

Ecological aspects of myxomycete assemblages in two Brazilian Cerrado landscapes

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Abstract: We investigated the ecological aspects of the myxobiota associated with both the mesophilic and gallery forests from a fragment of the Cerrado biome located in the municipality of Anápolis, Goiás, Brazil. Myxomycete assemblages were sampled in pre-established plots and compared using basic ecological calculations (α and β diversity, richness, abundance, similarity, evenness, functional diversity, and substrate ecology). A total of 55 records were obtained, corresponding to 19 species, 10 genera, and eight families. Of these, 37% were exclusive to the gallery forest, 26% to the mesophilic forest, and 37% common in both. No differences were found between species richness and composition between areas, however, the greater abundance and greater number of exclusive species in the gallery forest are suggestive of better conditions and resources for myxomycete communities in this forest formation. Furthermore, species were found to have different functional characteristics between the compared areas, which seemed to show a relationship with forest structure and the complexity of the niches. This is one of the first studies on the ecology of myxomycetes in the Cerrado biome providing relevant preliminary data for further research to be carried out in areas with little monitoring.

Keywords: Brazilian savanna, community ecology, functional diversity, myxogastrids, slime molds

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Introduction

Myxomycetes (plasmodial slime molds or myxogastrids) are a group of eukaryotic organisms characterized by distinct life cycle stages, two of which are more easily recognizable: one mobile and assimilative or amoeboid phase (plasmodium), and the other fixed and producing spores (sporocarp). It is by the sporocarp phase that the taxonomy of the group is based (Stephenson and Stempen 1994; Rojas and Stephenson 2017).

They are organisms associated to different types of substrates, ecosystems and ecological conditions (Rollins and Stephenson 2011). Even though most of the studies of myxomycetes have focused on taxonomy and geographic distribution, approaches to the ecology of the group have been growing in

Neotropical countries especially Mexico (Basanta et al. 2008; Estrada-Torres et al. 2009) and Costa Rica (Rojas and Stephenson 2007, 2008; Rojas et al. 2011; Rojas and Valverde 2015), the latter being the country best represented in relation to ecological studies of myxomycetes. These studies have evaluated how different environmental pressures affect the myxobiota and what are the mechanisms of adaptive responses to these new environmental conditions. In Brazil, this approach is not commonly used, and most studies have focused on substrate ecology and/or new substrate records (Araújo et al. 2012; Cavalcanti et al. 2015; Xavier-Santos et al. 2016; Lima and Cavalcanti 2017; Calaça et al. 2020; Moreira et al. 2021).

Currently, 255 species of myxomycetes are known in Brazil and approximately 40% of these occur in the Cerrado (Cavalcanti 2021), making it one of the richest biomes for myxomycetes in the country. This biome occupies a large part of the Brazilian territory and presents a great diversity of landscapes, including forest, savanna, and grassland formations (Ribeiro and Walter 2008). In this context, our study compared the myxomycete assemblages of two landscapes, the gallery forest and the mesophilic forest (semideciduous dry forest), of a Cerrado fragment in Central Brazil, considering different ecological parameters. This approach in tropical areas has the potential to increase knowledge about the ecological aspects in unique and poorly studied ecosystems, such as the Cerrado, and contribute to the active monitoring of tropical microorganisms in the context of climate change and conservation of natural resources.

Materials and methods

Study area

The study was carried out in the Reserva Ecológica da Universidade Estadual de Goiás, a fragment of Cerrado located in the Anápolis municipality, Goiás state, Brazil (16°23'40"S, 37°57'32"W; 1017 m). The regional climate is tropical (Cwb type) with a dry cold season (April to September) and a rainy warm season (October to March); with a mean annual temperature of 25 °C (Cardoso et al. 2014). The area comprises three Cerrado landscapes: cerrado *stricto sensu*, mesophilic forests and gallery forests.

The studied areas comprise two forest formations that differ in terms of floristic composition and water resources. The gallery forest is vegetation community that accompanies the small rivers and streams of the plateaus of Central Brazil, which has the characteristic of forming closed corridors (galleries) over the waterway. These are evergreen forests, usually not deciduous during the dry season. In contrast, mesophilic forests, also called semideciduous dry forests, occur in the interfluves in soils richer in nutrients and present different levels of deciduousness during the dry season (Ribeiro and Walter 2008; WWF 2015).

Field sampling

We delimited five plots of 25 m² in each area, in a 150 m transect from the edge to the interior, excluding the first 20 m to avoid the influence of edge conditions. Three collecting trips were carried out between 2016 and 2017, during which each plot was explored for 15 minutes to collect visible sporocarps. As established by Eliasson (1981), sporocarps of the same species found less than 20 cm apart were considered to be the same sample.

The taxonomic identification of the collected material was performed based on macro and microscopic characters. The taxonomic nomenclature used was according to Lado (2005-2021) and the genera and families were according to Poulain et al. (2011). The vouchers of the specimens studied were

deposited in the collection of myxomycetes in the herbarium of the Universidade Estadual de Goiás (HUEG).

Data analysis

The myxomycete assemblages were compared using ecological parameters of richness, relative frequency, abundance, diversity, evenness, and similarity, using the statistical software Past version 3.2. Species richness was estimated using the Chao1 index (Chao 1984) and the first order Jackknife (Jack1) (Gotelli 2009). Chao1 is a simple method that estimates total richness using the number of species that occurred only once (singletons) and the number of species that occurred twice (doubletons). Jack1 estimates total richness using single-occurring species (Colwell and Coddington 1994; Gotelli 2009). In the equation, $Chao_1$ and $Jack_1$ is the number of estimated species, S_{obs} is the number of species in the sample, F_1 is the number of singletons, F_2 is the number of doubletons and n is number of occurring:

$$Chao_1 = S_{obs} + \left(\frac{F_1^2}{2F_2} \right) \quad \text{and} \quad Jack_1 = S_{obs} + \left(\frac{n-1}{n} \right) * F_1$$

The α diversity was estimated by the Shannon-Wiener (H') index (Shannon 1948). In the equations, H' is ecological diversity, S is the number of species, p_i is the relative abundance of i^{th} species:

$$H' = - \sum_{i=1}^S (p_i * \ln(p_i))$$

The Shannon-Wiener index encompasses both attributes of a biological community, the number of species and their evenness, as the Pileou's evenness (J') is one of its components, which reflects the way in which individuals find themselves, distributed among the different species present in the sample. The evenness varies between 0 (minimum evenness) and 1 (maximum evenness). Pileou's evenness was calculated considering J' is the Pileou evenness, S is the total number of species and $\ln(S)$ is the species diversity under maximum equitability conditions:

$$J' = \frac{H'}{\ln(S)}$$

To verify the differences in Shannon index between areas, the modified t test of Hutcheson was used with a significance level of $p < 0.05$. To estimate the β diversity and measure the pattern of similarity between the areas, the Sørensen similarity index (S_s) was used (Stephenson 1989), where S_s is the Sorensen Coefficient, c is the number of species common to both communities, S_1 and S_2 is the number of species in community 1 and 2, respectively:

$$S_s = \frac{2 * c}{S_1 + S_2}$$

The S_s ranges from 0 to 1, when the value is 0: there is no similarity and when it is 1 there is total similarity (Ludwig and Reynolds 1988). To visualize the similarity of species composition between the areas, the Sørensen matrix was used to perform a Non-Metric Multidimensional Scale (NMDS) plot (Kruskal and Wish 1978). The NMDS performance was assessed with the stress coefficient (Clarke and Warwick 1994).

Functional diversity was evaluated according to Rojas and Valverde (2015) with minor adaptations. We considered the following morpho-functional parameters of the species: sporocarp type,

spore ornamentation, spore diameter, plasmodium and micro habit: corticolous, foliicolous and lignicolous (Andrade et al. 2006; Bezerra et al. 2008; Poulain et al. 2011). Data were expressed in percentage values; for the diameter of the spore the average of the measurements obtained within each species was considered and, subsequently, the frequency of richness within each evaluated landscape.

Results and Discussion

A total of 55 sporocarps of myxomycetes were recorded, corresponding to 19 species, 10 genera, and eight families (Fig. 1). Of these, 65% were recorded in the gallery forest and 35% in the mesophilic forest, with 37% and 26% of the total number of species, respectively, being exclusively recorded in them, and 37% common in both. Trichiaceae, Physaraceae, and Stemonitidaceae were the most representative families, with species recorded in both studied areas. The most frequent species were *Arcyria denudata*, *Ceratiomyxa fruticulosa*, *Hemitrichia calyculata*, and *Physarum album* (Table 1). These species are considered cosmopolitan and are widely distributed in neotropical regions (Lado and Basanta 2008), with records in several locations in the Cerrado biome (Cavalcanti 2021).

The diversity index found was $H'=2.4$ in the gallery forest and $H'=2.2$ in the mesophilic forest. In both areas, Pielou's evenness was $J'=0.9$, which indicates that the number of records is balanced among the species. Hutcheson's t-test showed that the diversity of the two areas was not significantly different ($t=0.50$, $d.f.=38$, $p>0.05$, Fig. 2) and the areas were similar in species composition ($S_s=0.54$) (Table 2). The NMDS showed that the species composition did not differ between the two areas (Fig. 2).

In most ecological studies of myxomycetes in Brazil, greater species diversity has been observed in humid forests, with low luminosity, even in different biomes (e.g., Atlantic Forest and Pampa) (Costa et al. 2014; Lima and Cavalcanti 2017). However, available data show different responses in other tropical regions. For example, in Costa Rica, Rojas and Valverde (2015) observed that a greater diversity of lignicolous species was found in dry than in humid forests, possibly justified by the high presence of available resources in dry forests, especially litter, resulting from the different levels of deciduousness.

A similar response had been previously recorded in another study carried out in Costa Rica by Schnittler and Stephenson (2000). Due to the availability of resources in dry forests and a shorter temporal window for sporocarp formation, myxomycetes are induced to form sporocarps very rapidly, in comparison with moister environments. As such, the same is not observed in forests with high humidity, where it is believed that myxomycetes remain in the vegetative phase for longer, without the formation of spores, reducing the efficiency of dispersion and colonization of new substrates (Schnittler and Stephenson 2000).

When comparing the areas studied by Schnittler and Stephenson (2000) and Rojas and Valverde (2015) with those in our study, we observed that despite the differences in the composition of species of fauna and flora, some physical and biological characteristics, such as the average temperature, and the presence of semideciduous forests are similar, but there is considerable variation in the average annual precipitation, with values between 1600-4000 mm for areas in Costa Rica and 1000-1200 mm for Brazil. This difference may indicate that the humid forests of the Cerrado, such as gallery forests, could have more suitable fructification windows (and niches by extension) for myxomycetes, justifying the greater number of sporocarps (abundance) and a higher number of exclusive species in the gallery forest (Tables 1 and 2).



Figure 1. Myxomycete species found in both the gallery and mesophilic forest of a Cerrado fragment in Central Brazil. **A)** *Arcyria cinerea*, **B)** *Arcyria denudata*, **C)** *Ceratiomyxa fruticulosa*, **D)** *Cribraria* cf. *intricata*, **E)** *Didymium iridis*, **F)** *Didymium squamulosum*, **G)** *Hemitrichia calyculata*, **H)** *Hemitrichia serpula*, **I)** *Metatrichia vesparia*, **J)** *Trichia* cf. *papillata*, **K)** *Lycogala epidendrum*, **L)** *Physarum album*, **M)** *Physarum nucleatum*, **N)** *Physarum viride*, **O)** *Physarum* sp. Species of the genus *Stemonitis* have not been documented. Scale bars = 0.5 mm.

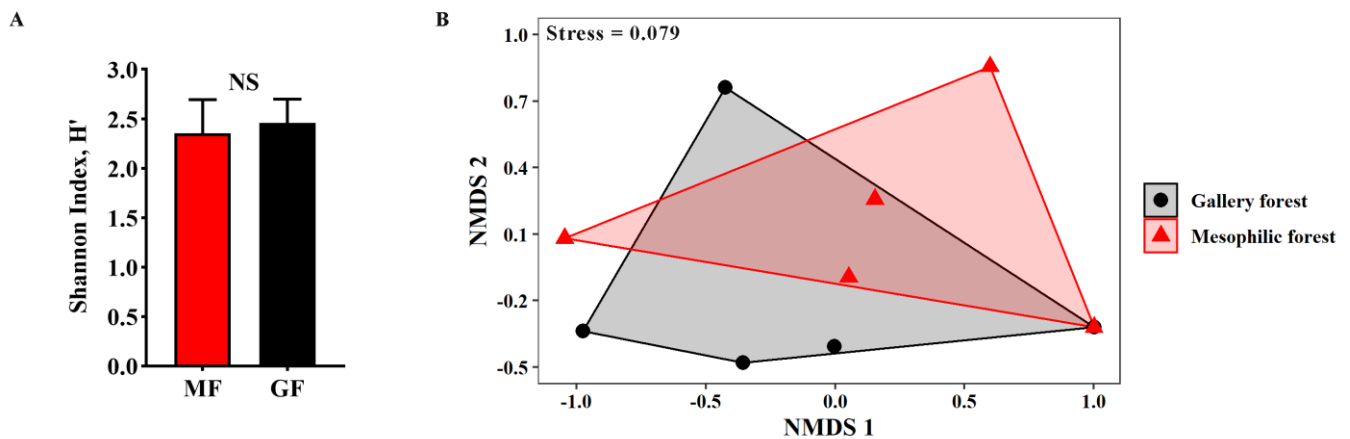


Figure 2. **A)** Shannon-Wiener index (H') of the two studied areas. MF = mesophilic forest, GF = gallery forest, NS = not significant (Hutcheson t-test $p > 0.05$). **B)** Non-Metric Multidimensional Scaling (NMDS) using Sørensen dissimilarity matrix. The figure suggests that the species composition is similar. The NMDS stress indicates good two-dimensional ordering (Claker 1993), thus preserving the classification order of the original matrix of communities.

The areas studied herein have different floristic compositions, structures, and environmental conditions. These and other pressures in forest environments directly affect the reproductive stage of myxomycetes, reflecting on their morphophysiological responses and the number of reproductive structures (Everhart and Keller 2008; Rojas and Valverde 2015). These functional traits are strategies resulting from the compensation of resources available in the habitat and become evident at various stages of the myxomycete life cycle (Everhart and Keller 2008). We observed that the studied myxomycete assemblages have both similar and distinct functional traits between the compared areas. It was common in both areas to record sporangium-type sporocarps, smooth and warted spore ornamentations, lignicolous habits and the presence of phaneroplasmodia in the amoeboid phase. Pseudoaethalia occurred only in the gallery forest; and in the mesophilic forest, spiny spore ornamentation was more frequent. The presence of species with larger spores occurred in the gallery forest and those with smaller dimensions in the mesophilic forest (Fig. 3). There was no difference in spore diameter between individuals of the same species in the evaluated areas.

Functional traits such as sporocarp type, the size and ornamentation of the spores, and plasmodium type may be allied to adaptations that favor the survival and perpetuation of the species. Sporocarps are essential for long-distance spore dispersal (Rojas *et al.* 2021), and with the presence of the stipe in this structure, characteristic of the sporangium, the species may increase their dispersal effectiveness due to the projection of the reproductive structure (Varga *et al.* 2019).

The different shapes, sizes and ornamentation of spores are the result of evolutionary pressures that aim to maximize the dispersion of spores in the air, reaching a long range and consequent colonization of new substrates (Keller and Everhart 2010). We suppose that the presence of more prominent ornaments, such as spines, can be more frequent in unfavorable environments, contributing to the spore dispersal and protection process.

Table 1. Number of records of myxomycetes by species and forest type recorded in the present study. Studied voucher information is provided. MF = mesophilic forest, GF = gallery forest, HUEG = Herbarium of the Universidade Estadual de Goiás.

Families/Species	GF	MF	Voucher in HUEG
Arcyriaceae			
<i>Arcyria cinerea</i>	3	1	11850, 11862-11864 11819, 11820, 11824, 11829, 11833, 11836, 11853,
<i>Arcyria denudata</i>	6	3	11855, 11857
Ceratiomyxaceae			
<i>Ceratiomyxa fruticulosa</i>	3	3	11821, 11831, 11834, 11843, 11854, 11859
Cribrariaceae			
<i>Cribraria cf. intricata</i>		1	11831
Didymiaceae			
<i>Didymium iridis</i>	1		11840
<i>Didymium squamulosum</i>	2		11839, 11861
Trichiaceae			
<i>Hemitrichia calyculata</i>	6	1	11827, 11835, 11841, 11846, 11849, 11852, 11887
<i>Hemitrichia serpula</i>	1	2	11822, 11823, 11856
<i>Metatrichia vesparia</i>	2		11828, 11851
<i>Trichia cf. papillata</i>	2		11848, 11888
Reticulariaceae			
<i>Lycogala epidendrum</i>	2		11832, 11838
Physaraceae			
<i>Physarum album</i>	4	3	11818, 11842, 11844, 11889-11892
<i>Physarum nucleatum</i>		1	11825
<i>Physarum viride</i>	2	1	11845, 11858, 11860
<i>Physarum sp.</i>		1	11826
Stemonitidaceae			
<i>Stemonitis fusca</i>	1		11837
<i>Stemonitis sp.1</i>		1	11847
<i>Stemonitis sp.2</i>	1		11949
<i>Stemonitis sp.3</i>		1	11830

The higher frequency of phaneroplasmodia occupying a greater extension of the wood surface in search of food may be advantageous for some species. This could suggest differences in competitive abilities associated with being more robust at the vegetative stage, and thus resulting in a greater number of sporocarps on the substrate (Everhart and Keller 2008). Furthermore, the high frequency of lignicolous species may be related to the presence of phaneroplasmodia in the amoeboid phase, and the expected high availability of substrates, as observed in the mesophilic forest. The lignicolous species are among the most common and widely known (Rufino and Cavalcanti 2007; Rojas *et al.* 2014).

Even though the species assemblages between the areas were similar, differences were observed, suggesting that the gallery forest displays more favorable conditions for myxomycetes. The same was observed in other taxonomic groups, equally influenced by microclimatic conditions, such as corticolous lichens (Rodrigues and Carregaro 2013) and bryophytes (Aquino *et al.* 2015; Rios *et al.* 2016). In contrast, the mesophilic forests have a more dynamic structural formation, due to the association with seasonality, where deciduousness of plant species in the dry season occur and, consequently, opening in the canopy modifies wind flow and water availability, affecting the conditions to form reproductive structures.

Interestingly, the studied myxomycete assemblages were constituted by species with wide distribution and poorly associated phenological patterns, also resistant to environmental disturbances such as fragmentation and fires (i.e., resilient of generalist species) (Kryvomaz and Stephenson 2017; Rojas et al. 2021; Stephenson et al. 2021), showing potential for dispersal and colonization of substrates.

Table 2. Ecological parameters calculated in the present study for the two considered forest types in the Cerrado Biome.

Parameter	Gallery Forests	Mesophilic Forest
Species richness	14	12
Abundance	36	19
Exclusive occurrence	7	5
Shannon-Wiener index (H')	2.4	2.2
Pielou's evenness index (J')	0.9	0.9
Sørensen's index (Ss)	0.54	

Our study demonstrated the similarity in myxomycete assemblages between the studied landscapes. However, these also showed morpho-functional characteristics influenced by the forest structure and the complexity of the system dynamics. Future research could directly elucidate the relationship between myxomycete diversity and their functional traits in other landscapes from Cerrado, by integrating the data from field collections and information from moist chamber analyses to record species that are fragile to environmental variations. Our data are part of one of the first studies on the ecology of myxomycetes in the Cerrado biome, providing a basis for further research to be carried out in areas with poor monitoring efforts.

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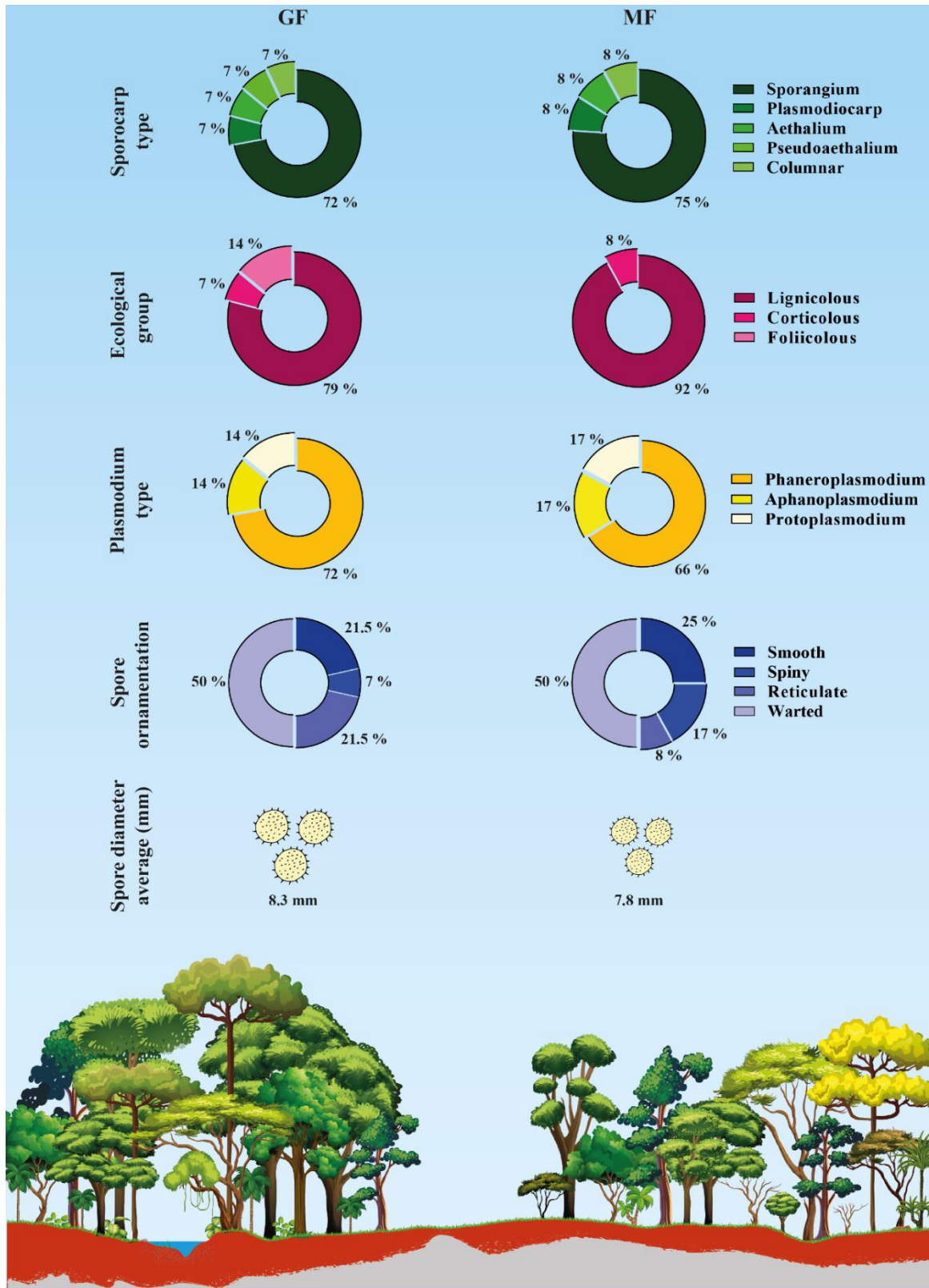


Figure 3. Functional traits evaluated the myxomycete species found in gallery forest and mesophilic forest in the Cerrado. GF = gallery forest, MF = mesophilic forest. Source of tree images: www.freepik.com.

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