

Altitudinal patterns of diversity of myxomycetes (Myxogastria) across tropical forests of Southern Vietnam

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Summary

The tropical forests of Vietnam are distinguished by a high species diversity of myxomycetes. The paper presents the results of analysis of the myxomycete diversity on the basis of field collecting of the fruit bodies, as well as moist chamber cultures prepared with samples taken from the bark surface of living trees and vines, ground and aerial litter and coarse woody debris. Detailed comparative analysis using methods of multidimensional statistics allowed us to reveal some trends in their distribution on high-altitude gradient, and also in various biotopes and substrates. Species richness and abundance are lower in middle-mountainous forests in comparison with lowland forests. In the mountain tropical forests these indicators decrease with increasing altitude and have minimal values in cloud forests. The abundance and species richness of myxomycetes decrease with an increase in the moisture content of substrates. The species composition of the substrate assemblages of mountain forests differs from that in the lowland forests. Some species which are common in temperate and boreal zone are registered also in the mountainous tropical forests of Vietnam.

Key words: Amoebozoa, biodiversity, ecology, slime molds, Southeast Asia, species inventory, tropical forests

Introduction

Synecological studies have successful outcome for only limited groups of protists that can be

detected in nature (or isolated in laboratory) using standard methods and can be determined up to species level without serious efforts. This permits the use of large data sets in comparative biogeographical

analyses. One such group is the myxomycetes or myxogastrids (Myxomycetes = Myxogastria).

The myxomycetes are a monophyletic group of terrestrial amoeboid fungus-like protists (Cavalier-Smith, 2013; Fiore-Donno et al., 2013; Kretzschmar et al., 2016) that produce aerial spore-bearing structures (sporocarps) and are often abundant in terrestrial ecosystems. In ecological terms they are phagotrophic bacterivores, helping to maintain the balance that exists in nature between bacterial and fungal decay (Madelin, 1984; Novozhilov et al., 2017b). Tiunov et al. (2015) suggested that a significant difference in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values shows that prey types and/or basal food sources may differ among different species of myxomycetes.

The vast majority of myxomycetes are endosporeous, which means that spores are produced inside the fruiting bodies. Approximately 1000 morphospecies of endosporeous myxomycetes have been described Lado (2005–2018), and these have been placed in five different taxonomic orders (Echinosteliida, Liceida, Physarida, Stemonitida and Trichiida). The Ceratiomyxida contains exosporeous species and forms a single clade separate from the sister clade that contains the other myxomycetes (Schnittler et al., 2012; Lado and Eliasson, 2017).

Only a few systematic species inventories are available for the tropical forests of Southeast Asia. The countries studied most extensively seem to be Thailand (Reinolds and Alexopoulos, 1971; Tran et al., 2008; Ko Ko et al., 2011) and the Philippines (Dagamac et al., 2017). A considerable number of inventories is as well available for tropical forests in Singapore (Rosing et al., 2011), Myanmar (Ko Ko et al., 2013), Cambodia (Ko Ko et al., 2015) and Laos (Ko Ko et al., 2012).

Up to date, only 57 species had been recorded from Vietnam (Van Hooff, 2009; Novozhilov and Mitchell, 2014; Novozhilov et al., 2014; Tran et al., 2014; Novozhilov and Stephenson, 2015; Novozhilov et al., 2017a).

The primary objective of the research was to obtain quantitative data about the distribution and ecology of different substrate assemblages of myxomycetes of various habitats of specially protected forests in Vietnam. We tried to find differences of species composition depending on altitudinal zonation (monsoon tropical lowland forests versus middle mountain and high mountain forests) and different substrates (bark, ground litter, air litter and decayed wood).

Material and methods

Systematic studies of species diversity, distribution patterns, substrate development and ecology of myxomycetes in Vietnam have been carried out since 2010 on the basis of the Joint Russian-Vietnamese Tropical Research and Technology Center (Novozhilov et al., 2017a).

We thus divided the survey effort, targeting different major vegetation types in three phases: (1) lowland monsoon semi-deciduous tropical forests (LF), (2) mountain tropical forests (MF) and (3) dry dipterocarp forests (DF).

In this paper we report the results of the first phase (Đông Nai Biosphere Reserve including Nam Cát Tiên National Park and Đông Nai Culture and Nature Reserve) with lowland monsoon forests (group A). The second part of the survey includes data from middle mountain forests (MM) and high mountain forests (HM) of Bidup-Núi Bà National Park and adjacent mountain regions of Chư Yang Sin National Park (Central Vietnam). In the middle mountain vegetation belt (800–1600 m) we studied four habitat groups (Kuznetsov et al., 2006): the mountain polydominant tropical forest with Fagaceae, Magnoliaceae, Theaceae, Podocarpaceae (group D); the mountain polydominant tropical forest with *Pinus krempfii*, *P. dalatensis*, *Fokienia hodginsi*, Elaeocarpaceae, Magnoliaceae, Theaceae, Podocarpaceae (group E); mountain opened coniferous forest with *Pinus kesiya* (group F). In the high mountain forest belt (1600–1800 m) we studied the high mountain evergreen mossy cloudy broad-leaved forest with Elaeocarpaceae, Ericaceae, Fagaceae, Guttiferaceae, Lauraceae, Magnoliaceae, Myrtaceae, Theaceae (group G). All localities with high degree of human disturbance (gardens and tree plantations) form the group X. All microhabitats suitable for myxomycete growth were subjected to a careful examination. Common and easily recognizable species were sometimes only recorded instead of being collected, whereas rare and not easily recognizable species were always preserved as herbarium specimens. The genus *Ceratiomyxa* was as well included in this study due to its ecological equivalence to the true myxomycetes. We defined all sporocarps which shared the same substrate and clustered together (thus likely to have developed from one plasmodium) as one colony. Mature sporocarps were mounted in small boxes and dried thoroughly using silica gel. Myxomycete taxa were

determined according to morphological characters of the fructifications, using standard monographs of the group (Martin and Alexopoulos, 1969) and various original descriptions from the literature (Poulain et al., 2011) applying a morphospecies concept. Nomenclature follows Lado (2005–2018). Voucher specimens are deposited in the Komarov Botanical Institute (LE).

During our quantitative survey, a total of 2548 substrate samples were collected for moist chamber cultures. These included bark from living trees and lianas (763 samples), ground plant litter (1083 samples), aerial litter attached to or trapped in the branches of living trees, lianas or giant grasses litter of grasses (404 samples), coarse woody debris (269), and the weathered dung (28) of herbivorous animals, such as cow and horse. Dung of herbivorous animals was encountered only in dry dipterocarp coast forest in Bình Châu – Phước Bửu Nature Reserve. Moist chamber cultures were prepared in accordance to M. Härkönen (Härkönen and Ukkola, 2000). All cultures consisted of moist filter paper and substrate sample in Petri dishes (9 cm diam.) and were incubated under ambient light condition and at room temperature (20–24°C) for up to 90 days and examined for the presence of myxomycetes on six occasions (days 2–4, 6–8, 11–14, 20–22, 40–44 and 85–90). A record is defined herein as one or more fruiting bodies of a species that developed from a moist chamber culture. All moist chamber cultures were prepared within 2–4 months after returning from the field survey.

To estimate the extent to which the survey was exhaustive, individual-based species accumulation curves (SAC) were constructed using the program EstimateS version 9.0 (Colwell, 2014) which calculates the expected richness function “Mao Tau” (Gotelli and Colwell, 2011). The proportion of the number of recorded species on the number of expected species according to the Chao1 estimator ($S*100/Chao1$) was used as an estimate for the completeness of a local species inventory. Diversity between the habitats (lowland versus highland) and substrates was compared using the classical richness indices of Fisher’s alpha, the Shannon index (considers richness and evenness) and Simpson index. Both diversity indices and distribution models were calculated in the ‘vegan’ package of R, using the functions *renyi* and *radfit*, respectively. Community composition between elevation was examined using (1) non-metric multidimensional scaling (NMDS) based on Bray Curtis distances

and (2) the statistical test PERMANOVA based on 999 permutations using the functions metaMDS and *adonis* of R, respectively. Indicator species analysis was performed with multipatt function from *indicspecies* (Cáceres and Legendre, 2009) package for R (R Core Team, 2017). For an estimation of species abundance, the ACOR scale (Stephenson et al., 1993) was adapted. It is based on the proportion of a species on the total number of records: R – rare (<0.5% for this survey), O – occasional (0.5–1.5%), C – common (1.5–3%), A – abundant (> 3%). Graphs were created with SigmaPlot 10.0.

Results and discussion

To the present time in 13 specially protected natural areas (SPAs) of Vietnam we registered a total of 2210 records coming from 789 field collections and 1421 collections obtained from 2547 moist chamber cultures prepared with samples taken from the bark surface of living trees and vines, ground and aerial litter, coarse woody debris and weathered dung of herbivorous animals. Determinations resulted in 159 taxa (155 morphospecies and four varieties) from 32 genera and 12 families (Table 1). We report 69 new records of myxomycete taxa for Vietnam and four of which are considered to be species new to science.

In this paper we analysed only part of this data relating to the lowland monsoon tropical forest (LF) of Nam Cát Tiên National Park (CT) and mountain forests (MF) of Bidup-Núi Bà National Park (BI) and Chư Yang Sin National Park (CY). In LF we registered 1108 records representing 107 taxa (104 morphospecies and three varieties) from 27 genera and 10 families (Novozhilov et al., 2017a), whereas in MF 496 records representing 84 taxa from 26 genera and 10 families.

The sampling effort (Fig. 1, A) was probably sufficient to recover all of the most common species in the whole studied area (136 taxa from 1604 records, 84% complete according to the final figure of the Chao1 estimator = 162 ± 12) as well as for LF (107 taxa from 1108 records, 86%, Chao1 = 125 ± 9) and MF (84 taxa of 496 records, 89%, Chao1 = 105 ± 11).

MYXOMYCETE DIVERSITY ACROSS ELEVATION GRADIENT

Despite the high number of 136 species recorded, only 26 taxa were found to be widely distributed

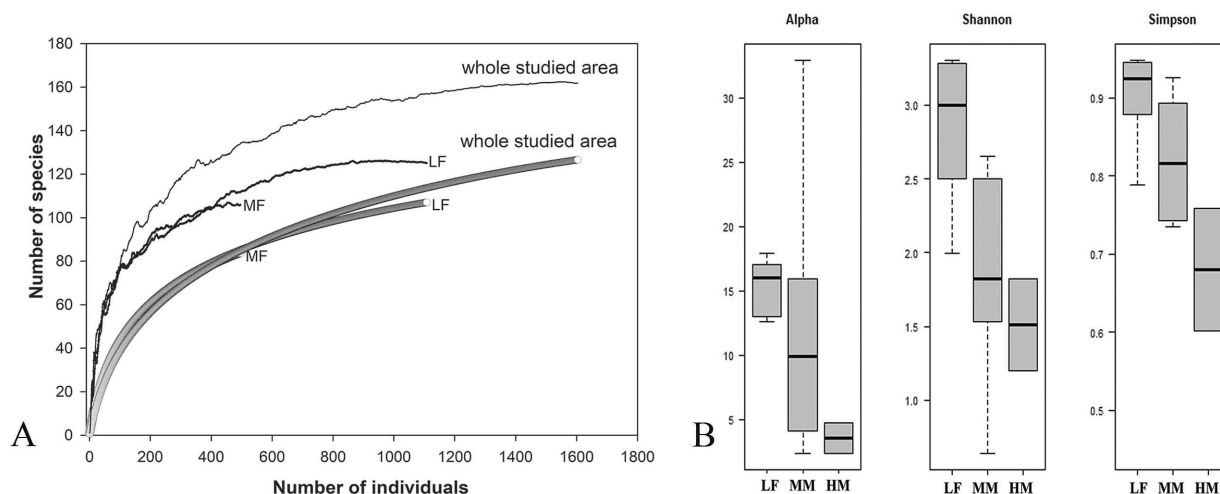


Fig. 1. A – Individual-based species accumulation curves (thick lines) and the Chao 1 (mean) estimator (thin jagged lines) of expected morphospecies richness for the whole studied area, the lowland monsoon forests (LF) and mountain forests (MF); B – box plot showing the comparison of three different diversity indices (Alpha = Fisher's alpha; Shannon = Shannon's H index and Simpson's index) in relations to vegetation types. Data from four study areas were pooled according to elevation (lowland versus mountain regions). *Abbreviations* for the habitat group are the same as those used in the text.

in the study area (present in 10 or more of the 154 studied localities).

Myxomycete diversity in terms of indexes of diversity (Fisher, H' , Simpson), percentage of positive cultures, the mean number of records per culture decreased from lowland forests to middle mountain forests and high mountain forests (Fig. 1, B).

At present we do not know the chief cause of this difference - poor sporulation activity in mountain regions, real low species richness or a deficiency of data. More research is needed for the final conclusion. According to the ACOR scale, 57% of all taxa in the lowland monsoon forests were rare, 24% were occasional, 11% were common and 8% were abundant. In the mountain forests 50% only

Table 1. Summary data for all myxomycete records, and these observed in the field and in moist chamber cultures (abbreviated as 'MC') for the 13 studied protected natural areas of Vietnam.

Reserve	BA	BC	BG	BI	BL	CT	CM	CY	KC	KK	KP	XS	YD
Rec	40	162	185	445	54	1108	20	51	17	26	32	50	19
Sp	17	40	57	75	23	107	9	30	13	14	14	27	12
Field collections													
Rec	1	0	119	206	13	347	0	17	17	26	26	16	0
Sp	1	0	41	54	13	60	0	13	13	14	11	15	0
Moist chamber cultures													
Number of cultures	40	273	211	668	86	954	69	105	NO	NO	61	50	30
Rec	39	162	66	239	41	761	20	34	0	0	6	34	19
Sp	17	40	26	34	16	77	9	17	0	0	4	15	12

Notes. Rec = number of specimens of myxomycetes identified to species level; Sp = number of morphospecies; BA = Ba Vì National Park; BC = Bình Châu - Phước Bửu Nature Reserve; BG = Bù Gia Mập National Park; BI = Bidup-Núi Bà National Park; BL = Lộc Bắc forestry; CT = Đồng Nai Biosphere Reserve (including Nam Cát Tiên National Park and Đồng Nai Culture and Nature Reserve), Đồng Nai Biosphere Reserve; CM = Chư Mom Ray National Park; CY = Chư Yang Sin National Park; KC = Kon Chư Răng Nature Reserve; KK = Kon Ka Kinh National Park; KP = Kon Plông Protected Forest (Thạch Nham); XS = Xuân Sơn National Park; YD = Yok Đôn National Park.

were rare, 36% were occasional, 6% were common and only 8% were abundant.

The five most abundant species in the lowland monsoon forests were *Arcyria cinerea* (83 records), *Perichaena chrysosperma* (68), *Cribraria microcarpa* (63), *Didymium floccosum* (54), *Diderma effusum* (50), *Cribraria violacea* (49), *Clastoderma debaryanum* (47), *Perichaena depressa* (37), *Lamproderma scintillans* (34). In the mountain forests, the list was headed by *Cribraria confusa* (61), *C. microcarpa* (47), *Physarum viride* (45), *Cribraria minutissima* (39), *A. cinerea* (33), *Comatracha spinisporum* (20), and *Clastoderma debaryanum* (15).

The most significant differences in the complexes of myxomycetes of lowland and mountain forests are revealed at the level of indicator species.

Results of the indicator species analysis showed that in the lowland monsoon forests the indicator species found on litter and bark were *Cribraria violacea* (indicator value = 0.617, $p = 0.007$), *Didymium floccosum* (indicator value = 0.556, $p = 0.027$), *Diderma effusum* (indicator value = 0.556, $p = 0.027$), *Perichaena chrysosperma* (indicator value = 0.553, $p = 0.031$), *P. depressa* (indicator value = 0.519, $p = 0.039$), *Lamproderma scintillans* (indicator value = 0.463, $p = 0.046$) whereas in the mountain forests the indicator species are *Cribraria confusa* (indicator value = 0.828, $p = 0.001$), *Stemonitis fusca* (indicator value = 0.813, $p = 0.003$), and *Comatracha spinispora* (indicator value = 0.682, $p = 0.007$).

Non-metric multidimensional scaling ordinations displayed that species composition of the lowland monsoon forests and middle mountain forest has more shared species than the high mountain forest whose dispersion ellipses clearly did not show clear overlap (Fig. 2, A). This differences among species composition of the three elevational zonation was and significantly different ($R^2 = 0.162$, $P = 0.008$, Stress = 0.196) from the PERMANOVA analysis. In terms of the different vegetation groups, the myxomycete assemblages also showed significant differences ($R^2 = 0.37$, $P = 0.001$, Stress = 0.196). The dispersion ellipses within mountain forests characterized of having opened coniferous forest with *Pinus kesiya* (group F) and the high mountain evergreen mossy cloudy broad-leaved forest (group G) form a separate cluster (Fig. 2, B) from other myxomycete assemblages of mountain vegetation. Myxomycetes of the middle mountain polydominant forest (group D) is different from the polydominant forest with dominance of

Podocarpaceae, Magnoliaceae, Myrtaceae, Calophyllaceae, Elaeocarpaceae, *Pinus krempfii* and *P. dalatensis* (group E) and have similarity with myxomycete diversity of the lowland forest (group A). The dispersion ellipses of the group A overlaps with the myxomycete assemblages of the habitat D, F and X (Fig. 2, B). Looking at species diversity, we estimate that 33% of all species found in natural forests occur as well commonly in plantations (group X).

SUBSTRATE-SPECIES RELATIONSHIPS

Regarding the major substrate types studied, species richness and diversity in the lowland and mountain forests was higher for aerial litter than for wood and bark, with ground litter housing the most diverse myxomycete assemblage. Interestingly, in tropical rain forests, aerial litter is often richer in species than ground litter (Schnittler et al., 2002; Stephenson et al., 2004a), whereas in monsoon tropical forests with a pronounced dry season, it seems to be the opposite. Wood-inhabiting (lignicolous) species seem to be more specialized than other myxomycete assemblages in the lowland monsoon forest. The mean values for similarity indices (records from the respective substrate type were compared with those from the other substrate types) support this statement: wood Ccs = 0.39 ± 0.18 ; ground litter Ccs = 0.44 ± 0.25 ; bark Ccs = 0.56 ± 0.26 ; aerial litter Ccs = 0.65 ± 0.19 (Novozhilov et al., 2017). Litter-inhabiting myxomycetes appear to be less specialized, although several fairly common taxa with a preference for litter can be listed: *Arcyria margino-undulata*, *Diachea leucopodia*, *Comatracha spinispora* and *Physarum echinosporum*. Typical species inhabiting aerial litter are *Cribraria microcarpa* and *Perichaena dictyonema*. As expected, the similarity between the myxomycete assemblages associated with ground litter (l) and aerial litter (alit) was high (Ccs = 0.83), apparently since both types of substrates contain many small dead twigs of lianas. The most abundant corticolous species exclusively found on bark were *Macbrideola scintillans*, *Licea operculata* and *Paradiacheopsis rigida*. Surprisingly, *Echinostelium minutum*, one of the most common corticolous species, may switch to ground litter in the tropical monsoon forest (13 of 27 records) occupying the coarse fraction of the ground litter.

Apparently, the distribution of myxomycetes inhabiting forests in southern Vietnam may be

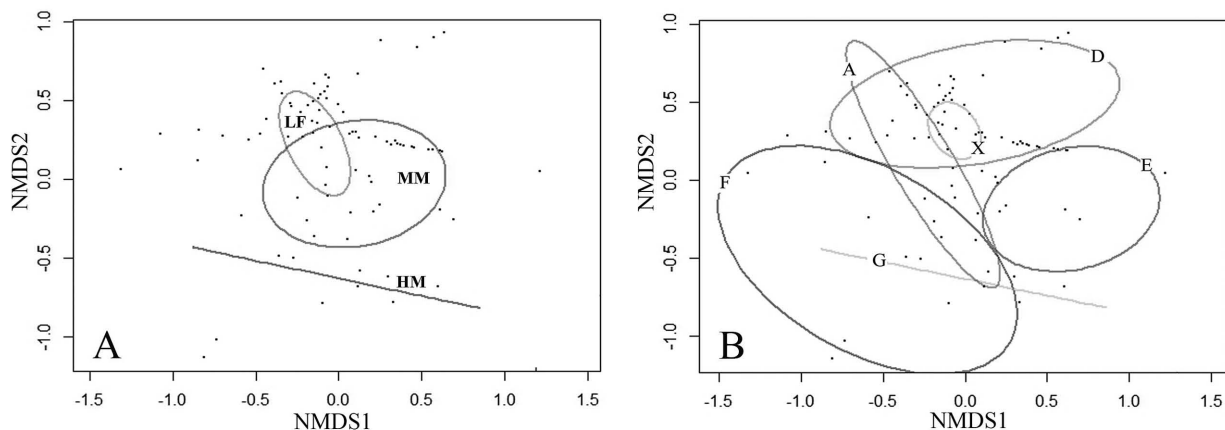


Fig. 2. Non-metric multidimensional scaling (NMDS) of species occurrences for the four surveys based on altitudinal zonation (A) and habitat groups (B). Black dots represent the position of myxomycete species in the ordination space. Ellipses denote dispersion based on standard deviation of point scores. Abbreviations for the altitudinal vegetation zonation and habitats are the same as those used in the text.

limited more by local vegetation, substrate availability, microclimate and soil types. We found several trends in distribution of myxomycetes in tropical forests of Vietnam. First, myxomycete species richness and abundance appear to be lower in the high mountain forests when compared to lowland tropical forests. Second, both abundance and richness of myxomycetes decrease with increasing moisture. Third, some microhabitats with no equivalents in temperate regions support distinct assemblages of myxomycetes. Compared with mountain forests, species assemblages of lowland monsoon forests are clearly different, and even common species of the mountain forests are replaced by others of the respective habitat in the lowland forests. Thus on bark of trees *Cribraria confusa* (the most common mountain species) is replaced by *C. violacea*, on ground litter *Comatricha spinispora* by *Diderma effusum* and *Lamproderma scintilans*. Interestingly in the tropical mountain forests of Vietnam several myxomycete taxa *Barbeyella minutissima*, *Echinostelium brooksii*, *E. colliculosum*, *Lamproderma columbinum*, *Licea kleistobolus*, *Lindbladia tubulina*, *Paradiacheopsis rigida* and *Trichia persimilis* were recorded that are known to be common in coniferous forests in temperate zones.

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