

Myxomycete assemblage turnover across a moisture and elevation gradient in Costa Rica

Alejandra Arenas-Taborda¹, María Carolina García-Chaves¹, Juan Pablo Niño-García¹ and Carlos Rojas²

¹ Escuela de Microbiología, Universidad de Antioquia, Medellín, Colombia

² Department of Biosystems Engineering and INII, University of Costa Rica, San Pedro de Montes de Oca, 11501 - Costa Rica

E-mail: alejandra.arenast@udea.edu.co

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Abstract: The formation of sporocarps in myxomycetes depends on environmental characteristics, among which, moisture and temperature seem to be relevant in tropical areas. Since temperature is linked to elevation, the effect of both of these variables can be studied along a natural moisture and elevation gradient. In the present study, myxomycete assemblages associated with three forest types representing a natural gradient of both climatic characteristics were studied during the same season in consecutive years. Species richness was higher in the driest studied locations and a clear separation among myxomycete assemblages across the gradient was documented. Such separation, however, highly likely implied the effect of sampling in different years. About 35% of the species were shared among forest types and 41% between sampling years. Using the ACOR scale, abundant and common myxomycetes were represented by species present in the three forest types, with clear changes in abundance across the gradient. However, occasional and rare myxomycete categories showed the loss of several species and the emergence of some others from the dry to the wet ecosystems, demonstrating a turnover of species across the different forest types within the gradient. These changes in species composition may be related to the El Niño Southern Oscillation events. Even though such turnover is a natural phenomenon based on species preferences for certain habitats, it is an important aspect to document, particularly in the less studied tropical regions of the world. In the small area studied herein, data showed that myxomycete dynamics are heavily influenced by the local microclimate. The increased speed and strength of ecological pressures on global biosystems represent a threat to microbial dynamics and perhaps myxomycetes can help offer some clues to understand such unbalances.

Keywords: ecology, Guanacaste, myxogastrids, slime molds

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Introduction

The myxomycetes are an interesting group of phagotrophic protists that despite being one of the least studied group of microorganisms, are comprised by about 1000 species described from all over the world (Lado 2005-2021). Most of the available information about the biogeography of myxomycetes has been generated in studies carried out in temperate regions of the Northern Hemisphere, but recent systematic studies from other parts of the world have revealed that ecological patterns of myxomycete assemblages associated with tropical ecosystems are quite different from those of temperate regions (Stephenson et al. 2008). For instance, it has been observed that, contrary to the general pattern observed

in temperate and boreal forests, myxomycete diversity and abundance in tropical systems decreases with increasing substrate moisture (Schnittler and Stephenson 2000). Considering the importance of moisture to induce the production of reproductive structures (sporocarps) in myxomycetes under natural conditions, it is relevant to provide further evidence in relation to the ecological differences that exist, for this group of microorganisms, on a local and regional scales across tropical ecosystems.

Moisture is one of the main environmental factors influencing the myxomycete life cycle and it seems logical that this variable would limit their occurrence in nature (Rubino and McCarthy 2003; Schnittler and Stephenson 2000; Stephenson *et al.* 2019). Myxomycetes tend to occur in relatively moist habitats since their spores, amoeboid cells and plasmodia require favorable conditions of moisture and temperature for germination and biological activity. However, constant humid conditions might limit their ability to disperse due to the reduced spore viability from fungal colonization on sporocarps (Stephenson *et al.* 1993). In addition, it has been proposed that strong and constant rainfall might wash myxomycete propagules from substrates, affecting their life cycle (Stephenson *et al.* 2020). As such, events like El Niño Southern Oscillation (ENSO) may have an effect on sporocarp production. Considering the great effect that rainfall has on the climate of tropical forests and the importance of moisture on the spatial and temporal patterns of occurrence in myxomycetes, it is relevant to evaluate whether seasonal changes in humidity at local spatial scales lead to changes on the diversity and distribution of myxomycetes on tropical habitats.

Despite having a small area, Costa Rica harbors a large diversity of biotic communities. Such flourish of biodiversity may be due to a combination of geographic and climatic factors that generates twenty-four different life zones (Rojas *et al.* 2010). In addition, the existence of large, protected areas represents a nice ‘field laboratory’ setting for research on myxomycetes, as it offers interesting gradients within short distances. For example, at La Selva Biological Station there is a moisture gradient facilitated by the presence of both low hills from the Cordillera Central and the great coastal plain of Sarapiquí, which give rise to two main life zones: Premontane Very Wet Tropical Forest and Very Wet Tropical Forest, in just 730.5 ha of land (Janzen 1991). Similar gradients occur throughout the country, but perhaps the most interesting ones are in the Guanacaste province, where seasonal tropical forests are located and where researchers have documented such seasonality to affect the metabolic activity of microbial communities (Waring and Powers 2016).

In the present study we explored the turnover in myxomycete assemblages across three different types of forest located within 50 kilometers from the west coast of Costa Rica. These forests represent a natural elevational and moisture gradient within the Guanacaste region. The objective of this effort was to evaluate the extent to which myxomycete diversity responds to changes in moisture at relatively small landscape-level scales. This approach is relevant to understand and document the effect of natural ecological variables on this group of organisms for potential climate change scenario and land use change monitoring.

Materials and methods

Study sites

Four study sites situated along a transect representing a three-point gradient of elevation and moisture across the Guanacaste region in Costa Rica were selected (Fig.1, Table 1). These sites were the Tenorio Volcano National Park (hereafter abbreviated as Tenorio), representative of premontane wet forests (PWF), the Miravalles National Park (Miravalles), an area with premontane moist transitional forests (PMTF) and two areas with lowland dry forests (LDF) represented by the Palo Verde National Park and the Horizontes Experimental Forest Station (Palo Verde and Horizontes, respectively).

The Tenorio Volcano and Miravalles National Parks are recently established protected areas. The first one, which takes its name from the Volcán Tenorio, contains 18402 ha of forests and volcanic terrain and has areas of cloud forest in the upper zones and wet forests in the lower ones (Wildlife Worldwilde; Centroamerica; Latinoamerica Salvaje 2021). The second study site, also on a volcano, represents the highest peak of the Guanacaste province with an elevation of 2028 m.a.s.l. In this study site, the low temperatures can reach 6°C, which is highly unusual for a province dominated by warmer lowlands.

Palo Verde National Park was created in 1978 and has an area of 18410 ha. The elevation of this study site varies from 0 to 268 m.a.s.l. The average precipitation is 1600 mm and temperatures range between 21-32°C. That combination of environmental factors allows the coexistence of habitats such as mangrove communities and dry forests (Janzen 1991). Finally, the Horizontes Experimental Forest Station, with an area of 7384 ha, is a former cattle farm and is currently part of the Guanacaste Conservation Area. The precipitation in this study site ranges between 1100-1500 mm per year and the average annual temperature ranges between 24-28°C. Since this area was used for cattle, forested zones are currently composed of successional, not old growth, forests (García 1996).

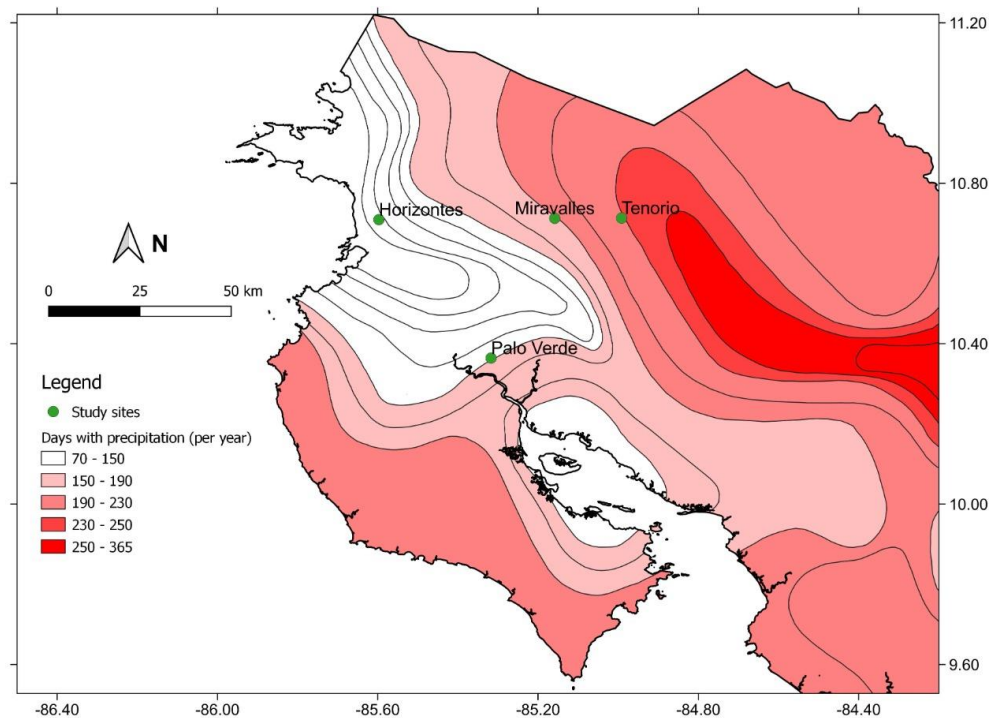


Figure 1. Isoline map showing the gradient of precipitation across the Guanacaste region in Costa Rica. Study sites are presented in green.

Sampling and recording

Two “disturbed” and two “non-disturbed” 20x50 m plots were established in each forest type using the concept of edge effect (Laurance 1991) for the determination of disturbance. The disturbed plots were located in the outer sections of the forest and the non-disturbed ones in the inner sections. Field surveys took place in June 2015 and June 2016; during each year a series of 15 samples of bark and 15 of twigs were collected from each of the four plots for a total of 120 substrate samples per forest type. In this manner, 360 samples were collected each year. For the lowland dry forest, Palo Verde was sampled during the first year and Horizontes during the second one. Differences in precipitation were recorded in both sampled years due to El Niño Southern Oscillation influence and for Palo Verde, recorded precipitation

values during 2015 and 2016 were 1165 and 1893 mm, respectively, for a difference of 728 mm or almost 40% (Rojas-Zeledón 2018).

With each one of the samples one moist chamber was set up in the laboratory using the protocol described by Stephenson and Stempen (1994). With this method, all moist chambers were studied for four months. All myxomycetes appearing in the moist chambers were recorded and identified by extracting the sporocarps from the culture and gluing them to pasteboard boxes. The collected material was deposited in the Myxogastrid Repository of the Engineering Research Institute at the University of Costa Rica.

Table 1. Elevation, annual precipitation, and temperature of the investigated areas in the Guanacaste region; designating the study sites using the Holdridge et al. (1971) classification of tropical forests.

Study site	Elevation of sampled zone (m.a.s.l.)	Average annual precipitation (mm)	Average annual temperature (°C)
Tenorio (PWF)	900	4000	19.5
Miravalles (PMTF)	1000	3500	29
Palo Verde (LDF)	100	1600	26.5
Horizontes (LDF)	100	1300	25.9

Analyses

First, some analyses were carried out to assess the method and the structure of collected data. Sample productivity was calculated for each forest type to assess the effectiveness of the methodology. For this, the number of recorded specimens was divided by the total number of moist chambers prepared and multiplied by 100 (to obtain the metric as a percentage). Second, to estimate the exhaustiveness of the survey, species accumulation curves (SAC) were constructed using the *specaccum* package in R and the rarefaction method.

For biodiversity purposes, alpha-diversity indices (Chao 1, Simpson, Shannon) were calculated for each forest type. The composition of the myxomycete assemblages from each forest type was examined with a principal coordinate analysis (PCoA) based on Bray-Curtis distances and, significant differences were demonstrated with the statistical test ANOSIM.

Finally, to evaluate the structural differences among myxomycete communities, the ACOR abundance scale was calculated for the species in each forest type and for the entire studied area. This was carried out as described by Stephenson et al. (1993). In this case, the relative abundances of species were calculated by considering the species count of each forest type and the entire studied area as the total number of species. The results obtained were used to construct bar plots to show the variation in myxomycete assemblage patterns. These analyses were made both for each forest type and each sampling year.

Results

A total of 526 specimens that corresponded to 46 species of myxomycetes were recorded across the three sampled forest types and during the two sampling years. The species accumulation curves (SACs) indicated that there was an adequate sampling of the three types of forest (Fig. 2), and suggested that the diversity of myxomycetes is higher in the Lowland Dry Forests (LDF) than in Premontane Wet Forests (PMF) or the Premontane Moist Transitional Forests (PMTF). In general, the productivity of moist chambers was higher in LDF (117%) than in PWF (60%) and PMTF samples (42%). Only seven out of

526 of the specimens (about 1%) could not be identified to the species level but could be referred to a species in the genus *Physarum* (these data were excluded from the rest of the analyses).

Diversity patterns of myxomycete assemblages

A clear separation in the myxomycete assemblages from all three different forest types was observed (ANOSIM, $p=0.002$) along the primary ordination axis (PCoA1), although PMTF showed a higher dispersion and larger overlap with the two other forests (Fig. 3). Interestingly, the distribution of samples along the secondary axis (PCoA2) seemed to be related with the two sampled years (ANOSIM, $p=0.013$), although this differentiation was more evident in the LDF dataset than in those from the other forests. These patterns were highly coherent with the differences found in alpha diversity since higher richness, diversity and, dominance were observed in LDF, whereas PMTF and PWF showed lower and similar diversity values (Fig. 4A). Also, differences in the diversity of myxomycetes between the two sampled years were less evident than among forests types. However, it was interesting to note that the diversity indices calculated for 2015 were relatively higher and more variable than those of 2016 (Fig. 4B). Similarly, myxomycete assemblages tended to have relatively higher dominance in the 2016 dataset, as shown by the Shannon and Simpson indices, regardless of the lower richness values.

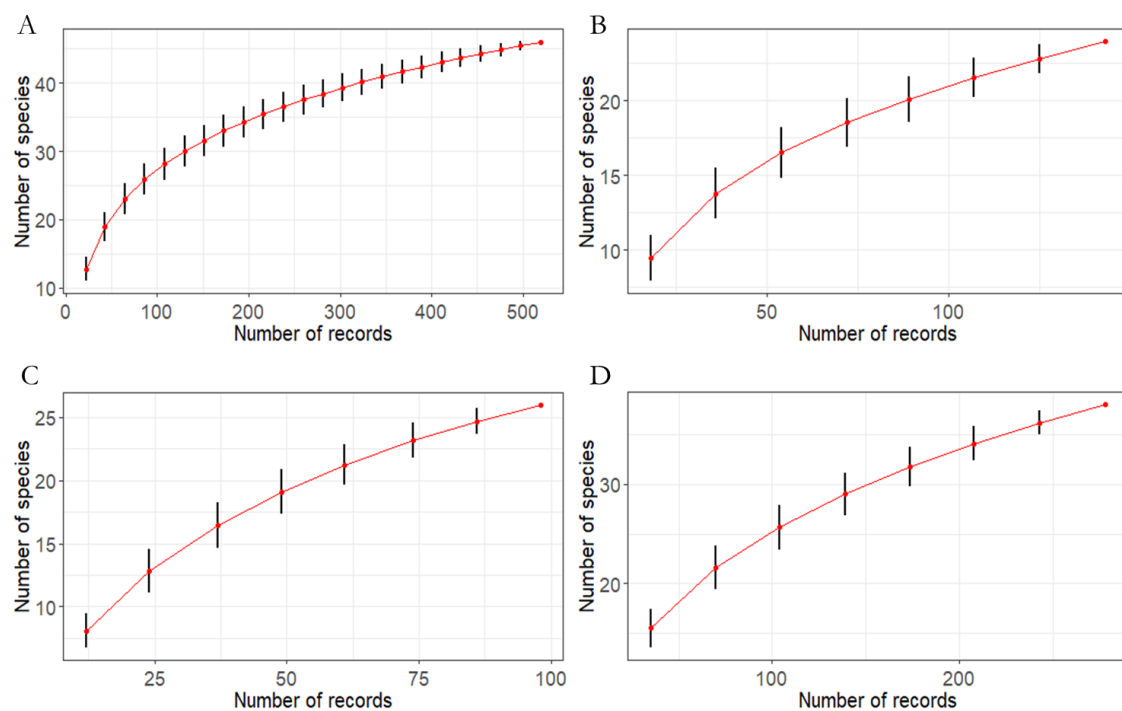


Figure 2. Species accumulation curves (SACs) calculated with the data collected in: A. the whole studied area, B. Premontane Wet Forest, C. Premontane Moist Transitional Forest, D. Lowland Dry Forest.

Commonness, rarity, and occurrence of myxomycetes species

Overall, 38 species were recorded in the Lowland Dry Forest, 26 species in the Premontane Moist Transitional Forest and 24 species in the Premontane Wet Forest (Fig. 5A). From the total of 46 recorded species, 35% were shared among the three forest types ($LDF \cap PWF \cap PMTF$), whereas between six and 28% of the species were unique. In line with the higher myxomycete diversity recorded in LDF (Fig. 4A), this forest also showed the higher number of unique species (Fig. 5A). In addition, between two and 13% of the species were shared by two forest (e.g. $LDF \cap PWF$). Similarly, the same comparison for the two

years when sampling took place showed that 41% of the species were found on both years (Fig. 5B), and the 2015 dataset showed the higher number of unique species (39%).

Based on the ACOR scale, about 24% of the observed species were classified as Abundant, 15% were Common, 22% were Occasional and 39% Rare (Supplementary Table 1). In general, Abundant and Common categories were dominated by species present on the three forest types (Fig. 6), with clear changes in abundance across the climatic gradient. Contrastingly, Occasional and Rare categories were constituted by a very different set of species in each forest type; demonstrating high species turnover from the LDF to PWF gradient (Fig. 6). Remarkably, some species such as *Physarum bivalve* and *Physarum decipiens* were not present in all sites across the studied gradient, even though they were part of the Abundant category. In contrast, a few species within the Occasional or Rare categories were recorded in all the sites across the gradient (*Didymium difforme*, *Didymium clavus* and *Cribraria microcarpa*) or at least in two forest types (*Physarum crateriforme*, *Hemitrichia minor*, *Comatracha pulchella*, *Didymium anellus*, *Physarum bogoriense* and *Physarum cinereum*).

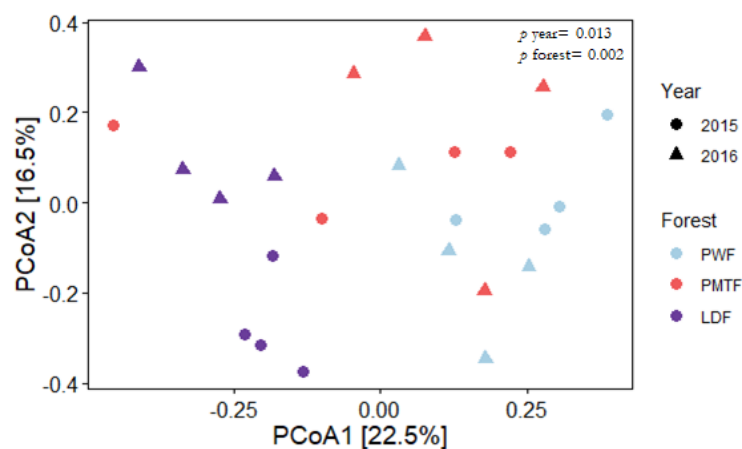


Figure 3. Distribution pattern of myxomycete assemblages differentiated by years (shape) and forests (color), using a Principal Coordinate Analysis (PCoA) with the Bray Curtis index. PWF=Premontane Wet Forest, PMTF=Premontane Moist Transitional Forest and LDF=Lowland Dry Forest datasets.

At the genus level, different species of the genera *Comatracha*, *Didymium* and *Physarum* were associated with one of the four ACOR categories, whereas species of *Lamproderma*, *Stemonitis*, *Clastoderma*, *Diachea*, *Hemitrichia*, *Licea*, *Lycogala* and *Trichia* were either Abundant or Rare, respectively. Finally, a similar analysis comparing the changes in relative abundance of myxomycete species between years showed little differences within the Abundant category but there seemed to be a high turnover of species from 2015 to 2016 within the other ACOR categories (Fig. 7).

Discussion

Climatic factors such as rainfall are important for the development of myxomycete sporocarps since the life cycle of these organisms requires a degree of water retention on substrates (Stephenson et al. 1993). Some substrates like litter and dung have higher retention values than bark (Schnittler 2001), which means that those are probably more susceptible to saturation. Since the moisture levels in moist chambers are not controlled within specific limits, this technique may have a double effect on results. First, providing the necessary moisture for sporocarp formation and second, by masking the effect of water

retention/saturation on substrates, which may impact negatively the formation of reproductive structures in some species (Stephenson and Stempen 1994).

Recent studies have shown that the internal moisture of the moist chambers is likely kept within non-significant limits for sporocarp production (Rojas et al. 2021a), but along with temperature these variables can have an effect on results. At the macroclimatic level, the month of June is usually rainy in Costa Rica (certainly the case for the studied years), with a dryer period known as the Veranillo de San Juan (Janzen 1991). Collecting material for myxomycete research during this month is associated with saturated substrates that require drying before moist chambers are set up.

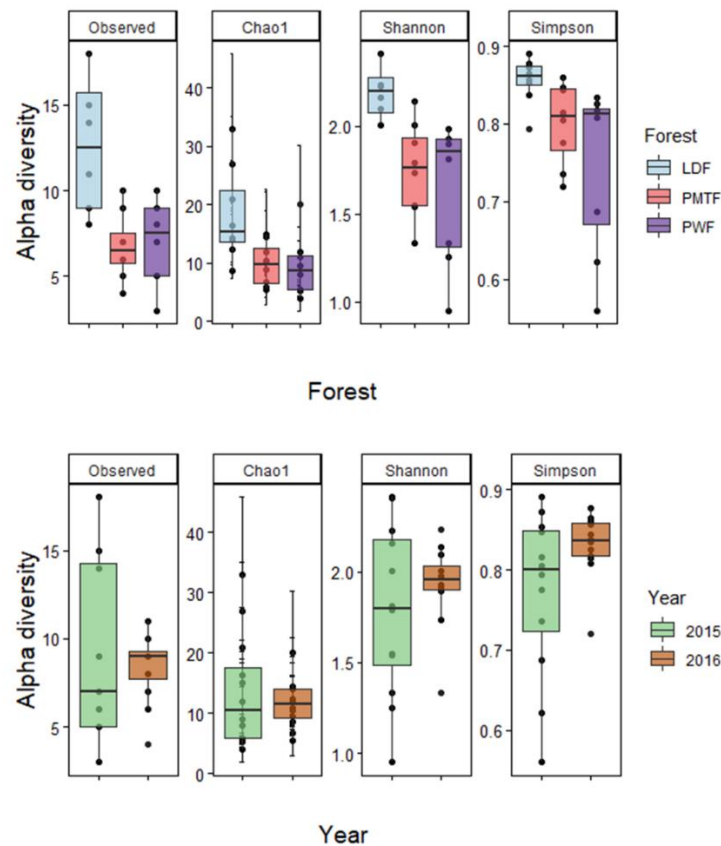


Figure 4. Comparison of alpha diversity indices of the myxomycete assemblages from A) different forest types and B) sampled years. PWF=Premontane Wet Forest, PMTF=Premontane Moist Transitional Forest samples and LDF=Lowland Dry Forest datasets.

Due to the natural differences in precipitation and atmospheric moisture among the three types of forests studied herein, the collected material showed noticeable differences in water saturation, even for such a small geographical area. Samples collected in Tenorio were completely saturated in water whereas samples from Palo Verde were wet but not soaked. Results seemed to have reflected these original differences in moisture by showing higher values of species richness and number of records in the latter and lower values in the former, which suggests that the washout effect previously reported in other studies (see Rojas et al. 2020) played a role in the recording of data across the gradient.

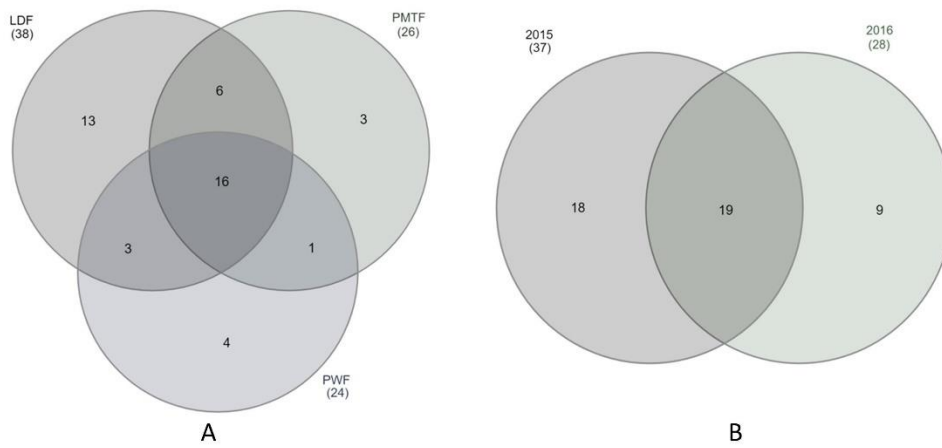


Figure 5. Number of myxomycete species shared across forests (A) and between years (B). The numbers in parentheses in the Venn Diagram correspond to the total number of species recorded for each forest type or each sampled year. PWF=Premontane Wet Forest, PMTF=Premontane Moist Transitional Forest samples and LDF=Lowland Dry Forest datasets.

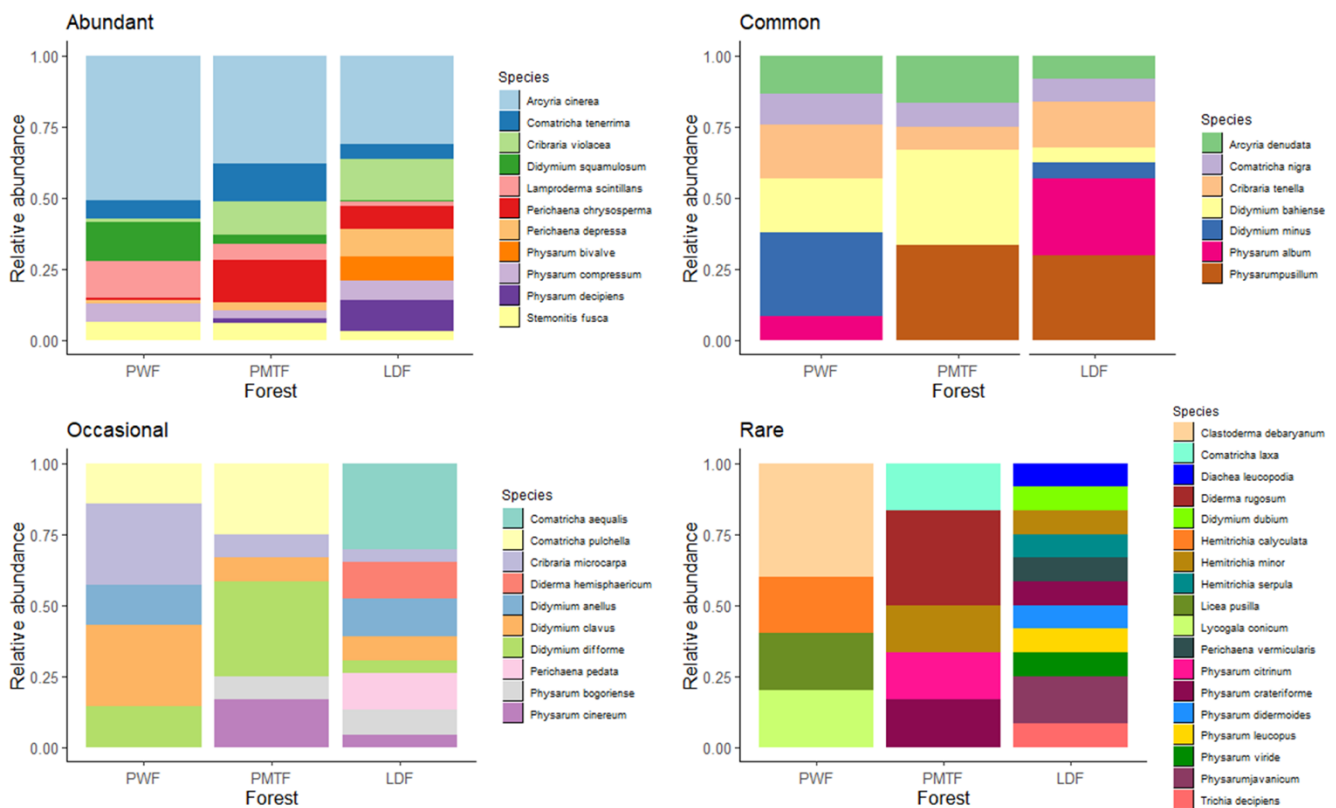


Figure 6. Relative abundance of myxomycete species arranged by forest types and separated according to the four categories of the ACOR scale.

Biogeographical analyses of myxomycete communities have shown clear floristic differences across latitudes that extend beyond the differences observed among diverse forest types (life zones herein)

within a region (Stephenson *et al.* 1993; Dagamac *et al.* 2017). However, as other authors have observed, both local climate and plant composition strongly influence the occurrence of sporocarps of myxomycetes, even within a small geographical area (Liu *et al.* 2015; Rojas and Stephenson 2008).

In the present study, the significant differences in the myxomycete assemblage composition found among forests and between years, seem to have been related to the subjacent dissimilarities in microclimates across the studied gradient. However, it is possible that differences in precipitation between years (32% higher in June 2016 vs June 2015, based on estimations from Costa Rica's National Meteorological Institute, León 2015; Ramírez 2016), associated with the ENSO, could explain the separations appreciated in the PCoA.

Such an observation would suggest that the climatic difference between collecting periods is a major variable explaining the differential production of sporocarps. However, since two different areas were surveyed for the lowland dry forest in the two distinct periods, this additional factor could have influenced yearly results as well. Despite the latter, based on previous tropical data (Tran *et al.* 2008), differences in myxomycete assemblages seem unlikely for Abundant and Common myxomycetes but not so much for rarer species.

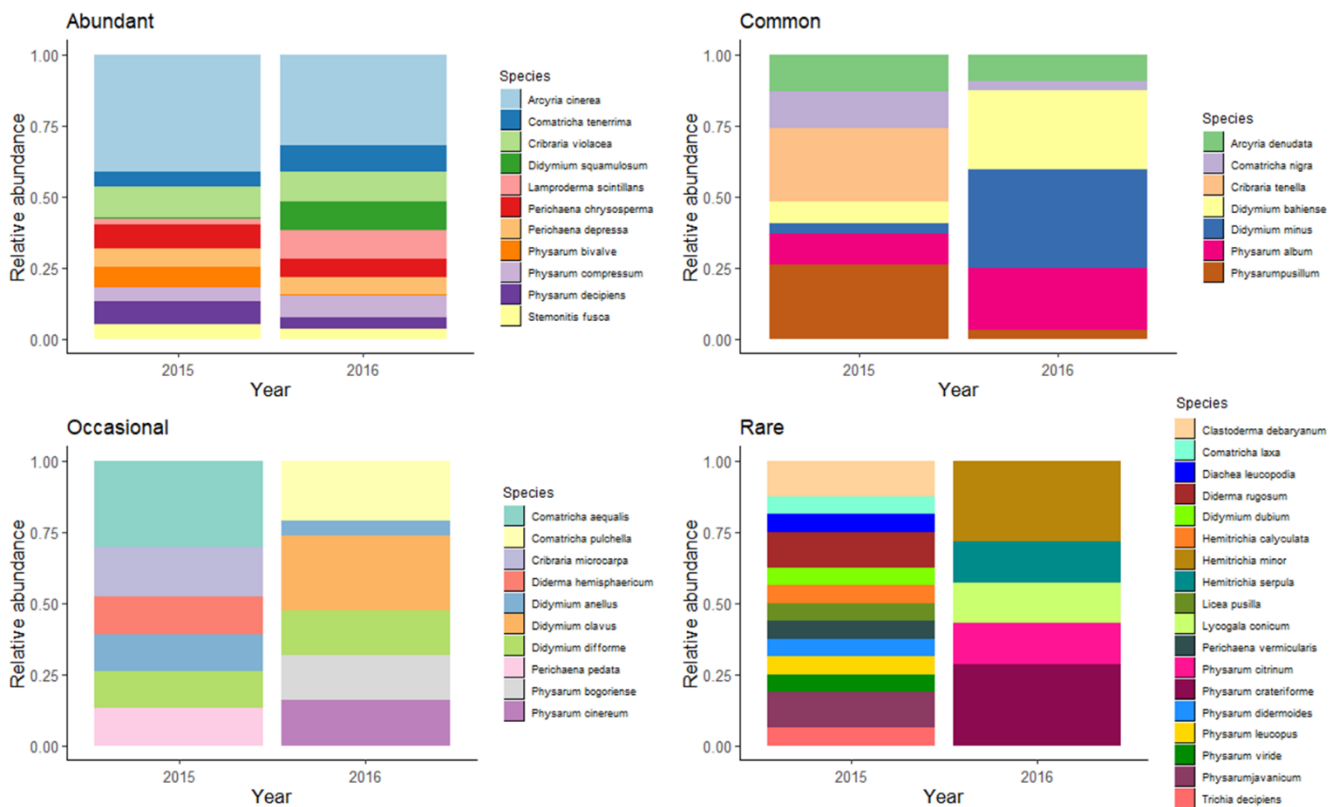


Figure 7. Relative abundance of myxomycete species arranged by year and separated according to the four categories of the ACOR scale.

Recently, the ENSO phenomenon was documented to affect positively the productivity of Rare species of myxomycetes in tropical conditions (Rojas *et al.* 2021b), supporting the previous observation

of Chiapetta et al. (2003) that sporocarp formation in *Fuligo septica* may be influenced by such events. The former observation was made in a non-seasonal forest where temporal variations in myxomycete assemblages are less pronounced than in dryer seasonal regions such as Guanacaste, where it is more likely for the effect to be more evident (see Lado et al. 2016).

As such, it seems that ENSO promotes the formation of sporocarps of rare myxomycetes in tropical forests, which increases the diversity of reproductive propagules in the air of those environments in a similar manner to seasonal observations (Surrant and Leventin 2005). If such spore load is more diverse, the probability of a higher diversity of myxomycetes to be recorded in laboratory conditions would be higher and very likely, the dominance would be lower since more species would be recorded.

Those predictions were exactly the results observed in the present study, with the more pronounced effect on the dryer of the three studied locations. However, the forced homogenization of microconditions imposed by the technique used for recording myxomycetes in the present study very likely limited the differences in results. In this manner, field-based experimentation of the same phenomenon would be highly valuable in other tropical areas for such hypothesis to be tested.

In general, the high turnover of myxomycetes species shown herein has been likely related with seasonality and ecosystem specific features like vegetation, also supported by previous research (Borg Dahl et al. 2019; Treviño-Zevallos and Lado 2020). In the present study, the ACOR scale classification allowed to identify that the turnover in Abundant and Common species was subtler than in rarer categories, and such effect was documented on particular species. For example, *Didymium squamulosum* is an Abundant species in wet ecosystems (Rojas et al. 2010; Treviño-Zevallos and Lado 2020) and such an observation is consistent with the results of the present study, where that species was Abundant in PWF during the rainier 2016. In contrast, Occasional and Rare species were more affected, as it was expected. However, it is important to mention that some species within genera such as *Lycogala* and *Hemitrichia*, almost never produce sporocarps in moist chambers. In this manner, studies with complementary collecting methods (i.e., field collections) are recommended for a more thorough evaluation of results.

The data presented herein showed that myxomycete results based on sporocarps using moist chambers can reflect ecological patterns taking place at higher-levels of organization (i.e., ecosystem dynamics based on climate). Hence, for monitoring purposes or environmental applications using myxomycetes, these data suggest that research should be focused on Occasional and Rare species. Finally, in order to continue building information in that direction, autoecological studies, rather than synecological ones are needed.

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Supplementary Table 1. Abundance and occurrence of myxomycete species based on the ACOR scale and the presence/absence analyses on Premontane Wet Forest (PWF), Premontane Moist Transitional Forest (PMTF) and Lowland Dry Forest (LDF).

Species	Abundance classification according to the ACOR scale	Occurrence classification according to the Venn diagram
<i>Arcyria cinerea</i>	Abundant	Shared across 3 forests
<i>Cribraria violacea</i>	Abundant	Shared across 3 forests
<i>Perichaena chrysosperma</i>	Abundant	Shared across 3 forests
<i>Comatracha tenerrima</i>	Abundant	Shared across 3 forests
<i>Physarum decipiens</i>	Abundant	Shared between LDF & PMTF
<i>Perichaena depressa</i>	Abundant	Shared across 3 forests
<i>Physarum compressum</i>	Abundant	Shared across 3 forests
<i>Lamproderma scintillans</i>	Abundant	Shared across 3 forests
<i>Physarum bivalve</i>	Abundant	Unique to LDF
<i>Didymium squamulosum</i>	Abundant	Shared across 3 forests
<i>Stemonitis fusca</i>	Abundant	Shared across 3 forests
<i>Physarum pusillum</i>	Common	Shared between LDF & PMTF
<i>Cribraria tenella</i>	Common	Shared across 3 forests
<i>Didymium bahiense</i>	Common	Shared across 3 forests
<i>Didymium minus</i>	Common	Shared between LDF & PWF
<i>Physarum album</i>	Common	Shared between LDF & PWF
<i>Arcyria denudata</i>	Common	Shared across 3 forests
<i>Comatracha nigra</i>	Common	Shared across 3 forests
<i>Comatracha aequalis</i>	Occasional	Unique to LDF
<i>Didymium difforme</i>	Occasional	Shared across 3 forests
<i>Didymium clavus</i>	Occasional	Shared across 3 forests
<i>Comatracha pulchella</i>	Occasional	Shared between PMTF & PWF
<i>Cribraria microcarpa</i>	Occasional	Shared across 3 forests
<i>Didymium anellus</i>	Occasional	Shared between LDF & PWF
<i>Diderma hemisphaericum</i>	Occasional	Unique to LDF
<i>Perichaena pedata</i>	Occasional	Unique to LDF
<i>Physarum bogoriense</i>	Occasional	Shared between LDF & PMTF
<i>Physarum cinereum</i>	Occasional	Shared between LDF & PMTF
<i>Clastoderma debaryanum</i>	Rare	Unique to PWF
<i>Diderma rugosum</i>	Rare	Unique to PMTF
<i>Hemitrichia minor</i>	Rare	Shared between LDF & PMTF
<i>Physarum crateriforme</i>	Rare	Shared between LDF & PMTF
<i>Physarum javanicum</i>	Rare	Unique to LDF
<i>Comatracha laxa</i>	Rare	Unique to PMTF
<i>Diachea leucopodia</i>	Rare	Unique to LDF
<i>Didymium dubium</i>	Rare	Unique to LDF
<i>Hemitrichia calyculata</i>	Rare	Unique to PWF

<i>Hemitrichia serpula</i>	Rare	Unique to LDF
<i>Licea pusilla</i>	Rare	Unique to PWF
<i>Lycogala conicum</i>	Rare	Unique to PWF
<i>Perichaena vermicularis</i>	Rare	Unique to LDF
<i>Physarum citrinum</i>	Rare	Unique to PMTF
<i>Physarum didermoides</i>	Rare	Unique to LDF
<i>Physarum leucopus</i>	Rare	Unique to LDF
<i>Physarum viride</i>	Rare	Unique to LDF
<i>Trichia decipiens</i>	Rare	Unique to LDF
