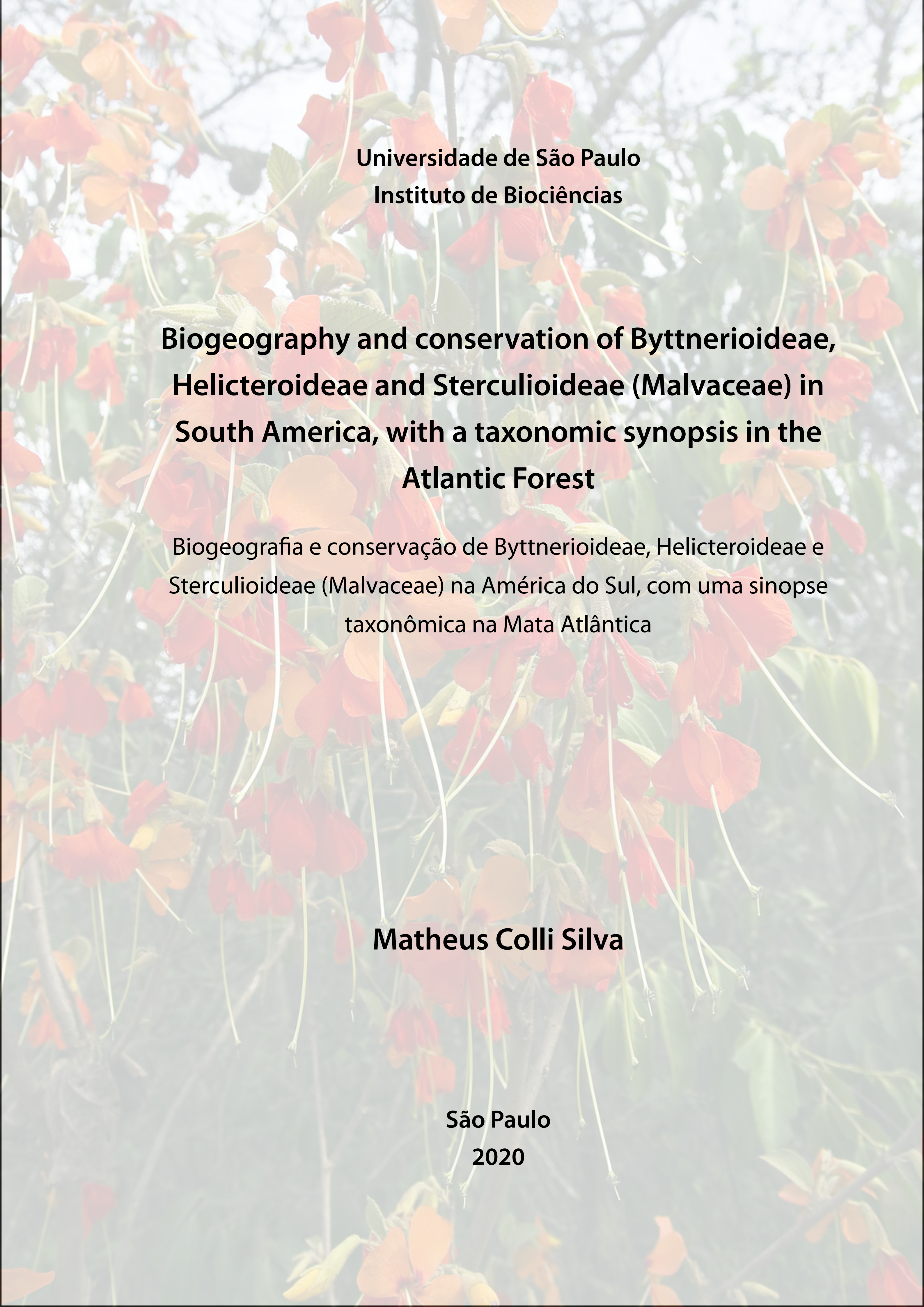

Universidade de São Paulo
Instituto de Biociências

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Matheus Colli Silva

São Paulo
2020

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Dissertação apresentada ao Instituto de Biociências da Universidade de São Paulo, para a obtenção de Título de **Mestre em Ciências Biológicas**, na área de **Botânica**.

Orientador: Prof. Dr. **José Rubens Pirani**

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UNIVERSO DA CULTURA O CENTRO ESTÁ EM TODA A PARTENO

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Índice *(Summary)*

Resumo

Mapear e discutir padrões biogeográficos é a base para o entendimento da evolução e diversificação das linhagens, especialmente importante para grupos pouco estudados, como é o caso de Malvaceae. Malvaceae é particularmente diversa na América do Sul, com altos índices de riqueza específica e endemismo, mas cujas questões básicas de biogeografia, conservação e taxonomia estão desatualizadas ou inexploradas. Paralelamente, a disponibilidade de dados nos repositórios online possibilita novos estudos de síntese com grupos diversos e em escala continental. Neste projeto, utilizamos como modelo três subfamílias de Malvaceae — Byttnerioideae, Helicteroideae e Sterculioideae — totalizando 271 espécies em 11 gêneros na América do Sul, para responder questões de síntese de padrões biogeográficos, viés de coleta, taxonomia e conservação dos grupos e das áreas onde os táxons ocorrem. Especificamente, nós (1) construímos uma base de dados de ocorrência para as espécies das três subfamílias, com base na consulta da literatura especializada e nas coleções dos herbários, buscando sintetizar o padrão espacial das subfamílias de Malvaceae na América do Sul, bem como estimando biorregiões e eventuais áreas com baixo esforço de coleta; (2) selecionamos espécies com padrão curiosamente disjunto para trazer novos insights na discussão sobre a biogeografia das áreas abertas e sazonalmente secas Neotropicais; (3) utilizamos a base de dados de ocorrência produzida para comparar a sua performance bom dados modelados ou obtidos automaticamente na representatividade das espécies na rede de unidades de conservação sul-americanas; (4) selecionamos dois gêneros — *Ayenia* e *Byttneria* — para realizar uma sinopse taxonômica na Mata Atlântica, uma contribuição necessária e importante à região e ao grupo; e (5) realizamos uma recircunscrição e um histórico nomenclatural sobre um nome mal aplicado — *Pterygota brasiliensis* Allemão — e revisamos a distribuição do gênero no planeta. Esta tese resultou em quatro capítulos e um anexo em formato de publicação, trazendo contribuições significativas sobre a evolução e conservação do grupo e das vegetações sul-americanas, bem como subsídios a estudos futuros com grupos de Malvaceae Neotropicais.

Palavras-chave: documentação da biodiversidade; Malvales; padrões espaciais; taxonomia; viés de coleta.

Abstract

Mapping and discussing biogeographical patterns are essential to understand the origin and evolution of lineages, especially important for current understudied taxonomical groups, such as the Malvaceae. Malvaceae is particularly diverse in South America, with high levels of species richness and endemism, but whose basic questions of biogeography, conservation and taxonomy are outdated and unassessed. Moreover, the current availability of larger online repositories allows the development of new comparative surveys with particularly diverse groups at a continental scale. In this thesis, we used as model three selected subfamilies of Malvaceae—Byttnerioideae, Helicteroideae and Sterculioideae—summing 271 species in 11 genera for South America, to assess questions of biogeography, collection bias, taxonomy and conservation of the groups and of the areas where the taxa occur. Specifically, we (1) built an occurrence database for all selected species via an extensive literature survey and consulting herbarium collections, towards synthetizing the overall distribution pattern of the subfamilies in South America, as well as to estimate bioregions and areas with low sampling efforts; (2) selected species with a particular disjunct pattern to bring insights on the discussion of the biogeography of open seasonally dry areas; (3) used the manual revisited database to compare its performance with an modeled and automatized built dataset when representing species inside South American protected areas network; (4) selected two genera—*Ayenia* and *Byttneria*—to provide a taxonomical synopsis of the group in the Atlantic Forest, a novel and important contribution for the region and for the group; and (5) performed a recircumscription and a nomenclatural historic of a misapplied name—*Pterygota brasiliensis* Allemão—also summarizing the distribution of the genus in the globe. This master thesis resulted in four manuscripts and one annex for publication and brought new subsidies and insights towards further assessments with Malvaceae groups on biogeography, evolution and conservation of the family and of different South American vegetations.

Keywords: biodiversity documentation; collection bias; Malvales; spatial patterns; taxonomy.

O estudo dos padrões biogeográficos é cada vez mais necessário num planeta onde o espaço geográfico tem passado por alterações rápidas (ver Miles et al., 2006). A situação é particularmente preocupante na América do Sul, um continente reconhecido pelos seus altos índices de riqueza de espécies e endemismo (Ulloa-Ulloa et al., 2017), mas cujo sistema de áreas protegidas pode não ser tão eficiente para garantir a manutenção dessa enorme diversidade (Oliveira et al., 2017; Colli-Silva et al., 2019). Isso é preocupante, pois o fato de muitas espécies desconhecidas ainda não terem sido descritas (o chamado déficit Lineano) e o fato de a distribuição geográfica da maioria dos táxons ser subestimada e enviesada (déficit Wallaceano), desafiam a priorização de políticas de conservação e de documentação da biodiversidade (ver mais em Hortal et al., 2015).

Na contramão deste panorama, esforços contínuos mostram que padrões biogeográficos são o resultado de processos que envolvem tanto variáveis bióticas como abióticas, e que, na verdade, os processos precisam ser compreendidos sob uma perspectiva integrativa (ver síntese em Antonelli et al., 2018). No caso das plantas, há trabalhos publicados sobre padrões de riqueza e endemismo, com destaque para grupos florestais (e.g. Nazareno et al., 2016), mas com alguns exemplos de grupos típicos de formações abertas ou sazonalmente secas (e.g. Linares-Palomino et al., 2011).

Definir padrões geográficos envolve o mapeamento dos registros de ocorrência, que pode ser feito considerando diferentes bases de dados, desde os registros das coleções biológicas até observações *in loco*, indicações de especialistas ou mesmo iniciativas de ciência cidadã (Graham & Jihmans, 2006; Lavoie, 2013). Nesse sentido, os materiais depositados nos herbários são a fonte de dados mais utilizada nos estudos de distribuição florística (Graham & Jihmans, 2006). Supostamente, essas bases são mais acuradas e confiáveis, uma vez que os registros são frequentemente reavaliados por taxonomistas (Ponder et al., 2002). Contudo, mesmo esses dados podem estar de alguma forma enviesados, e, consequentemente, subestimar ou superestimar o mapeamento da biodiversidade e a consequente obtenção de métricas de síntese de padrões espaciais (Meyer et al., 2015; Oliveira et al., 2016).

As bases de dados têm vantagens e desvantagens, e isso traz implicações relevantes em análises de "big-data", i.e., análises volumosas e automatizadas que envolvem dados de dezenas, centenas ou até milhares de espécies (ver Maldonado et al., 2015). Visando a contribuir com a conservação e documentação biológica na região Neotropical por meio de investigações nessa linha, escolhemos como modelo grupos que historicamente eram classificados como "Sterculiaceae", mas que hoje são subfamílias dentro de "Malvaceae *sensu lato*": Byttnerioideae, Helicteroideae e Sterculioideae. Malvaceae era circunscrito de modo menos abrangente que hoje, pois muitos de seus gêneros atuais eram inseridos em outros grupos — Bombacaceae, Malvaceae *sensu stricto*, Sterculiaceae e Tiliaceae — , hoje não mais reconhecidos, seja por não serem monofiléticos, seja por deixarem parafiléticos outros clados próximos (Péchon & Girord, 2014).

Embora todas as subfamílias tenham distribuição pantropical, muitos de seus gêneros são endêmicos da região Neotropical, com grupos centrados no continente sul-americano (Bayer & Kubitzki, 2005). Ainda que estes predominem nas formações abertas ou sazonalmente secas, há também clados tipicamente florestais, como observado em Sterculioideae (*Pterygota* e *Sterculia*), cujo centro de riqueza específica está localizado na Amazônia, bem como é o caso de alguns gêneros de Byttnerioideae, i.e., *Theobroma* (o grupo do cacau) e *Herrania* (Bayer & Kubitzki, 2005). A família é também diversa morfologicamente; conhecida pelas suas folhas actinódromas com tricomas estrelados, Malvaceae *sensu lato* compreende uma variedade de formas de vida, desde árvores a lianas e plantas rizomatosas, cujas flores e frutos contam uma arquitetura estrutural muito variável, mas elegante (Figura 1).

Por um lado, usar como modelo membros de um grupo mais inclusivo é interessante porque os padrões dentro de cada subfamília (ou dentro de cada gênero) podem indicar evidências históricas de certas linhagens que podem futuramente ser testadas. Por outro lado, trazer um grande *input* de dados referentes a grupos que são diversos do ponto de vista ecológico, filogenético, morfológico e biogeográfico é interessante pois, como cada subfamília se diversificou de modo mais ou menos independente (embora elas mantenham certa relação de ancestralidade próxima), a existência de padrões comuns entre todas elas pode indicar eventos históricos únicos e compartilhados (Riddle, 2017).

Finalmente, cabe destacar que Malvaceae conta atualmente com poucos especialistas ativos desde a sua recircunscrição, uma vez que os principais profissionais atuantes na América do Sul na segunda metade do século XX estão hoje aposentados (e.g. Gerleni Lopes Esteves) ou faleceram (Antonio Krapovickas e Carmen Leila Cristóbal). Além disso, os poucos especialistas ativos na América Latina têm produzido estudos com subfamílias específicas de Malvaceae, *i.e.*, Bombacoideae e Malvoideae. Consequentemente, outras subfamílias antes classificadas em Sterculiaceae e Tiliaceae, que também são bastante representativas, são ainda pouco focadas nos estudos básicos de taxonomia, evolução e biogeografia.

Dito isso, esta dissertação também conta com uma sinopse taxonômica para dois gêneros — *Ayenia* e *Byttneria* — que ocorrem na Mata Atlântica, um domínio florestal rico em espécies e muito ameaçado, mas que ainda conta com boa porção remanescente na região Sudeste e com muitas áreas com baixo esforço de coleta, com destaque para certas unidades de conservação (Oliveira et al., 2017). Conquanto tenha caráter diagnóstico, a elaboração da sinopse visou possibilitar ao autor uma experiência na área de taxonomia e no reconhecimento de espécies de Malvaceae —

atributos imprescindíveis na formação de um botânico especialista numa família, habilitando-o a permear com mais segurança na seara da biogeografia da biota Neotropical.

Através da criação de uma robusta base de dados de distribuição das espécies, a dissertação procura explorar as seguintes questões norteadoras: (1) As áreas de endemismo identificadas com os grupos focais corroboram biorregiões previamente reconhecidas na biota sul-americana? (2) Espécies desses grupos exibindo padrões de distribuição particulares trazem novos insights à história natural de regiões relativamente pouco exploradas, como as áreas abertas ou sazonalmente secas da América do Sul?; (3) Diferentes subfamílias de Malvaceae estão suficientemente bem representadas na rede de unidades de conservação da América do Sul e quais implicações isso possui em termos de conservação da biodiversidade?; e (4) Quais espécies de Byttnerieae ocorrem na Mata Atlântica, como elas podem ser identificadas e distinguidas, como elas estão distribuídas e qual seu estado de conservação?

Esta dissertação contém quatro manuscritos em formato de publicação que exploram as questões norteadoras aqui apresentadas, e um anexo com o manuscrito de um artigo recentemente publicado. O Capítulo 1 traz um estudo focado nos padrões gerais de distribuição, também definindo e discutindo biorregiões reconhecidas e questões de viés de coleta. Os dois capítulos seguintes pretendem explorar mais profundamente essa base de dados do Capítulo 1, seja do ponto de vista de padrões biogeográficos de espécies disjuntas (Capítulo 2), ou da perspectiva de conservação e documentação da biodiversidade (Capítulo 3). A seguir, o Capítulo 4 traz um estudo taxonômico sinóptico de dois gêneros — *Ayenia* e *Byttneria* — trazendo contribuições inéditas na área para a Mata Atlântica. Por fim, apresentamos o Anexo 1, que consiste num estudo nomenclatural de recircunscrição de um dos gêneros de estudo (*Basiloxylon*/*Pterygota*), que se mostrou necessário durante o andamento deste trabalho e que foi recentemente publicado.

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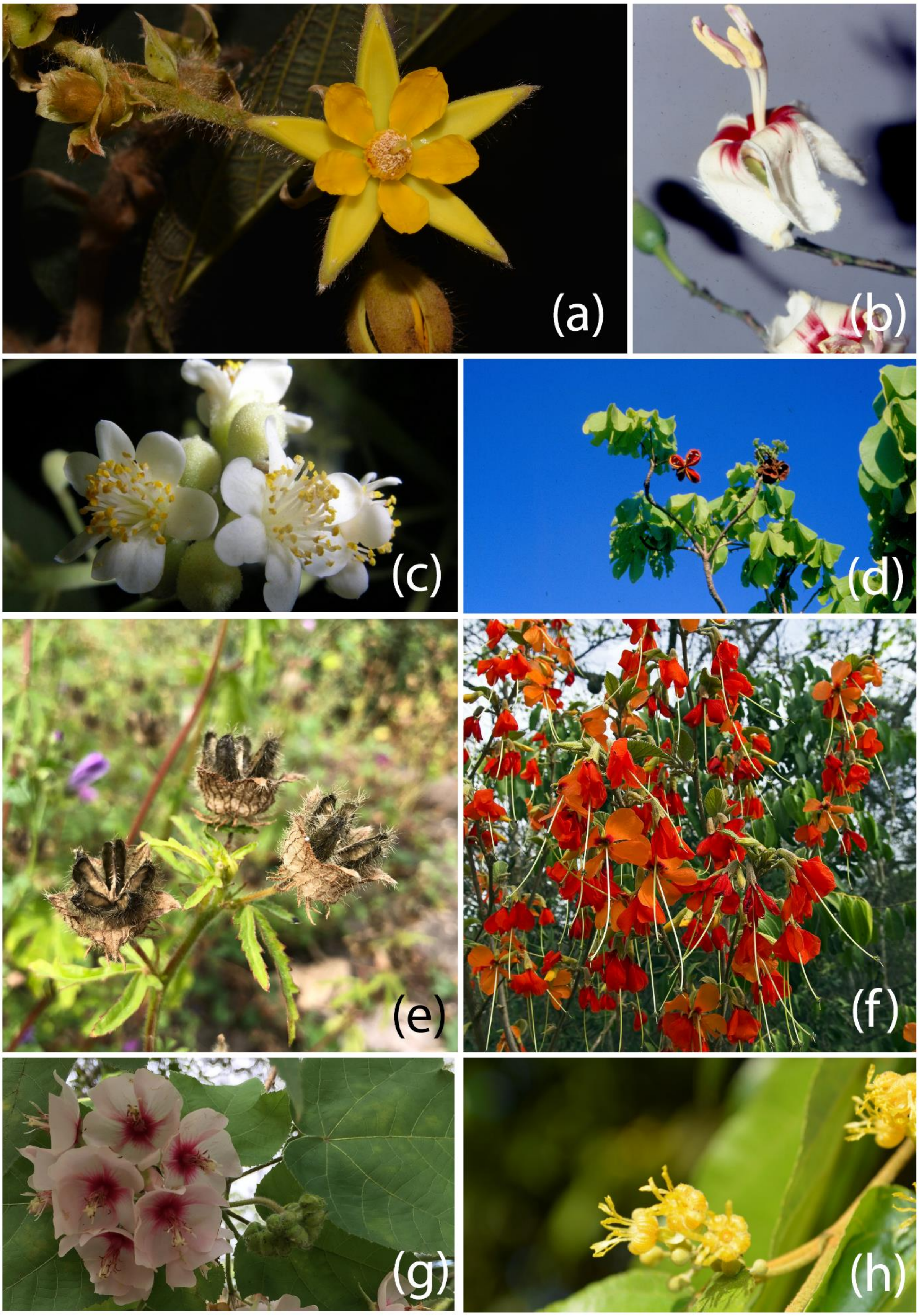
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Figura 1. Panorama geral da diversidade de Malvaceae *sensu lato* por principais subfamílias com representantes Neotropicais (exceto Tilioideae, subfamília com alguns representantes Neotropicais como *Triumfetta*, *Grewia* ou *Tilia*), com enfoque nas estruturas reprodutivas. (a) Flor e botões florais de *Apeiba tibourbou* Aubl. (Grewioideae), espécie amplamente distribuída por todo o território sul-americano; (b) Flor de *Ceiba erianthos* (Cav.) K.Schum. (Bombacoideae), espécie endêmica do Brasil, característica das regiões costeiras; (c) Flores de *Christiana africana* DC. (Brownlowioideae), ocorrendo na América do Sul disjuntamente na Amazônia e nas restingas do Sudeste e Nordeste do Brasil; (d) Frutos de *Sterculia striata* A.St.-Hil. & Naudin (Sterculioideae), uma das espécies de *Sterculia* predominante nas áreas abertas/sazonalmente secas do Brasil, além das áreas florestadas da Amazônia e Mata Atlântica; (e) Fruto do tipo esquizocarpo de *Hibiscus trionum* L. (Malvoideae), arbusto nativo da Europa e do Norte da África; (f) Flores de *Helicteres brevispira* A.St.-Hil. (Helicteroideae), arbusto típico dos Cerrados brasileiros que produz frutos espiralados e torcidos, o que dá o nome popular de “saca-rolha”; (g) Flores de *Dombeya burgessiae* Gerrard ex Harv. (Dombeyoideae), espécie Asiática cultivada nos jardins e áreas verdes brasileiras; (h) Flores de *Guazuma ulmifolia* Lam. (Byttnerioideae), árvore amplamente distribuída ao longo dos Neotrópicos, ocorrendo tanto em áreas abertas como fechadas, naturais ou antropizadas. Fotos: (a) Renato Goldenberg; (b, d) José Rubens Pirani; (c) Charles Rakotovao; (e, g, h) Matheus Colli-Silva; (f) Fernando Costa.

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Estimating bioregions and undercollected areas in South America by revisiting Byttnerioideae, Helicteroideae and Sterculioideae (Malvaceae) occurrence data*

Estimando biorregiões e áreas pouco coletadas na América do Sul através da revisão de dados de ocorrência de Byttnerioideae, Helicteroideae e Sterculioideae (Malvaceae)

Abstract

Revisiting biogeographical patterns is the first step towards fully assessing the natural history and conservation of particular groups, especially in species-rich lineages in regions with high levels of sampling bias, which is the case of South American Malvaceae. In this sense, we present and discuss a manually revisited database built for species of three selected subfamilies of Malvaceae—Byttnerioideae, Helicteroideae and Sterculioideae—in South America. Database was assembled from occurrence records by assessing online repositories and by an extensive literature survey. We retrieved 14,528 records of 271 species in 11 genera, 231 (85%) endemics to the continent. Different species are indicative to different bioregions and the collection efforts for the groups is heterogeneous within South America, being the Amazonia the area with highest levels of biasing effects. Occurrence records are widespread throughout South America, and most species are centered in the open seasonally dry formations, especially the Brazilian Cerrado, the Caatinga and Chaco's open grasslands. Furthermore, there are secondary centers of richness in the western region of the continent, in the Colombian and Ecuadorian portions of the Andes, as well as in the southern portion of the Brazilian Atlantic Forest. Amazonia—detected as the most undercollected area of South America—also has remarkable records from particular taxa, especially from the arborescent genera of Byttnerioideae (*Theobroma* and *Herrania*) and in Sterculioideae. Occurrence maps of species richness, a full list of revisited records and a summary of records per species are presented and discussed in light of the biogeographical patterns of the subfamilies.

Keywords: areas of endemism, biogeographical patterns, Malvales, Sterculiaceae.

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1. Introduction

Malvaceae is a widely species-rich family of flowering plants, with over 4,000 species in more than 200 genera (Bayer & Kubitzki, 2005). Malvaceae has typical actinodromous leaves densely covered by stellate hairs—following the trend of the order Malvales—, and a unique type of floral nectary, with glandular hairs on the inner surface of the calyx (Bayer & Kubitzki, 2005; Péchon & Gigord, 2014). Traditional classification systems have grouped several clades of Malvaceae *sensu lato* into Bombacaceae, Sterculiaceae, Tiliaceae, or Malvaceae *sensu stricto* (Péchon & Gigord, 2014). Nevertheless, circumscriptions were mainly based on strict morphological features which likely have evolved independently in the different lineages of Malvaceae *sensu lato* (Péchon & Gigord, 2014). In this respect, molecular phylogenetics also helped to elucidate the relationships of Malvaceae *sensu lato* to other families, improving the current circumscription of Malvales with 10 families (Stevens, 2001 onwards). Nowadays, Malvaceae is well-supported as monophyletic along with their ten families (Alverson et al., 1998; Baum et al., 1998; Bayer et al., 1999).

With the recircumscription of Malvaceae *sensu lato*, systematists are presently faced to a novel and challenging morphological, biogeographical and evolutionary scenario for the family. Current studies into specific groups of Malvaceae turned out to be fragmented, whereas taxonomical contributions have centered into particular groups of Malvaceae *sensu lato*, namely within the Malvoideae and the Bombacoideae. Particularly, as it was demonstrated that the former “Sterculiaceae” was polyphyletic, its genera were rearranged into three distinct subfamilies: Byttnerioideae, Helicteroideae and Sterculioideae. Seminal contributions on the taxonomy of genera in these groups were made by C.L. Cristóbal (1960; 1976; 1981; 1996; 2001), J. Cuatrecasas (1964) and further authors (Freytag, 1951; Schultes, 1958; Goldberg, 1967; Taroda, 1984, Taylor, 1989 (unpubl.); Saunders, 1995 (unpubl.)).

The almost complete lack of biogeographical analyses with these three subfamilies motivated the present study. This is allied to the emergent potential of herbarium collections as a main source to revisit large datasets towards assessing questions of biases and spatial patterns (Lavoie, 2013). In this sense, current increasing and availability of online repositories, as well as the development of new methods of biogeography and macroecology enhanced the prospection of such surveys. Subsequently, a more encompassing dataset can tackle potential areas with low sampling efforts—a documentation issue that seems to be recurrent in South America (Oliveira et al., 2016; 2019; Colli-Silva et al., *in press.*).

Byttnerioideae, Helicteroideae and Sterculioideae have several peculiar morphological features—some of these can be appreciated in Figure 1. Byttnerioideae is the most species-rich subfamily of the three; in South America, it is represented by shrubby-herbaceous to lianescent genera (*Ayenia* L., *Byttneria* Loefl., *Rayleya* Cristóbal, *Melochia* L. and *Waltheria* L.), but also by some arborescent groups (*Herrania* Goudot, *Guazuma* Adans. and *Theobroma* L.). Most of these genera are endemics to the Neotropical region, except for *Byttneria*, *Melochia* and *Waltheria* which have a pantropical distribution. Species of Byttnerioideae bear an eccentric corolla with each petal showing at least two distinct portions: a lower one—the "claw" (*sensu* Dorr, 1996; see also Cristóbal, 1976)—, and an upper expanded portion, or the "lamina" (Figures 1j-k).

On the other hand, Helicteroideae and Sterculioideae are quite distinct from the Byttnerioideae and from each other, varying from Amazonian large trees (e.g. in *Sterculia* and *Pterygota*—Figure 1b-c) to shrubs whose tubular flowers have a large androgynophore and often develop a twisted fruit in the case of *Helicteres*, the only genus of Helicteroideae in South America—Figures 1d-e. While *Pterygota* and *Sterculia* are pantropical, *Helicteres* have a remarkable Amphi-Pacific distribution.

In this work, we revisited and synthetized such distributional information of species of Byttnerioideae, Helicteroideae and Sterculioideae in South America, based on an extensive review from herbarium collections, online repositories and the literature. Also, we provided a robust dataset of revisited occurrence records that have subsided this study and shall facilitate further works with biogeography and conservation within the Neotropics (Chapters 2 and 3). We believe this is particularly essential for a group as the Malvaceae, whose basic biological and ecological panorama are heterogeneous but historically fragmented as we discussed above. Specifically, we here address to the following aspects that deserve proper assessment:

1. *Different sets of species, genera or subfamilies of Byttnerioideae, Helicteroideae and Sterculioideae are distributed in particular regions of South America.* Information available in the literature indicate that different subfamilies may have distinct spatial patterns, with particular genera being widespread throughout open seasonally dry areas, while other groups prevail in the moist areas of the Amazonia or Atlantic Forest. Our updated database will allow a proper verification of this probable spatial patterns.
2. *Different regions of South America exhibit particular sampling effort levels.* For the three subfamilies of this study, we believe that specific regions of the continent, namely the Amazonia, might be undercollected, and this fact should be assessed with the robust occurrence database built in here.

2. Methods

2.1. Database

The occurrence database was retrieved from an extensive taxonomical survey of online herbarium repositories and taxonomical works with Byttnerioideae, Helicteroideae and Sterculioideae groups in South America published so far. Database was built from November 2016 to November 2018. We included all available preserved specimen material from the major online repositories, as well as from South American local or regional sources. We consulted the following online repositories: (1) speciesLink network, `https://splink.org.br/`; (2) GBIF—the Global Information Biodiversity Facility, `https://gbif.org/`; (3) JABOT—the Brazilian Flora database maintained by the Rio de Janeiro Botanical Garden, `https://jabot.jbrj.gov.br/` and (4) JSTOR, `https://jstor.org/`. Also, we examined published taxonomical reviews for genera (Table 1). These works allowed us to validate and include new records absent in the online collections; also, we could redetermine and check specimen determinations, especially from species with scarcer collections.

Furthermore, we cross-checked all records with unprecise or with no location, georeferencing those if necessary. The georeferencing workflow (Figure 2) is based on Magdalena et al. (2018) and Bloom et al. (2018) frameworks. For coordinates that required *a posteriori* georeferencing—i.e. for exsiccatae with no geographical coordinates informed in the voucher label—, we assessed the gazetteer in the sheet labels and manually attributed a coordinate by using the "GeoLoc" georeferencing tool (`www.splink.cria.org.br/geoloc`). The "GeoLoc" tool provides a broad list of gazetteers based on the accumulated information of georeferenced vouchers deposited in the speciesLink network repository. The final revisited occurrence database is available in Supporting Information (Appendix S1).

All following analyses were run in R Environment (R Core Team, 2019). To check the first question of this work—different sets of species, genera or subfamilies of Byttnerioideae, Helicteroideae and Sterculioideae are distributed in particular areas of South America—we built maps considering (1) species richness and (2) record density, over 1° gridcells, for each subfamily and genus, using the "speciesgeocodeR" package v. 1.0-4 in R Environment (Töpel et al., 2016).

2.2. Estimating bioregions and biasing effects

To check if different sets of species are clustered in particular regions of South America (first question of this work), we used the “Infomap Bioregions”. The Infomap Bioregions platform contains an accessible and efficient clustering network analysis that estimates bioregions based on distribution data (Vilhena & Antonelli, 2015). Unlike parsimony or optimality-based criteria (check Szumik et al., 2002; Morrone, 2014), where only one record would be enough to state a particular occurrence in a geographical unit, clustering network approaches also consider record density to evaluate different scenarios of potential bioregions. Infomap Bioregions also provide a list of the most common and the most indicative species—i.e. species whose records are more expected in the potential bioregion than in a random scenario (Edler et al., 2016). We performed different cluster runs with cluster costs (i.e., the tune for splitting or lumping different bioregions), varying from 1.0 (which is the default of the platform) from 1.1, 1.2, 1.3 and 1.4 scores, performing 10 different trials in each step. Lastly, for the criteria of minimum/maximum records per cell and grid scale (check Edler et al., 2016) we set the default parameters: max cell size of 4°, min cell size of 1°, max cell capacity of 100 and min cell capacity of 10, patching sparse gridcells.

Finally, to address to the second main spatial aspect of this work—regarding the sampling bias—we quantified the biasing effect for our database through the “sampbias” package v. 1.0-2 (Zizka, 2017) in R Environment. The “sampbias” package provides a summary of biasing effects associated to human accessibility collections, such as surrounding cities, urban areas, rivers or roads (Zizka, 2017). Package functions also provide biasing effect metrics by statistically comparing the provided database with one under a random sampling scenario. Such metrics and maps were used for further discussion on possible over/undersampled areas in South America for our database.

3. Results

3.1. Richness patterns and biasing effects

We retrieved 14,528 records of 271 species in 11 genera for three subfamilies in South America. From the valid records of the 271 species, 205 belong to Byttnerioideae, 33 to Sterculioideae and 33 to Helicteroideae (Table 2). Figure 3 summarizes taxa distribution considering the different subfamilies, showing the record density and species richness in the study area. Table 2 lists all records per taxon, highlighting endemic species to the continent, which have revealed as the majority (231/271, c. 85% of all species, including 4 varieties, 2 per species).

Most taxa are centered in the open seasonally dry areas of South America, where open/dry habitats—the Cerrado, Caatinga and the Chaco—prevail (Figure 3). These areas hold lower levels of sampling bias for the group, whereas the Amazonia centers most of the undersampled, biased collections (Figure 4).

Byttnerioideae. With 206 species, Byttnerioideae is the most representative subfamily of the three (Figure 3b and 3f). Conversely, it has the lowest number of species endemics to South America. Most records are owed from Cristóbal's reviews (1960 for *Ayenia*; 1976, for *Byttneria*), but also from classical works with *Theobroma* and *Herrania* (Schultes, 1958; Cuatrecasas, 1964), *Melochia* (Goldberg, 1967) and an unpublished monography of *Waltheria* (Saunders, 1995 (unpubl.)). In the latter work, new taxa and combinations proposed by Saunders have never been validly published and should be properly assessed.

Helicteroideae. Most records of *Helicteres,* the only genera of Helicteroideae native to South America, are reported in Cristóbal's (2001) monography of the genus (Figure 3c and 3g). She described and revisited all the American species, recircumscribing taxa, updating species' information and proposing new combinations. From the nine new species Cristóbal described at that time, most were endemic to particular regions of central Brazil (*H. andersonii; H. cidii*, *H. denticulenta*, *H. krapovickasii*, *H. vallsii*), or to the Atlantic Forest phytogeographic domain (*H. laciniosa*, *H. pintonis*) and to the shrubby-arborescent dry "carrasco" vegetations in Bahia state, Brazil (*H. rufipila*).

Sterculioideae. South American genera of Sterculioideae are mainly found in forested areas, namely the Amazonia basin and the Brazilian coastal regions of the Atlantic Forest (Figure 3d and 3h). *Sterculia* is the most representative genus of the subfamily, with 30 species centered mainly in the eastern Amazonia, whereas *Pterygota* has three species—two in the Amazonia and one (*Pterygota brasiliensis* Allemão) endemic to the Brazilian Atlantic Forest according to its current circumscription (see Annex 1). A major contribution on the taxonomy of *Sterculia* was provided by Taylor (1986), including the proposal of six new species endemic to different spots of the Amazonian terra-firme forests. However, like Saunders (1995), Taylor never effectively published her results, so those names remain as non-valid and their circumscription should be reassessed.

3.2. Bioregions

We recovered 21 to 7 bioregions considering runs with different parameters (Figure 5a-d). A full list of the most common and indicative species per bioregion can be found in Supporting Information (Appendix S2). Mostly, bioregions are located in the following areas: (1) Amazon; (2) a central area merging the Brazilian Cerrado and Caatinga phytogeographic domains (or the Cerrado, Caatinga and the Espinhaço Range provinces according to Morrone (2014) and Colli-Silva et al. (2019)); (3) two bioregions in the Southern portion of the continent, between the southern portion of the Atlantic Forest and the southern grasslands of Brazil, Paraguay and Argentina; (4) one to three bioregions in the Western portion of the Andes; and (5) a disjunct bioregion encompassing Colombian and Venezuelan open/dry areas plus the mostly Brazilian tropical wetland vegetation of Pantanal.

Different bioregions are represented by different groups of species of different genera (Figure 5f). For instance, the Amazonian bioregion is almost represented by most of the *Sterculia* species, as well as arborescent Byttnerioideae (*Theobroma* spp.) and lianescent *Byttneria* spp. A second group is represented by *Waltheria*, *Melochia* and shrubby species of *Ayenia* and *Byttneria*, as well as for some *Helicteres* from Central Brazil. A third group is mainly represented by *Ayenia* and *Byttneria*, as well as by several *Melochia* species. A fourth group is a mixture of *Theobroma*, *Sterculia*, *Helicteres* and *Melochia* species, and the fifth is mostly composed by species of *Melochia* and *Waltheria* (Figure 5f).

4. Discussion

Both questions we stated before were corroborated (see section 1), so (1) different species in different genera exhibit a particular distribution pattern within South America, and (2) a differentiated sampling effort scenario was evidenced across different regions in the continent. In general, Byttnerioideae species are mainly centered in regions of open/dry habitats, while some genera in the other two subfamilies are typically from rainforests, namely the Amazonia and the southern portion of the Atlantic Forest. In the next sections, we discuss specific patterns for each subfamily, bringing some insights into the historical scenario of each group and future directions on taxonomy, biogeography and systematics and/or evolution given the reported patterns.

4.1. Sterculioideae

The Amazonian cluster shown in Figure 5f corresponds to one of the largest bioregions found in our survey, whose boundaries fairly coincide with the portion of the Amazonia, from northwestern Peru to the basin of the Amazon River. Most of the indicative species of Sterculioideae is also centered in western Brazil, close to northeastern Peru, or in the extreme north, near the Guianas. Those areas correspond, respectively, to the Madeira and Roraima provinces *sensu* Morrone (2014), which gives more support to their definitions as bioregions in their own right.

In fact, there is an estimation that more than a thousand species of woody plants are found in the moist forests of Amazonia or the Atlantic Forest disjunctly (Mori et al., 1981)—a pattern that, since then, have been increasingly reported in other plant groups (e.g. Prance, 1979; Santos et al., 2007; Thode et al., 2019). Such disjunctions have also been extensively reported for animals as well (e.g. Costa, 2003; Batalha-Filho et al., 2013; Rodrigues et al., 2014). This traces us back to the classical hypotheses of historical rainforest connections (see Ledo & Colli, 2017 for a good review on that) and, accordingly, novel approaches that evokes Miocene and Pliocene-Pleistocene past connections between Amazonia and Atlantic Forest, influenced by past climatic fluctuations.

Dispersal elements can also be evoked in here, as both genera are pantropical, with *Sterculia* seeds being dispersed by birds and *Pterygota* having winged seeds wind-dispersed (Bayer & Kubitzki, 2005; for *Pterygota*, check also Annex 1). In *Sterculia*, bird-mediated dispersal is likely to be an apomorphic state within the Sterculioideae, derived from an hypothetical ancestral with a dehiscent follicle with winged seeds wind-dispersed (Wilkie et al., 2006), facilitating long-dispersal through different areas such as among the moist forests of South America. In a historical perspective, *Pterygota* and *Sterculia* are likely to be a Paleogene lineage (Richardson et al., 2015; Hernández-Gutiérrez & Magallón, 2019), which can relate these events not only to vicariance promoted by the historical connections we have discussed above, but also to recent long dispersal events among different forested relics and gallery forests of open/dry biomes.

Supposedly, it is expected to find separate inner centers of endemism within each tropical rainforest too (see section 4.3 for a specific glance for the Atlantic Forest taxa). For the Amazonia, phytogeographical regions were first proposed by Ducke & Black (1954) based on the distribution of a large amount of species, with further refinements provided by some other authors such as Prance (1994). It is against this background that the Amazonia have been split in more than a dozen of provinces by Morrone (2014), mostly based on faunistic distributions—which likewise is more or less corroborated for plants as e.g. Sampaio (1945), Prance (1977), Daly & Prance (1988) or Hall & Harvey (2002) have shown. Nevertheless, such division is likely to be underestimated due to the lack of collections and the high levels of sampling bias in the area, as reported in here for our study groups. In the case of our survey, the highly sampling biased dataset did not allow to recover single bioregions within the Amazonia, which might make Sterculioideae not a good model to define or discuss potential inner bioregions and past connections in these areas.

4.2. Helicteroideae

In our survey, we reported 33 species of *Helicteres* occurring in South America—some of them widespread, others with a narrow distribution in specific savannic areas. Species are centered mainly in open seasonally dry areas of center and eastern Brazil, especially in the Cerrado, where the center of richness of the genus (and therefore of the whole subfamily) is located. Contrasting with current bioregion delimitations of Morrone (2014) for the Neotropics, it is congruent with the borders of the Cerrado province in the Chacoan dominion, where most of the Cerrado's open/dry vegetations are located.

Helicteres have tubular flowers mostly visited by hummingbirds, which likely is a very efficient pollinator for widespread species such as *H. sacarolha* (Griz & Machado, 2001; Silva et al., 2010). Dispersal in this group is authocoric or anemochoric, and seeds are liberated all at once, forming widespread and dense populations that rapidly grow and spread (Griz & Machado, 2001). This group, however, have several endemic species that can correspond to different endemism patterns within the Cerrado province.

Therefore, biology and distribution of species of the group allied with the remarkable Amphi-Pacific distribution of *Helicteres* makes us wonder how the whole genus (and the subfamily) have evolved in light of the heterogeneous geobiotic scenarios for the Neotropics and for other regions of the globe. This, allied with generating phylogenetic data—which, sadly, is still missing for Helicteroideae—can make this subfamily a good model to assess the inner endemism patterns of the Cerrado province and, subsequently, the evolution of open/dry, savannic biomes, which is less assessed when compared to forested vegetations (Pennington et al., 2000; Fiaschi & Pirani, 2009; see also Chapter 2).

4.3. Byttnerioideae

The center of species richness of Byttnerioideae is located in two main large regions: (1) the open/seasonally dry formation areas and (2) the Andes. However, secondary centers of richness can be found in the Amazonia and in the southern portion of the Atlantic Forest too, as well as through all the Chaco, Colombian and Venezuelan savannas and grasslands of southern Brazil, Argentina and Paraguay.

Many other plants and animals are endemics to open/dry habitats especially in the savannas and deciduous forests of the Caatinga and the Chacos (Mori, 1988; Prado & Gibbs, 1993; Pennington et al., 2000). For instance, the Caatinga is recognized as center of endemism of many birds besides the Byttnerioideae and other plant groups, and these biotic elements are likely related with Chacoan biota in Southwestern Brazil, Bolivia, Paraguay and Argentina (Mori, 1988).

Such endemism, relationship and habitat diversity might be related to different dispersal syndrome dynamics in particular genera and with the dynamics of open/dry vegetations themselves. In the case of Byttnerioideae, there are mentions of autochory and anemochory (Griz & Machado, 2001). These syndromes, allied to floral features, may optimize particular aspects of pollination in open/dry habitats such as in the Cerrado and Caatinga. In addition, xeromorphic characters typical in representatives of this group, such as scleromorphic or coriaceous leaves, with bundle sheath cells lignified, as described for some species of *Byttneria* (Cristóbal, 1964; Arbo, 1977) may be associated to ecological adaptations that have developed in a specific section of the genus—*Byttneria* sect. *Byttneria* (Whitlock & Hale, 2011).

Stablishing potential relations between vegetative characters and distributions of a rich genus as *Byttneria* seems to be a necessary task. Also, an investigation of leaf character evolution (including an anatomical framework) in light of a well sampled phylogeny of the genus should be envisaged for the future, as once attempted and suggested by Arbo (1997). In Chapter 2, we provide an in-depth analysis of open/dry habitats using selected species retrieved from the database we generated, discussing the potential role of multiple dispersal events as drivers for the centers of endemism we reported in here.

Nonetheless, we present some specific comments on the secondary centers found for this subfamily:

Amazonia. This area is mainly represented by species of *Herrania* and *Theobroma*, all arborescent, typical to the Amazonian lowland forests, occurring up to elevations of 1,000 m. These genera are quite distinct from other Byttnerioideae, as they are trees whose dispersal syndrome is likely zoochoric (Cuatrecasas, 1964; Barbosa et al., 2019), but more research is wanted to validate that (Richardson et al., 2015). There are some representatives widespread through all Amazonia (such as *T. subincanum* e *H. mariae*), but most of them are centered in eastern Brazilian Amazon and in Peru, Colombia, Venezuela and Ecuador, where the center of species richness of both genera is located.

This is a very unusual pattern even considering its closest genus of the tribe, *Guazuma*. *Guazuma* has a much wider distribution, with *G. ulmifolia* widespread through all the Neotropics. Nevertheless, biogeographical patterns of the Amazonia become problematic to discuss, as they are blurred due to biasing effects, with scarcer collection efforts and higher biasing levels in this area as we shown in here. Also, for *Theobroma*/*Herrania* this issue is even more problematic given the potential influence of cultivated specimens in defining the natural distribution of the species, especially of wild cacaos whose vouchers in the herbaria require revisitation.

Peri-Amazonian disjunctions. Surrounding the Amazonian rainforest, we found species with a particular disjunct pattern through different fragments of open seasonally dry formations, namely the dry deciduous forests or peri-Amazon seasonal savannas. Similar patterns were also found in vertebrates (Ederhard & Bermingham, 2004; Courtenay & Maffei, 2004; Quijada-Mascareñas et al., 2007; Azevedo et al., 2016) and widely suggested for plants (Granville, 1992; Prado & Gibbs, 1993; Pennington et al., 2000; 2004). In this sense, Werneck et al. (2011) analyzed these patterns, focusing on dry deciduous forest formations, suggesting a Pleistocenic connections through peri-Andean areas that can be rather questionable for the Malvaceae from our database, at least in under an species modeling approach (see Chapter 2). In fact, species of several plant families displaying some types of peri-Amazonian distributions may also inhabit or somewhat penetrate punctual sites of the forest, as was demonstrated by Granville (1992).

Atlantic Forest. This center emerged in our analysis mainly due to the distribution of species from the tribe Byttnerieae, especially species of *Byttneria*. Most species are typical to the southern portion of the Atlantic domain, and also to the Chaco or Brazilian grasslands (i.e. the Brazilian pampas), such as *Ayenia ekmanii*, *Waltheria carmensara*, *B. oranensis* e *A. acalyphifolia*. Our dataset could not recover good inner bioregions inside the coastal region of the Atlantic Forest; this area is, however, acknowledged by its high levels of species richness and endemism of plants and animals (Prance, 1982; Cracraft, 1985; DaSilva et al., 2017; Colli-Silva & Pirani, 2019), but apparently not so much for the Byttnerioideae neither Helicteroideae or Sterculioideae. This means that perhaps these three subfamilies of Malvaceae might not be a good choice as study case to explore evolution and diversification of moist forests.

Nevertheless, the Southern portion of the Atlantic Forest harbors some representatives of *Byttneria* as well, with a specific set of vegetative characters (see Chapter 4). Comparing with the modern bioregions of Morrone (2014), the bioregions is congruent with the Araucaria Forest province, more in Southern Brazil and Argentina, and the other two provinces of the Parana dominion (i.e. Atlantic and Parana Forest provinces).

5. Final remarks

In this survey, we provided a distribution synthesis of a fair sample of species of Malvaceae *sensu lato* in South America, detecting a large number of endemics but also a significative amount of widespread species—at least one per genus. Actually, such widespread pattern seems to be rather common for the Malvaceae *sensu lato*. For instance, in the Malvoideae, we have at least one representative per group whose is widespread through open or seasonally dry areas (Fryxell, 1997; Takeuchi & Esteves, 2017). This might also be related to the generalist pollination or wind-mediated propagule dispersal habits typical in the group. In fact, the presence of at least one widespread species within a genus is commonly reported in several Neotropical plant families.

The publication of this database updating the distribution and taxonomical determination of specimens may enable and stimulate further works with the group. A carefully revised database as ours can be used to improve the taxonomy of particular groups of Malvaceae, as well as to achieve a better understanding of their evolution and biogeographical history. Moreover, our database has the potential to be used as a study model for assessing broader questions of biodiversity patterns, documentation and conservation in South America.

6. Acknowledgments

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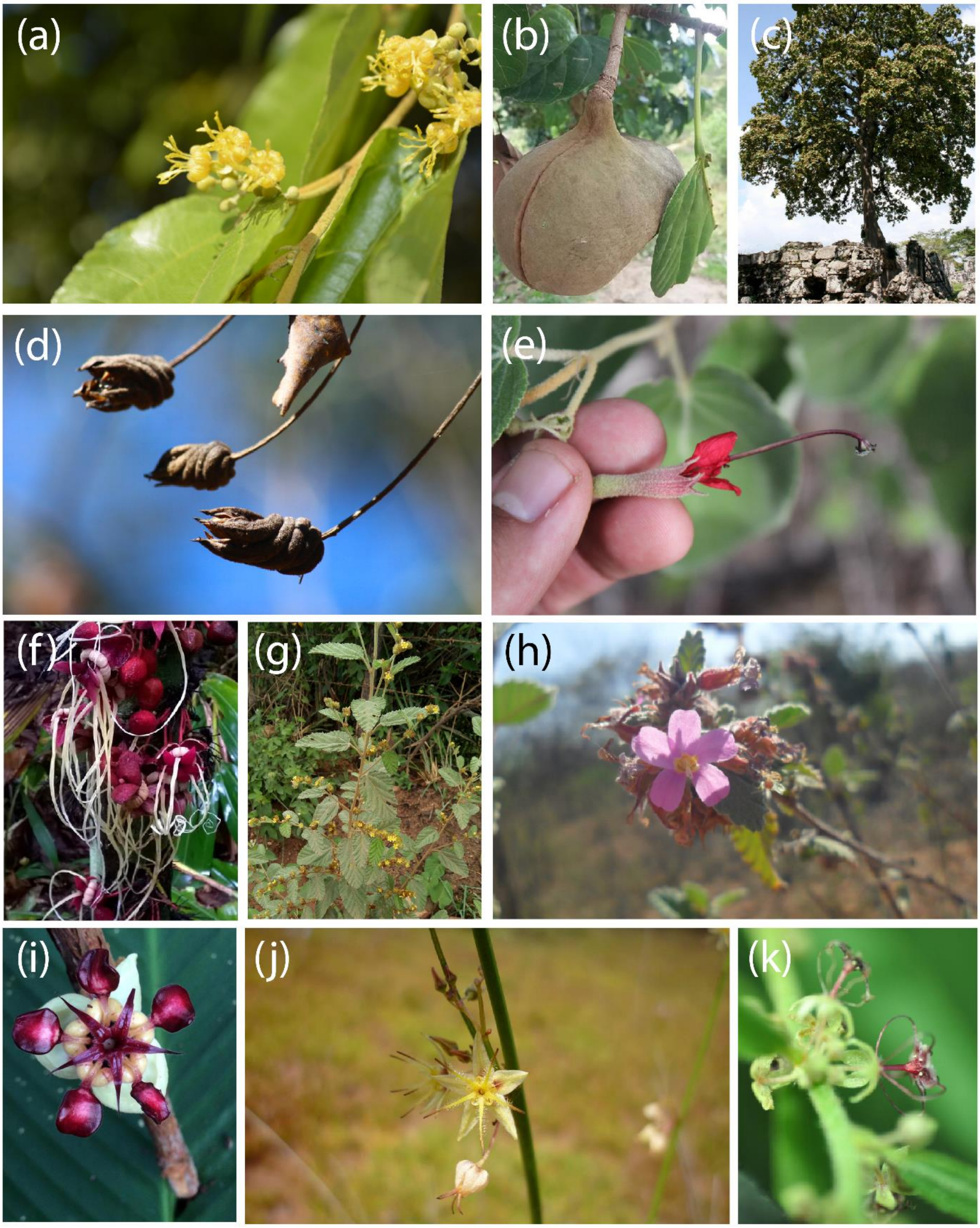
(a)
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Figure 1. A short glance of the morphological diversity in Byttnerioideae, Helicteroideae and Sterculioideae. (a) Flowers of *Guazuma ulmifolia* Lam. (Byttnerioideae), a tree widespread through all vegetations in the Neotropics; (b) Fruit of *Pterygota brasiliensis* Allemão (Sterculioideae), a tree endemic to the Brazilian Atlantic Forest (see Annex 1); (c) *Sterculia apetala* (Jacq.) H.Karst. (Sterculioideae)—tropical rainforest tree that can reach over 40 m; (d-e) Respectively, fruits and a flower of *Helicteres* (Helicteroideae), a shrubby-herbaceous genus mostly from open seasonally dry areas; (f) Flowers of *Herrania mariae* (Mart.) Decne. ex Goudot (Byttnerioideae), the Amazonian "cacau-jacaré" tree; (g) General aspect of a flowering specimen of *Waltheria indica* L. (Byttnerioideae), a ruderal species widespread through South America; (h) Flowering branch of *Melochia pyramidata* L. um (Byttnerioideae), another subshrub widespread through the continent; (i) Flower of *Theobroma grandiflorum* (Willd. ex Spreng.) K.Schum., the "cupuassu", a tree native to the Amazonia, economically important as its ally, the cocoa (*Theobroma cacao* L.)—note its unguiculate petals; (j) Flowers of *Byttneria* (Byttnerioideae), the most species-rich genus of the subfamily; (k) Flowers of *Ayenia angustifolia* A.St.-Hil. & Naudin (Byttnerioideae), an shrubby-herbaceous species allied to *Byttneria*. Photos by: (a) Matheus Colli-Silva; (b) Lukas Daneu; (c) Renato Mello-Silva; (d/j) Rodolph D. Santin; (e) Guilherme M. Antar; (f) Marco Lacerda (Sítio E-Jardim); (g/h) Thales S. Coutinho; (i) Luiz Otavio A. Teixeira (k) Roberta Dayrell.

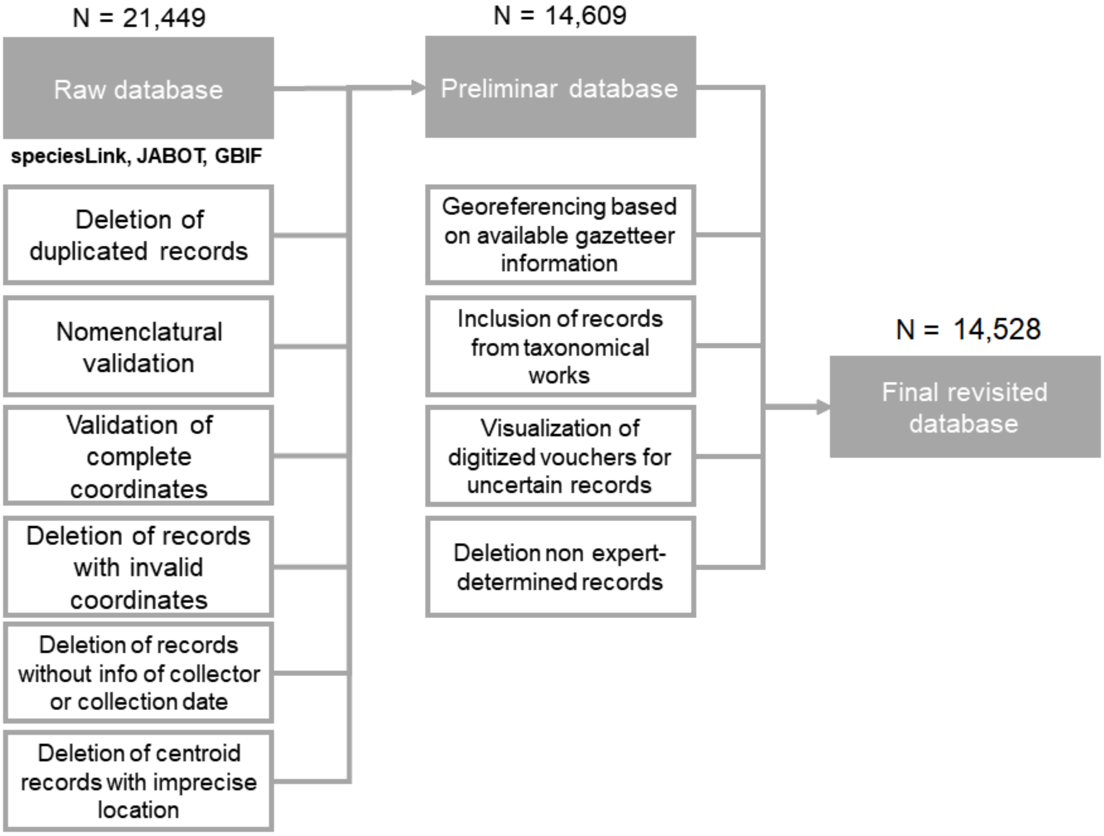

Figure 2. Summary of the workflow of the data cleaning performed in this survey. We also indicate the remaining number of records (N) for each cleaning step.

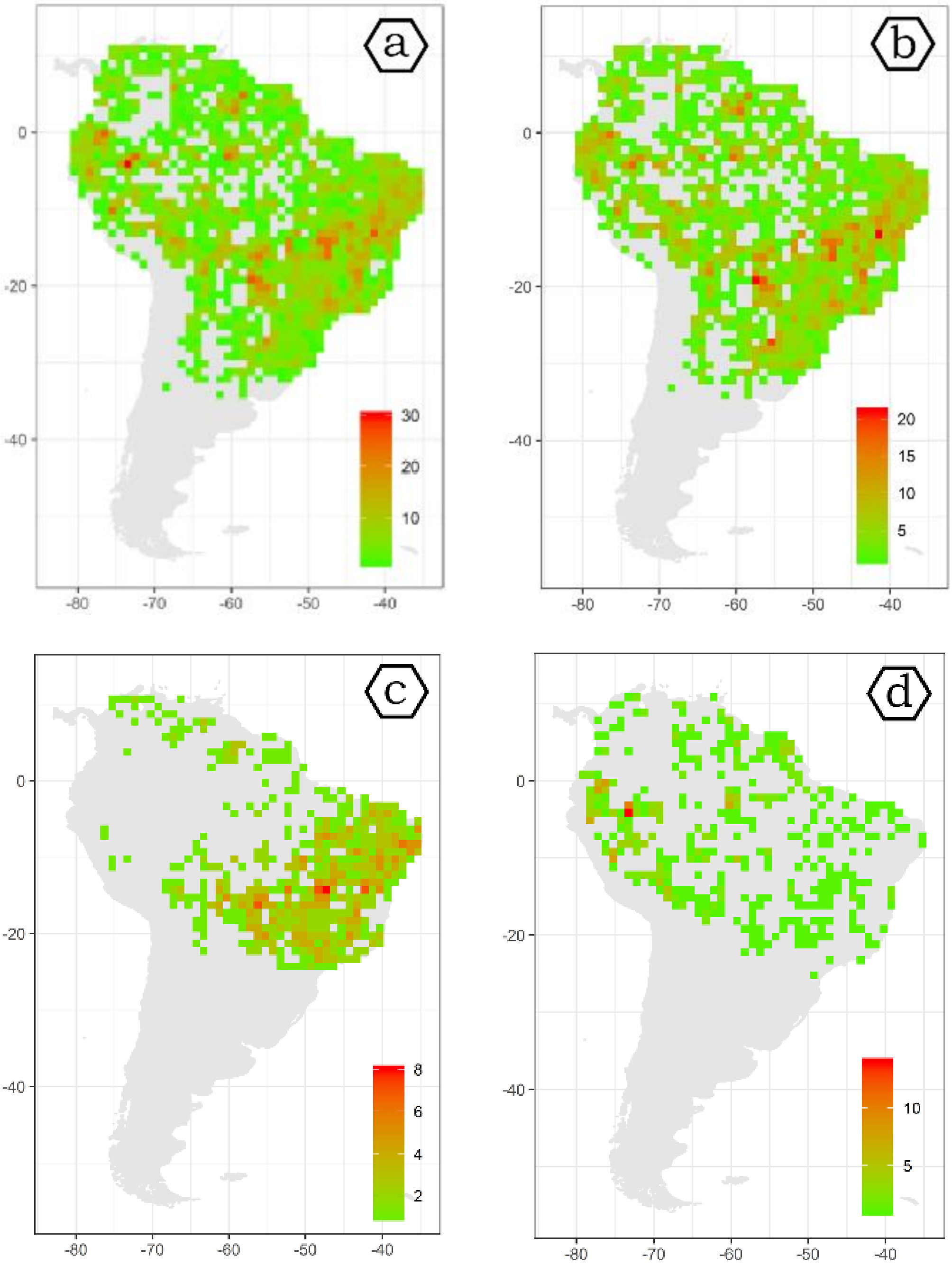

Figure 3. Distribution synthesis of the three selected subfamilies of Malvaceae, considering (a-d) record density in 1° gridcells. (a) record density for all species; (b) only Byttnerioideae; (c) Helicteroideae (therefore only *Helicteres*) (d) Sterculioideae *[Figure continues on the next page]*.

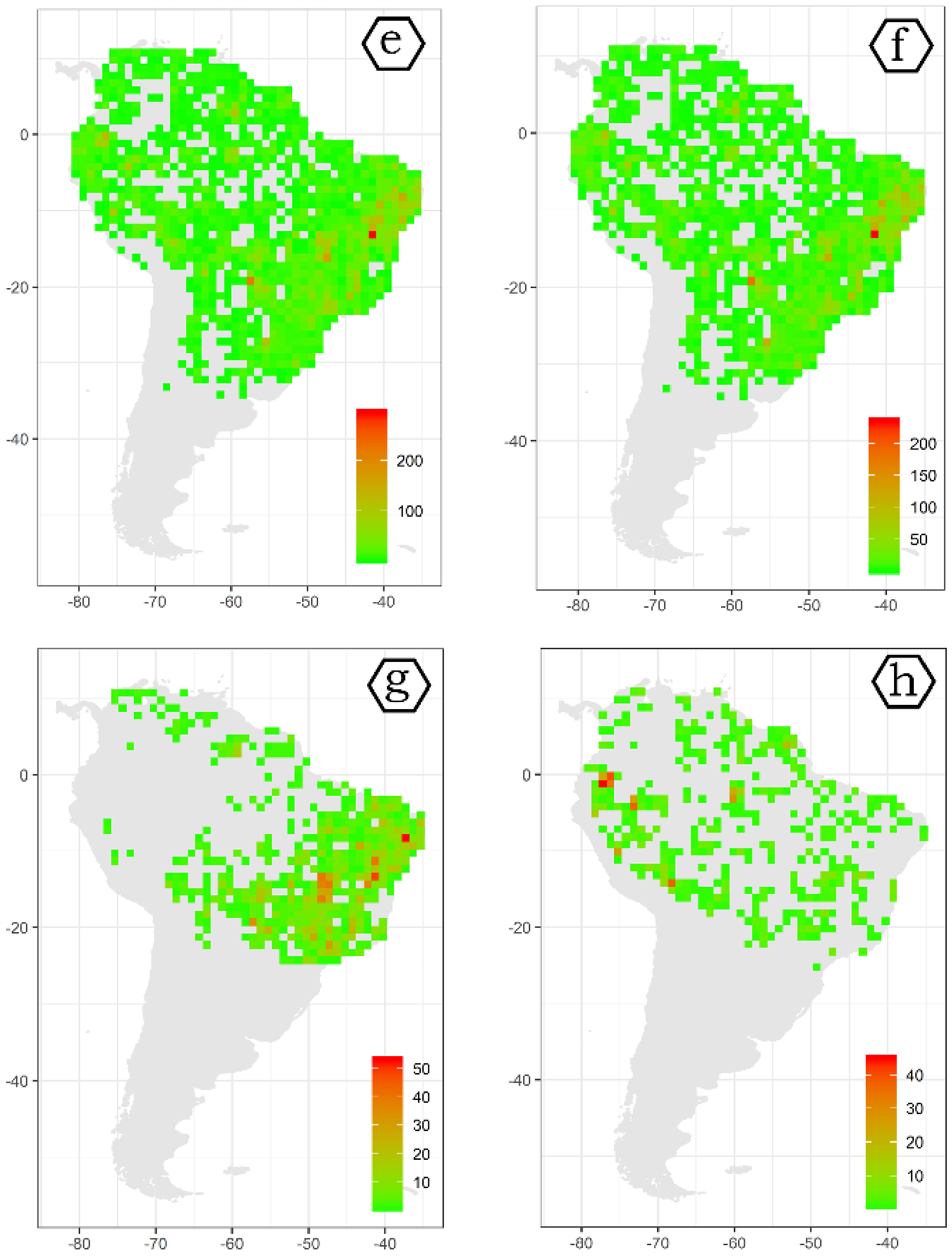

Figure 3 (cont.). Distribution synthesis of the three selected subfamilies of Malvaceae, considering (e-h) species richness in 1° gridcells. (e) species richness for all species; (f) only Byttnerioideae; (g) Helicteroideae; (h) Sterculioideae.

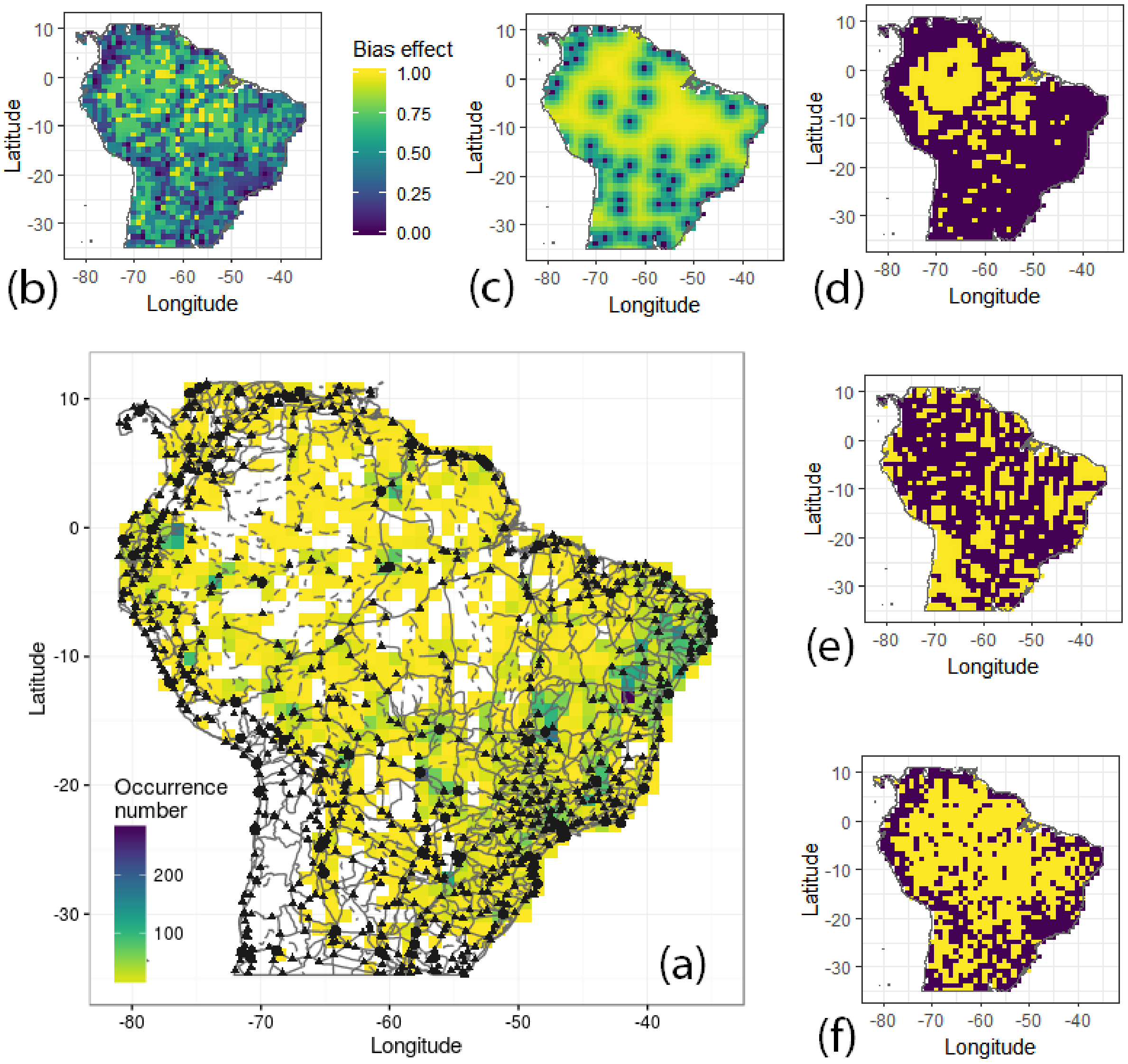

Figure 4. Sampling bias analysis (in 1° gridcells). (a) Records occurrence number per gridcell plotted upon, highlighting the road network of South America. (b) average sampling bias matrix considering (c) airports, (d) roads, (e) rivers and (f) urban areas. Bias effect scale near Figure 5b applies to all subsequent maps. Values closer to 1 reflect more biasing effects for the variables considered in here.

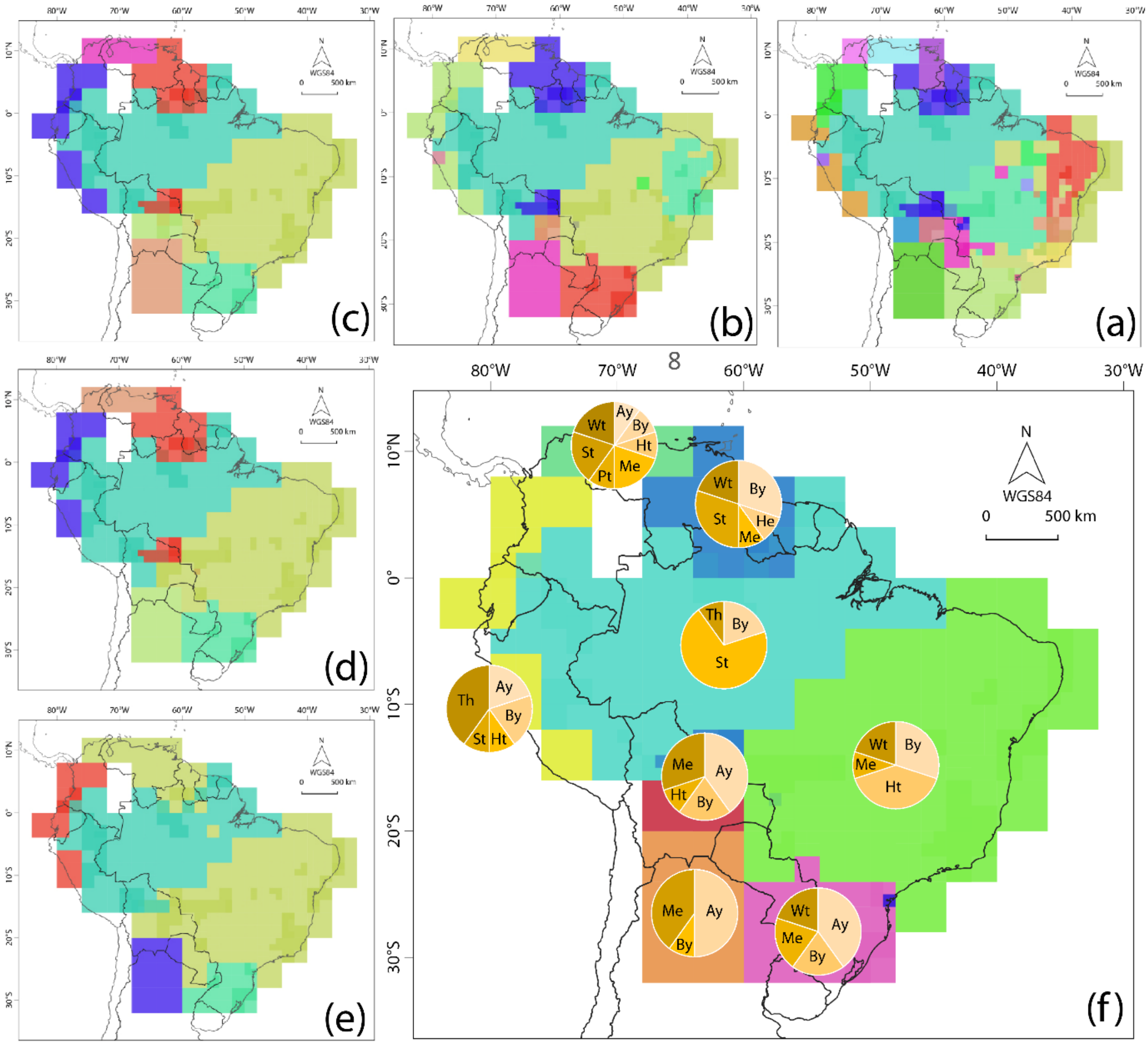

Figure 5. Estimated bioregions depicted in different colors, under distinct cluster costs: (a) 1.0, (b) 1.1, (c) 1.2, (d) 1.3 and (e) 1.4; (f) shows an average scenario (cluster cost of 1.2) in which the proportion of species per genera is presented for each bioregion. Genera represented in pie charts: Ay: *Ayenia*; By: *Byttneria*; He: *Herrania*; Ht: *Helicteres*; Me: *Melochia*; Pt: *Pterygota*; St: *Sterculia*; Th: *Theobroma*; Wt: *Waltheria*. . See Appendix S2 in Supporting Information for full results per bioregion.

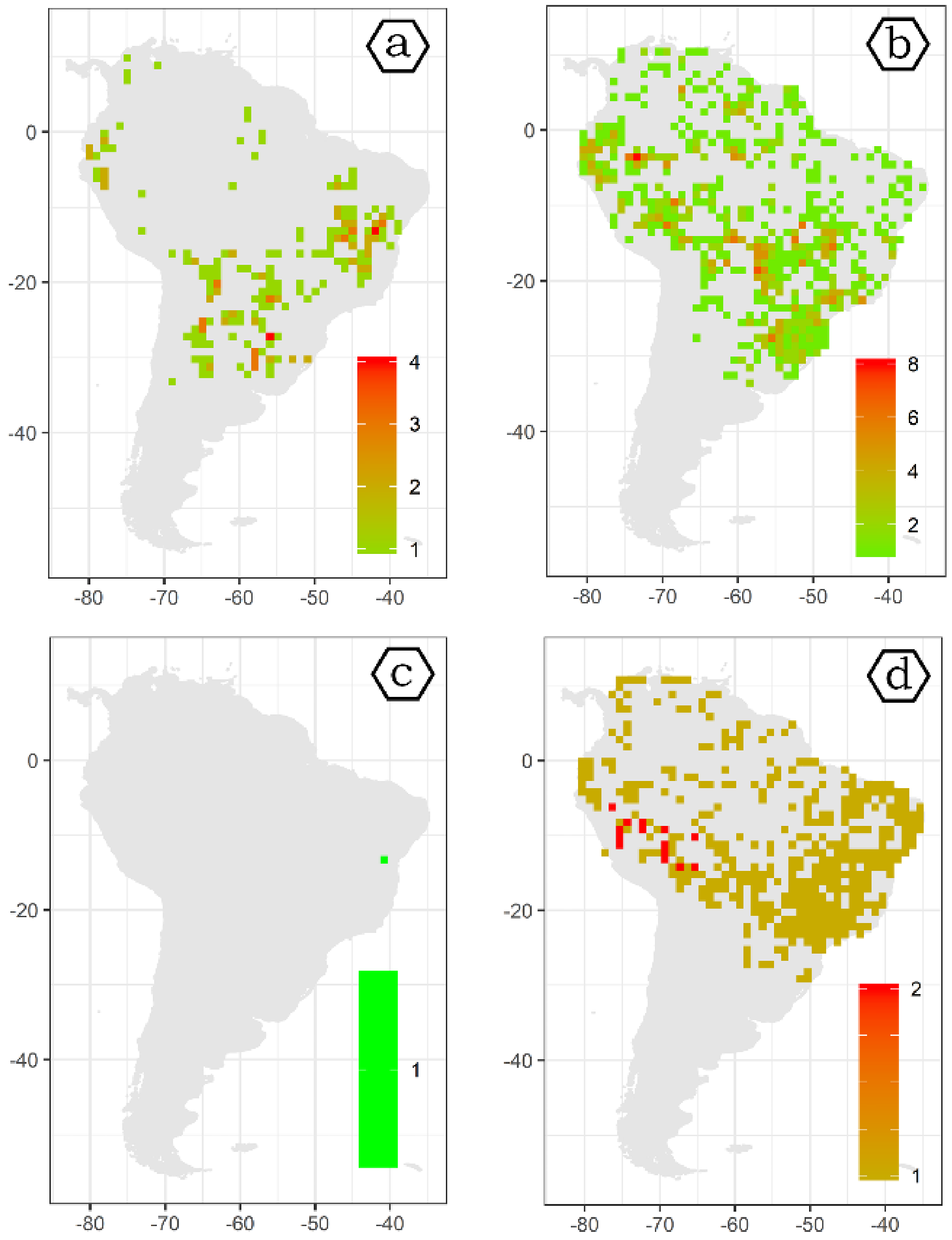

Figure 6a. Distribution synthesis of the genera of Byttnerioideae, considering (a-d) number of records. The density of records and species is at 1° gridcells. (a) Record density for Ayenia; (b) Byttneria; (c) Rayleya; and (d) Guazuma. *[Figure continues on next page]*.

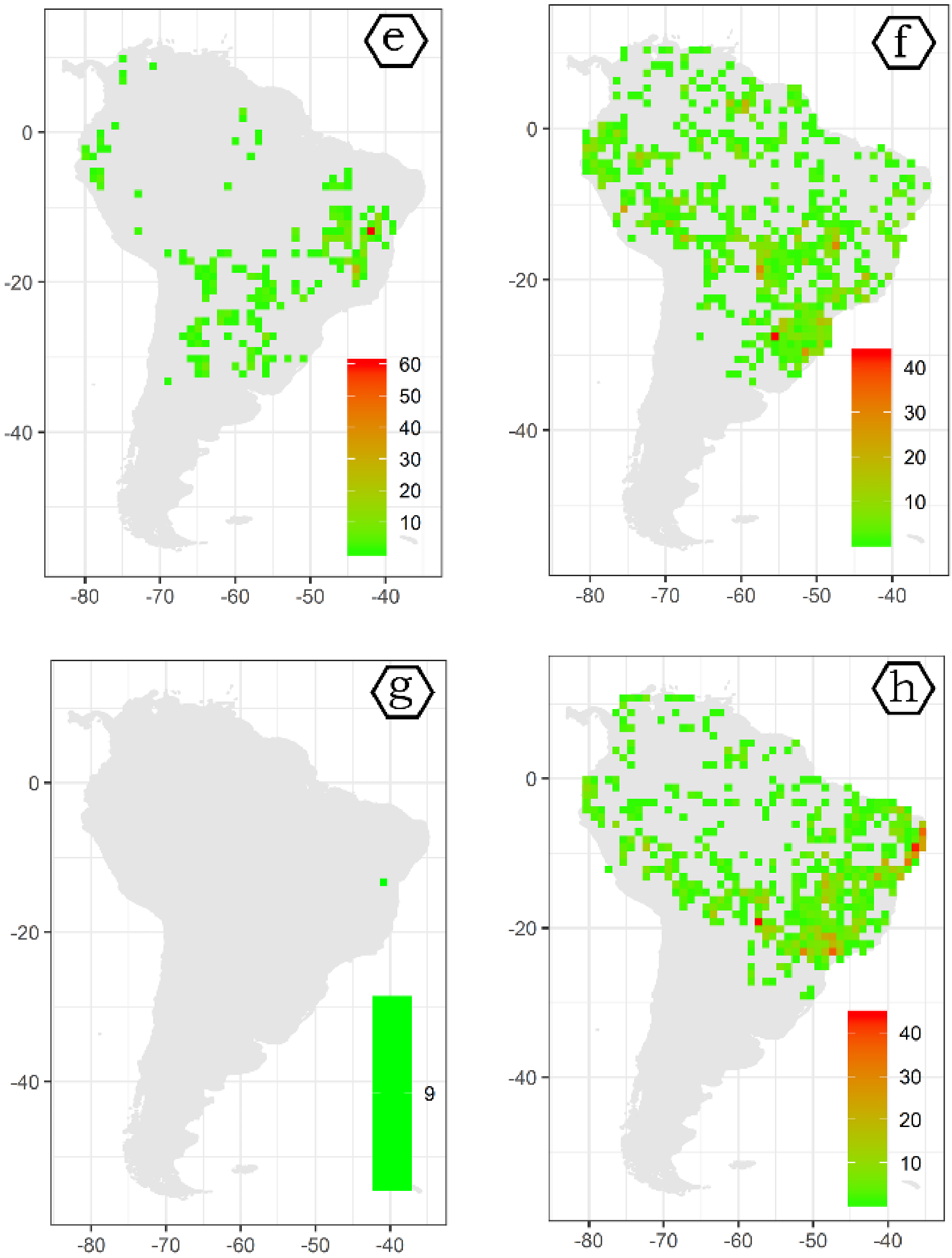

Figure 6a (cont.). Distribution synthesis of the genera of Byttnerioideae, considering (e-h) species richness in South America. The density of records and species is at 1° gridcells. (e) Species richness of *Ayenia*; (f) *Byttneria*; (g) *Rayleya* and (h) *Guazuma*.

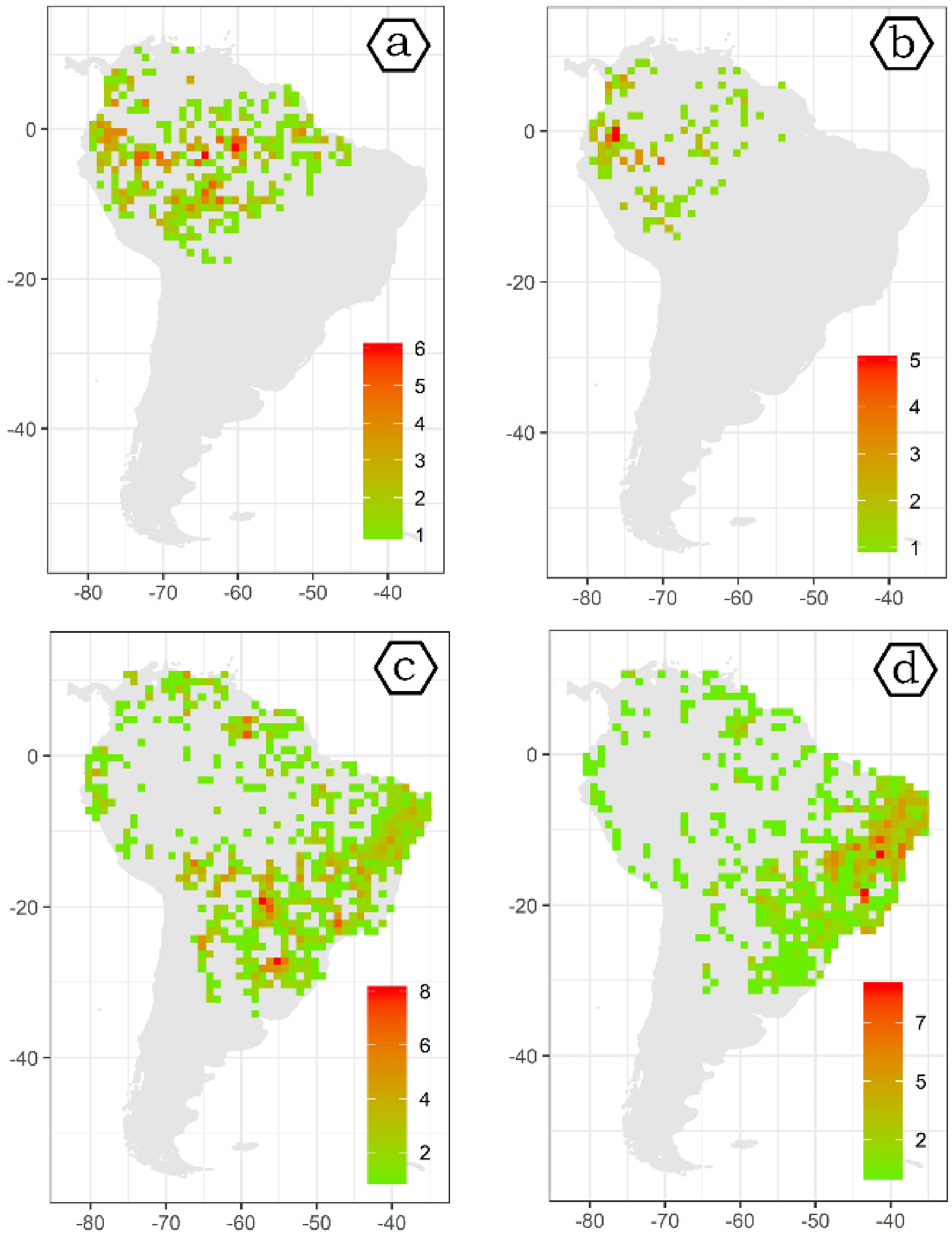

Figure 6b. Distribution synthesis of the genera of Byttnerioideae, considering (a-d) number of records and (e-h) species richness. Spatial scale is in 1° grid cells. (a) Density of records of *Theobroma*; (b) *Herrania*; (c) *Melochia*; and (d) *Waltheria*. (e) Species richness of *Theobroma*; (f) *Herrania*; (g) *Melochia* and (h) *Waltheria* [*Figure continues on next page]*.

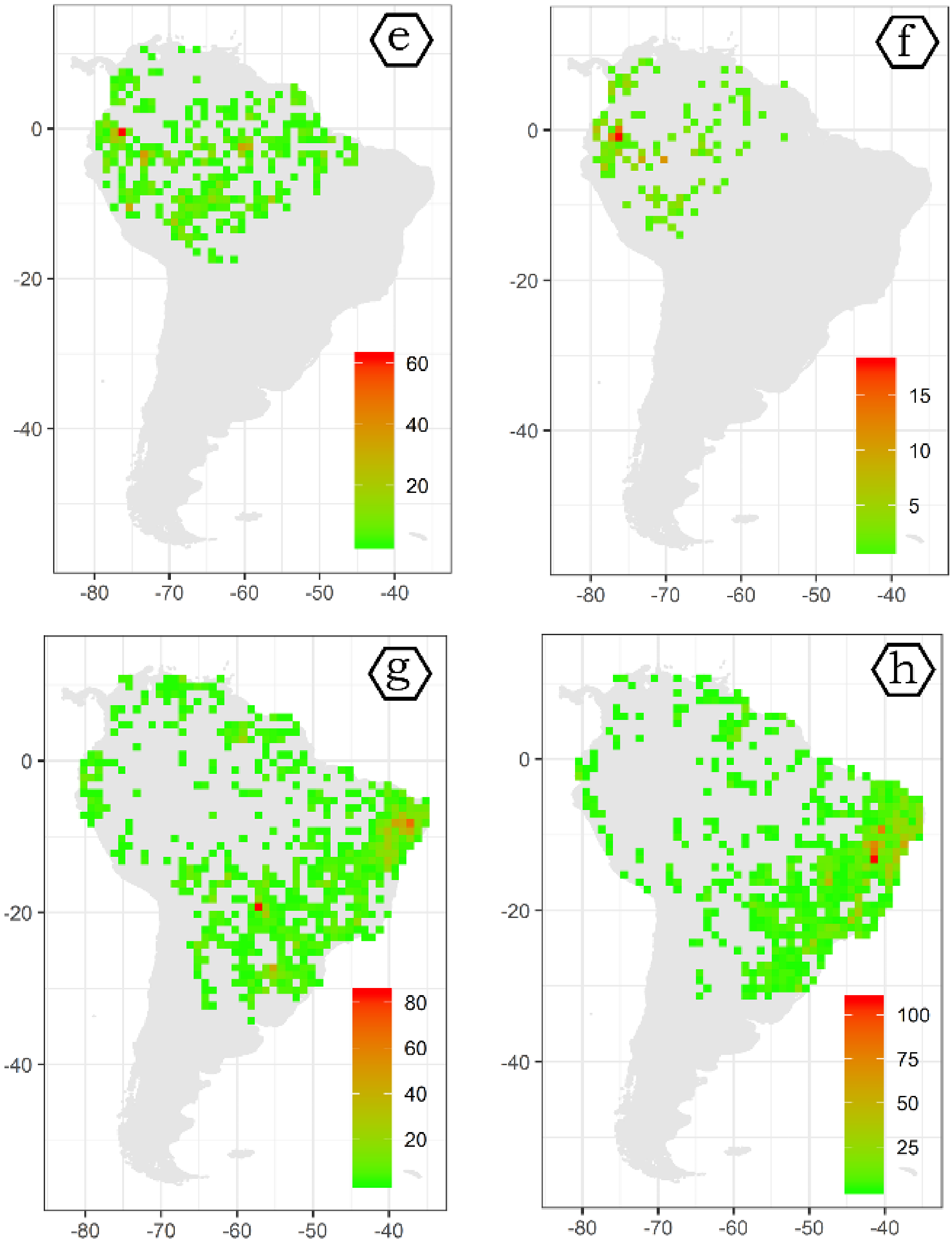

Figure 6b (cont.). Distribution synthesis of the genera of Byttnerioideae, considering (e-h) species richness. Spatial scale is in 1° grid cells. (e) Species richness of *Theobroma*; (f) *Herrania*; (g) *Melochia* and (h) *Waltheria*.

Table 1. Summary of the consulted works in the literature survey performed in this study. The known number of described species were obtained consulting the accepted names of online repositories (namely the Plant List, `www.plantlist.org`) plus information in the specific literature.

Genus	Main reference(s)	Total known	South American species (percent from the total)	New recs after literature survey	New species after literature survey
Ayenia	Cristóbal (1960)	≈80	33 (≈41%)	63	4
Byttneria	Cristóbal (1976)	≈140	76 (≈54%)	42	6
Guazuma	Freytag (1951)	3	2 (67%)	0	0
Helicteres	Cristóbal (2001)	≈60	33 (≈55%)	12	2
Herrania	Schultes (1958)	≈20	12 (≈60%)	25	0
Melochia	Goldberg (1967)	≈65	35 (≈54%)	69	1
Pterygota	Kostermans (1960) [Annex 1]	≈10	3 (≈30%)	0	0
Rayleya	Cristóbal (1981)	1	1 (100%)	0	0
Sterculia	Taroda (1984) Taylor (1986; unpubl.) Mondragón & Castillo (2011)	≈90	30 (≈33%)	15	0
Theobroma	Cuatrecasas (1964)	≈20	16 (≈80%)	44	1
Waltheria	Saunders (1995; unpubl.)	≈50	30 (≈60%)	88	11
Total		**≈539**	**271 (≈50%)**	**358**	**25**

Table 2. Summary of the species and total records of taxa from South America, based on our survey. Each supra-specific name (genus and subfamily) has the total number of species and the number of endemics to the continent for the group in parenthesis. All = Total number of occurrence records. Countries: AR = Argentina. BO = Bolivia. BR = Brazil. CH = Chile. CO = Colombia. EC = Ecuador. GF = French Guyana. GY = Guyana. PE = Peru. PY = Paraguay. SR = Suriname. UR = Uruguay. VE = Venezuela. End = taxa endemic to South America (indicated with an "X" if so). * = Name not validly published, but we considered it in this study still.

Taxon	All	AR	BO	BR	CH	CO	EC	GF	GY	PE	PY	SR	UR	VE	End
Byttnerioideae (206/170)	**10,749**	**535 (42/5)**	**579 (55/0)**	**8,058 (130/51)**	**0 (0/0)**	**186 (51/8)**	**500 (45/4)**	**118 (18/0)**	**195 (26/1)**	**612 (46/6)**	**38 (14/2)**	**93 (19/0)**	**3 (1/0)**	**140 (22/1)**	-
***Ayenia* L. (33/32)**	**557**	**95 (11/2)**	**32 (9/0)**	**385 (15/3)**	**0 (0/0)**	**5 (3/0)**	**10 (4/0)**	**0 (0/0)**	**6 (1/0)**	**15 (4/0)**	**5 (3/0)**	**0 (0/0)**	**3 (1/0)**	**1 (1/0)**	-
Ayenia acalyphifolia Griseb.	4	4	-	-	-	-	-	-	-	-	-	-	-	-	X
Ayenia acuminata Rusby	1	-	-	-	-	-	1	-	-	-	-	-	-	-	X
Ayenia aliculata Cristóbal	1	-	-	-	-	1	-	-	-	-	-	-	-	-	X
Ayenia angustifolia A.St.-Hil. & Naudin	214	-	-	214	-	-	-	-	-	-	-	-	-	-	X
Ayenia aprica Cristóbal	8	7	-	1	-	-	-	-	-	-	-	-	-	-	X
Ayenia blanchetiana K.Schum.	49	-	-	49	-	-	-	-	-	-	-	-	-	-	X
Ayenia boliviana Rusby	2	-	2	-	-	-	-	-	-	-	-	-	-	-	X
Ayenia cordobensis Hieron.	21	21	-	-	-	-	-	-	-	-	-	-	-	-	X
Ayenia ekmanii Cristóbal	11	3	-	3	-	-	-	-	-	-	2	-	3	-	X
Ayenia eliae Cristóbal	12	11	1	-	-	-	-	-	-	-	-	-	-	-	X
Ayenia erecta Mart.	6	-	-	6	-	-	-	-	-	-	-	-	-	-	X
Ayenia glabrescens K.Schum.	3	-	-	3	-	-	-	-	-	-	-	-	-	-	X
Ayenia hirta A.St.-Hil. & Naudin	2	-	-	2	-	-	-	-	-	-	-	-	-	-	X
Ayenia jussieui Cristóbal	11	-	-	-	-	-	3	-	-	8	-	-	-	-	X
Ayenia klugii Cristóbal & Arbo	3	-	-	-	-	1	2	-	-	-	-	-	-	-	X
Ayenia krapovickasii Cristóbal	4	-	4	-	-	-	-	-	-	-	-	-	-	-	X
Ayenia latifolia Cristóbal	9	-	-	9	-	-	-	-	-	-	-	-	-	-	X
Ayenia lingulata Griseb.	12	11	1	-	-	-	-	-	-	-	-	-	-	-	X
Ayenia luyensis Cristóbal	3	-	-	-	-	-	-	-	-	3	-	-	-	-	X
Ayenia magna L.	4	-	3	1	-	-	-	-	-	-	-	-	-	-	-

Taxon	All	AR	BO	BR	CH	CO	EC	GF	GY	PE	PY	SR	UR	VE	End
Ayenia mansfeldiana (Herter) Cristóbal	17	12	-	5	-	-	-	-	-	-	-	-	-	-	X
Ayenia noblickii Cristóbal	8	-	-	8	-	-	-	-	-	-	-	-	-	-	X
Ayenia nummularia Cristóbal	2	1	-	1	-	-	-	-	-	-	-	-	-	-	X
Ayenia odonellii Cristóbal	25	21	4	-	-	-	-	-	-	-	-	-	-	-	X
Ayenia peregrina Cristóbal	3	-	-	-	-	-	-	-	-	3	-	-	-	-	X
Ayenia praecipua Cristóbal	6	3	-	2	-	-	-	-	-	-	1	-	-	-	X
Ayenia praeclara Sandwith	8	-	-	7	-	-	-	-	-	1	-	-	-	-	X
Ayenia pusilla L.	4	-	-	-	-	-	4	-	-	-	-	-	-	-	X
Ayenia saligna Dorr	3	-	-	-	-	3	-	-	-	-	-	-	-	-	X
Ayenia schumanniana Kuntze	7	-	7	-	-	-	-	-	-	-	-	-	-	-	X
Ayenia spinulosa R.E.Fr.	2	-	-	-	-	-	-	-	-	-	2	-	-	-	X
Ayenia subtilis Cristóbal	2	1	1	-	-	-	-	-	-	-	-	-	-	-	X
Ayenia tomentosa L.	90	-	9	74	-	-	-	-	6	-	-	-	-	1	X
***Byttneria* Loefl. (76/73)**	**1,747**	**124 (11/1)**	**125 (18/0)**	**1,093 (52/21)**	**0 (0/0)**	**12 (10/2)**	**81 (16/4)**	**22 (4/0)**	**53 (6/0)**	**181 (26/6)**	**8 (4/0)**	**3 (2/0)**	**0 (0/0)**	**45 (10/1)**	**-**
Byttneria abutiloides A.St.-Hil. & Naudin	2	-	-	2	-	-	-	-	-	-	-	-	-	-	X
Byttneria aculeata Domb. ex Lam.	55	-	15	9	-	3	6	-	-	11	-	-	-	11	-
Byttneria affinis Pohl	1	-	-	1	-	-	-	-	-	-	-	-	-	-	X
Byttneria ancistrodonta Mildbr.	17	-	-	5	-	-	7	-	-	5	-	-	-	-	X
Byttneria aristeguietae Cristóbal	2	-	-	-	-	-	-	-	-	-	-	-	-	2	X
Byttneria asplundii Cristóbal	2	-	-	-	-	-	1	-	-	1	-	-	-	-	X
Byttneria asterotricha Mildbr.	32	-	2	9	-	-	11	-	-	10	-	-	-	-	X
Byttneria attenuatifolia Cristóbal	3	-	-	1	-	-	-	-	-	2	-	-	-	-	X
Byttneria aurantiaca Mildbr.	14	-	-	7	-	1	1	1	-	4	-	-	-	-	X
Byttneria australis Sieber ex Steud.	162	11	-	151	-	-	-	-	-	-	-	-	-	-	X
Byttneria benensis Britton	41	-	10	27	-	-	-	-	-	4	-	-	-	-	X
Byttneria beyrichiana K.Schum.	4	-	-	4	-	-	-	-	-	-	-	-	-	-	X
Byttneria catalpifolia Jacq. subsp. *catalpifolia*	99	-	26	26	-	1	8	-	2	30	-	2	-	4	-
Byttneria catalpifolia subsp. sidifolia (A.St.-Hil.) Cristóbal	20	2	-	18	-	-	-	-	-	-	-	-	-	-	-
Byttneria celtoides A.St.-Hil.	1	-	-	1	-	-	-	-	-	-	-	-	-	-	X
Byttneria cordata Lam.	7	-	-	-	-	-	1	-	-	6	-	-	-	-	X

Taxon	**All**	**AR**	**BO**	**BR**	**CH**	**CO**	**EC**	**GF**	**GY**	**PE**	**PY**	**SR**	**UR**	**VE**	**End**
Byttneria cordifolia Sagot	22	-	-	17	-	-	-	4	-	-	-	1	-	-	X
Byttneria coriacea Britton	52	-	1	24	-	-	1	-	-	26	-	-	-	-	X
Byttneria corylifolia Humb. & Bonpl. ex Roem. & Schult.	4	-	-	-	-	-	1	-	-	3	-	-	-	-	X
Byttneria cristobaliana Dorr	4	-	-	4	-	-	-	-	-	-	-	-	-	-	X
Byttneria dentata Pohl	16	-	1	15	-	-	-	-	-	-	-	-	-	-	X
Byttneria divaricata Benth.	92	1	7	62	-	-	-	-	19	-	-	-	-	3	X
Byttneria elliptica Pohl	11	-	-	11	-	-	-	-	-	-	-	-	-	-	X
Byttneria fernandesii Cristóbal	11	-	-	11	-	-	-	-	-	-	-	-	-	-	X
Byttneria filipes Mart. ex K.Schum.	113	15	9	89	-	-	-	-	-	-	-	-	-	-	X
Byttneria flexuosa Killip	1	-	-	-	-	-	1	-	-	-	-	-	-	-	X
Byttneria fulva Poepp. & Endl.	45	-	1	29	-	1	-	-	-	14	-	-	-	-	X
Byttneria gayana A.St.-Hil.	26	-	-	26	-	-	-	-	-	-	-	-	-	-	X
Byttneria genistella Triana & Planch.	65	-	7	34	-	1	-	-	12	-	-	-	-	11	X
Byttneria glabrescens Benth.	4	-	-	-	-	-	2	-	-	2	-	-	-	-	X
Byttneria glazioui Hochr.	15	-	-	15	-	-	-	-	-	-	-	-	-	-	X
Byttneria gracilipes Baill.	45	22	-	23	-	-	-	-	-	-	-	-	-	-	X
Byttneria hatschbachii Cristóbal	38	-	-	38	-	-	-	-	-	-	-	-	-	-	X
Byttneria hirsuta Ruiz & Pav.	21	-	5	-	-	-	-	-	-	16	-	-	-	-	X
Byttneria idroboi Cristóbal	1	-	-	-	-	1	-	-	-	-	-	-	-	-	X
Byttneria implacabilis Cristóbal	8	-	-	8	-	-	-	-	-	-	-	-	-	-	X
Byttneria irwinii Cristóbal	2	-	-	2	-	-	-	-	-	-	-	-	-	-	X
Byttneria jaculifolia Pohl	3	-	-	3	-	-	-	-	-	-	-	-	-	-	X
Byttneria lasiophylla Cristóbal	7	-	-	7	-	-	-	-	-	-	-	-	-	-	X
Byttneria lopez-mirandae Cristóbal	6	-	-	-	-	-	-	-	-	6	-	-	-	-	X
Byttneria loxensis Cristóbal	3	-	-	-	-	-	3	-	-	-	-	-	-	-	X
Byttneria melantha Mart. ex K.Schum.	3	-	-	-	-	-	-	-	-	3	-	-	-	-	X
Byttneria melastomaefolia A.St.-Hil.	104	-	-	104	-	-	-	-	-	-	-	-	-	-	X
Byttneria minytricha Cristóbal	2	-	-	-	-	-	-	-	-	2	-	-	-	-	X
Byttneria mollis Kunth	3	-	-	-	-	1	-	-	-	2	-	-	-	-	X
Byttneria morifolia Triana & Planch.	1	-	-	-	-	1	-	-	-	-	-	-	-	-	X

Taxon	All	AR	BO	BR	CH	CO	EC	GF	GY	PE	PY	SR	UR	VE	End
Byttneria morii L.C.Barnett & Dorr	15	-	-	-	-	-	-	11	4	-	-	-	-	-	X
Byttneria obliqua Benth.	29	-	1	27	-	-	-	-	-	-	-	-	-	1	X
Byttneria oblongata Pohl	35	-	2	33	-	-	-	-	-	-	-	-	-	-	X
Byttneria obtusata Benth. ex Hochr.	2	-	-	-	-	-	2	-	-	-	-	-	-	-	X
Byttneria oranensis Cristóbal	10	8	2	-	-	-	-	-	-	-	-	-	-	-	X
Byttneria ostenii Cristóbal	2	-	-	1	-	-	-	-	-	-	1	-	-	-	X
Byttneria ovata Lam.	18	-	-	-	-	-	16	-	-	2	-	-	-	-	X
Byttneria palustris Cristóbal	26	-	-	26	-	-	-	-	-	-	-	-	-	-	X
Byttneria parviflora Benth.	23	-	-	-	-	-	18	-	-	5	-	-	-	-	X
Byttneria pedersenii Cristóbal	22	22	-	-	-	-	-	-	-	-	-	-	-	-	X
Byttneria pescapraeifolia Britton	47	-	17	15	-	-	-	-	-	15	-	-	-	-	X
Byttneria petiolata Cristóbal	6	-	-	6	-	-	-	-	-	-	-	-	-	-	X
Byttneria piresii Cristóbal	9	-	-	4	-	-	-	-	-	-	-	-	-	5	X
Byttneria ramosissima Pohl	9	4	-	5	-	-	-	-	-	-	-	-	-	-	X
Byttneria rhamnifolia Benth.	39	-	2	34	-	1	-	-	-	1	-	-	-	1	X
Byttneria rojasii Cristóbal	3	-	-	1	-	-	-	-	-	-	2	-	-	-	X
Byttneria sagittifolia A.St.-Hil.	16	-	-	16	-	-	-	-	-	-	-	-	-	-	X
Byttneria scabra Pohl	134	21	9	78	-	1	-	6	14	-	-	-	-	5	X
Byttneria scalpellata Pohl	19	-	-	19	-	-	-	-	-	-	-	-	-	-	X
Byttneria schumannii Cristóbal	1	-	-	1	-	-	-	-	-	-	-	-	-	-	X
Byttneria sparrei Cristóbal	2	-	-	-	-	-	2	-	-	-	-	-	-	-	X
Byttneria stenophylla Cristóbal	8	-	-	6	-	-	-	-	-	-	2	-	-	-	X
Byttneria subsessilis Cristóbal	6	-	-	3	-	-	-	-	-	-	3	-	-	-	X
Byttneria triadenia Cristóbal	6	-	-	6	-	-	-	-	-	-	-	-	-	-	X
Byttneria tucumanensis Cristóbal	13	1	8	4	-	-	-	-	-	-	-	-	-	-	X
Byttneria uaupensis Spruce ex K.Schum.	6	-	-	1	-	-	-	-	2	1	-	-	-	2	X
Byttneria urosepala Mildbr.	5	-	-	-	-	-	-	-	-	5	-	-	-	-	X
Byttneria urticifolia K.Schum.	41	17	-	24	-	-	-	-	-	-	-	-	-	-	X
Byttneria vargasii Cristóbal	2	-	-	-	-	-	-	-	-	2	-	-	-	-	X
Byttneria weberbaueri Mildbr.	3	-	-	-	-	-	-	-	-	3	-	-	-	-	X

Taxon	All	AR	BO	BR	CH	CO	EC	GF	GY	PE	PY	SR	UR	VE	End
***Guazuma* Adans. (2/1)**	**1,792**	**13 (1/0)**	**105 (2/0)**	**1,506 (2/0)**	**0 (0/0)**	**31 (1/0)**	**46 (1/0)**	**5 (1/0)**	**12 (1/0)**	**84 (2/0)**	**0 (0/0)**	**3 (1/0)**	**0 (0/0)**	**22 (1/0)**	-
Guazuma crinita Mart.	47	-	2	15	-	-	-	-	-	30	-	-	-	-	X
Guazuma ulmifolia Lam.	1,745	13	99	1,472	-	31	42	4	12	48	-	3	-	21	-
***Herrania* Goudot (12/10)**	**255**	**0 (0/0)**	**2 (1/0)**	**64 (5/0)**	**0 (0/0)**	**43 (10/1)**	**76 (7/0)**	**1 (1/0)**	**9 (3/0)**	**60 (4/0)**	**0 (0/0)**	**1 (1/0)**	**0 (0/0)**	**20 (3/0)**	-
Herrania albiflora Goudot	8	-	-	-	-	4	-	-	-	-	-	-	-	4	X
Herrania balaensis P.Preuss	16	-	-	-	-	2	14	-	-	-	-	-	-	-	X
Herrania camargoana R.E.Schult.	6	-	-	3	-	2	-	-	-	-	-	-	-	1	X
Herrania cuatrecasasiana García-Barr.	9	-	-	-	-	5	3	-	-	1	-	-	-	-	X
Herrania kanukuensis R.E.Schult.	9	-	-	3	-	-	-	1	4	-	-	1	-	-	X
Herrania laciniifolia Goudot ex Triana, Planch. & Garc.Barr.	5	-	-	-	-	5	-	-	-	-	-	-	-	-	X
Herrania lemniscata R.E.Schult.	15	-	-	3	-	1	-	-	4	-	-	-	-	7	X
Herrania mariae Goudot	95	-	-	47	-	2	22	-	1	23	-	-	-	-	X
Herrania nitida (Poepp.) R.E.Schult.	48	-	-	5	-	6	18	-	-	19	-	-	-	-	X
Herrania nycterodendron R.E.Schult.	20	-	2	-	-	-	5	-	-	13	-	-	-	-	X
Herrania pulcherrima Goudot	16	-	-	-	-	13	3	-	-	-	-	-	-	-	-
Herrania purpurea (Pittier) R.E.Schult.	8	-	-	-	-	3	5	-	-	-	-	-	-	-	-
***Melochia* L. (35/20)**	**2,344**	**218 (15/1)**	**137 (15/1)**	**1,711 (22/6)**	**0 (0/0)**	**23 (10/0)**	**55 (8/0)**	**10 (3/0)**	**49 (9/1)**	**37 (9/0)**	**11 (2/0)**	**21 (5/0)**	**0 (0/0)**	**72 (13/0)**	-
Melochia anomala Griseb.	30	30	-	-	-	-	-	-	-	-	-	-	-	-	-
Melochia arenosa Benth.	114	-	13	77	-	-	-	-	16	-	-	1	-	7	-
Melochia argentina R.E.Fr.	27	21	6	-	-	-	-	-	-	-	-	-	-	-	X
Melochia betonicifolia Ruiz & Pav. ex K.Schum.	70	-	-	70	-	-	-	-	-	-	-	-	-	-	X
Melochia canescens Cristóbal	19	5	14	-	-	-	-	-	-	-	-	-	-	-	X
Melochia caracasana Jacq.	15	-	-	-	-	2	-	-	-	-	-	-	-	13	X
Melochia chamaedrys A.St.-Hil.	68	27	-	41	-	-	-	-	-	-	-	-	-	-	X
Melochia gardneri Sprague	7	-	-	7	-	-	-	-	-	-	-	-	-	-	X
Melochia goldbergii Cristóbal	12	6	-	-	-	-	-	-	-	-	6	-	-	-	X
Melochia graminifolia A.St.-Hil.	51	-	19	26	-	-	-	-	4	-	-	-	-	2	X
Melochia hassleriana Chodat	15	8	-	7	-	-	-	-	-	-	-	-	-	-	X
Melochia hermannioides A.St.-Hil.	15	14	1	-	-	-	-	-	-	-	-	-	-	-	X

Taxon	All	AR	BO	BR	CH	CO	EC	GF	GY	PE	PY	SR	UR	VE	End
Melochia illicioides K.Schum.	4	-	-	4	-	-	-	-	-	-	-	-	-	-	X
Melochia kerriifolia Triana & Planch.	9	-	-	6	-	2	-	-	-	-	-	-	-	1	-
Melochia lanceolata Benth.	11	-	-	2	-	-	-	-	2	-	-	7	-	-	X
Melochia leucantha J.F.Macbr.	4	-	-	-	-	-	-	-	-	4	-	-	-	-	X
Melochia lupulina Sw.	39	-	-	-	-	3	27	-	-	7	-	-	-	2	-
Melochia manducata C.Wright	6	-	-	-	-	1	1	-	-	1	-	-	-	3	-
Melochia melissaefolia Benth.	31	-	6	8	-	1	-	6	4	3	-	2	-	1	-
Melochia ministella Cristóbal	14	9	-	-	-	-	-	-	-	-	5	-	-	-	-
Melochia mollis Triana & Planch.	27	-	4	-	-	4	12	-	-	7	-	-	-	-	-
Melochia morongii Britton	12	5	1	6	-	-	-	-	-	-	-	-	-	-	X
Melochia nodiflora Sw.	6	-	-	1	-	4	-	-	-	-	-	-	-	1	-
Melochia parvifolia Kunth	107	2	3	82	-	-	-	-	9	-	-	-	-	11	-
Melochia pilosa Fawc. & Rendle	212	27	25	153	-	1	2	-	1	1	-	-	-	2	-
Melochia pyramidata L.	387	48	17	298	-	-	9	-	-	9	-	-	-	6	-
Melochia regnellii Gonçalez	7	-	-	7	-	-	-	-	-	-	-	-	-	-	-
Melochia sergipana Monteiro	2	-	-	2	-	-	-	-	-	-	-	-	-	-	-
Melochia simplex A.St.-Hil.	81	10	2	68	-	-	-	-	1	-	-	-	-	-	X
Melochia splendens A.St.-Hil. & Naudin	11	-	-	11	-	-	-	-	-	-	-	-	-	-	X
Melochia thymifolia (Presl) Goldberg	8	2	2	-	-	-	2	-	-	2	-	-	-	-	X
Melochia tomentosa L.	595	-	-	581	-	2	1	-	-	-	-	-	-	11	X
Melochia ulmifolia Benth.	48	-	-	31	-	-	-	3	5	-	-	9	-	-	X
Melochia villosa (Mill.) Fawc. & Rendle	272	4	16	223	-	3	1	1	7	3	-	2	-	12	-
Melochia werdermannii Goldberg	8	-	8	-	-	-	-	-	-	-	-	-	-	-	X
***Rayleya* Cristóbal (1/1)**	**9**	**0 (0/0)**	**0 (0/0)**	**9 (1/1)**	**0 (0/0)**	**0 (0/0)**	**0 (0/0)**	**0 (0/0)**	**0 (0/0)**	**0 (0/0)**	**0 (0/0)**	**0 (0/0)**	**0 (0/0)**	**0 (0/0)**	X
Rayleya bahiensis Cristóbal	9	-	-	9	-	-	-	-	-	-	-	-	-	-	X
***Theobroma* L. (16/12)**	**1,149**	**0 (0/0)**	**84 (4/0)**	**555 (10/3)**	**0 (0/0)**	**64 (11/4)**	**166 (5/0)**	**23 (2/0)**	**16 (2/0)**	**217 (6/0)**	**0 (0/0)**	**7 (1/0)**	**0 (0/0)**	**17 (3/0)**	-
Theobroma bernouillii Pittier	11	-	-	-	-	11	-	-	-	-	-	-	-	-	X
Theobroma bicolor Humb. & Bonpl.	28	-	-	-	-	3	18	-	-	5	-	-	-	2	X
Theobroma cacao L.	160	-	45	3	-	6	46	-	-	53	-	-	-	7	X

Taxon	All	AR	BO	BR	CH	CO	EC	GF	GY	PE	PY	SR	UR	VE	End
Theobroma canumanense Pires & Fróes ex Cuatrec.	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Theobroma chocoense Cuatrec.	7	-	-	-	-	7	-	-	-	-	-	-	-	-	-
Theobroma cirmolinae Cuatrec.	7	-	-	-	-	7	-	-	-	-	-	-	-	-	-
Theobroma gileri Cuatrec.	13	-	-	-	-	1	12	-	-	-	-	-	-	-	X
Theobroma glaucum H.Karst.	34	-	-	11	-	10	6	-	-	7	-	-	-	-	X
Theobroma grandiflorum (Willd. ex Spreng.) K.Schum.	29	-	-	29	-	-	-	-	-	-	-	-	-	-	X
Theobroma microcarpum Mart.	34	-	-	32	-	2	-	-	-	-	-	-	-	-	X
Theobroma nemorale Cuatrec.	6	-	-	-	-	6	-	-	-	-	-	-	-	-	-
Theobroma obovatum Klotzsch ex Bernoulli	118	-	1	67	-	3	-	-	1	46	-	-	-	-	X
Theobroma speciosum Willd.	245	-	33	198	-	-	-	-	-	14	-	-	-	-	X
Theobroma subincanum Mart.	360	-	5	124	-	8	84	17	15	92	-	7	-	8	X
Theobroma sylvestre Mart.	82	-	-	82	-	-	-	-	-	-	-	-	-	-	X
Theobroma velutinum Benoist	14	-	-	8	-	-	-	6	-	-	-	-	-	-	X
***Waltheria* L. (30/20)**	**2,896**	**71 (4/1)**	**43 (6/0)**	**2,604 (23/17)**	**0 (0/0)**	**16 (6/1)**	**27 (2/0)**	**16 (1/0)**	**62 (4/0)**	**25 (2/0)**	**3 (2/2)**	**4 (1/0)**	**0 (0/0)**	**25 (4/0)**	-
Waltheria ackermanniana K.Schum.	15	-	-	15	-	-	-	-	-	-	-	-	-	-	X
Waltheria albicans Turcz.	147	2	2	140	-	-	-	-	3	-	-	-	-	-	-
Waltheria berteroi (Spreng.) J.G.Saunders*	6	-	-	-	-	2	-	-	-	-	-	-	-	4	-
Waltheria biribiriensis J.G.Saunders*	9	-	-	9	-	-	-	-	-	-	-	-	-	-	X
Waltheria brachypetala Turcz.	317	-	-	317	-	-	-	-	-	-	-	-	-	-	X
Waltheria bracteosa A.St.-Hil. & Naudin	61	-	-	61	-	-	-	-	-	-	-	-	-	-	X
Waltheria carmensarae J.G.Saunders*	9	9	-	-	-	-	-	-	-	-	-	-	-	-	X
Waltheria carpinifolia A.St.-Hil. & Naudin	31	-	-	31	-	-	-	-	-	-	-	-	-	-	X
Waltheria cinerascens A.St.-Hil.	370	-	-	370	-	-	-	-	-	-	-	-	-	-	X
Waltheria collina K.Schum.	5	-	-	3	-	1	-	-	-	-	-	-	-	1	-
Waltheria communis A.St.-Hil.	400	46	10	344	-	-	-	-	-	-	-	-	-	-	X
Waltheria excelsa Turcz.	11	-	-	11	-	-	-	-	-	-	-	-	-	-	X
Waltheria ferruginea A.St.-Hil.	13	-	-	13	-	-	-	-	-	-	-	-	-	-	X
Waltheria flavovirens J.G.Saunders*	18	-	-	18	-	-	-	-	-	-	-	-	-	-	X
Waltheria glazioviana K.Schum.	2	-	-	2	-	-	-	-	-	-	-	-	-	-	-

Taxon	All	AR	BO	BR	CH	CO	EC	GF	GY	PE	PY	SR	UR	VE	End
Waltheria indica L.	1,141	14	25	1,010	-	8	2	16	39	9	-	4	-	14	-
Waltheria involucrata Benth.	42	-	-	15	-	2	-	-	19	-	-	-	-	6	X
Waltheria ladewii Rusby ex J.G.Saunders*	3	-	1	-	-	2	-	-	-	-	-	-	-	-	X
Waltheria macrophylla Hassl.	2	-	-	-	-	-	-	-	-	-	2	-	-	-	X
Waltheria maritima A.St.-Hil.	6	-	-	6	-	-	-	-	-	-	-	-	-	-	X
Waltheria operculata Rose	10	-	-	10	-	-	-	-	-	-	-	-	-	-	-
Waltheria ovata Cav.	42	-	1	-	-	-	25	-	-	16	-	-	-	-	X
Waltheria petiolata K.Schum.	8	-	-	8	-	-	-	-	-	-	-	-	-	-	-
Waltheria polyantha K.Schum.	3	-	-	3	-	-	-	-	-	-	-	-	-	-	X
Waltheria procumbens J.G.Saunders & Soria	1	-	-	-	-	-	-	-	-	-	1	-	-	-	X
Waltheria reclinata Rusby ex J.G.Saunders*	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Waltheria rotundifolia Schrank	12	-	-	12	-	-	-	-	-	-	-	-	-	-	-
Waltheria selloana K.Schum.	2	-	-	2	-	-	-	-	-	-	-	-	-	-	X
Waltheria vernonioides R.E.Fr.	5	-	-	5	-	-	-	-	-	-	-	-	-	-	X
Waltheria viscosissima A.St.-Hil.	204	-	4	199	-	-	-	-	1	-	-	-	-	-	-
Helicteroideae (33/29)	**2,663**	**3 (1/0)**	**115 (7/0)**	**2,434 (30/22)**	**0 (0/0)**	**14 (4/0)**	**0 (0/0)**	**20 (1/0)**	**33 (4/0)**	**6 (1/0)**	**0 (0/0)**	**3 (3/0)**	**0 (0/0)**	**35 (6/0)**	-
***Helicteres* L. (33/29)**	**2,663**	**3 (1/0)**	**115 (7/0)**	**2,434 (30/22)**	**0 (0/0)**	**14 (4/0)**	**0 (0/0)**	**20 (1/0)**	**33 (4/0)**	**6 (1/0)**	**0 (0/0)**	**3 (3/0)**	**0 (0/0)**	**35 (6/0)**	-
Helicteres andersonii Cristóbal	24	-	-	24	-	-	-	-	-	-	-	-	-	-	X
Helicteres aspera A.St.-Hil. & Naudin	20	-	-	20	-	-	-	-	-	-	-	-	-	-	X
Helicteres baruensis Benth.	186	-	-	171	-	1	-	-	10	-	-	1	-	3	-
Helicteres biflexa Cristóbal	2	-	-	2	-	-	-	-	-	-	-	-	-	-	X
Helicteres brevispira A.St.-Hil.	500	-	10	488	-	-	-	-	1	-	-	-	-	1	X
Helicteres carthagenensis Jacq.	10	-	-	-	-	7	-	-	-	-	-	-	-	3	-
Helicteres cidii Cristóbal	4	-	-	4	-	-	-	-	-	-	-	-	-	-	X
Helicteres corylifolia Buch.-Ham. ex Dillwyn	79	-	-	79	-	-	-	-	-	-	-	-	-	-	X
Helicteres denticulenta Cristóbal	10	-	-	10	-	-	-	-	-	-	-	-	-	-	X
Helicteres eichleri K.Schum.	123	-	-	123	-	-	-	-	-	-	-	-	-	-	X
Helicteres eitenii Leane	40	-	-	40	-	-	-	-	-	-	-	-	-	-	X
Helicteres gardneriana A.St.-Hil. & Naudin	50	-	24	26	-	-	-	-	-	-	-	-	-	-	X
Helicteres guazumifolia Pilg.	145	-	10	84	-	5	-	-	20	-	-	-	-	26	-

Taxon	All	AR	BO	BR	CH	CO	EC	GF	GY	PE	PY	SR	UR	VE	End
Helicteres heptandra L.B.Sm.	101	-	-	100	-	-	-	-	-	-	-	-	-	1	X
Helicteres jamaicensis Lam.	2	-	-	-	-	1	-	-	-	-	-	1	-	-	-
Helicteres krapovickasii Cristóbal	10	-	-	10	-	-	-	-	-	-	-	-	-	-	X
Helicteres laciniosa Cristóbal	20	-	-	20	-	-	-	-	-	-	-	-	-	-	X
Helicteres lenta Mart.	7	-	-	7	-	-	-	-	-	-	-	-	-	-	X
Helicteres lhotzkyana (Schott & Endl.) K.Schum. var. *lhotzkyana*	167	-	15	152	-	-	-	-	-	-	-	-	-	-	X
Helicteres lhotzkyana var. *pubinervis* Kuntze	48	3	45	-	-	-	-	-	-	-	-	-	-	-	X
Helicteres longepedunculata K.Schum.	2	-	-	2	-	-	-	-	-	-	-	-	-	-	X
Helicteres macropetala A.Juss.	57	-	-	57	-	-	-	-	-	-	-	-	-	-	X
Helicteres muscosa Mart.	129	-	-	129	-	-	-	-	-	-	-	-	-	-	X
Helicteres ovata Lam.	143	-	-	143	-	-	-	-	-	-	-	-	-	-	X
Helicteres pentandra L.	99	-	10	59	-	-	-	20	2	6	-	1	-	1	X
Helicteres pilgeri R.E.Fr.	12	-	-	12	-	-	-	-	-	-	-	-	-	-	X
Helicteres pintonis Cristóbal	2	-	-	2	-	-	-	-	-	-	-	-	-	-	X
Helicteres rufipila Cristóbal	2	-	-	2	-	-	-	-	-	-	-	-	-	-	X
Helicteres sacarolha A.Juss.	420	-	1	419	-	-	-	-	-	-	-	-	-	-	X
Helicteres urupensis Leane	1	-	-	1	-	-	-	-	-	-	-	-	-	-	X
Helicteres vallsii Cristóbal	8	-	-	8	-	-	-	-	-	-	-	-	-	-	X
Helicteres velutina K.Schum.	218	-	-	218	-	-	-	-	-	-	-	-	-	-	X
Helicteres vuarame Mart.	22	-	-	22	-	-	-	-	-	-	-	-	-	-	X
Sterculioideae (33/32)	**1,116**	**0 (0/0)**	**110 (8/0)**	**489 (17/3)**	**0 (0/0)**	**27 (11/3)**	**167 (11/0)**	**41 (6/0)**	**40 (5/1)**	**185 (17/0)**	**0 (0/0)**	**11 (2/0)**	**0 (0/0)**	**54 (8/2)**	-
***Pterygota* Schott. & Endl. (3/3)**	**63**	**0 (0/0)**	**31 (1/0)**	**10 (1/0)**	**0 (0/0)**	**5 (1/0)**	**0 (0/0)**	**0 (0/0)**	**0 (0/0)**	**13 (1/0)**	**0 (0/0)**	**0 (0/0)**	**0 (0/0)**	**4 (1/0)**	X
Pterygota amazonica L.O.Williams	44	-	31	-	-	-	-	-	-	13	-	-	-	-	X
Pterygota brasiliensis Allemão	10	-	-	10	-	-	-	-	-	-	-	-	-	-	X
Pterygota colombiana Cuatrec.	9	-	-	-	-	5	-	-	-	-	-	-	-	4	X
***Sterculia* L. (30/29)**	**1,053**	**0 (0/0)**	**79 (7/0)**	**479 (16/3)**	**0 (0/0)**	**22 (10/3)**	**167 (11/0)**	**41 (5/0)**	**32 (4/1)**	**172 (16/0)**	**0 (0/0)**	**11 (2/0)**	**0 (0/0)**	**50 (7/2)**	-
Sterculia abbreviata E.L.Taylor ex Mondragón	7	-	-	-	-	-	-	-	-	-	-	-	-	7	-
Sterculia aerisperma Cuatrec.	8	-	-	-	-	8	-	-	-	-	-	-	-	-	X
Sterculia antioquia E.L.Taylor*	2	-	-	-	-	2	-	-	-	-	-	-	-	-	X

Taxon	All	AR	BO	BR	CH	CO	EC	GF	GY	PE	PY	SR	UR	VE	End
Sterculia apeibophylla Ducke	71	-	9	26	-	1	17	-	-	18	-	-	-	-	X
Sterculia apetala H.Karst.	64	-	24	-	-	1	12	-	-	24	-	-	-	3	X
Sterculia chicomendesii E.L.Taylor*	11	-	-	9	-	-	-	-	-	2	-	-	-	-	X
Sterculia colombiana Sprague	65	-	-	-	-	-	55	-	-	10	-	-	-	-	X
Sterculia corrugata Little	5	-	-	-	-	-	4	-	-	1	-	-	-	-	X
Sterculia duckei E.L.Taylor ex J.A.C.Silva & M.F.Silva	10	-	-	10	-	-	-	-	-	-	-	-	-	-	X
Sterculia excelsa Mart.	69	-	1	62	-	-	-	2	4	-	-	-	-	-	X
Sterculia frondosa Spruce ex K.Schum.	103	-	-	44	-	-	25	11	-	23	-	-	-	-	X
Sterculia guapayensis Cuatrec.	9	-	-	-	-	1	-	-	-	8	-	-	-	-	X
Sterculia guianensis Sandwith	6	-	-	-	-	-	-	-	6	-	-	-	-	-	X
Sterculia kayae P.E.Berry	17	-	-	-	-	2	-	1	-	5	-	-	-	9	X
Sterculia killipiana E.L.Taylor*	22	-	-	6	-	2	-	-	-	14	-	-	-	-	X
Sterculia lisae E.L.Taylor*	6	-	-	6	-	-	-	-	-	-	-	-	-	-	X
Sterculia multiovula E.L.Taylor*	6	-	-	1	-	-	-	-	-	-	-	-	-	5	X
Sterculia parviflora (Ducke) E.L.Taylor	19	-	-	19	-	-	-	-	-	-	-	-	-	-	X
Sterculia pendula Ducke	4	-	-	3	-	-	-	-	-	1	-	-	-	-	X
Sterculia peruviana (D.R.Simpson) E.L.Taylor ex Brako & Zarucchi	17	-	-	-	-	1	3	-	-	9	-	-	-	4	X
Sterculia pruriens (Aubl.) K.Schum.	98	-	-	31	-	-	2	20	13	9	-	6	-	17	X
Sterculia rebeccae E.L.Taylor*	22	-	3	2	-	-	9	-	-	8	-	-	-	-	X
Sterculia recordiana Standl.	2	-	-	-	-	2	-	-	-	-	-	-	-	-	X
Sterculia rugosa R.Br.	11	-	-	-	-	-	2	-	9	-	-	-	-	-	X
Sterculia speciosa K.Schum.	7	-	-	3	-	-	1	1	-	2	-	-	-	-	X
Sterculia steyermarkii E.L.Taylor ex Mondragón	5	-	-	-	-	-	-	-	-	-	-	-	-	5	X
Sterculia stipulifera Ducke	21	-	1	11	-	-	-	-	-	9	-	-	-	-	X
Sterculia striata A.St.-Hil. & Naudin	262	-	20	242	-	-	-	-	-	-	-	-	-	-	X
Sterculia tessmannii Mildbr.	93	-	21	4	-	2	37	-	-	29	-	-	-	-	X
Sterculia villifera Steud.	11	-	-	-	-	-	-	6	-	-	-	5	-	-	X
Total (271/231)	**14,528**	**524 (43/5)**	**749 (70/0)**	**10,828 (177/76)**	**0 (0/0)**	**235 (66/11)**	**618 (54/4)**	**137 (19/0)**	**272 (34/2)**	**800 (71/6)**	**27 (11/2)**	**53 (16/0)**	**3 (1/0)**	**282 (49/3)**	-

Chapter 2 *(Capítulo 2)*

Current plant disjunctions in South American open seasonally dry formations are a natural pattern with species sharing traits related to long dispersal abilities*

Disjunções atuais de angiospermas nas formações abertas sazonalmente secas da América do Sul são um padrão natural e a maioria das espécies compartilham atributos associados à dispersão a longa distância

Abstract

Aim: To investigate whether reported disjunct distributions across long distances (the peri-Amazonian pattern) are a natural pattern rather than a potential sampling bias artifact in plant species from open seasonally dry formations of South America. Furthermore, to test hypotheses on the causes of these distributions, especially to distinguish the role of relict distributions and long-distance dispersal at species level, based on their potential habitat and traits such as lifeform and dispersal syndrome.

Location: South America.

Methods: We use species data from classical works plus data from the Brazilian Flora 2020 Project to report novel disjunct species across non-woody angiosperms and to assess their traits. Moreover, we selected species from the cacao family (Malvaceae) as a study model to investigate the drivers of these disjunctions at species level. Specifically, we use a novel, updated database of species geographical distributions together with paleoclimatic reconstructions to model the distribution of selected disjunct species through time.

Results: Modeling approaches reveal that the observed disjunctions for selected species are likely to be a natural pattern rather than a sampling bias artifact. However, response to past climatic conditions varied across species of the model group, but no general pattern of past continuous distributions emerged. Furthermore, we found peri-Amazonian disjunctions in at least 29 more species from open seasonally dry vegetation across taxonomical groups of angiosperms, most of them non-woody taxa. The majority of these species showed characters related to long distance dispersal.

Main conclusions: peri-Amazonian disjunctions, so far mainly reported for animals and woody plants, are likely to be a natural pattern spread in several plant lineages. Species traits and distribution models suggest a long distance-dispersal scenario over another one where current disjunctions are the relict of a large continuous range in the past. Nevertheless, our results call for the need of more research at genetic level to understand the biogeography of open seasonally dry vegetation in South America, considering species with different dispersal abilities.

Key-words: climatic niche, distribution patterns, Malvaceae, Neotropics, paleoclimate range size, species distribution models.

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1. Introduction

Tropical South America is globally acknowledged for its high species richness and endemism levels of plants and animals (Antonelli & Sanmartín, 2011; Hughes et al., 2013; Ulloa-Ulloa et al., 2017; Antonelli et al., 2018; Zizka, 2019). With this background, the classification of current biodiversity patterns into "biomes", "bioregions" or "areas of endemism" can help to understand the evolutionary history of particular groups or vegetations (Noguera-Urbano, 2016; Morrone, 2018; Mucina, 2019).

In South America, assessments of biodiversity patterns and historical biogeography have focused on evergreen forests—the Amazonia and the Atlantic Forest (e.g. Carnaval & Moritz, 2008; Hoorn et al., 2010; Sobral-Souza et al., 2015; Colli-Silva & Pirani, 2019; Thode et al., 2019)—and also on Andean-related formations (e.g. Anthelme et al., 2014; Godoy-Bürki et al., 2014; Quintana et al., 2017). In contrast, studies of taxa from the savannas and dry forested formations of open/dry habitats are relatively scarce (Pennington et al., 2000; Werneck, 2011; Werneck et al., 2012; Azevedo et al., 2016).

If explicitly considered for continental-scale analyses, the open seasonally dry formations (henceforth "OSDFs") are mostly treated as "vicariant agents" or "mechanisms" for the evolution of forest biota, rather than as relevant factors for the evolution of their biodiversity in their own right (Silva & Bates, 2002; Werneck, 2011). This is problematic, as OSDFs also comprise a startling variety of heterogeneous vegetations, including grasslands, savannas, and semi-arid to dry semideciduous and deciduous forests (Rizzini, 1997; Pennington et al., 2006; Ribeiro et al., 2008). Currently, most area of OSDFs is part of coherent blocks through different portions of South America, forming a remarkable peri-Amazonian pattern, from northeastern Brazil until Paraguay and Argentina, and then surrounding the Amazonia (Figure 1;

Prado & Gibbs, 1993; Rizzini, 1997; Pennington et al., 2004; Werneck, 2011).

Disjunct distributions across distant OSDFs have been reported for different animal groups at genus and species level; for instance, insects (Morrone & Coscarón, 1996), birds (Ederhard & Bermingham, 2004), reptiles (Quijada-Mascareñas et al., 2007; Werneck et al., 2012; Azevedo et al., 2016) and mammals (Courtenay & Maffei, 2004). For plants, Prado & Gibbs (1993), Prado (2000) and Pennington et al. (2000) described a large set of woody species potentially disjunct into dry deciduous forests, based mainly on dot-map distributions and expert knowledge. These authors, however, were fully aware that their plant dot-maps are ought to be easily misinterpreted, ought to reveal a sampling bias artifact rather than a natural disjunct pattern instead.

Against this trend, recent increase in spatial information of plant distributions from the digitization of collection records (Lavoie, 2013; Schmidt-Lebuhn et al., 2013) and floral treatments (e.g. BFG, 2018) enable to identify reliable disjunctions across plant groups and to cross-validate these among different data sources. Likewise, niche modeling frameworks have enhanced the possibility to evaluate the potential habitat of a species, testing, for instance, the potential distribution of a poorly collected taxon that might occur between non collected spots of an area (Kramer-Schadt et al., 2013). Nevertheless, Prado & Gibbs (1993), Prado (2000) and Pennington et al. (2000) suggest that the reported disjunctions might reflect past floristic links of a once more continuous open/dry forest through the “dry diagonal” (i.e. the Chaco + Cerrado + Caatinga) that form today the OSDFs and connects peri-Andean and Venezuelan/Colombian open/dry habitats. In fact, this culminated with Prado (2000) recognizing a new phytogeographical unit: the Tropical Seasonal Forests Region.

In this sense, mirroring the dynamics of evergreen forests, OSDFs may have changed their shape and extent through time, tracking climatic fluctuations in the

Quaternary (Moritz et al., 2000; Werneck et al., 2011; Costa et al., 2017) or even back in the Tertiary (Pennington et al., 2004). Consequently, disjunct distribution of OSDF species might have repeatedly shifted between continuous large ranges and smaller isolated ranges where other vegetations might have occupied, due to a potential expansion of semiarid vegetation in the continent (Ab'Sáber, 1977; Werneck, 2011; Sobral-Souza et al., 2015).

In summary, likely past expansions and contractions of OSDFs following climatic fluctuations would favor a vicariance scenario explaining current disjunct distributions as relics of past widespread distributions (Figure 1B), while independent long distance dispersal events could also have taken place in different groups at different times (Figure 1C) (Prado & Gibbs, 1993; Pennington et al., 2004; Quijada-Mascareñas et al., 2007; Werneck et al., 2011). Evidences favoring one or the other hypothetic scenarios have been obtained by means of confident methods applied to several groups of organisms; for instance, Pennington et al. (2006) present some of the works with dated phylogenies and population genetic analyses already carried with plant groups.

Here, we select species from two subfamilies of the cacao group (Malvaceae) as models to identify disjunct distributions in the OSDF of South America (especially tropical dry deciduous forests, where species in these groups prevail) and to evaluate their responses to past climatic conditions. We base our results and modeling approaches on a novel, high quality database on species occurrences of the family (see Chapter 1), and we use additional data to identify disjunctions in other plant groups. Also, we employ large-scale species distribution data and a species modeling framework to test potential disjunct patterns in plants and to summarize and report new peri-Amazonian distributions in OSDFs. Specifically, we aim at testing three hypotheses:

1. *peri-Amazonian disjunctions are likely to be a natural pattern rather than a sampling bias artifact.* The selection of point occurrences of taxa for a modeling framework approach should reveal consistent disjunct sets, suggesting a natural spatial pattern rather than a sampling bias artifact.
2. *The observed [natural, if question 1 is corroborated] disjunctions in selected taxa at species level are consequence of their common responses to Pleistocenic climatic fluctuations.* If the observed [natural] disjunctions are relicts of larger continuous distributions during Quaternary climatic fluctuations (as suggested by most works), we expect different species to respond similarly to past climatic fluctuations.
3. *Reported disjunct species should not share common traits related to long distance dispersal abilities.* If these widely suggested disjunctions are likely to be a natural pattern but consequence of a past widespread range of the whole vegetation, we would not expect to find particular dispersal modes related to an alternative scenario of either past or on-going multiple long dispersal through OSDF fragments.

2. Methods

2.1. A focus on Malvaceae as model group

For a more in depth study of the peri-Amazonian disjunctions, we selected species from the cacao group (Byttnerioideae, Helicteroideae and Sterculioideae) from the Malvaceae. The group has an expressive presence in OSDFs reflected in an updated occurrence database with high quality distribution information (Chapter 1). All entries in this database have been reviewed manually, including verification of common errors (Maldonado et al., 2015, Zizka et al., 2019), literature survey, revisiting herbarium collections and geo-referencing procedures (see Chapter 1 for more detail on the database).

We selected six species in five genera with disjunct distributions through South American OSDFs, as previously reported in taxonomical works for the groups (Cristóbal, 1960; 1976; 2001; Goldberg, 1967; Saunders (1995): *Ayenia tomentosa* L.; *Byttneria filipes* Mart. ex K.Schum; *Byttneria scabra* L.; *Helicteres heptandra* L.B.Sm., *Melochia graminifolia* A.St.-Hil., and *Waltheria albicans* Turcz. All species are shrubs to herbs with small flowers (except for *H. heptandra*, with tubular flowers up to 3 cm length) and dry indehiscent fruits bearing few, small seeds (Cristóbal, 1960; 1976; 2001). All species are disjunct through at least two different fragments of South American OSDFs (see Figure 1). Data for all occurrence points used in this study can be found in Supporting Information (Appendix S1).

2.2. Species distribution modeling

To check hypotheses 1 and 2 of this work—disjunctions are likely a natural pattern and, if so, natural disjunctions are consequence of common responses to past climatic conditions—we used a species distribution modeling framework to assess current and past potential distributions. We ran all further analyses in R Environment (R Core Team, 2018). A base script of these analyses can be found in Supporting Information (Appendix S2).

First, we downloaded bioclimatic variables for six time-slices from the Pliocene to the present time available in the PaleoClim project (Dolan et al., 2015; Hill, 2015; Karger et al., 2017; Brown et al., 2018): (1) Present (0 kybp—kiloyears before present); (2) Late Pleistocene (14.7-12.9 kybp), (3) Last Glacial Maximum (LGM, c. 22 kybp); (4) Last Inter Glacial period (LIG, c. 130 kybp), (5) Calabrian Pleistocene (c. 785 kybp) and (6) mid-Pliocene Warm period (3264-3025 kybp). We performed a VIF analysis

(Variance Inflation Factor) to remove redundant variables, keeping only variables whose multicollinearity scores were greater than > 0.7, by using the “car” package v. 3.0—6 (Fox et al., 2019). Following this procedure, we retained the following variables: (1) precipitation seasonality, (2) mean temperature of the wettest quarter and (3) mean temperature of the driest quarter.

We used the “sdm” package v. 1.0—81 (Naimi & Araujo, 2016) to model species distributions. We chose three different modeling algorithms (random forest model (rf), generalized additive models (gam) and bioclim), performing 5 runs and 5 k-folds cross-validation replications for each model.

In addition to the individual species distribution models, we projected suitable areas of OSDFs themselves through past time. To do so, we generated 1,000 random points within the current delimitations of OSDFs (based on Olson et al. (2001) delimitations—see also Figure 1) using the “sp” package v. 1.3-2 (Pebesma et al., 2018). We combined the savannas, Chaco and dry deciduous forests into a single group—the OSDFs—following the grouping of Antonelli et al. (2018), to simplify the complexity of open/dry habitats. We did that because species are widespread through these vegetations, and we were primarily interested to test the disjunct patterns of species—not the OSDFs—and their overall response to past climatic conditions. Thus, by grouping all open/dry biomes, we avoided unnecessary complexity when testing and discussing the main hypotheses of this work caused by the currently unclear and unstable nomenclature status of OSDFs (Werneck, 2011). A wider interpretation of the seasonally deciduous forests was likewise adopted by previous authors, including formations as diverse as tall forests on moister sites to cactus scrub on the driest, and the relationships between neotropical savannas and seasonally dry forests are considered as “notoriously complex” according to authors as Pennington et al. (2006).

Then, based on these random points plus the environmental layers, we projected the suitable area for OSDFs in all past time slices described above, as we did for the six selected species. We replicated that 10 times for each time slice, and historical projections were later used as background for plotting the projected extent of each species. We chose as cut-off thresholds for binary layers values at which the sum of sensitivity (true positive prediction rates) and specificity (true-negative prediction rates) scores per species were the highest.

Finally, we considered the Area Under the Curve (AUC) and the True Skill Statistic (TSS) scores for modeling evaluation. These indices compare the performance of the niche modeling considering an alternative null scenario (Philips & Dudík, 2008). Therefore, values closer to 1.0 indicates a better performance than a random scenario and should reflect better model predictions than values closer to 0.5—which would indicate that the modeling reflects exactly what the random scenario does (Phillips & Dudík, 2008).

2.3. Dispersal-related traits in other disjunct species

Prado & Gibbs (1993) and Pennington et al. (2000, 2004) summarize in their works a robust set of potentially disjunct species from groups of plants other than Malvaceae. As they only consider woody taxa, we generated a new dataset based on the Brazilian Flora 2020 Project database (henceforth "BFG database"), in order to get a more comprehensive approach including disjunct species with other lifeforms too. The BFG database has information on habitat, lifeform and taxonomy of algae, plant and fungi species of Brazil (BFG, 2018). Moreover, all information for a species is filed and checked by experts in taxonomy. Therefore, albeit still being under construction, BFG represents the most robust and voluminous datasets regarding the largest country of South America (BFG, 2018).

To identify novel species with disjunct OSDF distributions in BFG, we downloaded all relevant information available from `http://www.floradobrasil.jbrj.gov.br/` in June 2019. We selected only species that had a set of specific criteria which would potentially indicate they have a disjunct pattern of our interest. We selected only: (1) flowering plants native to Brazil, at species level; (2) correct names, letting aside names with uncertain nomenclatural or taxonomical status; (3) non-endemic species to Brazil—which was a proxy to keep only potentially disjunctions through discontinuous areas in the Caribbean coasts of Venezuela or Colombia; (4) only species assigned to occur in the following combination of phytogeographic domains: (a) Caatinga + Pantanal, (b) Pantanal only, (c) Caatinga only, or (d) Cerrado only. We did not consider species assigned to occur in the Cerrado + Caatinga or Cerrado + Caatinga + Pantanal domains to remove species with a potentially wide distribution. Lastly, we kept (5) species assigned to occur in OSDF vegetations, i.e. either in the following vegetation types according to the BFG: (a) Caatinga (*stricto sensu*), (b) high altitude grasslands; (c) grasslands; (d) "carrasco" vegetation; (e) Cerrado (*lato sensu*); and (e) seasonally deciduous forests. Data for all selected species can be found in Supporting Information (Table S1).

After this filtering, we manually checked the distribution of all species, using the information on the Global Biodiversity Information Facility (`www.gbif.org`), one of the largest existent biodiversity repositories (Robertson et al., 2014). From that, we manually evaluated if the distribution of each species was consistently disjunct, excluding those whose distribution records indicated a visually continuous distribution within OSDFs. All distribution maps with points of the selected species retrieved from the BFG can be found in Figure S1 in the Supporting Information. We acknowledge, that this procedure might not identify all disjointly species, but we believe it is a fair proxy to verify whether the pattern occurs across distinct taxonomical groups.

Finally, to test hypothesis 3—disjunct species share common traits related to long distance dispersal abilities—we gathered these novel potential disjunct species with the disjunct taxa reported by Prado & Gibbs (1993) and Pennington et al. (2000, 2004) based on dot-map distributions, and looked for information in the literature on dispersal syndromes for all species and lifeforms. This was done by means of an extensive literature survey and consults of specialists in taxonomy, and so a database of potentially disjunct species with main reported dispersal syndromes was elaborated. All information of consulted literature is presented in Table S1 in Supporting Information.

3. Results

3.1. Disjunctions in Malvaceae and Tertiary and Quaternary climatic fluctuations

Current predicted areas exhibited a consistently disjunct pattern for all species. All six species have recovered a potential fragmented habitat through at least two fragments of OSDFs (Figures 2 and 3). Conversely, modeled background distribution of the OSDFs did not varied significantly through time. Figures 2 and 3 show the projected distribution of the six study species for three selected time slices: the present, LGM and mid-Pliocene, were we found major changes through time (see Figure S1 in the Supporting Information for all time slices).

Suitable habitats varied differently for all species, whereas the total area predicted for the OSDFs remained almost stable through time (Figure 4), suggesting that the different species responded differently to past climatic fluctuations. Full information on the models and binary raster files can be found in Supporting Information for all time slices (Appendices S5 and S6). In general, we recovered good fittings for the models, with high AUC and TSS values (always greater than 0.9 and

0.7, respectively). Check Appendix S7 in Supporting Information for a full list of these calculations for all scenarios.

3.2. peri-Amazonian disjunctions and dispersal traits

When considering the BFG database, which includes distribution patterns for all lifeforms, we found 64 species with a potential similar disjunct pattern (Table S1 in Supporting Information). However, after manually checking their distribution data in GBIF, 29 species in 27 genera and 19 families were retained because their known records indicated a remarkably disjunct pattern in different OSDFs of South America (Table 1). Records retrieved from GBIF and maps with records for these species can be found in Table S1 in Supporting Information. For this database, there was a prevalence of both trees and herbs for different families, but Leguminosae, Poaceae and Euphorbiaceae have more species (Table 1). Furthermore, different dispersal syndromes were also found for distinct groups, with a particular presence of anemochory—11 species—followed by zoochory—7 species—and autochory—6 species (Table 1).

Woody disjunct species mentioned in Prado & Gibbs (1993) and Pennington et al. (2000, 2004) also revealed a scenario where the main dispersal syndrome is anemochory, followed by bird-mediated zoochory (Table 1). Lastly, when considering all data from our selected taxa of Malvaceae (Chapter 1), plus the BFG database and the classical taxonomical monographs, anemochory is the most mentioned syndrome for all lifeforms (32 species, or 45% of the total mentions), followed by bird-mediated zoochory (12 species, 17%), zoochory mediated by other animals (10 species, 11%) and hydrochory (5 species, 7%) (Table 1).

4. Discussion

Modeled species of Malvaceae selected from a highly accurate distribution database (Chapter 1) revealed that current disjunctions are likely to be a natural pattern rather than a continuous pattern potentially skewed by lack of collections. However, despite being a natural pattern, past paleoclimatic reconstructions revealed an inconsistent past distribution scenario, and species probably did not respond in similar ways to past climatic conditions.

Moreover, we reported other species with a potential disjunct pattern through South American OSDFs, supplementing the woody taxa list provided by previous works dealing with species from dry deciduous forests (Prado & Gibbs, 1993; Pennington et al., 2000, 2004). When looking for traits related to long-dispersal abilities, we found a prevalence of wind or bird mediated dispersal among different lifeforms, which can suggest a scenario where multiple long dispersal events may have taken place through OSDFs fragments as we discuss below.

4.1. Disjunctions as natural patterns

Previous biogeographical works have reported a significative variety of woody plants from dry deciduous forests with a potential disjunct pattern (Prado & Gibbs, 1993; Prado, 2000; Pennington et al., 2000, 2004). Nevertheless, these authors also recognized the possibility of some of these patterns be a false disjunction, consequence of a possible facile interpretation of the dot-map distributions or due to lack of collections in certain areas. In our survey, we avoided to run that risk and went deeper by testing if the observed disjunctions were in fact consistent disjunctions, and then we could properly proceed to model for past climatic conditions.

We feel confident that the distribution of the Malvaceae species in our study are truly fragmented because (1) our modeling results suggest no strong connections among potential habitats in current distributions—which otherwise would suggest a lack of collections between OSDF fragments; and because (2) while large areas of South America are indeed scarcely sampled for the Malvaceae (Chapter 1), the areas of low sampling do not generally overlap with the gaps relevant for the peri-Amazonian disjunctions (Chapter 1; see also Figure S2 in Supporting Information). In here, we here brought additional examples from herbs and shrubs (Table 1) to the vast literature reports of disjunctions in other groups of animals (e.g. Quijada-Mascareñas et al., 2007; Linares-Palomino et al., 2011; Werneck et al., 2011) and woody plants (Prado & Gibbs, 1993; Pennington et al., 2000, 2004, 2006). Such and increased and accurate species records, associated to our niche modeling approach, provide robust evidences that strengthen the disjunct pattern firstly described by authors in past decades that did not use specific and actual tools to properly verify it.

4.2. Species long dispersal abilities

Mostly, woody species of Table 1 have winged fruits or seeds which are pre-dispersed by birds, e.g. Anacardiaceae—*Astronium, Loxopterygium* spp., *Schinopsis* (Griz & Machado, 2001; Leite, 2002; Burnham & Carranco, 2004; Villaseñor-Sánchez et al., 2010), Apocynaceae—*Aspidosperma* (Griz & Machado, 2001; Vieira et al., 2008), Bignoniaceae—*Tabebuia* (Vieira et al., 2008), Leguminosae—*Amburana*, *Anadenanthera* (Vieira et al., 2008), Rhamnaceae—*Zizyphus* (Griz & Machado, 2001; Alves, 2008). These traits are likely related to long dispersal abilities (see Table S1 in Supporting Information for a full list). Similarly, when considering shrubby-herbaceous strata in the analysis, the grass family, Poaceae, was the second most common family retrieved from the BFG database. Poaceae is long known for having many species with high dispersal capabilities, which likely facilitated colonization and their further persistence and fragmentation in OSDFs (Cain et al., 2000; Linder et al., 2018).

For the Malvaceae, long dispersal abilities are not that obvious, given the morphology of fruits of most species, for instance in *Ayenia* and *Byttneria* (Whitlock & Hale, 2011), but also in other Byttnerioideae (Bayer & Kubitzki, 2005). All genera considered in our survey have dry deciduous fruits, with no specific structure that would intuitively attract a bird, nor that it is likely to be wind dispersed (Cristóbal, 1976; Whitlock & Hale, 2011). However, they often bear spines or hooks that can stick to bird feathers or mammal furs (Whitlock & Hale, 2011). This can also be enhanced to the high establishment rates of these species, where, after a rather rare dispersal event, they can rapidly colonize a new area (Whitlock & Hale, 2011).

Likewise, it is notable the presence of inflated or, in case of *Helicteres*, twisted dry fruits (Cristóbal, 2001), suggesting abiotic rather than biotic dispersal (Griz & Machado, 2001). Although there are reports of limited seed dispersal in *Helicteres* (Franceschinelli & Kesseli, 1998; Franceschinelli & Bawa, 2000), this genus is also known for having high turnover and colonization rates, with populations lasting one to two generations in a site (Franceschinelli & Kesseli, 1998; Franceschinelli & Bawa, 2000), and then rapidly expanding its distribution range through suitable habitats, similarly to what we described before for Byttnerioideae. As a matter of fact, in Malvaceae *sensu lato* there are lots of other examples of abiotic dispersal (Bayer & Kubitzki, 2005; Costa et al., 2015), especially for species from OSDFs worldwide (Griz & Machado, 2001). Some examples are genera of Bombacoideae or Gossypeae, with their remarkable kapok fruits whose seeds dispersal are wind-mediated (Stephens, 1958; Greene & Quesada, 2005).

Intuitively, these traits we presented are more associated to long dispersal events. This is, of course, a complex on-going debate, because OSDFs are a mosaic of different vegetations, bearing both dry deciduous forests (where most of disjunct species seem to prevail), but also the Venezuelan and Colombian savannas and forests and open areas of the South American “dry diagonal” (e.g. Prado & Gibbs, 1993; Prado 2000; Pennington et al. 2006; Whitlock et al., 2011). Even inside larger biomes, minor patches of different vegetations compose a mosaic where different species might occur. Such a mosaic may have diminished the distance of dispersal among areas, providing a “stepping-stone” route for species dispersal (Pennington et al., 2006; Olmstead, 2012; Hughes et al., 2012). Lastly, we only bring one evidence of trait related to long distance dispersal—the main dispersal mode—which is one important component of a still more complex set of traits and attributes that can be related to dispersal ability of a species (Pakeman & Quested, 2007).

4.3. Possible past scenarios for disjunctions

As disjunctions in OSDFs species are a natural spatial pattern, forested formations may have played an important role as environmental barriers, keeping species from open/dry habitats fragmented at least since the LGM (Werneck et al., 2011; Costa et al., 2017). An analogous situation can be traced with the dynamics of South American tropical rainforests. Current disjunctions of related lineages—i.e. one from the Atlantic Forest and another one from the Amazonia—, suggests at least two main past corridors through these forests (Bigarella et al., 1975; Costa, 2003; Ledo & Colli, 2017; Thode et al., 2019).

Intuitively, Quaternary dynamics of forested formations might have led to the observed disjunctions of forested species, separating relative lineages vicariance (Ledo & Colli, 2017; Thode et al., 2019). But when thinking on the natural history of species related to OSDFs, disjunction events would have happened even more recently than the disruption of South American rainforests (Werneck, 2011; Costa et al., 2017). In this regard, we consider two explanatory scenarios for species distribution: (1) multiple independent long-dispersal events; or (2) a shared history for all regional biota, where current observed disjunctions would represent relics of ancient widespread distributions—implying in similar responses to past climatic fluctuations.

We believe the scenario (1)—multiple independent on-going dispersal events—is more likely given our results, and it reflects diversification patterns described by Pennington et al. (2004) for dry deciduous forests. Accordingly, we would expect (i) different responses to past climatic conditions (alternative hypothesis 2 of this work)—which otherwise would indicate relics of past widespread distributions; and (ii) most taxa exhibiting high dispersal ability traits (hypothesis 3). Both conditions accord with our results, as (i) the distribution and extent of historical suitable areas for the modeled species varied differently through time, and thus different species responded differently to past climatic fluctuations and (ii) we found a prevalence of dispersal traits related to long dispersal in different groups and lifeforms (see section 4.2). This is not supported by similar works using distribution modeling framework using biome data (Werneck et al., 2011; 2012), although goes along with studies that use species occurrence rather than random samples of biomes as modeling inputs (Colinvaux et al., 2000; Collevatti et al., 2012).

An alternative scenario suggested by works such as Quijada-Masceñas et al. (2007) is somehow against our results too, except for one species in our work (*M. graminifolia*, see Figure 3e and 3h). Such scenario of an corridor of open/dry vegetations in the middle of the Amazonia Basin is not sustained by current palynological evidence, as described by Pennington et al. (2006). During the LGM, they suggest a partial expansion of savannic vegetations during the LGM through the Amazonian peripheries rather than in its central. Nevertheless, although such expansion would decrease the dispersal distances between open/dry areas, it would be limited for some regions (Pennington et al., 2006), then long-distance dispersal should be invoked by the areas in which Quijada-Mascareñas et al. (2007) partially base its proposed past corridor.

We believe our study contributes to this debate by bringing new examples of disjunct OSDF taxa (especially non-woody species), not only considering dot-map distributions but also potential habitats towards looking for past connections of species distributions. Additionally, there is a plenty scope to investigate the genetic structure of disjunct populations, by means of molecular population genetics, as previously claimed by Pennington et al. (2006). Published studies are scarce, and, for plants, somehow inconclusive. Naciri et al. (2006) for instance observed different differentiation events when comparing the populational structure of two equally disjunct species in dry deciduous forests. In this work, they demonstrate the potential of molecular populational studies on distinguishing vicariance and dispersal events in infraspecific levels, but the question if the main drivers for the disjunctions are recent dispersal events whether than relics of past connected areas remains open.

Such phylogeographical data, when associated to different lifeforms and dispersal modes, would certainly contribute to elucidate how and when species might have dispersed through that likely fragmented scenario. There are efforts towards that for animals already (Quijada-Mascareñas et al., 2007; Linares-Palomino et al., 2011) and, to a less extent, for woody plants (Quintana et al., 2017); but it would be interesting to consider the usually neglected shrubby-herbaceous component, using, for instance the Malvaceae taxa as study case. As a very representative family in open/dry habitats, diverse in terms of flower and fruit morphology, lifeforms and dispersal syndromes, this family constitute a good model to test questions related to the natural history of lineages related to OSDFs.

5. Conclusion

Independent data sources support reported peri-Amazonian disjunctions of plant species from open seasonally dry formations, suggesting that they represent a natural pattern and not an artefact of sampling effort (corroborating hypothesis 1). We found peri-Amazonian disjunctions in distantly related taxa of woody angiosperms and report additional non-woody species with similar pattern. For the past scenario, we did neither find a uniform response of the study species to past climate dynamics, nor a common pattern of past widespread distributions in these species (rejecting hypothesis 2), suggesting a more complex panorama of historical species distribution which is likely not only explained by bioclimatic variables. In contrast most species showing disjunct distributions displayed some type of trait facilitating long distance dispersal (providing a weak support for hypothesis 3).

Our results call for more detailed genetic and functional studies of the identified and discussed disjunct species, in order to achieve a better understanding of their recent population history and further elucidating the processes that generated and still maintain the current peri-Amazonian disjunctions. In general, open seasonally dry formations warrant biogeographical and population genetic research beyond considering them as vicariant agents for rainforest taxa.

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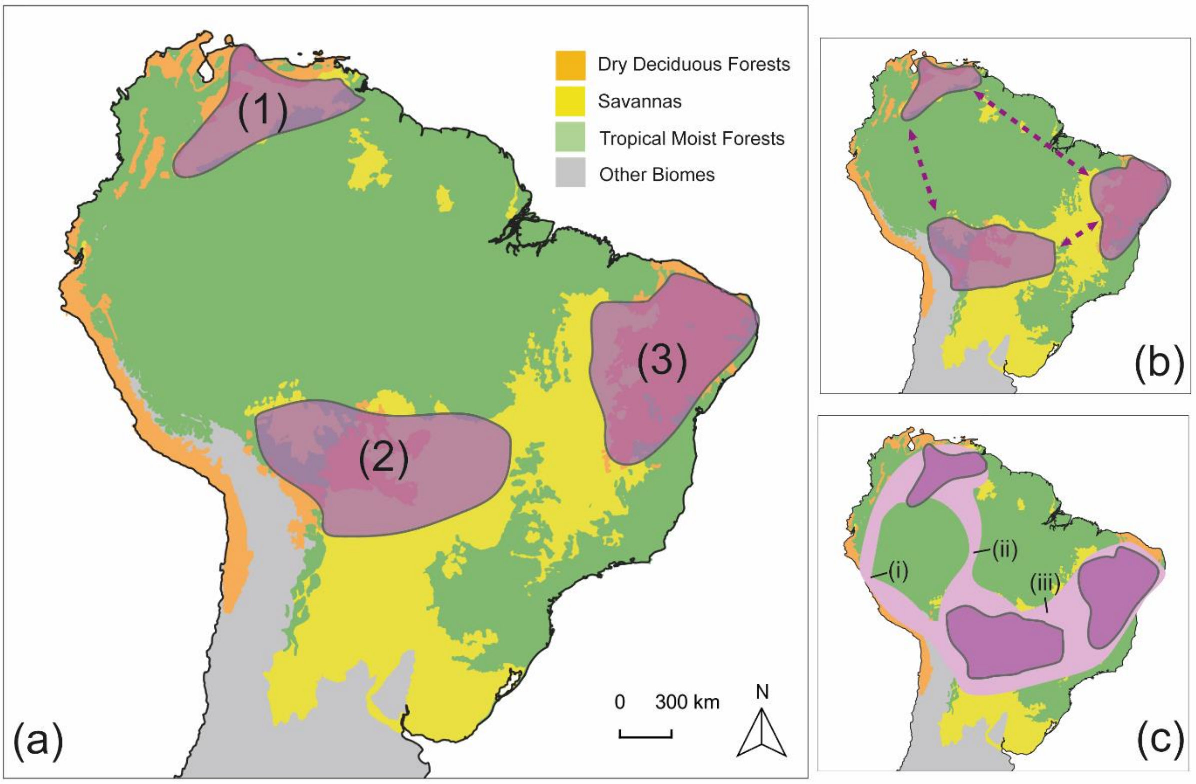

Figure 1. Open seasonally dry formations (OSDFs) across South America and main hypothetic scenarios for the origin of current disjunct species distributions. (a) Area of OSDFs with schematic examples of some of the "peri-Amazonian disjunctions" observed for plants in this study: (1) Caribbean open/dry coasts of northern Colombia and Venezuela, (2) Dry deciduous forests and marginal savannas of center-western South America, and (3) the Brazilian Caatinga. (b) Multiple-long dispersal scenario between these fragments, indicated by purple dashes. (c) Vicariance scenario, depicting possible past dry corridors connecting OSDTs, which could have allowed widespread species distribution, namely (i) a peri-Andean corridor; (ii) a corridor within the central Amazon basin (see Quijada-Mascareñas et al., 2007) and (iii) an alternative continuous distribution of species through Central Brazilian OSDFs, corresponding to the lack of collections between the areas (2) and (3). Delimitations based on Olson et al. (2001), Pennington et al. (2000, 2004) and Werneck (2011).

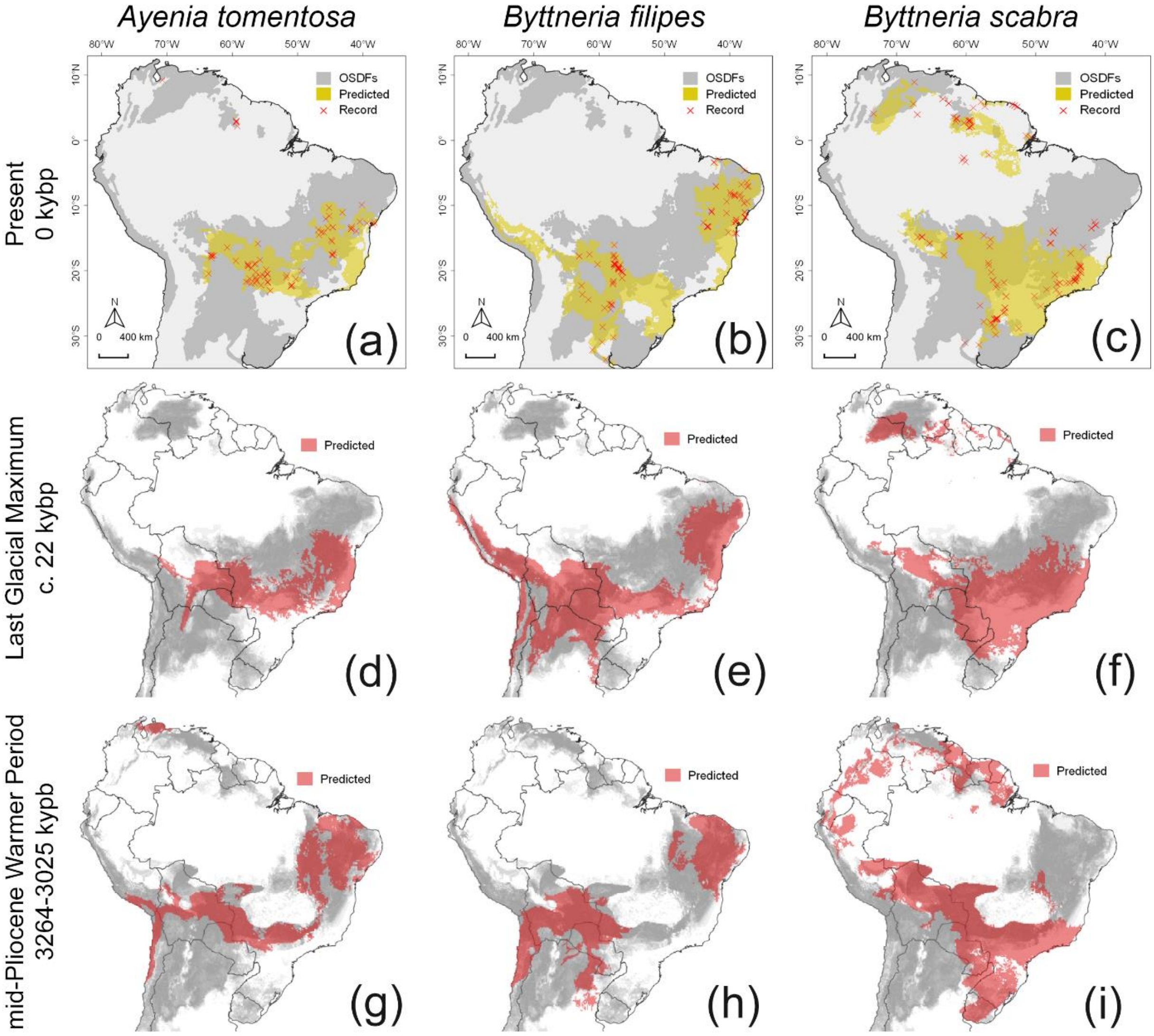

Figure 2. Model projections for *A. tomentosa*, *B. filipes* and *B. scabra* in selected past and present time slices. Grey shadings correspond to South American OSDFs. Maps **a-c:** present-time distribution for each species; yellow areas show modeling projections for the present period, with occurrence records marked as red crosses. Maps **d-i** are scaled based on the minimum and maximum model suitability values for each case. Files for all species and time slices can be found in Supporting Information (Appendix S6).

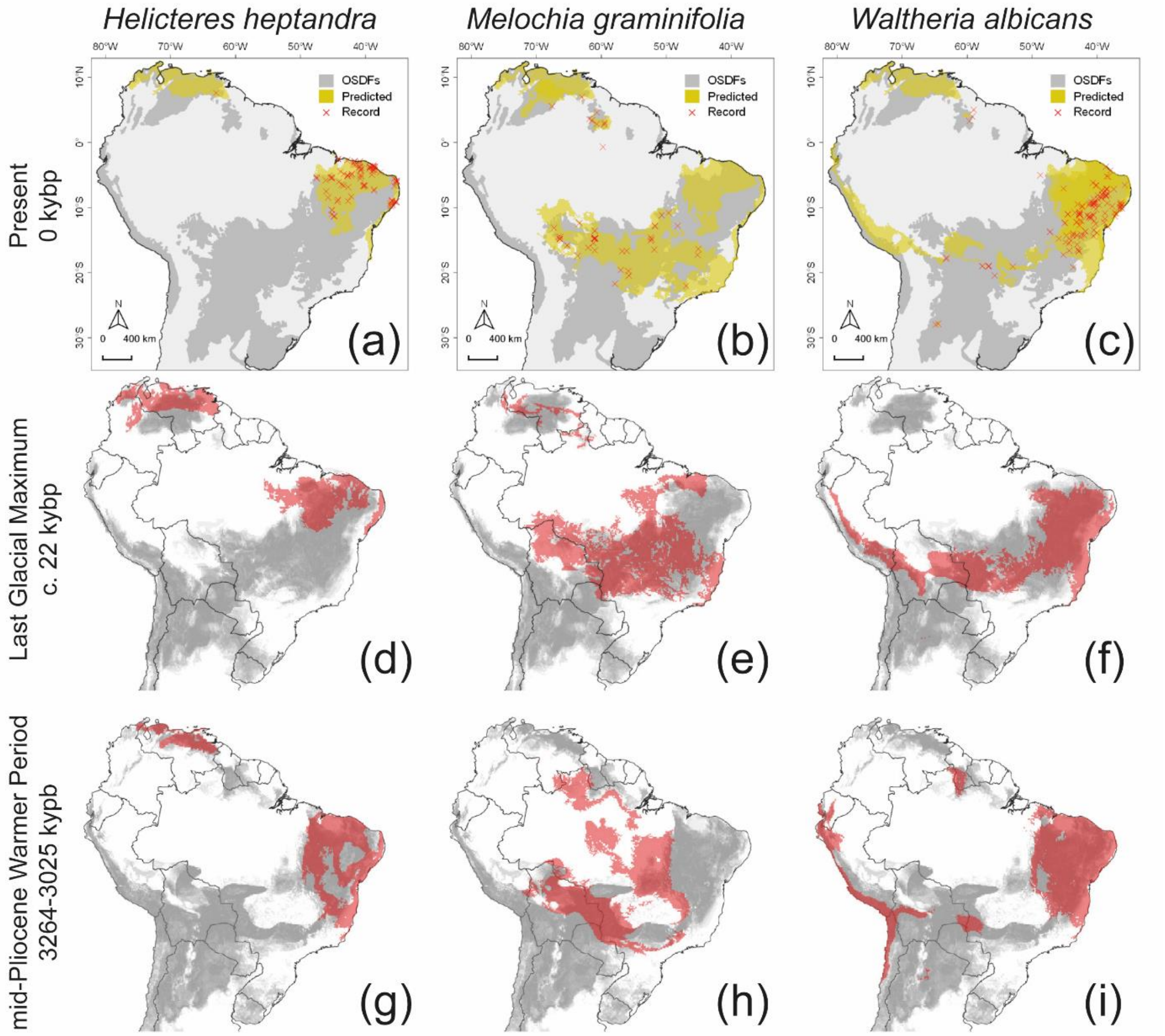

Figure 3. Model projections for *H. heptandra*, *M. graminifolia* and *W. albicans* in selected time slices. Grey shading corresponds to South American OSDFs. Maps **a-c**: present-time distribution for each species; yellow areas show modeling projections for the present period, with occurrence records marked as red crosses. Maps **d-i**: based on the minimum and maximum model suitability values for each case. Files for all species and time slices can be found in Supporting Information (Appendix S6).

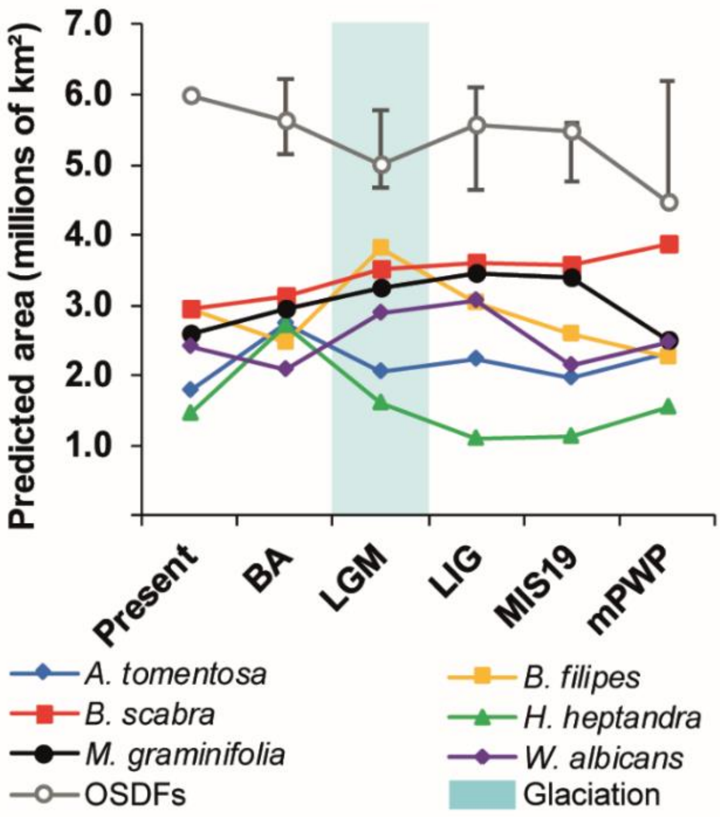

Figure 4. Total predicted area for the six selected species of Malvaceae and for the background scenario of the OSDFs. For the OSDF past projections, points indicate median values for 10 replicates and bar errors indicate minimum and maximum variation. Current = present time. BA = Late Pleistocene; LGM = Last Glacial Maximum; LIG = Last Inter Glacial; MIS19 = Marine Isotope Stage 19 in the Pleistocene (Calabrian); mPWP = mid-Pliocene Warm period, Late Pliocene. Blue background indicates a dry glacial period.

Table 1. Summary of the main distribution and traits of disjunct species, considering the selected Malvaceae for the modeling approach, as well as alternative independent databases: Brazilian Flora 2020 database and checking literature for woody (tree) species only (namely Prado & Gibbs (1993) and Pennington et al. (2000, 2004) dot-map distributions). Distribution within the fragments (1) to (3) according more or less to the established in Fig. 1 of this manuscript. Lifeforms: S = shrub/subshrub; H = herb; T = tree. Main dispersal syndromes: An = anemochory; ZoB = zoochory (bird-mediated); ZoO = zoochory (mediated by other animals); Hy = hydrochory; Au = autochory; ND = no data found. Dispersal syndromes were summarized according to our literature survey and specialists consulted. We list literature preferentially for the species listed, but if we found no citation of dispersal mode for the species we looked for information for relative species of the same genus; if we till found no information for the genus, we filled with "ND". All information and references for all sources can be found in Table S1 in Supporting Information.

Species	**Family**	**Fragments (Fig. 1)**			**Lifeform**	**Main dispersal syndrome**					
		(1)	**(2)**	**(3)**		**An**	**ZoB**	**ZoO**	**Hy**	**Au**	**ND**
Selected Malvaceae species for modeling (Chapter 1 database)											
Ayenia tomentosa L.	Malvaceae	X	X	X	S/H					X	
Byttneria filipes Mart. ex K.Schum.	Malvaceae		X	X	S/H					X	
Byttneria scabra L.	Malvaceae	X	X		S/H					X	
Helicteres heptandra L.B.Sm.	Malvaceae	X		X	S/H	X				X	
Melochia graminifolia A.St.-Hil.	Malvaceae	X	X		S/H					X	
Waltheria albicans Turcz.	Malvaceae	X	X	X	S/H					X	
Main dispersal syndrome (all species above)						**1**	**0**	**0**	**0**	**6**	**0**
Species from the BFG database											
Dicliptera ciliaris Juss.	Acanthaceae	X		X	S					X	
Annona spinescens Mart.	Annonaceae		X	X	T		X	X			
Erechtites missionum Malme	Compositae		X	X	S	X					
Fleischmannia prasiifolia (Griseb.) R.M.King & H.Rob.	Compositae		X	X	H	X					
Cordia glazioviana (Taub.) Gottschling & J.S.Mill.	Boraginaceae		X	X	T	X					
Lobelia fastigiata Kunth	Campanulaceae	X	X		H						X
Physostemon lanceolatum Mart. & Zucc.	Cleomaceae		X	X	H					X	

Species	Family	Fragments (Fig. 1)			Lifeform	Main dispersal syndrome					
		(1)	**(2)**	**(3)**		**An**	**ZoB**	**ZoO**	**Hy**	**Au**	**ND**
Rhynchospora curvula Griseb.	Cyperaceae	X		X	H	X					
Paepalanthus sessiliflorus Mart. ex Körn.	Eriocaulaceae	X		X	H	X					
Gymnanthes boticario Esser, M. F. A. Lucena & M. Alves	Euphorbiaceae		X	X	S/T					X	
Sebastiania larensis Croizat & Tamayo	Euphorbiaceae	X		X	S/T					X	
Aeschynomene rostrata Benth.	Leguminosae	X		X	S/H				X		
Aeschynomene scabra G.Don	Leguminosae	X	X	X	S/H				X		
Prosopis ruscifolia Griseb.	Leguminosae		X	X	T		X		X		
Senna gardneri (Benth.) H.S.Irwin & Barneby	Leguminosae	X		X	S/T					X	
Pusillanthus pubescens (Rizzini) Caires	Loranthaceae	X		X	H		X	X			
Pseudabutilon virgatum (Cav.) Fryxell	Malvaceae		X	X	S					X	
Phyllanthus chacoensis Morong	Phyllanthaceae		X	X	T		X	X			
Savia sessiliflora (Sw.) Willd.	Phyllanthaceae		X	X	T		X	X			
Bouteloua aristidoides (Kunth) Griseb.	Poaceae	X	X	X	H	X					
Digitaria aequatoriensis (Hitchc.) Henrard	Poaceae	X		X	H	X					
Digitaria tenuis (Nees) Henrard	Poaceae	X		X	H	X					
Enteropogon mollis (Nees) Clayton	Poaceae	X		X	H	X					
Pappophorum krapovickasii Roseng.	Poaceae		X	X	H	X					
Acanthocladus dichromus (Steud.) J.F.B.Pastore	Polygalaceae		X	X	T		X	X			
Ruprechtia apetala Wedd.	Polygonaceae		X	X	T	X					
Ziziphus guaranitica Malme	Rhamnaceae		X	X	S/T		X				
Zanthoxylum syncarpum Tul.	Rutaceae	X		X	T			X			
Kallstroemia tribuloides (Mart.) Steud.	Zygophyllaceae	X	X	X	S						X
Total mentions of dispersal syndrome (all species above)						**11**	**7**	**6**	**3**	**6**	**2**
Woody species mentioned in Prado & Gibbs (1993) and/or Pennington et al. (2000)											
Amburana cearensis (Allemão) A.C.Sm.	Leguminosae		X	X	T	X					
Myracrodruon urundeuva Allemão	Anacardiaceae		X	X	T	X					

Species	Family	Fragments (Fig. 1)			Lifeform	Main dispersal syndrome					
		(1)	**(2)**	**(3)**		**An**	**ZoB**	**ZoO**	**Hy**	**Au**	**ND**
Enterolobium contortisiliquum (Vell.) Morong	Leguminosae	X	X	X	T			X			
Astronium fraxinifolium Schott	Anacardiaceae	X	X	X	T	X	X				
Schinopsis brasiliensis Engl.	Anacardiaceae		X	X	T	X					
Aspidosperma cuspa (Kunth) S.F.Blake	Apocynaceae	X	X	X	T	X					
Aspidosperma discolor A.DC.	Apocynaceae	X		X	T	X					
Aspidosperma polyneuron Müll.Arg.	Apocynaceae	X	X	X	T	X					
Aspidosperma pyrifolium Mart. & Zucc.	Apocynaceae		X	X	T	X					
Aspidosperma riedelii Müll.Arg.	Apocynaceae		X	X	T	X					
Tabebuia aurea (Silva Manso) Benth. & Hook.f. ex S.Moore	Bignoniaceae	X	X	X	T	X					
Tabebuia caraiba (Mart.) Bureau	Bignoniaceae	X	X	X	T	X					
Tabebuia impetiginosa (Mart. ex DC.) Standl.	Bignoniaceae	X	X	X	T	X					
Commiphora leptophloeos (Mart.) J.B.Gillett	Burseraceae	X	X	X	T		X	X			
Celtis pubescens (Kunth) Spreng.	Cannabaceae	X	X	X	T		X				
Carica quercifolia (A. St.-Hil.) Hieron.	Caricaceae		X	X	T	X	X				
Albizia polyantha (Spreng.) G.P.Lewis	Leguminosae		X	X	T						X
Geoffroea spinosa Jacq.	Leguminosae	X	X	X	T			X	X		
Geoffroea striata (Willd.) Morong	Leguminosae	X	X	X	T			X	X		
Ziziphus joazeiro Mart.	Rhamnaceae		X	X	T		X				
Phyllostylon brasiliense Capan. ex Benth. & Hook.f.	Ulmaceae	X		X	T	X					
Phyllostylon rhamnoides (Poiss.) Taub.	Ulmaceae	X		X	T	X					
Total mentions of dispersal syndrome (all species above)						**15**	**5**	**4**	**2**	**0**	**1**
Total mentions of dispersal syndrome (all three sources)						**30**	**12**	**10**	**5**	**11**	**3**

Chapter 3 *(Capítulo 3)*

Cacao relatives reveal a controversial scenario of species coverage in South American protected areas*

O grupo do cacau revela efeitos de viés de documentação na avaliação e representatividade de espécies em unidades de conservação da América do Sul

Abstract

Biodiversity databases are the main frontline in assessing biogeographical patterns, whilst several subjects on plant diversity and threat status of large parts of the biomes around the globe are still sparsely known. For instance, for many areas and taxonomical groups it is unclear how well they are covered within the existent protected areas network (PAs), and if there is a bias of PAs towards different species or in different biomes. The increase of the availability of species occurrences from the digitization of herbarium specimens may remedy such lack of knowledge, especially in combination with species distribution models (SDMs), but SDM approaches are also ought to overrepresent the real occurrence of a taxon when suggesting suitable areas where it might still not occur. Here, we study the efficiency of the PAs network in South America to cover plant species of different distribution, abundance and threat status, using a distribution database of the cocoa family—Malvaceae—as study case. We modelled the distribution of 271 species from three subfamilies (Byttnerioideae, Helicteroideae, Sterculioideae) across South America, and evaluated how well the current network of PAs covers them. We found that 79 species lack any record inside any PA, and almost a third of these unprotected taxa were potentially threatened too. Our SDM approach suggests that the protected areas of biomes with little collection effort—namely the Amazonia—perform worse in covering different species than biomes with more collection efforts but with few delimitated PAs—namely the open/dry biomes, or the Atlantic Forest. However, modeling approaches suggest that the potential occurrence of many species in areas with few collections due to an controversial undercoverage scenario of collections in Amazonia. Our results show the need to strengthen efforts in field collections inside PAs and in maintaining herbarium collections, towards improving our knowledge on the flora of PAs. Also, poorly known taxa with few collections point to the important of carrying out field expeditions directed to seeking to recollect those taxa.

Keywords: biodiversity documentation; biological conservation; flowering plants; Neotropics; species distribution modeling.

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1. Introduction

Identifying spatial patterns of biodiversity is still a major challenge in biogeography, and is crucial due to accelerating land use change and habitat destruction (Lennon et al., 2004; Gaston et al., 2008; Diniz-Filho et al., 2013). In this sense, large scale databases of species distributions compiled from natural history collections, observation networks and, increasingly, citizen science initiatives have become a primary source for assessing biological patterns and important resources towards more effective conservation (Greve et al., 2016, Yesson et al., 2007; Robertson et al., 2014; Williams & Crouch, 2017).

For plants, georeferenced species occurrence records are mostly retrieved from herbarium collections (Pyke & Ehrlich, 2010; Lavoie, 2013; Schmidt-Lebuhn et al., 2013). Supposedly, biological collections are of higher quality then observational data, as taxonomical experts can repeatedly verify and update them (Graham & Jihmans, 2006; Pyke & Ehrlich, 2010). This is particularly important for megadiverse but underassessed regions such as extensive areas of the Neotropics (Feeley, 2015; Ulloa-Ulloa et al., 2017), since collections from this region have major taxonomical and geographical gaps (Oliveira et al., 2016; 2019; Daru et al., 2018).

Scarce data for large areas, e.g. the Amazonia (Feeley, 2015), and sampling bias towards more accessible regions (e.g., around cities, roads and waterways) are common situations for South America (Watson et al., 2014; Oliveira et al., 2017; Daru et al., 2018). For this reason, the South American protected area network (henceforth "South American PAs") may only include a biased subset of species and not fully represent the diversity of South America. As a result, conservation planning and evaluation are likely biased, since red lists mainly rely on known occurrence records in PAs for conservation assessment (e.g. Colli-Silva et al., 2016; Daru et al., 2018).

Currently, PAs correspond to c. 7% of the total area of South America, but historical planning has been heterogeneous throughout countries and time (Baldi et al., 2019). Hence, evaluating the efficacy of PAs is a major challenge given the heterogeneous sampling effort throughout PAs (Colli-Silva et al., 2016; Daru et al., 2018). For distribution data, information is often not standardized or even missing (Colli-Silva et al., 2016; 2020). Conversely, when larger amounts of data are available, these are often problematic due to issues such as the lack of complete or precise coordinates, misidentifications of museum specimens, and huge gaps in collections and documenting the flora of PAs (Yesson et al., 2007; Maldonado et al., 2015; Colli-Silva et al., 2019).

One attempt to overcome sampling gaps and biased sampling are species distribution models (SDMs) based on occurrence records and environmental variables (Hopkins, 2007; Kramer-Schadt et al., 2013; Guedes et al., 2017), and provide putative species distributions for areas with little data available. Therefore, SDMs alongside with quality assessment of point occurrence records can give an estimate of the fraction of biodiversity sampled in a given area, and points towards areas in need of further field sampling. Such a prioritization of collection effort is warranted in South America, where large areas are potentially species rich and poorly sampled, often also in PAs.

In this work we aim to estimate how well plants are accurately represented in South American Pas, using an expert-curated occurrence database from the cacao group (Malvaceae), a family which is widespread throughout the tropics, with particular diversity centers in different regions, including the Neotropics (Bayer & Kubitzki, 2005; see Chapter 1). Here, we focus on three of the nine recognized subfamilies *sensu* Alverson et al. (1998)—Byttnerioideae, Helicteroideae and Sterculioideae—which are species-rich in South America and include multiple species of importance such as cacao (*Theobroma cacao* L., Byttnerioideae), the West Indian elm (*Guazuma ulmifolia* Lam.) and the tropical chestnut trees (*Sterculia* spp.)

(Bayer & Kubitzki, 2005).

Specifically, we verify the following hypotheses:

1. *Different species are unequally represented and covered by South American PAs network.* As PAs are not randomly distributed across South America, we expect differences of species coverage in PAs among (a) genera, (b) threat levels and (c) biomes.
2. *Raw occurrence data underestimate the potential fraction of species in PAs.* Due to the biased sampling and knowledge gaps for large areas, raw occurrence data underestimate species coverage in South American PAs. Furthermore, potential habitats based on environmental predictors may give a more accurate picture of the potential but unknown coverage.
3. *Modeling approaches increase the accuracy of predicting species presence in PAs.* If the raw occurrence data underestimate the potential fraction of species in PAs, modeling approaches may accurately indicate areas where species are likely to occur.

2. Methods

2.1. Database of species occurrences

We retrieved the occurrence database from an extensive review of occurrence records of three selected subfamilies of the cacao group (Malvaceae): Byttnerioideae, Helicteroideae and Sterculioideae. Our database comprises 14,957 occurrence records for 271 species in 11 genera (Chapter 1). Sampled taxa occur in several environments, encompassing either narrowly distributed and widespread species prevailing in open seasonally dry areas (*Ayenia*, *Helicteres*, *Melochia*, *Rayleya*, *Waltheria*) and forested formations (*Herrania*, *Theobroma*, *Pterygota*, *Sterculia*), as well as species represented through different biomes (i.e. *Byttneria* and *Guazuma*). See Chapter 1 for details on the database.

2.2. Maps and South American PAs network

We downloaded the borders of PAs from the WDPA database (the World Database on Protected Areas) in September 2018, maintained by the United Nations Environment World Conservation Monitoring Centre (IUCN & UNEP-WCMC, 2016). A full list with all occurrence records, indicating those inside a PA is available in Appendix S1 in Supporting Information.

Maps were generated using the "speciesgeocodeR" package v. 2.0—10 (Töpel et al., 2016) and the QGIS software (`www.qgis.org`). We refer to "biomes" as large areas with a particular vegetation and potentially with a particular fauna and flora, that is subject to several abiotic conditions (Mucina, 2019), and following Olson et al. (2001) delimitations. To optimize data visualization, we distinguished species from the Amazonia from those from the Atlantic Forest instead of considering both as "Tropical and Subtropical Moist Broadleaf Forests".

2.3. Assessing the fraction of species in PAs

We ran all further analyses in the R Environment (R Core Team, 2018). To check hypothesis 1—species differ in their coverage in PAs—we compared the observed fraction of occurrences of each species in PAs with the fraction obtained from the same number of points randomly distributed across the study area. To do so, we swapped the n occurrence records for each species S 1000 times and assessed the fraction of occurrence records per replica within the South American PAs, using the "mobsim" package v. 0.1.0 (May, 2017).

We then visualized the statistical distribution of the obtained coverage fractions together with the observed distribution frequency for our database. To assess if PAs represent species insufficiently (hypothesis 1), we plotted these variables considering taxonomical groups and their distribution range, the potentially threatened species and species from different biomes. We assigned species whose > 70% of their records were within the borders of a particular biome as from that biome.

Then, we plotted the median value of the observed dataset in the graph. This approach enabled us to check if the assemblage of species is underrepresented, overrepresented or equally represented in PAs by comparing the position of the observed line with the frequency distribution of the median fraction of the replicas. We calculated the median fraction values too, but these measures were considerably different than the median values. Thus, we chose to keep only the median, as it is less sensitive to outliers and provides a more realistic idea than the mean for skewed distributions.

2.4. Preliminary conservation assessment

To estimate the threat level of the study species and compare it to their coverage in PAs, we performed a preliminary conservation assessment using the "ConR" package v. 1.2.3 in R based on our point occurrence database (Dauby et al., 2017). Functions in this package suggest preliminary threat categories based on distribution data and IUCN criterion B. The "ConR" package also considers the number of individual locations and subpopulations of each taxa in the assessment, along with estimating AOO (Area of Occupancy) and EOO (Extention of Occurrence) calculations (IUCN, 2001; Rodríguez et al., 2015). AOO and EOO calculations are two complimentary scores which reflects the distribution range of a taxon (IUCN, 2001). While EOO is a simple measure of the area of a minimum convex polygon encompassing all known point occurrences, AOO is the sum of the area within the EOO occupied by an occurrence record under 2 km gridcells (IUCN, 2001). Hence, in the absence of data for a full assessment, "ConR" provides a fair and rapid proxy to discuss potential conservation measures when only occurrence data is available.

2.5. Predicting species distributions

To check hypothesis 2—comparing the point occurrence database with a modeling framework—we modeled species ranges based on bioclimatic variables and on the *n* occurrence records for each species *s* of our study group. All analyses were performed with the "sdm" package v. 1.0—67 in R environment (Naimi & Araújo, 2017). Firstly, we downloaded 10 min resolution current bioclimatic variables from the WorldClim project (Fick & Hijmans, 2017; Karger et al., 2017). In order to eliminate redundant variables, we performed a Variance Inflation Factor (VIF) analysis, keeping only variables that were not strongly correlated (i.e. with a standard multicollinearity index < 0.7), using the "car" package v. 3.0—6 in R Environment (Fox et al., 2019). After this test, we kept the following bioclimatic variables: mean temperature of the wettest quarter, mean temperature of the driest quarter and precipitation seasonality.

To avoid modeling biases due to biased sampling, we used the "spThin" package v. 0.2.0 in R Environment for spatial thinning of species occurrence records according to the following workflow: (1) for species with more than 15 records, we adopted a spatial thinning buffer of 25 km radius with 50 repetitions (Aiello-Lammers et al., 2014), eliminating redundant points within this radius; (2) for taxa whose number of records where less than 15 and bigger than one, we used the original occurrence points, without thinning (Aiello-Lammers et al., 2014); and for species with one record, we only assumed as a proxy of predicted area a buffer of 25 km radius. This value is arbitrary, but it is an intermediate radius we believe it is suitable to not include or exclude more areas (Graham & Hijmans, 2006) and given the restrict niche of species with scarce records.

We adopted the "general additive", "random forest" and "bioclim" models, running the modeling over five replicates of cross-validations. Each model generated an output with suitability values for the predicted area of a species *S* (see Allouche et al., 2006). As binary raster indicated regions with highest suitability levels, we used those to estimate the predicted distribution area. For generating species binary raster predictions, we chose as cut-off thresholds the highest values of the sum of sensitivity (true positive prediction rates) and specificity (true-negative prediction rate). The modeling script is available in Appendix S2 in the Supporting Information and the projected distribution for all species are available in Appendix S3 in the Supporting Information. For modeling evaluation, we report the Area Under the Curve (AUC) and the True Skill Statistic (TSS) scores, following similar frameworks (Allouche et al., 2006). Values closer to 1.0 indicate a good fitting of the model, whereas values closer to 0.5 indicate the model is as good predictor as in a random case scenario.

Finally, to assess the fraction of species and endemic species in PAs for the modeling scenario, we assembled the predicted distributions for all species. Model outputs were crossed with point occurrence outputs, both in terms of coverage in PAs considering all species and only species endemic to each country of South America. We also assessed the fraction of the predicted area inside and outside protected areas per species, by intersecting the binary raster with PA delimitations.

2.6. Comparing the accuracy of different databases

To check if the raw occurrence data reports a divergent scenario of species coverage compared to a modeling scenario (hypothesis 2), we compared the accuracy of the species coverage under different scenarios: considering the point occurrences manually revisited, and the predicted area given in the SDM approach. Alternatively, we also compared a third scenario, by downloading all occurrence points of the species in GBIF database and subjecting the records to an automated cleaning, with no further review. We downloaded GBIF data using the “rgbif” v. 1.3.0 (Chamberlain et al., 2019) and cleaned them using “CoordinateCleaner” v. 2.0—11 in R (Zizka et al., 2019).

All sources were compared to a reference dataset of floral checklists in PAs of the GIFT database—the Global Inventory of Floras and Traits (Weigelt et al., 2019). The GIFT interface gathers information on PAs all over the world with revisited checklists and floras of selected PAs, based on an extensive consultation of published works of floras and checklists of species in PAs. All consulted works in the GIFT are available (Weigelt et al., 2019), as well as the whole database. Based on that list of references of works in the GIFT website, we selected 12 PAs in different countries of South America, and them looked for published checklists of them in the literature, as they were cited in the GIFT database as a reference (see `http://gift.uni-goettingen.de/about`). Table S1 in Supporting Information summarizes the selected references of consulted PAs in this survey.

We then manually checked the checklists from these selected PAs and compared the reported present/absent species with the occurring in (1) our manual revisited database and (2) the predicted by the modeled scenario. These three datasets were cross-tabulated with the reference data of the checklists available in the literature, and from that we created a confusion matrix with associated statistics of accuracy, also assessing true and false positive/negatives. Confusion matrix metrics were calculated using the “caret” package v. 6.0—84 in R (Kuhn, 2019).

3. Results

3.1. Occurrence in South American PAs

The presence of records inside South American PAs varied among species, biomes and threat levels. In total, 79 of the 271 species (29%) lack known occurrences in any PAs; of these, 67 (84%) were assigned as potentially threatened by our preliminary assessment (Figure 1). Furthermore, most of the potentially threatened and non-protected species were restricted to the Amazonia region (Figure 1; see Figure S1 and Table S1 in the Supporting Information for results per genus). In terms of treat status, 137 species (52%) have been considered as potentially threatened (i.e. as “Vulnerable”, “Endangered” or “Critically Endangered” according to the IUCN criteria) in our preliminary conservation assessment (Figure 1; see also Table S2 in Supporting Information for a full list per species). From that amount, 48% (67 species) had no known records within any South American PA (Figure 1).

3.2. Species coverage in PAs

In general, species are underrepresented when compared to the expected proportion in a random scenario, and potentially threatened species are less represented in PAs than non-threatened species (Figure 2). Noteworthy exceptions especially from forested formations—the Amazonia or the Atlantic Forest - are *Pterygota, Sterculia* and *Theobroma,* which are well represented in PAs. In contrast, examples of underrepresented genera are *Ayenia* and *Byttneria*, mostly from open seasonally dry formations, and *Herrania* in the Amazonia. Check Figure S1 in Supporting Information to see graphs per genus.

When considering only records from a specific biome rather than from the whole continent, the Amazonia revealed an undercoverage scenario (Figure 3). For the other biomes, species coverage was found as expected in a random scenario, considering the PAs network for these areas (Figure 3). However, the values of all fractions are still smaller than when compared with the Amazonia. For instance, although in the Deserts and Xeric Woodlands there is no undercoverage observed for our data, the median percent of records inside PAs is 7% against the ~29% for the Amazonia (Figure 3), a fraction four times more than of the open/dry habitats.

3.3. Species distribution models

Species distribution models predicted that species are more represented in PAs than the reported for the point distribution database (Figure 4; Table 1, Appendix S3). We observed AUC and TSS scores higher than 0.9 and 0.7, respectively for our distribution models (Appendix S3 in Supporting Information).

As expected, the distribution models indicated a larger range size for all species as compared to the raw occurrences and suggested moderate to high species richness in the sparsely sampled areas in central South America (Figure 4). The modelled species richness also suggested western Amazon, the Brazilian Caatinga and the dry deciduous forest formations of central-western Brazil as centers of species richness. Compared to the raw occurrences, the distribution models suggested a lower country-level endemism, especially in Peru, Paraguay and Bolivia (Table 1).

Furthermore, the models suggested higher species numbers than found by the raw occurrences for Brazil, Bolivia and Uruguay (see Table S4 in Supporting Information for a modelled species list for each country). Brazil, Bolivia and Uruguay are the countries projected to harbor more species , and Peru, Paraguay and Bolivia are the countries whose most known species endemic to the country are projected to occur in other countries as well (Table 1). A full list of number of species and endemic species to each country considering point-only and modeling approach can be found in Table S4 in Supporting Information.

When comparing the performance of different types of spatial data with the reference from the known flora of selected PAs, SDM presented the lowest sensivity levels, which reveals the high presence of potential false positives of occurrence inside PAs (Table 2). On the other hand, our manual revisited point database exhibited the highest levels of accuracy metrics, when comparing both with the SDM approach and when considering point occurrence databases obtained and cleaned automatedly (i.e. the from GBIF repository).

4. Discussion

Here, we verified three main hypotheses regarding the heterogeneous species coverage of South American PAs, using a Malvaceae distribution database (Chapter 1) as study case. Firstly, different species from this point distribution database exhibited an unequal coverage through South American PAs (hypothesis 1 of this work), as almost a third of all species have no occurrence records in any PAs. Moreover, most of these “non protected species” were revealed as potentially threatened or restrict to particular biomes, namely the open/dry habitats. Such undercoverage scenario for open/dry habitats is particularly problematic because these areas harbor most records of the species of the groups studied herein.

Secondly, we verified if raw occurrence data from our reviewed point distribution database were underestimated in terms of collections inside PAs (hypothesis 2 of this work). This was shown to be true for biomes with larger PAs delimitated but with few collection efforts—namely the Amazonia, where the observed fraction of species was less than the expected than in a random scenario (Figure 3). Furthermore, even though such undercoverage scenario was not found for open/dry areas, in percentage, very few species are documented in PAs of these biomes (7-13% *vs.* 16-28% for forested biomes; check Figure 3), reflecting the fact that, in contrast with the Amazonia and the Atlantic Forest, South American open/dry biomes have few areas delimited for protection (Baldi et al., 2019).

Lastly, we checked if alternative spatial data methods, namely the SDM framework, were more accurate in delimitating the potential occurrence of species in PAs, especially in areas with less collection effort, under the hypothesis they would increase the accuracy (hypothesis 3 of this work). However, we did not find such thing after cross-checking different databases—i.e. (1) our point distribution revisited database, (2) a automatedly generated and cleaned point database from GBIF, and (3) models derived from environmental layers and our point distribution revisited data. Actually, SDM data turned out to be the least accurate database of all, with lots of false positives in areas where species actually are not documented.

Hence, although global network PAs underwent through a significative expansion in recent decades, the increase was not homogeneous throughout the continent (Watson et al., 2014; Baldi et al., 2019). Thereupon, South American PAs must receive more efforts towards properly representing species and centers of plant endemism of open seasonally dry areas, such as those found in the Espinhaço Range and in the Chaco (Madriñan et al., 2013; Colli-Silva et al., 2019). Likewise, this is true when assessing species coverage of threatened taxa (Ribeiro et al., 2018) or biome coverage in South American PAs as well (Baldi et al., 2019).

4.1. The controversial scenario

Our results showed a good representation of our study group in the Atlantic Forest, where species are both relatively well sampled in the areas and well known in PAs (Rodrigues et al., 2004; Oliveira et al., 2017; Ribeiro et al., 2018). This contrasts with findings from the open/dry biomes—where the representation was as expected under a random distribution but with few species protected in absolute numbers—and from the Amazonia, where species were strongly underrepresented in the large delimited PAs (Figure 3). This trend is controversial, because, intuitively, well sampled areas should exhibit higher fraction of species in PAs, whereas less sampled areas should exhibit lower fractions of species in PAs. In fact, the Amazonia is long known for having larger PA's extent—including larger areas of alternative PAs, namely cultural heritage and indigenous territories (Watson et al., 2014; Baldi et al., 2019).

However, despite the fact that, in open/dry biomes, species coverage is as expected in the random scenario, the absolute percent of species is much lower than in forested biomes (see Figure 3). This is very much related to the fact the open/dry biomes have been historically much less neglected than forested biomes and, as we showed in our survey, demand delimitating more PAs. With much less delimited areas than forested environments, conservation priority in the savannas and dry deciduous forest go beyond financial issues, as discussed by Pennington et al. (2006). These authors point out several other issues on the effective conservation of open/dry biomes, including (1) the failure to consider different, naturally fragmented open/dry biomes as a single biome in their own right; (2) the non-consensus on the nomenclature of each biome (e.g. Cerrado vs. savannas; Caatinga vs. dry forest), that complexifies the identity of these habitats (unlike the long known "tropical/moist rainforests" in the Amazonia and Atlantic Forest); (3) the intensification of the fragmentation of an already fragmented biome due to anthropic pressure.

Alternatively, strict and larger PAs, such as some of the Atlantic Forest and the Amazonia, are also more effective in protecting their biodiversity, as they are less subject to intense human pressure (Jones et al., 2018). These areas are essential in representing the species of our survey, especially in countries where they mostly prevail, e.g. the Guianas, Argentina and Venezuela (Table 1). However, it is noteworthy that the Amazonia is also a well-known spot of collection gaps, with low levels of sampling effort for plants and animals (Hopkins, 2007; Feeley, 2015; Oliveira et al., 2016). This is also true for the Malvaceae groups studied herein (Chapter 1). Conversely, despite the high levels of species richness, endemism and their outstanding biome heterogeneity (see Werneck, 2011), open/dry biomes exhibit a relatively scarce PAs network (Espírito-Santo et al., 2009).

Put it differently, we likely do not protect what we know—i.e. in the open/dry biomes—, but sometimes we might not know what we potentially protect too—i.e. in the Amazonia. It is against this "controversial scenario" that occurrence records must be in the frontline of any distribution analyses, as data retrieved from biological collections are the safest proofing that "we know" the identity and distribution of a taxa (Graham & Jihmans, 2006; Pyke & Ehrlich, 2010). Accordingly, as gaps in biodiversity documentation hinder our current knowledge on biodiversity patterns (Gaston et al., 2004; Feeley, 2015), these gaps make biodiversity conservation problematic if the main goal is species representation (Rodrigues et al., 2004; Ribeiro et al., 2018).

4.2. The importance of fieldworks and floristic surveys in PAs

Underestimated levels of species coverage in South American Pas, such as the ones evidenced herein for cacao relatives, are consequence of (1) South American PAs network being unequally distributed through the continent and through particular biomes, and (2) sampling efforts varying from species with different extents. Hence, it is important to maintain not only herbarium collections (see section 4.1.), but also to carry out new field expeditions to (re)collect particular taxa, especially threatened species, where conservation assessments mostly rely on the frequency of new collections over time (Bachman et al., 2011; Watson et al., 2014; Colli-Silva et al., 2016; see also Chapter 2).

Also, as pointed out by Ribeiro et al. (2018), this is a great effort towards attending global commitments such the Global Strategy for Plant Conservation (GDB, 2016), where 75% of the country's threatened species should be represented within its PAs network. Furthermore, we highlight the lingering importance of floristic and taxonomical surveys within particular PAs (Giulietti et al., 1987; Stannard et al., 1995; Romero & Martins, 2002; Hopkins, 2005; Zappi et al., 2019). These surveys valorize and help to properly document PA's flora, along with updating the taxonomical knowledge on a particular genera or family. Likewise, floristic works in PAs also feed herbarium collections with new and updated records, increasing useful data for data consumers (Hopkins, 2007).

New field expeditions should also improve our knowledge on potential areas, habitats or biomes where a particular taxon might occur (Keeley & Silman, 2001; Warren & Seifert, 2011; Warren, 2012; Kramer-Schadt et al., 2013). Afterwards, in a SDM framework, we revealed that, in general, the predicted modeled area is larger than the current known (Table 1), which is expected in a SDM framework (Phillips et al., 2004; Guisan & Thuiller, 2005). However, albeit revealing potentially undercollected spots where species might occur, SDM frameworks are laxer, being limited in recovering suitable abiotic environments given distribution data (Phillips et al., 2004)—which are not the only determinants in determining species distribution (Jiménez-Valverde et al., 2008). Consequently, there is plenty of space for overestimate species distribution, especially regarding restrict taxa. In other words, even with the increasing of innovative SDM frameworks that can predict suitable areas for species (Jetz et al., 2008; Soley-Guardia et al., 2016), it seems that fieldwork, collections and deposition of preserved materials in herbaria are still critical measures to safely proof where a species occur—or at least to validate what a SDM potentially suggests (Feeley & Silman, 2011).

5. Conclusion

Species of the three subfamilies of the cacao family studied herein were generally undercovered in South American protected areas network, considering a point revisited distribution database. Mostly, such undercoverage affects more threatened species from genus of open/dry biomes, in countries with high levels of species richness or endemism such as Brazil and Colombia. In terms of biome coverage, Amazonian protected areas—the largest in area but with very scarce collection efforts—exhibited the worst coverage scenario. Nevertheless, although open/dry biomes have not exhibited low levels of sampling effort, they had very few species covered in their protected areas, because they have much less areas delimited for protection.

Furthermore, climate-based species distribution models indicated a much better coverage of species by the protected areas, suggesting that the future collection activity might reveal multiple species not yet collected in protected areas to be actually occurring there. However, data from local checklists suggests a higher accuracy of raw occurrence records than distribution models for determining the presence of species in the protected area network of South America.

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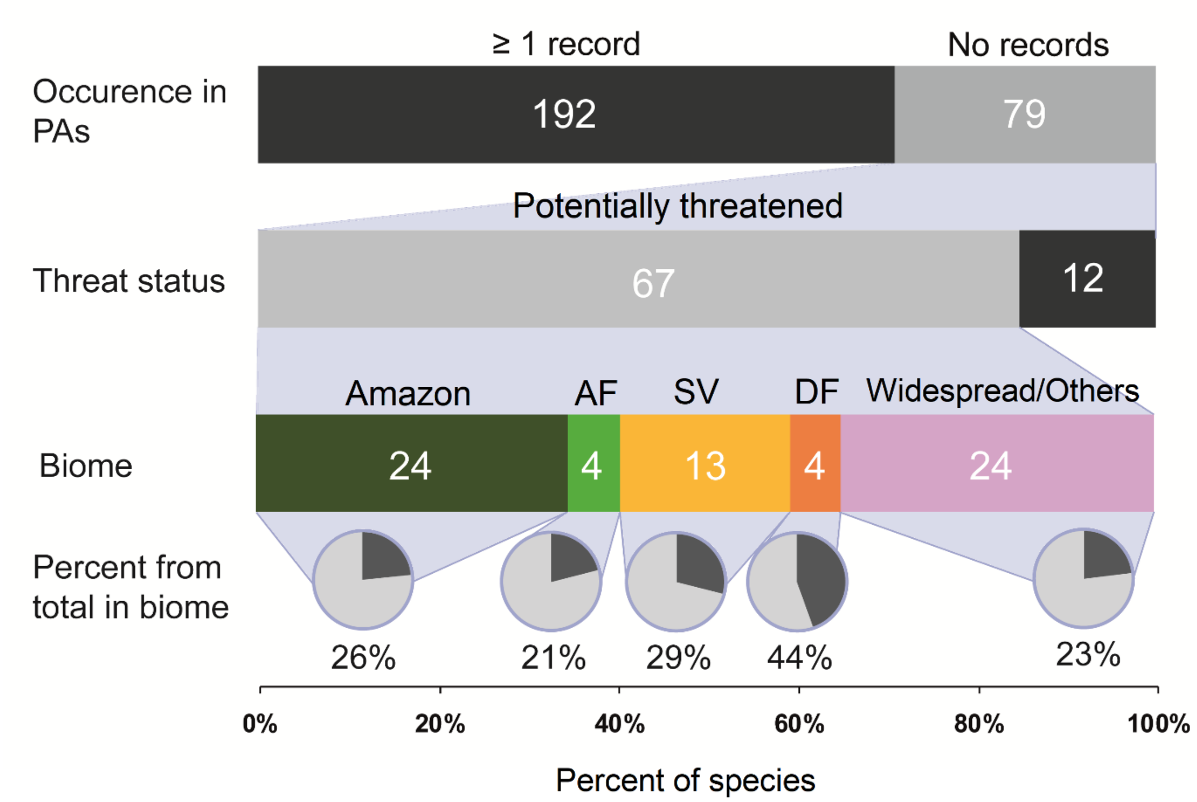

Figure 1. Main summary of species coverage in South American PAs, considering different variables for S species: whole assemblage (S = 271), indicating their known and unknown occurrence in PAs; (2) only threatened species (S = 137); (3) prevalent biome of threatened species, i.e. where at least 70% of the records of the S species are centered; (4) percent of threatened species from the total prevalent in each biome, namely: Amazon (S = 94), Atlantic Forest (AF; S = 19); Tropical grasslands and Savannas (Sav.; S = 45); Deserts and Xeric Woodlands (DF; S = 10). Check Tables S1 in Supporting Information for the full list per species and variable of interest.

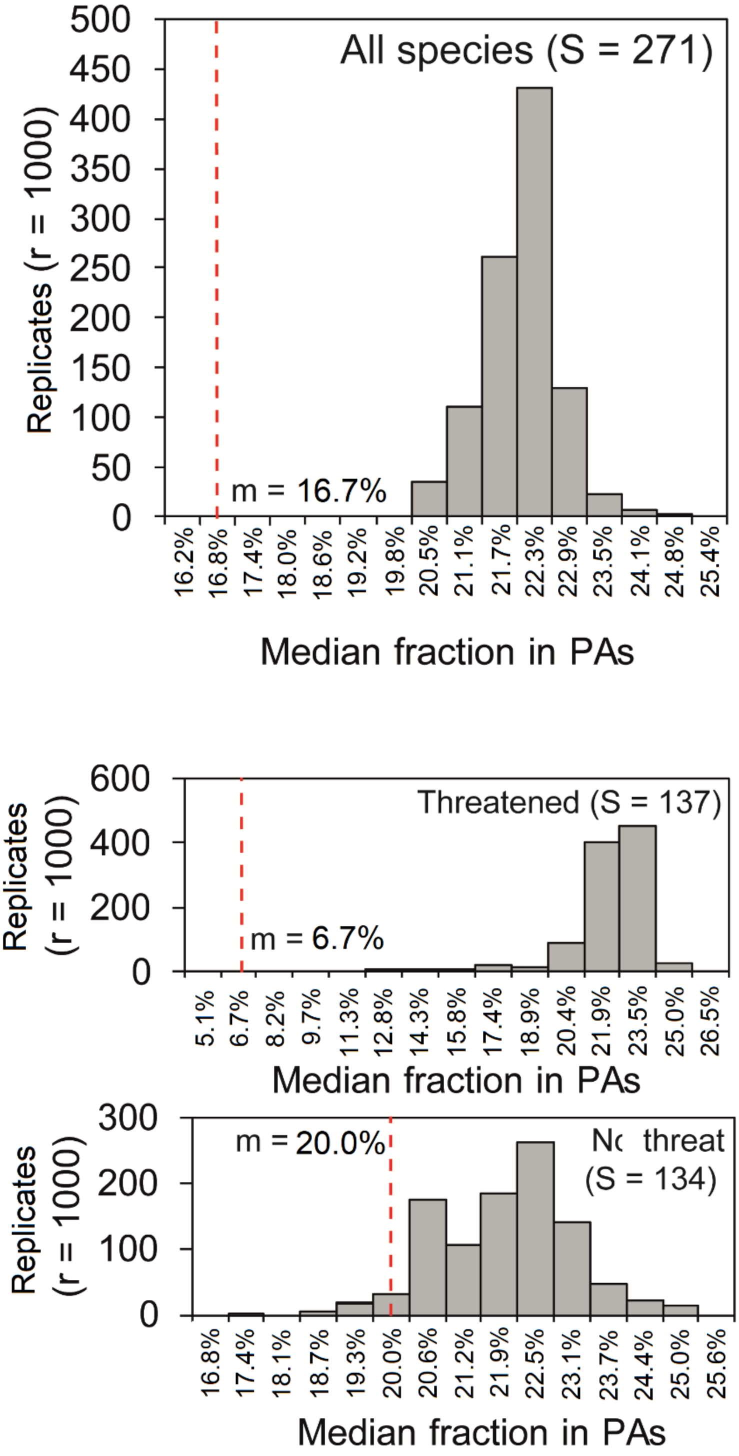

Figure 2. Distribution of the median fraction of species (S) in South American PAs considering a random scenario with 100 reps (r) and the red line indicating the real fraction given our data (m). Distribution data consider all species, then only threatened and only not threatened considering our preliminary conservation assessment. A full list of the fraction per species is available in Table S3 in Supporting Information.

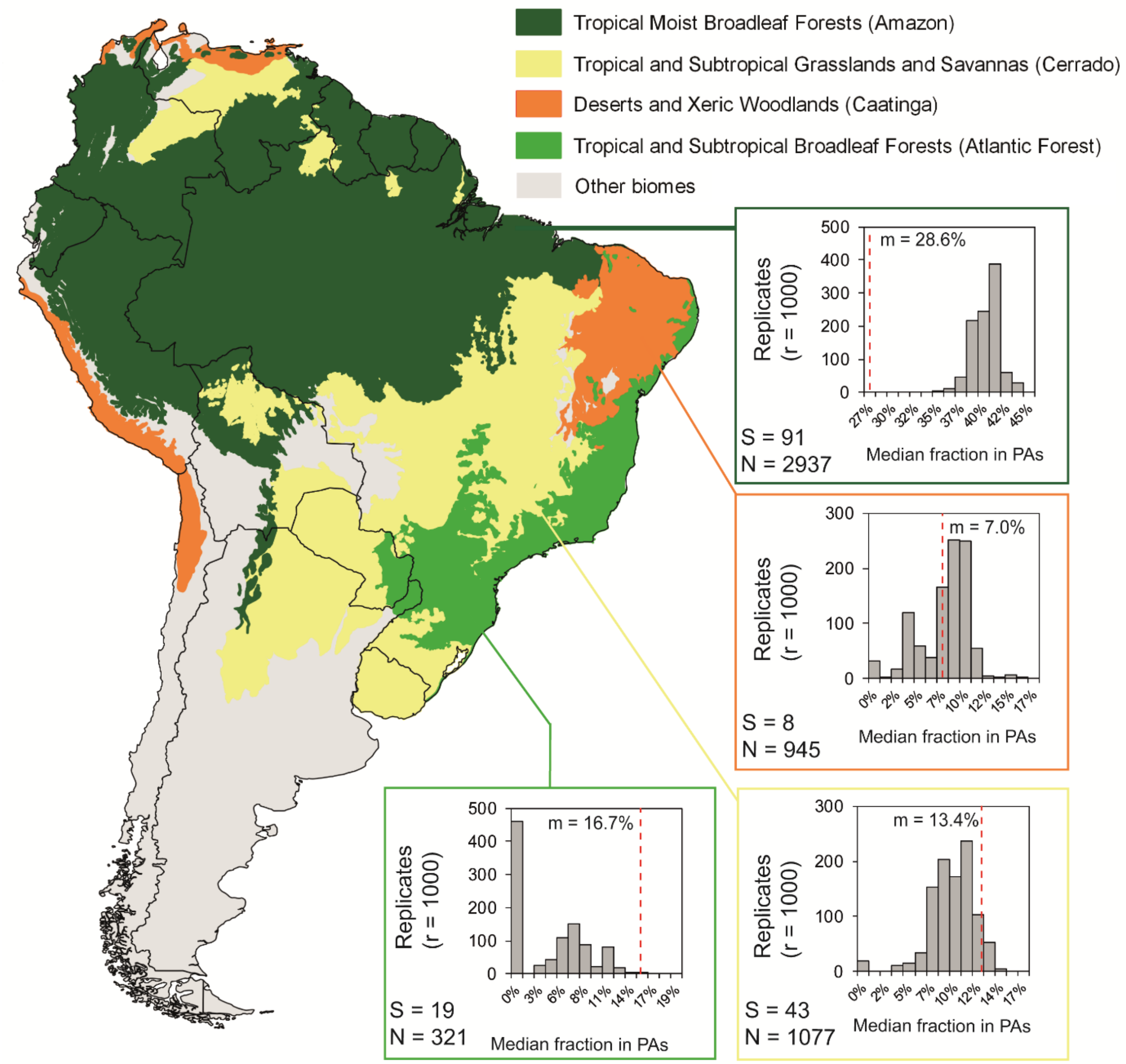

Figure 3. Distribution of the median fraction of species in South American PAs considering a random scenario with 1000 replicates (r) and the red line indicating the real fraction given our data (m). This figure consider species with > 70% of their records within the main biome delimitations sensu Olson et al. (2001), and random points were generated within each biome delimitation. A full list of the fraction per species is available in Table S1 in Supporting Information. S = number of species from the biome. N = total number of records from the biome.

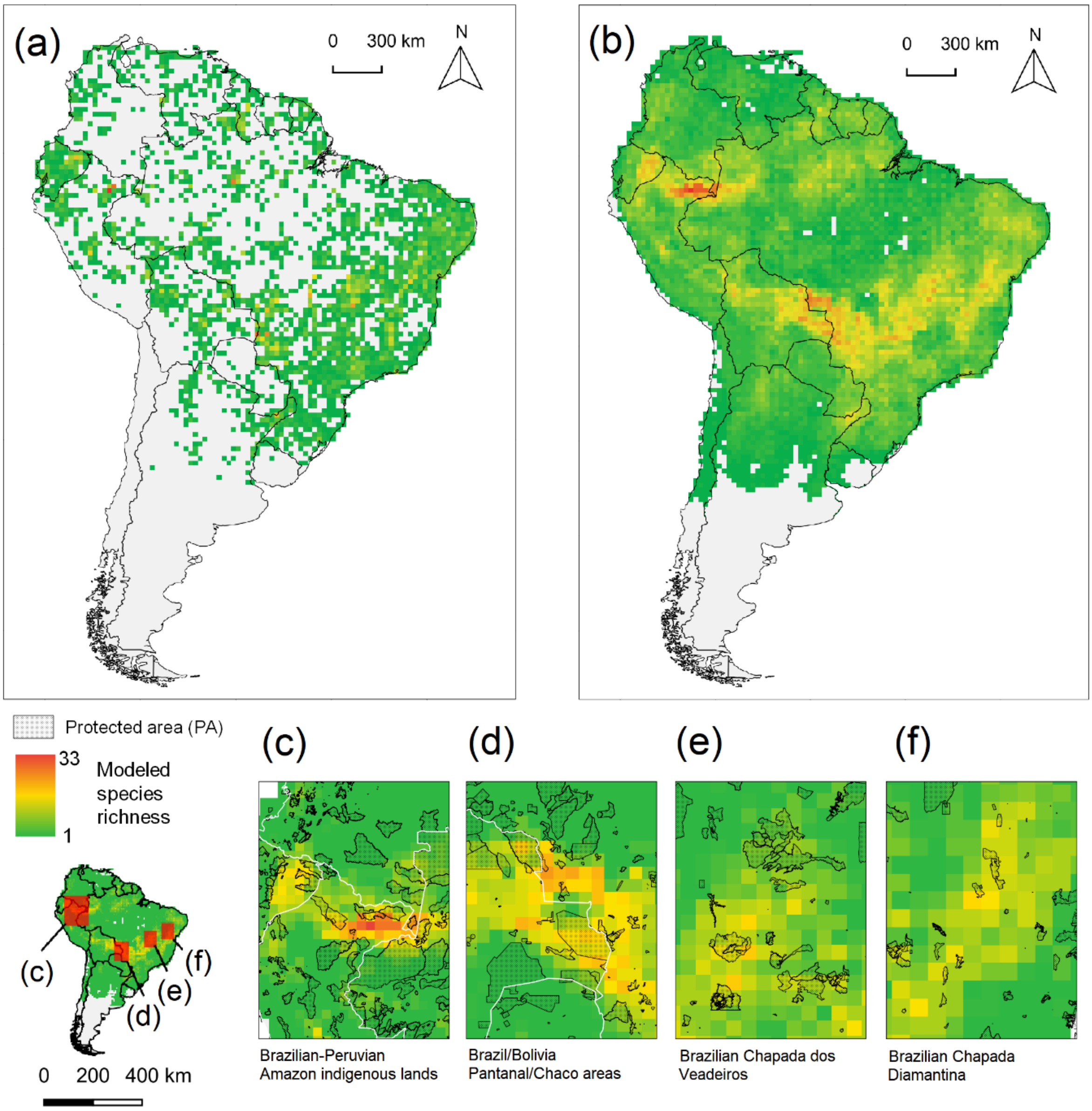

Figure 4. Species richness maps considering (a) manual revisited point occurrence database and (b) SDM predictions. From the map (b), we selected four major areas, from (c) to (f), with highest levels of predicted species richness, intersecting it with the South American PAs borders: (c) the Brazilian-Peruvian Amazon indigenous lands; (d) Brazil/Bolivia/Pantanal boundaries; (c) the Brazilian Chapada dos Veadeiros; and (d) the Brazilian Chapada Diamantina.

Table 1. Species richness and endemism levels based on known (point occurrences) and projected (species distribution modeling) frameworks. The last two columns indicate the estimated number of species considering both frameworks, as well as the number of species endemic to each country. For these, we also indicate the ratio of increase compared to the known values from point occurrences in parenthesis. Country codes: AR = Argentina; BO = Bolivia; BR = Brazil; CH = Chile; CO = Colombia; EC = Ecuador; GF = French Guyana; GY = Guyana; PE = Peru; PY = Paraguay; SR = Suriname; UR = Uruguay; VE = Venezuela. Check Table S4 in Supporting Information for a full list of species per country.

Country	Total no. of species			Endemic species to the country (Percent from the total)		
	Points	**Modeling**	**Increase**	**Points**	**Modeling**	**Decrease**
AR	44	49	11%	4 (9%)	3 (6%)	25%
BO	69	85	23%	4 (6%)	2 (2%)	50%
BR	179	201	12%	80 (45%)	67 (33%)	16%
CH	0	10	1000%	-	0 (0%)	-
CO	67	75	12%	13 (19%)	8 (11%)	38%
EC	54	57	6%	6 (11%)	1 (2%)	83%
GF	18	23	28%	0 (0%)	0 (0%)	-
GY	34	37	9%	1 (3%)	0 (0%)	100%
PE	17	47	176%	2 (12%)	0 (0%)	100%
PY	73	86	18%	9 (12%)	5 (6%)	44%
SR	16	22	38%	0 (0%)	0 (0%)	-
UR	2	13	550%	0 (0%)	0 (0%)	-
VE	48	63	31%	3 (6%)	1 (2%)	67%

Table 2. Confusion matrix metrics when comparing the GIFT database with (1) manual revisited occurrence database; (2) GBIF automated cleaned occurrence database; (3) modeling scenario given the manual occurrence records (SDM framework).

Calculation	(1) Manual revisited points	(2) GBIF point database	(3) SDM predictions
Accuracy	0.9852	0.87	0.75
95% Confidence Interval	(0.96, 1.00)	(0.82, 0.90)	(0.70, 0.80)
No Information Rate	0.79	0.94	0.65
Sensivity	1.00	0.86	0.93
Specificity	0.93	1.00	0.43
Balanced Accuracy	0.97	0.93	0.68

A synopsis of Byttnerieae (Malvaceae, Byttnerioideae) from Atlantic Forest, with notes on nomenclature and conservation*

Sinopse taxonômica de Byttnerieae (Byttnerioideae, Malvaceae) de Mata Atlântica, com notas sobre a nomenclatura e conservação

Abstract

This synopsis presents diagnostic characteristics and general comments on the morphological variability, distribution and conservation for the tribe Byttnerieae (Malvaceae, Byttnerioideae) of the Atlantic Forest. Byttnerieae is here represented by two allied genera: *Ayenia* and *Byttneria*. An extensive survey of the literature and available collections revealed the current occurrence of 20 species in the Atlantic Forest, being 11 species endemics to Brazil. Seven species are restricted to the southern portion of the domain (i.e. south to São Paulo state until Santa Catarina), with records prevailing in Brazil, with lower numbers in Argentina and Paraguay. Beyond the southern portion of the Atlantic Forest, there are three species endemics to Rio de Janeiro or Bahia states, while the others are distributed through South American open seasonally dry formations as well in ecotone regions to the Atlantic Forest. A diagnostic key for species and genera, with illustrations and notes on their distribution and a preliminary conservation assessment is presented. When convenient, we provide nomenclatural comments or updates for species: we designate lectotypes for six names (four synonyms and two correct names), update the authorship of one name, and first document the distribution of *A. glabrescens*, an endemic species from Bahian dry deciduous forests whose precise location was unknown.

Keywords: biogeography, conservation assessment, Malvales, Sterculiaceae, taxonomy.

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1. Introduction

Malvaceae is the species-richest family of Malvales, with over four thousand species in more than 200 genera (Bayer & Kubitzki, 2005). Traditionally, the name “Malvaceae” was less inclusive, because several genera were used to be ascribed to other three families—Bombacaceae, Sterculiaceae and Tiliaceae. The wider circumscription of Malvaceae was adopted as molecular phylogenies start to appear (Alverson et al., 1998; Baum et al., 1998; Bayer et al., 1999). Nowadays, nine subfamilies are recognized within “Malvaceae *sensu lato*” (*sensu* Alverson et al., 1998): Bombacoideae, Brownlowioideae, Byttnerioideae, Dombeyoideae, Grewioideae, Helicteroideae, Malvoideae, Sterculioideae and Tilioideae. Infrageneric and subfamily relationships, as well as evolutionary and biogeographical aspects require more efforts and are the core of new debates among malvologists (check e.g. von Balthazar et al., 2004; Tate et al. 2005; Duarte et al., 2011; Carvalho-Sobrinho et al., 2016). For instance, there is increasing evidence that Bombacoideae may be paraphyletic (Bayer & Kubitzki, 2005; von Balthazar et al., 2004; Hernández-Gutiérrez & Magallón, 2019), while morphological and molecular data indicate that each of the groups previously inserted into Sterculiaceae (i.e., Byttnerioideae, Helicteroideae and Sterculioideae) are each one monophyletic, but when assembled do not form a natural group (Whitlock et al., 2001; Richardson et al., 2015).

Malvaceae is generally diagnostic by its typical actinodromous leaves covered by stellate hairs—as it is common for other families in the order Malvales—, as well as by its unique type of floral nectary composed of glandular hairs located on the inner surface of the calyx of species (Bayer & Kubitzki, 2005). However, huge variation in lifeform, vegetative and reproductive features that likely evolved independently in the different subfamilies of Malvaceae *sensu lato* exists, considering its new phylogenetic scenario. Hence, with the recircumscription of Malvaceae *sensu lato*, systematists are presently faced to a novel morphological, biogeographical and evolutionary scenario for the family.

Currently, there are c. 70 genera and 750 species of Malvaceae *sensu lato* reported in Brazil, with c. 400 species endemic to the country (data retrieved from the Brazilian Flora 2020 Project). Therefore, Brazil encompasses most of the Malvaceae diversity in South America, and most or all the limits of particular phytogeographic domains prevail in the country, such as the Caatinga, the Cerrado and the Atlantic Forest. Particular subfamilies of Malvaceae are common in open seasonally dry formations of South America, occurring as expressive components of the Brazilian Caatinga and Cerrado, and also of the Chaco and Pampas open/dry habitats (see Chapter 1; Chapter 2).

Recent works into specific groups of Malvaceae turned out to be fragmented, whereas taxonomical contributions have centered into focused groups of Malvaceae *sensu lato*, namely within the Malvoideae and the Bombacoideae. Particularly, as it was demonstrated that the former “Sterculiaceae” was polyphyletic, its genera were rearranged into three distinct subfamilies: Byttnerioideae, Helicteroideae and Sterculioideae. Seminal contributions on the taxonomy of genera in these groups were made by C.L. Cristóbal (1960; 1976; 1981; 1996; 2001), J. Cuatrecasas (1964) and further authors (Freytag, 1951; Schultes, 1958; Goldberg, 1967; Taroda, 1984, Taylor, 1989 (unpubl.); Saunders, 1995 (unpubl.)).

In this regard, continuous efforts have been made on the taxonomy of Neotropical Malvaceae, with numerous remarkable contributions. Besides the classical monographs of Cristóbal (1960, 1976), we highlight several local floral studies as well, such as the “Flora da Serra do Cipó, Minas Gerais” (Esteves, 1992; Colli-Silva et al., 2019; Yoshikawa et al., 2019), the “Flora of Grão-Mogol, Minas Gerais” (Esteves, 2003; Cristóbal, 2006; Esteves & Krapovickas, 2009), the “São Paulo Phanerogamic Flora” (Duarte et al., 2007; Cruz & Esteves, 2009), as well as regional floras on specific groups (e.g. Gonçalves & Esteves, 2017). Nevertheless, we consider that the wider and novel diversity panorama of the family, which has arisen since its recircumscription in the early 2000s as we discussed above, still demands new efforts towards strengthening the taxonomical knowledge of the group.

Here, we bring novel contributions on Malvaceae by presenting a taxonomical synopsis with comments on the nomenclature, distribution and conservation of the Byttnerieae *sensu* Whitlock et al. (2001) from the Atlantic Forest domain. Byttnerieae is the most species-rich tribe of Byttnerioideae (Bayer & Kubitzki, 2005), and it is represented in the Neotropics by *Ayenia* L., *Byttneria* Loefl. and *Rayleya* Cristóbal, surpassing 200 species, most of them *Byttneria* (Chapter 1). Those species are usually shrubs or lianas with unguiculate petals that are adnate to a staminal tube (Whitlock et al., 2001). We update several aspects on the taxonomy and distribution of the tribe, by presenting an original taxonomical contribution to the rich Atlantic Forest flora.

2. Material and methods

Our work was mostly based on a selection of species from a manually verified and updated occurrence database of Byttnerioideae, Helicteroideae and Sterculioideae of South America, which is fully presented in Chapter 1. This database has c. 15,000 occurrence records that went through a manual data cleaning, validation and georeferencing procedures. Vouchers were assessed through the consultation of online repositories, including images of the types and of all other available specimens. Particularly relevant repositories are the virtual herbaria in the Brazilian online platforms 1) speciesLink network, `https://splink.org.br/`; 2) GBIF—the Global Information Biodiversity Facility, `https://gbif.org/`; 3) JABOT—the Brazilian Flora database maintained by the Rio de Janeiro Botanical Garden, `https://jabot.jbrj.gov.br/` and 4) JSTOR, `https://jstor.org/`. Additionally, we examined the following physical collections: K, R, RB, SP and SPF (acronyms according to Thiers, continuously updated), assembling a significative portion of the known collections of the Atlantic Forest domain for the group.

We based our work on Cristóbal's monographies of *Ayenia* and *Byttneria* (Cristóbal, 1960; 1976), but both genera received an updated taxonomical description accompanied by the state of art of their distribution, particularly within the Atlantic Forest domain. Habitat and updated geographical distribution were evaluated considering the designated on specific literature or in the examined voucher labels. We selected materials of Brazilian' first-level administrative divisions (henceforth "Brazilian states") of the Atlantic Forest, trying to represent one voucher per state in cases whose collections from the Atlantic Forest were not scarce. We also present brief comments on the nomenclature and conservation assessment of the taxa. A full list of names and exsiccatae can be found on section 8 (numerical list of taxa and list of exsiccatae) at the end of this manuscript.

For morphological terminologies of Byttnerieae, we followed the most recent literature of Cristóbal (1976) and Dorr (1996) for inflorescence and flower morphology, as well as for specific typologies of leaf nectaries. Further terminologies of leaf size, shape and venation were based on Ellis et al. (2009). For laminar sizes, we considered the measures taken from the leaves in the examined vouchers, as well as those present in the literature (Cristóbal, 1960) to estimate the leaf area and classifying according to Ellis et al. (2009) blade classes. Those are: lepyophyll (leaf area < 25 mm^2), nanophyll (25–225 m^2), microphyll (225–2,025 mm^2), notophyll (2,025–4,500 mm^2), mesophyll (4,500–18,225 mm^2), macrophyll (18,225–164,025 mm^2) or megaphyll (> 164,025 mm^2). By attributing blade area classes instead of informing leaf minimum/maximum length/wide values (as it is usually made in taxonomical treatments), we can have a fair approach of leaf dimensions without examining all vouchers for all species—which is the case of this synoptic work. Species descriptions emphasize vegetative features, especially in *Byttneria,* since they are very expressive and easier to access for taxonomic identification purposes.

Only mature parts of specimens were used for the synoptic descriptions and illustrations. Measures of leaves and inflorescences were taken from herbarium samples, while flowers and fruits were rehydrated before being measured and drawn. Photographs of rehydrated leaf structures and petals were taken through a Leica M125 stereomicroscope. Alternatively, we also present a section of "iconography", summarizing drawings made in previous works.

Lastly, for conservation assessment, species were preliminary categorized as either NT (Near Threatened), LC (Low Concerning), VU (Vulnerable), EN (Endangered) or CR (Critically Endangered) as suggested by the "ConR" package v. 1.2.4. in R Environment (Dauby et al., 2017). Then, we critically discussed the preliminary assessment considering our knowledge on the species particularities, suggesting an alternative category for further consideration when if we judged convenient. Maps were generated using QGIS software (`www.qgis.org`) based on point occurrence data.

3. Results and Discussion

We retrieved records for twenty species of Byttnerieae in the Atlantic Forest phytogeographic domain: six *Ayenia* and fourteen *Byttneria* species. Figure 1 summarizes the distribution for the species treated herein. Eleven taxa are endemic to Brazil (*B. abutiloides*, *B. australis*, *B. beyrichiana*, *B. cristobaliana*, *B. gayana*, *B. hatschbachii*, *B. implacabilis*, *B. triadenia*, *A. erecta*, *A. glabrescens* and *A. nummularia*) and six are endemic to the Atlantic Forest (*B. abutiloides*, *B. beyrichiana*, *B. cristobaliana*, *B. implacabilis*, *B. triadenia* and *A. glabrescens*). Interestingly, some *Byttneria* are centered in two main regions of the Atlantic Forest domain: (1) in the southern portion (with *B. australis*, *B. gracilipes*, *B. hatschbachii*, *B. pedersenii*, *B.*

urticifolia widespread, while *B. implacabilis* and *B. triadenia* are restrict to the coastal region of Santa Catarina and Paraná states, and *A. aprica* is known only from Rio Grande do Sul state and northeastern Argentina); (2) in the region between Rio de Janeiro and Espírito Santo states (with *B. abutiloides*, *B. beyrichiana* and *B. gayana*). Species extending beyond the Atlantic Forest domain may show conspicuously disjunct distributions, mainly *B. catalpifolia, B. filipes, B. scabra* and *A. tomentosa,* tough displaying distinct spatial patterns. Overall, both genera are scanty or almost absent from the central part of the Amazon basin, and the above mentioned disjunct species show a peri-Amazonian occurrence (Figure 1; see also discussion in Chapters 1 and 2).

As we have spotted some names with nomenclatural issues, we provide the second-step lectotypification for four synonyms, two lectotypificafions for correct names (*A. erecta* and *A. glabrescens*), and an authorship amendment of one name (*B. gracilipes*). Also, we first describe the distribution of *A. glabescens*, which was known only by the type with no precise location.

Despite of these new amendments, pioneer contributions of Cristóbal's for both genera are exceptional (Cristóbal, 1960; 1976), as she provided the most complete taxonomical treatment of *Ayenia* and *Byttneria* to date. According to Cristóbal, variation within vegetative characters, especially in the leaves, are important features for the taxonomy of the Byttnerieae, and in some cases those are more diagnostic than floral characters. For instance, in *Byttneria*, the variation of leaf shape and size are quite notable and therefore have been used as diagnostic for the circumscription of the species (Cristóbal, 1976; Arbo, 1977) (Figure 2). Here, we follow the same interpretations.

Ayenia and *Byttneria* differ in vegetative traits which can be easily assessed in the absence of reproductive structures. The main diagnostic feature to distinguish one genus to another is to check the presence of one to five extrafloral nectaries on the midvein (occasionally on the main veins) of the abaxial surface of the leaves of *Byttneria,* absent in *Ayenia* (Figure 2 and 3). However, flowers of *Ayenia* and *Byttneria* differ significantly (Figure 3), and some important floral characters help to distinguish species within each genus.

Morphological definitions of different portions of a clawed or unguiculate petal in *Ayenia* and *Byttneria* are tricky though. Dorr (1996) and Whitlock et al. (2001) pointed out inconsistences on the terminology of floral structures. The first possibility is to consider the traditional spatial definition: the “claw” as a narrow basal portion, and “lamina” as an expanded apical portion of an unguiculate petal, as adopted by Cristóbal (1960) in the monograph of *Ayenia*. Thus, as one compares *Ayenia* with *Byttneria* flowers, it is inferable that *Ayenia* would have a much lengthier claw than *Byttneria*; subsequently, the lamina of *Byttneria* should be understood as a complex structure, with a basal, expanded and bi-winged stalk-like portion followed by a filiform fringed laminar portion.

Conversely, when adopting Cristóbal’s (1976) definitions presented in the *Byttneria* monography, that very basal bi-winged portion of the lamina—what she further named as “hood”—would be actually a part of the claw, and not of the lamina. As a matter of fact, in *Ayenia*, the expanded upper portion is often accompanied by a filiform peltate appendix in its dorsal side (Figure 3); consequently, by comparison, it should be fair enough to infer that the so-called “appendix” in *Ayenia* is a reduced, almost vestigial part of the lamina, and the expanded portion should be part of the claw. Such debate is not conclusive, and novel developmental plus phylogenetic evidences are needed to clarify the potential homology of such structures. This is especially important because there is evidence that *Byttneria* is paraphyletic, and so the classification within Byttnerieae might change in the near future (W. Sharber pers. comm.).

Nonetheless, we chose to not merge those definitions and to maintain each specific terminology for each genus, following Cristóbal (1960; 1976) monographies. Thus, on one hand, the term "hood" is adopted only when regarding *Byttneria*. On the other hand, the so-called "appendix on the abaxial portion of a petal" is something unique to *Ayenia*—although there might be some homology between such structure in *Byttneria*, i.e. with the cylindrical and often fleshy lamina of this genus.

Identification key for the species of Byttnerieae from the Atlantic Forest

1. Shrubs, decumbent subshrubs to herbs. Leaf veins lacking extrafloral nectaries abaxially. Petals with a membranous claw, more prominent than the lamina, up to five times lengthier than it. Anthers with three thecae .... ***Ayenia***

  2. Decumbent subshrubs. Leaves suborbiculate. Stem and leaves densely pubescent. Base of the petal claw concave, subtriangular .... ***A. aprica***

  2'. Erect shrubs to subshrubs. Leaves ovate, elliptic or lanceolate, rarely suborbiculate (*A. nummularia*). Base of the petal claw convex, sometimes sub-rhomboid **3**

    3. Leaves glabrous, heterophyllous, with few sparse hairs, with different sizes in different branches .... ***A. glabrescens***

    3'. Leaves pubescent or tomentose, more or less of the same size **4**

      4. Leaves and branches conspicuously tomentose .... ***A. tomentosa***

      4'. Leaves and branches slightly pubescent, with few and sparse hairs **5**

        5. Leaf blade orbicular to sub-orbicular; adaxial face with branched hairs .... ***A. nummularia***

        5'. Leaf blade ovate, ovate-lanceolate, lanceolate or oblong; hairs simple, not branched **6**

          6. Leaf blade lanceolate, subcoriaceous, with prominent veins .... ***A. praecipua***

          6'. Leaf blade ovate, membranous, with flat veins .... ***A. erecta***

1'. Decumbent or erect shrubs or subshrubs to lianas. Leaves with one or more extrafloral nectaries on the abaxial side of the blade, each provided with one or more openings (i.e. uni or multiaperturate), usually visible at naked eye. Petals with a fleshy or membranous claw, smaller and less prominent than the upper portion (i.e. lamina). Anthers with two thecae .... ***Byttneria***

7. Leaves with a conspicuous uniaperturate nectary, visible at naked eye; venation prominent on both sides .... ***B.* sect. *Byttneria***

8. Petiole and branches ribbed and aculeate. Leaf blade lanceolate, margin untoothed or serrate or dentate only in the apex .... ***B. scabra***

8'. Petiole and branches unarmed. Leaf blade linear, ovate or elliptic, margin untoothed **9**

9. Leaves petiolate. Branches cylindrical .... ***B. hatschbachii***

9'. Leaves sessile to subsessile. Branches angulose .... ***B. pedersenii***

7'. Leaves with multiaperturate nectary whose region is usually visible at naked eye (multiple apertures are microscopic); venation prominent only on the abaxial side **10**

10. Lianas. Unarmed branches .... ***B.* sect. *Vahihara***

11. Leaf blade widely ovate, mesophyllous to macrophyllous (4,500–164,025 mm² of blade area). Petal lamina flat, untoothed or with erose margin. Fruits globose, flattened .... ***B. catalpifolia***

11'. Leaf blade ovate to lanceolate, notophyllous (2,025–4,500 mm² of blade area). Petal lamina narrow, cylindric. Fruits globose, spherical .... ***B. gayana***

10'. Shrubs or subshrubs erect to decumbent. Branches aculeate **12**

12. Thecae divergent. Fruits dehiscent .... ***B.* sect. *Urticifolia***

13. Leaf blade with (1-)3-5 extrafloral nectaries **14**

14. Claw and lamina of the petals pubescent ..... ***B. abutiloides***

14'. Claw glabrous and lamina of the petals pubescent **15**

15. Branches angulate and fistulose. Petal lamina fragile, cylindrical and with sparse hairs. Anthers subsessile .... ***B. implacabilis***

15'. Branches cylindrical and non fistulose. Lamina of the petals fleshy, densely pubescent. Anthers not sessile .... ***B. triadenia***

13'. Leaf blade with only one nectary **16**

16. Fruit sparsely aculeate with prickles c. 1 mm length. Leaf veins unarmed .... ***B. gracilipes***

16'. Fruit densely aculeate with prickles c. 3 mm length. Leaf veins aculeate .... ***B. urticifolia***

12'. Thecae non-divergent. Fruits indehiscent ...... ***B.* sect. *Crassipetala***

17. Petal lamina cylindrical, straight **18**

18. Leaf margin serrate. Fruit dehiscent, regularly pubescent .... ***B. beyrichiana***

18'. Leaf margin untoothed or, if serrate, toothed only in the apex. Fruit indehiscent, irregularly pubescent .... ***B. filipes***

19'. Petal lamina flat, markedly curved **20**

20. Leaves concolor leaves, not maculate. Secondary veins curved, not perpendicular to the midvein .... ***B. australis***

20'. Leaves maculate with a cinereous spot around the midvein. Secondary veins regularly spaced, perpendicular to the midvein .... ***B. cristobaliana***

I. *Ayenia* L., Kongl. Svenska Vetensk. Acad. Handl. 17: 24. 1756. Type: *Ayenia pusilla* L., Syst. Nat., 10(2): 1247. 1759.

Dayena Monier ex Mill., Figure Pl. Gard. Dict. 1: t. 118. 1756. Type: "*Dayenia inermis, foliis oblongis-cordatis*" [= *A. pusilla* L.].

Cybiostigma Turcz., Bull. Soc. Imp. Naturalistes Moscou 25(2): 155. 1852. Type: *C. sidaefolium* [= *A. mexicana* Turcz.].

Lorentzia Hieron., Bol. Acad. Nac. Cordova, 4: 96. 1881. Type: *L. cordobensis* [= *A. cordobensis* (Hieron.) Hieron.].

Shrubs, **subshrubs** or **herbs**; branches cylindrical, unarmed, glabrous or pubescent, hairs simple and stellate, hirsute or adpressed. **Leaves** simple, petiolate; blade entire, serrate or dentate, with stellate hairs. Inflorescence a cincinnus, axillary or terminal, with one or more flowers. **Flowers** bisexual, sometimes unisexual by abortion, actinomorphic, dichlamydeous and heterochlamydeous; calix symsepalous, pubescent, valvar aestivation; corolla choripetalous, petals purple to yellowish-green, unguiculate, lower basal portion (= claw) expanded, with an expanded portion (= hood) and usually an appendix in its abaxial face; upper portion (= lamina) less prominent and smaller than the claw, linear, glabrous; staminal tube campanulate to cylindrical; stamens 5, opposite to petals; anthers trithecae, divergent, free or partially connate on the base; staminodes 5, cucullate, alternate to petals; gynoecium syncarpous, 5-

carpelar, 5-celled; style 5, connate, stigma inconspicuous or capitate, with 5 globose lobes; ovules 2 per locule. **Fruit** schizocarpic, dry, spherical, aculeate, dehiscence septicidal or loculicidal; seeds ovoids, gray to black, smooth or tuberculate, not winged.

Ayenia is a Neotropical genus of shrubs to herbaceous plants with c. 70 species (Figure 1a-b), though only 68 species were recognized in the last monography by Cristóbal (1960). In Brazil, there are c. 20 species, occurring mostly in the open seasonally dry formations throughout the Cerrado or Caatinga phytogeographic domains. There are less representatives in the Atlantic Forest, and these usually grow in ecotone areas to other domains, such as the Brazilian Pampas, the Chaco or the Caatinga. Species of *Ayenia* may also inhabit disturbed areas.

Unlike its allied genus *Byttneria*, *Ayenia* has three thecae, a prominent androgynophore, a petal claw always more prominent than the petal lamina (Figure 5n), and a small aculeate fruit, with little infraspecific variation (Figure 5r-s). Besides, in *Ayenia* the vegetative variation is less expressive than in *Byttneria*, so species circumscription relies mostly on floral features as the size, form, margin and indumentum of the petals.

I.1. *Ayenia aprica* Cristóbal, Opera Lilloana 4: 126-128. 1957. Type: Argentina, Missiones, Candelaria, 1957, *J.E. Montes 10037*, holotype: LIL [photo! barcode: LIL932] (isotypes: CTES [photo! barcode: CTES1677], S [photo! barcode: S-R-11365]), SI [photo! barcode: SI563], UC [photo! barcode: UC1245111].

Synoptic description. Decumbent subshrubs. Leaf petiolate, leptophyllous (< 25 mm^2 of area), blade suborbiculate, symmetric, convex to rounded at apex, cordate at base, margin serrate (Figure 3a); primary venation actinodromous, major secondary veins craspedrodomous. Flowers pinkish to purple; claw hood entire, base subtriangular, concave, glabrous adaxially, pubescent abaxially, with a filiform appendix of almost half the size of the lamina; petal lamina cylindrical (Figure 5o). Fruit cylindrical, pubescent.

Iconography. Cristóbal (1960), fig. 42.

Distribution and habitat. Brazil (Rio Grande do Sul); Argentina (Missiones). A species occurring mostly in the southern portion of the Atlantic Forest, growing in transition areas between decidual forest formations and the Pampas (Figure 2d).

Selected material from the Atlantic Forest. BRAZIL. RIO GRANDE DO SUL: "Camino a Encruzilhada, 45 km", 12.II.1948, fl., *M.A. Palacios & A.R.C. Palacios 1296* (LIL, MO).

General comments. *Ayenia aprica* resembles *A. ekmanii*, especially given their distribution; however, they differ due to the following characters: (i) the base of the petal claw (obtuse in *A. ekmanii vs.* attenuate in *A. aprica*), (ii) the lifeform (small subshrubs in *A. ekmanii vs.* decumbent and larger shrubs in *A. aprica*), (iii) leaf indumentum (densely pubescent adaxially with hairs equally distributed in *A. aprica vs.* glabrous to slightly pubescent and concentrated on the midveins and secondary veins in *A. ekmanii*).

Preliminary conservation assessment. According to the IUCN criterium B, *A. aprica* is categorized as VU (Vulnerable), perhaps due to the relatively wide extension of occupancy (93,312 km^2). However, as collections of *A. aprica* are scarce, with only eight unique occurrences, such category may be underestimated. In fact, as the last collection in Brazil is from 1948, with no further novel collections (Cristóbal, 1960), we can expect that *A. aprica* may not occur in that region any longer.

I.2. *Ayenia erecta* Mart. ex K.Schum. in Mart., Fl. bras. 12(3): 103. 1886. Type: Brazil, Bahia ["*prov. Bahia*"], Juazeiro ["*Joazeiro*"], s.a., *C.F.P. Martius 2315*, syntypes: M 8x [photo! barcodes: M211151 (lectotype here designated), M211152, M211153, M211154, M211155, M211156, M211157, M211158].

Synoptic description. Erect subshrubs to herbs. Leaf petiolate, nanophyllous (25–225 mm^2 of area), blade ovate to oblong, symmetric, convex at apex, cordate at base, margin serrate, almost forming two lobes at the base (Figure 3b); primary venation pinnate, major secondary veins craspedrodomous. Flowers yellowish-green; claw hood entire, base rhomboid, convex, glabrous adaxially, pubescent abaxially, with an appendix smaller than half size of the lamina; petal lamina filiform (Figure 5p). Fruit small, almost glabrous, with pubescent prickles.

Iconography. Schumann in Martius (1886), v. XII, part. III, fasc. 96, pl. 23 (I); Cristóbal (1960), fig. 52.

Selected material from the Atlantic Forest. BRAZIL. BAHIA: Macarani, 2.VIII.2001, fl. & fr., *L.A. Mattos-Silva et al. 194* (CEPEC [photo!], IPA).

Distribution and habitat. Brazil (Bahia, Pernambuco). Brazil (Bahia, Pernambuco). A species mostly centered in decidual or riverine forests and in the arboreous Caatinga (the "carrascos"). In Atlantic Forest, it grows in different forested areas of Bahia (Figure 2d).

General comments. *Ayenia erecta* differs from other *Ayenia* due to the its shrubby-herbaceous lifeform and the conspicuous indumentum of its branches and seeds (Cristóbal, 1960). As Cristóbal (1960) did not examine several existent syntypes, we here designated a lectotype from the collection of the Munich Herbarium, whose vouchers are available online.

Preliminary conservation assessment. According to the IUCN criterium B, this species should be considered as EN (AOO = 20 km^2; EOO = 97,672 km^2). New collections of Caatinga and Atlantic Forest are desirable for a better definition of the species distribution and habitat.

I.3. *Ayenia glabrescens* K.Schum., Fl. bras. 12(3): 102. 1886. Lectotype here designated: Brazil, “In silvis Brasiliae”, s.a., *W. Neuwied s.n.*, F [online! barcode: F0073487F] (as isotype in the voucher).

Synoptic description. Decumbent subshrubs. Leaf petiolate, heterophyllous, usually nanophyllous (25–225 mm^2 of area), blade ovate to oblong, symmetric, acute at apex, obtuse to subcordate at base, margin irregularly serrate; primary venation actinodromous, major secondary veins craspedrodomous. Flowers purplish, claw hood entire, base triangular, convex, glabrous adaxially and pubescent abaxially, with an appendix with almost half the size of the lamina; petal lamina filiform. Fruit not seen.

Iconography. Schumann in Martius (1886), v. XII, part. III, fasc. 96, pl. 23 (II); Cristóbal (1960), fig. 55.

Selected material from the Atlantic Forest. BRAZIL. BAHIA: “Km 19 da rodovia Conquista/Barra da Choça”, 22.XI.1972, fl., *T.S. Santos 2510* (CEPEC, SPF!); Vitória da Conquista, “ca. 14 km na rodovia Vitória da Conquista/Brumado, 26.XII.1989, fl., *A.M. Carvalho 2606* (CEPEC, RB!, SPF!); Barra do Choca, “Estrada que liga a Rod. BR-116 a São Sebastião, 4 km a W da cidade”, 21.XI.1978, fl., *S.A. Mori 11263* (CEPEC [photo!], K!, NY [photo!], RB!)

Distribution and habitat. Brazil (Bahia). Endemic to the Atlantic Forest domain, growing in the dry deciduous forests of Bahia. The type had no precise location, so the distribution of *A. glabrescens* remained unknown since the 18th century. Furthermore, we determined new vouchers at K and SPF Herbaria from southern Bahia which are *A. glabrescens*. The type series is also likely to be from the Bahian

Atlantic Forest, given the documented journey of the collector of the species, Prince Maximilian of Wied, through the Brazilian coast (Moraes, 2009).

Nomenclatural notes. There was no record of *Ayenia glabrescens* other than the type until Cristóbal (1960) provided the genus monograph, when she alleged to not found the holotype, only seeing an isotype but not designating a lectotype. We also could not find the holotype during our survey, so we decided to designate the so-called "isotype" as a lectotype of *A. glabrescens*.

Preliminary conservation assessment. There are four preserved specimens for this taxon in the surroundings of Vitória da Conquista, in Bahia state. According to the IUCN preliminary assessment, this species is categorized as EN (Endangered), with an extension of occurrence of 550 km^2, and an area of occurrence of 12 km^2. There might be other specimens in these areas, but this will only be evident after further field expeditions nearby.

I.4. *Ayenia nummularia* Cristóbal, Opera Lilloana 4: 176. 1960. Type: Argentina, Missiones, San Ignacio, 1948, *G.J. Schwarz 6429* (holotype: LIL [photo! barcode: LIL893]).

Synoptic description. Decumbent subshrubs. Leaf petiolate, nanophyllous (25–225 mm^2 of area), blade ovate to oblong and symmetric, densely pubescent, obtuse at apex, cordate at base, margin irregularly dentate; primary venation actinodromous, major secondary veins craspedrodomous. Flowers yellowish-green; claw hood entire, base rhomboid and attenuate towards the apex, glabrous adaxially, pubescent abaxially, with an appendix smaller than half size of the lamina length; petal lamina filiform. Fruit not seen.

Iconography. Cristóbal (1960), fig. 62; Cruz & Esteves (2009), pl. 1, p. 265.

Distribution and habitat. Brazil (Mato Grosso do Sul); Argentina (Missiones). A species harboring in transitional areas between moist forests and open formations. In Brazil, there is one record in the Pantanal too (*Krapovickas 34513*, 1979), and in ecotone areas between Pantanal and the Atlantic Forest domains. Further collection efforts are required in areas between the two known records (Figure 2d).

General comments. *Ayenia nummularia* is remarkable by its ovate (orbiculate) leaves with 1-2 cm diam., distinct from *A. aprica,* which bears much smaller orbiculate leaves.

Preliminary conservation assessment. Species should be considered as DD (Data Deficient) due to scarce collections.

I.5. *Ayenia praecipua* Cristóbal, Opera Lilloana 4: 176. 1960. Type: Argentina, Missiones, Loreto, 1956, *J.E. Montes 10031* (holotype: LIL; isotype: SI [photo!]).

Synoptic description. Decumbent subshrubs. Leaf petiolate, nanophyllous (25–225 mm^2 of area), blade elliptic, symmetric, obtuse at apex, cordate at base, margin serrate with small teeth; veins prominent in both sides, primary venation pinnate, major secondary veins craspedrodomous. Flowers purplish; claw entire, base rhomboid, glabrous adaxially, pubescent abaxially, with an appendix smaller than half size of the lamina; petal lamina filiform. Fruit globose, with caducous prickles.

Iconography. Cristóbal (1960), fig. 66; Cruz & Esteves (2009), pl. 1, p. 265.

Distribution and habitat. Brazil (Mato Grosso do Sul); Argentina (Missiones); Paraguay (Caaguazú). As *A. nummularia*, *A. praecipua* is also common to transition areas between forested and open environments, with records in the Atlantic Forest, the Chaco and Pantanal (Figure 2d).

General comments. *Ayenia praecipua* is remarkable by its prominent veins, especially in both sides of the leaf. The number of available collections is higher than for *A. nummularia*, but still scarce.

Preliminary conservation assessment. According to the IUCN criterium B (AOO = 16 km^2; EOO = 33,628 km^2), this species should be categorized as EN (Endangered).

I.6. *Ayenia tomentosa* L., Syst. Nat., 10(2): 1247. 1759; Sp. Pl., 2(2): 1354. Neotype [designated in Dorr & Wiersema, 2010]: Guyana, Rapununi, Dadanawa, *Jansen-Jacobs 3986*, 1995, US [photo! barcode: US695591] (isoneotypes: NY [photo! barcode: NY609615], K [photo! barcode: K779797], P [photo! barcode: P6698037]).

Synoptic description. Small erect shrubs, densely tomentose. Leaf petiolate, microphyll (215–2,025 mm^2 of area), blade ovate to lanceolate, symmetric, acute at apex, cordate at base, margin crenate; primary venation pinnate, major secondary veins craspedrodomous (Figure 3c). Flowers lilac to purplish; claw filiform, entire margin, base triangular, glabrous adaxially, pubescent abaxially, with an appendix of the same length of the claw; petal lamina cylindric (Figure 5q). Fruit spherical, with caducous and pilose prickles.

Iconography. Cristóbal (1960), fig. 75; Cruz & Esteves (2009), pl. 1, p. 265.

Selected material from the Atlantic Forest. BRAZIL. BAHIA: Camaçari, “Monte Gordo”, 14.VII.1983, fl. & fr., *H.P. Bautista & G.C.P. Pinto 829* (FCAB, NY [photo!]). SÃO PAULO: Rancharia, 14.II.1970, fl. & fr., *G. Hatschbach et al. 23499* (MBM [photo!], NY [photo!], RFA, UPCB, US); *Souza 10927* (SPF! [barcode: SPF116565]).

Distribution and habitat. Brazil (Bahia, Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Piauí, São Paulo); Bolívia (Santa Cruz, Chuquisaca); Guyana (Upper Takutu-Upper Essequibo), Paraguay (Amambay), Venezuela (Mérida). This is the most widespread species of *Ayenia*, found in dry areas of Venezuela, in the

Guyana Shield, in open or seasonally dry areas of Central Brazil, in the Chaco and in riverine, decidual forests or anthropic areas, in transition between the Cerrado or Caatinga and the Atlantic Forest. In the Atlantic Forest, there are some representatives in Bahia, São Paulo and Mato Grosso do Sul states (Figure 2d).

General comments. *Ayenia tomentosa* is quite distinctive due to its shrubby lifeform and tomentose leaves, and also by bearing an androgynophore with almost the same length of the staminal tube.

Preliminary conservation assessment. *Ayenia tomentosa* is a widespread species through the South American continent that is LC (Low Concern) according to the IUCN criterium B.

II. *Byttneria* Loefl., *Iter Hispan.*: 313. 1758. *nom. cons. vs. Butneria* P. Browne, Civ. Nat. Hist. Jam., 166: 490, 1756 *et Butneria* Duhamel, Traité Arbr. Arbust., 1: 113-114, t. 45. 1755 (?*Calycanthus* L. Syst. Nat. 10: 1053. 1759). Type: *Byttneria scabra* L., Syst. Nat., 10(2): 939. 1759.

Chaetaea Jacquin, Enum. Plant. Carib., 1: 2. 1760. Type: *C. aculeata* Jacq. [= *B. aculeata* (Jacq.) Jacq.].

Pentaceros Meyer ("*Pentaceras*"), Prim. Fl. Esseq., 1: 136. 1818 [Nov 1830]. Type: *P. aculeatus* G.Mey. [= *B. divaricata* Benth.], *nom. rej. vs. Pentaceras* Hook.f. (filled as Rutaceae).

Heterophyllum Bojer ex Hook., Bot. Misc. 1: 291. 1830 [Apr-Jul 1830]. Type: *H. ramosum* Bojer ex Hook. [= *B. heterophylla* Hook.].

Shrubs erect to decumbent or **lianas**; branches with simple and stellate hairs; branches cylindrical, sometimes quadrangular or pentagonal, unarmed or aculeate. **Leaves** simple, alternate, estipulate, leaf petiolate or (sub-)sessile; margin entire or partially to totally serrate; abaxial side with 1-5 extrafloral nectaries each with one or more apertures, placed near the leaf base, on the midvein or main veins or at junction of the blade to the petiole; primary venation actinodromous, major secondary veins semicraspedodromous to eucamptodromous or brochidodromous.

Inflorescence axillary cymes, 3-9 flowers, with small bracts; peduncle usually very short to seemingly absent; bracteoles 1-2 per flower, usually persistent until the anthesis. **Flowers** bisexual, actinomorphic, dichlamydeous and heterochlamydeous; calyx symsepalous, sepals lobate, elliptical to filiform, valvar aestivation, corolla choripetalous, petals unguiculate, divided in a lower stalklike portion (= claw), membranous or fleshy, pubescent or glabrous, more or less narrowed, in which the petal sticks into the flower; a median winged portion (the "hood", which is herein considered as part of the claw); and an upper portion (= lamina), the latter also fleshy or membranous, cylindrical, rarely flat, glabrous or pubescent, equal or until 5 times larger than the claw in length; stamens 5, opposite to petals, with filaments united forming a campanulate to urceolate staminal tube; anthers bithecae, divergent, sessile or subsessile; staminodia 5, fleshy, alternate to petals, free or connate at the base, united to the staminal tube; gynoecium syncarpous, 5-carpelar and 5-locular; styles 5, connate almost up to the apex; stigma inconspicuous or capitate, with 5 globose lobes; ovules 2 per locule. **Fruit** a globose schizocarp, dehiscence septicidal or loculicidal, aculeate with acute to acicular prickles, persistent or caducous; seeds ovoid, brown or black, smooth or tuberculate, not winged.

Byttneria is a pantropical genus with c. 130 species, most of them found in the Neotropical region. In South America, there are c. 70 species, predominantly found along the open seasonally dry areas of the Brazilian Cerrado and Caatinga, but with other representatives in other forested and riverine areas. In the last review of the group, Cristóbal (1976) recognized six sections, based on morphological characters. In South America, there are species of the sections (1) *B.* sect. *Byttneria* (21 species, all Neotropical), (2) *B.* sect. *Vahihara* (Pantropical; 61 species, 13 Neotropical), (3) *B.* sect. *Urticifolia* (15 species, all Neotropical), and (4) *B.* sect. *Crassipetala* (Paleotropical and Neotropical; 22 species, 19 from the Neotropics).

Byttneria can be distinguished from its allied genus *Ayenia* by bearing an extrafloral nectary (sometimes more, three or up to five) on the abaxial side of the leaf blade, usually located at the base of the midveins. Nectary morphology is quite variable (Figure 2 and 4), as this structure may contains one or more apertures (i.e., it is uni or multiapertured) with variable pubescence and location. The nectary region is usually seen at naked eye, but the nectary cavity of one aperture can only be seen when the nectary is uniaperturate (Figure 4e-f). In species with multiaperturate nectary (Figure 4a-d), that region can be found at naked eye or under a stereomicroscope, but each aperture is microscopic, only seen with a higher magnification (Arbo, 1977).

Byttneria has no conspicuous androgynophore (while *Ayenia* and *Rayleya* do), with two thecae (unlike *Ayenia*), and the length of the petal claw is less than or equal to the petal lamina (in *Ayenia*, the claw length is much larger than the lamina in length). Further diagnostic characters are mostly vegetative, related to life form, leaf features, occurrence and size of the shoot prickles. Nevertheless, floral characters such as indumentum, size and form of the petal lamina and claw are also variable (Figures 3 and 5), and thus important for infrageneric delimitations.

Byng & Christenhusz (2018) proposed to synonymize all *Byttneria* to *Ayenia*, probably based on published phylogenies for the group (Whitlock et al., 2001; Whitlock & Hale, 2011). However, most branches on the phylogenies hitherto published are not strongly supported to allow any consistent taxonomical recircumscriptions. As a matter of fact, developing works on systematics of *Ayenia* revealed another panorama in the classification of the group (W. Sharber, pers. comm.), with *Byttneria* being paraphyletic and *Ayenia* being nested inside it. Therefore, in this work we do not adopt the proposal of Byng & Christenhusz (2018) and maintain the two genera as distinct for now.

II.1. *Byttneria abutiloides* A.St.-Hil. & Naudin, Ann. Sci. Nat., Bot. sér. 2, 18: 31. 1842. Type: Brazil, "*In montibus Serra dos Órgãos*" [Rio de Janeiro]. *G. Gardner 326*, 1838 (holotype: K!; isotypes: BM [photo!], G 2x [photo!], GH [photo!], MO [photo!], NY 2x [photo!], P 2x [photo!], S [photo!], W [photo!]).

Byttneria rivularis Gardner, London J. Bot. 2: 333. 1843, *nom. superfl.* Type: *G. Gardner 326*, 1838, holotype: probably BM [photo!]; isotypes: K [photo!], NY [photo!], S [photo!], W [photo!]).

Ayenia abutiloides (A.St.-Hil. & Naudin) Christenh. & Byng, Global Fl. 4: 134. 9 Feb 2018 [epublished].

Synoptic description. Decumbent shrubs, branches cylindrical, aculeate. Leaf petiolate, microphyllous (225–2,025 mm^2), blade ovate, symmetric, margin serrate, acute at apex, cordate at base; nectaries 3-5 per leaf, multiaperturate, dark, on the base of the midvein in the abaxial side; veins glabrous, primary venation actinodromous; major secondary veins semicraspedodromous. Flowers yellowish-green, petal claw membranous. Fruit spherical, densely aculeate.

Iconography. Cristóbal (1976), fig. 44.

Selected material from the Atlantic Forest. ESPÍRITO SANTO: Cachoeiro de Itapemirim, 5.V.1949, fl., *A.C. Brade 19762* (RB!, CTES).

Distribution and habitat. Brazil (Espírito Santo, Rio de Janeiro). Grows in humid areas near to watercourses in ombrophyllous forests (Figure 2b).

General comments. *Byttneria abutiloides* is one of the few species bearing more than one nectary on the abaxial side of the leaf. Additionally, its petal lamina size and indumentum make it easily distinguished from other species in the genus. All examined specimens are old, from densely forested regions, with unprecise location. Even inhabiting in a region with relatively high levels of collection effort, this is a species with a very scarce documentation (Oliveira et al., 2019; Colli-Silva et al., 2019).

Preliminary conservation assessment. According to the IUCN preliminary categories, *B. abutiloides* should be considered as EN (Endangered). However, given the scarce, old collections, we believe it should be considered not as threatened, but as Possibly Extinct (EX).

II.2. *Byttneria australis* A.St.-Hil., Fl. bras. Merid. 1(4): 145. 1825. Type: Brazil, "*Province de Sainte-Catherine*" [Santa Catarina], 1816, *Saint-Hilaire s.n.* (holotype: P [photo!]; isotype: F [photo!]).

Solanum brevipes Dunal in A.DC., Prodr. Syst. Nat. Regni Vegetabilis 13(1): 203-204. 1852 (as Solanaceae). Type: Brazil. Santa Catarina, 1834, *Bacle* s.n. (holotype unknown; lectotype here designated MPU [photo!])

Ayenia australis (A.St.-Hil.) Christenh. & Byng, Global Fl. 4: 135. 9 Feb 2018 [epublished].

Synoptic description. Erect shrubs, branches cylindrical, aculeate. Leaf petiolate, microphyllous (225–2,025 mm^2), blade oblanceolate, symmetric, untoothed margin, acuminate at apex, acute base (Figure 3d); nectary 1 per leaf, multiaperturate, located on the base of the midvein in the abaxial side; veins glabrous, primary venation pinnate; major secondary veins brochidodromous. Flowers yellowish-green, petal claw membranous, flat (Figures 5a-b and 6c). Fruit globose, with small prickles.

Iconography. Cristóbal (1976), figs. 5, 7 and 26; Cruz & Esteves (2009), pl. 1, p. 265.

Selected material from the Atlantic Forest. BRAZIL. SANTA CATARINA: Itajaí, 29.XII.1958, fl., *R. Reitz 6065* (HBR, NY, R!); Lomba Alta, 7.III.1949, fl., *F.K. Rawitscher s.n.* (SPF 80238) (SPF!); Botuverá, 1.IV.2007, fr., *J.A. Fazini* s.n. (FURB 27342) (FURB [photo!]). RIO GRANDE DO SUL: São Leopoldo, X.1941, *J.E. Leite 574* (NY [photo!]); Irai, Balneário Osvaldo Cruz, 23.I.1990, *A. Krapovickas & C.L. Cristóbal 43484* (K!; MO); Marcelino Ramos, 15.II.1993, fl., *J.A. Jarenkow 2320* (ESA [photo!], FLOR, ICN, MBM). PARANÁ: Cianorte, 24.VIII.1967, fl., *G. Hatschbach et al. 16973*

(MBM, NY [photo!]); São Mateus do Sul, 14.XI.1988, fl., *G. Hatschbach et al. 52524* (F, MBM, US [photo!], UPCB). SÃO PAULO: São Pedro, 15.VI.2000, *S. Gandolfi et al. s.n.* (ESA 4x [photo!]).

Distribution and habitat. Brazil (Paraná, São Paulo, Santa Catarina, Rio de Janeiro, Rio Grande do Sul). Mainly in disturbed forested areas of the southern portion of the Atlantic Forest, in moist environments, where it can be quite abundant. There are some records also in the grasslands of the Brazilian Pampas (Figure 2a).

General comments. Records of *Byttneria australis* are relatively abundant from its native areas. This species has a quite distinctive petal (Figures 5b and 6c), with the bi-winged portions of the hood and the lamina both fleshy and claw membranous.

Preliminary conservation assessment. *Byttneria australis* is typical to the southern portion of the Atlantic Forest of Brazil, but with a wide collection and several records inside protected areas. Thus, the IUCN criteria flags to be a “Least Concern” (LC) or “Near Threatened” (NT) taxon. Given it is an endemic species, we believe the latter category—Near Threatened—may suit better.

II.3. *Byttneria beyrichiana* K.Schum., in Mart., Fl. bras. 12(3): 96. 1886. Type: Brazil, Rio de Janeiro (“*Rio Janeiro*”), 1844, *Beyrich s.n.* (holotype: F [photo! barcode: F0BN9576], destroyed, photography only).

Byttneria beyrichiana var. *glazioviana* K.Schum. in Mart., Fl. bras. 12(3): 96. 1886. Type: Brazil, “*Habitat in Brasiliae provincial Rio de Janeiro prope metropolin*” [Rio de Janeiro], 1877, *Glaziou* 8571 (syntypes: K! [barcode: K1213508] (lectotype here designated), R! [barcode: R7734], G [photo! barcode: G358337].

Ayenia beyrichiana (K.Schum.) Christenh. & Byng, Global Fl. 4: 135. 9 Feb 2018 [epublished].

Synoptic description. Decumbent shrubs, branches cylindrical, aculeate. Leaf petiolate, notophyllous (2,025–4,500 mm^2), blade ovate, symmetric, margin slightly crenate to serrate, acuminate apex, truncate to concavo-convex base (Figure 3e);

nectary 1 per leaf, multiaperturate, located on the base of the midvein in the abaxial side; veins hairy, primary venation actinodromous; major secondary veins semicraspedodromous. Flowers purplish, petal claw membranous, flat (Figures 5c). Fruit subglobose, irregularly aculeate.

Iconography. Cristóbal (1976), fig. 21.

Selected material from the Atlantic Forest. BRAZIL. RIO DE JANEIRO: Rio de Janeiro, 3.III.1974, fl. & fr., *P. Carauta 1692* (CTES, MBM, NT [photo!]).

Distribution and habitat. Brazil (Rio de Janeiro), growing in the ombrophyllous forests of "Serra da Pedra Branca" (Figure 2b).

General comments. *Byttneria beyrichiana* is quite similar to another species from open or seasonally dry areas, *B. fernandesii*, which inhabits the Brazilian Caatinga, and also to the widespread *B. filipes*. Nevertheless, *B. beyrichiana* can be distinguished from *B. fernandesii* due to its aculeate branches (*vs.* unarmed branches in the latter) and its dehiscent fruit (*vs.* indehiscent). Conversely, the flowers of *B. beyrichiana* can be distinguished from *B. filipes* due to its glabrous petals (*vs.* pilose in the base in *B. filipes*). The variety described by Schumann in *Flora brasiliensis* was later treated as a synonym by Cristóbal (1976). As that variety was defined based on continuous and variable characters (i.e., small differences on the shape and density of the leaves indumentum and number of flowers per inflorescence), we here follow Cristobal's treatment.

Preliminary conservation assessment. This is a very narrow endemic species to Rio de Janeiro state, with its last collection from the early 1970s. Although according to the IUCN criterion B this species should be considered as EN when considering its population density (AOO = 16 km^2 and EOO = 2,481 km^2) we believe it should be classified as CR, given the old remain collections in the herbaria.

II.4. *Byttneria catalpifolia* Jacq., Pl. Rar. Hort. Schoenbr. 1: 21. 1797. Type: "*Crescit ad Caracas*", 1793, unknown collector (holotype: W according to Cristóbal (1976), but not seen in any virtual herbaria)

Ayenia catalpifolia (Jacq.) Christenh. & Byng, Global Fl. 4: 135. 9 Feb 2018 [epublished].

Synoptic description. Lianas, branches cylindrical, unarmed. Leaf petiolate, mesophyllous (4,500–18,225 mm^2), rarely macrophyllous (18,225–164,025 mm^2), blade widely ovate, symmetric, margin untoothed, straight to slightly acuminate apex, base widely cordate (Figure 3f); nectary 1 per leaf, multiaperturate, located on the base of the midvein in the abaxial side; veins prominent, especially at the abaxial side, primary venation actinodromous, with 3-4 veins leaving the petiole; major secondary veins brochidodromous. Flowers whitish to pink, petal claw membranous, flat. Fruit variable in shape and size and prickle density (Figure 5k-m), depending on the subspecies—see discussion below.

Iconography. Schumann in Martius (1886), v. XII, part. III, fasc. 96, pl. 20; Cristóbal (1976), figs. 7, 87-88; Cruz & Esteves (2009), pl. 1, p. 265.

Selected material from the Atlantic Forest. *Byttneria catalpifolia* subsp. *catalpifolia*—BRAZIL. BAHIA: Ilhéus, s.d., *J.S. J.S. Blanchet 2386*, (US); *J.S. J.S. Blanchet s.n.*, 1836 (NY 627561) (NY [photo!]). CEARÁ: Pacoti, "mata da Serrinha", 14.VI.1957, fr., *T.N. Guedes s.n.* (RB 114220) (RB!). PERNAMBUCO: Vicência, 30.VII.1968, *D. Andrade-Lima* 68-5422 (IPA 18856) (IPA); Nazaré da Mata, 15.VII.1953, fl. & fr., *J.C. Moraes 791*, (SPF!). *Byttneria catalpifolia* subsp. *sidifolia*—ARGENTINA. MISIONES: Iguazú, fl. & fr., 27.III.1970, *A. Krapovickas et al. 15737,* 1970 (CTES). BRAZIL. SÃO PAULO: Araras, fl., 02.IX.1984, *J.R. Pirani et al. 845* (SPF!); Limeira, 1954, *W. Hoehne s.n.* (SPF 15260) (SPF!); Timburi, fr., 14.VI.1995, *J.Y. Tamashiro 1265* (SPF!). PARANÁ: Terra Boa, 14.V.1969, fr., *G. Hatschbach et al. 21480* (NY [photo!]).

Distribution and habitat. *Byttneria catalpifolia* is one of the most widespread species of *Byttneria*, occurring throughout the Neotropics and with disjunct populations in tropical Africa and French Polynesian, found mainly in tropical forests (Figure 2c).

General comments. Cristóbal (1976) mentioned three subspecies of *B. catalpifolia*, two of them native to the Neotropics: the typical one and *B. catalpifolia* subsp. *sidifolia* (A.St-Hil.) Cristóbal. The populations from Africa were recognized as *B. catalpifolia* subsp. *africana* (Mast.) Exell & Mendonça, and mostly resemble *B. catalpifolia* subsp. *sidifolia.* Regarding the Neotropical taxa, *B. catalpifolia* subsp. *catalpifolia* differs from the subsp. *sidifolia* due to the following characters: (1) leaf indumentum pubescent, usually with denser stellate hairs (*vs.* less pubescent leaves, with scarcer stellate hairs); (2) margin of the petal lamina erose to sub-erose (*vs.* entire), and (3) fruit spherical, not flattened, smaller in dimensions but with larger prickle length and density (*vs.* flattened fruit with a lobed equatorial portion, larger in dimensions but with smaller and less dense prickles) (Figure 5k-m). In the Atlantic Forest, *B. catalpifolia* subsp. *catalpifolia* is more abundant in its northern portion, with records in Bahia, Espírito Santo and Pernambuco states. *Byttneria catalpifolia* subsp. *sidifolia* is more abundant in the southern portion of the domain, with records especially in Rio de Janeiro, Paraná and São Paulo states (Figure 2c). The orthographical variation, "*B. catalpaefolia*", found in older works and herbarium specimens, must be replaced in conformity with the Article 60.10 of the ICBN (Thurland et al., 2018).

Preliminary conservation assessment. Both subspecies are geographically widespread and have numerous herbarium records; therefore, they can be categorized as LC (Least Concern), as suggested by the preliminary assessment.

II.5. *Byttneria cristobaliana* Dorr, Kew Bull. 54(4): 991-992. 2000. Type: Brazil, Buerarema, 1995, *J.G. Jardim 637* (holotype: CEPEC; isotypes: NY [photo!], US [photo!], SP [photo!], CTES [photo!]).

Ayenia cristobaliana (Dorr) Christenh. & Byng, Global Fl. 4: 135. 9 Feb 2018 [epublished].

Distribution and habitat. Brazil (Bahia). A species found mainly in disturbed areas or in secondary ombrophyllous forests of the Atlantic Forest (Figure 2c).

Synoptic description. Decumbent shrubs, branches cylindrical, densely aculeate. Leaf petiolate, microphyllous (225–2,025 mm^2), blade linear-lanceolate, symmetric, margin untoothed, acuminate apex, cuneate to convex base; nectary 1 per leaf, multiaperturate, located on the base of the midvein in the abaxial side; veins pubescent, the main vein bordered by a cinereous portion, different in color from the rest of the blade (see Dorr, 1999); primary venation pinnate, major secondary veins brochidodromous. Flowers purple, petal claw membranous, flat. Fruit not seen.

Iconography. Dorr (1999), figs. 1-2.

Selected material from the Atlantic Forest. BRAZIL. BAHIA: Itabela, 17.V.1971, fl., *T.S. Santos 1657* (CEPEC [barcode: CEPEC6871]).

General comments. *Byttneria cristobaliana*, described by Dorr (1999), resembles *B. australis* and occurs in the southern portion of the Atlantic Forest. However, the two differ mainly due to the adaxial face markedly maculate in *B. cristobaliana* (*vs.* non maculate in *B. australis*). Besides, the petiole length in *B. cristobaliana* is smaller than in *B. australis*. Full description accompanied by illustrations can be found in Dorr (1999).

Preliminary conservation assessment. The collection of the species is rather scarce, and there are no records inside any protected areas since the description of the name. Hence, according to the IUCN criterium B (spatial parameters: AOO = 8 km^2, EOO = 17 km^2), we believe it should be categorized as EN (Endangered).

II.6. *Byttneria filipes* Mart. ex K.Schum. in Mart., Fl. bras. (in Martius) 12(3): 95. 1886. Lectotype [inadvertently designated by Cristóbal, 1972]: Brazil, Bahia, Jacobina ("*...ad Serra da Jacobina et Villa da Barra*"), 1995, *J.S. Blanchet 2660*, E [photo!] [here designated as the second-step lectotype] (isolectotypes: BM [photo!], G 4x [photo!], NY [photo!], K [photo!], F [photo!], GH [photo!], W, LE); syntypes: "*Locis haud indicates: Martius*", *Glaziou 10329* P 2x [photo!]; "*Etiam in Paraguay ad Villa* occidental", *Lorentz* s.n. GOET.

Byttneria martiana K.Schum. in Mart., Fl. bras. 12(3): 94. 1886. Type: Brazil, "*Habitat in Brasilia, loco haud indicato: C.F.P. Martius (Iter Brasil)*", M [barcode: M19639].

Byttneria paraguayensis (Britton) Chodat ("*Buttneria paraguayensis*"), Bull. Herb. Boissier ser. 2, 1: 403. 1901. Type: Brazil, "*l"Assomption*" [?Asunción], 1888-1889, *T. Morong* s.n., PH [photo!].

Byttneria filipes Mart. ex K.Schum. var. *puberula* Hassl., Trab. Mus. Farmacol 21: 86. 1909. Type: Paraguay, *T. Rojas* 124, GH [not seen].

Ayenia filipes (Mart. ex K.Schum.) Christenh. & Byng, Global Fl. 4: 135. 9 Feb 2018 [epublished].

Synoptic description. Decumbent shrubs, branches cylindrical, aculeate. Leaf petiolate, nanophyllous to microphyllous (25–2,025 mm^2), blade ovate-lanceolate, symmetric, margin untoothed, straight to slightly acuminate apex, convex base (Figure 3g); nectary 1 per leaf, multiaperturate, located on the base of the midvein in the abaxial side (Figure 4c); veins glabrous, prominent, primary venation pinnate, major secondary veins brochidodromous. Flowers yellowish-green, petal claw membranous, flat (Figures 5d and 6d). Fruit small, spherical, with irregular prickles.

Iconography. Cristóbal (1976), figs. 6, 7 and 19.

Selected material from the Atlantic Forest. BRAZIL. BAHIA: Itacaré, 3.X.1998, *J.G. Jardim 1849* (CEPEC; NY [photo! barcode: NY836715]); idem, 4.III.2004, *J.G. Jardim 4213*, 2004 (SPF! [barcode: SPF171593); Conde, 18.VIII.1995, fl. & fr., *G.*

Hatschbach et al. 63138 (CEPEC, ESA [photo!], FLOR, MBM [photo!], MO, SPF!, SPSF, UPCB).

Distribution and habitat. Brazil (Alagoas, Bahia, Ceará, Maranhão, Mato Grosso, Mato Grosso do Sul, Paraíba, Pernambuco, Piauí, Rio Grande do Norte, Sergipe). Also, in Argentina (Entre Ríos, Corrientes, Formosa), Paraguay (Amambay) and Bolivia (Santa Cruz). *Byttneria filipes* is a remarkably disjunct species (Chapter 2), known from riverine forests or arboreal formations of Caatinga and Atlantic Forest and also in the western portion of Brazil, in swampy areas of Pantanal, and the southern countries cited above (Figure 2c).

General comments. Cristóbal (1976) pointed out the morphological array of variation among the specimens of *B. filipes*, but she established no relation to the disjunct pattern of this taxon. Further assessment of herbarium collections and studies on population genetics should clarify the circumscription of *B. filipes.*

Preliminary conservation assessment. As this is a widespread species but with disjunct populations, we propose that *B. filipes* should be categorized as LC (Low Concern).

II.7. *Byttneria gayana* A.St.-Hil., Fl. bras. Merid. 1: 145-146. 1825. Type: Brazil, São Paulo, Lorena ("*Inveni in sylvis primaevis prope pagum disctum Pôrto da Caxueira, haud longe ab urbicula Lorena, província S. Pauli."*), 1848, *A. Saint-Hilaire 596* (holotype: P [photo!]; isotypes: P [photo!], F [photo!]).

Byttneria laevigata Schott ex Pohl, Pl. bras. 2: 70—71, t. 145. 1830. Lectotype [inadvertently designated by Cristóbal, 1972]: Brazil, Rio de Janeiro ("*Habitat inter frutices, cirea Metropolim Rio de Janeiro*"), *Schott* 5378, W 2x (barcodes: W0026559 [here designated as second-step lectotype] [photo!], W0026560 [second-step isolectotype] [photo!]).

Ayenia gayana (A.St.-Hil.) Christenh. & Byng, Global Fl. 4: 136. 9 Feb 2018 [epublished].

Synoptic description. Lianas, branches cylindrical, unarmed. Leaf petiolate, notophyll (2,025–4,500 mm^2), blade ovate to elliptic, symmetric, margin untoothed, acuminate apex, convex base (Figure 3h); nectary 1 per leaf, multiaperturate, located on the base of the midvein in the abaxial side; veins glabrous, flat, primary venation pinnate, major secondary veins brochidodromous. Flowers yellowish-green, petal claw membranous, flat (Figures 5f and 6b). Fruit small, with diminutive, sparse prickles.

Iconography. Cristóbal (1976), fig. 100.

Selected material from the Atlantic Forest. BRAZIL. BAHIA: Porto Seguro, 8.III.1974, *W.W. Thomas et al. 12018* (CEPEC, MO, US [photo!]); RIO DE JANEIRO: Magé, III.1978, fl., *P. Occhioni 8362* (MBM [photo!]); Rio de Janeiro, 21.II.1879, fl. & fr., *A. Glaziou 10330* (P 3x [photo!, R!); ESPÍRITO SANTO: Linhares, 20.II.1986, *L.A. Mattos-Silva 2008* (CEPEC, CVRD, RB [photo!]).

Distribution and habitat. Brazil (Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro). A species endemic to Brazil, mostly found in ombrophyllous forests of the Atlantic Forest, although also occurring in the Southern portion of the Chapada Diamantina plateau, at the central part of Bahia. Within the Atlantic Forest domain, four clustered populations are known: one in southern Bahia, others in Espírito Santo, Rio de Janeiro and Minas Gerais (Figure 2b).

General comments. *Byttneria gayana* resembles *B. catalpifolia*, but the leaves of the first are glabrous (*vs.* tomentose in the latter), and the petal lamina is glabrous (*vs.* pillose in *B. catalpifolia*). Furthermore, examination of materials from the four known disjunct populations revealed no significant morphological distinction among them. Nonetheless, further assessment is desirable to search for evidences of occurrence or lack of genetic flow among those four allopatric populations, to check whether an alternative, improved taxonomic circumscription would be necessary (distinguishing them as subspecies or even distinct species, for example).

Preliminary conservation assessment. According to the IUCN criterium B, *B. gayana* should be considered as NT or LC (Near Threatened or Low Concern), given its wide distribution through southeastern Brazil and southern Bahia. However, as each disjunct population have aggregated individuals, this species could be considered as LC rather NT.

II.8. *Byttneria gracilipes* Baill. ex Cristóbal, Adansonia 2: 167. 1861-62. Holotype [designated by Cristóbal, 1976]: unknown location, unknown collector, s.n., 1849, P [photo! barcode: P2286191] (isotype: F [photo! barcode: F73511F]).

Byttneria gracilipes Baill. Adansonia 9: 336. 1870. [*nom. illeg.*]

Byttneria gracilipes Le Maout & Decne. Traite Gen. Bot. 343. 1868 [*nom. illeg.*]

Ayenia gracilipes (Decne. ex Baill.) Christenh. & Byng, Global Fl. 4: 136. 9 Feb 2018 [epublished].

Synoptic description. Lianas, branches cylindrical, unarmed. Leaf petiolate, notophyll to mesophyll (2,025–18,225 mm^2), blade ovate, symmetric, margin serrate, straight to slightly acuminate apex, convex to slightly rounded base (Figure 3i); nectary 1 per leaf, multiaperturate, located on the base of the midvein in the abaxial side; veins glabrous, only the first mid veins prominent in the abaxial side, primary venation pinnate, with two basal secondary veins, major secondary veins semicraspedodromous. Flowers purple to yellowish-green, petal claw fleshy , flat (Figures 5e and 6a). Fruit small, densely aculeate with small, caducous prickles.

Iconography. Baillon (1861), p. 167; Le Maout & Decaisne (1868), p. 343; Cristóbal (1976), figs. 5, 55-56; Cruz & Esteves (2009), pl. 1, p. 265.

Selected material from the Atlantic Forest [Paratypes]: ARGENTINA. MISIONES: Cainguás, 30.VII.1987, fr., *R. Vanni et al. 875* (SPF!). BRAZIL. PARANÁ: Cerro Azul, 3.V.1977, bot., *G. Hatschbach et al. 39887* (MBM, NY [photo!], MO); SÃO PAULO: Águas da Prata, 21.III.1994, fl., *A.B. Martins et al. 31477*, (UEC [photo!]);

Corumbataí, 21.VIII.1995, fl., *O. Cesar 599*, (SPF!). ARGENTINA. MISIONES: Candelaria, 14.VI.1957, fl. & fr., *J.E. Montes 27254* (MBM [photo!]); Guaraní.

Distribution and habitat. Brazil (Paraná, Rio Grande do Sul, São Paulo) and Argentina (Missiones, Corrientes). A species restricted to the southern portion of the Atlantic Forest, in ombrophyllous forests. In Brazil, it also likely occurs in Santa Catarina state (Figure 2a).

General comments. *Byttneria gracilipes* is sympatric with *B. urticifolia* and they are often confused in herbaria, as pointed out by Cristóbal (1976). The two taxa can be distinguished by the notable presence of prickles on the leaf veins of *B. urticifolia*, absent in *B. gracilipes*. Besides, the fruit of *B. urticifolia* is much more densely aculeate than in *B. gracilipes*, which has smaller and sparser prickles.

Nomenclatural notes. Typification and authorship of *B. gracilipes* is problematic. Baillon (Adansonia 2: 167 (1861)) first mentioned this name when describing the floral development of *Byttneria*, but it consists of a *nomen nudum*. Nevertheless, he mentioned that a specimen of *B. gracilipes* was cultivated at the National Museum of Natural History of France, in Paris, where he developed most of his works (Stafleu & Cowan, 1976). In fact, there is a voucher in P [barcode: P2286191] from 1849 that might be from such specimen. In a latter work on floral development by Baillon published in 1870, *B. gracilipes* is mentioned once more, along with an illustration, but lacking a description or reference to a name from the previous works. Later on, Le Maout & Decaisne (1868) again mentioned *B. gracilipes*, now under an original illustration of *Byttneria* (Traite Gen. Bot.: 343), but also as a *nomen nudum*. Only one century later, Cristóbal (1976) provided a complete description of *B. gracilipes*, mentioning as holotype the preserved specimen of P mentioned by Baillon. Concurrently, she herself assigned a very fragmented material—a voucher of a leaf fragment with no label—from Field Museum (barcode: F73511F) as an isotype of a name with no valid designation. This information, however, is missing in her monography of *Byttneria*, and she is the true author who inadvertently validated the "*B. gracilipes*" in the publication of 1976. The precedence of the isotype designated by Cristóbal, however, remains dubious, and we could not check the physical collection of P to properly evaluate that.

Preliminary conservation assessment. According to the IUCN criterium B, this species should be considered as NT or LC due to its wide range (AOO = 136 km^2 and EOO = 297,684 km^2). We think the category NT is more suitable due to its occurrence in particular areas of the Southern portion of the Atlantic Forest.

II.9. *Byttneria hatschbachii* Cristóbal, Bonplandia 4: 307-310. 1976 (holotype: Brazil, Paraná, Arapoti, *G. Hatschbach et al.* 20042 (CTES [photo!])).

Ayenia hatschbachii (Cristóbal) Christenh. & Byng, Global Fl. 4: 136. 9 Feb 2018 [epublished].

Synoptic description. Erect subshrubs, branches pentagonal, unarmed. Leaf petiolate, mesophyll (4,500–18,225 mm^2), blade linear, symmetric, margin untoothed, straight at apex, with a small apiculous, cuneate at base (Figure 3j); nectary 1 per leaf, uniaperturate, located on the base of the midvein in the abaxial side; veins glabrous, yellow, very prominent in the abaxial side of a greenish leaf, primary venation pinnate, major secondary veins hemieucamptodromous. Flowers purple to yellowish-green, petal claw membranous, lamina with minute hair in its lower portion (Figures 5g and 6g). Fruit small, aculeate, caducous prickles.

Iconography. Cristóbal (1976), figs. 7 and 77; Cruz & Esteves (2009), pl. 1, p. 265.

Selected material from the Atlantic Forest. BRAZIL. PARANÁ: Sengés, 16.X.1997, fl., *G. Hatschbach et al. 67111* (ALCB, ESA [photo!], MBM [photo!], MO), Araucária, 28.X.1972, fl., *G. Hatschbach et al. 30570* (MBM [photo!], NY); Curitiba, 13.XI.1993, *A. Bidá 705* (NY, UPCB [photo!]); SÃO PAULO: Itapeva, *V.C. Souza 7047*, 2002 (ESA 2x [photo! barcodes: ESA26623, ESA21284], SPF! [barcode: SPF108063], SJRP [barcode: SJRP13032]); SANTA CATARINA: Lages, 22.X.2004, fl., *G. Hatschbach et al. 78348* (HUCS, UPCB).

Distribution and habitat. Brazil (Paraná, Rio Grande do Sul, São Paulo, Santa Catarina). A species endemic to Brazil, found at the southern portion of the Atlantic Forest, occurring from São Paulo to Rio Grande do Sul states, reaching the Brazilian Pampas. It inhabits in open or forested moist areas. In the Atlantic Forest, it is common in transitional portions of disturbed areas, particularly in Paraná and São Paulo states (Figure 2a).

General comments. *Byttneria hatschbachii* can be easily confused to *B. scalpellata* and *B. pedersenii*, as mentioned by Cristóbal (1976). The distinction between them rely mainly on the petiole length and leaf blade. *Byttneria hatschbachii* has the petiole lower than the length of the leaf blade, while they have almost the same length in *B. scalpellata*. The leaf blade is rounded in *B. hatschbachii vs.* attenuate in *B. pedersenii*. Besides, in *B. pedersenii* there are some axillary inflorescences with minute flowers, while in *B. hatschbachii*, the inflorescence is terminal.

Preliminary conservation assessment. The wide distribution of *B. hatschbachii* through its native area of occurrence classifies it as NT or LC (Near Threatened or Low Concern) according to the IUCN criterium B. We here propose the category NT rather than LC due to its endemicity in the Atlantic Forest.

II.10. *Byttneria implacabilis* Cristóbal, Bonplandia 4: 190—191. 1976. Holotype: Brazil, Santa Catarina, Garubá, 1973, *A. Krapovickas 23074*, CTES [photo!] (isotypes: RB [photo!], P [photo!], MO [photo!], US, SI, S [photo!]).

Ayenia implacabilis (Cristóbal) Christenh. & Byng, Global Fl. 4: 136. 9 Feb 2018 [epublished].

Synoptic description. Erect subshrubs, branches pentagonal, fistulose and densely aculeate, prickles regularly spread over minor stem branches. Leaf petiolate, notophyllous (2,025–4,500 mm²), blade ovate, symmetric, margin serrate, acuminate apex, convex to rounded base; nectary 1-3 per leaf, multiaperturate, located on the base of the midvein in the abaxial side; veins hairy, flat, primary venation pinnate, major secondary veins semicraspedodromous. Flowers yellowish-green, petal claw fleshy, lamina cylindrical, widely pubescent, with long hairs equally spaced on the lamina margin. Fruit small, aculeate, with acute prickles.

Iconography. Cristóbal (1976), fig. 46.

Selected material of the Atlantic Forest. BRAZIL. PARANÁ: Morretes, 18.III.1909, fr., *P. Dusén 8262* (MO [photo!]); idem, 24.I.1979, fl., *G. Hatschbach et al. 41947* (MBM [photo!], NY, SPF!); Guaratuba, 10.III.1963, fl., *G. Hatschbach et al. 9771*, (MBM [photo!], US). SANTA CATARINA: São Francisco do Sul, 08.IX.2006, *B. Mehlhaff 150* (JOI [barcode: JOI2169]).

Distribution and habitat. Brazil (Paraná, Santa Catarina). A narrow endemic species to the southern portion of the Brazilian Atlantic Forest, occurring in the coastal region of Paraná up to the northern littoral of Santa Catarina. It grows mainly on the understory of forested formations (Figure 2b).

General comments. *Byttneria implacabilis* is distinct mainly by its prominent and dense prickles. It is different from the remaining species due to the presence of multiaperturate nectary on the leaf blade, as well as aculeate and angulose branches, an unusual association of characters in *Byttneria*.

Preliminary conservation assessment. According to the IUCN criterium B, *B. implacabilis* should be categorized as EN (Endangered). Our proposition of such categorization relies on its endemism in a forested area that, although being under anthropic pressure, has a fair sampling effort and collection periodicity (the last collections are from 2006).

II.11. *Byttneria pedersenii* Cristóbal, Bonplandia 4: 271-275. 1976. Holotype: Paraguay, San Pedro, "*36 km N de San Estanislao*", 1968, *A. Krapovickas 13953*, CTES [photo!].

Ayenia subsessilis (Cristóbal) Christenh. & Byng, Global Fl. 4: 137. 9 Feb 2018 [epublished].

Distribution and habitat. Argentina (Missiones); Brazil (Mato Grosso do Sul); Paraguay (Caaguazú). Like *B. gracilipes* and *B. urticifolia*, *B. pedersenii* is also common to the ecotone areas between the Atlantic Forest the Pampas and the Chaco, with records through all Misiones province in Argentina, but some come from the frontier of Brazil and Paraguay (Figure 2b).

Synoptic description. Decumbent subshrubs, branches angulose, ribbed and fistulose, unarmed. Leaf subsessile, with a small winged and ribbed petiole inserted in the stem, notophyllous (2,025–4,500 mm^2), blade linear to slightly lanceolate, symmetric, margin untoothed, straight apex, cuneate base; nectary 1 per leaf, uniaperturate, located on the base of the midvein in the abaxial side (Figure 4e); veins yellow-greenish to ochraceous, prominent in the abaxial side, primary venation pinnate, major secondary veins hemieucamptodromous. Flowers yellowish-green to purple, petal claw membranous, lamina cylindrical, fleshy and pubescent only in its lower portion (Figures 5h and 6f). Fruit small, densely aculeate, with small prickles.

Iconography. Cristóbal (1976), figs. 1 and 79.

Selected material of the Atlantic Forest. ARGENTINA. MISIONES: Apóstoles, 01.II.1961, fl., *R.M. Crovetto 9360* (P [photo!]); Posadas, *Ekman 193*, 1907 (NY [photo! barcode: NY222222]). BRAZIL. MATO GROSSO DO SUL. Bela Vista, 16.XI.2002, fl., *G. Hatschbach et al. 74289* (MBM [photo!], K!).

General comments. *Byttneria pedersenii* resembles *B. hatschbachii*, but the former has axillary inflorescences with small flowers (*vs.* terminal inflorescences in the latter), and the base of its leaf blade is attenuate (*vs.* rounded, expanded in *B. hatschbachii*).

Preliminary conservation assessment. According to the IUCN criterium B, the species should be categorized as NT or LC (AOO = 152 km^2, EOO = 201,563 km^2). We suggest NT due to its endemism in this particular region of the continent.

II.12. *Byttneria scabra* L., Syst. Nat., 10(2): 939. 1759. Neotype designated by Dorr & Wieserma (2010): Venezuela, Bolívar, Alto Caroni, “alrededores de Sta. Elena de Uairén”, 1946, *Lasser 1445* US [photo! barcode: US837983] (isoneotypes: NY, VEN).

Ayenia scabra (L.) Christenh. & Byng, Global Fl. 4: 136. 9 Feb 2018 [epublished].

Byttneria longifolia Turcz. Bull. Soc. Imp. Naturalistes Moscou 25(2): 154. 1852. Syntypes: Venezuela, Caracas, *Funck 156*, P 2x [photo! barcodes: P2286217, P2286218] (lectotype here designated: P2286217); W.

Byttneria salicifolia Roem. & Schult., Syst. Veg, 5: 470. 1819. Type: Venezuela, Caripe, “*Couvent de Capucins entre les Ind. Chaymas*”, *Bonpland 306*, holotype: LZ [destroyed] (isotype: P [photo! barcode: P2286219] (here designated as lectotype)).

Byttneria scabra var. *brasiliensis* K.Schum. in Mart., Fl. bras. 12(3): 87. 1886. Syntypes: Brazil, “*In Brasiliae prov. S. Paulo*” [São Paulo], n.a., *Burchell 4262* (BR [photo! barcode: BR5430581]; lectotype here designated); “*In Brasilia australi, locis haud accuratius addictis*”, *Sello 3457* (P [photo! Barcode: P1900225]).

Byttneria scabra var. *dentata* A.St-Hil. & Naud., Fl. bras. Merid. 1(4): 144. 1825. Type: Brazil, “*In prov. Goyaz ad Rio Pilloens*”, n.a., holotype: *Pohl s.n.* (M [photo! barcode: M211166]); “*In Brasilia australi, locis haud accuratius addictis*”.

Byttneria scabra var. *hastata* K.Schum. in Mart., Fl. bras. 12(3): 87. 1886. Type: Brazil, Minas Gerais, Caldas (“*In prov. Minas Geraes apud Caldas*”), 1855, syntypes: *Lindberg 287a* (BR [photo! barcode: BR5430741 (lectotype here designated); S 2x [photo! barcodes: S12-17529, S12-17530]).

Byttneria scabra var. *latissima* K.Schum. in Mart., Fl. bras. 12(3): 87-88. 1886. Type: Brazil, Minas Gerais, Caldas (“*In provincia Minas Geraes prope Caldas*”), 1863, *Regnell III-282*, syntypes: S 5x [photo! barcodes: S12-17524 (lectotype here designated), S12-17525, S12-17526, S12-17531, S12-17532], P 2x [photo! barcodes: P1900143, P2285046].

Byttneria scabra. var. *serrata* K.Schum. in Mart., Fl. bras. 12(3): 87. 1886. Syntypes: Brazil, "*In prov. S. Paulo et Minarum apud Ypanema, Serra da Lapa, in campis S. Joao d"el Rey et Camapuam*" [São Paulo], n.a., *Martius Obs. 657* (M [photo! barcode: M211165]); "*prope Ytû*" (Itu), s.a., *Riedel 1967*, P [photo! barcode: P1900224 (lectotype here designated)]

Synoptic description. Decumbent subshrubs, branches angulose, aculeate, ribbed. Leaf petiolate, microphyllous (225–2,025 mm^2), blade variable in shape, but usually linear to slightly lanceolate, symmetric, margin usually untoothed, sometimes dentate only in the apex, convex apex, rounded base; nectary 1 per leaf, uniaperturate, located on the base of the midvein in the abaxial side; veins white-yellowish, prominent especially in the abaxial side, primary venation pinnate, major secondary veins semicraspedodromous. Flowers pinkish to purple, petal claw membranous, almost glabrous, with few hairs on the hood, lamina cylindrical, almost glabrous, with sparse hairs in the lower portion. Fruit small, subspherical, with densely sparse caducous prickles.

Iconography. Schumann in Martius (1886), v. XII, part. III, fasc. 96, pl. 19; Cristóbal (1976), figs. 5, 6, 60-61 and 75; Cruz & Esteves (2009), pl. 1, p. 265; Colli-Silva et al. (2019), fig. 2.

Selected material from the Atlantic Forest. BRAZIL. MATO GROSSO DO SUL: Mundo Novo, 10.XII.1982, fl., *G. Hatschbach et al. 45843* (MBM [photo!], MO); MINAS GERAIS: Poços de Caldas, 19.I.1980, fl., *A. Krapovickas et al. 35373* (MBM [photo!], MO); PARANÁ: Curitiba, "Capão da Imbuia", 05.XI.1974, *L.T. Dombrowski 5429* (HCF); Guai, 15.I.1971, fl. & fr., *G. Hatschbach et al. 25963* (MBM [photo!], NY, RFA, US); RIO GRANDE DO SUL: Soledade, 27.XI.2013, fl., *E. Pasini 982* (HUCS, ICN); SÃO PAULO: Patrocínio Paulista, 1893, fl., *A. Loefgren 2151* (SP!).

Distribution and habitat. Brazil (Bahia, Goiás, Distrito Federal, Amazonas, Amapá, Roraima, Mato Grosso, Mato Grosso do Sul, São Paulo, Paraná, Rio Grande do Sul); with disjunct records from Colombia (Vichada, Guainía), Venezuela (Bolívar, Guárico), in the Guianas and in Trinidad and Tobago. *Byttneria scabra* is one of the most widespread species of the genus, occurring mainly in open or seasonally dry areas of Cerrado, the Páramos and the *campo rupestre* vegetations, but also growing within forests in the Amazonian region and reaching the southernmost Brazilian states. In the Atlantic Forrest, it is common in the transitional zones with the Chaco, as well as in some forested or disturbed areas of Paraná, Minas Gerais and São Paulo states (Figure 2c).

General comments. *Byttneria scabra* is the type species of the genus and can be easily distinct from its allies of *Byttneria* sect. *Byttneria* by having both aculeate and angular branches. Several alternate names of *B. scabra* have been proposed through time, including half a dozen varieties recognized by Schumann in his monograph for Flora Brasiliensis. All of these, however, were later synonymized to *B. scabra* on Cristóbal's (1976) monograph, based on an extensive study of variability of shape, size and indumentum of the leaves. However, further studies on population genetics of this widespread and complex taxon would allow a reliable evaluation of its current taxonomic circumscription..

Preliminary conservation assessment. The species should be categorized as LC (Low Concern), considering its actual widespread distribution.

II.13. *Byttneria triadenia* Cristóbal Bonplandia 4: 194-197. 1976. Type: Brazil, Paraná, Paranaguá, 1969, *G. Hatschbach et al. 22866*, holotype: CTES [photo!] (isotypes: MBM).

Ayenia triadenia (Cristóbal) Christenh. & Byng, Global Fl. 4: 137. 9 Feb 2018 [epublished].

Synoptic description. Decumbent shrubs, branches cylindrical, aculeate. Leaf petiolate, microphyllous (225–2,025 mm^2), blade oblanceolate, symmetric, margin serrate with small teeth, straight apex, obtuse base (Figure 3k); nectaries 3 per leaf, multiaperturate, sometimes only visible in stereomicroscope (Figure 4d), located on the base of the midvein in the abaxial side; veins prominent in the abaxial side, primary venation pinnate, major secondary veins brochidodromous. Flowers yellowish-green and purple, petal claw purple, linear, cylindrical, glabrous; lamina cylindrical, fleshy, pubescent (Figures 5i and 6e). Fruit small, spherical, densely covered by small pubescent prickles.

Iconography. Cristóbal (1976), fig. 47.

Selected material from the Atlantic Forest. BRAZIL. PARANÁ: Guaratuba, 20.III.2002, fl., *J.M. Silva 3577* (ALCB 2x, ESA [photo!], HUCS, HUEFS [photo!], MBM [photo!], SPSF, SPF!).

Distribution and habitat. Brazil (Paraná). *Byttneria triadenia* occurs sympatrically with *B. implacabilis,* both endemic to the costal southern portion of the Atlantic Forest, with confirmed occurrence throughout all coastal region of Paraná state. Cristóbal (1976) also mentioned some records in Santa Catarina, but the location of these vouchers is unprecise. It grows mainly in forested and moist formations of the ombrophyllous forests (Figure 2b).

General comments. Besides co-occurring with *B. implacabilis* and other Byttnerieae in the southern coastal portion of the Atlantic Forest (see Chapter 1), this species is distinct from the remaining ones due to the presence of more than one nectary on the base of the midvein, as well as due to its prominent prickles and leaves and branches remarkably pubescent.

Preliminary conservation assessment. According to the IUCN criterium B, the species should be categorized as EN (Endangered), which we also agree.

II.14. *Byttneria urticifolia* Cristóbal Bonplandia 4: 194-197. 1976. Type: Brazil, Paraná, Paranaguá, 1969, *G. Hatschbach et al. 22866*, holotype: CTES [photo!] (isotypes: MBM).

Ayenia urticifolia (Cristóbal) Christenh. & Byng, Global Fl. 4: 137. 9 Feb 2018 [epublished].

Synoptic description. Decumbent subshrubs, branches slightly angulose, densely aculeate, ribbed, with canaliculate aculeate projections. Leaf petiolate, microphyllous (225–2,025 mm^2), blade ovate, symmetric, margin serrate, straight to acuminate apex, subcordate to cordate base (Figure 3l); nectary 1 per leaf, multiaperturate, located on the base of the midvein in the abaxial side; veins glabrous, midribs with prickles, primary venation acrodromous, major secondary veins craspedrodomous. Flowers purple to yellowish-green, petal claw carnose to linear, lamina membranous (Figure 5j). Fruit small, spherical, densely covered by small pubescent prickles.

Iconography. Cristóbal (1976), figs. 1, 5, 7, 54-55.

Selected material from the Atlantic Forest. ARGENTINA. MISIONES: Concepción. *H.A. Keller s.n.*, s.a. (CTES [CTES342419]); Cerro Azul, *A. Krapovickas s.n.*, s.a. (CTES [CTES32512]).

Distribution and habitat. Brazil (Rio Grande do Sul), and neighboring areas in Argentina (Misiones). A species distributed in the southern area of the Atlantic Forest, although more commonly found on dry grasslands and in transitional areas between forest and grasslands, in Rio Grande do Sul state and in Misiones, Argentina (Figure 2a).

General comments. *Byttneria urticifolia* resembles *B. gracilipes*, but has prickles on their leaf veins (absent in the latter), and its fruit is much more densely aculeate than in *B. gracilipes*, with smaller and sparser prickles.

Preliminary conservation assessment. According to the IUCN criterium B, this species should be considered as NT or LC (Near Threatened or Low Concern). We recommend NT due to its occurrence in particular areas of southern South America.

5. Final remarks

In this work we provided updated information on nomenclature, taxonomy, distribution and conservation data for the Byttnerieae, including two genera of Malvaceae *sensu lato* abundant in open/dry habitats, but also with representatives in moist forested environments, such as those of the Atlantic Forest. We described the occurrence of twenty species in two genera (fourteen for *Byttneria* and six for *Ayenia*), being eleven species endemics to this phytogeographic domain. Mostly, species are common in transitional areas between moist and open/dry habitats, especially in ecotone areas of the Atlantic Forest and the Brazilian Pampas.

For the endemic taxa, we have both taxa widely distributed in the southern portion of the Atlantic Forest, but also species very restricted to specific portions of the domain (such as endemics to Rio de Janeiro or Santa Catarina/Paraná states). We believe such information will enhance future studies with the taxonomy and evolution of these groups, and also give subsidies to future studies of conservation and natural history of the Atlantic Forest domain.

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8. Numerical list of taxa and list of exsiccatae

Numbers in parenthesis correspond to the following species-number list, as coded in their description in the main text.

NUMERICAL LIST OF TAXA

I. *Ayenia* L.

1. *A. aprica* Cristóbal
2. *A. erecta* Mart. ex K.Schum. in Mart.
3. *A. glabrescens* K.Schum. in Mart.
4. *A. nummularia* Cristóbal
5. *A. praecipua* Cristóbal
6. *A. tomentosa* L.

II. *Byttneria* Loefl.

1. *B. abutiloides* A.St.-Hil. & Naudin
2. *B. australis* A.St.-Hil.
3. *B. beyrichiana* K.Schum.
4. *B. catalpifolia* Jacq.
5. *B. cristobaliana* Dorr
6. *B. filipes* Mart. ex K.Schum. in Mart.
7. *B. gayana* A.St.-Hil.
8. *B. gracilipes* Baill. ex Cristóbal
9. *B. hatschbachii* Cristóbal
10. *B. implacabilis* Cristóbal
11. *B. pedersenii* Cristóbal
12. *B. scabra* L.
13. *B. triadenia* Cristóbal
14. *B. urticifolia* Cristóbal

LIST OF EXSICCATAE

Abrão et al. 4 (II-2); *Abruzzi* 578 (II-14); *Academia Brasileira de Ciências* 855 (I-2); *Acevedo-Rodriguez* 8968 (II-4); *Agostini* 1049 (II-4); *Alvarez s.n.* (II-8); *Amaral* 319 (I-6); 1090 (II-2); *Anderson* 7471a (II-12); 9112 (I-6); *Anderson et al.* 9112 (I-6); *Andrade-Lima* 52, 54 (II-6); *Arbo* 7993 (II-14); *Assunção* 805 (II-6); *Athayde et al.* 165 (II-10).

Baptista s.n. (II-2); *Barreto* 2607, 8472 (II-7); *Bautista* 829 (I-6); *Beck* 13131 (II-12); *Belem* 100 (I-6); *Bernacci et al.* 1470 (II-2); *Bidá* 75 (II-9); *Biganzoli* 354 (II-8); *Boom* 5002 (II-4); *Brade* 19762 (II-1); *Bresolin* 709 (II-2); *Brito* 103 (II-12); *Brunini* 168 (II-2); *Burnham* 1661 (II-4).

Carauta 1692 (II-3); *Carneiro* 97 (II-8); *Carrasco* 63 (II-4); *Carretero* 865 (II-4); *Carvalho* 55 (I-6); 2606 (I-3); *Caxambu* 841 (II-13); 4543 (II-7); 6659, 6765, 6837 (II-2); *Ceroni & Irgang* s.n. (II-14); *Cid-Moreira* 4684 (II-4); *Citadini-Zanette* 1843 (II-2); *Claros* 2316 (II-6); 9453 (II-4); *Clausen* 1514 (II-12); *Cordeiro et al.* s.n. (II-12); *Costa* 209, 237, 628 (II-12); *Crespo* 2043 (II-12); *Cristóbal* 21 (II-8); *Cruz* 2716, 3242, 3838, 4080 (II-4).

Dalpiaz s.n. (II-2); *Davidse* 14959, 22618 (II-12); *Delnatte* 169 (II-12); *Descole* 3389, s.n. (II-12); *DeWalt* 371 (II-4); *Diaz* 990 (II-12); *Diaz Santibanez* 6257, 7458 (II-4); *Dillenburg* 59 (II-14); *Dodson* 13837 (II-4); *Duarte* 42, 7645 (II-2); *Duarte & Hatschbach* 5326 (II-10); *Durigon* 211 (II-8); *Dusén* 8262 (II-10); 8913, 16574 (II-9).

Edwall 3397 (II-8); *Ely* s.n. (II-2).

Falkenberg 2937, 4534 (II-2); *Faxina* 166 (I-6); *Fazini* s.n. (II-2); *Fernandez* 16120 (II-12); *Fiaschi* 1948 (II-4); *Fleig* 43 (II-8); *Folli* 5929 (II-7); *Fortunato* 2042 (II-6); *Foster* 780 (II-4); *Freitas* 748, 889, 1083, s.n. (II-2); 889 (II-8); *Frey* 459 (II-6); *Funez* 1732, 6260 (II-2).

Gamarra 9459, 9795 (II-4); *Gasper* 1008 (II-2); *Gentry* 31000, 36047, 54630, 65767, 66016 (II-4); 73633 (II-6); *Gomes* 2383 (I-6); *Gonzales* 4483, 5300, 5423, 5588, 5765, 6399 (II-4); *Grandez Rios* 3609 (II-4); *Grupo Pedra do Cavalo* 85 (II-6); *Guaglianone* 3029 (II-12); *Guedes et al.* s.n. (I-6); *Guglieri-Caporal* 3179 (I-6); *Guillen* 302 (II-4); *Guimarães* 80 (II-8).

Harley 15491 (I-6); 1985, 21394 (II-6); 1687, 18797, 27312 (II-12); *Harling* 17975 (II-4); *Hatschbach* 23499, 42119, 45955, 64102, 66032, 73347 (I-6); 8778, 16973, 30332, 35178, 36618, s.n. (II-2); 29591, 35908, 36103, 63138, 76579 (II-6); 31472, 47737, 48698 (II-7); 39887 (II-8); 17259, 27116, 30057, 43379 (II-9); 20628, 41947 (II-10); 26148, 31525, 44791, 45843, 52524 (II-12); 22866 (II-13); *Hatschbach & Ahumada* 31472 (II-7); *Hatschbach & Cordeiro* 52524 (II-2); *Hatschbach & Pelanda* 35117 (II-2); *Hatschbach & Silva* 5497 (II-6); *Hatschbach & Zelma* 50359 (II-10); *Hatschbach et al.* 16973 (II-2); 56657 (I-2); 67111 (II-9); 77380, s.n. (I-6); s.n. (II-13); *Herrera* 69 (II-2); *Hopkins* 787 (II-12).

Jansen-Jacobs 472, 2411 (II-12); 3986 (I-6); *Jansen-Jacobs et al.* 3986 (I-6); *Jardim* 1646, 1908 (II-4); 1849 (II-6); *Jardim et al.* 637 (II-5); *Jarenkow* 712, 1308, 3557 (II-14); 2320 (II-2); *Juchum* 76 (I-6); *Juchum et al.* 76 (I-6).

Kassner-Filho 441 (II-2); *Kegler* 269 (II-2); *Keller* 76 (II-12); *Killeen* 3305, 7332 (II-4); 5680, 6728 (II-12); *Klein* 867, 7807 (II-2); *Klein & Bresolin* 10712 (II-2); *Klein & Souza* 10463 (II-2); *Korte* 52, 204, 544, 1245, 1850, 2703, 3622, 3957 (II-2); *Korte & Kniess* 544 (II-2); *Kostin* 41 (II-2); *Krapovickas* 9661 (I-4); 38733 (I-6); 28893 (II-2); 31516 (II-4); 34868, 35373 (II-12); *Krapovickas & Schinini* 32745 (I-6); *Kuhlmann* 1050 (II-7); *Kuntze s.n.* (II-6).

Leite 574 (II-2); *Liebsch* 89 (II-2); *Liesner* 7882, 9175 (II-4); *Lima* s.n. (II-8); *Lindeman* 766 (II-2); *Lindeman & Haas* 1363 (II-2); *Longhi* 612 (II-2); s.n. (II-14); *Lucheta* s.n. (II-2); *Lund* s.n. (II-1).

Maas et al. 5481 (II-12); *Macedo* 841 (I-6); *Macia* 6811 (II-4); *Magalhães* 279 (I-6); 90 (II-7); *Mamani* 958 (II-4); *Maranta* 305 (II-6); *Marchi* 122 (II-2); *Marchiori* 47 (II-2); 502 (II-8); *Martinez* 20813, 21897 (II-4); *Martins* 31477 (II-8); *Matos-Silva et al.* 194 (I-2); *Maturo* 295 (II-6); *Matzenbacher* s.n. (II-14); *Mondin* s.n. (II-2); *Montes* s.n. (I-1); 10032, 10033, s.n. (I-5); 556 (II-8); 9472, s.n. (II-11); 27254 (II-8); *Mostacedo* 2792 (I-6); *Múlgura* 2073, s.n. (I-1); 2198 (II-8); 2607, 3166 (II-2); s.n. (II-4); *Murakami* 1003 (II-4).

Nee 36439, 37716, 44845, 44874, 47574, 49800 (I-6); 35384, 44968 (II-4); 35638 (II-6); 37726 (II-12); *Neill* 6668 (II-4); *Nelson* 1421 (II-12); *Nicolini* s.n. (II-8); *Nicora* s.n. (I-1); 7995 (II-8); *Nuernberg & Mello* 481, 1080 (II-2).

Occhioni 8362 (II-7); *Oliveira* s.n. (II-7); *Ordones* 1174 (II-7),

Padilla 4255 (II-4); *Palacios & Cuezzo* 1296 (I-1); *Passos* s.n. (II-2); *Paz* 2721, 2790 (II-4); 246 (II-12); *Pereira* 2504 (II-12); *Pereira & Hatschbach* 7809 (II-2); *Pereira-Silva* 8129, 8427 (I-6); *Perez* 1178 (II-4); *Perry* 1203 (II-4); *Piccinini* 2499 (II-6); *Pinto* 211 (I-6); 213 (I-2); *Pirani* 2155 (I-6); 625 (II-2); *Pirani & Yano* 625 (II-2); *Pires* 5212, 9383 (II-12); *Pittier* 10722 (I-6); *Pivetta* 1117 (II-14); *Poliquesi* 7625 (II-8); *Porto et al.* 2168 (II-14); *Pott* 5692, 8444, 15442 (I-6); *Pott & Abreu* 4707 (I-6); *Pott et al.* 2327, 5551, 8486, 13968 (I-6); *Prata et al.* 1915 (I-6).

Queiroz 1719 (II-6); *Quinones* 1087 (II-12).

Rabelo 2273 (II-12); *Rabuske & Brack* 531 (II-2); *Raes* 109 (II-4); *Rambo* 38316, s.n. (II-2); *Reis* 2450 (II-2); *Reitz & Klein* 4021 (II-2); *Resende* 2042 (I-6); *Ribas* 2428 (II-

12); 4021, 5631 (II-2); *Ribas & Pereira* 2397 (I-6); *Riedel* 679 (I-5); *Rio de Janeiro Botanical Garden* 213 (II-7); *Ritter* s.n. (II-2); 4472, 4507, 4541, 4636 (II-6); *Rodrigues* 94 (II-2); *Rodriguez* 1627, 1690, 5363 (II-4); 669 (II-12); *Rodríguez* 545, 698 (II-2); *Rubio* 1797 (II-4).

Sacco 702 (II-14); *Santos* 2510 (I-3); 1657 (II-5); *Saulo* 71 (II-4); *Scarpa* 458 (II-6); *Scherer* s.n. (II-8); *Schinini* 30320 (II-6); 5958 (II-8); *Schlidwein* 2568, s.n. (II-2); *Schneider* 1601 (II-2); *Schultz* 110 (II-2); *Schultz & Irgang* 110 (II-2); *Schwarz* 6429 (I-4); 5459 (I-5); 2159, 2271, 5845, 6362, 7048, s.n. (II-11); *Schwindt* 484, 2029, 2879 (II-11); *Scipioni* s.n. (II-2); *Senna* 871 (II-2); *Sette-Silva* 65 (II-12); *Silberbauer-Gottsberger* 13371 (II-12); *Silva* 942 (I-6); 36, 1757, 9376 (II-2); *Silva & Cordeiro* 3577 (II-13); *Silva-Filho* s.n. (II-2); *Silva-Filho & Grings* s.n. (II-14); *Sinani* 343 (I-6); *Siqueira* 8, 1737, 2184, 2230 (II-2); 401 (II-7); *Siqueira-Filho* 1985 (I-6); *Smith & Klein* 276 (II-2); *Sobral* 3242 (II-2); 15356 (II-12); 1548 (II-14); *Sobral et al.* 721 (II-14); *Sopepi* 566, 2460 (II-4); *Souza* 5260, 10927 (I-6); *Steyermark* s.n. (II-4); *Stival-Santos* 208, 492, 1531 (II-2); *Stival-Santos & Silveira* 492 (II-2); *Stival-Santos et al.* 1531 (II-2).

Takahasi et al. 1081, 1350 (I-6); *Teixeira* s.n. (I-6); s.n. (II-8); *Temponi* 635 (II-2); *Thomas* 12018 (II-7)*;* 13936 (I-3); *Tiepolo & Svolenski* 700 (II-2); *Timana* 1542 (II-4); *Tipaz* 885 (II-4); *Toledo* 11715 (I-6); *Tonon* s.n. (II-8); *Tressens* 4549 (II-2); 5614 (II-8); 3972 (II-14).

Ungaretti 195 (II-2).

Vargas 10239 (II-4); *Velloso* s.n. (II-2); *Verdi* 693, 2681, 2767, 5333, 6368 (II-2); *Verdi et al.* 2767 (II-2); *Viana* 26 (II-6); *Vidal & Paula* 1213 (II-7); *Viégas* s.n. (II-2); s.n. (II-12); *Vieira* 1615 (II-10); *Vigo* 15113 (II-4); *Villalobos* 1559, 4655 (II-4); *Villanueva* 882 (II-12); *Villarroel* 3419 (II-12); *Virgas* s.n. (II-2).

Wasum 719 (II-2); *Werff* 13154 (II-4); *Wessler* s.n. (II-2).

Young 962 (II-4).

Zanatta s.n. (II-8); *Zanette* 1346 (II-2); *Zuloaga* 5044, 7211 (II-8).

Figure 1. General aspect of *Ayenia* (a-b) and *Byttneria* (c-d). *Ayenia* are small mainly shrubs to herbs, up to 0.5 m high, with some species forming rhizomes. On the other hand, *Byttneria* has a more variable set of lifeforms, from shrubs to subshrubs, herbs and lianas. Both species have small reproductive structures, with flowers varying from purplish to whitish, and aculeate fruits (b and d). Photos: (b) *Ayenia angustifolia*, by Gabriela Camargo; (d) *Byttneria scabra*, by Luciano Pedrosa. Voucher photos taken from (a) G. Hatschbach 36255 (*A. angustifolia)* and (c) G. Hatschbach 44791 (*B. scabra*), from MBM digitized collection Available at the speciesLink repository (`www.splink.org.br`).

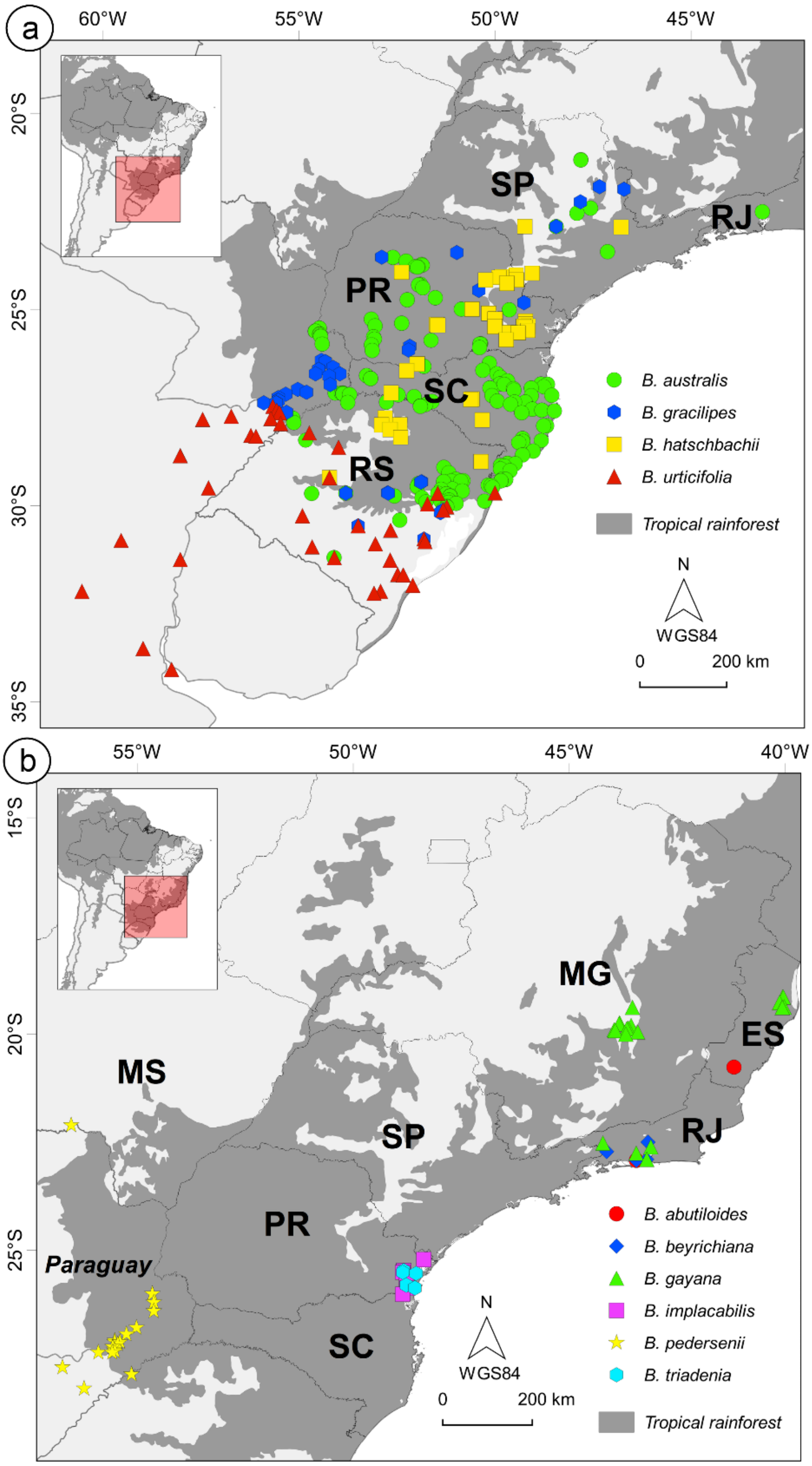

Figure 2. Distribution of the species of Byttnerieae that occur in the Atlantic Forest: (a) *Byttneria* species from the Southern Atlantic Forest portion; (b) endemic species of *Byttneria* from southern and central portions of the Atlantic Forest. We highlight the occurrence of species in the Atlantic Forest domain, and for Brazil in the following states: Espírito Santo (ES), Mato Grosso do Sul (MS), Minas Gerais (MG), Paraná (PR), Rio de Janeiro (RJ), Santa Catarina (SC), São Paulo (SP) and Rio Grande do Sul (RS). *[Continue on the next page]*

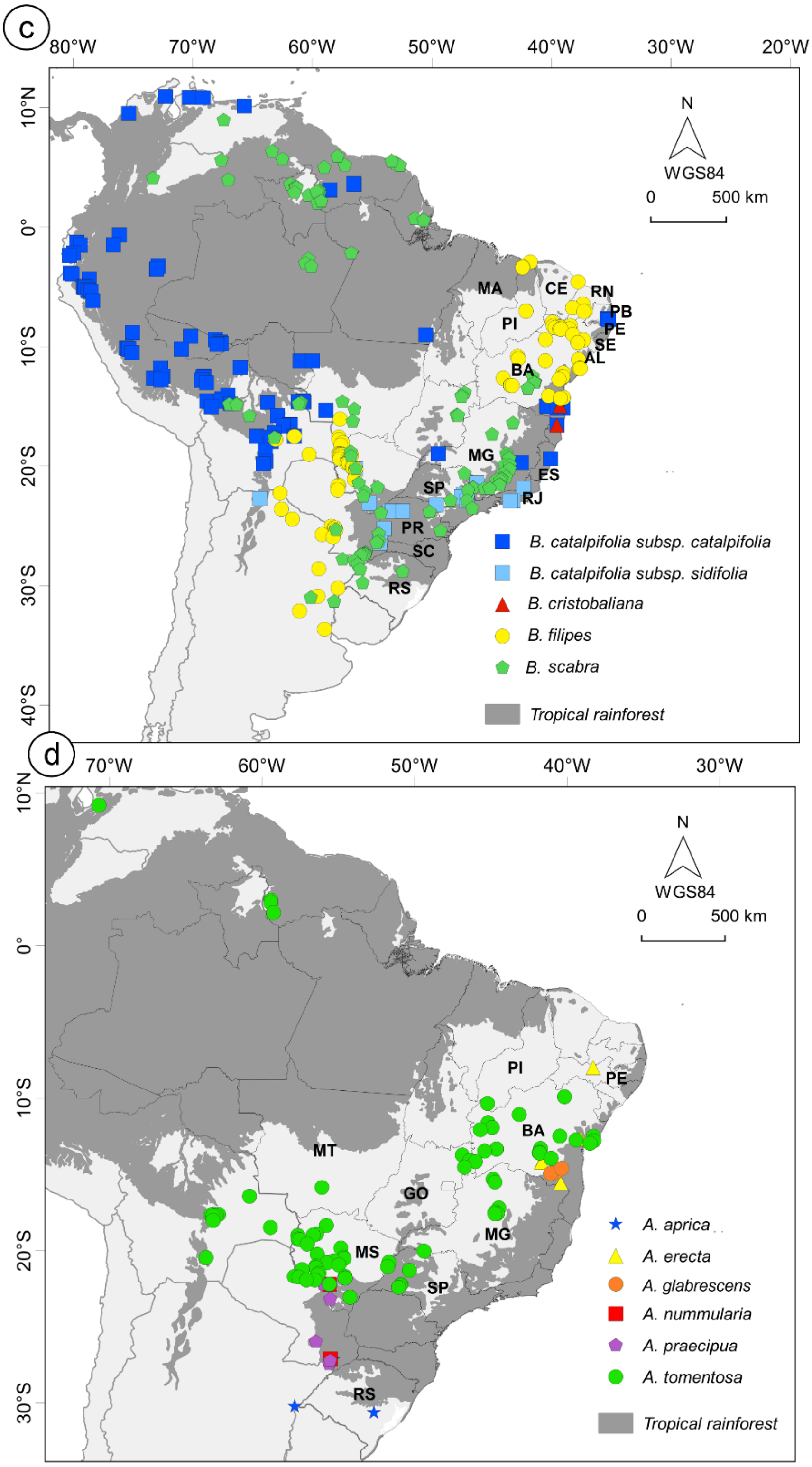

Figure 2 [cont.]. Distribution of the species of Byttnerieae that occur in the Atlantic Forest: (c) widespread species of *Byttneria*; and (d) species of *Ayenia*. We highlight the occurrence of species in the Atlantic Forest domain, and for Brazil in the following states: Alagoas (AL), Bahia (BA), Ceará (CE), Espírito Santo (ES), Maranhão (MA), Minas Gerais (MG), Paraíba (PB), Paraná (PR), Pernambuco (PE), Piauí (PI), Rio de Janeiro (RJ), Rio Grande do Norte (RN), Rio Grande do Sul (RS), Santa Catarina (SC), São Paulo (SP) and Sergipe (SE).

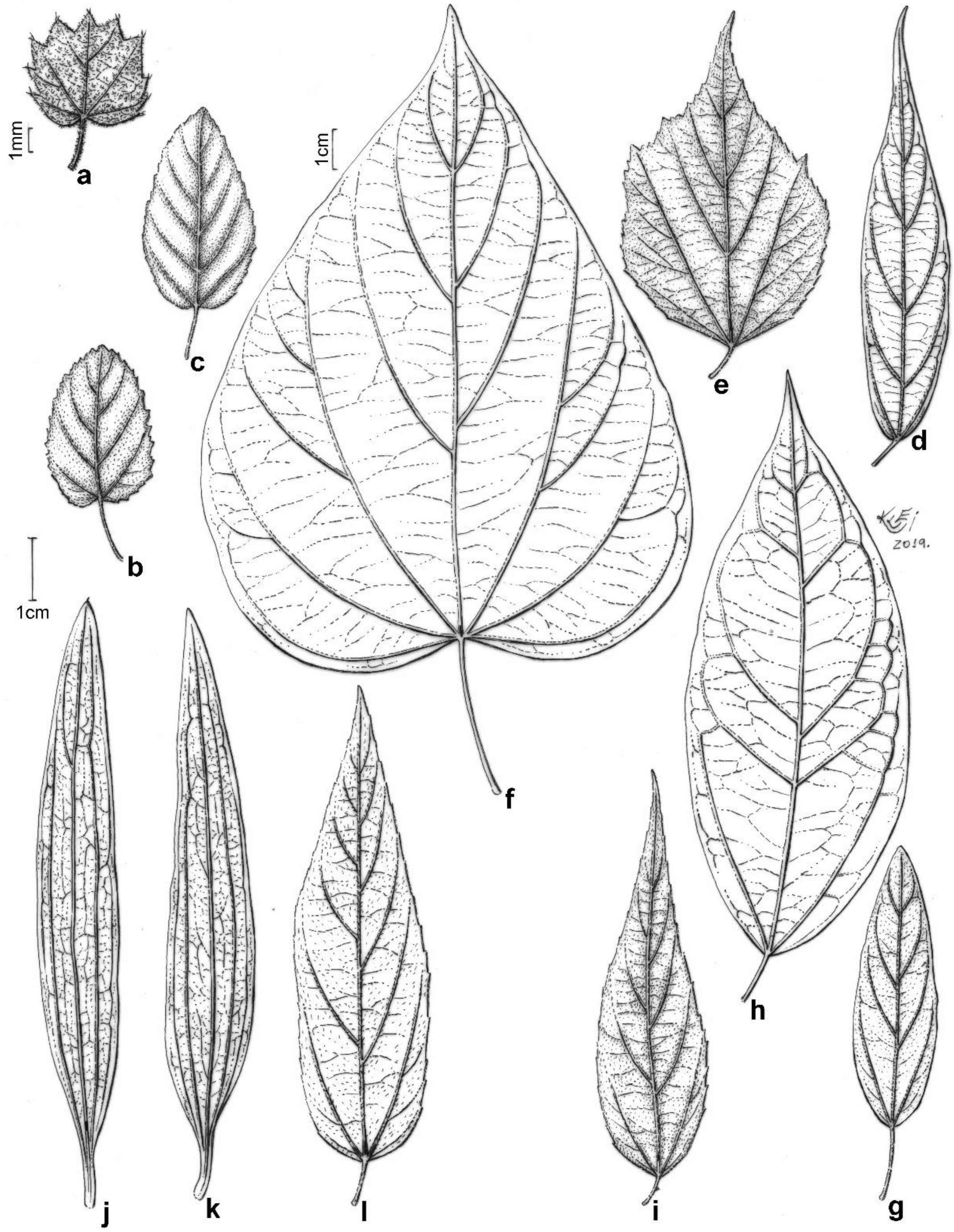

Figure 3. Leaves of selected Byttnerieae species of the Atlantic Forest, depicting variations in form and venation. (a) *A. aprica* (*Krapovickas* 24220 [RB198067]); (b) *A. erecta* (*Silva* 618 [RB762811]); (c) *A. tomentosa* (*Pirani* 2886 [SPF81745]); (d) *B. australis* (*Joly* s.n. [SPF80238]); (e) *B. beyrichiana* (*Carauta* 1692 [RB166547]); (f) *B. catalpifolia* subsp. *catalpifolia* (*Fiaschi* 1948 [SPF165690]); (g) *B. filipes* (*Zardini* 49866 [RB370921]); (h) *B. gayana* (*Kuhlmann* 1050 [SPF196846]); (i) *B. gracilipes* (*Martins* 31477 [SPF98515]); (j) *B. hatschbachii* (*Silva* 224 [SPF70631]); (k) *B. triadenia* (*Silva* 3577 [SPF156413]); (l) *B. urticifolia* (*Arbo* 5861 [SPF48433]). All leaves are on the same scale (indicated near (b), except for (a) and (f), where the proper scale is indicated near each particular illustration.

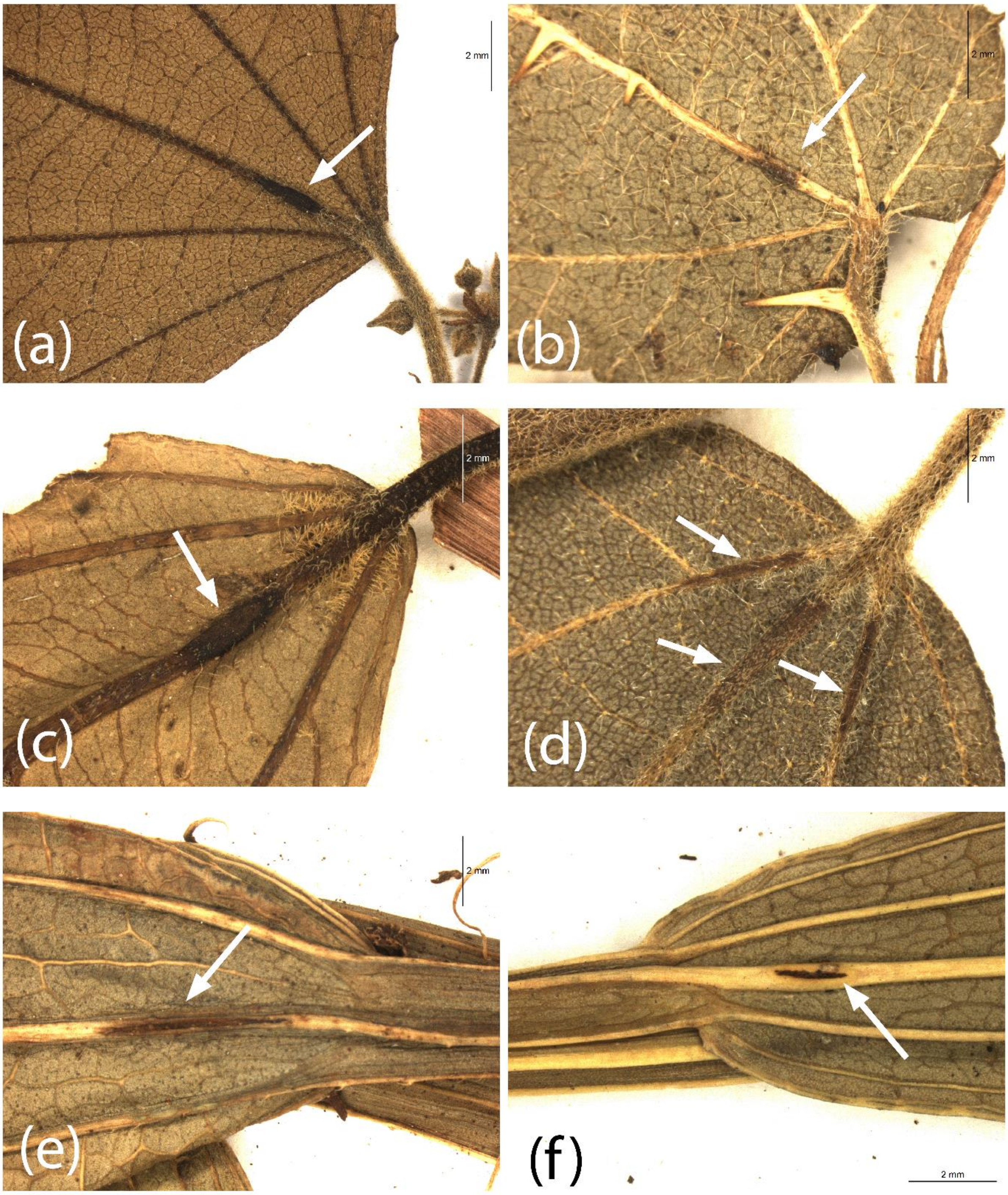

Figure 4. Selection of nectaries of some species of *Byttneria*, highlighting the diversity of form, number of appertures and position of the leaf nectary. (a) Multiaperturate nectary of *B. beyrichiana* (Carauta *1692 [RB166547]*); (b) *B. urticifolia* (also note the prickles on the midveins, something uncommon in the genus) (Arbo *5861 [SPF48433]*); (c) *B. filipes* (also note the concentration of hairs in the base of the midveins) (Zardini *49866 [RB370921]*); (d) *B. triadenia*, with three multiaperturate nectaria (Silva *3577 [SPF156413]*); (e) *B. pedersenii*, with a uniaperturate nectary with a large aperture (Vanni 659 *[SPF48513]*); (f) *B. triadenia*, with a uniaperturate nectary (Silva *3577 [SPF156413]*).

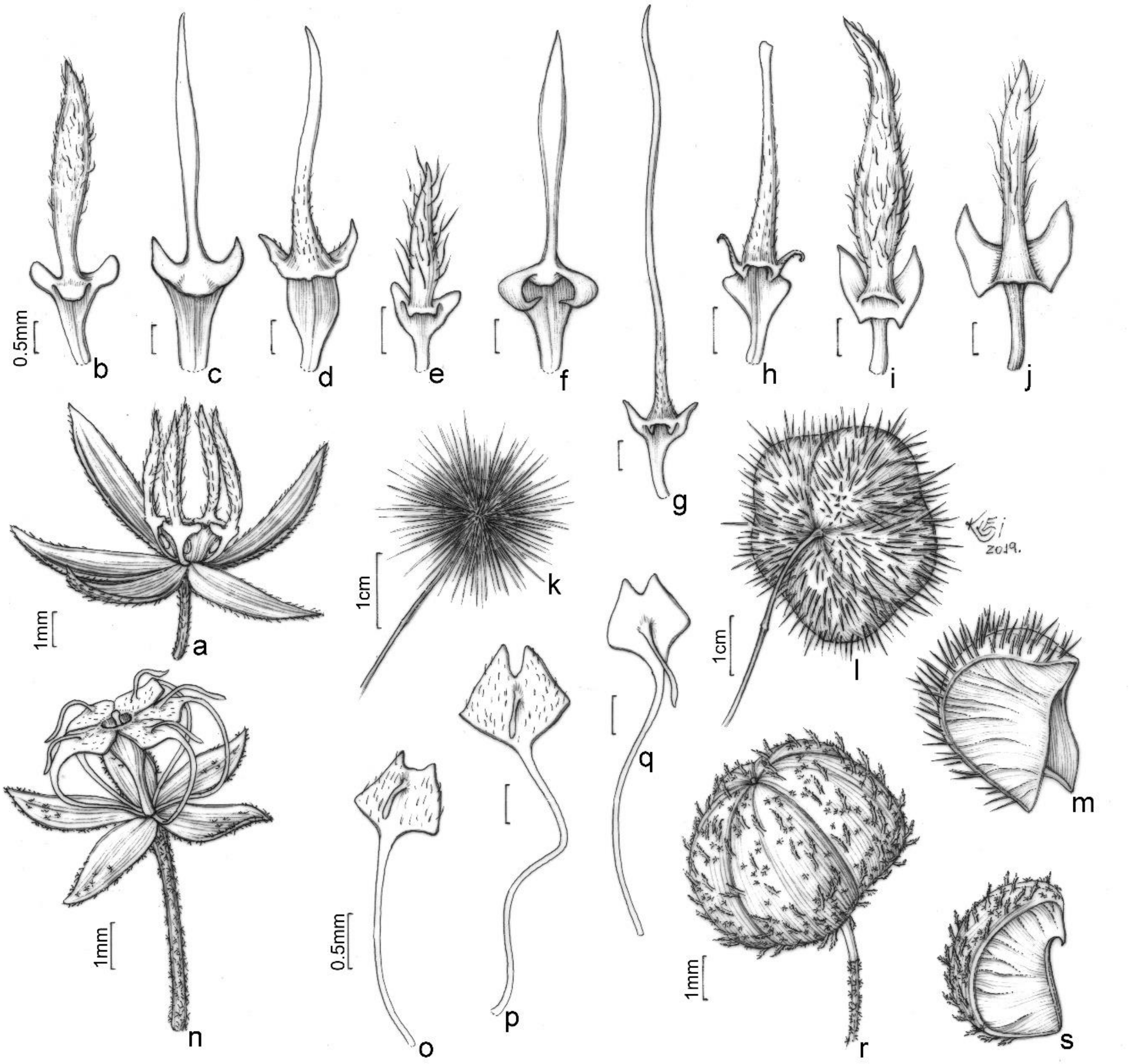

Figure 5. Some of the reproductive diversity of the Byttnerieae of the Atlantic Forest. (a) General aspect of the flower of *B. australis* (*Joly* s.n. [SPF80238]); (b-j) petals from selected *Byttneria* species in a same scale perspective. Petals from, respectively, (b) *B. australis* (*Joly* s.n. [SPF80238]), (c) *B. beyrichiana* (*Carauta* 1692 [RB166547]), (d) *B. filipes* (*Zardini* 49866 [RB370921]), (e) *B. gracilipes* (*Martins* 31477 [SPF98515]), (f) *B. gayana* (*Kuhlmann* 1050 [SPF196846]), (g) *B. hatschbachii* (*Silva* 224 [SPF70631]), (h) *B. pedersenii* (*Vanni 659* [SPF48513]), (i) *B. triadenia* (*Silva* 3577 [SPF156413]), (j) *B. urticifolia* (*Arbo* 5861 [SPF48433]). (k) fruit of *B. catalpifolia* subsp. *catalpifolia* (*Fiaschi* 1948 [SPF165690]); (l-m) fruit of *B. catalpifolia* subsp. *sidifolia* (general aspect in (l) and a mericarp in (m) (*Hatschbach* 62463 [SPF112502]); (n) General aspect of the flower of *A. erecta* (*Silva* 618 [RB762811]); (o-q) petals from (o) *A. aprica* (*Krapovickas* 24220 [RB198067]); (p) *A. erecta* (*Silva* 618 [RB762811]); (q) *A. tomentosa* (*Pirani* 2886 [SPF81745]). (r-s) Fruit and a mericarp of *A. tomentosa* (*Pirani* 2886 [SPF81745]).

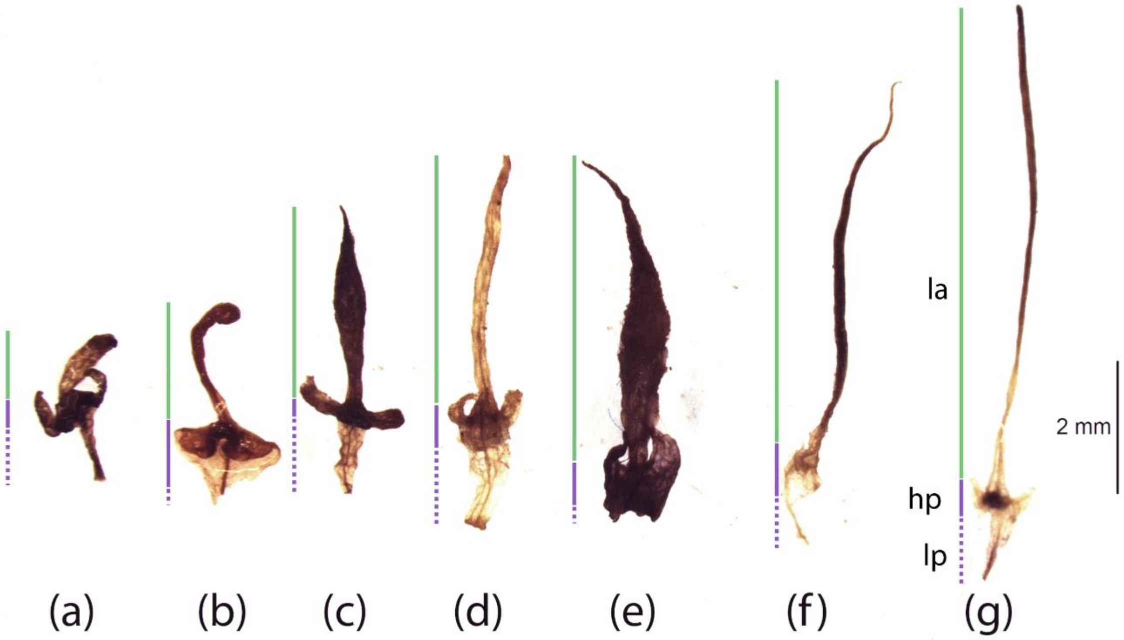

Figure 6. A selection of the morphological variation in a petal of *Byttneria* spp. The petals in this group is unguiculate, divided in a lower laminar and smaller portion—the claw (purple lines)—and an upper expanded bigger portion—the lamina (green lines). Furthermore, the claw is still divided in a lower portion in which the petal inserts in the flower axis (lp, dashed purple lines) and a upper biwinged portion called “hood” (hp, continuous purple lines). The size, form and indumentum of each portion of a petal varies between *Byttneria* species. (a) *B. gracilipes* (Martins *31477 [SPF98515]*); (b) *B. gayana* (Kuhlmann *1050 [SPF196846]*); (c) *B. australis* (Joly *s.n. [SPF80238]*); (d) *B. filipes* (Zardini *49866 [RB370921]*); (e) *B. triadenia* (Silva *3577 [SPF156413]*); (f) *B. pedersenii* (Vanni 659 *[SPF48513*); (g) *B. hatschbachii* (Silva *224 [SPF70631]*).

Notes on the circumscription of *Pterygota* (Malvaceae, Sterculioideae) with special reference to a Brazilian taxon with a misapplied name[*]

Notas sobre a circunscrição de Pterygota *(Malvaceae, Sterculioideae) com particular referência a um táxon brasileiro com nome mal aplicado*

Pending taxonomical problems regarding *Pterygota* Schott & Endl. are related to troublesome circumscription and historical-nomenclatural issues. For instance, *Pterygota brasiliensis* Allemão is cited as *Basiloxylon brasiliensis* (Allemão) K.Schum in some publications, e.g. the Catalog of Plants and Fungi of Brazil (Forzza et al. 2010) and the Checklist of Vascular Plants of the Americas (Ulloa-Ulloa et al. 2017). Conversely, it is referred as *P. brasiliensis* in other works, such as the checklist of species from the Brazilian Atlantic Forest (Dutra et al. 2015) and now in the Brazilian Flora 2020 Project (Ferreira-Júnior 2018). Here, we review and standardize taxonomical issues regarding *Pterygota*, something which has not been addressed since the end of the 1960s, focusing on the Brazilian species *P. brasiliensis.*

Herbarium collections of K, RB, SP and SPF herbaria were visited and analyzed, as well as all digital material Available at online databases (Virtual Herbarium of Flora and Fungi, `http://www.inct.splink.org.br`; Rio de Janeiro Botanical Garden database, `http://jabot.jbrj.gov.br`; C.V. Staar Virtual Herbarium `http://sweetgum.nybg.org/science/vh`; Global Biodiversity Information Facility, `http://www.gbif.org`, and Tropicos® database, of the Missouri Botanical Garden, `www.tropicos.org`). For *Pterygota brasiliensis*, taxonomical literature was also

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consulted to evaluate the nomenclatural history of the names. A distribution map of *Pterygota* was elaborated based on a large record distribution database of some Malvaceae groups maintained by the authors. Such database underwent an intense process of taxonomical validation, data cleaning, and review of records, and it should be available soon (Chapter 1).

Pterygota is a genus traditionally classified in Sterculiaceae, currently Malvaceae *sensu lato*, Sterculioideae. There are about 20 described specific names (Hinsley 2014) proposed in this genus of large trees, mostly found in primary or secondary formations of tropical rainforests. Essentially, *Pterygota* is distinct from its allied *Sterculia* by having winged seeds, usually in higher number than those of the latter. Nevertheless, *Pterygota*'s dispersal ability is relatively more restrict than in *Sterculia* (Yamada & Suzuki 1999). *Pterygota* is a relatively recent genus, with estimates of its origin in the Lower Miocene (≈7 Mya), within the Sterculioideae lineage, which separated from its sister group in the early Oligocene (≈36 Mya) (Richardson et al. 2015). Also, it is noteworthy that two African species are included in the IUCN Red List of Threatened Species (Hawthorne 1998).

There are three main centers of occurrence of the genus (Figure 1). (i) Central Africa, with at least three species; (ii) Southeastern Asia, containing at least four species, including *Pterygota alata* (Roxb.) R.Br., which is cultivated elsewhere in tropical countries, and (iii) the Neotropics with four disjunct species: *P. excelsa* (Standl. & L.O. Williams) Kosterm. In Panama and Costa Rica; *P. colombiana* in Colombia and Venezuela; *P. amazonica* L.O. Williams in Peru and Bolivia; and *P. brasiliensis* Allemão, which has a natural distribution along the coastal Brazilian Atlantic Forest, from Pernambuco to Rio de Janeiro, with some cultivated specimens there and in some other places of Brazil.

As a matter of fact, checked records of *P. brasiliensis* from Amazonia are related to misidentifications. They belong to other *Pterygota* species, either still undescribed or not properly determined, although they might be distinguishable after evaluating the leaf morphology and size (Williams 1968). Some of these records may constitute the first Brazilian records of *P. amazonica*, a species currently known only from the Amazonian forests of Bolivia and Peru (Dorr 1992). It is also noteworthy that *Pterygota excelsa* (Standl. & L.O. Williams) Kosterm. (basionym of *Basiloxylon excelsum* Standl. & L.O.Williams), from Panama region (Robyns & Cuatrecasas 1964), went through a similar issue of nomenclatural incongruence, but today is consistently recognized as *Pterygota* rather than *Basiloxylon* (Williams 1968).

That said, we herein proceed to comment on the nomenclatural issue of *Pterygota brasiliensis*, a Brazilian taxon with a misapplied name. Firstly, in the protologue of *Pterygota brasiliensis*, Allemão & Allemão (1862: 7) presented a short description and designated as holotype a vegetative specimen from Ceará, Brazil. Later, in 1886, Schumann wrote a footnote in Flora Brasiliensis (1886a: 12) about a collection made in Rio de Janeiro under the name of *Sterculia rex* Mart. He stated it should belong to a new genus, distinct from *Sterculia*, indicating the species as *Basiloxylon rex* (Mart.) K.Schum. (Kostermans 1960). This is the first mention ever of the name *Basiloxylon*. In the same year, Schumann validated his designation in Flora Brasiliensis designation, thus validating the publication of the name *B. rex* (Schumann 1886b: 82-83). Concurrently, however, Schumann himself also reduced *P. brasiliensis* to a synonym of *Basiloxylon brasiliensis* (Allemão) K.Schum., without mentioning *B. rex* which was previously described by him (Schumann 1895: 98). Furthermore, Schumann synonymized an older name (P. brasiliensis) to a newer one, without mentioning *B. rex* he once described; hence, he did not follow the nomenclatural principle of publication priority, as pointed out by Williams (1968).

Few years later, naturalist Paul Standley noted the striking similarity between specimens of *Pterygota* and *Basiloxylon* (Williams 1968). However, only 50 years later this problematic issue was effectively revisited, when Kostermans wrote, in 1959, a footnote on the isosyntype of *B. rex* (Glaziou 10310, K (barcode: K380924)), and synonymized *B. rex* to *P. brasiliensis*. He also warned another issue: several vouchers determined as *B. brasiliensis* could actually be samples from a native species native to India, *Pterygota alata* (Roxb.) R.Br (Kostermans 1960).

Now regarding that: if what Kostermans has suggested in his note is true, we should expect some evidence on the introduction of *P. alata* in Brazil. In fact, there is a possibility that Luiz D'Abreu, after an expedition to Goa and other localities in India, brought to Brazil some seeds of *P. alata*, along with several other exotic species he effectively did bring to the country. However, so far, our literature survey found no documentation nor records of *P. alata* introduction in Brazil by humans, and the specimens cultivated at Rio de Janeiro Botanical Garden were planted only a few decades ago (pers. comm. with Marcus Nadruz, curator of the Rio de Janeiro Botanical Garden Arboretum). Besides, species' references do not appear in any historical archives documenting cultivated plants introduced in Rio de Janeiro, such as the Hortus Fluminensis (Rodrigues 1894).

Anyhow, misconception regarding the use of those binomials is comprehensible. Indeed, although with disjunct geographical distributions, the similarity between materials of *Pterygota alata* and *P. brasiliensis* is remarkable, leading to the possibility of considering that the two are conspecific. Kostermans (1960) pointed out differences between these two species are slight: *P. alata* has larger flowers and its calyx has denser indumentum than that of *P. brasiliensis*, with relatively smaller flowers and a sparse indumentum. Moreover, a kind of sac is often present at the junction of the petiole and lamina in *P. brasiliensis*, while it is absent in *P. alata*. Assessing such traits as discrete character states reliable for taxonomical purposes is still difficult since herbarium specimens usually lack flowers and are mostly only fruiting or sterile material. Also, we found variability in the presence and prominence of this sac in the leaf base of *P. brasiliensis*, with some specimens with a flat structure.

Still, striking morphological similarity between *P. alata* and *P. brasiliensis* (which may be actually a single transatlantic disjunct species) carries along a wider question: how a recent genus, dating from Miocene, when continents were completely drifted apart, came to has so close morphological types at disjunct parts of a pantropical distribution? Was this pattern caused by a putative long-distance dispersal event, even considering the documented seed dispersal limitation? Phylogeographical studies, associated to systematics and historical biogeography are needed to elucidate such complex history and patterns of *Pterygota*, as well as their relations to Sterculioideae allies. The results shall then bring light to a better taxonomy of the group. For now, we must at least stress the need to keep *Basiloxylon* as an incorrect name and universalize the adoption of *Pterygota brasiliensis* Allemão as the correct name for this native and endemic species of the Brazilian Atlantic Forest domain.

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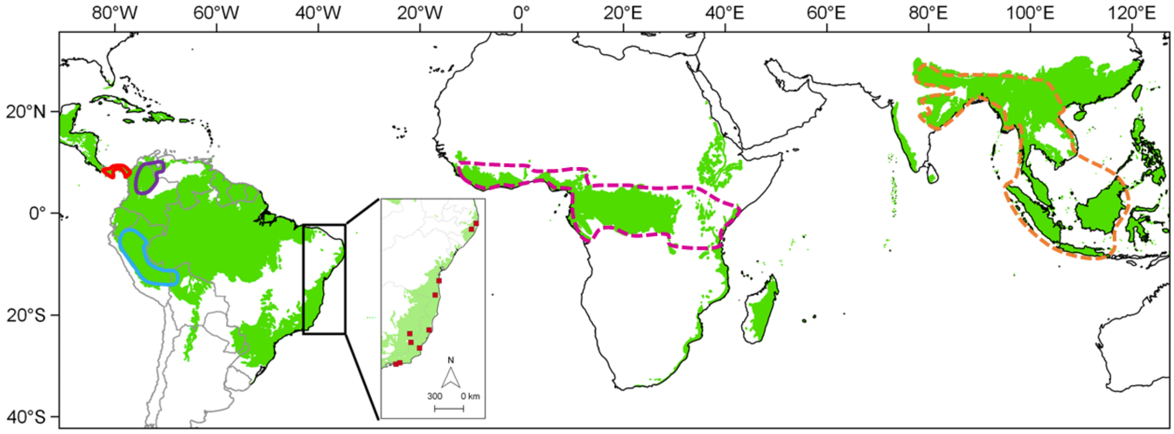

Figure 1. Distribution map of *Pterygota*, based on Hinsley (2014) and on our record database. Green highlights the tropical forests of the world. Neotropical species: *P. brasiliensis* (square points through all Brazilian Atlantic coast, zoomed in the map); *P. colombiana* (purple outline), *P. amazonica* (blue outline) and *P. excelsa* (red outline). Central Africa (pink dashed outline), with at least three species. And Eastern Asia (orange dashed outline), with at least five species, including *P. alata*, which is cultivated elsewhere.

Conclusions *(Conclusões)*

Nesta dissertação, explorei, sob perspectivas diferentes, mas complementares, aspectos da biogeografia, taxonomia e conservação na América do Sul, usando como modelo de estudo múltiplos dados acerca de 271 espécies em 11 gêneros e três subfamílias de um grupo muito expressivo na região Neotropical e na América do Sul — Malvaceae. Sumariamente, concluo que:

1. *Diferentes grupos estão distribuídos heterogeneamente pelo continente sul-americano (Capítulo 1).* Diferentes gêneros ou conjuntos de espécies estão restritos a determinadas áreas do continente, e alguns grupos de espécies coincidem com áreas de endemismo já reconhecidas na literatura para outros grupos de plantas ou animais. Além disso, a distribuição de espécies e de eventos de coleta num mesmo ponto é heterogênea e enviesada em regiões específicas do continente, notadamente na Amazônia.
2. *A partir de uma base revisada de pontos de ocorrência e espécies, e dela selecionando táxons com um padrão biogeográfico particular, foi possível discutir possíveis cenários biogeográficos nas áreas abertas ou sazonalmente secas da América do Sul, sugerindo que eventos de dispersão a longa distância devem ter tido papel importante na história natural da região e de parte da biota que a compõe (Capítulo 2).* Sob uma perspectiva de modelagem de distribuição de espécies, aliado ao conhecimento sobre espécies de Malvaceae selecionadas e de outras selecionadas de uma base de dados reconhecida — a do projeto da Flora do Brasil 2020 —, procuramos discutir cenários explanatórios para as disjunções reportadas em diferentes grupos de plantas ou animais. Concluímos que o padrão disjunto é natural — i.e., provavelmente não é consequência de viés de coleta na área — e que diferentes espécies responderam diferentemente às mudanças

climáticas no Quaternário que protagonizam a história natural da região. Isso, aliado a atributos que intuitivamente estão associados à dispersão a longa distância, sugere que essas espécies possam manter eventos de dispersão em áreas abertas ou sazonalmente secas.

3. *Usando-se dessa mesma base revisada de pontos de ocorrência, é possível discutir o panorama de representatividade de espécies no contexto da rede de unidades de conservação (UCs) da América do Sul, detectando as regiões do continente onde há sub ou sobre-representação (Capítulo 3).* Também adotando-se de elementos de modelagem de distribuição de espécies, foi possível concluir que diferentes espécies estão heterogeneamente representadas pelas UCs sul-americanas, variando de acordo com área de distribuição, bioma e grupo taxonômico. Por conseguinte, em alguns biomas — notadamente a Amazônia — a falta de coletas e do conhecimento sobre registros dentro de UCs dificulta saber o quanto nós potencialmente protegemos nas UCs mas não dispomos de registros nos herbários para comprovar tal representatividade.

4. *A base revisada dessas espécies permitiu realizar trabalhos taxonômicos e nomenclaturais no âmbito da Mata Atlântica, um importante domínio fitogeográfico da região Neotropical (Capítulo 4 e Anexo).* Nesse sentido, trouxemos contribuições taxonômicas e nomenclaturais para três gêneros (*Ayenia*, *Byttneria* e *Pterygota*), notadamente descrevendo pela primeira vez a localização de uma espécie antes só conhecida pelo tipo nomenclatural e com distribuição desconhecida, estabilizando a nomenclatura de espécies por via de lectotipificações, atualização da nomenclatura e estado de conhecimento dos gêneros (Capítulo 4) e resolvendo um problema nomenclatural referente a *Pterygota brasiliensis,* espécie que vinha sendo denominada com um nome mal aplicado (ver Anexo).

Em suma, esta dissertação reflete os focos em que concentrei minha pesquisa, com perspectivas de aprofundamento num doutorado, e potencialmente durante minha carreira como pesquisador-docente no Brasil. As minhas contribuições já publicadas e em vias de finalização contemplam tanto (1) o campo teórico e metodológico da biogeografia, especialmente da biogeografia de padrões espaciais; (2) a biogeografia, conservação e documentação da biodiversidade no contexto da América do Sul, um continente com altos índices de riqueza de espécies e endemismos; (3) novos insights sobre a história natural de regiões importantes da região Neotropical, sobretudo as vegetações abertas ou sazonalmente secas que predominam a longo da Diagonal Aberta da América do Sul.

Além disso, o trabalho também trouxe contribuições (4) no conhecimento específico sobre a taxonomia, biogeografia, história, conservação e documentação do grupo focal de estudo — Byttnerioideae, Helicteroideae e Sterculioideae — o que se estende às Malvaceae como um todo. Trata-se certamente de um grupo que, assim como outras grandes famílias tropicais, deve ser estudado minuciosamente em direção de novos insights e contribuições sobre questões não só mais particulares do grupo em si, como também questões mais gerais de biogeografia, documentação e conservação da biota em escala continental a global.

Por último destaco a importância da manutenção de estudo de dados primários, sobretudo dos materiais depositados nos herbários. Uma revisão ampla e comparada de dados de ocorrência com um enfoque taxonômico particular por si só rendeu cinco capítulos, dois deles apenas versando questões mais amplas do campo da biogeografia. Esse método de trabalho é aqui fortemente preconizado — focado não só na taxonomia, mas também em questões selecionadas mais amplas — seja aplicado em outras dissertações ou teses com outros grupos de plantas. Cada grupo tem sua história, que se reflete em padrões específicos, únicos. Portanto, cada grupo traz também uma contribuição única do ponto de vista de padrões biogeográficos, documentação da biodiversidade e conservação de um bioma, país ou continente.