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REGULAR PAPER

Myxomycete diversity in a humid montane forest on the eastern slopes of the Peruvian Andes

Italo F. Treviño-Zevallos[1,2,*] & Carlos Lado[1]

[1]Real Jardín Botánico, CSIC. Plaza de Murillo 2, 28014 Madrid, Spain
[2]Universidad Nacional de San Agustín de Arequipa, Av. Alcides Carrión s.n., Arequipa, Peru
*Corresponding author: ifrant01@gmail.com

Background – The humid montane forests on the eastern slopes of the Peruvian Andes are known for their high biodiversity and natural resources. While their incredibly rich plant and animal communities are still in the process of being discovered, the diversity of smaller organisms such as the Myxomycetes are even more scarcely known. In this work, we document the Myxomycete diversity in these montane forests and evaluate species abundance, occurrence by substrates, distribution, and seasonality, thus documenting population status and species ecology.
Material and methods – The study was carried out at the Wayqecha Biological Station located in the Cusco region of Peru. Two sampling campaigns took place in late January (wet season) and early May (dry season) of 2018. We performed a species inventory and evaluated alpha diversity, assemblage similarity, and abundance of Myxomycetes within six 100 m^2 plots. We documented variations of species richness and abundance between seasons as well as between substrates.
Results – We recorded a total of 81 taxa of Myxomycetes. The order Physarales was the most diverse, and the most abundant species were *Didymium squamulosum* and *Diderma deplanatum* during the wet and dry season, respectively. The substrate with highest diversity overall was dead leaves. Diversity was similar in both seasons but with a notable species turnover.
Conclusion – The humid montane forest on the eastern slopes of the Andes in Peru revealed an unexpected richness in Myxomycetes. Based on our results, we conclude that this type of forest harbours one of the greatest Myxomycetes diversities in the Peruvian territory, also due to the important seasonal species turnover.

Keywords – Amoebozoa; biodiversity hotspot; myxobiota; neotropics; Peru; tropical forest.

INTRODUCTION

The Myxomycetes are currently placed within the eukaryotic supergroup Amoebozoa but are traditionally studied by mycologists (Rojas & Stephenson 2007). These organisms vary considerably in size, ranging from less than 100 µm in some species to several centimetres in others (Keller et al. 2017). They are usually associated with humid environments due to their need for water to complete their life cycle (Lado et al. 2016). The Myxomycetes are common in a variety of terrestrial ecosystems where they feed on bacteria, yeasts, fungal spores, and other soil microbes. They contribute to the decomposition of plant material and to soil fertility by unlocking nutrients. As a whole, the class Myxomycetes has a worldwide distribution, but some individual species are highly specialized and may live in very selective and even extreme environments (Lado et al. 2017).

The humid montane forest growing on the eastern slopes of the Peruvian Andes is a particular biome of utmost importance for the conservation of biodiversity and natural resources (Young & León 1999). This type of forest is known to

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have the highest rate of endemism in the entire South American continent and is considered as one of the most important biodiversity hotspots in the world (Tejedor et al. 2012). It can therefore be expected that Myxomycetes are also present and highly diverse in this type of forest, especially considering the variety of (plant) substrates and the high humidity. However, studies on Myxomycetes in tropical montane forests, as well as more generally in the Neotropics, are sparse (Rojas & Stephenson 2007; Rojas et al. 2011; Schnittler & Stephenson 2000; Schnittler et al. 2002; Treviño-Zevallos & Lado 2020). Diversity, species abundance, distribution, and seasonality of these organisms are therefore still largely unknown.

Myxomycetes have however been studied in the Amazonian lowland forest of Madre de Dios, where 62 species from 19 genera have been reported (Rojas & Stephenson 2013). Arid biomes, such as those found along the Pacific coast (the Lomas formation) or on the western slopes of the Andes (Cactus belt, grasslands), are comparatively better known. These environments have been surveyed by Lado et al. (2016, 2019) and Wrigley de Basanta et al. (2015), representing about 90% of all Peruvian Myxomycete records. More than 100 species have been reported there, and two new species have recently been described (Wrigley de Basanta et al. 2019; Lado et al. 2019).

The main goal of this study is to obtain data on the diversity and the assemblage of Myxomycetes that inhabit humid montane forests that grow on the eastern slopes of the Andes. The specific objectives are (i) to characterize species composition and abundance, (ii) to determine their occurrences per substrate, and (iii) to compare Myxomycetes diversity between the dry and the wet season.

MATERIAL AND METHODS

Study area

The study was conducted at the Wayqecha Biological Station (WBS), a private conservation area of approximately 594 ha located in the Kosñipata district, Paucartambo province, Cusco region, near km 117 on the Cusco–Pilcopata road. The station coordinates are 13°10′30″S, 71°35′12″W and the area has an elevation range of 2300–3500 m a.s.l. (fig. 1). The WBS is managed by ACCA (Asociación para la Conservación de la Cuenca Amazónica) and borders the Manu

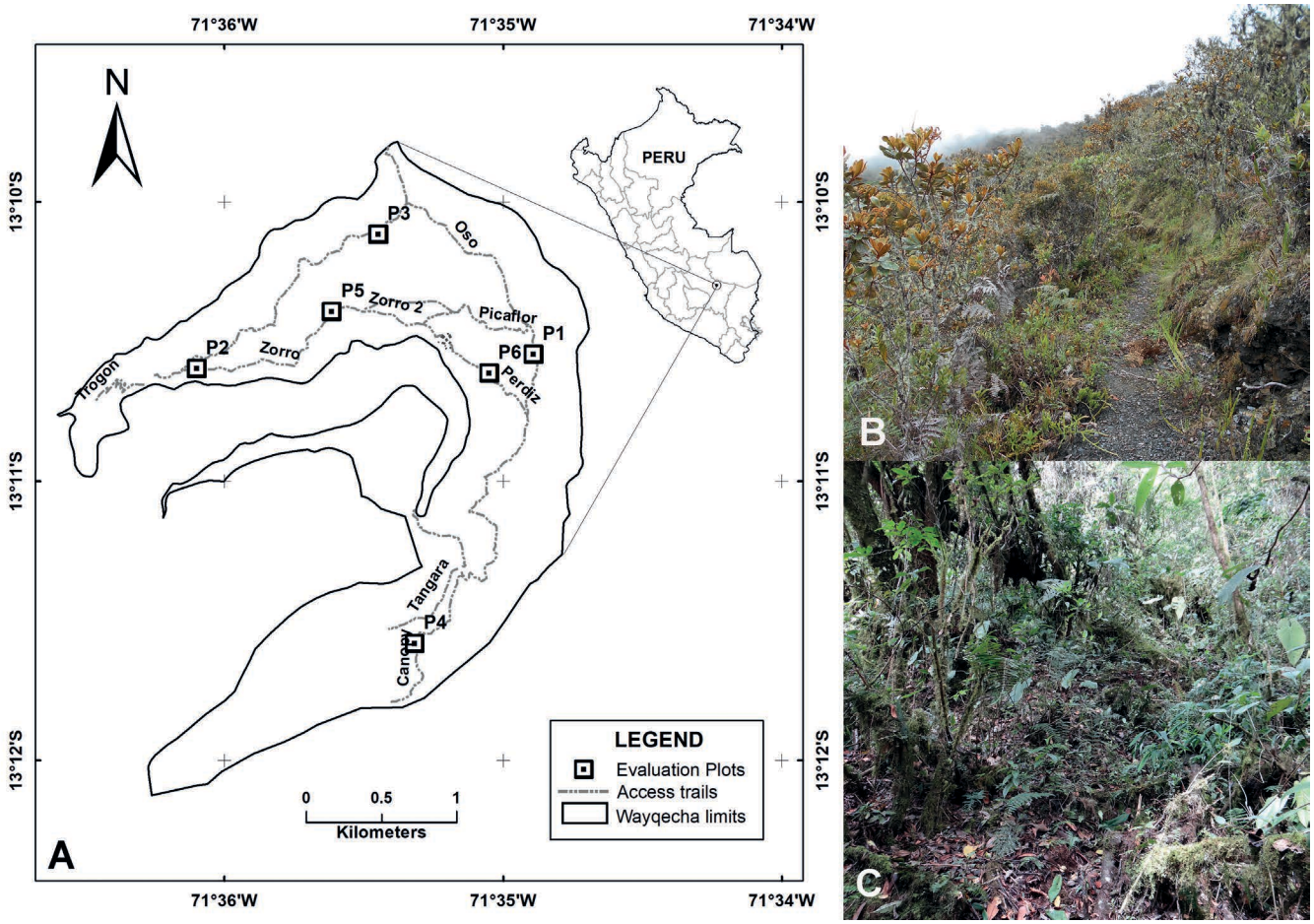

Figure 1 – **A**. Map of the Wayqecha Biological Station showing the location of the six plots (P1–P6). **B**–**C**. Examples of the vegetation at the Wayqecha Biological Station. Photographs: I. Treviño. Data of trails and limits of Wayqecha Biological Station provided by ACCA (Asociación para la Conservación de la Cuenca Amazónica). Map created with ArcGis version 10.2.2 (Esri 2014). © Esri and its licensors, all rights reserved. This map is not distributed under the terms of the Creative Commons license of this publication. For permission to reuse, please contact the rights holder.

National Park (Rivera 2007; Medina et al. 2012). The vegetation is dominated by trees of the genera *Weinmannia*, *Myrsine*, and *Clethra*, arborescent ferns of genus *Cyathea*, and shrubs of the family Ericaceae. Epiphytic bromeliads, ferns, bryophytes, and orchids are also abundant and divers. Transitional zones and Andean grasslands are present in the parts of the area with the highest elevation. The forest is continually saturated with rain and fog, except during a relatively short dry season between the months of May and July. The precipitation ranges from < 10 mm, in the months of June and July, to > 100 mm, in the months of January to March, and the average temperature is 11°C with little seasonal variation (Repasky et al. 2010).

Sampling

The sampling was done by two people during two weeks, one week in late January (wettest month of the wet season) and another week in early May (second driest month of the dry season) of 2018. The sampling was carried out in six plots of 100 m^2 (10 × 10 m) located at least 20 meters away from the access trails and distributed evenly over the WBS. The plots were selected to account for the variation in plant associations and elevations found in the WBS. The time spent to sample each plot was two hours. We recorded and collected all species and documented individual abundances on each plot up to a height of 2 m. Individuals were defined as a colony of Myxomycetes with more than three fruiting bodies and situated at a distance > 50 cm away from other colonies of the same species. This minimum number of fruiting bodies was chosen because it represents the number that is necessary for the identification of the species: (at least) one fruiting body is kept for the observation of microscopic characters and two others for measurements and observation of macroscopic features.

In addition to the species inventory, five samples (leaf litter with twig remains) were taken from each plot for moist chamber culturing, following the protocols detailed in Wrigley de Basanta & Estrada-Torres (2017). The purpose of these cultures was to observe small species not detectable in the field. Finally, an intensive survey of Myxomycetes was performed along the access trails of WBS in order to collect fruiting bodies using an opportunistic approach (O'Dell et al. 2011). The collections were placed in plastic boxes to avoid contamination and subsequently gathered in cardboard boxes for desiccation. For each collection, we noted the substrate and added georeferenced data and a code number.

Identification and occurrence by substrates

The species were identified using the monographs of Farr (1976), Lado & Pando (1997), Martin & Alexopoulos (1969), Nannenga-Bremekamp (1991), Poulain et al. (2011), and other specialized literature. The nomenclature follows Lado (2005–2020). The specimens were deposited in the South Peruvian Herbarium (HSP) with duplicates of some collections in the Herbarium of the Royal Botanic Garden of Madrid (MA).

The recorded Myxomycetes were classified based on their occurrence on the type of substrate. We adapted the classification of Ing (1994) with the following considerations:

- Foliicolous – Growing on leaves of plants or fronds of ferns, alive or in a state of decomposition and fallen to the ground.
- Lignicolous (A) – Growing on dead trunks or fallen branches of decomposing trees.
- Lignicolous (B) – Growing in small branches or stems of decomposing plants of < 1 cm in diameter.
- Muscicolous – Growing on bryophyte thallus.
- Floricolous – Growing on the remains of flowers or inflorescences.

The corticolous type was not considered in this survey due to the characteristics of the surface of the bark of the trees, which were covered with a coarse layer of mosses, lichens, ferns, bromeliads, and other epiphytic plants, or residues of organic matter, thus rendering substrate classification inaccurate.

Data analyses

We compiled a list of all taxa of Myxomycetes recorded at the WBS. The list includes the species obtained from the plots, from the intensive search, and from the moist chamber cultures. The occurrence by season and by substrate type were also included. Abundance, sampling effort, alpha-beta diversity, and seasonality were only analysed for the plots. A rank-abundance plot was made to document the abundance of taxa according to the season (Zar 1996). The sampling effort was evaluated using the estimators Chao1 and ACE (Colwell & Coddington 1994; Colwell et al. 2004) in EstimateS v.9.1.0 (Colwell 2013). The upper limit of abundance for rare or infrequent species was set to 3, considering species with a relative abundance of ≤ 0.05 to be rare (Stephenson et al. 1993). The Clench function, $Sn = (a * n) / [1+ (b * n)]$, where Sn is the number of species accumulated for a unit of collection effort (n), was also calculated. This function was used to infer the proportion of recorded species as compared to the estimated total. The parameters for this function were calculated in Statistica v.12 (Statsoft Inc 2013) using the Simplex and Quasi-Newton adjustment methods (Jiménez-Valverde & Hortal 2003). Alpha and beta diversity were estimated using Shannon (log 2) and Jaccard indices, respectively. These indices were computed in Primer-E v.6.1.6 (Clarke & Gorley 2005). Finally, we performed a χ^2 test (Zar 1996) in order to evaluate whether Myxomycetes community composition depended on the season (wet season vs. dry season).

RESULTS

Myxomycetes diversity in WBS

A total of 81 taxa in 6 orders, 10 families, and 22 genera were recorded in WBS (table 1). Fifty taxa were recorded in the plots, and an additional 28 and 3 taxa were found in the intensive survey and the moist chamber cultures, respectively.

The order Physarales showed the greatest richness with 45 species and one variety, followed by the order Trichiales

Table 1 – **List of the Myxomycetes taxa found in the humid montane forest at the Wayqecha Biological Station, Peru.**
For each taxon, information is given on how it was sampled, in which season it was collected, and on which substrate it was found. Is = Intensive survey; Pl = plot. Fl = Floricolous; Mu = Muscicolous; L(A) = Lignicolous (A); L(B) = Lignicolous (B); Fo = Foliicolous. *Obtained from moist chamber culture.

Taxa	Sampling		Season		Occurrence by substrate					
	Is	Pl	Wet	Dry	Fl	Mu	L(A)	L (B)	Fo	Total
Arcyria affinis Rostaf.	X	X	X	X			2		1	3
Arcyria cinerea (Bull.) Pers.*	X	X	X	X			4	1	2	7
Arcyria denudata (L.) Wettst.	X			X					1	1
Arcyria pomiformis (Leers) Rostaf.		X	X						1	1
Arcyria sp. 1		X		X			1			1
Calomyxa sp. 1	X	X	X	X			1	1	1	3
Clastoderma debaryanum A.Blytt		X		X			1			1
Comatricha alta Preuss		X	X	X			2			2
Comatricha laxa Rostaf.	X	X	X						2	2
Comatricha pulchella (C.Bab.) Rostaf.	X		X						1	1
Comatricha sp. 1	X		X				1		1	2
Craterium aureum (Schumach.) Rostaf.	X	X	X					2	6	8
Craterium leucocephalum (Pers. ex J.F.Gmel.) Ditmar	X		X						1	1
Craterium minutum (Leers) Fr.	X	X	X	X			2		8	10
Craterium obovatum Peck		X		X					2	2
Craterium sp. 1		X		X					1	1
Cribraria cf. *paucicostata* Nann.-Bremek.	X		X				1			1
Cribraria mirabilis (Rostaf.) Massee		X	X				1			1
Cribraria splendens (Schrad.) Pers.	X		X				1			1
Cribraria vulgaris Schrad.	X	X	X	X			5		2	7
Diachea leucopodia (Bull.) Rostaf.	X		X						2	2
Diachea sp. 1		X	X						1	1
Diderma deplanatum Fr.	X	X	X	X	1	31	2		27	61
Diderma cf. *globosum* Pers.	X	X	X	X					3	3
Diderma effusum (Schwein.) Morgan	X			X					1	1
Diderma fragile Aramb.	X	X		X		3			1	4
Diderma miniatum Nann.-Bremek.	X			X					4	4
Diderma subdictyospermum (Rostaf.) E.Sheld.	X	X		X		4	2	2	6	14
Diderma sp. 1	X	X		X		2			3	5
Diderma sp. 2	X		X				1			1
Didymium clavus (Alb. & Schwein.) Rabenh.		X	X	X				2	9	11
Didymium dubium Rostaf.	X		X						1	1
Didymium cf. *iridis* (Ditmar) Fr.	X	X	X	X		2		1	7	10
Didymium minus (Lister) Morgan	X		X						1	1
Didymium nigripes (Link) Fr.	X	X	X	X		6	2	8	62	78
Didymium squamulosum (Alb. & Schwein.) Fr. & Palmquist	X	X	X	X		2		11	65	78
Didymium sp. 1		X	X						1	1
Didymium sp. 2		X		X					1	1
Hemitrichia calyculata (Speg.) M.L.Farr	X	X	X	X			14		1	15
Hemitrichia pardina (Minakata) Ing	X	X	X	X			1		2	3
Hemitrichia serpula (Scop.) Rostaf. ex Lister	X			X			2			2
Lamproderma scintillans (Berk. & Broome) Morgan		X	X					1		1

Table 1 (continued) – List of the Myxomycetes taxa found in the humid montane forest at the Wayqecha Biological Station, Peru. For each taxon, information is given on how it was sampled, in which season it was collected, and on which substrate it was found. Is = Intensive survey; Pl = plot. Fl = Floricolous; Mu = Muscicolous; L(A) = Lignicolous (A); L(B) = Lignicolous (B); Fo = Foliicolous. *Obtained from moist chamber culture.

Taxa	Sampling		Season		Occurrence by substrate					
	Is	Pl	Wet	Dry	Fl	Mu	L(A)	L (B)	Fo	Total
Leocarpus sp. 1	X		X				1			1
Licea sp. 1*				X					1	1
Macbrideola spinosispora L.M.Walker, G.Moreno & S.L.Stephenson*				X					1	1
Metatrichia floriformis (Schwein.) Nann.-Bremek.	X	X		X			5		1	6
Metatrichia vesparia (Batsch) Nann.-Bremek. ex G.W.Martin & Alexop.		X	X	X			2			2
Paradiacheopsis sp. 1	X		X				1			1
Perichaena chrysosperma (Curr.) Lister	X		X				1			1
Perichaena depressa Lib.*				X				3		3
Physarum album (Bull.) Chevall.	X	X	X	X			9	2	13	24
Physarum auripigmentum G.W. Martin	X		X						1	1
Physarum bivalve Pers.	X	X	X	X		2			6	8
Physarum brunneolum (W.Phillips) Massee	X			X		1				1
Physarum cinereum (Batsch) Pers.		X		X					1	1
Physarum compressum Alb. & Schwein.		X	X	X					5	5
Physarum galbeum Wingate		X	X	X			3		1	4
Physarum laevisporum Agnihothr.	X		X	X	1				2	3
Physarum cf. *luteolum* Peck	X		X						1	1
Physarum melleum (Berk. & Broome) Massee	X	X	X	X					4	4
Physarum cf. *oblatum* T.Macbr.	X		X						2	2
Physarum penetrale Rex		X		X			1			1
Physarum pusillum (Berk. & M.A.Curtis) G.Lister	X	X	X	X		3	1		8	12
Physarum robustum (Lister) Nann.-Bremek.		X	X			1	1			2
Physarum viride var. *aurantium* (Bull.) Lister	X	X	X	X			6		2	8
Physarum viride (Bull.) Pers. var. *viride*	X		X				1			1
Physarum sp. 1	X			X					1	1
Physarum sp. 2		X	X	X		3				3
Physarum sp. 3	X	X	X	X			1		2	3
Physarum sp. 4	X	X	X	X			2			2
Physarum sp. 5		X	X						3	3
Physarum sp. 6	X	X	X	X					12	12
Stemonitis axifera (Bull.) T.Macbr.	X		X				1			1
Stemonitis pallida Wingate	X			X			1			1
Stemonitis splendens Rostaf.	X			X			2			2
Stemonitopsis typhina (F.H.Wigg.) Nann.-Bremek.	X			X			1			1
Trichia cf. *affinis* de Bary	X	X	X	X		1	8		2	11
Trichia decipiens (Pers.) T.Macbr.	X	X	X	X			10		1	11
Trichia cf. *subfusca* Rex	X	X	X	X			3			3
Trichia verrucosa Berk.	X	X	X	X		1	12		4	17
Tubifera ferruginosa (Batsch) J.F.Gmel.	X		X				1			1
Number of taxa	**58**	**50**	**58**	**54**	**2**	**14**	**42**	**11**	**55**	**81**

(17 spp.), Stemonitidales (11 spp.), Cribrariales (6 spp.), and Echinosteliales (1 sp.). The genus *Physarum* was the most diverse with 21 species and one variety, followed by *Diderma* and *Didymium* with 8 species each. The genera *Calomyxa*, *Clastoderma*, *Licea*, *Leocarpus*, *Lamproderma*, *Macbrideola*, *Paradiacheopsis*, *Stemonitopsis*, and *Tubifera*, were represented by only one species. In terms of number of collected specimens, the most collected species were *Didymium squamulosum* and *Diderma deplanatum* with 79 and 64 collections respectively. Note that 18 taxa belonging to the genera *Arcyria*, *Calomyxa*, *Comatricha*, *Craterium*, *Diachea*, *Didymium*, *Leocarpus*, *Licea*, *Paradiacheopsis*, and *Physarum* were only identified to the genus level (indicated with "sp." in table 1).

Abundance in the plots

In the evaluated plots, 155 and 160 individuals of Myxomycetes were recorded for the wet and dry season respectively. The rank-abundance plot shows that the most commonly recorded species for the wet season was *Didymium squamulosum* (Relative Abundance, RA = 21.9%), followed by *Didymium nigripes* (RA = 18.7%), *Didymium clavus* (RA = 6.5%), *Physarum pusillum* (RA = 5.8%), and *Physarum album* (RA = 5.2%) (fig. 2A). During the dry season, the most abundant species was *Diderma deplanatum* (RA = 29.4%), followed by *Didymium nigripes* (RA = 11.9%), *Didymium squamulosum* (RA = 11.3%), *Diderma subdyctiospermum* (RA = 7.5%), and *Physarum album* (RA = 3.1%) (fig. 2B). Overall, 58.3% of the species observed during the wet season had less than three records versus 65% during the dry season. Many species were only represented by one record, i.e., 55.3% for the wet season and 38.9% for the dry season.

Alpha-beta diversity and sampling effort in the plots

The alpha diversity in the six plots, according to the Shannon index, was 4.076 bits / individual for the wet season and 3.964 bits / individual for the dry season. The similarity between the two periods was 0.46 according to the Jaccard index. A total of 50 species were recorded in the six plots. According to the Chao1 and ACE estimators, the expected number of species if the sampling effort had been exhaustive would be 59 and 65 respectively (fig. 3A). This means that our sampling represents 85% or 77% of the estimated number of species, which suggests that the sampling effort was adequate. Based on the Clench function, the expected number of species in plots would be 77 ($r^2 = 0.99997$; fig. 3B), indicating that we recorded 65% of all possible species in the sampling area. Furthermore, our EstimateS analysis showed that only 11 additional species would have been found if the sampling effort had been duplicated.

Table 2 – **Total number of records and number of species (between brackets) for the different Myxomycetes orders according to the seasons.**

Order	Wet season	Dry season
Echinosteliales		1 (1)
Cribrariales	1 (1)	2 (1)
Physarales	134 (24)	131 (25)
Stemonitidales	3 (3)	1 (1)
Trichiales	17 (8)	25 (10)
Total	**155 (36)**	**160 (38)**

Myxomycetes richness in the plots by season

The highest number of collections were made for the order Physarales during both the dry and the wet season, while the order Echinosteliales was the least represented with only one species observed during the dry season (table 2).

According to χ^2 test, the number of Myxomycete species ($\chi^2 = 2.1902$; d.f. = 4; p = 0.70083) and the number of collections per order ($\chi^2 = 3.8127$; d.f. = 4; p = 0.4319) were not different between the two seasons.

Occurrence by type of substrate

When evaluating the substrates on which the Myxomycetes were collected, we found that the foliicolous species dominated the assemblages (302 collections, 58%), followed by

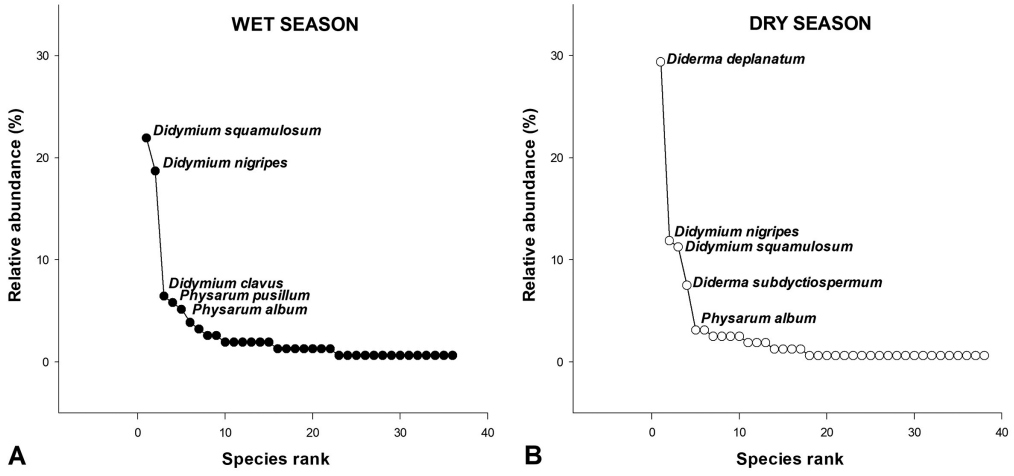

Figure 2 – Rank-abundance plots for the Myxomycete taxa found at the Wayqecha Biological Station. **A**. Wet season. **B**. Dry season.

lignicolous (A) (120 collections, 23%), muscicolous (62 collections, 11.9%), lignicolous (B) (34 collections, 6.5%), and floricolous (2 collections, 0.38%). Fifty-two of the 81 taxa (64%) were observed on a single type of substrate, of which 27 species (33.3%) were foliicolous, 21 species (25.9%) lignicolous (A), 2 species (2.5%) lignicolous (B), and 2 species (2.5%) muscicolous.

DISCUSSION

This study is, to our knowledge, the first inventory of Myxomycetes from the humid montane forests of Peru. We recorded a total of 81 taxa in 6 orders, 10 families, and 22 genera in the entire survey. The Physarales were the most diverse and abundant order, with a total of 45 species and 402 collections. Our data show a higher Physarales species richness as compared to the humid montane forests in Ecuador (Schnittler et al. 2002) or to the Amazonian lowlands in Peru (Rojas 2013), where only 32 and 20 species of Physarales were recorded respectively. This may be due to the higher amount of organic litter and the variety of substrates in the forest, which is enhanced by the presence of hemiepiphytic and epiphytic plants that are very abundant in WBS. Another explanation could be the timing of the survey, since Schnittler et al. (2002) performed their study during September–October, while this study was performed at two different periods of the year, i.e., late January and early May.

The order Physarales was also the most diverse and abundant in the surveyed plots. It is represented there by 30 taxa, with *Didymium squamulosum*, *Didymium nigripes*, and *Diderma deplanatum* as the most abundant species. However, notable changes among their populations were observed according to the season. *Didymium squamulosum* and *Didymium nigripes*, the most abundant species during the wet season, declined with almost 40% during the dry season. In contrast, *Diderma deplanatum* increased its population size 8-fold from the wet to the dry season, becoming the most abundant species in the dry season. This suggests that the most suitable conditions for the fructification of *D. deplanatum* occurs during the dry season. The type of substrate seems to be important for the development of Myxomycetes fructifications in humid montane forests as well: *D. squamulosum* and *D. nigripes* clearly behaved as foliicolous species, while *D. deplanatum* is muscicolous. It is possible that the latter species is favoured because of its tendency to grow on mosses, which, in addition to being abundant, also retain water well during dry conditions; this in contrast to forest litter.

The species richness found in the plots was higher than in other similar studies in the Neotropics. Rojas & Stephenson (2007) found less species (37 vs. 50 in our work) in Costa Rica, despite a larger plot size (20 × 50 m vs. 10 × 10 m in our study). This difference is probably related to the habitat type and productivity of the dominant trees: Costa Rican sites were dominated by *Quercus costaricensis* versus *Weinmannia*, *Myrsine*, and *Clethra* in WBS.

The percentage of species found only once reached 55.3% during the wet season and 38.9% during the dry season. Similar values were obtained by Schnittler & Stephenson (2000) in moist chamber cultures from Costa Rica, where 58.3% of the taxa were represented by ≤ 3 records. This suggest that some factors might affect the fruiting rate of Myxomycetes in the humid montane forest. According to Stephenson (1989), one of these factors might be the pH of the substrates, which is considered to be important in determining myxomycete abundance and distribution patterns.

Our results are different from those obtained in the Peruvian lowland Amazon (Rojas & Stephenson 2013) where the substrate with the highest abundance of Myxomycetes was decaying wood versus leaf litter in our study. This might be due to higher humidity in humid montane forest leaf litter as compared to lowland forest litter due to the characteristic presence of fog in this habitat. Also, the thickness of the leaf litter (> 10 cm) offers Myxomycetes a moisture gradient between adjacent leaves, allowing the plasmodia to move towards different layers of leaves according to their requirements, or start the development of sporophores. This behaviour of the plasmodia was also observed in a warm temperate forest in western Japan (Takahashi 2015). Plasmodia grew within the wet lower layers of the large accumulations of

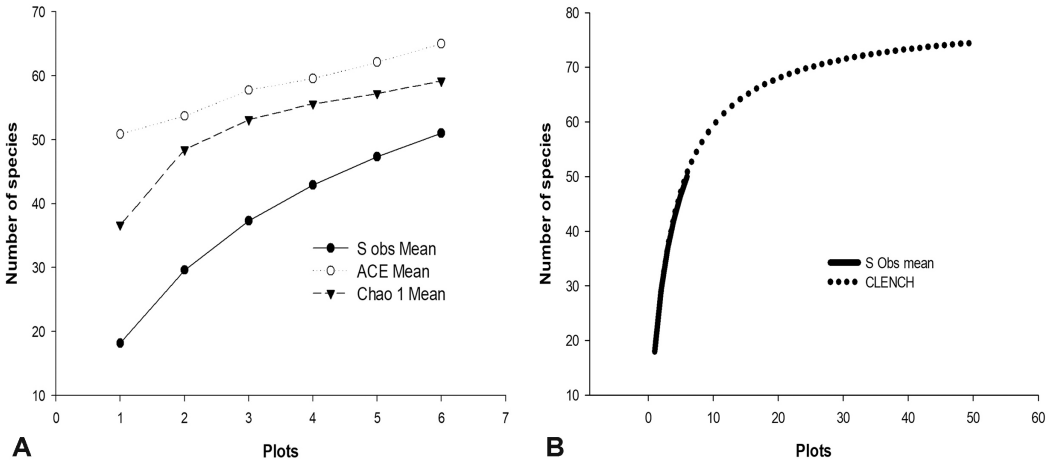

Figure 3 – **A**. Species accumulation curves using ACE and Chao1. **B**. Species accumulation curve using the Clench adjustment. Photographs by Italo Treviño.

leaves before migrating to the drier upper layers and finally fruiting on the surface leaves. This behaviour increases survival chance and allows sclerotizing and subsequent recovery of the plasmodium when humidity and temperature become favourable again (Tran et al. 2006). Likewise, a well-defined stratification of Myxomycete composition on leaf litter may result from the effects of competition and/or other microenvironmental influences (Rollins & Stephenson 2012).

The alpha diversity has a similar value for both seasons (see Shannon index), yet the most abundant species are different between the seasons (see Jaccard index). If we consider all recorded species in WBS, more than 60% were only observed during a single season, suggesting the existence of two communities that fructify at different periods of the year. Similar observations were made for Myxomycete communities in different forest types in northern Thailand (Ko Ko et al. 2011), where only 41.8% of the species recorded were common either during the warm-wet or during the cool-dry season. However, a much larger sampling period (3–5 years) would provide more conclusive data.

The estimators Chao1 and ACE, as well as the Clench function, indicate a higher richness of species expected than recorded. It is possible that some species have not been recorded because they did not develop sporophores during the sampling period. Their state of development (spore, plasmodium, or amoeba) may be undetectable in the field (Gao et al. 2018; Shchepin et al. 2019). The moist chamber approach is a valuable alternative to direct field observation to detect small and inconspicuous species. Here, *Licea* sp. 1 and *Macbrideola spinosispora*, two species making extremely small sporophores (0.4 mm, only observable at a 20× magnification) were only observed in moist chambers. However, the number of positive cultures obtained in this study (30%) is low compared to other studies (Schnittler et al. 2002; Rojas & Stephenson 2013). On the other hand, the use of an intensive survey, as a complementary method to the use of plots, allowed for a better approximation of the real number of species that inhabit the study area.

Although it has been suggested (Liu et al. 2015) that the elevated air moisture found in humid forests does not favour Myxomycetes, we found a considerable species richness in humid montane forests. As Tran et al. (2006) indicated, the taxonomy and ecology of the assemblages of tropical Myxomycetes is still incompletely known. Many biomes have still not been surveyed for Myxomycetes, be it in Peru or in other Neotropical countries, which suggests that further explorations will probably yield many new discoveries.

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REFERENCES

Clarke K.R., Gorley R.N. (2005) PRIMER: getting started with v6 (Plymouth routines in multivariate ecological research). Plymouth, PRIMER-E Ltd.

Colwell R. (2013) EstimateS, version 9.1.0. Statistical estimation of species richness and shared species from samples. Available at http://viceroy.eeb.uconn.edu/estimates [accessed 14 Aug. 2020].

Colwell R., Coddington J. (1994) Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society* 345(1311): 101–118. https://www.jstor.org/stable/56143

Colwell R.K., Mao C.X., Chang J. (2004) Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology* 85(10): 2717–2727. https://doi.org/10.1890/03-0557

Esri (2014) ArcGIS for Desktop, version 10.2.2. Environmental Systems Research Institute, Redlands, CA, USA. Available at http://www.esri.com/ [accessed 17 Aug. 2020].

Farr M. (1976) The Myxomycetes. Flora Neotropica Monograph No. 16. New York, New York Botanical Garden Press

Gao Y., Yan S., Wang G., He G., Chen S. (2018) Myxomycete diversity and ecology in the Baotianman national nature reserve, a subtropical mountain forest in central China. *Fungal Ecology* 35: 10–19. https://doi.org/10.1016/j.funeco.2018.06.002

Ing B. (1994) The phytosociology of Myxomycetes. *New Phytologist* 126(2): 175–201. https://doi.org/10.1111/j.1469-8137.1994.tb03937.x

Jiménez-Valverde J., Hortal J. (2003) Las curvas de acumulación de especies y la necesidad de evaluar la calidad de los inventarios biológicos. *Revista Ibérica de Aracnología* 8: 151–161.

Keller H.W., Everhart S.E. Kilgore C.M. (2017) The Myxomycetes: introduction, basic biology, life cycles, genetics, and reproduction. In: Stephenson S.L., Rojas C. (eds) Myxomycetes. Biology, systematics, biogeography and ecology: 1–40. San Diego, Elsevier. https://doi.org/10.1016/B978-0-12-805089-7.00001-9

Ko Ko T.W., Stephenson S.L., Hyde K.D., Lumyong S. (2011) Influence of seasonality on the occurrence of myxomycetes. *Chiang Mai Journal of Science* 38: 71–84.

Lado C. (2005–2020) An online nomenclatural information system of Eumycetozoa. Real Jardín Botánico, CSIC, Madrid, Spain. Available at https://www.nomen.eumycetozoa.com [accessed 20 Jan. 2020].

Lado C., Pando F. (1997) Myxomycetes, I. Ceratiomyxales, Liceales, Echinosteliales Trichiales. *Flora Mycologica Iberica*, vol. 2. Madrid, Berlin, Stuttgart, Real Jardín Botánico, CSIC - J. Cramer.

Lado C., Wrigley de Basanta D., Estrada-Torres A., Stephenson S.L. (2016) Myxomycete diversity in the coastal desert of Peru with emphasis on the lomas formations. *Anales del Jardín Botánico de Madrid* 73(1): e032. https://doi.org/10.3989/ajbm.2436

Lado C., Estrada-Torres A., Wrigley de Basanta D., Schnittler M., Stephenson S.L. (2017) A rapid biodiversity assessment of Myxomycetes from a primary tropical moist forest of the Amazon basin in Ecuador. *Nova Hedwigia* 104(1–3): 293–321. https://doi.org/10.1127/nova_hedwigia/2016/0372

Lado C., Wrigley de Basanta D., Estrada-Torres A., Stephenson S.L., Treviño-Zevallos I. (2019) Diversity of Myxomycetes in arid zones of Peru part II: the cactus belt and transition zones.

Anales del Jardín Botánico de Madrid 76(2): e083. https://doi.org/10.3989/ajbm.2520

Liu Q.S., Yan, S.Z., Chen S.L. (2015) Species diversity of Myxomycetes associated with different terrestrial ecosystems, substrata (microhabitats) and environmental factors. *Mycological Progress* 14: 27. https://doi.org/10.1007/s11557-015-1048-9

Martin G.W., Alexopoulos C.J. (1969) The Myxomycetes. Iowa, University of Iowa Press.

Medina C., Zeballos H., López E. (2012) Diversidad de mamíferos en los bosques montanos del valle de Kosñipata, Cusco, Perú. *Mastozoología neotropical* 19(1): 85–104.

Nannenga-Bremekamp N.E. (1991) A guide to temperate Myxomycetes. Bristol, Biopress Limited.

O'Dell T.E., Lodge D.J., Mueller G.M. (2011) Approaches to sampling Macrofungi. In: Mueller G.M., Bills G., Foster M.S. (eds) Biodiversity of fungi: inventory and monitoring methods: 163–168. San Diego, Elsevier.

Poulain M., Meyer M., Bozonnet J. (2011) Les Myxomycètes. Sévrier, Fédération Mycologique et Botanique Dauphiné – Savoie.

Repasky R., Janovec J., Christenson E., Pinder J., Barfield K. (2010) Diversity and abundance of orchids in a Peruvian cloud forest. *Journal of the Botanical Research Institute of Texas* 4: 317–332. https://www.jstor.org/stable/41972014

Rivera G. (2007) Composición florística y análisis de diversidad arbórea en un área de bosque montano en el centro de investigación Wayqecha, Kosñipata Cusco. Degree Thesis. Universidad Nacional Agraria La Molina, Perú.

Rojas C., Stephenson S.L. (2007) Distribution and ecology of Myxomycetes in the high-elevation oak forests of Cerro Bellavista, Costa Rica. *Mycologia* 99: 534–543. https://doi.org/10.3852/mycologia.99.4.534

Rojas C., Stephenson S.L. (2013) Effect of forest disturbance on Myxomycete assemblages in the southwestern Peruvian Amazon. *Fungal Diversity* 59: 45–53. https://doi.org/10.1007/s13225-012-0181-x

Rojas C., Stephenson S.L., Pavlich M. (2011) New additions to the Myxobiota of Peru. *Mycosphere* 2(5): 583–592. https://doi.org/10.5943/mycosphere/2/5/8

Rollins A.W, Stephenson S.L. (2012) Myxogastrid distribution within the leaf litter microhabitat. *Mycosphere* 3(5): 543–549. https://doi.org/10.5943/mycosphere/3/5/2

Shchepin O.N, Schnittler M., Dagamac N.H.A, Leontyev D.V., Novozhilov Y.K. (2019) Unexplored diversity of microscopic Myxomycetes: evidence from environmental DNA. *Plant Ecology and Evolution* 152(3): 499–506. https://doi.org/10.5091/plecevo.2019.1621

Schnittler M., Stephenson S.L. (2000) Myxomycete biodiversity in four different forest types in Costa Rica. *Mycologia* 92(4): 626–637. https://doi.org/10.1080/00275514.2000.12061203

Schnittler M., Lado C., Stephenson S. (2002) Rapid biodiversity assessment of a tropical Myxomycete assemblage - Maquipucuna Cloud Forest Reserve, Ecuador. *Fungal Diversity* 9: 135–167.

Statsoft Inc (2013) Statistica (data analysis software system) v.12. Available at https://www.tibco.com/resources/product-download/tibco-statistica-trial-download-windows [accessed 14 Aug. 2020].

Stephenson S. (1989) Distribution and ecology of Myxomycetes in temperate forests. II. Patterns of occurrence on bark surface of living trees, leaf litter, and dung. *Mycologia* 81(4): 608–621. https://doi.org/10.2307/3760136

Stephenson S.L., Kalyanasundaran I., Lakhanpal T.N. (1993) A biogeographical comparative study of Myxomycetes in the mid-Appalachians in the eastern North America and two regions of India. *Journal of Biogeography* 20(6): 645–657. https://doi.org/10.2307/2845520

Takahashi K. (2015) Distribution of Myxomycetes on varied leaf litter types in a mixed forest in warm-temperate western Japan. *Open Journal of Forestry* 5: 686–696. https://doi.org/10.4236/ojf.2015.57061

Tejedor N., Alvarez E., Arango S., Araujo A., Blundo C., Boza T., La Torre M.A., Gaviria J., Gutierrez N., Jørgensen P., León B., López R., Malizia L., Millán B., Moraes M., Pacheco S., Rey J., Reynel C., Timana de la Flor M., Ulloa C., Vacas O., Newton A. (2012) Evaluación del estado de conservación de los bosques montanos en los Andes tropicales. *Ecosistemas* 21(1–2): 148–166.

Tran T.M.H., Stephenson S.L., Hyde K.D., Mongkolporn O. (2006) Distribution and occurrence of Myxomycetes in tropical forests of northern Thailand. *Fungal Diversity* 22: 227–242.

Treviño-Zevallos I., Lado C. (2020) New records of Myxomycetes from Peru. *Check List* 16(2): 253–264. https://doi.org/10.15560/16.2.253

Wrigley de Basanta D., Lado C., García-Martín J.M., Estrada-Torres A. (2015) *Didymium xerophilum*, a new myxomycete from the tropical Andes. *Mycologia* 107(1): 157–168. https://doi.org/10.3852/14-058

Wrigley de Basanta D., Estrada-Torres A. (2017) Techniques for recording and isolating Myxomycetes. In: Stephenson S.L., Rojas C. (eds) Myxomycetes. Biology, Systematics, Biogeography and Ecology: 333–363. San Diego, Elsevier. https://doi.org/10.1016/B978-0-12-805089-7.00010-X

Wrigley de Basanta D., Estrada-Torres A., Lado C. (2019) *Licea aurea* a new Myxomycete from the Peruvian Andes. *Phytotaxa 391*(3): 218–224. https://doi.org/10.11646/phytotaxa.391.3.5.

Young K.R., León B. (1999) Peru's humid Eastern montane forests: an overview of their physical settings, biological diversity, human use and settlement, and conservation needs. DIVA Technical Report 5. Kalø, Denmark, Centre for Research on the Cultural and Biological Diversity of Andean Rainforests (DIVA).

Zar J.H. (1996) Biostatistical analysis. New Jersey, Prentice Hall.

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