
Myxomycete ecology along an elevation gradient on Cocos Island, Costa Rica

Rojas, C. * and Stephenson, S.L.

Department of Biological Sciences, University of Arkansas, Fayetteville, AR, 72701, USA

Rojas, C. and Stephenson, S.L. (2008). Myxomycete ecology along an elevation gradient on Cocos Island, Costa Rica. *Fungal Diversity* 29: 117-127.

The marine biota of Cocos Island is well known; however, the terrestrial biota is poorly understood. In an effort to document the myxomycetes of the island and to determine their ecological distribution along an elevation gradient, a survey was carried out in 2005. Forty-one species were recorded, mostly from moist chamber cultures prepared with samples of various types of substrate material collected from a series of selected study sites. The assemblage of species on Cocos Island was found to be more similar to that reported from previous studies in Puerto Rico than those obtained from other investigations carried out in continental Costa Rica. This suggests that the very isolation provided by the ocean may influence the biotic interactions and ecological factors involved in determining the distribution patterns and dispersal potential of myxomycetes in the various microhabitats in which these organisms occur. Decreasing diversity with increasing elevation and the role of certain microenvironmental factors in maintaining myxomycete assemblages in particular microhabitats is also discussed. The data generated in this study also contributes to the body of knowledge required to evaluate some of the biogeographical and ecological hypotheses currently under discussion within the scientific community.

Key words: community ecology, eumycetozoans, island biogeography, Neotropics

Article Information

Received 29 August 2007

Accepted 7 October 2007

Published online 31 March 2008

*Corresponding author: C. Rojas; e-mail: crojas@uark.edu

Introduction

Cocos Island is a small oceanic land mass located approximately 550 km southeast of the Pacific coast of Costa Rica (Hogue and Miller, 1981). The rugged topography found in the island is thought to be the product of volcanic and tectonic activity associated with the Galapagos hotspot approximately 2 million years ago (Castillo *et al.*, 1988; Walther, 2002). The geographic isolation of Cocos Island has produced a distinct assemblage of species and high levels of endemism (e.g. Hogue and Miller, 1981). The extremely wet climate and oceanic character give Cocos an ecological character that is not shared with either the Galapagos Archipelago or any of the other islands (e.g., Malpelo or Coiba) in this region of the world (Kirkendall and Jordal, 2006).

Even though isolated islands such as Cocos potentially represent living laboratories for studies of biogeography and evolution,

relatively little is known about their biota and the ecological dynamics of the organisms present. This is particularly true for protists, a group for which most species have been proposed to be cosmopolitan (de Wit and Bouvier, 2006). Interestingly, recent evidence relating to myxomycete distribution and ecology in the Neotropics (e.g., Lado *et al.*, 2003; Stephenson *et al.*, 2004; Rojas and Stephenson, 2007) seems to show that some species within the group appear to respond more directly to microenvironmental factors than predicted by the neutral theory, which may indicate that the ubiquity theory does not necessarily explain myxomycete distribution patterns. This same observation has also been made for other protists (Foissner, 2006).

Continental Costa Rica represents a good starting point for studying the dynamics of the assemblages of myxomycetes associated with tropical ecosystems. These organisms have been well investigated throughout most areas

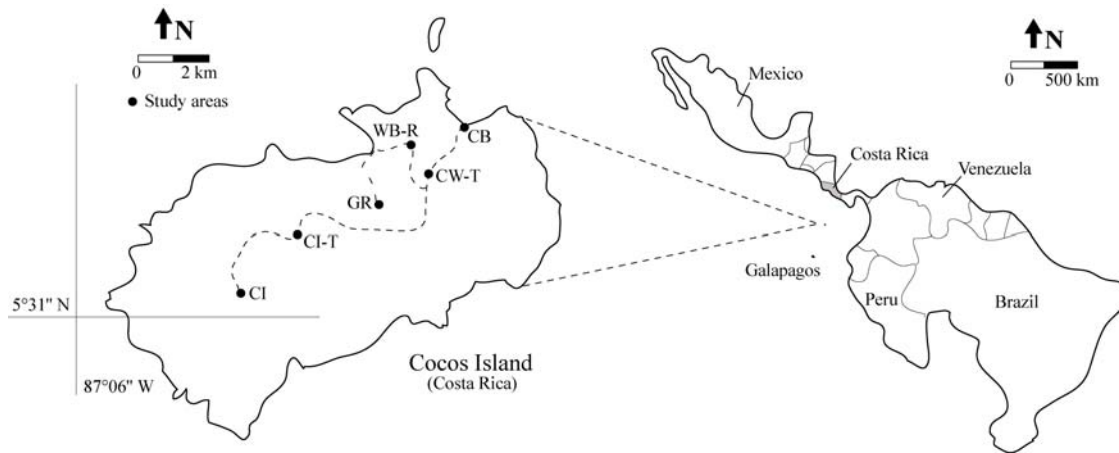


Fig 1 Geographical location of Cocos Island in the eastern Pacific (**right**) and a detailed map of the trail system and study sites used in the present investigation. Abbreviations used for study sites are explained in Material and Methods.

of the country (e.g. Schnittler and Stephenson, 2000), where a series of ecological patterns has been documented. One of the more important of these is the general pattern of decreasing myxomycete diversity with increasing elevation. Moreover, higher levels of diversity appear to exist in temperate rather than tropical regions of the Northern Hemisphere investigated to date (Stephenson *et al.*, 2004). The myxomycetes of insular tropical communities have been studied in the past (e.g. Eliasson and Nannenga-Bremekamp, 1983; Eliasson, 1991; Pando, 1997; Novozhilov *et al.*, 2001) but never in the context of the relative isolation, geologic history and ecological situation that an island such as Cocos provides. The overall objective of the present study was to investigate the diversity, species assemblages and substrate specificity of myxomycetes along an elevational gradient on Cocos Island.

Materials and methods

The vegetation of Cocos Island consists primarily of lowland tropical moist forests, according to the Holdridge life zone classification system (Beauvais and Matagne, 1998). The island is located between latitudes 5°30'06" to 5°33'26" N and longitudes 87°05'46" to 87°01'47" W and is within the Costa Rican continental waters jurisdiction (Montoya, 2007). The surveys reported herein were carried out during a visit to the island in April 2005, during a period when weather conditions were moderately dry. Because this island is a

world historical treasure and a world heritage site, study areas had to be selected within the context of the trail system already in place.

A. Selected study areas

Six study sites situated along a transect that represents an elevation gradient across the island were selected. The starting point for the transect was in the northeastern portion of Cocos Island at Chatham Bay, and the ending point was at Cerro Iglesias in the southwestern portion of the island (Fig 1). A brief description of each of the study sites is provided below.

Chatham Bay (CB – 5°32'56"N, 87°02'42"W)

This study site encompasses the only sandy beach and represents one of the two bays of the island. The vegetation is typical of lowland coastal areas throughout the Neotropics, with *Erythrina fusca*, *Ochroma pyramidalis* and *Terminalia catappa* as common tree species (e.g. Porter, 1973). The forest shows a simple vertical structure, sometimes with only two discrete vegetation layers and intermediate-to large-sized canopy gaps. The areas surveyed for myxomycetes occurred at elevations between 5 and 15 m.

Chatham-Wafer Trail (CW-T – 5°32'29"N, 87°02'53"W)

In the trail from Chatham Bay to the interior of the island there is an area of open

savannah-like forest dominated by grasses, sedges and ferns of the family Dennstaedtiaceae. The vegetation at this study site has a very limited vertical structure, with only two subordinate layers within the understory and no other structural components present. Although this type of vegetation is found at intermediate elevations between 75 and 150 m, it is characterized by the absence of canopy, which creates a virtually open area.

Wafer Bay Ridge (WB-R – 5°32'39"N, 87°02'57"W)

This study site represents the first non-coastal area of forest vegetation along the elevation gradient. It is located on a ridge between Chatham and Wafer bays. Three of the most common trees in this moist forest are *Ficus pertusa*, *Ocotea insularis* and the endemic *Cecropia pittieri*. The vertical structure of the forest is quite different from that of coastal areas, with more than three discrete vegetation layers and intermediate-sized canopy gaps that give the forest a more closed appearance than is the case in coastal areas. This study site occurs at an elevation of approximately 100 m.

Genio River (GR – 5°32'21"N, 87°03'18"W)

The portion of the island in which this study site occurs resembles Wafer Bay Ridge in plant composition and stratification; however, it is characterized by the typical structure of a gallery forest, with trees following a more linear arrangement along the river. Common plant species in this area include *Rustia occidentalis*, *Pilea gomeziana* and the endemic *Hoffmannia piratarum*. Elevations in this portion of the island range between 100 and 150 m.

Cerro Iglesias Trail (CI-T – 5°32'03"N, 87°03'56"W)

Located at a higher elevation (ca 400 m) on the Cerro Iglesias trail, the forest at this study site resembles the premontane cloud forests of continental areas at the same latitude (e.g. Monteverde in Costa Rica), although at a much lower elevation. The most abundant plants include the canopy dominants *Sacoglottis*

holdridgei, *Ocotea insularis* and *Clusia rosea* and large ferns of the genus *Cyathea* in the understory. However, *Euterpe precatoria* is commonly observed extending beyond the canopy. The vertical structure of this forest is characterized by more than three non-discrete layers of vegetation and intermediate-sized canopy gaps.

Cerro Iglesias (CI – 5°31'41"N, 87°04'12"W)

This study site represents the highest point on the island. The general characteristics and structure of the forest are essentially the same as for Cerro Iglesias Trail. The canopy of this area is dominated by *Sacoglottis holdridgei* and the understory by *Cyathea alfonsiana* (Montoya, 2007). However, the very top of the mountain, which coincides with the end of the trail, is represented by an open area that is clearly the product of human influence. The elevation in this area is 575.5 m (Castillo *et al.*, 1998, Montoya, 2007).

B. Field and laboratory studies

A series of 130 moist chamber cultures was prepared in the laboratory from samples of dead plant material collected in study areas. For this part of the study, samples of both ground litter and aerial litter (dead but still attached plant parts above the ground) were collected in the Chatham Bay, Chatham-Wafer Trail, Cerro Iglesias Trail and Cerro Iglesias study sites. Samples of bark and twigs were collected only in the Wafer Bay Ridge and Chatham Bay study sites, respectively, whereas only samples of aerial litter were obtained in the Genio River study site. All samples were processed and studied using the laboratory protocol given by Stephenson and Stempen (1994).

In addition to the laboratory study, specimens of myxomycetes that fruited in the field under natural conditions were collected and curated using the protocols described by Cannon and Sutton (2004) and Stephenson and Stempen (1994). Following this methodology, myxomycetes are searched for in an opportunistic manner in the microhabitats provided by different types of dead plant material. When observed, the specimen along with a small

Table 1. Species of myxomycetes recorded from Cocos Island and ecological parameters associated with the species in question. Note: A = Abundant, C = Common, O = Occasional, R = Rare 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), FC/MC = total number of field collections (FC) and moist chamber records (MC) for each species, SD = standard deviation.

Species	Abundance	FC/MC	pH (SD) ^a	Elevation ^b
<i>Arcyria afroalpina</i> Rammeloo	R	0/1	3.61 (NA)	575
<i>Arcyria cinerea</i> (Bull.) Pers.	A	0/56	4.91 (1.21)	10-575
<i>Arcyria minuta</i> Buchet	C	0/4	6.34 (1.34)	10
<i>Clastoderma debaryanum</i> A.Blytt	C	0/5	5.71 (1.55)	10-400
<i>Clastoderma pachypus</i> Nann.-Bremek.	R	0/2	4.27 (NA)	400
<i>Collaria arcyriionema</i> (Rostaf.) Nann.-Bremek. ex Lado	A	0/20	6.04 (0.96)	10-150
<i>Collaria lurida</i> (Lister) Nann.-Bremek.	C	0/7	4.28 (1.62)	10-250
<i>Comatricha elegans</i> (Racib.) G.Lister	C	0/5	6.21 (0.85)	10-150
<i>Comatricha laxa</i> Rostaf.	R	0/1	3.33 (NA)	250
<i>Comatricha nigra</i> (Pers. ex J.F.Gmel.) J.Schröt.	O	0/3	3.94 (1.19)	150-575
<i>Comatricha pulchella</i> (C.Bab.) Rostaf.	C	0/7	4.65 (1.21)	10-400
<i>Comatricha tenerrima</i> (M.A.Curtis) G.Lister	A	0/9	6.11 (1.01)	10-575
<i>Craterium aureum</i> (Schumach.) Rostaf.	R	0/1	6.14 (NA)	150
<i>Cribraria intricata</i> Schrad.	R	1/0	NA	150
<i>Cribraria microcarpa</i> (Schrad.) Pers.	A	0/22	4.84 (0.80)	10-575
<i>Cribraria violacea</i> Rex	A	0/12	7.06 (0.78)	10-100
<i>Diachea leucopodia</i> (Bull.) Rostaf.	C	4/3	5.43 (0.71)	10
<i>Diderma effusum</i> (Schwein.) Morgan	A	0/10	5.14 (1.50)	10-575
<i>Diderma hemisphaericum</i> (Bull.) Hornem.	R	0/1	5.90 (NA)	150
<i>Didymium iridis</i> (Ditmar) Fr.	O	0/3	5.88 (0.73)	10
<i>Didymium minus</i> (Lister) Morgan	R	0/1	5.29 (NA)	150
<i>Didymium squamulosum</i> (Alb. & Schwein.) Fr.	C	0/5	5.99 (1.31)	10-150
<i>Echinostelium minutum</i> de Bary	R	0/1	4.27 (NA)	400
<i>Hemitrichia minor</i> G.Lister	O	0/2	4.64 (2.24)	10-250
<i>Hemitrichia serpula</i> (Scop.) Rostaf. ex Lister	O	1/2	4.92 (0.17)	10-575
<i>Lamproderma scintillans</i> (Berk. & Broome) Morgan	C	0/5	6.17 (0.36)	10-150
<i>Licea</i> sp.	O	0/2	5.29 (0.65)	100-150
<i>Macbrideola scintillans</i> H.C.Gilbert	R	0/1	4.02 (NA)	100
<i>Perichaena chrysosperma</i> (Curr.) Lister	A	0/10	7.10 (0.39)	10
<i>Perichaena depressa</i> Lib.	A	0/10	6.12 (0.97)	10-150
<i>Perichaena pedata</i> (Lister & G.Lister) Lister ex E.Jahn	R	0/1	4.97 (NA)	400
<i>Physarum compressum</i> Alb. & Schwein.	O	0/2	7.44 (0.02)	10
<i>Physarum javanicum</i> Racib.	R	0/1	6.35 (NA)	10
<i>Physarum melleum</i> (Berk. & Broome) Masee	C	6/0	NA	10
<i>Physarum pusillum</i> (Berk. & M.A.Curtis) G.Lister	R	0/1	6.62 (NA)	150
<i>Physarum serpula</i> Morgan	O	0/2	6.45 (1.21)	10
<i>Physarum superbum</i> Hagelst.	R	0/1	7.43 (NA)	10
<i>Stemonitis flavogenita</i> E.Jahn	R	0/1	6.05 (NA)	10
<i>Stemonitis fusca</i> Roth	A	0/8	5.59 (0.90)	10-150
<i>Stemonitopsis hyperopta</i> (Meyl.) Nann.-Bremek.	R	1/0	NA	10
<i>Tubifera bombardata</i> (Berk. & Broome) G.W.Martin	R	1/0	NA	150

^amean pH of the moist chamber cultures in which the species was recorded

^belevation (m) or range of elevations over which a species was recorded

portion of the substrate upon which fruiting occurred are collected and returned to the laboratory, after which they are glued to paper strips, placed in small pasteboard boxes and allowed to dry at room temperature. In the current study, no specimens still in the plasmodial stage were collected. In addition, pH was not measured for field collections. The morphological concept of species in current use for myxomycetes was applied to all of the collected material. Nomenclature follows Hernández-Crespo and Lado (2005) except for *Tubifera bombardata*, for which the treatment of Martin and Alexopoulos (1969) is used. Nomenclature for plants follows Trusty *et al.* (2006).

C. Data analysis

Sørensen's coefficient of community index was calculated for each of the data sets from those study sites where samples of both ground litter and aerial litter or bark and twigs were collected equally. The Shannon-Wiener index was obtained for the same study sites as well as for the entire assemblage of myxomycetes recorded from Cocos Island. The taxonomic diversity index was calculated for the combinations of ground litter-aerial litter and bark-twigs, using the methodology outlined by Stephenson *et al.* (1993).

Species were classified according to their abundance using a protocol similar to that described by Stephenson *et al.* (1993). In this system of classification, species representing more than 3% of the total number of specimens were considered as abundant, those falling between 1.5-3% as common, between 0.5-1.5% as occasional and those less than 0.5% as rare.

A species accumulation curve was generated for each type of substrate, using both field and laboratory data based on the abundance-based coverage estimator (ACE) values calculated by the program EstimateS (Colwell, 2006) with a cutoff value of 1.5% in abundance. These sets of data were adjusted

later according to the formula $y = \frac{ax}{b+x}$ as suggested by Raaijmakers (1987). Since the coefficient of variation for all the datasets was higher than 0.5, an estimation of the total

number of species to be expected for each substrate was calculated using the program SPADE (Chao and Shen, 2003) by using the ACE values as recommended by Chao *et al.* (2006).

Results

Two hundred and forty-one specimens representing 41 species of myxomycetes were recorded from the various study sites. The numbers of records from field and laboratory conditions are shown in Table 1. Moist chamber cultures were especially productive, with 92% of all moist chambers and 93% of those prepared with samples of aerial litter or ground litter showing some evidence (either fruiting bodies or plasmodia) of the presence of myxomycetes. None of the 41 species was a new record for the country of Costa Rica or the entire Neotropical region; however, they do represent the first records of this group of organisms from Cocos Island. Only four species were represented exclusively by specimens that had fruited under field conditions. As such, specimens obtained by means of the moist chamber culture technique made up more than 90% of the total number of all species recorded during the entire study. Interestingly, 34% of all specimens were recovered from twigs and bark, although samples of these substrates represented only 20% of all substrate samples collected. In fact, twigs were the substrate characterized by the highest mean number of fruitings per moist chamber culture ($t = 1.96$, d.f. = 136, $p < 0.05$), with a value of 3.70. The corresponding values for aerial litter, ground litter and bark were 1.23, 1.30 and 1.95, respectively.

The species accumulation curves (Fig 2) appear to indicate that for all the different types of substrates examined, adequate sampling was carried out; however, there seem to be two different trends in the analysis. The species accumulation curves for the two types of litter (ground and aerial) and the two non-litter substrates (bark and twigs) seem to be more similar to each other than to either member of the contrasting substrate type. The ACE values for the maximum number of species to be found in the different substrates indicate that

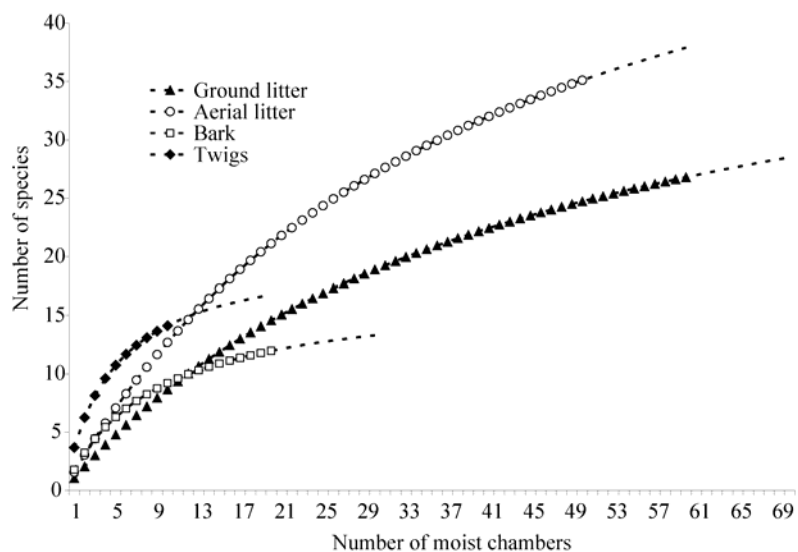


Fig 2 Species accumulation curves for the assemblages of myxomycetes associated with the four different types of substrates investigated. In each instance, the dashed line represents a prediction of the curve using the modified equation obtained from the ACE values. The calculated maximum values of species richness using SPADE were 48 for aerial litter, 39 for ground litter, 14 for bark and 17 for twigs.

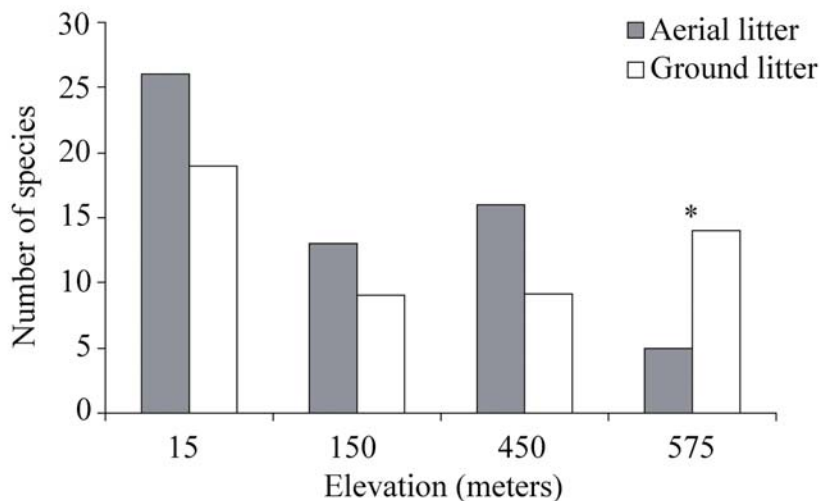


Fig 3 Number of species by substrate type in relation to elevation for both ground litter and aerial litter where the two types of litter were collected equally. The asterisk indicates a statistically significant relationship.

Table 2. Sørensen's coefficient of community values for pairwise combinations of the assemblages of species from the four different study sites where samples of both aerial litter and ground litter were collected equally (upper right) and numbers of species shared in common (lower left).

	Chatham Bay	Chatham-Wafer Trail	Cerro Iglesias Trail	Cerro Iglesias
Chatham Bay	***	0.40	0.22	0.38
Chatham-Wafer Trail	6	***	0.31	0.44
Cerro Iglesias Trail	3	3	***	0.40
Cerro Iglesias	4	4	3	***

the survey accounted for the 62%, 69%, 93% and 88% of the species in aerial litter, ground litter, bark and twigs, respectively. The Shannon-Wiener and taxonomic diversity indices calculated for the assemblage of species on the island were 1.31 and 2.27, respectively, whereas the values for the latter index calculated for the combinations of aerial litter-ground litter and bark-twigs were 2.14 and 1.37, respectively.

When the aerial and ground litter data sets for Chatham Bay, Chatham-Wafer trail, Cerro Iglesias trail and Cerro Iglesias were analyzed, the obtained values for the Shannon-Wiener index were 1.17, 0.92, 0.7 and 0.64, respectively. These diversity values correlate with elevation (Shannon-Wiener index versus elevation, Pearson's product moment = -0.96, $p < 0.05$). Interestingly, pH showed the same pattern (pH versus elevation, Pearson's product moment = -0.76, $p < 0.001$). With the single exception of the Cerro Iglesias, all of the other study sites yielded higher numbers of fruitings for aerial litter than for ground litter (Fig 3, $\chi^2 = 4.43$, $g1 = 1$, $p < 0.05$). In spite of this difference in substrate preference, the highest values for Sørensen's coefficient of community were obtained when data from this study site were included. It is interesting to note that the Cerro Iglesias Trail study site was the least similar to all of the other study sites (Table 2). When only species associated with bark and twigs from the Chatham Bay and Wafer Ridge study sites were considered, no appreciable difference was apparent in their diversity index values (0.70 and 0.72, respectively), and the Sørensen's coefficient of community index for the two sites was 0.3.

Discussion

As mentioned earlier in this paper, information on the assemblages of myxomycetes associated with insular ecosystems is limited. Although the 41 species recorded in the present study have also been reported for continental Costa Rica and neighboring countries, they represent a useful set of data to use in an effort to better understand the

biogeography of myxomycetes in one region of the world. For example, species such as *Arcyria cinerea*, *Cribraria violacea*, *Collaria arcyronema* and *Perichaena chrysosperma* were abundant in both the present study and in the moist tropical forests studied by Schnittler and Stephenson (2000). However, some of the other more abundant species recorded in the present study, including such examples as *Cribraria microcarpa*, *Comatricha tenerrima*, *Diderma effusum* and *Stemonitis fusca*, were not particularly common in the latter study but were reported as among the more common taxa present in Puerto Rico (Stephenson *et al.*, 2004). It has been suggested (e.g. Stephenson, 1989) that such differences in abundance can be explained on the basis of the differences that exist in resource availability and microenvironmental characteristics. However, until recently, very few studies have addressed these questions and thus have generated the data required to test this hypothesis.

In a previous study carried out in the tropical forests of Puerto Rico (Novozhilov *et al.*, 2001), both the species composition of the assemblage of myxomycetes present and their patterns of abundance were similar to those found in the present study. For example, *Physarum serpula*, a rare species on Cocos Island, was also recorded by Novozhilov *et al.* (2001) but not recorded by Schnittler and Stephenson (2000) in Costa Rica. Even more interesting is a comparison of the list of species reported for a previous study in Puerto Rico (Stephenson *et al.*, 1999) and the same type of data compiled in the present study. Eighteen species, representing 80% of the data set for Puerto Rico, are shared between the two studies. This contrasts to the much lower proportion (only 39%) of species shared in common between the present study and those reported by Schnittler and Stephenson (2000) for a series of moist tropical forest study sites in Costa Rica. It is obvious that differences in the overall collecting effort and the types of substrate available can influence these values; however, there would seem to be some evidence that the two islands have a more similar species composition for a comparable type of forest than either does with their continental counterpart.

A clear pattern obtained in this study is the low number of species traditionally regarded as corticolous, especially those belonging to such genera as *Echinostelium*, *Licea* and *Macbrideola*. This is not surprising, especially when it is considered that these genera seem to be more abundant in temperate forests (see Stephenson *et al.*, 1993) than tropical forests. In previous studies in the Neotropical region, this pattern has been well documented (e.g. Schnittler and Stephenson, 2000, Novozhilov *et al.*, 2001).

Another interesting result is that more than 90% of the moist chamber cultures prepared with samples of ground litter and aerial litter in the present study were positive for myxomycetes. Stephenson *et al.* (2004) reported values for positive cultures ranging from 39 to 79% for ground litter samples collected from tropical forests in Puerto Rico and indicated that these values were lower than those usually reported for comparable substrates in temperate forests. However, Schnittler and Stephenson (2000) also reported high values for cultures prepared using samples of litter substrates collected in moist tropical forests of continental Costa Rica, which suggests that such values are not exceptional. The fact that more than 90% of the specimens obtained in the present study were obtained from moist chamber cultures seems to suggest that a more exhaustive field survey would be necessary to document the myxobiota of the island more completely. However, the logistical constraints inherent in carrying out field research in this part of the world make such a task difficult to accomplish. A recent study (Stephenson *et al.*, 2008b) of the myxomycetes associated with woody twigs has provided evidence that this substrate is an underestimated but important microhabitat for some species. In the present study, in spite of the fact that twigs were not collected from study sites located at the higher elevations, more than 30% of the total number of records were recorded on this substrate.

Each of the species accumulation curves show an apparently normal pattern for the type of substrate being considered. Bark has been reported to yield lower numbers of myxomycetes than ground litter in the tropics (e.g. Schnittler and Stephenson, 2000), which is

exactly the reverse of the pattern that has been observed in temperate forests (e.g. Stephenson, 1989; Stephenson *et al.*, 1993). This may explain, at least in part, why the two curves representing litter substrates do not flatten in the figure. Interestingly, the ACE values for the maximum number of species indicate that the survey was more complete for woody substrates such as bark and twigs than for aerial litter and ground litter. These estimates however, may represent underestimations simply because all of the different substrates were not investigated with equal intensity, a variable that clearly could not be controlled in the present study due to logistical constraints such as the time available for collecting in more remote portions of the island. In any case, it seems likely that most of the common species on Cocos Island were successfully recorded during the course of the present study.

A similar situation occurs with respect to the Shannon-Wiener index of diversity. The algorithm used in the calculation of the index depends upon sample size and therefore indices obtained for data sets derived using different sampling efforts are not directly comparable. Schnittler and Stephenson (2000) used a methodology similar to that of the present study and analyzed 111 moist chambers from moist tropical forests in Costa Rica. In this study they obtained a diversity index value of 2.97, much higher than the value (1.31) obtained after processing 130 moist chambers in the present study. The isolation of Cocos Island may play a role in accounting for this difference.

On the other hand, similar values for the taxonomic diversity index would be expected if species of myxomycetes are distributed more or less equally in different ecosystems and geographical locations, as predicted by both the ubiquity theory of protist distribution (Finley, 2002; Fenchel and Finley, 2004) and the neutral theory of biodiversity (Hubbell, 2001). However, in a comparative study of the assemblages of myxomycetes associated with temperate and tropical regions, Stephenson *et al.* (1993) reported values higher than 3.0 for tropical regions of India. The latter study was based only upon specimens collected in the field and did not involve a moist chamber component. In a similar study carried out in

northern Thailand, Tran *et al.* (2006) reported an overall value of 3.44, whereas Stephenson *et al.* (1999) obtained a value of 1.76 for a study carried out in Puerto Rico. The latter value is lower than what might be expected for a tropical region, but their study was limited to the ground litter microhabitat and considered only specimens obtained from moist chamber cultures. Interestingly, the value obtained for Cocos Island (2.27) falls between the values reported for India and Puerto Rico. However, there is at least some evidence that tropical insular assemblages are characterized by lower species/genera ratios than continental ones, which may reflect fundamental but as yet undetermined differences in the biotic interactions and ecological factors involved in determining the distribution patterns and dispersal potential of myxomycetes (Stephenson *et al.*, 2008a). For these organisms, the more limited habitat space and taxonomic (and thus resource) diversity of available substrates on an island may favor interspecific competition over intraspecific interactions, assuming that more closely related species have more similar microenvironmental requirements. Data obtained from studies carried out in arid areas of northern Chile (Lado *et al.*, 2007) and Russia (Novozhilov *et al.*, 2006), which are biogeographically isolated in an ecological sense, provide evidence to support for such a hypothesis. In fact, this apparent resource partitioning among the members of the assemblage of species of myxomycetes present in a particular ecosystem may represent one of the more important factors determining both the local and global distribution within the group.

A clear pattern of decreasing diversity with increasing elevation was apparent in the present study, based on the Shannon-Wiener index values obtained for some of the study sites. The occurrence of such a pattern in tropical regions was discussed by Stephenson *et al.* (2004). Apparently, a lower number of plant species is associated with this phenomenon, but the effect of abiotic factors probably also plays an important role in determining the distribution patterns of myxomycetes. In the present study, pH was also observed to decrease with elevation,

suggesting that microenvironmental conditions also change at higher elevations. Recent studies (e.g. Schnittler *et al.*, 2006; Rojas and Stephenson, 2007) have demonstrated the importance of some microenvironmental characteristics in determining the occurrence of some species of myxomycetes, which suggests that if myxomycetes respond to microenvironmental factors when fruiting, they would probably respond as well to macroenvironmental factors such as differences in elevation and plant communities.

One interesting pattern that emerged from the present study is that species richness was higher for aerial litter than for ground litter except in the study area at the highest elevation, where more species were associated with ground litter. It is generally assumed that wind plays a major role in dispersing the spores of myxomycetes (Stephenson *et al.*, 2008a). Schnittler *et al.* (2006) demonstrated that even a slight breeze can have the potential effect of causing the spore of a myxomycete to be dispersed more than one kilometer from its starting point. As such, the occurrence of myxomycetes in aerial microhabitats would not seem surprising. With this in mind, it seems logical to attribute the apparent lower diversity of aerial substrates at higher elevations to the possible removal of spores by the usually higher winds associated with such sites. However, the leaching effect of the sometimes almost horizontal wind-driven precipitation that occurs over mountain peaks also could reduce the number of spores associated with aerial substrates.

Comparisons among the various study sites did not reveal large numbers of species shared in common, which also accounts for the relatively low coefficient of community values obtained for pairwise comparisons of these study sites. It is clear that these differences could be attributed, at least in part, to the different plant communities present in the study sites. Tran *et al.* (2007) reported a similar situation for a series of study sites in northern Thailand; however, the Cerro Iglesias Trail study site was characterized by a coefficient of community value even lower that might have been anticipated, when the assemblage of species was compared with those of the two

lower elevations. Interestingly, Cerro Iglesias shared more species with these communities, which suggests that wind dispersal, presumably more efficient in open areas, is a major factor determining the composition of species on the island. The forest surrounding the Cerro Iglesias Trail is more closed than the other three study sites, which would be expected to place some constraint on wind dispersal. Interestingly, the assemblages of species associated with bark and twigs did not show differences in diversity that could be related to elevation, suggesting that the two study sites involved (Chatham Bay and Wafer Bay Ridge) may have similar environmental characteristics. One possibly important aspect is that both bays are located in the northern portion of the island, where they would be subjected to the influence of tides, winds and rain in similar manner. The low coefficient of community value for these two study sites seems to be related to taxonomic differences in the plant communities present.

In summary, the data obtained in the present study indicate that both the species composition of the assemblages of myxomycetes present and their diversity along the elevation gradient represented by the transect of study sites conform to a similar pattern reported for other areas of Neotropics. Moreover, these same data provided additional evidence that the distribution of myxomycetes in nature is not well explained by the ubiquity theory. Instead, wind and the composition of the plant communities present seem to be the most important factors determining the occurrence of myxomycetes on the island, and perhaps for other insular ecosystems as well.

Acknowledgements

Appreciation is extended to Luis Diego Gomez and Michel Montoya, the *Biocursos* program of the Organization for Tropical Studies and the Eumycetozoan Laboratory at the University of Arkansas for their logistical support and to the authorities in the Cocos Island Conservation Area office in San Jose for granting permission to conduct this study and to the park rangers who assisted in the field work. We also thank Maria Julia Vargas and the Herbarium of the University of Costa Rica (USJ) for their valuable help with pre-processing and shipping the samples and specimens. This project was funded by National Science Foundation grant DEB-0316284.

References

- Beauvais, J and Matagne, P. (1998). The Holdridge's concept of "life zone": A Tropical point of view in ecology. *Ecologie* 29: 557-564.
- Cannon, P. and Sutton, B. (2004). Microfungi on wood and plant debris. In: *Biodiversity of fungi: Inventory and monitoring methods* (eds. G. Mueller, G. Bills and M. Foster). Elsevier Academic Press, Burlington Massachusetts: 217-239.
- Castillo, P., Batiza, R., Vanko, D., Malavassi, E., Barquero, J. and Fernandez, E. (1988). Anomalous young volcanoes on old hot-spot traces. I. Geology and petrology of Cocos Island. *Geological Society of America Bulletin* 100: 1400-1414.
- Chao, A. and Shen, T.J. (2003). SPADE (Species Prediction And Diversity Estimation). Version 3.1. Persistent URL <chao.stat.nthu.edu.tw>.
- Colwell, R.K. (2006). EstimateS: Statistical estimation of species richness and shared species from samples. Version 8.0. Persistent URL <purl.oclc.org/estimates>.
- de Wit, R. and Bouvier, T. (2006). 'Everything is everywhere, but, the environment selects'; what did Baas Becking and Beijerinck really say? *Environmental Microbiology* 8: 755-758.
- Eliasson, U. (1991). The myxomycete biota of the Hawaiian islands, USA. *Mycological Research* 95: 257-267.
- Eliasson, U. and Nannenga-Bremekamp, N. (1983). Myxomycetes of the scalesia forest, Galapagos Islands, Ecuador. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series C Biological and Medical Sciences*. 86: 143-154.
- Fenchel, T. and Finlay, B. (2004). The ubiquity of small species: patterns of local and global diversity. *BioScience* 54: 777-784.
- Finlay, B. (2002). Global dispersal of free-living microbial eukaryotic species. *Science* 296: 1061-1063.
- Foissner, W. (2006). Biogeography and dispersal of microorganisms: a review emphasizing protists. *Acta Protozool.* 45: 111-136.
- Hernández-Crespo, J.C. and Lado, C. (2005). An on-line nomenclatural information system of Eumycetozoa. Revised on 17-V-2007. Persistent URL <nomen.eumycetozoa.com>.
- Hogue, C. and Miller, S. (1981). Entomofauna of Cocos Island, Costa Rica. *Atoll Research Bulletin* 250: 1-29.
- Hubbell, S. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton New Jersey.
- Kirkendall, L. and Jordal, B. (2006). The bark and ambrosia beetles (*Curculionidae*, *Scolytinae*) of Cocos Island, Costa Rica and the role of mating systems in island zoogeography. *Biological Journal of the Linnean Society* 89: 729-743.

- Lado, C., Estrada-Torres, A. and Stephenson, S.L. (2007). Myxomycetes collected in the first phase of a north-south transect of Chile. *Fungal Diversity* 25: 81-101.
- Lado, C., Estrada-Torres, A., Stephenson, S.L., Wrigley de Basanta, D. and Schnittler M. (2003). Biodiversity assessment of myxomycetes from two tropical forest reserves in Mexico. *Fungal Diversity* 12:67-110.
- Martin, G.W. and Alexopoulos, C.J. (1969). *The Myxomycetes*. University of Iowa Press, Iowa City.
- Novozhilov, Y.K., Schnittler, M., Rollins, A. and Stephenson, S.L. (2001). Myxomycetes from different forest types in Puerto Rico. *Mycologia* 77: 285-299.
- Novozhilov, Y.K., Zemlianskaia, I.V., Schnittler, M. and Stephenson, S.L. (2006). Myxomycete diversity and ecology in the arid regions of the Lower Volga River Basin (Russia). *Fungal Diversity* 23:193-241.
- Montoya, M. (2007). Conozca la Isla del Coco: una guía para su visita. In: *Biocursos para amantes de la naturaleza: Conozca el parque nacional Isla del Coco, la isla del tesoro (26 abril al 6 de mayo 2007)*. (ed. Organization for Tropical Studies). Organization for Tropical Studies. San José, Costa Rica. 35-176.
- Pando, F. (1997). Catálogo preliminar de los Mixomicetes del Parque Nacional de Coiba (Panamá). In: *Flora y fauna del Parque Nacional de Coiba (Panamá)*. (ed. S. Castroviejo). Agencia Española de Cooperación Internacional. Madrid: 191-204.
- Porter, D. (1973). The vegetation of Panama: a review. In: *Vegetation and vegetation history of northern Latin America*. (ed. A. Graham). Elsevier Scientific Publishing Company, Amsterdam London New York: 177-183.
- Raaijmakers, J.G.W. (1987). Statistical analysis of the Michaelis-Menten equation. *Biometrics* 43: 793-803.
- Rojas, C. and Stephenson, S.L. (2007). Distribution and ecology of myxomycetes in the high-elevation oak forests of Cerro Bellavista, Costa Rica. *Mycologia* 99: 534-543.
- Schnittler, M. and Stephenson, S.L. (2000). Myxomycete biodiversity in four different forest types in Costa Rica. *Mycologia* 92: 626-637.
- Schnittler, M., Unterseher, M. and Tesmer, J. (2006). Species richness and ecological characterization of myxomycetes and myxomycete-like organisms in the canopy of a temperate deciduous forest. *Mycologia* 98: 223-232.
- Stephenson, S.L. (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: 608-621.
- Stephenson, S.L., Kalyanasundaram, I. and Lakhanpal, T. (1993). A comparative biogeographical study of Myxomycetes in the mid-Appalachians of eastern North America and two regions of India. *Journal of Biogeography* 20: 645-657.
- Stephenson, S.L. and Stempen, H. (1994). *Myxomycetes: a handbook of slime molds*. Timber Press, Portland Oregon.
- Stephenson, S.L., Landolt, J. and Moore, D. (1999). Protostelids, dictyostelids and myxomycetes in the litter microhabitat of the Luquillo Experimental Forest, Puerto Rico. *Mycological Research* 103: 209-214.
- Stephenson, S.L., Schnittler, M., Lado, C., Estrada-Torres, A., Wrigley de Basanta, D., Landolt, J., Novozhilov, Y.K., Clark, J., Moore, D. and Spiegel, F. (2004). Studies of neotropical mycetozoans. *Systematics and Geography of Plants* 74: 87-108.
- Stephenson, S.L., Schnittler, M. and Novozhilov, Y.K. (2008a) Myxomycete diversity and distribution from the fossil record to the present. *Biodiversity and Conservation* 17: 285-301.
- Stephenson, S.L., Urban, L., Rojas, C. and McDonald, M. (2008b). Myxomycetes associated with woody twigs. *Revista Mexicana de Micología* (in press).
- Tran, H.T.M., Stephenson, S.L., Hyde, K.D. and Mongkolporn, O. (2006). Distribution and occurrence of myxomycetes in tropical forests of northern Thailand. *Fungal Diversity* 22: 227-242.
- Trusty, J.L., Kesler, H.C. and Haug-Delgado, G. (2006). Vascular flora of Isla del Coco, Costa Rica. *Proceedings of the California Academy of Sciences (Fourth Series)* 57: 247-355.
- Walther, C. (2002). Crustal structure of the Cocos Ridge northeast of Cocos Island, Panamá Basin. *Geophys Res Lett* DOI:10.1029/2001GL014267.