



Current knowledge of the occurrence and distribution of Sapindales in Brazil: a data synthesis from the Brazilian Flora 2020 project

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Abstract

The Sapindales comprise one of the hallmark orders in the Neotropics, being an important component of forested and open formations, especially in Brazil. In recent decades, there have been many efforts made to unravel the Brazilian flora and its distribution; among them is the Brazilian Flora 2020 Project, the main goal of which was to produce updated monographs about Brazilian plant groups. In this work, we present a synthesis of the occurrence and distributions of species and genera of Sapindales in Brazil, noting species endemic to the country, as well as the prevalence of the order in Brazilian phytogeographic domains and vegetations. We have shown that Brazil has 1003 native species in 119 genera of six families of Sapindales, with 388 (43%) species endemic to the country, and the Rutaceae and Sapindaceae families being the richest in species, genera and endemics. Diverse species and life forms are found in virtually all vegetations and phytogeographic domains, but mostly in rainforests of the Amazonian and Atlantic Forest domains. Life forms vary greatly across different families, with a prevalence of lianas in Sapindaceae and of trees in Rutaceae. We discuss our results in light of the current patterns of the families and their assemblage in different vegetation and phytogeographic domains of Brazil.

Keywords Biogeography · Distribution · Online databases · Phytogeographic domains · Vegetation types

1 Introduction

With nine recognized families (Anacardiaceae, Biebersteinaceae, Burseraceae, Kirkiaaceae, Meliaceae, Nitriariaceae, Rutaceae, Sapindaceae and Simaroubaceae), the order Sapindales has ca. 5200 species across 473 genera, mostly tropical, varying from trees to shrubs and lianas, seldomly herbs (Stevens 2001). An alternative estimate ascribes 472 genera and 6142 species to the order (Christenhusz and Byng 2016), which, regardless, makes it one of the dominant groups of malvid eudicots of the globe. As a matter of fact, the Sapindales correspond to ca. 3% of eudicots diversity, and high levels of diversification have been inferred for the group (Magallón and Castillo 2009).

Historically, Sapindales circumscription has been somewhat controversial. Some authors have considered Sapindales in a narrow sense, with current families being placed either in Rutales (Anacardiaceae, Burseraceae, Kirkiaaceae,

Meliaceae, Rutaceae, Simaroubaceae) or Sapindales *sensu stricto*, incl. Sapindaceae (e.g., Scholz 1964; Takhtajan 1980; Dahlgren 1980; Thorne 1992). With the advent of molecular systematics, novel phylogenies based on molecular evidence have recurrently corroborated a wider circumscription of Sapindales, supporting the monophyly of Sapindales *sensu lato*, including most families of the former Rutales (i.e., not including Biebersteinaceae and Sapindaceae) in its current circumscription (Gadek et al. 1996; Muellner-Riehl et al. 2016).

Although phylogenetic relationships in the order are supported solely by molecular evidence and no morphological synapomorphies have been identified so far, many Sapindales share some diagnostic features, e.g.: leaves mostly pinnately compound and flowers bearing a well-developed nectariferous disk (Cronquist 1981; Gadek et al. 1996). Furthermore, the order represents a diverse and economically important group of flowering plants, including citrus, cashew, mango, pistachio, frankincense, myrrh, mahogany, tree-of-heaven, lychee, rambutan and maple. Many representatives of Sapindales are widely used in the timber industry or as foods or medicinal components. The latter is likely associated with the diversified and unique set of secondary

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metabolites typical to the order, with species producing bioactive compounds rich in terpenoids, limonoids and terpenes (Waterman 2007).

The Neotropical region encompasses from two-fifths to half of all known Sapindales diversity. The three families not represented in the Neotropical region (Biebersteiniaceae, Kirkiaeae and Nitriaceae) correspond to only four genera and 27 species of an order that has a total of almost 6000 species. Moreover, there are tribes entirely endemic to the Neotropics (e.g., Rutaceae-Galipeeae, Colli-Silva and Pirani 2019) or almost so (e.g., Sapindaceae-Paullinieae, Acevedo-Rodríguez et al. 2017).

Brazil is the country with the richest flora of Earth, having more than 30,000 flowering plants (Ulloa-Ulloa et al. 2017; BFG 2021a). In Brazil, the Sapindales have been the subject of several floristic treatments focusing on specific groups and families, especially on regional scales (e.g., Albuquerque 1976; Pirani 1997; 2002; Somner 2009). Recent studies have shed light on historical biogeography, phylogenetic relationships, and the evolution of morphological and anatomical features in selected clades of Neotropical Sapindales. In addition, new collections and updated determinations of known records have provided new information for a synthesis of the occurrence and distributions of Sapindales. These studies have been allied with national initiatives that aim to gather all information of the Brazilian flora towards meeting Target 1 of the Global Strategy for Plant Conservation by the end of 2020 (BFG 2018), namely: the Brazilian Flora 2020 Project (BFG 2015, 2018, 2021a), the REFLORA/CNPq Program (<http://cnpq.br/apresentacao-reflora>) and the Center of Reference in Environmental Information (<http://www.cria.org.br/>).

This study aims to provide a synthesis of the distribution of the Sapindales in Brazil, highlighting species endemic to the country and their prevalence in each phytogeographic domain and vegetation type. All information compiled in the Brazilian Flora 2020 Project (henceforth, just “BFG project”) will be better displayed in the form of graphs, tables and statistical analysis, and data will be interpreted according to the current literature. Our goal is to look for additional evidence that may contribute to a better understanding of the biogeographic diversification history of tropical groups. Also, our results shall be contrasted and discussed considering the known occurrence of Sapindales worldwide.

2 Material and methods

The list of Sapindales of Brazil was compiled from the taxonomic list of the BFG database (BFG 2021a). The database was downloaded on January 6, 2021, and it is available at GBIF.org (BFG 2021b). The BFG project is an initiative based at the Rio de Janeiro Botanical Garden, but with the

collaboration of hundreds of taxonomists. Monographs of some genera across all families of Sapindales were produced by specialists in each family, including description of distribution in each Brazilian federative unit, life form, origin (whether native or introduced to Brazil) and habitat (vegetation types and phytogeographic domains). Definitions of life forms, vegetation types and phytogeographic domains strictly followed the Brazilian Flora 2020 categories, unless explicitly mentioned.

Data were compiled and analyzed in the R Environment (R Core Team 2020). The BFG project also maintains an accurate nomenclatural database including synonyms used in the literature, based on monographs and taxonomic treatments that specialists likely consulted to build said monographs. Selected information of taxonomic groups was eventually vetted by contacting specialists in the group. Aiming at an overall picture, we also compared the Brazilian records with estimates of Sapindalean generic and specific richness worldwide, according to Christenhusz and Byng (2016); and in the Neotropical region, according to recent family treatments prepared by specialists and published by Smith et al. (2004) and Kubitzki (2011), as well as in the APweb site (Stevens 2001 onwards).

In conjunction with graphs and descriptive tables, we statistically compared the relationships between vegetation types, phytogeographic domains and life forms for each family, through Fisher's exact test for count data, at 0.05 significance levels, using the “stats” package in R Environment (R Core Team 2020). Maps were built using QGIS software (www.qgis.org), with information on the extensions of Brazil's phytogeographic domains extracted from Sobral and Stehmann (2009). The frequency of life forms for each variable (vegetation type and phytogeographic domain) was tested for each family, in relation to their frequency of all other families. In other words, we statistically assessed the difference between the occurrence of a given family versus the occurrence of all other families together for a given variable.

3 Results

Occurrence and endemism in Brazil – In Brazil, there are 1003 species of Sapindales in 119 genera and six families; 910 species are native and almost half of them (388, 43%) are endemic to the country (Table 1; Fig. 1). Of the order's native species, 51% of those recorded to the Neotropics are in Brazil (Table 1). A comprehensive list of entries can be found as Supplementary Material (Table S1).

The richest family in number of native species is Sapindaceae, with 418 species, comprising almost half of the order's diversity in Brazil (Table 1). Conversely, even though Rutaceae is the richest family of Sapindales globally, with

Table 1 Estimates of genera and species richness of families of Sapindales occurring in Brazil: worldwide according to Christenhusz and Byng (2016); estimates in the Neotropics according mostly to Smith et al. (2004); estimates in Brazil compiled from the species list of the Brazilian Flora 2020 Project (2020)

Family	Taxa	World	Neotropics (% world)	Brazil (% Neotrop.)	Native (% Brazil)	Introduced (% Brazil)	Endemic (% native)
Ana	Genera	83	33 (40%)	15 (45%)	12 (80%)	4 (27%)	1 (8%)
	Species	860	170 (20%)	64 (38%)	58 (91%)	6 (9%)	19 (33%)
Bur	Genera	19	8 (42%)	5 (63%)	5 (100%)	0 (0%)	0 (0%)
	Species	615	295 (48%)	116 (39%)	115 (99%)	0 (0%)	26 (23%)
Mel	Genera	53	11 (21%)	11 (100%)	6 (55%)	7 (64%)	0 (0%)
	Species	600	130 (22%)	101 (78%)	92 (91%)	9 (9%)	25 (27%)
Rut	Genera	154	58 (38%)	49 (84%)	31 (63%)	26 (53%)	5 (16%)
	Species	2070	360 (17%)	249 (69%)	191 (77%)	41 (16%)	106 (55%)
Sap	Genera	142	35 (25%)	32 (91%)	26 (81%)	8 (25%)	2 (8%)
	Species	1860	968 (52%)	437 (45%)	418 (96%)	18 (4%)	191 (46%)
Sim	Genera	23	7 (30%)	7 (100%)	7 (100%)	0 (0%)	0 (0%)
	Species	117	55 (47%)	36 (65%)	36 (100%)	0 (0%)	21 (58%)
All	Genera	474	152 (32%)	119 (78%)	87 (73%)	45 (38%)	8 (9%)
	Species	6122	1978 (32%)	1003 (51%)	910 (91%)	74 (7%)	388 (43%)

Recognized taxa of Sapindales in Brazil, per family, including fractions (%) relative to all families. Each column includes, respectively, summaries for all species (incl. native, naturalized and cultivated species), genera, native species only and endemic species to Brazil only. Estimates from Christenhusz and Byng (2016) slightly differ from family treatments published in Kubitzki's work (see references), and from the APweb site (Stevens 2001 onwards)

154 genera and 2100 species, the richest family of Sapindales is by far Sapindaceae, with almost half of all known native species of the order. Rutaceae is a nearly cosmopolitan group, most diverse in Australasia (Kubitzki et al. 2011), and in Brazil comprises a quarter of all known diversity of the order (Table 1). These two families are followed by Meliaceae and Burseraceae, with c. 10% of Sapindales diversity each, and then by Anacardiaceae and Simaroubaceae (Table 1).

Sapindales also stand out in terms of species endemism, with half of all species of the order being endemic to Brazil and around two-fifths (43%) (i.e., 388 out of 910 native spp.) are endemic to the country (Table 1). The composition pattern of species endemism is similar to the species richness pattern, with Sapindaceae bearing nearly half of Sapindales endemic species (191 spp.), followed by Rutaceae, with 106 endemics (Table 1). The Rutaceae also account for nearly a third of Sapindales endemic species (Table 1).

The Rutaceae are conspicuous in having the greatest number of introduced species in Brazil: ca. 23% (41 of 249 species registered in Brazil) are cultivated or naturalized in the country. Most cultivated taxa of Rutaceae belongs to *Citrus*, a genus related to a wealthy industry developed since the beginning of the twentieth century in some areas of the country.

Life forms, vegetation types and phytogeographic domains – Species of Sapindales can be found virtually all throughout the six phytogeographic domains of Brazil (Figs. 1, 2a). However, most species occur in the two forest domains (Amazon and Atlantic rain forests), and that is particularly true for Burseraceae (Fig. 2a). Simaroubaceae is most diverse in the Cerrado, and the Anacardiaceae is most diverse in the Cerrado and in the Pampa (Fig. 2a). Except for the two latter families, Sapindales are more speciose in Amazonia (Fig. 2a); nevertheless, the scenario changes when considering only endemic species (Fig. 2b), as all are restricted to the Atlantic Forest, rather than to the Amazon domain. Furthermore, for some families the number of endemic species associated with a single domain is much more evident, viz. Burseraceae in the Amazon rainforest, or Simaroubaceae in the Cerrado (Fig. 2b).

Nearly half of all species of Sapindales in Brazil are trees, followed by shrubs and lianas, and exceptionally herbs (Fig. 2c). Most Meliaceae and Burseraceae are trees, while 56% of Sapindaceae are lianas (Fig. 2c). Life form distribution is also statistically different for Rutaceae and Sapindaceae according to the vegetation types and phytogeographic domains (Tables 2 and 3). In Sapindaceae, the statistical prevalence of lianas has been shown for Atlantic Forest formations (namely the Atlantic ombrophylous forests and *restinga*), while they were less common than expected for

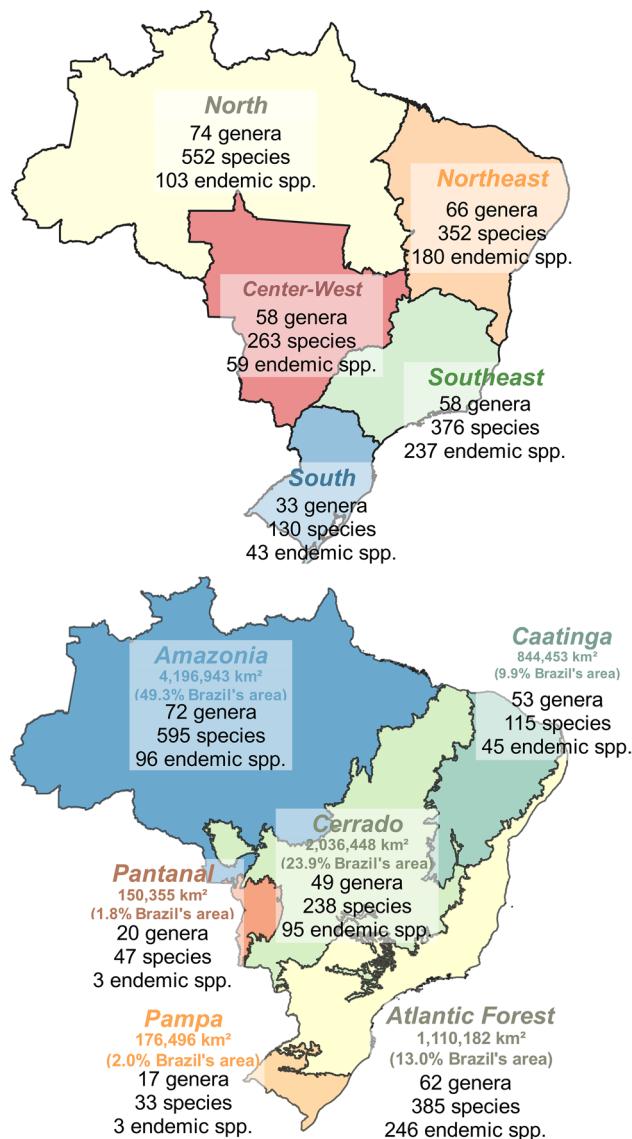


Fig. 1 Sapindales distribution in Brazil, considering its political delimitations in regions (left) and its major phytogeographic domains (right). Area and percentage of phytogeographic domains obtained from Sobral and Stehmann (2009)

Amazonian and open dry formations (Table 3). Conversely, in Rutaceae, trees have been shown to be a much more common component of the Atlantic ombrophylous forests, while (sub-)shrubs have been established to be less common than expected in those regions (Tables 2 and 3).

When considering the composition of Sapindales families in each vegetation type, the scenario is also heterogeneous, and members of all families can be found somewhat equally distributed through each vegetation type (Fig. 2d). Following Fig. 2a, b for phytogeographic domains, the majority of Sapindales occurs in ombrophylous forests of the Atlantic Forest (Fig. 2d), followed by other forested seasonal or

riverine formations (i.e., riverine and seasonally semideciduous forests).

Lastly, when contrasting life form distribution with phytogeographic domains and vegetation types, Rutaceae is the only family that is found in all phytogeographic domains (Table 2) but not in all vegetation types (Table 3). Simaroubaceae has no confirmed records in Pantanal, and Burseraceae has no records in the Pampa (Table 2); both families lack records of species in many vegetation types as well (Table 3). It should be noted that even though there is a lack of Burseraceae records in Pantanal in the Flora do Brasil database, we are aware of the occurrence of *Comiphora leptophloeos* (Mart.) Gillett and *Protium heptaphyllum* (Aubl.) Marchand in the Pantanal area (see Pirani and Silva-Luz 2018).

4 Discussion

Overall distribution patterns – While the center of generic and species richness of Sapindales is not in Brazil nor in the Neotropics, three families have around half of their species in these areas, showing a very expressive regional diversification of the group: Sapindaceae (968 Neotropical spp., or 52% of the world total), Burseraceae (295, 48%), and Simaroubaceae (55, 47%) (Table 1). Three Sapindalean families are not represented in the Neotropics (Biebersteiniaeae, Kirkiaeae, and Nitrariaceae), and the other families are better represented in Australasia (Rutaceae, Kubitzki et al. 2011), and Africa or Tropical Asia (Anacardiaceae and Meliaceae, Pell et al. 2011; Mabberley et al. 1995).

An exceptional case of a large and mostly north temperate genus is *Acer* (Sapindaceae), with around 126 species in North America, Europe, Northern Asia, and Japan (Acevedo-Rodríguez et al. 2011). Extra-tropical species belonging to the Brazilian genera of Sapindales are scattered: a few species of *Zanthoxylum* (Rutaceae) also occur in eastern North America, and one species in Chile (*Z. mayu* Bertero, in the Juan Fernández Archipelago). In Anacardiaceae, *Lithraea* reaches Uruguay and Chile, and *Schinus* extends to Patagonia; in Meliaceae, *Swietenia* extends to southern Florida (USA). In Sapindaceae *Cupania*, *Matayba* and *Serjania* have some subtropical species, and a variety of the widespread soapberry *Sapindus saponaria* L. occurs as a deciduous tree with winter hardiness along several temperate areas in the United States. Finally, in Simaroubaceae, one species of *Simarouba* reaches Florida, and a few *Castela* species occur in northern Mexico, Arizona and California.

Nonetheless, it is noteworthy that 89% of the Neotropical genera and 51% of the Neotropical species of Sapindales are found in Brazil. In fact, all Neotropical genera from three of the order's six largest families are found in the country: Meliaceae, Sapindaceae, Simaroubaceae, in addition to

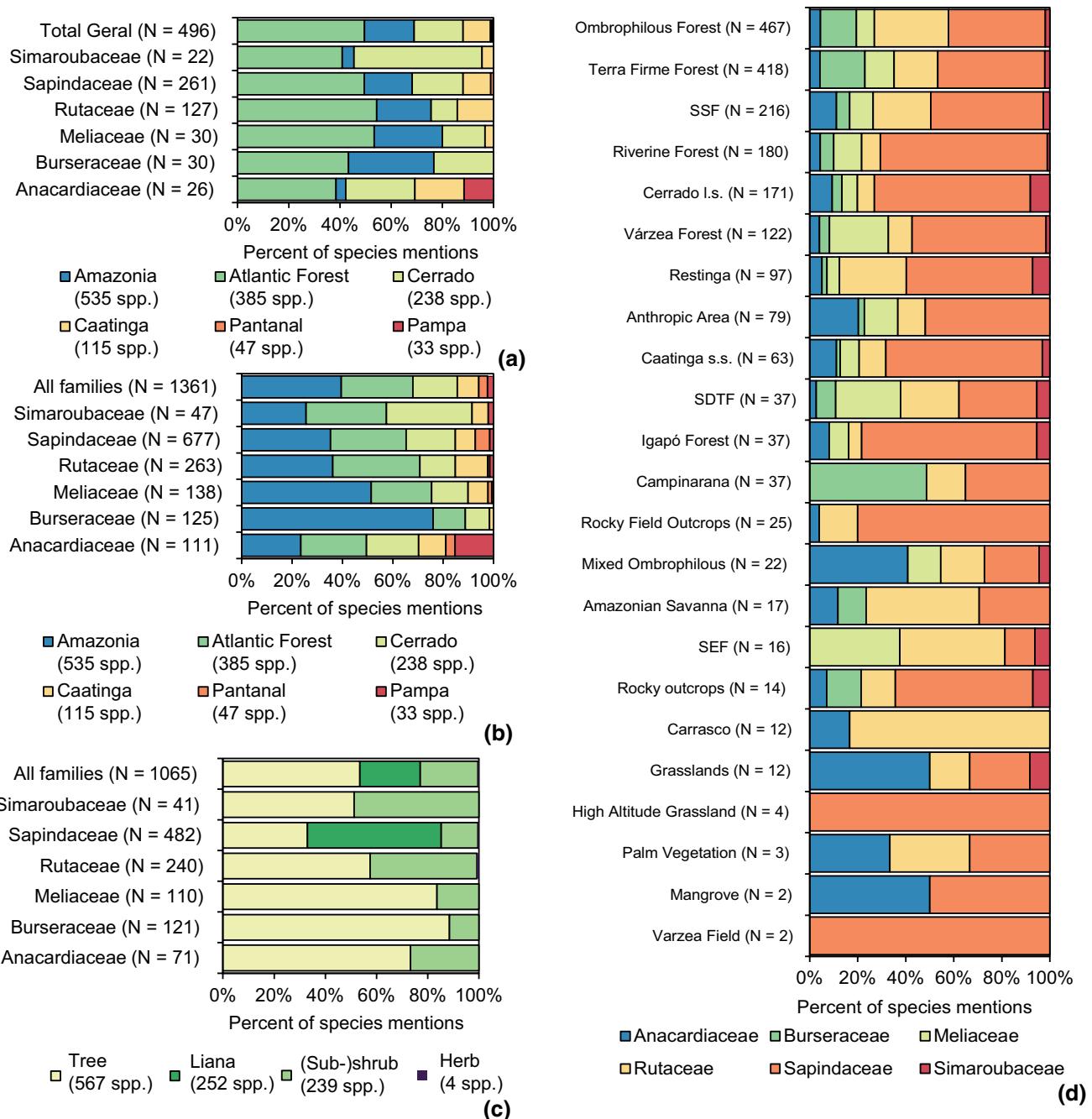


Fig. 2 General summary of species profile of Sapindales from Brazil. Charts summarize **a** lifeform composition for each family; **b** species occurrence in each Brazilian phytogeographic domain; **c** Brazilian endemic species occurrence in each phytogeographic domain; **d** species occurrence in each Brazilian vegetation type. Data according to the Brazilian Flora 2020 Project classification. Mention numbers (N) do not correspond to numbers of unique species, as one species can occur in more than one phytogeographic domain or vegetation type. SSDF Seasonal Semideciduous Forests; SDTF Seasonal Deciduous Forests; SEF Seasonal Evergreen Forest. Check Table S1 in Supplementary Material for a full list of all species and the variables concerned

almost all Rutaceae genera. Three of those families bear more than a half of their Neotropical species in Brazil: Simaroubaceae (65%), Rutaceae (69%), and Meliaceae (78%) (Table 1). This overall picture may reflect either Brazil's continental size or its tropical location. With much of its

territorial extent lying within the tropics, the “latitudinal species gradient” applies here, as species' richness tend to be higher at tropical latitudes (Hillebrand 2004). In this sense, high-latitude (or high-altitude) frost-prone regions, presumably, are less conducive to diversification and/or more prone

Table 2 Fisher's exact test summary (at 0.05 significance level) on relations among lifeform prevalence and each Brazilian phytogeographic domain

Phytogeographic domain	Lifeform	Ana	Bur	Mel	Rut	Sap	Sim
Amazonia	Liana	—	—	—	—	<	—
	(Sub-)shrub	—	—	—	—	<	—
	Tree	—	—	—	—	>	—
	Herb	—	—	—	—	<	—
Atlantic forest	Liana	—	—	—	—	>	—
	(Sub-)shrub	—	—	—	>	<	—
	Tree	—	—	—	<	<	—
	Herb	—	—	—	>	>	—
Caatinga	Liana	—	—	—	—	<	—
	(Sub-)shrub	—	—	—	—	>	—
	Tree	—	—	—	—	<	—
	Herb	—	—	—	—	>	—
Cerrado	Liana	—	—	—	—	<	—
	(Sub-)shrub	—	—	—	—	>	—
	Tree	—	—	—	—	>	—
	Herb	—	—	—	—	>	—
Pampa	Liana	—	NA	—	—	—	—
	(Sub-)shrub	—	NA	—	—	—	—
	Tree	—	NA	—	—	—	—
	Herb	—	NA	—	—	—	—
Pantanal	Liana	—	NA	—	—	>	NA
	(Sub-)shrub	—	NA	—	—	<	NA
	Tree	—	NA	—	—	<	NA
	Herb	—	NA	—	—	>	NA

In each family, statistics include if each lifeform is more (">") or less prevalent ("<") than the expected (in relation to all other families) in a particular phytogeographic domain, otherwise it will be as prevalent expected ("—"). Ana. = Anacardiaceae; Bur. = Burseraceae; Mel. = Meliaceae; Rut. = Rutaceae; Sap. = Sapindaceae; Sim. = Simaroubaceae; "NA" = no confirmed records for the cell. The full dataset used to build this table is available as Supplementary Material (Table S2)

to extinction than tropical regions in the order (Davies et al. 2004).

Several genera of Sapindales have their main center of species diversity in Brazil. Remarkable examples are *Spondias* (Anacardiaceae); *Trichilia* (Meliaceae); *Conchocarpus*, *Galipea* and *Pilocarpus* (Rutaceae); *Cupania*, *Matayba* and *Paullinia* (Sapindaceae); and *Homalolepis* (Simaroubaceae), although most of these genera are rather small. Moreover, phylogenies of the six Sapindalean families suggest geographic patterns consistent with Wiens and Donoghue (2004) hypothesis: early diverging lineages are tropical and likely to show tropical niche conservatism, while the few temperate branches diversified more recently (as seen for instance in the dated Sapindales phylogeny of Mueller-Riehl et al. 2016). A noteworthy exception to this trend is found in Sapindaceae, where *Xanthoceras* (China) and the clade *Acer* + *Aesculus*, which emerge as earlier diverging lineages, are all temperate groups.

Main patterns of life forms of Brazilian Sapindales – In association with a broad ecological range of Sapindales, our results showed that life forms are quite diverse within the order. Some are rain forest giants such as *Cedrela* and *Carapa* trees (Meliaceae) reaching up to 50 m tall, and six Amazonian species of *Anacardium* (Anacardiaceae) that are trees of the canopy or emergent: especially *A. excelsum* (Kunth) Skeels and *A. giganteum* Hancock ex Engl., which can reach 40–50 m tall and 300 cm in diameter (Mitchell and Mori 1987). Other huge Amazonian Sapindalean trees include *Euxylophora paraensis* Huber, which can be more than 40 m tall, and the 30 m tall *Zanthoxylum ekmani* (Urb.) Alain and *Z. compactum* (Huber ex Albuq.) P.G.Waterman (Pirani and Groppo 2020). In the Atlantic Forest domain, *Balfourodendron riedelianum* (Engl.) Engl. can reach up to 30 m in height.

But apart from rainforest giants, the Brazilian Sapindales also include numerous medium-sized trees and understorey treelets and shrubs with varied architectures, as well as lianas, subshrubs and seldom herbs (e.g., *Ertela*, Rutaceae).

Table 3 Summary of the relations among lifeform prevalence and each vegetation type informed by the Brazilian Flora 2020 Project

Lifeform	Scenarios ($\alpha=0.05$)	Anacardiaceae	Burseraceae	Meliaceae	Rutaceae	Sapindaceae	Simaroubaceae
Liana	More common	—	—	—	—	Ombrophilous forest, Restinga	—
	Less common	—	—	—	—	Anthropic área, Caatinga (s.s.), Cerrado (l.s.), Inundated Forest (Várzea), Riverine Forest, Seasonally Semideciduous Forest, Terra Firme Forest	—
(Sub-)shrub	More common	—	—	—	—	Anthropic area, Caatinga (s.s.), Cerrado (l.s.), Riverine Forest, Inundated Forest (Várzea), Ombrophilous Forest, Restinga	—
	Less common	—	—	—	—	Seasonally semideciduous forest; Terra Firme forest	—
Tree	More common	—	—	—	—	Anthropic Area, Riverine Forest, Terra Firme Forest, Inundated Forest (Várzea)	—
	Less common	—	—	—	—	Caatinga (s.s.), Cerrado (l.s.), Ombrophilous Forest, Restinga, Seasonally Semideciduous Forest	—
Herb	More common	—	—	—	—	Ombrophilous forest	—
	Less common	—	—	—	—	Caatinga (s.s.), Cerrado (l.s.), Riverine Forest, Terra Firme Forest, Seasonally Semideciduous Forest, Ombrophilous Forest, Anthropic area, Inundated Forest (Várzea), Restinga	—

Table 3 (continued)

Lifeform	Scenarios ($\alpha=0.05$)	Anacardiaceae	Burseraceae	Meliaceae	Rutaceae	Sapindaceae	Simaroubaceae
No confirmed occurrences	Campinarana; high-altitude grasslands; seasonal evergreen forest; varzea field	Carrasco Vegetation; Grasslands; High-Altitude Grasslands; Inundated Forest (Igapó); Mangrove; Mixed Ombrophilous Forest; Palm Vegetation; Rocky Fields ("campo rupestre"); Seasonal Evergreen Forest; Varzea Field	Amazonian Savanna; Campinarana; Carrasco Vegetation; Grassland; High-Altitude Grassland; Mangrove; Palm Vegetation; Rocky Field ("campo rupestre"); Rocky outcrop vegetation; Várzea Field	Amazonian Savanna; Campinarana; Carrasco Vegetation; Grassland; High-Altitude Grassland; Mangrove; Palm Vegetation; Rocky Field ("campo rupestre"); Rocky outcrop vegetation; Várzea Field	High-Altitude Grassland; Mangrove; Várzea Field	Carrasco Vegetation	Amazonian Savanna; Anthropic area; Campinarana; Carrasco Vegetation; High-Altitude Grassland; Mangrove; Palm Vegetation; Rocky Field ("campo rupestre"); Várzea Field

For each family, the table includes all formations in which a given lifeform is more or less common than the expected (in relation to the occurrence of all other families) according to Fisher's exact test results (at 0.05 significance level, besides which formations have, for a given lifeform, no confirmed records for any species for the family. The full dataset used to build this table is available as Supplementary Material (Table S2)

Geoxyllic (sub-)shrubs with shoots that re-sprout annually from a woody underground stem system are observed in four of the six families. Thorny plants occur in various forms: branches often spinose due to modified shoot apices are found in *Castela* (Simaroubaceae), *Commiphora* (Burseraceae), and some species of *Schinus* (Anacardiaceae); while in *Zanthoxylum* (Rutaceae) many species are aculeate on the trunk or leaves. Most species are evergreen, but genera such as *Carapa* and *Cedrela* (Meliaceae); *Astronium*, *Cyrtocarpa* and *Spondias* (Anacardiaceae); and *Bursera* and *Commiphora* (Burseraceae) are seasonally deciduous. Two Amazonian species of myrmecophytes, with hollow stems inhabited by ants, are known in Rutaceae (*Zanthoxylum compactum* (Huber ex Albuq.) P.G.Waterman) and in Simaroubaceae (*Picrolemma sprucei* Hook.f.). The genus *Sohnreyia* (Rutaceae) consists of pachycaul, hapaxanthic (=semelparous) trees in the Amazon.

Burseraceae and Meliaceae are families with few non-arbooreal species, but in Brazil, they lack some habits such as lianas and geophytes (Daly et al. 2011; Weeks et al. 2014; Heads 2019). In contrast, our results showed that the lianescence habit prevails in Sapindaceae (Fig. 2a), which is a remarkable Neotropical pattern. While lianas are very rare or absent in most Sapindales, in Sapindaceae they are numerous. Moreover, all Sapindaceae lianas belong to a single clade, the tribe Paullinieae, recently re-circumscribed to include only six genera (*Thinouia*, *Lophostigma*, *Cardiospermum*, *Paullinia*, *Serjania* and *Urvillea*) of climbers or climber-derived shrubs with stipulate leaves and a pair of inflorescence tendrils (Acevedo-Rodríguez et al. 2017).

Main patterns among vegetations – Tropical rain forests (Amazon and Atlantic Forest) – The Sapindales are more diverse across almost all vegetation types, except for the grasslands that favor Anacardiaceae, and Amazonian Campinarana, rich in Burseraceae (Fig. 1d). In fact, Anacardiaceae has conspicuous components in Brazil's Cerrado *lato sensu*, such as four suffrutescent species of *Anacardium* (e.g., Mitchell and Mori 1987)—two of which are usually locally abundant—as well as shrubs (or treelets) of *Lithraea* and *Astronium*. Also, Anacardiaceae is the only Sapindales family with a noteworthy presence in the Pampa domain (Figs. 2b, c), mainly due to the presence of eleven species of *Schinus* represented there. Conversely, the remarkable presence of Burseraceae in the Amazonian Campinarana is expressed in studies associating environmental heterogeneity with edaphic specialist and generalist tree species of *Protium*—some of them inhabiting that vegetation—which have revealed lineages with habitat specialization in white sand or flooded soils across the Amazon Basin (Fine et al. 2012, 2014).

Finally, in Rutaceae, a biogeographic analysis was performed with the subtribe Galipeinæ (Colli-Silva and Pirani 2019), revealing two main centers of diversity, a major one

in the Atlantic Forest and a secondary one in the Amazon rain forest, with only a few species widespread through the Cerrado (8 spp.) and Caatinga (8 spp.; *Conchocarpus hamadryadicus* Pirani and Kallunki is the only species endemic to this domain). Rather, *Conchocarpus* is the richest genus of Galipeinae in the Atlantic Forest (34 spp.) and in the Amazon (8 spp.), where *Raputia* is also represented by eight species (Colli-Silva and Pirani 2019).

Regarding the Amazonian domain, the prevailing rain forests are ancient ecosystems that have existed continuously for about 55 million years (Maslin et al. 2005). Nevertheless, recent rapid radiations in Amazonian rain forest groups have been documented, including in Meliaceae (Pennington and Clarkson 2013; Koenen et al. 2015; Clarkson et al. 2016). The main causes of these rapid radiations taking place during the tertiary and quaternary may be explained using ecological niche models that correlate geological and climatic events including: (1) the Andean uplift from the early to mid-Miocene, promoting climatic and hydrological changes and acting as a barrier to dispersal of organisms (Antonelli and Sanmartín 2011); (2) formation of the Panama Isthmus, completed in the late Miocene, resulting in a massive interchange of land species (Burnham and Graham 1999); (3) climatic fluctuations in the quaternary, when Amazonian rainforests became drier and colder, resulting in changes in the structure and floristic composition including colonization by cool-adapted taxa (e.g., Antonelli and Sanmartín 2011; D'Apolito et al. 2017).

Therefore, the fact that the diversity of all these Sapindales taxa is concentrated in the two rain forest domains may reflect the overall history of South American forests (check Buso et al. 2014). It is currently accepted that since the early Eocene, there was a large continuous area of tropical moist forest extending from the Mesoamerican Pacific to the South American coast, but Pliocene periods of climatic cooling and drying favored the expansion of a “diagonal of open formations” or “dry diagonal” (Prado and Gibbs 1993) in central South America—presently comprising the Caatinga, Cerrado and Chaco domains—disrupting the connection between Atlantic Forest and Amazonian forests (Gentry 1982; Fiaschi and Pirani 2009). We argue that as both rainforest domains have ever since been disturbed by a series of environmental variables and historical evolutionary events, they house multiple areas of endemism for several groups of plants and animals (e.g., Pausas and Austin 2001), including Sapindales lineages.

Open/seasonally dry formations – Another remarkable pattern observed refers to the floristic affinities between lowland rain forests and savanna woodlands. Besides ascribing this pattern to the Annonaceae, Chrysobalanaceae, Combretaceae, Ebenaceae, Leguminosae, Moraceae, Myrtaceae, and Rubiaceae, Heads (2019) added the sapindalean families

Anacardiaceae, Burseraceae, Meliaceae and Sapindaceae. In fact, in Brazil, closely related species pairs or higher groups are found in both environments (forests and savannas), as in well-known genera such as *Anacardium* (Anacardiaceae); *Protium* (Burseraceae); *Esenbeckia*, *Hortia* and *Pilocarpus* (Rutaceae); *Cardiospermum*, *Matayba* and *Talisia* (Sapindaceae); and *Homalolepis* (Simaroubaceae). In the monospecific genus *Cabralea* (Meliaceae), each of the two subspecies currently recognized is restricted to rain forests or to the Cerrado (Pennington et al. 1981).

Some genera that are mainly arborescent also include heliophytic, shrubby to geoxyllic species inhabiting open, dry formations such as the Cerrado and *campo rupestre*, on genera that are mainly arborescent is also a particularly interesting subject. In Brazilian Sapindales, geoxyllic savanna taxa whose underground systems have already been documented in detail include *Anacardium humile* A.St.-Hil. and *A. nanum* A.St.-Hil. (Anacardiaceae, e.g., Lopez-Naranjo 1977); *Hortia oreadica* Groppo, Kallunki and Pirani (Rutaceae, Groppo et al. 2012); and five species of *Homalolepis*, markedly *H. suffruticosa* (Engl.) Devecchi and Pirani (Simaroubaceae, Devecchi et al. 2018; Melo-de-Pinna et al. 2021). The presence of a nutrient reserve supply in the underground system and the remarkable capacity for regeneration of aerial shots and leaves certainly enable these plants to cope with the periodic fires that take place during the dry season in the Cerrado (e.g., Groppo and Pirani 2012; Melo-de-Pinna et al. 2021).

The above species fit the pattern in which savanna or *campo rupestre* taxa descend directly from forest lineages, previously documented in phylogeny-based studies on diversification of other families as Leguminosae and Melastomataceae (Simon et al. 2009; Rando et al. 2016), Asteraceae (Loeuille et al. 2015), Malvaceae-Bombacoideae (Zizka et al. 2020), in Rutaceae with *Metrodorea* (Dias et al. 2015) and *Spiranthera* (Brito et al. 2017), and Simaroubaceae with *Homalolepis* (Devecchi et al. 2018). This latter genus belongs to a clade formed by two forest genera, *Simaba* and *Simarouba*, plus 25 species of *Homalolepis* found in Brazil, three of them occurring in the Amazon, 11 occurring in the Atlantic Forest, and 13 are in the Cerrado. According to this pattern, several lineages that are current components of the Cerrado flora seem to have evolved more recently from forest ancestors, in a process involving life form transitions and morphological and ecological adaptations (Simon et al. 2009; Zizka et al. 2020). Studies of paleovegetation and paleoclimate also suggest that forest cover has dominated tropical South America since the early Paleogene, while savannas with geoxyllics and pyrophytes expanded only from the Miocene (e.g., Beerling and Osborne 2006; Simon et al. 2009; Graham 2011). Similar patterns have been also described for African savannas (Maurin et al. 2014; Pennington and Hughes 2014), and there is evidence that most

dry habitats of the world expanded from the Miocene as well (Arakaki et al. 2011).

Some taxa of Brazilian Sapindales have a strong presence in seasonally dry tropical forests (SDTF), which in Brazil correspond to forests included within the Caatinga domain as well as other smaller, disjunct areas (Prado and Gibbs 1993; Pennington et al. 2009; Colli-Silva et al. 2021). For example, about 50% of the species of *Trichilia* section *Trichilia* are confined to seasonally dry forests or occur both in seasonally dry and in lowland rain forest (Clarkson et al. 2016). As a particular formation within the SDTFs, deciduous forests are often associated with limestone outcrops, and it is interesting to notice the close connection between Meliaceae and limestone; 22 out of 48 genera of the family (46%) have been reported from that substrate (Heads 2019). In this work, we include species of *Trichilia* which are conspicuous elements in limestone vegetation, e.g., *T. catigua* A. Juss., *T. clausenii* C. DC., and *T. hirta* L.

Other genera of Sapindales are likewise expressive in SDTFs. *Esenbeckia* (Rutaceae) has two centers of diversity, one in Central America and the other in South America (Kaastra 1982). Like *Esenbeckia*, other genera of Sapindales have at least five species each in dry areas of Caatinga, including *Pilocarpus* (Rutaceae) and *Cardiospermum* (Sapindaceae). The taxa inhabiting dry habitats could be part of lineages with phylogenetic structure and diversification patterns similar to the previously found in Leguminosae and other groups (Pennington et al. 2009; Särkinen et al. 2011; Werneck et al. 2011; Hughes et al. 2015). Other genera have at least one species endemic to caatinga vegetation, such as pantropical *Zanthoxylum* (Rutaceae) with *Z. stelligerum* Turcz. and *Z. hamadryadicum* Pirani, neotropical *Pilocarpus* with *P. sulcatus* Skorupa and *P. trachylophus* Holmes, and *Schinopsis* (Anacardiaceae) with *S. brasiliensis* Engl., the latter a small genus in which the only other Brazilian species is found in the Cerrado and in the Chaco (a SDTF area). Likewise, the sole species of *Apterokarpos* (Anacardiaceae) is endemic to dry formations of the Caatinga, while its sister group is a clade composed of monospecific *Cardenasioidendron* from Bolivian SDTFs, and *Loxopterygium*, with three species disjunct in other SDTFs of northern Peru and Ecuador, and in the Piedmont nucleus of SDTF in northern Argentina and southern Bolivia (Pennington et al. 2009; Silva-Luz et al. 2019).

Montane formations – Taxa of Sapindales are poorly represented at higher elevations, and mountainous areas in Brazil are scarce. However, some species are conspicuous in lower montane forests (Daly et al. 2012, 2020) and a few species occur near or above the tree line in the Andes and East Africa. In Meliaceae, the American genera that reach the highest altitudes are *Trichilia*, with a species recorded at 3300 m in Bolivia, and *Cedrela*, with two species recorded

at 3100 and 3400 m and in subpáramo in the Andes (Pennington and Muellner 2010; Heads 2019). In the latter genus, the widespread *C. fissilis* Vell., distributed from Colombia to southern Brazil, shows a wide ecological range from lowland, evergreen or seasonal forests, to gallery forest, to (sub-)montane forests as a component of *Araucaria* forest in Southern Brazil (Pennington et al. 1981; Pennington and Muellner 2010). *Cabralea canjerana* (Vell.) Mart. (Meliaceae), *Tapirira guianensis* Aubl. (Anacardiaceae) and *Protium heptaphyllum* (Aubl.) Marchand (Burseraceae) are other remarkable lowland forests species which also occur in mountainous regions in central-eastern and southeastern Brazil from 900 m.

In Anacardiaceae, *Schinus* has species at high altitudes in Andean dry vegetation, and in Brazil, some other species occur in the *Araucaria* Forest. Examples from other Sapindales families include *Picrasma crenata* (Vell.) Engl. (Simaroubaceae), inhabiting high slopes of *Araucaria* forests; trees of *Zanthoxylum acuminatum* (Sw.) Sw. (Rutaceae) are recorded at 2000 m, and *Z. fagara* (L.) Sarg. at 2500 m, although in Brazil they usually occur at lower altitudes. Most species of *Raveniopsis* are restricted to rocky, humid, acid soils on top of tepuis (Guayana Shield in Northern South America, mostly in Venezuela), and in Brazil *R. aracaënsis* Kallunki and Steyermark is endemic to Serra do Aracá in northern Amazonas, inhabiting cloud forest between 1150 and 1400 m altitude, while *R. peduncularis* Pittier and Lasser is known from tepuis in Venezuela, above 1600 m altitude, but only at 1200 m in Brazil, Upper Rio Negro, near the border with Venezuela (Pirani and Groppo 2020).

5 Final remarks

Brazil's vast environmental heterogeneity encompasses several vegetation types and phytogeographic domains. The wide diversity of vegetational types found in the country includes rainforests (Amazonian and Atlantic forests), semi-desert deciduous vegetation (Caatinga), rocky grasslands (*campo rupestre*), savanna woodland vegetation (Cerrado), and steppe-like vegetation (Pampa) as its main vegetations. Even though Amazonian rainforests account for about one-third of the South American continent (Fig. 1), three other terrestrial biomes are noteworthy for their size and ecological importance and lie almost entirely on Brazilian territory: the Cerrado, the Caatinga and the Atlantic Forest. Historical factors that may have played a major role in the assembly and evolution of the Neotropical flora were roughly classified as abiotic (e.g., climatic, geological and hydrological changes) and biotic (e.g., soil adaptations; niche conservatism; interactions with pollinators and dispersers) by Antonelli and Sanmartín (2011).

We believe that a similar biogeographic scenario and patterns as discussed above will likely be recovered in many other groups of Sapindales, when likewise submitted to explicit analyses. Specifically, particularly speciose genera that can be targeted for other studies include *Protium* (Burseraceae); *Guarea* and *Trichilia* (Meliaceae); *Conchocarpus* and *Zanthoxylum* (Rutaceae); and *Matayba*, *Paullinia*, *Serjania* and *Talisia* (Sapindaceae), most of them with more species in Amazonia, except for *Conchocarpus*, *Cupania* and *Serjania*, which are richer in the Atlantic Forest, and *Matayba* which is represented equally in the two forest domains. Thus, we argue further biogeographic studies on these taxa using dated phylogenies would improve our knowledge of the evolutionary paths that lineages followed and the main historical factors that may have molded the present spatial and ecological patterns in those groups.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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