

Checklist and geographic distribution of Myrtaceae species occurring in campinaranas of the Brazilian Amazon

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ABSTRACT

White-sand vegetation (campinarana) is a type of vegetation restricted to oligotrophic and highly leached white sand soils in the Amazon phytogeographic domain that includes grassland to forest phytophysionomies. Campinaranas cover about 5% of this phytogeographic domain and are impacted by various anthropic activities that put plant species, especially endemic ones, at risk. Myrtaceae has significant representativeness in oligotrophic edaphic environments, but floristic and taxonomic studies on the family in campinaranas are still few and geographically limited. We present a checklist of Myrtaceae species known from campinaranas of the Brazilian Amazon based on the survey of herbarium specimens and literature data in order to assess the level of endemism of these species for this vegetation type. We compiled occurrence records of 72 species and six genera. *Myrcia* and *Eugenia* were the genera with the highest number of species. Overall, 38 species (53%) occurred only in the Amazon and two were endemic to campinaranas (*Eugenia campina* and *Myrcia psammophila*). Four species are new records for the Brazilian Amazon: *Blepharocalyx salicifolius*, *Eugenia hatschbachii*, *Myrcia anceps* and *Myrcia racemosa*. The specific richness of Myrtaceae in Brazilian campinaranas is likely to be underestimated since extensive areas, especially those farther from the riverbanks, in the states of Amazonas and Roraima, have not yet been intensively surveyed.

KEYWORDS: white sand vegetation; floristics; oligotrophic soils; endemisms; *Myrcia*; *Eugenia*

Checklist e distribuição geográfica das espécies de Myrtaceae que ocorrem em campinaranas da Amazônia brasileira

RESUMO

Campinarana é um tipo de vegetação restrita a solos de areia branca oligotróficos e altamente lixiviados no domínio fitogeográfico amazônico, que inclui fitofisionomias campestres a florestais. Campinaranas cobrem aproximadamente 5% deste domínio fitogeográfico e estão sujeitas ao impacto de várias atividades antrópicas que colocam em risco as espécies vegetais, especialmente as endêmicas. Myrtaceae possui uma representatividade significativa em ambientes edáficos oligotróficos, mas estudos florísticos e taxonômicos sobre a família em campinaranas ainda são escassos e geograficamente limitados. Nós apresentamos um checklist de espécies de Myrtaceae em campinaranas da Amazônia Brasileira, com base no levantamento de espécimes de herbários e dados de literatura, com o objetivo de verificar o nível de endemismo dessas espécies para este tipo de vegetação. Nós compilamos registros de ocorrência de 72 espécies e seis gêneros. *Myrcia* e *Eugenia* foram os gêneros com maior riqueza específica. Do total de espécies, 38 (53%) ocorreram somente na Amazônia e duas foram endêmicas das campinaranas (*Eugenia campina* e *Myrcia psammophila*). Quatro espécies constituem novos registros para a Amazônia brasileira: *Blepharocalyx salicifolius*, *Eugenia hatschbachii*, *Myrcia anceps* e *Myrcia racemosa*. A riqueza específica de Myrtaceae nas campinaranas brasileiras provavelmente está subestimada, pois extensas áreas, especialmente aquelas mais distantes dos rios nos estados de Amazonas e Roraima, ainda não foram intensamente amostradas.

PALAVRAS-CHAVE: vegetação de areia branca; florística; solos oligotróficos; endemismos; *Myrcia*; *Eugenia*

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INTRODUCTION

Campinarana is the term used in Brazil to define a type of vegetation restricted to oligotrophic and highly leached white-sand soils in the Amazon phytogeographic domain that is formed by open vegetation, from grassland to forest phytophysiognomies, usually forming islands embedded in other types of vegetation (Fine and Bruna 2016; Guimarães and Bueno 2016). Campinaranas currently cover about 5% (335.000 km²) of the area of the Amazon phytogeographic domain and 2.8% (217.039 km²) of the Brazilian Amazon domain (Adeney *et al.* 2016; García-Villacorta *et al.* 2016). They are impacted by anthropic activities such as sand extraction, deforestation and vegetation burning for cattle ranching and charcoal production, resulting in fragmentation and severe area reduction that lead to species extinction, especially endemic ones (Ferreira *et al.* 2013; Adeney *et al.* 2016; Oliveira-Filho *et al.* 2021).

In recent decades, an increasing number of studies have focused on campinaranas and their importance for species diversity patterns, evolutionary processes and ecosystem services in the Brazilian Amazon, but they are still few and limited in scope (e.g., Ferreira *et al.* 2014; Adeney *et al.* 2016; Daly *et al.* 2016; Demarchi *et al.* 2022). Floristic and taxonomic studies have shown that Myrtaceae is one of the most well-represented botanical families in campinaranas (e.g., Ferreira 2009; Demarchi *et al.* 2022). Myrtaceae is also frequently represented in other Amazonian oligotrophic environments (e.g., Amazonian savannas and sandy coastal vegetation known in Brazil as restinga), where *Eugenia* L. and *Myrcia* DC. are the genera with the highest species richness (Silva *et al.* 2010; Da Rocha and Da Costa Neto 2019; Da Silva e Silva *et al.* 2021). The occurrence of these genera in limiting

environments such as campinaranas has been associated with adaptations in anatomical traits and morphological plasticity, such as reduction in leaf area and parenchyma tissue, and a well-developed cuticle, which enhance resistance to high light incidence, and clustering and diameter change of stem vessels, which indicate an investment in hydraulic efficiency (Amorim and Júnior 2016; Lemos *et al.* 2019, 2020).

Considering the scarcity of published information on the identification and distribution of Myrtaceae in Brazilian campinaranas, and its importance for the biogeography, conservation and ecological restoration policies of these environments, the objective of the present study was to provide a checklist of Myrtaceae species that occur in campinaranas in the Brazilian Amazon with emphasis on endemic species.

MATERIAL AND METHODS

Study area

The campinarana areas considered in this study are distributed in the states of Acre, Amapá, Amazonas, Pará, Rondônia and Roraima, corresponding to 27 localities in the Brazilian Amazon (Figure 1; Supplementary Material, Table S1). The climate in Brazilian campinaranas is predominantly of the Af type (humid tropical, without a pronounced dry season) according to the Köppen classification (Alvares *et al.* 2013). Annual precipitation ranges from 1,800 to 3,000 mm and average annual temperature ranges from 24 to 28 °C (INMET 2024). The types of soil found in campinaranas are commonly sandy, classified as sopsols or neosols, which undergo high leaching, resulting in a low nutrient content, which characterizes them as oligotrophic (Mendonça *et al.* 2015; Atwell *et al.* 2023).

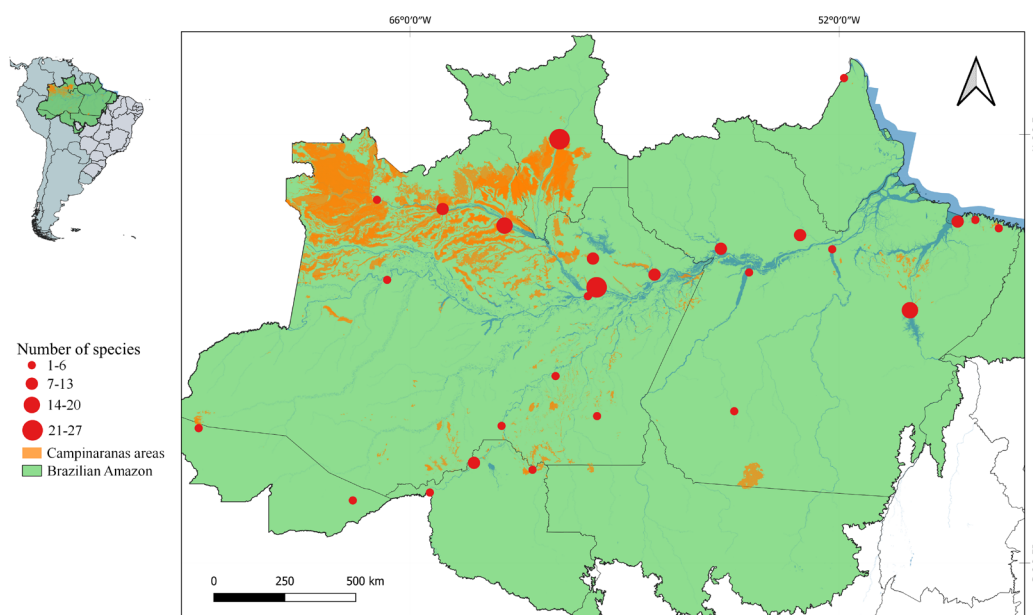


Figure 1. Locality records of specimens of Myrtaceae collected in campinaranas in the Brazilian Amazon phytogeographic domain and number of species per locality.

Data collection and treatment

Specimens of Myrtaceae species from campinaranas were compiled through consultation in person to the herbaria HBRA, HCP, HIFPA, HE, IAN and MG (acronyms according to Thiers 2023). Online herbarium records were also obtained from SpeciesLink (<https://specieslink.net>, accessed on 29 Feb 2023) using “campina” (an obsolete term for campinarana), “campinarana” and/or “white sand” as search terms. We considered published floristic surveys conducted in Brazilian Amazonian campinaranas by Anderson *et al.* (1975), Ferreira *et al.* (2013), Ferreira *et al.* (2014), Daly *et al.* (2016) and Demarchi *et al.* (2022), and also the technical report by Silveira (2003) and the doctoral thesis by Ferreira (2009). The species names used in these sources were revised and are cited here according to Flora e Funga do Brasil (<https://floradobrasil.jbrj.gov.br/>, accessed on 26 Feb 2023). Only herborized specimens were analyzed for this study. The identity of species that constitute new occurrences for Brazilian Amazonian campinaranas were confirmed by Myrtaceae taxonomists (see Acknowledgments). Geographic distribution data, including distribution in phytogeographic domains, were obtained from Flora e Funga do Brasil (<https://floradobrasil.jbrj.gov.br/>, accessed on 26 Feb 2023) and Global Biodiversity Information Facility (<https://gbif.org>, accessed on 09 Feb 2023). We adopted the classification of vegetation types by Flora e Funga do Brasil. The resulting list of Myrtaceae is presented in alphabetical order of genera and species and testimonial material is provided for each record. We also elaborated a Venn diagram showing the number of Myrtaceae species shared among the sampled Brazilian Amazonian campinaranas and other phytogeographic domains in Brazil, as well as a diagram showing the occurrence of Myrtaceae species found in Brazilian Amazonian campinaranas in other Brazilian vegetation types. For this, we used PowerPoint software version 2016 of the Office package (<https://www.microsoft.com/pt-br/microsoft-365/previous-versions/microsoft-office-2016>) and the Illustration software (<https://www.adobe.com/br/products/illustrator.html>).

RESULTS

We recorded 72 Myrtaceae species distributed in six genera in the 27 campinarana localities (Table 1). The genera with

the greatest number of species were *Myrcia* (38 species) and *Eugenia* (21), both representing 82% of all recorded species, followed by *Psidium* L. and *Calycolpus* O.Berg (4 each), *Blepharocalyx* O.Berg and *Myrciaria* O.Berg (2 each) and *Siphoneugena* O.Berg (1).

The number of recorded species ranged from one to 27 species per locality (Figure 1), with highest numbers in the municipalities of Caracaraí (Roraima) and Manaus (Amazonas) with 22 and 27 species, respectively (Supplementary Material, Table S1). Overall, 38 (53%) species were endemic to the Amazon, although most were not restricted to campinaranas. The remaining species had a wide geographic distribution in Brazil, 19 species (26%) occurring in three or more phytogeographic domains. Cerrado (Brazilian savanna) and Atlantic Forest were the domains with the highest number of species shared with campinaranas (27 and 25, respectively). Species occurring in campinaranas rarely occurred in the Pantanal (3) or Pampa (southern Brazilian grasslands) (2) (Figure 2).

Almost all species that occurred in campinaranas also occurred in other types of vegetation in Brazil (Figure 3), mostly in terra firme forest (65% of the 72 species), followed by seasonally flooded forests, including várzea (forests periodically flooded by white water rivers), igapó (forests flooded by black water rivers) and gallery forests (48%), and ombrophilous forest (rainforest) (31%). Two species occurred exclusively in campinaranas: *Eugenia campina* Sobral & M.A.D. Souza and *Myrcia psammophila* Gaem & Farroñay. However, both species have a punctual distribution: *E. campina* was recorded in two localities, one in the state of Pará and another in the state of Amazonas, and *M. psammophila* was found only in a single site in Amazonas. In addition to the latter two species, *Eugenia hatschbachii* Mazine, *Myrcia cuprea* (O.Berg) Kiaersk. and *Myrcia saxatilis* (Amshoff) McVaugh were recorded only in campinarana and in vegetation types that develop in oligotrophic soils (restingas, cerrado (lato sensu) or Amazonian savanna). We report four species as new records for the Brazilian Amazon: *Blepharocalyx salicifolius* (Kunth) O.Berg, *E. hatschbachii*, *Myrcia anceps* (Spreng.) O.Berg and *Myrcia racemosa* (O.Berg) Kiaersk.

Table 1. Species of Myrtaceae recorded in 27 campinarana sites throughout the Brazilian Amazon and their occurrence in Brazilian phytogeographic domains and vegetation types. New occurrences for the Brazilian Amazon are marked with an asterisk (*).

Species	Herbarium voucher	Phytogeographic domain	Vegetation type
<i>Blepharocalyx eggersii</i> (Kiaersk.) Landrum	Ferreira, CAC 12970 (INPA)	Amazon, Atlantic Forest	Campinarana, terra firme forest, ombrophilous forest (rainforest), restinga
* <i>Blepharocalyx salicifolius</i> (Kunth) O.Berg	Dácio, IMS 1309 (INPA)	Amazon, Caatinga, Cerrado, Atlantic Forest, Pampa	Anthropic area, grassland, campinarana, rupestrian fields, cerrado (lato sensu), seasonally deciduous forest, seasonally semideciduous forest, ombrophilous forest (rainforest), mixed ombrophilous forest, restinga
<i>Calycolpus calophyllus</i> (Kunth) O.Berg	Lima, DF 304 (INPA)	Amazon	Campinarana, várzea forest, amazonian savanna
<i>Calycolpus goetheanus</i> (Mart. ex DC.) O.Berg	Souza, MAD 482 (IAN)	Amazon, Cerrado	Campinarana, terra firme forest, várzea forest, amazonian savanna

Table 1. Continued.

Species	Herbarium voucher	Phytogeographic domain	Vegetation type
<i>Calycolpus revolutus</i> (Schauer) O.Berg	Souza, MAD 482 (IAN)	Amazon	Campinarana, terra firme forest, amazonian savanna
<i>Calycolpus roraimensis</i> Steyerl.	Perigolo, NA 218 (INPA)	Amazon	Campinarana, amazonian savanna, rock outcrop vegetation
<i>Eugenia biflora</i> (L.) DC.	Black, GA 8695 (IAN)	Amazon, Caatinga, Cerrado	Campinarana, cerrado (lato sensu), terra firme forest, várzea forest
<i>Eugenia caducipetala</i> M.A.D.Souza & Scudeller	Carvalho-Sobrinho, JG 960 (INPA)	Amazon	Campinarana, terra firme forest
<i>Eugenia calva</i> McVaugh	Souza, MAD de 190 (INPA)	Amazon	Campinarana, várzea forest
<i>Eugenia citrifolia</i> Poir.	Labiak, P.H. 5616 (UFPR)	Amazon	Campinarana, terra firme forest
<i>Eugenia egensis</i> DC.	Cabral, FN 1258 (INPA)	Amazon, Cerrado, Atlantic Forest	campinarana, cerrado (lato sensu), terra firme forest, várzea forest, seasonally deciduous forest
<i>Eugenia florida</i> DC.	Pereira-Silva, G 16514 (IAN)	Amazon, Caatinga, Cerrado, Atlantic Forest	Campinarana, caatinga (stricto sensu), cerrado (lato sensu), terra firme forest, várzea forest, Seasonal semideciduous forest, ombrophilous forest (rainforest)
<i>Eugenia gomesiana</i> O.Berg	Cabral, FN 377 (INPA)	Amazon	Campinarana, riverine forest and/or gallery forest, igapó forest, terra firme forest, várzea forest
* <i>Eugenia hatschbachii</i> Mazine	Assunção, PACL 1135 (INPA)	Amazon, Cerrado	Campinarana, cerrado (lato sensu)
<i>Eugenia inundata</i> DC.	Nitta, A 17591 (IAN)	Amazon, Cerrado	Campinarana, igapó forest, várzea forest
<i>Eugenia moschata</i> (Aubl.) Nied. ex T.Durand & B.D.Jacks.	Roosmalen, MGMV 1319 (INPA)	Amazon, Cerrado	Campinarana, cerrado (lato sensu), terra firme forest, várzea forest
<i>Eugenia omissa</i> McVaugh	Prance, GT 3323 (INPA)	Amazon	Campinarana, terra firme forest
<i>Eugenia patens</i> Poir.	Medeiros, H 1081 (HUFESJ)	Amazon	Campinarana, terra firme forest, várzea forest
<i>Eugenia patrisii</i> Vahl	Daly, DC 944 (IAN)	Amazon	Campinarana, várzea forest
<i>Eugenia protenta</i> McVaugh	Thomas, WW 5342 (INPA)	Amazon	Campinarana, terra firme forest
<i>Eugenia puniceifolia</i> (Kunth) DC.	Oliveira, E 4765 (IAN)	Amazon, Caatinga, Cerrado, Atlantic Forest, Pantanal	Campinarana, caatinga (stricto sensu), campinarana, rupestrian fields, cerrado (lato sensu), seasonal semideciduous forest, restinga, rock outcrop vegetation
<i>Eugenia pusilliflora</i> M.L.Kawasaki & B.Holst	Nelson, BW 637 (INPA)	Amazon	Campinarana, terra firme forest
<i>Eugenia roseiflora</i> McVaugh	L. Alencar 228 (US)	Amazon	Campinarana, várzea forest
<i>Eugenia stictopetala</i> Mart. ex DC.	Daly, DC 1007 (INPA)	Amazon, Caatinga, Cerrado, Atlantic Forest	Campinarana, rupestrian fields, cerrado (lato sensu), terra firme forest, ombrophilous forest (rainforest)
<i>Eugenia stipitata</i> McVaugh	Fróes, RL 32483 (IAN)	Amazon	Campinarana, terra firme forest, várzea forest
<i>Eugenia subterminalis</i> DC.	Souza, MAD de 109 (INPA)	Amazon, Caatinga, Cerrado, Atlantic Forest	Campinarana, seasonal evergreen forest, seasonal semideciduous forest, ombrophilous forest (rainforest), mixed ombrophilous forest
<i>Eugenia campina</i> Sobral & M.A.D.Souza	Anderson, AB 313 (INPA)	Amazon	Campinarana
<i>Myrcia aliena</i> McVaugh	Daly, DC 10612 (UFACPZ)	Amazon	Campinarana, terra firme forest, várzea forest
<i>Myrcia amapensis</i> McVaugh	Pires, MJ 592 (INPA)	Amazon	Campinarana, terra firme forest, restinga, amazonian savanna
<i>Myrcia amazonica</i> DC.	Souza, MAD 327 (IAN)	Amazon, Cerrado, Atlantic Forest	Campinarana, cerrado (lato sensu), riverine forest and/or gallery forest, terra firme forest, seasonal semideciduous forest, ombrophilous forest (rainforest)
* <i>Myrcia anceps</i> (Spreng.) O.Berg	Rocha, GPE 191 (UB)	Amazon, Atlantic Forest	Campinarana, seasonal semideciduous forest, ombrophilous forest (rainforest)
<i>Myrcia bracteata</i> (Rich.) DC.	Assunção, PACL 1657 (INPA)	Amazon, Cerrado	Campinarana, terra firme forest
<i>Myrcia caudata</i> (McVaugh) E.Lucas & C.E.Wilson	Sakagawa, S 439 (INPA)	Amazon	Campinarana, riverine forest and/or gallery forest, terra firme forest
<i>Myrcia clusiifolia</i> (Kunth) DC.	Holanda, ASS 372 (INPA)	Amazon	Campinarana, cerrado (lato sensu), terra firme forest
<i>Myrcia crebra</i> (McVaugh) A.R.Lourenço & E.Lucas	Lourenço, AR 339 (BHCB)	Amazon	Campinarana, terra firme forest, várzea forest
<i>Myrcia cuprea</i> (O.Berg) Kiaersk.	Conceição, LA 9 (IAN)	Amazon	Campinarana, restinga, amazonian savanna
<i>Myrcia cuspidata</i> (Mart. ex DC.) A.R.Lourenço & E.Lucas	Farroñay, FJ 1305 (INPA)	Amazon	Campinarana, igapó forest, terra firme forest, várzea forest
<i>Myrcia decorticans</i> DC.	Black, GA 18944 (IAN)	Amazon, Atlantic Forest	Campinarana, ombrophilous forest (rainforest), restinga
<i>Myrcia deflexa</i> (Poir.) DC.	Damasceno, B 18 (IAN)	Amazon, Cerrado	Campinarana, riverine forest and/or gallery forest, terra firme forest, seasonal evergreen forest
<i>Myrcia eximia</i> DC.	Coelho, C.A. 417 (INPA)	Amazon, Cerrado, Atlantic Forest	Campinarana, cerrado (lato sensu), ombrophilous forest (rainforest)
<i>Myrcia florifera</i> (McVaugh) Gaem & E.Lucas	Melo, A 885 (INPA)	Amazon	Campinarana, riverine forest and/or gallery forest, terra firme forest

Table 1. Continued.

Species	Herbarium voucher	Phytogeographic domain	Vegetation type
<i>Myrcia gigas</i> McVaugh	Junqueira, AB 881 (INPA)	Amazon	Campinarana, igapó forest, terra firme forest, várzea forest
<i>Myrcia glabra</i> (O.Berg) D.Legrand	Demarchi, LO 1330 (INPA)	Amazon, Atlantic Forest	Campinarana, ombrophilous forest (rainforest), restinga
<i>Myrcia grandis</i> McVaugh	Damasco, G 591 (INPA)	Amazon	Campinarana, terra firme forest
<i>Myrcia guianensis</i> (Aubl.) DC.	Souza, MAD 1640 (IAN)	Amazon, Caatinga, Cerrado, Atlantic Forest, Pantanal	Caatinga (stricto sensu), campinarana, rupestrian fields, cerrado (lato sensu), terra firme forest, seasonally deciduous forest, seasonal semideciduous forest, ombrophilous forest (rainforest), mixed ombrophilous forest, restinga
<i>Myrcia hylobates</i> (Standl. ex Amshoff) E.Lucas & K.Samra	Ferreira, CAC 10067 (CEN)	Amazon, Atlantic Forest	Campinarana, terra firme forest, ombrophilous forest (rainforest)
<i>Myrcia inaequiloba</i> (DC.) Lemée	Lima, DF 305 (INPA)	Amazon, Atlantic Forest	Campinarana, riverine forest and/or gallery forest, terra firme forest, várzea forest
<i>Myrcia intonsa</i> (McVaugh) B.Holst	Carvalho-Sobrinho, JG 1503 (INPA)	Amazon	Campinarana, terra firme forest
<i>Myrcia megapaniculata</i> A.R.Lourenço & Parraos.	Perigolo, NA 206 (IAN)	Amazon	Campinarana, terra firme forest, várzea forest
<i>Myrcia multiflora</i> (Lam.) DC.	Pires, MJ 662 (INPA)	Amazon, Caatinga, Cerrado, Atlantic Forest, Pampa	Anthropic area, rupestrian fields, campinarana, cerrado (lato sensu), terra firme forest, seasonal semideciduous forest, ombrophilous forest (rainforest), mixed ombrophilous forest
<i>Myrcia neoforsteri</i> A.R.Lourenço & E.Lucas	Lourenço, AR 339 (INPA)	Amazon	Campinarana, terra firme forest, várzea forest
<i>Myrcia ovata</i> Cambess.	Carvalho, FA de 1747 (INPA)	Amazon, Atlantic Forest	Campinarana, ombrophilous forest (rainforest), restinga
<i>Myrcia paivae</i> O.Berg	Gaem, PH 135 (UFSCar)	Amazon	Campinarana, terra firme forest, várzea forest
<i>Myrcia platyclada</i> DC.	Vicentini, A 1398 (SP)	Amazon	Campinarana, terra firme forest
<i>Myrcia psammophila</i> Gaem & Farroñay	Farroñay, FJ 1305 (INPA)	Amazon	Campinarana
<i>Myrcia pyrifolia</i> (Desv. ex Ham.) Nied.	Black, GA 18952 (IAN)	Amazon	Campinarana, terra firme forest, várzea forest
* <i>Myrcia racemosa</i> (O.Berg) Kiaersk.	Carvalho, FA de 1837 (INPA)	Amazon, Cerrado, Atlantic Forest	Anthropic area, campinarana, ombrophilous forest (rainforest), restinga
<i>Myrcia rufipila</i> McVaugh	Lisboa, P.L.B. 1403 (MG)	Amazon	Campinarana, terra firme forest
<i>Myrcia saxatilis</i> (Amshoff) McVaugh	Demarchi, LO 1377 (INPA)	Amazon	Campinarana, amazonian savanna
<i>Myrcia servata</i> McVaugh	Souza, MAD 506 (IAN)	Amazon	Campinarana, terra firme forest, várzea forest, amazonian savanna
<i>Myrcia splendens</i> (Sw.) DC.	Simon, MF 1005 (IAN)	Amazon, Caatinga, Cerrado, Atlantic Forest, Pantanal	Campinarana, rupestrian fields, cerrado (lato sensu), riverine forest and/or gallery forest, terra firme forest, seasonal evergreen forest, Seasonal semideciduous forest, ombrophilous forest (rainforest)
<i>Myrcia sylvatica</i> (G.Mey.) DC.	Mansano, VF 869 (IAN)	Amazon, Caatinga, Cerrado, Atlantic Forest	Campinarana, terra firme forest, várzea forest, ombrophilous forest (rainforest)
<i>Myrcia tomentosa</i> (Aubl.) DC.	UB 217225	Amazon, Caatinga, Cerrado, Atlantic Forest	Campinarana, caatinga (stricto sensu), high altitude grassland, rupestrian fields, cerrado (lato sensu), riverine forest and/or gallery forest, terra firme forest, várzea forest, seasonal semideciduous forest, ombrophilous forest (rainforest), restinga
<i>Myrcia uaupensis</i> (O.Berg) Gaem & E.Lucas	Krukoff, BA 7232 (SP)	Amazon	Campinarana, igapó forest, terra firme forest, ombrophilous forest (rainforest)
<i>Myrcia umbraticola</i> (Kunth) E.Lucas & C.E.Wilson	Campos, P 1230 (INPA)	Amazon	Campinarana, igapó forest, ombrophilous forest (rainforest)
<i>Myrciaria dubia</i> (Kunth) McVaugh	Pires, JM 6742 (IAN)	Amazon, Cerrado	Campinarana, várzea forest
<i>Myrciaria floribunda</i> (H.West ex Willd.) O.Berg	HBRA6158	Amazon, Caatinga, Cerrado, Atlantic Forest	Campinarana, rupestrian fields, cerrado (lato sensu), riverine forest and/or gallery forest, terra firme forest, várzea forest, seasonally deciduous forest, seasonal evergreen forest, Seasonal semideciduous forest, ombrophilous forest (rainforest), mixed ombrophilous forest, restinga
<i>Psidium acutangulum</i> DC.	Souza, MAD 1769 (IAN)	Amazon	Campinarana, várzea forest
<i>Psidium guineense</i> Sw.	Lourenço, AR 334 (INPA)	Amazon, Caatinga, Cerrado, Atlantic Forest	Campinarana, anthropic area, caatinga, high altitude grassland, rupestrian fields, cerrado, seasonal semideciduous forest, ombrophilous forest (rainforest)
<i>Psidium guyanense</i> Pers.	Coradin, L 120 (IAN)	Amazon, Cerrado	Campinarana, cerrado (lato sensu), terra firme forest, amazonian savanna
<i>Psidium salutare</i> (Kunth) O.Berg	Coradin, L 141 (IAN)	Amazon, Cerrado, Atlantic Forest	Campinarana, caatinga (stricto sensu), grassland, rupestrian fields, cerrado (lato sensu), seasonal semideciduous forest, mixed ombrophilous forest
<i>Siphoneugena dussii</i> (Krug & Urb.) Proença	Prance, GT 25051 (MO)	Amazon, Caatinga, Cerrado, Atlantic Forest	Campinarana, caatinga (stricto sensu), cerrado (lato sensu), terra firme forest, seasonal semideciduous forest

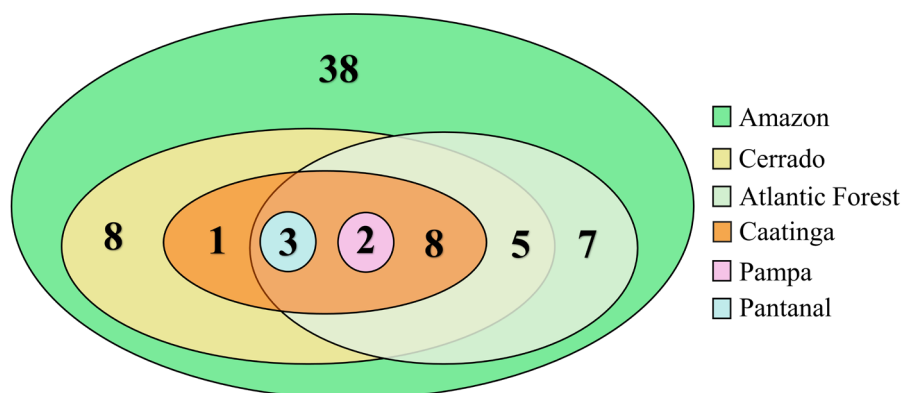


Figure 2. Venn diagram showing the number of Myrtaceae species shared among campinaranas of the Brazilian Amazon and other phylogeographic domains in Brazil.

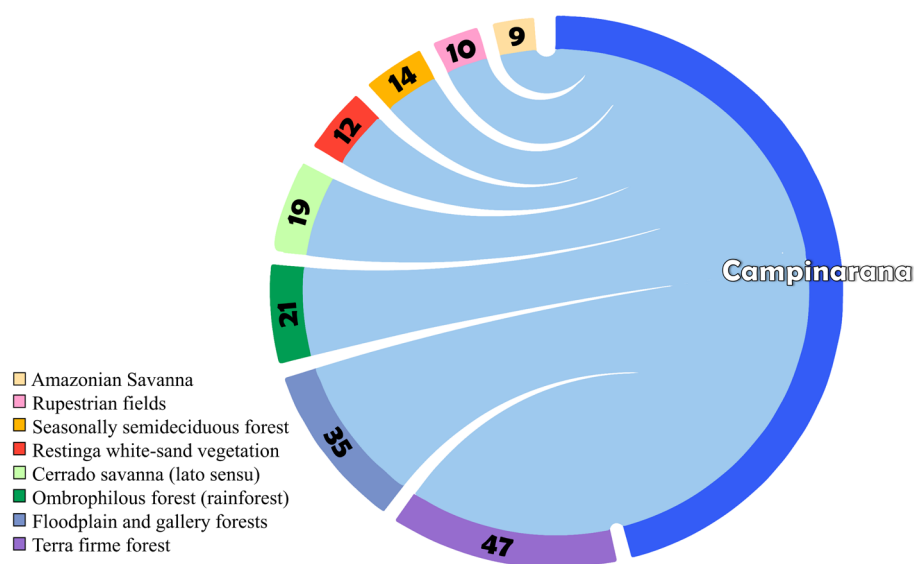


Figure 3. Diagram showing the occurrence of 72 Myrtaceae species found in campinaranas of the Brazilian Amazon and other Brazilian vegetation types. Each species occurred in one to eleven other vegetation types besides campinaranas.

DISCUSSION

Myrtaceae frequently occur in environments of the Amazonian phylogeographic domain with limiting conditions, such as savannas and restingas (Silva *et al.* 2010; Da Rocha and Da Costa Neto 2019; Da Silva e Silva *et al.* 2021). *Myrcia* and *Eugenia* were the genera with the highest richness of species recorded both in campinaranas (Ferreira 2009; Demarchi *et al.* 2022; this study) and restingas (Amaral *et al.* 2008; Silva *et al.* 2010; Lourenço and Barbosa 2012) in Brazil. However, our results indicate a higher number of Myrtaceae species in campinaranas than in Amazonian restingas (Amaral *et al.* 2008; Silva *et al.* 2010; Da Silva e Silva *et al.* 2021; Flora e Funga do Brasil (<https://is.gd/VtfAvj>) and Amazonian savannas (Magnusson *et al.* 2008; Da Rocha and Da Costa Neto 2019; Campos *et al.* 2021; Flora e Funga do Brasil

(<https://is.gd/07yG7L>). This is likely related to the less hostile conditions of campinaranas compared to Amazonian savannas, which undergo seasonal fire regimes, and restingas, influenced by saline and windy coastal conditions.

The high number of species of Myrtaceae in campinaranas can also be associated with anatomical adaptations in this family that enable different mechanisms of colonization, establishment and development, conferring phenotypic plasticity to successfully resist limiting environmental conditions (Arruda *et al.* 2009; Melo Júnior and Torres Boeger 2015; Amorim and Melo Júnior 2017; Lemos *et al.* 2018; Gavilanes *et al.* 2020; Radersma *et al.* 2020; Amboni *et al.* 2022). For example, changes in leaf anatomy are decisive in the acclimatization capacity of species exposed to different environmental conditions (Donato and De Morretes 2009; Amorim and Melo Júnior 2017; Lemos *et al.* 2018). The

leaves of *Eugenia glazioviana* Kiaersk developed xeromorphic anatomical features in response to water stress (Esposito-Polesi et al. 2011) and similar results have been observed in *Eugenia luschnathiana* (O.Berg) Klotzsch ex B.D.Jacks. Also, morphological data of *Myrcia splendens* (Sw.) DC. (Amorim and Júnior 2016) and *Myrcia guianenses* (Aubl.) DC. (Lemos et al. 2020) showed that plasticity is an advantageous feature in response to certain abiotic factors, such as increased temperature and water deficit. The presence in campinaranas of species with a preference for oligotrophic soils, such as *E. hatschbachii*, *M. cuprea* and *M. saxatilis*, reinforces the existence of specialist species in these environments, as previously reported (Fine et al. 2010; Silva et al. 2010; Ferreira et al. 2013; Adeney et al. 2016; Daly et al. 2016; Fine and Baraloto 2016; García-Villacorta et al. 2016; Demarchi et al. 2022). Anatomical and physiological plasticity in plant species confers the ability to adjust and achieve high fitness under different environmental conditions (Sultan 2000) and provide insights into how species can deal with possible natural or anthropogenic climatic and environmental changes (Valladares et al. 2014).

The highest number of species recorded in the campinaranas of Amazonas and Roraima is likely related to the larger size of the campinarana areas and the greater number of floristic studies conducted in these states (Adeney et al. 2016). It is also notable that collections are concentrated in areas near the riverbanks (Figure 1), which helps to understand why these species are well distributed among the wetlands (Figure 3). However, this sampling concentration may mask the true richness of campinarana flora, since vegetation islands farther from the riverbank will have less influence from flooded areas, and other species may compose these landscapes (García-Villacorta et al. 2016; Demarchi et al. 2022).

Most species in our checklist are restricted to the Amazon phytogeographic domain (53%), corroborating that most woody species in the Amazon are endemic or rare (ter Steege et al. 2013). On the other hand, the greatest diversity of the family is concentrated in the Atlantic Forest (Santos et al. 2017), and plant species originating from Cerrado are often found in campinaranas (Guimarães and Bueno 2016). This scenario, combined with the high dispersal capacity of Myrtaceae (Gressler et al. 2006), justifies Cerrado and Atlantic Forest as the domains with the highest number of species shared with campinaranas. Campinaranas are embedded mainly in terra firme forests (Adeney et al. 2016), which probably explains why terra firme forest was the type of vegetation with the highest number of species shared with campinaranas. However, campinaranas are also expected to be strongly influenced by other vegetation types due to factors such as geographic proximity (Vicentini 2004; Adeney et al. 2016), variation in abiotic conditions within campinarana islands, such as the increase in temperature and decrease in humidity in more open physiognomies and variation in water table position (García Villacorta et al. 2016; Demarchi et al. 2018).

Little is known about the conservation status of Myrtaceae. For the two endemic species recorded in our study, only *E. campina* was evaluated for its preliminary conservation status, being classified as of Least Concern (LC) (De Souza and Sobral 2018). Species endemic to campinaranas were also recorded for Clusiaceae (Demarchi et al. 2021), Fabaceae (Rando and De Lima 2020) and Malvaceae (Guevara Andino and Fernández-Alonso 2018), highlighting the need for further floristic and taxonomic surveys to assess the species diversity and composition in this vegetation type.

CONCLUSIONS

We conclude that Myrtaceae species in Brazilian Amazonian campinaranas are mostly endemic to the Amazonian phytogeographical domain. Four species of Myrtaceae were recorded for the first time in the Brazilian Amazon. Some species are specialists in soils with limiting conditions and a significant portion has plastic anatomical and morphological characteristics, in addition to long-distance dispersal mechanisms, that favor occupation and survival in campinaranas. The specific richness of Myrtaceae (72 species) recorded for Brazilian campinaranas is relatively high, but is probably underestimated, since extensive areas of campinaranas, especially those further away from riverbanks in the states of Amazonas and Roraima, have not yet been intensively surveyed. Therefore, we emphasize the need to know the floristic diversity of campinaranas (not only Myrtaceae) to identify areas of special interest for conservation.

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DATA AVAILABILITY: All data supporting the results of this study have been published in this article. All species records mentioned have a voucher number listed in Table 1 and can be accessed at <https://specieslink.net/> or in the respective herbaria. The coordinates of each locality and species per locality are in the supplementary material



SUPPLEMENTARY MATERIAL

Natividade et al. Checklist and geographic distribution of Myrtaceae species occurring in campinaranas of the Brazilian Amazon

Table S1. Species of Myrtaceae recorded in each of 27 localities of campinarana in six states of the Brazilian Amazon.

State	Municipality	Coordinates	Species	State	Municipality	Coordinates	Species				
Acre	Mâncio Lima	7°35'36.0"S, 72°56'08.4"W	<i>Eugenia patens</i>				<i>Myrcia guianensis</i>				
			<i>Myrcia aliena</i>				<i>Myrcia multiflora</i>				
			<i>Myrcia bracteata</i>				<i>Myrcia paivae</i>				
			<i>Myrcia hylobates</i>				<i>Myrcia platyclada</i>				
	Rio Branco	9°51'25.2"S, 67°35'11.7"W	<i>Eugenia pusilliflora</i>				<i>Myrcia saxatilis</i>				
			<i>Myrcia guianensis</i>				<i>Myrcia servata</i>				
			<i>Myrciaria floribunda</i>				<i>Myrcia splendens</i>				
	Amapá	Oiapoque	3°49'55.3"N, 51°47'27.3"W				<i>Psidium acutangulum</i>			<i>Myrcia sylvatica</i>	
	Amazonas	Apuí	7°12'00.6"S, 59°54'00.8"W				<i>Eugenia hatschbachii</i>				<i>Myrcia umbraticola</i>
							<i>Eugenia moschata</i>	Manicoré	5°52'58.9"S, 61°14'31.5"W	<i>Myrcia umbraticola</i>	
Barcelos		0°27'53.5"N, 63°28'31.1"W	<i>Calycolpus calophyllus</i>	Presidente Figueiredo	2°01'32.7"S, 60°02'39.4"W	<i>Eugenia biflora</i>					
			<i>Eugenia citrifolia</i>			<i>Eugenia caducipetala</i>					
			<i>Eugenia egensis</i>			<i>Eugenia moschata</i>					
			<i>Eugenia gomesiana</i>			<i>Eugenia protenta</i>					
			<i>Eugenia puniceifolia</i>			<i>Eugenia stictopetala</i>					
			<i>Myrcia bracteata</i>			<i>Myrcia caudata</i>					
			<i>Myrcia clusiifolia</i>			<i>Myrcia clusiifolia</i>					
<i>Myrcia gigas</i>		<i>Myrcia grandis</i>									
<i>Myrcia grandis</i>		<i>Myrcia guianensis</i>									
<i>Myrcia intonsa</i>		<i>Myrcia intonsa</i>									
<i>Myrcia racemosa</i>		<i>Myrcia saxatilis</i>									
<i>Myrcia saxatilis</i>		<i>Myrcia servata</i>									
<i>Myrcia servata</i>		<i>Myrcia splendens</i>									
<i>Myrcia splendens</i>		<i>Myrcia sylvatica</i>									
<i>Myrcia sylvatica</i>		<i>Myrcia umbraticola</i>									
<i>Myrcia umbraticola</i>											
Humaitá		7°31'11.5"S, 63°01'00.5"W	<i>Eugenia calva</i>	Santa Isabel do Rio Negro	0°12'12"S, 65°07'34"W	<i>Eugenia egensis</i>					
	<i>Eugenia florida</i>		<i>Eugenia gomesiana</i>								
	<i>Eugenia omissa</i>		<i>Eugenia moschata</i>								
	<i>Myrcia splendens</i>		<i>Eugenia puniceifolia</i>								
	<i>Myrcia uaupensis</i>		<i>Myrcia grandis</i>								
Iranduba	3°15'40.8"S, 60°11'01.1"W	<i>Eugenia biflora</i>			<i>Myrcia inaequiloba</i>						
		<i>Eugenia puniceifolia</i>			<i>Myrcia saxatilis</i>						
		<i>Myrcia amazonica</i>			<i>Myrcia sylvatica</i>						
		<i>Myrcia psammophila</i>			<i>Myrcia uaupensis</i>						
		<i>Myrcia umbraticola</i>			<i>Myrcia umbraticola</i>						
Jutaí	2°49'15.2"S, 66°41'40.3"W	<i>Myrcia bracteata</i>									
Machadinho	8°53'55.9"S, 61°58'32.6"W	<i>Myrcia splendens</i>	São Gabriel da Cachoeira	0°12'00.2"N, 67°33'08.5"W	<i>Eugenia roseiflora</i>						
		<i>Psidium acutangulum</i>			<i>Myrcia ovata</i>						
		<i>Calycolpus goetheanus</i>			<i>Myrcia racemosa</i>						
Manaus	2°48'46.7"S, 59°52'34.6"W	<i>Calycolpus revolutus</i>			<i>Myrcia splendens</i>						
		<i>Eugenia biflora</i>	São Sebastião do Uatumã	2°35'18.9"S, 58°01'06.2"W	<i>Eugenia biflora</i>						
		<i>Eugenia calva</i>			<i>Myrcia clusiifolia</i>						
		<i>Eugenia campina</i>			<i>Myrcia glabra</i>						
		<i>Eugenia inundata</i>			<i>Myrcia grandis</i>						
		<i>Eugenia moschata</i>			<i>Myrcia guianensis</i>						
		<i>Eugenia patrisii</i>			<i>Myrcia saxatilis</i>						
		<i>Eugenia protenta</i>			<i>Myrcia splendens</i>						
		<i>Eugenia puniceifolia</i>									
		<i>Eugenia subterminalis</i>									
		<i>Eugenia stictopetala</i>									
		<i>Myrcia amazonica</i>									
		<i>Myrcia bracteata</i>									
		<i>Myrcia caudata</i>									
<i>Myrcia clusiifolia</i>											
<i>Myrcia cuspidata</i>											
<i>Myrcia eximia</i>											
Pará	Almeirim	0°43'12.6"S, 52°31'11.7"W	<i>Eugenia puniceifolia</i>			<i>Myrcia amapensis</i>					
			<i>Myrcia amazonica</i>			<i>Myrcia cuprea</i>					
			<i>Myrcia bracteata</i>			<i>Myrcia multiflora</i>					
			<i>Myrcia caudata</i>			<i>Myrcia splendens</i>					
	Alter do Chão	2°25'26.7"S, 54°48'37.3"W	<i>Myrcia clusiifolia</i>			<i>Eugenia biflora</i>					
			<i>Myrcia cuspidata</i>			<i>Eugenia puniceifolia</i>					
			<i>Myrcia eximia</i>								

Table S1. Continued.

State	Municipality	Coordinates	Species	State	Municipality	Coordinates	Species
			<i>Myrcia guianensis</i>				<i>Eugenia puniceifolia</i>
			<i>Myrcia multiflora</i>				<i>Myrcia amazonica</i>
			<i>Siphoneugena dussii</i>				<i>Myrcia bracteata</i>
	Bragança	1°04'03.0"S, 46°43'34.0"W	<i>Myrcia cuprea</i>				<i>Myrcia cuprea</i>
			<i>Myrcia guianensis</i>				<i>Myrcia decorticans</i>
	Martins Pinheiro	0°46'51.8"S, 47°33'26.2"W	<i>Eugenia puniceifolia</i>				<i>Myrcia deflexa</i>
			<i>Myrcia bracteata</i>				<i>Myrcia pyrifolia</i>
			<i>Psidium guineense</i>				<i>Myrcia splendens</i>
			<i>Psidium guyanense</i>				<i>Myrcia sylvatica</i>
			<i>Psidium salutare</i>				<i>Myrciaria dúbia</i>
							<i>Psidium guineense</i>
	Novo Progresso	7°08'52.0"S, 55°22'52.0"W	<i>Myrcia guianensis</i>	Roraima	Abunã	9°38'32.0"S, 65°02'42.0"W	<i>Myrcia megapaniculata</i>
			<i>Myrcia tomentosa</i>				<i>Psidium acutangulum</i>
	Oriximiná	1°39'25.6"S, 56°00'42.6"W	<i>Eugenia biflora</i>		Porto Velho	8°39'18.5"S, 63°56'51.8"W	<i>Calycolpus roraimensis</i>
			<i>Eugenia campina</i>				<i>Eugenia florida</i>
			<i>Eugenia puniceifolia</i>				<i>Myrcia amazonica</i>
			<i>Myrcia amazonica</i>				<i>Myrcia anceps</i>
			<i>Myrcia bracteata</i>				<i>Myrcia caudata</i>
			<i>Myrcia guianensis</i>				<i>Myrcia cuspidata</i>
			<i>Myrcia pyrifolia</i>				<i>Myrcia</i>
			<i>Myrcia servata</i>				<i>megapaniculata</i>
			<i>Myrcia splendens</i>				<i>Myrcia splendens</i>
			<i>Myrcia sylvatica</i>	Roraima	Caracará	1°50'29.0"N, 61°07'40.0"W	<i>Blepharocalyx eggersii</i>
	Porto de Moz	1°45'01.5"S, 52°13'31.8"W	<i>Eugenia stipitata</i>				<i>Blepharocalyx salicifolius</i>
			<i>Myrcia multiflora</i>				<i>Calycolpus calophyllus</i>
	Tucuruí	3°44'09.2"S, 49°44'07.3"W	<i>Calycolpus goetheanus</i>				<i>Calycolpus goetheanus</i>
			<i>Eugenia biflora</i>				<i>Eugenia egensis</i>
			<i>Eugenia gomesiana</i>				<i>Eugenia florida</i>
			<i>Eugenia moschata</i>				<i>Eugenia gomesiana</i>
			<i>Eugenia patens</i>				<i>Eugenia patrisii</i>
			<i>Eugenia patrisii</i>				<i>Myrcia clusiifolia</i>
			<i>Eugenia protenta</i>				<i>Myrcia crebra</i>
			<i>Eugenia puniceifolia</i>				<i>Myrcia florifera</i>
			<i>Eugenia stictopetala</i>				<i>Myrcia grandis</i>
			<i>Myrcia amazonica</i>				<i>Myrcia guianensis</i>
			<i>Myrcia guianensis</i>				<i>Myrcia inaequiloba</i>
			<i>Myrcia inaequiloba</i>				<i>Myrcia neoforsteri</i>
			<i>Myrcia multiflora</i>				<i>Myrcia pyrifolia</i>
			<i>Myrcia rufipila</i>				<i>Myrcia saxatilis</i>
			<i>Myrcia splendens</i>				<i>Myrcia splendens</i>
			<i>Myrcia sylvatica</i>				<i>Myrcia umbraticola</i>
			<i>Myrcia tomentosa</i>				<i>Myrciaria floribunda</i>
	Vigia de Nazaré	0°49'32.2"S, 48°06'25.2"W	<i>Calycolpus goetheanus</i>				<i>Psidium guineense</i>
			<i>Eugenia biflora</i>				