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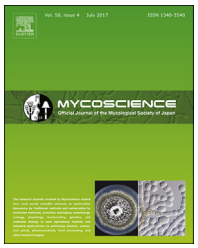

Full paper

Corticolous myxomycetes assemblages in a seasonally dry tropical forest in Brazil

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ABSTRACT

Corticolous myxomycetes are a distinct ecological group consisting of species typically associated with the outer bark surface of living trees. The current study aimed to characterize the community structure of corticolous myxomycetes and their associated trees, analyzing the influence of geographic distance, bark pH, and tree diameter on myxomycete assemblages in a Neotropical Seasonal Dry Tropical Forest (SDTF) in Brazil. The myxomycete community composition significantly varied with the increase of the geographic distance between the studied plots, and tree bark pH was able to explain the species composition exclusively recorded in one of the three transects.

1. Introduction

The monophyletic Myxomycetes lineage, including Myxogastria and Ceratiomyxida (Cavalier-Smith et al. 2015), comprises amoeboid protists with a trophic stage involving a unicellular, multinucleate, plasmodium and a reproductive stage, developing as a sporocarp, where the meiotic spores are produced (Fiore-Donno et al. 2010; Cavalier-Smith 2013). Myxomycetes are ubiquitous in all terrestrial ecosystems across different climates and vegetation zones: (i) tropical [Schnittler and Stephenson 2000 (Central America);

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Stephenson et al. 2004 (South America); Tran et al. 2006 (Asia); Ndiritu et al. 2009 (Africa)]; (ii) temperate (Stephenson 1989; Snell and Keller 2003; Schnittler et al. 2006); (iii) boreal [Schnittler and Novozhilov 1996; Novozhilov et al. 1999 (Asia)]; (iv) tundra [Stephenson et al. 2007 (Southern Hemisphere); Stephenson et al. 2000 (Northern Hemisphere)] and (v) montane/alpine [Ronikier and Ronikier 2009 (worldwide); Novozhilov et al. 2013]. They inhabit litter and woody plant debris, dung and soil, and the surface of living plants and fungi (Stephenson 2011). Environmental factors such as substrate pH, moisture, and temperature influence both trophic and reproductive stages of the myxomycete life cycle, suggesting that distribution in nature is not random (Stephenson 1989; Tesmer and Schnittler 2007; de Lima and Cavalcanti 2015; Liu et al. 2015).

A distinct ecological group of myxomycetes consists of species typically associated with the outer bark surface of living trees (Clayton et al. 2014; Schnittler et al. 2016). The term "corticolous myxomycetes" was originally used to describe these species that complete their entire life cycle on the bark of living trees (Keller and Brooks 1976). As many of the corticolous myxomycetes species are rather inconspicuous, or sporadic in their occurrence, they are difficult to detect in the field (Stephenson 2011). A convenient manner to study them is the moist chamber culture method originally devised by Gilbert and Martin (1933).

The Caatinga phytogeographic domain of Northeastern Brazil is the largest nuclei of Seasonally Dry Tropical Forests (SDTF) that are scattered in the Neotropics (Prado 2000; Queiroz 2006). A dry season in the Caatinga can last 6–11 mo and the mean annual precipitation is less than 1000 mm (Queiroz 2006; Oliveira-Filho et al. 2013). The vegetation in Caatinga exhibits remarkable adaptations that allow it to thrive under strong seasonality. Typically, the woodland is composed of small to medium-sized trees and shrubs, often bearing thorns and small leaves that are deciduous in the dry season (Queiroz 2006). Recently, fossil-calibrated plant phylogenies, dating back to early Miocene, have tracked the ancient evolutionary history of the Caatinga dry woodland (Queiroz and Lavin 2011; Pennington and Lavin 2016). The few studies reporting the occurrence of corticolous myxomycetes species in the Caatinga (Gottsberger 1968; Góes-Neto and Cavalcanti 2002; Silva and Cavalcanti 2012) are all taxonomic surveys upon field-collected myxomycete specimens. No study, however, has attempted to understand the community structure of corticolous myxomycetes in the Caatinga. In order to fill this ecological gap, the current study aimed to characterize the community structure of corticolous myxomycetes and their associated trees, and to analyze the influence of geographic distance, bark pH, and tree diameter on myxomycetes assemblages within the seasonally dry setting of the Brazilian Caatinga.

2. Material and methods

2.1. Study area

The study area is a fragment of seasonally dry tropical forest (Biome Caatinga) located in the northeastern of Brazil (municipality of Ipirá in the state of Bahia) (12°10′36.1″S–12°10′51.3″S; 39°46′10.2″W–39°46′14.9″W; elevation: 280 m). The site is a remnant of a previously larger pristine forested area. The region has a tropical semiarid climate with a mean annual temperature of 23.7 °C and a mean annual rainfall of 754 mm, mainly concentrated in winter (Jun–Jul), corresponding to BSw in Köppen system of climate classification (Kottek et al. 2006).

2.2. Sampling strategy

The point-center quarter method (PCQM) was used to survey the tree community (Cottam and Curtis 1956). A total of 30 points was distributed along three 100 m long transects. The distance between each point was 10 m, so that each transect contained 10 points. The nearest tree to the sampling point in each one of the four quarters was sampled. The following inclusion criteria for selection of the trees were adopted: (i) trees with fissured outer bark and (ii) DBH (trunk diam at breast height) $\geq$ 2 cm at 1.30 m above the soil. A fragment of bark with about 10 cm was sampled from each host tree with a sterile knife, taking care not to damage the underlying tree living tissues, and the samples were deposited in sterile plastic bags.

2.3. Moist chambers

Moist chambers were made with collected substrata using 9-cm plastic Petri dishes covered with a sterilized paper filter at the bottom. A total of 118 moist chambers was prepared, comprising one for each sampled individual tree. Substrata were placed on the filter paper and sterilized distilled water (pH 7.0) was added enough to submerge the material (Mitchell 1977). After 24 h, the excess of water was drained off and pH (Digimed, DM20, Brazil) was measured (Stephenson 1985). Moist chambers were incubated in the laboratory in a diffuse light/dark environment at room temperature (23–25 °C) and examined, initially daily, and later twice a week, during two months, with a stereomicroscope, for the presence of plasmodia and/or sporocarp. Plasmodia types were classified as protoplasmodium, aphanoplasmodium, phaneroplasmodium or intermediate (trichiaceous) plasmodium (Everhart and Keller 2008). A group of sporocarps originated from the same plasmodium was considered as an individual (Eliasson 1981).

2.4. Identification of myxomycetes and trees

Trees were sampled according to standard botanical methods (Mori et al. 2011) and vouchers of living trees were identified at species level using taxonomic keys from specific literature (Queiroz 2009), and stored in the Herbarium of the State University at Feira de Santana (HUEFS). The tree families are circumscribed according to the phylogenetic classification proposed by the Angiosperm Phylogeny Group (Byng et al. 2016). The myxomycetes were identified using taxonomic identification keys (Martin and Alexopoulos 1969; Lado and Pando 1997; Poulain et al. 2011; Lado et al. 2016) and representative samples of each identified species were deposited in the HUEFS.

Table 1 – Phytosociological parameters of tree species recovered in a seasonally dry tropical forest in Brazil.

Species	Families	Transects			No. Ind	Plant structure parameters					HC	MR
		T1	T2	T3		RD	RDo	RF	IVI	CV		
Aspidosperma polyneuron	Apocynaceae	1	0	0	1	0.83	3.19	1.27	5.29	4.02	1	1
Averrhoidium gardnerianum	Sapindaceae	16	17	8	41	34.17	18.53	29.11	81.81	52.70	41	8
Bougainvillea spectabilis	Nyctaginaceae	2	1	0	3	2.50	0.70	3.80	7.00	3.20	3	1
Caesalpinia pyramidalis	Leguminosae	5	15	23	43	35.83	31.17	30.38	97.39	67.01	43	11
Capparis flexuosa	Capparaceae	1	1	0	2	1.67	0.63	2.53	4.83	2.30	2	0
Cordia superba	Boraginaceae	0	1	0	1	0.83	0.45	1.27	2.55	1.28	1	0
Diospyros inconstans	Ebenaceae	2	0	0	2	1.67	0.35	2.53	4.55	2.02	2	0
Goniorrhachis marginata	Leguminosae	1	0	2	3	2.50	4.81	2.53	9.84	7.31	3	1
Muellera campestris	Leguminosae	0	2	0	2	1.67	1.76	1.27	4.70	3.43	2	0
Parapiptadenia blanchetii	Leguminosae	0	0	1	1	0.83	0.17	1.27	2.27	1.00	1	0
Ruprechtia laxiflora	Polygonaceae	1	1	0	2	1.67	7.69	2.53	11.89	9.35	2	0
Schinopsis brasiliensis	Anacardiaceae	0	0	2	2	1.67	4.59	2.53	8.79	6.26	2	1
Schoepfia brasiliensis	Schoepfiaceae	3	0	1	4	3.33	2.90	3.80	10.03	6.23	4	1
Sideroxylon obtusifolium	Sapotaceae	0	2	3	5	4.17	16.41	6.33	26.90	20.57	5	3
Syagrus coronata	Arecaceae	4	0	0	4	3.33	3.54	3.80	10.67	6.88	4	1
Ziziphus cotinifolia	Rhamnaceae	2	0	0	2	1.67	2.20	2.53	6.39	3.86	2	0
											118	–

Notes: T1: First Transect; T2: Second Transect; T3: Third Transect; RD: Relative density; RDo: Relative dominance; RF: Relative frequency; IVI: Importance value index; CV: Cover value; HC: Number of tree individual species sampled. MR: Myxomycete species richness.

2.5. *Data analyses*

The phytosociological (plant community structure) parameters of density, relative frequency, dominance, and importance value per species were calculated for each tree species (Martins 1993). The accumulation curve was fitted for each transect based on the Chao2 estimator (Chao 1987), and the species richness was estimated using the non-parametric richness incidence-based coverage estimator Chao2 and abundance-based coverage estimator (Unterseher et al. 2011).

The diversity was estimated using Shannon (H') index ($H' = -\Sigma pi \ln pi$), where pi is the relative abundance (the

Table 2 – List of myxomycete species found in a SDTF in Brazil with corresponding relative frequencies, tree species and bark pH organized by transects.

Myxomycete species	Orders	RF (%)	Transect	Tree species	pH*
Licea minima Fr.	Liceales	1.96	1	*C. pyramidalis*	5.4
Hemitrichia serpula (Scop.) Rotaf. ex Lister	Trichiales	1.96	1	*A. gardnerianum*	5.9
Arcyria denudata (L.) Wettst.	Trichiales	1.96	2	*A. gardnerianum*	5.5
Physarum tenerum Rex	Physarales	3.92	2	*C. pyramidalis*	5.14 (4.9–5.7)
Comatricha laxa Rostaf.	Stemonitales	5.9	2	*A. gardnerianum*	5.6 (5.3–5.8)
Stemonitis fusca Roth	Stemonitales	3.92	2	*C. pyramidalis* *A. gardnerianum*	5.35 (5.3–5.4)
Stemonitis pallida Wingate in Macbride	Stemonitales	1.96	2	*Sideroxylon obtusifolium*	6.6
Clastoderma debaryanum Blytt	Echinosteliales	1.96	3	*C. pyramidalis*	4.9
Perichaena depressa Libert	Trichiales	1.96	3	*C. pyramidalis*	7.5
Comatricha elegans (Racib.) G. Lister	Stemonitales	1.96	3	*A. gardnerianum*	4.8
Comatricha pulchella (C. Bab.) Rostaf.	Stemonitales	5.9	3	*C. pyramidalis* *A. gardnerianum*	4.46 (4.3–4.9)
Stemonitis flavogenita Jahn	Stemonitales	1.96	3	*C. pyramidalis*	6.3
Stemonitis herbatica Peck	Stemonitales	1.96	3	*C. pyramidalis*	4.6
Physarum bogoriense Racib.	Physarales	5.9	1,2	*A. gardnerianum*	6.34 (5.6–5.8)
Physarum vernum Sommerf	Physarales	3.92	1,2	*Sideroxylon obtusifolium*	7.2
Cribraria violacea Rex	Liceales	7.85	2,3	*Sideroxylon obtusifolium* *Schinopsis brasiliensis*	6.34 (6.0–6.8)
Arcyria cinerea (Bull.) Pers.	Trichiales	31.38	1,2,3	*Aspidosperma polyneuron* *Averrhoidium gardnerianum* *Bougainvillea spectabilis* *Sideroxylon obtusifolium* *Caesalpinia pyramidalis* *Schoepfia brasiliensis*	5.78 (4.7–7.5)
Physarum serpula Morgan	Physarales	9.8	1,2,3	*C. pyramidalis* *Goniorrhachis marginata*	6.15 (5.8–7.1)

RF: relative frequency. * bark pH median (inferior and superior pH values).

Table 3 – Diversity indices of trees and myxomycetes communities in the three transects in a seasonally dry tropical forest in Brazil.

	Trees				Myxomycetes			
	T_1	T_2	T_3	$T_{(1, 2, 3)}$	T_1	T_2	T_3	$T_{(1, 2, 3)}$
Species	8	7	7	18	7	10	10	18
Individuals	39	41	41	121	11	19	17	51
Diversity (H′)	1.91	1.39	1.35	1.81	1.29	2.06	2.04	2.42
Evenness (J)	0.79	0.67	0.69	0.65	0.80	0.89	0.93	0.84
Chao	13.7	12	8	20.2	9.5	19	21.5	31.5

Notes: T_1: Transect 1; T_2: Transect 2; T_3: Transect 3; $T_{(1, 2, 3)}$: Total value of each variable in all the transects.

proportion of the total number of individuals or records represented by *ith* species), which is a heterogeneity index, influenced by both species richness and evenness. The evenness of species diversity was calculated using the Pielou formula: $H'/H'\max$, where H' = Shannon index and $H'\max$ = the possible maximum diversity of the number of species (S) present in the community, defined by the formula $H'\max = \ln S$. As an indicator for overall myxomycete taxonomic diversity and to compare with previous studies, it was used the mean number of species per genus (S/G) (Stephenson et al. 1993).

The multiple regression on matrices (MRM) was used to evaluate the relative importance of the geographic distance, bark pH and tree diameter on myxomycetes community similarity (Goslee and Urban 2007). To further examine the relative importance of each predictor variable at the three transect scales, we have investigated scale-specific MRM models. This method is useful to evaluate the β-diversity and to determine if the dissimilarity observed between communities is associated to the environmental variables and/or geographic distance (spatial distance). Moreover, it allows assessing the sign and magnitude of these relationships: a positive coefficient indicates that a large difference for an environmental variable corresponds to a large turnover in species composition. The MRM models were performed with all the variables. The non-significant variable with the highest *P* value was removed and then the test was repeated. This procedure was done iteratively with all variables presenting *P* values highest than 0.5 (Vaz et al. 2014). We have tested the significance of each model by performing 10,000 permutations. All analyses were done using the software package R (R Development Core Team 2016).

3. Results

A total of 46.7% of moist chambers were positive, i.e., exhibited plasmodia, and 85.7% of them produced sporocarps (Table 1). A total of 51 myxomycete isolates were identified as belonging to 18 species (Table 2). The simultaneous presence of two plasmodia was observed in only 5.4% of the positive moist chambers, occurring the following possibilities: (i) both plasmodia were aphanoplasmodia, (ii) one aphanoplasmodium and one phaneroplasmodium, or (iii) both were of

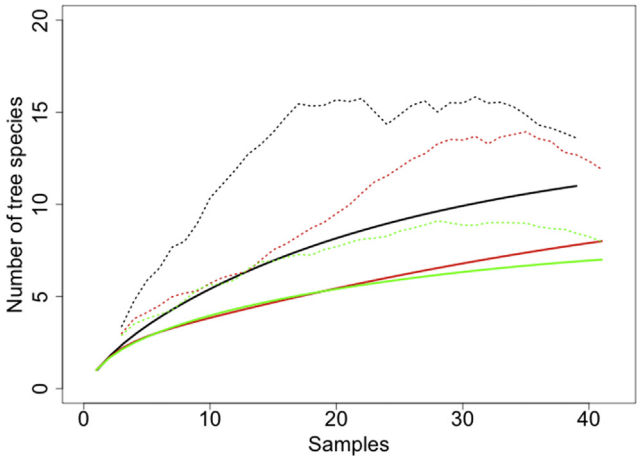

Fig. 1 – Rarefaction curve of the number of tree species against the number of samples in each transect. Thick lines: sample-based species and thin jagged lines: Chao 2 (mean) estimator of expected tree species richness for the first transect (black lines), second transect (red lines) and the third transect (green lines). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

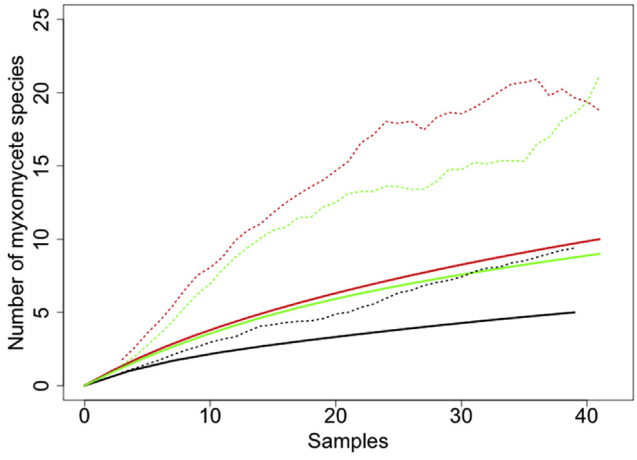

Fig. 2 – Rarefaction curve of the number of myxomycete species against the number of samples in each transect. Thick lines: sample-based species and thin jagged lines: Chao 2 (mean) estimator of expected myxomycetes species richness for the first transect (black lines), second transect (red lines) and the third transect (green lines). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

intermediate (or trichiaceous) form. The myxomycete species were distributed among the following orders: Stemonitales (38.9%), followed by Physarales (22.2%), Trichiales (22.2%), Liceales (11.1%) and Echinosteliales (5.6%). *Arcyria cinerea* was the most frequent species, followed by *Physarum serpula*, which were the only two species that occurred in all the three transects.

The myxomycete assemblages sampled in the three transects were associated with 118 host trees, which belonged to 16 species and 16 genera of 15 distinct families of angiosperms (Table 1). The plant species *Caesalpinia pyramidalis* (Leguminosae) and *Averrhoidium gardnerianum* (Sapindaceae) exhibited the highest cover value, relative frequency, dominance, and density not only in the totality of sampled area but also in each transect. Nevertheless, most *A. gardnerianum* individuals occurred in transects 1 and 2 rather than in the transect 3 whereas the opposite spatial distribution pattern was exhibited by *C. pyramidalis* (Table 1). Both tree species showed rough and hard barks with lenticels. The tree community diversity and richness were similar in all transects (Table 3).

The species accumulation curve did not reach an asymptote for any transect for both trees (Fig. 1) and myxomycetes communities (Fig. 2), indicating that the total number of expected species was not captured. The sampling effort, based on ACE and Chao2 estimator, was 87.3% and 79.4% for trees, and 72.1% and 57.1% for myxomycetes, respectively. The Shannon diversity index were similar in all transects whereas the evenness value was slightly lower in the third transect (Table 3). The mean number of myxomycetes species per genus (S/G) was two, and the lowest diversity and evenness values of myxomycetes were found in the first transect (Table 3).

The ordinate axis in Fig. 3 represents the mean percentage of isolating a myxomycete species in accordance to the tree species (abscissa axis). Only three tree species harbored more than one myxomycete species (Fig. 3): *Caesalpinia pyramidalis*, *A. gardnerianum* and *Sideroxylon obtusifolium* showed the highest number of distinct myxomycete species whereas *A. polyneuron*, *B. spectabilis*, *Schinopsis brasiliensis*, *Goniorrhachis marginata*, harbored only one species. There were no myxomycete species exclusively isolated from any tree species (Fig. 3).

The MRM analysis allowed us to evaluate the independent contribution of the geographic distance and environmental variables to the community structure of the myxomycetes. The results (Table 4) showed that geographic distance was statistically significant in all transects, and bark pH had an effect on community similarity in the third transect.

4. Discussion

Ecological studies of corticolous myxomycetes and the unveiling of factors influencing their distribution have been largely performed in temperate and boreal biomes (Novozhilov et al. 2007; Everhart and Keller 2008; Everhart et al. 2008; Clayton et al. 2014; Takahashi 2014; Schnittler et al. 2016). Few studies were carried out in Neotropical seasonally dry tropical forests (Maimoni-Rodella and Gottsberger 1980; Schnittler and Stephenson 2000; Wrigley de Basanta et al. 2012). According to the species accumulation curves, the sampling effort was not sufficient to adequately capture tree and myxomycete species richness (69.2% and 78.3%) respectively. Although the plateau was not reached, other studies conducted in SDTFs had similar results (Schnittler and Stephenson 2000; Wrigley de Basanta et al. 2012).

The Brazilian SDTF had a higher myxomycetes diversity as measured by both Shannon and the S/G index. The Shannon index ($H' = 2.53$) for myxomycetes was higher than that of the Costa Rican SDTF ($H' = 1.11$) (Schnittler and Stephenson 2000). The mean number of myxomycetes species per genus (S/G) was also higher than in Costa Rica site (S/G: 1.78) (Schnittler

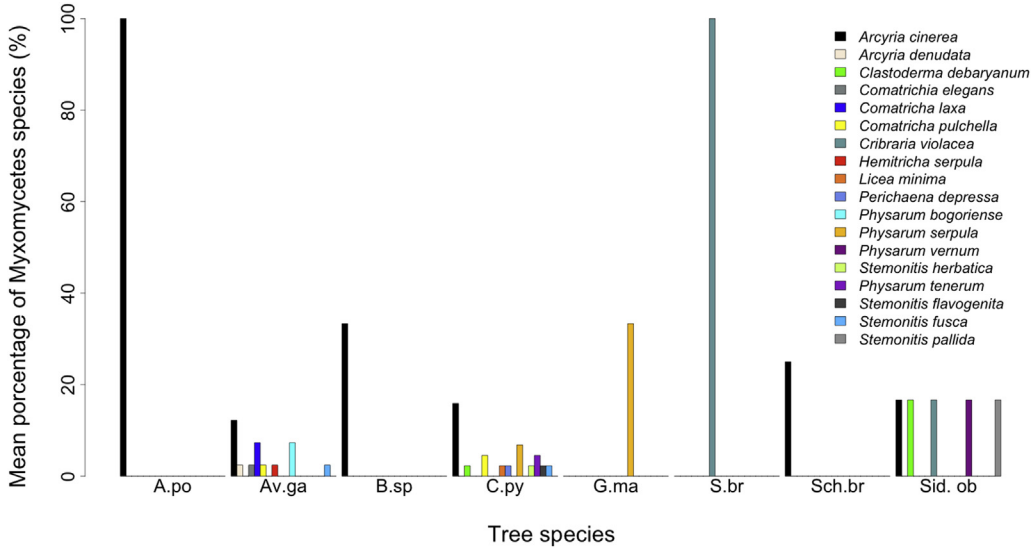

Fig. 3 – The plots represent the mean percentage of myxomycete species obtained by tree species. A.po: *Aspidosperma polyneuron*, Av.ga: *Averrhoidium gardnerianum*, B.sp: *Bougainvillea spectabilis*, C.py: *Caesalpinia pyramidalis*, G.ma: *Goniorrhachis marginata*, S.br: *Schinopsis brasiliensis*, Sch.br: *Schoepfia brasiliensis*, Sid. ob: *Sideroxylon obtusifolium*.

Table 4 – Results of the multiple regression on matrices (MRM) analysis of the myxomycete community.

	All transects ($R^2 = 0.004^*$)	Third transect ($R^2 = 0.04^*$)
Ln (geographic distance)	0.057*	–
pH	–	0.174*
Diameter breast height	–	–

The variation (R^2) of the community dissimilarity that is explained by the remaining variables and the partial regression coefficients (β) of the final model are shown. Where a partial regression is shown, its significance level (via one-way tests) is <0.05. *$P \leq 0.05$.

and Stephenson 2000) and both were lower than in Madagascar site (Wrigley de Basanta et al. 2012) (S/G = 3.1). The lower number of species per genus (2) indicates a greater taxonomic diversity.

The dispersal of a microorganism is the transport and successful establishment of either the entire organism or its propagules (spores) from one location to another (Hanson et al. 2012). Most species of myxomycetes produce a high number of small and light spores that are air dispersed (Tesmer and Schnittler 2007), implying that, there is no dispersal limitation (Black et al. 2004). However, the MRM analysis showed that myxomycete community similarity decayed with increasing distance when all transects were considered (Table 4). This suggests that environmental factors select for the myxomycetes that are better adapted to the conditions of the substrate they reach (Liu et al. 2015).

The geographic distance, bark pH and tree diameter were still not sufficient to explain most of the variability in myxomycete species distribution, suggesting that other factors must be assessed to better clarify this question. Furthermore, there is no association between myxomycetes assemblages and distinct tree species, as well as in other studies (Snell and Keller 2003). However, bark pH was statistically significant to explain the myxomycetes species distributions along one of the transects. Individual trees within this section had a lower bark pH, irrespective of taxonomy. Two of the transects were near a stream and had a denser and higher canopy, while the third transect had a sparse and lower canopy, allowing for direct sunlight and, consequently, dryer conditions. The following myxomycete species only occurred in the third transect: *Clastoderma debaryanum*, *Comatrichia elegans*, and *Comatrichia pulchella*. *Clastoderma debaryanum* and *Comatrichia* spp. are acidophilic species and have been found on acidic tree barks (Schnittler 2001; Härkönen et al. 2004; Schnittler et al. 2016). Therefore, bark pH acts as a selective factor for the establishment of an acidophilic myxomycete assemblage in the third transect.

5. Conclusion

This work revealed a high diversity of corticolous myxomycetes in a seasonally dry tropical forest in Brazil. The small and light spores of Myxomycetes suggest that there is no dispersal limitation. However, in our work, the myxomycetes community composition was influenced by geographic distance. Then, even if the spores can disperse, the abiotic and biotic factors they encounter influence their establishment. One such factor, bark pH, was able to explain the species exclusively recorded in only one of the three transects. Nevertheless, future studies are necessary to understand the influence of other environmental variables on the structure of myxomycetes assemblages in seasonal dry tropical forests.

Disclosure

The authors declare no conflicts of interest. All the experiments undertaken in this study comply with the current laws of the country where they were performed.

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