

Distribution and ecology of myxomycetes in the high-elevation oak forests of Cerro Bellavista, Costa Rica

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Abstract: Myxomycetes associated with a high-elevation (>3000 m) oak forest in the Talamanca Range of Costa Rica were studied for 7 mo. Field collections were supplemented with collections obtained from moist chamber cultures prepared with samples of bark and ground litter of *Quercus costaricensis*. Various microenvironmental parameters including pH, substrate moisture and diameter, height above the ground and canopy openness were recorded for each field collection, whereas macroenvironmental data for temperature and precipitation were obtained from a meteorological station near the study area. Niche breadth and niche overlap indices were calculated to assess possible resource partitioning by myxomycetes. Thirty-seven species were recorded, including 11 new records for Costa Rica, eight for Central America and one for the neotropics. Both PCA and NMS multivariate analyses indicated that pH and height above the ground explained most of the observed variation, although substrate diameter also seemed to be an important factor. Precipitation showed an inverse correlation with the number of fruitings, confirming its importance as a macroenvironmental factor. Niche overlap values were not higher for closely related species and values for niche breadths were similar for most of the more common species, suggesting that most members of the assemblage of myxomycetes present in the study site are ecological generalists.

Key words: biodiversity, community ecology, eumycetozoans, slime molds, Talamanca Range

INTRODUCTION

The myxomycetes (plasmodial slime molds or myxogastriids) are a relatively small and homogeneous group of eukaryotic, phagotrophic organisms (Stephenson and Stempen 1994) phylogenetically related to the amoeboid protists (Adl et al 2005) but traditionally studied by mycologists. Only about 880 species are known worldwide (Hernández-Crespo and

Lado 2005). The myxomycete life cycle consists of two vegetative stages, one a uninucleate amoeba, with or without flagella, the other a multinucleate unicellular structure known as a plasmodium (Martin and Alexopoulos 1969). Under suitable conditions the plasmodium gives rise to the reproductive stage, a somewhat fungus-like fruiting body.

Most ecological studies of myxomycetes have been carried out in temperate regions of the world (e.g. Härkönen 1977, Stephenson 1989, Novozhilov et al 1999, Schnittler 2001b), and only recently have certain regions of the tropics been investigated. However most regions of the tropics remain understudied and thus have considerable potential for future studies (Schnittler and Stephenson 2000, Stephenson et al 2004b). Results obtained from recent studies suggest that the relative abundance of myxomycete fruiting bodies decreases with decreasing latitude (Schnittler and Stephenson 2002) and increasing elevation, apparently in response (at least in part) to increasing environmental moisture (Stephenson et al 2004b). Stephenson et al (2000) suggested that distribution ranges in myxomycetes can be large, although factors related to microclimate and vegetation influence their presence and dispersal potential. For example some species display strong preferences for specific substrates or exhibit distribution patterns that can be related to microenvironmental variables such as pH and moisture (Novozhilov et al 2005). However distribution patterns of myxomycetes have yet to be studied in high-elevation forests of the tropics and basic questions relating to the assemblages of myxomycetes present in these forests and whether the abundance of fruitings is correlated with the actual number of taxa present at a particular locality warrant further investigation.

In Costa Rica many forests above 3000 m are dominated by a single species of oak (*Quercus costaricensis* Liebm.). These high-elevation oak forests are characterized by an almost constant cloud coverage, and for this reason they often are referred to as “cloud forests” (Kappelle et al 1992). Other major groups of organisms such as animals, plants and fungi have distinctive assemblages of species associated with these forests, and the assemblages usually differ from those found at intermediate elevations or in lowland moist sites in the same region (Kappelle 1996).

The lack of ecological data on myxomycetes in the

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neotropics, especially in high-elevation forests, suggested the study described herein, in which an effort was made first to characterize the assemblage of species associated with a high-elevation oak forest in Costa Rica and then to investigate some of the ecological patterns displayed by these species. Particular emphasis was placed on assessing patterns of sporulation phenology, seasonal abundance and microhabitat occurrence in relation to macro- and microenvironmental factors and the range of available microhabitats.

MATERIALS AND METHODS

The study reported herein was carried out in 2004 in a high-elevation oak-dominated forest community in the mountains of south central Costa Rica. The forest examined would be classified as a montane moist forest according to the Holdridge life zone system (Beauvais and Matagne 1998). The actual study site is on the eastern slope of Cerro Bellavista and within the boundaries of the Cerro de la Muerte Biological Station (9°33'42"N, 83°44'27"W) in the province of San Jose, Costa Rica. Elevations within the study area are 3142–3230 m above sea level. The forest is characterized by a canopy that is 20–25 m tall and dominated by *Quercus costaricensis*. In the subcanopy (5–15 m tall) the most common trees are members of the genera *Weinmannia*, *Comarostaphylis*, *Schefflera*, *Drymis*, *Myrsine* and *Oreopanax*. The understory is dominated by ferns and the bamboo-like grass *Chusquea*. The mean annual temperature in this region of Costa Rica is 10.9 C, and precipitation averages around 3000 mm per year (data from the National Meteorological Institute, Costa Rica).

Field sampling was carried out during the two periods of the year characterized by a different precipitation regime. The first period (referred to as the “dry season”) occurs between December and the beginning of the rains in May, whereas as the second period (the “rainy season”) encompasses the rest of the year. However it should be noted that recognizing these two periods as distinct is somewhat arbitrary because the annual climate exhibits a rather superficial seasonality and forests are mostly evergreen throughout the year. Three collecting trips were made in each of the two seasons, and these extended over a total of 7 mo. The laboratory component of the study was carried out during an additional 8 mo. Samples for laboratory study were collected only in the first trip of each season, but field collections were obtained on every trip.

Plots and collections.—Three 20 × 50 m (0.1 ha) plots were established in portions of the study area clearly dominated by oak trees. Although no analysis of tree dominance was carried out, Jimenez et al (1988) reported a density of about 500 stems per hectare (DBH >10) for the oak forests in this portion of the Talamanca Range. To minimize any marginal effects the boundary for each plot was located at least 50 m from the forest edge. The opportunistic sampling protocol (Cannon and Sutton 2004) was used to search for fruitings of myxomycetes in each plot. This method is effective for

studying myxomycetes, especially when the forest structure is particularly complex as is the case in many areas of the tropics because it lets the researcher make an a priori selection of substrates. For this reason primary emphasis was placed on examining dead leaves, decaying wood and twigs for myxomycetes. No specimens still in the plasmodial stage were collected. Nomenclature follows Hernández-Crespo and Lado (2005) except for *Arcyria leiocarpa* and *Stemonitis smithii*, where the treatment of Martin and Alexopoulos (1969) is used.

All specimens obtained in the field were collected and curated in the manner described by Stephenson and Stempen (1994). To complement field collections, 120 moist chamber cultures were prepared with samples of bark and ground litter collected from each plot. Sixty moist chambers were prepared with samples collected during the dry season and another 60 with samples collected during the rainy season. In this part of the study samples were collected in paper bags, transported to the laboratory and placed in standard 9 mm diam Petri dishes lined with filter paper. Distilled water was added to each dish and the sample material in each culture remained soaked for 24 h, after which excess water was poured off. Cultures were examined every week for approximately 4 mo.

Environmental measurements.—General climatic data for the total period during which the study was carried out were obtained directly from the Villa Mills meteorological station, 5 km south of the study site, through the National Meteorological Institute (IMN) in San Jose, Costa Rica. Microenvironmental variables were measured or determined directly in the field. For example the type of substrate on which a fruiting occurred along with its diameter (for woody substrates) and height above ground were recorded for each specimen collected.

Canopy openness, measured with a spherical densiometer, was used as an indicator of the quantity of light reaching the forest floor. To determine this parameter, each plot was divided in 10 subplots of 10 × 10 m, and these were subdivided further into four 5 × 5 m areas. In each of the latter, four measurements of canopy openness were obtained and the mean value was calculated. Each specimen collected in the plot was assigned the average value of the specific area in which it occurred.

The stage of wood decay was recorded for discrete categories as described by Stephenson et al (2004a), except that in the present study categories 2 and 4 were not used. As such only three categories (1, 3 and 5) were recorded for wood decay and these were considered to represent early, intermediate and late decay stages. Substrate moisture was measured by collecting small samples of substrate from the same microsites on which fruitings occurred. Within 24 h of returning from the field these samples were weighed and placed in a constant temperature oven for 72 h at 65 C. Afterward it was assumed that most of the water content of the substrates had been lost and samples were reweighed. The difference between dry and original weights was used to obtain the percentage moisture for each sample.

Data analysis.—Shannon-Wiener and taxonomic diversity indices (Stephenson et al 1993) were calculated for the total

assemblage of species in an effort to quantify overall myxomycete biodiversity in the forest studied. Sørensen's coefficient of community was calculated for the sets of specimens obtained on different collecting dates to evaluate temporal differences in species composition.

A multivariate analysis of microenvironmental measurements was carried out to evaluate the possible effects of micro- and macroenvironmental variables. To avoid the "noise" produced by the less common species, all species were classified according to their abundance before performing the analysis. In this classification, species representing more than 3% of the total number of collections were considered as abundant, those falling between 1.5–3% as common, between 0.5 and up to 1.5% as occasional and those less than 0.5% as rare (Stephenson et al 1993). A nonmetric multidimensional scaling ordination (NMS) was performed with the numeric microenvironmental variables for only the species classified as abundant. This ordination was carried out with the program PC-ORD by exploring 50 runs of real data and 50 runs of randomized data using the autopilot function and the scores generated by weighted averaging. Sørensen distances and a Monte Carlo test of significance were used. A principal component analysis (PCA) based on correlations also was performed with the same set of data to evaluate the relative importance of the different variables to structure and composition of the community and to evaluate similarities with the previous ordination.

Values obtained for niche breadth and niche overlap were calculated in the manner described by Stephenson (1988). These were evaluated for the most abundant species with Levin's estimators, as recommended by Maurer (1982) and Petraitis (1985). In this case substrate moisture and diameter, pH, height above the ground and canopy openness (and thus the level of light) were used as potential indicators of resource partitioning. This type of analysis has the potential to examine the evidence for potential interactions that might occur within particular taxonomic groups. Such interactions might not be revealed on a spatial analysis, especially if they occur between closely related species.

RESULTS

Thirty-seven species were collected (TABLE I), with 27 of these recorded during the dry season and 20 during the rainy season. Most species were represented by fruitings that occurred in the field under natural conditions, and only four taxa were recovered from moist chamber cultures. Eleven of the 37 species are new records for Costa Rica, nine are new records for the Central America and one (*Diacheopsis* sp.) is a new record for the neotropics. The most abundant species were *Cribraria piriformis*, *Ceratiomyxa fruticulosa*, *Cribraria mirabilis* and *Cribraria vulgaris*. Most fruitings were recorded on logs, twigs and bryophytes, although a few occurred on ground litter. For the entire study the value calculated for Shannon's index

of diversity was 3.27, whereas the values for the dry season and the rainy season were respectively 1.09 and 1.30; the index of taxonomic diversity for the total assemblage of species present was 2.11. Eighty-two percent of all field collections consisted of stalked fruiting bodies, and 75% of the species recorded were examples that typically produce stalked fruiting bodies.

The PCA analysis indicated that 60% of the total variation was explained by pH and height above the ground (not shown). However, according to the NMS analysis, height above the ground, substrate diameter and pH were the most important microenvironmental variables accounting for the variation in the data when a cutoff value of 0.01 is applied (FIG. 1). Of note, pH values above 4.5 are absent when height above the ground reaches 1 m (pH vs. height above ground, Pearson's product moment = -0.43 , $P < 0.0001$) and values this high were rarely recorded for substrates with a diameter greater than 20 cm (pH vs. height above ground, Pearson's product moment = -0.36 , $P < 0.0001$). Those relationships are explained by the fact that substrates with diameters >25 cm are rare near the ground (substrate diameter vs. height above ground, Pearson's product moment = 0.45 , $P < 0.0001$). In fact a deeper analysis indicated that *Didymium squamulosum*, *Lycogala epidendrum* and *Metatrichia floriformis* seem to group together both for high pH and lower heights. These species also differ from other taxa in their relatively high values for substrate pH ($F = 8.00$, $df = 11$, $P < 0.0001$). Conversely examples of species showing a preference for more acidic and higher substrates include *Cribraria mirabilis* and *Trichia botrytis*.

Substrate moisture, pH and canopy openness showed significant differences when a comparison between the two seasons was made. Of interest, height above the ground also showed a significant difference from the dry to the rainy season. Temporal differences also appear to be apparent in the type of substrate ($\chi^2 = 31.7$, $df = 8$, $P < 0.0001$), with logs and twigs more commonly recorded during the dry season and logs and bryophytes during the rainy period.

Of interest, the only macroenvironmental factor that appears to have an important influence on the occurrence of myxomycetes is precipitation, which had an inverse but significant correlation with the number of fruitings recorded (FIG. 2, precipitation vs. number of fruitings, Pearson's product moment = -0.77 , $p < 0.05$). However a multiple regression analysis showed that the combined effect of temperature and precipitation seems to have an even greater influence (precipitation and temperature vs. number of fruitings, Pearson's product moment = 0.95 , $P <$

TABLE I. Myxomycetes recorded at Cerro Bellavista and mean values for the most important associated microenvironmental variables. Abbreviations are given only for the most abundant species. Note: NF/MC = Total number of field collections (NF) and moist chamber records (MC) for each species, SD = Standard deviation, HAG = Height above ground in centimeters, SubD = Substrate diameter in centimeters, O = Occasional, R = Rare, C = Common, A = Abundant and NA = Not available (i.e. when a particular species was recorded only in moist chamber culture or when the number of specimens for that particular species was only one)

Species	Abundance	NF/MC	pH (SD)	HAG	SubD	Abbreviation
<i>Arcyria cinerea</i> (Bull.) Pers.	O	2/0	4.25 (0.20)	72.50	23.50	
<i>Arcyria denudata</i> (L.) Wettst.	R	1/0	4.30 (NA)	5.00	6.00	
<i>Arcyria leiocarpha</i> (Cooke) Martin & Alexop.	O	3/0	4.67 (0.35)	108.33	26.33	
<i>Ceratiomyxa fruticulosa</i> (Mull.) Macbride	A	19/0	4.67 (0.76)	34.47	6.89	CERfru
<i>Clastoderma debaryanum</i> Blytt	C	5/0	4.72 (0.37)	10.00	18.40	
<i>Comatricha pulchella</i> (Bab.) Rostaf. ^a	C	4/0	4.23 (0.91)	5.00	6.75	
<i>Comatricha tenerrima</i> (Curtis) G. Lister	O	2/0	4.90 (0.84)	5.00	3.00	
<i>Cribraria intricata</i> Schrad.	C	6/0	4.30 (0.42)	57.50	25.67	
<i>Cribraria mirabilis</i> (Rostaf.) Masee ^b	A	15/0	4.58 (0.58)	50.00	16.60	CRImir
<i>Cribraria piriformis</i> Schrad.	A	20/0	3.90 (0.79)	31.20	20.40	CRIPyr
<i>Cribraria vulgaris</i> Schrad.	A	14/0	3.83 (0.70)	68.57	18.64	CRIVul
<i>Diacheopsis</i> sp. ^c	R	1/0	4.40 (NA)	150.00	20.00	
<i>Diderma chondrioderma</i> (de Bary & Rostaf.) G. Lister	R	1/0	6.90 (NA)	5.00	7.00	
<i>Diderma</i> sp.	O	2/0	5.75 (1.09)	5.00	4.00	
<i>Didymium dubium</i> Rostaf. ^b	R	0/1	NA	NA	NA	
<i>Didymium squamulosum</i> (Alb. & Schwein.) Fr.	A	9/0	5.80 (1.08)	5.22	1.67	DDYsqu
<i>Hemitrichia calyculata</i> (Speg.) Farr	A	9/0	4.97 (0.58)	20.00	10.33	HEMcal
<i>Hemitrichia serpula</i> (Scop.) Rostaf. ex Lister	A	0/7	NA	NA	NA	HEMser
<i>Lamproderma columbinum</i> (Pers.) Rostaf. ^b	A	12/0	4.21 (0.58)	27.50	20.50	LAMcol
<i>Lamproderma cribrarioides</i> (Fr.) R.E.Fr. ^b	O	3/0	4.70 (0.69)	6.67	18.00	
<i>Lamproderma echinulatum</i> (Berk.) Rostaf. ^b	C	5/0	4.88 (0.79)	25.00	29.00	
<i>Lamproderma sauteri</i> Rostaf. ^b	R	1/0	4.60 (NA)	5.00	5.00	
<i>Leocarpus fragilis</i> (Dicks.) Rostaf. ^b	O	2/0	6.15 (0.63)	30.00	9.50	
<i>Lycogala epidendrum</i> (L.) Fr.	A	10/0	5.52 (0.87)	16.40	7.95	LYCepi
<i>Metatrichia floriformis</i> (Schwein.) Nann.-Bremek.	A	13/0	5.52 (0.72)	7.62	14.00	METflo
<i>Perichaena depressa</i> Lib.	R	0/1	NA	NA	NA	
<i>Physarum brunneolum</i> (Phillips) Masee ^b	R	1/0	4.70 (NA)	100.00	10.00	
<i>Physarum contextum</i> (Pers.) Pers. ^a	R	1/0	5.80 (NA)	5.00	10.00	
<i>Physarum leucopus</i> Link	R	1/0	6.50 (NA)	80.00	4.00	
<i>Physarum melleum</i> (Berk. & Broome) Masee	R	0/1	NA	NA	NA	
<i>Stemonitis fusca</i> Roth	O	2/0	5.35 (0.07)	32.50	45.00	
<i>Stemonitis smithii</i> Macbride	O	4/0	5.28 (0.18)	11.25	10.25	
<i>Stemonitopsis hyperopta</i> (Meyl.) Nann.-Bremek.	O	3/1	4.10 (0.36)	48.33	6.67	
<i>Trichia botrytis</i> (Gmel.) Pers.	A	10/0	4.30 (0.51)	74.50	7.80	TRIBot
<i>Trichia decipiens</i> (Pers.) Macbride	O	3/0	4.77 (0.32)	30.00	10.00	
<i>Trichia favoginea</i> (Batsch.) Pers.	A	7/1	4.41 (1.09)	32.14	22.00	TRIfav
<i>Trichia verrucosa</i> Berk.	A	8/0	4.95 (1.32)	34.38	11.31	TRIVer

^aNew record for Costa Rica.

^bNew record for Central America.

^cNew record for the neotropics.

0.05). A significant relationship was not observed when the number of species was considered (precipitation and temperature vs. number of species, Pearson's product moment = 0.87, $P < 0.05$).

The coefficient of similarity value calculated for species assemblages associated with the two seasons was 0.48. Major differences in abundance were noted for members of such genera as *Lamproderma* and *Lycogala*, which invariably were absent during the

rainy period, or *Didymium* and *Leocarpus*, never recorded for the dry season. When the values calculated for niche breadth and overlap are examined it is clear that the values for most species are similar and relatively high (TABLE II). If niche breadth values represent the mathematical result of a proportionally higher number of fruitings recorded in the field, then some correlation between these two variables should exist for the community as a whole.

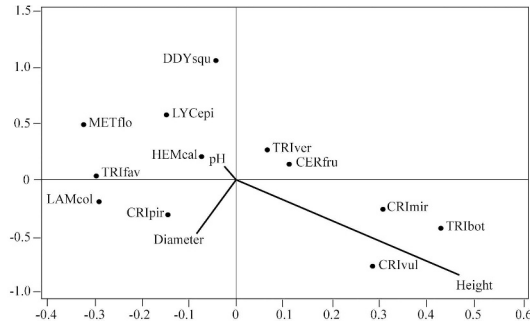


FIG. 1. Ordination of species and microenvironmental variables with nonmetric multidimensional scaling (NMS). Points define the abundant species. Lines indicate the direction and strength of the most important microenvironmental variables. (For abbreviations used for species see TABLE I.)

However the actual correlation is weak (niche breadth vs. number of fruitings, Pearson's product moment = 0.09, $P > 0.05$). Posterior analysis indicated that *Lamproderma columbinum* has a broader niche and *Dydimium squamulosum* a narrower niche than the other species ($F = 14.5$, $df = 7$, $P < 0.05$). When these two species are excluded from the analysis, no appreciable differences in niche breadth values can be noted among the rest of the taxa present ($F = 5.07$, $df = 5$, $P > 0.05$).

One might expect intrageneric overlap to be higher than intergeneric overlap due to the theoretical relatedness in resource use by closely related species. However an analysis of the niche overlap values calculated for *Cribraria* and *Trichia*, the two most diverse genera, does not reveal significant differences in the values between species within each genus or among the species of the two genera ($F = 1.20$, $df = 2$, $P > 0.05$).

DISCUSSION

The number of species recorded in the present study is comparable to the totals reported for studies carried out elsewhere in the tropics (e.g. Schnittler and Stephenson 2000, Stephenson et al 2004a). However limiting the study to selected substrates might have underestimated the actual number of taxa present. Schnittler (2001a) and Schnittler and Stephenson (2002) have described new microhabitats for myxomycetes in the neotropics, and unpubl data suggest that a number of others probably exist. Preliminary surveys of the study area in 2001 and 2003 indicated that at least four plant species could be serving as living microhabitats for some species of myxomycetes. However these plants were not considered in the present study and some of the species of

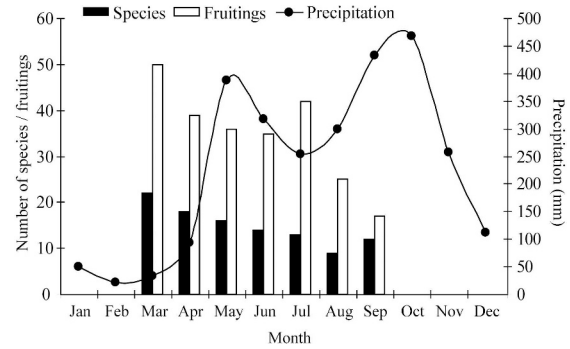


FIG. 2. Numbers of species and fruitings recorded during 7 mo of field work in the current study. The line indicates the average value of monthly precipitation for Cerro Bellavista, based on data provided by the National Weather Institute in Costa Rica.

myxomycetes typically associated with the microhabitats they provide were not recorded in the present study either. In any case it is clear that surveys of nontraditional substrates would yield new records for any particular locality, especially in the neotropics as discussed by Stephenson et al (2004b).

In a similar study carried out in the seasonal tropical forests of Guanacaste in Costa Rica, Schnittler and Stephenson (2000) reported a Shannon's index of 1.11. Such a low value can be obtained for a single locality in temperate regions (e.g. Stephenson 1989), but it seems more typical for the apparently less diverse tropical regions of the world (Stephenson et al 2004b). As such the value obtained in the present study (3.27) seems more comparable to those obtained for temperate rather than tropical regions, and the values obtained for the different periods of study suggest that diversity is similar throughout the year. The taxonomic diversity index (2.11) obtained in the present study contrasts dramatically with values reported for other areas in the tropics. For example Stephenson et al (1993) obtained a value of 3.93 for the set of data contained in a published checklist of the myxomycetes of Costa Rica (Alexopoulos and Saenz 1976) and reported a value of 4.13 for southern India.

When these values are considered together the apparent conclusion is that tropical areas appear to be characterized by lower overall numbers of species but richer intrageneric diversity. However the set of data from Cerro Bellavista shows a different pattern. The assemblage of species contains a relatively higher number of species, and this number is especially impressive when one considers that for tropical regions myxomycete diversity seems to decrease as elevation increases (Stephenson et al 2004b). Of note, the assemblage at Cerro Bellavista is dramatically poor in terms of the number of species per genus, which

TABLE II. Niche breadth and niche overlap values for the 12 most abundant species recorded at Cerro Bellavista. Just one value per species pair is shown. (For abbreviations refer to TABLE I.)

Species	Niche breadth	Species and Niche overlap values											
		CERfru	CRImir	CRIPir	CRIVul	DDYsqu	HEMcal	LAMcol	LYCepi	METFlo	TRIBot	TRIfav	TRIVer
CERfru	2.54	***	0.96	0.95	0.87	0.80	0.97	0.84	0.95	0.82	0.86	0.94	0.97
CRImir	2.98		***	0.97	0.96	0.63	0.93	0.93	0.87	0.74	0.92	0.97	0.99
CRIPir	2.95			***	0.90	0.70	0.97	0.92	0.92	0.86	0.82	0.99	0.97
CRIVul	3.03				***	0.47	0.82	0.93	0.73	0.57	0.96	0.90	0.93
DDYsqu	2.00					***	0.87	0.62	0.92	0.91	0.59	0.75	0.79
HEMcal	2.60						***	0.85	0.98	0.92	0.79	0.96	0.96
LAMcol	3.86							***	0.76	0.70	0.80	0.94	0.91
LYCepi	2.25								***	0.95	0.74	0.92	0.92
METFlo	2.16									***	0.62	0.88	0.85
TRIBot	2.63										***	0.82	0.89
TRIfav	3.00											***	0.96
TRIVer	3.04												***

resembles the apparent pattern for temperate areas. This suggests that resource partitioning among species should be lower than in typical tropical assemblages, where requirements of particular species might be expected to be more similar due to higher numbers of closely related taxa.

Ceratiomyxa fruticulosa was the only species found to be abundant both in the present study and a previous study of cloud forests in Ecuador (Stephenson et al 2004a). However *Didymium squamulosum*, *Lycogala epidendrum* and *Metatrichia floriformis*, reported as common in Ecuador, are three of the species that form a cluster that seems to be related to a basic pH in the ordination presented (FIG. 1).

When pH values are compared it is clear that most substrates at Cerro Bellavista are only slightly more acidic (values of 2.7–7.1) than those in Ecuador (3.3–9.8). However none of the species associated with low pH values in the present study, including the three common species of *Cribraria*, were reported from Ecuador (Stephenson et al 2004a). Moreover in their study of a cloud forest in the northern part of Costa Rica, Schnittler and Stephenson (2000) did not report the same species recorded in the present study. The forests investigated in these three studies were different in terms of plant composition and architecture. Consequently it seems obvious that the differences in climatic conditions and plant composition that exist among these three areas are playing an important role in determining the species composition of the assemblages of myxomycetes present.

The only common species shared between the present study and cloud forests in Ecuador (Schnittler and Stephenson 2000) occurred only on leaf litter, which suggests that lignicolous substrates might have a more important influence on the distribution of

myxomycetes, as has been suggested for plant communities in other parts of the world (e.g. Stephenson 1988, Schnittler 2001b). Of note, oak is absent both in Ecuador (Ulloa and Møller 1993) and in the cloud forest studied by Schnittler and Stephenson (2000) in Costa Rica.

An interesting result of the present study is the high proportion of stalked species (75%) and records of those species (82%). The values we obtained are similar to those reported for temperate deciduous (but mostly oak) forests in the Mountain Lake region of southwestern Virginia (Stephenson 1988), where the same percentage (74%) was recorded for both species that typically produce stalked fruiting bodies and the total number of records represented by these species. This would suggest that whatever ecological factors (presumably those related to levels of substrate and/or atmospheric moisture) are involved in determining the relative proportions of sessile vs. stalked forms in the assemblage of myxomycetes present in a particular type of habitat are fairly comparable for high-elevation oak forests in Costa Rica and mid-latitude oak forests in eastern North America.

Records of new taxa.—Studies of myxomycetes in Costa Rica (e.g. Schnittler and Stephenson 2000) have increased the number of species known from the country to 126. However these studies did not consider high-elevation communities. Although there are few records from an elevation of approximately 2700 m near the El Empalme area (Alexopoulos and Saenz 1976), the highest area studied in detail thus far is the Monteverde Biological Reserve at around 1500 m (Schnittler and Stephenson 2000). However both the structure of the forest and climatic conditions in these two areas are very different from those

at Cerro Bellavista. Therefore the new records generated in the present study are probably not unexpected.

Four species of the genus *Lamproderma* were recorded in the present study, and none of these had been reported previously for the Central American region. Also three of the four most abundant species recorded in Cerro Bellavista are members of the order Liceales, which was the single most abundant order. Stephenson and Stempen (1994) indicated that both *Lamproderma* and *Cribraria*, a member of the Liceales, are characteristic genera of temperate forests. *Cribraria mirabilis*, one of the new records, is well known in temperate areas, especially in Europe (Lado and Pando 1997) but appears to be rare in the tropics. Of interest, this species was one of the most abundant myxomycetes in the present study.

Leocarpus fragilis, another species typical of temperate regions, also was recorded at Cerro Bellavista. This species was collected previously (Martin Schnittler, unpubl data) in the paramo of the Cerro Chirripó (ca. 3700 m). Both mountains are in the Talamanca region and represent two of the highest peaks in Costa Rica, which suggests that *L. fragilis* might be restricted to high elevations of the country. This is apparently the case in Colombia (Uribe-Meléndez 1995).

As a general observation it seems that the assemblage of myxomycetes at Cerro Bellavista more closely resembles, both taxonomically and ecologically, the assemblages associated with temperate forests rather than those of tropical forests.

Microenvironmental factors.—The PCA analysis indicates that pH and height above the ground account for much of the variation associated with the more common species. Other studies (e.g. Härkönen 1977, Schnittler et al 2006) have found that pH is an important ecological factor for myxomycetes and height above the ground also seems to have some influence on the distribution of the organisms, especially on a macro scale when forest canopies are studied (e.g. Black et al 2004). The results from the PCA analysis are not surprising when the forest dynamics of Cerro Bellavista, where there is a slight seasonality affecting the phenology of oak trees, are considered (Kappelle 1996). The variation that occurs in the canopy coverage represents an important factor because it largely determines the effective vertical precipitation reaching the forest floor and the extent to which leaching of nutrients from the canopy takes place (e.g. Milla et al 2005), thus influencing the substrate humidity and pH values in the lower strata of the forest.

In the present study compositional differences in the species assemblages recorded for the different seasons might be expected to make this pattern even more evident, especially when species recorded only in one of the two seasons are considered. *Lycogala epidendrum* and *Didymium squamulosum* for example were recorded during only one season. Similarly it seems that substrate moisture does not affect the assemblage of species in Cerro Bellavista as has been observed in other studies (e.g. Schnittler et al 2006). However the major effect of horizontal precipitation in the study area is that maintains relatively high water content for most substrates throughout the entire year.

Substrate diameter is another important variable (FIG. 1). This is not surprising either, especially when it is obvious that most of the twigs and lower diameter logs are associated with the ground level. For example Schnittler et al (2006) found these factors did not explain the variation in their data when they studied a community of canopy myxomycetes in Germany. However the assemblages of species present in the canopy and aerial strata of tropical forests are different from those found at ground level (Black et al 2004); therefore it would not be surprising if their community ecology is different.

Cribraria vulgaris, *C. mirabilis* and *Trichia botrytis* were recorded at the highest positions, whereas three other species (*Trichia favoginea*, *C. piriformis* and *Lamproderma columbinum*) were recorded for substrates with the largest diameters. Of note, most of those species were recorded in both seasons, which suggests that these variables are not as macroenvironmentally dependent as is the case for pH. Consequently the composition of the species assemblage observed in a particular season is a combination of preferences for both dynamic and more static microenvironmental conditions, depending on the responses of particular taxa.

Associated with the microenvironmental variation that exists between the seasons, there was a significant difference in the height above the ground at which fruitings were recorded, with higher values being recorded during the rainy season. This pattern does not seem to have been reported for myxomycetes in previous studies.

In general the myxomycetes seemed to fruit preferentially on logs and twigs on the ground. However bryophytes were very important during the rainy season. Of interest, although bryophytes have been reported as apparently favorable substrates for myxomycetes (Stephenson and Studlar 1985), they do not seem to be more abundant above the ground in the oak forests of Costa Rica (Holz et al 2002). Consequently the apparent change in height above

the ground of the myxomycetes at Cerro Bellavista for the two different seasons does not necessarily seem to be the result of species that are able to grow on bryophytes, as the data appear to show.

Macroenvironmental factors.—Data (FIG. 2) seem to indicate that the sporulation patterns of myxomycetes in the study area are linked intimately with precipitation. However, for this particular forest, it is difficult to evaluate the effect of seasonal climate variables on the community due to its tropical evergreen character. Although patterns of seasonality are known for some species of myxomycetes in temperate regions, there is a lack of mid- and long-term studies in the tropics (Stephenson et al 2004b).

In one of the few other studies of seasonal differences in myxomycetes, Maimoni-Rodella and Gottsberger (1980) examined the sporulation pattern of the species present in a lowland tropical rainforest in Brazil. Although these authors reported an overall pattern similar to that of the present study, they also considered temperature to be the more important factor in the tropics because water often is not a limiting factor. Of note, Ogata et al (1996) found a positive correlation between both precipitation and temperature and the overall abundance of fruitings in a study carried out in eastern central Mexico. These authors agreed with Maimoni-Rodella and Gottsberger (1980) when suggesting that slight changes in temperature during the period studied might be responsible for changes observed in the community composition. However both of these studies were carried out in ecological situations totally different from the present study, which is also reflected in the very different species composition, as already discussed.

For the general area considered in the present study Kappelle (1996) found that temperature is the most important variable explaining the dynamics of the overall ecosystem. It is interesting to note that our data suggest that temperature has a positive additive effect on the model when both factors are examined together. More than one environmental factor apparently affects the timing of sporulation in myxomycetes. However the main effect of precipitation in the present study contrasts dramatically with the negligible effect of substrate moisture in the microenvironmental analysis. This seems to indicate that, as has been observed in other studies, myxomycetes have an optimal range of substrate moisture conditions, which is hypothesized to be constantly maintained by the cloud coverage in the study area but exceeded when rain occurs and temperature drops.

Climatic data for Cerro Bellavista indicate that temperature varies only about 1.7 C from February to

October, whereas monthly precipitation increases dramatically from around 21 mm to more than 450 mm over the same period. However the effect of horizontal precipitation at high elevation in the tropics is known to be correlated with temperature because the latter affects the water content in the atmosphere. For example Stephenson and Stempen (1994) suggested that atmospheric humidity could be the most important macroenvironmental variable determining the timing of sporulation for myxomycetes. This variable did not seem as important in the present study; however it is known that high environmental humidity is associated with high horizontal precipitation and high precipitation recycling (Dominguez et al 2006). Results obtained in the present study seem to indicate that myxomycete fruitings increase in number as precipitation drops and decrease with increasing precipitation. However similar studies carried out in lowland tropical forests in other parts of the neotropics might reveal the relative effect of each factor on the sporulation pattern and abundance of myxomycetes.

Niche breadth and overlap.—The values calculated for niche breadth are mathematical constructs that are determined by the original values of resource utilization used as input for the equations to generate a value for a particular species. One assumes a normal distribution in the resource utilization requirements; consequently there is an increasing probability of finding increasingly more narrow niches as more input data are used. This is due to the fact that values closer to the mean are more common than extreme values. For this reason is important to test whether the niche breadth values are the product of a probabilistic artifact or external factors. The nonsignificant and weak correlation between the number of fruitings found in the field and values for niche breadth suggests that these two variables are independent, which makes niche breadth useful for making inferences about biotic interactions.

The observed niche breadths include examples that show significant differences for some species when *Lamproderma columbinum* and *Didymium squamulosum* are included in the analyses. Of note, these two species are found at the extremes of the niche breadth distribution for the study area, at least suggesting that they are characterized by ecological strategies different from those of the other taxa present. *Didymium squamulosum* was the only abundant species in which the fruiting bodies contained calcium carbonate, which may influence its ecological distribution. *Lamproderma columbinum* seems to exhibit a strong substrate preference for bryophytes, even though its niche breadth is the broadest overall.

When analyzing niche overlap it has been noted that closely related species, for example those belonging to the same genus, have more similar resource requirements than less related species, presumably as a result of their common evolutionary path (Morin 1999). However, when the intrageneric niche overlap values are evaluated with the two most diverse genera in this study, no differences were found. In fact the values obtained for species within each genus differ only slightly from the values obtained for species across genera. The implication would seem to be that they reflect a common ecological strategy. In fact it appears that the assemblage of myxomycetes consists of a majority of generalist species and few that are specialists.

In summary the results obtained in the present study provide new and relevant data on the ecological patterns displayed by myxomycetes in the neotropics. The new records for the region also contribute to our knowledge of the biogeographical patterns of myxomycetes. When the influence of both macro- and microenvironmental variables on the sporulation of myxomycetes at Cerro Bellavista was evaluated, information generated in the study indicates that a combination of factors determines the timing of this phenomenon, whereas analyses of niche breadth suggest that the species of myxomycetes present are mostly ecological generalists that are well adapted to changing microenvironmental conditions.

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