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Ecological characterization of a tropical myxomycete assemblage—Maquipucuna Cloud Forest Reserve, Ecuador

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Abstract: The assemblage of myxomycetes (plasmodial slime molds) associated with cloud forests of the Maquipucuna Cloud Forest Reserve in the western Andes was investigated. Within three study sites located along a gradient extending from 1200 to 2700 m above sea level, a clear pattern of decreasing myxomycete diversity and productivity with elevation was apparent. As such, these data conform to the pattern of ''reverse diversity'' for myxomycetes in the neotropics, with higher diversity for less mesic forest types than for more mesic forest types. Canonical correspondence analysis of myxomycete abundances in relation to microhabitat parameters revealed three major ecological assemblages: wood-, litter- and inflorescence-inhabiting species. All three assemblages include a number of specialized species, with the assemblage associated with litter being the most diverse and the one associated with inflorescences being the most distinctive. In addition, samples from the microhabitat represented by the cover of epiphyllic liverworts on living leaves regularly produce myxomycetes in moist chamber culture but with few sporocarps and no evidence of any specialized species. At least near ground level, bark-inhabiting (corticolous) myxomycetes are uncommon in the cloud forests sampled in the present study.

Key words: biodiversity, cloud forest, distribution, ecology, western Andes

INTRODUCTION

The myxomycetes (plasmodial slime molds) are a small group of fungus-like organisms, with approximately 875 species described worldwide (Lado 2001). The majority of species are probably cosmopolitan, but a few species appear to be confined to the tropics or subtropics and some others have been collected only in temperate regions (Alexopoulos 1963, Farr 1976, Martin et al 1983). Myxomycetes appear to be particularly abundant in temperate forests, but at least some species apparently occur in any terrestrial ecosystem with plants and plant detritus (Stephenson and Stempen 1994). For example, they have been reported from deserts (e.g., Blackwell and Gilbertson 1980) and high-latitude tundra (Stephenson and Laursen 1993), where harsh environmental conditions place severe constraints on living organisms.

Most of what is known about the assemblages of myxomycetes associated with particular types of terrestrial ecosystems has been derived from studies carried out in temperate regions of the Northern Hemisphere; few studies have been conducted in tropical/subtropical regions of the world (Schnittler and Stephenson 2002). The purpose of this study was to obtain data on the ecology and biodiversity of the assemblage of myxomycetes associated with the Maquipucuna Cloud Forest in the western Andes of South America. Specific objectives were (i) to characterize the assemblage of commonly occurring species by assessing their abundances and (ii) to obtain data on the distribution of myxomycetes along an elevational gradient. Microhabitat preferences and taxonomic descriptions of all the species of myxomycetes encountered are provided in Schnittler et al (2002).

MATERIALS AND METHODS

Study sites.—The Maquipucuna Cloud Forest Reserve has been described by Schnittler et al (2002). Within this reserve, three study sites were selected; each of these represented a different type of primary forest, with no or only a limited degree of human disturbance at the lowermost site.

Study site 1 (Moist Forest, abbreviation *MF*) is situated in a small valley ca. 1.2 km SW of the Maquipucuna Foundation Lodge, elevation 1300 ± 100 m (00°07′15″N, 78°38′05″W ± 250 m). The annual rainfall at this site is approximately 2500 mm (2453 mm registered at the village of Nanegalito, ca. 5 km SW of the study site and situated at approximately the same elevation). In spite of this rather high value, the influence of a dry season is still appreciable, with less than 100 mm average monthly rainfall from May

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to November. Leaves of understory shrubs, as well as the litter layer on the forest floor, can dry out almost completely during a week without rain. The canopy, formed by trees with medium to large evergreen leaves, is closed except for tree fall gaps and stream valleys. The bark of trees at this site ranges from smooth to deeply furrowed or flaky but is mostly soft and noticeably hydrophilic. It is covered by thin mats of leafy liverworts in sheltered places but also frequently occurs free of epiphytes. Lianas as well as climbing plants belonging to the family Araceae are common, whereas other epiphytes are rather rare. Along small streams and in slightly disturbed areas near the Lodge, tall herbs of the order Zingiberales were locally abundant, particularly *Costus guanaiensis* Rusby and *Heliconia griggsiana* L.B. Sm. (names follow Jørgensen and León-Yánez [1989]), with their decaying floral parts providing a microhabitat only recently known to support myxomycetes (Schnittler and Stephenson 2002). The forest at this site can be assigned to the Tropical Moist Forest type sensu Holdridge et al (1971).

Study site 2 (Wet Forest, *WF*) is a middle-elevation cloud forest, located near the NNW-exposed first summit of the Cerro de Sosa massif, ca. 3.5 km S of the Maquipucuna Foundation Lodge, elevation 1900 ± 150 m (00°05′40″N, 78°37′00″W ± 1 km). Annual rainfall is probably 3300–3700 mm, and daily cloud exposure is common during the dry season. The almost closed forest canopy is formed by tall evergreen trees, with members of the families Clusiaceae, Cunoniaceae and Lauraceae the most abundant. The influence of the dry season is much less apparent than at Site 1, with rainfall common also during May–November. The litter layer on the forest floor stays continuously wet in deeper layers and leaves of understory plants are covered with thin but nearly closed mats of epiphyllic liverworts, sometimes mosses. The bark surface of most trees is covered with a thick, almost closed mat of mosses and liverworts. Bark texture is mostly smooth or slowly peeling, with large but smooth flakes. Members of the family Araceae are the predominant epiphytic plants; lianas are considerably less common than at Site 1. In the Holdridge classification, this site would be assigned to the Tropical Premontane Wet Forest.

Site 3 (Rain Forest, *RF*) is a high-elevation cloud forest near the highest summit (Cerro Montechristi) of the Maquipucuna Reserve, elevation 2700 ± 75 m, (00°03′15″N 78°35′55″W ± 500 m). Annual rainfall probably is 3500–4000 mm, with daily, long periods of cloud exposure occurring during the dry season. At this elevation, no real dry season occurs. Long curtains of epiphytic mosses, together with a lush cover of epiphytic bromeliads, ferns and members of the family Cyclanthaceae are characteristic features of this cloud forest. However, true lianas are absent. The litter layer on the forest floor stays continuously wet throughout the year and is often covered by a film of water. Leaf surfaces of understory plants dry out for only a short period during the day or remain wet. Trees are small, 10–20 m tall, and the canopy is only about 70% closed. The bark of trees is almost completely covered with lush, 2–5 cm thick mats of mostly mosses and hymenophyllaceous ferns. In the Holdridge system, this site would be considered Tropical Lower Montane Rain Forest.

Sampling procedures.—Within each of the three study sites, series of substratum samples from the different microhabitats being investigated were collected along a transect ca. 200 m in length. Over a distance of no more than 10 m, several samples were collected and pooled to produce a composite sample of 15–25 g for each substratum type. Sampling was repeated as often as necessary over the transect to obtain an adequate sample size. As noted above, the study sites differed somewhat in the types of microhabitats present, so the numbers of samples collected varied at each site. Immediately after the field survey, all samples were placed in moist chamber cultures and maintained for up to 4 mo (see Schnittler et al [2002] for more detail). In addition to collecting substratum samples, a ca. 2.5 km portion of the trail (and extending out to about 3 m on each side) through the study site was examined carefully for the presence of myxomycete fruiting bodies on three occasions during the period of the survey, and the actual period of time spent looking for myxomycetes was noted.

For both samples and collections of myxomycete fruiting bodies, data on a series of microhabitat parameters were recorded. The substratum type was classified as *b* for bark of living trees, *w* for decaying wood, *ll* for leafy litter on the forest floor, *la* for leafy aerial litter (still attached or trapped in the branches of understory shrubs and trees), *lh* for litter of fleshy herbaceous plants, *lw* for decaying stems of aerial lianas, *ep* for covers of epiphyllic liverworts on living leaves of understory shrubs and small trees and *li* for living inflorescences of tall herbs, all belonging to the order Zingiberales. Measurements were recorded for substratum pH, using a flat surface electrode and an Orion model 610 pH meter, substratum diameter (or thickness), and sampling height. The stage of decomposition of coarse woody debris and forest floor litter was estimated and then assigned to one of five classes: 1, dead but still not decayed substrata (e.g., corky layers of bark, recently fallen trunks and branches of trees, completely intact leaves); 2, slightly decayed (wood with bark still attached but the cambium already decayed, wood solid [only the tip of a knife penetrates], leaves decolored but the basic structure still preserved); 3, moderately decayed (wood with loose bark or already decorticated, wood still firm but appearing softer and often with abundant fungal growth [knife penetrates when firm pressure is applied], leaves with a partly destroyed structure); 4, strongly decayed (wood partly destroyed, mostly decorticated, soft and of spongy consistency, easily broken by hand [knife penetrates easily], leaves thoroughly destroyed, single leaves not recognizable); and 5, almost completely decayed (shapeless, soft masses of destroyed wood, destroyed leaf remnants). The extent of contact of the substratum with the ground was estimated as 1, high above ground (usually more than 1 m); 2, near the ground but no direct contact; 3, partial contact with the ground; 4, lying directly on the ground, thus taking up moisture from the soil; and 5, half buried in the soil or noticeably at the soil-litter interface. Substratum moisture at the time of collecting was roughly estimated as 1, dry; 2, moist; 3, wet (water-saturated); and 4, covered with a film of water. Using a similar scale, three microclimate parameters of the immediate environment of the substratum were estimated as means of

the probable prevailing conditions each day: light intensity (ranging from 1, full sun, to 5, full shade), wind exposure (4 classes), and air moisture (1, rather dry; 2, moist; and 3, saturated most of the day).

For all field and moist chamber records of myxomycetes, numbers of sporocarps were determined or (for such species as *Lycogala epidendrum*) the respective volume of an aethalium or pseudoaethalium estimated. For *Ceratiomyxa,* the total coverage (i.e., square centimeters occupied by the entire fruiting) was noted. For statistical analyses, all these absolute measures were converted into weighted abundances. The latter were calculated by dividing the absolute measures (e.g., number of sporocarps) by the mean value obtained for all records for a particular species. Consequently, the sum of all weighted abundances for a particular species is equal to the number of records. For example, *Arcyria cinerea* was represented by 108 records (25 from specimens obtained as field collections and 83 from specimens appearing in moist chamber culture). This figure (108) is the same as the sum of the individual values calculated for weighted abundance (e.g., 0.1 + 1.7 + 0.6 + 1.6 + 104.0 = 108) of *A. cinerea* on each substratum type. Such weighted abundances were used for all comparative analyses because they equalize inherent differences in the ratio of sporocarp number per fruiting/average sporocarp size that exist for some species of myxomycetes (e.g., for an *Echinostelium,* 200 sporocarps is a relatively small fruiting, but for a *Physarum* this would represent a rather large fruiting). It was assumed that sporocarps that shared the same substratum and were separated by a distance that could be overcome by a migrating plasmodium had been derived from the same plasmodium (sensu Stephenson 1988). These were considered as representing one record.

Data analysis.—Diversity indices were calculated for the various datasets by using Shannon's formula (Shannon and Weaver 1963):

$$\text{diversity } (H') = -\sum (P_i \ln P_i)$$

where P_i is the proportion (in terms of weighted abundance) of all records represented by species *i.* Preferences of species for a certain substratum type were calculated as the percentage of the total records of this species occurring on the respective substratum.

Canonical correspondence analysis (CCA), as described by ter Braak (1986, 1987a), was used to determine the response of the myxomycete assemblage to environmental factors. Each myxomycete record was coded in the environmental dimensions according to the states described above for each parameter. For pH, substratum diameter and sampling height, numerical values were used. For all myxomycete records, weighted abundance values were used. The given eigenvalues, ranging between 0 and 1, are a measure for the degree in which species distribution can be explained by the respective ordination axis (ter Braak 1987b). Calculations were carried out with the program CANOCO (Ter Braak 1988). For biplots, species scores and those of the environmental variables on the canonical axes were symmetrical scaled to mean 1 and SD 1. The centroids of the environmental variables were associated with species by a Euclidian distance matrix. More detailed information on the use of these methods to analyze distributional relationships in myxomycetes is provided by Schnittler (2001b) and Schnittler and Stephenson (2002).

RESULTS

Of the 1033 records of myxomycetes generated in the present study, 936 (with 564 of those collected in the field and 443 obtained from moist chamber cultures) could be determined to species and were considered in the subsequent ecological analyses. The annotated species list (see Schnittler et al [2002]) consists of 77 taxa, which yields a Shannon diversity index of 4.98. TABLE I shows the statistical data for the 36 more common species (i.e., those classified as at least occurring occasionally in Schnittler et al [2002]). Almost half these taxa belong to the order Physarales, members of which are characterized by a phaneroplasmodium, which is robust, can achieve considerable size in some species and appears to tolerate the two extremes of the moisture gradient better than the other types of plasmodia found in myxomycetes. None of the more common species recorded in the present study produces a protoplasmodium.

Myxomycete distribution in the investigated forest types.—Although the initial sampling effort was essentially the same for each of the three study sites, remarkable differences were apparent with respect to the relative abundance of fruitings in the field (TABLE II). With the hours spent by the first two authors for field collecting tallied, the number of fruitings observed per hour was calculated. If the value for Site 1 (Moist Forest, 6.9) is considered as 100%, myxomycete abundance for sites 2 (Wet Forest) and 3 (Rain Forest) were only 37% and 21%, respectively. The same trend was evident when assessing productivity of the moist chamber cultures. With a mean of 1.05 records per moist chamber culture for site 1 considered as 100%, values for sites 2 and 3 were 93% and 58%, respectively. TABLE III presents results for the four types of substrata (bark of living trees, forest floor litter, aerial leafy litter and leaves with a cover of epiphyllic liverworts) available at all three sites. Although productivity varied widely among the substratum types, all displayed a pattern of decreasing productivity with increasing elevation. When reviewing absolute numbers of field records for the three study sites (TABLE II), the two higher elevation sites (*WF* and *RF*) produced only 18% and 9% of the total records for litter- and wood-inhabiting myxomycetes, respectively.

A similar pattern holds true for species diversity (TABLE II). The highest number of species (66) was recorded for Site 1 (Moist Forest), at the lowest ele-

vation, and all but two of the species recorded from the field (*Fuligo septica* and *Trichia varia*) were present. Site 2 (Wet Forest) had a significantly lower number (14) of species. Records obtained from moist chamber cultures followed the same pattern, with the number of species (13) recorded from Site 2 less than half the number (28) for Site 1. When comparing the results for moist chamber cultures prepared with samples from comparable substratum types, all types showed lower diversity values at higher elevations (TABLE III). This trend was strongest for litter substrata and least pronounced for the substratum type represented by covers of epiphyllic liverworts on living leaves.

The mean numbers of sporocarps per record generally were greater for field collections than for collections obtained from moist chamber cultures (TABLE II). Also, for this parameter, the highest study site seems to be less productive than the two at lower elevations (TABLES II, III).

Myxomycete-substratum relationships.—Litter (consisting of the substratum types *ll, la, lh* and *lw,* as defined under Materials and Methods) was the most productive substratum, both in terms of records as well as in terms of species, with 56 species identified from 485 records (284 from the field, including five plasmodia and eight indeterminable collections; 201 from moist chamber cultures, including 57 plasmodia). Decaying wood was the substratum recorded for 34 species from 222 records (all from the field, including four indeterminable collections). An unexpected result was the discovery of two substratum types as new for myxomycetes. The first of these is represented by the cover of epiphyllic liverworts that occurs on living leaves (10 species from 141 records, all from moist chamber, including two plasmodia). The second consists of the decaying corolla and other flower parts on otherwise living (seed-producing) inflorescences of living plants (14 species from 166 records, 76 observed in the field, including eight indeterminable collections and 90 from moist chamber cultures, including 10 plasmodia). Myxomycetes associated with these substratum types are the subject of two papers (Schnittler 2001a, Schnittler and Stephenson 2002). Bark of living trees was relatively unproductive (14 species from 18 records, eight from the field, 10 from moist chambers, including two plasmodia).

Of the 34 species inhabiting wood (substratum type *w*), 30 were found exclusively on this substratum and the average specificity of a wood-inhabiting species was 75%. Average specificity values were lower for litter (substratum types *ll, la, lh* and *lw,* 57 species, 66%), bark (*b,* 14, 59%), inflorescences (*in,* 14, 53%) and epiphyllic liverworts (*ep,* 10, 33%). Shannon diversity indices were highest for litter (4.73), followed by wood (4.34), bark (3.66), inflorescences (3.17) and epiphyllic liverworts (2.10).

A rather high proportion of all myxomycete records originated from substrata above the ground. For litter (substratum types *ll, la, lh* and *lw*) as well as for wood, about one-third (94 of 284 collections [32.8%]; and 75 of 230 collections [32.6%]) of all field collections came from aerial substrata that were not in direct contact with the ground. In addition, living inflorescences as well as leaves with a cover of epiphyllic liverworts are two substratum types found only above the ground.

The biplot of the CCA for all myxomycete records that could be determined to species (FIG. 1) reveals three separate myxomycete assemblages, the first inhabiting litter, the second associated with wood and the third found on inflorescences. The assemblage associated with litter was the most species rich (19 of 36 of the more common myxomycetes, see TABLE I), with most of the species present apparently adapted to substrata with a circumneutral pH. The assemblage associated with wood (13 of the more common species) contains a number of examples adapted to substrata with a rather acidic pH, including a few specialists such as *Ceratiomyxa morchella* (two records with substratum pH values of 3.7 and 4.0, respectively). Inflorescences harbour the most distinctive species assemblage, with four of the more common species clearly preferring this substratum, all apparently adapted to the high pH characteristic of this substratum type. Other than the substratum type (i.e., wood, litter and inflorescences) itself, pH appears to be the single most important environmental parameter. For obvious reasons (i.e., the host species of *Heliconia* and *Costus* inhabit forest gaps and inflorescences develop 2.5–3.5 m above ground), sampling height, light intensity and wind exposure classify with the substratum type represented by inflorescences. Substratum and air moisture tend to be higher on decaying wood, and no myxomycete species was clearly associated with substrata in contact with the ground (parameter soil), which keeps these substrata from drying out. The parameters litter and bark are close to each other because a few species with a preference for litter (e.g., *Didymium clavus* and *D. squamulosum*) were found occasionally on bark. Among litter-inhabiting myxomycetes, *Didymium nigripes, Diderma hemisphaericum* and the species of *Craterium* are common, whereas the most common species (*Didymium iridis*) behaves as a generalist, occurring frequently also on inflorescences and in association with epiphyllic liverworts (TABLE I). *Hemitrichia calyculata* and *H. serpula,* the latter requiring high substratum

TABLE I. Summary data on numbers of records (rec) and sporocarps for field collections and those from moist chamber cultures, numbers of records and weighted abundances (abu) for the main substratum types and pH (mean values and range) for the more common (≧ 5 records) species of myxomycetes recorded in the present study

		Field collections			Moist chamber culture collections			Substratum type[b]										pH[c]	
			Sporocarps[a]			Sporocarps[a]		*b*		*l*		*in*		*ep*		*w*			
Scientific name	Abbr.	Rec	Sum	Mean	Rec	Sum	Mean	Rec	Abu	Rec	Abu	Rec	Abu	Rec	Abu	Rec	Abu	Mean	Range
Arcyria cinerea	ARCcin	25	12 809	512	83	594	7	1	0.1	32	1.7	11	0.6	41	1.6	**23**[d]	**104.0**	7.0	3.5–8.8
Arcyria denudata	ARCden	24	6822	284	—			—		2	1.1	—		—		**22**	**22.9**	5.8	3.5–7.0
Arcyria globosa	ARCglo	9	670	74	1	2	2	—		**10**	**10.0**	—		—		—		6.8	5.8–7.6
Ceratiomyxa fruticulosa	CERfru	37	n.d.		—			—		4	4.0	—		—		**33**	**33.0**	5.6	3.3–7.7
Comatricha pulchella	COMpul	4	195	49	2	4	2	—		**5**	**5.9**	—		1	0.1	—		6.9	5.7–7.9
Craterium aureum	CRAaur	7	3795	542	—			—		**7**	**7.0**	—		—		—		6.8	6.2–7.1
Craterium leucocephalum	CRAleu	26	12 469	480	—			—		**26**	**26.0**	—		—		—		6.9	6.3–7.6
Cribraria cancellata	CRIcan	15	5530	369	—			—		—		—		—		**15**	**15.0**	5.5	4.2–7.1
Cribraria intricata	CRIint	5	2300	460	—			—		1	0.9	—		—		**4**	**4.1**	4.6	3.3–6.5
Cribraria tenella	CRIten	15	13 863	924	—			—		1	0.0	—		—		**14**	**15.0**	5.3	3.5–6.5
Diderma effusum	DIDeff	13	811	62	2	16	8	—		**13**	**14.7**	—		2	0.3	—		7.1	6.6–8.2
Diderma hemisphaericum	DIDhem	16	454	28	6	41	7	—		**21**	**21.9**	—		1	0.1	—		6.9	4.4–7.9
Didymium anellus	DDYane	7	2120	303	2	14	7	—		**9**	**9.0**	—		—		—		7.1	6.4–8.3
Didymium bahiense	DDYbah	12	2015	168	—			2	0.3	**6**	**10.6**	4	1.1	—		—		7.6	6.0–9.2
Didymium clavus	DDYcla	14	1300	93	2	9	5	—		**16**	**16.0**	—		—		—		7.0	6.3–7.9
Didymium iridis	DDYiri	16	1606	100	95	1012	11	—		**57**	**78.8**	11	16.4	43	15.8	—		7.5	5.7–8.9
Didymium nigripes	DDYnig	15	2855	190	—			—		**15**	**15.0**	—		—		—		7.1	6.4–8.8
Didymium squamulosum	DDYsqu	27	7564	280	53	302	6	1	10.2	**30**	**62.2**	7	4.9	42	2.8	—		7.5	5.4–9.2
Hemitrichia calyculata	HEMcal	38	2600	68	—			—		1	0.4	—		—		**37**	**37.6**	6.0	3.3–7.4
Hemitrichia serpula	HEMser	19	5280	278	—			—		**10**	**12.3**	—		—		9	6.7	7.0	4.3–9.2
Lamproderma arcyrionema	LAManm	5	240	48	2	65	33	—		**5**	**3.6**	—		—		2	3.4	6.6	3.5–7.9
Lamproderma scintillans	LAMsci	3	80	27	16	224	14	1	2.8	**17**	**15.9**	—		1	0.3	—		7.0	6.3–7.6
Lycogala epidendrum	LYCepi	6	n.d.		—			—		—		—		—		**6**	**6.0**	6.3	5.1–7.5
Metatrichia floriformis	METflo	5	345	69	—			—		—		—		—		**5**	**5.0**	5.7	4.4–6.3
Perichaena cf. *dictyonema*	PERdic	—			14	406	29	—		1	0.5	**13**	**13.5**	—		—		8.3	7.9–8.8
Perichaena vermicularis	PERver	4	97	24	15	33	2	—		6	7.3	**13**	**11.7**	—		—		7.7	6.9–9.1
Physarum cinereum	PHYcin	5	1000	200	—			—		**4**	**4.7**	1	0.4	—		—		7.1	6.5–8.5
Physarum compressum	PHYcom	46	7447	162	38	481	13	—		**45**	**68.1**	32	14.7	6	0.6	1	0.6	8.0	6.2–9.7
Physarum didermoides	PHYdio	17	3420	201	5	1083	217	—		—		**22**	**22.0**	—		—		8.6	6.8–9.8
Physarum melleum	PHYmel	13	3280	252	—			—		**12**	**12.7**	—		—		1	0.3	7.1	6.3–8.2

TABLE I. Continued

Scientific name	Abbr.	Field collections			Moist chamber culture collections			Substratum type[b]										pH[c]	
		Sporocarps[a]			Sporocarps[a]			*b*		*l*		*in*		*ep*		*w*			
		Rec	Sum	Mean	Rec	Sum	Mean	Rec	Abu	Rec	Abu	Rec	Abu	Rec	Abu	Rec	Abu	Mean	Range
Physarum nutans	PHYnut	12	3230	269	—			—		4	1.4	—		—		**8**	**10.6**	5.7	3.7–7.4
Physarum pusillum	PHYpus	23	1334	58	11	37	3	—		5	26.9	**28**	**6.8**	—		1	0.2	8.0	6.8–9.8
Physarum sp.	PHYsp.	7	560	80	—			—		**7**	**7.0**	—		—		—		6.7	5.8–7.1
Stemonitis axifera	STEaxi	7	606	87	—			—		1	0.5	—		—		**6**	**6.5**	5.1	3.5–7.5
Stemonitis fusca	STEfus	8	4975	622	—			—		2	0.7	—		—		**6**	**7.3**	5.7	4.5–7.5
Tubifera microcarpa	TUBmic	5	1720	344	—			—		—		—		—		**5**	**5.0**	5.6	4.2–6.4

[a] Sum and mean number of sporocarps per record for field collections and moist chamber culture collections for a particular species.

[b] Number of records and weighted abundances per substratum type (b—bark of living trees, l—various types of ground and aerial litter, in—living inflorescences, ep—epiphyllic liverworts on living leaves, w—decaying wood).

[c] Mean and range of pH recorded for all records (from both field collections and those from moist chamber cultures) for a given species.

[d] Values for the preferred substratum type for each species (based on weighted abundances) are indicated in bold.

moisture, were the two species occurring most frequently on wood. The highly variable *Arcyria cinerea* occurred not only on wood but even more often on epiphyllic liverworts. As reported in Schnittler (2001a), the latter collections belong to a quite distinct dwarf form that perhaps warrants description as a separate taxon. Due to their low sporocarp numbers, as compared with the typical, wood-inhabiting form, they do not significantly alter the species scores of this complex species.

DISCUSSION

The study reported herein is one of the very few in which an effort was made to record sporocarp numbers for every myxomycete fruiting observed in field or obtained in moist chamber cultures. As demonstrated by Schnittler (2001b), the obtained abundance measures appear to represent an important key for characterizing ecological niches for myxomycetes.

Myxomycete distribution in the investigated forest types.—As is obvious from the data presented in TABLES II and III, several parameters (field records encountered per hour, records and mean number of sporocarps per moist chamber cultures as well as number of species) indicate a pattern of decreasing myxomycete diversity with increasing elevation and annual rainfall. This conforms to the results of a study of four forest types in Costa Rica (FIG. 2; Schnittler and Stephenson 2000). A similar pattern was first reported for the Luquillo Mountains of Puerto Rico (Stephenson et al 1999, Novozhilov et al 2000). Thus, in spite of the general concept of myxomycetes preferring humid environments, species diversity and productivity of neotropical myxomycetes seems to be highest in dry forests.

As hypothesized by Alexopoulos (1970), high humidity tends to promote the colonization of myxomycete fruiting bodies by myxomyceticolous fungi. These parasitic fungi ''smother'' a fruiting body, covering it with a mycelial mat. Fungal hyphae invade protoplasts of individual spores, thus rendering them useless for dispersal (Rogerson and Stephenson 1993). Even without a fungus being present, myxomycete spores in a sporocarp on a continuously wet substratum have problems drying out, which is a precondition for becoming airborne and thus being dispersed. This could explain the reverse pattern of decreasing myxomycete diversity with increasing elevation and rainfall and is supported by several lines of evidence. First, as was also the case for the Costa Rican study, species diversity and records per culture were higher for aerial leafy litter than for the same

TABLE II. Numbers recorded for myxomycetes collected in the field or obtained from moist chamber cultures for the three study sites

	Study site[a]		
	MF	*WF*	*RF*
Field collections			
Field records	549	32	9
Collecting hours	80	12	6
Records per hour	6.9	2.6	1.5
Sporocarps per record	269	584	198
Number of species	66	14	5
Moist chamber culture collections			
Number of moist chamber cultures	220	155	100
Records from moist chamber cultures	230	152	61
Records per culture	1.05	0.98	0.61
Sporocarps per record	16	8	8
Number of species	28	13	12

[a] According to the Holdridge classification, abbreviations for the study sites are: *MF*—Tropical Moist Forest, *WF*—Tropical Premontane Wet Forest, *RF*—Lower Premontane Rain Forest.

[b] Sporocarp counts were not applied to those taxa (e.g., members of such genera as *Ceratiomyxa, Fuligo* or *Lycogala*) that do not produce fruitings with distinct sporocarps.

TABLE III. Moist chamber productivity for the four substratum types available in all three study sites

	Study site[a]		
Substratum type	*MF*	*WF*	*RF*
Bark of living trees			
Cultures prepared	33	24	19
No. of records	6	2	2
Records per culture	0.18	0.08	0.10
Sporocarps per record	11.8	6.0	1.5
No. of species	4	2	2
Forest floor litter			
Cultures prepared	44	42	41
No. of records	53	20	16
Records per culture	1.20	0.48	0.39
Sporocarps per record	6.5	7.5	3.8
No. of species	9	4	5
Aerial leafy litter			
Cultures prepared	21	21	20
No. of records	29	16	6
Records per culture	1.38	0.76	0.30
Sporocarps per record	9.1	4.6	3.8
No. of species	10	6	3
Epiphyllic liverworts			
Cultures prepared	21	20	20
No. of records	52	51	33
Records per culture	2.47	2.55	1.65
Sporocarps per record	5.9	7.4	6.9
No. of species	5	6	5

[a] Abbreviations for study sites are the same as those used in TABLE II.

substratum from the forest floor (TABLE III). Both substrata should be identical in origin and nutrient content, but the more exposed aerial litter has a greater chance to dry out during a brief period of

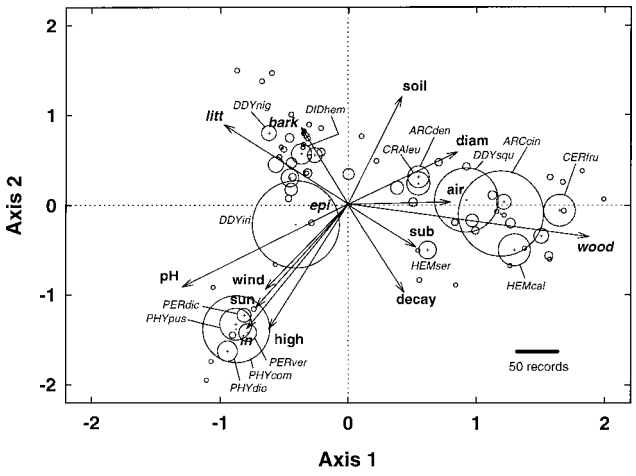

FIG. 1. Canonical correspondence analysis of 936 myxomycete records (representing 77 taxa) with ten environmental parameters (the substratum types **litt**er, **b**ark, **w**ood, **in**florescences and **epi**phyllic liverworts on living leaves; extent of contact with **soil**; **pH**; **diam**eter and **decay** stage of the substratum; **sub**stratum and **air** moisture; sampling **heigh**t, **wind** and **sun** exposure) being considered. Species scores were calculated using weighted abundances for the species; the diameter of the circle around each species score indicates the relative number of records. Abbreviations of the names used for more common species are the same as those given in TABLE I. Eigenvalues for the first four axes are 0.71, 0.50, 0.45 and 0.39, respectively.

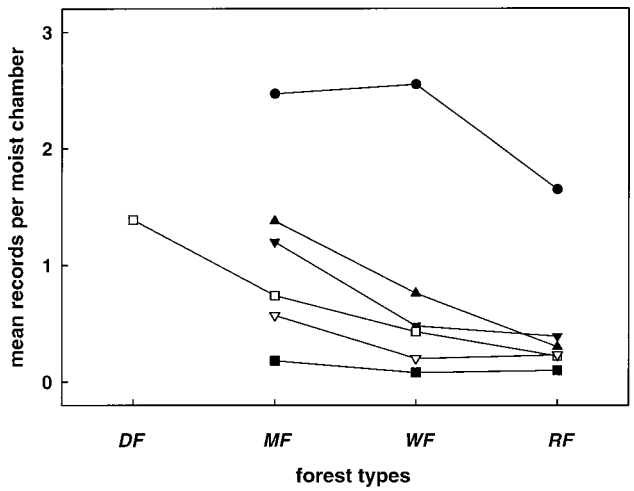

FIG 2. Productivity of moist chamber cultures prepared with substratum samples from Maquipucuna (bark of living trees, solid rectangles; leaf litter from the forest floor, solid inverted triangles; aerial leaf litter, solid triangles; covers of epiphyllic liverworts on living leaves, solid circles) and the Area de Conservación de Guanacaste in Costa Rica (bark, open rectangles; leaf litter from the forest floor, open inverted triangles). Except for leaf litter from the forest floor (40 cultures), each dot represents the mean number of records per culture from a series of 20 ± 2 cultures prepared with material from the forest types Tropical Dry Forest (*DF,* and present only in Costa Rica), Moist Forest (*MF*), Wet Forest (*WF*), and Lower Premontane Rain Forest (*RF*).

clear weather. Second, the same pattern of higher species numbers for aerial versus ground substrata was obtained in a series of substratum colonization experiments carried out in Puerto Rico, where sterile straws were used as baits for another group of myxomycete-like organisms, the protostelids (Moore and Spiegel 2000). Third, myxomycetes inhabiting epiphyllic liverworts on living leaves, a two-dimensional aerial microhabitat that dries out quickly during a few hours of sunshine, seems to be an exception to the pattern mentioned above, at least for species numbers and productivity (in terms of sporocarps) per moist chamber culture. Fourth, wood, as a substratum that rarely dries out in humid tropical forests, displays lower species diversity in the tropics than in temperate regions (Stephenson et al 1993). Fifth, if the stalked fructification of myxomycetes is perceived as the primary evolutionary solution for the dilemma pointed out above, the majority of the taxa encountered in the present study should be stalked. With more than 80% of all species recorded in the entire study producing stalked fruiting bodies, this is indeed the case. Except for *Diderma effusum,* where the fruiting bodies are effectively preserved for eventual out-drying by a thick limy peridium, the only sessile species (*Perichaena* cf. *dictyonema* and *P. vermicularis*) represented among the more common species occurred on inflorescences, a very exposed habitat that has an excellent chance of drying out. With one exception, all the species for which the primary substratum was decaying wood (which has the least chance of drying out) are stalked. The exception is *Lycogala epidendrum,* an aethalium-forming species with a different, puffball-like mode of spore dispersal (i.e., the hydrophobic spores are dispersed from the aethalium by the force of falling raindrops).

In summary, it can be concluded that, in addition to the (still unknown) supply of food organisms, physical features of the substratum and climate are the major factors determining the distribution of myxomycetes.

Myxomycete-substratum relationships.—In this study, five main types of substrata were found to support assemblages of myxomycetes; these were decaying wood, litter, the bark of living trees, living inflorescences and covers of epiphyllic liverworts on living leaves. The latter two are new for myxomycetes.

While based on myxomycete abundances measured as sporocarp numbers, the CCA (FIG. 1) actually reflects myxomycete occurrences only from the first three assemblages. Epiphyllic liverwort-inhabiting myxomycetes were detected regularly in moist chamber cultures, but the respective sporocarp numbers were low (TABLE I). Bark-inhabiting (corticolous) myxomycetes were found to be rare in terms of both records and sporocarp numbers. Litter, wood and inflorescences each supported a relatively distinct assemblage of myxomycetes. Differences in pH seem to be a major distinguishing factor, as indicated by the mean pH value of all species preferring the respective substratum types: litter 7.1, inflorescences 8.1 and wood 5.7.

Wood-inhabiting myxomycetes are the primary focus of most studies of this group of organisms. However, quantitative (i.e., where all myxomycete occurrences were recorded) data are available from only two other studies carried out in neotropical forests (Veracruz, Mexico, Ogata et al [1996]; Sao Paulo State, Brazil, Maimoni-Rodella and Gottsberger [1980]). In both studies, the most common species of myxomycetes included many of the same examples found to be abundant in the present study. Among these were *Ceratiomyxa fruticulosa, Arcyria cinerea* and *Hemitrichia calyculata.* The latter was the most common wood-inhabiting species in all three studies and also was reported as most abundant in a survey from equatorial Guinea (Lado and Teyssiere 1998). Whereas these common species inhabit decaying wood characterized by a mostly circumneutral pH (TABLE I), a second group of less abundant species

is associated with decaying wood that is acidic, with pH values of 4 and lower. Prominent examples are *Cribraria intricata* and *C. tenella,* or *Ceratiomyxa morchella,* found abundantly on acidic logs in a survey carried out in eastern Ecuador (Schnittler, unpublished data). Wood-inhabiting myxomycetes displayed the highest average specificity (75%) of all substratum types.

As was also the case for the Costa Rican study (Schnittler and Stephenson 2000), litter (substratum groups *ll, la, lh* and *lw*) was the most productive substratum at Maquipucuna, both in terms of records and numbers of species. Compared with wood, litter-inhabiting myxomycetes have a clearly lower degree of specificity (61–35%). It seems to be a general trend in the tropics that litter substrata are richer in species than wood (cf. Stephenson et al [1993]), whereas decaying wood and the bark of living trees are the two most diverse substratum types in temperate regions (Stephenson 1988, 1989). In the present study, 14 of 19 of the more common species preferring litter belong to the order Physarales.

Inflorescence-inhabiting myxomycetes form a distinct assemblage with a few but highly specialized species as described in detail by Schnittler and Stephenson (2002).

The few species (*Cribraria confusa, Licea perexigua* and *Enerthenema papillatum*) occurring exclusively on bark all were rare, indicating that bark at the height (ca. 1.5 m) sampled in the present study is not a suitable substratum for myxomycetes in neotropical forests. This correlates well with the results reported for Costa Rica by Schnittler and Stephenson (2000), where bark was ecologically important for myxomycetes only in Tropical Dry Forests. The mean sporocarp numbers for cultures prepared with bark (TABLE III), which clearly decrease with increasing elevation and annual rainfall, suggest a leaching effect of heavy rains, which wash out nutrients, myxomycete propagules or both. It is possible that substratum samples from the tree canopy, where the bark is exposed to direct sunlight and dries out much faster, would yield a more diverse assemblage of corticolous myxomycetes.

As described by Schnittler (2001a), the myxomycete assemblage associated with epiphyllic liverworts on living leaves has no clearly specialized species, which is underscored by the low average specificity (33%) of species recorded for this substratum type. The three most common species, the dwarf form of *Arcyria cinerea, Didymium iridis* and *D. squamulosum,* occurred frequently on other types of aerial litter. Most likely, in nature this substratum supports only small populations of myxamoebae without the potential to produce substantial numbers of fruitings.

Although the great majority of the taxa encountered in this study were uniform in terms of their morphological characters, a few of the more common taxa were found to be variable. Because of the apomictic mode of reproduction characteristic of many myxomycetes, as discussed by Clark (2000), the application of the morphological species concept becomes rather problematic in some instances. In addition to *Arcyria cinerea,* as mentioned above, *Didymium iridis* is a good example of a taxon whose morphological limits are difficult to define. In our study, this species behaved as a generalist, occurring on various types of litter, inflorescences and epiphyllic liverworts. Clark and Mires (1999) characterized *D. iridis* as a complex species with numerous biotypes difficult to accommodate properly within the traditional morphological species concept. Also investigated, but much more uniform morphologically, was *Physarum melleum* (Clark and Stephenson 2000), in the present study almost restricted to leafy ground litter. This indicates the possible value of (yet to be developed) molecular markers for a more complete understanding of myxomycete ecology.

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