SUBSTRATE ASSEMBLAGES OF MYXOMYCETES (MYXOGASTRIA) ON THE BARK OF LIVING TREES AND AERIAL LITTER IN VIETNAMESE FORESTS

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1. INTRODUCTION

Myxomycetes (Myxogastria) are amoeboid, fungi-like, spore-producing protists, that have traditionally been studied by mycologists. The group comprises more than 1000 morphospecies in 5 orders [1]. Both zoological and botanical nomenclature codes can be applied to these organisms since in the latter case they are considered as one of the groups in the Amoebozoa clade [2], forming sporocarps - a type of fruiting bodies [3]. Myxomycetes play an important role in soil ecosystems: they significantly influence the population of other microorganisms and constitute up to 25% of the complete amoeboid diversity [4, 5, 6].

One of the main factors influencing distribution of myxomycetes is the accessibility of suitable substrates. Myxomycete trophic stages (myxamoeba, zoospores and plasmodia) primarily inhabit soil or substrates directly connected with it, such as rotten wood, ground litter, leaves and stems of living grasses, mosses, lichens, weathered dung of herbivorous animals, etc. However, there exist species whose life cycle stages pass on the bark of living trees and also in the leaf and branch litter under the forest canopy [7]. The latter habitat is present more often in various tropical and subtropical biomes. In addition to vascular plant debris, aerial habitats of myxomycetes include liverworts and lichens, covering tree leaves in the understory layer [8, 9], inflorescences of giant grasses [10, 11], and also soil, accumulating straight in the canopy [9] and usually connected with large epiphytes.

Corticolous myxomycetes [3, 12] and myxomycete assemblages of aerial litter [12, 14] have been recorded in both Neotropics and Paleotropics, including Vietnam [10, 15, 16]. The described habitats significantly differ in physical parameters, but can be suitable for similar myxomycete species; however, the comparative analysis of myxomycete diversity of these two substrate assemblages in Vietnam has not been fulfilled.

The aim of this work is to compare the species and taxonomic composition of these two ecological assemblages of myxomycetes, occurring high above soil and ground litter.

2. MATERIALS AND METHODS

There are two main types of myxomycete species registration: traditional field records and the moist chamber culture technique in the laboratory. During this work we used the latter method, since it is more suitable to reveal species inhabiting the bark of living plants and aerial litter as they have minute sporocarps which are challenging to notice in the field and also tend to be easily destructed by invertebrates. The analysis was based on the data from three national parks, where myxomycetes were studied the most intensively during the last 10 years, namely Phia Oac-Phia Den, Bidoup Nui Ba and Cat Tien (Fig. 1).

For every specimen there were geographic coordinates, vegetation type and data on substrate noted down, such as a) substrate type; b) height above ground (for bark samples); c) intensity of light exposure; d) exposure to wind; e) texture of the bark surface (for bark samples). These parameters were registered in the field using a specially developed module system and then transferred to the database. The substrate pH was measured later in the laboratory.

Figure 1. Location of the studied

Substrate samples for every moist chamber were collected from exactly one separate microhabitat and placed in paper bags. In the laboratory samples were set in Petri dishes covered with moist filter paper in the bottom. Cultures were stored at room temperature (20-24ºC) and diffused light and checked 7 times (on 2-4, 6-8, 11-13, 21-24, 40-43, 50-55, 60-62, 90-95 days from the experiment start) using the Zeiss Stemi stereo microscope.

Determination of specimens was performed using species keys, monographs [17, 18, 19] and various websites on the Internet (http://www.discoverlife.org; http://www.eumycetozoa.com; http://slimemold.uark.edu). Features of sporocarps and spores were studied via light microscopy (Zeiss Stemi stereo microscope, Zeiss Axio Imager A1 light microscope) and in some cases JSM-6390 scanning electron microscope(SEM). Also, we referred to the modified myxomycete phylogeny system [17].

Evaluation of species composition of substrate assemblages was carried out using individual-based richness estimator Chao1, calculated via EstimateS 9.1.0 [20]. In order to assess completeness of the revealed species composition, ratio of the expected number of species (based on the Chao1 index) to the recorded number of species was used (S*100/Chao1, %). Species composition similarity of substrate assemblages was calculated using the corrected Chao-Sørensen index [21].

Species diversity (alpha diversity) was calculated using the Shannon’s diversity index $H' = -\sum_{i=1}^{R} p_i \ln p_i$, where p_i - the relative abundance (number of individuals of species i to the total number of individuals of all species ratio), and also the Simpson’s diversity index $D = 1/\sum_{i=1}^{R} p_i^2$. The mean number of species per genus (S/G) was used as an index of general taxonomic diversity [22].

The ACOR scale was used to assess the species abundance [23]. It is based on the ratio of the number of individual species records to the total number of records: R - rare (<0.5%, 1-3 records), O - occasional (0.5-1.5%, 3-10 records), C - common (1.5-3%, 11-20 records), A - abundant (> 3%, more than 21 records).

Indicator species analysis was performed considering 40 species having more than three records (667 records in total). For this, "multipatt" function from "indicspecies" package in R with "IndVal.g" as association function and 9999 permutations was used [24].

The annotated species list is given below. Every species name is provided with the following data in brackets: species abundance according to the ACOR scale, number of specimens found on bark (b) and aerial litter (alit), number of specimens found in each of the three national parks. The specimen collection is stored in the mycological herbarium of BIN RAS (LE-F).

3. RESULTS AND DISCUSSION

Arcyria cinerea (Bull.) Pers. [A, 51] b: 29, alit: 22; BID: 4, CAT: 41, PHO: 6.

Arcyria denudata (L.) Wettst. [R, 3] b: 2, alit: 1; BID: 2, CAT: 1.

Arcyria margino-undulata Nann.-Bremek. & Y.Yamam. [R, 1] b: 1; PHO: 1.

Arcyria minuta Buchet [O, 6] b: 2, alit: 4; CAT: 6.

Badhamia affinis Rostaf. [R, 2] b: 2; CAT: 2.

Clastoderma debaryanum A. Blytt [A, 44] b: 40, alit: 4; BID: 11, CAT: 30, PHO: 3.

Colloderma oculatum (C. Lippert) G. Lister [R, 1] b: 1; PHO: 1.

Collaria arcyrionema (Rostaf.) Nann.-Bremek. ex Lado [R, 1] alit: 1; CAT: 1.

Collaria lurida (Lister) Nann.-Bremek. [R, 1] alit: 1; CAT: 1.

Comatricha elegans (Racib.) G. Lister [R, 2] b: 1, alit: 1; BID: 1, CAT: 1.

Comatricha pulchella (C. Bab.) Rostaf. [R, 1] alit: 1; BID: 1.

Comatricha spinispora Novozh. & D.W.Mitch. [R, 4] b: 3, alit: 1; BID: 2, CAT: 1, PHO: 1.

Comatricha tenerrima (M. A. Curtis) G. Lister [O, 6] b: 3, alit: 3; BID: 3, CAT: 3.

Cribraria confusa Nann.-Bremek. & Y. Yamam. [A, 86] b: 85, alit: 1; BID: 52, CAT: 31, PHO: 3 (Fig. 2a, d).

Cribraria intricata Schrad. [R, 3] b: 3; CAT: 3.

Cribraria lepida Meyl. [R, 1] b: 1; CAT: 1.

Cribraria microcarpa (Schrad.) Pers. [A, 49] b: 27, alit: 22; BID: 17, CAT: 27, PHO: 5 (Fig. 2b, e).

Cribraria minutissima Schwein. [A, 36] b: 36; BID: 36 (Fig. 2c, f).

Cribraria tecta Hooff [R, 2] b: 2; CAT: 1, PHO: 1.

Cribraria tenella var. *concinna* G. Lister [R, 1] alit: 1; CAT: 1.

Cribraria violacea Rex [A, 34] b: 26, alit: 8; CAT: 32, PHO: 2.

Didymium difforme (Pers.) Gray [O, 5] b: 5; PHO: 5.

Scale bars: n = 2 µm; e = 50 µm; k, q = 10 µm; d, f, i = 100 µm; a, h, m, o = 200 µm; b, c, j, l, p = 500 µm; g = 1000 µm.

Didymium floccoides Nann.-Bremek. & Y.Yamam. [C, 14] b: 7, alit: 7; CAT: 13, PHO: 1.

Didymium iridis (Ditmar) Fr. [O, 8] b: 6, alit: 2; CAT: 4, PHO: 4.

Didymium minus (Lister) Morgan [O, 6] b: 6; CAT: 6.

Didymium nigripes (Link) Fr. [O, 12] b: 9, alit: 3; CAT: 11, PHO: 1.

Didymium verrucosporum A.L.Welden [R, 1] alit: 1; CAT: 1.

Diachea leucopodia (Bull.) Rostaf. [R, 2] b: 2; PHO: 2.

Diderma chondrioderma (de Bary & Rostaf.) Kuntze [R, 1] b: 1; PHO: 1.

Diderma deplanatum Fr. [C, 19] b: 19; PHO: 19.

Diderma effusum (Schwein.) Morgan [C, 18] b: 13, alit: 5; BID: 1, CAT: 17.

Diderma hemisphaericum (Bull.) Hornem. [O, 6] b: 4, alit: 2; BID: 1, CAT: 5.

Diderma pseudotestaceum Novozh. & D.W.Mitch. [R, 1] b: 1; CAT: 1.

Diderma rugosum (Rex) T.Macbr. [R, 2] b: 2; CAT: 2.

Echinostelium apitectum K.D.Whitney [O, 5] b: 5; BID: 5.

Echinostelium brooksii K.D.Whitney [R, 3] b: 3; BID: 3.

Echinostelium colliculosum K.D.Whitney & H. W. Keller [R, 4] b: 4; BID: 4.

Echinostelium elachiston Alexop. [R, 1] b: 1; CAT: 1.

Echinostelium minutum de Bary [A, 29] b: 23, alit: 6; BID: 5, CAT: 14, PHO: 10.

Enerthenema papillatum (Pers.) Rostaf. [R, 3] b: 3; BID: 3.

Hemitrichia calyculata (Speg.) M.L.Farr [R, 3] b: 2, alit: 1; CAT: 3.

Hemitrichia leiotricha (Lister) G.Lister [R, 1] b: 1; PHO: 1.

Hemitrichia minor G.Lister [R, 1] b: 1; BID: 1.

Hemitrichia pardina (Minakata) Ing [R, 3] b: 2, alit: 1; CAT: 2, PHO: 1.

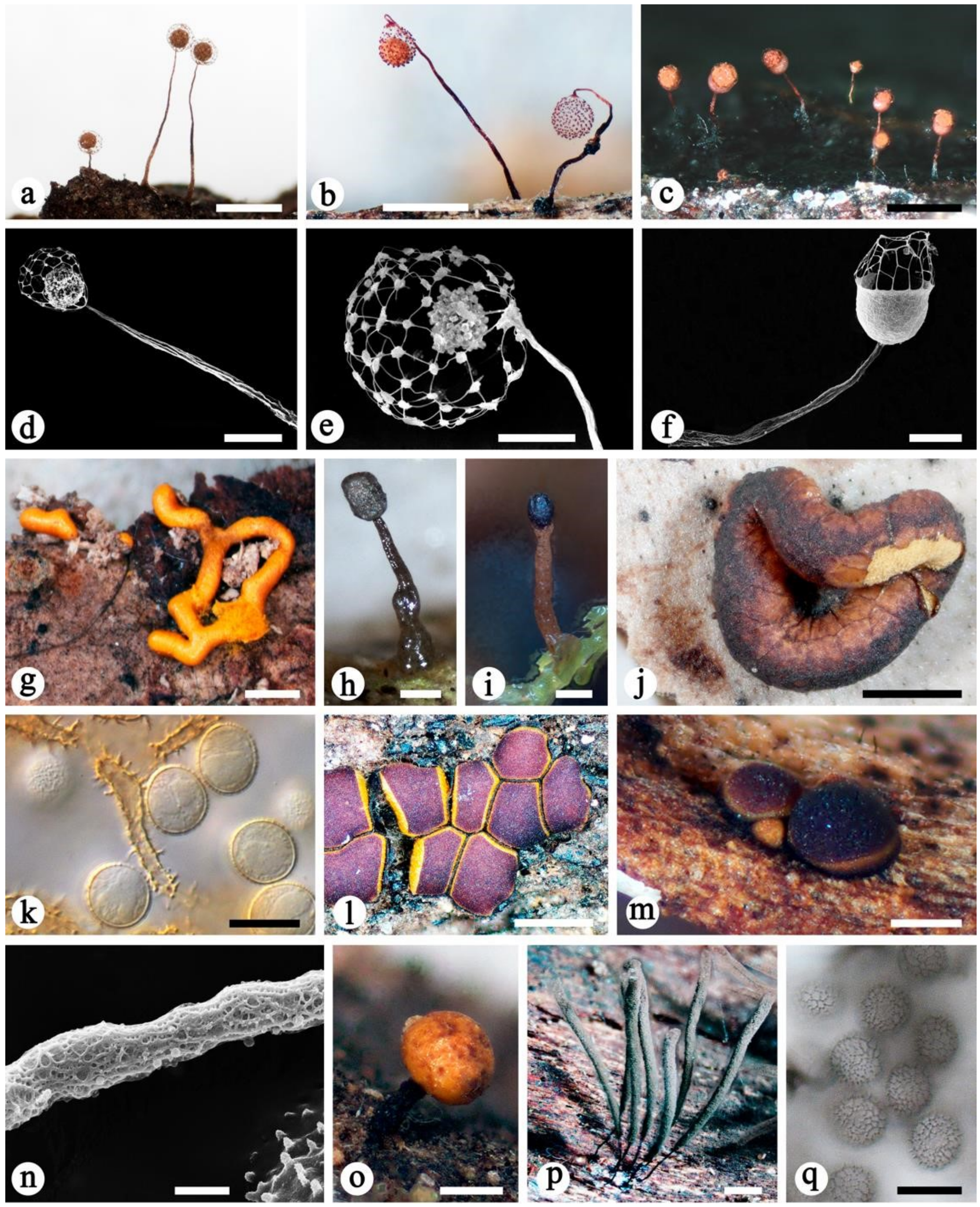

Figure 2. *Cribraria confusa* (a, d): a - General view of sporocarps, d - Sporangium under SEM; *Cribraria macrocarpa* (b, e): b - General view of sporocarps, e - Top of the sporangium under SEM; *Cribraria minutissima* (c, f): c - General view of sporocarps, f - Sporangium under SEM; *Hemitrichia serpula*: g - Plasmodiocarp; *Licea operculata*: h, i - Sporocarps; *Perichaena chrysosperma* (j, k): j - Plasmodiocarp, k - Spores and part of capillitial threads; *Perichaena depressa*: l - Sporocarps; *Perichaena dictyonema* (m, n): m - Sporangia, n - Capillitial thread; *Perichaena pedata*: o - Sporangium; *Stemonitis fusca* (p, q): p - Sporangia, q - Spores

Hemitrichia serpula (Scop.) Rostaf. ex Lister [C, 15] b: 3, alit: 12; CAT: 14, PHO: 1 (Fig. 2g).

Lamproderma scintillans (Berk. & Broome) Morgan [C, 14] b: 9, alit: 5; CAT: 14.

Licea biforis Morgan [R, 2] b: 2; CAT: 2.

Licea bulbosa Nann.-Bremek. & Y.Yamam. [R, 1] b: 1; PHO: 1.

Licea eleanorae Ing [R, 1] b: 1; CAT: 1.

Licea kleistobolus G.W.Martin [R, 4] b: 4; BID: 3, CAT: 1.

Licea operculata (Wingate) G.W.Martin [A, 30] b: 30; BID: 1, CAT: 11, PHO: 18 (Fig. 2h, i).

Licea scyphoides T.E.Brooks & H.W.Keller [R, 3] b: 3; CAT: 3.

Macbrideola argentea Nann.-Bremek. & Y. Yamam. [R, 2] b: 2; CAT: 2.

Macbrideola cornea (G.Lister & Cran) Alexop. [R, 1] b: 1; PHO: 1.

Macbrideola ovoidea Nann.-Bremek. & Y.Yamam. [R, 1] b: 1; CAT: 1.

Macbrideola scintillans H.C.Gilbert [C, 14] b: 14; BID: 1, CAT: 13.

Metatrichia vesparia (Batsch) Nann.-Bremek. ex G.W.Martin & Alexop [C, 13] b: 9, alit: 4; CAT: 13.

Paradiacheopsis longipes Hoof & Nann.-Bremek. [O, 5] b: 4, alit: 1; BID: 1, PHO: 4.

Paradiacheopsis rigida (Brândză) Nann.-Bremek. [O, 6] b: 6; CAT: 6.

Paradiacheopsis solitaria (Nann.-Bremek.) Nann.-Bremek. [O, 5] b: 5; BID: 1, PHO: 4.

Perichaena calongei Lado, D.Wrigley & Estrada [R, 2] alit: 2; PHO: 2.

Perichaena chrysosperma (Curr.) Lister [A, 57] b: 27, alit: 30; BID: 1, CAT: 56 (Fig. 2j, k).

Perichaena depressa Lib. [O, 12] b: 4, alit: 8; CAT: 12 (Fig. 2l).

Perichaena dictyonema Rammeloo [R, 4] alit: 4; CAT: 3, PHO: 1 (Fig. 2m, n).

Perichaena echinolophospora Novozh. & S.L.Stephenson [R, 1] b: 1; CAT: 1.

Perichaena pedata (Lister & G.Lister) Lister ex E.Jahn [R, 4] alit: 4; CAT: 3, PHO: 1 (Fig. 2o).

Perichaena vermicularis (Schwein.) Rostaf. [R, 3] b: 1, alit: 2; CAT: 3.

Physarum album (Bull.) Chevall. [O, 5] b: 4, alit: 1; CAT: 5.

Physarum compressum Alb. & Schwein. [O, 8] b: 6, alit: 2; CAT: 8.

Physarum decipiens M.A.Curtis [R, 1] b: 1; CAT: 1.

Physarum flavicomum Berk. [R, 1] alit: 1; CAT: 1.

Physarum lakhanpalii Nann.-Bremek. & Y.Yamam. [R, 1] b: 1; PHO: 1.

Physarum melleum (Berk. & Broome) Massee [R, 1] alit: 1; CAT: 1.

Physarum oblatum T.Macbr. [R, 4] b: 1, alit: 3; CAT: 4.

Physarum penetrale Rex [R, 1] alit: 1; CAT: 1.

Physarum pusillum (Berk. & M.A.Curtis) G. Lister [R, 2] alit: 2; CAT: 2.

Physarum roseum Berk. & Broome [O, 5] b: 3, alit: 2; CAT: 4, PHO: 1.

Physarum sulphureum Alb. & Schwein. [R, 1] alit: 1; CAT: 1.

Physarum superbum Hagelst. [O, 9] b: 8, alit: 1; CAT: 9.

Physarum viride (Bull.) Pers. [R, 1] b: 1; CAT: 1.

Stemonitis fusca Roth [O, 11] b: 1, alit: 10; BID: 1, CAT: 10 (Fig. 2p, q).

Stemonitis mussooriensis G.W.Martin, K.S.Thind & Sohi [R, 1] b: 1; CAT: 1.

Stemonitopsis aequalis (Peck) Y.Yamam. [R, 2] alit: 2; CAT: 2.

Trichia ambigua Schirmer, L.G.Krieglst. & Flatau [O, 7] b: 7; PHO: 7.

Trichia decipiens var. *olivacea* (Meyl.) Meyl. [R, 1] b: 1; PHO: 1.

Trichia erecta Rex [R, 1] b: 1; BID: 1.

Trichia scabra Rostaf. [R, 1] b: 1; PHO: 1.

As a total, 1009 moist chamber cultures were studied during the experiment and 747 records were made. They resulted in 87 species from 5 orders, 9 families, and 23 genera, that were encountered on both substrates. *Clastoderma debaryanum* and *Echinostelium minutum* were indicated as abundant, the former was 10 times more restricted to bark and the later - about 3.5 times more. Another abundant species, *Perichaena chrysosperma,* demonstrated no substrate preferences (27 records on bark vs 30 records on litter). Forty-seven species were considered rare, which is more than a half of the total number, and 9 species were marked as abundant. Both bark and aerial litter were almost evenly studied: 74.5 and 72.5 per cent respective. Comparison of study completeness in each reserves demonstrates an obvious dependency: the more records are made, the more the value is. The abundance-based Chao-Sørensen index equals 0.76, which implies a high proportion of actual and estimated shared species, although there were only 31 of them.

The analysis of indicator species resulted in 11 species with significant indicator values for one of the two substrate types (Table 2, Fig. 2). For the moist chambers with aerial litter, eight species showed high indicator values, including *Perichaena chrysosperma*, *Cribraria macrocarpa*, and *Arcyria cinerea*. Five species demonstrated high indicator values for the bark of living trees, with *Cribraria confusa*, *C. minutissima*, and *Licea operculata* having the highest IndVal.g values.

In the case of *Arcyria cinerea*, indicator values are quite biased since this species is considered ubiquitous and occupies a whole range of various substrate, so it is also very abundant on aerial litter. The same is true for other species: *Perichaena chrysosperma* and *Cribraria microcarpa* occur less often than the aforementioned species. The data from literature [14] and our results show that these species also inhabit ground litter, wood, and the bark of living trees. Rest of the *Perichaena* species listed here (*P. depressa, P. dictyonema,* and *P. pedata*) are common bark inhabitants and were expected to be identified as indicators. The similar situation is with all indicator species of the corticolous assemblage.

The most peculiar case is the abundance of *Stemonitis fusca* on aerial litter, since this is a typical lignicolous species in regions with boreal and temperate climate. Such substrate switches might occur in tropical forests due to the specific environmental conditions.

Table 1. Parameters characterizing myxomycete diversity on the bark of living trees (b) and aerial litter (alit) in three national parks in Vietnam

	All	PHO	BID	CAT	b	alit
Rec	747	112	162	473	549	198
Sp	87	33	26	63	73	45
G	23	16	15	20	21	16
Sp/G	3.8	2.1	1.7	3.2	3.5	2.8
Chao1	123.86	70.91	47.86	91.81	98.05	61.91
SD	18.53	24.41	17.39	16.67	13.64	10.61
Comp. (%)	70.2	46.5	54.3	68.6	74.5	72.7
H'	3.62	2.94	2.3	3.44	3.47	3.2
D	22.61	12.35	5.77	20.78	18.71	15.48

PHO - Phia Oac; BID - Bidoup Nui Ba; CAT - Cat Tien; Rec = number of specimens; Sp = number of morphospecies; G = number of genera; Sp/G = morphospecies number / genera number; Chao1 = estimated species number; SD = Chao1 standard deviation; Comp. (%) = ratio of the revealed number of species to the estimated number of species; H' = Shannon's diversity index; D = Simpson's (inverse) diversity index

Table 2. Myxomycete species with a significant indicator value for one of the substrate types

Substrate	Species (records)	Comp. A	Comp. B	IndVal.g	p-value
alit	*Perichaena chrysosperma* (57)	0.75	0.25	0.433	0.0001**
alit	*Cribraria microcarpa* (49)	0.6875	0.18333	0.355	0.0036*
alit	*Arcyria cinerea* (51)	0.67195	0.18333	0.351	0.006*
alit	*Hemitrichia serpula* (15)	0.91525	0.1	0.303	0.0002**
alit	*Stemonitis fusca* (11)	0.96429	0.08333	0.283	0.0001**
alit	*Perichaena depressa* (12)	0.84375	0.06667	0.237	0.0039*
alit	*Perichaena dictyonema* (4)	1	0.03333	0.183	0.0051*
alit	*Perichaena pedata* (4)	1	0.03333	0.183	0.0052*
b	*Cribraria confusa* (86)	0.96921	0.26235	0.504	0.0001**
b	*Cribraria minutissima* (36)	1	0.10494	0.324	0.001**
b	*Licea operculata* (30)	1	0.08642	0.294	0.0018*

*For a species, "Comp. A" is the probability that the surveyed site belongs to the target site group given the fact that the species has been found, and "Comp. B" is the probability of finding the species in sites belonging to the site group. IndVal.g is a function of both components. Significance levels: ** <0.001, * 0.001-0.01. Abbreviations: alit - aerial litter, b - bark of living trees.*

4. CONCLUSION

- A total of 747 records of 87 myxomycetes were recovered from the 1009 moist chamber cultures prepared. Altogether, 87 morphospecies of myxomycetes were recorded.

- Two types of myxomycete assemblages were studied: on bark and on aerial litter. Both of them were characterized by the same survey completeness but by different indicator species.

- As a result, *Perichaena chrysosperma*, *Cribraria macrocarpa*, and *Arcyria cinerea* were recognized as indicator species for aerial litter whereas *Cribraria confusa*, *C. minutissima*, and *Licea operculata* - for bark.

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SUMMARY

SUBSTRATE ASSEMBLAGES OF MYXOMYCETES (MYXOGASTRIA) ON THE BARK OF LIVING TREES AND AERIAL LITTER IN VIETNAMESE FORESTS

Myxomycete (Myxogastria) are amoeboid protists, usually associated with soil or nearby substrates, as their trophic stages require moist conditions and sufficient number of microorganisms to feed on. However, they are able to inhabit places that have no direct connection with soil. In this paper myxomycete assemblages encountered on bark and aerial liter, a unique substrate of tropical forest, were studied. The material was collected in different years in various vegetation types of 3 national parks, Phia Oac-Phia Den, Bidoup-Nui Ba and Cat Tien, located in distant parts of Vietnam during the last 10 years. Taxonomic diversity was revealed via the experiment using moist chamber cultures. A total of 1009 cultures resulted in 747 records, assigned to 87 morphospecies from 5 orders, 9 families, and 23 genera. Seventy-three species were recorded on the bark of living plants and 45 were found on aerial litter, and the study for each substrate was completed for 74.5 and 72.7 per cent respectively. More than a half of the total number of species was presented by singletons and doubletons. The analysis of indicator species was performed, which confirmed the dominance of specialist species on bark (*Cribraria confusa*, *C. minutissima*, and *Licea operculata*) and aerial litter (*Perichaena depressa*, *P. dictyonema*, and *P. pedata*). Some species, such as *Perichaena chrysosperma,* demonstrated no specific substrate preference. A typical lignicolous species in temperate regions, *Stemonitis fusca*, appeared to be abundant on aerial litter, showing a change in substrate preferences, which is common for several myxomycete species in tropics. High-quality photographs, including those obtained with SEM, of 10 indicator morphospecies are provided.

Keywords: *Amoebozoa, Myxomycetes, tropics, biodiversity, corticulous species.*

Nhận bài ngày 05 tháng 7 năm 2021

Phản biện xong ngày 07 tháng 10 năm 2021

Hoàn thiện ngày 18 tháng 10 năm 2021

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