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Beyond forests in the Amazon: biogeography and floristic relationships of the Amazonian savannas

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Open habitats such as grasslands occupy < 5% of the Amazon and are currently grouped under the broad term Amazonian savanna, covering an area of *c*. 267 000 km^2, mostly in Brazil and Bolivia. These habitats are found isolated within an extensive rainforest matrix, having a distinct flora from the latter. The lower Amazon River is home to several patches of savanna that occupy both south and north banks of the river, in Santarém, Alenquer and Monte Alegre. Although having an abundance of herbaceous plants, most studies on these open areas focus only on tree species, ignoring the relevant non-woody component of the vegetation. Our objectives were to provide new surveys of seed plants for two Amazonian savanna sites and to take the opportunity to revisit the biogeographical links between Amazonian savanna, Amazonian canga vegetation and the central Brazilian cerrado (CBC) and caatinga, analysing woody and herbaceous plants. We created a floristic database that includes sites of Amazonian savannas, including campinarana, coastal scrub (restinga), CBC and Amazonian campos rupestres (on canga or other substrate). We compared those sites using multivariate analyses to find out the degree of floristic resemblance between sites. We prepared a new list of 406 species of seed plants [336 in Parque Estadual de Monte Alegre (PEMA) and 117 in Serra do Itauajuri (SI)], including 23 new records for the state of Pará and some putative new species for science. The Amazonian savannas form three loosely arranged groups, whereas the Amazonian canga formed a cohesive assemblage. Both groups were contrasted against cerrado and caatinga sites and had a distinctive flora from both. Sites from north-western Pará (Alter do Chão, PEMA and SI) were grouped with their northern counterparts in Roraima. An improved representation of the flora of these sites is provided, with more insight into the relationship between the Amazonian savanna sites and other vegetation types. It is worrying that recent changes of the Brazilian legislation place open environments, such as PEMA, in the path of vulnerability to disturbance and destruction.

ADDITIONAL KEYWORDS: Amazon Rainforest – cerrado – flora – multivariate analysis – Parque Estadual de Monte Alegre.

The Amazon is renowned for being the most diverse rainforest on earth and stands out as the primary source of Neotropical diversity (Antonelli *et al.*, 2018). This biome comprises *c.* 6 000 000 km^2 and spreads across Brazil, Peru, Bolivia, Colombia, Venezuela and the Guianas. In Brazil, *c*. 80% of the area is covered by forest, whereas < 5% comprises open formations such as grasslands and open woodlands (IBGE, 2019), grouped by Pires & Prance (1985) under the broader term 'Amazonian savanna'. The savanna is currently estimated to cover an area of *c*. 267 000 km^2, mostly in Brazil and Bolivia (*c.* 90% of the total area), with sites in Venezuela, Guyana and Suriname (Carvalho & Mustin, 2017). The Amazonian savannas are isolated patches of open habitats with distinct flora, found within a matrix of extensive rainforest (Viana *et al.*, 2016). As an indicator, *c*. 40 seed plant

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species endemic to Brazil are considered exclusive to Amazonian savanna (FBO2020, under construction). It has been established that changing climate during the Quaternary caused a reduction of the forest cover extent, allowing for the spread of savannas, opening opportunities for species migration between the central Brazilian cerrado (CBC) and the Venezuelan llanos (Cardoso Da Silva & Bates, 2002). However, plant population genetic evidence sources propose that the connection between the Amazonian savanna and the Brazilian cerrado is older than the last glacial maximum from the Pleistocene [i.e. 21 thousand years ago (kya)] and that these areas remained in isolation for a long time (130 kya or more), pointing at little connection during the last millennia (Buzatti *et al.*, 2018; Resende-Moreira *et al.*, 2018). Indeed, modelling studies suggest the distribution of the cerrado was wider *c*. 120–130 kya and included connections with the disjunct savannas of the Guyana shield (Werneck *et al.*, 2012; Bueno *et al.*, 2017). Highlighted as of particular importance for conservation (Barbosa-Silva *et al.*, 2016; Carvalho & Mustin, 2017), the Amazonian savanna is under increasing risk as mechanized agriculture advances as the world population increases exponentially. Human interventions leading to conversion of savanna into large-scale agriculture, cattle-ranching and mining sites, and increased frequency of fires and other threats to the quality of habitats have been recorded (Reis *et al.*, 2015; Carvalho & Mustin, 2017).

In the state of Pará, the region of Santarém in the lower Amazon River is home to several patches of savanna (Andrade-Lima, 1959; Oliveira Jr *et al.*, 1999; Magnusson *et al.*, 2008) that occupy both south and north banks of the river, including the Municipalities of Santarém, Alenquer and Monte Alegre. With great archaeological relevance, Monte Alegre is among the top prehistoric human settlements in lowland Amazonia and harbours abundant rupestrian pictographs in caves, shelters and open-air walls (Fig. 1). The first reports of these paintings were made by English naturalist Alfred Wallace in 1848, and subsequently Canadian geologist Charles F. Hartt explored the site and published drawings and findings in *The American Naturalist* in 1871 (Lima & Figueirôa, 2010). Hartt's studies were followed by anthropologist Curt Nimuendajú in 1924, geographer Friedrich Katzer in 1933 and ethnographer Manfred Rauschert 1954–1955, leading to the full excavation of the cave (*Caverna da Pedra Pintada*) by anthropologist Anne Roosevelt in 1996 (Davis, 2016). In relation to the Monte Alegre pictographs and their astronomical significance, Davis (2016) suggested that the fact that this area is covered in low-growing cerrado vegetation may have facilitated the fascinating sky observations made by the occupants of the site thousands of years ago. These research activities were important for the designation of the area as a conservation unit, leading to the creation of a state park, the Parque Estadual de Monte Alegre (PEMA) in November 2001, aimed at protecting the heritage site and surrounding natural environment. Despite the attention received in archaeological terms, the vegetation of this part of the Amazon is poorly understood and, until recently, only two botanical expeditions were carried out, a first survey by Adolpho Ducke in 1923 (Ducke, 1930) and a more complete account made by Dárdano de Andrade-Lima (Andrade-Lima, 1959). Back in 1953, Andrade-Lima made plant collections on horseback in what is now known as PEMA and in the Serra do Itauajuri (SI), a massif that lies to the north of the park. He provided a list of *c*. 60 species for both sites and described the local open vegetation as similar both to the Brazilian cerrado and to the natural fields on Marajó Island, known as campos tesos.

The majority of vegetation studies in the Amazon have a focus on tree species (ter Steege *et al.*, 2013), and the same trend is reflected in research concerning savannas in the Amazon (Miranda & Carneiro Filho, 1994; Magnusson *et al.*, 2008) and elsewhere in Brazil (Ratter *et al.*, 1996; Ratter, Bridgewater & Ribeiro, 2003; Pennington, Lewis & Ratter, 2006; Pontara *et al.*, 2018). Analyses based solely on the woody component of a flora may not be effective in detecting floristic and biogeographic links, considering that the non-woody plants represent a considerably large proportion of the species richness, more so in open vegetation types [Brazil Flora Group (BFG), 2015].

The main objectives of this study are: (1) to provide a comprehensive survey of seed plants in the Amazonian savanna for two sites in Monte Alegre, reducing the current knowledge gap about its flora; (2) to take the opportunity provided by the completion of these lists to revisit the biogeographical links between Amazonian savanna, Amazonian canga vegetation and the CBC considering woody and herbaceous plants and (3) to evaluate the role of the Amazon River as a barrier to species dispersal between patches of Amazonian savannas.

MATERIAL AND METHODS

The study area

Two new comprehensive floristic lists of seed plants for Amazonian savannas were prepared for the Municipality of Monte Alegre in Pará state, lower Amazon. The region comprises outcrops of Palaeozoic and Tertiary rocks that are unusual in the Amazonian context, where geologically recent sedimentary cover predominates (Maurity *et al.*, 1995). The plant collections were carried out in two locations, the PEMA, a state park of 5,800 ha, located at 2°00'55"S

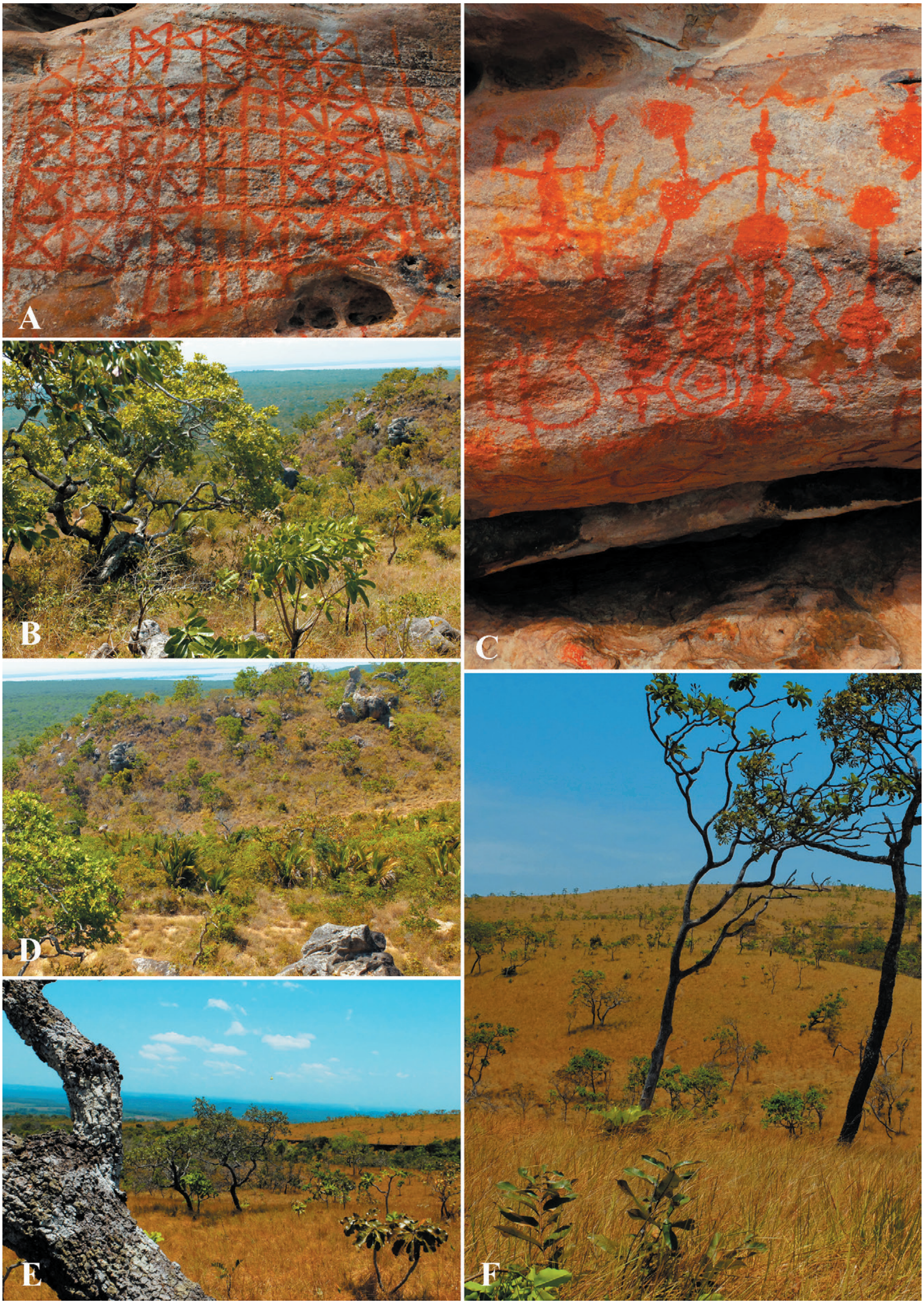

Figure 1. A, C, Rupestrian pictographs in caves at the Parque Estadual de Monte Alegre (PEMA). B, D, Savanna of PEMA. E, F, savanna of the Serra do Itauajuri (SI).

and 54°09’36”W, and the SI, with an area of 760 ha, between 1°50’03”S and 54°3’26”W (Fig. 2). Both areas are found in the geological formation known as the Domo de Monte Alegre, an inverted dome-like structure comprising a flat, low lying central part, low relief with altimetric dimensions < 50 m and raised edges, highlighting the hills to the north and south with higher elevations (Almeida & Vizeu, 2007; Makino, Moura & Chemale Jr, 2007). This formation is a result of the uplifting of Palaeozoic rocks, mainly of the Faro sedimentary formation, estimated to be 325–345 Myr old (Pastana, 1999). The PEMA is found at the southern edge of the dome and comprises three main ridges, known as Serra do Ererê, with elevations up to 250 m a.s.l., Serra do Paituna, to the south, reaching 170 m a.s.l., and unnamed hills to the south-east, up to 160 m a.s.l. About 15 km north on a straight line from Monte Alegre, the SI can be easily accessed via the PA-423 highway. Located in the north-eastern flank of the dome, it comprises a plateau reaching 400 m a.s.l., with steep edges to the south and west. Two of these outcrops were sampled, recording plants in different vegetation types, comprising sandstone campo rupestre (Fig. 1C, D), park savanna on deep sandy soil, savanna on shallow (Fig. 1E, F), rocky soil and stream margin with buriti (*Mauritia flexuosa* L.f.) palms. The local forest was not a focus for this study, which was devoted only to the savannas.

Collections and data handling

Botanical expeditions to the PEMA and SI were carried out in October 2016 (five people, three days), September 2017 (two people, four days) and June 2018 (four people, four days). The specimens collected during the expeditions were pressed in the field, dried in an electric stove and deposited at the herbarium of the Museu Paraense Emilio Goeldi (MG) in Belém, Brazil. When available, duplicates were sent to specialists in other herbaria. We recorded field information regarding vegetation, habitat, substrate, life form, habit and plant details in a database in

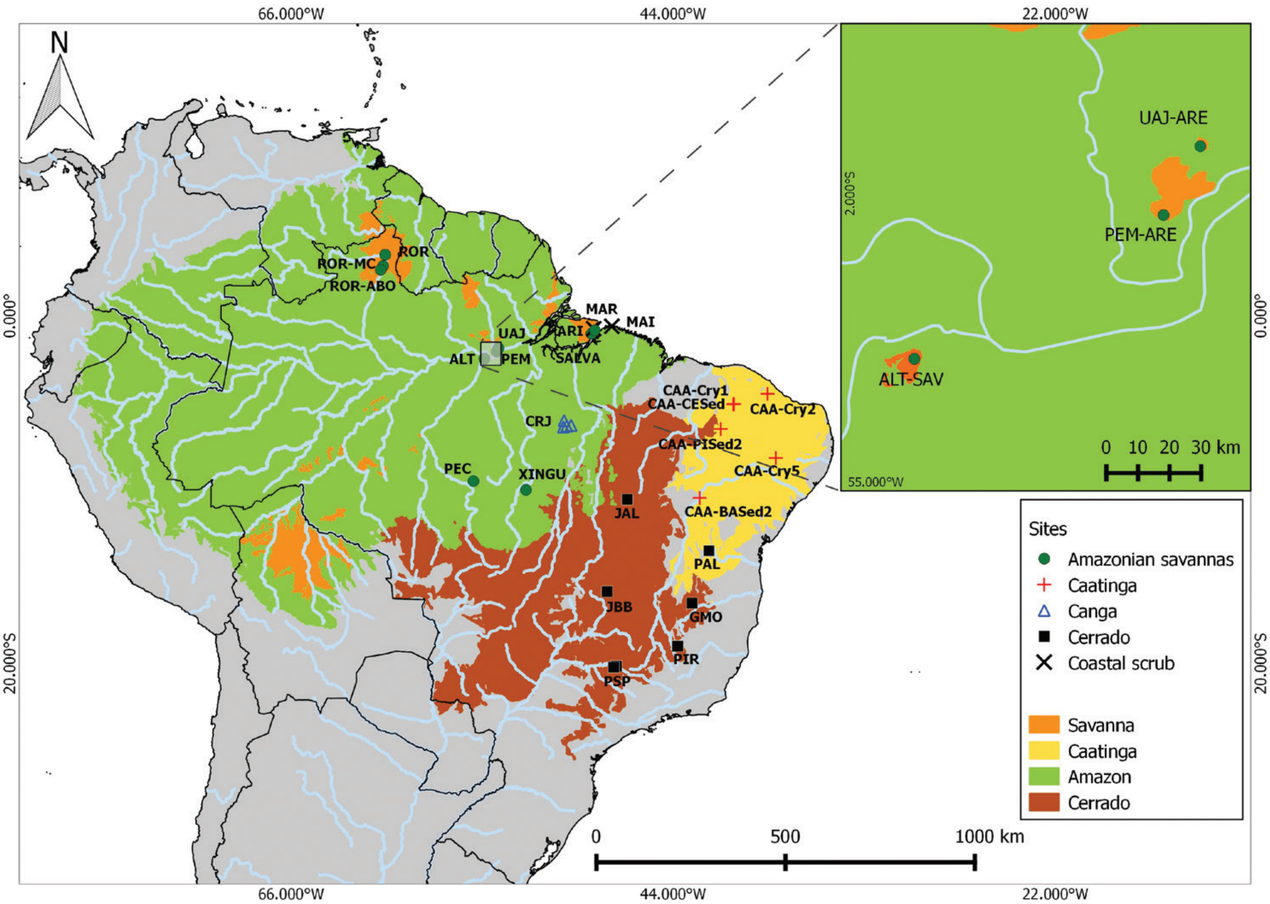

Figure 2. Areas compared in biogeographical database and area of study of the new floristic lists of Amazonian savannas, Parque Estadual de Monte Alegre (PEMA) and SI.

BRAHMS software (BRAHMS7, 2018), with plant images linked to each specimen. Collections from these sites were consulted at MG, IAN and IPA (Dárdano de Andrade Lima collections) herbaria by the authors. A web search for records available for these sites in the Virtual Herbarium of Flora and Fungi of Brazil (INCT, 2018, http://splink.cria.org.br/) recovered specimens from BHCB, IAN, INPA, NY, SP, HUEFS, R, RB and UB (herbarium abbreviations according to Thiers, 2011). Specimens were identified using available literature, by comparison with herbarium specimens and consulting specialists (listed under acknowledgements). The final species list organized by seed plant family, genus and species followed APG IV (2016). Life form, substrate, new records and the current accepted nomenclature follow the database of the Flora do Brasil Online 2020 (FBO2020, under construction). Conservation status for the species was verified in the Brazilian plant red list (Martinelli & Moraes, 2013). A complete list of exsiccatae collected during this project is provided as an electronic supplement for those willing to identify specimens from the study area (see the Supporting Information S1).

Biogeographical database

The Amazonian savannas are scattered across the Amazon Forest biome, and the individual savanna patches can be located hundreds of kilometres apart, separated by a matrix of rainforests and large rivers. In eastern Amazonia, they are distributed from Roraima state on the border with Venezuela, to Marajó Island in the Amazon estuary (Fig. 2). To compare the biogeographical affinities of the Amazonian savannas with other vegetation types we added our newly produced lists to published floristic surveys reporting species composition for localities in the Amazon: savannas, campo rupestre on canga and restinga vegetation (coastal scrubland). This database comprising open Amazonian vegetation was compared to the two main tropical open vegetation types found in Brazil: the CBC, to which the Amazonian savannas are thought to be floristically related, and the deciduous caatinga in the semi-arid region of north-eastern Brazil. All species were compiled in a BRAHMS database (BRAHMS7, 2018) and all species names were updated to match the Flora of Brazil 2020 (FBO2020, under construction). The comprehensive floristic list database previously used to study Brazilian campo rupestre (Zappi *et al.*, 2017, 2019) was expanded to include areas of CBC, Amazonian savannas (including campinarana, reflecting Coutinho, 2016) and coastal scrub (restinga). Lists from selected sites were incorporated into a matrix (Table 1 and Fig. 2).

Floristic comparison and distribution of the Amazonian savannas

The geographical distribution of the species listed for Monte Alegre (PEMA and SI) was analysed using the Brazilian Flora website (FBO2020, under construction) and categorized into endemic/non-endemic to Brazil, to the state of Pará and to northern Brazil. Their presence per biome was ascertained (Amazon rainforest, cerrado, caatinga, Atlantic rainforest). Species were also ranked according to their distribution in other Brazilian states and regions. Species lists resulting from the groupings formed by the biogeographical analyses were compared by means of Venn diagrams using the Venny algorithm (Oliveros, 2018).

Biogeographical analysis

After updating the species nomenclature, we produced a clean species presence-absence matrix S2, excluding invasive species according to Giulietti *et al.* (2018), species determined as aff. and taxa not fully determined to species. We then performed multivariate analyses on the matrix using the 'vegan' package in R (Oksanen *et al.*, 2010; R Core Team, 2018). We used NMDS ordination and UPGMA clustering analyses using Bray Curtis distance to compare the floristic resemblance between sites. To test the significance of the floristic groups defined by each vegetation type (Amazonian savanna, Amazonian canga, restinga vegetation, CBC and caatinga).

RESULTS

Monte Alegre and Serra do Itauajuri species list

Five hundred and forty-two new collections were consolidated with 450 previously collected specimens, found mostly at MG, IAN and IPA herbaria. A final count of 406 species of seed plants was recorded (336 in PEMA and 117 in SI), corresponding to 271 genera and 93 plant families (92 families of angiosperms and one family of gymnosperms) (Table 2). Of these, 288 species were exclusive to PEMA and 69 species were only found at SI, with an overlap of 48 species (Table 2). These findings include 23 new records for the state of Pará; these were not yet listed in the FBO2020 (under construction) at the point of conclusion of the identification phase, but may have been added since, based on the material resulting from our fieldwork. Of these 23, seven species were newly recorded for the Amazon rainforest [*Byrsonima lancifolia* A.Juss., *Cissus duarteana* Cambess., *Lepidaploa remotiflora* (Rich.) H.Rob., *Riencourtia oblongifolia* Gardner, *Vitex flavens* Kunth, *Paspalum gemmosum* Chase

Table 1. Sites included in the Amazonian savanna analysis coded by site symbols: dot = Amazonian savanna; triangle = Amazonian canga; square = Central Brazilian Cerrado; black X = restinga of Marajó; grey cross = caatinga. BA (Bahia), CE (Ceará), DF (Distrito Federal), MG (Minas Gerais), MT (Mato Grosso), PA (Pará), PE (Pernambuco), PI (Piauí), SP (São Paulo) and TO (Tocantins)

Site symbol	Area code	Area name	Species number	Coordinates (DMS) S	Coordinates (DMS) W	Reference
•	ALT-SAV	Alter do Chão, PA	116	2°29’40”	54°53’29”	(Magnusson *et al.*, 2008: 200)
•	ARI-CSO	Cachoeira do Arari, Marajó, PA	15	1°02’00”	48°43’41”	(Lisboa, 2012)
+	CAA-BASed2	Vila Ibirara, Dunas do Rio São Francisco, BA	86	10°48’21”	42°49’30”	(Rocha *et al.*, 2004)
+	CAA-Cry1	Reserva Natural de Serra das Almas, CE	124	5°04’48”	40°31’12”	(Araújo *et al.*, 2011)
+	CAA-Cry2	Reserva Não me Deixes, CE	103	4°56’02”	38°35’20”	(Carvalho da Costa *et al.*, 2007)
+	CAA-CESed1	Reserva Natural de Serra das Almas, CE	124	51°00’	40°33’36”	(Araújo *et al.*, 2011)
+	CAA-CESed2	Reserva Natural de Serra das Almas, CE	217	5°08’36”	40°52’48”	(Araújo *et al.*, 2011: 201)
+	CAA-Cry5	RPPN Maurício Dantas, PE	88	8°11’04”	38°06’51”	(Costa *et al.*, 2009)
+	CAA-PISed2	Fazenda do Morro do Baixio, PE	113	6°30’41”	41°16’53”	(Mendes and Castro, 2009)
▲	CRJ-S11A	Carajás – Serra Sul, PA	227	6°18’57”	50°23’43”	(Mota *et al.*, 2018)
▲	CRJ-S11B	Carajás – Serra Sul, PA	198	6°20’33”	50°26’57”	(Mota *et al.*, 2018)
▲	CRJ-S11C	Carajás – Serra Sul, PA	177	6°23’19”	50°22’52”	(Mota *et al.*, 2018)
▲	CRJ-S11D	Carajás – Serra Sul, PA	419	6°23’50”	50°20’26”	(Mota *et al.*, 2018)
▲	CRJ-SB	Carajás – Serra da Bocaina, PA	219	6°18’14”	49°53’57”	(Mota *et al.*, 2018)
▲	CRJ-SN1	Carajás – Serra Norte, PA	376	6°01’54”	50°18’11”	(Mota *et al.*, 2018)
▲	CRJ-SN2	Carajás – Serra Norte, PA	124	6°03’31”	50°14’38”	(Mota *et al.* 2018)
▲	CRJ-SN3	Carajás – Serra Norte, PA	216	6°01’52”	50°12’11”	(Mota *et al.*, 2018)
▲	CRJ-SN4	Carajás – Serra Norte, PA	302	6°06’24”	50°10’56”	(Mota *et al.*, 2018)
▲	CRJ-SN5	Carajás – Serra Norte, PA	287	6°07’02”	50°07’58”	(Mota *et al.*, 2018)
▲	CRJ-SN6	Carajás – Serra Norte, PA	98	6°07’47”	50°10’31”	(Mota *et al.*, 2018)
▲	CRJ-SN7	Carajás – Serra Norte, PA	110	6°09’31”	50°10’10”	(Mota *et al.*, 2018)
▲	CRJ-SN8	Carajás – Serra Norte, PA	99	6°11’11”	50°09’26”	(Mota *et al.*, 2018)
▲	CRJ-ST	Carajás – Serra do Tarzan, PA	208	6°20’40”	50°08’49”	(Mota *et al.*, 2018)
■	GMO-CCE	Parque Estadual de Grão Mogol, MG	348	16°31’59”	42°55’59”	(Pirani *et al.*, 2009)
■	JAL-ALL	Parque Nacional do Jalapão, TO	517	10°34’01”	46°39’57”	Antar *et al.*, 2019
■	JBB-CER	Estação Ecológica JBB, DF	612	15°51’41”	47°49’43”	(Chacon *et al.*, 2009)
×	MAI-RES	Ilha de Maiandeua, PA	52	0°36’20”	47°33’01”	(Bastos, 1988)
×	MAR-RES	Salvaterra, Marajó, PA	95	0°44’48”	48°35’49”	(Lisboa, 2012)
■	PAL-CER	Pico das Almas, BA	257	13°30’52”	41°57’52”	(Stannard, 1995)
•	PEC-AFL	Parque Estadual do Cristalino, MT	206	9°30’32”	55°31’24”	(Zappi *et al.*, 2011)
•	PEM-ARE	Parque Estadual de Monte Alegre, PA (PEMA)	328	2°03’39”	54°10’48”	Devecchi *et al.* (This study)
■	PIR-CER	Serra do Cipó, MG	200	19°00’	43°45’47”	(Zappi *et al.*, 2014)
■	PIR-CEA	Serra do Cipó, MG	34	19°00’	43°45’47”	(Zappi *et al.*, 2014)
■	PIR-CERU	Serra do Cipó, MG		19°00’	43°45’47”	(Zappi *et al.*, 2014)

Table 1. Continued

Site symbol	Area code	Area name	Species number	Coordinates (DMS) S	Coordinates (DMS) W	Reference
■	PSP-DES	Distrito de Estreito, SP	163	20º09'09"	47º17'27"	(Sasaki and Mello-Silva, 2008)
■	PSP-FBJ	Parque Estadual das Furnas do Bom Jesus	326	20º13'07"	47º26'29"	(Sasaki and Mello-Silva, 2008)
•	ROR-ABO	Campo Experimental Água Boa, RR	83	2º52'16"	60º43'13"	(Araújo *et al.*, 2017)
•	ROR-CER	Savana do Rio Branco, RR	64	3º30'49"	60º35'42"	(Takeuchi, 1960)
•	ROR-MC	Campus do Cauamé, RR	78	2º38'36"	60º51'35"	(Araújo *et al.*, 2017)
•	SALVA	Salvaterra, Marajó, PA	56	0º50'07"	48º32'21"	(Lisboa, 2012)
•	UAJ-ARE	Serra do Itauajuri, PA (SI)	113	1º51'53"	54º04'31"	Devecchi *et al.* (this study)
•	XINGU	Parque Estadual do Xingu, MT	189	9º54'22"	52º38'50"	(Zappi *et al.*, 2016)

ex Renvoize and *Maranta divaricata* Roscoe]. Also, *Asemeia monticola* (Kunth) J.F.B.Pastore & J.R.Abbott, *Pseudobombax longiflorum* (Mart.) A.Robyns, *Homalolepis pohliana* (F.Boas) Devecchi & Pirani and *Praxelis diffusa* (Rich.) Pruski were new records for this biome, all formerly recorded for cerrado. Besides these, at least two species new to science were found (members of Acanthaceae and Melastomataceae); no species listed as endangered were recorded so far. The richest families were Fabaceae (62 species), Poaceae (37 species), Rubiaceae (21 species), Cyperaceae (20 species) and Myrtaceae (18 species). The richest genera were *Chamaecrista* Moench (ten species), *Rhynchospora* Vahl (eight species), *Eugenia* P.Micheli ex L. and *Myrcia* DC. ex Guill. (seven species each), *Paspalum* L. (six species), *Mimosa* L. and *Paepalanthus* Mart. (five species each); 72.6% (196 genera) were represented by a single species.

Concerning plant habit, we found that 37.2% were herbs, 21% trees, 20.2% shrubs, 12.5% lianas and 9.1% subshrubs. Regarding substrate, the vast majority of the recorded plants were terrestrial (95%); the rest were rupicolous, aquatic, epiphytic or parasitic.

Species distribution breakdown

The geographical distribution breakdown of the 392 fully named species listed hereby has provided evidence of six species only known from Pará, 14 restricted to the northern region of Brazil (including or not the north-eastern state of Maranhão, which has strong floristic connections with the Amazonian region); a further 20 species were endemic to Brazil but found in more than one region. When analysed on the basis on biome, the same set of species show a trend of first Amazon rainforest then cerrado distribution (Fig. 3); caatinga and Atlantic rainforest make smaller contributions in terms of species percentages. Most species (40.9%) are widely distributed, occurring in all biomes considered.

Biogeographical analysis

Our matrix comparing the floristic affinities of the Amazonian savannas with other open vegetation types of Brazil had 8213 records for 3304 species in 49 sites belonging to five vegetation types (Amazonian savannas, Amazonian canga, coastal restinga vegetation in the Amazon, CBC and north-eastern Brazil semi-arid caatinga). Analyses revealed that the Amazonian savannas do not form one single cohesive floristic assemblage; they form three groups in the UPGMA analysis (Fig. 4A). Most sites grouped as a 'core Amazonian savanna', joining the lavrado vegetation of Roraima and other savannas scattered throughout the Amazon, including some on Marajó Island, in the estuary of the Amazon River. Sites in northern Mato Grosso state (XINGU and PEC-AFL) formed a second group, closer to the clearly defined, cohesive Amazonian canga (Fig. 4A, B) than to other savannas. The Amazonian cangas comprise rich grasslands surrounded by forests restricted to the iron-rich mountaintops in south-eastern Pará (Mota *et al.*, 2018); they were the most cohesive group in our analysis. One Amazonian savanna site (ARI-CSO) appears as an outlier. The CBC sites from central Brazil formed a single group, including both core (PIR-CER, PIR-CEA, PIR-CERUP, GMO-CCE, JBB-CER, JAL-ALL, PSP-FBJ, PSP-DES) and a disjunct cerrado site (PAL) from the state of Bahia in north-eastern Brazil. In the NMDS, most Amazonian savannas were positioned between the CBC and the Amazonian canga sites. Caatinga was the most distinctive vegetation, differing floristically from CBC, Amazonian savannas and Amazonian canga. Sites of Amazonian campo

Table 2. List of species collected in the savanna at the Parque Estadual de Monte Alegre (PEMA) and Serra do Itauajuri (SI). Native problem (*) and invasive (**) species are indicated according to Giulietti *et al.* (2018). Habit: HER – herb, SUB – subshrub, SHR – shrub, LIA – climber or liana, TRE – tree (including palms).

Family and species	Life form	Substrate	PEMA	SI	Both	New for Pará
Acanthaceae						
Justicia sp. nov.	SHR	Terrestrial	X			X
Ruellia costata (Nees) Hiern	SUB	Terrestrial		X		
Ruellia geminiflora Kunth	SUB	Terrestrial	X			
Amaranthaceae						
Alternanthera brasiliana (L.) Kuntze	HER	Terrestrial	X			
Alternanthera martii R.E.Fr.	SUB	Terrestrial	X			
Cyathula prostrata Blume	SUB	Terrestrial		X		
Amaryllidaceae						
Bomarea edulis (Tussac) Herb.	LIA	Terrestrial	X			
Hippeastrum puniceum (Lam.) Kuntze	HER	Terrestrial	X			
Anacardiaceae						
Anacardium occidentale L.	TRE	Terrestrial	X	X	X	
Tapirira guianensis Aubl.	TRE	Terrestrial	X			
Annonaceae						
Xylopia aromatica (Lam.) Mart.	SHR	Terrestrial	X			
Apocynaceae						
Aspidosperma subincanum Mart.	TRE	Terrestrial	X			
Blepharodon pictum (Vahl) W.D.Stevens	LIA	Terrestrial	X			
Himatanthus drasticus (Mart.) Plumel	TRE	Terrestrial	X	X	X	
Mandevilla tenuifolia (J.C.Mikan) Woodson	LIA	Terrestrial	X	X	X	
Odontadenia hypoglauca Müll.Arg.	LIA	Terrestrial	X			
Odontadenia lutea (Vell.) Markgr.	SHR	Terrestrial	X	X	X	
Odontadenia nitida (Vahl) Müll.Arg.	LIA	Terrestrial	X			
Oxypetalum capitatum Mart.	HER	Terrestrial		X		
Tabernaemontana angulata Mart. ex Müll.Arg.	SHR	Terrestrial	X			
Araceae						
Anthurium bonplandii Bunting	HER	Epiphytic	X			
Anthurium gracile (Rudge) Lindl.	HER	Rupicolous	X			
Philodendron acutatum Schott	LIA	Epiphytic	X	X	X	
Arecaceae						
Attalea phalerata Mart. ex Spreng.	TRE	Terrestrial	X			
Attalea spectabilis Mart.	TRE	Terrestrial	X			
Mauritia flexuosa L.f.	TRE	Terrestrial	X			
Syagrus cocoides Mart.	TRE	Terrestrial	X	X	X	
Asteraceae						
Aspilia paraensis (Huber) J.U.Santos	SUB	Terrestrial	X			
Chromolaena odorata (L.) R.M.King & H.Rob.	SHR	Terrestrial	X			
Ichthyothere cunabi Mart.	SHR	Terrestrial		X		
Ichthyothere terminalis (Spreng.) S.F.Blake	HER	Terrestrial	X	X	X	
Lepidaploa arenaria (Mart. ex DC.) H.Rob.	SHR	Terrestrial	X			
Lepidaploa remotiflora (Rich.) H.Rob.	SHR	Terrestrial		X		X
Lepidaploa silvae (H.Rob.) H.Rob.	SHR	Terrestrial	X			
Praxelis asperulacea (Baker) R.M.King & H.Rob.	HER	Terrestrial		X		
Praxelis diffusa (Rich.) Pruski	HER	Terrestrial		X		
Riencourtia oblongifolia Gardner	HER	Terrestrial	X	X	X	X
Riencourtia pedunculosa (Rich.) Pruski	HER	Terrestrial	X	X	X	
Tridax procumbens L.	HER	Terrestrial	X			X
Begoniaceae						
Begonia humilis Aiton	HER	Terrestrial	X	X	X	

Table 2. Continued

Family and species	**Life form**	**Substrate**	**PEMA**	**SI**	**Both**	**New for Pará**
Begonia semiovata Liebm.	HER	Terrestrial	X			
Bignoniaceae						
Adenocalymma allamandiflorum (Bureau ex K.Schum.) L.G.Lohmann	LIA	Terrestrial	X			
Adenocalymma magnificum Mart. ex DC.	LIA	Terrestrial	X			
Bignonia noterophila Mart. ex DC.	LIA	Terrestrial	X			
Cuspidaria inaequalis (DC. ex Splitg.) L.G.Lohmann	LIA	Terrestrial		X		
Handroanthus ochraceus (Cham.) Mattos	TRE	Terrestrial	X			
Jacaranda duckei Vattimo	TRE	Terrestrial	X	X	X	
Tabebuia aurea (Silva Manso) Benth. & Hook.f. ex S.Moore	TRE	Terrestrial	X			
Tanaecium sp.	LIA	Terrestrial	X			
Bixaceae						
Bixa orellana L.	SHR	Terrestrial	X			
Cochlospermum regium (Mart. ex Schrank) Pilg.	SHR	Terrestrial	X			
Cochlospermum vitifolium (Willd.) Spreng.	SHR	Terrestrial	X			
Boraginaceae						
Cordia tetrandra Aubl.	TRE	Terrestrial	X			
Heliotropium indicum L.	HER	Terrestrial	X			
Bromeliaceae						
Bromelia sp.	HER	Terrestrial	X			
Burseraceae						
Protium heptaphyllum (Aubl.) Marchand	TRE	Terrestrial	X			
Cactaceae						
Cereus hexagonus (L.) Mill.	SHR	Rupicolous	X			
Hylocereus setaceus (Salm-Dyck) R.Bauer	LIA	Rupicolous	X			
Capparaceae						
Cynophalla flexuosa (L.) J.Presl	SHR	Terrestrial	X			
Caricaceae						
Vasconcellea microcarpa (Jacq.) A.DC.	SHR	Terrestrial		X		
Caryophyllaceae						
Polycarpaea corymbosa (L.) Lam.	HER	Terrestrial	X			
Celastraceae						
Anthodon decussatus Ruiz & Pav.	LIA	Terrestrial	X			
Cheiloclinium hippocrateoides (Peyr.) A.C.Sm.	LIA	Terrestrial	X			
Cheiloclinium serratum (Cambess.) A.C.Sm.	LIA	Terrestrial	X			
Maytenus guyanensis Klotzsch ex Reissek	SHR	Terrestrial	X			
Peritassa laevigata (Hoffmanns. ex Link) A.C.Sm.	LIA	Terrestrial	X			
Chrysobalanaceae						
Couepia guianensis Aubl.	TRE	Terrestrial	X			
Hirtella ciliata Mart. & Zucc.	TRE	Terrestrial	X			
Hirtella racemosa Lam.	SHR	Terrestrial	X			
Licania canescens Benoist	TRE	Terrestrial	X			
Licania cymosa Fritsch	TRE	Terrestrial	X			
Cleomaceae						
Physostemon guianense (Aubl.) Malme	HER	Terrestrial	X			
Clusiaceae						
Clusia columnaris Engl.	TRE	Terrestrial	X			
Combretaceae						
Combretum rotundifolium Rich.	LIA	Terrestrial	X			
Connaraceae						
Connarus erianthus Benth. ex Baker	TRE	Terrestrial	X			

Table 2. Continued

Family and species	**Life form**	**Substrate**	**PEMA**	**SI**	**Both**	**New for Pará**
Connarus favosus Planch.	SHR	Terrestrial	X			
Convolvulaceae						
Camonea umbellata (L.) A.R.Simões & Staples	LIA	Terrestrial	X			
Evolvulus filipes Mart.	HER	Terrestrial	X			
Ipomoea alba L.	LIA	Terrestrial	X			
Ipomoea asarifolia (Desr.) Roem. & Schult.	LIA	Terrestrial	X			
Ipomoea goyazensis Gardner	LIA	Terrestrial		X		
Ipomoea piurensis O'Donell	LIA	Terrestrial	X			
Jacquemontia gracillima (Choisy) Hallier f.	HER	Terrestrial	X			X
Jacquemontia guyanensis (Aubl.) Meisn.	LIA	Terrestrial	X			
Costaceae						
Costus spiralis (Jacq.) Roscoe	HER	Terrestrial		X		
Cucurbitaceae						
Ceratosanthes cf. *hilariana* Cong.	LIA	Terrestrial	X			X
Cyperaceae						
Bulbostylis capillaris (L.) C.B.Clarke	HER	Terrestrial	X			
Bulbostylis conifera (Kunth) C.B.Clarke	HER	Terrestrial	X			
Bulbostylis junciformis (Kunth) C.B.Clarke	HER	Terrestrial	X	X	X	
Bulbostylis paradoxa (Spreng.) Lindm.	HER	Terrestrial		X		
Cyperus aggregatus (Willd.) Endl.*	HER	Terrestrial	X			
Cyperus amabilis Vahl	HER	Terrestrial	X	X	X	
Cyperus laxus Lam.	HER	Terrestrial	X			
Lagenocarpus verticillatus (Spreng.) T.Koyama & Maguire	HER	Terrestrial	X			
Rhynchospora barbata (Vahl) Kunth	HER	Terrestrial	X			
Rhynchospora cephalotes (L.) Vahl	HER	Terrestrial	X	X	X	
Rhynchospora dentinux C.B.Clarke	HER	Terrestrial		X		
Rhynchospora divaricata (Ham.) M.T.Strong	HER	Terrestrial		X		
Rhynchospora cf. filiformis Vahl.	HER	Terrestrial	X			
Rhynchospora globosa (Kunth) Roem. & Schult.	HER	Terrestrial	X			
Rhynchospora hirsuta (Vahl) Vahl	HER	Terrestrial	X			
Rhynchospora trichochaeta C.B.Clarke	HER	Terrestrial		X		
Scleria bracteata Cav.	HER	Terrestrial	X			
Scleria cyperina Willd. ex Kunth	HER	Terrestrial		X		
Scleria secans (L.) Urb.	HER	Terrestrial	X			
Scleria verticillata Muhl.	HER	Terrestrial	X	X	X	
Dilleniaceae						
Curatella americana L.	SHR	Terrestrial	X	X	X	
Davilla pedicellaris Benth.	LIA	Terrestrial	X			
Dioscoreaceae						
Dioscorea amaranthoides C.Presl	LIA	Terrestrial	X			
Ebenaceae						
Diospyros sericea A.DC.	SHR	Terrestrial	X			X
Eriocaulaceae						
Paepalanthus bifidus (Schrad.) Kunth	HER	Terrestrial	X			
Paepalanthus fasciculatus (Rottb.) Kunth	HER	Terrestrial	X			
Paepalanthus fasciculoides Hensold	HER	Terrestrial	X			
Paepalanthus polytrichoides Kunth	HER	Terrestrial	X			
Paepalanthus subtilis Miq.	HER	Terrestrial	X	X	X	
Syngonanthus biformis (N.E.Br.) Gleason	HER	Terrestrial		X		
Syngonanthus caulescens (Poir.) Ruhland	HER	Terrestrial	X			
Syngonanthus davidsei Huft	HER	Terrestrial		X		

Table 2. Continued

Family and species	Life form	Substrate	PEMA	SI	Both	New for Pará
Erythroxylaceae						
Erythroxylum citrifolium A.St.-Hil.	TRE	Terrestrial	X			
Erythroxylum rufum Cav.	TRE	Terrestrial	X			
Euphorbiaceae						
Alchornea discolor Poepp.	SHR	Terrestrial	X			
Croton glandulosus L.	SUB	Terrestrial	X			
Croton paraensis Müll.Arg.	HER	Terrestrial	X			
Euphorbia hyssopifolia L.	HER	Terrestrial	X			
Jatropha gossypiifolia L.	SHR	Terrestrial	X			
Mabea angustifolia Spruce ex Benth.	SHR	Terrestrial		X		
Manihot caerulescens Pohl	SHR	Terrestrial	X			
Maprounea guianensis Aubl.	TRE	Terrestrial	X			
Microstachys corniculata (Vahl) Griseb.	SUB	Terrestrial	X			
Fabaceae						
Abarema cochleata (Willd.) Barneby & J.W.Grimes	TRE	Terrestrial	X			
Aeschynomene brasiliana (Poir.) DC.	SUB	Terrestrial		X		
Aeschynomene histrix Poir.	SUB	Terrestrial	X	X	X	
Aeschynomene paniculata Willd. ex Vogel	HER	Terrestrial	X	X	X	
Anadenanthera peregrina (L.) Speg.	SHR	Terrestrial	X			
Ancistrotropis firmula (Mart. ex Benth.) A.Delgado	LIA	Terrestrial		X		
Bauhinia platypetala Burch. ex Benth.	SHR	Terrestrial	X			
Bauhinia ungulata L.	SHR	Terrestrial	X			
Bowdichia virgilioides Kunth	TRE	Terrestrial	X	X	X	
Calliandra surinamensis Benth.	SHR	Terrestrial	X			
Calopogonium mucunoides Desv.	LIA	Terrestrial	X			
Centrosema brasilianum (L.) Benth.	LIA	Terrestrial	X			
Chamaecrista bahiae (H.S.Irwin) H.S.Irwin & Barneby	TRE	Terrestrial	X			
Chamaecrista calycioides (DC. ex Collad.) Grenne	HER	Terrestrial		X		
Chamaecrista desvauxii (Collad.) Killip	HER	Terrestrial		X		
Chamaecrista diphylla (L.) Greene	SUB	Terrestrial	X	X	X	
Chamaecrista fagonioides (Vogel) H.S.Irwin & Barneby	SUB	Terrestrial	X			
Chamaecrista flexuosa (L.) Greene	SUB	Terrestrial	X	X	X	
Chamaecrista hispidula (Vahl) H.S.Irwin & Barneby	SUB	Terrestrial	X	X	X	
Chamaecrista nictitans (L.) Moench	SUB	Terrestrial	X			
Chamaecrista ramosa (Vogel) H.S.Irwin & Barneby	SUB	Terrestrial	X			
Chamaecrista viscosa (Kunth) H.S.Irwin & Barneby	SHR	Terrestrial	X			
Clitoria guianensis (Aubl.) Benth.	HER	Terrestrial		X		
Copaifera martii Hayne	TRE	Terrestrial	X			
Crotalaria maypurensis Kunth	SUB	Terrestrial	X	X	X	
Crotalaria stipularia Desv.	SUB	Terrestrial	X			
Derris floribunda (Benth.) Ducke	LIA	Terrestrial	X			X
Desmodium barbatum (L.) Benth.**	SUB	Terrestrial		X		
Desmodium distortum (Aubl.) J.F.Macbr.	SUB	Terrestrial	X	X	X	
Dioclea coriacea Benth.	LIA	Terrestrial	X	X	X	
Dioclea guianensis Benth.	LIA	Terrestrial	X	X	X	
Eriosema crinitum (Kunth) G.Don	HER	Terrestrial		X		
Eriosema rufum (Kunth) G.Don	HER	Terrestrial	X			
Eriosema simplicifolium (Kunth) G.Don	SUB	Terrestrial		X		
Galactia jussiaeana Kunth	SUB	Terrestrial	X	X	X	
Helicotropis linearis (Kunth) A.Delgado	LIA	Terrestrial		X		

Table 2. Continued

Family and species	Life form	Substrate	PEMA	SI	Both	New for Pará
Hymenaea parvifolia Huber	TRE	Terrestrial	X			
Hymenolobium petraeum Ducke	TRE	Terrestrial	X			
Inga heterophylla Willd.	TRE	Terrestrial	X			
Inga laurina (Sw.) Willd.	TRE	Terrestrial	X			
Machaerium acutifolium Vogel	TRE	Terrestrial		X		
Macrolobium acaciifolium (Benth.) Benth.	TRE	Terrestrial	X			
Macroptilium gracile (Poepp. ex Benth.) Urb.	HER	Terrestrial		X		
Mimosa debilis Humb. & Bonpl. ex Willd.	SUB	Terrestrial	X			
Mimosa orthocarpa Spruce ex Benth.	SUB	Terrestrial	X			
Mimosa pudica L.*	SHR	Terrestrial	X			
Mimosa sensitiva L.	SHR	Terrestrial	X			
Mimosa xanthocentra Mart.	SHR	Terrestrial	X			
Peltogyne paradoxa Ducke	TRE	Terrestrial		X		
Periandra mediterranea (Vell.) Taub.	SHR	Terrestrial	X			
Plathymenia reticulata Benth.	TRE	Terrestrial	X	X	X	
Platymiscium trinitatis Benth.	TRE	Terrestrial	X			
Schnella glabra (Jacq.) Dugand	LIA	Terrestrial	X			
Senna latifolia (G.Mey.) H.S.Irwin & Barneby	SHR	Terrestrial	X			
Senna silvestris (Vell.) H.S.Irwin & Barneby	SHR	Terrestrial	X			
Senna spectabilis (DC.) H.S.Irwin & Barneby	TRE/SHR	Terrestrial	X			
Stylosanthes gracilis Kunth	SUB	Terrestrial	X	X	X	
Stylosanthes viscosa (L.) Sw.	SUB	Terrestrial	X			
Tachigali vulgaris L.G.Silva & H.C.Lima	TRE	Terrestrial	X			
Tephrosia adunca Benth.	SUB	Terrestrial		X		
Tephrosia domingensis (Willd.) Pers.	SUB	Terrestrial		X		
Zornia latifolia Sm.	SUB	Terrestrial	X			
Gentianaceae						
Curtia tenella (Mart.) Cham.	HER	Terrestrial		X		
Neurotheca loeselioides (Spruce ex Progel) Baill.	HER	Terrestrial		X		
Schultesia benthamiana Klotzsch ex Griseb.	HER	Terrestrial		X		
Gesneriaceae						
Gloxinia erinoides (DC.) Roalson & Boggan	HER	Rupicolous	X			
Seemannia purpurascens Rusby	HER	Terrestrial		X		
Gnetaceae						
Gnetum cf. *nodiflorum* Brongn.	LIA	Terrestrial		X		
Heliconiaceae						
Heliconia hirsuta L.f.	HER	Terrestrial	X			
Humiriaceae						
Sacoglottis guianensis Benth.	TRE	Terrestrial	X			
Sacoglottis mattogrossensis Malme	TRE	Terrestrial	X			
Hypericaceae						
Vismia gracilis Hieron.	TRE	Terrestrial	X	X	X	
Icacinaceae						
Casimirella rupestris (Ducke) R.A.Howard	LIA	Terrestrial	X			
Krameriaceae						
Krameria tomentosa A.St.-Hil.	SHR	Terrestrial	X			
Lamiaceae						
Aegiphila integrifolia (Jacq.) Moldenke	SHR	Terrestrial	X			
Aegiphila verticillata Vell.	SHR	Terrestrial	X			
Amasonia hirta Benth.	SUB	Terrestrial	X	X	X	
Hyptis atrorubens Poit.	HER	Terrestrial	X			
Hyptis recurvata Poit.	HER	Terrestrial	X			

Table 2. Continued

Family and species	Life form	Substrate	PEMA	SI	Both	New for Pará
Mesosphaerum suaveolens (L.) Kuntze*	SUB	Terrestrial	X			
Vitex flavens Kunth	TRE	Terrestrial	X			X
Vitex triflora Vahl	TRE	Terrestrial	X			
Lauraceae						
Cassytha filiformis L.	LIA	Holoparasite	X			
Nectandra amazonum Nees	TRE	Terrestrial	X			
Ocotea fasciculata (Nees) Mez	TRE	Terrestrial	X			
Lecythidaceae						
Eschweilera ovata (Cambess.) Mart. ex Miers	TRE	Terrestrial	X			
Lecythis lurida (Miers) S.A.Mori	TRE	Terrestrial	X			
Lentibulariaceae						
Utricularia hispida Lam.	HER	Aquatic	X			X
Utricularia subulata L.	HER	Aquatic	X	X	X	
Utricularia trichophylla Spruce ex Oliv.	HER	Aquatic	X			
Loganiaceae						
Antonia ovata Pohl	TRE	Terrestrial	X	X	X	
Mitreola petiolata (J.F.Gmel.) Torr. & A.Gray	HER	Terrestrial		X		
Loranthaceae						
Oryctanthus florulentus (Rich.) Tiegh.	SHR	Hemiparasite	X			
Psittacanthus biternatus (Hoffmanns.) G.Don	SHR	Hemiparasite	X			
Psittacanthus plagiophyllus Eichler	SHR	Hemiparasite	X			
Struthanthus polyrhizus (Mart.) Mart.	SHR/LIA	Hemiparasite	X			X
Lythraceae						
Cuphea tenuissima Koehne	HER	Terrestrial	X			
Lafoensia vandelliana Cham. & Schltdl.	TRE	Terrestrial	X			
Malpighiaceae						
Byrsonima crassifolia (L.) Kunth	TRE	Terrestrial	X	X	X	
Byrsonima lancifolia A.Juss.	SHR	Terrestrial	X			X
Diplopterys pubipetala(A.Juss.) W.R.Anderson & C.C.Davis	LIA	Terrestrial	X	X	X	
Heteropterys macrostachya A.Juss.	LIA	Terrestrial	X			X
Heteropterys nervosa A.Juss.	LIA	Terrestrial	X			
Janusia janusioides (A.Juss.) W.R.Anderson	LIA	Terrestrial	X	X	X	
Malvaceae						
Eriotheca globosa (Aubl.) A. Robyns	TRE	Terrestrial	X			
Helicteres pentandra L.	SHR	Terrestrial	X			
Luehea paniculata Mart. & Zucc.	SHR	Terrestrial	X			X
Pavonia malacophylla (Link & Otto) Garcke	SHR	Terrestrial	X			
Peltaea surumuensis (Ulbr.) Krapov. & Cristóbal	SHR	Terrestrial	X			
Pseudobombax cf. longiflorum (Mart.) A. Robyns	SHR	Terrestrial	X			
Waltheria indica L.*	SUB	Terrestrial	X			
Marantaceae						
Koernickanthe orbiculata (Körn.) L.Andersson	HER	Terrestrial	X			
Maranta sp.	HER	Terrestrial	X			
Monotagma laxum (Poepp. & Endl.) K.Schum.	HER	Terrestrial	X			
Marcgraviaceae						
Norantea guianensis Aubl.	LIA	Hemiepiphyte	X			
Melastomataceae						
Aciotis acuminifolia (Mart. ex DC.) Triana	HER	Terrestrial	X			
Aciotis annua (Mart. ex DC.) Triana	HER	Terrestrial	X	X	X	
Bellucia dichotoma Cogn.	TRE	Terrestrial	X			
Clidemia rubra (Aubl.) Mart.	SUB	Terrestrial		X		

Table 2. Continued

Family and species	Life form	Substrate	PEMA	SI	Both	New for Pará
Comolia sp. nov.	HER	Terrestrial, Aquatic		X		X
Miconia alborufescens Naudin	SHR	Terrestrial	X			
Miconia rufescens (Aubl.) DC.	SHR	Terrestrial	X			
Miconia secundiflora Cogn.	SHR	Terrestrial	X			
Noterophila limnobios (DC.) Mart.	HER	Aquatic	X			
Rhynchanthera grandiflora (Aubl.) DC.	SHR	Terrestrial	X			
Tibouchina aspera Aubl.	SUB	Terrestrial	X			
Tococa guianensis Aubl.	SHR	Terrestrial	X			
Meliaceae						
Trichilia elegans A.Juss.	TRE	Terrestrial	X			
Menispermaceae						
Abuta grandifolia (Mart.) Sandwith	LIA	Terrestrial	X			
Cissampelos ovalifolia DC.	SUB	Terrestrial	X			
Molluginaceae						
Mollugo verticillata L.	HER	Terrestrial	X			
Moraceae						
Dorstenia tubicina Ruiz & Pav.	HER	Terrestrial	X			
Ficus americana Aubl.	TRE	Terrestrial	X			
Ficus pakkensis Standl.	TRE	Terrestrial	X			
Ficus paludica Standl.	SHR	Terrestrial	X			
Ficus sp.	SHR	Terrestrial	X			
Myristicaceae						
Virola sebifera Aubl.	TRE	Terrestrial	X	X	X	
Myrtaceae						
Calycolpus goetheanus (Mart. ex DC.) O.Berg	TRE	Terrestrial	X			
Campomanesia grandiflora (Aubl.) Sagot	TRE	Terrestrial	X			
Eugenia biflora (L.) DC.	SHR	Terrestrial	X			
Eugenia flavescens DC.	TRE	Terrestrial	X			
Eugenia moschata (Aubl.) Nied. ex T.Durand & B.D.Jacks.	TRE	Terrestrial	X			
Eugenia protenta McVaugh	TRE	Terrestrial	X			
Eugenia punicifolia (Kunth) DC.	TRE	Terrestrial	X			
Eugenia sp.	TRE	Terrestrial	X			
Eugenia stictopetala Mart. ex DC.	TRE	Terrestrial	X			
Myrcia amazonica DC.	SHR	Terrestrial		X		
Myrcia bracteata (Rich.) DC.	TRE	Terrestrial	X			
Myrcia guianensis (Aubl.) DC.	SHR	Terrestrial	X			
Myrcia multiflora (Lam.) DC.	SHR	Terrestrial	X			
Myrcia splendens (Sw.) DC.	SHR	Terrestrial	X			
Myrcia tomentosa (Aubl.) DC.	TRE	Terrestrial	X			
Myrcia umbraticola (O.Berg) E.Lucas & C.E.Wilson	TRE	Terrestrial	X			
Myrciaria floribunda (H.West. ex Willd.) O.Berg	TRE	Terrestrial	X			
Psidium acutangulum DC.	SHR	Terrestrial	X			
Nyctaginaceae						
Neea ovalifolia Spruce ex J.A.Schmidt	SHR	Terrestrial	X			
Ochnaceae						
Ouratea attenuata Tiegh.	TRE	Terrestrial	X			X
Ouratea castaneaefolia (DC.) Engl.	SHR	Terrestrial	X	X	X	
Sauvagesia ramosissima Spruce ex Eichler	HER	Terrestrial	X			
Sauvagesia tenella Lam.	HER	Terrestrial	X			

Table 2. Continued

Family and species	Life form	Substrate	PEMA	SI	Both	New for Pará
Olacaceae						
Heisteria ovata Benth.	TRE	Terrestrial	X			
Onagraceae						
Ludwigia octovalvis (Jacq.) P.H.Raven*	HER	Terrestrial		X		
Opiliaceae						
Agonandra brasiliensis Miers ex Benth. & Hook.f.	TRE	Terrestrial	X			
Orchidaceae						
Cyrtopodium cristatum Lindl.	HER	Terrestrial		X		
Epidendrum nocturnum Jacq.	HER	Epiphytic		X		
Galeandra cristata Lindl.	HER	Epiphytic	X			
Galeandra montana Barb.Rodr.	HER	Terrestrial		X		
Orobanchaceae						
Agalinis hispidula (Mart.) D'Arcy	HER	Aquatic		X		
Buchnera palustris (Aubl.) Spreng.	HER	Terrestrial		X		
Buchnera rosea Kunth	HER	Terrestrial		X		
Passifloraceae						
Passiflora acuminata DC.	LIA	Terrestrial	X			
Passiflora coccinea Aubl.	LIA	Terrestrial	X			
Passiflora costata Mast.	LIA	Terrestrial	X			
Phyllanthaceae						
Phyllanthus niruri L.	HER	Terrestrial	X			
Richeria grandis Vahl	TRE	Terrestrial		X		
Piperaceae						
Piper sp.	SHR	Terrestrial		X		
Plantaginaceae						
Conobea aquatica Aubl.	HER	Aquatic	X			
Poaceae						
Andropogon fastigiatus Sw.	HER	Terrestrial	X			
Andropogon leucostachyus Kunth	HER	Terrestrial		X		
Anthaenantia lanata (Kunth) Benth.	HER	Terrestrial		X		
Aristida capillacea Lam.	HER	Terrestrial		X		
Aristida longifolia Trin.	HER	Terrestrial	X			
Axonopus aureus P.Beauv.	HER	Terrestrial	X			
Axonopus capillaris (Lam.) Chase*	HER	Terrestrial	X			
Eragrostis maypurensis (Kunth) Steud.	HER	Terrestrial	X			
Gymnopogon foliosus (Willd.) Nees	HER	Terrestrial	X			
Gynerium sagittatum (Aubl.) P.Beauv.	HER	Terrestrial	X			X
Hildaea tenuis (J.Presl & C.Presl) C.Silva & R.P.Oliveira	HER	Terrestrial		X		
Ichnanthus calvescens (Nees ex Trin.) Doll	HER	Terrestrial		X		
Ichnanthus hoffmannseggii (Roem. & Schult.) Döll	HER	Terrestrial	X			
Ichnanthus leptophyllus (Nees ex Trin.) Doll	HER	Terrestrial	X			
Ichnanthus sp.	HER	Terrestrial		X		
Lasiacis ligulata Hitchc. & Chase	HER	Terrestrial	X			
Melinis repens (Willd.) Zizka	HER	Terrestrial	X			X
Mesosetum loliiforme (Hochst.) Chase	HER	Terrestrial	X			
Olyra caudata Trin.	HER	Terrestrial	X			
Orthoclada laxa (Rich.) P.Beauv.	HER	Terrestrial	X			
Pariana sp.	HER	Terrestrial	X			
Paspalum conjugatum P.J.Bergius	HER	Terrestrial	X			
Paspalum gemmosum Chase ex Renvoize	HER	Terrestrial	X			X
Paspalum multicaule Poir.*	HER	Terrestrial	X			

Table 2. Continued

Family and species	Life form	Substrate	PEMA	SI	Both	New for Pará
Paspalum parvulum (A.G.Burm.) S.Denham	HER	Terrestrial	X			
Paspalum spissum Swallen	HER	Terrestrial		X		
Paspalum subsesquiglume Doll.	HER	Terrestrial		X		
Sacciolepis myuros (Lam.) Chase	HER	Terrestrial		X		
Schizachyrium sp.	HER	Terrestrial		X		
Setaria vulpiseta (Lam.) Roem. & Schult.	HER	Terrestrial	X			
Spheneria kegelii (C.A.Müll.) Pilg.	HER	Terrestrial	X			
Streptogyna americana C.E.Hubb.	HER	Terrestrial	X			
Streptostachys asperifolia Desv.	HER	Terrestrial	X			
Trachypogon spicatus (L.f.) Kuntze	HER	Terrestrial	X			
Trachypogon vestitus Andersson	HER	Terrestrial	X			X
Trichanthecium cyanescens (Nees ex Trin.) Zuloaga & Morrone	HER	Terrestrial	X			
Trichanthecium pyrularium (Hitchc. & Chase) Zuloaga & Morrone	HER	Terrestrial		X		
Polygalaceae						
Asemeia mollis (Kunth) J.F.B.Pastore & J.R.Abbott	HER	Terrestrial		X		
Asemeia monticola (Kunth) J.F.B.Pastore & J.R.Abbott	HER	Terrestrial	X	X	X	
Asemeia violacea (Aubl.) J.F.B.Pastore & J.R.Abbott	HER	Terrestrial		X		
Bredemeyera floribunda Willd.	LIA	Terrestrial	X			
Polygala appressa Benth.	HER	Terrestrial	X			
Polygala asperuloides Kunth	HER	Terrestrial		X		
Polygala trichosperma L.	HER	Terrestrial	X			
Portulacaceae						
Portulaca mucronata Link	HER	Terrestrial	X			
Primulaceae						
Cybianthus detergens Mart.	SHR	Terrestrial	X			
Proteaceae						
Roupala montana Aubl.	TRE	Terrestrial	X	X	X	
Rhabdodendraceae						
Rhabdodendron amazonicum (Spruce ex Benth.) Huber	SHR	Terrestrial	X			
Rubiaceae						
Alibertia edulis (Rich.) A.Rich.	SHR	Terrestrial	X			
Borreria cerradoana E.L.Cabral, R.M.Salas & J.D.Soto	HER	Terrestrial	X			X
Borreria hispida Spruce ex K.Schum.	HER	Terrestrial	X	X	X	
Borreria verticillata (L.) G.Mey.*	SHR	Terrestrial	X			
Chiococca alba (L.) Hitchc.	SHR	Terrestrial	X			
Chomelia malaneoides Müll.Arg.	SHR	Terrestrial	X			
Cordiera myrciifolia (K.Schum.) C.H.Perss. & Delprete	SHR	Terrestrial	X			
Declieuxia fruticosa (Willd. ex Roem. & Schult.) Kuntze	SUB	Terrestrial	X			
Guettarda spruceana Müll.Arg.	TRE	Terrestrial	X			
Ixora martinsii Standl.	SHR	Terrestrial	X			
Mitracarpus hirtus (L.) DC.	HER	Terrestrial	X			
Mitracarpus strigosus (Thunb.) P.L.R.Moraes, De Smedt & Hjertson	HER	Terrestrial	X			
Palicourea crocea (Sw.) Roem. & Schult.	HER	Terrestrial	X			X
Palicourea guianensis Aubl.	SHR	Terrestrial	X			

Table 2. Continued

Family and species	Life form	Substrate	PEMA	SI	Both	New for Pará
Palicourea rigida Kunth	SHR	Terrestrial		X		
Perama hirsuta Aubl.	HER	Terrestrial	X			
Psychotria bracteocardia (DC.) Müll.Arg.	SHR	Terrestrial	X			
Psychotria hoffmannseggiana (Willd. ex Schult.) Müll.Arg.	SHR	Terrestrial	X	X	X	
Tocoyena formosa (Cham. & Schltdl.) K.Schum.	TRE	Terrestrial		X		
Tocoyena hispidula Standl.	TRE	Terrestrial	X			
Tocoyena longiflora Aubl.	SHR	Terrestrial		X		
Salicaceae						
Casearia commersoniana Cambess.	TRE	Terrestrial	X			
Casearia grandiflora Cambess.	SHR	Terrestrial	X			
Casearia javitensis Kunth	SHR	Terrestrial	X			
Casearia sylvestris Sw.	TRE	Terrestrial	X			
Santalaceae						
Phoradendron obtusissimum (Miq.) Eichler	HER	Hemiparasite	X			
Sapindaceae						
Allophylus strictus Radlk.	SHR	Terrestrial	X			
Matayba guianensis Aubl.	SHR	Terrestrial	X			
Paullinia interrupta Benth.	LIA	Terrestrial	X			
Pseudima frutescens (Aubl.) Radlk.	SHR	Terrestrial	X			
Serjania paucidentata DC.	LIA	Terrestrial	X			
Sapotaceae						
Chrysophyllum argenteum Jacq.	TRE	Terrestrial	X			
Pouteria macrophylla (Lam.) Eyma	TRE	Terrestrial	X			
Pouteria ramiflora (Mart.) Radlk.	TRE	Terrestrial	X			
Simaroubaceae						
Homalolepis pohliana (Boas) Devecchi & Pirani	SHR	Terrestrial	X			
Simaba guianensis Aubl.	TRE	Terrestrial	X			
Simarouba amara Aubl.	TRE	Terrestrial	X	X	X	
Solanaceae						
Cestrum latifolium Lam.	SHR	Terrestrial		X		
Schwenckia americana Rooyen ex L.	HER	Terrestrial	X			
Turneraceae						
Piriqueta cistoides (L.) Griseb.	HER	Terrestrial	X			
Turnera brasiliensis Willd. ex Schult.	SUB	Terrestrial	X			
Turnera coerulea DC.	SUB	Terrestrial	X	X	X	
Verbenaceae						
Clerodendrum aculeatum (L.) Schltdl.	SHR	Terrestrial	X			
Lantana camara L.**	SHR	Terrestrial	X			
Violaceae						
Pombalia calceolaria (L.) Paula-Souza	HER	Terrestrial	X			
Rinorea guianensis Aubl.	TRE	Terrestrial	X			
Vitaceae						
Cissus duarteana Cambess.	LIA	Terrestrial	X			X
Cissus erosa Rich.	LIA	Terrestrial	X			
Vochysiaceae						
Qualea grandiflora Mart.	TRE	Terrestrial	X	X	X	
Salvertia convallariodora A.St.-Hil.	TRE	Terrestrial	X	X	X	
Xyridaceae						
Xyris fallax Malme	HER	Terrestrial	X			
Species total by locality			PEMA (336), SI (117), both (48)			

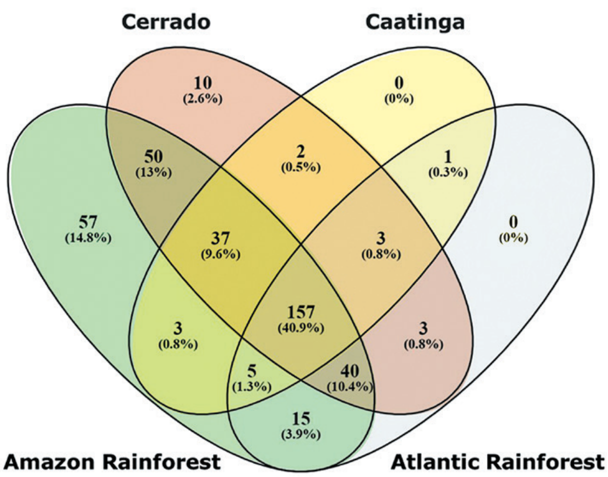

Figure 3. Venn diagram showing overlap between four major Brazilian biomes for 392 species from PEMA and SI in the Monte Alegre region.

rupestre and campinarana in Mato Grosso state (XINGU, PEC-AFL) are interposed between the Amazonian canga and the Amazonian savanna sites, whereas the savanna in Roraima (ROR) appears to have more affinity with the coastal campos from Marajó Island (SALVA).

The breakdown of the species analysed shows that the Amazonian savannas have comparable species overlap with the cerrado and the Amazonian canga vegetation groups. The species common to all three vegetations are relatively few (Fig. 5A, B). The diagram (Fig. 5C) shows that there are 22 species that overlap between all three sites in the Monte Alegre-Santarém region, and some of these representative taxa are illustrated in Figure 6.

DISCUSSION

The biogeographic analyses show that the savannas from central Amazonia in Pará (Monte Alegre and Alter do Chão) are floristically related, despite being on opposite sides of the Amazon River. Meanwhile there are further, weaker connections between them and other Amazonian savannas. Four large groups were identified: Amazonian savanna, Amazonian canga, CBC and Caatinga. The Amazonian canga sites around Carajás appear to be distinct from the Amazonian savanna, being related to two savannic sites in northern Mato Grosso, but not to the other Amazon savannas or the CBC. The low similarity between Amazonian savannas and CBC sites is second only to the tenuous link between them and the caatinga, a deciduous vegetation adapted to the Brazilian semi-arid region, with low and erratic rainfall (Moro *et al.*, 2016). Caatinga is indeed an outgroup of the 'open vegetation' in our analyses. In terms of species overlap, the Amazonian savanna flora is represented by a distinct set of species that are widely distributed in open vegetation, and endemism levels are low in comparison with the Amazonian canga and CBC (Zappi *et al.*, 2019).

Amazonian savannas in Monte Alegre

At first sight, PEMA and SI sites present strong physiognomic differences (Fig. 1), as the site at PEMA falls within the description of Amazonian campo rupestre (Pires & Prance, 1985), with abundant sandstone outcrops that decompose into sandy expanses of land covered by scant herbs and occasional groups of trees. SI, meanwhile, is a flat plateau with occasional exposed layers of rock, where the soil is covered by a continuous herbaceous layer and scattered trees with gnarled trunks, resembling cerrado vegetation (Fig. 1). Indeed, despite the fact of being located at some distance, and on opposing banks of the Amazon River, PEMA has paired with the Amazonian savanna at Alter do Chão (Magnusson *et al.*, 2008) in our biogeographical analyses, before the pair grouped with SI. However, these three areas are more similar to each other than to other savanna sites to the north, south and west of the Amazon. The Amazon River has been considered a determinant for the distribution and speciation of several organisms (Patton, da Silva & Malcolm, 1994; Hall & Harvey, 2002; Nazareno, Dick & Lohmann, 2017). However, the high similarity revealed in our study between sites on both sides of the river (PEMA and Alter do Chão) shows that the barrier the river represents is either recent or semi-permeable, as seen for other Amazonian rivers (Moraes *et al.*, 2016), and does not play an expressive role in the distribution of Amazonian savanna species in that region.

When considering endemism, the species found in Monte Alegre appeared to be widespread in other savannas of the continent. Only 5% of all species listed were endemic to the Amazon rainforest biome, and this is consistent with the trend of low levels of endemism expected for the Amazon region as a whole [Brazil Flora Group (BFG), 2015], but considerably different to what was found in the Amazonian canga, where endemic plants are more common, reflecting the selection pressure made by the particular edaphic conditions in canga outcrops (Mota *et al.*, 2018).

Affinities of the Amazonian savannas

Former work focusing on woody species attributed low support to the Amazonian savanna as a group (Ratter *et al.*, 1996, 2003), with sites like Alter do Chão

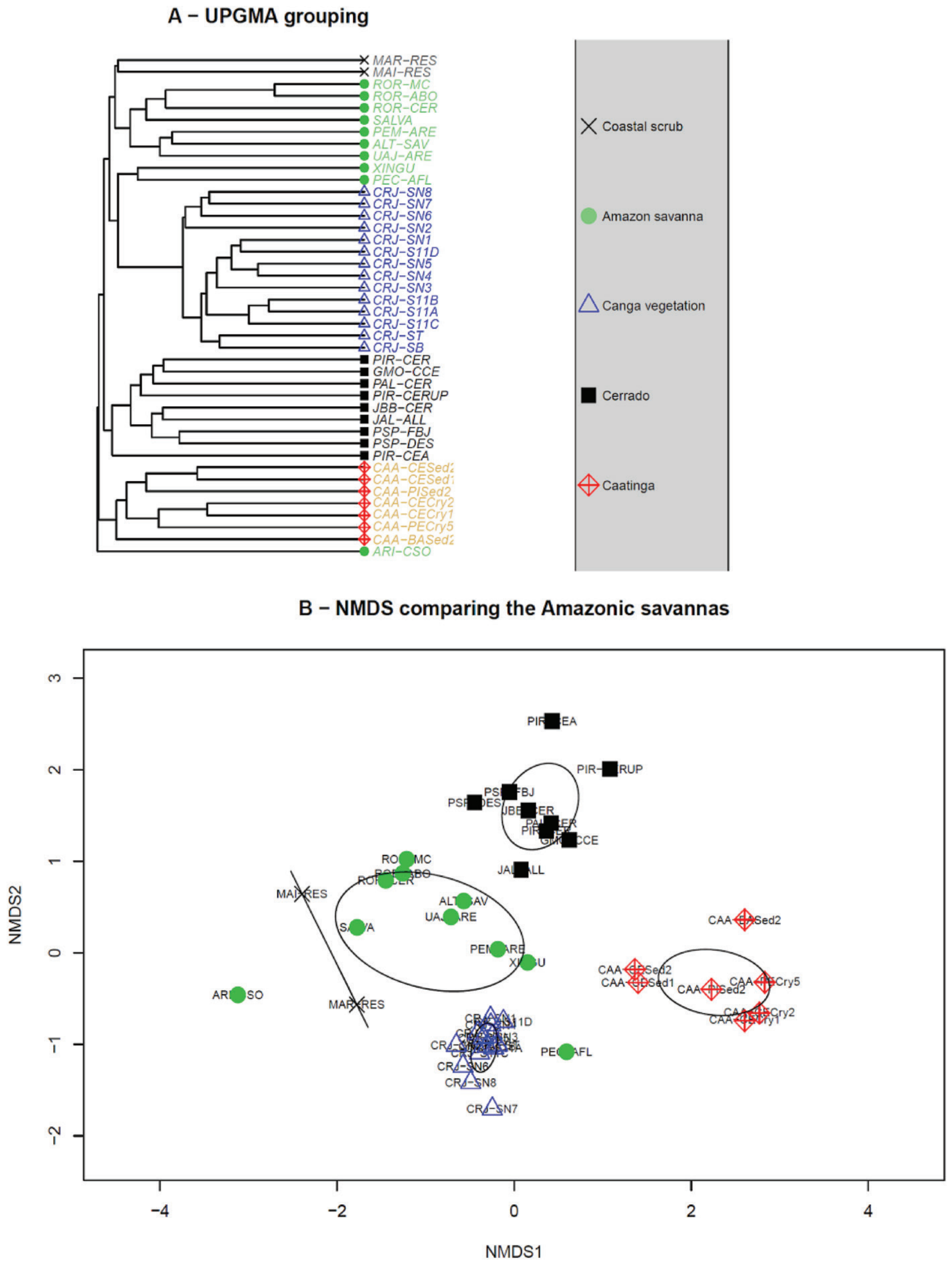

Figure 4. A, UPGMA of open vegetation comparing the five main groups (coastal scrub, Amazonian savanna, Amazonian canga, cerrado and caatinga). B, NMDS showing relationships between the five groups.

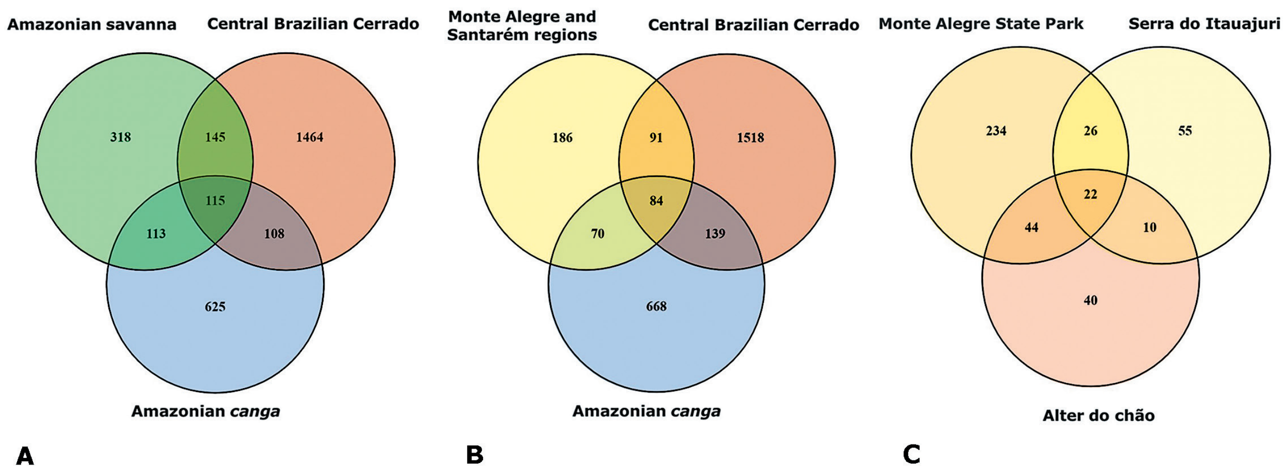

Figure 5. A, Venn diagram showing overlap between Amazonian savanna, Amazonian canga and CBC for 1888 species (total analysis). B, Venn diagram showing overlap between Monte Alegre and Santarém regions (Parque Estadual de Monte Alegre, Serra do Itauajuri and Alter do Chão) and Amazonian canga and CBC for 2756 species. C, Species overlap between Amazonian savanna sites around Monte Alegre and Santarém.

(Magnusson *et al.*, 2008), near our study sites of PEMA and SI, appearing as outliers for a group of savannas of central Brazil that include the Brazilian states of Tocantins and Maranhão. Using comprehensive floristic lists (woody and non-woody plants were analysed), we show that there are considerable differences in the flora of Amazonian savannas located in distant sites. Open habitats in coastal sites (the campos tesos and restinga vegetation) were different floristically from other central Amazonian savannas, and these savannas from central Amazonia had stronger connections with the lavrados of Roraima, on the border with Venezuela. The sites from north-western Pará (Alter do Chão, PEMA and SI) were grouped with northern counterparts in Roraima (Figs 2, 3), showing this pattern. Previous authors (e.g. Ratter *et al.* 2003) have suggested the Amazon savannas to be a subgroup with impoverished plant diversity within the Cerrado Domain.

We also tested the hypothesis that the Amazonian canga might be related to the Amazonian savanna, and our findings disagreed with the nomenclature used by some recent papers (Lanes *et al.*, 2018; Souza-Filho *et al.*, 2019) that refer to the canga of Carajás, in Pará, as Amazonian savanna. In our analyses, Amazonian canga forms a cohesive group, distantly paired with two sites from Mato Grosso (PEC and Xingu, cf. Zappi *et al.*, 2011, 2016) and isolated from the Amazonian savanna. The Amazonian canga sites have high similarity support and count with unique origins, diversification and endemism (Giulietti *et al.*, under review; Mota *et al.*, 2018; Zappi *et al.*, 2019). The link between Mato Grosso sites (PEC and Xingu) and the Amazonian canga is surprising. These sites occur over different rock types (sandstone in PEC, granitic in Xingu) and reunite a series of different physiognomies (campinarana and campo rupestre on arenitic rocks and granite outcrops in PEC, campinarana and granitic outcrops in Xingu), and share 13 species with the Amazonian canga sites [*Ananas ananassoides* (Baker) L.B.Sm.*, *Andropogon bicornis* L.*, *Crotalaria maypurensis* Kunth*, *Emmotum nitens* (Benth.) Miers*, *Fridericia cinnamomea* (DC.) L.G.Lohmann, *Ipomoea asplundii* O'Donnell, *Mimosa somnians* Humb. & Bonpl. ex Willd.*, *Myrcia splendens* (Sw.) DC.*, *Pseudobombax longiflorum* (Mart.) A.Robyns, *Rhynchospora pubera* (Vahl) Boekeler*, *Syagrus cocoides* Mart., *Syngonanthus caulescens* (Poir.) Ruhland and *Vochysia haenkeana* Mart.], seven (*) of which being frequent in the Amazonian canga of Carajás, occurring on most or all outcrops; the others have been recorded infrequently, on one to four outcrops.

Former analyses of cerrado and Amazonian savanna using woody species have quoted 30% (Ratter *et al.*, 1996) to 50% of species as unique to a single site (Ratter *et al.*, 2003), whereas in our study we found that 1000 out of 3304 species (30%) were singletons. The breakdown of these figures reveals that, from 830 plant species listed for Amazonian savanna, 311 species, or 37%, were singletons. The Amazonian canga group is much more cohesive, with 23% of the species appearing only once. On the other hand, the cerrado sites span over a much wider geographical area and include some outstanding diverse localities (with 400 or more species each), and the unique species count for individual sites reaches 56%, which is closer to the value found by Ratter *et al.* (2003).

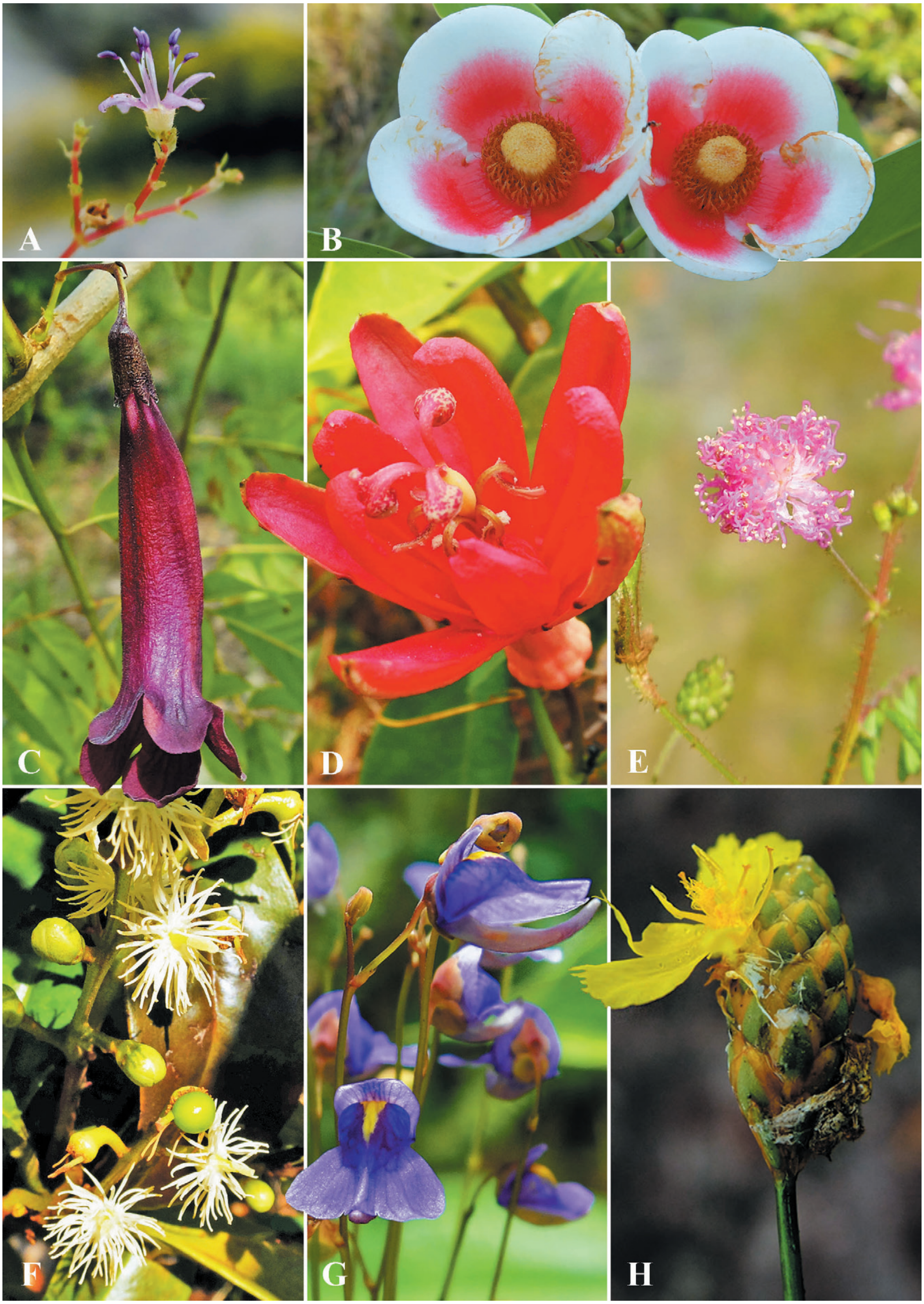

Figure 6. Species representative of the Amazonian savannas found at PEMA, SI and Alter do Chão. A, *Aciotis annua* (Mart. ex DC.) Triana. B, *Clusia columnaris* Engl. C, *Jacaranda duckei* Vattimo. D, *Passiflora coccinea* Aubl. E, *Mimosa orthocarpa* Spruce ex Benth. F, *Rhabdodendron amazonicum* (Spruce ex Benth.) Huber. G, *Utricularia hispida* Lam. H, *Xyris fallax* Malme.

Climatic models estimate that during the Last Interglacial Maximum (LIG) of the Pleistocene (130 kya), the cerrado had a wider distribution and formed a corridor of open habitats in the central Amazon, roughly where we find patches of Amazonian savanna today (Bueno *et al.*, 2017). Studies of population genetic of different species revealed high concordance with the climatic modelling, showing genetic Pleistocene connections between populations of species with disjunct distribution between the CBC and the Amazonian savannas (Buzatti *et al.*, 2018; Resende-Moreira *et al.*, 2018). This shows that, during some timeframe, species from the cerrado were able to migrate to sites now occupied by rainforests (Bueno *et al.* 2017), but that for at least some 12 000 years these disjunct populations have been isolated from the ancestral ones in CBC (Buzatti *et al.*, 2018; Resende-Moreira *et al.*, 2018). Rezende-Moreira *et al.* (2018) drew attention to the fact that the maximum expansion of the studied species was during the LIG (130 kya), highlighting a less recent connection between the Amazonian savannas and the CBC biome. This may explain the strong segregation found between the Amazonian savannas and the cerrado. On the other hand, the subset of widely distributed cerrado species found in the Amazonian savannas, coupled with the relative lack of endemism detected in the latter vegetation, may suggest that the connection between CBC and the Amazonian savannas is recent, and that time since isolation was not long enough to produce a distinct flora. Moreover, isolation can be overcame by episodic dispersal during glacial cycles, when open and drier habitats expanded (Pennington *et al.*, 2004; Franco *et al.*, 2017). For instance, the presence of the cactus *Cereus hexagonus* (L.) Mill. in some of the sites studied (PEMA and CRJ) may represent a link to the dry forest from Lara-Falcón region in Venezuela (Lima *et al.*, 2018).

From an ecological standpoint, Coutinho (2016) considered that the ecology of the cerrado, with deep soils and water table, differs from that of the Amazonian savannas, where the soils are often waterlogged due to the presence of rocks lying at the surface or not far below it. Araújo *et al.* (2017) found that the waterlogged savannas (also known as campinaranas) have considerable higher herbaceous plant diversity and abundance than the more drained sites. Similar sites in the Amazon were already described as swampy savannas (Pires-O'Brien, 1992). The soil in PEMA and SI is indeed shallow, and the bedrock is often close to the surface, as was observed in other Amazonian savanna sites (ALT-SAV, SALVA and PEC-AFL) visited by members of our research team. Therefore it is plausible that the Amazonian savanna fits within the definition of pedo-biome (Langan, Higgins & Scheiter, 2017), where communities of plant species able to survive rooting restrictions and temporary waterlogging explain the distribution of savanna in close proximity with rainforest.

Study limitations

The uncertain, peripheral position retrieved for certain samples, such as ARI (Lisboa, 2012), that consists of only a few species, or lists where species are not fully identified, exemplifies how the quality of information is paramount to perform this type of study. Paradoxically, one of the most challenging aspects of running analyses that integrate woody and herbaceous species information is the scarcity of species lists comprising both woody and non-woody plants for the majority of biomes and vegetation types. Moreover, even for comprehensive lists, their compilation had different constraints, with different collecting effort and coverage. One of the contributions of the present study is to provide two new lists, with 336 (PEMA) and 117 (SI) species, respectively, and to recommend that, in order to make phytosociological comparisons, the minimum collecting effort should ideally amass around 100 species of seed plants with all habits.

CONCLUSIONS

As well as the new data published here, which contribute towards knowledge of Amazonian seed plants, we have taken into account the herbaceous component of the open vegetation to make floristic comparisons with a wider tropical area. Therefore, we provide an improved representation of the flora of these sites, gaining more insight into the relationships between the Amazonian savanna sites and other vegetation types. We show that what is being called Amazonian cerrado should now be treated as Amazon savannas, as they are floristically more related to the lavrados of northern Amazon in Roraima than to the typical CBC. The Amazonian canga of Carajás stand out both from the Amazonian savanna and from the CBC. Unfortunately, recent changes of legislation in Brazil put such open environments, especially riverside areas such as PEMA, in the path of vulnerability to disturbance and destruction (Grasel *et al.*, 2019).

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DATA AVAILABILITY STATEMENT

All supplementary data can be accesssed at Figshare repository: https://doi.org/10.6084/m9.figshare.9169766

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SUPPORTING INFORMATION

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

S1. List of exsiccatae collected during the project
S2. Matrix: presence-absence matrix
S3. Data analysed
S4. Venn diagram data
S5. Amazonic Savannas script, R