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Diversity and Ecological Associations of Pluteaceae (Fungi, Agaricomycetes, Agaricales) in Brazilian Biomes

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ABSTRACT

The Pluteaceae family is recorded in 10 Brazilian states, containing lignicolous, terricolous and humicolous species that perform fundamental functions as saprobes. This study aimed to contribute to a better understanding of the interactions and ecological importance of the family. For this, through a synthesis of taxonomic, morphological, and molecular data, the phylogenetic relationships of the group were reconstructed by Maximum Likelihood and Maximum Parsimony. Georeferenced data were used to elucidate the distribution of the species in Brazilian biomes. Phylogenetically, the family integrated a monophyletic clade, where the genera *Pluteus* and *Volvariella* were internally related as sister clades. In relation to the ecology of Pluteaceae, the Southeastern Region was very important, containing about 32% of the family species occurring near watersheds. 62% of the species of the group have occurrence restricted to the Atlantic Forest biome, and many of them are associated with native arboreal substrates, such as *Roupala* sp., *Dicksonia* sp., *Clitoria* sp., and *Astrocaryum aculeatissimum*. In general, the largely lignicolous family acts in the ecosystems as nutrient cycles, mainly related to wood. Also, species of the family with colonization in litterfall and terricolous represented unique interactions involving native arboreal groups and occurrences in areas of intense anthropic action, such as agriculture. Thus, with the compiled data in this study, it was possible to infer that Pluteaceae is directly associated with the regeneration of Brazilian biomes, actively helping in their maintenance.

Keywords: Evolutionary relationships, Ecology of Agaricales, Ecosystems.

Diversidade e Associações Ecológicas de Pluteaceae (Fungi, Agaricomycetes, Agaricales) nos Biomas Brasileiros

RESUMO

A família Pluteaceae é registrada em 10 estados brasileiros, contendo espécies lignícolas, terrícolas e húmicas que desempenham papéis fundamentais como sapróbios. Este estudo teve como objetivo contribuir para uma melhor compreensão das interações e da importância ecológica da família. Para tanto, através de uma síntese de dados taxonômicos, morfológicos e moleculares, as relações filogenéticas do grupo foram reconstruídas por Máxima Verossimilhança e Máxima Parcimônia. Os dados georreferenciados foram utilizados para elucidar a distribuição das espécies nos biomas brasileiros. Filogeneticamente, a família integrou um clado monofilético, onde os gêneros *Pluteus* e *Volvariella* se relacionaram internamente como clados irmãos. Em relação à ecologia de Pluteaceae, a Região Sudeste foi muito importante, contendo cerca de 32% das espécies da família ocorrendo próximas a bacias hidrográficas. 62% das espécies do grupo possuem ocorrência restrita ao bioma Mata Atlântica, e muitas delas estão associadas a substratos arbóreos nativos, tais como *Roupala* sp., *Dicksonia* sp., *Clitoria* sp. e *Astrocaryum aculeatissimum*. Em geral, a família é em grande parte lignícola e atua nos ecossistemas como cicladores de nutrientes, principalmente os relacionados à madeira. Além disso, espécies da família de colonização em serapilheira e terrícolas apresentaram interações únicas envolvendo grupos arbóreos nativos, e ocorrências em áreas de intensa ação antrópica como a da agricultura. Assim, com os dados compilados neste estudo, foi

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possível inferir que Pluteaceae está diretamente associada à regeneração dos biomas brasileiros, auxiliando ativamente na sua manutenção.

Palavras-Chaves: Relações evolutivas, Ecologia de Agaricales, Ecossistemas.

1. Introduction

Agaricales include the fungi popularly known as mushrooms, being a temporary phase called basidiome that emerges on the soil surface during the reproductive cycle (Azevedo & Barata, 2018). This important structure also underlies most of the taxonomic classification of its group, through its morphological, anatomical, and microchemical characters (Putzke & Putzke, 2017). However, phylogeny is increasingly contributing to a better understanding of the evolutionary relationships of these individuals (James et al., 2006). With approximately 364 species (Ainsworth, 2008), Pluteaceae (Agaricales, Basidiomycota) contains distinctive macromorphological features for the agaricoids fungi, such as the presence of a well-developed volva in some species of *Volvariella*, annulus absent as in *Pluteus* or rarely present as in *Chamaeota*, also have a pink to pinkish-brown spore print (Putzke & Wartchow, 2008).

In the Brazil, about 104 species (including cf. and var.) of Pluteaceae have already been listed (Putzke & Wartchow, 2008; Maia et al., 2015; Putzke & Putzke, 2018). Many of them after revisions were reported as similar or not belonging to their taxonomic designation (Menolli, 2013; Menolli et al., 2015; Menolli & Capelari, 2016). The family is composed of four distinct genera: *Pluteus*, *Volvariella*, *Chamaeota*, and recently by *Volvopluteus* segregated from *Volvariella* (Singer, 1986; Ainsworth, 2008; Justo et al., 2011). Among the main microscopic features, hymenial cystidia are usually present, metuloid or not metuloid with thick-walled, inverse hymenophore trama, basidiospores globose to ellipsoid, thick-walled, smooth, inamyloid, and cynaphilic (Singer, 1986).

In relation to the ecology of the family, in Brazil many are associated with native vegetation, composed of forests and woodlands, also in riparian zones (Menolli et al., 2015). The species are saprobic with lignicolous, terricolous, and humicolous habits, occurring in 10 Brazilian states: Amazonas - AM, Bahia - BA, Mato Grosso - MT, Minas Gerais - MG, Pará - PA, Paraná - PR, Rio de Janeiro - RJ, Rio Grande do Sul - RS, Rondônia - RO, and São Paulo - SP (Putzke & Wartchow, 2008; Maia et al., 2015; Putzke & Putzke, 2018). For the members of this group, the genera *Pluteus* and *Volvariella* have been distributed in three of the six Brazilian biomes (Amazon, Atlantic Forest, and Pampa). Most *Pluteus* species grow on wood (trunks and branches) or litterfall, while *Volvariella* on the soil (Menolli & Capelari, 2016).

The designation lignicolous for the family marks an important ecological interaction, even though there are exceptions, most species of Pluteaceae grow on wood causing its decomposition (de Mattos, 2020). Thus, they act in the cycling go organic matter through its reintegration into the ecosystem (Lonsdale et al., 2008; Carvalho et al., 2022). Carbon is the main source of the relationship between fungi and vegetation (Baldrian et al., 2016). However, this interaction depends of vectors, such as the type of vegetation, soil conditions, and species diversity (Abrego & Salcedo, 2014; Walthert & Meier, 2017; Copot & Tănase, 2019). Also, geographic, climatic, precipitation, and temperature conditions directly influence the communities of saprobe fungi (Tedersoo et al., 2014; Borgmann-Winter et al., 2022).

In this form, due to the significance of Pluteaceae for Brazilian biomes, this study aimed to contribute to a better understanding of the interactions and ecological importance of the family. For this, a review was performed in the form of a synthesis involving taxonomic, morphological, molecular, and biogeographic data, where distinct characters of the group bionomy were elucidated.

2. Material and Methods

2.1 Bibliographical search and database

For the species of Pluteaceae with occurrence in Brazil (Table 1), a search bibliographic was made containing data of public digital platforms and printed works. The following keywords were used: Pluteaceae, taxonomic description, and new species. The data available in Putzke & Putzke (2018) for the family were used as the guide for research.

Table 1 - Pluteaceae species with occurrence in Brazil with molecular and geographical data.

Species	Access code	BRA states	References
Pluteus albostipitatus	HM562130.1	PR, RS, AM, SP	Menolli et al. (2015)
**Pluteus amazonicus*	KF937355.1	AM	Singer (1961)
**Pluteus anomocystidiatus*	-	PR	Menolli (2013); Menolli et al. (2015)
Pluteus angustisporus	-	PR	Menolli (2013)
Pluteus aquosus	-	RS	Wartchow et al. (2006)
Pluteus argentinensis	-	MG, SP	Rosa & Capelari (2009); Menolli (2013); Dias & Cortez (2013)
**Pluteus aureolatus*	KM983680.1	AM	Menolli (2013)
**Pluteus aureovenatus*	HM562160.1	SP	Menolli et al. (2010)
Pluteus beniensis	JQ065029.1	PR, RS	Wartchow et al. (2006); de Meijer (2006); Menolli & Capelari (2016)
**Pluteus brunneocrinitus*	KM983692.1	SP	Menolli (2013); Menolli et al. (2015)
Pluteus brunneopictus	JF908623.1	RS	Menolli & Capelari (2016)
**Pluteus cebolinhae*	KM983713.1	SP	Menolli (2013); Menolli et al. (2015)
Pluteus cervinus	-	RS, PR	Menolli (2013); Dias & Cortez (2013)
Pluteus chrysophlebius	HM562088.1	PR	Menolli et al. (2010); Menolli (2013); Menolli et al. (2015)
Pluteus chusqueae	-	PR	Menolli (2013)
**Pluteus crassocystidiatus*	-	PR	Menolli et al. (2015)
**Pluteus crassus*	MW050978.1	PR	de Meijer (2006); Menolli (2013)
Pluteus crinitus	KM983691.1	AM	Menolli (2013); Menolli et al. (2015)
Pluteus cubensis	-	PR	Rosa et al. (2003); Xavier-Santos et al. (2004); de Meijer (2006); Rosa & Capelari (2009); Menolli et al. (2015)
**Pluteus densifibrillosus*	HM562159.1	SP	Menolli et al. (2010)
Pluteus diptychocystis	KM983674.1	SP, RN	Menolli (2013); Menolli & Capelari (2016)
Pluteus dominicanus	FJ816665.1	SP	Menolli et al. (2010)
Pluteus eludens	HM562185.1	PR	Menolli (2013)
**Pluteus elvaniae*	-	RS	Wartchow (2018)
Pluteus cf. *fastigiatus*	-	AM	Menolli & Capelari (2016)
Pluteus cf. *fernandezianus*	JQ065028.1	RS	Menolli (2013)
Pluteus fibulatus	-	PR, RS	Menolli (2013)
**Pluteus fluminensis*	FJ816664.1	RJ, PR	Menolli et al. (2010); Menolli & Capelari (2016)
Pluteus fuligineovenosus	FJ816662.1	SP	Menolli & Capelari (2016)
Pluteus cf. *fuliginosus*	-	SP	Menolli & Capelari (2016)
Pluteus fusconigricans	-	PR	Menolli (2013)

Pluteus glaucotinctus	HM562157.1	PR, SP	Wartchow et al. (2006) Menolli & Capelari (2008); Menolli (2013)
Pluteus glaucus	-	SP	Stijve & de Meijer (1993); Guzmán & Guevera (1998)
Pluteus globiger	JQ065030.1	RS, PR	Wartchow et al. (2006); Dias & Cortez (2013)
**Pluteus halonatus*	-	AM	Menolli et al. (2015)
Pluteus harrissi	-	SP, MG, PR	de Meijer (2006); Rosa & Capelari (2009); Menolli (2013)
Pluteus haywardii	-	MG	Rosa & Capelari (2009);
**Pluteus hispidulopsis*	-	RN	Menolli et al. (2015)
Pluteus homolae	-	SP	Menolli (2013)
**Pluteus hylaeicola*	-	PA, PR	Menolli (2013); Menolli et al. (2015)
Pluteus iguazuensis	-	RS, PR, AM	de Meijer (2006); Drehmel et al. (2008); Menolli (2013); Menolli & Capelari (2016)
Pluteus jamaicensis	FJ816657.1	SP	Menolli et al. (2010)
**Pluteus karstedtiae*	KM983682.1	SP, RJ	Menolli (2013)
Pluteus longistriatus	HM562172.1	SP, RJ, PR	Menolli et al. (2010); Menolli (2013)
Pluteus maculosipes	-	PR	Menolli (2013)
Pluteus meridionalis	KJ009767.1	SP	Menolli et al. (2014)
Pluteus nanus	KF306030.1	RS	Menolli & Capelari (2016)
**Pluteus necopinatus*	KM983693.1	RJ	Menolli (2013)
**Pluteus neochrysaegis*	-	PR	Menolli (2013)
Pluteus nigrolineatus	FJ375245.1	RS	Wartchow et al. (2006)
**Pluteus paucicystidiatus*	-	SP	Menolli (2013)
Pluteus phlebophorus	HM562039.1	RS	Singer (1961); Menolli & Capelari (2016)
Pluteus pluvialis	-	RS	Menolli & Capelari (2016)
Pluteus pulverulentus	GU551943.1	PR	de Meijer (2006); Menolli & Capelari (2016)
**Pluteus puttemansii*	HM562164.1	SP	Menolli et al. (2010)
Pluteus riberaltensis	HM562162.1	SP	de Meijer (2006); Menolli et al. (2010);
Pluteus rimosellus	-	PR	Menolli (2013)
Pluteus rimosoaffinis	KM983706.1	BA, SP, PR, RS	de Meijer (2006); Menolli (2013)
Pluteus riograndensis	-	PR, RS	Raithelhuber (1991); Menolli & Capelari (2016)
Pluteus salicinus	JF908625.1	PR	Stijve & de Meijer (1993); de Meijer (2006)
Pluteus sapiicola	KM983707.1	PR	Menolli (2013)
Pluteus striatocystis	-	PR	Menolli (2013)
**Pluteus subfibrillosus*	-	RJ, PR, RS	Menolli et al. (2014)
**Pluteus sublaevigatus*	-	SP, PR	Menolli et al. (2010); Menolli (2013)
Pluteus umbrionalbidus	-	RS, PR, MG, SP	Singer (1958); Rosa & Capelari (2009); Menolli et al. (2010)
Pluteus variipes	-	SP	Menolli & Capelari (2016)
**Pluteus varzeicola*	-	AM	Singer (1961)
Pluteus velutinus	KR022027.1	PA	Menolli (2013)
Pluteus viscidulus	HM562110.1	RS	Singer (1961)

Pluteus xylophilus	HM562163.1	RS, SP, PR	de Meijer (2006); Menolli et al. (2010); Menolli (2013)
Volvariella bombycina	HM562212.1	RS, SP, PR	Sobestiansky (2005); de Meijer (2006); Menolli & Capelari (2008)
Volvariella cubensis	-	PE	Wartchow (2009)
Volvariella earlei	HM246497.1	PR	de Meijer (2006)
Volvariella gloiocephala	JN182873.1	RS, PR	de Meijer (2006)
**Volvariella heterospora*	-	SP	Menolli & Capelari (2008)
Volvariella macrospora	-	AM	Singer (1961)
**Volvariella nullicystidiata*	-	SP	Menolli & Capelari (2008)
**Volvariella oswaldoi*	-	PE	Batista (1957); Putzke (1994)
Volvariella perciliata	EU920672.1	SP, RS	de Meijer (2006); Menolli & Capelari (2008)
Volvariella pusilla	HM246494.1	RS	Singer (1961)
**Volvariella rondoniensis*	-	RO, PR	de Meijer (2006)
Volvariella speciosa	-	PE	Batista (1957)
Volvariella cf. *striata*	-	PE	de Meijer (2006)
Volvariella taylori	-	PR	de Meijer (2006)
Volvariella volvacea	HM367073.1	PR	de Meijer (2006)

Note: Accession numbers with prefixes are available in National Center for Biotechnology Information (NCBI) GenBank (www.ncbi.nlm.nih.gov). Occurrence/sampling location according to references. (-) Indicates species without molecular data but with computed morphological data (see methodology in 2.2). (*) Indicates species with occurrence only in Brazil. Source: Authors (2021).

2.2 *Molecular and taxonomic data*

For the species of Pluteaceae, a search of molecular data was performed in the National Center for Biotechnology Information (NCBI) GenBank (https://www.ncbi.nlm.nih.gov/). The markers were selected according to their availability for species during the *blast* search. After a preliminary evaluation, parts of the 5.8S, 18S and ITS1-2 genes were tested considering their mutations rates. In total, 44 species of Pluteaceae in a matrix with 529 characters were selected (Table 1). As outgroups, *Amanita campinaranae*, *Amanita craseoderma*, and *Amanita lippiae* were used due to their phylogenetic proximity with the family (Matheny et al., 2006). All sequences were aligned in CodonCode Aligner v.3.7 (Richterich, 2004) with the option *muscle* and *gap* activated.

A matrix with morphological characters according to the bibliography was elaborated. The data available in Putzke & Putzke (2018) was used for the build of the matrix. The following morphological characters were used: presence or absence of volvulus; with or without annulus; diameter and form of the pileus; lamellae form and insertion; size and form of the stipe; morphology of spores and basidia; the arrangement of the lamella trama; cortical layer type; fibulae; habit; habitat, and substrate. The matrix integrated 88 species (three outgroups) and 73 binary characters. In the program Mesquite v.2.7 (Maddison & Maddison, 2007) the data were compilated.

The molecular and morphological data were concatenated in SequenceMatrix v.1.8 (Vaidya et al., 2011). Constructed matrix was used for Maximum Parsimony (MP) *bootstrap* in TNT v.1.5 (Goloboff, et al., 2008) with “Traditional” searches for more parsimonious trees starting at 1.000 replications with the TBR algorithm, keeping 100 cladograms at each step of the heuristic search (*hold* = 100). In TNT, the nodes containing the synapomorphies were analyzed using the “*Collapse*” function. For Maximum Likelihood (ML), conducted in RAxML-GUI v.1.5 (Silvestro & Michalak, 2012) with GTR model, keep 200 rounds calculated with 1.000 repetitions for the fast *bootstrap* reconstruction of the more likelihood, using the “*New Rapid Hill-Climbing”* algorithm (Stamatakis et al., 2008), and ML search activated. ML tree was used as the master tree, and therefore its topology and branch lengths were used for the presentation of the relationships built in this study.

2.3 Georeferencing of specimens

A file in the Excel program (Walkenbach, 2010) containing the geographical origin of the specimens described to Brazil and their geographical coordinates in decimal (latitude and longitude) was prepared, according to the data available in the literature (Table 1). The proportions of species distributions in biomes were computed, and the percentages were calculated in Excel by Fávero & Belfiore (2017) model. The projection from the place of occurrence of specimens in Brazilian biomes was performed in the program R v.3.6 (Ihaka & Gentleman, 1996). For the plotting of data, the packages "*phytools*" and "*mapdata*" (Revell, 2012; Becker & Wilks, 2016) were used.

3. Results

3.1 Phylogenetic analysis of the dataset

The survey conducted to Pluteaceae occurring in Brazil compiled 85 species from family and three outgroups in a matrix with 602 characters (molecular and morphological data). *Pluteus* and *Volvariella* genera with occurrence in Brazil had moderate to high MP and ML *bootstrap* support in phylogeny, according to the relationships (Figure 1).

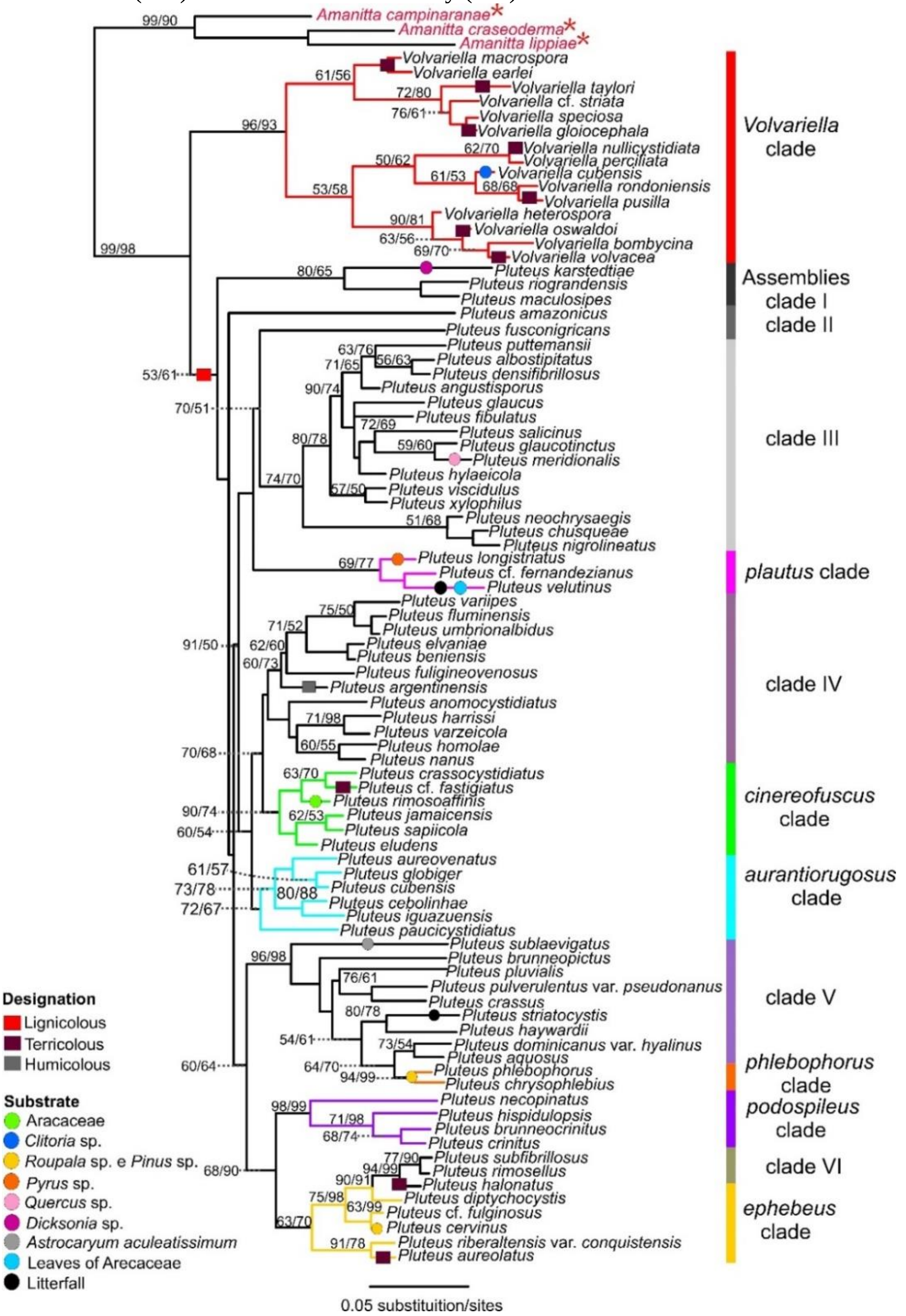
The clade *Volvariella* was listed as internally monophyletic, maintaining high support (ML = 96% and BP = 93%), and externally as clade sister of *Pluteus* (Figure 1). Due to the internal topology of the group not being well resolved in the literature, the precepts by Justo et al. (2011) were maintained according to the identification key for the Brazilian species of *Volvariella* (Putzke & Putzke, 2018).

Pluteus clade was related as monophyletic with moderate support (ML = 53% and MP = 61%). However, many of the relationships among closely related species have been recovered internally. Clades already described in the literature maintained high *bootstrap* support for the species belonging to the sections: *Volvariella* (ML = 96% and MP = 93%), *plautus* (ML = 69% and MP = 77%), *cinerofuscus* (ML = 90% and MP = 74%), *aurantiorugosus* (ML = 72% and MP = 76%), *phlebophorus* (ML = 94% and MP = 99%), *podospileus* (ML = 98% and MP = 99%), and *ephebeus* (ML = 63% and MP = 70%). *Pluteus* assemblages containing the remaining species reconstructed clades with moderate to high *bootstrap* support (Figure 1).

Synapomorphies related to the habit, habitat, and substrate were recovered according to the inferred description for each species, and many of them integrated the same section and share some designation. The clades of assemblies III, IV, V, and VI, *cinerofuscus*, *aurantiorugosus*, *phlebophorus*, *podospileus*, and *ephebeus* were part of the lignicolous. The presence of terricolous species among the lignicolous clades demonstrates the emergence of this behavior more than once during the evolutionary history of the group, according to breach length in the IV and VI assemblages, in *Volvariella*, *cinerofuscus*, and *ephebeus* clades (Figure 1).

Overall, speciation processes in relation to the arboreal association character were dispersed in the phylogeny, where most of the designated species formed paraphyletic and polyphyletic internal subclades, such as *P. karstedtiae* associated with *Dicksonia* sp. (Dicksoniaceae); *P. meridionalis* to *Quercus* sp. (Fagaceae); *P. longistriatus* to *Pyrus* sp. (Rosaceae); *P. cervinus*, *P. chrysophlebius* and *P. phlebophorus* with *Roupala* sp. (Proteaceae) and *Pinus* sp. (Pinaceae); *V. cubensis* to *Clitoria* sp. (Fagaceae); *P.rimosoaffinis* to Aracaceae; and *P. sublaevigatus* to *Astrocaryum aculeatissimum* (Arecaceae). Among the other associations, the arboreal species were not identified in the literature, being described only as branches and trunks of Gymnosperms or Angiosperms (Figure 1).

Figure 1 - ML master tree with reconstructed phylogenetic relationships. Supports obtained in *bootstrap* Maximum Likelihood (ML) and Maximum Parsimony (MP) with values next to the branches.



Note: Outgroups with red asterisk. Source: Authors (2021).

Some clades showed speciation in relation to substrate type and maintained close relationships, such as *phlebophorus* (ML = 94% and MP = 99%), which grows on branches and trunks of *Roupala* sp. and *Pinus* sp. However, some species such as *P. cervinus* maintained distant relationships even though they shared the same substrate type. Other similarities involving distant species of litterfall such as *P. striatocystis* and *P. velutinus* related within the pluteoid clade, but with distinct recent ancestry.

3.2 Distribution and characteristics of the species in the biomes

Among the Pluteaceae species analyzed, about 81% occur only in a single biome, 14% occur in two distinct biomes, and only 5% occur in three of the six Brazilian biomes. 62% of species occur only in the Atlantic Forest, 8% only in the Pampa, and 9% only in the Amazon. 17% occur in both Atlantic Forest and Pampa, 2% in the Amazon and Atlantic Forest, 2% occur in all three biomes (Atlantic Forest, Amazon, and Pampa), and there are not species that share occurrence in the Pampa and Amazon. It is important to emphasize the lack of occurrence records of Pluteaceae in the Cerrado, Pantanal, and Caatinga (Figure 2).

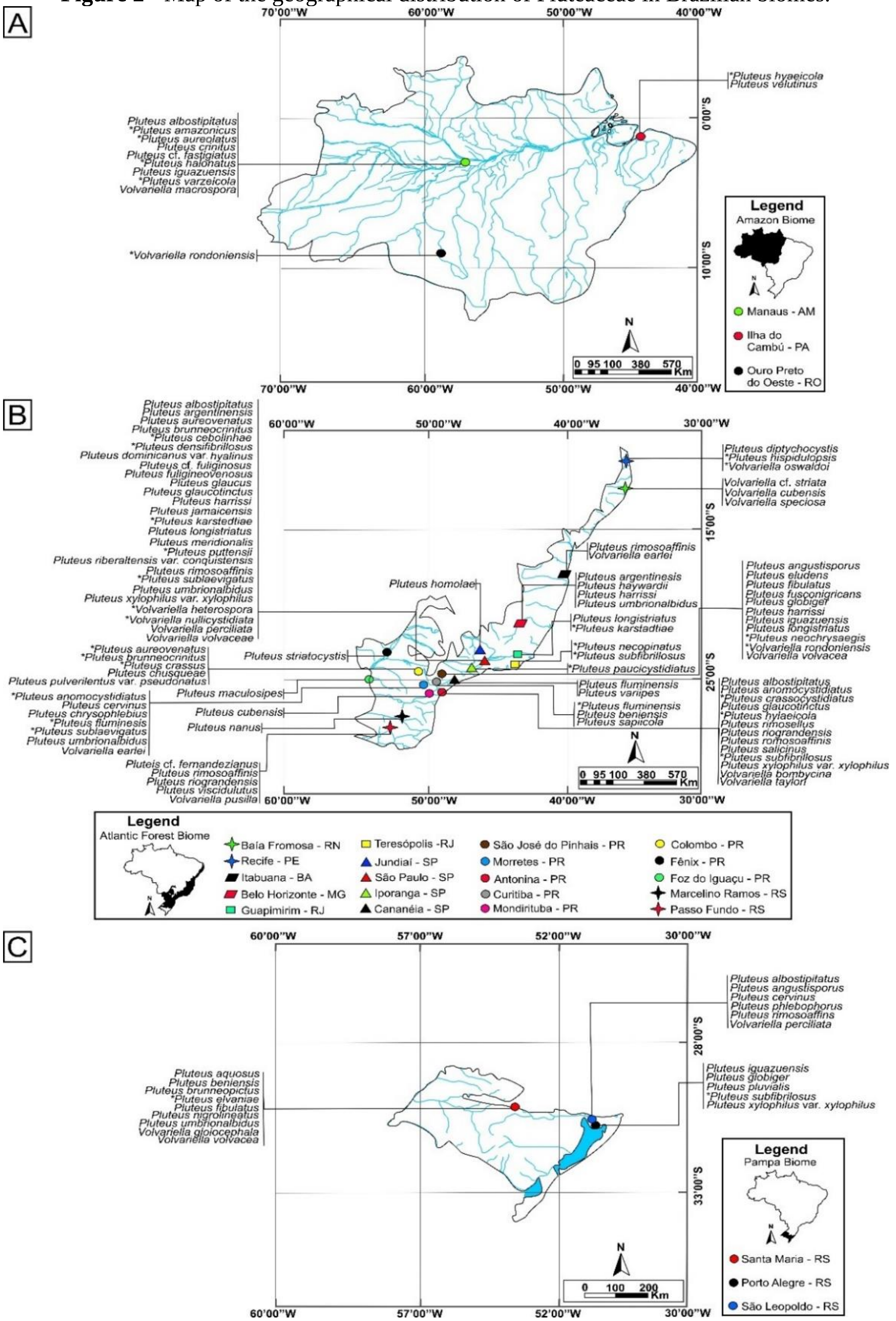
The Southeastern and Southern Regions of Brazil, composed of Atlantic Forest and a portion of the Pampa biome, were the Brazilian regions with the highest occurrence and diversity of species of Pluteaceae. In these regions, 32% of the species of the family occurred near waterways and hydrographic basins that are important to the region, such as in Parque Estadual das Fontes do Ipiranga - SP, Parque Estadual da Cantareira - SP, and Reserva Natural Rio Cachoeira in Antonina - PR. For these species, 50% were restricted to these regions (Figure 2).

In the Northeastern Region, the Atlantic Forest domain was found a higher occurrence of restricted and phylogenetically close species of Pluteaceae, such as *V. oswaldoi*, *V. cubensis*, *V. speciosa*, and *V.* cf. *striata*. While the Amazon biome showed a higher occurrence of restricted species, but distantly related as *V. macrospora*, *P. amazonicus*, *P. velutinus*, *P. varzeicula*, *P.* cf. *fastigiatus*, *P. crinitus*, *P. holonatus*, and *P. aureolatus* (Figure 2).

The Pampa biome and Atlantic Forest showed the occurrence of most phylogenetically close species with the concomitant distribution. Among them *P. cervinus*, *P. subfibrilosus*, *P. beniensis*, *P. umbrionalbidus*, *P. fibulatus*, *P. angustisporus*, *P. albostipiatus*, *P. iguazuensis*, and *P. globiger* that had occurred in both the biomes, are closely related and have a lignicolous habit. As well as *V. nullicystidiata*, *V. perciliata*, *V. speciosa*, and *V.* cf. *striata*, which are terricolous species (Figures 1 and 2).

Generalist species of occurrence in all three biomes and different localities maintained distant relationships but internally integrated into the pluteoid clade. Being them *P. iguazuensis*, *P. rimozoafins*, *P. umbrionalbidus*, *P. longistriatus*, *P. harrissi*, *P. xylophilus*, and *P. albostipiatus*, with exception of *V. volvacea*, which is part of the sister clade *Volvariella* (Figures 1 and 2).

Figure 2 - Map of the geographical distribution of Pluteaceae in Brazilian biomes.



Note: * Indicates endemic species from Brazil. Amazon Biome (A). Atlantic Forest Biome (B). Pampa Biome (C). Map follows with the main water resources. Source: Authors (2021).

4. Discussion

4.1 Diversity of Pluteaceae near watercourses

The Parque Estadual das Fontes do Ipiranga - SP is an Atlantic Forest fragment is integrated by riparian zone that protects the water resources of Riacho do Ipiranga (Tanus et al., 2012). In this location the species *P. meridionalis*, *P. riberaltensis*, *P.* cf. *fuliginosus*, *P. argentinensis*, and *P. aureovenatus* endemic from Brazil had an occurrence record (Rosa & Capelari, 2009; Menolli et al., 2010; Dias & Cortez, 2013; Menolli, 2013; Menolli & Capelari, 2016). In a study conducted by Leal & Gugliotta (2008) in the region, 108 species of Basidiomycetes were registered, but none of them belonged to Pluteaceae. However, the major ecological importance listed for the region was at the fungal succession involved in the action that transforming source of organic matter, dynamizing the trophic chain at the area. Thus, it is possible to infer that the pluteoid group plays this same ecological role since they are designated also saprobic.

Integrating part of Serra da Cantareira, the Parque Estadual da Cantareira - SP Atlantic Forest domain, were registered endemic species, such as *P. brunneocrinitus*, *P. dominicanus* var. *hyalinus*, *P. jamaicensise*, and *P. fuligineovenosus* that occur only in this biome. Some the species endemic from Brazil also were found in area as *P. densifibrillosus*, *V. heterospora*, and *V. nullicystidiata* (de Meijer, 2006; Menolli & Capelari, 2008; Menolli et al., 2010; Menolli, 2013; Menolli et al., 2015; Menolli & Capelari, 2016). Containing micro-watersheds of Ribeirão Santa Inês, Ribeirão das Águas Claras, Ribeirão São Pedro, Rio Baquirivu, Rio Cabuçu, and Córrego Cabuçu (Brasil, 2006), riparian zones along waterways of region play roles in water drainage, nutrient absorption and retention, and also serve as a filter for metropolitan air pollution (Feitosa & Ribeiro, 2005). For the fungal community of this area, in a study involving 23 species of wood-degrading Basidiomycota pointed that the macronutrients: nitrogen, potassium, calcium, magnesium, sulfur, and phosphorus; and micronutrients: boron, chlorine, molybdenum, copper, iron, zinc, and manganese; were more abundant in this soil due to fungal presence (Hamaguchi & Vitali, 2014). The Pluteaceae species that occur in this region are also lignicolous. Therefore, the group also acts in this area as nutrient cycling, mainly connected to the wood.

The Reserva Natural Rio Cachoeira in Antonina - PR, Atlantic Forest domain, has recorded most of the restricted pluteoid species in biome single. *P. rimosoaffinis*, *P. crassocystidiatus*, *P. anomocystidiatus*, *P. salicinus*, *V. bombycine*, and *V. taylori* were recorded in this area. Also, the local shown greater pluteoid diversyty containing species generalist as *P. albostipitatus*, *P. glaucotinctus*, *P. rimosellus*, *P. subfibrillosus*, *P. xylophilus*, *P. riograndensis*, and *P. hylaeicola* that is endemic from Brazil (Raithelhuber, 1991; Sobestiansky, 2005; de Meijer, 2006; Menolli & Capelari, 2008; Menolli, 2013; Menolli et al., 2014; Menolli et al., 2015; Menolli & Capelari, 2016). The 8.600 hectare reserve consists of Dense Alluvial Ombrophylous Forest in Rio das Cachoeiras and its effluents, which is going through a regeneration period due to the high anthropic action of the past (IBGE, 2020). In this aspect, the saprobe fungi assist at various levels during the forest regeneration process (Xavier & de Holanda, 2015). Abrahão et al. (2019) when analyzing the abundance of macrofungi in this region, inferred that 30% of the 796 species collected were associated with the riparian zone, listed as having the highest diversity when compared to the Semideciduous Forest. Borba et al. (2015) showed that the diversity of Basidiomycetes, including species of Pluteaceae in Atlantic Forest in Parque Natural Municipal Nascentes do Garcia, Blumenau - SC, was related to microclimate and vegetation type, both important factors for the diversity of this group in the riparian zone at local.

In general, the Atlantic Forest biome exhibited a diverse group of Pluteaceae species occurring near important watersheds and water resources. The biome has high rates of endemism, not only for Pluteaceae, but also for many other fungal species (Putzke & Putzke, 2017). The regions mentioned above come from anthropic action and significant habitat loss (IBGE, 2020). Even with public policies that seek its preservation, there is a need for further studies aimed at the importance of their bionomy. In this premise, fungi act by providing nutritional raw material mainly those related to cycling processes, acting directly on the regeneration of the environment (Leal & Gugliotta, 2008).

4.2 Pluteoid interactions with arboreal species

Pluteaceae is a family lignicolous and little proportion terricolous, where the *Volvariella* clade contained most of the species with occurrence on the soil (Singer, 1986; Putzke & Wartchow, 2008; Maia et al., 2015; Putzke & Putzke, 2018). For the Brazilian species, distinct specifications occur because some besides growing on wood (Gymnosperms and Angiosperms), also cause its decomposition, such as the clade *phlebophorus*, *podospileus*, *ephebeus*, *aurantiorugosus*, and *cinerofuscus* (de Meijer, 2006; Menolli & Capelari, 2008; Menolli, 2013; Menolli et al., 2014; Menolli et al., 2015; Menolli & Capelari, 2016). Others have relationships specific with substrates, such as *P. meridionalis* which grows on branches of *Quercus* sp. (Menolli et al., 2014). The pluteoid species have an important function in the cycling of matter from the native arboreal (Kew, 2018). At the Atlantic Forest fragment site, it contributes to carbon cycling (Baldrian et al., 2016), assisting in the homeostasis of the ecosystem.

P. cervinus grows on branches and trunks of *Roupala* sp. (native) and *Pinus* sp. (exotic) (Menolli, 2013), occurring in two distinct biomes and sharing between them the same substrate type. In Pampa and in Atlantic Forest, both the local contained artificial forests of *Pinus* sp. that were introduced for reforestation (Vasquez et al., 2007) due to its rapid growth and adaptation to acidic soils (da Silva et al., 2018). Also, *P. phlebophorus* and *P. chrysophlebius* share these same substrates in these biomes (Miranda-Melo et al., 2007; Menolli et al., 2010; Menolli, 2013). In this premise, Xavier & Holanda (2015) reports that for these regions, lignicolous fungi act at various stages of decomposition and have a positive correlation in the regeneration of native vegetation.

Containing a distribution along the Brazilian coast in the Atlantic Forest domain, *Astrocaryum aculeatissimum* is the substrate associated with endemic species from Brazil *P. sublaevigatus* (Menolli et al., 2010; Menolli, 2013). At southeast coast, the native Brazilian palm acts as an ecological filter (Brancalion et al., 2010). Its fruits are consumed for small rodents, such as *Dasyprocta leporina* (agouti), *Trinomys iheringi* (rodents), and *Sciurus aestuans* (squirrel) (Oliveira et al., 2018). These consumers of the fruit are also largely its dispersers, aiding in the wide distribution of the species throughout the coast. Being that for *P. sublaevigatus*, the wide distribution of the host species may have aided in its occurrence in long of the Brazilian coast. Tedersoo et al. (2014) report that the distribution of the host arboreal species is directly related to its fungus-associated distribution.

P. longistriatus have as substrate *Pyrus* sp., popularly known in Brazil as pera or common pear (Menolli et al., 2010; Menolli, 2013). The fruit tree is exotic of nutritional and commercial value, introduced in Brazil of Asian origin. The pera acclimates well to the forests of the southeast, and its abundance is associated with its cultivation and dispersal of the seeds through the massive consumption of the fruit by the fauna (Veasey et al., 2011). Edman & Jonsson (2001) infer that the saprobic fungi are capable of numerous adaptations, as spores can travel up to 500 km and develop in a completely new location if conditions are suitable, especially when the substrate is also abundant.

P. karstedtiae had occurrences recorded in the Atlantic Forest domain. The pluteoid is endemic from Brazil and has as substrate *Dicksonia* sp. (Menolli, 2013). This genus contains about 20 cosmopolitan species, but some are native to Central and South America, and are endangered, such as *Dicksonia sellowiana* (Large & Braggins, 2004). In this form, fungi as *P. karstedtiae* that develop on branches and fallen leaves on the ground can help control soil quality, such as humidity, nitrogen, phosphorus, and carbon concentration, which are essential for the beneficial development of these plants (Sariyildiz, 2015).

P. rimosoaffinis grow on branches of Arecaceae (Menolli & Capelari, 2016). In general, these palms are distributed all over the country, are fruitful, and they also have economic importance in the manufacture of fibers (Baker & Dransfield, 2016). These species realized important interactions with saprophytic fungi for example, of the 14 genera described for Diatrypaceae (Ascomycetes, Xylariales), 9 were reported in associated with species of Arecaceae in South America (Konta, 2020). The occurrence of *P. rimosoaffinis* in Pampa and Atlantic Forest biomes, at diversified points corroborates with the theory of Vanderwal (2017), that infer the influence of fungal composition linked to the abundance of host arboreal species. In their study, the author links the abundance of saprobes *Bulgaria inquinans* (Phacidiaceae) and *Daedalea quercina* (Fomitopsidaceae) to the distribution of *Quercus* sp. at a forest in Romênia (Vanderwal, 2017).

V. cubensis shown occurrence only in the Atlantic Forest domain and has as substrate *Clitoria* sp. (Wartchow, 2009), native from tropical and subtropical forests (Gondim et al., 2005). For this arboreal species, the conservation status in Brazil has been aggravating in recent years, where some are threatened with extinction, such as *Clitoria froes* (IUCN, 2021). This factor may be related to the occurrence of *V. cubensis*, mainly to its endemism in the Northeast Region of the country. According to Hottola & Siitonen (2008), the density index of endemic trees and the associated saprobic leads to the conclusion that the greater the endemism of the plant, the lower the fungal occurrence.

In the Atlantic Forest and Pampa biomes, pluteoid species have mainly native Brazilian tree species as substrate. For the two biomes the fragmentation and habitat loss is constant, which is an aggravating factor for their conservation status (Vasquez et al., 2007). In the Atlantic Forest the urbanization, and in Pampa the agriculture and livestock are examples of anthropic actions in these ecosystems (IBGE, 2020). Thus, the species of Pluteaceae with specific substrate, such as those mentioned above, act together with the host tree species, mainly linked to nutrients from the same. In this form, they guarantee cycling and the return of these nutrients to the soil, which can later be used by new seedlings.

4.3 Pluteoid associations with litterfall

The litterfall substrate is unique and contains a large amount of macro and micronutrients compared to branches or trunks (Costa et al., 2015). Only two pluteoid species were reported associated with this substrate in Brazil. However, according to dos Santos et al. (2015), the macrofungi that are capable of colonizing litterfall are highly adapted to chemically varying conditions, which underscores their importance in these ecosystems.

P. velutinus is endemic from the Amazon domain grows on leaf sheaths of Arecaceae (Menolli, 2013). These palms have many associations with Basidiomycetes fungi. In the study carried in the Amazon biome by Mendoza et al. (2018) involving 12 fungal families, some species were associated with diverse portions of this plant, such as *Auricularia auricula-judae* (Auriculariaceae) to the trunk, *Hexagonia hydnoides* (Polyporaceae) to the branches, and *Mycena zephirus* (Mycenaceae) on leaves. In this context, the interaction of fungal species in relation to the diversity of the arboreal substrate can be associated with the trophic speciation of the group and its adaptation to the habitat (Albuquerque et al., 2010). For other samples described of *P. velutinus*, as in Italia, the species has been reported colonizing branches of *Quercus cerris* (Ferisin & Dovana, 2016), and in Russia on branches of *Castanea sativa* (Kalinina et al., 2020). In general, *P. velutinus* grow on wood (Pradeep et al., 2012), and in Brazil to Amazon biome the report on litterfall of palm trees is unique (Menolli, 2013).

P. striatocystis was the only specimen pluteoid in the Central-Western Region recorded in litterfall at the Atlantic Forest (Menolli, 2013). Inserted in an area that preserves one of the last remnants of the tropical forest due to high anthropic action (Scherer & Bispo, 2011). For the world, this is the second occurrence, the first registration was effectuated in Africa (Pegler, 1977), where *P. striatocystis* also was reported growing in litterfall. Santana et al. (2017) infer that the tropical forest ecosystems form a very varied substrate due to the climatic conditions of temperature and humidity, and this factor influences the broad fungal colonization. In the study of dos Santos et al. (2015) involving a checklist of fungi with occurred in tropical forests, the authors inferred that the litterfall fungi are the vastest group in distribution at intercontinental tropical regions.

However, the two species of Pluteaceae recorded in association with litter play an essential role as saprobes. Only one had a record in the Amazon domain, which holds the largest equatorial forest in the world (IBGE, 2020). In terms of conservation, the Amazon biome suffers large-scale habitat losses, in the face of the advance of deforestation linked to public development policies (Mendoza et al., 2018). The occurrence of pluteoid species in this region, as well as in the Atlantic Forest domain can assist in policies aimed at the conservation of both biomes since they are unprecedented records for Brazil, as well as for the world.

4.4 Soil nutrient cyclers

P. argentinensis grows in the soil and on dicotyledons humus (Rosa & Capelari, 2009; Menolli, 2013; Dias & Cortez, 2013). This important characteristic of the species reinforces an ecological association already reported by Nobre et al. (2010) when analyzing macrofungal species associated with wood humus, where the substrate was rich in modified lignin. The lignicolous fungi contain enzymes capable of degrading complex compounds, such as lignin and sometimes also hemicellulose and cellulose (Junior et al., 2021). The humus resulting from this important process can remain in the soil for hundreds of years and is essential for the continued renewal of the flora since this substrate increases the aeration, nutrient, and water absorption capacity of the soil (Abreu et al., 2022).

P. cf. *fastigiatus*, *P. aureolatus*, and *P. halonatus* with occurrence in Amazon biome were recorded growing solitary on soil (Menolli, 2013; Menolli et al., 2015; Menolli & Capelari, 2016). Medrado et al. (2019) infer that soil colonization is influenced by several biotic and abiotic factors, such as climate, soil chemical characteristics, and plant species growing in the area. In our reconstructions, the phylogenetic relationships among these species showed close. According to Mummey et al. (2010), the habitat of fungi may be a primary factor determinant for the structuration from your community. Corroborated with this theory, *P. aureolatus*, *P. halonatus*, and *P.*cf. *fastigiatus* were the only of the genus *Pluteus* with terricolous habitat. However, these soil saprobes are part of a large group of systematic fungi, with succession layers in diversified periods that change according to the seasons of the year. This characteristic helps in their constant performance in the nutritional maintenance of the soil (Oliveira et al., 2019).

Volvariella clade is predominantly terricolous with a large distribution in Atlantic Forest and Pampa biomes. *V. nullicystidiata*, *V. earlei*, *V. taylori*, *V. gloiocephala*, and *V. volvacea* occurs in both the biomes at more than one locality (de Meijer, 2006; Menolli & Capelari, 2008). Figueiredo et al. (2020) detailed the importance of terricolous macrofungi in the Atlantic Forest in the extreme south of Bahia. In the study, 77 of the sampled species (Basidiomycota and Ascomycota), 51% were associated with secondary vegetation in the middle stage of regeneration. According to the Secretaria do Meio Ambiente (Brasil, 2017), the fungi in the region perform an ecological action associated with the regeneration of the flora.

The presence of fungi in the soil brings numerous benefits, mainly related to carbon cycling (Baldrian et al., 2016). In the Brazilian biomes that suffer from anthropic action, the deconstruction of plant organic biomass by the enzymatic action of fungi is one of the most active interactions in these ecosystems (Floudas et al., 2012). *V. macrospora* was found in clay soil (Singer, 1961) and was reported in actuation as a nutrient drain and in aerating of the soil (Bononi et al. 2008).

In Atlantic Forest, the species endemic from Brazil *V. oswaldoi* had an occurrence registered on substrates of cotton crop culture of genera *Gossypium* sp. (Malvaceae) (Batista, 1957; Putzke, 1994). *V. pusilla* in the same biome also was found in agricultural soil (Singer, 1961). The saprobic fungi interacted in agricultural soil is inferred to Carrenho et al. (2007) as an aid in the degradation of organic matter and nutrient transport, also in energy flow and pathogen control. In a study conducted with the fungi *Hysterangium incarceratum* (Hysterangiaceae), *Laccaria fraterna* (Hydnangiaceae), and *Pisolithus tinctorius* (Sclerodermataceae), that have mycorrhizal associations in agricultural areas, a simulation of the levels of heavy metals (Al, As, Cd, Cr, Ni, and Pb) was performed by Ray et al. (2005), inferring to these fungi the accumulation of these metals benefiting the soil. *Thelephora terrestris* (Thelephoraceae) and *Suillus bovinus* (Suillaceae) associated with the culture of *Pinus sylvestris* also have been evaluated, and all species shown actuation as protectors on copper levels (Van-Tichelen et al., 2001; Ray et al., 2005).

For pluteoid species that have the soil as substrate, there is an important interaction related to the cycling of organic matter from agriculture. In Brazil, mainly in the Amazon, Atlantic Forest and Pampa biomes, areas of intercropped cultivation occur (IBGE, 2020). Thus, the fungal presence is a natural aid since the fungus rapidly degrades the rest of the organic matter, returning nutrients to the soil that will serve as a nutritional basis for the new crop.

5. Conclusion

Pluteaceae is a group lignicolous fungi, mainly the members of the genus *Pluteus*. The pluteoid act helping in the cycling of wood compounds that are difficult to degrade. Also, the terricolous *Volvariella* are saprobes that play key ecological roles on the soil. The data compiled in the literature and the relationships built in this study showed that the species of the family with occurrence in Brazil performed ecological importance unique for the biomes.

The Atlantic Forest biome showed a great diversity of species described, containing interactions ecological important to the regions near watercourses. Association pluteoid specifics with the native arboreal Brazilian and distribution of group showed how much the fungal-arboreal interaction is important for these regions. Terricolous fungal of the family present in areas of intense anthropic action play important actions that should be better analyzed in a future study. Thus, it is possible to infer that the family is actively associated with the cycling of nutrients and the regeneration of the flora in Brazilian biomes.

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