2	D	CA 9	28	1	3	2.32805	2.57805
2	D	CA 10	8	3	6	3.39208	3.89208
2	D	CA 11	71	1	3	2.37622	2.62622
2	D	CA 12	18	2	3	2.15245	2.40245
2	D	CA 13	13	1	5	3.05566	3.75566
2	D	CA 14	17	2	5	2.10821	2.85821
2	D	CA 15	29	1	3	2.12116	2.37116
2	D	CA 16	44	1	3	2.35441	2.60441
2	D	CA 17	11	2	4	2.14286	2.39286

2	D	CA 18	135	1	3	2.33658	2.58658
2	D	CA 19	13	1	4	2.73744	2.98744
2	D	CA 20	57	1	3	2.53234	2.78234
2	D	CA 21	9	1	3	2.66959	2.91959
2	D	CA 22	8	1	3	2.17647	2.42647
2	D	CA 23	5	1	3	2.1	2.35
2	D	CA 24	26	1	3	2.50599	2.7599
2	D	CA 25	9	2	6	2.17406	3.42406
2	D	CA 26	7	1	5	3.06823	3.31823
2	D	CA 27	14	1	4	2.24574	2.49574

Table S2.4. Species per consensus area at 40% cutoff of similarity under the loose rule in the Default Analysis at two degrees of grid size. In red, the 29 species with ambiguous membership to consensus areas. Minimum score: species minimum index score in the individual areas aggregated in the consensus area. Maximum score: species maximum index score in the individual areas aggregated in the consensus area.

Consensus Area	Species	Minimum Score	Maximum Score
CA 0	*Adenocalymma ackermannii**	0	0.833
	Adenocalymma apetiolatum	0	0.75
	Adenocalymma apparicianum	0	0.741
	Adenocalymma aurantiacum	0	0.846
	*Adenocalymma bullatum**	0	0.917
	Adenocalymma candolleanum	0	0.831
	Adenocalymma cinereum	0	0.889
	Adenocalymma cristicalyx	0	0.774
	Adenocalymma cymbalum	0	0.802
	*Adenocalymma dichilum**	0	0.875
	*Adenocalymma divaricatum**	0	0.634
	Adenocalymma gibbosum	0	0.714
	Adenocalymma grandifolium	0	0.917
	Adenocalymma hirtum	0	0.762
	*Adenocalymma hypostictum**	0	0.717
	Adenocalymma lineare	0	0.75
	Adenocalymma macrophyllum	0	0.861
	Adenocalymma pubescens	0	0.72
	Adenocalymma salmoneum	0	0.958
	Adenocalymma scabriusculum	0	0.701
	Adenocalymma sessile	0	0.969
	Adenocalymma subsessilifolium	0	0.825
	*Adenocalymma subspicatum**	0	0.804
	Adenocalymma trifoliatum	0	0.904
	Adenocalymma ubatubense	0	0.636
	Amphilophium bauhinioides	0	0.833
	*Amphilophium bracteatum**	0	0.559

*Amphilophium dolichoides**	0	0.514
Amphilophium frutescens	0	0.705
Anemopaegma album	0	0.795
*Anemopaegma citrinum**	0	0.854
Anemopaegma goyazense	0	0.566
Anemopaegma heringeri	0	0.75
Anemopaegma hilarianum	0	0.857
Anemopaegma laeve	0	0.835
Anemopaegma scabriusculum	0	0.814
Anemopaegma setilobum	0	1
Anemopaegma velutinum	0	0.848
Bignonia costata	0	0.731
Cuspidaria argentea	0	0.824
Cuspidaria cratensis	0	0.731
*Cuspidaria lasiantha**	0	0.754
Cuspidaria multiflora	0	0.828
Cuspidaria octoptera	0	0.79
*Dolichandra unguiculata**	0	0.711
Fridericia bahiensis	0	0.721
Fridericia cuneifolia	0	0.839
Fridericia dispar	0	0.656
Fridericia elegans	0	0.719
*Fridericia erubescens**	0	0.601
*Fridericia formosa**	0	0.672
Fridericia leucopogon	0	0.817
Fridericia limae	0	0.811
Fridericia rego	0	0.782
Fridericia simplex	0	0.75
Fridericia subexserta	0	0.667
Fridericia subincana	0	0.796
Fridericia subverticillata	0	0.75
Fridericia trachyphylla	0	0.808
Fridericia tynanthoides	0	0.744
Lundia damazioi	0	0.875
*Lundia gardneri**	0	0.762
*Lundia helicocalyx**	0	0.583
*Lundia obliqua**	0	0.625
Lundia virginalis	0	0.765
*Mansoa hirsuta**	0	0.729
Mansoa hymenaea	0	0.865
Mansoa lanceolata	0	0.759
Mansoa minensis	0	0.813
Mansoa paganuccii	0	0.785
Martinella insignis	0	0.725
Pleonotoma castelnaei	0	0.766

	*Pleonotoma stichadenia**	0	0.81
	Tanaecium cyrtanthum	0	0.788
	Tanaecium neobrasiliense	0	0.756
	Tanaecium paradoxum	0	0.75
	Tanaecium parviflorum	0	0.853
	*Tynanthus fasciculatus**	0	0.827
	Tynanthus labiatus	0	0.778
	Xylophragma corchoroides	0	0.82
	*Xylophragma harleyi**	0	0.732
	Xylophragma heterocalyx	0	0.62
	Xylophragma myrianthum	0	0.5
CA 1	*Adenocalymma bullatum**	0	0.548
	Cuspidaria pulchella	0	0.767
	*Fridericia formosa**	0.646	0.757
	*Lundia obliqua**	0.484	0.847
	Pleonotoma fluminensis	0	0.652
	*Tynanthus fasciculatus**	0.586	0.736
CA 2	*Adenocalymma mirabile*	0	0.74
	*Adenocalymma subspicatum**	0	0.364
	Anemopaegma mirabile	0	0.5
	Fridericia crassa	0.524	0.75
	Fridericia pliciflora	0	0.781
	*Lundia helicocalyx**	0.536	0.881
CA 3	*Amphilophium obovatum*	0.667	0.763
	Amphilophium pauciflorum	0	0.722
	Fridericia grosourdyana	0.705	0.841
	Pleonotoma echitidea	0	0.613
CA 4	*Adenocalymma allamandiflorum*	0	0.634
	Adenocalymma gracielzae	0	0.662
	Adenocalymma magnificum	0	0.552
	Adenocalymma velutinum	0	0.788
	Mansoa angustidens	0	0.4
	Pleonotoma bracteata	0	0.787
	Pyrostegia millingtonioides	0	0.75
CA 5	*Adenocalymma ackermannii**	0	0.75
	*Adenocalymma dichilum**	0	0.688
	*Adenocalymma hypostictum**	0.605	0.833
	*Amphilophium blanchetii**	0	0.7
	Amphilophium perbracteatum	0.625	0.75
	*Lundia gardneri**	0	0.513
	Mansoa ivanii	0.667	0.833
	Mansoa longicalyx	0.625	0.75
	*Xylophragma harleyi**	0	0.388
CA 6	*Adenocalymma divaricatum**	0.654	0.824
	Anemopaegma gracile	0	0.802

	Fridericia erubescens*	0.753	0.867
	Pleonotoma stichadenia*	0	0.777
CA 7	_Bignonia lilacina_	0.658	0.717
	Cuspidaria inaequalis	0.786	0.831
	Lundia densiflora	0.802	0.847
	Tanaecium bilabiatum*	0	0.815
CA 8	_Adenocalymma ackermannii*_	0.75	0.833
	Adenocalymma flavum	0.571	0.688
	Adenocalymma hypostictum*	0.288	0.587
	Martinella insignis*	0	0.405
CA 9	_Adenocalymma coriaceum_	0.697	0.697
	Anemopaegma citrinum*	0.828	0.828
	Cuspidaria lasiantha*	0.803	0.803
CA 10	_Adenocalymma album_	0.857	0.917
	Adenocalymma saulense	0.786	0.833
	Amphilophium cremersii	0	0.632
	Anemopaegma granvillei	0.75	0.792
	Fridericia oligantha	0.359	0.368
	Tynanthus sastrei	0	0.75
CA 11	_Adenocalymma bracteatum_	0.792	0.792
	Anemopaegma arvense	0.776	0.776
	Fridericia craterophora	0.808	0.808
CA 12	_Fridericia floribunda_	0.419	0.556
	Tanaecium caudiculatum	0.75	0.8
	Tynanthus guatemalensis	0.861	0.933
CA 13	_Adenocalymma dusenii*_	0.846	0.846
	Adenocalymma hatschbachii*	0.865	0.865
	Amphilophium bracteatum*	0.647	0.647
	Amphilophium dolichoides*	0.647	0.647
	Amphilophium dusenianum	0.5	0.5
CA 14	_Adenocalymma aspericarpum_	0.603	0.629
	Adenocalymma magdalenense*	0	0.788
	Amphilophium steyermarkii	0	0.571
	Bignonia cuneata	0	0.771
	Bignonia pterocalyx	0.691	0.71
CA 15	_Dolichandra unguiculata*_	0.802	0.802
	Fridericia speciosa	0.669	0.669
	Mansoa glaziovii	0.651	0.651
CA 16	_Bignonia bracteomana_	0.839	0.839
	Fridericia nicotianiflora	0.705	0.705
	Tanaecium affine	0.811	0.811
CA 17	_Adenocalymma magdalenense*_	0	0.652
	Bignonia neouliginosa*	0.5	0.889
	Pachyptera erythraea*	0.711	0.857
	Tanaecium exitiosum*	0	0.786

CA 18	*Anemopaegma paraense*	0.739	0.739
	Lundia erionema	0.798	0.798
	*Tanaecium bilabiatum**	0.799	0.799
CA 19	*Adenocalymma dichilum**	0.758	0.758
	*Amphilophium blanchetii**	0.685	0.685
	*Lundia gardneri**	0.697	0.697
	*Mansoa hirsuta**	0.597	0.597
CA 20	*Fridericia pearcei*	0.848	0.848
	Lundia spruceana	0.841	0.841
	Tanaecium xanthophyllum	0.844	0.844
CA 21	*Adenocalymma dusenii**	1	1
	*Adenocalymma hatschbachii**	0.947	0.947
	Anemopaegma nebulosum	0.722	0.722
CA 22	*Adenocalymma dugandii*	0.719	0.719
	Amphilophium chocoense	0.781	0.781
	*Tanaecium exitiosum**	0.676	0.676
CA 23	*Adenocalymma molle*	0.8	0.8
	Cuspidaria cinerea	0.5	0.5
	Tynanthus densiflorus	0.8	0.8
CA 24	*Adenocalymma paulistarum*	0.84	0.84
	Fridericia mutabilis	0.849	0.849
	Tynanthus micranthus	0.817	0.817
CA 25	*Amphilophium arenarium*	0	0.321
	Amphilophium monophyllum	0.55	0.722
	Anemopaegma salicifolium	0.781	0.821
	Fridericia carichanensis	0	0.303
	Pleonotoma dendrotricha	0	0.688
	Pleonotoma exserta	0.5	0.875
CA 26	*Adenocalymma arthropetiolatum*	0.55	0.55
	Adenocalymma chocoense	0.714	0.714
	*Bignonia neouliginosa**	0.458	0.458
	*Pachyptera erythraea**	0.767	0.767
	Tynanthus croatianus	0.579	0.579
CA 27	*Anemopaegma longipetiolatum*	0.461	0.461
	Fridericia fagoides	0.467	0.467
	Fridericia whitei	0.568	0.568
	Tanaecium tetramerum	0.75	0.75

Table S2.5. Summary of the consensus areas at 40% of cutoff of similarity with the loose rule for the Default Analysis at three degrees. When the column for species is accompanied by a number inside a parenthesis, this indicates the number of higher taxa that participate in the consensus.

Spatial Scale	Analysis	Consensus Area	Size	Individual Areas	Species	Minimum Score	Maximum Score
3	D	CA 0	88	37	17	2.3109	6.01263
3	D	CA 1	237	7	2(3)	2.63879	2.8979
3	D	CA 2	58	28	16	2.07361	4.55947
3	D	CA 3	66	23	19	2.0124	3.5124
3	D	CA 4	24	1	3	2.25928	2.50928
3	D	CA 5	48	110	102	2.1814	20.76971
3	D	CA 6	15	3	6	2.42947	2.67947
3	D	CA 7	38	16	13	2.17574	4.07727
3	D	CA 8	30	23	20	2.11548	4.96222
3	D	CA 9	108	13	7(1)	2.12217	3.37217
3	D	CA 10	26	3	6	2.19583	2.94583
3	D	CA 11	19	16	19	2.01481	4.29814
3	D	CA 12	45	6	6	2.02172	3.02172
3	D	CA 13	8	1	4	2.32813	2.57813
3	D	CA 14	19	7	17	2.33636	5.83034
3	D	CA 15	17	1	4	2.24906	2.49906
3	D	CA 16	13	5	13	3.33889	6.29142
3	D	CA 17	59	2	4	2.15983	2.40983
3	D	CA 18	22	5	7	2.04987	2.54987
3	D	CA 19	28	2	7	2.98892	4.23892
3	D	CA 20	27	2	5	2.74221	3.24221
3	D	CA 21	29	1	3	2.01193	2.26193
3	D	CA 22	150	1	2(1)	2.58829	2.83289
3	D	CA 23	25	1	4	2.8632	3.1132
3	D	CA 24	8	1	3	2.0625	2.3125
3	D	CA 25	16	1	5	3.15538	3.40538
3	D	CA 26	12	1	7	4.57343	4.82343
3	D	CA 27	27	1	3	2.06841	2.31841
3	D	CA 28	19	1	4	2.63827	2.88827
3	D	CA 29	9	1	4	2.39855	2.64855
3	D	CA 30	8	2	7	3.42857	4.42857
3	D	CA 31	15	1	3	2.10795	2.35795
3	D	CA 32	27	1	5	3.78037	4.03037
3	D	CA 33	24	1	3	2.09763	2.34763

Table S2.6. Species per consensus area at 40% cutoff of similarity under the loose rule in the Default Analysis at three degrees of grid size. In red, the 61 species with ambiguous membership to consensus areas. Minimum score: species minimum index score in the individual areas aggregated in the consensus area. Maximum score: species maximum index score in the individual areas aggregated in the consensus area.

Consensus Area	Species	Minimum Score	Maximum Score
CA 0	*Adenocalymma bracteosum*	0	0.785
	*Adenocalymma impressum**	0	0.728
	*Adenocalymma schomburgkii**	0	0.864
	*Amphilophium granulosum**	0	0.811
	Amphilophium racemosum	0	0.861

	*Anemopaegma paraense**	0	0.837
	Bignonia lilacina	0	0.829
	Bignonia nocturna	0	0.785
	Cuspidaria inaequalis	0	0.879
	Fridericia fanshawei	0	0.798
	*Fridericia nigrescens**	0	0.592
	*Fridericia prancei**	0	0.755
	*Fridericia tuberculata**	0	0.756
	Lundia densiflora	0	0.881
	Lundia erionema	0	0.795
	*Pleonotoma clematis**	0	0.794
	Tanaecium bilabiatum	0	0.881
CA 1	*Amphilophium crucigerum*	0	0.891
	Dolichandra unguis-cati	0.836	0.875
	GRP-2	0	0.953
	GRP-15	0	0.939
	GRP-16	0	0.945
CA 2	*Adenocalymma bracteatum*	0	0.882
	Adenocalymma nodosum	0	0.78
	Anemopaegma acutifolium	0	0.845
	Anemopaegma arvense	0	0.908
	Anemopaegma chamberlaynii	0	0.794
	Anemopaegma glaucum	0	0.805
	Cuspidaria bracteata	0	0.7
	*Cuspidaria convoluta**	0	0.667
	Cuspidaria pulchra	0	0.703
	Cuspidaria sceptrum	0	0.787
	Cuspidaria simplicifolia	0	0.632
	Fridericia craterophora	0	0.807
	*Fridericia samydoides**	0	0.817
	Mansoa difficilis	0	0.806
	Perianthomega vellozoi	0	0.65
	Stizophyllum perforatum	0	0.833
CA 3	*Adenocalymma schomburgkii**	0	0.781
	Adenocalymma tanaeciicarpum	0	0.754
	*Amphilophium granulosum**	0	0.69
	Amphilophium magnoliifolium	0	0.729
	Amphilophium pulverulentum	0	0.809
	*Anemopaegma foetidum**	0	0.779
	*Anemopaegma ionanthum**	0	0.517
	Anemopaegma oligoneuron	0	0.823
	*Anemopaegma paraense**	0	0.665
	*Anemopaegma robustum**	0	0.762
	Bignonia sordida	0	0.824
	*Cuspidaria subincana**	0	0.678

	*Dolichandra steyermarkii**	0	0.667
	Fridericia egensis	0	0.78
	*Fridericia nigrescens**	0	0.773
	*Fridericia prancei**	0	0.679
	*Pleonotoma clematis**	0	0.695
	*Pleonotoma jasminifolia**	0	0.662
	Tanaecium duckei	0	0.665
CA 4	*Adenocalymma divaricatum**	0.623	0.623
	*Adenocalymma scabriusculum**	0.82	0.82
	*Fridericia dispar**	0.816	0.816
CA 5	*Adenocalymma alboaurantiacum*	0	0.761
	Adenocalymma aurantiacum	0	0.917
	Adenocalymma bullatum	0	0.75
	Adenocalymma candolleanum	0	0.809
	Adenocalymma cinereum	0	0.833
	Adenocalymma coriaceum	0	0.917
	Adenocalymma cristicalyx	0	0.732
	Adenocalymma cymbalum	0	0.8
	Adenocalymma dichilum	0	0.844
	*Adenocalymma divaricatum**	0	0.815
	Adenocalymma dusenii	0	0.705
	Adenocalymma flavum	0	0.667
	Adenocalymma gibbosum	0	0.667
	Adenocalymma grandifolium	0	0.917
	Adenocalymma hatschbachii	0	0.75
	Adenocalymma hirtum	0	0.667
	Adenocalymma hypostictum	0	0.875
	Adenocalymma macrophyllum	0	0.833
	*Adenocalymma paulistarum**	0	0.685
	Adenocalymma pedunculatum	0	0.736
	Adenocalymma pubescens	0	0.789
	Adenocalymma salmoneum	0	0.833
	*Adenocalymma scabriusculum**	0	0.771
	Adenocalymma sessile	0	0.833
	Adenocalymma subsessilifolium	0	0.958
	Adenocalymma trifoliatum	0	1
	Adenocalymma ubatubense	0	0.75
	Amphilophium bauhinioides	0	0.824
	Amphilophium blanchetii	0	0.792
	Amphilophium bracteatum	0	0.833
	Amphilophium dolichoides	0	0.8
	Amphilophium dusenianum	0	0.909
	Amphilophium frutescens	0	0.625
	Amphilophium scabriusculum	0	0.764

Anemopaegma album	0	0.75
Anemopaegma citrinum	0	0.923
Anemopaegma goyazense	0	0.636
Anemopaegma gracile	0	0.774
Anemopaegma hilarianum	0	0.846
Anemopaegma laeve	0	0.908
*Anemopaegma mirabile**	0	0.688
Anemopaegma nebulosum	0	0.667
Anemopaegma pabstii	0	0.792
Anemopaegma scabriusculum	0	0.875
Anemopaegma setilobum	0	0.833
Anemopaegma velutinum	0	0.815
Bignonia costata	0	0.792
*Cuspidaria argentea**	0	0.846
*Cuspidaria cratensis**	0	0.778
Cuspidaria lasiantha	0	0.875
Cuspidaria multiflora	0	0.813
Cuspidaria octoptera	0	0.906
*Cuspidaria pulchella**	0	0.703
Dolichandra unguiculata	0	0.75
Fridericia bahiensis	0	0.861
Fridericia cuneifolia	0	0.875
*Fridericia dispar**	0	0.623
Fridericia elegans	0	0.75
Fridericia erubescens	0	0.82
Fridericia formosa	0	0.833
Fridericia leucopogon	0	0.844
*Fridericia limae**	0	0.714
Fridericia rego	0	0.774
*Fridericia samydoides**	0	0.705
Fridericia simplex	0	0.803
Fridericia speciosa	0	0.897
Fridericia subexserta	0	0.667
Fridericia subincana	0	0.69
Fridericia trachyphylla	0	0.875
Fridericia tynanthoides	0	0.7
Lundia damazioi	0	0.813
Lundia gardneri	0	0.886
Lundia longa	0	0.546
Lundia obliqua	0	0.853
*Lundia virginalis**	0	0.825
*Mansoa glaziovii**	0	0.757
*Mansoa hirsuta**	0	0.765
Mansoa hymenaea	0	0.63
Mansoa ivanii	0	0.833

	Mansoa lanceolata	0	0.758
	Mansoa longicalyx	0	0.75
	Mansoa minensis	0	0.958
	Mansoa onohualcoides	0	0.598
	Mansoa paganuccii	0	0.776
	Martinella insignis	0	0.75
	Pleonotoma castelnaei	0	0.806
	Pleonotoma fluminensis	0	0.667
	*Pleonotoma orientalis**	0	0.451
	Pleonotoma stichadenia	0	0.793
	*Pleonotoma tetraquetra**	0	0.728
	Tanaecium cyrtanthum	0	0.848
	Tanaecium neobrasiliense	0	0.846
	*Tanaecium paradoxum**	0	0.75
	Tanaecium parviflorum	0	0.845
	*Tynanthus cognatus**	0	0.612
	Tynanthus fasciculatus	0	0.794
	Tynanthus labiatus	0	0.808
	*Tynanthus micranthus**	0	0.717
	Xylophragma corchoroides	0	0.875
	Xylophragma harleyi	0	0.797
	Xylophragma heterocalyx	0	0.705
	*Xylophragma myrianthum**	0	0.766
CA 6	*Amphilophium parkeri**	0.648	0.708
	*Amphilophium porphyrotrichum**	0	0.727
	*Bignonia microcalyx**	0	0.528
	Fridericia mollis	0.487	0.592
	*Fridericia oligantha**	0	0.8
	*Pleonotoma echitidea**	0	0.771
CA 7	*Adenocalymma uleanum*	0	0.821
	Amphilophium cuneifolium	0	0.589
	Amphilophium nunezii	0	0.703
	Anemopaegma insculptum	0	0.642
	Bignonia sanctae	0	0.733
	Bignonia uleana	0	0.906
	Cuspidaria emmonsii	0	0.833
	*Fridericia arthrerion**	0	0.729
	*Fridericia pearcei**	0	0.811
	Fridericia poeppigii	0	0.83
	*Lundia spruceana**	0	0.788
	*Pleonotoma pavettiflora**	0	0.645
	*Tanaecium xanthophyllum**	0	0.871
CA 8	*Adenocalymma arthropetiolatum*	0	0.75
	Adenocalymma aspericarpum	0	0.818
	Adenocalymma chocoense	0	0.792

	Adenocalymma dugandii*	0	0.792
	Adenocalymma magdalenense	0	0.813
	Amphilophium chocoense*	0	0.656
	Amphilophium steyermarkii*	0	0.886
	Anemopaegma karstenii	0	0.653
	Anemopaegma santaritense*	0	0.905
	Anemopaegma villosum*	0	0.75
	Bignonia cuneata	0	0.75
	Bignonia neouliginosa	0	0.917
	Bignonia phellosperma	0	0.938
	Bignonia pterocalyx	0	0.886
	Fridericia oxycarpa	0	0.806
	Pachyptera erythraea	0	0.875
	Tanaecium crucigerum	0	0.786
	Tanaecium exitiosum	0	0.813
	Tynanthus croatianus	0	0.667
	Tynanthus macranthus	0	0.813
CA 9	_Dolichandra steyermarkii*_	0	0.758
	Lundia puberula	0	0.856
	Mansoa alliacea	0	0.763
	Mansoa standleyi	0	0.811
	Martinella obovata	0	0.85
	Pachyptera kerere	0	0.852
	Pleonotoma variabilis	0	0.864
	GRP-26	0	0.863
CA 10	_Cuspidaria pulchella*_	0	0.787
	Fridericia samydoides*	0	0.745
	Lundia nitidula	0.569	0.867
	Lundia virginalis*	0	0.667
	Pleonotoma tetraquetra*	0	0.776
	Xylophragma myrianthum*	0	0.75
CA 11	_Amphilophium arenarium_	0	0.563
	Amphilophium monophyllum	0	0.773
	Amphilophium obovatum	0	0.679
	Amphilophium pauciflorum	0	0.667
	Amphilophium porphyrotrichum*	0	0.611
	Anemopaegma alatum	0	0.548
	Anemopaegma grandifolium	0	0.554
	Anemopaegma jucundum*	0	0.676
	Anemopaegma robustum*	0	0.481
	Anemopaegma salicifolium	0	0.8
	Bignonia microcalyx*	0	0.833
	Cuspidaria monophylla*	0	0.6
	Fridericia carichanensis*	0	0.893
	Fridericia grosourdyana	0	0.833

	Fridericia oligantha*	0	0.385
	Pleonotoma dendrotricha	0	0.7
	Pleonotoma echitidea*	0	0.795
	Pleonotoma exserta	0	0.8
	Tanaecium apiculatum	0	0.7
CA 12	_Amphilophium granulosum*_	0	0.598
	Cuspidaria bracteolata	0	0.68
	Fridericia prancei*	0.602	0.787
	Martinella iquitoensis	0	0.76
	Pleonotoma jasminifolia*	0	0.866
	Tanaecium truncatum	0	0.734
CA 13	_Adenocalymma dugandii*_	0.719	0.719
	Amphilophium chocoense*	0.656	0.656
	Anemopaegma santaritense*	0.453	0.453
	Bignonia magnifica	0.5	0.5
CA 14	_Adenocalymma adenophorum*_	0	0.808
	Adenocalymma cidii*	0	0.643
	Adenocalymma longilineum	0	0.796
	Adenocalymma molle	0	0.792
	Adenocalymma moringifolium	0	0.443
	Amphilophium laeve*	0	0.5
	Amphilophium lohmanniae*	0	0.542
	Amphilophium reticulatum	0	0.667
	Anemopaegma ionanthum*	0	0.396
	Anemopaegma jucundum*	0	0.676
	Cuspidaria cinerea	0	0.75
	Cuspidaria monophylla*	0	0.6
	Cuspidaria subincana*	0	0.454
	Fridericia lauta	0	0.769
	Pachyptera aromatica	0	0.771
	Pleonotoma longiflora	0	0.75
	Tynanthus densiflorus	0	0.75
CA 15	_Adenocalymma adenophorum*_	0.647	0.647
	Amphilophium lohmanniae*	0.721	0.721
	Anemopaegma foetidum*	0.423	0.423
	Cuspidaria subincana*	0.458	0.458
CA 16	_Adenocalymma apparicianum_	0	0.5
	Adenocalymma mirabile	0	0.861
	Adenocalymma subspicatum	0	0.722
	Anemopaegma mirabile*	0	0.667
	Cuspidaria argentea*	0	1
	Cuspidaria cratensis*	0	0.895
	Fridericia crassa	0.5	0.722
	Fridericia limae*	0	0.473
	Fridericia pliciflora	0	0.75

	Lundia helicocalyx	0.591	0.857
	*Mansoa hirsuta**	0	0.406
	*Pleonotoma orientalis**	0	0.311
	*Tanaecium paradoxum**	0	0.563
CA 17	*Adenocalymma biternatum*	0.754	0.775
	*Adenocalymma impressum**	0.723	0.731
	Fridericia spicata	0	0.748
	*Fridericia tuberculata**	0	0.653
CA 18	*Amphilophium sandwithii*	0	0.818
	Anemopaegma longipetiolatum	0	0.742
	Fridericia caudigera	0	0.919
	Fridericia fagoides	0	0.733
	Fridericia truncata	0	0.513
	Fridericia whitei	0	0.548
	Tanaecium tetramerum	0	0.75
CA 19	*Adenocalymma paulistarum**	0	0.737
	Anemopaegma prostratum	0	0.708
	Bignonia binata	0.654	0.767
	*Cuspidaria convoluta**	0.507	0.769
	Fridericia mutabilis	0	0.769
	*Fridericia samydoides**	0.654	0.746
	*Tynanthus micranthus**	0	0.737
CA 20	*Amphilophium dasytrichum*	0.704	0.769
	*Fridericia arthrerion**	0.589	0.592
	*Pleonotoma pavettiflora**	0.724	0.74
	*Tanaecium xanthophyllum**	0	0.461
	Xylophragma platyphyllum	0.614	0.644
CA 21	*Adenocalymma subincanum*	0.606	0.606
	Lundia laevis	0.647	0.647
	Tanaecium ornithophilum	0.759	0.759
CA 22	*Bignonia sciuripabulum*	0.827	0.827
	Pyrostegia venusta	0.861	0.861
	GRP-14	0.895	0.895
CA 23	*Cuspidaria convoluta**	0.584	0.584
	*Fridericia samydoides**	0.88	0.88
	*Mansoa glaziovii**	0.77	0.77
	*Tynanthus cognatus**	0.629	0.629
CA 24	*Adenocalymma calcareum*	0.5	0.5
	*Adenocalymma cidii**	0.625	0.625
	*Amphilophium laeve**	0.938	0.938
CA 25	*Bignonia potosina**	0.526	0.526
	Fridericia costaricensis	0.639	0.639
	*Fridericia floribunda**	0.662	0.662
	Tanaecium caudiculatum	0.656	0.656
	Tynanthus guatemalensis	0.672	0.672

CA 26	*Adenocalymma allamandiflorum*	0.768	0.768
	Adenocalymma gracielzae	0.586	0.586
	Adenocalymma magnificum	0.688	0.688
	Adenocalymma velutinum	0.583	0.583
	Mansoa angustidens	0.574	0.574
	Pleonotoma bracteata	0.625	0.625
	Pyrostegia millingtonioides	0.75	0.75
CA 27	*Amphilophium carolinae*	0.742	0.742
	Bignonia callistegioides	0.75	0.75
	Dolichandra cynanchoides	0.576	0.576
CA 28	*Anemopaegma colombianum*	0.724	0.724
	*Bignonia bracteomana**	0.517	0.517
	*Tanaecium affine**	0.635	0.635
	Tynanthus panurensis	0.762	0.762
CA 29	*Amphilophium steyermarkii**	0.556	0.556
	Anemopaegma rugosum	0.611	0.611
	*Anemopaegma villosum**	0.667	0.667
	*Fridericia carichanensis**	0.565	0.565
CA 30	*Adenocalymma album*	0.75	1
	Adenocalymma saulense	0	0.75
	Amphilophium cremersii	0.571	0.595
	*Amphilophium parkeri**	0	0.583
	Anemopaegma granvillei	0	0.813
	*Fridericia oligantha**	0.5	0.875
	Tynanthus sastrei	0.625	0.75
CA 31	*Amphilophium buccinatorium*	0.783	0.783
	*Fridericia floribunda**	0.708	0.708
	*Fridericia viscida**	0.616	0.616
CA 32	*Bignonia bracteomana**	0.815	0.815
CA 33	Fridericia nicotianiflora	0.759	0.759
	*Fridericia pearcei**	0.723	0.723
	*Lundia spruceana**	0.738	0.738
	*Tanaecium affine**	0.745	0.745
	Amphilophium laxiflorum	0.683	0.683
	*Bignonia potosina**	0.689	0.689
	*Fridericia viscida**	0.726	0.726

Table S2.7. List of the 97 species that do not give score to any pattern of endemism in the Default analysis. Note that all the disjunct species that were filled manually and referred in Table S1.1 (Appendix S1) are in this list.

Species
Adenocalymma albiflorum
Adenocalymma apurense
Adenocalymma bracteolatum
Adenocalymma cladotrichum
Adenocalymma contractum
Adenocalymma flaviflorum
Adenocalymma juliae
Adenocalymma marginatum
Adenocalymma nervosum
Adenocalymma patulum
Adenocalymma peregrinum
Adenocalymma sastrei
Adenocalymma validum
Amphilophium aschersonii
Amphilophium campinae
Amphilophium ecuadorense
Amphilophium elongatum
Amphilophium falcatum
Amphilophium gnaphalanthum
Amphilophium lactiflorum
Amphilophium mansoanum
Amphilophium occidentale
Amphilophium paniculatum
Amphilophium pannosum
Amphilophium pilosum
Amphilophium rodriguesii
Amphilophium stamineum
Anemopaegma brevipes
Anemopaegma chrysanthum
Anemopaegma chrysoleucum
Anemopaegma flavum
Anemopaegma floridum
Anemopaegma longidens
Anemopaegma orbiculatum
Anemopaegma parkeri
Anemopaegma patelliforme
Anemopaegma puberulum
Bignonia aequinoctialis
Bignonia campanulata
Bignonia capreolata
Bignonia cararensis
Bignonia corymbosa
Bignonia decora
Bignonia diversifolia
Bignonia hyacinthina
Bignonia longiflora
Bignonia neoheterophylla
Bignonia noterophila
Bignonia prieurii
Bignonia ramentacea
Callichlamys latifolia
Cuspidaria floribunda
Cuspidaria lachnaea
Cuspidaria lateriflora
Cuspidaria weberbaueri
Dolichandra chodatii
Dolichandra dentata
Dolichandra hispida
Dolichandra quadrivalvis
Dolichandra uncata
Fridericia candicans
Fridericia chica
Fridericia cinerea
Fridericia cinnamomea
Fridericia conjugata
Fridericia florida
Fridericia japurensis
Fridericia mollissima
Fridericia patellifera
Fridericia platyphylla
Fridericia podopogon
Fridericia pubescens
Fridericia schumanniana
Fridericia trailii
Fridericia triplinervia
Lundia corymbifera
Manaosella cordifolia
Mansoa gentryi
Mansoa parvifolia
Mansoa sagotii
Mansoa verrucifera
Pachyptera ventricosa
Pleonotoma fissicalyx
Pleonotoma melioides
Stizophyllum inaequilaterum
Stizophyllum riparium
Tanaecium dichotomum
Tanaecium jaroba
Tanaecium pyramidatum
Tanaecium revillae
Tanaecium selloi
Tanaecium tetragonolobum
Tynanthus polyanthus
Tynanthus pubescens
Tynanthus schumannianus
Xylophragma pratense
Xylophragma seemannianum

Table S2.8. Summary of the consensus areas at 40% of cutoff of similarity with the loose rule for the Strict Analysis at one degrees.

Spatial Scale	Analysis	Consensus Area	Size	Individual Areas	Species	Minimum Score	Maximum Score
1	S	CA 0	31	2	4	2.50319	2.75319
1	S	CA 1	18	1	4	3.14999	3.66999
1	S	CA 2	7	1	3	2.47321	2.72321

1	S	CA 3	7	1	3	2.32571	2.48571
1	S	CA 4	14	1	3	2.4381	2.6881
1	S	CA 5	7	1	3	2.38839	2.63839
1	S	CA 6	6	1	3	2.54762	2.79762

Table S2.9. Species per consensus area at 40% cutoff of similarity under the loose rule in the Strict Analysis at one degrees of grid size. Minimum score: species minimum index score in the individual areas aggregated in the consensus area. Maximum score: species maximum index score in the individual areas aggregated in the consensus area.

Consensus Area	Species	Minimum Score	Maximum Score
CA 0	*Adenocalymma grandifolium*	0.846	0.87
	Adenocalymma trifoliatum	0	0.894
	Fridericia leucopogon	0.784	0.836
	Lundia damazioi	0	0.797
CA 1	*Adenocalymma cinereum*	0.732	0.732
	Adenocalymma macrophyllum	0.895	0.895
	Adenocalymma salmoneum	0.932	0.932
	Anemopaegma setilobum	0.861	0.861
CA 2	*Adenocalymma molle*	0.844	0.844
	Amphilophium reticulatum	0.786	0.786
	Tynanthus densiflorus	0.844	0.844
CA 3	*Fridericia elegans*	0.75	0.75
	Fridericia subexserta	0.786	0.786
	Fridericia subverticillata	0.7	0.7
CA 4	*Adenocalymma album*	0.933	0.933
	Adenocalymma saulense	0.683	0.683
	Tynanthus sastrei	0.821	0.821
CA 5	*Amphilophium perbracteatum*	0.821	0.821
	Mansoa ivanii	0.781	0.781
	Mansoa longicalyx	0.786	0.786
CA 6	*Adenocalymma apetiolatum*	0.917	0.917
	Adenocalymma lineare	0.917	0.917
	Tynanthus espiritosantensis	0.714	0.714

Table S2.10. Summary of the consensus areas at 40% of cutoff of similarity with the loose rule for the Strict Analysis at two degrees.

Spatial Scale	Analysis	Consensus Area	Size	Individual Areas	Species	Minimum Score	Maximum Score
2	S	CA 0	29	38	35	2.69444	9.52832
2	S	CA 1	19	2	5	3.10328	3.35328
2	S	CA 2	18	3	5	2.25699	3.25699
2	S	CA 3	167	2	4	2.39523	2.64523
2	S	CA 4	11	1	3	2.38622	2.63622
2	S	CA 5	37	2	4	2.28389	2.5338
2	S	CA 6	16	1	3	2.48727	2.73727
2	S	CA 7	11	2	6	3.42947	3.92947
2	S	CA 8	26	1	3	2.50599	2.75599
2	S	CA 9	135	1	3	2.33658	2.58658
2	S	CA 10	9	1	3	2.66959	2.91959

2	S	CA 11	10	1	4	3.07095	3.32095
2	S	CA 12	47	1	3	2.49357	2.74357
2	S	CA 13	25	1	3	3.07095	3.32095
2	S	CA 14	44	1	3	2.35441	2.60441
2	S	CA 15	5	1	3	2.54242	2.79242
2	S	CA 16	8	1	4	3.06597	3.31597
2	S	CA 17	5	1	4	2.89675	3.14675
2	S	CA 18	6	1	7	5.19744	5.44744
2	S	CA 19	20	1	3	2.32614	2.57614
2	S	CA 20	5	1	4	3.55	3.8
2	S	CA 21	57	1	3	2.53234	2.78234

Table S2.11. Species per consensus area at 40% cutoff of similarity under the loose rule in the Strict Analysis at two degrees of grid size. In red, the 11 species with ambiguous membership to consensus areas. Minimum score: species minimum index score in the individual areas aggregated in the consensus area. Maximum score: species maximum index score in the individual areas aggregated in the consensus area.

Consensus Area	Species	Minimum Score	Minimum Score
CA 0	*Adenocalymma apetiolatum*	0	0.667
	Adenocalymma aurantiacum	0	1
	Adenocalymma bullatum	0	0.778
	Adenocalymma cinereum	0	0.938
	Adenocalymma cymbalum	0	0.782
	Adenocalymma grandifolium	0	0.917
	Adenocalymma lineare	0	0.667
	Adenocalymma macrophyllum	0	0.906
	Adenocalymma salmoneum	0	0.958
	Adenocalymma sessile	0	0.969
	Adenocalymma subsessilifolium	0	0.867
	Amphilophium bauhinioides	0	0.833
	Amphilophium frutescens	0	0.853
	Anemopaegma citrinum	0	0.854
	Anemopaegma heringeri	0	0.714
	Anemopaegma hilarianum	0	0.907
	Anemopaegma setilobum	0	1
	Cuspidaria lasiantha	0	0.718
	Cuspidaria octoptera	0	0.914
	Fridericia cuneifolia	0	0.838
	Fridericia elegans	0	0.667
	Fridericia leucopogon	0	0.81
	Fridericia rego	0	0.737
	Fridericia subincana	0	0.875
	Fridericia trachyphylla	0	0.864
	Fridericia tynanthoides	0	0.782
	Lundia damazioi	0	0.875
	Lundia virginalis	0	0.722
	Mansoa hymenaea	0	0.84
	Mansoa lanceolata	0	0.806
	Mansoa minensis	0	0.813
	Pleonotoma stichadenia	0	0.754
	Tanaecium neobrasiliense	0	0.756
	Tynanthus labiatus	0	0.821
	Xylophragma corchoroides	0	0.9
CA 1	*Adenocalymma dichilum*	0.853	0.853
	Anemopaegma album	0.731	0.763
	Anemopaegma velutinum	0.744	0.808

	Lundia gardneri	0	0.792
	Tanaecium neobrasiliense	0	0.679
CA 2	*Adenocalymma bullatum*	0	0.75
	Cuspidaria pulchella	0	0.767
	Fridericia formosa	0.683	0.757
	Lundia obliqua	0	0.847
	Tynanthus fasciculatus	0.736	0.8
CA 3	*Bignonia lilacina*	0	0.717
	Cuspidaria inaequalis	0.791	0.831
	Lundia densiflora	0.799	0.847
	Tanaecium bilabiatum	0	0.829
CA 4	*Adenocalymma hirtum*	0.795	0.795
	Amphilophium frutescens	0.86	0.86
	Fridericia subincana	0.731	0.731
CA 5	*Adenocalymma pubescens*	0.72	0.747
	Anemopaegma scabriusculum	0.806	0.814
	Fridericia bahiensis	0	0.826
	Pleonotoma castelnaei	0	0.75
CA 6	*Adenocalymma aspericarpum*	0.859	0.859
	Amphilophium steyermarkii	0.779	0.779
	Bignonia pterocalyx	0.848	0.848
CA 7	*Adenocalymma ackermannii*	0	0.75
	Adenocalymma hypostictum	0.674	0.833
	Amphilophium blanchetii	0	0.7
	Amphilophium perbracteatum	0.667	0.688
	Mansoa ivanii	0.722	0.75
	Mansoa longicalyx	0.667	0.688
CA 8	*Adenocalymma paulistarum*	0.84	0.84
	Fridericia mutabilis	0.849	0.849
	Tynanthus micranthus	0.817	0.817
CA 9	*Anemopaegma paraense*	0.739	0.739
	Lundia erionema	0.798	0.798
	Tanaecium bilabiatum	0.799	0.799
CA 10	*Adenocalymma dusenii*	1	1
	Adenocalymma hatschbachii	0.947	0.947
	Anemopaegma nebulosum	0.722	0.722
CA 11	*Adenocalymma mirabile*	0.74	0.74
	Fridericia crassa	0.725	0.725
	Fridericia pliciflora	0.725	0.725
	Lundia helicocalyx	0.881	0.881
CA 12	*Adenocalymma divaricatum*	0.824	0.824
	Anemopaegma gracile	0.802	0.802
	Fridericia erubescens	0.867	0.867
CA 13	*Adenocalymma candolleanum*	0.692	0.692
	Fridericia limae	0.863	0.863
	Mansoa paganuccii	0.782	0.782
CA 14	*Bignonia bracteomana*	0.839	0.839
	Fridericia nicotianiflora	0.705	0.705
	Tanaecium affine	0.811	0.811
CA 15	*Adenocalymma arthropetiolatum*	0.833	0.833
	Adenocalymma chocoense	0.8	0.8
	Tynanthus croatianus	0.909	0.909
CA 16	*Amphilophium monophyllum*	0.722	0.722
	Anemopaegma salicifolium	0.781	0.781
	Pleonotoma dendrotricha	0.688	0.688
	Pleonotoma exserta	0.875	0.875

CA 17	*Adenocalymma apetiolatum*	0.7	0.7
	Adenocalymma hirtum	0.679	0.679
	Adenocalymma lineare	0.7	0.7
	Martinella insignis	0.818	0.818
CA 18	*Adenocalymma bullatum*	0.808	0.808
	Adenocalymma grandifolium	0.8	0.8
	Anemopaegma heringeri	0.75	0.75
	Bignonia costata	0.731	0.731
	Fridericia elegans	0.692	0.692
	Fridericia subexserta	0.667	0.667
	Fridericia subverticillata	0.75	0.75
CA 19	*Adenocalymma subspicatum*	0.713	0.713
	Cuspidaria argentea	0.83	0.83
	Cuspidaria cratensis	0.784	0.784
CA 20	*Adenocalymma album*	1	1
	Adenocalymma saulense	0.9	0.9
	Anemopaegma granvillei	0.85	0.85
	Tynanthus sastrei	0.8	0.8
CA 21	*Fridericia pearcei*	0.848	0.848
	Lundia spruceana	0.841	0.841
	Tanaecium xanthophyllum	0.844	0.844

Table S2.12. Summary of the consensus areas at 40% of cutoff of similarity with the loose rule for the Strict Analysis at three degrees.

Spatial Scale	Analysis	Consensus Area	Size	Individual Areas	Species	Minimum Score	Maximum Score
3	S	CA 0	36	56	37	2.24894	7.54386
3	S	CA 1	26	47	53	2.29716	14.00688
3	S	CA 2	90	34	13	2.51735	6.01263
3	S	CA 3	237	6	5	2.23876	3.73876
3	S	CA 4	14	1	4	2.90583	3.15583
3	S	CA 5	17	6	6	2.23876	3.73876
3	S	CA 6	25	5	7	2.37473	4.17455
3	S	CA 7	13	1	5	3.51893	3.76893
3	S	CA 8	7	2	6	3.89103	4.14103
3	S	CA 9	17	3	5	2.47059	3.97059
3	S	CA 10	27	2	5	2.40182	3.90182
3	S	CA 11	42	4	8	3.23329	4.73329
3	S	CA 12	107	9	5	2.54709	3.29709
3	S	CA 13	7	2	5	3.58494	3.83494
3	S	CA 14	9	1	4	2.99778	3.24778
3	S	CA 15	5	1	3	2.27727	2.52727
3	S	CA 16	7	3	3	2.0625	2.3125
3	S	CA 17	10	1	3	2.525	2.775
3	S	CA 18	10	2	5	3.64722	3.89722
3	S	CA 19	9	1	4	3.28636	3.53363
3	S	CA 20	4	1	4	3.3125	3.5625
3	S	CA 21	87	1	3	2.34352	2.59352
3	S	CA 22	6	2	5	2.29167	3.54167
3	S	CA 23	31	1	5	3.93021	4.18021
3	S	CA 24	11	1	3	2.24513	2.49513
3	S	CA 25	4	1	3	2.5625	2.8125
3	S	CA 26	12	1	3	2.56038	2.81038
3	S	CA 27	7	1	5	3.78214	4.03214

3	S	CA 28	39	1	3	2.40214	2.65214
3	S	CA 29	47	1	3	2.33291	2.58291
3	S	CA 30	12	1	3	2.33636	2.58636
3	S	CA 31	20	1	3	2.50272	2.75272
3	S	CA 32	4	1	3	2.51389	2.76389
3	S	CA 33	6	1	4	3.21875	3.46875
3	S	CA 34	150	1	3	2.58289	2.83289

Table S2.13. Species per consensus area at 40% cutoff of similarity under the loose rule in the Strict Analysis at three degrees of grid size. In red, the 41 species with ambiguous membership to consensus areas. Minimum score: species minimum index score in the individual areas aggregated in the consensus area. Maximum score: species maximum index score in the individual areas aggregated in the consensus area.

Consensus Area	Species	Minimum Score	Maximum Score
CA 0	*Adenocalymma candolleanum*	0	0.821
	Adenocalymma cristicalyx	0	0.732
	Adenocalymma cymbalum	0	0.705
	Adenocalymma dichilum	0	0.958
	Adenocalymma divaricatum	0	0.898
	Adenocalymma hypostictum	0	0.781
	Adenocalymma pubescens	0	0.875
	Adenocalymma scabriusculum	0	0.716
	Amphilophium blanchetii	0	0.85
	Anemopaegma album	0	0.783
	Anemopaegma gracile	0	0.745
	Anemopaegma laeve	0	0.939
	Anemopaegma mirabile	0	0.714
	Anemopaegma pabstii	0	0.855
	Anemopaegma scabriusculum	0	0.895
	Anemopaegma velutinum	0	0.932
	Cuspidaria argentea	0	0.909
	Cuspidaria cratensis	0	0.826
	Cuspidaria lasiantha	0	0.803
	Cuspidaria multiflora	0	1
	Fridericia bahiensis	0	0.906
	Fridericia dispar	0	0.719
	Fridericia erubescens	0	0.929
	Fridericia limae	0	0.859
	Fridericia simplex	0	0.893
	Lundia gardneri	0	0.941
	Mansoa hirsuta	0	0.909
	Mansoa ivanii	0	0.833
	Mansoa longicalyx	0	0.75
	Mansoa paganuccii	0	0.904
	Pleonotoma castelnaei	0	0.886
	Pleonotoma stichadenia	0	0.779
	Tanaecium cyrtanthum	0	0.875
	Tanaecium neobrasiliense	0	0.765
	Tanaecium paradoxum	0	0.786

	Tanaecium parviflorum	0	0.845
	Xylophragma harleyi	0	0.87
CA 1	*Adenocalymma aurantiacum*	0	0.917
	Adenocalymma bullatum	0	0.875
	Adenocalymma cinereum	0	0.9
	Adenocalymma coriaceum	0	0.696
	Adenocalymma cymbalum	0	0.833
	Adenocalymma gibbosum	0	0.7
	Adenocalymma grandifolium	0	1
	Adenocalymma hirtum	0	0.725
	Adenocalymma macrophyllum	0	0.9
	Adenocalymma salmoneum	0	0.9
	Adenocalymma sessile	0	0.9
	Adenocalymma subsessilifolium	0	0.909
	Adenocalymma trifoliatum	0	0.75
	Adenocalymma ubatubense	0	0.875
	Amphilophium bauhinioides	0	0.923
	Amphilophium bracteatum	0	0.929
	Amphilophium dolichoides	0	0.8
	Amphilophium frutescens	0	0.75
	Anemopaegma album	0	0.661
	Anemopaegma citrinum	0	0.958
	Anemopaegma hilarianum	0	0.958
	Anemopaegma setilobum	0	0.9
	Bignonia costata	0	0.938
	Cuspidaria lasiantha	0	0.893
	Cuspidaria octoptera	0	0.825
	Cuspidaria pulchella	0	0.677
	Dolichandra unguiculata	0	0.938
	Fridericia cuneifolia	0	0.776
	Fridericia elegans	0	0.8
	Fridericia formosa	0	0.833
	Fridericia leucopogon	0	0.893
	Fridericia rego	0	0.896
	Fridericia speciosa	0	0.879
	Fridericia subexserta	0	0.75
	Fridericia subincana	0	0.9
	Fridericia trachyphylla	0	0.95
	Fridericia tynanthoides	0	0.7
	Lundia damazioi	0	0.864
	Lundia gardneri	0	0.727
	Lundia obliqua	0	0.792
	Lundia virginalis	0	0.914
	Mansoa glaziovii	0	0.679
	Mansoa hymenaea	0	0.813
	Mansoa lanceolata	0	0.875
	Mansoa minensis	0	0.846
	Pleonotoma stichadenia	0	0.72
	Pleonotoma tetraquetra	0	0.75
	Tanaecium neobrasiliense	0	0.75
	Tynanthus fasciculatus	0	0.885
	Tynanthus labiatus	0	0.833

	Xylophragma corchoroides	0	0.821
	Xylophragma harleyi	0	0.797
	Xylophragma heterocalyx	0	0.667
CA 2	*Adenocalymma bracteosum*	0	0.78
	Adenocalymma impressum	0	0.848
	Amphilophium granulosum	0	0.846
	Amphilophium racemosum	0	0.856
	Anemopaegma paraense	0	0.832
	Bignonia lilacina	0	0.829
	Bignonia nocturna	0	0.75
	Cuspidaria inaequalis	0	0.878
	Fridericia fanshawei	0	0.821
	Fridericia tuberculata	0	0.849
	Lundia densiflora	0	0.881
	Lundia erionema	0	0.795
	Tanaecium bilabiatum	0	0.881
CA 3	*Amphilophium crucigerum*	0	0.891
	Dolichandra unguis	0.836	0.875
	GRP-2	0	0.953
	GRP-15	0	0.939
	GRP-16	0	0.945
CA 4	*Cuspidaria octoptera*	0.732	0.732
	Lundia virginalis	0.694	0.694
	Pleonotoma tetraquetra	0.676	0.676
	Xylophragma myrianthum	0.804	0.804
CA 5	*Adenocalymma allamandiflorum*	0	0.938
	Adenocalymma gracielzae	0	0.771
	Adenocalymma magnificum	0	1
	Mansoa angustidens	0	0.828
	Pleonotoma bracteata	0	0.75
	Pyrostegia millingtonioides	0	0.714
CA 6	*Cuspidaria pulchella*	0	0.727
	Dolichandra unguiculata	0	0.744
	Fridericia samydoides	0	0.883
	Fridericia speciosa	0	0.838
	Lundia obliqua	0	0.75
	Mansoa glaziovii	0.744	0.821
	Tynanthus cognatus	0	0.698
CA 7	*Adenocalymma paulistarum*	0.661	0.661
	Amphilophium bracteatum	0.685	0.685
	Cuspidaria pulchella	0.742	0.742
	Lundia obliqua	0.769	0.769
	Tynanthus micranthus	0.661	0.661
CA 8	*Adenocalymma adenophorum*	0.808	0.917
	Adenocalymma molle	0.792	0.792
	Amphilophium reticulatum	0.667	0.667
	Cuspidaria cinerea	0	0.769
	Pleonotoma longiflora	0	0.875
	Tynanthus densiflorus	0.75	0.75
CA 9	*Adenocalymma coriaceum*	0.75	0.941
	Amphilophium scabriusculum	0.667	0.779
	Anemopaegma citrinum	0	0.75

	Cuspidaria lasiantha	0.676	0.75
	Xylophragma corchoroides	0	0.821
CA 10	*Bignonia bracteomana*	0.813	0.815
	Fridericia nicotianiflora	0.759	0.802
	Fridericia pearcei	0	0.723
	Lundia spruceana	0	0.738
	Tanaecium affine	0.745	0.787
CA 11	*Adenocalymma bracteatum*	0	0.872
	Adenocalymma nodosum	0	0.78
	Anemopaegma acutifolium	0	0.845
	Anemopaegma arvense	0.762	0.821
	Anemopaegma glaucum	0	0.781
	Cuspidaria sceptrum	0	0.816
	Fridericia craterophora	0.731	0.815
	Stizophyllum perforatum	0	0.747
CA 12	*Lundia puberula*	0	0.856
	Martinella obovata	0.797	0.85
	Pachyptera kerere	0	0.852
	Pleonotoma variabilis	0	0.864
	GRP-26	0	0.863
CA 13	*Amphilophium arenarium*	0.688	0.833
	Amphilophium monophyllum	0.667	0.731
	Anemopaegma salicifolium	0.75	0.8
	Pleonotoma dendrotricha	0.667	0.7
	Pleonotoma exserta	0.75	0.8
CA 14	*Adenocalymma bullatum*	0.667	0.667
	Cuspidaria pulchella	0.72	0.72
	Fridericia formosa	0.722	0.722
	Lundia obliqua	0.889	0.889
CA 15	*Adenocalymma dugandii*	0.727	0.727
	Pachyptera erythraea	0.8	0.8
	Tanaecium exitiosum	0.75	0.75
CA 16	*Amphilophium obovatum*	0.708	0.708
	Amphilophium pauciflorum	0.667	0.667
	Fridericia grosourdyana	0.688	0.885
CA 17	*Adenocalymma aspericarpum*	0.85	0.85
	Adenocalymma magdalenense	0.75	0.75
	Bignonia pterocalyx	0.925	0.925
CA 18	*Adenocalymma dusenii*	0.684	0.75
	Adenocalymma hatschbachii	0.667	0.667
	Amphilophium bracteatum	0.763	0.763
	Amphilophium dolichoides	0.696	0.75
	Amphilophium dusenianum	0.717	0.85
CA 19	*Adenocalymma subspicatum*	0.722	0.722
	Cuspidaria argentea	1	1
	Cuspidaria cratensis	0.895	0.895
	Fridericia pliciflora	0.667	0.667
CA 20	*Adenocalymma album*	1	1
	Adenocalymma saulense	0.75	0.75
	Anemopaegma granvillei	0.813	0.813
	Tynanthus sastrei	0.75	0.75
CA 21	*Mansoa alliacea*	0.742	0.742

	Mansoa standleyi	0.811	0.811
	Pleonotoma variabilis	0.79	0.79
CA 22	*Adenocalymma flavum*	0	0.75
	Adenocalymma hirtum	0	0.875
	Amphilophium frutescens	0.667	0.917
	Fridericia tynanthoides	0	0.833
	Martinella insignis	0.75	0.875
CA 23	*Bignonia uleana*	0.731	0.731
	Fridericia arthrerion	0.729	0.729
	Fridericia pearcei	0.811	0.811
	Lundia spruceana	0.788	0.788
	Tanaecium xanthophyllum	0.871	0.871
CA 24	*Fridericia floribunda*	0.768	0.768
	Tanaecium caudiculatum	0.727	0.727
	Tynanthus guatemalensis	0.75	0.75
CA 25	*Adenocalymma arthropetiolatum*	0.875	0.875
	Adenocalymma chocoense	0.938	0.938
	Tynanthus croatianus	0.75	0.75
CA 26	*Adenocalymma paulistarum*	0.875	0.875
	Fridericia mutabilis	0.865	0.865
	Tynanthus micranthus	0.82	0.82
CA 27	*Adenocalymma magdalenense*	0.857	0.857
	Bignonia neouliginosa	0.857	0.857
	Bignonia pterocalyx	0.675	0.675
	Pachyptera erythraea	0.714	0.714
	Tanaecium exitiosum	0.679	0.679
CA 28	*Adenocalymma bracteatum*	0.802	0.802
	Anemopaegma chamberlaynii	0.794	0.794
	Mansoa difficilis	0.806	0.806
CA 29	*Adenocalymma schomburgkii*	0.735	0.735
	Bignonia sordida	0.824	0.824
	Fridericia nigrescens	0.773	0.773
CA 30	*Adenocalymma longilineum*	0.796	0.796
	Fridericia lauta	0.769	0.769
	Pachyptera aromatica	0.771	0.771
CA 31	*Adenocalymma uleanum*	0.838	0.838
	Bignonia uleana	0.815	0.815
	Cuspidaria emmonsii	0.85	0.85
CA 32	*Adenocalymma dusenii*	0.889	0.889
	Adenocalymma hatschbachii	0.875	0.875
	Anemopaegma nebulosum	0.75	0.75
CA 33	*Adenocalymma mirabile*	0.719	0.719
	Fridericia crassa	0.833	0.833
	Fridericia pliciflora	0.75	0.75
	Lundia helicocalyx	0.917	0.917
CA 34	*Bignonia sciuripabulum*	0.827	0.827
	Pyrostegia venusta	0.861	0.861
	GRP-14	0.895	0.895

Appendix 3

Unraveling distribution patterns of Neotropical lianas: An analysis of endemicity of tribe Bignonieae (Bignoniaceae)

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Supporting information: Appendix S3

Comparison among consensus areas considering different spatial scales and elevation.

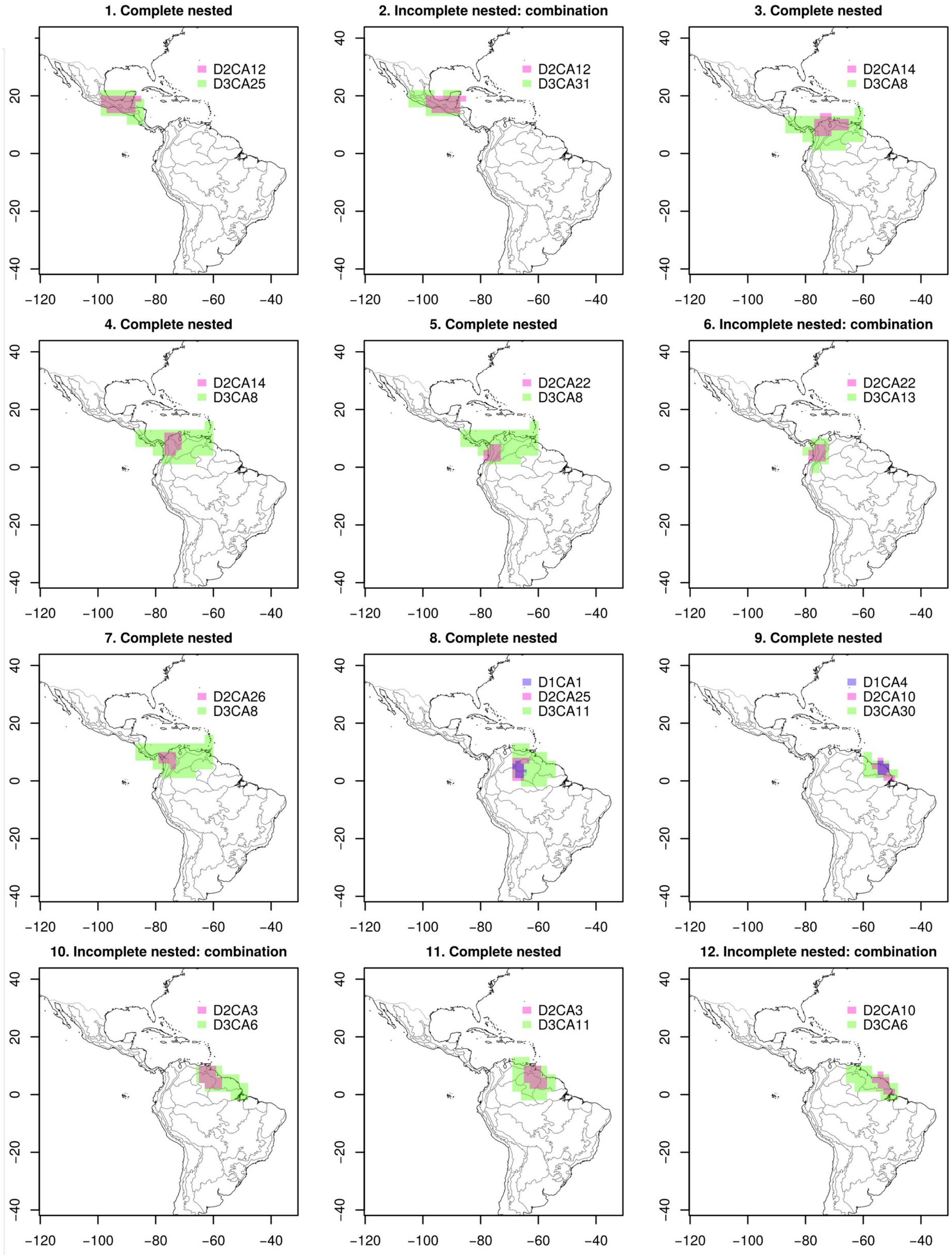
Table S3.1. Effect of spatial scale over species composition among the areas located in the same geographical region at the Default analysis. **Region:** geographical region. **Map ID***:* number of the corresponding map that depicts the referred areas in the Figure S1 (Below). **1, 2** and **3**: spatial scale in degrees at which the area is recovered. **Class**: The kind of effect over species composition among the compared areas: Identical: The areas are composed by the same species across scales. Complete nested: A pattern of successive and complete inclusion of defining species from areas at the finer scales into areas at the broader scales: Incomplete nested combination: patterns at successive spatial scales are included but species composition might change by losing or adding species at specific spatial scales. Reverse nested: a patterns from a finer spatial scale includes a pattern from a coarser scale. **Description:** refers to the specific effect observe between the areas. **Species:** it refers to the species that are shared or lost in the incomplete nested patterns.

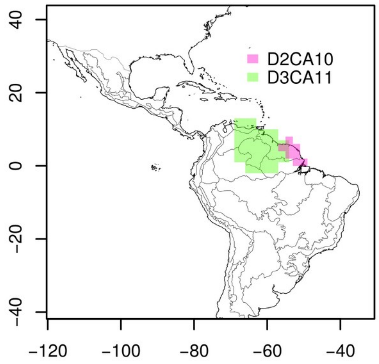
Geographic sector	Map ID	1	2	3	Class	Description	Species
Central America centered	1		D2CA12	D3CA25	Complete nested	Species sequentially included in broader patterns.	
	2		D2CA12	D3CA31	Incomplete nested: combination	Species from different scales are mixed. Only few species are shared among patterns.	Shared: *Fridericia floribunda*
Northwestern South America centered	3		D2CA14	D3CA8	Complete nested	Species sequentially included in broader patterns.	
	4		D2CA17	D3CA8	Complete nested	Species sequentially included in broader patterns.	
	5		D2CA22	D3CA8	Complete nested	Species sequentially included in broader patterns.	
	6		S2CA22	D3CA13	Incomplete nested: combination	Species from different scales are mixed. Only few species are shared among patterns.	Shared: *Adenocalymma divaricatum, Amphilophium chocoense*
	7		D2CA26	D3CA8	Complete nested	Species sequentially included in broader patterns.	
Guiana Shield centered	8	D1CA1	D2CA25	D3CA11	Complete nested	Species sequentially included in broader patterns.	
	9	D1CA4	D2CA10	D3CA30	Complete nested	Species sequentially included in broader patterns.	
	10		D2CA3	D3CA6	Incomplete nested: combination	Species from different scales are mixed. Only few species are shared among patterns.	Shared: *Pleonotoma echitidea*
	11		D2CA3	D3CA11	Complete nested	Species sequentially included in broader patterns.	
	12		D2CA10	D3CA6	Incomplete nested: combination	Species from different scales are mixed. Only few species are shared among patterns.	Shared: *Fridericia oligantha*
	13		D2CA10	D3CA11	Incomplete nested: combination	Species from different scales are mixed. Only few species are shared among patterns.	Shared: *Fridericia oligantha*
	14		D2CA10	D3CA30	Complete nested	Species sequentially included in broader patterns.	
Amazon basin centered	15	D1CA7	D2CA23	D3CA14	Incomplete nested: combination	D1CA7 and D2CA23 have each a species that is unique to them, and all of their species are included in D3CA14.	
	16		D2CA4	D3CA26	Identical	Identical in both scales.	
	17		D2CA7	D3CA0	Complete nested	Species sequentially included in broader patterns.	
	18		D2CA16	D3CA28	Complete nested	Species sequentially included in broader patterns.	
	19		D2CA16	D3CA32	Complete nested	Species sequentially included in broader patterns.	
	20		D2CA18	D3CA0	Complete nested	Species sequentially included in broader patterns.	
	21		D2CA18	D3CA3	Incomplete nested: combination	Species from different scales are mixed. Only few species are shared among patterns.	Shared: *Adenocalymma bracteolatum*
	22		D2CA20	D3CA20	Incomplete nested: combination	Species from different scales are mixed. Only few species are shared among patterns.	Shared: *Tanaecium truncatum*

	23		D2CA20	D3CA32	Incomplete nested: combination	Species from different scales are mixed. Only few species are shared among patterns.	Shared: *Fridericia pearcei, Lundia spruceana*
	24		D2CA23	D3CA14	Complete nested	Species sequentially included in broader patterns.	
	25		D2CA25	D3CA11	Complete nested	Species sequentially included in broader patterns.	
	26		D2CA25	D3CA29	Incomplete nested: combination	Species from different scales are mixed. Only few species are shared among patterns.	Shared: *Fridericia carichanensis*
	27		D2CA27	D3CA18	Incomplete nested: combination	Species sequentially included in broader patterns.	
Eastern South America centered	28	D1CA0	D2CA0	D3CA5	Incomplete nested: combination	Defining species of D1CA0 are completely included at two degrees. Two and three degrees share 75 species in common, 8 species are unique to D2CA0 and 27 species are unique to D3CA5.	
	29	D1CA0	D2CA1	D3CA5	Incomplete nested: combination	Species from one and two degrees are mixed. Only few species are shared among patterns. Species at two degrees completely included in the broader scale.	Shared: *Adenocalymma bullatum, Tynanthus fasciculatus*
	30	D1CA2	D2CA0	D3CA5	Incomplete nested: combination	Defining species of D1CA0 are completely included at two degrees. Two and three degrees share 75 species in common, 8 species are unique to D2CA0 and 27 species are unique to D3CA5.	
	31	D1CA3	D2CA0	D3CA5	Incomplete nested: combination	Defining species of D1CA0 are completely included at two degrees. Two and three degrees share 75 species in common, 8 species are unique to D2CA0 and 27 species are unique to D3CA5.	
	32	D1CA5	D2CA0	D3CA5	Incomplete nested: lost	Species from one degree included at two and three degrees, but one is species is absent from them. See . Two and three degrees share 75 species in common, 8 species are unique to D2CA0 and 27 species are unique to D3CA5.	Lost: *Anemopaegma pachyphyllum*
	33	D1CA5	D2CA1	D3CA5	Incomplete nested: combination	Species from one and two degrees are mixed. Only few species are shared among patterns. Species at two degrees completely included in the broader scale.	*Shared: Adenocalymma bracteosum*
	34	D1CA6	D2CA5	D3CA5	Incomplete nested: lost	Species sequentially included in broader patterns, but one species from D1CA6 and two from D2CA5 are absent at the D3CA5.	Lost: *Amphilophium perbracteatum, Adenocalymma ackermannii*
	35	D1CA8	D2CA0	D3CA5	Incomplete nested: combination	Defining species of D1CA8 are completely included at two degrees but one of its species its lost at three degrees. Two and three degrees share 75 species in common, 8 species are unique to D2CA0 and 27 species are unique to D3CA5.	Lost: *Adenocalymma ackermannii*
	36	D1CA8	D2CA1	D3CA5	Incomplete nested: combination	Overlap by sharing species at one and two degrees; species at 2 degrees included at three degrees.	Shared: *Adenocalymma bullatum*
	37	D1CA9	D2CA0	D3CA5	Incomplete nested: lost	Species from one degree included at two and three degrees, but one is species is absent from them.	*Lost: Tynanthus espiritosantensis*
	38	D1CA9	D2CA8	D3CA5	Incomplete nested:	D1CA9 and D2CA8 shared one species; D1CA9	Shared: *Martinella*

			combination	and D3CA5share two species. One species from D2CA8 is lost at three degrees.	*insignis, Adenocalymma hirtum. Lost: Adenocalymma ackermannii*
39	D2CA0	D3CA4	Reverse nested	Defining species at three degrees completely included at two degrees.	
40	D2CA0	D3CA5	Incomplete nested: combination	Two and three degrees share 75 species in common, 8 species are unique to D2CA0 and 27 species are unique to D3CA5.	
41	D2CA0	D3CA10	Incomplete nested: combination	Species from different scales are mixed. Only few species are shared among patterns.	Shared: *Lundia virginalis, Xylophragma myrianthum*
42	D2CA0	D3CA16	Incomplete nested: combination	Two and three degrees share 8 species in common, 75 species are unique to D2CA0 and 5 are unique to D3CA16.	
43	D2CA1	D3CA5	Complete nested	Species sequentially included in broader patterns.	
44	D2CA1	D3CA10	Incomplete nested: combination	Species from different scales are mixed. Only few species are shared among patterns.	Shared: *Cuspidaria pulchella*
45	D2CA2	D3CA16	Complete nested	Species sequentially included in broader patterns.	
46	D2CA5	D3CA5	Incomplete nested: lost	Species from two degrees included at three degrees, with two species absent in the latter scale.	Lost: *Adenocalymma ackermannii, Amphilophium perbracteatum*
47	D2CA6	D3CA4	Incomplete nested: combination	Species from different scales are mixed. Only few species are shared among patterns.	Shared: *Adenocalymma divaricatum*
48	D2CA6	D3CA5	Complete nested	Species sequentially included in broader patterns.	
49	D2CA8	D3CA5	Incomplete nested: lost	Species from two degrees included at three degrees, with one species absent in the latter scale.	Lost: *Adenocalymma ackermanii*
50	D2CA9	D3CA5	Complete nested	Species sequentially included in broader patterns.	
51	D2CA13	D3CA5	Complete nested	Species sequentially included in broader patterns.	
52	D2CA15	D3CA5	Complete nested	Species sequentially included in broader patterns.	
53	D2CA15	D3CA23	Incomplete nested: combination	Species from different scales are mixed. Only few species are shared among patterns.	Shared: *Mansoa glaziovii*
54	D2CA19	D3CA5	Complete nested	Species sequentially included in broader patterns.	
55	D2CA19	D3CA16	Incomplete nested: combination	Species from different scales are mixed. Only few species are shared among patterns.	Shared: *Mansoa hirsuta*
56	D2CA21	D3CA5	Complete nested	Species sequentially included in broader patterns.	
57	D2CA24	D3CA5	Incomplete nested: combination	Species from different scales are mixed. Only few species are shared among patterns.	Shared: *Adenocalymma paulistarum, Tynanthus macranthus*
58	D2CA24	D3CA19	Complete nested	Species sequentially included in broader patterns.	
59	D2CA11	D3CA2	Reverse nested	Defining species at three degrees completely included at two degrees.	

Figure S3.1. Maps of consensus areas at different spatial scales as referred in Table S.3.1. *Nested:* A pattern of successive and complete inclusion of defining species from areas at the finer scales into areas at the broader scales; *Reverse nested*: A pattern of complete inclusion of defining species of an area at the broader scale into a bigger area at the finer scale; *Nested and combined:* A pattern of incomplete inclusion between areas at different scales in which some species are unique to specific scales; *Nested with lost:* A pattern of incomplete inclusion between areas at different scales in which some species from the finer scale are lost at the broader scales; *Overlapped:* Areas at different scales overlap by sharing few species; *Overlapped and nested:* A pattern where two areas overlap by sharing few species, which in turn are both included in another area at the broader scale; and *Identical:* areas at different scales are defined exactly by the same species.





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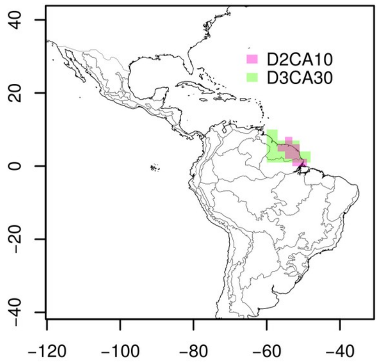

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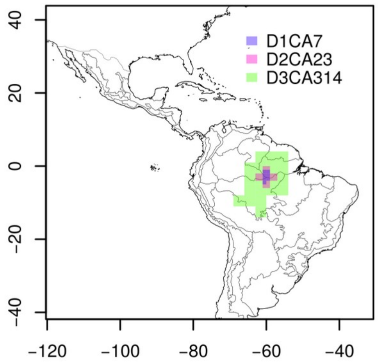

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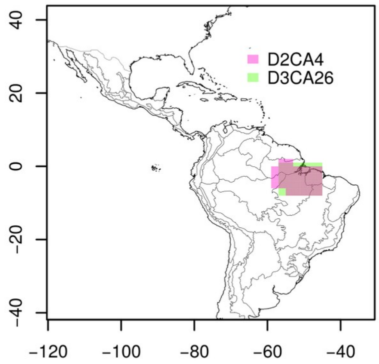

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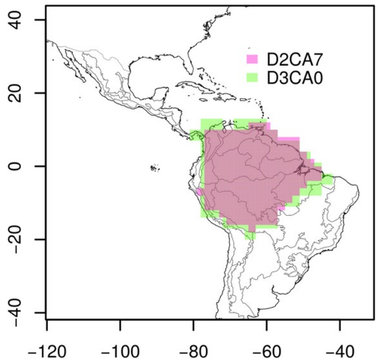

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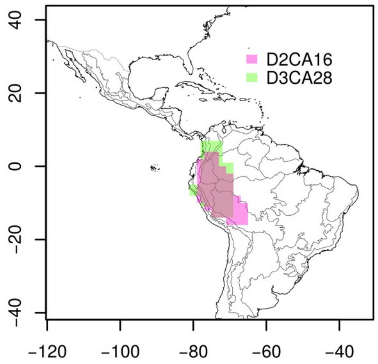

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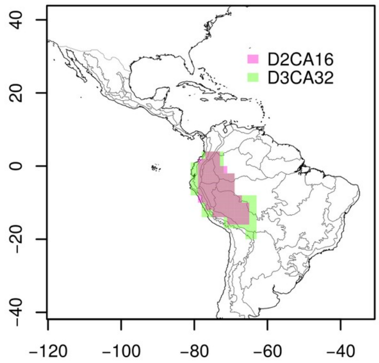

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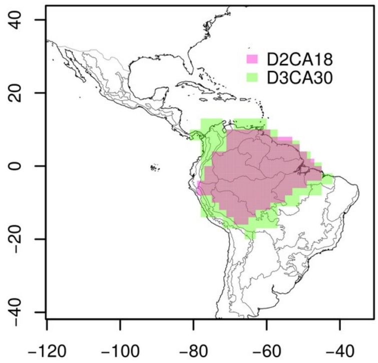

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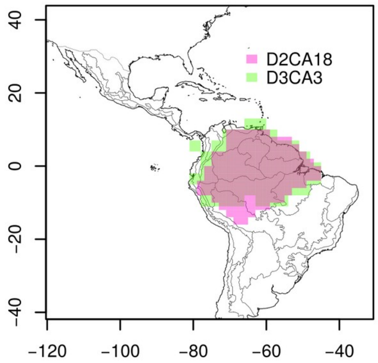

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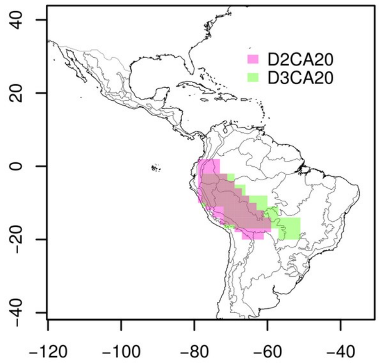

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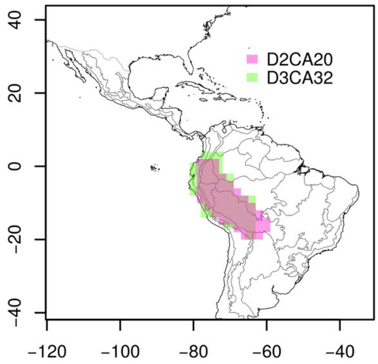

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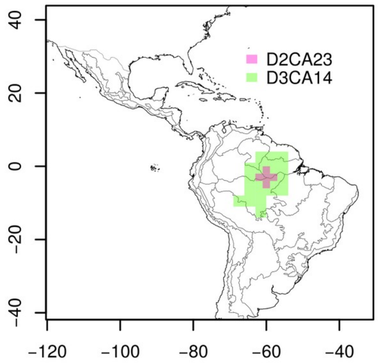

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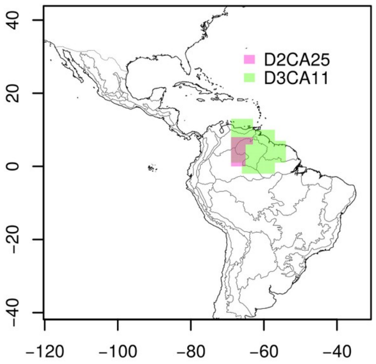
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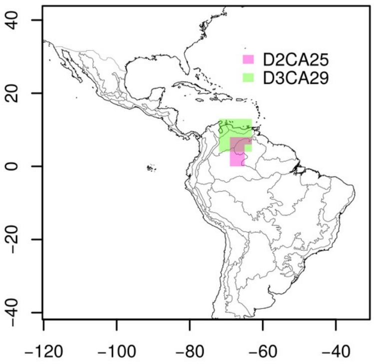
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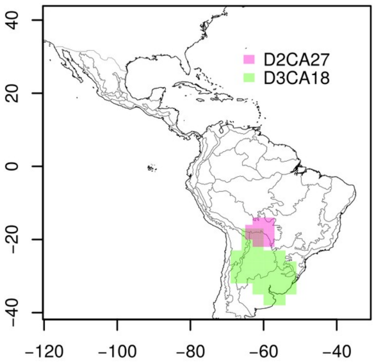
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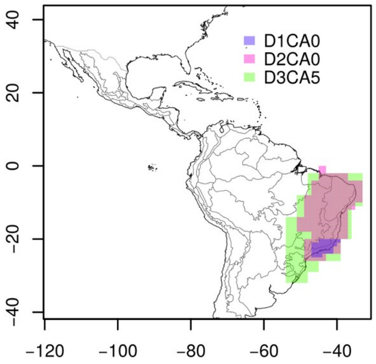
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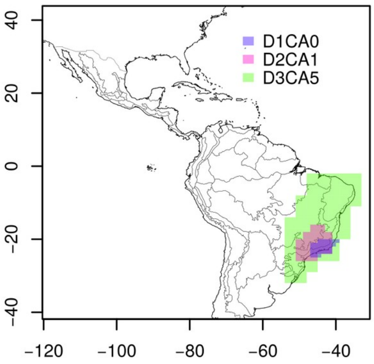
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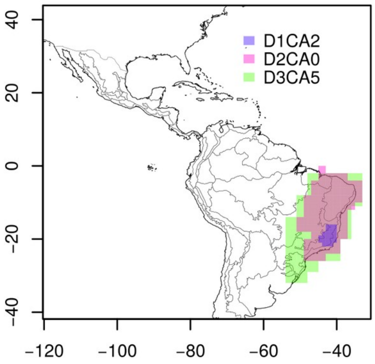
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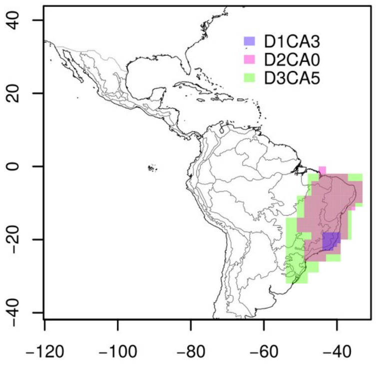
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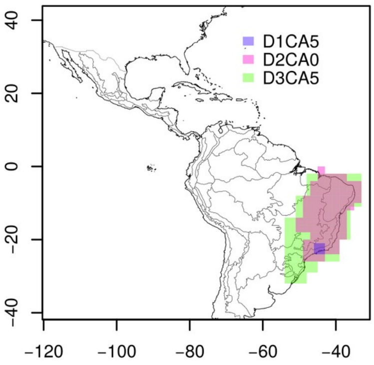
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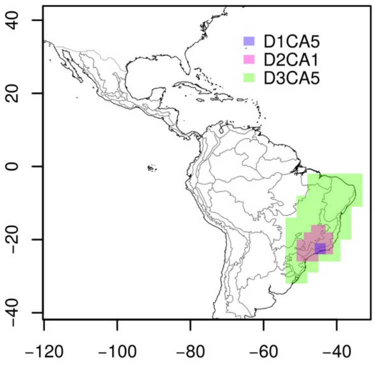
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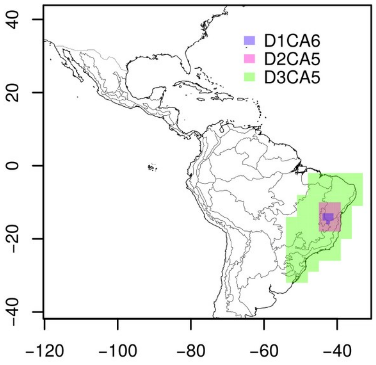
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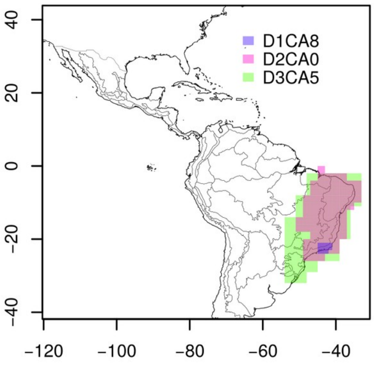
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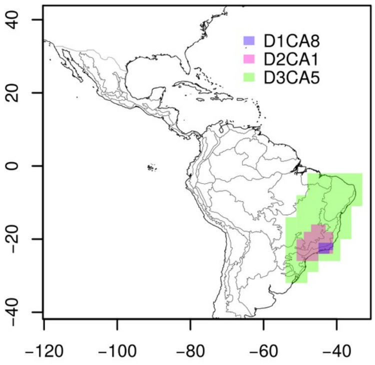
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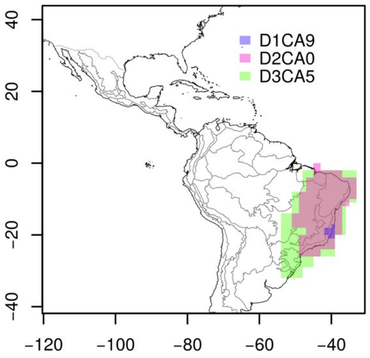

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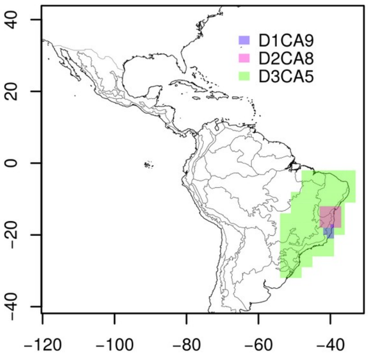

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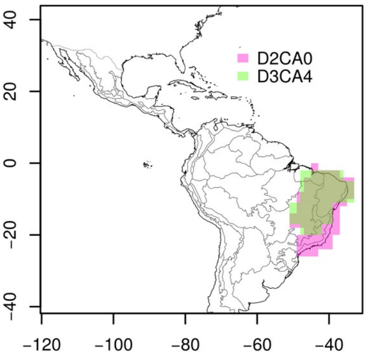

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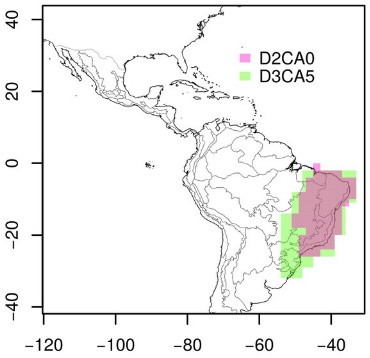

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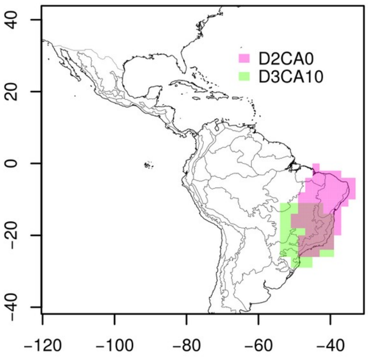

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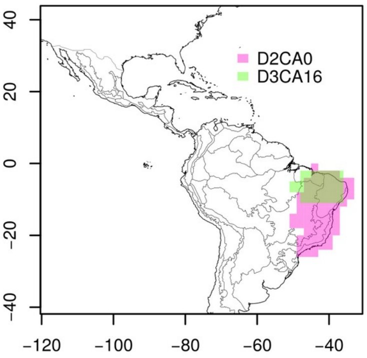

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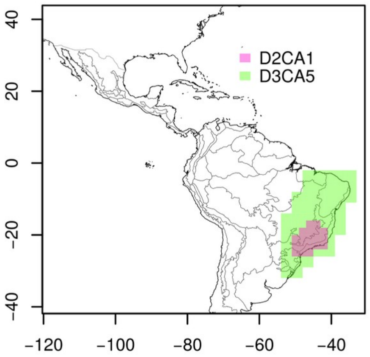

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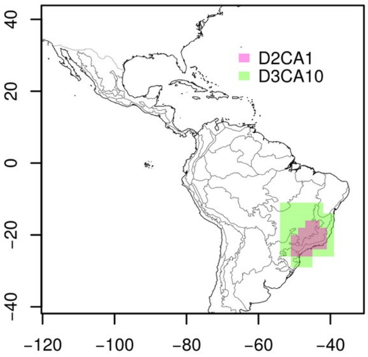

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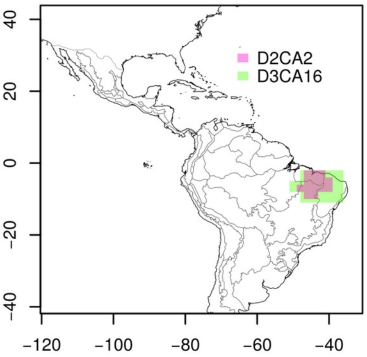

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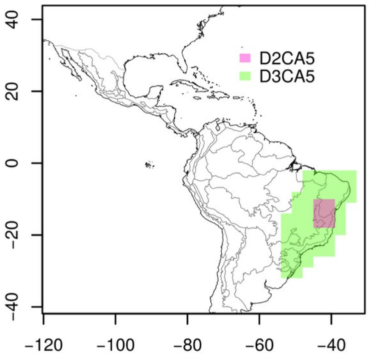

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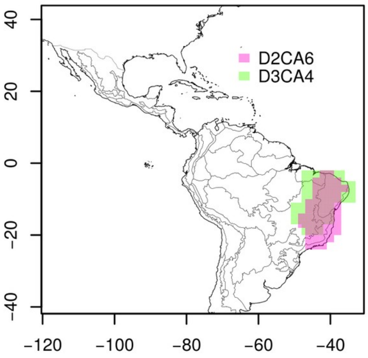

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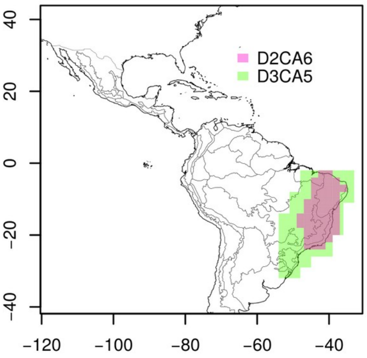

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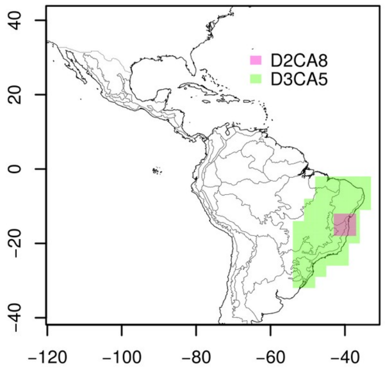

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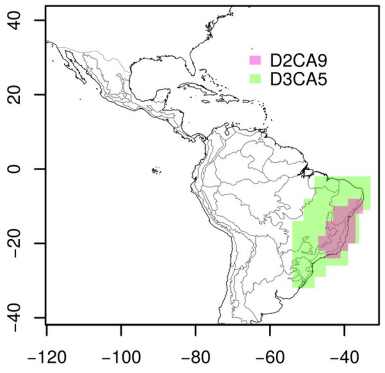

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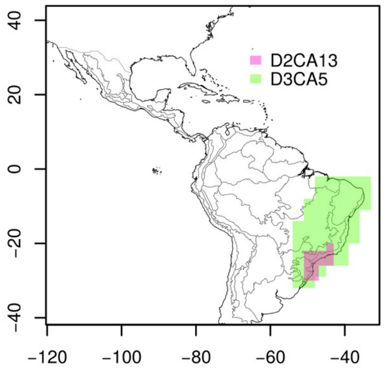

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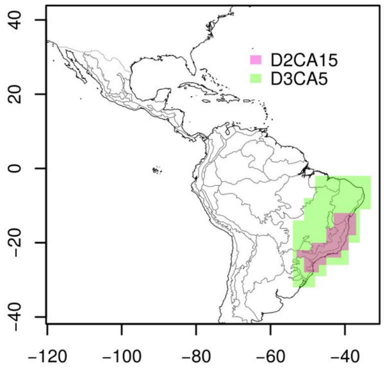

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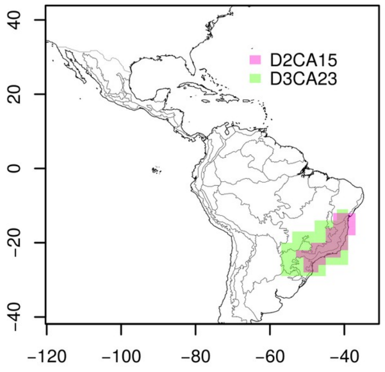

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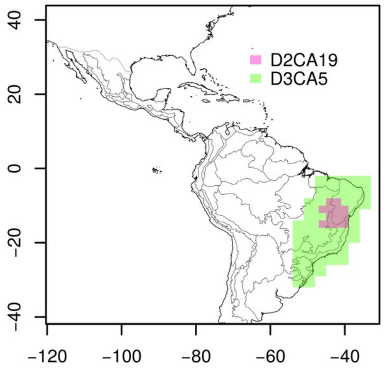

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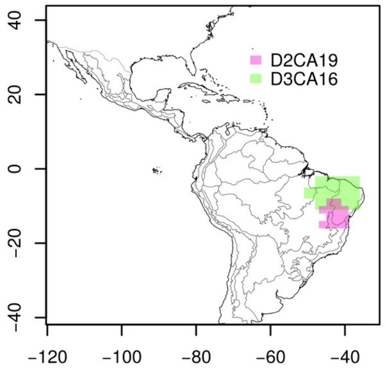

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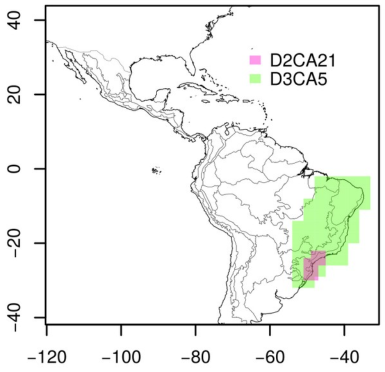

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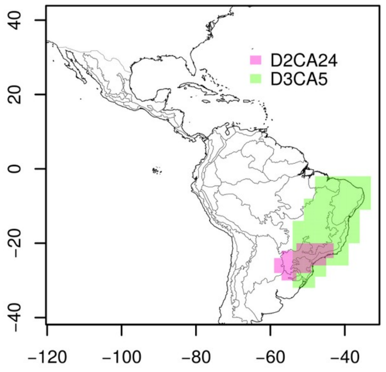

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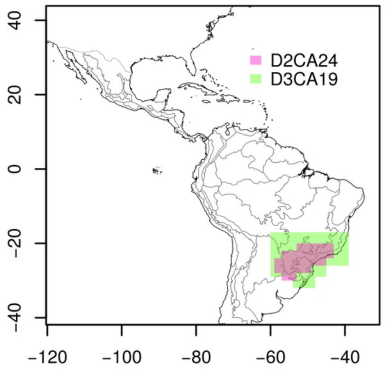

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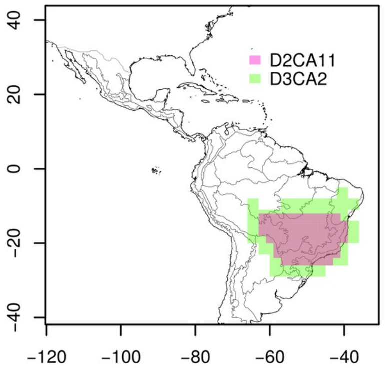
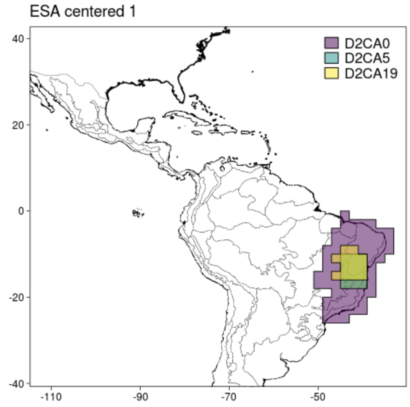
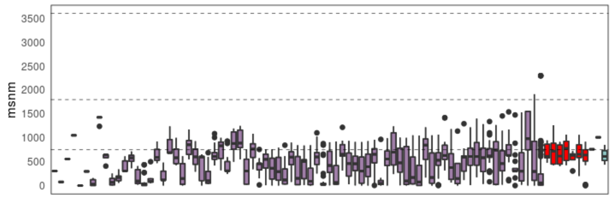
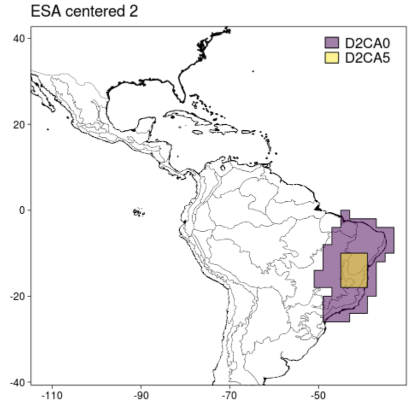


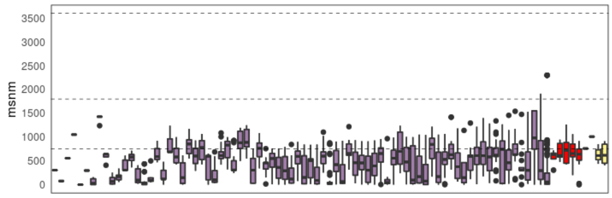
Figure S3.2. Ten groups of consensus areas with ambiguous species for which the ambiguity exists between patterns at different altitudinal profiles. Each figure consist of the (1) Map of consensus areas on the left, (2) a boxplot for each scoring species showing their elevation above sea level on the top-right position, and (3) a table showing the range of endemicity scores the conflicting species had in each area. The box plot colors indicate species belonging to different consensus areas, with the red color highlighting ambiguous species. The dashed lines refer to the approximated lower boundaries between different altitudinal belts for Lowlands and Lower Mountain forest (750 masl), Upper Mountain Forest (1800 masl), Subalpine Forests (3600 masl), and snowy highlands (4500 masl) (Prance, 1989; Frahm and Gardstein, 1991). The table shows in the column names the consensus area and its range of endemicity scores. The value "*NA*" means that the species is not present in that particular consensus area. This visualization allow us to see if the ambiguous species might belong preferentially to patterns at a specific altitudinal belt.



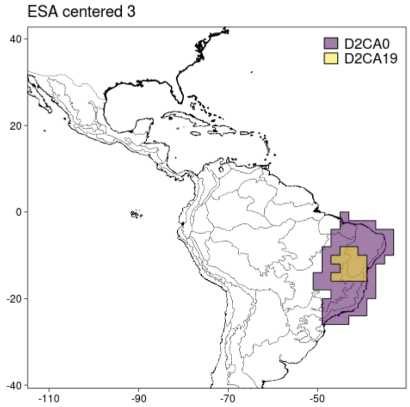


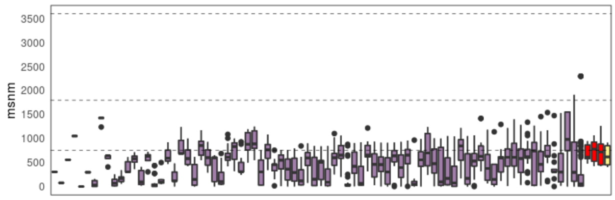
Species	D2CA0 2.08138 - 12.01492	D2CA5 3.6317 - 4.6317	D2CA19 2.73744 - 2.98744
Adenocalymma ackermannii	0 - 0.833	NA	0 - 0.75
Adenocalymma dichilum	0 - 0.875	0.758 - 0.758	0 - 0.688
Adenocalymma hypostictum	0 - 0.717	NA	0.605 - 0.833
Amphilophium blanchetii	NA	0.685 - 0.685	0 - 0.7
Lundia gardneri	0 - 0.762	0.697 - 0.697	0 - 0.513
Mansoa hirsuta	0 - 0.729	0.597 - 0.597	NA
Xylophragma harleyi	0 - 0.732	NA	0 - 0.388



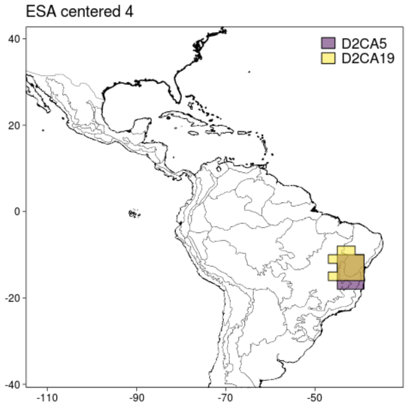


Species	D2CA0 2.08138 - 12.01492	D2CA5 3.6317 - 4.6317
Adenocalymma ackermannii	0 - 0.833	0 - 0.75
Adenocalymma dichilum	0 - 0.875	0 - 0.688
Adenocalymma hypostictum	0 - 0.717	0.605 - 0.833
Lundia gardneri	0 - 0.762	0 - 0.513
Xylophragma harleyi	0 - 0.732	0 - 0.388





Species	D2CA0 2.08138 - 12.01492	D2CA19 2.73744 - 2.98744
Adenocalymma dichilum	0 - 0.875	0.758 - 0.758
Lundia gardneri	0 - 0.762	0.697 - 0.697
Mansoa hirsuta	0 - 0.729	0.597 - 0.597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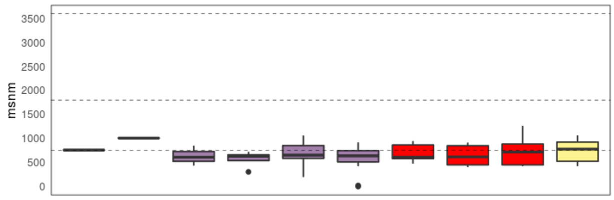
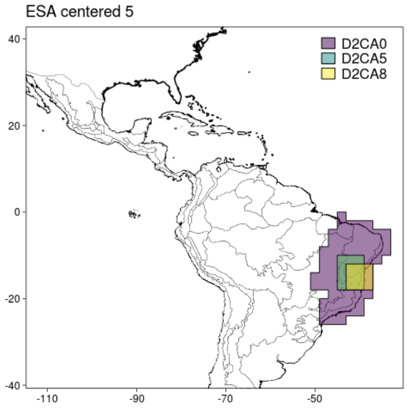


Species	D2CA5 3.6317 - 4.6317	D2CA19 2.73744 - 2.98744
Adenocalymma dichilum	0.758 - 0.758	0 - 0.688
Amphilophium blanchetii	0.685 - 0.685	0 - 0.7
Lundia gardneri	0.697 - 0.697	0 - 0.513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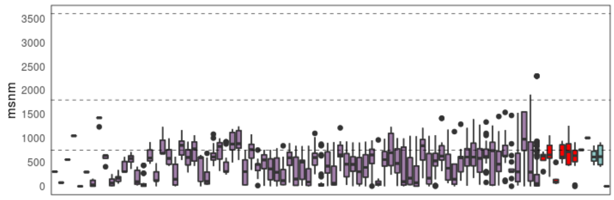
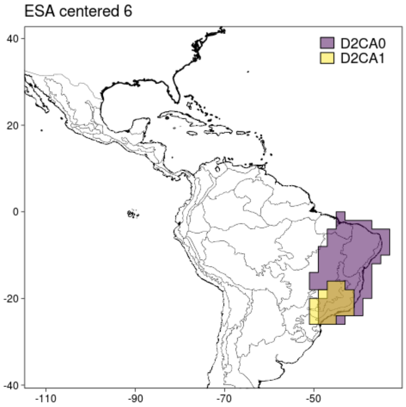


Species	D2CA0 2.08138 - 12.01492	D2CA5 3.6317 - 4.6317	D2CA8 2.02446 - 2.27446
Adenocalymma ackermannii	0 - 0.833	0 - 0.75	0.75 - 0.833
Adenocalymma dichilum	0 - 0.875	0 - 0.688	NA
Adenocalymma hypostictum	0 - 0.717	0.605 - 0.833	0.288 - 0.587
Lundia gardneri	0 - 0.762	0 - 0.513	NA
Martinella insignis	0 - 0.725	NA	0 - 0.405
Xylophragma harleyi	0 - 0.732	0 - 0.388	NA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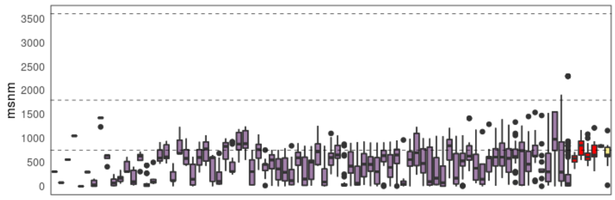
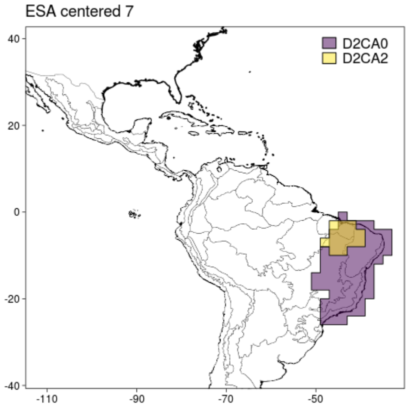


Species	D2CA0 2.08138 - 12.01492	D2CA1 2.86547 - 3.11547
Adenocalymma bullatum	0 - 0.917	0 - 0.548
Fridericia formosa	0 - 0.672	0.646 - 0.757
Lundia obliqua	0 - 0.625	0.484 - 0.847
Tynanthus fasciculatus	0 - 0.827	0.586 - 0.736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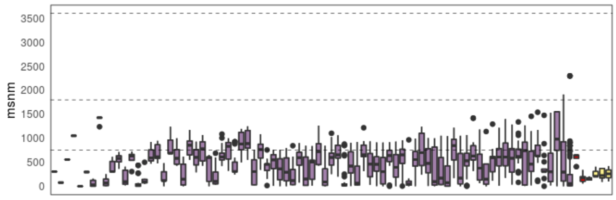
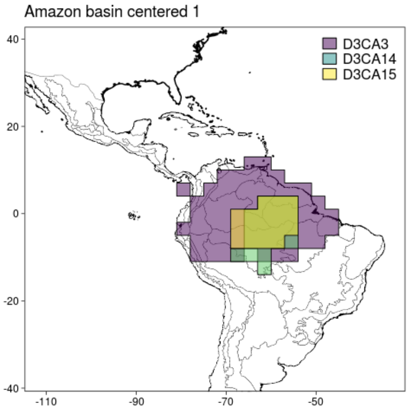
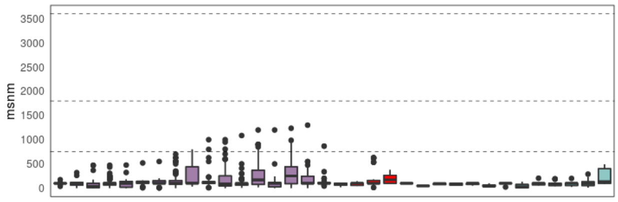
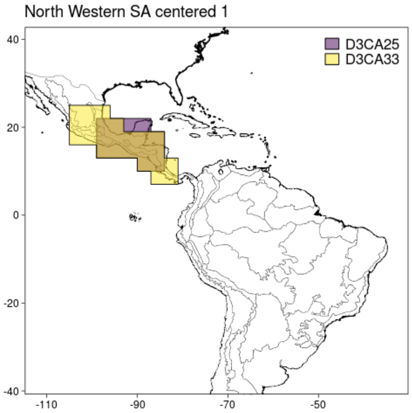


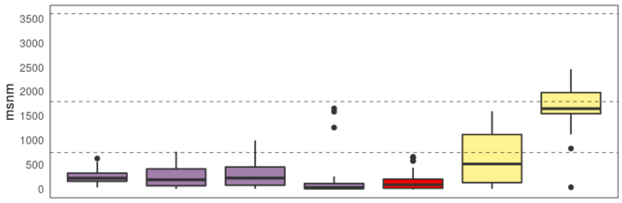
Species	D2CA0 2.08138 - 12.01492	D2CA2 2.2487 - 2.4987
Adenocalymma subspicatum	0 - 0.804	0 - 0.364
Lundia helicocalyx	0 - 0.583	0.536 - 0.881



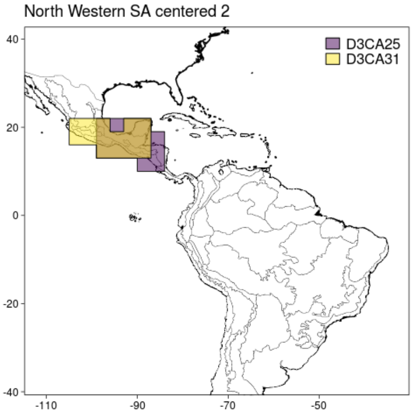


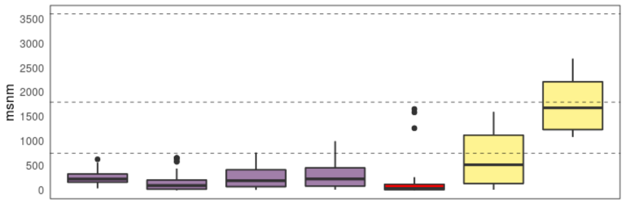
Species	D3CA3 2.0124 - 3.5124	D3CA14 2.33636 - 5.83034	D3CA15 2.24906 - 2.49906
Adenocalymma adenophorum	0 - 0.808	0.647 - 0.647	NA
Amphilophium lohmanniae	0 - 0.542	0.721 - 0.721	NA
Anemopaegma foetidum	NA	0.423 - 0.423	0 - 0.779
Anemopaegma ionanthum	0 - 0.396	NA	0 - 0.517
Cuspidaria subincana	0 - 0.454	0.458 - 0.458	0 - 0.678





Species	D3CA25 3.15538 - 3.40538	D3CA33 2.09763 - 2.34763
Bignonia potosina	0.526 - 0.526	0.689 - 0.689





Species	D3CA25 3.15538 - 3.40538	D3CA31 2.10795 - 2.35795
Fridericia floribunda	0.662 - 0.662	0.708 - 0.708

Table S2. Species giving score to areas only at one, two or three degrees. Changes in spatial scale might create inconsistencies in the composition of patterns if species have few occurrence points defining their distributions. Species with few points that score at a finer scale might not score at coarser spatial scales. This can happen even when the group of species with which the poor sampled species used to define the pattern at the finer spatial scale appeared at the broader scale.

At one and three degrees but absent at two.	At one and two degrees but absent at three.	Unique to one degree	Unique to two degrees
Amphilophium reticulatum	*Adenocalymma apetiolatum*	*Anemopaegma pachyphyllum*	*Adenocalymma ackermannii*
	Adenocalymma lineare	*Tynanthus espiritosantensis*	*Anemopaegma heringeri*
	Amphilophium perbracteatum		
	Fridericia subverticillata		

CHAPTER 3.

Do shared distribution patterns entail common causes? A case study of the Grinnellian climatic niche and areas of endemism using neotropical lianas (Bignonieae, Bignoniaceae)

To be submitted to the *Journal of Global Ecology and Biogeography*

Do shared distribution patterns entail common causes? A case study of the Grinnellian climatic niche and areas of endemism using neotropical lianas (Bignonieae, Bignoniaceae)

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Data availability statement

R scripts available at <https://github.com/jupanago/Rcode_Bignonieae_niche>

Biosketch

Juan Pablo Narváez-Gómez is a plant scientist with a deep interest in the biogeography of neotropical plants. This work is a part of his PhD thesis at the Institute of Biosciences of the University of São Paulo on the biogeography of neotropical lianas of the tribe Bignonieae (Bignoniaceae). He is also a public engagement enthusiast and is currently a PhD student at Dr. Lohmann's Lab.

Abstract

Aim: We characterize the Grinnellian niche of species from different areas of endemism as a means to identify common ecological processes that involve the contemporary climate as a driving factor of shared distribution patterns.

Location: Continental area of the Neotropics.

Major taxa studied: The tribe Bignonieae (Bignoniaceae), the largest clade of neotropical lianas.

Methods: We grouped the studied species into areas of endemism (AoE) at 2-degree resolution, and used a Principal Component Analysis (PCA) to characterize the species Grinnellian climatic niche using occurrence point locality data and the bioclimatic variables of the CHELSA 1.2. database. Species were grouped by area of endemism, and the niche occupation and partitioning were characterized by measuring the niche breadth and niche relative position using the mean distance among PCA scores and centroids in multivariate space. The similarity among endemic species of the same AoE was calculated using the Schoener D metric of niche overlap. Tests of equivalence and similarity in environmental space were performed to find common tendencies of niche conservation or divergence among species.

Results: We found that areas of endemism were formed by species with very different climatic niches. Variation in niche breadth and relative position in climatic space was high and negatively related to overlap values. Variation in niche property was related to the geographical location of the areas of endemism. The tests of equivalence and similarity did not identify any evidence of conserved or divergent Grinnellian niches for endemic taxa.

Main conclusions: Differences in the niche of endemic species are not associated with their membership to a particular area of endemism but reflect the climatic heterogeneity of these areas instead. No common processes were found among species sharing the same sympatric distribution. Our findings corroborate earlier findings that the correlations between endemism and contemporary climate are related to the spatial autocorrelation between climate and geography.

Keywords: **ENDEMISM, CONTEMPORARY CLIMATE, GRINNELLIAN NICHE, LIANAS, BIGNONIEAE**

Introduction

Areas of endemism (AoE) refer to the pattern of non-random congruence among the distributional limits of two or more species that occur nowhere else and show an extensive degree of sympatry (Szumik & Goloboff, 2004). An AoE represents an instantaneous photograph of both the ongoing ecological process affecting species range dynamics and the evolutionary processes leading to speciation that result in the confining of species to particular regions of the world (Weeks *et al.*, 2016). Among the possible causes of endemism, climate has gained attention in recent years (Harrison & Noss, 2017). Climate stability and landscape features buffering the effects of past climate change would drive the accumulation and the ecological specialization of narrow range species in centers of endemism (Dynesius & Jansson, 2000; Jansson, 2003). Similarly, the correlation between contemporary climate heterogeneity and species ecological tolerance has underlaid a diverse range of hypotheses about how climate regulates species distributions that involve (1) physiological restrains over species distribution limits (Stephenson, 1990); (2) areas with unusual climates filtering species with specific adaptations (Ohlemüller *et al.*, 2008); (3) climate seasonal effects over range size (Addo-Bediako *et al.*, 2000); (4) climatic heterogeneity promoting diversification by niche partitioning (Jetz & Rahbek, 2002); and (5) climate indirect effects by changes in the distribution of related and ecologically important species (Thomas, 2010). Some studies have identified a strong correlation between contemporary climate and endemism, but this correlation is not necessary evidence of climate as a causal factor (Zuloaga *et al.*, 2019). Despite all the attempts to understand the relationship between climate and endemism, the specific mechanisms shaping this relationship are still unknown.

Biogeographical patterns can be understood as a product of the interaction between the Grinnellian climatic niche and the geographic range of multiple species with shared distribution limits (Pearson & Dawson, 2003; Soberón, 2007; Wiens, 2011). The Grinnellian niche refers to the multivariate space formed by the non-interactive climatic environmental factors that allow the indefinite growth of a species' population (Soberón, 2010). This concept has provided the means to study processes such as ecological specialization, habitat suitability tracking, and speciation in three ways. First, understanding how niche breadth and range size are correlated at different spatial scales has been possible through the characterization of the Grinnellian niche position and the range of climatic conditions encompassed by a species in the climatic space (i.e., its niche breadth) (Devictor *et al.*, 2010; Nakazawa, 2013; Slatyer *et al.*, 2013). Second, species range dynamics have been inferred by environmental niche models used to estimate area climatic suitability through space and time (Graham *et al.*, 2010), and the role of niche shifts and expansions in the colonization capacity of invasive species (Guisan *et al.*, 2014). Finally, the study of the Grinnellian niche of sister species with sympatric and allopatric distributions has produced insights about the relative frequency of different modes of speciation (Anacker & Strauss, 2014; Li *et al.*, 2018), as well as insights into the role of niche conservatism and divergence in these processes (Cardillo & Warren, 2016). Therefore, the climatic Grinnellian niche provides a wide range of applications to study the basic processes leading to the confining of species in areas of endemism.

Plants exhibit a strong relationship between climate and distribution (Parmesan & Hanley, 2015) and can serve as good models to explore the relationship between the climatic niche and endemism. Water-energy balance is known to regulate the distribution of biomes around the world and the distributional limits of many groups of plants (Stephenson, 1990). Climate is also key for the establishment of the distribution of plant habits (Hawkins *et al.*, 2011), the latitudinal diversity gradient, and the compositional changes of regional floras (Chen *et al.*, 2015). The plant tribe Bignonieae (Bignoniaceae) is an excellent model to examine the relationship between endemism and the climatic niche. This monophyletic group of lianas includes 393 species grouped in 20 genera, representing half of the species currently included in the family Bignoniaceae (Lohmann & Taylor, 2014). Bignonieae extends from 35°S to 39°N and is an important component of Neotropical forest canopies, occupying both wet and dry environments across different biogeographical areas. Some aspects of the ecology of Bignonieae suggest that climate might be an important driver of its distribution. For instance, Bignonieae patterns of diversity are correlated with evapotranspiration (Meyer *et al.*, 2018), and patterns of endemism are correlated with continental climate (Gentry, 1979). Furthermore, habitat specialization to abiotic factors has been shown to contribute to community assembly in this tribe (Alcantara *et al.*, 2014). Although patterns of endemism in the tribe exhibit similar arrangements to other plant distribution patterns suspected to have resulted from past climatic events in the Neotropics, the relationship between climate and endemism has not been studied (Chapter 2).

Given the affinity between the species of Bignonieae and climate, and their tendency to specialize to abiotic conditions, we would expect that species with similar distribution patterns might exhibit similar patterns of niche partitioning that can, in turn, be recognized by similar variation trends in their niche position, breadth, and similarity. More precisely, if climate was a causal factor determining the formation of an area of endemism, one would be able to detect its effect by identifying similarities in the climatic niche of its species. For example, if the climate of the area acted as a filter for specific conditions, species with similar physiological tolerances would be expected. This could be manifested as a closer position in climatic environmental space, narrow niche breadth, and high overlap values among the species in the area of endemism. If the environmental heterogeneity of the area of endemism was important, we would expect endemic species to occupy different regions of the environmental space, with narrow or wide niche breadth and low values of niche overlap. Detecting these patterns of niche space partitioning and changes in the properties of the niche can inform us about how endemic species and the AoE in which they occur are related to climate as a possible causal factor.

In this study, we aim to characterize the climatic niche of the species of Bignonieae that belong to different areas of endemism (*sensu* Szumik & Goloboff, 2004) in order to frame hypotheses about the possible ecological processes behind their patterns of endemism across the Neotropics. Specifically, we wanted to assess whether the properties of the climatic niche such as position, breadth, and overlap vary in a predictable fashion among species belonging to different areas of endemism and whether this could be associated with the process of ecological specialization in the climatic space. In this context, we searched for patterns of variation in niche properties and overlap in species that share similar distribution patterns and occur in extensive sympatry as part of Areas of endemism. To achieve this goal, we took an exploratory approach in the multivariate environmental space in order to visualize and detect patterns of variation in the niche properties.

Methods

Species occurrence database

The database comprises 386 species of all 20 genera recognized within tribe Bignonieae and contains 28,763 records that encompass their complete geographical extent. Overall, 304 species have ten or more records, while 60 species have between three and nine records, and 22 species have less than three records. This Bignonieae dataset was assembled by LGL from herbarium records that she examined from multiple collections, especially MO (Missouri Botanical Garden), and more recently verified and complemented during the development of other spatial studies (Chapter 1, for a full description). The taxonomy follows Lohmann and Taylor (2014), with updates from subsequent taxonomic treatments of tribe Bignonieae (see Chapter 1, for a full description).

Areas of Endemism (AoE)

We used the AoEs of the tribe Bignonieae from a previous analysis of endemicity in which AoEs were defined at different spatial scales (see Chapter 2 for a full description). We selected the 28 AoEs defined at the spatial resolution of 2 degrees, which were formed by 166 endemic species out of the 386 sampled species of tribe Bignonieae. These areas are distributed across the complete geographical extent of Bignonieae, covering almost the entire Neotropical region, except the Antilles. Some AoEs overlap in geographic space, in their margins or in nested patterns. At this resolution, the AoEs have the least degree of ambiguity among the patterns of endemism discovered across spatial scales (Chapter 2). The number of endemic species per AoE is not balanced, with most AoEs being defined by three to nine species (27 AoEs), except from one area that is formed by 83 species. Most species belong exclusively to a single AoE.

Environmental space

To build the climatic space of the areas of endemism in Bignonieae, we used the bioclimatic variables of the CHELSA 1.2 climatic database (Karger *et al.*, 2017), at the spatial resolution of 10 arc minutes.. This resolution is equivalent to cell sizes of 18.5 km (an area of approximately 343 km^2) at the equator, which is appropriate to study the effect of climate over broad distribution patterns at regional scales (Pearson & Dawson, 2003). We used the species occurrence data points of all species of Bignonieae and one point per grid cell of each AoE to extract the climatic information for each of the CHELSA bioclimatic layers using the R programming language package "raster" (Hijmans, 2019). To reduce the redundancy associated with collinearity and spatial autocorrelation, and to allow a better separation between the environmental conditions of the AoEs and species climatic niches in the multivariate space, we discarded highly correlated variables using Pearson correlation coefficients greater than 0.7 as threshold (Zuur *et al.*, 2010; Dormann *et al.*, 2013). We scaled and standardized the set of uncorrelated variables and conducted a Principal

Component Analysis (PCA) to build the final climatic space using the *rda* function of the "vegan" package (Oksanen et al. 2019) implemented in R (R Core Team, 2020). To check that this reduced environment contained the variables that better explain the variation of the complete dataset of species occurrence and AoEs, we conducted a second but more general PCA using all the bioclimatic variables and manually checked the loading of each variable.

Measuring the niche overlap between endemic species using this environmental space was computationally intensive. We decided to create a second climatic environmental space using the same bioclimatic variables, but only including the values for the occurrence points of the endemic species. This approach reduced the amount of data in the environmental space, conserved the structure of correlation between bioclimatic variables, and eased the calculations of overlap and the performance of the equivalence and similarity tests.

Characterizing environmental spaces and the climatic niche of species

Measures of niche breadth and position were taken in the climatic multivariate space as properties of the climatic niche (Thuiller *et al.*, 2005; Broennimann *et al.*, 2006). We calculated niche breadth as the mean distance of the principal component scores of each species occurrence point to the centroid of the species cloud of points in multidimensional space using the R package "usedist" (Bittinger, 2020). This package uses the distance matrix between all the principal component scores to calculate the distance between points and find the centroids in multivariate space (Bittinger, 2020). This measure of dispersion is an appropriate approximation to estimate the Grinnellian niche breadth and ecological specialization in environmental space (Carnes *et al.*, 1982; Devictor *et al.*, 2010). To check whether this approximation was reliable, we compared it to the mean distance to centroid obtained independently using the *betadisper* function of the "vegan" package (Anderson, 2006) (Oksanen et al. 2019). Both measures were positively correlated and increased monotonically. This analysis was conducted using a Virtual Machine in the Microsoft Azure Cloud service (https://azure.microsoft.com) (Fig. S1.1, see Appendix S1 in Supporting Information). To aid the interpretation of the results, we used the quartiles of the data to classify the niche breadth into three categories: (i) narrow (below the first quartile), (ii) medium (between the first and third quartiles), and (iii) wide (above the third quartile).

Similarly, the niche position of endemic species was calculated as the distance between the centroid of the species niche and the centroid of the AoEs' environment in the multivariate space using the R package "usedist" (Bittinger, 2020). This measure provided the relative position of the species in relation to the average environmental conditions in the area of endemism. This measure also provided an indirect measure of whether the species is occupying the most or the least frequent environmental conditions in the area, as well as the degree of aggregation and proximity of species niches inside the environmental space encompassed by the AoEs. Together with the niche breadth, it characterizes how the climatic space is partitioned and occupied. To aid the interpretation of the results, we used the quartiles of the data to classify the niche breadth into three categories: (i) near (below the first quartile), (ii) middling (between the first and third quartiles), and (iii) far (above the third quartile) distance from the species centroid to the centroid of the area of endemism.

The niche overlap between species was calculated in environmental space using Schoener's D and Hellinger's I metrics (Warren *et al.*, 2008; Broennimann *et al.*, 2012), implemented in the R package "ecospat" (Di Cola *et al.*, 2017). The overlap was calculated using a smooth density kernel that accounts for bias in the environmental space by counting and weighing the abundance of environmental conditions in which the species is found (Broennimann et al., 2012). Given that Schoener's D and Hellinger's I were positively correlated and changed monotonically, we only report the commonly used Schoener`s D values (Rödder & Engler, 2011). To interpret and describe the results, we classified niche overlap into five categories: (i) Limited ($D < 0.2$), (ii) Low ($0.2 < D <= 0.4$), (iii) Moderate ($0.4 < D <= 0.6$), (iv) High ($0.6 < D <= 0.8$), and (v) Very High ($D > 0.8$) (Rödder & Engler, 2011).

Strategy for the comparison of niche properties among areas of endemism

We looked for patterns of variation in the breadth, position, and overlap among the endemic species between and within areas of endemism. Each area of endemism was considered as an independent group of species, and areas of endemism were grouped by their geographic location: 1. Mesoamerica (Meso_1), 2. Northern Andes (N_Andes_1-4), 3. Guiana Shield centered (Guiana_1-3), 4. Amazonia-Basin Centered (Amazonia_1-6), 5. South-Eastern South America-Dry Diagonal (D_Diagonal_1-3), 5. South-Eastern South America-Throughout the Dry Diagonal and Atlantic Forest (DD_AF_1-6); and 6. South-Eastern South America-Atlantic Forest (Atl_Forest_1-5) (J.P. Narváez-Gómez, personal communication.). To look for differences among areas of endemism we used the Welch's ANOVA which is robust to violations of assumptions of normality and heteroscedasticity (Welch, 1951; Keselman *et al.*, 2008). These statistical analyses were implemented using the R package "onewaytests" (Dag *et al.*, 2018). Visualizations were conducted using the R package "ggplot2" (Wickham, 2016).

Test of equivalence and similarity of niche overlap

To assess how similar are the endemic species belonging to an AoE, we applied the equivalence and similarity tests of niche overlap to all the species pair comparisons within the area (Broennimann et al., 2012; Di Cola et al., 2017). These tests randomly sample the species climatic niche to simulate a null distribution of niche overlap values. This process was repeated 100 times, and if the observed niche overlap among a species pair lies outside the 95% of the density of the distribution, then the null hypothesis of no similarity or equivalency is rejected. While the simulation of the equivalence test is symmetrical by randomly sampling the niches of both species under comparison, the similarity test randomly samples one of the niches at a time. The equivalence test assesses whether the overlap remains constant between species despite the randomization of the climatic space. The similarity test can be interpreted as a background test that looks for similarities given the environmental differences observed in the area where the species occur (Warren et al., 2008). Both tests are two-tailed with two different alternative hypotheses. The lower alternative predicts that the niches are less similar or equivalent than expected by chance (low overlap), while the greater alternative predicts that the niches are more similar or equivalent than expected by chance (high overlap) (Di Cola et al., 2017). The biological interpretation of the no rejection of the null hypotheses in each case suggests the lower alternative as a possible niche differentiation, while suggesting the greater alternative as a possible niche conservation (Warren *et al.*, 2014).

The results from these tests allow us to identify whether species niches express recognizable tendencies to be more or less similar than expected by chance, and whether these similarities are more related to the characteristics of their environments than to intrinsic biological processes given the occurrence data available. The tests and simulations were implemented in the Scientific Computation Cluster Santos Dumont of the Brazilian National Scientific Computation Laboratory (https://sdumont.lncc.br/index.php).

Results

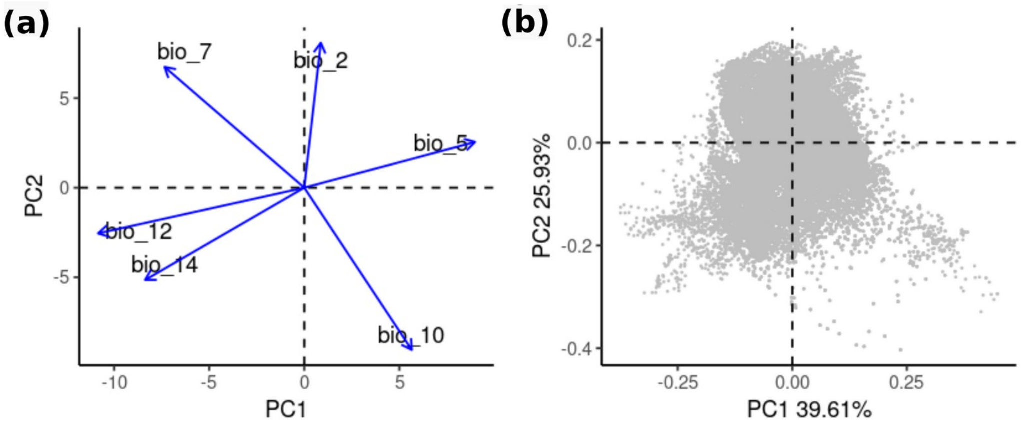
The environmental space of the areas of endemism of Bignonieae

The environmental climatic space of areas of endemism (AoEs) and the species of the tribe Bignonieae were built using the bioclimatic variables Mean Temperature of Warmest Quarter (bio_10), Max Temperature of Warmest Month (bio_5), Temperature Annual Range (bio_7), Annual Precipitation (bio_12), Precipitation of Driest Month (bio_14), and Mean Diurnal Range (bio_2). These variables represent the temperature fluctuation, seasonality in precipitation, and water availability in the study region (Fig. 1). The first principal component of this climatic space (Fig. 1) accounted for 39.61% of the variation among data from areas and species, and was positively correlated with bio_5, bio_10, and bio_2, and negatively correlated with bio_12, bio_14, and bio_7. In turn, the second principal component accounted for 25.93% of the variation, and was positively correlated with bio_2, bio_7, and bio_5, and negatively correlated with bio_10, bio_14, and bio_12. A plot of the PC1 and PC2 showed that the environmental space encompassed by each area of endemism is neither unique nor exclusive because they have a high degree of overlap (Fig. 2).

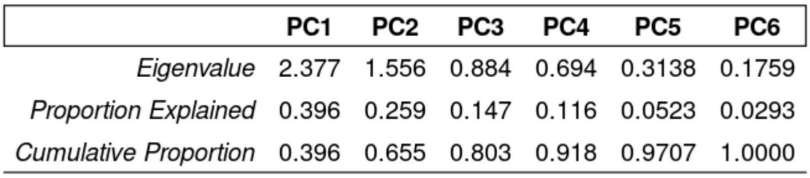
Variation in the properties of the climatic niche of endemic species

There were significant differences among the niche properties across all AoEs (Fig. 3A-B, Table 1). While some areas (i.e., Andes_4, Guiana_1, Amazonia_1-3-5-6, D_Diagonal:3, DD_AF_4-5-6, and Atl_Forest_3-4; Fig. 4a) included species with only narrow or medium breadth niches, others included a mix of species with different niche breadths (i.e., N_Andes_1-3, DD_AF_1; Fig. 4a). Likewise, while some species of the same AoE showed niches close to the average climatic conditions in the area (i.e., Amazonia_2-4-5-6, and DD_AF_6; Fig. 4b), others were more distant and located in the less frequent climatic conditions (i.e., Andes_1-4, and DD_AF_2; Fig. 4b). This heterogeneity in the niche properties was mirrored by overall lower and moderate values of niche overlap across AoEs (Fig. 4c).

When looking specifically at the niche differences between areas of endemism located over the same geographical region, the differences in niche properties were less evident (Fig. 3, Table 1). While in some regions significant differences among niche breadth were detected suggesting different levels of climatic specialization, in other regions the non-significant differences suggest that endemic species belonging to different AoEs have very similar levels of specialization in climatic space, relative to the region over which they are located (Table 1). Areas located over the Andes and the Atlantic Forest or those located over the Dry Diagonal and the Atlantic Forest had greater variation in niche breadth and position, and showed lower values of niche overlap (Fig. 3). On the other hand, areas located over Amazonia showed lower variation in niche breadth and position, while showing higher values of niche overlap.

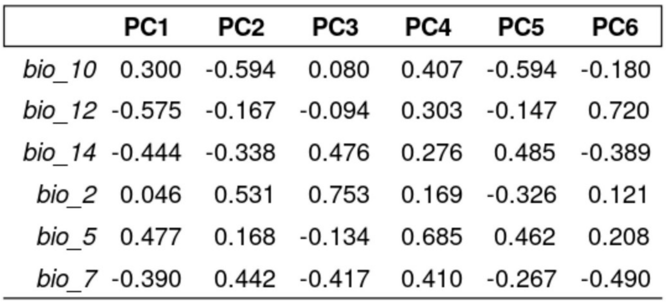


(c)



	PC1	PC2	PC3	PC4	PC5	PC6
Eigenvalue	2.377	1.556	0.884	0.694	0.3138	0.1759
Proportion Explained	0.396	0.259	0.147	0.116	0.0523	0.0293
Cumulative Proportion	0.396	0.655	0.803	0.918	0.9707	1.0000

(d)



	PC1	PC2	PC3	PC4	PC5	PC6
bio_10	0.300	-0.594	0.080	0.407	-0.594	-0.180
bio_12	-0.575	-0.167	-0.094	0.303	-0.147	0.720
bio_14	-0.444	-0.338	0.476	0.276	0.485	-0.389
bio_2	0.046	0.531	0.753	0.169	-0.326	0.121
bio_5	0.477	0.168	-0.134	0.685	0.462	0.208
bio_7	-0.390	0.442	-0.417	0.410	-0.267	-0.490

Figure 1. Principal Component Analysis (PCA) of the climatic environmental space of Bignonieae. This environment considers the environment formed by the uncorrelated bioclimatic variables from CHELSA 1.2 that were extracted for all Areas of Endemism (AoEs) using one point per pixel and all occurrences of tribe Bignonieae. (a) PCA scaling 2 the variables contributing to the principal components. (b) PCA scaling 1 showing the species occurrences and the extracted points from areas of endemism. Percentages indicate the variance explained by each principal component. (c) Table with the proportion of the variability explained by each principal component. (d) Variable contribution to principal components showed as correlation coefficients.

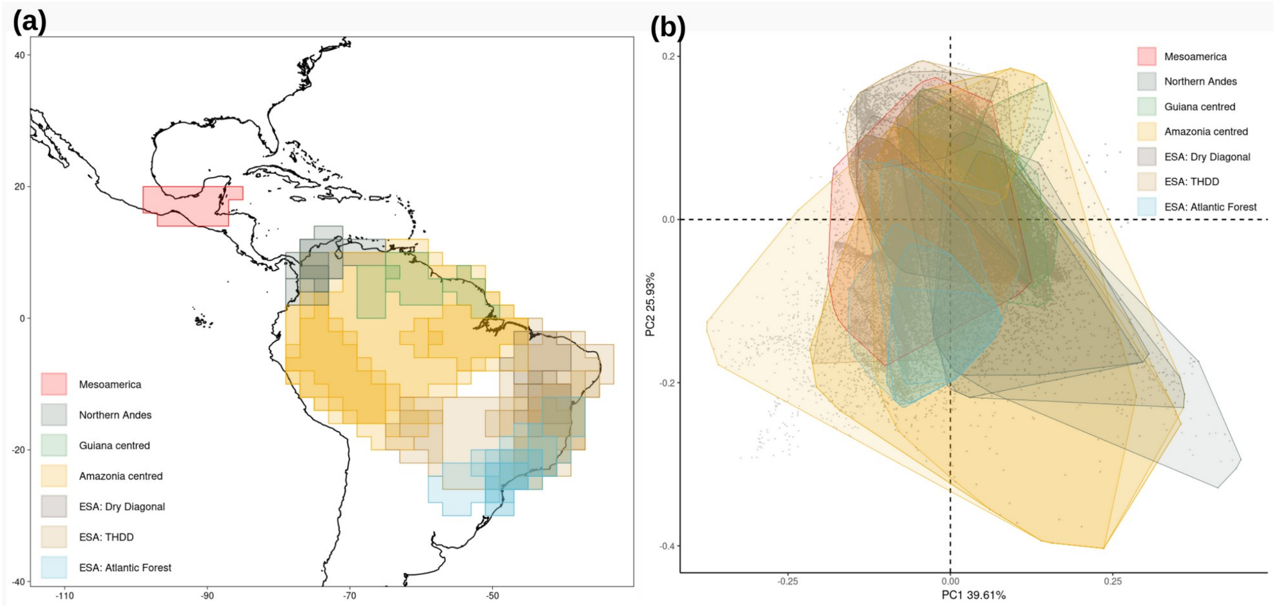


Figure 2. (a) Areas of endemism (AoEs) of the tribe Bignonieae (Bignoniaceae) and (b) the corresponding principal component analysis representing their environmental spaces like convex hulls. Colors indicate the approximate geographic regions over which these areas are located. Gray dots represent each one of the species occurrence data points and the background (i.e., a point per each of the 2 degree cells composing the AoEs). Note the high degree of overlap in both geographical and environmental spaces, as well as the apparent delimitation of broad geographical regions and their environmental spaces. See Panels 1-28 for detailed information about endemic species in each AoE.

Conservation and divergence of endemic species niches

The tests of equivalence and similarity did not support divergence nor conservation of the niches among endemic species belonging to different AoEs given the available distributional data and background environment (Fig. 5a-d). The null hypothesis that niches are no more equivalent than expected by chance was not rejected for most of the species pair comparisons within AoEs (Fig. 5a). Conversely, the null hypothesis of the niches being no less equivalent than expected by chance was rejected for a high number of species pairwise comparisons within AoEs (Fig. 5b). However, the null hypothesis of no less similarity than expected by chance given the environmental background was not rejected in any of the pairwise species comparisons (Fig. 5d). This means that the difference detected by the equivalence test with the alternative lower hypothesis is not significant because species niches are as different as expected by the environmental differences across AoEs. Similarly, the null hypothesis of no more similarity than expected by chance was rejected only for a few species pairs. However, given that the equivalence test with the greater alternative rejected a significant conservation of their niches (Fig. 5c). This similarity can be attributed to reasons other than niche conservatism.

TABLE 1. Statistical test of difference among Areas of Endemism (AoE) of the tribe Bignonieae that occur within the same geographical regions. The column "region" denotes the comparison across all AoEs in the denoted geographic region. The region "All" refers to the comparison of all AoEs regardless of the of the region to which they belong. The asterisk (*) indicates which tests were significant.

Niche property	Region	F	num_DF	den_DF	p, α = 0.05	
Niche relative position	All	15.8457	27	27.052	1.344E-10	*
	Northern Andes	1.8435	3	5.278	0.2514	
	Guiana centered	3.9141	2	5.832	0.08358	
	Amazonia centered	4.0232	5	6.571	0.05297	
	Dry Diagonal	1.1308	2	7.13	0.3745	
	Dry Diangonal & Atlantic Forest (DD_AF)	48.0991	5	7.456	1.703E-05	*
	Atlantic Forest	0.3931	4	5.484	0.807	
Niche breadth	All	38.9477	27	26.31	3.77E-15	*
	Northern Andes	0.256	3	5.632	0.8545	
	Guiana centered	3.1496	2	6.649	0.1091	
	Amazonia centered	178.551	5	6.484	8.043E-07	*
	Dry Diagonal	0.3528	2	5.075	0.7187	
	Dry Diangonal & Atlantic Forest (DD_AF)	25.4096	5	7.34	0.0001779	*
	Atlantic Forest	5.3018	4	6.061	0.03521	*
Overlap: Schoener D	All	26.1468	27	50.368	3.514E-21	*
	Northern Andes	9.1651	3	13.547	0.001433	*
	Guiana centered	6.5956	2	20.826	0.00604	*
	Amazonia centered	37.8007	5	10.348	2.575E-06	*
	Dry Diagonal	47.6042	2	18.664	4.683E-08	*
	Dry Diangonal & Atlantic Forest (DD_AF)	48.8838	5	10.834	4.513E-07	*
	Atlantic Forest	1.2897	4	8.238	0.349	

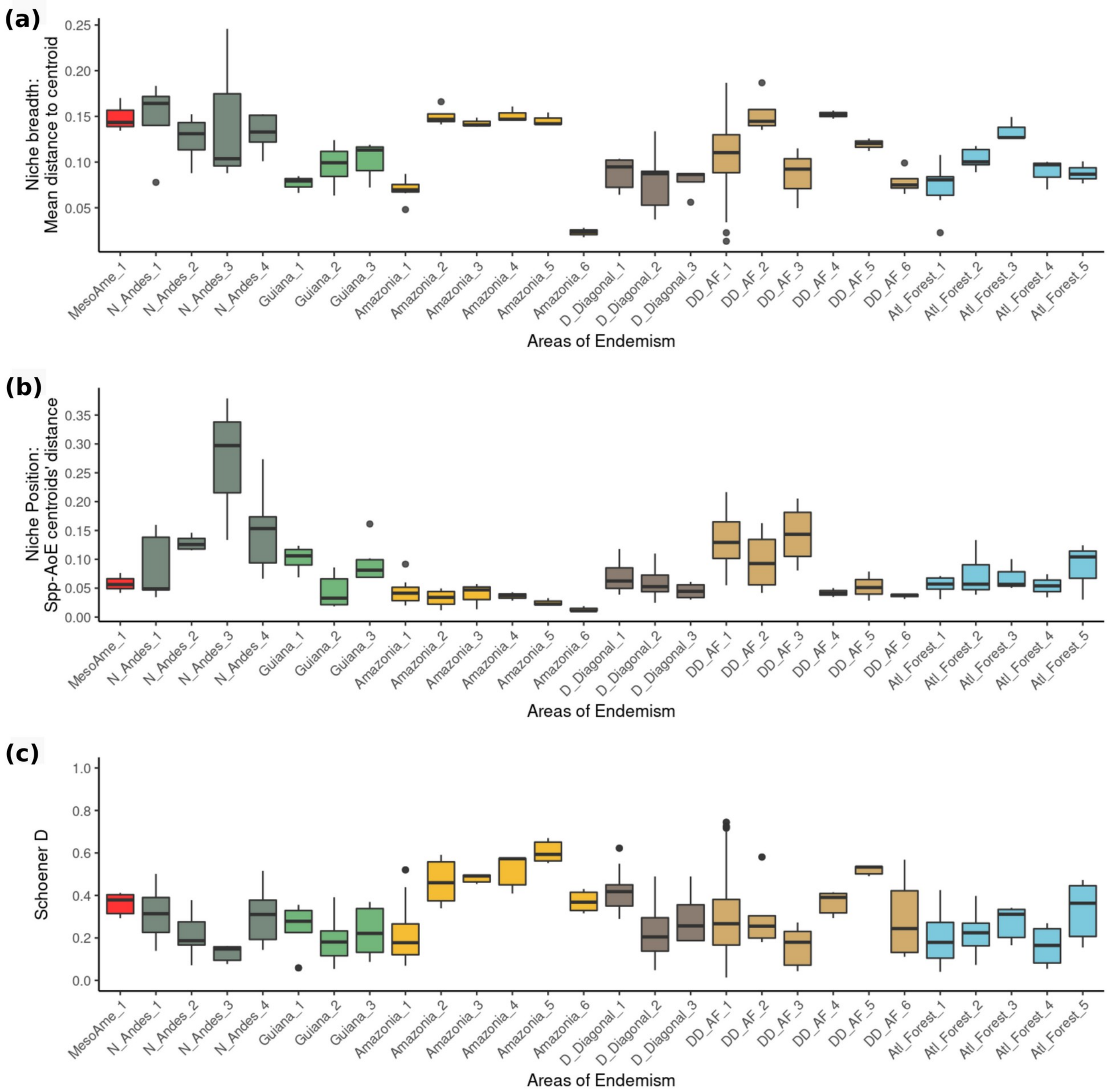


Figure 3. Distribution of the values for the niche properties of position and breadth, and the overlap among species pairwise comparisons for species belonging to different Areas of Endemism (AoEs). Colors identify the regions over which these AoEs occur. The Welch' ANOVA tests associated with these areas are shown in Table 1. (a) Niche breadth measured as the mean distance to centroid of every species record to the centroid of the species niche in the environmental space. (b) Niche position measured as the mean distance between endemic species centroids and the centroid of the Area of Endemism in environmental space, representing a relative measure of position in climatic space. (c) Overlap between endemic species assessed by the Schoener D metric. Note that only one area was identified in Mesoamerica. For detailed information about endemic species in each AoE, refer to Panels 1-28 in Supplementary Material.

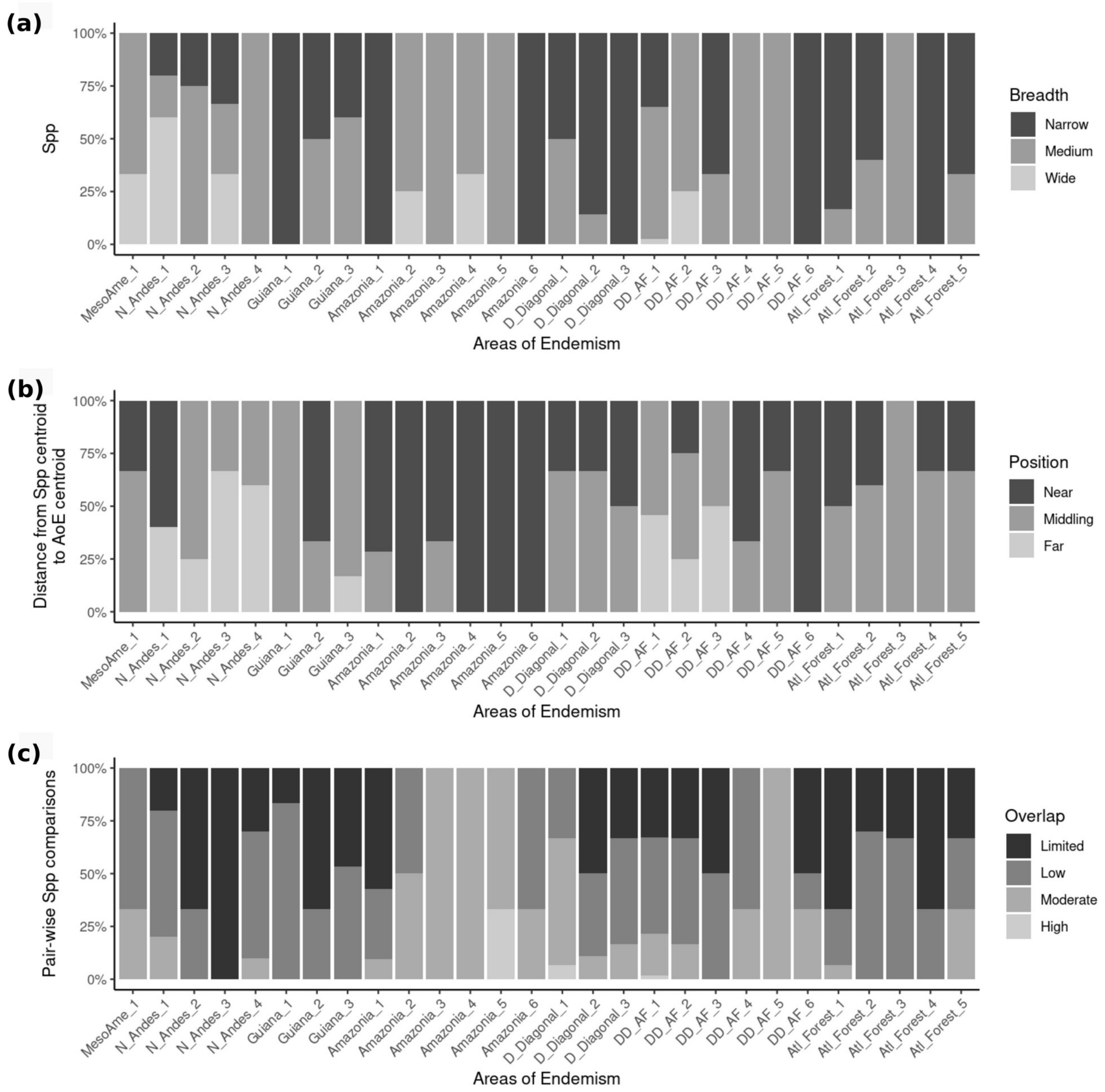


Figure 4. Overview of niche property variation within each Area of Endemism (AoE). For each niche property and niche overlap, categories were defined to visualize how the species niche differs inside each AoE. (a) Niche breadth, (b) Niche relative position, and (c) Schoener D overlap. Categories for niche breadth and position were defined using the quartiles of the values distribution, and the categories of overlap f were taken from Rödder & Engler (2011): Limited (D < 0.2), Low (0.2 < D <= 0.4), Moderate (0.4 < D <= 0.6), High (0.6 < D <= 0.8), and Very High (D < 0.8) (Rödder & Engler, 2011). For detailed information about endemic species in each AoE, refer to Panels 1-28 in Supplementary Material.

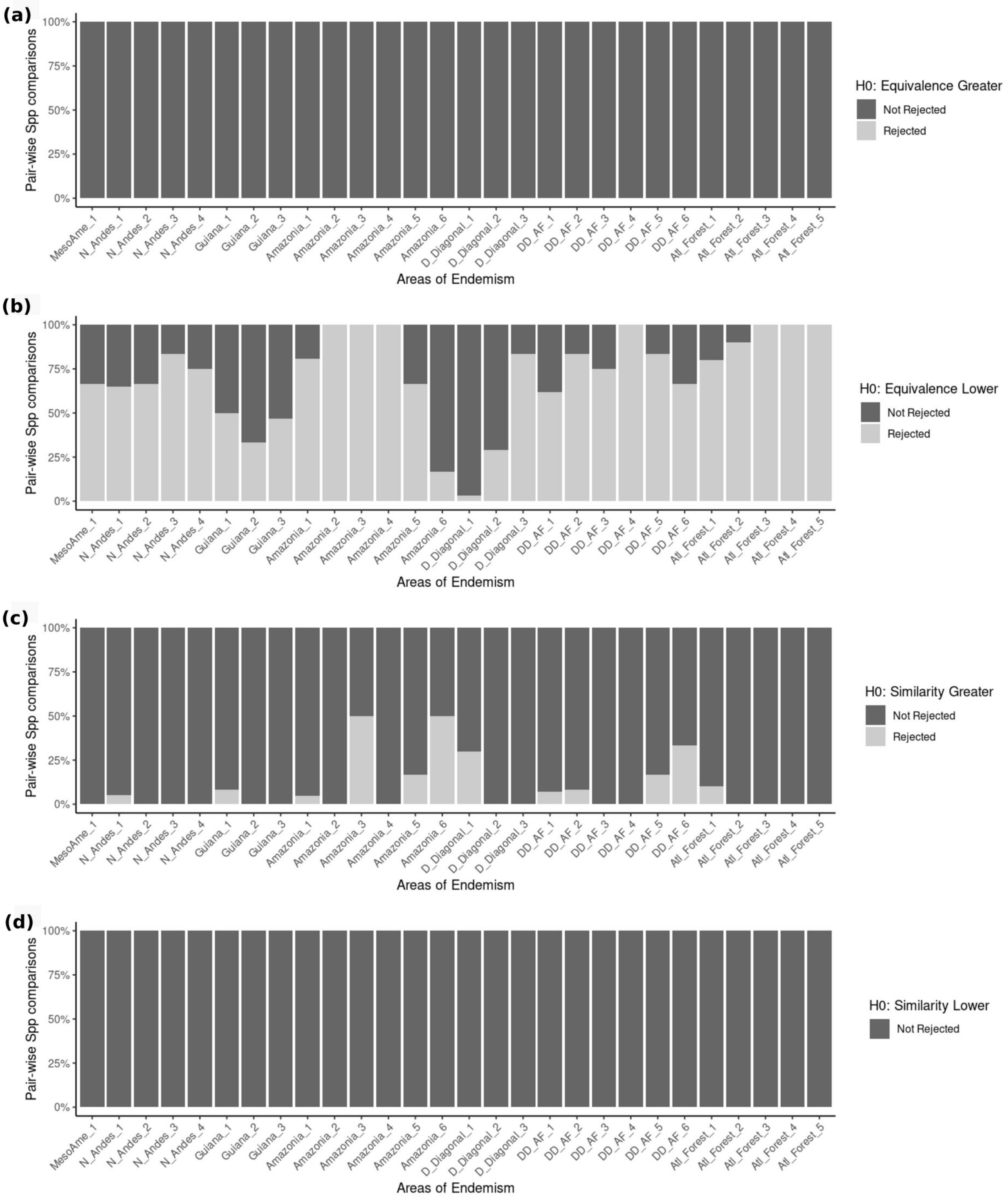


Figure 5. Equivalence and similarity tests for pairwise species comparisons within each Area of Endemism (AoE). Percentages indicate the proportion of pairwise comparisons that reject the null hypotheses. The test of equivalence and similarity are two tailed tests using two alternative hypotheses: The alternative lower test for significant differences among the species niches, while the alternative lower test for significant similarities among species niches. The equivalence test examines if the two niches are identical (conserved) or different (divergent). The similarity test evaluates if this similarity or difference is significant given the environmental background. (a) Equivalence alternative greater, (b) Equivalence alternative lower, (c) Similarity alternative greater, (d) Similarity alternative lower. For many pairwise comparisons the equivalence lower null hypothesis was rejected, while the similarity lower null hypothesis was not. This means that species within areas of endemism are no less equivalent than expected by chance given the environment. Species niches are as different as expected given the environmental heterogeneity of the AoEs.

Discussion

In order to characterize the relationship between climate and areas of endemism (AoEs) in Bignonieae, we explored the trends of variation in the properties of the climatic niche of endemic species belonging to different AoEs. We expected to find a correspondence between patterns of sympatric geographic distributions and patterns of variation in the properties of the climatic niche as a proxy for common ecological processes leading to specialization in climatic multivariate space. Although common trends in niche breadth and position of the endemic species were identified for some AoEs (Fig. 3), the niche overlap among species was generally low, and no tendency for conservation or divergence of the climatic niche could be attributed to ecological processes (Fig. 5). Differences among species could be attributed to environmental climatic heterogeneity across AoEs instead. Therefore, no evidence that membership to AoEs is associated with shared ecological processes in climatic space was found given the available distributional data.

The environmental space of AoEs was built using bioclimatic variables that represent the temperature fluctuation, seasonality in precipitation, and water availability in the Neotropics (Fig. 1). Our findings indicate that the contemporary climate circumscribed by each AoE of Bignonieae overlapped extensively (Fig. 2), suggesting that AoEs are not associated with unique climates, but encompass geographic regions that are climatically heterogeneous instead. This result weakens the role of exclusive and rare climates as important drivers of endemism in this tribe (Ohlemüller *et al.*, 2008). Previous observations of Bignonieae distributions asserted that patterns of endemism were associated with continental climatic regimes (Gentry, 1979). However, the presence of similar climates among AoEs suggest that the confinement of endemic species to these regions is not related to contemporary climate as a factor limiting species distributions.

The species climatic niches fell within the boundaries of the climatic space defined by the AoEs to which they belonged to (see Appendix S2 in Supporting Information). However, their niche properties differed substantially within and between AoEs (Fig. 3). The higher variation in niche breadth and relative position to the average climatic conditions in the AoEs suggests that endemic species are partitioning and specializing in different zones of the climatic space. This finding explains why the values of overlap were generally low among most species (Fig. 3), suggesting that species of the same AoEs are occupying localities with different environments. The niche specialization into different zones of the climatic space is consistent with previous studies that showed the importance of abiotic specialization in the assembly of communities of Bignonieae (Alcantara *et al.*, 2014), and with the lack of niche conservatism in species of the Bignonieae genus *Tynanthus* (Medeiros *et al.*, 2015). These results support the role that niche lability might have in the colonization of areas with different climates in this clade (Lohmann *et al.*, 2013; Donoghue & Edwards, 2014).

The range of variation in niche properties seems to be related to the landscape complexity of the regions over which the AoEs are located and to express a negative relationship between variation in niche breadth, relative position, and overlap. AoEs located over regions with more heterogeneous landscapes (e.g., those encompassing mountains) showed a mixture of species with different niche breadths and positions, and low values of niche overlap (i.e., the Northern Andes, the Atlantic Forest, and Dry Diagonal-Atlantic Forest; Fig. 3). The AoEs located over regions with more homogeneous landscapes such as the Amazonian Lowlands (Fig. 3) included species with more similar niche breadths and positions and relatively higher values of overlap. Topographical and environmental heterogeneity are related to higher levels of endemism and richness because they increase the niche space available and the opportunities to specialize into different regions of the environmental space (Irl *et al.*, 2015). This means that AoEs encompassing montane regions will include a mixture of species that despite their high degree of sympatry are nonetheless specializing into different environments. Similarly, AoEs encompassing regions with more homogeneous environment will consist of species that are closer in the environmental space and with more similar climatic preferences. These results suggest that niche differences could be driven by spatial autocorrelation and species dispersal capacity rather than biological or ecological processes (Warren *et al.*, 2014).

This hypothesis is also supported by the tests of niche equivalence and similarity of niche overlap which showed that the niches of the endemic species are not more or less equivalent or similar than expected given the environmental heterogeneity of the AoEs (Fig. 5). Our exploration of the climatic niche of the species of Bignonieae led us to conclude that the sympatric distributions described by the areas of endemism have no corresponding patterns of variation in the properties of the climatic niche. The AoEs of the tribe Bignonieae are formed by species with very different climatic niches. Therefore, the membership to these areas was not a proxy to discover common processes involving the contemporary climate that were responsible for the formation or maintenance of these patterns. Other causes such as history, dispersal limitations, and biotic interactions must be responsible for areas of endemism within tribe Bignonieae (Lohmann *et al.*, 2013; Chapter 2). Although strong correlations among endemism, climate, and other habitat characteristics (e.g., topography) have been reported (Irl et al., 2015), our findings are consistent with studies for other taxa that showed that the relationship between endemism and contemporary climates can be caused by spatial autocorrelation between climate and geography (Zuloaga *et al.*, 2018).

In our study, we defined the Grinnellian niche of endemic species under the contemporary climate and asked whether the variation in niche properties might provide us with clues about common ecological processes associated with the membership to areas of endemism. Previous analyses of the Grinnellian niche in the context of endemism have demonstrated (1) the importance of using endemic species to fully account for the realized ecological niche in environmental niche modeling (Broennimann *et al.*, 2006; Thuiller *et al.*, 2005); (2) the applicability of climate suitability for the identification of areas of endemism (Escalante *et al.*, 2013; Linder *et al.*, 2013); (4) the relevance of the climatic niche to understand the temporal dynamics of areas of endemism (Gámez *et al.*, 2014); (5) and the differences among patterns of niche partitioning and occupation by endemic and non-endemic species in selected biomes (Sánchez-Tapia *et al.*, 2018). Together these approaches show that using the Grinnellian niche to explore patterns of partition and occupation of the climatic space can reveal relevant aspects of climate as a causal factor of particular areas of endemism.

Nevertheless, a few caveats must be taken into account regarding the biological and methodological dimensions of our results. We took a broad scale approach and looked at the species geographical limit using the niche concept as a tool. Spatial scale can affect the relationship among geographic range, niche properties, and niche overlap among endemic species belonging to the same AoE (Li *et al.*, 2018; Daru *et al.*, 2020). While the climatic niches of sympatric species are expected to be conserved at large spatial scales given the effects of habitat filtering across broad regions, niche divergence is expected at the local scale where factors such as microclimate differences, soil variation, and pollinator availability impact species interactions and specialization patterns across different axes of the niche space (i.e., competitive exclusion) (Silvertown *et al.*, 2006). Studies of the climatic niche of the species of Bignonieae using climatic data with higher resolution and additional information such as soil composition or canopy height should allow us to see how niches are partitioning the climatic space at local scales.

Two important assumptions behind the overlap estimation methods used here (Broennimann *et al.*, 2012) are that species distribution are at equilibrium with environmental conditions, and that the niche is well characterized by the occurrence data. However, these assumptions are rarely met because species distributions obtained from occurrence data suffer from geographical biases in collection effort that limit the knowledge of the environmental tolerance of species (Meyer *et al.*, 2016). Moreover, the dimensions of species niches depend on the environment available in the region where the species is found at a specific point in time (Jiménez *et al.*, 2019). This means that niche measurements and overlap among species can be underestimated by spatial and temporal biases in species occurrence and environmental data (Wiens *et al.*, 2009). Increasing the amount of distributional data can generate different results for Bignonieae if the niche of its species is not well represented by the data at hand.

Here we attempt to unravel the causes of patterns of endemism within tribe Bignonieae by studying the relationship between sympatric distributions and the occupation of the contemporary climatic niche. No relationship was recovered and we confirmed the tendency of species niches to specialize in different regions of the climatic space. This niche specialization supports that niche evolution and lability are important factors explaining distributions in this clade of tropical lianas. Further modeling approaches aiming at studying the effects of past climate change over species distributions tracking species movement through time can help to unravel the historical climatic factors associated with patterns of endemism in Bignonieae. Furthermore, studies using complete species phylogenies to study niche transitions across evolutionary history will certainly help to improve our understanding of the biogeography of these plants.

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Data availability statement

R scripts available at <https://github.com/jupanago/Rcode_Bignonieae_niche>

Appendix 1

Do shared distribution patterns entail common causes? A case study of the Grinnellian climatic niche and areas of endemism using neotropical lianas (Bignonieae, Bignoniaceae)

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Supplementary material Appendix S1 – Niche breadth in PCA and PCoA.

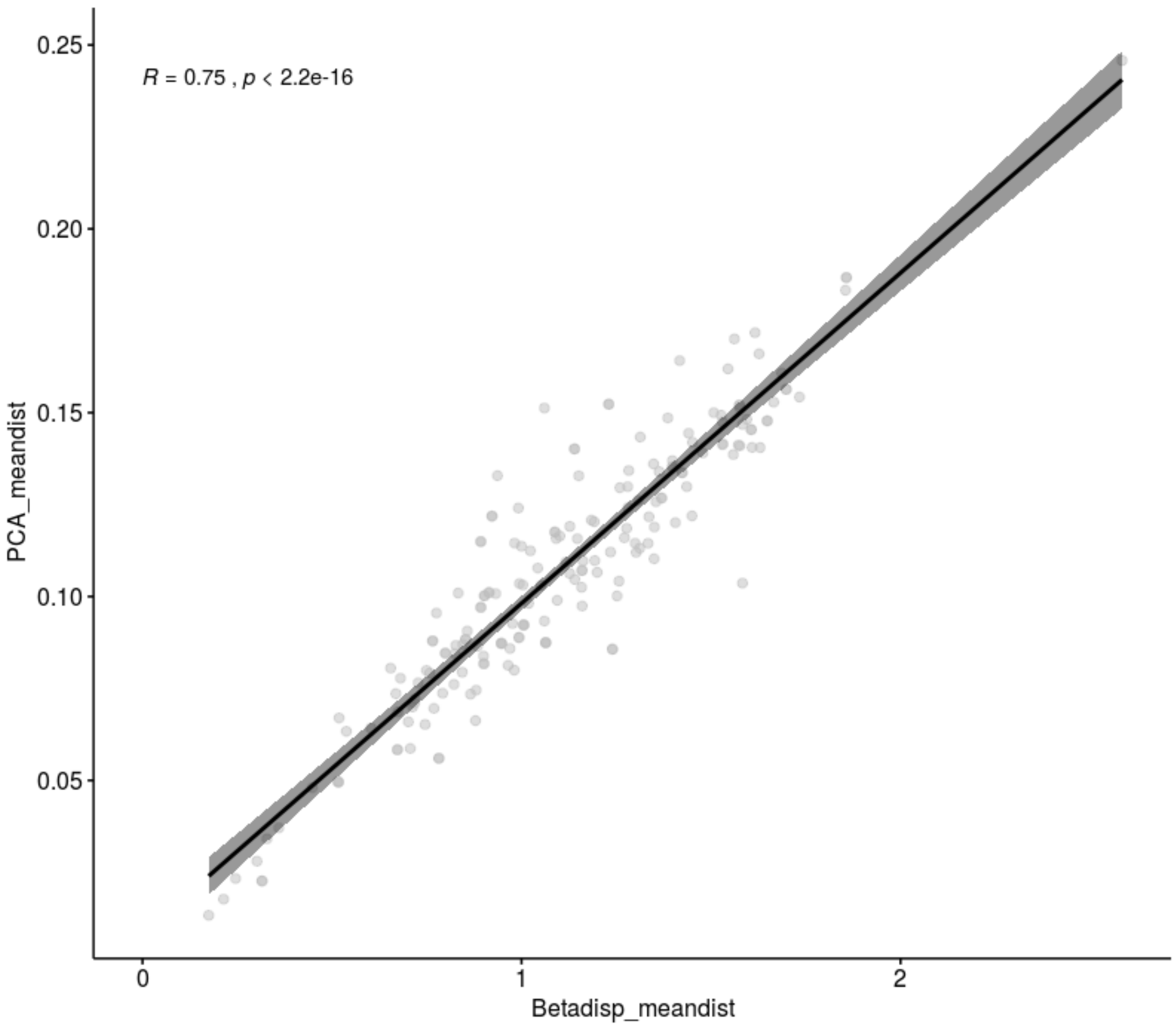

Figure S1.1. Pearson correlation between the niche breadth calculated as a mean distance to the centroid of the PC scores of the PCA describing the climatic environment of the Areas of Endemism and the same measure but with the PCoA calculated by the function betadisper of the R package "vegan" (Oksanen et al., 2019). Note that both measures of niche breadth were positively correlated and increased monotonically.

Appendix 2

Do shared distribution patterns entail common causes? A case study of the Grinnellian climatic niche and areas of endemism using neotropical lianas (Bignonieae, Bignoniaceae)

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Supplementary material Appendix S2 – Panels of Niches properties for Areas of Endemism of the Tribe Bignonieae

The following panels help to visualize the niche properties of the endemic species of particular areas of endemism.

a. The map of the area of endemism, its name, the approximated geographical region, the kind of patterns it has, and the number of endemic species.

b. The environmental space of the area of endemism represented as a convex hull.

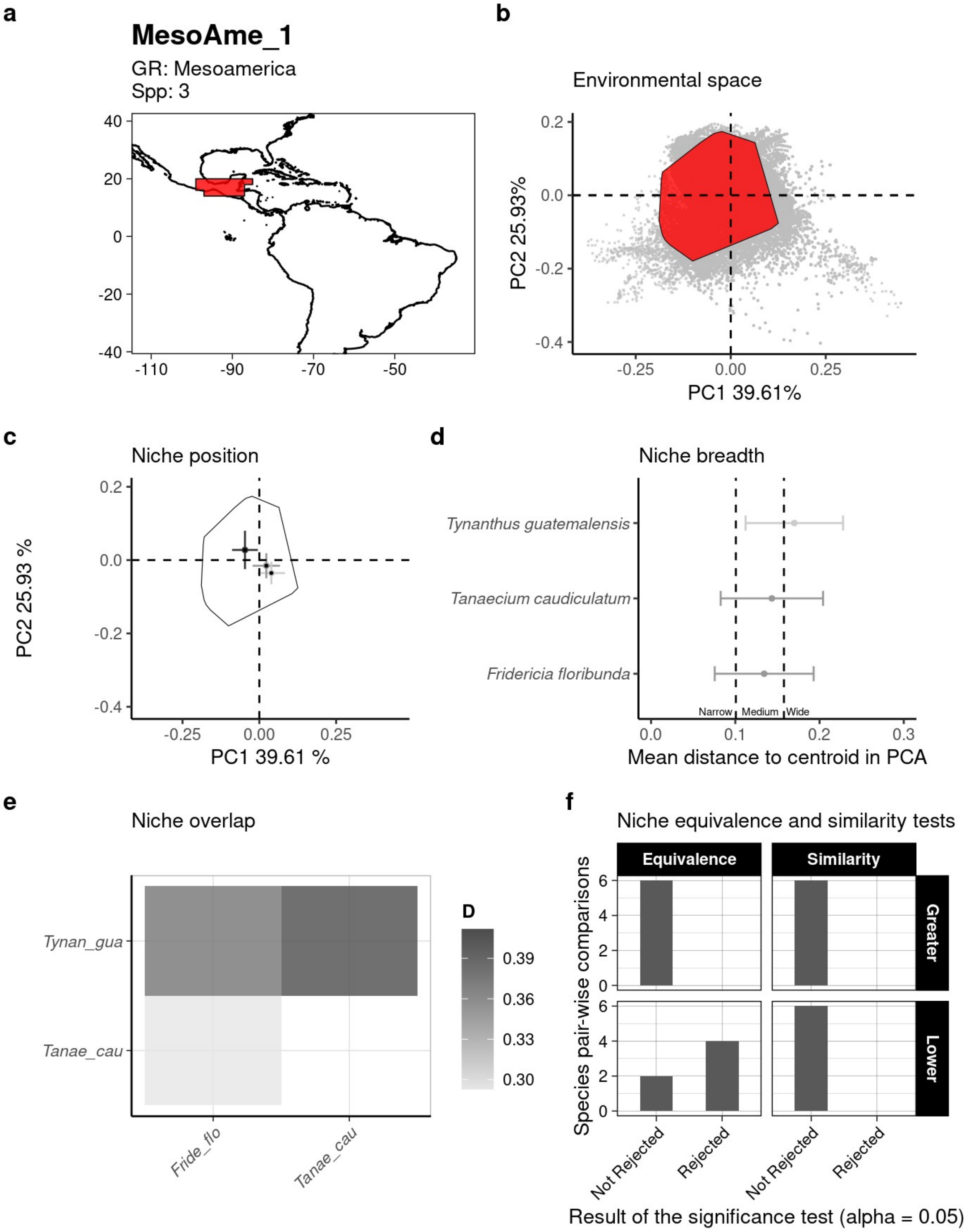
c. An approximate representation of the niche position of endemics species inside the environment of the Area of Endemism depicted in the PC1 and PC2 only. The value of niche position was calculated using the 6 principal components of the PCA, therefore this depiction is only an heuristic device to visualize possible patterns.

d. Niche breadth of endemic species. Doted lines indicate the first and third quartile used to categorize niche breadth as Narrow, Medium and Wide.

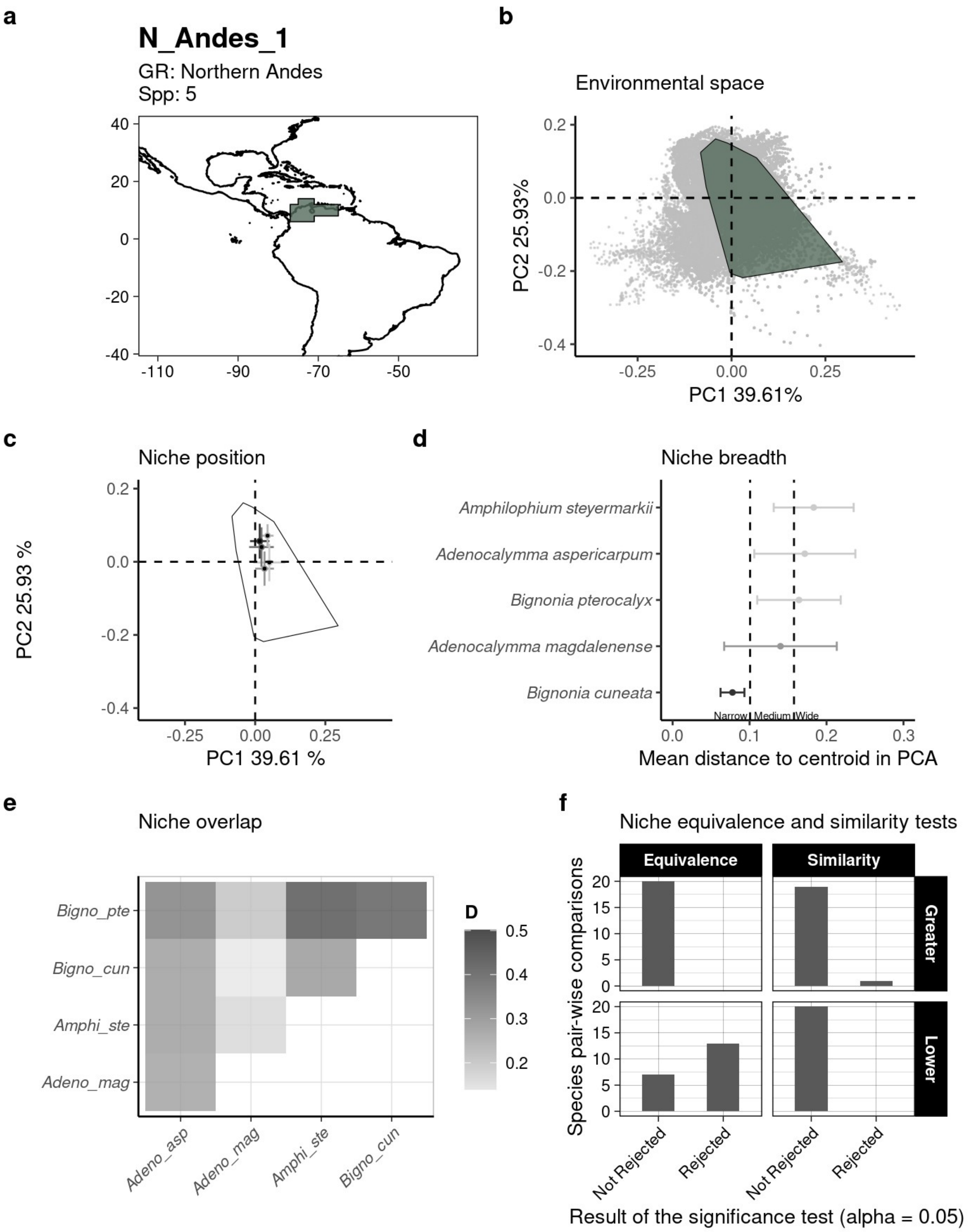
e. Schoener D overlap for endemic species in the Area.

f. Results of the equivalence and similarity tests under the alternative hypothesis of Lower (Divergence) and Greater (Conservatism). X axis indicates if the test has a $p>0.05$ (Rejected) or $p<=0.05$ (Not Rejected). Y axis indicates the number of pair comparisons between endemic species evaluated. Similarity tests imply more pair comparisons than the equivalence tests (Further details within the methods).

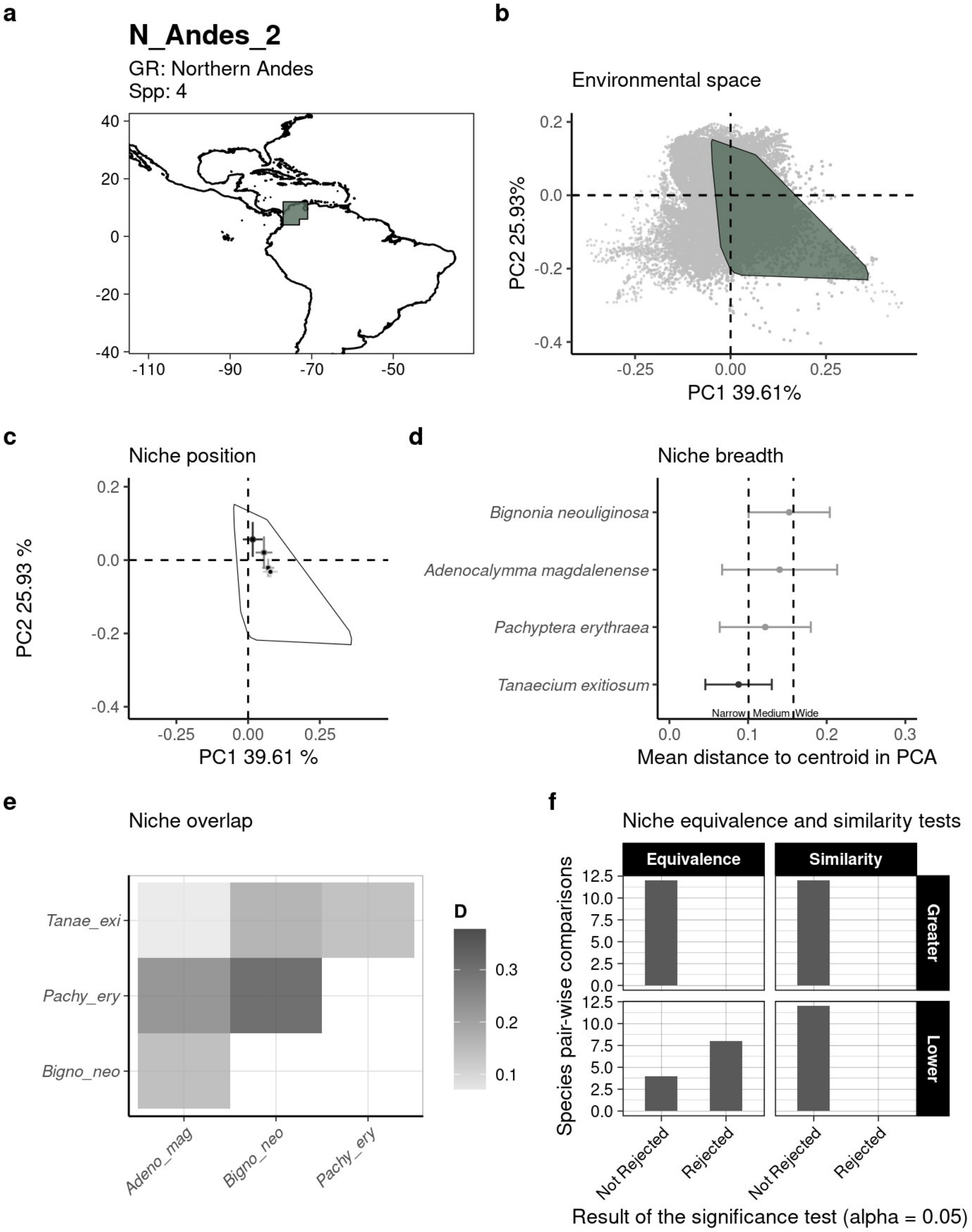
Panel 1: MesoAme_1



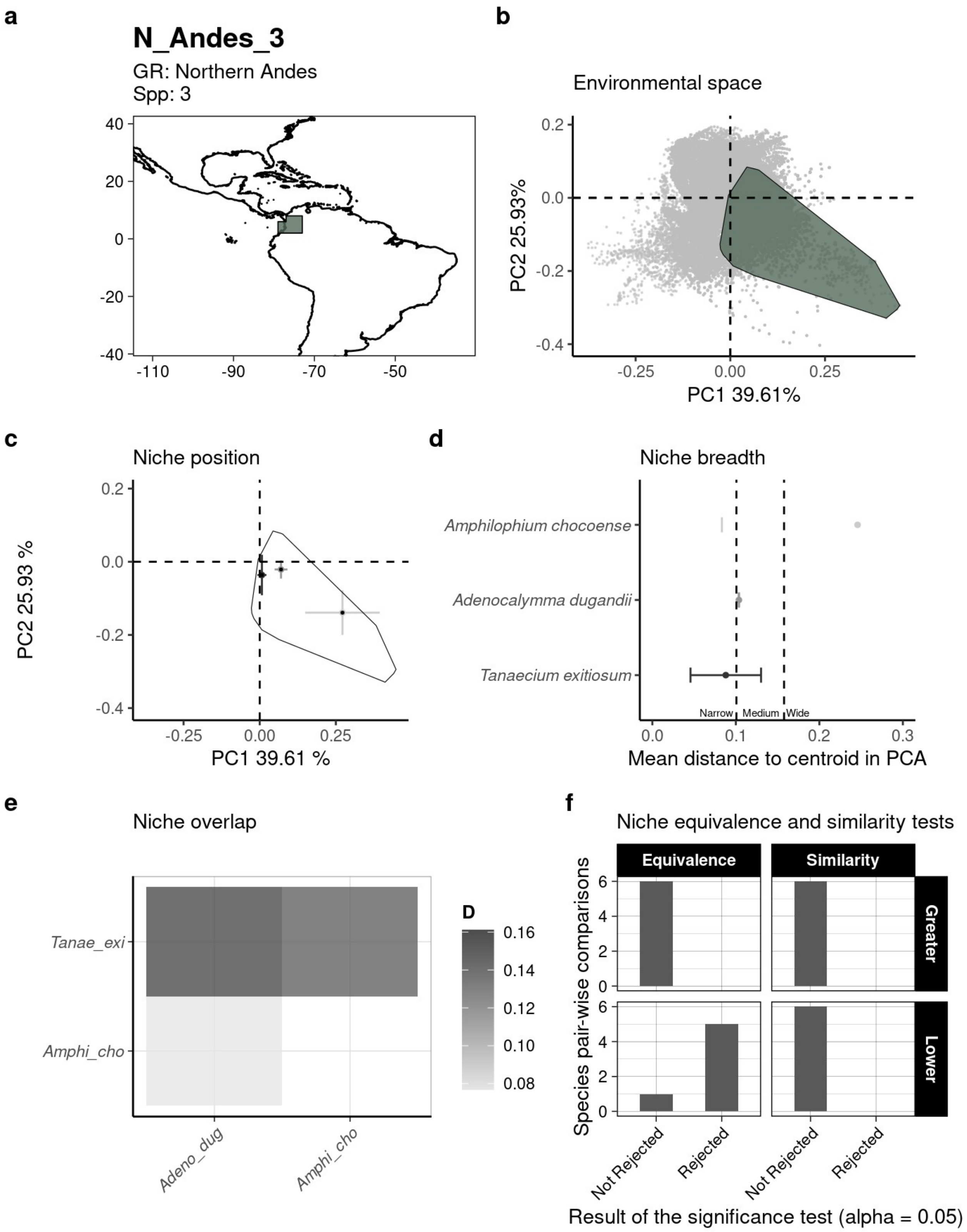
Panel 2: N_Andes_1



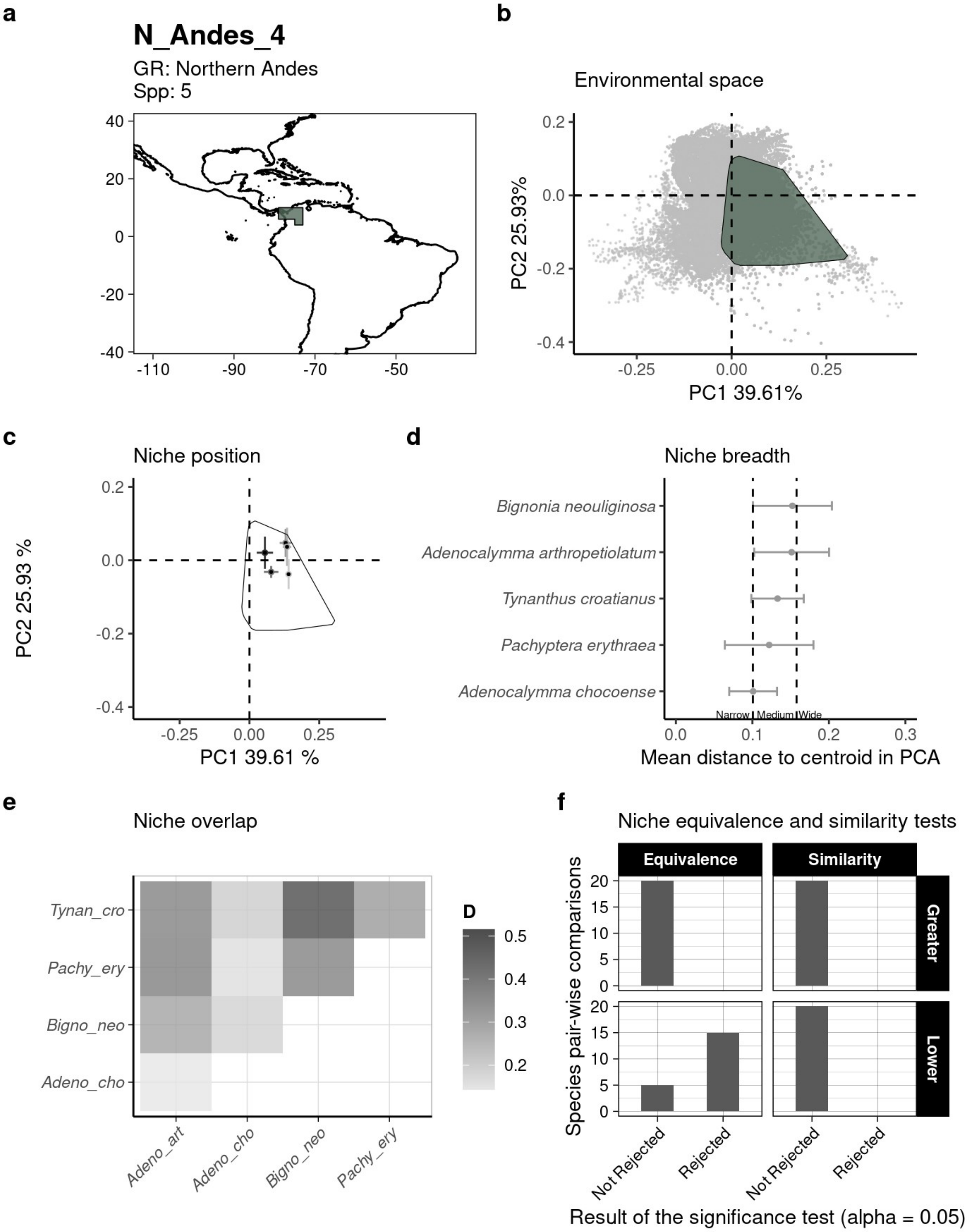
Panel 3: N_Andes_2



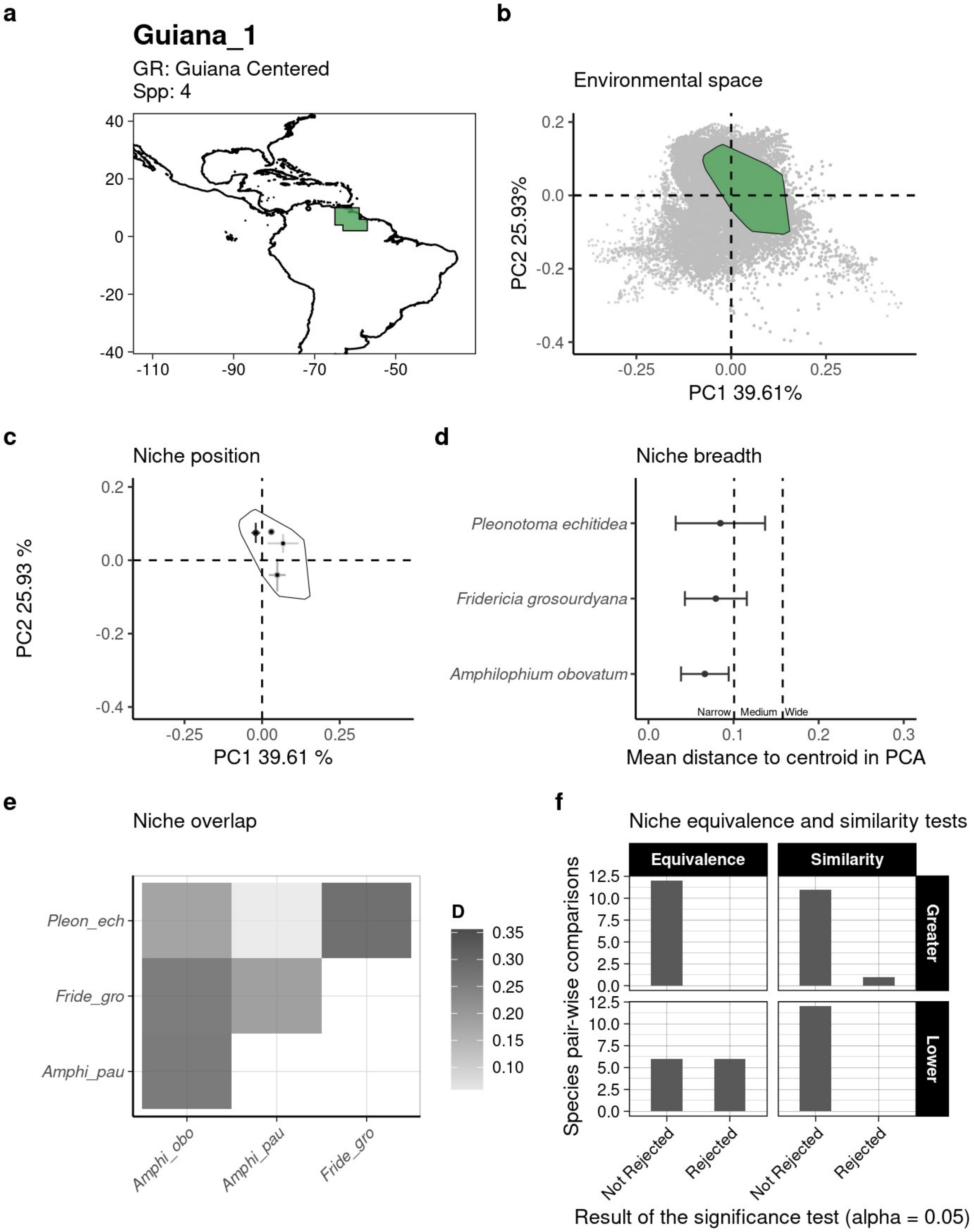
Panel 4: N_Andes_3



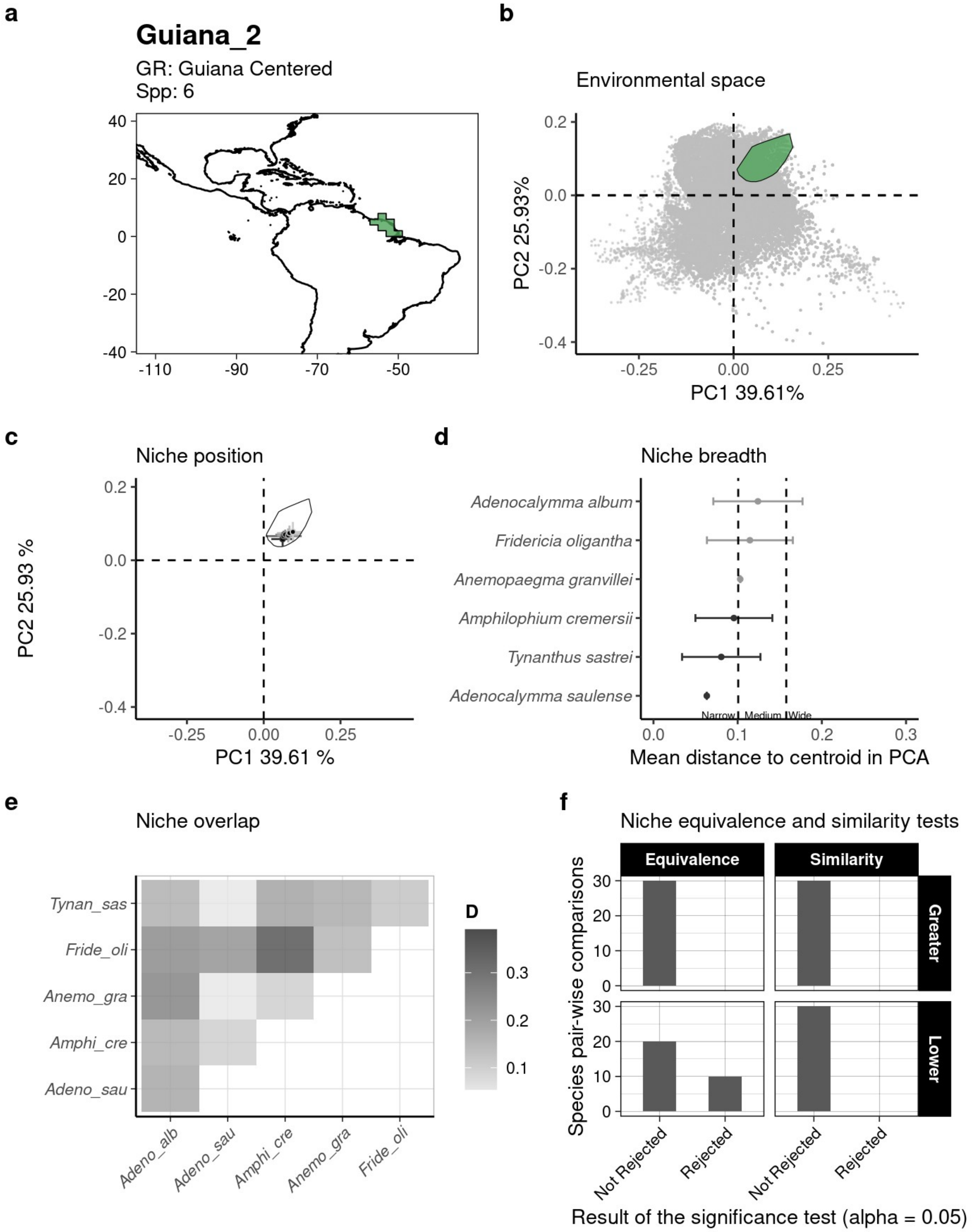
Panel 5: N_Andes_4



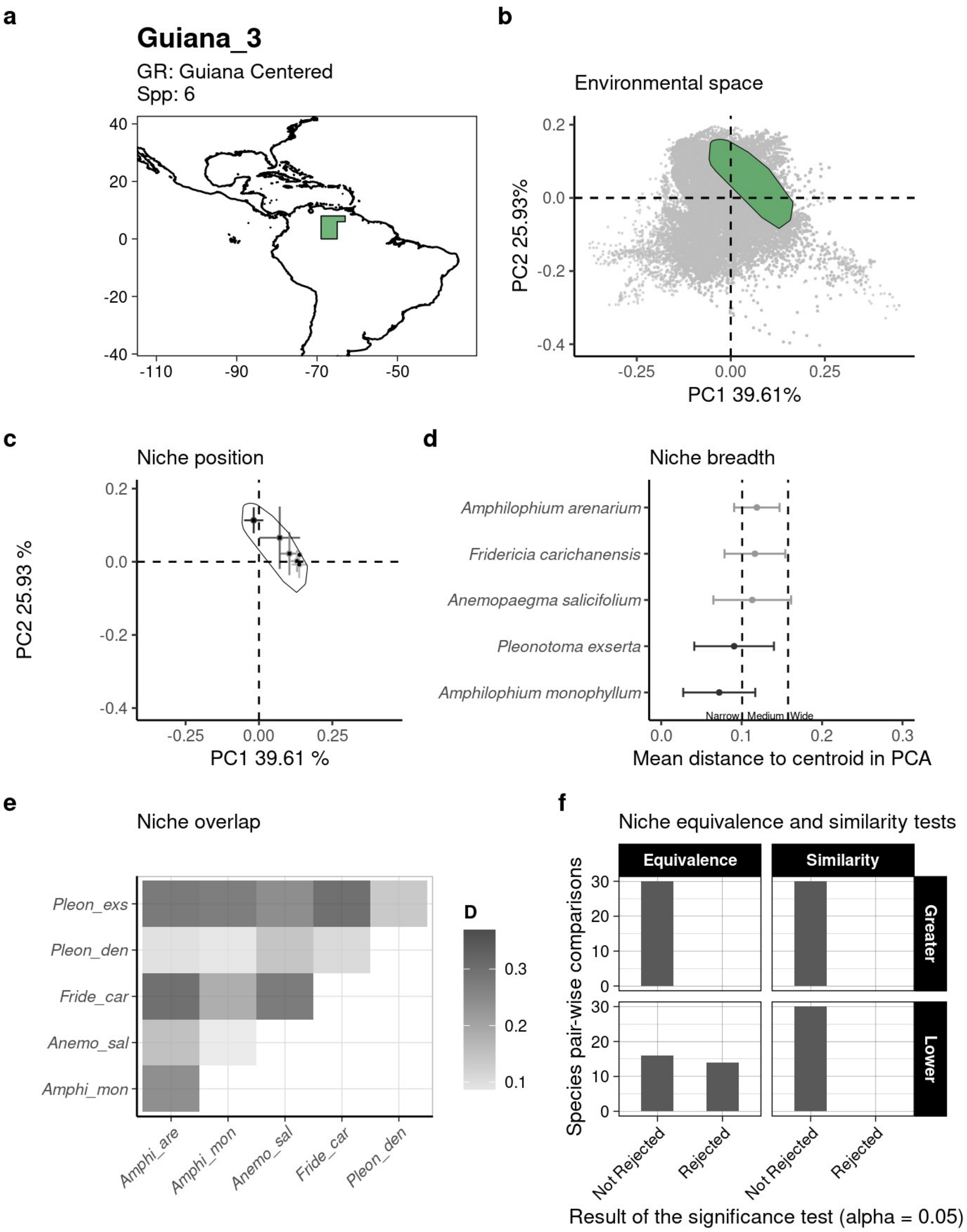
Panel 6: Guiana_1



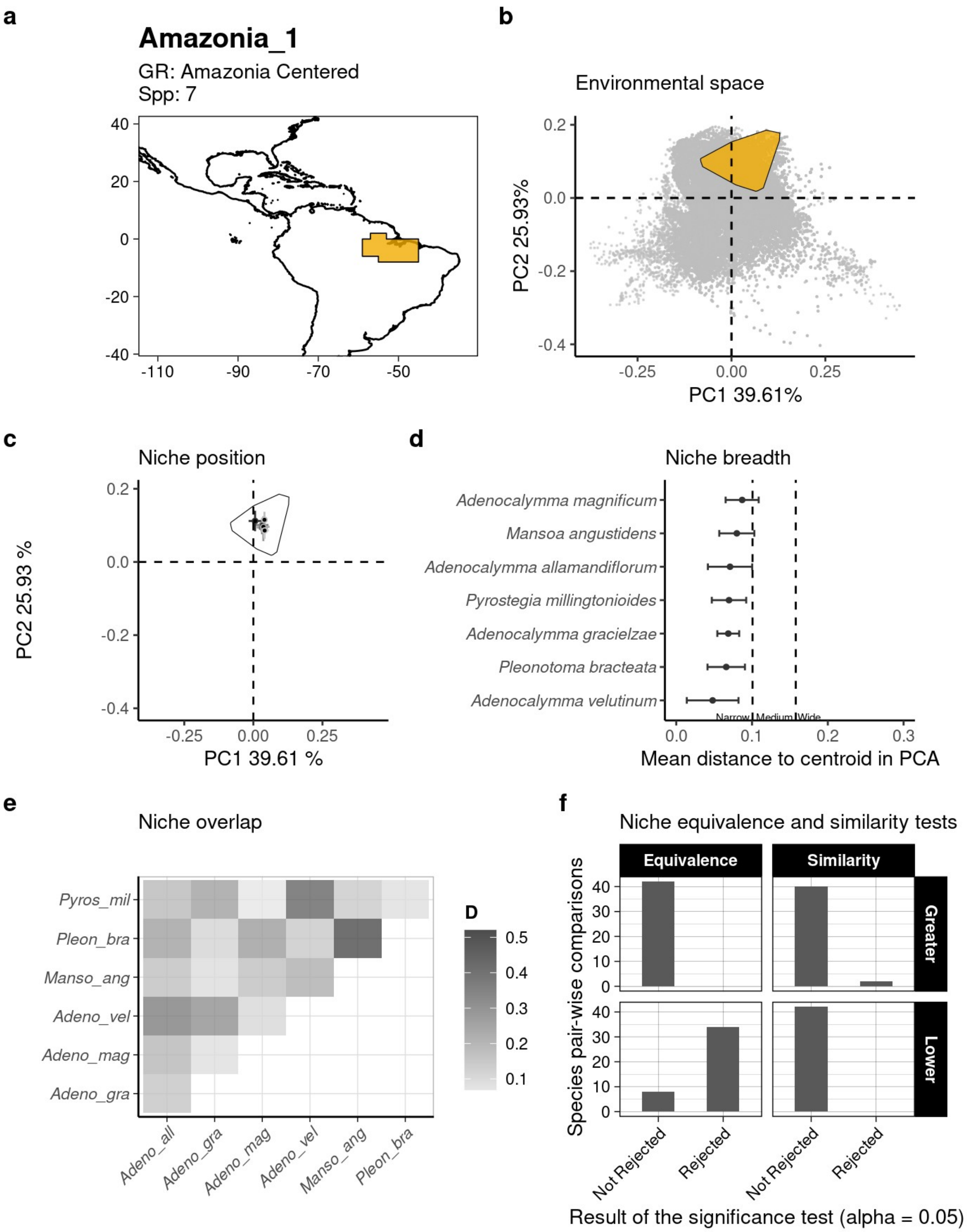
Panel 7: Guiana_2



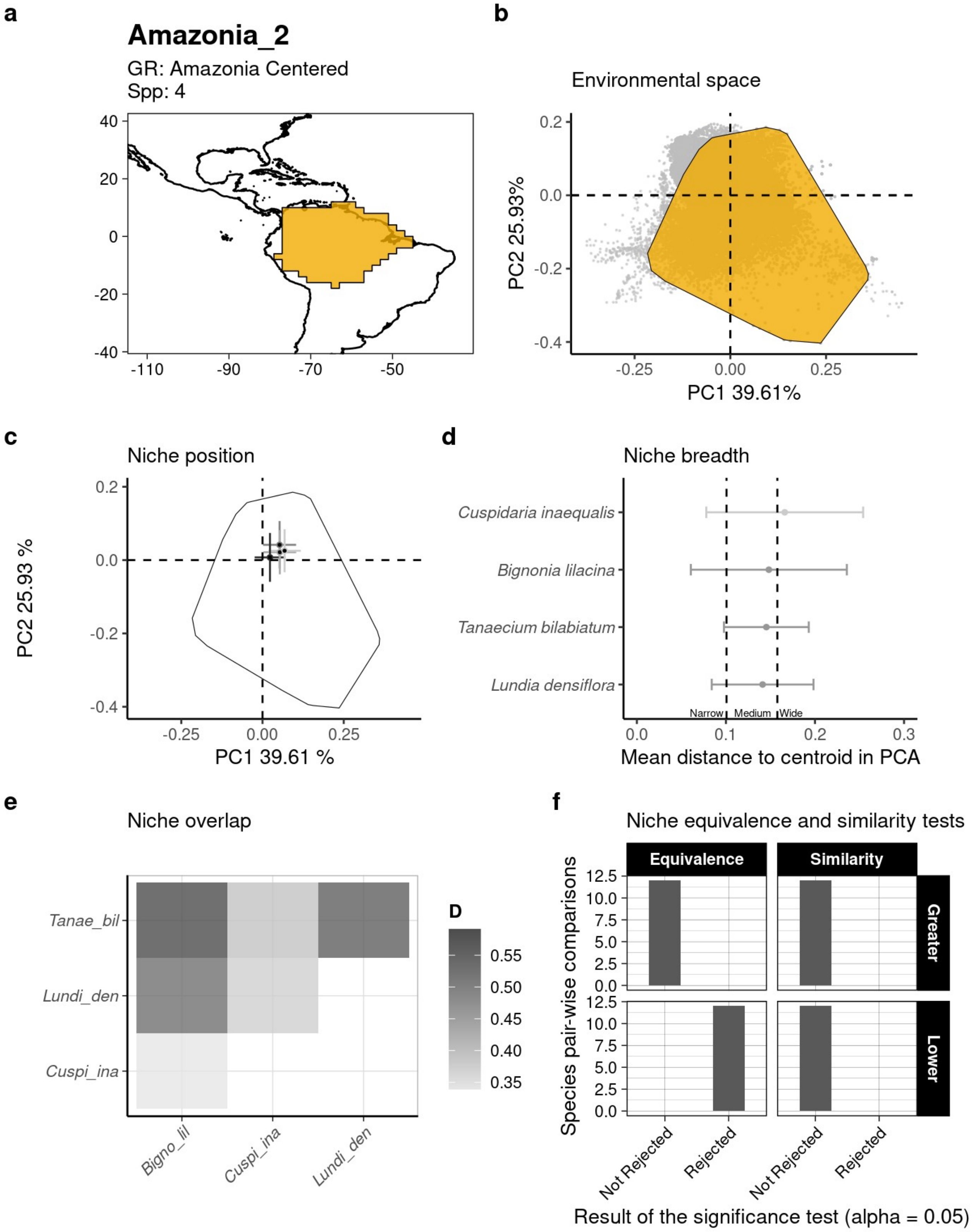
Panel 8: Guiana_3



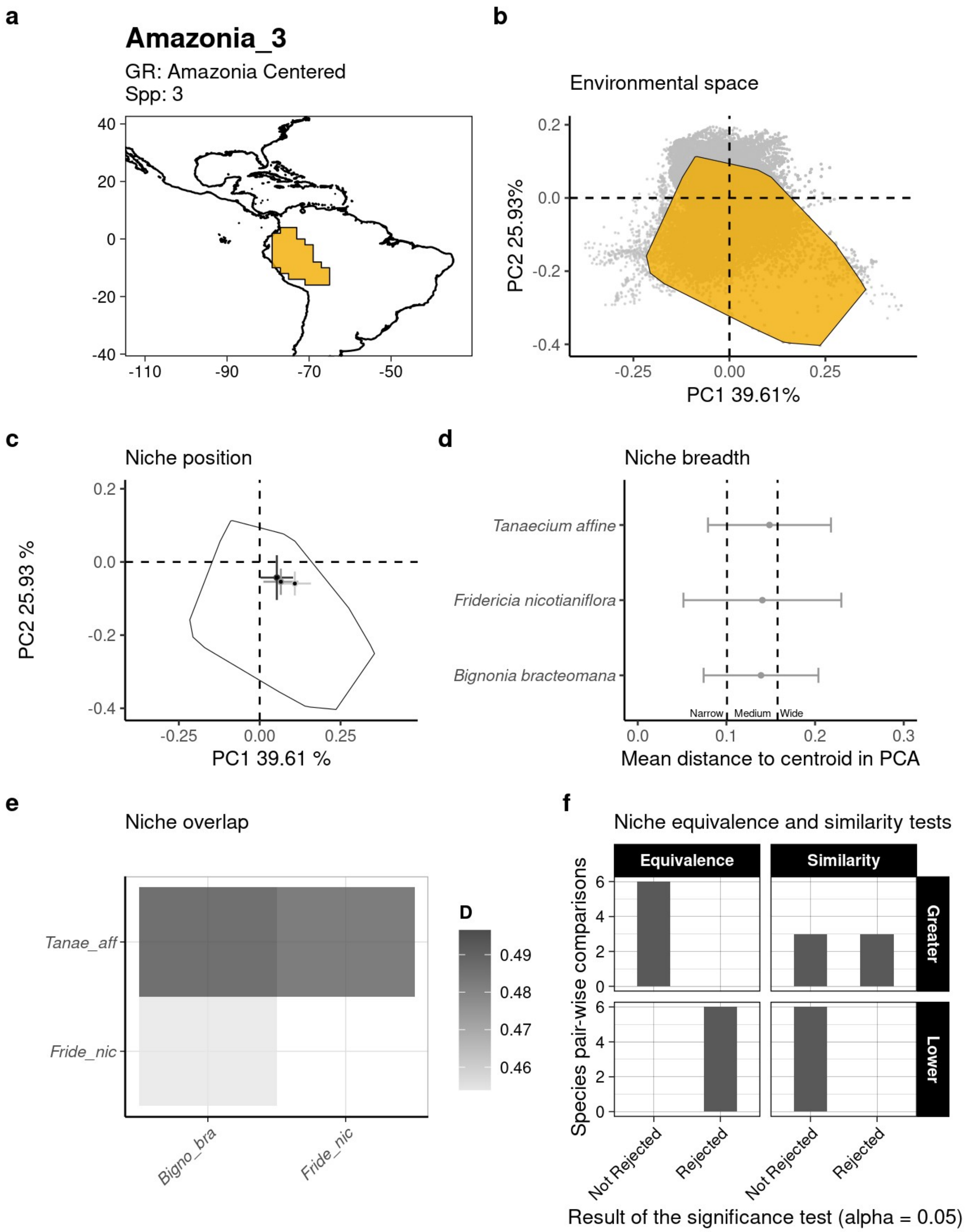
Panel 9: Amazonia_1



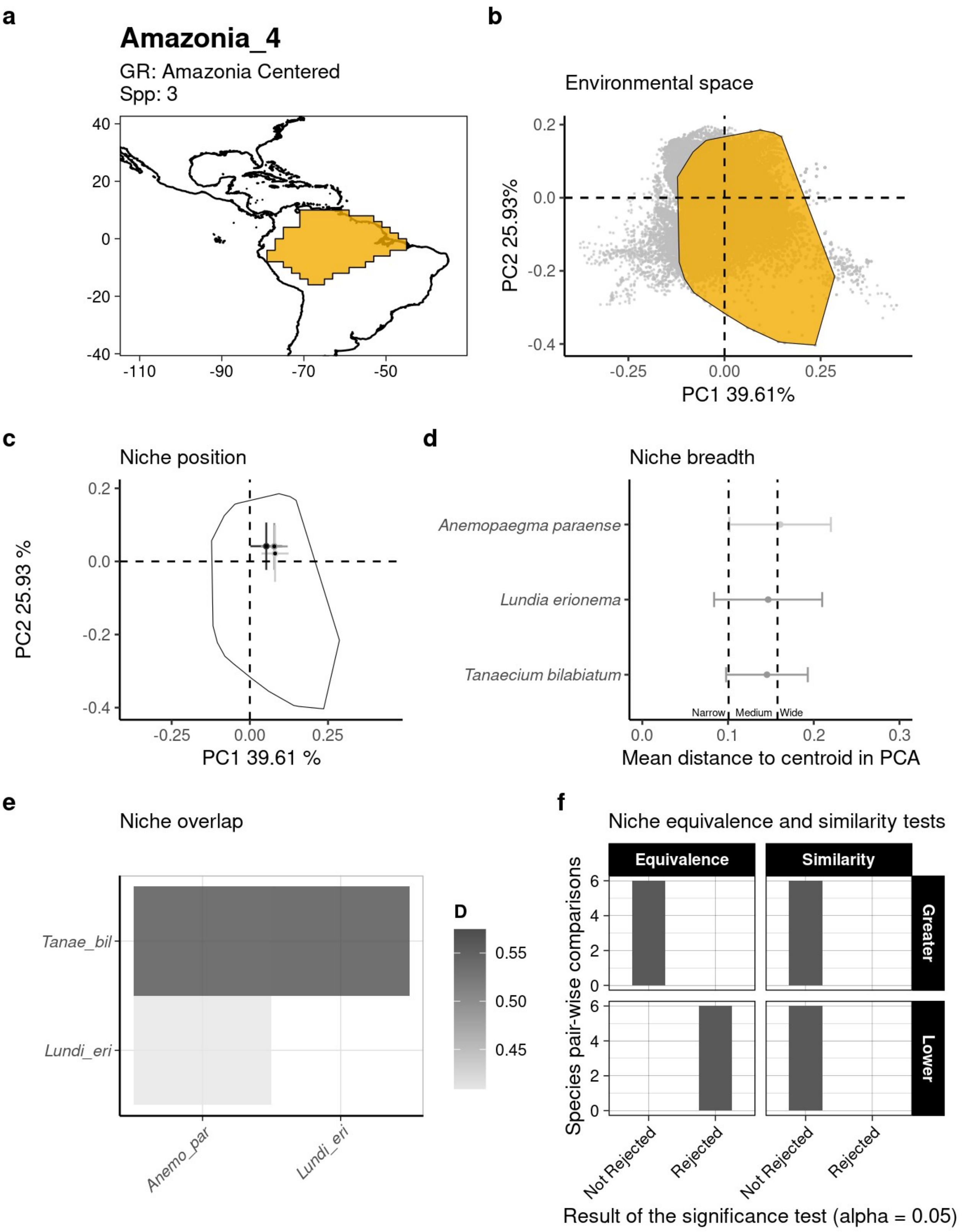
Panel 10: Amazonia_2



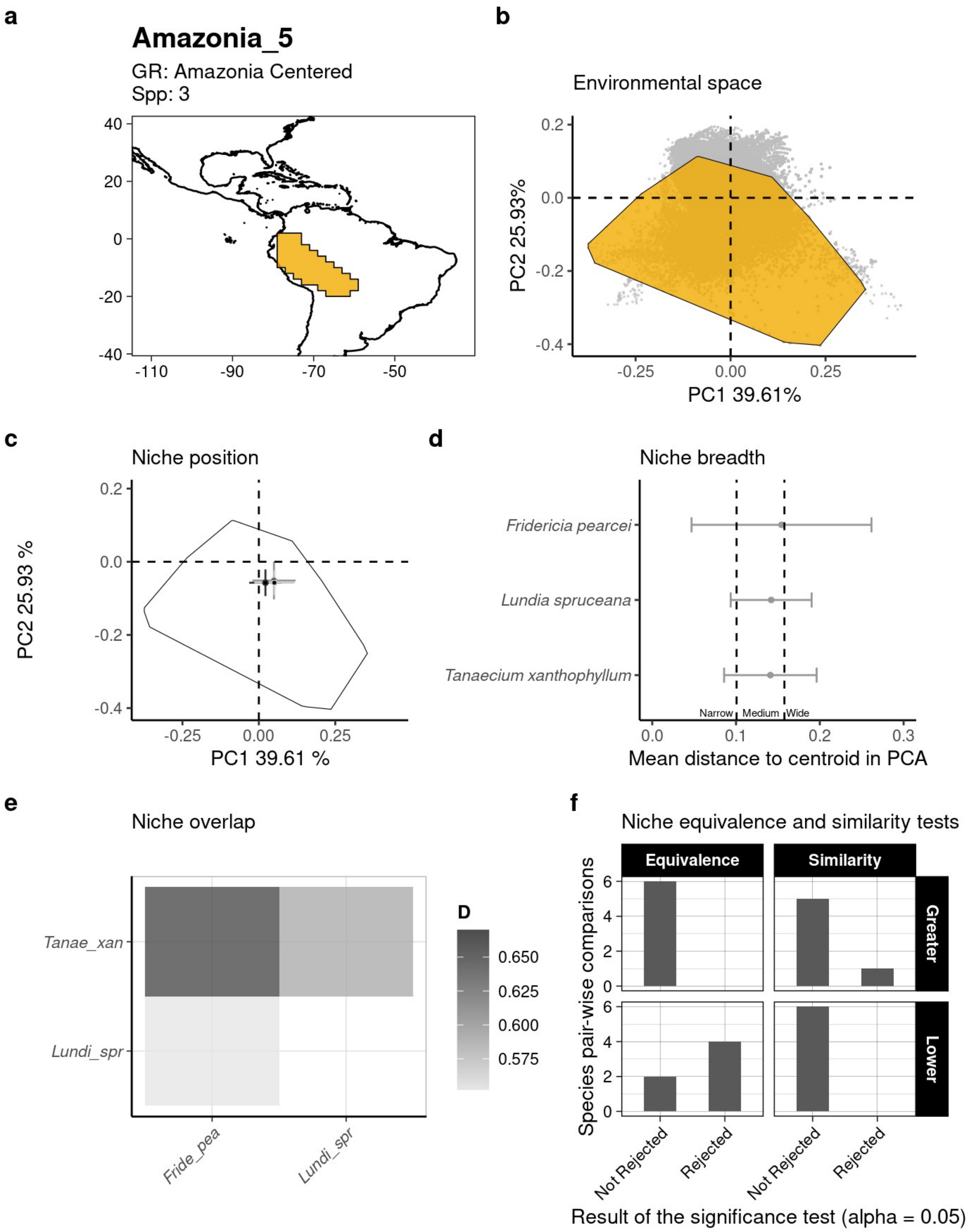
Panel 11: Amazonia_3



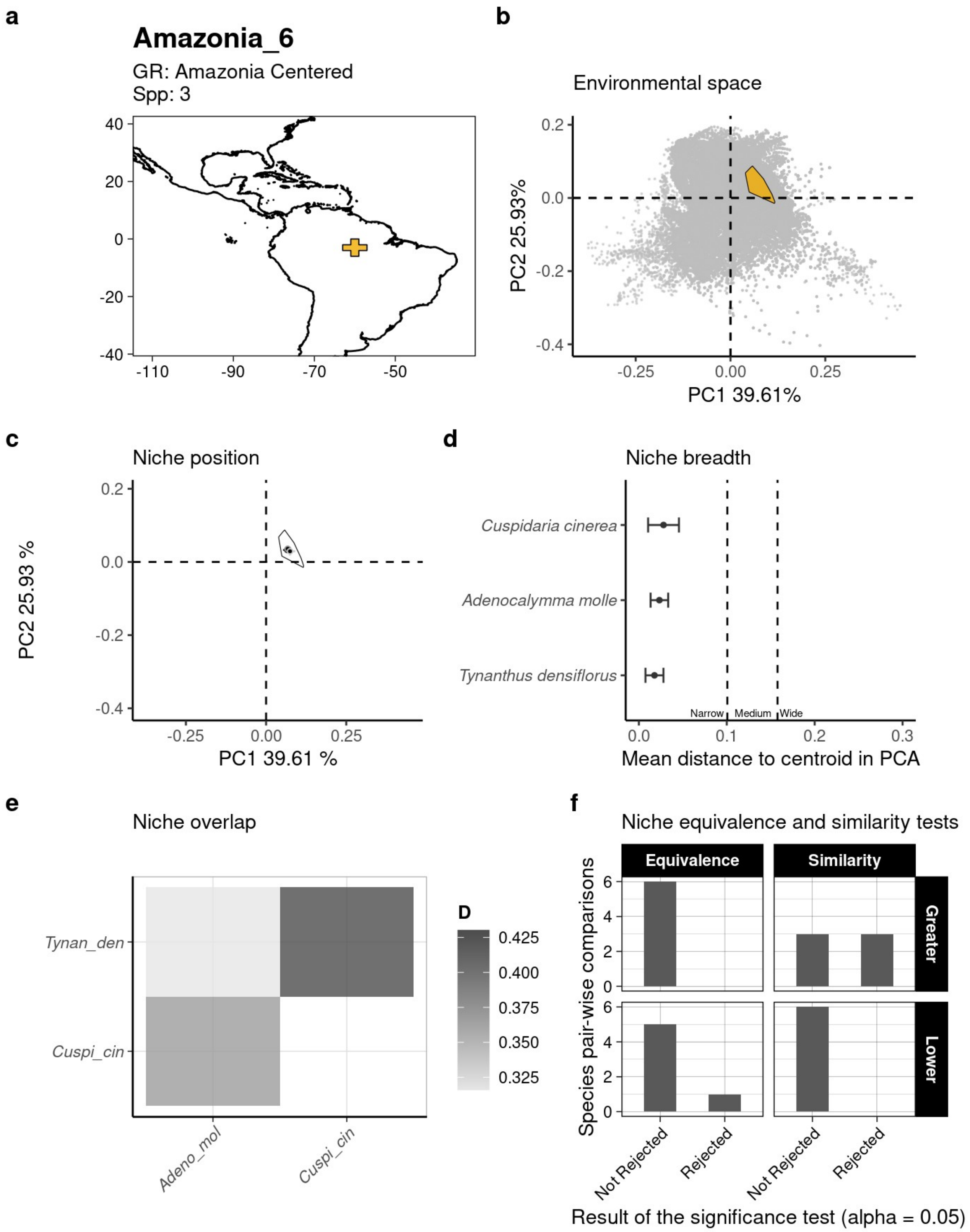
Panel 12: Amazonia_4



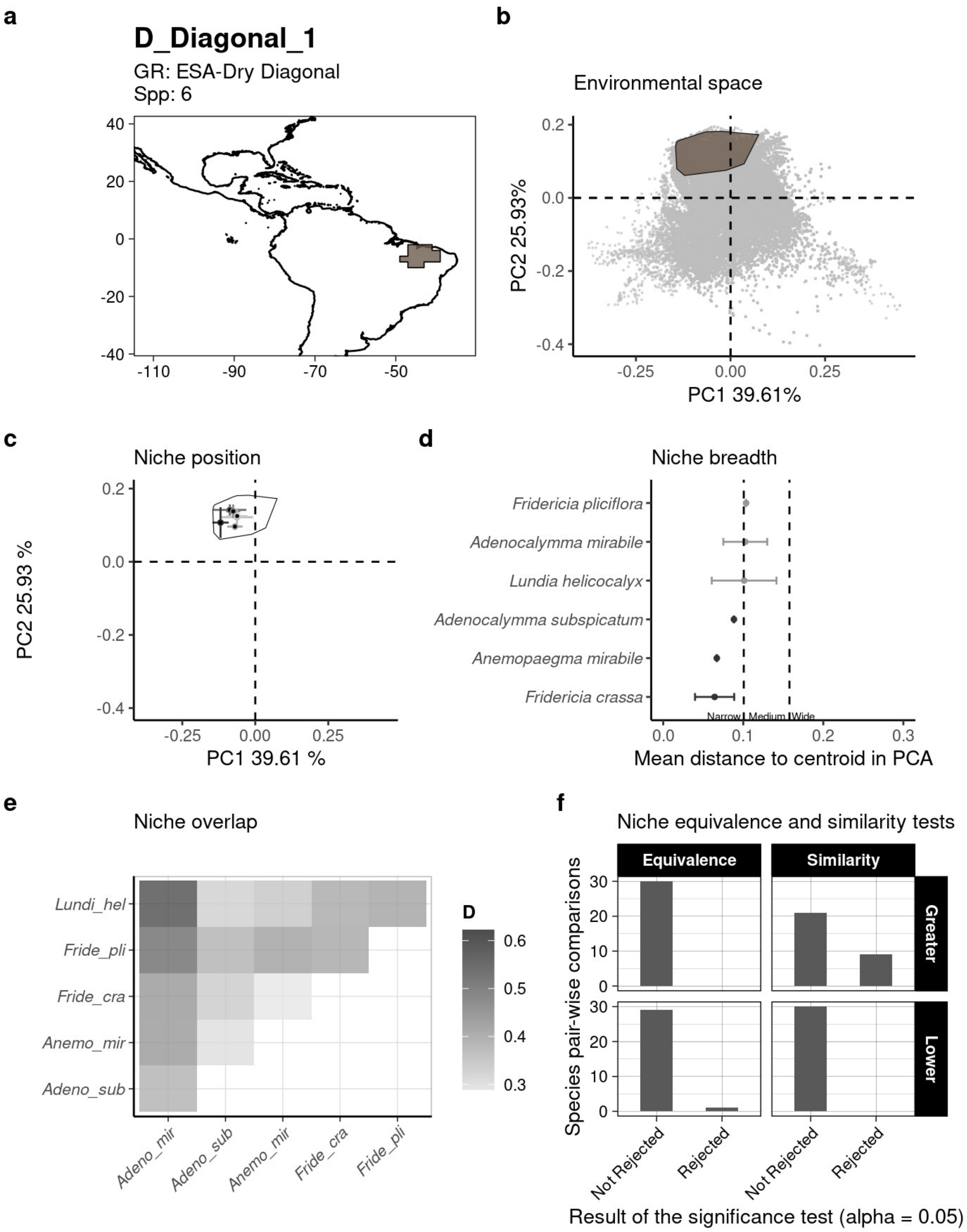
Panel 13: Amazonia_5



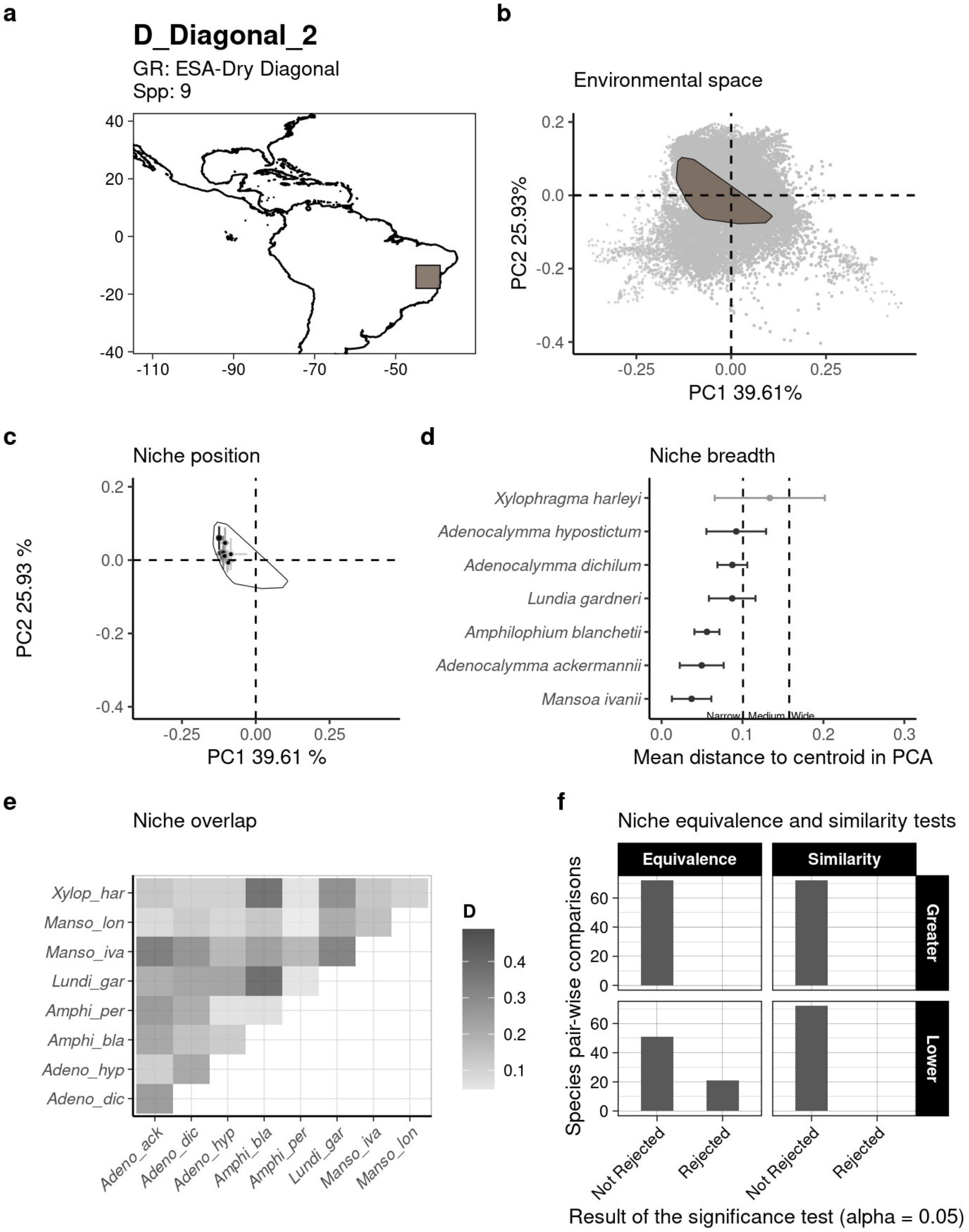
Panel 14: Amazonia_6



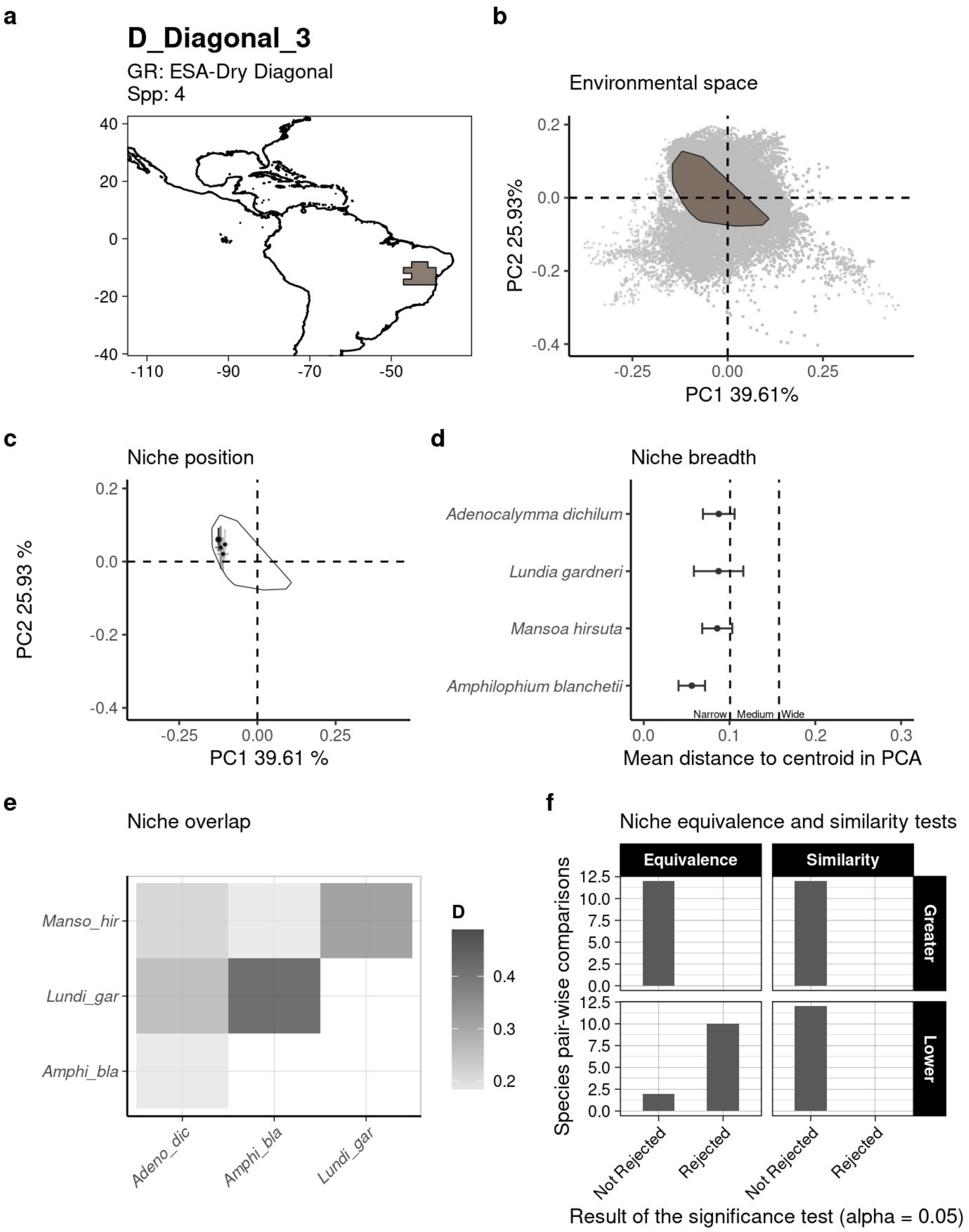
Panel 15: D_Diagonal_1



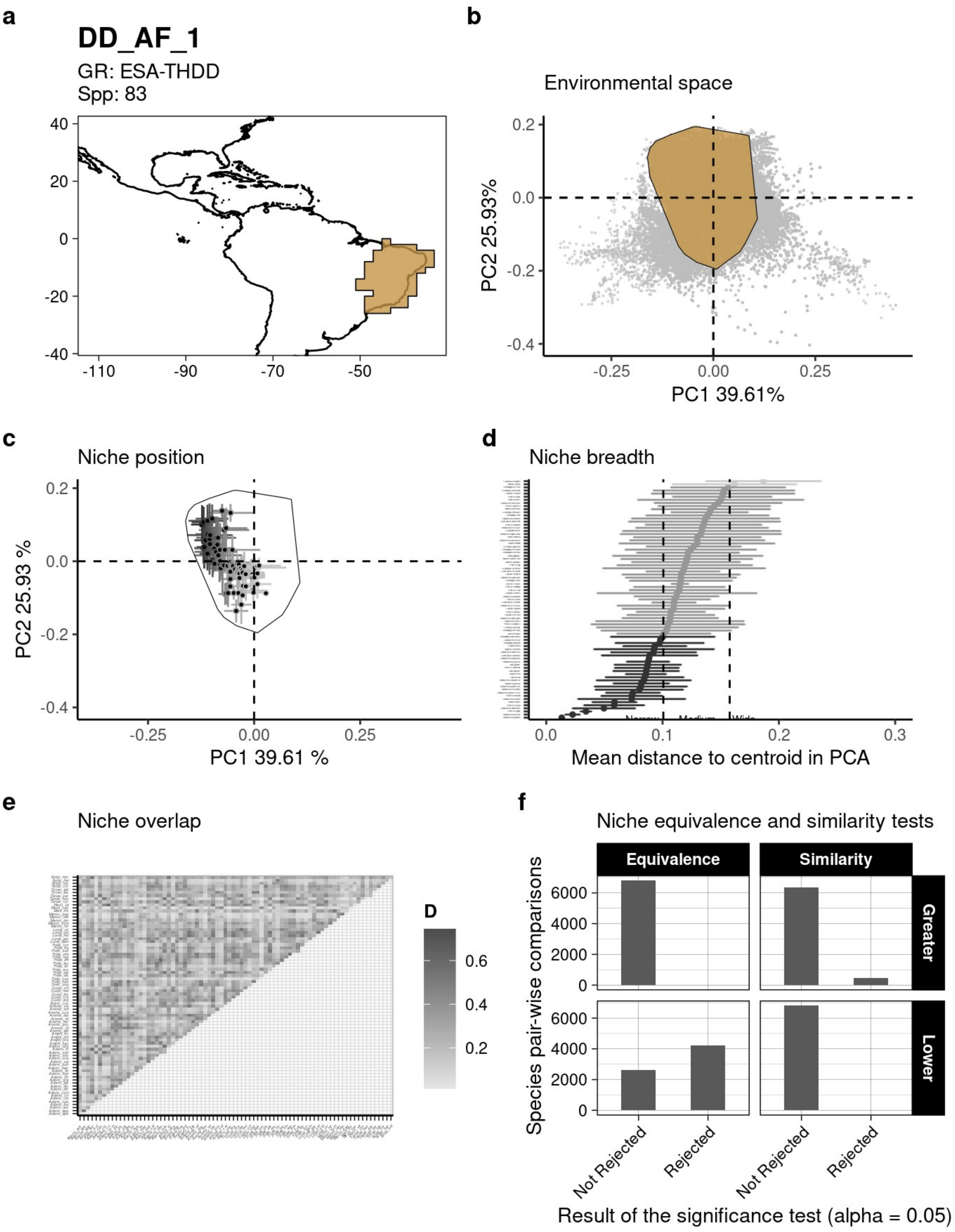
Panel 16: D_Diagonal_2



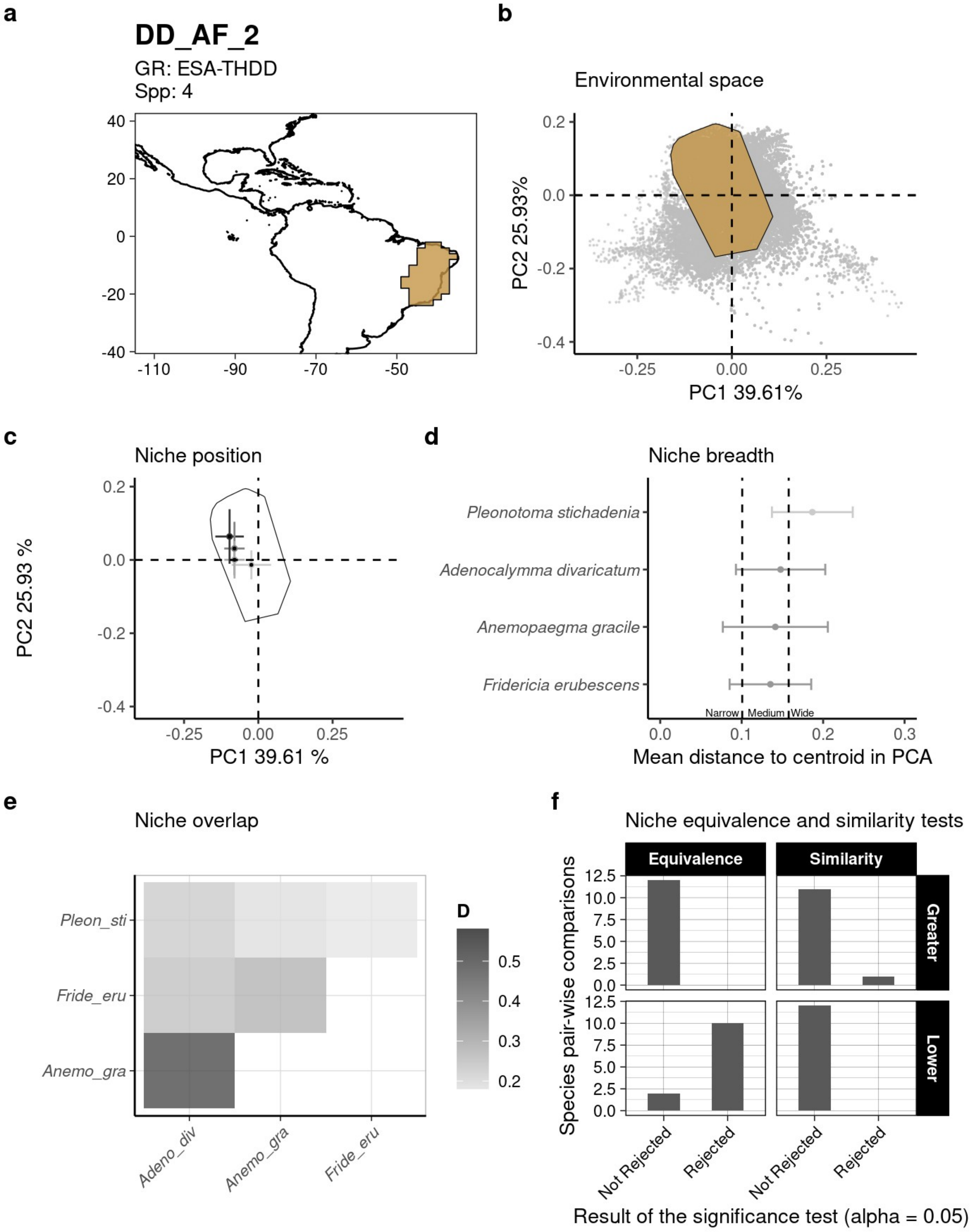
Panel 17: D_Diagonal_3



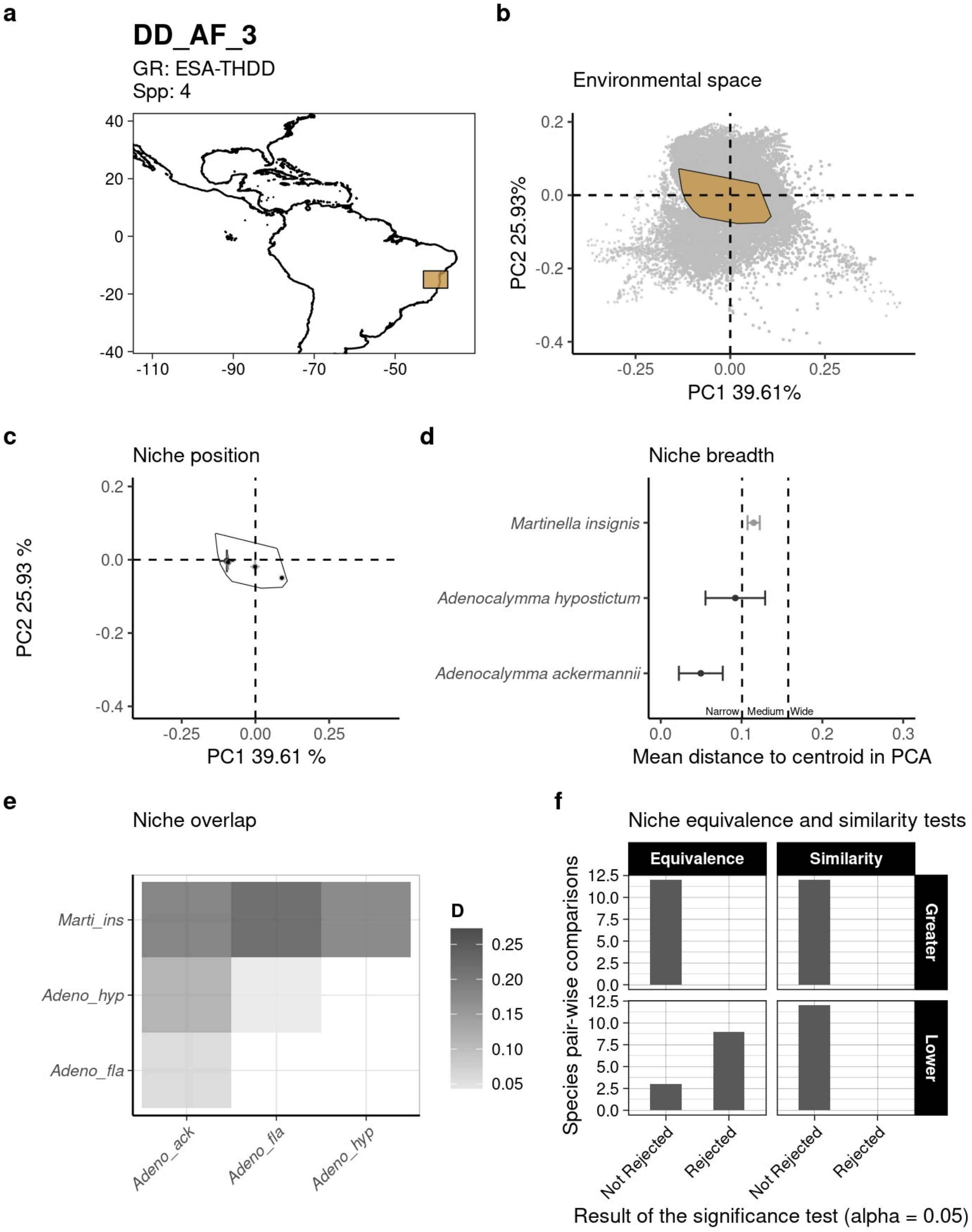
Panel 18: DD_AF_1



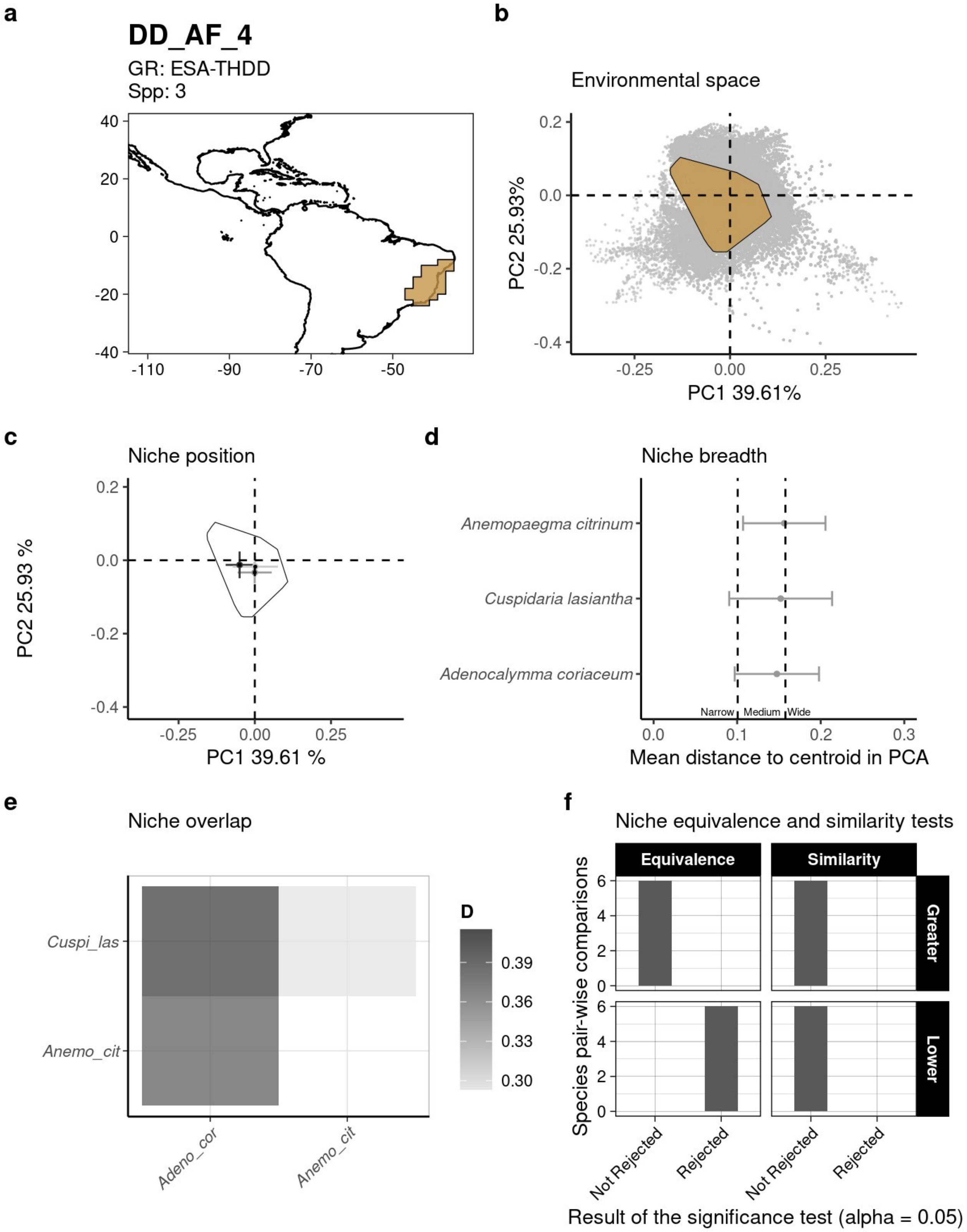
Panel 19: DD_AF_2



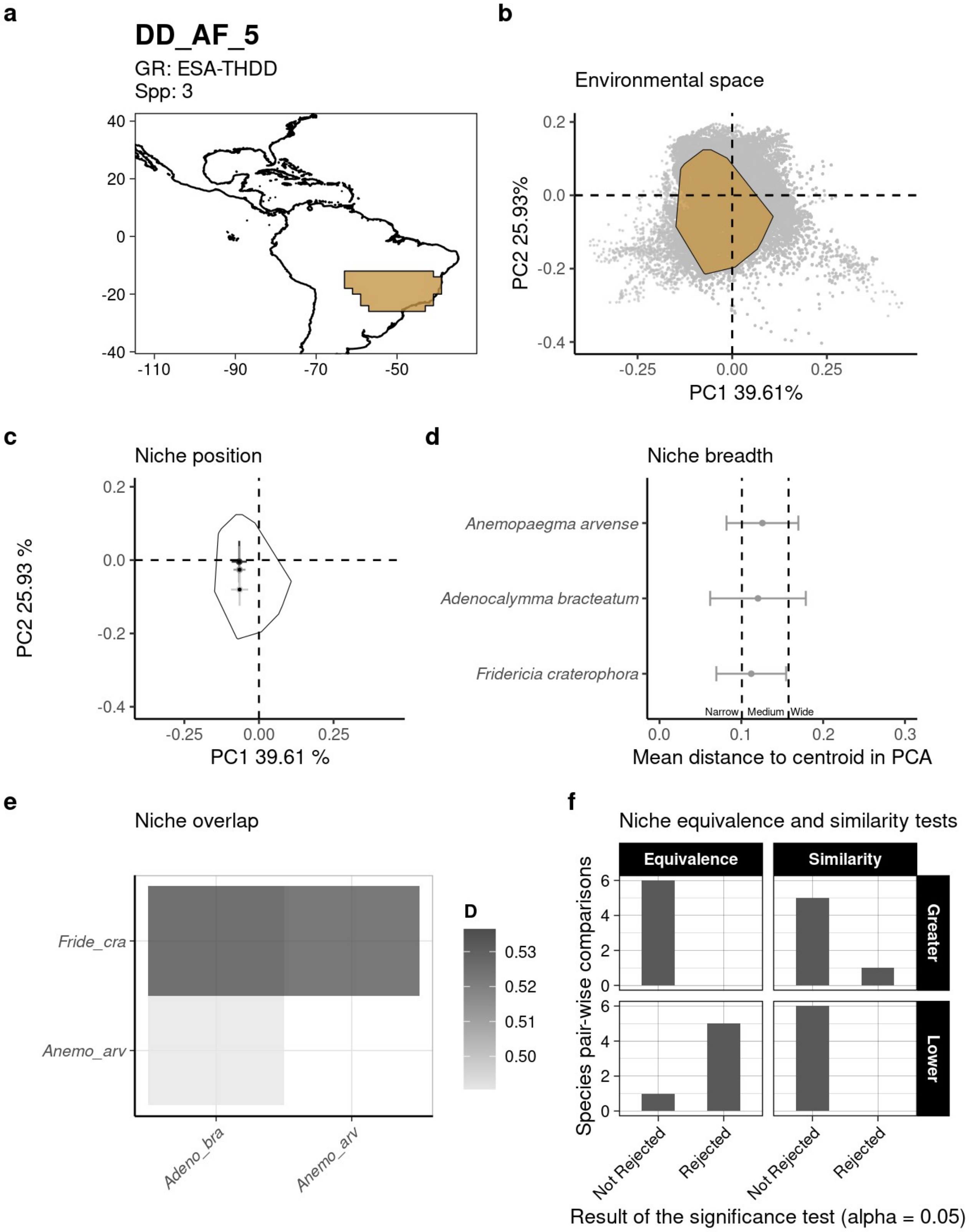
Panel 20: DD_AF_3



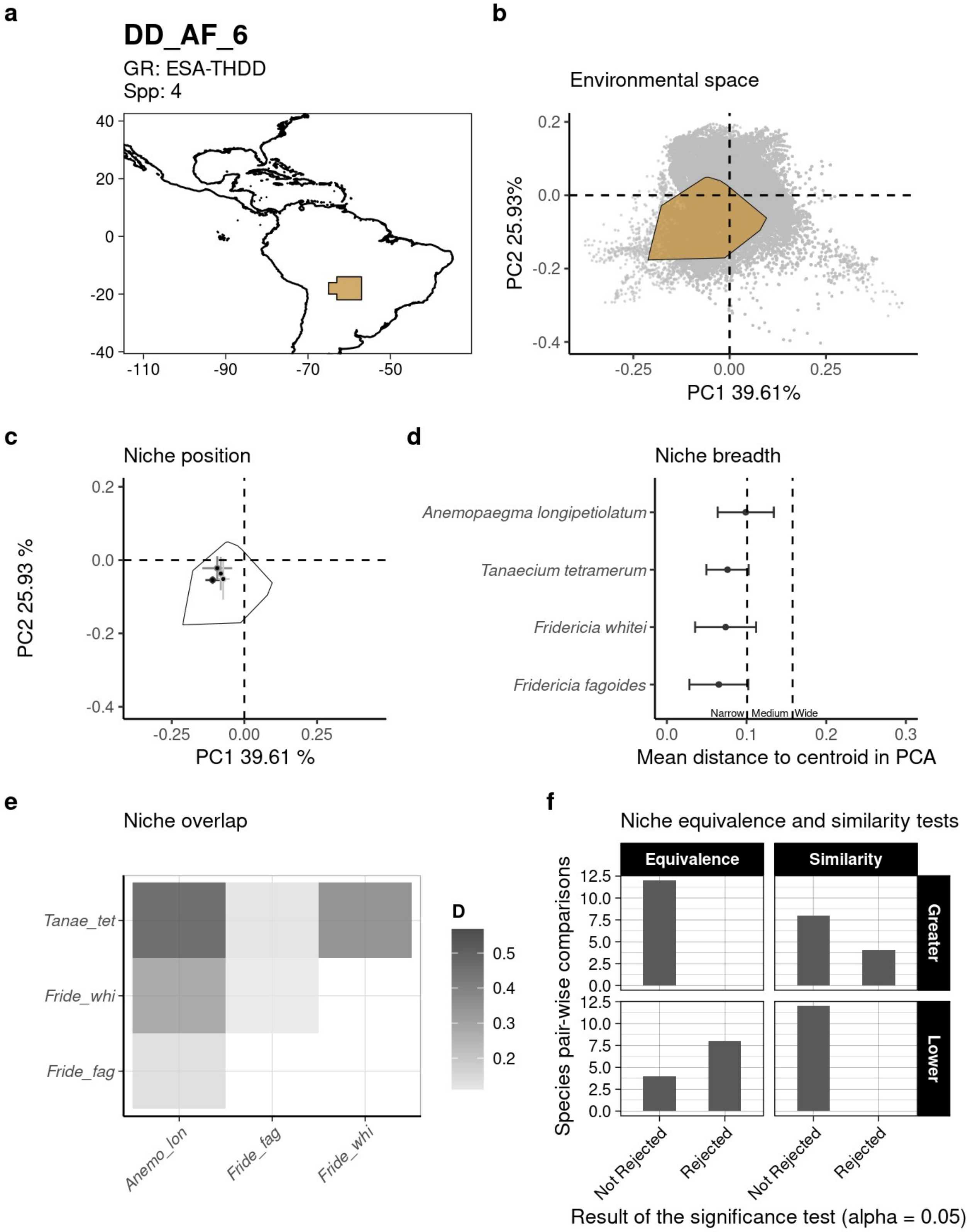
Panel 21: DD_AF_4



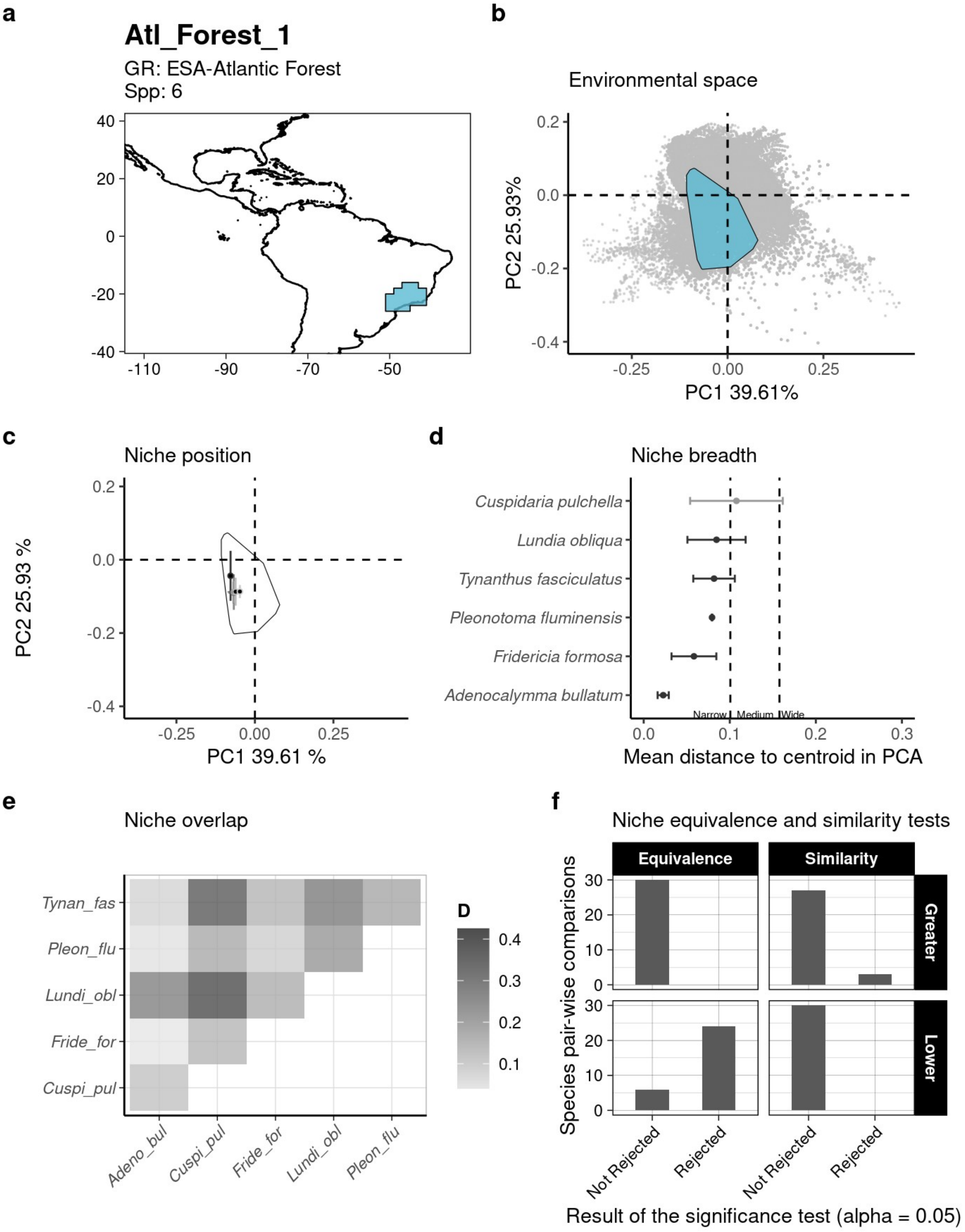
Panel 22: DD_AF_5



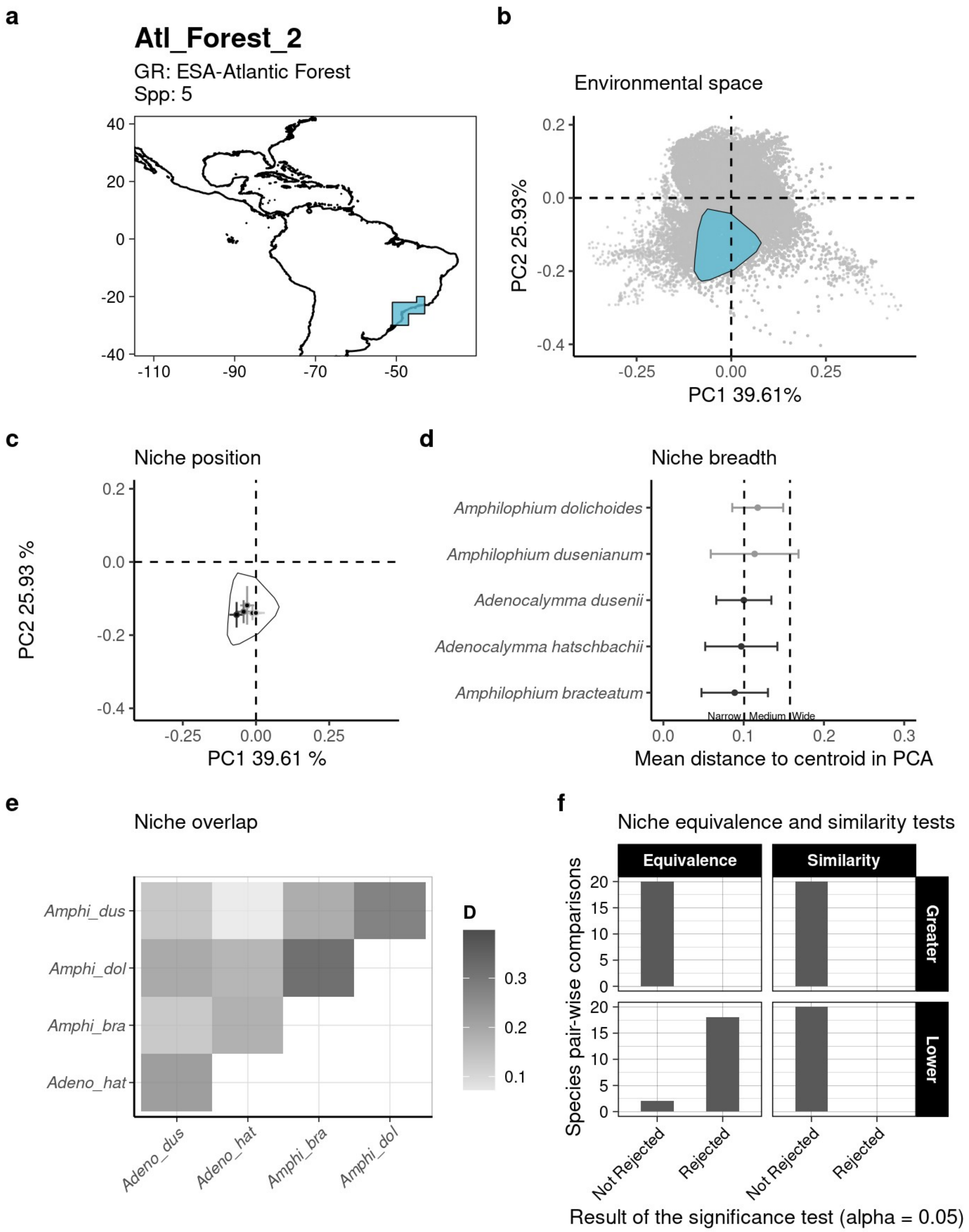
Panel 23: DD_AF_6



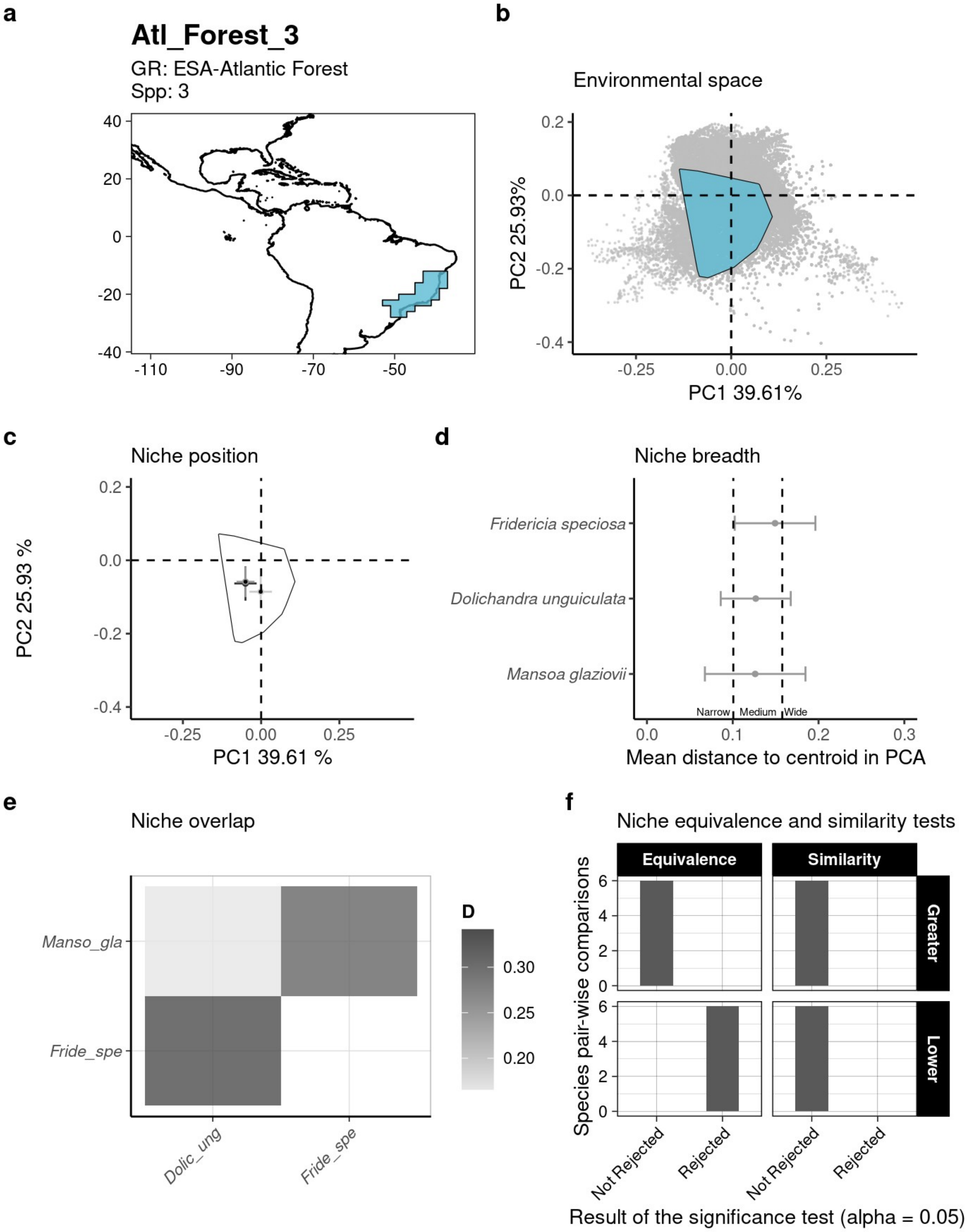
Panel 24: Atl_Forest_1



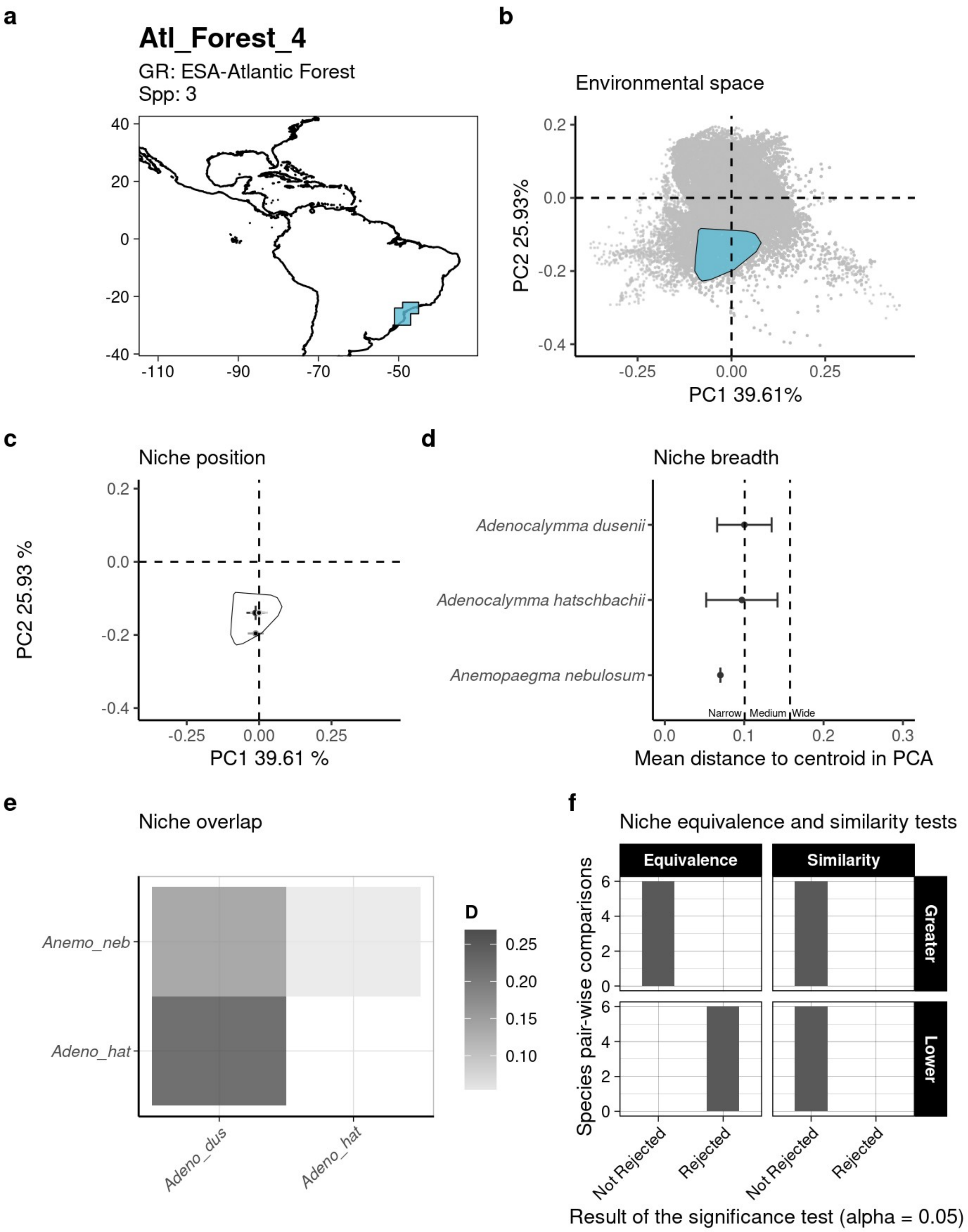
Panel 25: Atl_Forest_2



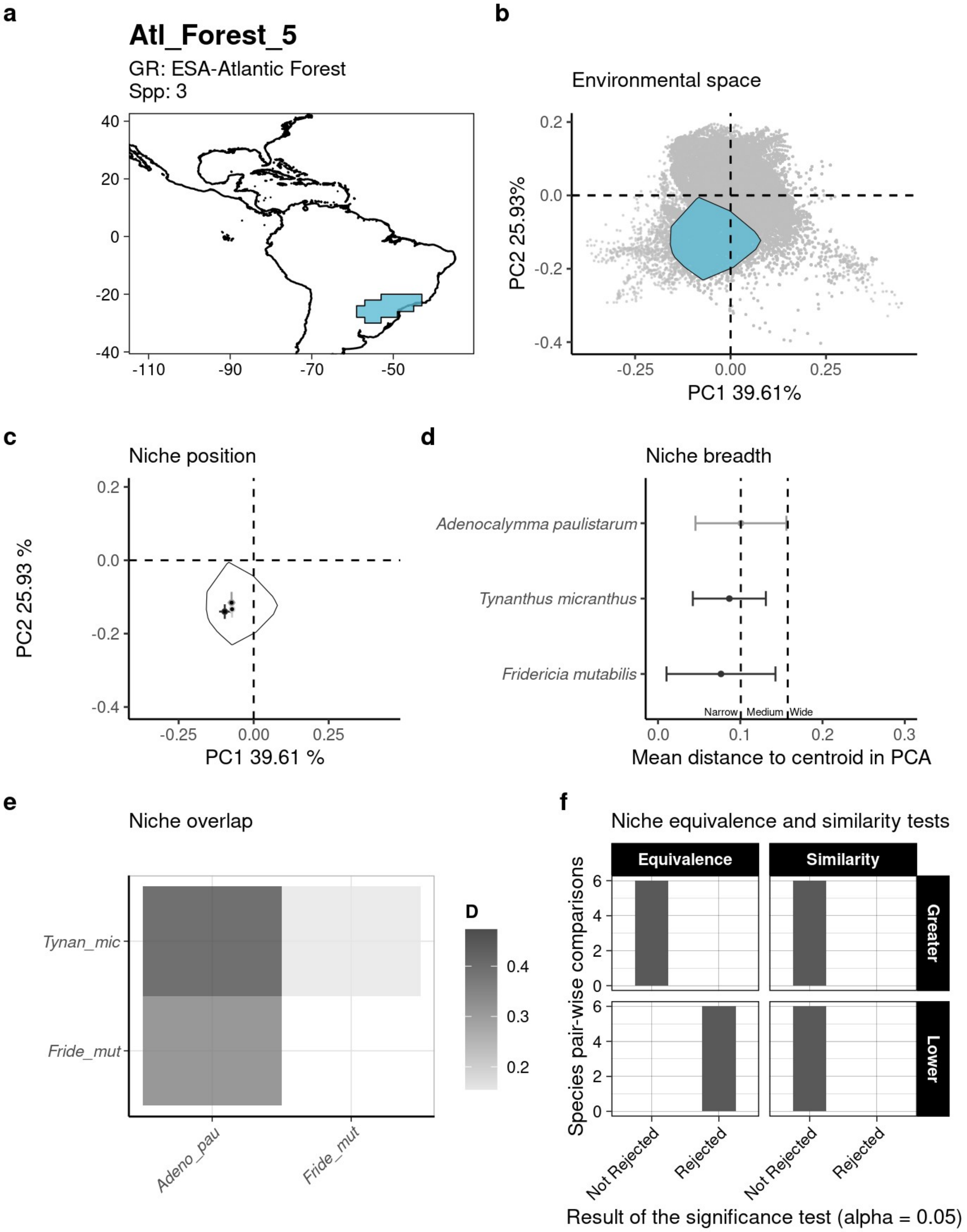
Panel 26: Atl_Forest_3



Panel 27: Atl_Forest_4



Panel 28: Atl_Forest_5



Conclusion

In this work we used the tribe Bignonieae (Bignoniaceae) as a model to unravel species distribution patterns and their relationship with climate. The first step towards this goal was to evaluate our knowledge about Bignonieae species distribution patterns (Chapter 1). The second step was to describe Bignonieae areas of endemism and evaluate the patters recovered in the context of Neotropical biogeographical hypotheses (Chapter 2). The third step was to study how the climatic niche of endemic species varied across areas (Chapter 3).

We showed that the Bignonieae distribution database assembled by Dr. Lúcia Lohmann and colleagues is in good shape, containing high-quality geographical data and covering almost the complete species diversity of the tribe. Our analysis of spatial biases and completeness identified the areas for which future survey efforts would maximize the spatial coverage of the database and increase the representation of the overall species diversity. New surveys are needed across the Neotropics, especially in the Amazon, where several localities have never been sampled. The high quality of this database reflects the fact that Bignonieae is among the best studied clades of Neotropical plants to date. However, knowledge gaps indicate the high need for additional botanical explorations throughout the Neotropics, especially in the Amazon.

Numerous areas of endemism were recovered for Bignonieae across the Neotropics, especially at coarser spatial scales. These areas were characterized by numerous nested and overlapping patterns while presenting low spatial congruence with the Neotropical regionalization schemes proposed by Gentry based on plant data and by Morrone based on multiple taxa. By thoroughly describing the areas of endemism of Bignonieae, we were able to identify explanatory hypotheses for species sets that define each area. We showed that ambiguity in species membership to areas of endemism is low but constant across spatial scales. How to best deal with this ambiguity remains to be determined, which would be particularly relevant while proposing subsequent exploratory hypothesis about the drivers of areas of endemism.

We were unable to identify common ecological processes among species shared by the areas of endemism by exploring the properties of the climatic niche of endemic species. Differences among Bignonieae species were mainly due to the heterogeneity of the contemporary climate that characterized the areas of endemism corroborating earlier findings. Niche specialization was shown to represent an important factor shaping Bignonieae species distributions.

Overall, this study allowed us to identify priorities for Bignonieae biogeography research, namely: (i) species distribution models must be produced to better define priority areas for new survey efforts and conservation; and (ii) the role of past climate change during the Quaternary seems to have been significant given the similarity among areas of endemism and other patterns thought to have been driven by similar factors.

We adopted an explicit spatial approach to test hypotheses associated with the relationship between patterns of species distributions and climate. More specifically, we treated areas of endemism as open questions, looked at species distributions in detail, made inferential steps explicit, used present day information to make inferences about the past, and applied innovative approaches to unravel the causes and processes behind species distribution patterns. Even though the data is not perfect, it represents one of the best plant datasets available to date. Even though patterns have inherent ambiguities and the causal inferences depend on methodological assumptions, we used approaches available to date to systematically explore the plausibility of different explanatory hypotheses based on the evidence available. Research on areas of endemism using a spatial explicit approach is a developing field that will greatly benefit from the establishment of clear connections through posterior analyses. We hope that this work will encourage future studies aiming to find new ways to address old questions.

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