

Biogeographical assessment of myxomycete assemblages from Neotropical and Asian Palaeotropical forests

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ABSTRACT

Aim Lowland/highland and Neotropical/Asian Palaeotropical assemblages of myxomycetes were compared to test the null hypothesis that neither species diversity nor species composition differs between the two ecoregions. This can be expected if myxomycetes behave as ubiquists and are capable of unlimited long distance dispersal.

Location Four pairs (lowland/highland) of comprehensive regional surveys encompassing *c*. 7500 specimens were compared; these represented Neotropical (Yasuni/Maquipucuna in Ecuador; Guanacaste/Monteverde in Costa Rica) and Asian Palaeotropical forests (Cat Tien/Bi Dup Nui Ba in Vietnam; Chiang Mai in Thailand/South Luzon in the Philippines).

Methods Each survey was carried out in an area characterized by relatively homogenous vegetation consisting of natural or near-natural forests, and incorporated both field collecting and the use of moist chamber cultures, and all observed fructifications were recorded. Analyses of diversity (i.e. richness) and community composition were carried out with ESTIMATES and R.

Results Between 400 and 2500 records per survey were obtained. Species accumulation curves indicated moderate to nearly exhaustive completeness (70–94% of expected species richness recorded). Multivariate analyses suggest that geographical separation (Neotropic versus Palaeotropic) explained the observed differences in composition of myxomycete assemblages better than habitat differences (lowland versus highland forests).

Main Conclusion Both geographically restricted morphospecies and differences in myxomycete assemblages provide evidence that myxomycetes are not ubiquists but tend to follow the moderate endemicity hypothesis of protist biogeography.

Keywords

Amoebozoa, community ecology, dispersal barriers, endemicity, morphospecies, myxomycete, plasmodial slime moulds

INTRODUCTION

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Myxomycetes (plasmodial slime moulds) are one of the few protist groups that can be studied in the field, based on their above-ground macroscopic fructifications which release airborne spores (Schnittler *et al.*, 2012). Most of our knowledge about myxomycete assemblages has been derived from surveys which have recorded fructifications in the field or from moist chamber cultures (Stephenson *et al.*, 2008). In terms of biogeography, most studies have been carried out in temperate regions of the Northern Hemisphere, including alpine and subalpine mountains (Ronikier & Ronikier, 2009; Novozhilov *et al.*, 2013), tundra (Novozhilov *et al.*, 1999; Stephenson *et al.*, 2000), winter-cold deserts (Schnittler & Novozhilov, 2000; Schnittler, 2001; Novozhilov & Schnittler, 2008) and temperate grasslands (Rollins & Stephenson, 2013). Only recently have other parts of the world, such as tropical zones, warm deserts or the Patagonian steppe been

Journal of Biogeography

studied systematically (Estrada-Torres *et al.*, 2009; Wrigley de Basanta *et al.*, 2010; Lado *et al.*, 2013, 2014, 2016). At the level of morphologically recognizable taxa, many myx-omycete species display cross-continental distribution patterns (Stephenson *et al.*, 2008). Even remote islands such as the Galapagos Islands (Eliasson & Nannenga-Bremekamp, 1983), the Hawaiian archipelago (Eliasson, 1991), Macquarie Island (Stephenson *et al.*, 2007) or Bohol Island (Macabago *et al.*, 2017) do not seem to have endemic taxa present.

In contrast, numerous myxomycete species described within the last few decades (Schnittler & Mitchell, 2000) are known from only one or a few localities. Moreover, certain vegetation types contain species that are locally abundant but do not occur elsewhere. This is best documented for deserts; examples include Physarum pseudonotabile Novozh., Schnittler & Okun in Central Asia (Novozhilov & Schnittler, 2008; Novozhilov et al., 2013), or Perichaena calongei Lado, D. Wrigley & Estrada, Didymium infundibuliforme D. Wrigley, Lado & Estrada and Physarum atacamense D. Wrigley, Lado & Estrada in South America (Lado et al., 2009; Wrigley de Basanta et al., 2009, 2012; Araujo et al., 2015). Whether this is due to the lack of data from many areas of the world or due to some morphologically recognizable myxomycete species occurring with a limited distribution is a question being debated. In spite of their capability for long distance dispersal via spores (Kamono et al., 2009), it seems that in keeping with other eukaryotic protists such as testate amoebae, ciliates and diatoms (Foissner, 2006, 2008), myxomycetes may support the moderate endemicity hypothesis (Foissner, 1999) for protist biogeography. This hypothesis recognizes that cosmopolitan species of protists may exist in nature but due to geographical barriers, about 30% of all species can show geographically restricted distributions.

Various studies have reported species of myxomycetes fruiting predominantly in specific vegetation types (Schnittler & Stephenson, 2000), on particular substrates (Wrigley de Basanta et al., 2008; Tucker et al., 2011), or during certain seasons (Rojas & Stephenson, 2007; Dagamac et al., 2012). The unresolved question is whether such differences are entirely the result of microhabitat preferences (wherever suitable substrata occur under suitable microclimatic conditions, the respective species will fruit), as suggested for Barbeyella minutissima Meyl. (Schnittler et al., 2000). If microhabitat suitability represents the only factor determining occurrence, effective long-distance dispersal or persistent populations of amoebae must be assumed. Indeed, 18S rRNA gene sequences of the commonly highland fruiting nivicolous genus Meriderma were already detected in lowland regions, indicating persistence (presumably of amoebae) where this taxon never fruits (Fiore-Donno et al., 2016). Furthermore, another explanation is to assume the existence of barriers to distribution, at least between continents (Estrada-Torres et al., 2013; Aguilar et al., 2014). Long-distance dispersal has been reported for myxomycetes (Kamono et al., 2009), and the patchy occurrence of nivicolous myxomycetes in mountain ranges of the Northern and Southern Hemispheres corroborates this (Ronikier & Lado, 2015). Thus, transcontinental dispersal events may happen, but it is unknown if the frequency of gene flow mediated by spore dispersal is sufficient to prevent allopatric speciation from occurring between transcontinental populations. As has been shown for the much better documented ferns and fern allies (usually possessing much larger spores), species may show transcontinental distribution patterns or may be restricted to one continent only (Karst *et al.*, 2005).

An adequate 'field laboratory' to address the question of myxomycetes distribution would be a major ecosystem that is stable for a long period of time and is globally distributed - in other words, tropical regions covered naturally by rain forests. For myxomycetes, many diversity assessments have been carried out in Neotropical forests. These range from country checklists (Brazil, Cavalcanti, 2010; Colombia, Rojas et al., 2012a; Costa Rica, Rojas et al., 2010; El Salvador, Rojas et al., 2013) to abundance-based diversity assessments of natural habitats (Lado et al., 2003; Rojas & Stephenson, 2012). About half of the c. 1000 known morphospecies of myxomycetes (Lado, 2005-2016) have been recorded from the Neotropics (Lado & Wrigley de Basanta, 2008). Our knowledge of myxomycete diversity of the Asian Palaeotropics is more limited, and c. 200 taxa are known. Nevertheless, several investigations have been carried out in lowland and montane vegetation types of Southeast Asia, including Thailand (Tran et al., 2008; KoKo et al., 2010), Singapore (Rosing et al., 2011), Laos (KoKo et al., 2012), Vietnam (Novozhilov & Mitchell, 2014; Novozhilov et al., 2014; Tran et al., 2014; Novozhilov & Stephenson, 2015) and the Philippines (Dagamac et al., 2015a,b, 2017).

This study compared myxomycete assemblages between Neotropical and Asian Palaeotropical forests with the objective of answering several questions: First, are there differences in species composition and/or species abundance between (1) different vegetation types within a particular region (tropical lowland versus highland forests) or (2) comparable vegetation types on different continents (Asian Palaeotropics: Thailand, Philippines and Vietnam versus Neotropics: Costa Rica and Ecuador)? Second, are there species apparently restricted to only one of the regions in question? Third, does a comparison of regional survey data provide evidence to support the 'moderate endemicity' hypothesis (Foissner, 2006) for eukaryotic protists?

MATERIALS AND METHODS

Compilation of regional datasets

A double-paired design (four Neotropical and four Asian Palaeotropical/four lowland and four highland areas, Fig. 1, Table 1) was chosen to identify differences in species composition and abundance associated with geography and/or elevation as a proxy for habitat type. Five criteria were applied to select the eight datasets used in this study. (1) The *area* for each survey should be relatively homogenous for a major



Figure 1 World map showing the eight areas surveyed for myxomycetes that were used in this study, the number of records found and the total number of species accounted on each survey. [Colour figure can be viewed at wileyonlinelibrary.com]

Table 1 Characteristics of the eight investigated areas in the Neotropical and Asian Palaeotropics; naming the investigated area,
literature references, elevation and geographical coordinates, the number of moist chamber cultures prepared and vegetation types,
applying by Holdridge et al. (1971) classification of tropical forests. Surveys are listed in the sequence Neotropical/Palaeotropical (N/P)
and lowland/highland (L/H) for each region.

Region	Reference	Elevation (m a.s.l.)	Location	Moist chamber cultures	Vegetation type
NL: Costa Rica, Guanacaste	Schnittler & Stephenson (2000)	10-300	08 [°] 47′–10 [°] 58′ N 82 [°] 49′–85 [°] 56′ W	476	Tropical dry forest (excluding volcano Cacao)
NL: Ecuador, Yasuni	Lado et al. (2017)	200-275	04 [°] 00′–04 [°] 04′ N 76 [°] 22′–76 [°] 25′ W	225	Tropical moist forest, Amazonian lowland forest
NH: Costa Rica, Monteverde	Rojas et al. (2010)	1000-1500	10 [°] 16′–10 [°] 19′ N 84 [°] 44′–84 [°] 48′ W	<i>c</i> . 700	Tropical montane wet forest
NH: Ecuador, Maquipucuna	Schnittler <i>et al.</i> (2002), Stephenson <i>et al.</i> (2004a)	1250-2720	03 [°] 15′–07 [°] 28′ N 78 [°] 34′–78 [°] 28′ W	475	Tropical montane wet forest
PL: Philippines, South Luzon	Dagamac et al. (2017, 2015b)	10–524	12°75′–14°10″N 120°54′–124°09′ E	1500	Tropical moist forest
PL: Vietnam, Cat Tien	Novozhilov et al. (2017)	72–247	11°16′–11°27′ N 107°03′–107°26′ E	954	Tropical moist forest
PH: Thailand, Chiang Mai	Dagamac, N.H.A., Unterseher, M. & Schnittler, M., unpublished data; Rojas <i>et al.</i> (2012b), KoKo <i>et al.</i> (2010);	900–2500	18 [°] 48′–20 [°] 10′ N 98 [°] 29′–99 [°] 72′ E	<i>c</i> . 1000	Tropical montane wet forest
PH: Vietnam, Bi Dup Nui Ba	Novozhilov, personal communication	1375–1747	12 [°] 07'–12 [°] 11' N 108 [°] 38'–108 [°] 42' E	922	Tropical montane wet forest

forest type. (2) The two *components* of a survey should include at least 100 records from the field collections plus 100 records obtained by the moist chamber culture technique, with all major substrata (bark, aerial and ground litter) roughly equally represented. (3) *Records* should include all fructifications observed in the field or in cultures, which may be determined on the spot or collected for later determination. This allowed abundance estimates to be compiled for all of the species present, but excluded many published studies which provided only pure species lists without abundance data. (4) The *exhaustiveness* of a survey should exceed 70% in order to recover the majority of species likely to occur in a particular region. In a strict sense, this could not be verified. As a proxy criterion, we checked if the Chao1 estimator for an individual-based accumulation curve (including all records from each survey) converged (standard deviation should not monotonously increase but decrease with increasing number of records) and if its final value indicated a completeness of at least 70% (ratio observed to expected species). (5) The *habitats* studied within a survey should include at least pockets of natural or near-natural forests, to reflect the natural species inventory to a significant degree.

Moist chamber cultures and specimen determination

Moist chamber cultures were prepared in 9 cm Petri dishes using standard procedures (e.g. Schnittler, 2001), incubated under ambient light at room temperature (c. 20-24 °C) for up to 90 days and checked regularly on at least five occasions. To maintain moisture, distilled water was added over the first 6 weeks of the incubation period. Mature fructifications were transferred to herbarium boxes, with one record defined as a colony of fructifications from a single taxon developing in one culture. Myxomycete taxa were determined according to morphological characters of the fructifications, using standard monographs of the group (e.g. Nannenga-Bremekamp, 1967, 1991; Martin & Alexopoulos, 1969; Farr, 1976; Neubert et al., 1995-2000; Lado & Pando, 1997; Poulain et al., 2011) and public repositories (Eumycetozoan Project at http://slimemold.uark.edu/; Discover Life at http://www.discoverlife.org). Nomenclature follows Lado (2005-2016). Voucher specimens are deposited in the herbarium of the University of Arkansas (UARK), the Botanical State Collection Munich (M), the herbarium of the University of Costa Rica at San Jose (USJ), the Real Jardín Botánico de Madrid, (MA-fungi), the University of Santo Tomas, Manila (USTH) and the Komarov Botanical Institute (LE).

Data analysis

Individual-based species accumulation curves were constructed for each study area using ESTIMATES 9.1 (Colwell, 2013, 100 randomizations). In accordance with Unterseher et al. (2008), first a non-parametric estimator was calculated using the 'default settings' of ESTIMATES (Chao1, Chao et al., 2005); second species accumulation curves were fitted with the hyperbolic function y = ax/(b + x), with the parameter *a* providing an estimate for species richness. Myxomycete abundance was classified according to the ACOR scale of Stephenson et al. (1993), based upon the proportion of a species to the total number of records for each survey: Rrare (< 0.5%), O-occasional (> 0.5-1.5%), C-common (> 1.5-3%), A-abundant (> 3%). Abundance-based datasets from each of the eight study areas (see Appendix S2 in Supporting Information) and environmental variables (geographical region and elevation, Table 1) were analysed in R (R Core Team, 2015). Diversity between the geographical regions (Neotropics versus Palaeotropics) and habitats (lowland versus highland) was compared using the classical richness indices of Fisher's alpha, the Shannon index (considers richness and evenness) and the first three numbers of Hill's diversity series (Hill, 1973; Morris et al., 2014); differences

were tested for significance by a Wilcoxon test. In addition, the most probable abundance distribution model was determined from rank-abundance plots (Whittaker, 1965) testing five models following Wilson (1991): Null (fits the broken stick model), Preemption (fits the geometric series or Motomura model), log-Normal, Zipf and Mandelbrot. Both diversity indices and distribution models were calculated in the 'vegan' package of R, using the functions *renyi* and *radfit*, respectively. Community composition between geography and elevation was examined using (1) clustering analysis and non-metric multidimensional scaling (NMDS) based on Bray Curtis distances and (2) the statistical test PERMANOVA based on 999 permutations using the functions *hclust*, *metaMDS* and *adonis* of R (see Appendix S3 for input files).

RESULTS

Basic data, sampling intensity and species composition

Altogether, the surveys from eight areas (Table 1, see Fig. S3 in Appendix S1) included a total of 7585 myxomycete records (2844 from Neotropical and 4741 from Asian Palaeotropical forests). A total of 239 taxa (species and varieties) were recorded. Neotropical forests were less diverse (150 taxa) than Asian Palaeotropical forests (196 taxa, see Appendix S2 for a collated list). This difference remained if the rarefied values (based on the lower number of 2844 records) from an analysis of the species accumulation curves were considered: 150.0 vs. 172.8 taxa.

On both continents, numerous taxa were represented by only one record (singleton) for the entire region (Neotropics: 40 taxa, 27% of all taxa; Palaeotropics: 43 taxa, 22%). The eight surveys were between 70% and 88% complete according to the Chao1 estimator, and between 76% and 94% according to a hyperbolic regression (Table 2, see Fig. S1 in Appendix S1). If the degree of exhaustiveness was estimated by a hyperbolic function y = ax/(b + x), the fit was better (R = 0.885, a = 97.3, P < 0.0001) than for the final values of the Chao1 estimator (R = 0.716, a = 94.3, P < 0.0001, Fig. 2). Even for the South Luzon survey that had the highest number of records, the survey was no more than 91% (Chao1) and 94% (hyperbolic regression) complete. With increasing sampling effort the number of singleton species declined (linear regression y = ax + b for a scatter plot of records per survey versus number of singleton species: R = 0.676, a = -0.0077, P = 0.0066).

According to the ACOR scale, 72% of all taxa in the four Neotropical surveys (pooled to a common species list, see Appendix S2 and Fig S2 in Appendix S1) were rare, 17% were occasional, 7% were common and 5% were abundant. In spite of being represented by 1.7 times more records, 80% of all taxa from the Asian Palaeotropical surveys were rare, 7% were occasional, 11% were common and only 3% were abundant. The five most abundant species in the Neotropical forest were *Didymium iridis* (211 records), *Didymium*

Table 2 Statistical analysis of individual-based species accumulation curves of myxomycetes for the eight regional surveys in the tropics (giving the area by name and classified as L = lowland, H = highland), showing numbers of records (Rec), species (Sp), rarified species (SpR), and values for numbers of species to expect according to the Chaol estimator (mean \pm SD) and a fit with a hyperbolic function y = ax/(b + x), with *a* as the estimator for the number of species to be expected. The per cent values denote the proportion of species found on the number of species expected.

C	Found			Expected: Chao1			Expected: Hyperbolic			
Area	Rec	Sp	SpR	Chao1	SD	%	а	SD	R	%
NL: Guanacaste	441	80	80.0	104.9	13.0	76.2	101.2	0.3	0.999	79.0
NL: Yasuni	924	92	75.8	126.5	19.3	72.8	103.2	0.2	0.996	89.2
NH: Monteverde	522	76	71.2	108.3	16.0	70.2	99.7	0.4	0.997	76.3
NH: Maquipucuna	957	85	66.1	105.8	10.9	80.3	97.7	0.3	0.992	87.0
PL: South Luzon	2045	80	57.1	86.0	4.7	93.0	85.6	0.1	0.994	93.5
PL: Cat Tien	1105	105	81.2	120.3	8.3	87.3	120.4	0.2	0.996	87.2
PH: Chiang Mai	1147	133	96.4	151.2	8.4	88.0	162.5	0.3	0.997	81.8
PH: Bi Dup Nui Ba	444	74	73.8	94.0	10.5	78.8	100.2	0.3	0.998	73.8



Figure 2 Relationship between the number of records and exhaustiveness of a survey (number of myxomycete species found as proportion of the number of species to expect) for eight tropical surveys according to the Chaol estimator \pm SD (a) and a hyperbolic regression (b). The values for eight regional surveys were in turn fitted with a hyperbolic function y = ax/(b + x), indicated as a solid line with 95% confidence intervals as dotted lines. This fit results in estimates of the maximum exhaustiveness for an infinite number of records of 94.2% (Chaol, R = 0.716) and 97.3% (hyperbolic regression, R = 0.885).

squamulosum (194), Physarum compressum (190), the dwarf form of Arcyria cinerea (172, described in Schnittler, 2000) and Hemitrichia calyculata (119). In the Asian Palaeotropical forests, the list was headed by Arcyria cinerea (933), Didymium squamulosum (194), Perichaena depressa (155), Cribraria microcarpa (149) and Diderma hemisphaericum (144).

Non-metric multidimensional scaling ordinations display contrasting signals of species turnover for geographical (Neotropical versus Asian Palaeotropical) and elevational (lowland versus highland) differences. Species composition of Neotropical forests differed significantly from that of Asian Palaeotropical forests ($R^2 = 0.278$, P = 0.088); dispersion ellipses of the two assemblages in NMDS did not overlap (Fig. 3a). Cluster analysis using Bray Curtis dissimilarity (Fig. 3c) confirmed this bipartition. In contrast, there is no significant difference between lowland and highland sample groups (Fig. 3b, $R^2 = 0.117$, P = 0.474).

Species abundance distribution and diversity

The rank-abundance plots tested for different abundance distribution models showed comparable results for Neotropical and Asian Palaeotropical forests. For datasets pooled for the two different geographical regions, log-Normal was the best fitting model; for the comparison of lowlands versus highlands the log-Normal model best fit for the former and Mandelbrot model provided a slightly better fit for the latter (Fig. 4). Boxplots for several estimators of species diversity (Fig. 5) were not always higher for the Palaeotropics (Fig. 5a), as would be expected from a comparison of species richness. The trend for elevational differences is clearer, since all five indices were higher for lowland than for highland forests (Fig. 5b). However, none of these differences was significant (comparison between lowland and highland areas, see Table S1 of Appendix S1, P > 0.05; between Neotropical and



Figure 3 Non-metric multidimensional scaling (NMDS) of species occurrences for the eight surveys based on (a) geographic location and (b) elevational location. Black dots represent the position of myxomycete species in the ordination space. Coloured circles and squares represent the regions/areas; coloured ellipses denote dispersion based on standard deviation of point scores. (c) Clustering analysis using Bray Curtis dissimilarity distance based on species composition (species and abundances). [Colour figure can be viewed at wileyonlinelibrary.com]

Asian Palaeotropical forests, P > 0.05). Similarly, species richness was not higher in lowland forests, since rarefied means were 73.5 \pm 11.2 for lowland and 76.9 \pm 13.4 for highland areas (rarefied figures based on the lowest number of 441 records for a survey, Table 2). This was caused by the very high taxon number for one highland survey (northern Thailand, 133 taxa, rarefied value 96.4).

DISCUSSION

Differences in species abundances and composition between the Neotropics and Asian Palaeotropics

In recent years, abundance-based myxomycete data from the Asian Palaeotropics have become available, allowing a comparison with Neotropical inventories. Almost all myxomycete surveys revealed a high proportion of rare taxa, often found only once in an area (e.g. Schnittler *et al.*, 2002). To compensate for the random component introduced by the rather high proportion of rare species (between 15% and 38% of all species in our surveys were represented by single records) we considered only surveys recording species abundances. Four pairs of large datasets were compiled to test the *prima facie* null hypothesis that neither diversity nor species composition differs between Neotropical and Asian Palaeotropical forests. Given that similar macroecological conditions exist between regions, this can be expected if there is efficient long-distance dispersal by spores.

For a regional survey, there was some degree of heterogeneity in targeted microhabitats and/or substrata. Even for large datasets, such as that from South Luzon, the number of species recorded was lower than the number of expected species. This was predicted to be the case even for infinitely large surveys, as indicated by final percentages of 92% (estimated via analysis of species accumulation curves based on the Chao1 estimator) and 97% (hyperbolic regression, Fig. 2) and a higher sampling effort seems to reduce the proportion of rare species for a survey. These results reflected the unavoidable degree of heterogeneity for surveys covering a larger area. Nevertheless, the species accumulation curves generated for the eight study areas suggest that the sampling effort was sufficient to recover most of the species that are realistically possible to recover.

Asian Palaeotropic forests seemed to be richer in species of myxomycetes than Neotropic forests (rarefied species numbers: 172.8 vs. 150.0). The presence of conifers (*Pinus* spp.) with acidic bark and wood in the mountains of Vietnam (Bi Dup Nui Ba) and Thailand (Chiang Mai) may contribute,



Figure 4 Rank abundance plots based on the abundance of species for the (a, b) geographical (Neotropics versus Palaeotropic) and (c, d) elevational (Lowland versus Highland) gradient fitted with five species distribution models. All records from region or elevation (four surveys each) were pooled. The model showing the best fit is highlighted by a thick line. [Colour figure can be viewed at wileyonlinelibrary.com]

since here several myxomycete taxa (Barbeyella minutissima Meyl., Echinostelium brooksii Whitney, E. colliculosum Whitney & Keller, Lamproderma columbinum (Pers.) Rostaf., Licea kleistobolus Martin, Lindbladia tubulina Fr., Paradiacheopsis rigida (Brândza) Nann.-Bremek., and Trichia persimilis Karst.) were recorded that are known to be common in coniferous forests in temperate zones. Neotropical highland regions investigated in this study lack conifers, but these do occur, together with some of the species of myxomycete mentioned above, on the summits of Mexican volcanoes (Lado & Wrigley de Basanta, 2008). In addition, northern Thailand (Chiang Mai) yielded the highest number of species (133), and this was the only dataset compiled from several researchers working independently. For this area, we cannot avoid the possibility that in a few cases a particular taxon was assigned to two different names, causing overestimation of species numbers. The dataset from northern Thailand also contained the highest proportion of rare species (69.2%); and the number of singleton species (33) was above average (23.5).

The higher species richness of Asian Palaeotropical forests was not reflected by all of the computed diversity indices, but all indices were consistently higher for lowland than for highland forests (Fig. 5b). These differences were not statistically significant (Wilcoxon test) but were in congruence with observations that myxomycete diversity in tropical forests decreases with increasing elevation (Schnittler & Stephenson, 2000; Stephenson *et al.*, 2004b; Rojas & Stephenson, 2008). In constantly wet highland forests, myxomycetes seemed to utilize aerial litter, which dries out faster, more often than ground microhabitats (Schnittler & Stephenson, 2000; Lado *et al.*, 2003, 2017). Therefore, the moisture regime, not elevation *per se* may be the driver of differences in the abundance of fruiting bodies (Rojas *et al.*, 2016).

Interestingly, when we consider species composition, a statistically significant difference was observed among myxomycete assemblages in relation to geography (Neotropics versus Palaeotropics) but not in relation to habitat type (lowland versus highland forests). As in fungal endophytes (Langenfeld *et al.*, 2013), soil protist assemblages (Foissner, 2007; Bates *et al.*, 2013), and marine ciliates (Stock *et al.*, 2013), geographical location best explains the differences in assemblage composition. A biogeographical study of myx-omycetes that focused only on tropical highland forests found a similar pattern: a cluster analysis separated myx-omycete assemblages recorded from Thailand from those of



Figure 5 Box plot showing the comparison of five different diversity indices (Alpha = Fisher's alpha; Shannon = Shannon's H index; N0 = species richness; N1 = exponent of Shannon diversity and N2 = inverse of Simpson) in relations to (a) geography and (b) elevation. Data from four study areas were pooled according to (a) geography (Neo- versus Palaeotropics) and (b) elevation (lowland versus highland regions).

the Americas (Rojas *et al.*, 2012b). Although elevation determined habitat availability (Rojas *et al.*, 2010; Dagamac *et al.*, 2014) and forest types (Novozhilov *et al.*, 2000; Rojas *et al.*, 2011), the high overlap of species composition between assemblages of lowland and highland areas showed that myxomycetes seem to find in both elevations suitable microhabitats for fruiting.

Are there myxomycetes restricted to the tropics?

Several species were found in a single survey or a pair of surveys only. Comatricha spinispora Novozh. & Mitchell (26 records), Diderma pseudostestaceum Novozh. & Mitchell (14), D. cattiense Novozh. & Mitchell (18) and Perichaena echinolophospora Novozh. & Stephenson (4) were found only in surveys conducted in Vietnam. Craterium paraguayense (Speg.) G. Lister (4) and Lamproderma muscorum (Lev.) Hagelst. (7) were reported exclusively from the Costa Rican highlands (Monteverde) dataset and Diachea silvaepluvialis Farr (6) was found exclusively in Ecuador (Yasuni). More species were found exclusively in either the Neotropical (35) or the Asian Palaeotropical region (68), of which 24 and 30 species, respectively, were singletons. For instance, Ceratiomyxa morchella Welden (45 records) and C. sphaerosperma Boedijn (24) were found only in the Neotropical region; Physarum echinosporum Lister (55) and Cribraria minutissima Schwein. (41) occurred exclusively in surveys from the Asian Palaeotropical region. However, at this point, we have to consider the low taxonomic resolution provided by a morphological-based approach. All studies that entered the 'biospecies' level via cultivation and compatibility experiments (Clark & Haskins, 2013) or via molecular markers (Feng & Schnittler, 2015) found that a given 'morphospecies' comprised several putative biospecies (defined as reproductively isolated units). A first local survey based on fructifications with a full barcoding component estimated the relationship between morphospecies and ribotypes, the latter indicating the existence of different biospecies, to be 1:2-10 (Feng & Schnittler, 2017). Therefore, a cosmopolitan morphospecies such as Arcyria cinerea (Bull.) Pers., is likely to consist of several biospecies (Clark et al., 2002) if studied by molecular methods, and therefore putative biospecies may be more restricted in distribution. This is not obvious when looking at distribution ranges of myxomycetes (see examples in Stephenson et al., 2008) since many morphospecies appear to have large or even cosmopolitan ranges. In other words, as in the case of pyrenomycetous fungi (Vasilyeva & Stephenson, 2014), we should expect at least some species to be restricted to certain regions of the world.

Morphological-based surveys support moderate endemicity for eukaryotic protist

Given the apparent rarity of fructifications for many myxomycetes (Stephenson, 2011), abundance data are important to identify cases of moderate endemicity. Ceratiomyxa morchella Welden (Neotropics) and Physarum echinosporum Lister (Asian Palaeotropics) may be good examples, both representing unmistakable morphospecies that were common only in one of the two regions. For this finding, we can assume that despite intense surveys in similar tropical environments, geographical barriers between continents have played a role in the apparent differences noted for species abundance and composition. We can also expect that geographical differences found in this study will become more evident if large datasets on molecular diversity become available for myxomycetes. In a related morphological-based approach, Estrada-Torres et al. (2013) considered numerous environmental factors and found that historical geography explained best the distribution of myxomycete assemblages in the Americas. Even if this study used presence/absence data only, they similarly noted that some species (e.g. Diderma tehuacanense Estrada, D. Wrigley & Lado and Perichaena stipitata Lado, Estrada & D.Wrigley) were found exclusively in one area.

In summary, biogeographic patterns of myxomycetes in the tropics provided evidence that species composition is different and this is due to at least some morphologically recognizable taxa that are indeed restricted to particular geographical areas, some appeared to be regionally or locally endemic, and thus we may expect moderate endemicity to be the rule rather than the exception.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Supplementary figures and tables.Appendix S2 Collated database of the study areas.Appendix S3 Input files used in R.

BIOSKETCH

Nikki Heherson A. Dagamac is broadly interested in biogeography and biodiversity of tropical myxomycetes. The group worked for a number of decades on developing a better understanding of the global distribution patterns, taxonomy and ecology of myxomycetes.

Author contributions: M.S. conceptualized and designed the present study; data from the Neotropical region were taken from surveys of M.S., Y.K.N., C.L., C.R. and S.L.S; data from the Palaeotropical region originated from field surveys of N.H.A.D., Y.K.N., T.E.D.C., M.U. and M.S; N.H.A.D. compiled all data from the eight surveys, assembled the initial species lists and collated the dataset; N.H.A.D., M.U. and M.S. performed the ecological analysis of the dataset and interpreted the results; N.H.A.D. and M.S. prepared the manuscript, which was approved by all authors and improved by Y.K.N., C.L. and C.R. S.L.S. did the English correction of the text.

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