# The myxomycetes of the La Selva Biological Station (Costa Rica)

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**Abstract:** A compilation of all species of myxomycetes recorded from the La Selva Biological Station was carried out with the objective of summarizing and then analysing the most complete dataset from a single locality in Costa Rica. These data indicated that 85 species have been recorded from La Selva between 1963 and 2012. This result arbitrarily makes La Selva the single “most diverse” locality in Costa Rica. Given that the site is among the most intensively studied tropical forests in the country, this is clearly a consequence of an unequal sampling effort across a much larger territory. In the dataset presented herein, the majority of species recorded were members of the dark-spored clade of myxomycetes and were associated with decaying wood and ground litter. As a result of the present study, five species not reported previously for Costa Rica were added to the list of myxomycetes for the country. Finally, a maximum entropy distribution model showed that the La Selva myxomycete dataset influenced the response of probabilities associated with low elevation forests of Costa Rica despite the fact that La Selva represents only 0.03% of the total area of the country. These results indicate that the dataset compiled herein represents an important contribution to our understanding of the overall distribution of lowland tropical myxomycetes.

**Zusammenfassung:** Eine Liste aller Myxomyceten-Arten, die von der Biologischen Station La Selva aufgezeichnet wurden, wurde ermittelt mit dem Ziel der Zusammenstellung und nachfolgenden Analyse der umfassendsten Datenmenge von einer einzigen Lokalität in Costa Rica. Diese Daten zeigten, dass 85 Arten von La Selva zwischen 1963 und 2012 registriert wurden. Das macht La Selva willkürlich zum alleinigen "höchst diversen" Ort in Costa Rica. Da dieser Ort zu den am intensivsten untersuchten tropischen Wäldern im Land gehört, ist dies eindeutig eine Folge ungleicher Sammelbemühungen in einem viel größeren Gebiet. In dem hier dargestellten Datenbestand gehörte der Großteil der Arten zum Clade der dunkelsporige Myxomyceten und war mit vermoderndem Holz und Streuresten assoziiert. Als Ergebnis der vorliegenden Studie wurden fünf Myxomyceten-Arten neu für Costa Rica erfasst. Schließlich zeigte ein Maximum Entropieverteilungs-Modell, das die La Selva Myxomyceten Datenmenge die Auftritts-Wahrscheinlichkeiten beeinflusst, die im Zusammenhang mit Tieflandwäldern von Costa Rica stehen, trotz der Tatsache, dass La Selva nur 0,03% der Gesamtfläche des Landes repräsentiert. Diese Ergebnisse zeigen, dass die hier zusammengestellte Datenmenge einen wichtigen Beitrag zum Verständnis der Gesamtverteilung der tropischen Tiefland-Myxomyceten liefert.

The myxomycetes (also called plasmodial slime molds or myxogastrids) are a group of amoeboid protists that occur in association with decaying plant material in most terrestrial ecosystems around the world (STEPHENSON 2003). In recent decades, particular research efforts have focused on various aspects related to the global distribution and biodiversity of the group (see STEPHENSON & al. 2008). Most of these comprehensive biogeographical analyses (e.g., ESTRADA-TORRES & al. 2013), although incredibly valuable, consider only large-scale global patterns, and there are few locality-based analyses of biodiversity. The lack of locality-based studies is largely due to the limited number of localities in the world with comprehensive high quality datasets available for this type of analysis.

The La Selva Biological Station (LSBS) is one exceptional locality for which an appropriate amount of data is available for such a locality-based study. Located in the northeastern Caribbean lowlands of Costa Rica, LSBS is comprised of a 1500 ha patch of mixed lowland wet forests (MCDADE & HARSTHORN 1994). A mecca for biological research in the Neotropics, LSBS has been the location of numerous myxomycete collections for more than 50 years. As one of the leading tropical research sites in the world, a very large amount of ecological information is available relating to a variety of organisms and biological systems present (e.g., WHITFIELD & al. 2007). In fact, according to the Organization for Tropical Studies web site (www.ots.ac.cr), the large amount of research carried out at LSBS has yielded more than 2655 scientific publications.

With the logistical support provided by the Organization for Tropical Studies, all three authors of this paper have collected information about myxomycetes at LSBS at different times over the past two decades. A variety of standard techniques were used for collecting myxomycete data (see STEPHENSON & STEMPEN 1994 for collecting protocols), and a number of different microhabitats were surveyed. The primary objective of the research effort described in this paper was to compile all of this available information into a single concise dataset for analysis. In addition to a presentation of the full dataset, short discussions will touch briefly on a few of the experiments from which these data were derived. The physical and temporal distribution of all collections, the variety of technical methods used, and the overall number of records compiled herein make this dataset valuable and unique in terms of tropical myxomycete research. This new LSBS dataset will allow meaningful investigations into the large amount of ecological data on myxomycetes that can be considered for this locality.

**Materials and methods**

The La Selva Biological Station (LSBS) is located in the Caribbean Lowlands of Costa Rica in the primarily agricultural county of Sarapiquí. Historical climatic data collected since the station opened in 1953 show an annual precipitation of approximately 4000 mm and a temperature range that falls between 19 and 31°C and is therefore classified as a lowland tropical wet forest (HOLDRIDGE & al. 1971). The research station itself is under the administration of the Organization for Tropical Studies (OTS) and hosts hundreds of students and researchers from all over the world every year. Both the University of Costa Rica and the University of Arkansas are member institutions of OTS and, as a result, there is a long-term link between the authors and LSBS.

A preliminary database of myxomycete records from La Selva was generated using historical information from the University of Costa Rica Herbarium (USJ) and the United States National Fungus Collection (BPI) in Beltsville, Maryland. This initial database was then updated to include the 719

records of specimens collected by the three authors on different occasions between 1994 and 2012. This produced a complete dataset consisting of 952 records.

The collections made by the authors include both specimens that had fruited in the field under natural conditions and specimens appearing in moist chamber cultures, whereas the initial database was composed of only field collected specimens. All field collections were obtained using the general opportunistic approach in the manner described by CANNON & SUTTON (2004), and all moist chamber cultures in which fruiting bodies appeared were prepared in the laboratory using field-collected dead plant material, as described by STEPHENSON & STEMPEN (1994). All collections obtained by the authors have been curated using the protocol of STEPHENSON & STEMPEN (1994) and deposited in either the Mycological Herbarium at the University of Arkansas (UARK) or the University of Costa Rica Herbarium (USJ). The studies used as a reference for the reporting of new records for Costa Rica were those of ROJAS & al. (2010) and ROJAS & CALVO (2014). Nomenclature follows the treatment of LADO (2005–2012). The genus *Ceratiomyxa*, although now recognized as a sister group to the myxomycetes (FIORE-DONNO & al. 2010), was included in this dataset due its historical inclusion within the myxomycetes.

Once the database was compiled and any inconsistencies corrected, basic species diversity analyses were carried out. For this evaluation, a general species accumulation curve was created and corrected using the formula $y=a*x/(b+x)$, where $a$ represents the maximum number of species for the studied locality within the context of the sampling effort and techniques used for the detection of the occurrences being considered, $b$ is a constant derived from the best fitting model applied to the original dataset and $x$ is the number of records used to construct the model.

Also, the number of records per year and primary substrate types on which they occurred were calculated in order to analyze the completeness of the surveys carried out at this locality.

Next, an analysis of the number of stalked vs non-stalked records was carried out. This analysis was carried out to evaluate, albeit briefly, the hypothesis that high moisture levels on substrate surfaces of myxomycete microhabitats in lowland tropical moist forests favor the formation of stalked fruiting bodies, as suggested by SCHNITTLER & STEPHENSOn (2000). In a similar manner, an analysis of the relative distribution of records within the five classical myxomycete taxonomic orders as well as the two main phylogenetic clades (dark-spored and bright-spored; FIORE-DONNO & al. 2005) was carried out. Although similar taxonomic evaluations have been carried out in the past that have examined the distribution of records with respect to the different taxonomic orders of myxomycetes, a more modern approach that also considers the major phylogenetic clades is not yet commonly used by researchers.

A more detailed analysis of ecological patterns was carried out on a subset of data consisting of 126 records for which functional trait information had been recorded. The objective of this analysis was to examine potential differences in the strategies used by different myxomycete species to produce the various fruiting structure morphologies found throughout the group. This subset of data was collected by the second author in 2007 following a protocol designed to compare functional characters in myxomycetes from both tropical dry and wet forests in Costa Rica. In this survey, lignicolous myxomycetes were collected in both old-growth (~50 yr) and late successional patches (~30 yr) of forest on a series of 30 logs, using the sampling protocol described by ROJAS & VALVERDE (2015). For sporangiate collections, some functional traits such as stipe volume, sporotheca diameter and spore diameter were recorded. In addition, a series of environmental parameters (e.g., log volume, pH, substrate moisture, substrate diameter, canopy openness and height above the ground) were measured or determined for each collection. These environmental and functional characteristics were then analyzed in relation to the type of forest (successional stage) where the records were obtained.

The same subset of data as described above was next combined with a similar subset of data collected by the first author in order to analyze the effect of forest age on the myxomycete communities at La Selva. Unlike the dataset above, which is composed entirely of records from field collections, this second subset was derived entirely from moist chamber cultures and contained 263 records. Substrates for culture (ground litter, aerial litter, small pieces of woody debris and the bark of living trees) were collected in 2011 with three replicates, within two old-growth sites (~40 yr) and two successional forest (~20 yr) sites and placed into moist chamber culture. The newly combined dataset contained a total of 360 records. Species abundance, richness and Shannon diversity (*H'*) (SHANNON & WEAVER 1963) were analyzed in relation to the type of forest (successional stage). To investigate the differ-

ences in the community composition between the two forests, coefficient of community (CC) and percentage similarity (PS) indices were calculated (MUELLER-DOMBOIS & ELLENBERG 1974, GAUCH 1982). The CC considers only the presence or absence of each species and is calculated with the formula, $CC = 2c/(a+b)$ where $a$ and $b$ are the total number of species in each community and $c$ is the number of species common between them. The values range from 0 (no species in common) to 1.0 (all species in common). The PS considers not only presence of each species but the relative abundance in the communities and is calculated with the formula, $PS = \Sigma min(a,b, \ldots x)$ where *min* is the lesser of the two relative abundances of species ($a,b, \ldots x$) in the communities. The values of PS range between 0 (no species in common) to 1.0 (all species in common and in equal relative abundances).

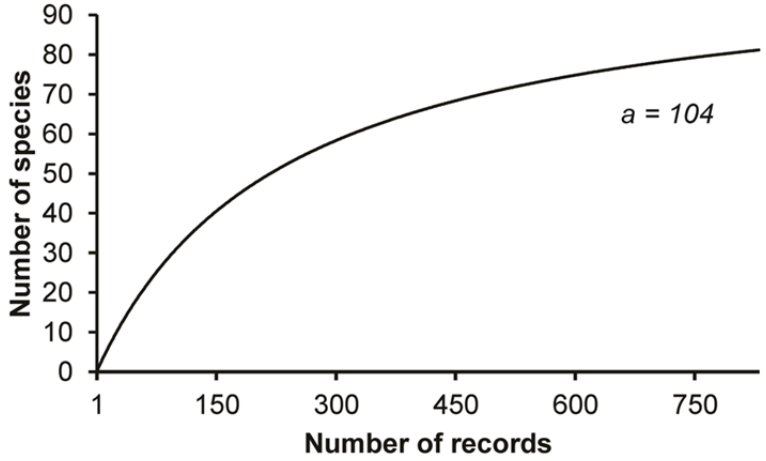


Fig. 1. Species accumulation curve constructed with the dataset of myxomycete records obtained during the period of 1963-2012 for the La Selva Biological Station. The parameter *a* represents the maximum number of species to be found at that locality using the same collecting effort and protocols.

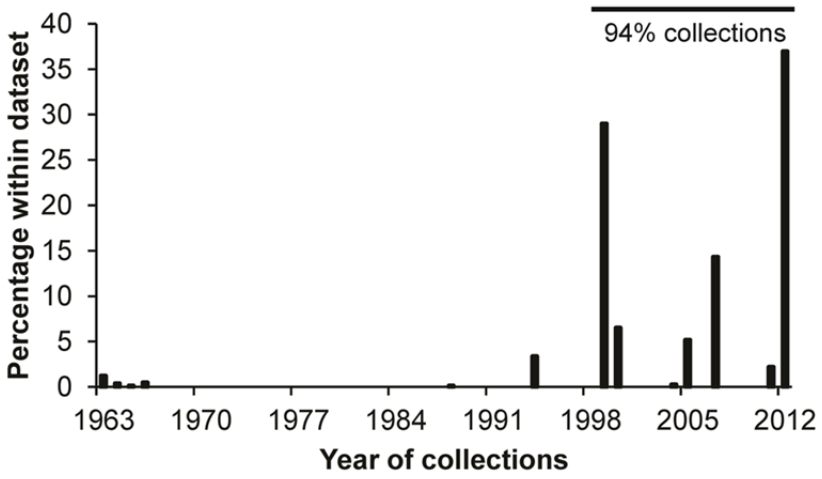


Fig. 2. Distribution of myxomycete records collected during the period of 1963-2012 at the La Selva Biological Station.

Finally, a niche-based analysis of potential myxomycete distribution in Costa Rica was carried out using a GIS approach to test the overall weight contributed by the LSBS dataset for the entire country. For this analysis, elevation, isothermality, annual temperature range, annual precipitation and the coefficient of precipitation variation for Costa Rica were obtained from WorldClim (www.worldclim.org) and used as biophysical variables to generate probability maps for the occurrence of myxomycetes in Costa Rica. These maps were generated by including and excluding the LSBS dataset separately in MaxEnt, version 3.3.3 (see PHILLIPS & al. [2006] for theoretical considera-

tions) and adjusted to the Holdridge life zones in ArcMap 10.1 using the CR05 and CRTM05 official datum and projection.

As the very last step, an annotated list of species for LSBS was generated. In the list, each species name is followed by information indicating the method used to obtain the record in question and the type of substrate from which it was collected. The method used to obtain the record was abbreviated as *FC* for field collections or *MC* for collections from moist chamber cultures. Substrate type was abbreviated as *AL* for aerial litter, *WB* for decaying wood and bark, *FI* for flowers and inflorescences, *GL* for ground litter and *PL* for living plants. An asterisk before the name indicates that the species represents a new record for Costa Rica.

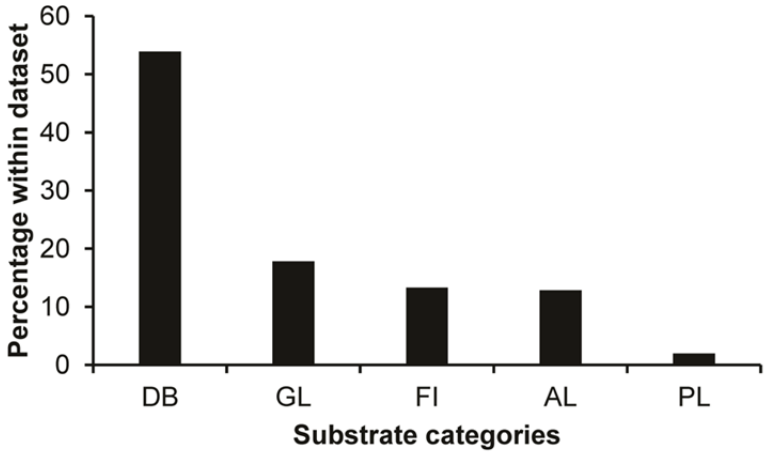


Fig. 3. Distribution of myxomycete records in the five most common substrate categories. Abbreviations are DB = decaying bark and wood, GL = ground litter, FI = flowers and inflorescences, AL = aerial litter, PL = living plants.

## Results

A total of 85 species have been recorded at the La Selva Biological Station in Costa Rica, according to the dataset compiled in the present study. One additional species, *Perichaena longipes*, was also recorded at LSBS, but because it was new to science and had not yet been described, it was not included here. The records of this species at LSBS have instead been included in the recent species description by WALKER & al. (2015). Sampling appeared to be nearly exhaustive according to the species accumulation curve, which estimated that approximately 104 species could be expected using the protocols and techniques used in the present study (Fig. 1). Five of the species on the list compiled for LSBS were not previously documented for Costa Rica, thereby increasing the total number of species for the country to 217.

When all of the records in the database were considered, approximately 74% represented stalked species, whereas only 26% are species that do not produce a stalk. The five most commonly encountered species, according to the dataset, were *Arcyria cinerea*, *Physarum didermoides*, *Physarum compressum*, *Didymium iridis* and *Hemitrichia calyculata*. These species represented 11.1, 4.8, 4.6, 4.5 and 3.8% of the total number of all records, respectively. Thirty four species with only one record (singletons) for the country were recorded. Some rarely encountered species at LSBS included *Tubifera casparyi*, *Trichia varia* and *Trichia botrytis*.

The majority of the records from LSBS were collected in the past 20 years (see Fig. 2), but other information to which the authors had access dated as far back as 1963. Dead bark and decaying wood, both on the forest floor, were the substrates upon which most specimens were recorded, followed by ground litter, flowers and inflorescences, aerial litter and living plants (Fig. 3).

With the subset of 126 records for which environmental and functional information was collected, some differences in the functional parameters were found to exist between the two forests of different successional stages within LSBS (Tab. 1). For instance, pH of the substrate and the mean height above the ground at which myxomycete fruiting bodies occurred were higher in old-growth patches in comparison with successional ones. Similarly, the number of individual fruiting bodies per fruiting for sporangiate forms was significantly higher for old-growth patches.

Tab. 1. Average and standard deviation (in parentheses) values for all environmental and functional parameters measured for a subdataset of myxomycetes collected at LSBS and used for ecological analysis in the present study. The results of the statistical hypothesis testing are also shown in the last column.

| Parameter | Old-growth | Successional | Statistical testing |
|---|---|---|---|
| *Environmental* | | | |
| Log volumen ($m^3$) | 7.9 (5.0) | 8.7 (8.0) | $t$ = 0.61, $d.f$ = 100, $P$ = 0.71 |
| pH (1-14 scale) | 6.1 (1.0) | 5.7 (1.2) | $t$ = -1.71, $d.f$ = 107, $P$ = 0.04* |
| Moisture (%) | 44.4 (9.1) | 43.0 (6.8) | $t$ = 0.93, $d.f$ = 113, $P$ = 0.17 |
| Substrate diameter (cm) | 28.0 (13.4) | 31.3 (21.0) | $t$ = 0.95, $d.f$ = 91, $P$ = 0.82 |
| Canopy openness (%) | 54.2 (14.4) | 60.0 (15.4) | $t$ = 2.28, $d.f$ = 113, $P$ = 0.98 |
| Height above ground (cm) | 26.7 (30.4) | 18.3 (18.9) | $t$ = -1.82, $d.f$ = 105, $P$ = 0.03* |
| *Functional* | | | |
| Stipe volume ($mm^3$) | 5.8 (6.6) | 3.0 (3.3) | $t$ = 1.69, $d.f$ = 33, $P$ = 0.05 |
| Spore diameter (mm) | 7.1 (1.2) | 6.8 (1.1) | $t$ = 2.03, $d.f$ = 21, $P$ = 0.97 |
| Sporotheca diameter (mm) | 1.0 (0.8) | 1.9 (1.8) | $t$ = 0.83, $d.f$ = 35, $P$ = 0.20 |
| Number of fruiting bodies/fruiting | 52.4 (98.3) | 26 (56.0) | $t$ = -1.81, $d.f$ = 100, $P$ = 0.03* |

* Results were statistically significant using an alpha value of 0.05.

Tab. 2. Myxomycete community composition in old-growth and successional forests at LSBS. The results of the statistical hypothesis testing are also shown in the last column.

| Parameter | Old-growth | Successional | Total | Statistical testing |
|---|---|---|---|---|
| Fruiting body abundance | 171 | 189 | 189 | $X^2$ = 0.09, $d.f$ = 1, $P$ = 0.34 |
| Species richness | 41 | 37 | 53 | $X^2$ = 7.55, $d.f$ = 1, $P$ = 0.006* |
| Shannon diversity ($H'$) | 1.40 | 1.29 | 1.42 | $X^2$ = 0.01, $d.f$ = 1, $P$ = 0.91 |

* Results were statistically significant using an alpha value of 0.05.

The distribution of myxomycetes from LSBS across the five classical taxonomic orders showed that most species and records belonged to the order *Physarales*. Interestingly, the second and third most common orders by number of recorded species were the *Stemonitales* and *Trichiales*, whereas the same ordination performed using the number of records of each species showed that *Trichiales* and *Liceales* were more commonly recorded. Therefore, the dark-spored clade of myxomycetes (containing the

orders *Physarales* and *Stemonitales*) dominated the assemblage of species at LSBS, both in terms of species and records.

The subset of data used to analyze myxomycete communities between old-growth and successional forests at LSBS contained 360 records representing 53 species. Richness, but not abundance, was significantly different between the two forest types (Tab. 2). Total Shannon diversity was 1.42, with similar values in the old-growth and successional forests individually with values of 1.40 and 1.29, respectively. However, the composition of the communities was quite different. Of the 53 species considered in this analysis, only 25 of these were found in both forest types; the CC was calculated to be 0.64 and the PS was 0.56. As such, it appears that there may be a shift in the community composition of myxomycetes over time during forest succession, but overall only richness appears to be affected significantly.

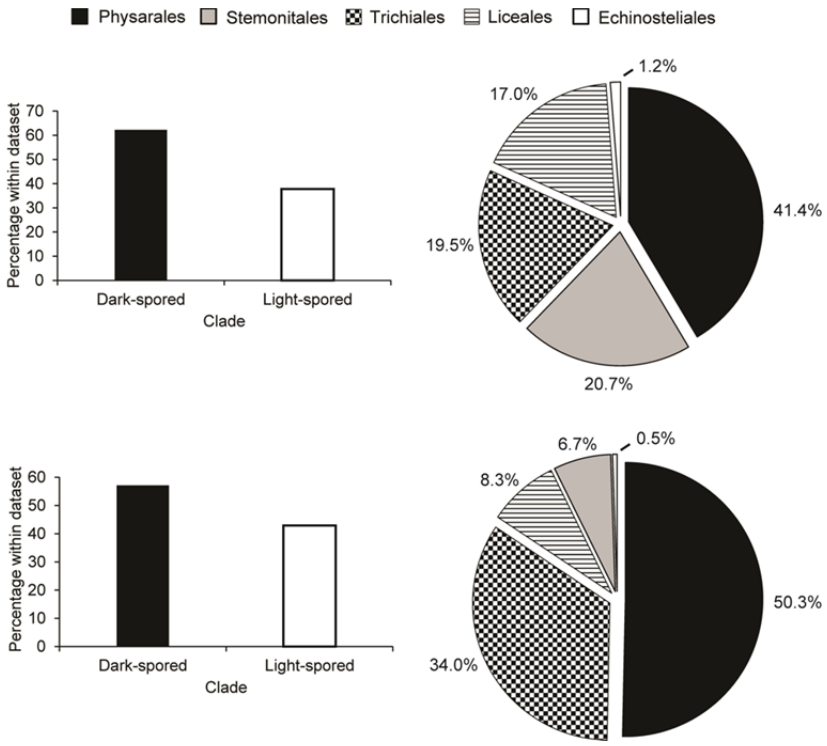


Fig. 4. Distribution of myxomycete species (top) and records (bottom) according to phylogenetic clade (left) and taxonomic orders (right). The pattern code for the orders provided on top of the figure applies only to the pie charts.

The predictive model for the distribution of myxomycetes showed that for Costa Rica as a whole, the LSBS dataset did not provide a sufficiently strong influence to be used in a large scale distribution model (Fig. 5). However, due to the smaller number of sampling sites for myxomycete distribution located at lower elevations in Costa Rica, information from LSBS (a lower elevation Caribbean site) represented an important dataset that modified the response of the predictive model in areas with similar elevations. In particular, the northwestern section of Costa Rica (the Guanacaste Province) and the lower elevation areas along both slopes of the mountain ranges dividing the country were the most affected by the inclusion of the LSBS dataset in the model.

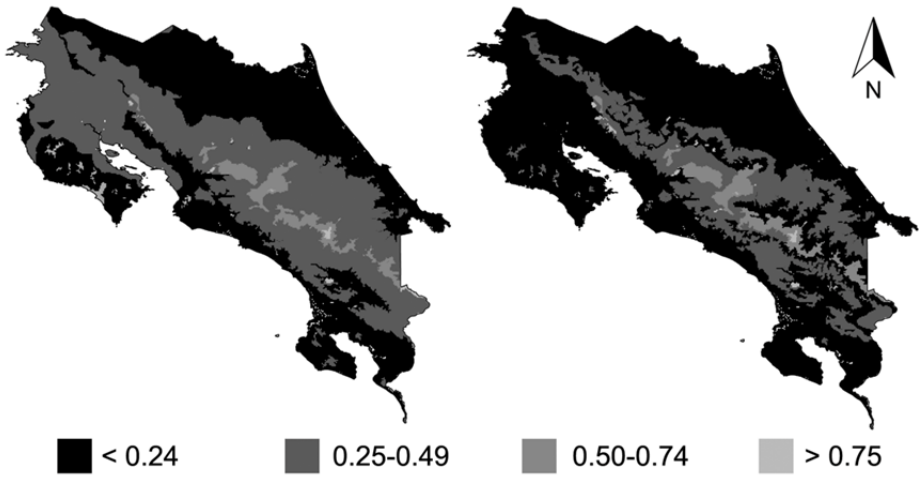


Fig. 5. Maximum entropy distribution maps for myxomycetes in Costa Rica including (left) and excluding (right) the LSBS dataset. The grey areas on the maps represent the different probabilistic categories associated with the Holdridge life zone classification of forest types.

In terms of myxomycete diversity in general and in lowland tropical wet forests in particular, this new dataset from LSBS is an important contribution. For this reason, the annotated list of myxomycete species from LSBS is provided below.

## List of Myxomycetes recorded at La Selva Biological Station during the period of 1963-2012

For abbreviations see Material and methods.

*Arcyria afroalpina* RAMMELOO – MC, on GL.
*Arcyria cinerea* (BULL.) PERS. – FC and MC, on AL, WB, GL and PL.
*Arcyria denudata* (L.) WETTST. – FC and MC, on WB.
*Arcyria pomiformis* (LEERS) ROSTAF. – MC, on AL.
* *Calonema aureum* MORGAN – MC, on WB.
*Ceratiomyxa fruticulosa* (O. F. MÜLL.) T. MACBR. – FC, on WB and GL.
*Ceratiomyxa morchella* A. L. WELDEN – FC, on WB.
*Ceratiomyxa sphaerosperma* BOEDIJN – FC, on WB and GL.
*Clastoderma debaryanum* A. BLYTT – MC, on AL.
*Collaria arcyrionema* (ROSTAF.) NANN.-BREMEK. ex LADO – FC and MC, on WB.
* *Comatricha alta* PREUSS – MC, on WB.
*Comatricha laxa* ROSTAF. – MC, on AL and WB.
* *Comatricha lurida* (LISTER) NANN.-BREMEK. – MC, on AL.
*Comatricha nigra* (PERS. ex J. F. GMEL.) J. SCHRÖT. – MC, on GL.
*Comatricha pulchella* (C. BAB.) ROSTAF. – MC, on AL, WB and GL.
*Comatricha tenerrima* (M. A. CURTIS) G. LISTER – MC, on WB.
*Craterium aureum* (SCHUMACH.) ROSTAF. – MC, on AL and GL.
*Cribraria cancellata* (BATSCH) NANN.-BREMEK. – FC and MC, on WB.
*Cribraria intricata* SCHRAD. – FC, on WB.
*Cribraria languescens* REX – FC, on WB.

*Cribraria microcarpa* (SCHRAD.) PERS. – MC, on AL and WB
*Cribraria splendens* (SCHRAD.) PErs. – FC, on WB.
*Cribraria tenella* SCHRAD. – FC, on WB.
*Cribraria violacea* REX – MC, on AL and WB.
*Diachea leucopodia* (BULL.) ROSTAF. – MC, on WB.
*Dictydiaethalium plumbeum* (SCHUMACH.) ROSTAF. – FC, on WB.
*Diderma effusum* (SCHWEIN.) MORGAN – FC and MC, on Al, WB and GL.
*Diderma hemisphaericum* (BULL.) HORNEM. – FC, on FI.
* *Diderma rimosum* ELIASSON & NANN.-BREMEK. – FC, on WB.
*Diderma saundersii* (BERK. & BROOME ex MASSEE) E. Sheld. – FC, on GL.
*Didymium clavus* (ALB. & SCHWEIN.) RABENH. – FC and MC, on AL and GL.
*Didymium difforme* (PERS.) GRAY – FC, on GL.
*Didymium iridis* (DITMAR) FR. – FC and MC, on AL, WB, FI, GL and PL.
*Didymium nigripes* (LINK) FR. – MC, on GL.
*Didymium squamulosum* (ALB. & SCHWEIN.) FR. & PALMQUIST – FC and MC, on AL, GL and PL.
*Echinostelium minutum* DE BARY – MC, on AL and WB.
*Fuligo megaspora* STURGIS – FC, on WB.
*Hemitrichia calyculata* (SPEG.) M. L. FARR – FC and MC, on WB and GL.
*Hemitrichia pardina* (MINAKATA) ING – MC, on AL and WB.
*Hemitrichia serpula* (SCOP.) ROSTAF. ex LISTER – FC and MC, on AL, WB and GL.
*Lamproderma scintillans* (BERK. & BROOME) MORGAN – FC and MC, on AL, WB, GL and PL.
*Licea biforis* MORGAN – MC, on AL.
*Licea operculata* (WINGATE) G.W. MARTIN – MC, on AL and WB.
*Lycogala conicum* PERS. – FC, on WB.
*Lycogala epidendrum* (L.) FR. – FC and MC, on WB and PL.
*Metatrichia floriformis* (SCHWEIN.) NANN.-BREMek. – FC, on WB.
*Metatrichia vesparia* (BATSCH) NANN.-BREMEK. ex G.W. MARTIN & ALEXOP. – FC, on WB.
*Perichaena chrysosperma* (CURR.) LISTER – FC and MC, on AL and WB.
*Perichaena dictyonema* RAMMELOO – FC, on FI.
*Perichaena pedata* (LISTER & G. LISTER) LISTER ex E. JAHN – MC, on GL.
*Physarella oblonga* (BERK. & M. A. CURTIS) MORGAN – FC, on WB.
*Physarum album* (BULL.) CHEVALL. – FC and MC, on AL and WB.
*Physarum auriscalpium* COOKE – FC, on FI.
*Physarum bivalve* PERS. – MC, on WB.
*Physarum bogoriense* RACIB. – MC, on WB.
*Physarum compressum* ALB. & SCHWEIN. – FC and MC, on AL, WB, FI, GL and PL.
*Physarum didermoides* (PERS.) ROSTAF. – FC, on WB, FI and GL.
*Physarum flavicomum* BERK. – FC, on GL.
*Physarum globuliferum* (BULL.) PERS. – MC, on WB.
*Physarum leucophaeum* FR. & PALMQUIST – FC, on GL.
*Physarum melleum* (BERK. & BROOME) MASSEE – FC and MC, on AL, WB and GL.
*Physarum nucleatum* REX – FC, on WB.
*Physarum oblatum* T. MACBR. – MC, on AL.

*Physarum pezizoideum* (JUNGH.) PAVILL. & LAGARDE – FC, on WB.
*Physarum polycephalum* SCHWEIN. – FC, on GL.
*Physarum pusillum* (BERK. & M. A. CURTIS) G. LISTER – FC, on FI and PL.
*Physarum roseum* BERK. & BROOME – MC, on AL and WB.
*Physarum stellatum* (MASSEE) G. W. MARTIN – FC and MC, on WB.
* *Physarum sulphureum* ALB. & SCHWEIN. – MC, on AL.
*Physarum superbum* HAGELST. – FC, on FI.
*Physarum tenerum* REX – FC, on WB.
*Physarum viride* (BULL.) PERS. – FC and MC, on WB
*Stemonaria longa* (PECK) NANN.-BREMEK., R. SHARMA & Y. YAMAM. – FC, on WB.
*Stemonitis axifera* (BULL.) T. MACBR. – FC, on WB.
*Stemonitis foliicola* ING – FC, on GL.
*Stemonitis fusca* ROTH – FC and MC, on WB.
*Stemonitis splendens* ROSTAF. – FC, on GL.
*Stemonitopsis subcaespitosa* (PECK) NANN.-BREMEK. – FC, on WB.
*Stemonitopsis typhina* (F. H. WIGG.) NANN.-BREMEK. – FC, on WB.
*Symphytocarpus herbaticus* ING – FC, on WB.
*Trichia botrytis* (J. F. GMEL.) PERS. – FC, on WB.
*Trichia favoginea* (BATSCH) PERS. – MC, on WB.
*Trichia varia* (PERS. ex J. F. GMEL.) PERS. – FC; on WB.
*Tubifera casparyi* (ROSTAF.) T. MACBR. – FC, on PL.
*Tubifera ferruginosa* (BATSCH) J. F. GMEL. – MC, on WB.

## Discussion

The new dataset generated in the present study includes all available myxomycete records for LSBS in Costa Rica, and it represents one of the most complete datasets for any single locality in the Neotropics. Several factors other than its overall size add to the value of this dataset. First, the records were collected using different protocols. Second, these collections were made over a period of 50 years. Therefore, the presence of variation in the diversity and taxonomic composition between the different subdatasets was not surprising. Due to the heterogeneity of the full dataset, information can potentially be extracted in a variety of ways and allow one to ask a greater variety of questions. Therefore, this dataset offers a valuable body of information that can aid in our understanding of myxomycete distribution in the general biogeographical region in which LSBS is located.

The total land cover of LSBS is only approximately 0.03% of the total area of Costa Rica, but because of the large concentration of surveys that have taken place here over the years, it may not be surprising that LSBS includes approximately 40% of the myxomycete biota of Costa Rica (see ROJAS & al. 2010). This makes LSBS the most diverse locality for myxomycetes in the entire country, although due to the reasons stated above, this is clearly an artefact (at least in part) of the intensive sampling effort. In spite of this, the results presented herein suggest that lowland tropical wet forests have a complex diversity of myxomycetes. This diversity will likely continue

to increase with the incorporation of newly available molecular methods and as even more microhabitats are examined.

The high percentage of stalked forms in the LSBS dataset (74%) seems to support the hypothesis that the high levels of moisture in the tropics promote stalk formation in myxomycetes or at least provides an advantage for those species characterized by the presence of a stalk. This could be evidence of the influence of environmental variables on the phenotype that is expressed in myxomycete morphology. Some evidence for the latter (i.e., thicker spore walls in dry vs. wet forests for the same species) has been recently documented by ROJAS & VALVERDE (2015). However, a larger number of single locality datasets with enough information to address such hypotheses is still needed. Therefore, this is only an observation about this LSBS dataset in particular and it cannot be used to draw more comprehensive conclusions regarding the hypothesis.

When the LSBS dataset is compared to the dataset consisting of myxomycete data for the entire territory of Costa Rica (as presented in ROJAS & al. 2010), it is interesting to note that *Arcyria* was the most commonly recorded genus at LSBS, whereas *Physarum* and *Didymium* were the two most common genera in the dataset for the entire country. At LSBS, *Physarum* and *Didymium* also are prominent genera, but perhaps the higher numbers of *A. cinerea* recorded for the locality are simply related to the use of the moist chamber culture collecting technique, since this species is commonly abundant using this protocol. Moist chamber cultures were used at a much higher frequency in the LSBS dataset as compared to the collecting techniques used for the country as a whole.

The distribution of species among the taxonomic orders was similar between the LSBS dataset and the entire dataset for Costa Rica. Previous research has shown that members of the Physarales are the most commonly recorded myxomycetes in tropical forests, making our results unsurprising (see STEPHENSON & al. 1993). However, it should be pointed out that many members of the orders *Liceales* and *Echinosteliales* may be underestimated in this and many other studies carried out in the tropics due to protocol biases. Such information regarding taxonomic distribution patterns is valuable as our knowledge of myxomycete ecology and evolution continues to grow. However, at present the significance of the results obtained remain difficult to interpret.

It is interesting that forest age does not seem to have a great effect on the myxomycete community at LSBS. We found little difference in species abundance or diversity between old-growth and successional forests, although the species richness and community composition does seem to change. Only 25 of the 53 species in this subset of data were found in both the old-growth and successional study sites. Other research at LSBS does indicate that the woody vegetation is quite resilient, and that the forests at LSBS are characterized by rapid recovery in both biomass and species richness (LETCHER & CHAZDON 2009). Given the close association between myxomycetes and aboveground vegetation, perhaps the myxomycete community has had a similar recovery. Myxomycetes certainly have characteristics that should be amenable to rapid recovery such as their ease in dispersal due to the small spore size, large population sizes and also the ability to resist a variety of harsh conditions by transitioning to one of three possible resting stages (spores, microcysts and sclerotia). But much like the aforementioned taxonomic analyses, to accurately interpret these data will require a

greater knowledge base relating to myxomycete ecology and a species based understanding of physiology and habitat preference.

Independent of that fact, it seems that forest characteristics are indeed related to the quality and variety of microhabitats utilized by myxomycetes at LSBS. In this context, differences between old-growth and successional forest patches may require further study at single localities when using more conclusive approaches. Similar observations have been made since the work of SCHNITTLER & STEPHENSON (2000), and the topic is still a point of discussion by researchers who study myxomycetes.

Finally, the importance of locality-based myxomycete surveys carried out using a systematic approach became clear when the distribution models were generated. The LSBS dataset did not have an effect on the probability distribution of myxomycetes in most of the territory of Costa Rica, whereas for areas with similar biophysical conditions, the effect was far from negligible. In this way, regardless of the use of such models as predictive tools, this approach provides interesting information about the quality and potential use of particular datasets, as it has been demonstrated herein. Therefore, the use of such techniques for analysis of myxomycete distribution should be carried out with caution, and researchers should consider that for most areas in the world, there is simply not a sufficiently large body of occurrence information for a truly thorough analysis. However, for some commonly recorded and abundant species, or for genotypic information, ecological niche modeling may be an interesting analysis approach to explore.

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