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Biogeography and Microhabitat Distribution of Myxomycetes in High-Elevation Areas of the Neotropics

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BIOGEOGRAPHY AND MICROHABITAT DISTRIBUTION OF MYXOMYCETES IN HIGH-ELEVATION AREAS OF THE NEOTROPICS

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy in Biology

By

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ABSTRACT

Myxomycetes are a group of amoeboid organisms with the capacity of forming fruiting bodies that resemble some macrofungi. The ecology and global distribution of species within the group have been studied only during the last half century. For this reason, a number of questions regarding the nature of the interactions that exist between myxomycetes and their environment still lack the empirical evidence required to obtain complete answers. In the Neotropical region, species assemblages have been moderately well studied, but their biogeography and macroecology have received little attention. In high-elevation areas of this region, the situation is especially precarious, due the lack of formal studies that have considered these potentially threatened ecosystems. In order to fill in some of the information gaps for which previous studies had not provided conclusive evidence, a number of projects outlined in this dissertation were carried out.

The main objective of the research described herein was to study the biogeography and ecology of the myxomycete assemblages associated with high-elevation areas of the northern Neotropics. However, an appreciable effort was directed towards other ecosystems in order to obtain comparative data that could be used to assess other specific questions formulated during the course of the research. With the data generated in this investigation, a number of patterns could be detected at different ecological levels. Among these were that myxomycetes respond to differences in macro- and microenvironmental characteristics of the ecosystems in which they occur. In the first case, myxomycetes seem to respond more or less collectively to some of the parameters that could be measured or determined. However, at the microhabitat level, the selective responses seem to be specific for particular species. This general pattern appears to be

consistent and independent of the geographical and historical characteristics of the area. However, the latter seem to have a strong effect on the composition of the assemblage of species present in a particular area.

These observations support the idea that myxomycetes are not neutrally distributed across biomes and ecosystems on earth. In fact, structural differences in the assemblages studied along a latitudinal gradient from the United States to Costa Rica suggest that some myxomycetes have regional distributions. As specific results of this study, the first comprehensive ecological analysis of myxomycetes for a tropical country, a series of updated species diversity lists for three Neotropical countries and a comparison of myxomycete assemblages across three different biogeographical provinces were carried out. It is envisioned that the data generated during this investigation will be used in future studies relating to both myxomycetes and the ecosystems studied. In any case, the data presented herein represent valuable contribution to what is known about the threatened high-elevation forests in the Neotropics.

This dissertation is approved for
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DEDICATION

To the circle of fire.

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LIST OF THE ORIGINAL ARTICLES INCLUDED IN THIS DISSERTATION

Rojas C, Stephenson SL. 2007. Distribution and ecology of myxomycetes in the high-elevation oak forests of Cerro Bellavista, Costa Rica. Mycologia 99: 534-543.

Rojas C, Stephenson SL. 2008. Myxomycete ecology along an elevation gradient on Cocos Island, Costa Rica. Fungal Diversity 29: 117-127.

Rojas C, Schnittler M, Biffi D, Stephenson SL. 2008. Microhabitat and niche separation in species of *Ceratiomyxa*. Mycologia 100: 843-850.

Rojas C, Valverde R, Stephenson SL, Vargas MJ. 2009. Ecological patterns of Costa Rican Myxomycetes. Fungal Ecology (in press). doi 10.1016/j.funeco.2009.08.002.

Chapter 1

Introduction

Myxomycetes and research on these organisms in the Neotropics

The myxomycetes (plasmodial slime molds or myxogastrids) comprise a group of amoebae that form part of the super group Amebozoa (Adl et al. 2005). Their phylogenetic position is currently supported by molecular studies that show their monophyletic character within that super group (see Pawlowski and Burki 2009). In the past, they have been considered members of a group known as the Eumycetozoa (Olive 1975). This hypothetical group included, along with the myxomycetes, two other groups of amoebae known as dictyostelids and protostelids. However, the integrity of the Eumycetozoa as a natural group has been recently questioned on the basis of molecular evidence showing that the protostelids are probably not monophyletic (Shadwick et al. 2009).

This fact does not affect the current recognized position of myxomycetes within the Amebozoa but it changes the concepts and nomenclatural treatments of the particular subgroups of organisms to which they are related. Given this scenario and for the purpose of this dissertation, myxomycetes will simply be treated as a group of amebozoans that is taxonomically distinct from both dictyostelid and protostelid amoebae.

Life cycle

The life cycle of myxomycetes has been described in detail by a number of authors (e.g., Martin and Alexopoulos 1969, Stephenson and Stempen 1994, Everhart and Keller 2008). Most of these descriptions, however, seem to be incomplete in the sense that they depict only some of the observed stages or conversions that myxomycetes can undergo during their life. In general, these descriptions serve the purpose of illustrating the most important life cycle stages of these organisms; however, the absence of complete life cycles has implications for a complete ecological understanding of the group.

The first aspect to consider regarding the life cycle of myxomycetes is that these organisms have three important life stages that differ dramatically from one another. These stages are represented by one reproductive phase and two vegetative ones that will be explained in the following paragraphs. In this way, individuals undergo a process of modifications over their life span in order to complete the entire cycle.

Although myxomycetes are amoeboid organisms, they have the capacity to produce spores (Martin and Alexopoulos 1969, Stephenson and Stempen 1994).This capacity is also shared with dictyostelid, protostelioid amoebae and the genus *Copromyxa*, the only other "fruiting-capable" groups within the Amebozoa (Cavalier-Smith 2003, Adl et al. 2005). The spores produced by myxomycetes are contained within a spore-holding structure known as a fruiting body. There are several types of fruiting bodies or sporocarps (Figure 1); however, the most common one is a stalked globose

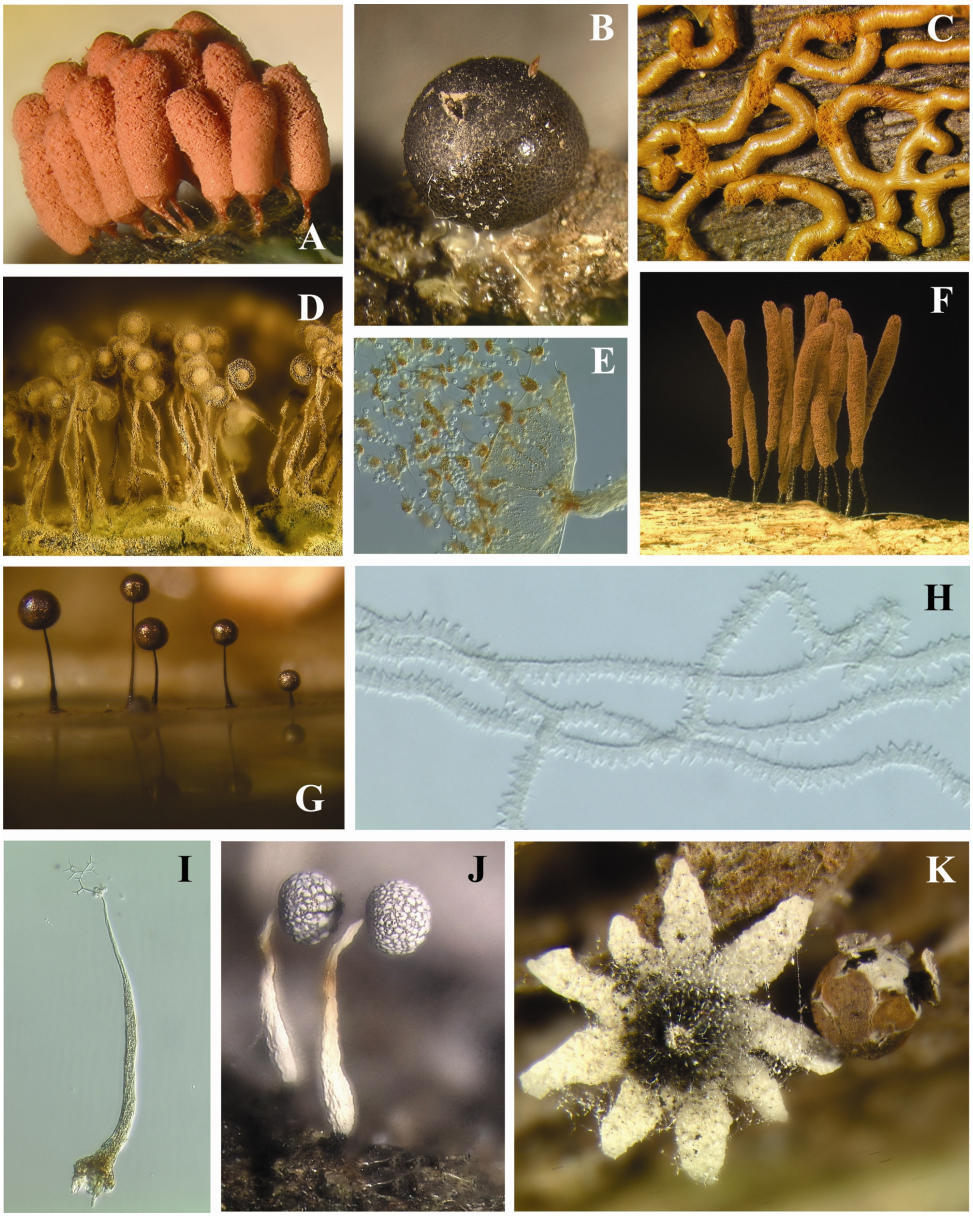

Figure 1. Myxomycete fruiting bodies and associated structures. A. Sporangia of *Arcyria insignis*; B. Aethalium of *Lycogala epidendrum*; C. Plasmodiocarp of *Hemitrichia serpula*; D. Sporangia of *Cribraria intricata*; E. Peridial net of *C. intricata*; F. Sporangia of *Stemonitis axifera*; G. Sporangia of *Lamproderma scintillans*; H. Capillitium of *A. denudata*; I. Sporangium of *Echinostelium minutum*; J. Sporangia of *Physarum stellatum* and K. Sporangia of *Physarum brunneolum*. Images not at the same scale.

structure known as a sporangium. This type of structure depicts the typical reproductive stage in myxomycetes. As the fruiting body develops (Figure 2A), the process of spore formation takes place as well. The newly formed spores, which are produced by meiotic divisions, are released to the environment once the fruiting body develops completely (Figure 2B). It is because of this capacity to produce spores within fruiting bodies that myxomycetes were once considered part of the Fungi (Alexopoulos et al. 1996).

These spores, with typical diameters ranging between 5 and 15 μm (Tesmer and Schnittler 2007), are dispersed with the aid of a number of environmental factors including wind and rain. However, it has also been observed that insects (e.g., Blackwell 1984) and even vertebrates (e.g., Townsend et al. 2005) can act as dispersion vectors. Once the spores reach a suitable substrate, they germinate (Figure 2C) and give rise to a haploid ameboid cell known as a myxamoeba (Figure 2E). Apparently, as a product of environmental conditions, among which the most important is high moisture, these myxamoebae can undergo a process of transformation in which two anterior flagella are produced. When this occurs, the resulting individuals are known as swarm cells (Figure 2F). The inter-conversion between myxamoebae and swarm cells occurs in both directions. If environmental conditions are not favorable for these vegetative cells, myxamoebae can enter a resting stage in which they divide and produce microcysts (Figure 2G), which can in turn form myxamoebae once conditions are favorable again.

If conditions favor the free-living style of both myxamoebae and swarm cells, these cell types can act as gametes. Thus far, studies show that both myxamoebae and swarm cells mate only with other individuals of the same cell type that carry compatible reproductive alleles (Figure 2H, e.g., Clark 1995) in a process known as heterothallism.

However, non-heterothallic strains for species with heterothallic systems are known to be very common as well (Clark et al. 2004). In fact, it has been observed that these systems can inter-convert (Collins 1980) and that some morphospecies are a mixture of heterothallic and non-heterothallic lineages (Clark and Stephenson 2003). Non-heterothallic lineages of myxomycetes seem to continue their life cycle via apomixis (Figures 2M, N and O, e.g., Haskins and Therrien 1978). These lineages are characterized by the lack of genetic crossing and ploidy changes between vegetative and reproductive stages (Clark et al. 2003).

Assuming that the cycle is heterothallic, after two compatible gametes undergo somatogamy, their nuclei fuse and a zygote is formed (Figure 2I). The zygote starts growing and its nucleus divides rapidly to finally form a macroscopic unicellular multinucleate structure known as a plasmodium (Figure 2J). During this vegetative stage, myxomycetes can grow as large as one meter or more in diameter and become very conspicuous even for the untrained eye. Due the gelatinous texture of the plasmodium, myxomycetes are colloquially referred to as plasmodial slime molds (Stephenson and Stempen 1994) or simply slime molds.

Depending on environmental conditions, the plasmodium can undergo a transformation into a resting structure known as a sclerotium (Figure 2K), in which myxomycetes can survive until favorable conditions return. In that case, the sclerotium usually re-transforms and re-generates a plasmodium. The process of sporocarp formation (Figure 2L) takes place once the plasmodium matures or it is old. In this way, fruiting bodies are formed, the life cycle is completed and myxomycetes are able to produce spores again.

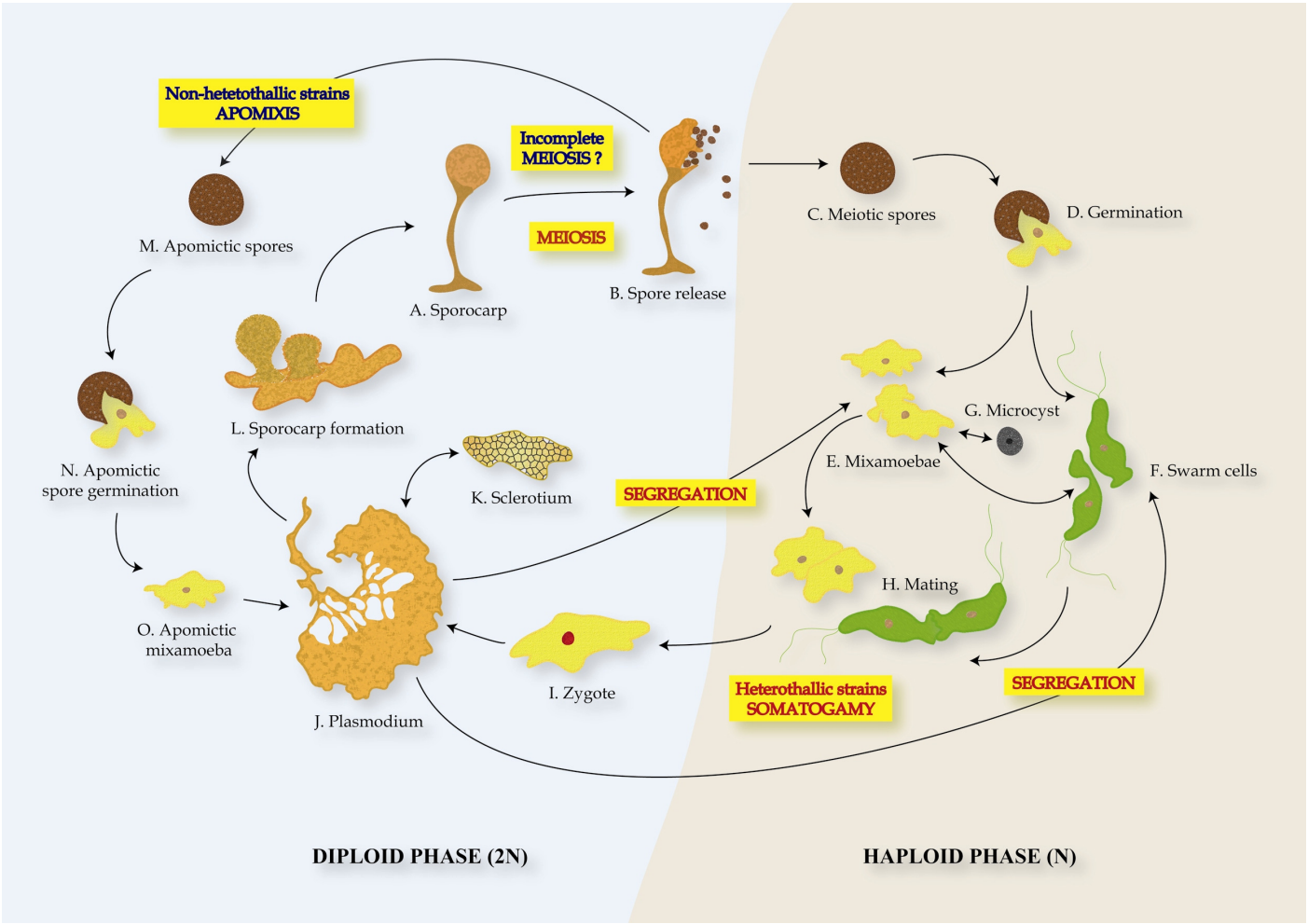

Figure 2. Life cycle of myxomycetes, including both heterothallic and non-heterothallic types.

Classification

The current view on the phylogenetic position of myxomycetes is that the group should be treated as a clade within the super group Amebozoa (see Pawlowski and Burki 2009, Shadwick et al. 2009). Contrary to the situation with other taxonomic groups within the Amebozoa, most myxomycete genera and species have remained in the group since they were described. Over time, a large number of corrections have been made on both the taxonomic and nomenclatural treatments (e.g., Keller and Brooks 1976, Nannenga-Bremekamp 1984, Gams 2005, Lado et al. 2005) but the integrity of the myxomycetes as a group has been unquestioned.

Even though this situation has been the general pattern, there are particular cases that represent exceptions. The genus *Ceratiomyxa* J.Schröt., for example, was traditionally considered a myxomycete by a number of authors (e.g., Martin and Alexopoulos 1969), until L. S. Olive (1970) proposed the genus belongs to the group of protostelioid amoebae that he called protostelids at that time and which were thought to be paraphyletic. Almost 40 years later, molecular evidence shows that this genus is neither a protostelioid amoeba nor a myxomycete but a deeply diverging sister group to the latter (Fiore-Donno et al. 2010). A similar situation occurred with the genus *Schenella*, which was originally thought to be a myxomycete (Macbride 1911) but is now considered to be a fungus (see Estrada-Torres et al. 2005).

In spite of this constant process of classification changes, Hernández-Crespo and Lado (2005) reported about 915 formally accepted names of myxomycetes in 59 different genera. Whether or not all those names correspond to actual biological species or some of them are examples of species complexes is an issue to be resolved by myxomycete

taxonomists in the future. The fact is that a similar scenario is observed in most groups of protists. For this reason, some authors have argued that a nested classification system is not appropriate at the moment (see Adl et al. 2005) and that phylogenetic relationships among groups should be elucidated or clarified before a proper system is established.

For myxomycetes, only recently has a higher order classification of the group been carried out using molecular analysis (see Fiore-Donno et al. 2005). This study provided evidence supporting an older classification of myxomycetes based on spore color (Lister and Lister 1925). In this system, species with light-colored spores are separate from species with dark-colored spores. Lister and Lister (1925) gave these two groups the category of orders but more recent authors have considered that myxomycetes are composed of up to six different orders (e.g., Martin and Alexopoulos 1969).

With this scenario is clear that there is still more work to be done at the higher category level in myxomycetes before a clearer picture is available. Before that, perhaps the best way to classify myxomycetes is that proposed by Adl et al. (2005) in which a non-categorical system is used. The only problem with this is that most modern myxomycete researchers have used the system proposed by Martin and Alexopoulos (1969), which is also the most commonly used system today (e.g., Stephenson 2003). For that reason, a reference in publications to this system is still needed regarding myxomycetes. That approach has been followed in this dissertation.

According to Martin and Alexopoulos (1969), myxomycetes are classified into two main groups depending on the position of the spores in relation to the fruiting body. Those species with spores borne outside of the fruiting body are considered part of the order Ceratiomyxales, the group that includes the genus *Ceratiomyxa*, as already

discussed. The rest of the species belong to the orders Echinosteliales, Liceales, Trichiales, Physarales and Stemonitales, which are groups characterized by bearing the spores borne inside the fruiting body. The main differences between the latter groups are based on morphological characters such as spore color, presence, shape and ornamentation of the internal structures of the fruiting body and presence of calcium carbonate. However, it is anticipated that the relationships among orders and genera will undergo a number of changes when fine-scale molecular analyses are carried out on a wide range of species. For instance, the recently studied relationship between physaraceous and stemonitaceous myxomycetes has already led to some changes in classification being proposed (see Fiore-Donno et al. 2008).

Ecological study

Historically, myxomycetes have been studied by a larger number of trained taxonomists than ecologists. Even though in earlier publications there is some basic ecological information about myxomycete species (e.g., Lister 1894, Fries 1899), most of the ecological analyses of the group have been carried out during the last decades (e.g., Maimoni-Rodella and Gottsberger 1980, Eliasson 1981, Stephenson 1988, Stephenson et al. 2003).

The majority of the studies on myxomycetes to date have been conducted in the temperate areas of the Northern Hemisphere (Stephenson et al. 2004b), notably Europe and North America. The most comprehensive treatments of the group (e.g., de Bary 1859, Lister 1894, Martin and Alexopoulos 1969) are a testimony of that fact. Even though some other geographical locations of the world have been studied more intensively in the

last 50 years or so, there are still some areas that are highly underrepresented (see Figure 3). Unfortunately, this is a pattern that can be generalized to most groups of organisms as well.

Most of the current ecological patterns known for the myxomycetes are based on this highly skewed research scheme followed in the past. For this reason, whether or not the ecological information currently available is enough to provide reasonably supported hypotheses remains problematic. For example, when the currently available geospatial information on myxomycete distribution is used to generate niche models, it is obvious that a similar research effort in underrepresented areas (e.g., the tropics, see Stephenson et al. 2004b) is necessary before a more accurate and biologically meaningful distribution map can be generated (Figure 4).

In any case, based on the best available information, myxomycetes are known to occur in most terrestrial ecosystems (Stephenson 2003). The general latitudinal pattern shows that the diversity of these organisms is higher in temperate than in tropical or boreal areas (Schnittler 2001a). However, as recently mentioned, due the discrepancy that exists among the research efforts carried out at the different latitudes in the world, this pattern is still highly arguable.

Myxomycetes have long been known to occur on decaying wood, litter, soil, herbivore dung and the bark surface of living trees in the forest (Stephenson and Stempen 1994). Each of these substrates is known to support a different assemblage of species (Stephenson 2003). In recent years they have been documented on less traditional substrates such as inflorescences (e.g., Schnittler and Stephenson 2002), twigs (Stephenson et al. 2008), bryophytes (e.g., Schnittler 2001c) and lianas (e.g., Wrigley de

Basanta et al. 2008). These types of non-traditional substrates have been reported from tropical areas of the world.

In a similar manner, modern trends in myxomycete research have included the study of desert areas (e.g., Schnittler 2001b, Lado et al. 2007), islands (e.g., Eliasson 2004, Stephenson et al. 2007b, Rojas and Stephenson 2008) and mountains (e.g., Rojas and Stephenson 2007, Novozhilov and Schnittler 2008, Ronikier and Ronikier 2009), all of which are areas that had received little attention in the past. The study of these areas has increased not only the number of known species for some countries in the world, but also the capacity to conduct ecological comparisons. These were hard to carry out in the past due the lack of information about certain habitat types and geographical areas. With the information obtained from these projects, it seems that myxomycetes show distribution patterns that are associated with forest type, precipitation and elevation as described for abudant species by Stephenson et al. (2007a). In the first comprehensive ecological analysis for a tropical country, Rojas et al. (2009) found that the distribution pattern for the myxomycetes in Costa Rica supports this hypothesis.

Due to this new tendency of data acquisition from underrepresented geographical areas in the world, there seems to be a trend towards the publication of results from such areas. Just recently, for example, published reports have been made for New Zealand (Stephenson 2003), the Neotropics (Lado and Wrigley de Basanta 2008), Africa (Ndiritu et al. 2009) and the North American grasslands (Rollins 2009). Also, a revision of the myxomycetes from Costa Rica is in progress (Rojas, Schnittler and Stephenson, *in preparation*).

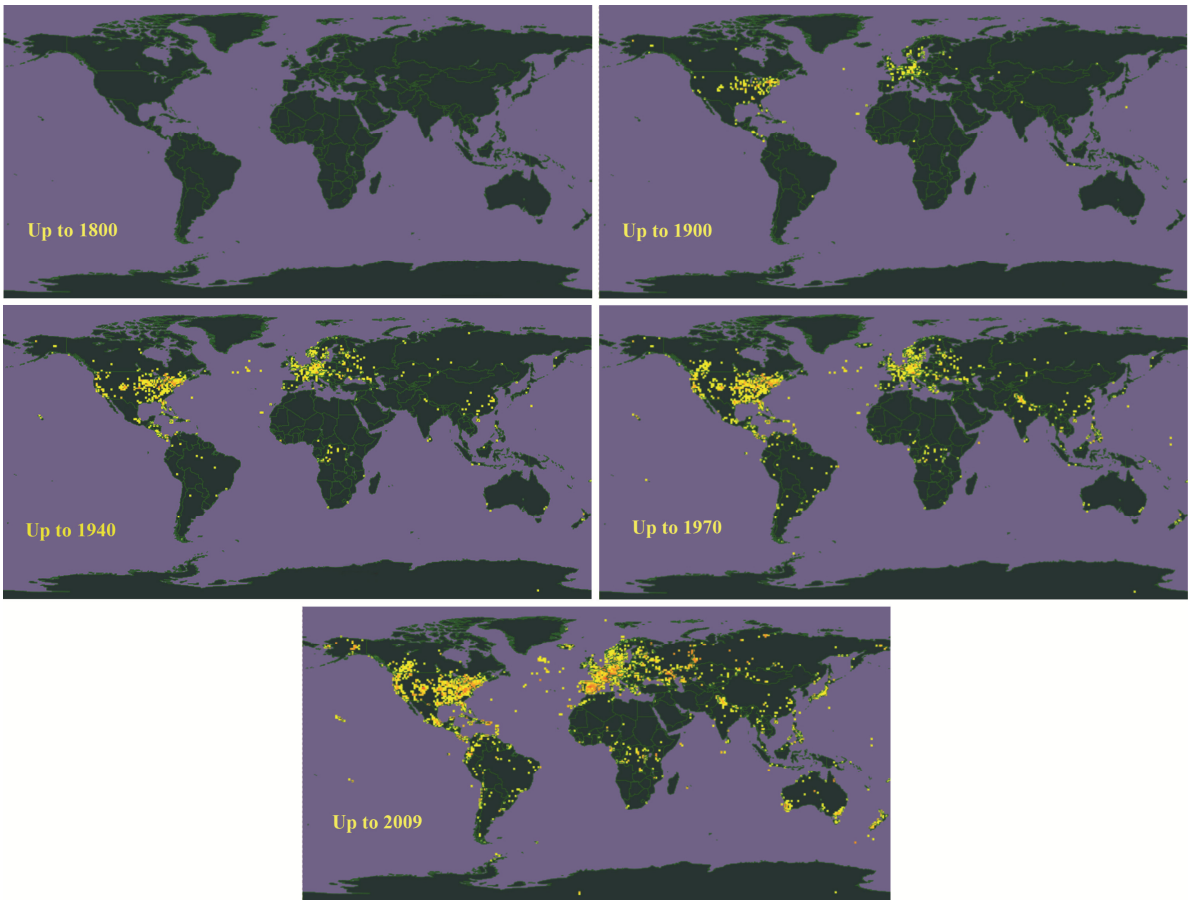

Figure 3. Geographical distribution of myxomycete records at different time intervals, beginning in 1800 and based on data obtained from the Global Biodiversity Information Facility online portal (http://www.gbif.org) on October 11, 2009 (a total of 147,792 records).

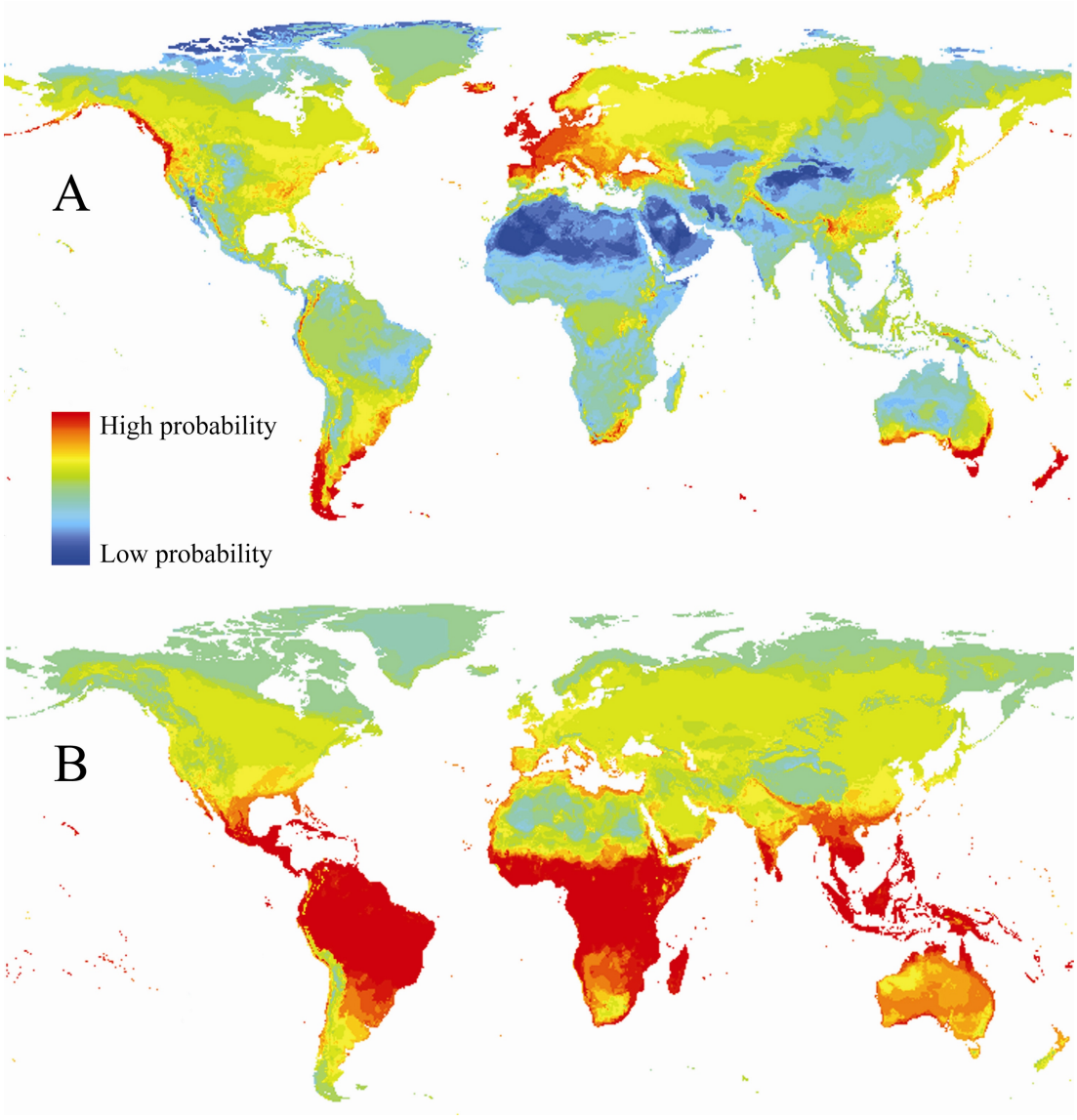

Figure 4. Probable distribution of the fundamental niche of myxomycetes calculated from (a) the current geographical distribution of records as retrieved from the Global Biodiversity Information Facility and (b) assuming a more even distribution of the research effort in tropical areas. Maps generated using openModeller (Muñoz et al. 2009).

There is no doubt that these studies largely represent the current tendency of incorporating ecological aspects into the myxomycete research. However, it seems that in years to come, the use of molecular techniques to evaluate ecological aspects of the group will become more common, especially since it has the potential to generate important information that otherwise would be impossible to obtain. Examples of the latter are the recent studies of Win Ko Ko et al. (2009) and Kamono et al. (2009).

Research in Neotropical areas

The Neotropics, or New World Tropics, are *sensu stricto* the area that occurs between the Tropic of Cancer and the Tropic of Capricorn on the American continents. Some authors have considered, however, that when used to refer to the biogeographical province, the term also should include some of the subtropical areas in Mexico and South America (e.g., Udvary 1975). More recently, the term has been used in the same way when considering information on endemic taxa and movement of species (Olson et al. 2001). The latter meaning is an operational definition used for a number of practical purposes, including biogeographical, palaeoecological and climate change research as well as the distribution of conservation efforts and international consideration of the ecological regions of the world. For this reason, and for the purpose of this dissertation, the term Neotropics or Neotropic/Neotropical region will be used in this sense of Olson et al. (2001, see Figure 5).

Research on myxomycetes has been carried out in the Neotropical region for more than 100 years, as diagramed on Figure 3. According to Lado and Wrigley de Basanta (2008), the first known reports of a myxomycete in the Neotropical area were

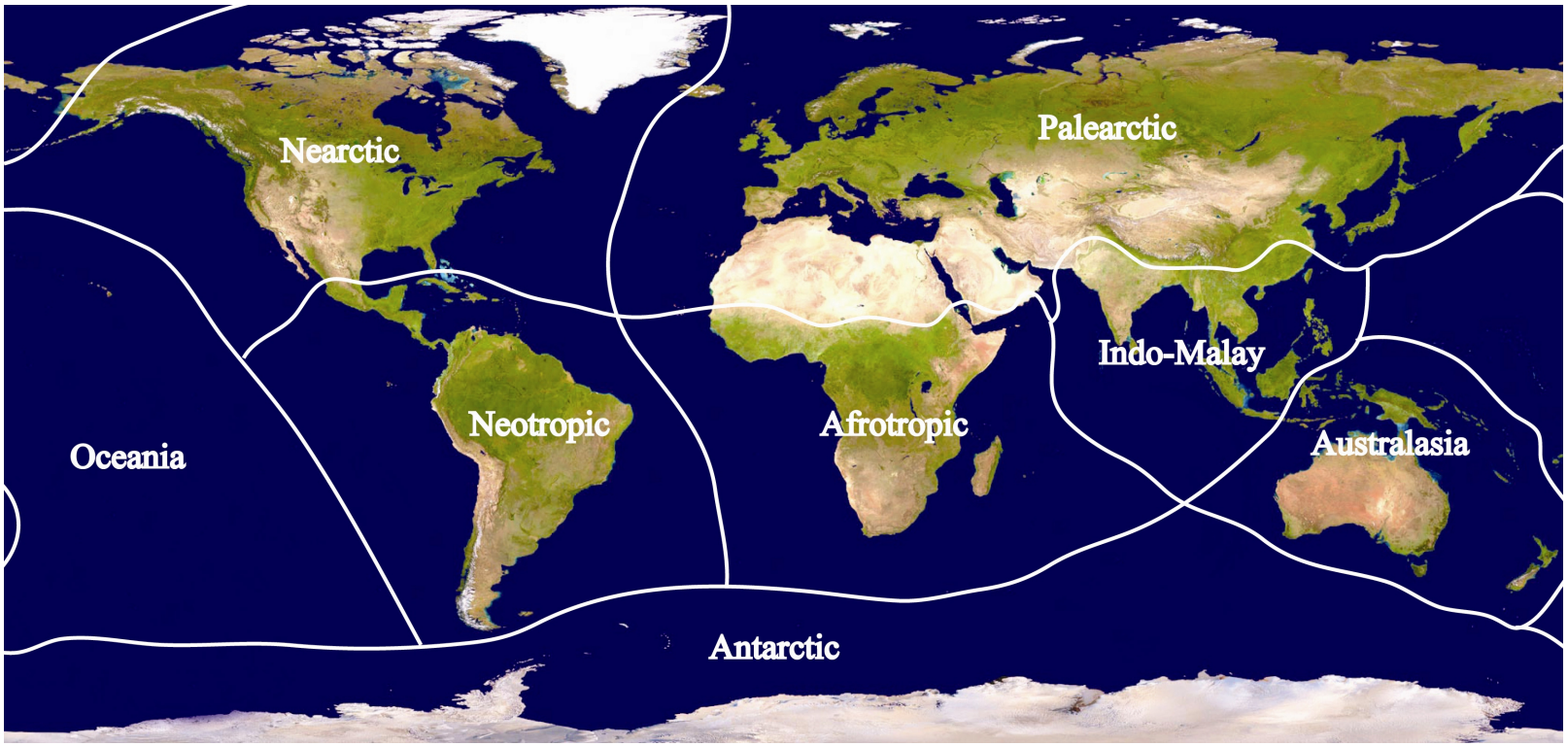

Figure 5. Biogeographical regions of the world as understood in the context of this dissertation. Based on Olson et al. (2001).

from Chile and Peru in 1828 and 1829, respectively (Bertero 1828, Rudolphi 1829). Even though research efforts at that time were limited, myxomycetes have continued to be collected in the Neotropics since then. In a similar way to the history of other types of scientific research in the New World, European investigators took the lead in Neotropical myxomycete research. A former French soldier from Napoleon Bonaparte's army, Jean Pierre François Camille Montagne, was the first to report a series of myxomycetes from Brazil, Chile, Cuba, Puerto Rico and Guyana (Montagne 1837, 1852, 1855) after retiring from the military service and dedicating himself to the study of cryptogams in South America. Similarly, another French mycologist, Joseph Henri Levéillé, was the responsible for the first reports of myxomycetes in Colombia (Levéillé 1863).

In spite of these isolated efforts, it was not until the decade of the 1880's that more serious fungal surveys were carried out in the southern Neotropics. A number of recognized mycologists such as the Italians Carlos Luis Spegazzini and Augusto Napoleone Berlese, the British George Edward Massee and the French Narcisse Théophile Patouillard generated important information on the distribution and taxonomy of myxomycetes in Argentina, Brazil, Colombia, Cuba, Guyana, Paraguay, Uruguay, Venezuela and the Caribbean (e.g., Spegazzini 1880a, 1880b, 1880c, 1881, 1882, 1886, 1887, 1889; Berlese 1888, Massee 1889, Patouillard and Gaillard 1888). These types of exploratory surveys continued in other countries in South America for the next decades.

It was not until the end of the 19th century that the first American mycologist published a report on Neotropical myxomycetes. With his study in Nicaragua, Thomas Houston Macbride also reported the first myxomycetes for the Central American region (Macbride 1893). Two years later, the recognized Italian mycologist Pier Andrea

Saccardo published his 11th volume of the *Sylloge Fungorum* and recognized the new species described by Macbride for Central America (Saccardo 1895), thus giving the former credit for his study.

From that moment on, myxomycete research in the Neotropics began to take place more systematically in the Northern countries of Latin America, while it consolidated in South America. In the early years of the 20th century, myxomycete exploration finally took place in countries such as Costa Rica and Mexico (e.g., Hennings 1902, Saccardo and Sydow 1902). With the establishment of Panama as a country and the completion of the canal by the United States in 1914, the period of biological exploration in the next few decades included the study of myxomycetes in that area as well (Standley 1927, 1933).

By that time, the incipient study of Fungi and myxomycete occurrence and distribution in the Neotropics had already taken researchers to virtually all major regions within the area. This period of exploration continued until the mid-20th century. By 1950, the only countries in the whole Neotropics for which there were no published reports of myxomycetes were Belize, Guatemala, French Guiana, Haiti and Honduras (see Lado and Wrigley de Basanta 2008). The first published report of myxomycetes from these areas occurred as late as the end of the 20th century in the case of Belize (Ing and Haynes 1999).

In spite of this, information on myxomycetes from the Neotropical area was somehow available for the majority of the countries by the decade of the 1970s. For that reason, Marie Leonore Farr, an American myxomycologist generated a monograph for Neotropical myxomycetes at the end of that decade (Farr 1976). Her work, published by

the New York Botanical Garden, became the point of reference for myxomycete occurrence and distribution in the Neotropics for years to come. During the next decade, recognized myxomycete studies in the Neotropics were practically absent in all countries except for Brazil, Ecuador and Mexico. These studies were principally carried out by Laise Cavalcanti from the University of Pernambuco in Brazil (e.g., Cavalcanti and Oliveira 1985, Cavalcanti and Pôrto 1985), Elly Nannenga-Bremekamp from the National Botanic Garden of Belgium (e.g., Eliasson and Nannenga-Bremekamp 1983, Nannenga-Bremekamp 1989) and Gastón Guzmán from the Xalapa Institute of Ecology in Mexico (e.g., Guzmán and Guzmán-Dávalos 1981, Guzman and Villareal 1984).

During the past 20 years, the research effort in the Neotropics has had different objectives in different areas. For example, the Neotropical area that has received most of the effort in relation to occurrence of myxomycetes is Mexico. Lado and Wrigley de Basanta (2008) calculated that approximately 72% of all the published articles about Mexican myxomycetes have been produced since 1990. The first complex ecological studies have taken place during the late part of this time period as well. Most of the ecological analyses on Neotropical myxomycetes have occurred in Costa Rica (e.g., Schnittler and Stephenson 2000, Schnittler 2001c, Schnittler and Stephenson 2002, Rojas and Stephenson 2007, 2008), Ecuador (e.g., Schnittler 2001c, Schnittler and Stephenson 2002, Schnittler et al. 2002, Stephenson et al. 2004a) and Puerto Rico (e.g., Novozhilov et al. 2000, Schnittler and Stephenson 2002, Wrigley de Basanta et al. 2008).

Most areas of South America have not been studied in the last two decades. This of course, is not conclusive; some exceptions include the already mentioned studies in Ecuador, some projects in Chile (e.g., Lado et al. 2007, Wrigley de Basanta et al. 2009)

and Argentina (e.g., Crespo and Lugo 2003, Wrigley de Basanta et al. 2009) and a series of regional studies in Brazil (e.g., Cavalcanti and Mobin 2002, Maimoni-Rodella and Cavalcanti 2006). There are also some other ecological studies currently going on in some areas of the Peruvian Amazon and Andes and the Aburrá Valley in Colombia (Rojas and Stephenson, unpublished data).

Previous to this dissertation work there were no comparative studies for high-elevation myxomycete communities in the Neotropics, no comprehensive ecological analyses for any tropical country in the world and only limited information on the biogeography of myxomycetes in the northern Neotropical area.

High-elevation Neotropical forests and the contextual framework of this dissertation

Most of the information available for high-elevation forests in the Neotropical area refers to these ecosystems as Neotropical cloud forests. The problem with the use of this term is that "cloud forests" *per se* encompass a series of environments that vary dramatically in elevation, precipitation and temperature regimes (Brown and Kappelle 2001). If latitudinal differences are considered as well, it is not surprising that there are a number of regional terms that have been used to refer to these forests. For example, they are referred to "bosque mesófilo de montaña" (mountain mesophyll forest) in Mexico (e.g., Ponce-Vargas et al. 2006), "bosque nuboso" (cloud forest) in Costa Rica (e.g., Vargas 1990), "selva andina" (andean jungle) in Colombia (e.g., Cleef et al. 2003) and "yunga" (yunga) in Argentina (e.g., Hilgert and Gil 2006.).

Due this discrepancy in terms, some authors prefer to use the term "montane cloud forests" (see Bubb et al. 2004) to delimit those tropical forests located at elevations above the premontane level. Following the Holdridge system of forest classification in the Neotropical region (Holdridge et al. 1971), these "montane cloud forests" are limited to the lower montane, montane and subalpine levels. In the Northern section of the Neotropics, however, some regions such as central Panama, Nicaragua, Belize and most Caribbean islands do not have this forest type (see Figure 6) as a result of their topographic characteristics.

Most researchers agree that on oceanic islands the elevation at which "cloud forests" occur is dramatically lower (Brown and Kappelle 2001). This has been attributed to the "Massenerhebung" effect (Grubb 1971). When mountains are isolated, the effect of winds and drastic temperature differences between the mountain and the atmosphere is accentuated by the isolation of the mountain, thus generating colder environments at lower elevations in relation to mountains that are surrounded by land masses and/or other mountains (Barry 1992). Because of this, some mountain environments in oceanic islands (e.g., Ascension Island in the South Atlantic) have "cloud forests" just like their continental counterparts.

However, given the ambiguity associated with the terms "cloud forest" and "montane cloud forest" when regional or global studies are conducted, it is more convenient to define the operational unit in which the study is carried out. Since the majority of definitions are used in a colloquial way to refer to different forest types, a different approach should be used to avoid confusion. Unfortunately, mountain forests

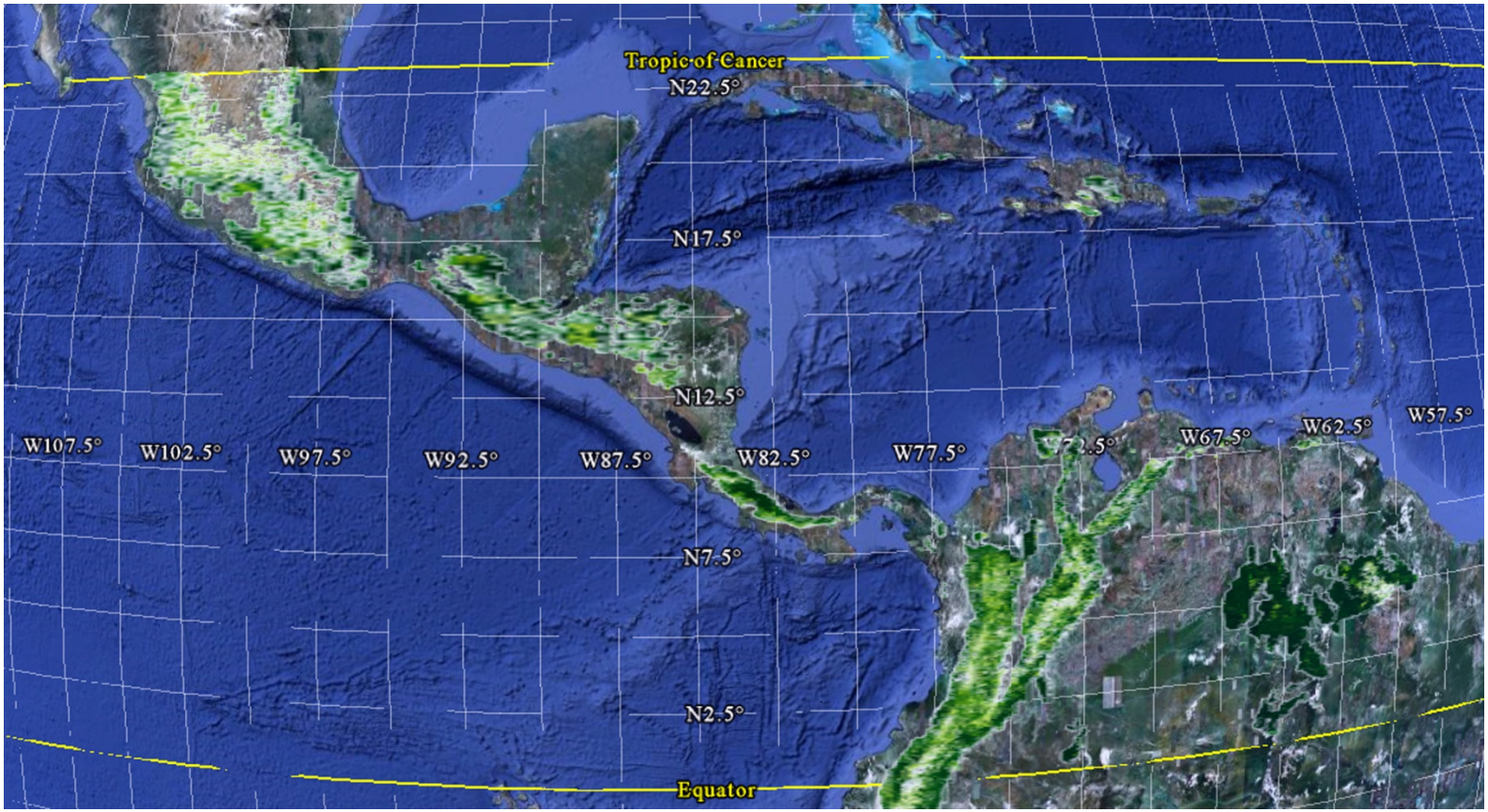

Figure 6. Composite satellite image of the Northern section of the Neotropical region centered over Nicaragua showing the distribution of cloud forests *sensu lato* as green polygons. Darker green areas show montane cloud forests. According to Mulligan and Burke (2005).

cannot be defined only using elevation as a parameter. Most researchers agree that the concept of mountain should also include the characteristic steep slopes that generate the highly energetic instability in the environment (Kapos et al. 2000). Since this approach is not standard in biological investigations, the term montane forest is ambiguous as well. For this dissertation, habitat characteristics such as cloud coverage and slope degree are not as important as other factors such as forest structure and geographic location of the areas.

For this reason, in order to avoid confusions with terms that are associated with other meanings, the term ***high-elevation Neotropical forest*** is used herein to refer to those montane habitats in the Neotropics that represent the highest extreme of the forest extension before the tree line is reached.

For the Neotropical region, these high-elevation forests occur over a wide latitudinal range from Mexico to Argentina (Brown and Kappelle 2001). The accepted northernmost remnant of this type of forest occurs in the Cumbres de Monterrey National Park, which is located in the Mexican state of Nuevo León at approximately 31˚N (Luna et al. 2001). In South America, the southernmost section of this forest type is found in the Sierra del Aconquija at approximately 29˚S in the provinces of Catamarca in Argentina (Brown et al. 2001).

As expected, distinct high-elevation areas along the Neotropics have been influenced in various ways by different historical and biological factors, thus shaping the forests in diverse ways. For example, it is believed that the vegetation in the Mexican high-elevation forests has a clear Neartic and Paleartic origin (Rzedowski 1991b) but a strong Neotropical influence, especially at the herbaceous level (Rzedowski 1991a).

Approximately 46% of the plant genera present in these forests are distributed across the Neotropics (Luna et al. 2001). At the other extreme, the vegetation of the yungas in Argentina is known to have common elements of Neotropical distribution but characteristic species of Gondwanic origin (Brown et al. 2001). In the middle of the Americas, the vegetation of the high-elevation forests of Costa Rica shows that approximately 46% of the genera originated in the Neotropics but around 28% of them are either Asian or Arctic in origin (Kappelle 2001).

Research questions in this dissertation

This dissertation was designed to study the biogeography and ecology of myxomycete assemblages in high-elevation areas of the northern Neotropics. However, in order to obtain comparative data, an appreciable effort was directed towards other types of forest and research objectives as well.

The main objective of the overall project was to investigate the distribution of myxomycetes in tropical areas in order to compare the results obtained with known patterns in myxomycete ecology and general ecological theories. For this, three basic questions were formulated at the beginning of this project. The first question is biogeographical in nature and considers whether myxomycete species with a Nearctic affinity or those with a Palearctic affinity are more common than Neotropical species in the temperate-like environments represented by high-elevation forests in the Neotropics. For this question, the two basic hypotheses are given below.

Ho: There are no differences in the species composition of myxomycete communities between temperate and high-elevation Neotropical forests.

Ha: There are differences in the species composition of myxomycete communities between temperate and high-elevation Neotropical forests.

The prediction of this question is based on preliminary studies carried out in the Talamanca Range in Costa Rica (Rojas 2005). According to these studies, it seems that myxomycete assemblages in high-elevation Neotropical forests more closely resemble the assemblages found in temperate forests with a strong Nearctic affinity than species assemblages characteristic of low-elevation Neotropical forests.

The second question, ecological in this case, examines the distribution of myxomycete species in high-elevation and low-elevation Neotropical forests by studying the macro- and microenvironments within which these species occur. These macro- and microenvironments are defined by a series of environmental conditions and determine which of the two hypotheses listed below explain the presence of myxomycetes in the high-elevation communities.

Ho: There are no specific macro- and microenvironmental conditions correlated with the presence of myxomycetes in high-elevation forests as opposed to low-elevation forests in the Neotropics.

Ha: There are specific macro- and microenvironmental conditions correlated with the presence of myxomycetes in high-elevation forests as opposed to low-elevation forests in the Neotropics.

In this case, the prediction is that different myxomycete species show different levels of association with different sets of macro- and microenvironmental conditions, thus making the species assemblages in low-elevation areas different from those in high-elevation areas. This is based on previous patterns of distribution reported for other areas of the Neotropics (see Stephenson et al. 2004b).

The third question is intended to evaluate more carefully the interaction (in terms of niche overlap) among closely related species in a taxonomic group with a known Neotropical affinity in order to determine if this approach is useful in explaining their distribution across the region. For this question, the two hypotheses are given below.

Ho: There are no differences in the niche overlap among closely related species with high Neotropical affinity that help explain their distribution across the region.
Ha: There are differences in the niche overlap among closely related species with high Neotropical affinity that help explain their distribution across the region.

For this question the prediction is that even at this fine level, differences in the interaction among species should be detectable and can be observed using a niche-based approach. This is supported by the fact that for some genera with Neotropical species, differences in distribution reported in the literature indicate they may be associated with particular conditions of their environment (see Martin and Alexopoulos 1969). This can mean that those species could show separation of niches by means of resource partitioning.

Even though the study of the three questions mentioned above represent the basis of this dissertation, a number of different other problems are treated within each the chapters that follow. Due the highly heterogenic methodologies used in different chapters to find evidence addresing the different hypotheses, a number of different other issues related to current myxomycete research are treated separately in the chapters as well. However, as mentioned earlier, all of these approaches were used to provide evidence to answer the three basic questions explained above.

Study areas

For the study of the research questions explained in the last section, a series of study areas were selected in different parts of the world, especially across the Americas (Figure 7). These areas are different in terms of forest composition and structure as would be expected, given the different influencing elements that have shaped the different forests worldwide. However, they all represent forest habitats with similar characteristics for the study of the particular aspects that this dissertation addresses.

With the only purpose of keeping the information organized, all the study areas from which data were collected have been arranged into groups. These groups correspond to the Chapter organization of this dissertation and follow the objective-centered set of three research questions explained in the last section. With the exception of some non-visited study sites included in two external complementary datasets used for Chapters 2, 5 and 9, the study areas investigated by the author of this dissertation follow the arrangement given in Table 1.

Figure 7. Map of the major land masses in the world showing the locations of the study areas used for this dissertation.

Table 1. Study areas visited during the course of this dissertation, according to the chapters that contain information from them. Note: NP = national park, SPA = special protection area, BS = biological station, CFP = cloud forest preserve.

Study area (Country)	Chapter 2	Chapter 3	Chapter 4	Chapter 5	Chapter 6	Chapter 7	Chapter 8	Chapter 9
Great Smoky Mountains NP (USA)					**X**	**X**		
Doi Inthanon NP (Thailand)					**X**	**X**		
La Malinche NP (Mexico)					**X**	**X**		**X**
Cofre de Perote NP (Mexico)					**X**	**X**		**X**
La Ventoza SPA (Guatemala)					**X**	**X**		**X**
Llanos de San Miguel SPA (Guatemala)					**X**	**X**		**X**
Cerro de la Muerte/Tapantí NP (Costa Rica)	**X**	**X**		**X**	**X**	**X**	**X**	
Chirripo NP (Costa Rica)	**X**			**X**	**X**	**X**	**X**	
La Selva BS (Costa Rica)	**X**			**X**			**X**	
Palo Verde BS (Costa Rica)	**X**			**X**			**X**	
Las Cruces BS (Costa Rica)	**X**			**X**			**X**	

Table 1. Continued.

Cahuita NP (Costa Rica)	**X**		**X**	**X**
Monteverde CFP (Costa Rica)	**X**		**X**	**X**
Cocos Island NP (Costa Rica)	**X**	**X**	**X**	**X**
Los Amigos BS (Peru)			**X**	

A brief overview of the study areas is provided below. Dissertation chapters indicate for how long these areas were surveyed and what type of information has been obtained from them. Study areas have been organized by biogeographical provinces using the scheme in Figure 5 and arrangement in Table 1.

Nearctic Province – high-elevation temperate forest of the United States

As explained earlier, this dissertation focuses on myxomycete dynamics in high-elevation Neotropical forests. However, since the climatic characteristics of these areas resemble those of temperate areas, they have often been considered temperate islands in a tropical landscape. In fact, for certain areas in the Neotropics and some groups of organisms, high-elevation Neotropical ecosystems seem to act as biogeographical islands (see Cleef and Chaverri 2005) and explain patterns proposed by the theory of island biogeography (MacArthur and Wilson 1967).

For this reason, one true temperate area was selected to establish adequate comparisons with the other study areas in the Neotropics. This temperate study area corresponds to part of the higher portions of the Great Smoky Mountain National Park known as Andrews Bald, located in the state of North Carolina, United States at 35°32'19" N and 83°29'38" W, with an elevation of approximately 1750 m (Figure 8). The “balds” in this part of the Appalachians are treeless areas covered by grasses, sedges, and forbs (Jenkins 2007). Even though the origin of these open grassy areas has been a matter of debate for a long time (e.g., Lindsay and Bratton 1979), they resemble structurally the grassy areas found in tropical mountains beyond the tree line.

The area of the Appalachians where Andrews Bald is located consists of rocks of Precambrian age (King et al. 1958) that formed the Appalachian Range during the Alleghenian orogeny after the North American plate collided with the African plate (Rast 1984). The area seems to have escaped the Wisconsin glaciation. Evidence shows that the glacial border was less than 250 miles to the north of this area, but current vegetation seems to have been highly influenced by this period (Braun 1951).

Whether or not the "balds" of the Smoky Mountains are a natural product or the result of anthropogenic influence, the structure of the plant layer is very different from that in the forested areas surrounding the open areas (Linday and Bratton 1980). At present, in Andrews Bald the dominant plant is the mountain oat grass, *Danthonia compressa*; however, other common plants found in this area include *Potentilla canadensis*, *Rumex acetosella* and *Cinna latifolia* (Jenkins 2007). Two of the common non-herbaceous plants that occur in this area include serviceberry, *Amelanchier laevis* and fir, *Abies fraseri* (Linday and Bratton 1980).

Indo-Malay Province – high-elevation tropical forest in Thailand

In a similar way to the selection of a temperate area for comparison with the Neotropical study sites selected, one tropical area was selected outside of the Neotropics. This area is within Doi Inthanon National Park in northwestern Thailand, located approximately between 18°31' - 18°33' N and 98°28' - 98°31' E. This mountain represents the highest peak in Thailand at 2562 m and it is part of the Shan Highlands complex (Gupta 2005), which is considered by some as an eastern extension of the foothills of the Himalayas.

The latest evidence shows that the Doi Inthanon core complex was formed during the Late Triassic (Dunning et al. 1995) and the final development occurred between the Late Cretaceous and the Miocene (Macdonald et al. 1993). Apparently, the forests of these high-elevation areas in Southeast Asia did not change as much as those in low-elevation areas as a product of the last glacial maximum around 18,000 years ago (Heaney 1991). Today, the forest vegetation is dominated by the oak tree *Quercus eumorpha* and the myrtaceous tree *Syzygium angkae*, which together seem to represent around 40% of the plants in the area (Khamyong et al. 2004). However, other plants such as *Litsea martabanica*, *Helicia nilagirica*, *Lindera caudate* and *Schima wallichi* are common. At lower elevations, the pine tree *Pinus kesiya* is a common species in the pine-oak mixed forest assemblage (see Turnbull et al. 1980).

In the Doi Inthanon area, two study sites were selected on the basis of tree species assemblages in the forest (Figure 9). The first study site corresponds to the oak-dominated higher elevation parts of the forest on the road to the Napamaytanidol Chedi temples and is located at 18°31'34" N and 98°29'44" E approximately 1700 m above sea level. The second study site is located at 18°31'9" N and 98°31'4" E in the pine-oak mixed forest area around 1400 m above sea level. Both areas are located along the road number 1009 in the territory protected by the National Park.

Neotropic province – high-elevation tropical forests in Mexico

The majority of the study sites used during the course of this dissertation are located in the Neotropics. As explained in a previous section, this biogeographical area encompasses all the territories of South and Central America as well as the Caribbean,

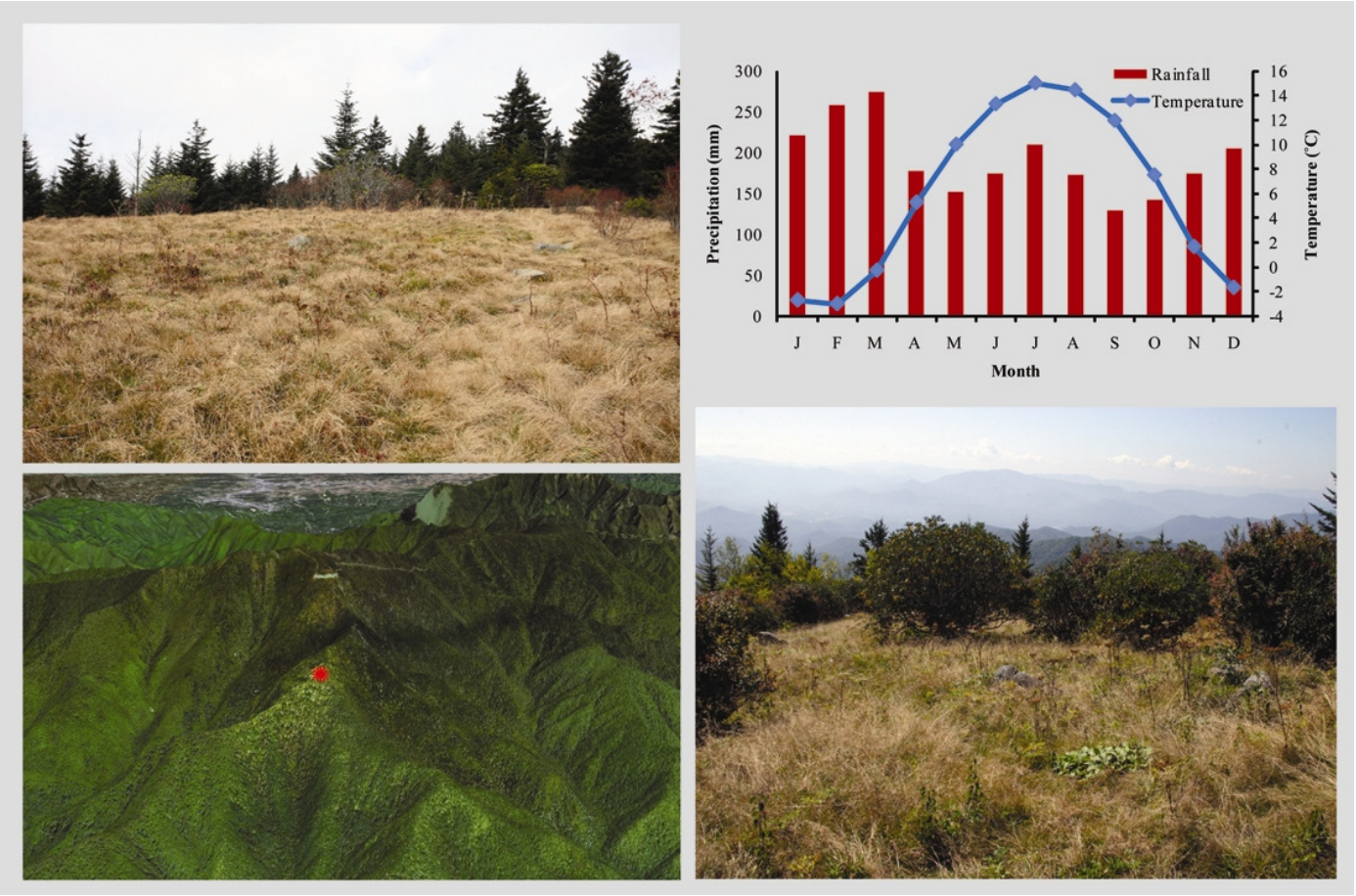

Figure 8. Andrews Bald, the study site in the Great Smoky Mountains National Park. Satellite image imposed over digital elevation model on lower left indicating the position of the site as a red star. Climograph made using data obtained by the United States National Park Service at Clingmans Dome.

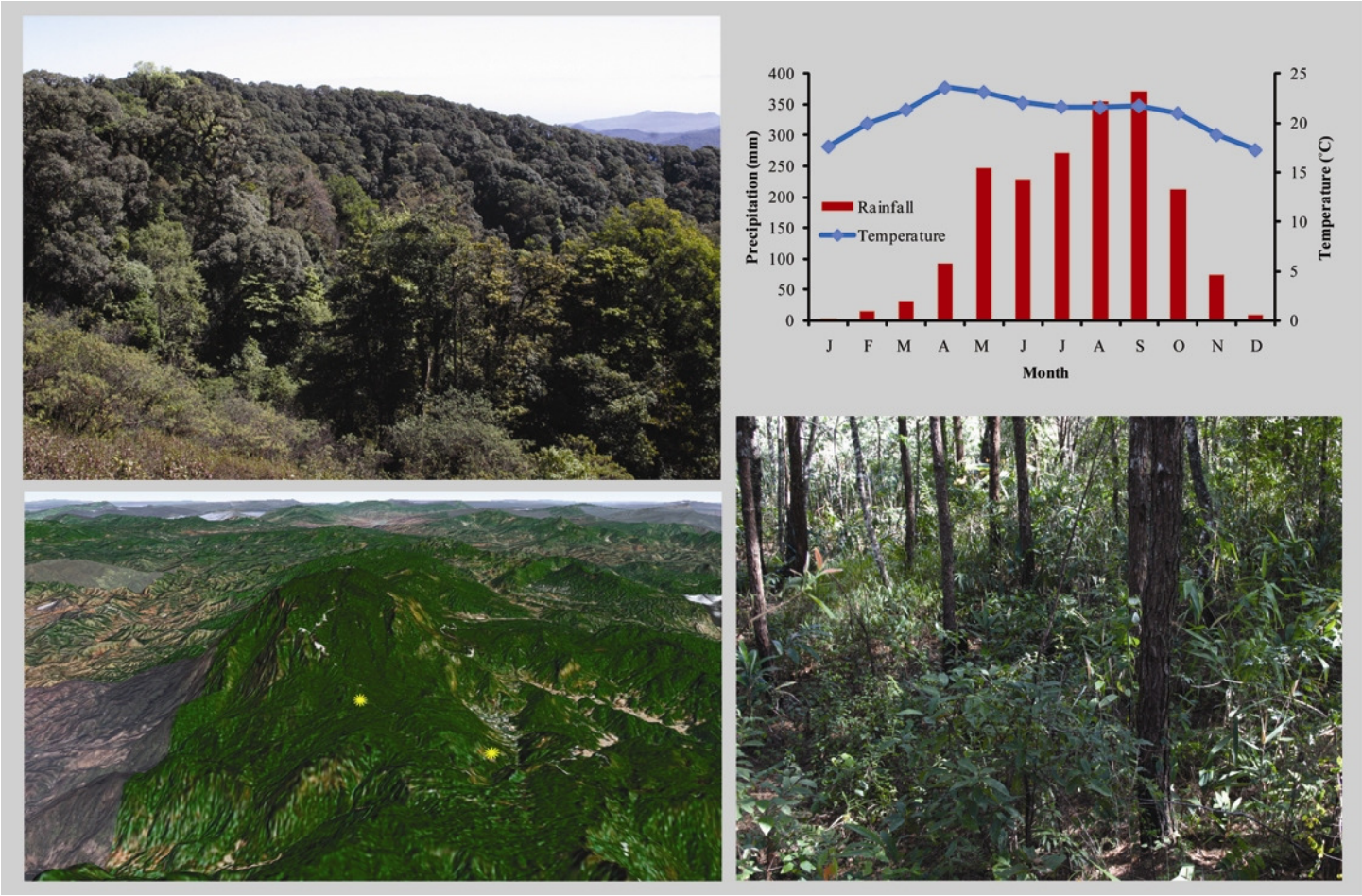

Figure 9. Doi Inthanon, the study area in northwestern Thailand. Satellite image imposed over digital elevation model on lower left indicating the position of the two study sites as yellow stars. Climograph made using data from Kanzaki et al. (2004).

and includes a large portion of the Mexican territories (see Figure 5). For practical purposes, all the study sites in this region will be described in order from north to south (see Figure 7).

In Mexico, two high-elevation study areas on the Trans-Mexican Volcanic Belt (TMVB) were selected. The TMVB is a partial consequence of the subduction of the Cocos plate underneath the North American plate along the middle America trench (Nixon 1982) and it is composed by a series of volcanoes of late Tertiary and Quaternary origin (Castro-Govea and Siebe 2007). Due its active nature, it has been suggested that volcanic cones along this belt have been formed as recently as 0.2 million years (García-Palomo et al. 2002). The TMVB is very important in the regional context as it encompasses the area where the highest peaks of Mexico are located (de Blij 2005).

The two study areas selected in Mexico are located in the eastern section of the TMVB. The first one is the La Malinche National Park (Figure 10). This area surrounds a non-active volcano of the same name and it is located between the states of Puebla and Tlaxcala in the central part of the country at approximately 19˚14'00" N and 98˚01'55" W at elevations of ca 3000-4600 m (Castro-Govea and Siebe 2007). The park covers 46,093 hectares, of which 12,932 belong to the state of Puebla and 33,161 to Tlaxcala (López-Dominguez and Acosta-Pérez 2005). In the past this mountain has been referred to Matlalcueyetl but is now more commonly called La Malintzin or La Malinche (Riley 2002).

The oldest rocks in the vicinity of La Malinche are dated at 9.7 million years (Carrazco-Núñez et al. 1997); however, due the stratovolcanic nature of this mountain, soils are formed by a series of sediment layers radiocarbon-dated between 102 and

46,000 years old (Castro-Govea and Siebe 2007). Evidence shows that glaciers and moraines were common in higher parts of the mountain (Heyne 1994) and that temperature changes since the last glaciation have shaped the vegetation present at different times (see D'Antoni 1993). For example, at elevations higher than 3100 m, it seems that the vegetation and forest structure has changed from alpine grasslands around 10,000 years ago to the typical forests found in most areas today (Straka and Ohngemach 1989).

The current vegetation of the La Malinche forests is dominated by pine trees. The two most common species are *Pinus montezumae* in the lower elevations and *P. hartwegii* in the highest areas; however, other trees such as *Alnus jorullensis*, *Quercus laurina* and *Abies religiosa* are common in certain areas of the mountain (Montoya et al. 2004). For example, in particular areas *A. religiosa* dominates the vegetation but the species usually forms mixed patches with *P. hartwegii* and *Juniperus monticola*. The highest parts of La Malinche are characterized by the dominance of grasses and lack of trees. The typical vegetation in these areas is dominated by the tussock grasses *Festuca tolucensis* and *Calamagrostis tolucensis*. However, sometimes individuals of *Juniperus monticola* and *P. hartwegii*, the only tree species that resist under the prevailing environmental conditions (Villers-Ruiz et al. 2006), are found in these areas as well.

The second study site in Mexico is the Cofre de Perote National Park area (Figure 11). In a similar way to La Malinche, this area surrounds a volcano of the same name. Located in the state of Veracruz between 19˚26' - 19˚31' N and 97˚07' - 97˚11' W at elevations between ca 3100 – 4100 m, this shield volcano is the result of a complex

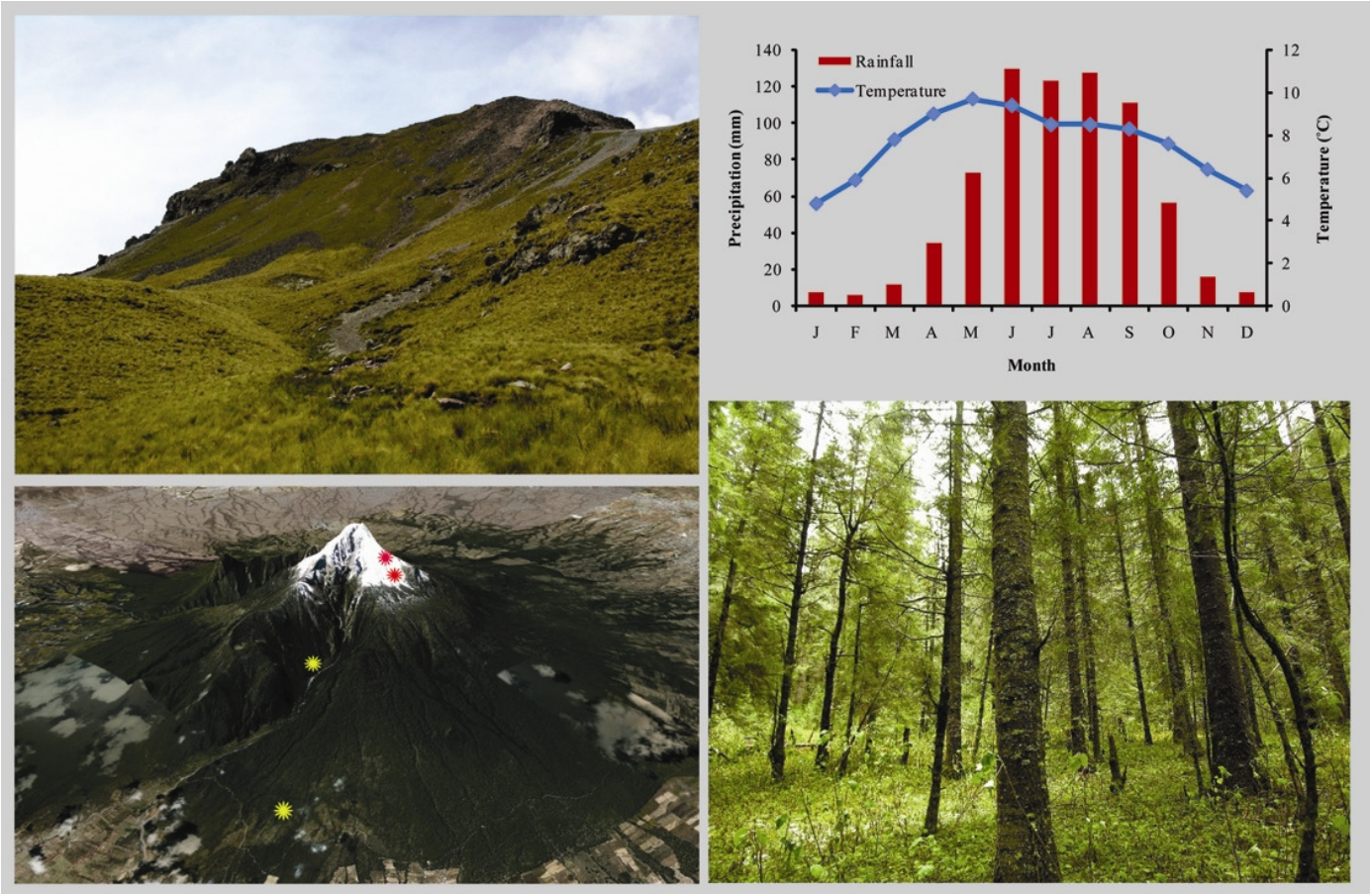

Figure 10. La Malinche, one of the study areas in Mexico. Satellite image imposed over digital elevation model on lower left indicating the position of the four study sites as yellow (forest) and red (grass) stars. Climograph made using data from the Mexican Meteorological Service.

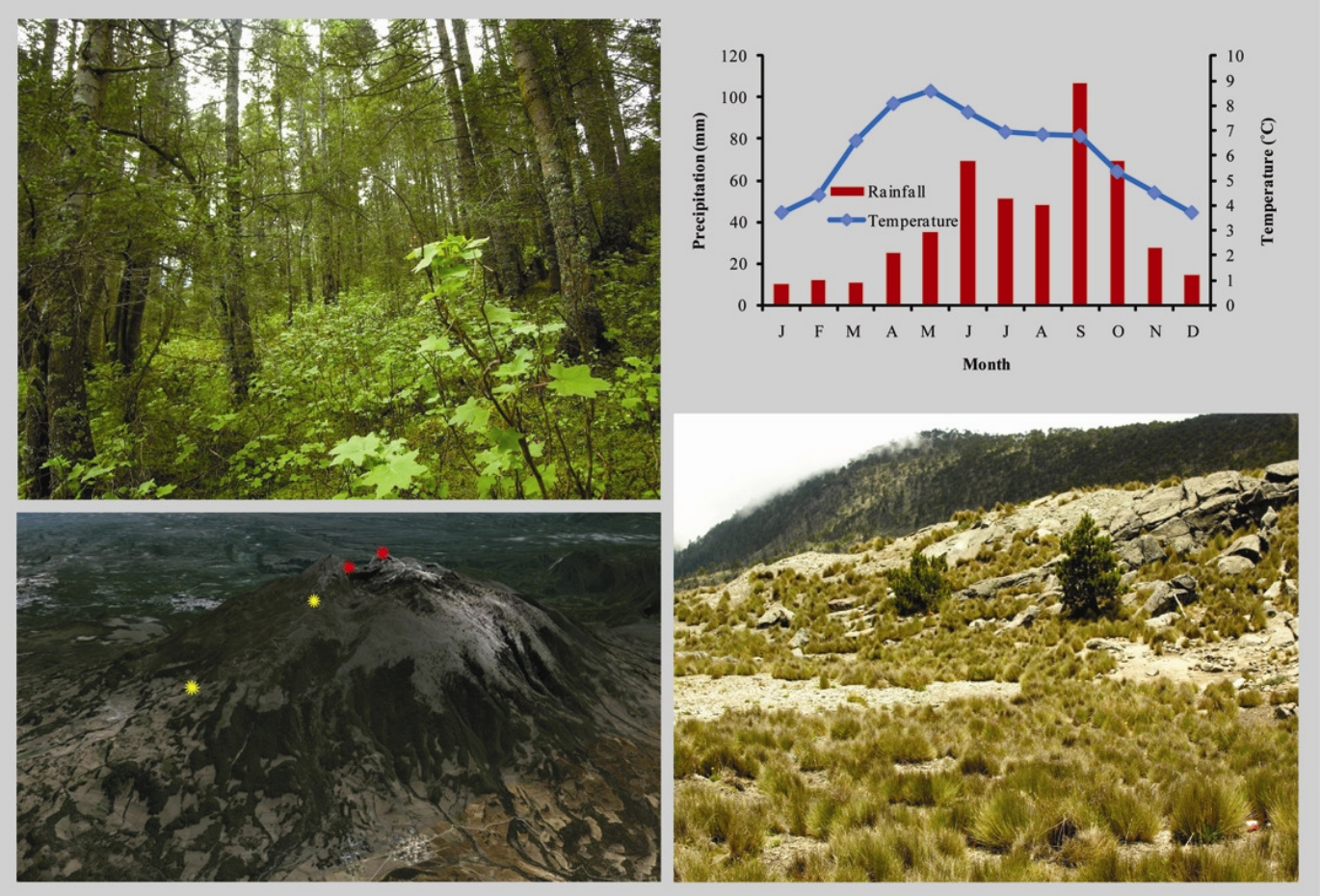

Figure 11. Cofre de Perote, one of the study areas in Mexico. Satellite image imposed over digital elevation model on lower left indicating the position of the four study sites as yellow (forest) and red (grass) stars. Climograph made using data from the Mexican Meteorological Service.

geological process that started around 1.3 million years ago (Carrasco-Núñez et al. 2009). However, in comparison to La Malinche or other volcanoes in the TMVB, the geology of Cofre de Perote has been poorly studied (Ferrari 2000).

Cofre de Perote shows an elevational vegetation pattern similar to that of La Malinche. At lower elevations a mixture of species of pine trees or a mixed pine-oak forest dominates the landscape; however, at higher elevations *Pinus hartwegii* is the only species found in the pine forest ecosystem that occurs just below the tree line (Narave 1985). Around 3000 m in elevation, a belt that constitutes the fir (*Abies religiosa*) forest is also present. In this sense, it has been noticed that the floristic resemblance between the understory plants of this and the fir forest in La Malinche is very low (Sánchez-González 2005). Beyond the tree line, the only habitat present is what Narave (1985) denominated "high altitude moors". This vegetation type corresponds to the tussock grass-dominated environment found at La Malinche as well.

Neotropic province – high-elevation tropical forests in Guatemala

In Guatemala, two study areas were selected in the western part of the country. These areas are located between 15˚27' - 15˚30' N and 91˚27' - 91˚28' W on the Cuchumatanes Plateau (Figure 12), a high-elevation formation with a complex geological history (see Anderson et al. 1973). This area has received the most profound human impact in Guatemala in the last 50 years (Islebe and Véliz 2001) and since 1989 is under special protection by the Guatemalan government (see article 90 of the Guatemalan Law of Protected Areas).

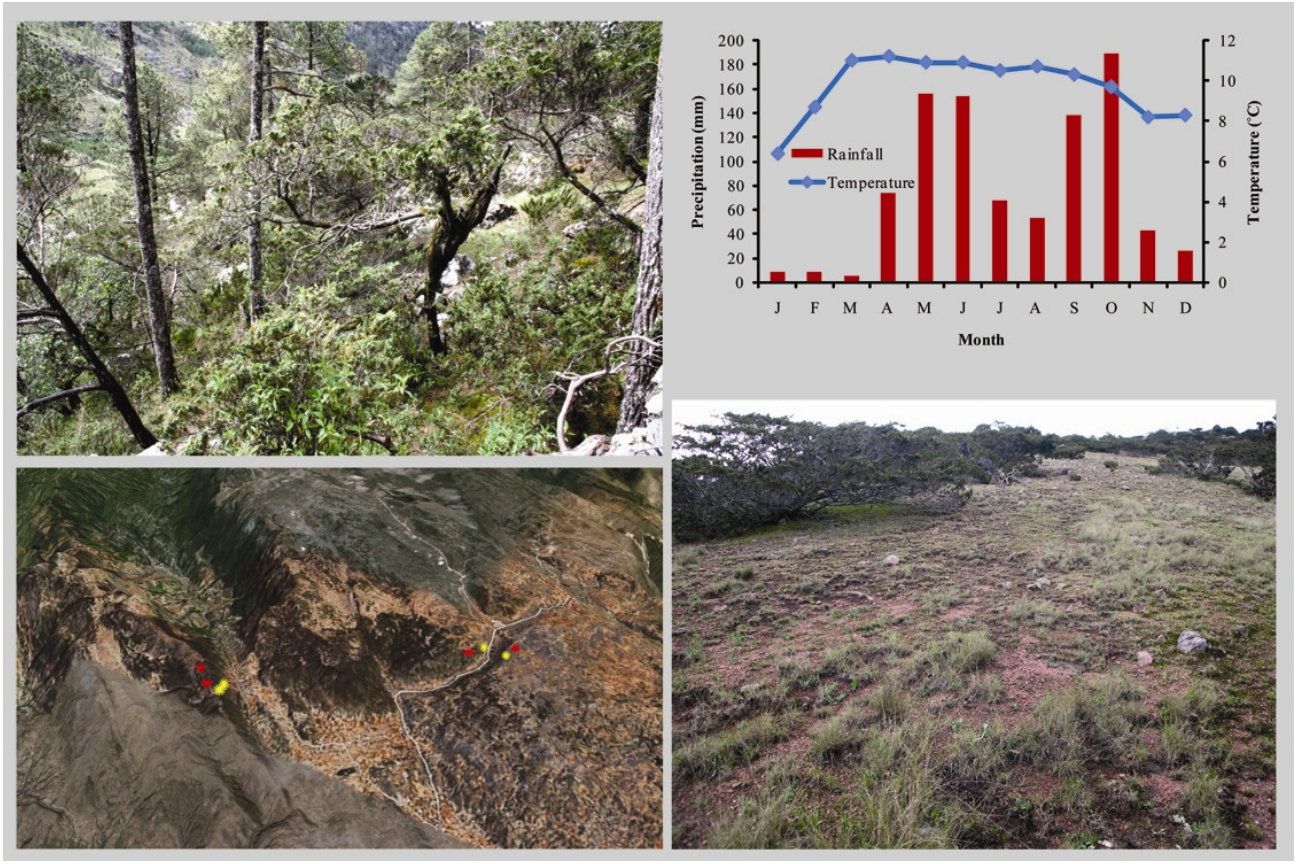

Figure 12. Los Cuchumatanes, the study area in Guatemala. Satellite image imposed over digital elevation model on lower left indicating the position of the study sites as yellow (forest) and red (grass) stars. La Ventoza is located on the left side and Llanos de San Miguel on the right one. Climograph made using an approximation from the Guatemalan National Institute of Sismology, Volcanology, Meteorology and Hydrology.

The selected sites in the Cuchumatanes are located along the Chixoy-Polochic fault in the Todos Santos formation, an area characterized by rocks of Cretaceous origin (Anderson et al. 1973). This area supported an ice cap of approximately 60 km^2 during the last glaciation and represents, along with the Talamanca Range in Costa Rica, the only glaciated areas that occurred at that time in Central America (Lachniet 2004).

As was the case in Mexico, two study sites in this area were selected. They correspond to the villages of La Ventoza and Llanos de San Miguel located at 15˚27'46" N and 91˚32'00" W at approximately 3400 m and 15˚30'10" N and 91˚29'50" W at approximately 3300 m, respectively. However, due the more or less homogeneous climate of the Cuchumatanes plateau and its general topographic and edaphic characteristics, these two areas are usually considered part of the same biological unit. In this common environment, a number of different plant associations have been described. The dominant taxonomic groups of these forests have been found to be very similar to those in the mountains of Mexico, thus supporting the concept of a phytogeographical unit for high-elevation environments denominated Megamexico (Islebe and Velázquez 1994). For the Cuchumanates areas some of the most characteristic plant associations are *Relbunium microphyllum – Agrostis tolucensis*, *Hypnum cypressiforme – Juniperus standleyi, Lachemilla vulcanica – Pinus hartwegii* and the *Agave hurteri – Alnus firmifolia* (Islebe et al. 1995).

Neotropic province – high-elevation tropical forests in Costa Rica

The southernmost high-elevation sites selected for this dissertation are located on the Talamanca Range in Costa Rica. This geologic formation is the largest and highest

mountain belt in southern Central America and is located on the Chorotega tectonic block between northern Costa Rica and the Panama Canal Zone (Coates and Obando 1996). The Talamanca Range seems to be the product of the rapid uplifting of one of the youngest exposed plutonic suites in the world around 5 million years ago, which is related to the subduction of the Cocos Plate underneath the Caribbean plate (Drummond et al. 1995).

As mentioned earlier, there is evidence that some areas in the Talamanca Range supported glaciers in the Late Pleistocene (Lachniet 2004). The presence of cirques, U-shaped valleys and moraines, is especially evident on Cerro Chirripó and Cerro de la Muerte, two of the highest peaks in Costa Rica (Kappelle 2001). For the first of these, glaciers are thought to have retreated after the Young Dryas event, around 9,700 years ago (Orvis and Horn 2005). At present, both areas are protected by the Costa Rican government in the form of National Parks.

The two study sites selected in Costa Rica correspond to the two already mentioned peaks of the Talamanca Range. The first of these areas, the Cerro de la Muerte also known as Cerro Buenavista, Macizo de la Muerte or Death's Massif, is located at 9˚33' N and 83˚45' W and reaches a maximum elevation of 3491 m (Lachniet et al. 2005, Figure 13). This area was annexed to the already existing Tapantí National Park in the year 2000 by presidential decree number 28307-MINAE with the objective of protecting the fragile paramo ecosystem present in the highest elevations. The dominant vegetation of this paramo includes the bamboo *Chusquea subtessellata*, the ericaceous shrub *Pernettya coriacea* and the asteraceous herb *Gamochaeta americana* (Chaverri and Cleef 2005). However, below the tree line, the Cerro de la Muerte is well recognized for the

plant communities formed by *Quercus costaricensis – Myrsine pittieri* around 3100 m and *Quercus costaricensis – Quercus copeyensis* around 2900 m (Kappelle 1996).

The second study area in Costa Rica corresponds to the Chirripó National Park (Figure 14). This protected area includes the Cerro Chirripó, the highest mountain in Costa Rica, which is located around 9˚28' and 83˚29' W, and reaches an official elevation of 3819 m (Lachniet et al. 2005). In a similar way to Cerro de la Muerte, the highest parts of Chirripó are dominated by the paramo vegetation already mentioned and the forested areas immediately below the tree line by oak forests. For Chirripó, the oak forests immediately below the tree line are dominated in the canopy by a mixture of *Quercus costaricensis* and *Q. copeyensis*, but the understory is clearly dominated by the bamboo *Chusquea* (Kappelle 1996).

Neotropic province – intermediate elevation tropical forests in Costa Rica

In addition to the high-elevation sites explained before, a series of secondary study sites was selected at intermediate and low elevations in Costa Rica and Peru. The objective of the selection of these areas was to acquire comparative datasets for the effort carried out in high-elevation areas in order to obtain more information about the ecology of myxomycetes in the Neotropics.

In this manner, two intermediate elevation areas were studied in Costa Rica. Even though these areas are located in the premontane belt according to Holdridge et al. (1971), they are located in different mountain ranges and represent different life zones in the country. The first of these areas is the Monteverde Cloud Forest Preserve (Figure 15), which is located on the Tilarán Range in northwestern Costa Rica at 10˚17'49" N and

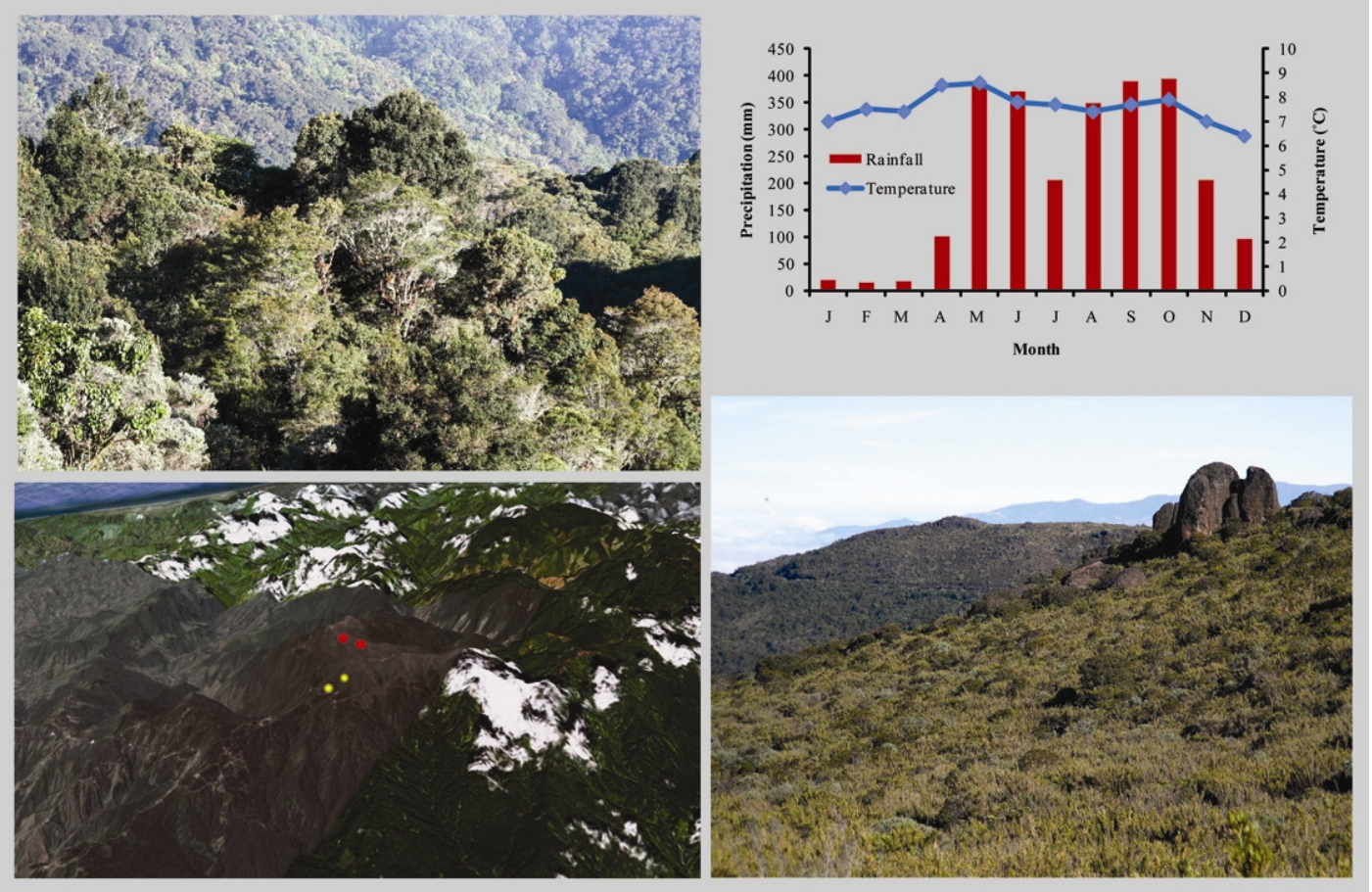

Figure 13. Cerro de la Muerte, one of the study areas in Costa Rica. Satellite image imposed over digital elevation model on lower left indicating the position of the four study sites as yellow (forest) and red (paramo) stars. Climograph made using data from Herrera (2005).

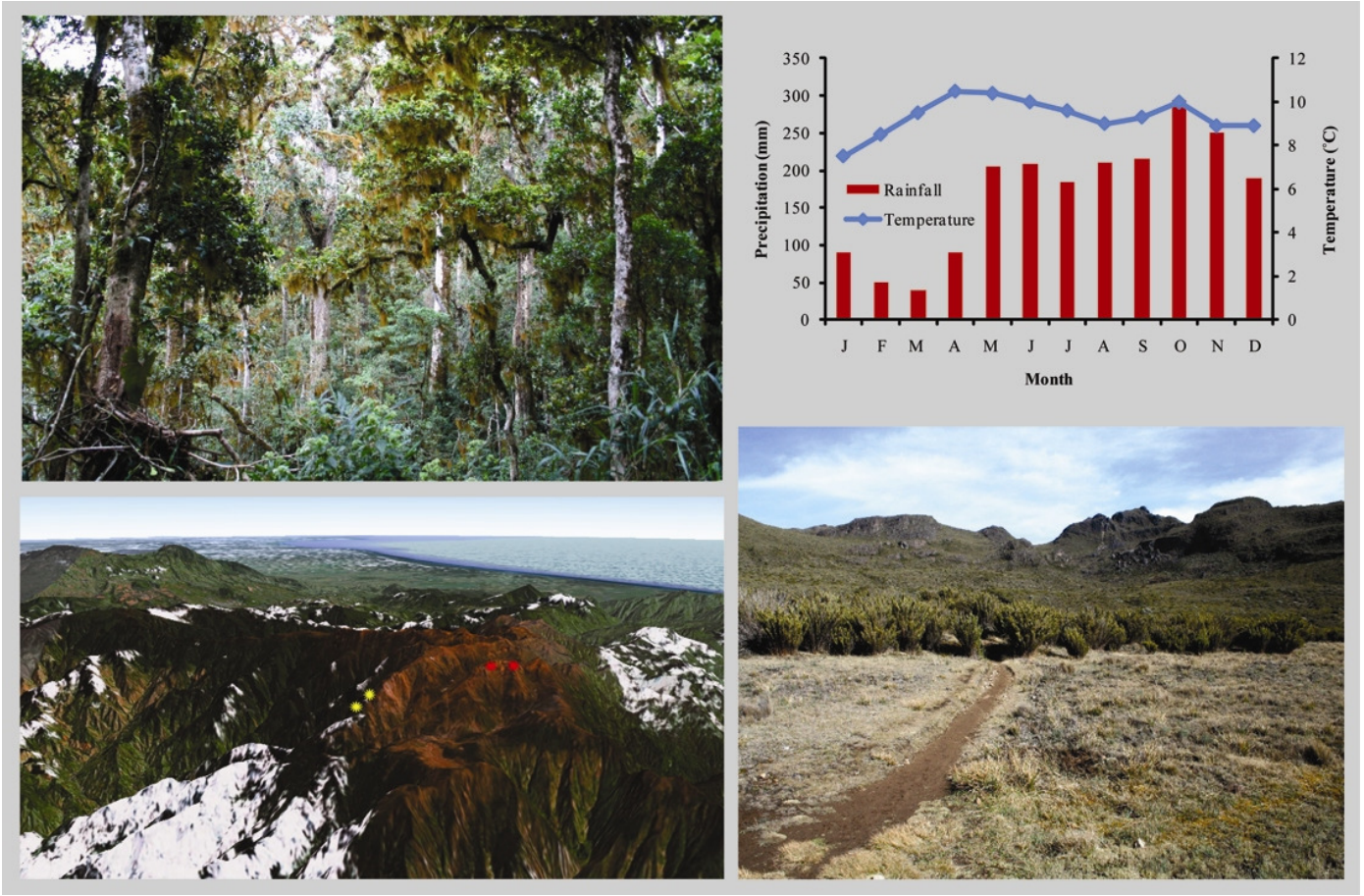

Figure 14. Cerro Chirripó, one of the study areas in Costa Rica. Satellite image imposed over digital elevation model on lower left indicating the position of the four study sites as yellow (forest) and red (paramo) stars. Climograph made using data from Herrera (2005).

84˚47'0" W and approximately 1500 m in elevation. The mountains of Monteverde are the product of the volcanic activity in the Guanacaste Volcanic Range and have been dated to be 1-2 million years old (Gillot et al. 1994). The forests present in this area are conspicuously rich in mosses and epiphytes. They have even been considered the area of the highest known orchid diversity on earth (Haber 2000). In spite of this, the most representative plant families at Monteverde are the Lauraceae, Rubiaceae, Fabaceae, Moraceae and Meliaceae (see Kappelle 2001).

The other intermediate elevation site in Costa Rica corresponds to the Las Cruces Biological Station/Wilson Botanical Gardens (Figure 16), an area administered by the Organization for Tropical Studies. This site is located in southwestern Costa Rica on the Cruces Pacific Coastal Range at 8˚47'7" N and 82˚57'32" W and approximately 1200 m in elevation. The formation of this area apparently occurred during the late Eocene-Miocene and the common sedimentary rocks of the region are mixed with gabbroic sills, which have been dated at about 12 million years old (MacMillan et al. 2001). Even though the Wilson Botanical Gardens are a mixture of exotic and native plants, they represent one of the most important *ex-situ* conservation efforts for palm trees worldwide. In fact, the Arecaceae (the palm tree family) along with the Araceae and Bromeliaceae are the most represented plant families in the herbarium of Las Cruces (Quirós 2009).

Neotropical province – low-elevation tropical forests in Costa Rica

In a manner similar to what was described for the last study sites, three low-elevation forests were studied in Costa Rica. Two of these sites represent lowland rainforests, whereas the third is a lowland seasonal dry forest. The first site is the La

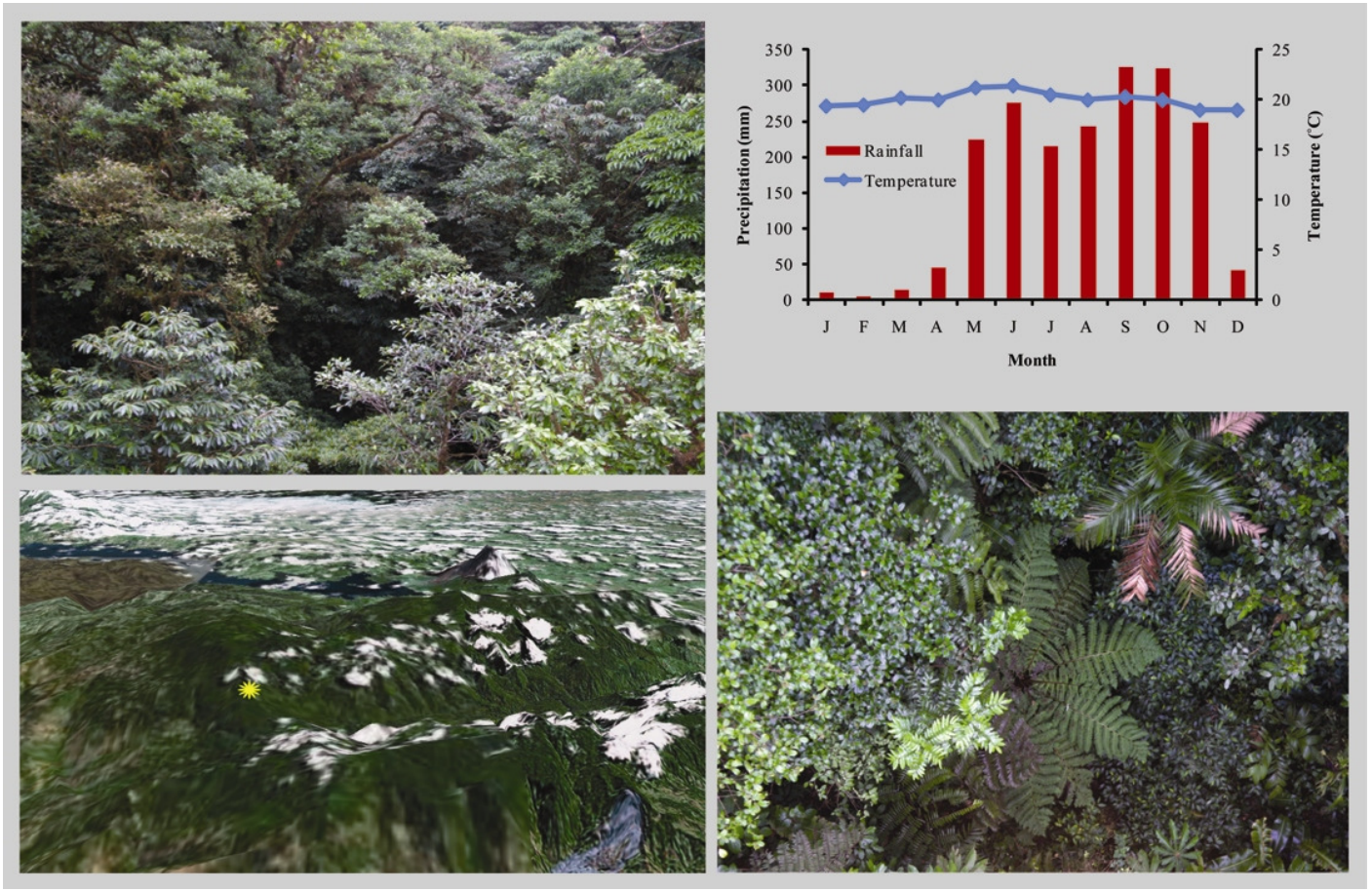

Figure 15. Monteverde, one of the intermediate elevation study areas in Costa Rica. Satellite image imposed over digital elevation model on lower left indicating the location of the Cloud Forest Reserve. Climograph made using data from the Costa Rican Meteorological Institute.

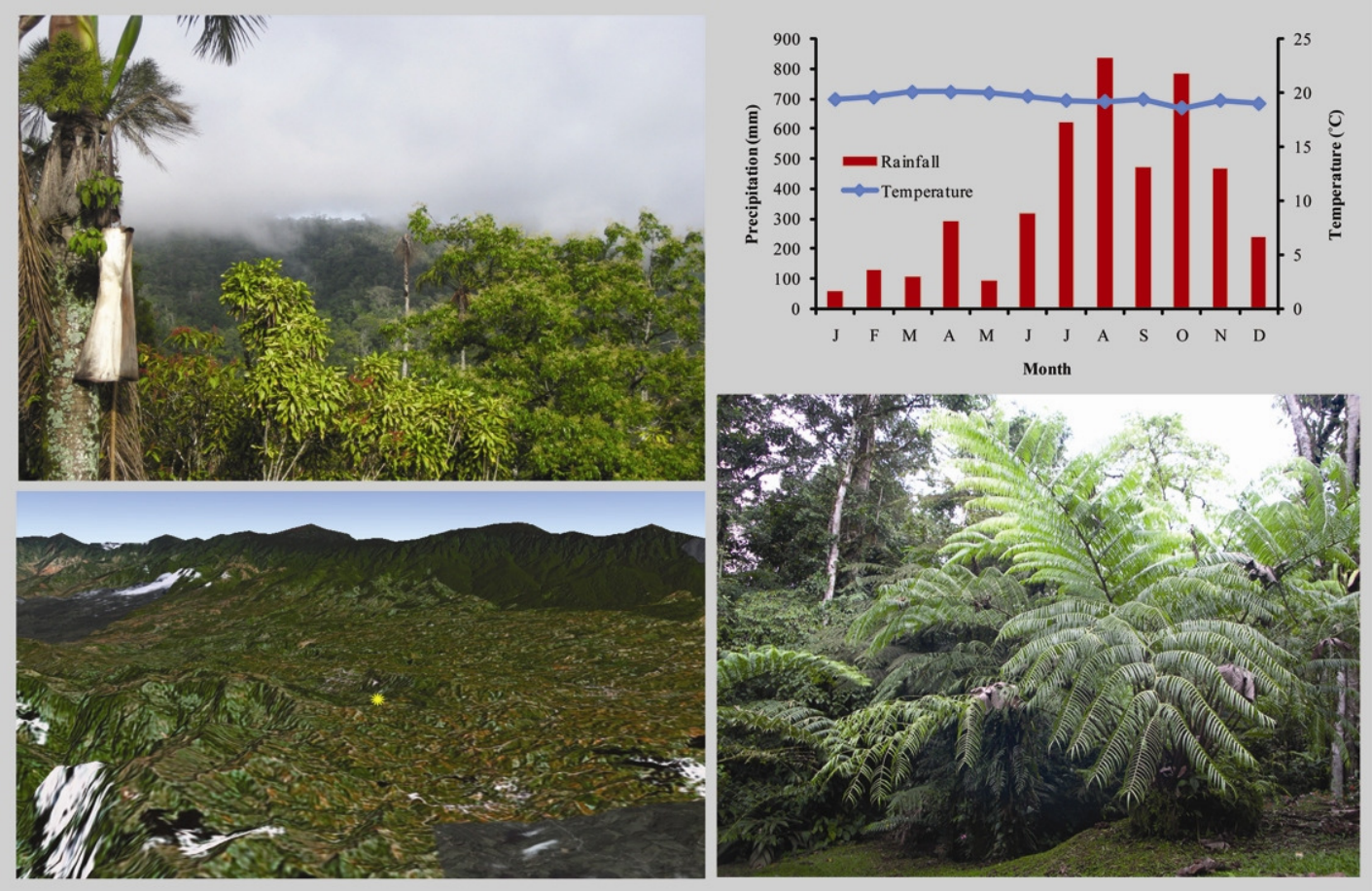

Figure 16. Las Cruces, one of the intermediate elevation study areas in Costa Rica. Satellite image imposed over digital elevation model on lower left indicating the location of the Biological Station. Climograph made using data from the Organization for Tropical Studies.

Selva Biological Station, which is located on the Caribbean slope of Costa Rica at 10˚25'54" N and 84˚00'47" W with an elevation of approximately 50 m (Figure 17). La Selva is one of the most widely recognized tropical biological stations in the world and is completely administered by the Organization for Tropical Studies. Most of the geological features in this area are formed by lower Pleistocene lava flows, alluvial deposits and Tertiary volcanic hills (Sanford et al. 2000). The forests in this area correspond to lowland tropical rain forests and are distinctive because of the abundance of *Pentaclethra macroloba* and the palm trees *Socratea exorrhiza*, *Welfia georgii* and *Iriartea deltoidea* (see Hartshorn and Hammel 2000).

The second low-elevation site selected corresponds to the Cahuita National Park. This area is located on the Caribbean coast of Costa Rica at 9˚44' N and 82˚49' W and approximately 10-15 m in elevation (Figure 18). This area is the product of moderately weathered rocks formed during the late Miocene-early Pleistocene (Sprechmann 1984) and is characterized by sedimentary soils with high contents of calcium (Salazar et al. 2004). The marine sector of this National Park contains the most developed coral reef along the Caribbean coast of Costa Rica (Cortés and Risk 1985). The vegetation in this area is typical of the Caribbean coast of Central America with families such as the Arecaceae, Moraceae, Combretaceae, Euphorbiaceae and Malvaceae as the most common groups in the forest (see Sánchez 1983).

The last low-elevation site in Costa Rica is the Palo Verde National Park, which is located in the Tempisque basin in northwestern Costa Rica at 10˚20' N and 85˚20' W and an elevation of approximately 20 m (Figure 19). This area is under a joint administration from the Costa Rican National Park Service and the Organization for Tropical Studies

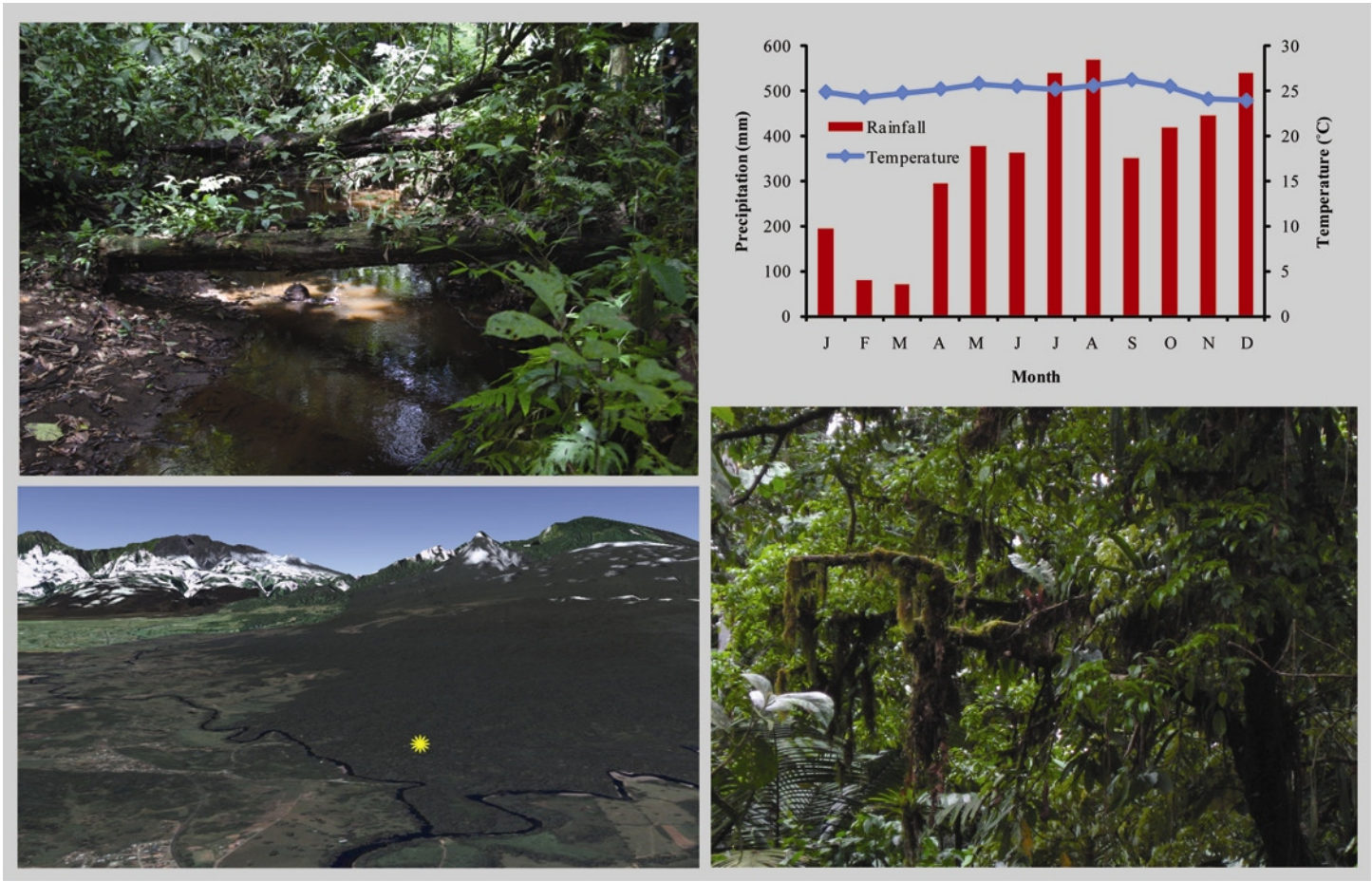

Figure 17. La Selva, one of the low-elevation study areas in Costa Rica. Satellite image imposed over digital elevation model on lower left indicating the location of the Biological Station. Climograph made using data from the Organization for Tropical Studies.

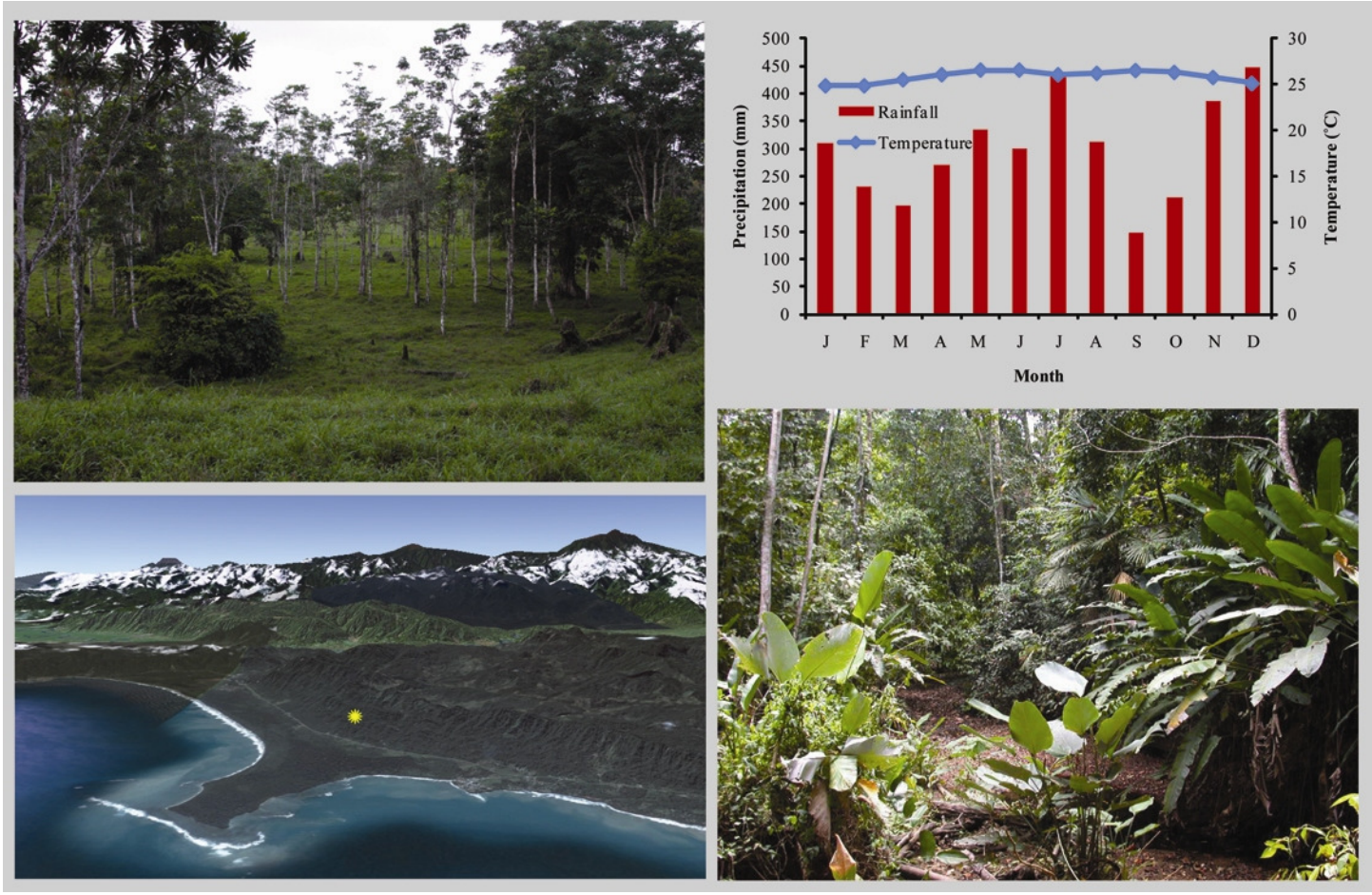

Figure 18. Cahuita, one of the low-elevation study areas in Costa Rica. Satellite image imposed over digital elevation model on lower left indicating the location of the collecting area. Climograph made using data from the Costa Rican Meteorological Institute.

and is located in one of the oldest geological regions of Costa Rica. The rocks of this area are thought to have originated in the upper Paleocene-lower Eocene around 56 million years ago (Jaccard et al. 2001). The forest present in this area is a seasonal tropical dry forest with *Acacia*, *Bombacopsis*, *Enterolobium*, *Hymenaea* and *Tabebiua* as common genera (Chavarría et al. 2001).

Neotropic province – insular forests in Costa Rica

In order to study the ecology of Neotropical myxomycetes in the context of a true oceanic island, one more territory of Costa Rica was selected. This is Cocos Island, an oceanic island in the eastern tropical pacific that gave rise to a National Park of the same name. This island is located approximately 550 km southeast from the Pacific coast of Costa Rica between 5º30' - 5º33' N and 87º01' - 87º05' W (Figure 20, Montoya 2007) and it is the summit of a seamount that lies on the Cocos plate (Castillo et al. 1988).

This island is thought to be around 2 million years old (Castillo et al. 1988) and contains one of most pristine insular forests in the world. The number of vascular plants is close to 235 species, around 30% of which are endemic to the island (Trusty et al. 2006). Even though the terrestrial section of the national park is very understudied, some previous investigations have treated the flora (e.g., Gómez 1975, Dauphin 1999, Bernecker-Lücking 2000) and the mycoflora (e.g., Gómez 1983) of the island.

Neotropic province – low elevation tropical forests in Peru

The last study area established for this dissertation is located in the southwestern portion of the Amazon Basin in South America. The specific site corresponds to the Los

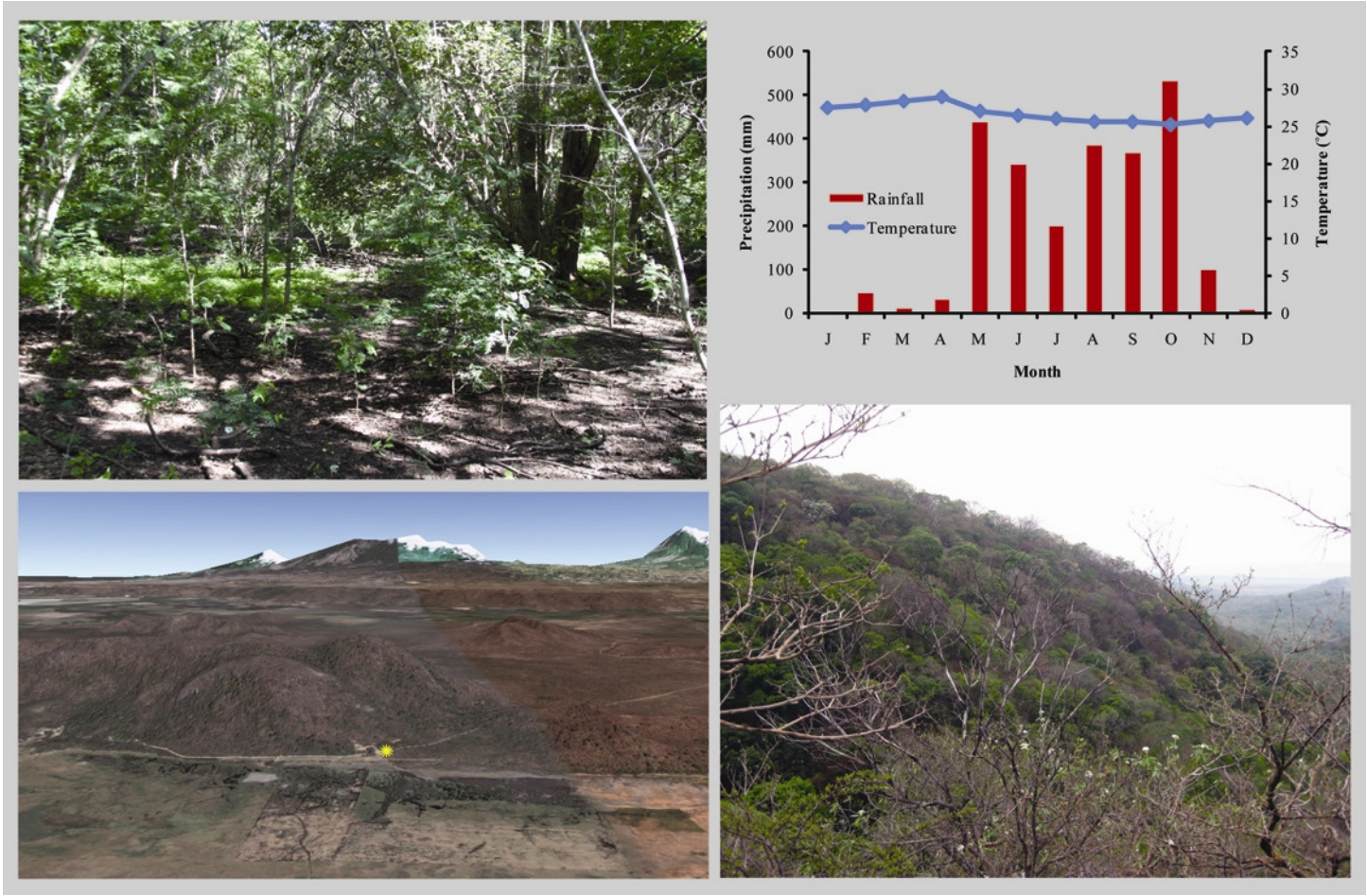

Figure 19. Palo Verde, one of the low-elevation study areas in Costa Rica. Satellite image imposed over digital elevation model on lower left indicating the location of the Biological Station. Climograph made using data from the Organization for Tropical Studies.

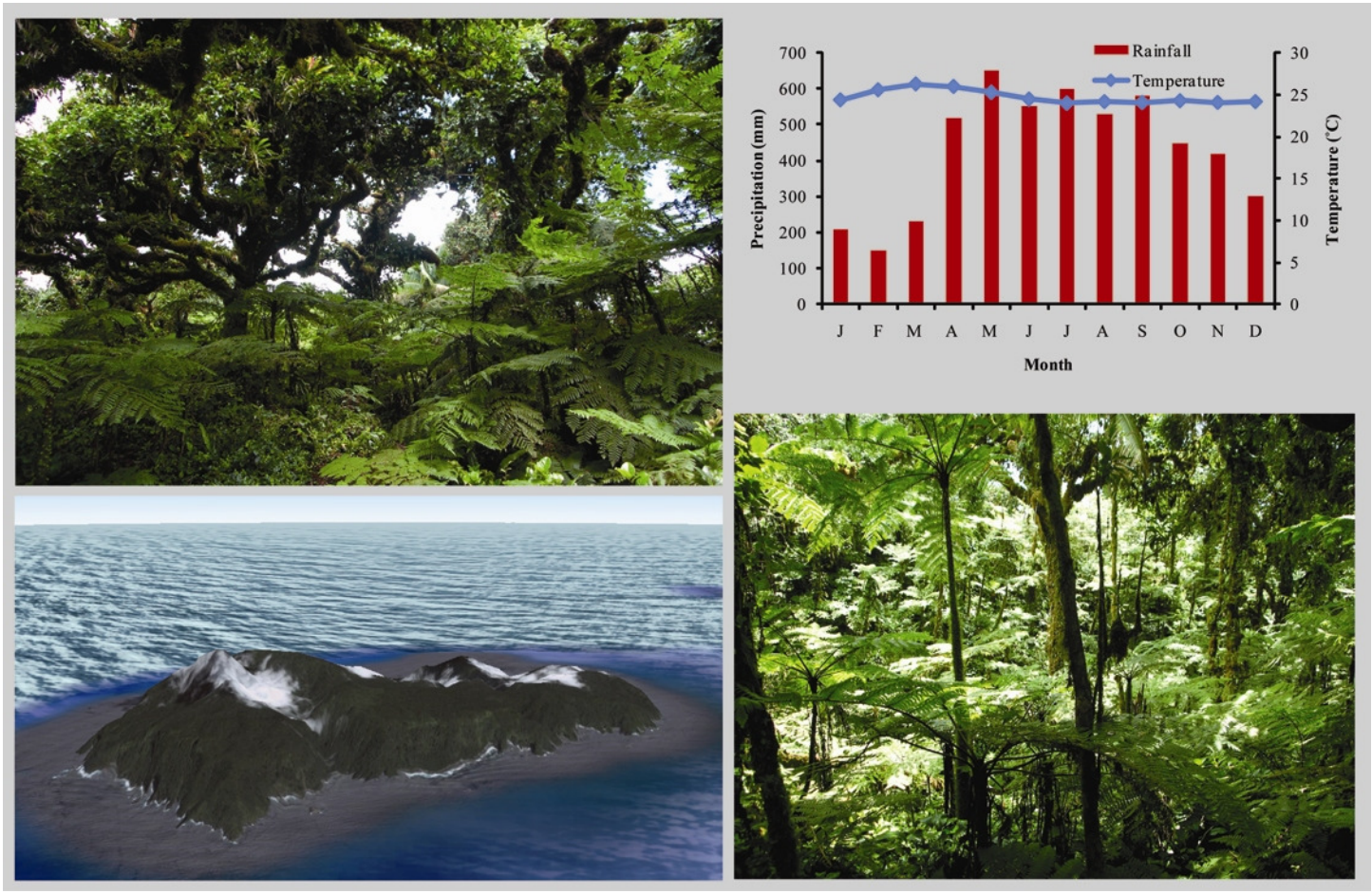

Figure 20. Cocos Island, the oceanic island studied in this dissertation. Satellite image imposed over digital elevation model on lower left showing the island. Climograph made using data from Alfaro (2008).

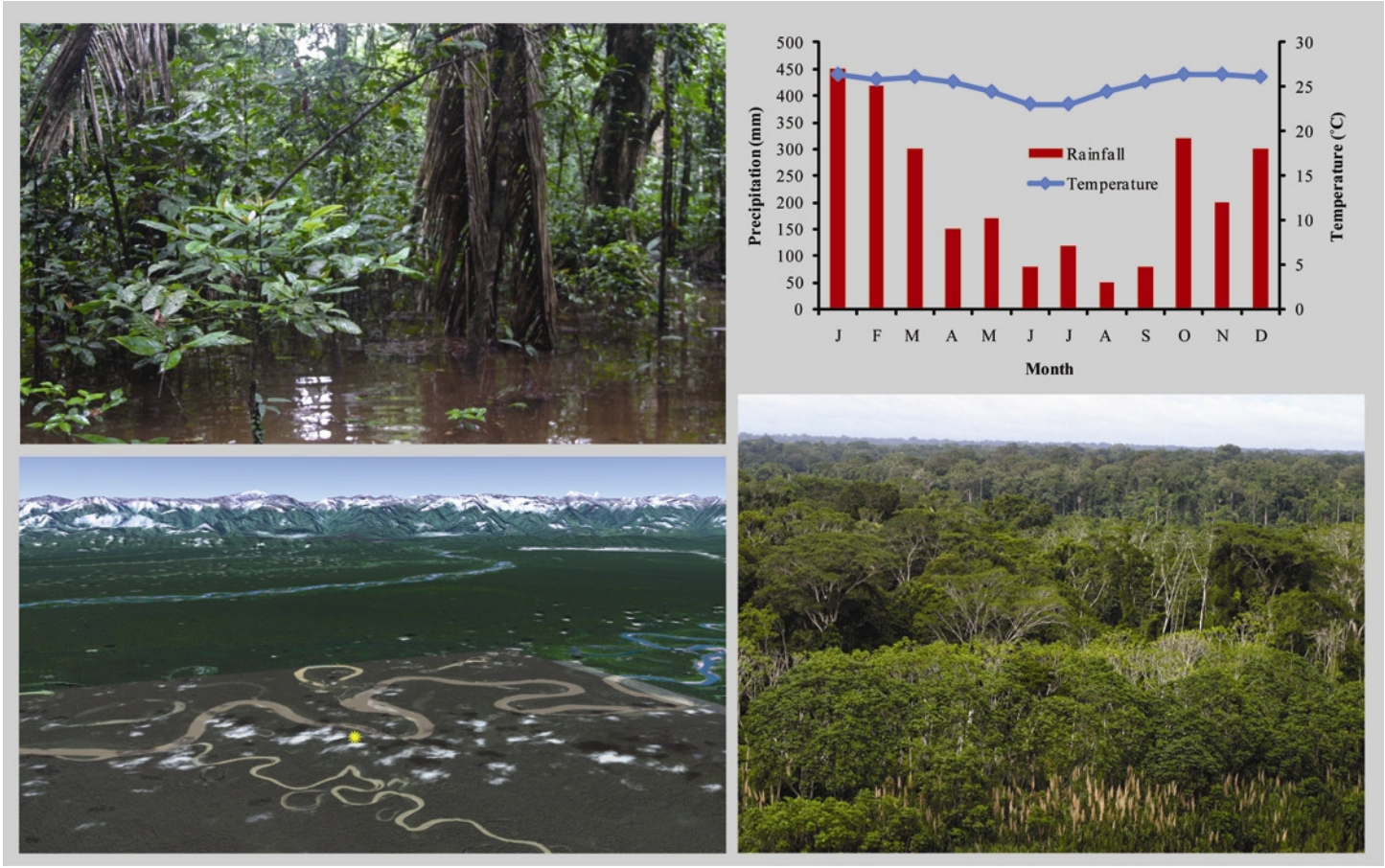

Figure 21. Los Amigos, the low-elevation study area in southeastern Peru. Satellite image imposed over digital elevation model on lower left indicating the location of the Biological Station. Climograph made using data from the Peruvian National System of Meteorology and Hydrology.

Amigos Biological Station which is located at 12˚34' N and 70˚06' W, with an elevation of approximately 250 m (Figure 21). This area is administered by Amazon Conservation Association by means of a public land concession from the Peruvian government.

This station is located on the Madre de Dios geological formation in Peru, an area that seems to have been finally shaped during the late Cenozoic (Campbell et al. 2001). In general, this area is formed by a series of alluvial, lacustrine, and tidal deposits, some of which have been dated as recent as 30,000 years old (see Pitman 2008). The vegetation present in this area is associated to lowland tropical moist forests with a strong influence of the Madre de Dios River system watershed. Some of the more commonly represented plant families in this area include the Arecaceae, Myristicaceae, Moraceae, and Violaceae (Pitman 2000). A current ongoing inventory project of the biota present at Los Amigos is taking place in this area.

Dissertation structure

For practical purposes this dissertation has been divided in a series of chapters, each of which deals with specific aspects of myxomycete ecology and biogeography in the Neotropics, with emphasis, as indicated earlier, on the northern part of the region. All the chapters presented herein have been structured in a peer-review journal format. During the course of this project, some chapters have been submitted and published in professional journals. Although these published chapters have included one or more coauthors and collaborators, all the work described in the chapters was designed, carried out, analyzed and presented by the author of this dissertation. The work of the collaborators has been limited to particular tasks within the context of the research

process, including such things as sharing complementary datasets, providing assistance in the field, logistic or technical support and editing of manuscripts to be submitted for publication. Working with other people in this fashion is a common practice of professionals in all branches of science. However, the complementary datasets mentioned above were compiled, corrected and double-checked with the original authors (unless deceased) by the author of this dissertation.

Following the working scheme of the present dissertation, all chapters have been written so as to provide answers to the questions mentioned in a previous section. In this way, Chapter 2 gives a general overview of myxomycete ecology in Costa Rica. This chapter represents, to our knowledge, the first comprehensive published study of myxomycete ecology for a tropical country and includes a dataset of records that has been compiled from the best information sources available today. This information has been carefully examined using a Geographic Information System (GIS) approach and analyzed using both macro- and micro-ecological methods. This chapter provides a solid basis for comparative studies involving other tropical areas of the world, including those considered in other chapters of this dissertation. For this chapter, the senior author collected some of the examined material in the field, compiled and corrected the entire dataset, analyzed the data and wrote the manuscript submitted for publication. The role of the coauthors was limited to logistical help in the field and during visits to herbaria, help during the field component of the research and checking and suggesting edits to the final manuscript.

Once an overview of the ecology of Costa Rican myxomycetes was available, it was possible to carry out a finer analysis for a particular area of the country. This

approach has been followed in order to provide information related to the microenvironments in which myxomycetes are found in the Neotropics, one of the main three questions of this project. In this way, Chapter 3 summarizes one of the studies carried out during the course of this dissertation. This chapter analyzes the importance of a series of microenvironmental parameters in the sporulation patterns of myxomycetes for an oak forest in the Talamanca Range in south-central Costa Rica. An introduction to the study of resource partitioning in myxomycetes by means of niche analyses is included in this chapter as well. For this chapter, the senior author collected all the data in the field, carried out the laboratory work, generated and analyzed the dataset and wrote the manuscript to be submitted for publication. The coauthor contributed with logistical help during the research and checked and suggested edits in the final manuscript.

Following a similar approach, but also with the purpose of studying ecological factors that might account for biogeographical patterns, Chapter 4 introduces the study of myxomycetes in oceanic islands by means of an ecological analysis along an elevational transect on Cocos Island of the western coast of Costa Rica. This chapter analyzes the similarity of the species assemblages found in this island at different elevations with previous studies in other oceanic tropical islands and similar forests in mainland Costa Rica. An introduction to the concept of ecological isolation in tropical myxomycetes is presented in this chapter. This constitutes an important contribution to future studies of myxomycete biogeography. For this chapter, the roles of the senior author and the coauthor of the published manuscript were the same as indicated above for the previous chapter.

The third question of study in this dissertation is related with the interaction among closely related species. For this, a microenvironmental niche-based approach has been followed to produce Chapter 5. In this chapter, a solid database constructed with information on three species of a myxomycete-like organism has been used to study the process of separation of niches. The chapter compares and contrasts the ecology and the distributional patterns of the three species in question, for which very few ecological data were available prior to this dissertation. In this case, the senior author collected some of the data in the field, carried out most of the laboratory work, compiled and analyzed the dataset and wrote the manuscript to be submitted for publication. The coauthors contributed logistical support during the research process, provided a complimentary dataset for analysis and checked and suggested edits to the final version of the manuscript.

The following two chapters (6 and 7) focus on the results obtained from the series of high-elevation study areas selected for this dissertation. In this way, Chapter 6 compares the structure of the different high-elevation myxomycete assemblages considered in this dissertation. This chapter incorporates the analysis of data in a macroecological frame in which a series of both macro- and microenvironmental conditions are analyzed in order to generate data relevant to myxomycete distribution in the region. A comparison with some of the previously presented chapters of this dissertation is also incorporated in this analysis. The entire process involved in generating the data that yielded this chapter was carried out by the author of this dissertation.

In a similar manner, Chapter 7 summarizes the biogeographical aspects of the assemblages studied by comparing the species composition of all the Neotropical study

sites and the two external areas. This chapter also introduces the analysis of results in the context of ecological theories that are related to the distribution and biogeography of organisms. Particular emphasis on the use of neutral models and niche-based models of community structure and species distribution is found in this chapter. For this, the analysis has been carried out taking in consideration the results presented in the previous chapters of this dissertation. As was the case for Chapter 6, the entire process involved in generating the data that yielded this chapter was carried out by the author of this dissertation.

All the analyses carried out in the last chapters have generated two byproducts during the course of this dissertation. The first one of these, is the review of Costa Rican myxomycetes that is presented in Chapter 8, which summarizes the most important studies carried out during the past century in this region of Central America. In order to make the review more meaningful for future projects in the area, a series of basic ecological annotations and specimen locations have been included for each of the species presented in this chapter. The second byproduct is the report on the new species of myxomycetes from Mexico and Guatemala that is presented in Chapter 9. In a similar way to the last chapter, this report includes basic ecological information regarding the microhabitats in which the different species of myxomycetes were found. In both instances, the author of this dissertation was responsible for the entire process involved in generating the manuscript.

With exception of the present introductory chapter, the other chapters of this dissertation represent considerations of various aspects of the body of data generated for the selected study areas during the period of my graduate study. The process of research

involved in generating these data has been carried out under the premise of studying the ecology and biogeography of myxomycetes in high-elevation areas of the Neotropics. For this reason, a final section containing general observations and concluding remarks has been included in Chapter 10. In this final chapter, a series of general comments relating to the ecology and biogeography of tropical myxomycetes, with particular emphasis on the high-elevation areas, has been included.

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Chapter 2

Ecological patterns of Costa Rican Myxomycetes

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Rojas C, Valverde R, Stephenson SL, Vargas MJ. 2009. Ecological patterns of Costa Rican Myxomycetes. Fungal Ecology (*in press*). doi 10.1016/j.funeco.2009.08.002.

Abstract: Ecological patterns of tropical myxomycetes have been subjected to study only during the last decade. However, an exhaustive analysis of an extensive dataset for a single tropical country is lacking. For this reason, the present study was designed with the primary objective of examining the ecological distribution patterns of myxomycetes in Costa Rica. A database that includes historical records was compiled, and factors such as forest type and substrate preference were analyzed in an effort to understand these patterns at both the macro- and microenvironmental levels. Microenvironmental parameters that may drive abiotic preferences were analyzed. The ecological distribution of species showed a complex pattern; however, elevation seemed to be a key factor in determining the distribution of the group of species analyzed. In the same way, nonwoody substrates seemed to represent the most important factor explaining the niches occupied by myxomycetes in lowland regions of the country.

Index descriptors: Central America, community ecology, eumycetozoans, Neotropics.

Introduction

The plasmodial slime molds (myxomycetes or myxogastrids) comprise a group of amoeboid protists (Fahrni *et al.* 2003) known worldwide. Their life cycle includes the particular capacity to produce meiotic spores within spore-bearing structures during the reproductive stage (Alexopoulos *et al.* 1996). In the vegetative stage, these organisms survive as complex macroscopic multinucleate, single-celled structures known as plasmodia that feed upon microorganisms and are able to move short distances across or within particular substrates (Stephenson & Stempen 1994).

This combination of characteristics is thought to give myxomycetes a competitive advantage over other groups of amoebae with respect to their migratory rates and effective colonization capacity. Interestingly, most of the species in the group do not show the cosmopolitan distribution that is predicted by models based on these ideas (e.g., Finlay 2002). For example, Fenchel & Finlay (2004) proposed that organisms smaller than 1 mm should occur "everywhere" as long as suitable habitats permit their existence. However, data are still being collected to determine whether or not this pattern applies to myxomycetes. For instance, Schnittler & Stephenson (2000) reported a number of shared species between the tropical forests of Costa Rica and the temperate forests in the eastern United States, but within the Neotropical region it seems that some of the macroscopic species of the genus *Ceratiomyxa* are not evenly distributed in similar environments (Rojas *et al.* 2008). The more general idea, based on the most recent data available, is that

some species of myxomycetes seem to show clear biogeographical patterns that conform more closely to the predictions of mathematical models and empirical data obtained from field surveys made for other groups of protists (e.g., Chao et al. 2006).

The latter pattern seems more obvious when recent ecological studies of myxomycetes are considered. Most such studies have found that some species of myxomycetes seem to be largely restricted to particular environments, apparently as a product of their preference for specific vegetation types (e.g., Schnittler & Stephenson 2002), substrates (e.g., Wrigley de Basanta *et al.* 2008) or microenviromental conditions (e.g., Rojas & Stephenson 2007). However, very few efforts have been made to relate particular species of myxomycetes to different types of forest ecosystems, even though this is the first step in evaluating ecological patterns at a larger scale. The major constraint for this type of analysis is the availability of an exhaustive set of biological data along with information on the spatial distribution of forest types for the area being considered.

In this sense, Costa Rica represents a good starting point for tropical areas. Although research on myxomycetes has not been carried out consistently and systematically throughout the past century, there are a number of important baseline studies (e.g., Welden 1954; Alexopoulos & Sáenz 1975; Farr 1976). However, even more relevant are the systematic studies of myxomycetes that have been carried out in the country during the period of 1994-2007, most of which were summarized by Stephenson *et al.* (2004b). Fortunately, a well developed system of digital geographic information data also exists for the country (e.g., Vaughan *et al.* 1998). In fact, the widely known

forest type classification system developed by Leslie Holdridge (Holdridge *et al.* 1971) has already been incorporated into the Digital Atlas of Costa Rica (ITCR 2004).

The reasons that this has taken place are simple. This country represents only 0.03% of the terrestrial surface on the Earth but contains more than 4.5% of the known terrestrial species on the planet (Obando 2008). The geographic position, the influence of wind and ocean currents and geological history of Costa Rica provide this country with a unique set of conditions for the establishment of life forms. The interaction of these abiotic conditions has given rise to 24 different forest types or life zones, each of which presumably has a particular assemblage of species.

Given all these conditions, we decided to carry out the project described herein to develop a more complete understanding of the ecological dynamics of tropical myxomycetes. For that reason, the primary objectives of this project were (1) to analyze the distributional patterns of myxomycetes in relation to different forest types and on different substrates and (2) to assess microenvironmental factors as abiotic driving forces for myxomycete distribution in Costa Rica. This study has considerable implications for future projects, since it is the first comprehensive study in which an effort has been made to analyze the effect of both macro- (e.g., forest types) and microenvironmental (e.g., substrates) factors on the distribution patterns of myxomycetes in a tropical country. It also provides baseline ecological data on myxomycete communities that can serve as a starting point for future studies in the tropics.

Materials and methods

This study considered specimens and information generated throughout the period of 1905 to 2007. These specimens were collected by a number of different individuals using different methodologies. However, every possible effort has been made to decrease the effect of this time-related constraint and to make use of the available information in an objective manner. Throughout this paper, the forest type classification used refers to the Holdridge life zone classification system (Holdridge *et al.* 1971), and the nomenclature used for myxomycetes follows Hernández-Crespo & Lado (2005). All species identifications are based on the morphological species concept, and for field-collected specimens, no material still in the plasmodial stage was considered.

Database construction

Approximately 95% of the database used in this paper was compiled from records of specimens collected by the authors and by Dr. Martin Schnittler between 1994 and 2007. The remaining 5% of the database was derived from older records obtained from the herbaria of the University of Costa Rica (USJ), the United States National Fungus Collections (BPI) and the National Museum of Costa Rica (CR). External records from the Global Biodiversity Information Facility (GBIF) primary database also were considered.

The final database included 4811 records of specimens of myxomycetes collected between 1905 and 2007. To avoid duplication of records, all records were carefully examined. In addition, a thorough evaluation of the nomenclature was carried out in order to standardize the nomenclatural treatment of species in the database.

Collecting protocols

For those specimens obtained after 1994, a combination of field and laboratory techniques was used. In the first instance, the opportunistic sampling protocol described by Cannon & Sutton (2004) was utilized. This method is highly effective in studying microorganisms for which ecological patterns are still poorly known. It consists of a randomly-based sampling effort with very few pre-defined collecting parameters. In the present study, specimens were collected in the forest understory from dead plant material. Specimens collected in this manner were curated according to the protocol described by Stephenson & Stempen (1994). Once collected, specimens of myxomycetes were glued to paper strips, placed in small pasteboard boxes and allowed to dry at room temperature. Specimens collected before 1994 are presumed to have been collected in a similar manner, since these sampling and collecting techniques have been widely used in the past (e.g., Martin & Alexopoulos 1969). For example, Constantine Alexopoulos and Jose Alberto Sáenz carried out the first major survey of myxomycetes in Costa Rica by using the same basic methodology described above (see Alexopoulos & Sáenz 1975).

Laboratory isolation of myxomycetes from samples of organic material collected in the field and used to establish moist chamber cultures was carried out only after 1994. For this part of the study, a series of samples consisting of dead plant material was randomly collected and brought back to the laboratory. Subsamples of this material were placed on pieces of filter paper in Petri dishes and soaked with distilled water for 24 hours. Afterwards, excess water was poured off the plate, and the resulting cultures were

maintained and examined for the presence of myxomycetes over a period of approximately two months.

Recognition of forest types

As already noted, forest types are referred to as life zones in the Holdridge system of ecosystem classification. In order to recognize the appropriate forest type for each of the records in the main database, an examination of the geographical coordinates was carried out. Both the coordinates and the elevation of all collecting localities for each record were manually reviewed and checked for consistency using the cartographic sheets of the 1:200000 ecological map of Costa Rica (Bolaños & Watson 1993). However, when original coordinates and/or elevation were not available for collections made before 1994, the geographic centroid of the closest known locality provided the information for the record. The locality information for these collections was obtained by studying the field trip records present at the USJ and CR herbaria for the collectors and years being evaluated.

After the georeference evaluation, a transformation of datum from WSG84 to Ocotepeque was performed. The latter datum is the official reference of the National Geographic Institute of Costa Rica, and it was considered necessary to do this in order to minimize the spatial error when plotting records on official maps. According to Fallas (2003), when such a transformation is performed, the maximum root mean square positioning error oscillates around 4 m, even when low cost GPS units are used to obtain the original coordinates using the WSG84 datum. This degree of geographic accuracy exceeds the requirements of the type of biological analysis presented in this paper, but it

follows the protocol currently being used for the country. However, this does not mean that the actual accuracy of records after the transformation was in all cases less than 4 m. Each GPS reading carries inherent errors on its own due to atmospheric conditions, forest structure and position of satellites. Nevertheless, it is thought that the final database contains very accurate geographic information.

After this correction, the original Holdridge life zone layer provided in the Digital Atlas of Costa Rica (ITCR 2004) was used to create a map of the country with independent data representing the different forest types. For this, a series of sub layers corresponding to the 24 different life zones was created by using the metadata information to identify the individual polygons representing each one of the zones. A modified map was created and used to plot all the records, using the corrected coordinates. After this, a complete matching record-life zone report was generated and used to assign the forest type to each one of the records. All GIS work was performed using the program ARCmap, version 9.2.

Substrate and species classification

The range of substrates upon which myxomycetes occur is very broad. For this reason, in the present study, a list of 10 substrate categories was created and all records were arbitrarily assigned to one of these categories. Categories were created from observed patterns of occurrence in tropical areas and some of them represent substrates that are unique to this part of the world. From nonwoody to increasingly woody, substrate categories (with the abbreviations used given in parentheses) are dung (DU), flowers and

inflorescences (FI), living plants (LP), living cryptogams (LC), ground litter (GL), aerial litter (AL), lianas (LI), fruits (FR), twigs (TW) and dead bark and wood (DBW).

Since the collecting effort in each of the forest types was obviously different, species were placed into four main categories of abundance in order to decrease the potential risk of accepting a poorly supported hypothesis during the statistical analysis. In this classification, species representing more than 1.5% of the total number of collections were considered as abundant, those falling between 0.5–1.5% as common, between 0.15–< 0.05% as occasional and those less than 0.05% as rare (modified from Stephenson *et al.* 1993). According to this system, only species making up more than 1.5% of the total number of collections were considered as well represented, whereas those making up less than 1.5% were considered as not well represented in the country. Only those species falling in the first category were used to evaluate forest type and substrate preferences as well as the overall effect of environmental factors on the inherent variation of the dataset as revealed through applying multivariate techniques and niche breadth analyses. This is due to the larger number of records available and thus the lower potential minimum error during the analyses.

Species occurrences

The observed distributions of records among forest types and on various substrates were analyzed independently in an effort to assess the effects of both macro- and microenvironmental factors. The idea was to test whether or not species occurrences were significantly higher or lower than the expected probability for the particular macro- and microenvironmental categories. For the former, the expected probability was

considered as a function of the entire area covered by the forest type in question. With this system, the probability of finding a species would be higher in those ecosystems with larger areas. For substrates, it was considered that the probability of finding a particular type was a function of the exhaustiveness of the survey and not a function of the relative abundance of substrate types. When the opportunistic protocol is used, a non conscious *a priori* assessment of the ecosystem is carried out and the sampling effort starts being gradually directed toward rarer substrates. This results in a more or less equal sampling effort of all available substrates in relation to their relative availability.

However, since the distribution of substrates is not equal among forest types, it was considered that the probability of finding a species on a particular substrate for a specific forest type was a function of the number of substrates present in that forest type. This means that substrates had different associated probabilities depending upon the forest type being considered, which conforms to the opportunistic collecting protocol used as well. In all cases goodness of fit Chi-Square tests were performed between the observed and the expected distributions to look for statistical differences, and forest types or substrates that showed a marked deviation from the expected probability were recognized as "key" categories.

Analysis of microenvironmental conditions

Some recent studies of myxomycetes have provided evidence of the importance of certain environmental factors in determining the spatial distribution of particular species. In order to evaluate the importance of a group of seven microenvironmental

parameters in the distribution of species throughout the country, a niche breadth calculation and a multivariate analysis were carried out.

For both analyses the environmental factors evaluated were (1) elevation, (2) evapotranspiration rate (extrapolated from the forest type analysis) in the forest being considered, (3) mean temperature, (4) diameter of the substrate, (5) wind exposure, (6) light exposure and (7) substrate type. For wind and light exposure, the discrete category protocol used by Stephenson *et al.* (2004a) was utilized, whereas for substrate type an ordinal classification of substrates was developed, based on their woodiness using the sequence described in a previous section. For the multivariate analysis, both a principal component analysis (PCA) and a non-metric multidimensional scaling ordination (NMS) were carried out using the program PC-ORD, version 5.17 (McCune & Mefford, 2006). The first analysis was based upon correlations among variables. For the second analysis, the scores were generated using the autopilot option and weighted averaging from an exploration of 50 runs of real data and 50 runs of randomized data using Sørensen distances. Some species had to be excluded from these analyses due the lack of microenvironmental information on them in the main database.

Results

Altogether, 188 species of myxomycetes were recorded in the database. Many of these were new records for Costa Rica; however, a complete taxonomic treatment of Costa Rican myxomycetes will be the subject of a future paper. The records included in the database represent 18 out of the 24 forest types recognized for Costa Rica. The geographic location of all study sites is shown in Fig. 1. In a similar way, a depiction of

the collecting efforts over time is presented in Fig. 2, where it is clearly apparent that the majority of specimens have been obtained in the last decade or so.

Well represented species accounted for approximately 10% of the total number of species found in the country, whereas species with fewer than 5 records represented exactly 50% of the total. When the preference of well represented species was evaluated in relation to forest types and substrates, there were some readily apparent patterns in the analysis (Table 1). It is clear that all species have broad niches; however, *Collaria arcyrionema* and *Perichaena vermicularis* show the narrowest ones. At the same time, *Arcyria cinerea* and *A. insignis* seem to show a preference for lowland moist forests, whereas *A. denudata* displays a preference for montane rain forests. In fact, *A. denudata* was so underrepresented in lowland moist forests that it seems unlikely to be collected in that forest type. Interestingly, both *A. cinerea* and *A. denudata* showed a clear preference for dead bark and wood, whereas *A. insignis* seems to be preferentially associated with living plants and flowers and inflorescences (Fig. 3). In a similar fashion, *Ceratiomyxa fruticulosa* seems to occur preferentially on dead bark and wood in premontane and lower montane moist forests but was infrequent in lowland moist forests.

An interesting case is represented by a group of species consisting of *Collaria arcyrionema, Diderma hemisphaericum, Didymium iridis, Didymium squamulosum, Lamproderma scintillans*, *Perichaena depressa* and *Physarum pusillum*. All these species seem to be strongly associated with ground litter, although in different forest types. Most of them were preferentially found in lowland moist forests; however, it is interesting to note that *Diderma hemisphericum, Didymium iridis* and *Didymium squamulosum* were highly underrepresented in premontane and lower montane forests.

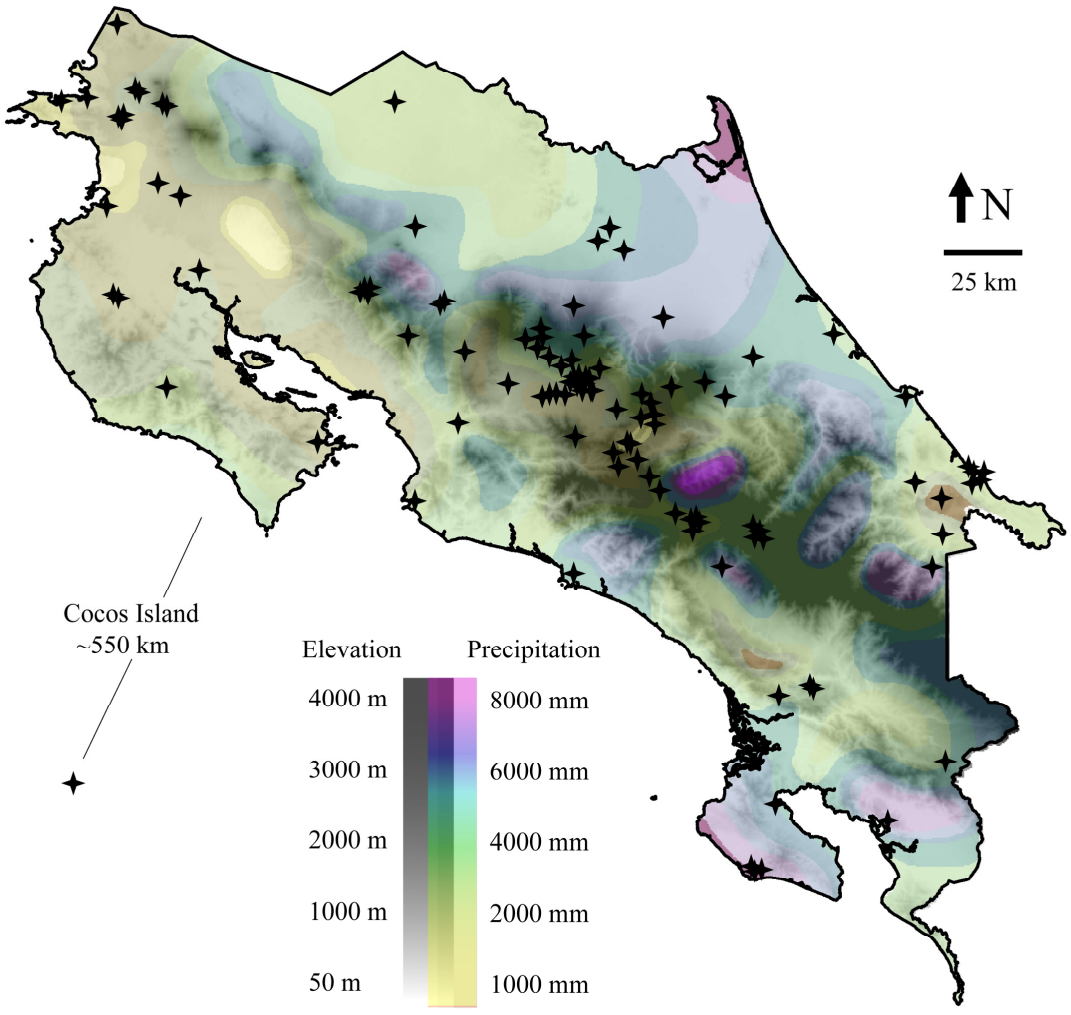

Figure 1. Map of Costa Rica showing the localities where specimens included in the database were collected. The Lambert CR-N equal-area projection is used.

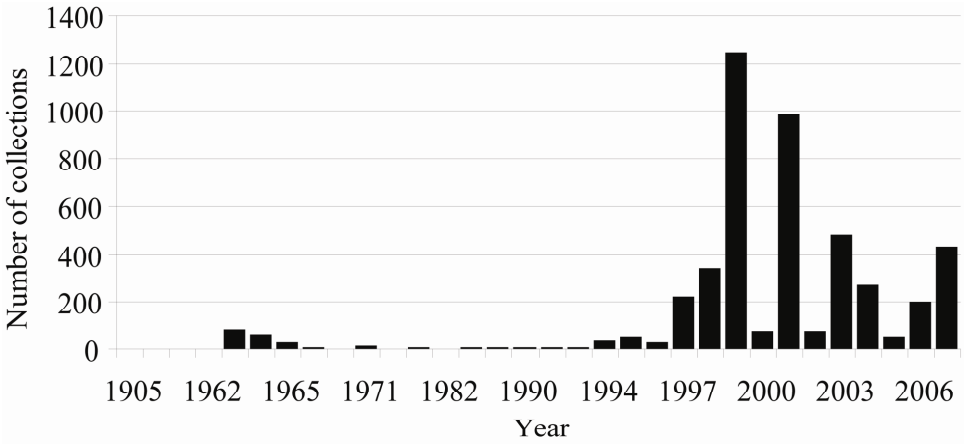

Figure 2. Number of myxomycete collections per year for the period between 1905 and 2007. Documented sampling during the period between 1963 and 1965 corresponds to collections made by C.J. Alexopoulos and J.A. Sáenz. The collecting effort after 1994 largely represents the product of projects funded by three grants from the National Science Foundation (to SLS).

Table 1. List of well represented myxomycete species, niche breadths and associated life zones and substrates with a higher or lower occurrence than expected from the calculated probabilities. For substrate and forest type abbreviations see materials and methods. Total number of records included = 1703. Note: SC=Species Code, NB=Niche Breadth.

Species	SC	NB	Key forest type (TP*)	Key substrate (TP*)
Arcyria cinerea	ARCcin	4.20	LMF (3.0), LMFTd (-15.1)	DBW (3.0), TW (-2.5)
Arcyria denudata	ARCden	n.a.+	PMFTL (2.6), MRF (5.0), LMF (-4.0)	DBW (3.6), GL (-3.1)
Arcyria insignis	ARCins	3.63	LMF (2.0), PWF (-25.2)	LP (2.6), AL (-7.5), GL (-3.6)
Ceratiomyxa fruticulosa	CERfru	4.40	LMMF (6.0), PWFTp (8.5), LMF (-27.0)	DBW (5.4), GL (-4.7)
Collaria arcyrionema	COLarc	3.51	LMF (2.3), PWTTL (-7.3)	GL (2.2)
Cribraria violacea	CRIvio	n.a.+	LDF (21.0), LMF (-2.6)	DBW (3.0), TW (-3.0), AL (-3.0)
Diderma hemisphaericum	DIDhem	4.42	PMFTL (-14.0), PWTTL (-20.4)	GL (3.6), DBW (-4.2)
Didymium iridis	DDYiri	5.70	PMFTL (-5.2), PRF (-23.0)	GL (3.9), DBW (-6.1)
Didymium squamulosum	DDYsqu	4.39	PMFTL (-22.0), LMWF (-5.3)	GL (4.8), TW (-13.8),
Hemitrichia calyculata	HEMcal	5.60	LWF (-3.8), MRF (-7.1)	DBW (5.1), GL (-2.7), TW (-8.3)
Hemitrichia serpula	HEMser	5.28	LDF (-10.6), MRF (8.5)	DBW (3.5), TW (-2.8)

Table 1. Continued

Species	SC	NB	Key forest type (TP*)	Key substrate (TP*)
Lamproderma scintillans	LAMsci	n.a.[+]	LMF (2.4), PRF (-3.9)	GL (3.4), DBW (-20.3)
Lycogala epidendrum	LYCepi	5.68	MRF (17.2), LMF (-4.7)	DBW (2.8), GL (-4.1)
Perichaena chrysosperma	PERchr	4.16	PMF (13.4), PWTTL (-11.5)	DBW (1.85), TW (-1.6)
Perichaena depressa	PERdep	4.84	LMF (2.5), PWF (-15.6), PRF (-12.5)	GL (2.4)
Perichaena vermicularis	PERver	3.60	LMF (2.6), LDF (6.4)	AL (2.1)
Physarum compressum	PHYcom	n.a.[+]	PMFTL (-13.1), PRF (-25.0)	FI (2.4), GL (2.7), DBW (-2.2)
Physarum didermoides	PHYdid	4.58	PRF (-19.4), LMFTP (-36.2)	FI (3.4), GL (-3.2), AL (-25.0)
Physarum pusillum	PHYpus	5.17	LMF (4.3), PMFTL (-20.1), PWF(-5.6)	GL (1.8)
Stemonitis fusca	STEfus	6.15	MRF (12.4), PMF (6.5)	DBW (2.8), AL (-2.5)

* Times the probability. It denotes the number of times over or under (negative) the expected probability that the species was found in the life zone or substrate. In all cases the χ^2 test showed significant differences between observed and expected distributions with associated probabilities oscillating between 0.005 and < 0.0001.

[+] n.a. = not available. Values were not calculated due the lack of environmental information for these species.

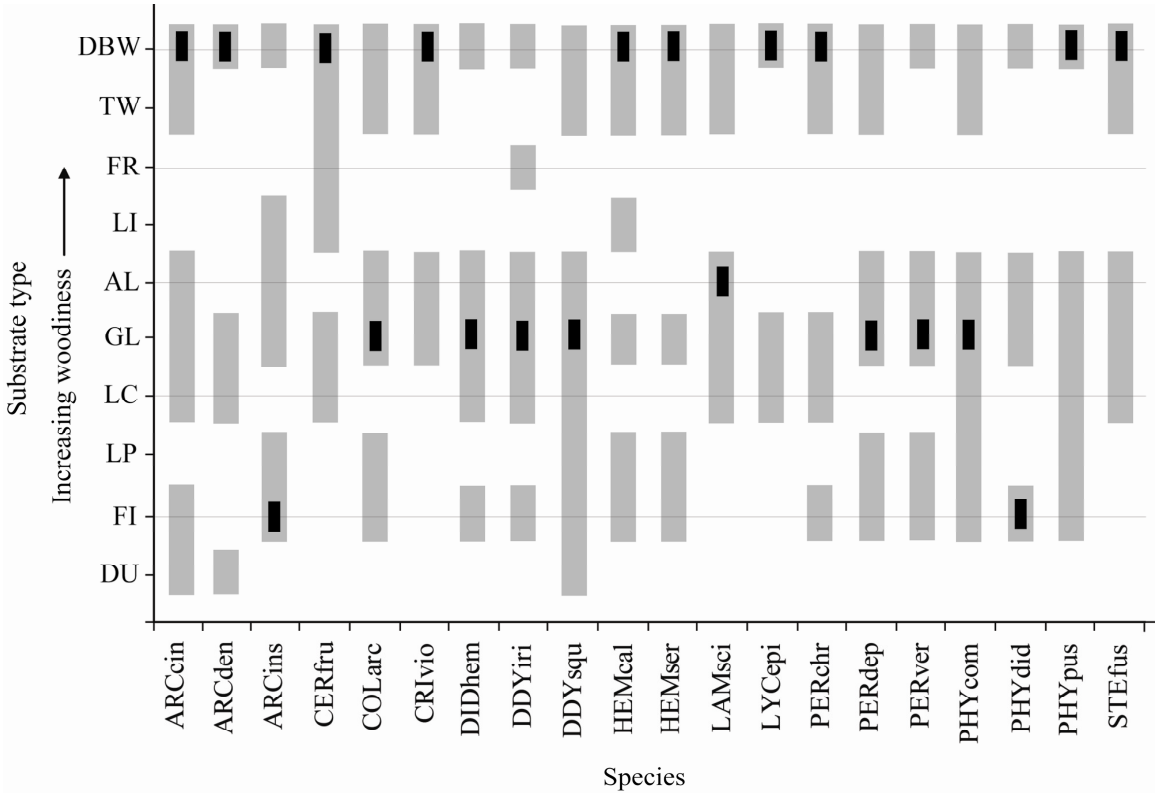

Figure 3. Diagram showing the distribution of substrates observed for the well represented species of myxomycetes in Costa Rica. Black squares indicate the preferred substrate for each one of the species.

The three species in the genus *Perichaena* display another interesting pattern. All are highly associated with moist forests. However, both *P. depressa* and *P. vermicularis* seem to prefer lowland forests, whereas *P. chrysosperma* was found more commonly in premontane forests. Interestingly, all three are associated with different substrates.

This was not the case for the two species in the genus *Hemitrichia*. Both *H. calyculata* and *H. serpula* were found preferentially on dead bark and wood; however, they seem to be associated with different forest types. Two of the less abundant species (*Lamproderma columbinum* and *L. scintillans*) displayed a preference for a uncommon substrate for myxomycetes, since they occurred on living cryptogams (bryophytes).

Interestingly, *Physarum compressum* and *Ph. didermoides* appear to be highly associated with flowers and inflorescences and are very much underrepresented at higher elevations. In contrast, it seems clear that *Stemonitis fusca* and *Lycogala epidendrum* prefer montane rain forests and grow preferentially on dead bark and wood. A clearer picture of the significant differences between abundant species in relation with elevation can be observed in Fig. 4 (F=35.05, d.f. = 1, P = 0.001). In a similar fashion, species present only in these montane environments included *Cribraria mirabilis*, *Enerthenema papillatum*, *Leocarpus fragilis* and *Trichia verrucosa* (not shown in the table). Interestingly, none of the common species was found to be present in only one region of the country (see Table 2) or to grow preferentially above the ground on aerial substrates.

The results obtained from the multivariate analysis seem to support the same tendencies observed in the previous analyses. The PCA determined that elevation, wind exposure and substrate are the three most important environmental parameters explaining the hyperdimensional variation observed in the present study. These three factors alone

accounted for over 90% of the total variation in the dataset. The NMS ordination performed (Fig. 5) shows the multidimensional arrangement of the abundant species in relation with these three factors. A pattern of elevation and substrate preferences similar to the one observed in the previous analyses is evident.

Discussion

The total number of species reported for Costa Rica in this paper is larger than the figure obtained in any other comparable study of which we are aware. Recently, Rojas and Stephenson (2007) increased the total number of species known from this country to 137. Since studies of myxomycetes have been more common in Costa Rica than in other countries in Central America, it would be expected that some of the species newly reported for Costa Rica also represent new records for the region. However, as indicated earlier, the taxonomic aspects of the database compiled in the present study will be addressed in a separate analysis.

It is interesting to note that the majority of records of myxomycetes for Costa Rica have been made during the last 14 years. This is not surprising, considering that this country has been at the forefront of mycological research in Central America for the past two decades. However, it is noteworthy that this research effort has already considered 75% of the forest types recognized for the country. Even though there are still areas that need further investigation, most of the country has already been studied, at least when forest types are considered. In any case, the body of information used to construct the database presented in this paper represents an exhaustive effort made over a period of a number of years. This is obviously reflected in the completeness of the study in terms of

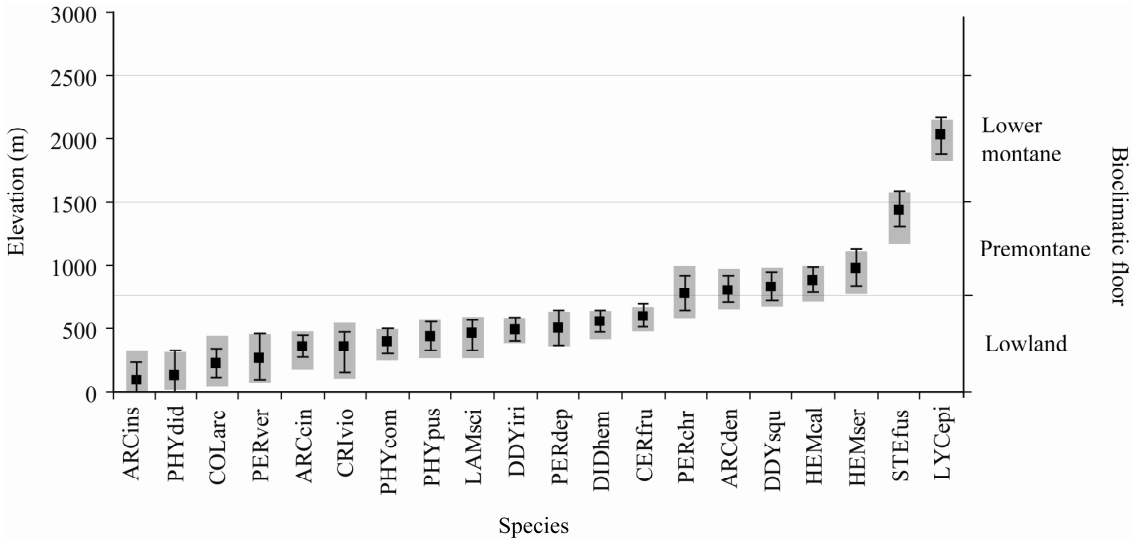

Figure 4. Diagram showing the relationship observed between well represented species of myxomycetes and elevation in Costa Rica. Black squares indicate the average elevation of records, bars show the standard error and gray areas encompass the 95% confidence interval.

Table 2. List of well represented myxomycete species and their relative abundance according to major forest types. For species code see Table 1 and for abundance classification see materials and methods. A = Abundant, C = Common, O = Ocassional and R = Rare. Total number of records included = 3108.

Species code	**Forest type ***										
	PRF	LMRF	MRF	SRP	LWF	PWF	LMWF	LMF	PMF	LMMF	LDF
ARCcin	C	C	R		C	C	R	A	O	R	O
ARCden	R		C			R	R	R	R	R	R
ARCins						R	R	A	R		R
CERfru	O	R	O		R	O	R	R	R	R	O
COLarc	R				O	O		C	R		
CRIvio	R	R			O	R	R	O	R		C
DIDhem	R	O	R		C	C	R	C	O		R
DDYiri	R	O	R		C	C	R	C	R		R
DDYsqu	R	C	O	R	C	C	R	O	O		R
HEMcal	R	R	C	R	O	C	R	C	R	R	R
HEMser	R		O		R	R	R	R	R	R	O

Table 2. Continued

Species code	Forest type *										
	PRF	LMRF	MRF	SRP	LWF	PWF	LMWF	LMF	PMF	LMMF	LDF
LAMsci	R	O	R		O	O		C	R		O
LYCepi		R	C			R	O	R	R		R
PERchr		O	R	R	O	R		O	O		R
PERdep	R		O	R	O	R		C	R	R	O
PERver		R	R		O	R	R	C			O
PHYcom	R	O	R	R	A	C	R	C	O		R
PHYdid	R		R		C	R		C	R		R
PHYpus	R	R	O		O	R	R	A	R	R	R
STEfus		R	O	R	O	R	R	R	O	R	

* PRF = Premontane Rain Forest, LMRF = Lower Montane Rain Forest, MRF = Montaner Rain Forest, SRP = Subalpine Rain Paramo, LWF = Lowland Wet Forest, PWF = Premontane Wet Forest, LMWF = Lower Montane Wet Forest = LMF = Lowland Moist Forest, PMF = Premontane Moist Forest, LMMF = Lower Montane Moist Forest, LDF = Lowland Dry Forest.

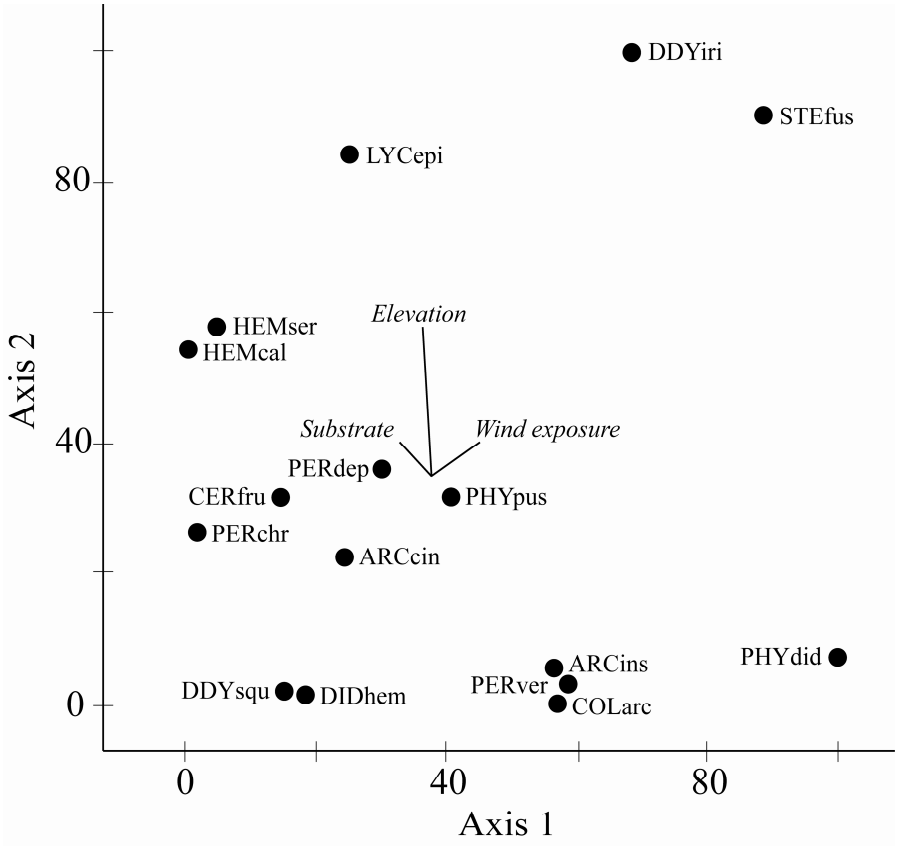

Figure 5. Ordination of records using nonmetric multidimensional scaling (NMS). Circles define the position of species and lines indicate the direction of the most important microenvironmental variables. Abbreviations used for species follow the codes provided in Table 1.

surveyed macro- and microenvironments. Some other studies (e.g., Schnittler & Stephenson 2000, 2002) have already addressed particular ecological situations in Costa Rica; however, a complete analysis for the entire country has never been carried out.

In any case, the fact that more than 50% of the total number of records are made up of species with fewer than 5 records would be interesting to address in the future. It is known that different abundance distributions are associated with different ecological strategies of biological groups (McGill *et al.* 2007).

Forest type and substrate preference

It is interesting to note that species within the same genera show differences at one or both environmental levels. For example, the well represented species recorded in the genus *Arcyria* seem to prefer dead bark and wood over other substrates, although one of the species shows a clear preference for nonwoody substrates. A similar pattern was reported by Stephenson *et al.* (1993) for members of the order Trichiales in the tropical forests of southern India, which is the order in which the genus *Arcyria* is traditionally placed. Similarly, species in the genus *Perichaena*, another member of the Trichiales, were found on different substrates but preferentially in lowland moist forests. This forest type has already been noted as an especially suitable habitat for the genus (e.g., Schnittler & Stephenson 2000).

Another pattern of substrate preference is seen in *C. fruticulosa, S. fusca, L. epidendrum* and all species in the genus *Hemitrichia*. All of the members of this group were found mostly on dead bark and wood. This is clear in Fig 3. For these species, even the multivariate analyses show that the substrate factor is an important factor in

explaining their distribution. Evidently, given the high number of available substrates in tropical regions, it seems that a preference for dead bark and wood in these regions might be associated with broader niches. This is the general trend observed in the niche breadth values shown in Table 1. Interestingly, previous studies have shown broad niches for all of these species in both temperate (e.g., Stephenson 1988) and tropical areas (e.g., Rojas & Stephenson 2007). However, for the first species, this pattern conforms to the recorded substrate preferences across the Neotropical region (Rojas *et al.* 2008).

One of the more noteworthy patterns is displayed by *S. fusca* and *L. epidendrum*, both of which showed a preference for higher elevation forests, which also may be an indication of their preference for cooler, more temperate environments. The same can be said for the group of species that has been found only in high elevation areas. In fact, two of these (*Enerthenema papillatum* and *Leocarpus fragilis*) belong to an ecological group of what have been considered traditionally as "temperate" species. Not surprisingly, Fig 4 shows that elevation is not only an important environmental factor but also a variable that explains the vertical distribution of those species most abundant at high elevations in Costa Rica.

In the same way, the group of species highly associated with ground litter, inflorescences and bryophytes displays a microhabitat distribution pattern that has been observed previously in forest ecosystems in Costa Rica (Schnittler 2001; Schnittler & Stephenson 2000, 2002). However, in contrast to the preference for dead bark and wood, these species are in theory likely to show more narrow niches as a response to their substrate preferences. The evidence provided in this paper partially supports this hypothesis. The narrowest niche, for example, was found in the ground litter inhabitant

Collaria arcyrionema. Although very little information on niche relationships is available for tropical regions, in the high elevation oak forests of Costa Rica, *Didymium squamulosum*, another of the ground litter-inhabiting species, showed a very narrow niche (Rojas & Stephenson 2007).

Paradoxically, most of the species in this ecological group are absent from high elevation forests. Results from multivariate analysis also suggest that lowland forests are important in the vertical distribution of these species. This may be an indication that they somehow depend on the higher litter decomposition rates occurring at lower elevations. For example, in their study of myxomycete communities in different forest types in Costa Rica, Schnittler & Stephenson (2000) found all of the species reported herein that show a preference for ground litter substrates were more abundant on litter from lowland moist forests rather than litter from lowland dry forests. This is interesting because there is evidence showing that the process of decomposition occurs more rapidly in moist tropical forests (Palace *et al.* 2008). Schnittler & Stephenson (2002) observed that both *Physarum compressum* and *Ph. didermoides*, the two most common inflorescence-inhabiting species in their study, were the most abundant species found on inflorescences from all tropical areas for which they had data. In their study, even the preference factor, a form of mathematical algorithm to evaluate the constancy of species growing on inflorescences over litter, was determined as "infinite" (reported as ∞) for *Ph. didermoides*. The exact mechanisms driving the ecology of species of myxomycetes that appear to be restricted to inflorescences in the tropics have not yet been studied carefully, but this does seem to be a clearly apparent pattern found in tropical forests.

What is evident from all of these analyses is that myxomycetes in Costa Rica seem to show patterns of preference for particular macro- and microenvironmental situations. The high levels of preference for forest types and substrates observed for particular species suggest that myxomycetes are not randomly distributed across the country. In fact, what this dataset also suggests is that myxomycetes in Costa Rica show levels of preference for different sets of environmental conditions that drive their distribution in the country in different ways. The fact that this is also apparent when species are analyzed within a given forest type or substrate provides additional support for such a concept. It is true that some forest types have been surveyed more extensively than others, but in practically all cases a given pattern of preference can be observed. It seems possible that the latter situation is an indication that the three important abiotic factors identified in the present study also are major determinants for other Neotropical myxomycete metacommunities.

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Chapter 3

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

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Rojas C, Stephenson SL. 2007. Distribution and ecology of myxomycetes in the high-elevation oak forests of Cerro Bellavista, Costa Rica. Mycologia 99: 534-543.

Abstract: Myxomycetes associated with a high-elevation (>3000 m) oak forest in the Talamanca Range of Costa Rica were studied over a period of seven months. 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 located 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 quite 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 myxogastrids) 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, and 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 levels of environmental moisture (Stephenson *et al* 2004b). Stephenson *et al* (2000) suggested that distribution ranges in myxomycetes can be very 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 or not 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 are often 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 present 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 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 during 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 located 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 general study area range between 3142 and 3230 m above sea level. The forest present 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, since the annual climate of this region of Costa Rica 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 seven months. The laboratory component of the study was carried out during an additional eight months. 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 x 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. In order to minimize any edge 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 allows the researcher to 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 diameter Petri dishes lined with filter paper. Distilled water was added to each dish and the sample material in each culture remained soaked for 24 hours, after which excess water was poured off. Cultures were examined every week for approximately four months.

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, located 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 upon 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 ten subplots of 10 x 10 m, and these were further subdivided into four 5 x 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 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 upon which fruitings occurred. Within 24 hours of returning from the field, these samples were weighed and then placed in a constant temperature oven for 72 hours at 65 C. After this period, 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 effect 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– < 1.5% as occasional

and those less than 0.5% as rare (Stephenson *et al* 1993). A nonmetric multidimensional scaling ordination (NMS) was performed using the numeric microenvironmental variables for only the species classified as abundant. This ordination was carried out using 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 was also 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 using 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 during the entire study (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 1.09 and 1.30, respectively; 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). Interestingly, pH values above 4.5 are absent when height above the ground reaches 1 m (pH versus 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 versus 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 versus 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*

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
Arcyria cinerea (Bull.) Pers.	O	2 /0	4.25 (0.20)	72.50	23.50	
Arcyria denudata (L.) Wettst.	R	1/0	4.30 (NA)	5.00	6.00	
Arcyria leiocarpa (Cooke) Martin & Alexop.	O	3/0	4.67 (0.35)	108.33	26.33	
Ceratiomyxa fruticulosa (Mull.) Macbride	A	19/0	4.67 (0.76)	34.47	6.89	CERfru
Clastoderma debaryanum Blytt	C	5/0	4.72 (0.37)	10.00	18.40	
Comatricha pulchella (Bab.) Rostaf [a]	C	4/0	4.23 (0.91)	5.00	6.75	
Comatricha tenerrima (Curtis) G. Lister	O	2/0	4.90 (0.84)	5.00	3.00	
Cribraria intricata Schrad.	C	6/0	4.30 (0.42)	57.50	25.67	
Cribraria mirabilis (Rostaf.) Massee [b]	A	15/0	4.58 (0.58)	50.00	16.60	CRImir
Cribraria piriformis Schrad.	A	20/0	3.90 (0.79)	31.20	20.40	CRIpir

TABLE I. Continued

Species	Abundance	NF/MC	pH (SD)	HAG	SubD	Abbreviation
Cribraria vulgaris Schrad.	A	14/0	3.83 (0.70)	68.57	18.64	CRIvul
Diacheopsis sp. [c]	R	1/0	4.40 (NA)	150.00	20.00	
Diderma chondrioderma (de Bary & Rostaf.) G.Lister	R	1/0	6.90 (NA)	5.00	7.00	
Diderma sp.	O	2/0	5.75 (1.09)	5.00	4.00	
Didymium dubium Rostaf. [b]	R	0/1	NA	NA	NA	
Didymium squamulosum (Alb. & Schwein.) Fr.	A	9/0	5.80 (1.08)	5.22	1.67	DDYsqu
Hemitrichia calyculata (Speg.) Farr	A	9/0	4.97 (0.58)	20.00	10.33	HEMcal
Hemitrichia serpula (Scop.) Rostaf. ex Lister	A	0/7	NA	NA	NA	HEMser
Lamproderma columbinum (Pers.) Rostaf. [b]	A	12/0	4.21 (0.58)	27.50	20.50	LAMcol
Lamproderma cribrarioides (Fr.) R.E.Fr. [b]	O	3/0	4.70 (0.69)	6.67	18.00	
Lamproderma echinulatum (Berk.) Rostaf. [b]	C	5/0	4.88 (0.79)	25.00	29.00	
Lamproderma sauteri Rostaf. [b]	R	1/0	4.60 (NA)	5.00	5.00	
Leocarpus fragilis (Dicks.) Rostaf. [b]	O	2/0	6.15 (0.63)	30.00	9.50	
Lycogala epidendrum (L.) Fr.	A	10/0	5.52 (0.87)	16.40	7.95	LYCepi

TABLE I. Continued

Species	Abundance	NF/MC	pH (SD)	HAG	SubD	Abbreviation
Metatrichia floriformis (Schwein.) Nann.- Bremek.	A	13/0	5.52 (0.72)	7.62	14.00	METflo
Perichaena depressa Lib.	R	0/1	NA	NA	NA	
Physarum brunneolum (Phillips) Massee [b]	R	1/0	4.70 (NA)	100.00	10.00	
Physarum contextum (Pers.) Pers. [a]	R	1/0	5.80 (NA)	5.00	10.00	
Physarum leucopus Link	R	1/0	6.50 (NA)	80.00	4.00	
Physarum melleum (Berk. & Broome) Massee	R	0/1	NA	NA	NA	
Stemonitis fusca Roth	O	2/0	5.35 (0.07)	32.50	45.00	
Stemonitis smithii Macbride	O	4/0	5.28 (0.18)	11.25	10.25	
Stemonitopsis hyperopta (Meyl.) Nann.- Bremek.	O	3/1	4.10 (0.36)	48.33	6.67	
Trichia botrytis (Gmel.) Pers.	A	10/0	4.30 (0.51)	74.50	7.80	TRIbot
Trichia decipiens (Pers.) Macbride	O	3/0	4.77 (0.32)	30.00	10.00	
Trichia favoginea (Batsch.) Pers.	A	7/1	4.41 (1.09)	32.14	22.00	TRIfav
Trichia verrucosa Berk.	A	8/0	4.95 (1.32)	34.38	11.31	TRIver

[a] New record for Costa Rica, [b] New record for Central America, [c] New record for the Neotropics

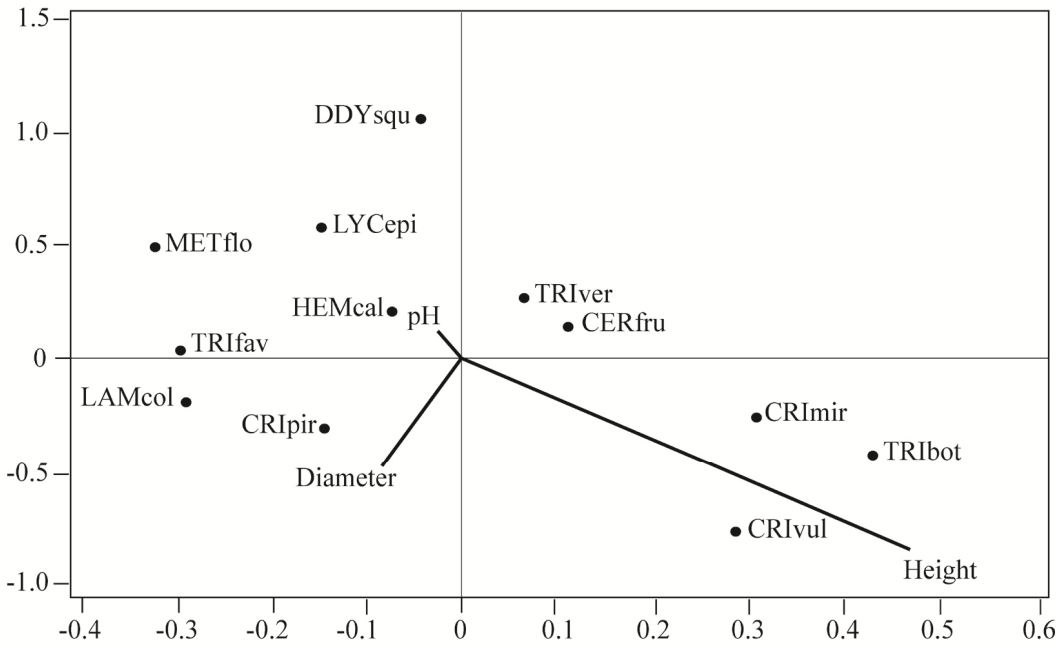

Figure 1. Ordination of species and microenvironmental variables using nonmetric multidimensional scaling (NMS). Points define the abundant species. Lines indicate the direction and strength of the most important microenvironmental variables. For abbreviations used for species see TABLE I.

floriformis seem to group together both for high pH and lower heights. These species also differ from the other taxa in their relatively high values for substrate pH (F=8.00, d.f.=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. Interestingly, 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 (χ^2=31.7, d.f.=8, $P <$ 0.0001), with logs and twigs more commonly recorded during the dry season and logs and bryophytes during the rainy period.

Interestingly, the only macroenvironmental factor that appears to have an important influence on the occurence of myxomycetes is precipitation, which had a inverse but significant correlation with the number of fruitings recorded (FIG. 2, precipitation versus 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 versus number of fruitings, Pearson's product moment = 0.95, $P < 0.05$). A significant relationship was not observed when the number of species was considered (precipitation and temperature versus 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 were invariably absent during the rainy period, or *Didymium* and *Leocarpus*, never recorded for the dry season. When the

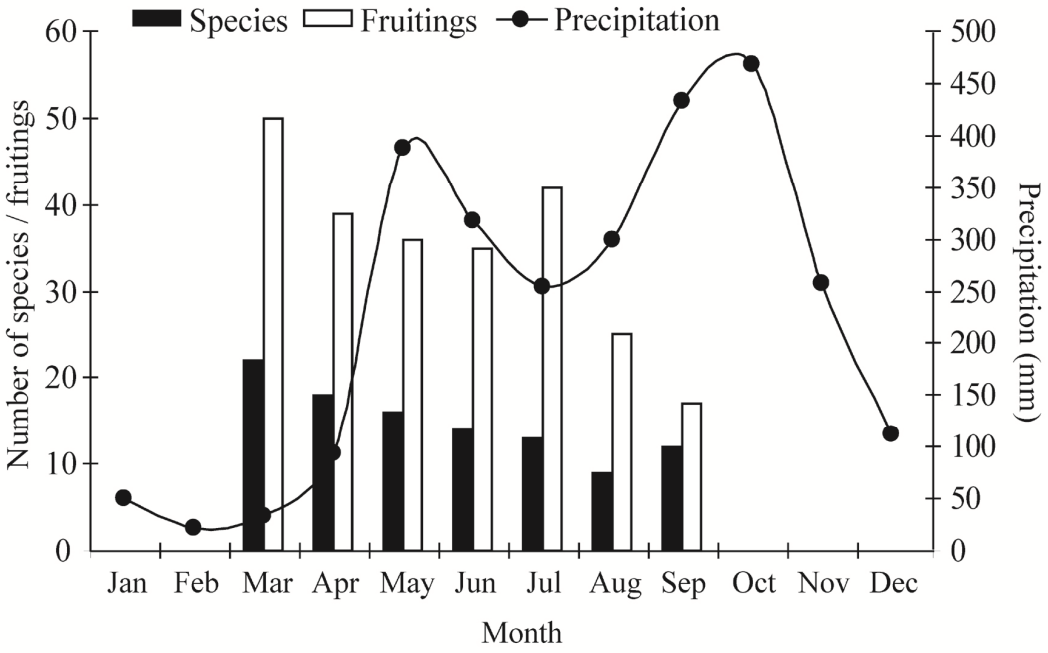

Figure 2. Numbers of species and fruitings recorded during seven months of field work in the current study. The line indicates the average value of monthly precipitation for Cerro Bellavista, based on data provided by the National Weather Institute in Costa Rica.

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. Note: NB=Niche Breadth.

Species	**NB**	**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												***

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. However, the actual correlation is extremely weak (niche breadth versus 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 ($F=14.5$, d.f=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 ($F=5.07$, d.f=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 ($F=1.20$, d.f.=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 & Stephenson 2000, Stephenson *et al* 2004a). However, limiting the study to selected substrates may have underestimated the actual number of taxa present. Recently, Schnittler (2001a) and Schnittler and Stephenson (2002) have described new microhabitats for myxomycetes in the Neotropics, and unpublished data suggest that a number of others probably exist.

Preliminary surveys of the general 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 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 present 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). Interestingly, the assemblage at Cerro Bellavista is dramatically poor in terms of the number of species per genus, which 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 in Fig. 1.

When pH values are compared, it is clear that most substrates at Cerro Bellavista are only slightly more acidic (values from 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 very 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 may 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). Interestingly, 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 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 versus 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.— Recent 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 elevation (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. Interestingly, this species was one of the most abundant myxomycetes in the present study.

Leocarpus fragilis, another species typical of temperate regions, was also recorded at Cerro Bellavista. This species was collected previously (Martin Schnittler, unpublished data) in the paramo of the Cerro Chirripó (ca. 3700 m). Both mountains are located in the Talamanca region and represent two of the highest peaks in Costa Rica, which suggests that *L. fragilis* may be restricted to high elevation areas 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. Many 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 since 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 a relatively high water content for most substrates throughout the entire year.

Substrate diameter is another important variable as shown in FIG. 1. This is not surprising either, especially when it is very obvious that most of the twigs and lower diameter logs are associated with the ground level. For example, Schnittler *et al* (2006) did not find these factors to 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 the 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. Interestingly, 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. Interestingly, 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 presented in FIG. 2 seem to indicate that the sporulation patterns of myxomycetes in the study area are intimately linked with precipitation levels. 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, since water often is not a limiting factor. Interestingly, 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. Apparently, more than one environmental factor 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 of time. However, the effect of horizontal precipitation in high elevation areas in the tropics is known to be correlated with temperature, since 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 levels of environmental humidity are associated with high horizontal precipitation and high levels of precipitation recycling (Dominguez *et al* 2006). Results

obtained in the present study seem to indicate that myxomycete fruitings increase in number as precipitation levels drops and decrease with increasing levels of 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 or not the niche breadth values obtained 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. Interestingly, 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 produced contain 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 using 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 of these similar values would seem to be that they reflect a common ecological strategy. In fact, it appears that the assemblage of myxomycetes present consists of a majority of generalist species and very 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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Chapter 4

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

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Rojas C, Stephenson SL. 2008. Myxomycete ecology along an elevation gradient on Cocos Island, Costa Rica. Fungal Diversity 29: 117-127.

Abstract: 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

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 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 5º30'06" to 5º33'26" N and longitudes 87º05'46" to 87º01'47" W and is within the Costa Rican continental waters

jurisdiction (Montoya, 2006). 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 cattapa* 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 occidentales*, *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 holdridge*, *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 holdridge* 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 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 bombarda*, 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 $y = ax/(b+x)$ 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

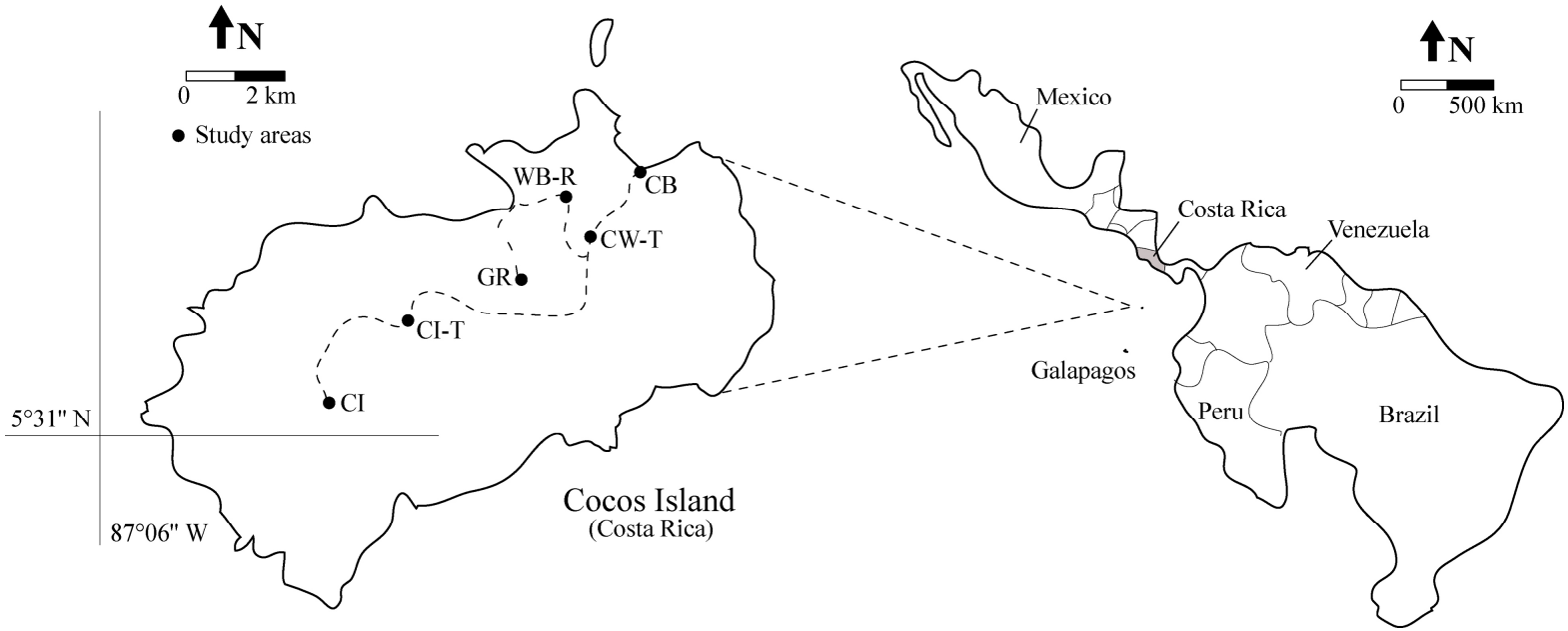

Figure 1. Geographical location of Cocos Island in the eastern Pacific (right) and a detailed map of the trail system and study sites used in the present investigation. Abbreviations used for study sites are explained in Material and Methods.

Table 1. Species of myxomycetes recorded from Cocos Island and ecological parameters associated with the species in question. Note: A = Abundant, C = Common, O = Ocassional, 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]
Arcyria afroalpina Rammeloo	R	0/1	3.61 (NA)	575
Arcyria cinerea (Bull.) Pers.	A	0/56	4.91 (1.21)	10-575
Arcyria minuta Buchet	C	0/4	6.34 (1.34)	10
Clastoderma debaryanum A. Blytt.	C	0/5	5.71 (1.55)	10-400
Clastoderma pachypus Nann.-Bremek.	R	0/2	4.27 NA)	400
Collaria arcyrionema (Rostaf.) Nann.-Bremek. ex Lado	A	0/20	6.04 (0.96)	10-150
Collaria lurida (Lister) Nann.-Bremek.	C	0/7	4.28 (1.62)	10-250
Comatricha elegans (Racib.) G.Lister	C	0/5	6.21 (0.85)	10-150
Comatricha laxa Rostaf.	R	0/1	3.33 (NA)	250
Comatricha nigra (Pers. ex J.F.Gmel.) J.Schröt.	O	0/3	3.94 (1.19)	150-575

Table 1. Continued

Comatricha pulchella (C.Bab.) Rostaf.	C	0/7	4.65 (1.21)	10-400
Comatricha tenerrima (M.A.Curtis) G.Lister	A	0/9	6.11 (1.01)	10-575
Craterium aureum (Schumach.) Rostaf.	R	0/1	6.14 (NA)	150
Cribraria intricata Schrad.	R	1/0	NA	150
Cribraria microcarpa (Schrad.) Pers.	A	0/22	4.84 (0.80)	10-575
Cribraria violacea Rex	A	0/12	7.06 (0.78)	10-100
Diachea leucopodia (Bull.) Rostaf.	C	4/3	5.43 (0.71)	10
Diderma effusum (Schwein.) Morgan	A	0/10	5.14 (1.50)	10-575
Diderma hemisphaericum (Bull.) Hornem.	R	0/1	5.90 (NA)	150
Didymium iridis (Ditmar) Fr.	O	0/3	5.88 (0.73)	10
Didymium minus (Lister) Morgan	R	0/1	5.29 (NA)	150
Didymium squamulosum (Alb. & Schwein.) Fr.	C	0/5	5.99 (1.31)	10-150
Echinostelium minutum de Bary	R	0/1	4.27 (NA)	400

Table 1. Continued

Echinostelium minutum de Bary	R	0/1	4.27 (NA)	400
Hemitrichia minor G.Lister	O	0/2	4.64 (2.24)	10-250
Hemitrichia serpula (Scop.) Rostaf. ex Lister	O	1/2	4.92 (0.17)	10-575
Lamproderma scintillans (Berk. & Broome) Morgan	C	0/5	6.17 (0.36)	10-150
Licea sp.	O	0/2	5.29 (0.65)	100-150
Macbrideola scintillans H.C.Gilbert	R	0/1	4.02 (NA)	100
Perichaena chrysosperma (Curr.) Lister	A	0/10	7.10 (0.39)	10
Perichaena depressa Lib.	A	0/10	6.12 (0.97)	10-150
Perichaena pedata (Lister & G.Lister) Lister ex E.Jahn	R	0/1	4.97 (NA)	400
Physarum compressum Alb. & Schwein.	O	0/2	7.44 (0.02)	10
Physarum javanicum Racib.	R	0/1	6.35 (NA)	10
Physarum melleum (Berk. & Broome) Massee	C	6/0	NA	10
Physarum pusillum (Berk. & M.A.Curtis) G.Lister	R	0/1	6.62 (NA)	150

Table 1. Continued

Physarum serpula Morgan	O	0/2	6.45 (1.21)	10
Physarum superbum Hagelst.	R	0/1	7.43 (NA)	10
Stemonitis flavogenita E.Jahn	R	0/1	6.05 (NA)	10
Stemonitis fusca Roth	A	0/8	5.59 (0.90)	10-150
Stemonitopsis hyperopta (Meyl.) Nann.-Bremek.	R	1/0	NA	10
Tubifera bombarda (Berk. & Broome) G. W Martin	R	1/0	NA	150

[a]mean pH of the moist chamber cultures in which the species was recorded

[b]elevation (m) or range of elevations over which a species was recorded

different substrates indicate that 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 values obtained 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 = -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, $\chi^2 = 4.43$, gl = 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.

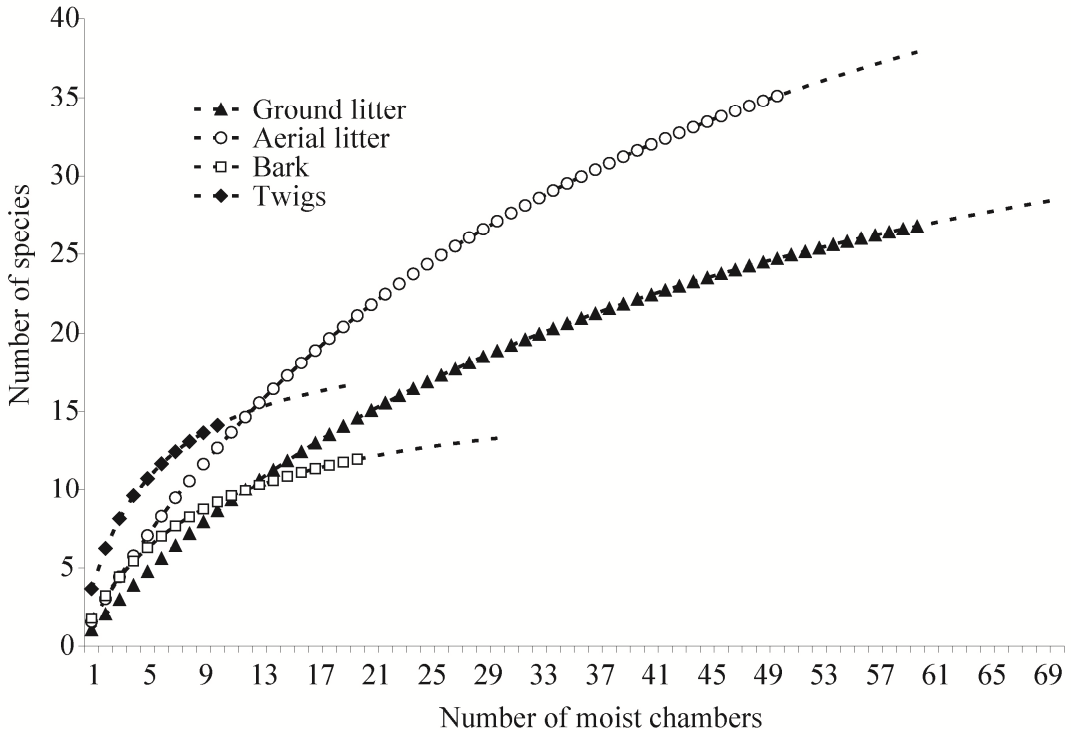

Figure 2. Species accumulation curves for the assemblages of myxomycetes associated with the four different types of substrates investigated. In each instance, the dashed line represents a prediction of the curve using the modified equation obtained from the ACE values. The calculated maximum values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

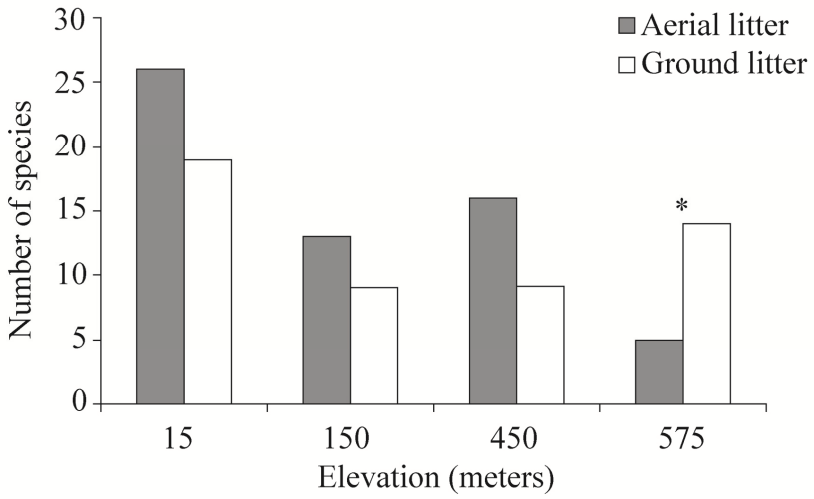

Figure 3. Number of species by substrate type in relation to elevation for both ground litter and aerial litter where the two types of litter were collected equally. The asterisk indicates a statistically significant relationship.

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 arcyrionema* 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

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	***

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*., 2007b) of the myxomyetes 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*., 2007a). 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*., 2007a). 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

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Chapter 5

Microhabitat and niche separation in species of *Ceratiomyxa*

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Abstract: The eumycetozoan genus *Ceratiomyxa* appears to have a cosmopolitan distribution, although two of the three macroscopic species within the genus have been reported only from tropical regions of the world. In theory, these two tropical species might be expected to display more narrow niches than their cosmopolitan counterpart, due to their specialization for tropical environments. However, ecological data documenting niche separation in eumycetozoans are largely lacking. As part of several investigations carried out in the Neotropics, the ecology of the three macroscopic species of *Ceratiomyxa* was studied. The results from in situ measurements of environmental factors associated with their fructifications reveal a clear separation of niches between the two tropical species, which may be an indication of resource partitioning within the genus. As expected in theory, the cosmopolitan *C. fruticulosa* shows the broadest niche

of the three species. Moreover, the niche overlap value between *C. morchella* and *C. sphaerosperma* along with results from a multivariate CDA analysis seem to indicate that these two species are more specialized than *C. fruticulosa*.
Key words: community ecology, Eumycetozoans, niche overlap, Neotropics, resource partitioning

Introduction

The eumycetozoans are a group of amoeboid protists (Fahrni et al 2003) whose life cycle includes the particular capacity to produce spores and spore-holding structures during their reproductive stages (Alexopoulos 1996). The three different taxonomic groups recognized for the eumycetozoans are the myxomycetes (plasmodial slime molds or myxogastrids), the dictyostelids (cellular slime molds) and the protostelids (Adl et al 2005). Although the genus *Ceratiomyxa* has been considered as a protostelid slime mold (Olive 1970), most researchers treat it as a myxomycete (e.g., Tran et al 2006, Stephenson et al 2008). In fact, recent molecular analyses suggest that there is strong support showing that the genus is a sister group to the myxomycetes and not to the protostelids (Fiore-Donno et al 2007). Interestingly, three out of the four species making up the genus have a macroscopic habit and resemble myxomycetes both morphologically and ecologically.

Although the genus *Ceratiomyxa* is widely distributed, only the most common species *C. fruticulosa* has a cosmopolitan distribution. The other two macroscopic species appear to be restricted to the tropics (Stephenson et al 2008), where they also seem to be less abundant than *C. fruticulosa*. A high degree of specialization has been documented

in *C. sphaerosperma* (Novozhilov et al 2001); however, a proper niche analysis for all the macroscopic species in the genus has not yet been carried out. In fact, there have been few previous studies of this type for any species of eumycetozoans (e.g., Stephenson 1988, Schnittler 2001). The problem inherent in doing such an analysis is that without enough ecological information about the species, it is hard to construct an adequate experimental design to evaluate these aspects.

In the past, most studies involving *Ceratiomyxa* have had a strictly taxonomic approach (Olive 1970, Olive and Stoianovitch 1979, Scheetz et al 1980), with no real considerations of ecology. However, the increasing number of biogeographical studies of myxomycetes over the last decade (reviewed in Stephenson et al 2004b) has provided evidence that the three macroscopic species have different geographical distributions, both at the world and at the ecosystem level. Presumably, the differences in distribution noted for closely related organisms result from differential responses to intrinsic ecological properties such as their ability to colonize particular substrates or utilize different resources available in their immediate environment. When this phenomenon occurs, it is often hypothesized that there is a higher niche overlap in species that are closely related phylogenetically (e.g., intrageneric taxa) than in less closely related species (Morin 1999). Unfortunately, the effect of biotic interactions among sympatric species is still poorly understood for eumycetozoans. For that reason, this project was designed to provide a body of data on niche overlap and resource partitioning in *Ceratiomyxa* in an effort to evaluate niche breadth and overlap among the species within the genus.

Materials and Methods

This study described herein includes data collected during the ten-year period 1998-2008 in several Neotropical countries. Only data on *Ceratiomyxa fruticulosa*, *C. morchella* and *C. sphaerosperma* (abbreviated as CERfru, CERmor and CERsph, respectively) are considered in this paper. The morphological species concept was used to identify the three macroscopic intrageneric forms currently recognized in the genus *Ceratiomyxa* (FIG 1), the nomenclature used follows Hernández-Crespo and Lado (2005) and the forest classification system is that of Holdridge et al (1971).

Study sites.— The data considered herein were collected in 14 different study areas across the Neotropics. For those areas in which collections were made in different study sites within the general study area, a georeference centroid for the geographic location, rather than the exact location, is provided. Two of the surveyed areas are in South America. (1) Los Amigos Biological Station (in the rest of this paper referred to as Los Amigos, exact coordinates: 12°34'09.0" S, 70°06'00.4" W, elevation 200-300 m) in the southern Amazonia of Peru. This area is administrated by Amazon Conservation Association and is located in the Department of Madre de Dios in the watershed of the Los Amigos River, between Manu National Park and the city of Puerto Maldonado in the middle of one of the world's biodiversity hotspots. The forests of this area are classified as lowland tropical wet forests. (2) Yasuní National Park (Yasuní, collecting area centroid coordinates: 0°40'16.80" S, 76°23'25.20" W, elevation 200-300 m) in the northeastern Amazonia of Ecuador in the province of Orellana. This other area of high diversity is characterized by lowland tropical wet forests. (3) Maquipucuna Cloud Forest Reserve (Maquipucuna, collecting area centroid coordinates: 0°6'08.40" N, 78°37'4.20"

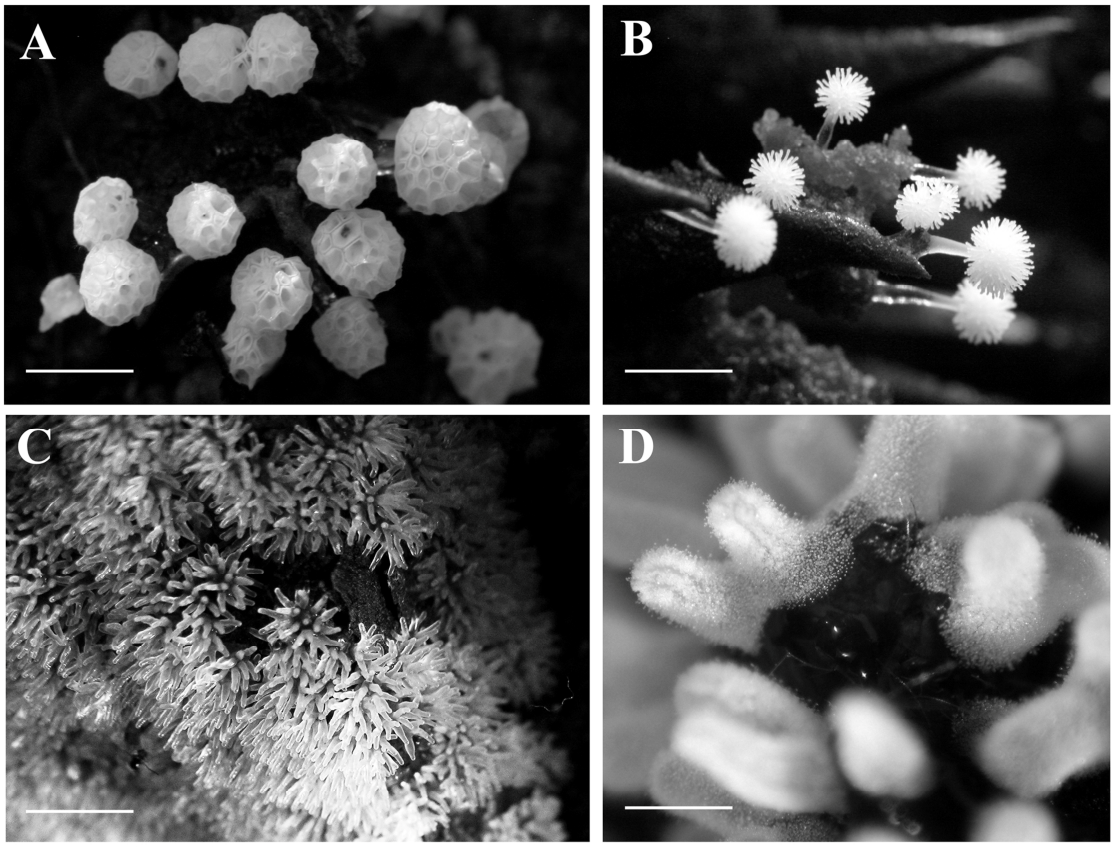

FIGURE 1. Typical morphology of the fructifications produced by the three macroscopic species of *Ceratiomyxa*. A, fructifications of *C. morchella*; B, fructifications of *C. sphaerosperma*; C, columnoid form of the fructification of *C. fruticulosa* and D, detail of the columns in *C. fruticulosa*. Scale bar represents 3 mm in A and B, 20 mm in C and 4 mm in D.

W, elevation 1200-2700 m) on the western slope of the Ecuadorian Andes in the provice of Pichincha. In this area, due the elevational and precipitation gradients, both premontane tropical wet forests and lower montane tropical moist forests are present, depending on the elevation. A complete description of this area is provided by Schnittler et al (2002).

The study areas in Central America are all located in Costa Rica and include the three biological stations of the Organization for Tropical Studies. (4) Las Cruces Biological Station (Las Cruces, exact coordinates: 8°47'12.00" N, 82°57'16.80" W, elevation 1000-1100 m) located in the Panamanian border on the southern Pacific coastal range of Costa Rica in the vicinity of the town of San Vito in the province of Puntarenas. The forests in this study area are premontane tropical wet forest. (5) La Selva Biological Station (La Selva, exact coordinates: 10°25'51.75"N, 84° 0'14.08"W, elevation 50-80 m) in northeastern Costa Rica. La Selva is located in the province of Heredia near the town of Puerto Viejo de Sarapiquí, and the forests are classified as lowland tropical wet forests. (6) Palo Verde Biological Station (Palo Verde, exact coordinates: 10°20'42.54"N, 85°20'18.18"W, elevation 5-20 m) in the north pacific region of Costa Rica. This station is located within the territory of the Palo Verde National Park near the town of Bagaces in the province of Guanacaste. The forests are classified as lowland tropical dry forests and are characterized by a definite seasonality, which is influenced mainly by the precipitation regime.

Other study areas in Costa Rica were located throughout the country. (7) Cahuita (Cahuita, exact coordinates: 9°45'16.20"N, 82°52'6.60"W, elevation 5-20 m). This area corresponds to a coastal town on the south Caribbean coast of Costa Rica in the vicinity

of the Cahuita National Park in the province of Limón. The forests here are represented by lowland tropical wet forests. (8) Cerro de la Muerte Biological Station (Cerro, exact coordinates: 9°33'53.00"N, 83°44'32.00"W, elevation 3200-3300 m) in the highest elevations of the Talamanca Range in central southern Costa Rica in the province of San José. A complete description of this area is provided by Rojas & Stephenson (2007). The forests of these mountains are classified as montane tropical moist forests. (9) Monteverde Cloud Forest Reserve (Monteverde, collecting area centroid coordinates: 10°17'9.60"N, 84°46'14.40"W, elevation 800-1500 m), part of the Tilarán Range along the Pacific coast in central northern Costa Rica in the province of Puntarenas. This area, near the town of Santa Elena, encompasses one of the most famous cloud forests in the world in which the systematic study of its biodiversity has played a key role in the understanding of the climate change effect over tropical areas. According to the Holdridge life zone system the ecosystems present are characterized by premontane tropical wet forests.

The northwestern province of Guanacaste in Costa Rica was represented by three study areas (see Schnittler & Stephenson 2000 for details). (10) Santa Rosa National Park (Santa Rosa, collecting area centroid coordinates: 10°50'37.80"N, 85°36'45.00"W, elevation 250-300 m) near the city of Liberia. This area is characterized by lowland tropical dry forests with high degree of seasonality. (11) Maritza Biological Station (Maritza, collecting area centroid coordinates: 10°56'60.00"N, 85°29'18.00"W, elevation 600-700 m), located in the northernmost section of the Guanacaste range in Costa Rica; on the western slope of the Orosí volcano. The forests in this area are tropical premontane transitional wet forests showing the seasonal influence of the lower elevation dry forests

and the upper elevation wet forests. (12) Cacao Biological Station (Cacao, collecting area centroid coordinates: 10°55'21.00"N, 85°28'4.80"W, elevation 1100-1200 m) on the western slope of the Cacao volcano. The forests in this area correspond to tropical premontane transitional wet forests as well. However, this place is associated with a higher precipitation than the Maritza Biological Station area.

The northernmost study areas were located in Puerto Rico and the Yucatan of Mexico. (13) El Verde Field Station (El Verde, exact coordinates: 10°50'37.80"N, 85°36'45.00"W elevation 350-450 m) in the municipality of Luquillo in northeastern Puerto Rico. This area shows the typical lowland tropical wet forests of most of the Caribbean. However, the sampled area corresponds to the so-called tabonuco forest dominated by the palm Dacryodes excelsa Vahn. A complete description of this area is provided by Stephenson et al (1999). (14) El Eden Ecological Reserve (El Eden, collecting area centroid coordinates: 21°12'44.40"N, 87°11'43.20"W, elevation 5-10 m) located in the state of Quintana Roo in southeastern Mexico. This area is characterized by having lowland tropical dry forests with a very strong seasonal effect provided by the high precipitation coming from the Atlantic Ocean during part of the year. A complete description of this area is provided by Lado et al (2003).

Sampling.— In all study areas, the opportunistic method of collecting recommended for microscopic fungi by Cannon and Sutton (2004) was applied. Using this protocol, a thorough survey for fructifications was made on decayed logs, twigs and fruits along some of the trails that are present in all of the specific study sites. The selection of the trails to be surveyed was based on the overall characteristics of the forest and for the case of Los Amigos, La Selva and Palo Verde, determined by using the GIS-

based forest coverage maps present at these stations. In all cases, the ecosystem type (ET) was defined as the forest type already mentioned for each study area according to the Holdridge life zone system and the forest subtype (FT) was determined as primary, secondary and disturbed depending upon the overall appearance and known ecological characteristics such as vertical structure, canopy openness and plant composition.

Microhabitats.— In order to evaluate both direct and multivariable responses of the species to their environment, a series of microenvironmental parameters was measured or determined directly in the field when fructifications were found. These microenvironmental parameters included pH, substrate moisture (SM), substrate type (ST), diameter or thickness of the substrate (DS) as an index of substrate mass, height above the ground (HAG) and canopy openness (CO) as a way to evaluate light availability. The first and second parameters were measured using a calibrated pH meter and an electronic moisture meter when possible, whereas the other parameters were determined as described in Stephenson et al (2004a). With this commonly used protocol, the level of light availability is assessed with a system that uses five discrete categories and can be easily transformed into a standard percentage scale comparable to the readings obtained with the moisture meter. In addition, the categorical arrangement used for ecosystem type and forest subtype was considered part of the microenvironmental setting.

Classification of non-continuous parameters.— For non-continuous parameters an ordinal classification of records was determined by using a series of ecological categories (sensu Stephenson 1988) developed specifically for each parameter. With this approach, the ecosystem type (ET) was ordered using categories based upon increasing levels of precipitation and elevation. These were (1) basal floor dry forest, (2) basal floor

transitional wet forest, (3) premontane floor transitional wet forest, (4) premontane floor wet forest, (5) lower montane floor moist forest and (6) montane floor moist forest. In a similar fashion, the forest type (FT) was classified according to the level of human disturbance, which ranged from (1) pristine primary forests to the (2) secondary and (3) disturbed areas. The substrate type (ST) classes were ordered in five categories that included (1) bark, (2) wood, (3) leaves, (4) herbaceous material and (5) fruits and seeds.

Data analysis.— A classification of records on the basis of their occurrence in the study areas (communities) was estimated using the Bray-Curtis distance measure with the program PAST (Hammer et al 2001) for those areas with the three species present. This estimator, commonly used to evaluate similarity, is sensible to low numbers for some of the species in the communities under study and is very robust for small datasets (Clarke et al 2006). The values obtained with this estimator range from 0 in case of total correspondence of abundances of both positive and negative matches to 1 in case of total dissimilarity. In addition to this analysis, a comparison of the abundance of the three species according to forest subtype was also carried out for the whole dataset using the Pearson's algorithm for the Chi-square test.

In order to evaluate the formal structure of the records for each species in the hyperspace constructed from the data for the various microenviromental parameters and the importance of the latter for the distribution of records, a Canonical Discriminant Analysis (CDA) and a Principal Components Analysis (PCA) were performed using the program PC-Ord, version 5.11. The former type of analysis is appropriate to discriminate groups and determine the contribution of variables in datasets that have a b number of sampling units containing a c number of non-overlapping groups, whereas the second is

useful to determine the relative importance of those variables in the multidimensional spatial ordination (Kenkel et al 2002). These analyses were carried out by considering the six direct microenvironmental parameters mentioned already in addition to ecosystem type and forest subtypes.

Also, the same first six microenvironmental variables were used to evaluate the niche breadth and the niche overlap of the three species. For this part of the analysis, the estimators were obtained by using the MacArthur-Levins (MacArthur and Levins 1967) approach in the manner described by Stephenson (1988). The niche overlap was also calculated by using the Shannon-Wiener Communication Theory formula (Shannon and Weaver 1949) as a way to compare the overlap between species when the niche breadth is not taken into account. This is important when it is considered that the biological interpretation of the overlap in a multivariate analysis depends upon the characteristics of the parameter distributions. For that reason, these parametric analyses were also performed, following the recommendations of Stine and Heyse (2001).

Results

A total of 408 records of *Ceratiomyxa* were recorded from the field surveys. *Ceratiomyxa fruticulosa* was the single most common species, representing 77% of the total number of records, with *C. morchella* and *C. sphaerosperma* contributing 15% and 8%, respectively. The three species co-occurring at the same time were recorded only for Los Amigos, Yasuní and Monteverde, with the last one being the only non-lowland tropical moist forest with all occurrences. Interestingly, the values of the Bray-Curtis distance estimates were 0.78, 0.67 and 0.23 for the pairwise combinations Monteverde-

Yasuní, Monteverde-Los Amigos, Yasuní-Los Amigos, respectively. These were the only study areas for which all three species were present.

The three species were found in the three subtypes of forest; however, there are differences in the relative abundance at which they seem to occur in each type. For example, *C. fruticulosa* is found more frequently than the other two species in secondary forests and this factor seems to account for the overall differences in their occurrence (χ^2 = 33.95, g.l. = 4, P < 0.0001). When the records of *C. morchella* and *C. sphaerosperma* are compared independently from those of *C. fruticulosa*, the former two species do not differ in their occurrence (χ^2= 1.26, g.l. = 2, P > 0.05). Interestingly, all species were found in similar proportions in disturbed areas. When the preferred substrates for each of the species are considered, it is very clear that both *C. fruticulosa* and *C. morchella* seem to have preference for decaying wood. For these two species, >90% of the observations were recorded on the latter substrate. That is not the case for *C. sphaerosperma*, for which approximately 87% of the records were found on herbaceous substrates.

The CDA analysis in FIG. 2 shows a separation of the *C. morchella* and *C. sphaerosperma* two-dimensional hyperspaces. However, it also shows that their respective hyperspaces are contained almost entirely within the much more extensive hyperspace of *C. fruticulosa*. The PCA analysis in FIG. 3 shows that the most important microenvironmental parameters appear to be substrate type, pH and diameter of the substrate, respectively. With exception of canopy openness, all microenvironmental parameters showed significant differences (not shown) among the three species. The data presented in TABLE I summarize the range and average values for these parameters.

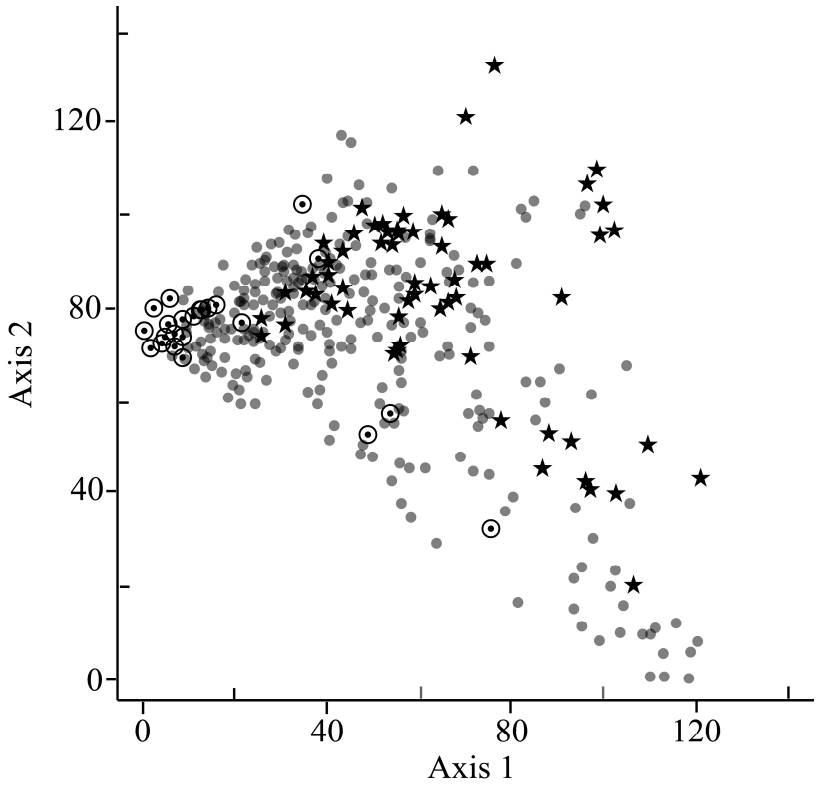

FIGURE 2. Canonical Discriminate Analysis ordination that shows the two dimensional hyperspaces occupied by the three species of *Ceratiomyxa*. Note: gray circles = *C. fruticulosa*, black stars = *C. morchella* and black circles with enclosed points = *C. sphaerosperma*. For abbreviations see Materials and Methods.

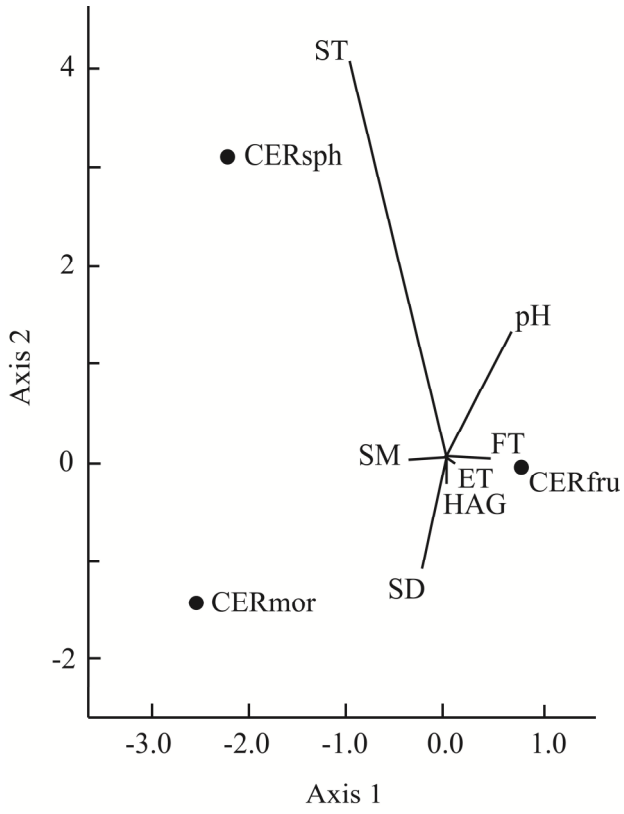

FIGURE 3. Principal Component Analysis diagram showing the position of the three species of *Ceratiomyxa* in the hyperspace constructed with the microenvironmental variables. Note: ET = ecosystem type, FT = forest subtype. For other abbreviations see Material and Methods.

TABLE I. Range and average values (in parentheses) for five of the microenvironmental parameters obtained for the three species of *Ceratiomyxa*. For abbreviations see Materials and Methods.

Species	pH	SM (%)	SD (cm)	HAG (cm)	CO (%)
CERfru	3.03 – 8.85 (5.67)	23 – 100 (68)	1 – 150 (25)	0.0 – 25.0 (3.7)	8.3– 100.0 (48.0)
CERmor	2.98 – 5.99 (4.06)	27 – 100 (77)	8 – 150 (46)	0.5 – 19.0 (4.3)	30.0 – 70.0 (45.4)
CERsph	2.88 – 8.29 (6.38)	35 – 100 (78)	0 – 30 (5)	0.0 – 12.0 (1.2)	25.0 – 80.0 (46.4)

TABLE II. Niche breadth and niche overlap values for the species of *Ceratiomyxa* recorded at the study sites. Just one value per species pair is shown. The first value corresponds to the MacArthur-Levins calculation and the value in parenthesis to the Shannon-Wiener estimate. For abbreviations refer to Materials and Methods.

Species	Niche breadth	Species and niche overlap values		
		CERfru	CERmor	CERsph
CERfru	4.50	***	0.96 (0.96)	0.70 (0.70)
CERmor	4.30		***	0.64 (0.56)
CERsph	3.40			***

The niche breadth and overlap values obtained with the MacArthur-Levins and Shannon-Wiener protocols are shown in TABLE II. The inclusion of niche breadth in the first case does not have a significant effect on the calculated values for either algorithm (χ^2= 6.60, g.l. = 4, P > 0.05). *Ceratiomyxa fruticulosa* shows the broadest niche, closely followed by *C. morchella* and *C. sphaerospema*. Similarly, the highest niche overlap occurs between *C. fruticulosa* and the other two species and the lowest value is associated with the combination *C. morchella – C. sphaerosperma*. Niche overlap is higher between *C. fruticulosa* and *C. morchella* than between the former and *C. sphaerosperma*. Interestingly, the latter species shows significant differences from the other two when a comparison of substrate types is considered (χ^2= 129.9, d.f. = 10, P < 0.0001).

Discussion

Members of the genus *Ceratiomyxa* represent some of the more commonly encounterd eumycetozoans in tropical regions. However, also in tropical regions many studies have recorded only one species, *C. fruticulosa* (e.g., Hochgesand and Gottsberger 1996, Ogata et al 1996). The other two macroscopic species within the genus are more difficult to find and normally represent occasional to rare observations. In spite of that, some studies such as those of Pando (1996) and Novozhilov et al (2001) represent instances in which appreciable numbers of records of *C. sphaerosperma* were documented. In spite of these situations, what is currently known about the overall pattern of abundance for the three species seems to correspond to the relative frequencies recorded in the present study. This suggests that for the latter, the survey was carried out

effectively, even though for some of the study areas *C. morchella* and *C. sphaerosperma* were never recorded. In any case, it has been suggested that the former species is more abundant in the Amazon forests than in Central America (Stephenson et al 2008), which seems to conform with the results obtained in the present study.

When the mathematical distance between the study areas with the three species present is evaluated, a similar pattern is apparent. It is interesting to note that the values obtained show an increasing degree of dissimilarity with increasing geographical distance from the southernmost study area (Los Amigos) and with differences in the forest type. This can be observed in the higher Bray-Curtis distance value for both the pairwise combinations of Los Amigos and Yasuní with Monteverde than for the combination of Los Amigos and Yasuní. Interestingly, of these three areas, the only one that is not represented by a lowland tropical rainforest is Monteverde, which may also be an indication that differences in forest type can play a role in the distribution of the species within the genus.

In fact, a similar pattern can be observed in the occurrence of the three species in the evaluated subtypes of forest. The low abundance of *C. morchella* and *C. sphaerosperma* in secondary forests is likely to be the product, at least in part, of differences in the microhabitats available, which in turn are the product of variations in the forest structure of the three sub types of forests. This might be particularly true with respect to the availability of particular substrates for which one of the species of *Ceratiomyxa* seems to show a preference, an observation that has been reported for myxomycetes in previous studies (e.g., Stephenson 1988).

Interestingly, some of these correlations are apparent when the micro-environmental parameters are evaluated independently. For example, the average pH value for the three species differs significantly in the present study (not shown before, $F = 53.95$, $d.f = 2$, $p < 0.0001$, TABLE I), being higher for *C. fruticulosa* and *C. sphaerosperma* than for *C. morchella*. Such a pattern was reported previously by Stephenson et al (2008). Interestingly, it is known that the higher heterogeneity of organisms and resources in secondary tropical forests affects the acidity levels of the substrates in different ways (e.g., Herrera and Finegan 1997), a situation that may have a stronger negative effect on the presence of species such as *C. morchella* and *C. sphaerosperma* that seem to be more pH-specific than *C. fruticulosa*.

Also noted in the present study is that one the strongest tendencies observed was the occurrence of *C. sphaerosperma* on substrates different than those on which *C. fruticulosa* and *C. morchella* were recorded. In fact, for purposes of comparison, all the observations of *C. morchella* reported herein were found on decaying wood, whereas 87% of all records of *C. sphaerosperma* came from herbaceous plant litter. This is not the first time that *C. sphaerosperma* has been reported to be restricted to particular types of substrates. Novozhilov et al (2001) recorded this species only on the decaying fruits of *Andira inermis*, which suggested a pattern of high abundance associated with a particular plant. In any case, the important point to consider is that *C. sphaerosperma* was recorded as exploiting a resource that neither of the other two species appears to utilize. When such a phenomenon occurs, it is logical to think that the niche overlap between the species involved is lower than between species that share the same substrate in a similar way. Based upon the other analyses carried out, this seems to be the case for the

macroscopic species of *Ceratiomyxa*. For example, in FIG. 2 the hyperspaces obtained for *C. morchella* and *C. sphaerosperma* are both smaller than that obtained for *C. fruticulosa*. The hyperspaces of the two tropical species seem to be comparable in size; however, FIG. 3 shows that *C. sphaerosperma* is clearly associated with higher pH values and lower diameter substrates than *C. morchella*. Moreoever, the niche breadth values in TABLE II show the same pattern. This makes sense when one considers that the characteristics of the substrates utilized by these two less common species of *Ceratiomyxa* are different, as already discussed.

Interestingly, for these two species, the overlap in their hyperspaces is very low, which can be interpreted as an indication of resource partitioning and specialization within the genus. On the other hand, one might think that *C. fruticulosa* is less specialized for particular resources than the two other species simply because it is the only species in the genus that occurs throughout the world. Although the data in TABLE II seem to indicate such a situation, our dataset is too limited for a truly definitive conclusion. Nevertheless, these data do seem to suggest the idea that *C. fruticulosa* is more of a generalist, based both on the multivariate and niche breadth and overlap analyses. These results conform with what was reported by Stephenson (1988) for the same species in upland forests of a study area in eastern North America. Another interesting observation is that *C. fruticulosa* seems to have a much more variable morphology than the two other macroscopic species in the genus. This has been observed both in the color of fresh fructifications (pink to pale yellow to white) and the appearance of the sporophores, which can vary from highly branched (*var. arbuscula* [Berk. & Broome] Minakata) to an almost poroid appearance (*var. poroides* [Alb. & Schwein.] G. Lister).

What seems to be readily apparent is that the niches of *C. morchella* and *C. sphaerosperma* are clearly defined by the characteristics of their microhabitat and that *C. fruticulosa* seems to be the least specialist of the three macroscopic species. These apparent microenviromental preferences might account, at least in part, for their distribution patterns and interspecific interactions. However, since little information on various aspects of the ecology of eumycetozoans is available, especially at the level of species, this is certainly something that warrants additional study.

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Chapter 6

Macroecology of high-elevation myxomycete assemblages in the northern Neotropics

Abstract: A number of recent studies have been directed towards developing a more complete understanding of myxomycete ecology in high-elevation areas of the Neotropics. However, the lack of comparative data obtained using standard methodologies makes the results from these studies somewhat speculative. The objective of the investigation described was to examine the evidence for macroecological patterns in myxomycete assemblages in the northern Neotropics. First, a series of study areas was selected in Mexico, Guatemala and Costa Rica. In addition, two other study areas (one in the United States and the other in Thailand) were selected in order to compare the diversity-environment relationships using data from the Neotropics with comparable data from a temperate forest in North America and a tropical forest in Asia. A standard methodology for collecting and processing samples of substrate material was used for all study areas. Altogether, 2592 moist chamber cultures were prepared from the samples collected during the course of the investigation, and these samples yielded a total of 1377 myxomycete records representing 89 different species. A trend of decreasing species richness with decreasing latitude was observed for the species assemblages associated with the study areas in the Neotropics. This contrasted with a lack of significant differences among these same study areas when species diversity was analyzed. Species assemblages in the Neotropical study areas became increasingly similar to the temperate study area as latitude increased. The difference in species richness between study areas in

Mexico and Thailand along with the results obtained for a series of macroclimatic patterns evaluated in the study areas of the Neotropical region suggest that forest structure plays an important role in the structure of myxomycete assemblages. In contrast, the soil chemical characteristics and the pH of the substrates present seem to be indirectly related to the diversity estimators used for analysis, which suggests that their role with respect to the dynamics of the myxomycete assemblages considered is probably more important at a smaller ecological scale.

Keywords: alpha and beta diversity, community structure, Cofre de Perote, Cuchumatanes, Doi Inthanon, Malinche, mycetozoans, Talamanca.

Introduction

The myxomycetes (plasmodial slime molds or myxogastrids) comprise a monophyletic group of amoebozoans (see Pawlowski and Burki 2009) that have the capacity to produce fruiting bodies during the reproductive stage of their life cycle (Martin and Alexopoulos 1969). These microorganisms have been collected in most terrestrial ecosystems (Stephenson 2003). Although myxomycetes have been known since the middle of the 17th century (see Stephenson et al. 2008a), most studies published on the group are taxonomic in nature and contain relatively little ecological information. In fact, it was not until the second half of the 20th century that studies directed specifically to myxomycete ecology began to be carried out (e.g., Blackwell and Gilbertson 1984, Venkataramani and Kalyanasundaram 1986, Stephenson 1988, Stephenson et al. 1993).

One of the problems with our knowledge of myxomycete ecology is that the information currently available does not seem to provide enough evidence to properly develop and test hypotheses relating to the distribution of myxomycetes across the planet. This is based on the fact that the majority of ecological studies have been carried out in the temperate forests of the northern hemisphere (Stephenson et al. 2008a). In spite of this situation, during the past two decades there has been more studies of myxomycetes in previously underrepresented areas of the world, and this has already generated valuable information for some of these poorly known areas (e.g., Stephenson et al. 1992, Tran et al. 2006, Nderitu et al. 2009). In fact, very recent studies (e.g., Novozhilov and Schnittler 2008, Estrada-Torres et al. 2009) of myxomycetes in several underrepresented ecosystems have contributed a body of new information on a number of important ecological relationships that had not been observed previously.

For the New World tropics (or Neotropics), most ecological research is fairly recent. According to Lado and Wrigley de Basanta (2008), approximately 53% of published papers on Neotropical myxomycetes have been produced since the appearance of the Neotropical monograph by Marie Farr (Farr 1976). The majority of these studies have centered their efforts on myxomycetes in low- and mid-elevation areas. This has generated a somewhat biased view of the distribution and ecology of myxomycetes in the Neotropics, since some macro- and microhabitats are underrepresented as an artifact of this restricted sampling. In spite of that, recent efforts have been made to alleviate this problem and studies of higher elevation areas in the Neotropics have also been carried out (e.g., Schnittler et al. 2002, Rodríguez-Palma et al. 2005, Rojas and Stephenson 2007).

Most comparative studies of Neotropical myxomycetes have considered species assemblages occurring in different forest types within a single country (e.g., Novozhilov et al. 2000, Schnittler and Stephenson 2000) or those associated with particular microhabitats or belonging to certain taxonomic groups (e.g., Schnittler and Stephenson 2002, Rojas et al. 2008). As such, a more comprehensive analysis of the ecology of myxomycete assemblages in the Neotropical region is possible only when there are more baseline information, especially for understudied forests and other vegetation types that occupy high-elevation areas in the Neotropics.

For these areas, the different taxonomic composition and structure of the forest might influence assemblages of myxomycetes in different ways. For example, previous studies have shown that some myxomycete species seem to be very substrate specific (e.g., Stephenson et al 2008b, Wrigley de Basanta et al. 2008) or largely influenced by environmental factors (e.g., Rojas and Stephenson 2007). This specificity is likely to have an effect on the macroecological characteristics of different assemblages. However, these types of comparative studies are scarce; and for the high-elevation areas of the Neotropical region empirical data is practically non-existent. Such type of information gaps partially explain the lack of clarity in the distribution pattern for most myxomycete species, which in most cases remains still unclear.

For those reasons, this project was designed with the idea of providing basic information on myxomycete assemblages in poorly known high-elevation areas of the northern Neotropics. The overall objectives of the project were (1) to study macroecological aspects of myxomycete assemblages in these areas and (2) to use modern ecological methodology to generate comparative baseline data for this region of

the world. Such an approach offers both the opportunity to generate basic information for these understudied areas as well as the flexibility of applying additional types of ecological analysis in the context of future projects.

Materials and methods

This investigation was carried out entirely during the period of 2006 to 2009. For practical purposes, the morphological concept of species was used for species identification and names of species follow the taxonomic treatment provided by Lado (2005-2010). However, a more complete evaluation of the species present in the study areas is the subject of a separate paper due to the biogeographical implications that fall outside of the scope designed for this paper.

Study areas

A series of eight high-elevation study areas was selected for this investigation. Six of these are located in the northern Neotropics, one in North America and one in southeastern Asia. For the Neotropical region, two study sites were established in each of the six study areas, whereas only one study site was established in North America and Asia. Each study site contained two collecting plots approximately 0.1 ha in size. Consequently, a total of 28 different plots in 14 study sites were surveyed to obtain the data generated in this investigation.

The North American study area (Area 1) investigated was Andrews Bald (hereafter referred to as Andrews Bald; with collecting plots located at 35°32' N and 83°29' W, 1750 meter above sea level – m asl –). This area is located in the highlands of

the Great Smoky Mountains National Park, approximately 2.5 kilometers south of Clingmans Dome, in Swain County, North Carolina in the United States. As a typical "bald", the vegetation in this open area is dominated by grasses, sedges and forbs, with *Abies fraseri* (Pursh) Poir. dominant in the surrounding forest. In this area, only the open locations were sampled. The second study area (Area 2) investigated is located in Southeast Asia on Doi Inthanon (Doi Inthanon, collecting plots located between 18°31'–18°33' N and 98°28'– 98°31' E, between 1400–1700 m asl). This study site is located in the province of Chiang Mai, Thailand, on Doi Inthanon, which is the highest mountain in the country (2565 m asl). The forests of the highest portions of Doi Inthanon are dominated by *Quercus eumorpha* Kurz, although at lower elevations a mixed assemblage containing *Pinus kesiya* Royle ex Gordon is also found. In this study area, only forested study sites were used.

In the Neotropical region, study areas were selected in Mexico, Guatemala and Costa Rica. For the first country the study areas are (Area 3) Matlalcueyetl (Malinche, collecting plots located between 19˚14'–19˚16' N and 97˚59'–98˚02' W, 3100–4050 m asl), a volcano located in the Trans Mexican Volcanic Belt between the states of Puebla and Tlaxcala and (Area 4) Cofre de Perote (Perote, collecting plots located between 19˚29'–19˚31' N and 97˚09'–97˚10' W, 3400–4200 m asl), a shield volcano located in the state of Veracruz. In these two study areas, most of the forests at lower elevations are dominated by *Pinus hartwegii* Lindl. and *Abies religiosa* (Kunth.) Schltdl. et Cham, whereas the highest elevations are dominated by the tussock grasses *Festuca tolucensis* Kunth and *Calamagrostis tolucensis* (Kunth) Trin. ex Steud. In both cases, study sites were established in both forested and non-forested (high-elevation grasslands) locations.

The study areas selected in Guatemala are (Area 5) Llanos de San Miguel (Llanos, collecting plots located at 15˚30' N and 91˚29' W, 3400–3500 m asl) and (Area 6) La Ventoza (Ventoza, collecting plots located at 15˚27' N and 91˚32' W, 3400–3600 m asl). These two study areas are located on the Cuchumanates Plateau, which is within the Department of Huehuetenango in the northwestern section of the country. As with the case for Mexico, study sites in these areas were established on the basis of plant dominance. Both forested sites dominated by *Juniperus standleyi* Steyerm. or *Pinus hartwegii* Lindl. and non-forested sites dominated by the tussock grass *Agrostis tolucensis* Kunth or *Agave hurteri* Trel. were sampled.

The southernmost study areas are located on the Talamanca Range in south-central Costa Rica. These are (Area 7) Cerro Buenavista or Cerro de la Muerte (Cerro, collecting plots located at 9˚33' N and 83˚44'–83˚45' W, 3150–3450 m asl) and (Area 8) Macizo del Chirripó (Chirripo, collecting plots located between 9˚26'–9˚27' N and 83˚29'–83˚31' W, 3150–3500 m asl). These two study areas are located within the province of San José and have characteristic *Quercus* L. dominated forests below the tree line and treeless areas dominated by the dwarf bamboo *Chusquea subtessellata* Hitch. at the highest elevations. Study sites were established in both forested and non-forested areas.

Experimental design

In order to obtain representative records of myxomycetes from the study areas being surveyed, collecting trips were made during the summers of 2006 and 2007. On each visit, 16 samples of dead plant material were collected directly from each one of the

plots. However, for the study area in southeastern Asia, this same number of samples was collected only once in early 2008.

A total of 864 samples of dead plant material were collected during the entire study. Four samples of sorted material that correspond to ground litter (GL), aerial litter (AL), twigs (TW) and bark (BA) were collected randomly from each plot during each visit. As considered herein, the term ground litter is used to refer to leaves and non-woody plant material present on the forest floor, aerial litter is defined as decomposing plant material that occurred above the ground and remained attached to the aerial portions of living plants before being collected, twigs are small decomposing woody branches present on the forest floor and bark refers to the periderm of mature living trees.

Each sample was used to prepare a series of three moist chamber cultures in the manner described by Stephenson and Stempen (1994). In total, 2592 moist chamber cultures were prepared during the entire study. Dead plant material from each sample was placed in a Petri dish lined with filter paper; pH-neutral water was added to the dish and the plant material soaked for approximately 24 hours, after which substrate pH was measured and excess water was poured off. All cultures were systematically observed on a weekly basis for approximately ten consecutive weeks.

When fruiting bodies were observed, these were removed from the moist chamber culture and carefully glued to paper trays set in small pasteboard boxes. All specimens curated in this manner were identified and deposited in the herbarium of the University of Arkansas (UARK) for future reference. The identification of all specimens took place at the Laboratory for Mycetozoan Research of the University of Arkansas during the period 2007-2009. In addition, a database of records was compiled and used for analysis.

Soil samples

In addition to the plant material collected for moist chamber cultures, a series of soil samples was collected from study areas in the Neotropics to determine soil chemical characteristics and to examine the evidence for possible correlations with various ecological parameters of the myxomycete assemblage present in those study areas. Soil samples were sent to Brookside Laboratories Inc. (New Knoxville, Ohio) for analysis of levels of macronutrients and trace elements, organic matter, total exchange capacity, pH and soluble sulfur.

Data analysis

All collections of myxomycetes were assigned to the substrate sample from which they were recovered and not simply to the moist chamber culture in which they appeared. The completeness of the survey for the methodology used was calculated by first obtaining the maximum number of species to be expected for each of the study sites using the prediction platform and the multinomial model in the program SPADE (Chao and Shen 2003). For this, the values for the abundance-based coverage estimator (ACE) were used as recommended by Chao et al. (2006). The relationship between the observed and expected numbers of species for each of the study sites was calculated and considered as the degree of completeness.

An analysis of alpha and beta diversity was also carried out on each dataset. For this, the Shannon, Simpson and Fisher indices of diversity were calculated with SPADE for each study areas using the bias-corrected maximum likelihood estimator, the

maximum likelihood estimator and the classic formula of each index, respectively. The calculation of alpha diversity was performed using different indices to avoid interpretation problems that commonly appear when only one estimator is used. According to Magurran (2004), even though the Shannon index is very popular in biological research, its interpretation is more complicated than most biologists assume due the variable effect of addition of species on the resulting value in most circumstances. In contrast, the Simpson and Fisher indices are more intuitive; provide a better calculation for small sample sizes and help with the interpretation of the former. In a same manner as described for the previous calculation of alpha diversity, the taxonomic diversity index value *sensu* Stephenson et al. (1993) was also calculated for each study areas. This estimator simply reflects the relationship between the number of species and genera in a given dataset, but this provides important information on the intrageneric diversity of myxomycete assemblages. As a complement to the latter calculations, both the values for the Sørensen coefficient of community similarity (= Sørensen quantitative index) and the Bray-Curtis distance measure were estimated for all combinations of study areas in order to evaluate the degree of similarity among them. For the latter, the classic formula for the Sørensen similarity index (Sørensen 1948) was used. These two measurements of similarity were used for their slightly different formulation and potential interpretation. The coefficient of community similarity index takes into consideration the relative abundance of species in the calculation and ranges from 0 when assemblages are totally different to 1 when the two assemblages are the same. On the other hand, the distance measure for species assemblages calculated using the classic Bray-Curtis index is based on presence/absence data only and ranges from 0 when

assemblages are the same (no distance) to 1 when they have opposite presence/absence patterns (maximum distance).

In addition to these analyses, several other aspects of the ecology of myxomycetes were also examined. Possible relationships between species richness, species diversity and taxonomic diversity with sampling period, latitude, substrate type, substrate pH and soil chemical characteristics were evaluated using either analysis of variance or linear regression analysis, depending on the parameter characteristics of the data subset. In those instances in which analysis of variance revealed significant differences, *post-hoc* Tukey tests were carried out to evaluate the direction of the distribution. When linear regressions were carried out, a posterior analysis of variance testing the probability of the regression occurring as a result of random events was also done. All of these tests were performed using the statistical package JPM, version 8.0, and a rejection value of 0.05 for null hypotheses.

The particular relationship between myxomycetes and the substrate upon which they fruited in the laboratory was more carefully evaluated for the most abundant species only. This is due the fact that a number of recent studies have shown that particular species of myxomycetes seems to be highly substrate-specific. For this analysis, a categorization of the species was carried out on the original dataset on the basis of their relative abundance following a modification from Stephenson et al. (1993). Those species with overall abundance values higher than 1.5% were considered as Abundant (A), those falling between 1.5-0.5% as Common (C), between 0.5-0.15% as Occasional (O) and those falling below 0.15% as Rare (R).

Only those species falling in the abundant category were considered for the substrate analysis since the probability of obtaining statistical errors driving to wrong conclusions is increased when not well represented species are included. In a similar way as the previous evaluations, an Analysis of Variance and posterior Tukey tests were performed when necessary. The statistical program JMP was also used for this analysis.

Multivariate analysis

In addition to the latter, a Principal Components Analysis (PCA) was performed with a series of macro- and microenvironmental parameters collected in order to evaluate the variation exhibited in the database generated. For this analysis, only those records corresponding to species considered as abundant (A) were used in a similar way as with the substrate specificity evaluation. The environmental parameters included correspond to: mean annual temperature and precipitation of the study areas (provided by meteorological institutes in the countries involved), elevation, pH of the substrate, host plant, habitat type and substrate type.

For the last three mentioned parameters, an ordination of categories was carried out prior to the analysis in a similar way as described by Rojas et al. (2008). The values for pH were transformed to concentration of H^+ ions in solution to avoid the inclusion of logarithm-based scales in the evaluation. The PCA analysis was performed after re-scaling all variables on PC-ORD, version 5.30 (McCune and Mefford 2006).

Results

A total of 1377 myxomycete records representing 89 different species were obtained from all of the moist chamber cultures prepared during the course of the study. Forty-four percent of the records were from Mexico, 29% from Guatemala, 11% from the United States, 10% from Costa Rica and 6% from Thailand. For the Neotropical countries, moist chamber cultures showed a strong but not statistically significant tendency to yield fewer myxomycetes as latitude decreased ($R^2 = 0.98$, $F(1,1) = 66.18$, $P = 0.07$). The single most frequently recovered species was *Didymium difforme*, followed closely by *Stemonitis fusca* and *Arcyria cinerea* (Table 1).

The numbers of positive moist chamber cultures were essentially the same for the data sets obtained for the United States and Mexico (*mean* = 96.8 and 96.5, *standard deviation* = 4.41 and 2.77, respectively), but both were significantly higher than the values calculated for the sets obtained from Guatemala, Thailand and Costa Rica (*mean* = 87.4, 78.1 and 64.8, *standard deviation* = 3.31, not calculated for replication absence and 15.47, respectively; $t(8) = 2.77$, $P < 0.05$, $r = 0.67$). This pattern did not change when equal efforts were compared by excluding the data sets from the United States and Thailand from the analysis ($t(5) = 3.18$, $P < 0.05$, $r = 0.81$).

A different pattern was observed when the numbers of species found in each the study areas were compared (Fig. 1). There were significant differences in the number of species found among study areas ($F(2,3) = 12.3$, $P = 0.035$, $R^2 = 0.82$). The values obtained for Mexico (*mean* = 50.0, *standard deviation* = 8.48) were higher (Tukey $P < 0.05$) than those found in Guatemala (*mean* = 29.0, *standard deviation* = 5.65), the United States (*mean* = 23.5, *standard deviation* = 0.70), Thailand (20) and Costa Rica

(*mean* = 19.0, *standard deviation* = 4.24). There were no differences in the study areas when sampling periods are compared ($F(1,34) = 2,75$, $P = 0.11$, $R^2 = 0.07$) or when the overall distribution of records for the different substrates among the study areas is compared ($F(3,32)= 1.72$, $P = 0.18$, $R^2 = 0.13$). The latter pattern is still evident even when the data sets from the United States and Thailand are excluded from the analysis ($F(1,22) = 2,24$, $P = 0.15$, $R^2 = 0.09$ and $F(2,20)= 1.68$, $P = 0.20$, $R^2 = 0.20$, respectively). In fact, when the effects of both sampling period and substrate or substrate and country on the number of myxomycetes found are evaluated in a combined model (see Table 2), no significant differences were found for either one ($F(7,28) = 1.19$, $P = 0.33$, $R^2 =0.23$ and $F(19,16) = 1,96$, $P = 0.08$, $R^2 = 0.69$, respectively).

Both the highest species richness and diversity were recorded for the forested area of Perote in Mexico. However, the forests of La Malinche were characterized by the highest value for taxonomic diversity (Table 1). When non-forested areas are considered, no statistical differences were found for the Shannon ($F(3,3)= 0.65$, $P = 0.63$, $R^2 = 0.39$), Simpson ($F(3,3)= 0.05$, $P = 0.97$, $R^2 = 0.05$) or Fisher ($F(3,3)= 0.88$, $P = 0.53$, $R^2 = 0.46$) indices of diversity among the different study areas. Moreover, the taxonomic diversity index does not show significant differences among the study areas ($F(3,3) = 0.87$, $P = 0.54$, $R^2 = 0.46$). For forested areas statistical differences among the study areas were observed when the taxonomic diversity index was evaluated ($F(3,3)= 29.65$, $P = 0.009$, $R^2 = 0.97$), but differences are not apparent when the Shannon ($F(3,3) = 5.15$, $P = 0.10$, $R^2 = 0.83$), Simpson ($F(3,3) = 0.57$, $P = 0.67$, $R^2 = 0.36$) or Fisher ($F(3,3) = 4.61$, $P = 0.12$, $R^2 = 0.82$) indices of diversity are evaluated. These differences seem to be

Table 1. Summary data for each of the study areas used in the present investigation. The ten most frequent species and their abundances are shown in addition to general aspects of the survey, a summary of the substrate pH values and soil analysis.

COUNTRY	**US**	**TH**	**MX**				**GU**				**CR**			
Study area	**AB**	**DI**	**CP**		**LM**		**LL**		**LV**		**CM**		**CH**	
Vegetation type	**NF**	**F**	**F**	**NF**	**F**	**NF**	**F**	**NF**	**F**	**NF**	**F**	**NF**	**F**	**NF**
Species														
DDYdif	5	2	47	33	61	35	7	6	12	3	0	0	0	0
STEfus	7	0	9	13	6	8	36	10	27	21	5	6	8	4
ARCcin	38	6	4	4	6	0	7	12	4	3	1	1	4	4
DDYiri	3	8	5	0	5	3	6	14	16	7	0	0	5	1
DDYsqu	0	4	5	6	8	2	19	3	2	5	0	3	5	1
COMnig	8	0	23	2	3	6	2	0	4	4	1	2	3	1
PHYcom	0	0	8	8	11	1	6	3	4	2	1	2	3	9
PERdep	0	2	6	8	12	4	6	5	5	5	0	0	2	2
PHYbiv	20	0	5	7	2	3	0	1	2	1	2	0	0	0
DDYbah	0	0	3	0	5	1	5	0	12	1	2	1	0	1

Table 1. Continued.

Survey														
Number of records	153	88	178	138	191	107	115	85	117	72	21	34	43	35
Species richness	33	20	40	32	39	26	20	21	23	22	12	16	13	13
MNS (ACE)	45	27	74	41	46	33	23	27	28	31	19	23	16	20
Completeness (%)	74	75	54	79	85	80	89	79	84	71	64	70	80	66
Shannon's ID	2.99	2.55	3.10	3.04	3.03	2.79	2.49	2.84	2.73	2.80	2.74	2.90	2.50	2.54
Simpson's ID	0.10	0.14	0.10	0.09	0.12	0.13	0.15	0.08	0.10	0.12	0.11	0.08	0.11	0.12
Fisher's ID	12.90	8.07	16.05	13.07	14.82	10.93	6.99	8.92	8.56	10.80	11.63	11.79	6.33	7.49
TDI	2.06	1.53	2.66	2.28	3.00	2.36	2.22	2.10	2.30	2.20	1.50	2.66	1.62	2.16
Substrate pH														
Average pH	5.15	5.29	5.98	5.90	6.22	5.38	5.42	5.40	5.09	5.06	4.96	4.70	5.26	5.49
Minimum pH	3.91	4.17	3.63	4.04	3.82	3.94	4.16	4.09	3.75	4.43	3.84	3.72	4.37	4.00

Table 1. Continued.

Maximum pH	7.57	6.60	8.01	7.38	7.47	7.52	6.93	6.71	6.33	5.86	5.78	5.24	6.45	6.33
Soil parameters														
pH	n.a.	n.a.	5.8	5.2	4.8	4.8	4.5	5.2	4.1	4.0	5.3	4.9	4.8	5.7
Organic matter (%)	n.a.	n.a.	42.00	3.38	11.00	3.82	83.15	32.23	34.05	17.93	40.68	48.97	36.49	21.31
TEC	n.a.	n.a.	29.68	7.82	15.46	10.98	29.63	41.14	27.37	21.79	21.06	29.19	22.17	23.18

Abbreviations used: US= United States, TH = Thailand, MX = Mexico, GU = Guatemala, CR = Costa Rica, AB = Andrews Bald, DI = Doi INthanon, CP = Cofre de Perote, LM = La Malinche, LL = Llanos de San Miguel, LV = La Ventoza, CM = Cerro de la Muerte, CH = Macizo del Chirripó, F = forested, NF = non-forested, MNS = maximum expected number of species, ID = index of diversity, TDI = taxonomic diversity index, TEC = total exchange capacity.

Species codes: DDYdif = *Didymium difforme* (Pers.) Gray; STEfus = *Stemonitis fusca* Roth; ARCcin = *Arcyria cinerea* (Bull.) Pers., DDYiri = *Didymium iridis* (Ditmar) Fr., DDYsqu = *Didymium squamulosum* (Alb. & Schwein.) Fr.; COMnig = *Comatricha nigra* (Pers. ex J.F.Gmel.) J.Schröt., PHYcom = *Physarum compressum* Alb. & Schwein., PERdep = *Perichaena depressa* Lib.; PHYbiv = *Physarum bivalve* Pers. and DDYbah = *Didymium bahiense* Gottsb.

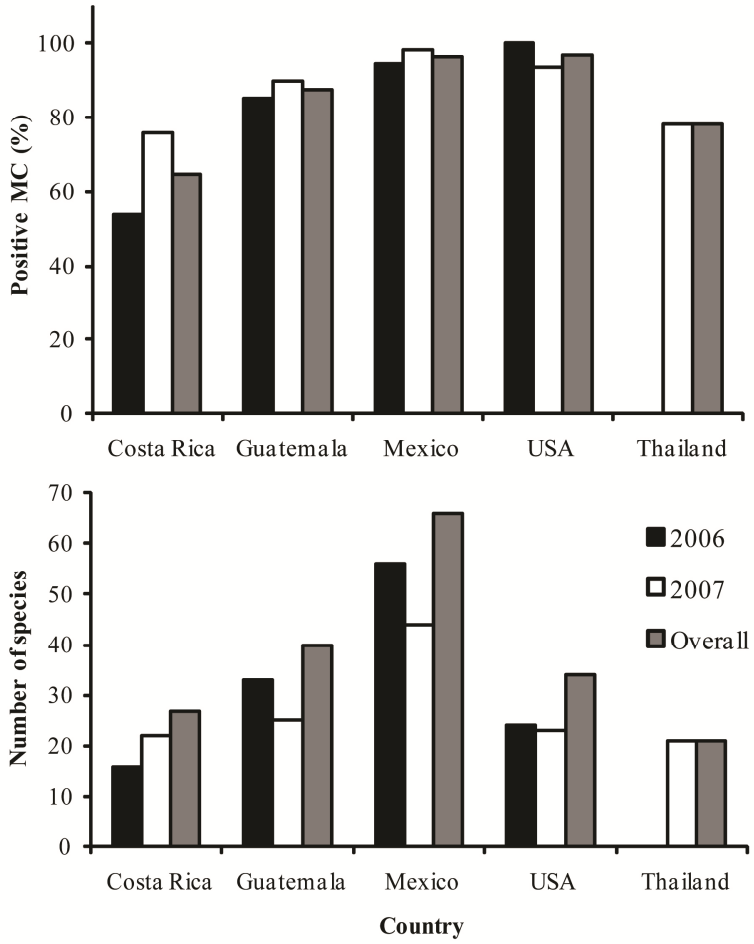

Figure 1. Comparison of the number of positive moist chamber cultures and number of species obtained on each one of the countries evaluated arranged by sampling period.

associated with the higher value for La Malinche (Tukey $P < 0.05$) when compared to the other study areas and are even more evident when Doi Inthanon is excluded from the analysis (Tukey $P < 0.005$). For the entire dataset, no differences in species diversity and taxonomic diversity between forested and non-forested sites were apparent (for Shannon index $F(1,5) = 1.05$, $P = 0.35$, $R^2 = 0.17$; others not shown; for taxonomic diversity index F $(1,5) = 0.0006$, $P = 0.98$, $R^2 = 0.0001$).

When species richness values were evaluated, significant differences were apparent both among non-forested study sites ($F(3,3) = 13.93$, $P = 0.02$, $R^2 = 0.93$) and forested study sites ($F(3,3) = 140.61$, $P < 0.001$, $R^2 = 0.99$) in study areas across the entire region of study. This pattern is maintained when Doi Inthanon is excluded from the analysis ($F(2,3) = 206.18$, $P < 0.001$, $R^2 = 0.99$). It would seem noteworthy that the distributions of values in these analyses seem to show different patterns. For non-forested sites, both Cerro and Chirripo in Costa Rica show significantly lower values (Tukey $P < 0.05$), whereas in forested sites both Perote and Maliche show significantly higher values (Tukey $P < 0.005$). When Doi Inthanon is not included in the analysis, the latter pattern is maintained (Tukey $P < 0.005$). For the complete dataset, differences in species richness between forested and non-forested sites appear to be absent ($F(1,5) = 4.32$, $P = 0.09$, $R^2 = 0.46$). The correlations between species diversity, species richness and taxonomic diversity index in relation to latitude for all study areas across the Americas are presented in Fig 2.

Both the number of records and the species richness recorded in each study area showed a weak but significant correlation with average pH (R^2=0.53; F (1,12) = 13.53, P = 0.003

Table 2. Number of species of myxomycetes recorded in each one of the countries, arranged by sampling period and the substrate from which they were recovered. The order of countries reflects the abundance of myxomycetes from highest (top) to lowest (bottom).

Country	**Sampling period**	**Substrates**			
		GL	**AL**	**T**	**B**
Mexico	2006	26	32	24	17
	2007	15	13	13	9
Guatemala	2006	17	25	13	10
	2007	15	13	13	9
United States	2006	8	7	10	5
	2007	9	9	11	8
Costa Rica	2006	4	10	8	4
	2007	3	20	4	9
Thailand	2008	4	11	7	6

and R^2=0.51; F (1,12) = 12.50, P = 0.004, respectively) and a moderate correlation with maximum pH (R^2 = 0.72; F (1,12) = 31.59, P = 0.0001 and R^2 = 0.66; F (1,12) = 23.82, P = 0.0004). Only species diversity using the Shannon index values showed a weak correlation with minimum pH (R^2=0.30; F (1,12)=5.43, P = 0.03). In contrast, none of these parameters seemed to be associated with soil conditions, except for the diversity index values, which show a moderately weak significant negative correlation with the level of sodium (in ppm, R^2 = -0.62, F (1, 10)=16.90, P = 0.002) and the taxonomic diversity index, which is weakly correlated with the level of phosphorus (in ppm, R^2=0.54, F against random (1,10)= 12.18, P = 0.005). The relationship between the organic content and the total exchange capacity of the soil with the species richness recorded in each of the study areas in the Neotropical region was not significant (F(3,8) = 1.15, P = 0.38, R^2 = 0.30), as can be noted in Figure 3. A similar result was obtained for the relationship of these two factors and the total number of records (F(3,8) = 1.03, P = 0.42, R^2 = 0.28) or the diversity value (for the Shannon index, F(3,8) = 1.07, P = 0.41, R^2 = 0.28) obtained for the study areas.

The values obtained for the Sørensen coefficient of community similarity index and the Bray-Curtis distance measure are normally distributed and can be observed in Table 3. The highest value and thus the greatest similarity for the first estimator was obtained for the Chirripo forested-non forested comparison, but high values were also obtained for the Llanos forested-Ventoza forested and non-forested comparisons as well as for the pairwise comparison of Perote forested and all other Mexican study areas. In a similar fashion, the lowest value for the Bray-Curtis distance measure, and thus greatest similarity, was found to exist for the Perote forested-non forested comparison, whereas

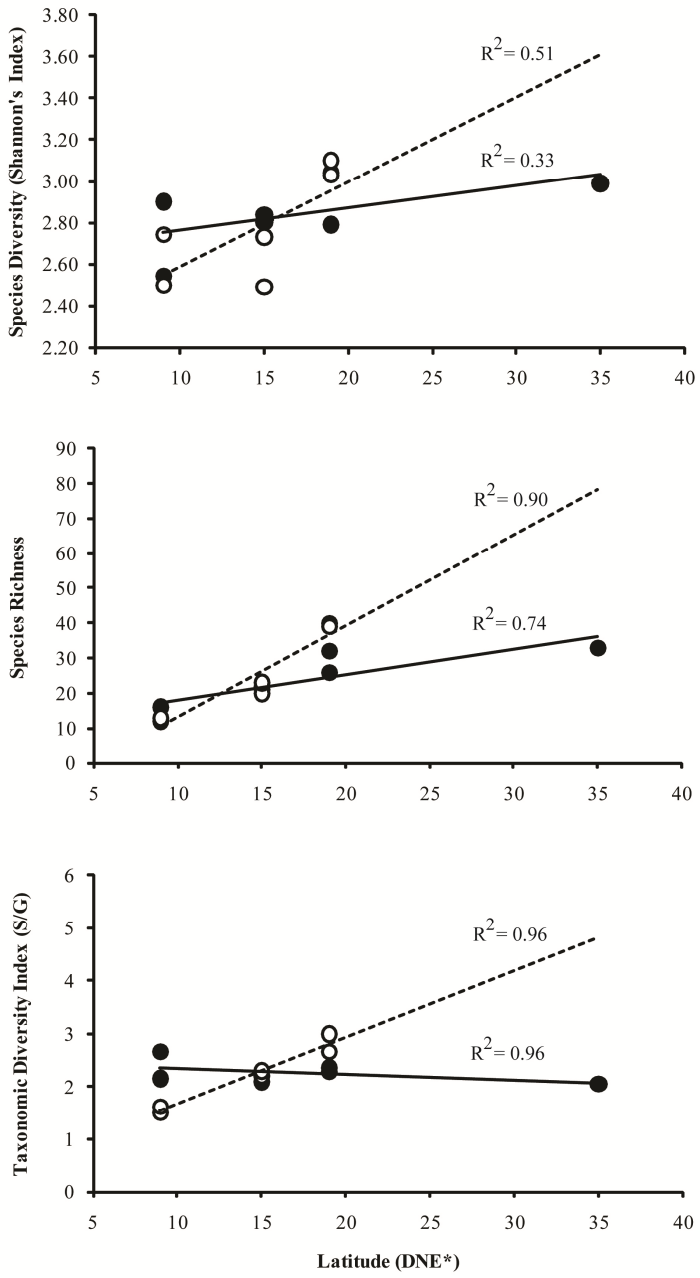

Figure 2. Comparisons of the regression analyses for species diversity, species richness and taxonomic diversity index in relation to latitude for the study areas in the Americas. Filled circles and continuous lines represent non-forested study sites, whereas open circles and dotted lines represent forested ones. Values for the Pearson Product Moment coefficient are given in each case.

other low values existed between Perote forested and Perote non-forested and the other Mexican study areas. The Llanos forested-Ventoza forested and non-forested study areas also showed a low value for the Bray-Curtis distance measure. Both the Sørensen and the Bray-Curtis values of all study areas in the Neotropical region showed moderate but significant correlations with latitude when paired with Andrews Bald (Fig. 4, $R^2 = 0.72$, $F(1,10) = 26.44$ $P = 0.0004$ and $R^2 = -0.71$, $F(1,10) = 24.99$ $P = 0.0005$, respectively). The same pattern for both the Sørensen and the Bray-Curtis values was evident when only the non-forested areas are taken in consideration for the analysis. However, the correlation was higher than in the previous analysis when the Sørensen coefficient was used ($R^2 = 0.83$, $F(1,4) = 20.76$ $P = 0.01$) but similar when the Bray-Curtis distance measure was considered ($R^2 = -0.71$, $F(1,4) = 10.01$ $P = 0.03$).

The Principal Component Analysis performed on the dataset of records and environmental parameters revealed that approximately 70% of the variation is explained by elevation, substrate pH and habitat type, the first three components in order of importance. The most frequently encountered species are widely dispersed in the multidimensional space formed by the environmental parameters but seem to be arranged into ecological groups. In Figure 5, group A is composed by two species primarily found in forested areas with relatively high pH values, group B is formed by two species encountered in non-forested areas with intermediate pH values and group C is composed by species primarily found in non-forested areas with relatively low pH values. An analysis of variance on the first three components did not show any significant differences among them.

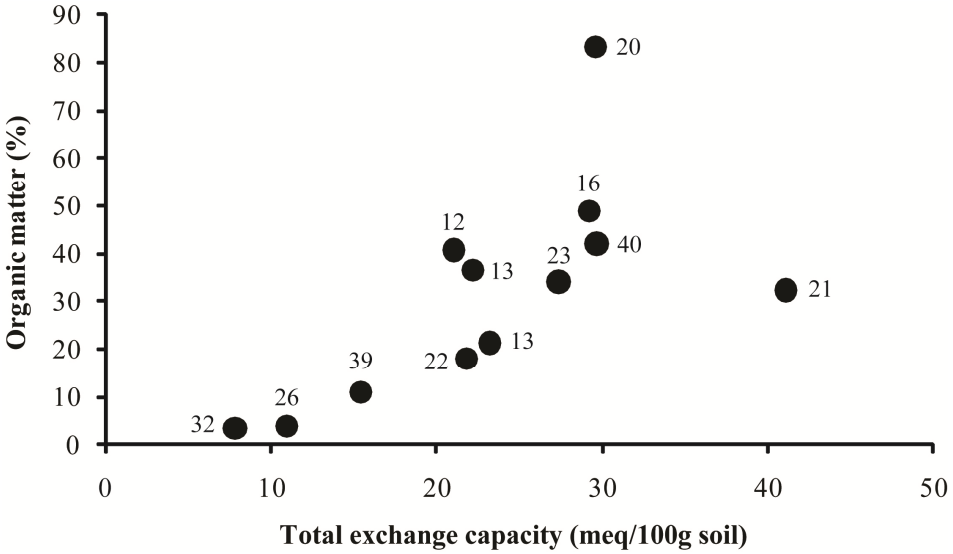

Figure 3. Illustration of the non-significant relation between soil richness (as the correlation between TEC and organic matter) and species richness in the study areas.

Table 3. Values for the Sørensen coefficient of community (upper right) and the Bray-Curtis distance (lower left) across study areas. Letter codes are used for all study areas (see below).

	A	B	C	D	E	F	G	H	I	J	K	L	M	N
A	---	0.30	0.52	0.40	0.47	0.37	0.30	0.29	0.42	0.36	0.26	0.20	0.26	0.26
B	0.85	---	0.30	0.26	0.27	0.21	0.35	0.24	0.32	0.23	0.15	0.22	0.30	0.30
C	0.72	0.84	---	0.58	0.62	0.57	0.43	0.49	0.44	0.45	0.34	0.32	0.33	0.45
D	0.75	0.84	0.36	---	0.59	0.51	0.46	0.49	0.47	0.40	0.40	0.33	0.35	0.44
E	0.73	0.83	0.39	0.42	---	0.64	0.54	0.46	0.64	0.52	0.35	0.36	0.46	0.46
F	0.76	0.89	0.41	0.43	0.46	---	0.47	0.51	0.48	0.45	0.31	0.23	0.30	0.46
G	0.79	0.76	0.63	0.58	0.58	0.70	---	0.43	0.65	0.66	0.50	0.50	0.54	0.54
H	0.73	0.75	0.66	0.62	0.68	0.65	0.54	---	0.45	0.60	0.30	0.27	0.35	0.41
I	0.74	0.78	0.63	0.60	0.58	0.64	0.37	0.48	---	0.62	0.40	0.51	0.55	0.55
J	0.76	0.74	0.65	0.63	0.67	0.67	0.37	0.45	0.38	---	0.47	0.47	0.57	0.51
K	0.86	0.94	0.84	0.79	0.83	0.81	0.77	0.81	0.79	0.72	---	0.57	0.48	0.48
L	0.83	0.88	0.82	0.77	0.78	0.82	0.73	0.78	0.72	0.62	0.49	---	0.55	0.55

Table 3. Continued.

M	0.79	0.75	0.71	0.70	0.69	0.74	0.60	0.60	0.61	0.46	0.68	0.53	---	0.69
N	0.86	0.85	0.71	0.67	0.72	0.78	0.69	0.73	0.73	0.68	0.67	0.62	0.46	---

Letter codes: A = Andrews Bald, B = Doi Inthanon, C = Perote forested, D = Perote non-forested, E = Malinche forested, F = Malinche non-forested, G = Llanos forested, H = Llanos non-forested, I = Ventoza forested, J = Ventoza non-forested, K = Cerro forested, L = Cerro non-forested, M = Chirripo forested, N = Chirripo non-forested.

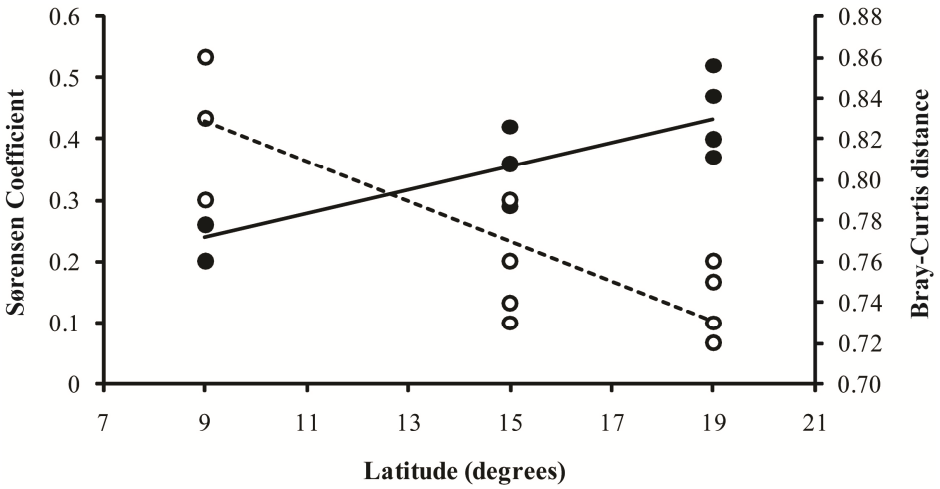

Figure 4. Relation between the beta diversity estimators used and latitude for the study areas in the Neotropics in comparison with Andrews Bald. Filled circles and continuous line represent the Sørensen coefficient index, whereas open circles and dotted line represent the Bray-Curtis distance.

Discussion

The total number of myxomycete records and species obtained in this investigation represent an overview of the myxomycete biota of high-elevation areas of the northern Neotropics. With the exception of *Didymium bahiense*, the most frequently encountered myxomycetes in the present study are also known from most countries in the Neotropics (see Lado and Wrigley de Basanta 2008). The most abundant species (*Didymium difforme*) was not recovered from any of the study areas in Costa Rica, where collections of this species have been made in the past. Field observations in these same mountains have indicated that *D. difforme* frequently grows on living plants such as *Cirsium subcoriaceum* (Less.) Petr. and *Bomarea costaricensis* Kranzlin. These two plants tend to occur in areas with particular edaphic conditions that are not characteristic of the two study areas used in the present investigation (see Chaverri 2008), an observation that might account for the apparent absence of *D. difforme*. The two next most common myxomycete species in the study areas, *Stemonitis fusca* and *Arcyria cinerea*, are among the most frequently encountered species in myxomycete surveys throughout the world. For this reason, they have been referred to as "cosmopolitan" in the past (e.g., Martin and Alexopoulos 1969). Whether or not they represent single biological entities that have a truly worldwide distribution is an issue that requires further investigation. However, it did not seem surprising to find these two species in the study areas evaluated in the present investigation, especially considering that the substrates upon which they typically occur are among those sampled.

For the three Neotropical countries evaluated, the frequency of myxomycete occurrence in moist chamber cultures decreased linearly at an average rate of almost 8%

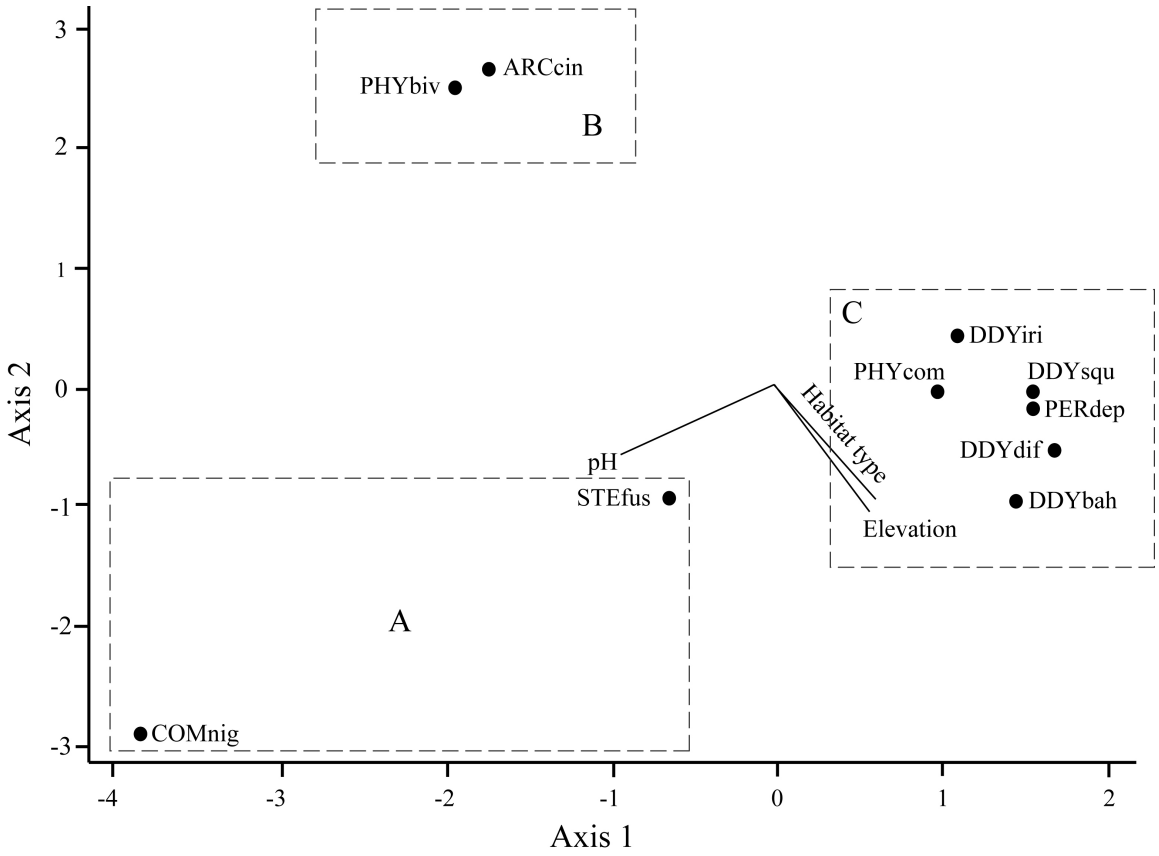

Figure 5. Principal Component Analysis ordination of the ten most frequently encountered myxomycetes in the study areas and apparent grouping of species based on the first and second most important environmental parameters. For abbreviations of species names see Table 1.

for each degree of latitude from Mexico to Costa Rica when only data from the three Central American study areas are considered. If the plant assemblages in these areas were the primary factor accounting for this pattern, then one would expect a similar degree of dissimilarity among the forests that occur along this latitudinal gradient. This does not seem to be the case. The taxonomic composition of high-elevation forests in Guatemala is more closely related to those in Mexico rather than to those in Costa Rica (Islebe and Kappelle 1994). It is possible that macroclimatic factors in the study areas play an important role in causing this pattern. Although under laboratory situations all moist chamber cultures were maintained at similar environmental conditions, substrates in the field are subjected to a number of environmental factors that differ among areas.

For example, both temperature and precipitation data obtained from different meteorological institutes in the countries studied differ among study areas. However, only precipitation shows a significant increment from Mexico to Costa Rica (not shown before, $F(2,57) = 16.25$, $P < 0.0001$, $R^2 = 0.35$) and by extension a high correlation with the percentage of positive moist chamber cultures along the latitudinal gradient (not shown before $R^2 = 0.99$, $F(1,1) = 110.59$, $P = 0.06$). In these mountain areas, the combined effect of rainfall and steep slopes probably accounts for an appreciable degree of "spore washing" from the different substrates reached by myxomycete spores, which might indirectly influence the patterns of higher occurrence of myxomycetes and the percentage of positive moist chamber cultures observed.

For the number of species observed at each different latitude, some other factors such as the taxa present and their particular ecology should be taken in consideration. However, since very little information on the ecology of myxomycete species is

supported by empirical data obtained using standard methodologies, the interpretation of this type of result is highly speculative. In the present study, one factor that should not be ignored is the unequal sampling effort for the two non-Neotropical study areas. Although the results obtained for these study areas cannot be properly compared with those from the study areas in the Neotropical region, the North American study area, which corresponds to a non-forested site, shows a greater species richness than the combined study sites for both study areas in Costa Rica. In a previous study in this same country, Schnittler and Stephenson (2000) reported that the total number of species obtained in moist chamber cultures for bark and litter were comparable for Costa Rica and temperate forests of Virginia in the United States. Our results do not conform to those from this previous study, but it is important to take into account the effect of major differences in the forest type from which material for laboratory study was collected, which were not very similar for these two studies.

Recent data indicates that the relative abundance of some species differs among forest types in Costa Rica (Rojas et al. 2009), which very likely has an impact on the density distribution of air-borne spores for different myxomycete taxa in different parts of the country. If this is the case, species that are better represented in a given forest type would have a higher probability of reaching suitable substrates within that same forest type than to be dispersed successfully to other forest types. Therefore, even though both studies may be used for comparisons, it is clear that the species composition and habitat characteristics of both assemblages are very different, which potentially explains the differences.

The number of species of myxomycetes recorded from Doi Inthanon was significantly lower (Table 1) than the number of species found at a similar latitude in Mexico. The forests in both regions of the world are seasonal and have similar dominant trees (*Quercus*-*Pinus* assemblages). However, the structure of the forest is very different for the two study areas. For Doi Inthanon, the high tree diversity (see Khamyong et al. 2004) results in a complex multilayered forest with a well-developed understory and subcanopy, whereas the forests of La Malinche and Perote are relatively simple in terms of their vertical structure, due the limitation of light reaching the lower parts of the forest (see Villers-Ruiz et al. 2006).

Also, both the precipitation and temperature regimes of the two regions are different. At Doi Inthanon (annual average temperature around 20˚C) temperatures are about three times higher than for either La Malinche or Perote, and the latter two areas receive between four and five times less precipitation than the study area in Thailand (around 160 mm rain/year for the last one). As mentioned earlier, it seems likely that higher levels of precipitation have an effect upon the colonization of substrates by myxomycetes, which would have to be considered along with the obvious detrimental effect of rain drops on the fragile myxomycete fruiting bodies. For instance, in the high-elevation oak forests of Costa Rica, precipitation levels seem to have an inverse relationship with the number of fruiting bodies and species of myxomycetes present at a given time (Rojas and Stephenson 2007), with the complex vertical structure of the Costa Rican forests also representing a factor of some (albeit undetermined) importance. The forest at Doi Inthanon should retain more water from evapotranspiration than the forests of La Malinche and Perote, which are also more exposed to the influence of the trade

winds. Presumably, the latter would serve to maintain higher levels of humidity within the forest in the first study area, which may have an effect on the number of myxoamoebae that begin the sexual cycle of myxomycete and ultimately produce fruiting bodies, as has been previously reported (see Stephenson and Stempen 1994).

No significant differences were found for both sampling period and overall distribution of substrates among the various study areas. This seems to be another indication that macroclimatic differences are an important driving force accounting for myxomycete distributional patterns at the larger scale in the region of study. Although the taxonomic composition of the plant assemblages of high-elevation areas in Mexico and Costa Rica are very different, myxomycetes seem to show similar patterns of occurrence on the substrates that were examined. This would not mean that the macroecological patterns of myxomycete assemblages for these two areas do not differ at all. The diversity indicators evaluated in this study showed that the Mexican study areas are richer and more taxonomically diverse than the more southern areas in the Neotropics. These differences seem to be associated more with the forested sites than with the non-forested sites, providing support to the idea that forest structure may account under certain conditions for the differences that exist between areas. The lack of differences at the diversity level for these study areas provides evidence at a different level.

It is thought that more evenly distributed assemblages of species are composed of taxa with similar competitive abilities. This concept has generated a number of theoretical models that attempt to explain the differences that exist among biological systems (see Magurran 2004). However, a common idea is that diversity is associated with both richness and relative abundance of the taxonomic units involved. In this way,

areas characterized by differing species richness but having similar diversity support assemblages of species with similar abilities that are occupying the niches available in the system. This is usually associated with a generalist pattern of resource utilization. For myxomycetes, even though it has been observed that related organisms seem to show specialized niches (e.g., Rojas et al. 2008), it has also been observed that levels of niche overlap are high for particular species in some assemblages (e.g., Stephenson et al. 1988). For the high-elevation areas of Costa Rica, Rojas and Stephenson (2007) observed high overlap values in most of the species comparisons that they considered when habitat use niches were studied.

If this high niche overlap is a generalized pattern in resource-limited systems such as the high-elevation areas in the Neotropics considered in the present study, then one would expect the different assemblages in the region studied to show a similar pattern of diversity, independent of their species richness. The data obtained herein may provide some evidence for the latter pattern, suggesting that the assemblages of myxomycetes in these areas are predominantly dominated by species that are likely to be present throughout the entire geographical area of study. Most of the frequently encountered species recorded from the study area in the Neotropics were also present at Andrews Bald and Doi Inthanon. Even though these species can represent taxa with widespread distributions and narrow niches, this does not seem to be the case based on previous ecological data on other tropical groups (see Rojas et al. 2008).

As mentioned earlier, macroclimatic factors seem to influence the distributional patterns of myxomycetes in the region of study. However, microclimatic factors such as substrate pH and soil chemical characteristics do not seem to be as important in

explaining the occurrence of myxomycetes (as a group) in the study areas. Both average and maximum pH showed a correlative trend with the number of records and species richness, suggesting that high pH levels might offer more suitable conditions for myxomycetes. The significant correlation of species diversity and minimum pH appears to suggest that beyond a certain point, acidity becomes a limiting factor for the occurrence of particular species, perhaps relating to the fact that a particular food resource is no longer available. Similar observations have been reported previously in the literature (e.g., Feest and Madelin 1988), also suggesting that simple physiological tolerance of myxomycete species to low acidity conditions does not seem to be the reason for this type of pattern (see Stephenson and Landolt 1996).

It is perhaps surprising that the majority of the chemical characteristics of the soil did not show any evidence of a relationship with the indicators analyzed for myxomycetes. Soil characteristics would indirectly influence the occurrence of myxomycete fruiting bodies, since these actually occur on plant debris and not directly on the ground. However, one would suspect that better soil conditions (i.e., higher levels of macronutrients) would have an impact on the plant assemblages in the study areas, which would likely affect the myxomycetes occurring on the plant debris present. Data reported by Stephenson and Landolt (1996) suggest that higher levels of calcium, magnesium and phosphorus might be correlated with higher species richness and possibly diversity. In the present study, only diversity — both at the ecological and taxonomic level — showed some relationship with chemical characteristics of the soil. However, only a moderately weak negative correlation with sodium was observed. This is interesting, since high levels of sodium in soils are usually associated with poorly drained soils with low

permeability (Marx et al. 1996) and are known to affect negatively particular species of bacteria (e.g., Gannon et al. 1991).

The highest levels of sodium were recorded for Chirripo (not shown), where the typical low-diversity paramo ecosystem occurs. In this area, dominated by the dwarf bamboo *Chusquea*, only some isolated trees occur (see Chaverri 2008). However, it seems that the low diversity of myxomycetes in this area is not the product of the *Chusquea*-dominated environment *per se*, but more of an indirect effect of the lack of a vertical forest structure in the treeless paramo. On the other hand, the weak correlation between the taxonomic diversity index and higher levels of phosphorus reflects that higher inputs of plant nutrients have a positive effect upon the production of plant structures (Mengel and Kirkby 2001). The availability of a higher number of plant structures increases by default the probability of myxomycetes to find more suitable microhabitats as expected. Obviously, this is not surprising. Also, the lack of a correlation between the levels of organic matter and the total exchange capacity (total cations) of the soil and any of the diversity indicators analyzed suggests that the relationship between soil richness and myxomycete diversity is not direct. As indicated earlier, it seems that the myxomycete indicators are only showing in an indirect way the effects of soil conditions on the plant assemblages and forest structure in the study areas.

The apparent patterns explained earlier seem to be somehow contradictory with the PCA analysis performed on the most frequently encountered species. For all study areas, the three most important variables do not show any significant differences; whereas in this analysis they appear to be explaining a large percentage of the variation exhibited in the dataset. This result is not contradictory and actually seems to be an

indication that the environmental parameters evaluated might not have a strong effect on the occurrence of the myxomycetes in the study areas when they are considered as a group, but are reflected when particular species are evaluated. A similar pattern was recently observed for the species assemblages present in different forest types in Costa Rica (see Rojas et al. 2009). This observation seems to provide an indication of the level of resolution at which ecological patterns for different taxonomic levels can be observed. Such pattern would also indicate that the dominant species of myxomycetes in the high-elevation areas evaluated may show individual environmental preferences in certain conditions, an aspect to evaluate in future projects.

The grouping of species observed in the PCA ordination may provide evidence for the latter type of ecological strategies that some myxomycete species are showing. For example, the two species in group A are characterized by long stalks and evanescent peridia; whereas the two species in group B show stalks of intermediate length and both dehiscent and non dehiscent peridia, and those in group C are sessile (including all records of *Physarum compressum* observed in this study) to short stalked and show primarily thick peridia. The combination of absence of stalk and thick peridium seems to be a very good adaptation for resistance in environments with harsh environmental conditions (see Estrada-Torres et al. 2009), which would easily explain the higher frequency of this form in the environmentally tougher non-forested areas. In forested conditions there seems to be a change in resource allocation and forms tend to have longer stalks and weaker peridia, which would presumably increase the potential capacity of the species in these areas to disperse and colonize the preferred milder microenvironments. In any case, our data is only suggestive and not conclusive in this

sense and experimental testing would definitely provide a better understanding of this phenomenon.

Finally, higher levels of similarity between study sites on the same mountain or study areas within the same country indicate the existence of regional species assemblages, suggesting that limitations on dispersal are not strong in these regions. Both the Sørensen index and the Bray-Curtis distance measure values for the different assemblage comparisons show a similar trend, even though the latter does not consider the relative abundance of the species. This similar pattern for both estimators may indicate that colonization processes are relatively more important in structuring the species assemblage of myxomycetes in the study areas. As expected, species assemblages in the study areas of the Neotropical region showed a decreasing degree of similarity with increasing distance from Andrews Bald. The relative abundance of the species present seems to play a secondary but non negligible role in the structure of the assemblage. The similarity of myxomycete assemblages when compared to Andrews Bald was slightly more significant when species abundance was included in the calculation. This similarity seems to be another indication that macroclimatic factors such as the precipitation of the areas discussed earlier, influence the abundance patterns of the myxomycetes present.

In summary, the data provided herein seem to indicate that myxomycetes in high-elevation areas of the Neotropics are subjected to a number of processes that shape the composition of the assemblages of species present. Among those processes, our data suggest that macroclimatic factors are important and that the composition of plant species in these high-elevation forests might not be as important in constructing these assemblages as it is the structure of forest. An experimental approach is needed to further

evaluate the mentioned factors. However, a number of limitations in relation to myxomycete manipulation in laboratory conditions represent an obstacle for experimentation at the moment.

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Chapter 7

Biogeographical aspects of high-elevation myxomycete assemblages in the northern Neotropics

Abstract: The biogeographical relationships of myxomycete assemblages around the world have been the subject of only a limited number of studies in the past. This study represented an effort to apply some of the relatively well-known biogeographical and ecological models to the observed structure of myxomycete assemblages, with emphasis on the northern Neotropical region. A series of 28 experimental plots located in 14 study sites within five different countries was surveyed during two consecutive years using a standard methodology that included both field collections and specimens obtained from moist chamber cultures. Results showed that myxomycetes in high-elevation areas of the northern Neotropics seem to have different levels of preference for macro- and microenvironments, varying degrees of niche breadth and overlap, and different patterns of species occurrence in comparable areas. In a similar manner, species assemblages along a latitudinal gradient that extends from Mexico to Costa Rica showed a decreasing level of similarity with an assemblage studied in the temperate forests of the eastern United Stated and were clearly distinct from an assemblage in Southeast Asia. The implication of these results is that myxomycete ecology in the study areas does not support neutral models of species distribution and appears to be better explained by niche-based models.

Keywords: community ecology, Central America, Doi Inthanon, Great Smoky Mountains, Mexico, myxogastria

Introduction

The myxomycetes or myxogastrids comprise a group of ameboid protists (Pawlowski and Burki 2009) known to occur throughout the world in microhabitats such as soil, decaying wood, bark, soft decomposing plant parts and herbivore dung (Stephenson 2003). The life cycle of these organisms involves a number of stages, including the production of fruiting bodies containing spores and the development of a mobile multinucleate macroscopic form known as a plasmodium (see Martin and Alexopoulos 1969), that would seem to have a positive effect on the dispersal capabilities of the whatever species might be considered. However, empirical data from several previous studies show that a number of myxomycetes seem to exhibit distribution ranges that appear to be associated with macro- and microenvironmental characteristics of the habitats in which they occur (see Stephenson et al. 2007).

Most of the studies on the group have been carried out in temperate forests of the northern Hemisphere (Stephenson 2003). However, an increasing number of investigations have taken place in recent years in other parts of the world (e.g., Tran et al. 2008, Ndiritu et al. 2009). These recent studies have generated important information relating to myxomycete diversity and patterns of occurrence at different ecological scales. However, despite these recent efforts, most tropical areas remain understudied. Even those areas such as the Neotropics, in which most recent ecological studies of tropical

myxomycetes have been carried out thus far, continue to generate important information on the global distribution and occurrence of the group.

The information generated in the context of the research directed towards tropical myxomycetes has contributed greatly to our understanding of the strategies utilized by these microorganisms in a number of ecological situations that are absent in temperate areas (e.g., Schnittler and Stephenson 2002, Wrigley de Basanta et al. 2008). Such studies have also been important in that they have investigated the different assemblages of myxomycetes in the tropical forests of Central and South America (see review by Stephenson et al. 2004b). However, in spite of this increasing research effort in the Neotropics, myxomycete assemblages associated with high-elevation areas have not been studied with the same intensity as low-elevation assemblages. For that reason, several recent studies (e.g., Schnittler et al. 2002, Rojas and Stephenson 2007) have been carried out in several mountainous areas of the Neotropics.

Unfortunately, due the impact of anthropogenic factors on mountain forests around the world (see Bubb et al. 2004), from which most high-elevations areas of the Neotropics do not escape (Brown and Kappelle 2001), the myxomycetes occurring in these areas are threatened as much as other organisms. The very fragmentation of these high-elevation forests provides the opportunity of studying several ecological aspects of the biology of myxomycetes that have not been fully considered in previous studies. In fact, the study of these organisms in areas with a high susceptibility to future climate change scenarios has the potential of providing important information regarding both the organisms considered and the ecosystems studied.

Moreover, these same myxomycete assemblages in high-elevation areas of the Neotropics represent an excellent choice to revisit classic macroecological and biogeographical questions for which the available evidence is not yet conclusive. For instance, a large number of widely accepted patterns of species distribution have been proposed based upon information obtained for macroscopic organisms, but the focus on larger organisms has historically limited the contribution of less conspicuous groups to the study of such patterns (see Secretariat of the Convention on Biological Diversity 2008). In contrast, modern ecological study has included the monitoring of organisms in space and time, the essence of biogeography (Cox and Moore 2000), as one of the priorities to understand how life on the earth responds to changing environments. As such, it is not surprising that the determination of species diversity, the key for biogeographical studies, has been recently considered one of the top 25 issues for science to address in the present century (Pennisi 2005).

In this context, the study described herein was designed with the main objective of providing baseline information on the biogeographical relationships of the myxomycete assemblages occurring in high-elevation areas of the northern Neotropics. The approach used was intended primarily to generate information that can be used in future studies, but it also provides information relating to the habitats studied, some of which might be changing rapidly.

Materials and methods

The present study was carried out during the period of 2006-2009. For species identification, the morphological species concept was used, following the taxonomic

treatment of Lado (2005-2010). Country codes follow the two-letter format recommended in the ISO 3166-1.

Study areas

A series of eight study areas was selected for investigation of the assemblages of myxomycetes present. Six of these areas are located in the northern section of the Neotropical region, one in eastern North America and one in Southeast Asia. For the Neotropics, two study sites that correspond to forested (F) and non-forested zones (NF) were selected in all study areas. A non-forested area was selected in eastern North America and a forested area was selected in Southeast Asia. In all cases, two experimental plots with an area of approximately 0.1 ha were established. As a result of this effort, a total of 28 experimental plots located in 14 study sites were used for this investigation.

The Neotropical areas are located in Mexico, Guatemala and Costa Rica. In the first country they correspond to (A) the Matlalcueyetl (=La Malinche) Volcano (hereafter abbreviated as MA, elevation 3100–4000 m), which is located between the states of Puebla and Tlaxcala and (B) the Cofre de Perote Volcano (PE, elevation 3400–4200 m) in the state of Veracruz. In Guatemala, the two study areas are located on the Cuchumatanes Plateau and correspond to (C) Llanos de San Miguel (LL, elevation 3400–3500 m) and (D) La Ventoza (VE, elevation 3400–3600 m). In Costa Rica, the two study areas are part of the Talamanca Range and correspond to (E) Cerro Buenavista or Cerro de la Muerte (CE, 3150–3450 m) and (F) Macizo del Chirripó (CH, 3150–3500 m). The forests in all these areas are very different in terms of their taxonomic composition, being

dominated by *Pinus* and *Abies* in Mexico, *Juniperus* and *Pinus* in Guatemala and *Quercus* in Costa Rica. Non-forested zones in the study areas are dominated by the tussock grasses *Festuca* and *Agrostis* in Mexico and Guatemala and by the dwarf bamboo *Chusquea* in Costa Rica.

The two external study areas correspond to (G) Andrews Bald (AB, elevation 1750 m), a non-forested area dominated by grasses, sedges and forbs and located in a high-elevation area of the Great Smoky Mountain National Park in North Carolina, United States and (H) Doi Inthanon (DI, 1400–1700 m), the highest mountain in Thailand, located in the province of Chiang Mai. The forests in the latter case are dominated by *Quercus* at higher elevations and by a *Quercus*-*Pinus* mixture at lower elevations.

Material studied

In order to obtain a representative sample of myxomycetes for analysis, all study areas in the Americas were visited on two occasions during the summers of 2006 and 2007. The study area corresponding to Doi Inthanon was visited only once during January of 2008. In all study areas a series of collections of 16 samples of material for laboratory study was obtained during each visit. Each collection consisted of four samples each of ground litter, aerial litter, twigs and bark collected randomly from each one of the experimental plots. As used herein, ground litter refers to dead plant material deposited on the forest floor and aerial litter corresponds to dead but still attached plant material that has not been in contact with the ground.

A total of 864 samples of material were collected for the entire study. Each sample was used to prepare three moist chamber cultures in the manner described by Stephenson and Stempen (1994), for a total of 2592 moist chamber cultures. In all cases, a small portion of the material for examination was placed in a standard size Petri dish previously lined with filter paper. After this, pH-neutral water was added until all the material was submerged in the liquid. The plate remained in this condition for 24 hours, after which excess of water was poured off. All moist chamber cultures were examined over a period of 10 weeks and the internal moisture of the plates was maintained by adding little amounts of water occasionally during the observation period.

When fruiting bodies of myxomycetes were observed, they were extracted from the moist chamber culture and placed into small pasteboard boxes that were deposited in the mycological herbarium of the University of Arkansas (UARK) for future reference. Identification of the species represented by the specimens of myxomycetes took place between 2006 and 2009 at the Laboratory for Mycetozoan Research of the University of Arkansas.

In addition to the moist chamber component, a series of field collections of myxomycetes was obtained from all study areas during each visit. For this, the opportunistic sampling protocol described by Cannon and Sutton (2004) was utilized. With this method, myxomycete fruiting bodies were searched for in each study area in a random fashion to minimize human errors and maximize the probability of finding rare species. When fruiting bodies were found, they were brought back to the laboratory and curated in the same way described earlier. The database used for analysis was created using the records obtained using the two different protocols.

General data analysis

In order to evaluate the completeness of the survey, a series of rarefaction curves was constructed using the records obtained from the moist chamber cultures. Species accumulation curves for each study area were generated using the abundance-based coverage estimator (ACE) values calculated by the program EstimateS, version 8.0 (Colwell 2006) with a cutoff value of 1.5% in abundance. These curves were adjusted later according to the formula $y = \frac{(ax)}{(b+x)}$ as suggested by Raaijmakers (1987). In addition to the latter, a series of rank-abundance plots was created for each one of the study areas. This approach has the advantage of being useful for evaluating species richness and evenness patterns among species assemblages (Magurran 2004), in a similar way to a classic alpha diversity analysis.

In addition to the latter, the relationships among species assemblages in the different study areas were evaluated by performing a cluster analysis using two different methods in the program PC-ORD, version 5.30 (McCune and Mefford 2006). The first approach evaluated corresponds to Ward's method, a general-purpose linkage procedure that minimizes distortions in the space created by the matrix of data. This method uses analysis of variance and Euclidean distances to evaluate the separation between groups. The second approach used is the furthest neighbor method, in which the distance between groups is determined by the greatest distance between any two species in the different groups. This method uses the Bray-Curtis distance index to determine spatial relationships among groups according to the classic formula for the Sorensen coefficient

of similarity and seems to be particularly useful in cases when the groups evaluated form naturally distinct units (McCune and Mefford 2006).

Evaluation of ecological models

The biogeographical relationships and both macro- and microecological aspects of the assemblages of myxomycetes associated with high-elevation areas also was studied. For this, an examination of four ecological models of species distribution was carried out, using different approaches and the database constructed with the records obtained from the various study areas.

The first model examined is the one often called the *ubiquity theory*, as revived by Fenchel and Finlay (2004). This theory basically proposes that microscopic organisms should occur everywhere on earth as long as suitable habitats permit their existence. To evaluate whether or not myxomycetes in the study areas show evidence of conforming to this theory, three secondary approaches were followed. For all these analyses, species from the original moist chamber culture or field collection datasets were placed in categories on the basis of their relative abundance, following a modification of the approach described by Stephenson et al. (1993). Those species with overall abundance values higher than 1.5% were considered as Abundant (A), those falling between 1.5-0.5% as Common (C), between 0.5-0.15% as Occasional (O) and those falling below 0.15% as Rare (R). Only those species falling in the abundant category were considered for the ubiquity theory evaluation, since the probability of obtaining statistical errors leading to wrong conclusions (Type I error) is increased when species that are not well-represented are included

Using this methodology, the first approach consisted of an evaluation of the occurrence and relative abundance of the most frequently encountered species in relation to the various study areas, using a probabilistic approach. For this analysis, the relative abundance of each species in the complete dataset was considered a product of both the capacity of the species to occur in a given environment and the existence of such environment. Since all study areas presented comparable environments and were surveyed at comparable times using a standard effort, the expected abundance of each species was hypothesized to be similar (not significantly different) across all study areas. The expected abundance values were calculated for each species as a product of the total number of records across study areas and tested against the observed values, using a standard Chi-Square formula with a rejection value of 0.05 for the null hypothesis, as calculated using the software program JMP, version 8.0. It is clear that there are a number of underlying reasons why species would not show such pattern. However, this approach still offers the possibility of providing information in relation to the occurrence of selected species in the studied areas.

The second approach, which represented an effort to assess the ubiquity theory, evaluated the particular relationship that exists between myxomycetes and the type of substrate upon which they occurred in the laboratory. A number of recent studies have shown that some species of myxomycetes appear to be highly substrate-specific. If this is a real pattern, it would provide evidence against the ubiquity theory, since organisms would not be expected to occur preferentially in certain microhabitats when a number of other suitable microhabitats are potentially available. For this evaluation, a series of analyses of variance was used to test the preference of the myxomycetes observed for one

of the four different substrate types collected. This examination was carried out on both the entire dataset and a series of subsets arranged by country. When null hypotheses were rejected, *post-hoc* Tukey tests were also performed to evaluate the direction of the distributions.

The third approach used to study the ubiquity theory consisted of an evaluation of the microenvironments in which species collected in the field were found. For this analysis, a series of microenvironmental variables associated with the field records was measured *in situ*. These variables correspond to a number of characteristics of the substrates upon which fruiting bodies were collected. These include pH, moisture, diameter, distance from the ground, substrate type and exposure to light. The first four variables were measured directly in the field using electronic devices (e.g., calibrated pH, moisture and distance meters), whereas light exposure was recorded using the protocol explained by Stephenson et al. (2004a). With this method, a categorical classification of light conditions is used to record this variable.

All these microenvironmental parameters were used to perform a multivariate analysis intended to provide information on the variation exhibited by the dataset. For this evaluation, a Principal Component Analysis (PCA) was carried out using the program PC-ORD, version 5.30 (McCune and Mefford 2006), with only the most abundant species being used in the calculations. In a similar manner, the same variables were also used to calculate the niche breadth and niche overlap of particular species using the MacArthur-Levins estimator in a similar manner to that described by Rojas et al. (2008). The idea behind using this approach is to evaluate the relationship between microenvironmental preference and niche breadth, which can provide important

information regarding the intrinsic ecological characteristics of myxomycete species and their relationship with observed distribution patterns.

In addition to the latter, an examination of species occurrence in relation to two microenvironmental parameters was carried out only for Cerro Buenavista in Costa Rica. To do this, two sets of data loggers were placed in the two experimental plots and records for temperature and relative humidity were obtained *in situ* for a period of one year. For both experimental plots, one data logger was located at ground level and the second one at 1 m above the ground. For those records of myxomycetes collected from a height of less than 50 cm above the ground, the data logger at ground provided the microenvironmental information, whereas records collected at heights above 50 cm were associated with the readings from the higher data logger. With this information, an analysis of the average temperature and humidity obtained at 7:00 AM in relation to the records found in the experimental plots was carried out using analysis of variance and *post-hoc* Tukey tests, using JMP, version 8.0.

The second model for evaluation corresponded to the *Unified neutral theory of biodiversity and biogeography* (UNT) proposed by Hubbell (2001). According to this theory, species within the same trophic level are ecologically equivalent and their existence is determined by a fundamental biodiversity constant. The relative abundances of the species in a guild are determined by two parameters, one denominated θ (theta), which controls the appearance of new species in the regional species pool, and a second one denominated *m*, which determines the immigration from the regional species pool into the individual communities. To evaluate this model, only records of myxomycetes obtained from moist chambers were used. The two parameters mentioned above were

calculated for each of the study areas, using a maximum likelihood-based estimation in the manner described by Etienne (2005) and with the program TeTame, version 2.0 (Chave and Jabot 2008). After this, a simple correlation analysis of these values and both the observed species richness and abundance values was performed with JMP, version 8.0, using a rejection value of 0.05 for the null hypothesis. This analysis is intended to provide evidence relating to a possible explanation of myxomycete distribution by means of neutral parameters.

The last two models examined represent an effort to assess whether or not niche-based methods are useful for an analysis of myxomycete distribution patterns. Although there are a number of niche-based models that have been used to explain community dynamics, it has been proposed that only the broken stick and the geometric series models properly explain the patterns found in nature (Dewdney 2003). Other models seem to have limitations in their biological interpretation due to their mathematical formulation (see Magurran 2004). The first of the models tested is based upon the fact that species occurring in the same area are dynamic enough to generate, in time, a mature and stable community where each taxon has similar competitive abilities. The second approach, the geometric series, is a theoretical construct based on the idea that niche preemption takes place by favoring the earliest inhabitants within a functional group in a particular ecosystem.

In order to evaluate which of these two niche-based models best explains the distribution of myxomycetes in the study areas, a series of tests was carried out. For this, all species were sorted from most to least abundant and then ranked on the basis of their abundance values. Following the method of Fattorini (2005), regression analysis was

used and the best fit model was selected, based on the correlation estimator. According to this concept, the model with the highest estimator is considered to be the better one to explain the observed pattern in nature.

In the first case, the analysis considered the distribution of observed abundance values and the theoretical values expected with the broken stick model. The latter were obtained by using the formula $A = b_o + b_i \log R$, where A is the species abundance, R is the respective rank and both b_o and b_i are optimized fitting parameters obtained from a system of equations for each observed dataset. For the geometric series model, values were obtained using the formula $\log A = b_o + b_i R$, where all parameters are the same as in the previous case. The correlation estimator obtained to evaluate the broken stick model distribution was the Pearson's product moment (R^2), whereas the fit index (FI) was calculated to test the geometric series model. The latter was obtained using the formula $FI = 1 - (RSS/TSS)$, where $TSS = \sum_{i=1}^{n} (Yi - Ya)^2$ and $RSS = \sum_{i=1}^{n} (Yi - Yb)^2$. In these calculations, Yi is the observed value, Yb is the backtransformed value of Y in the transformed space and Ya is the mean of the backtransformed data.

Results

A total of 1522 records including 149 field collections were obtained during the course of the present investigation. This effort generated a total number of 114 species for the complete study, 89 of which were recovered only from moist chamber cultures, 24 were only found in the field and 10 were recorded using both methods. The rarefaction curves generated with the data from moist chambers (Fig. 1) show that the sampling effort used with this methodology was adequate to recover most of the species from each

of the study areas. Only Doi Inthanon shows evidence of under sampling of the assemblage of myxomycetes present. The rank/abundance plots generated (Fig. 2) show similar structural patterns for the assemblages of myxomycetes in the various study areas, with the most obvious difference among study areas apparent for those in Costa Rica. The number of ranks is relatively similar in all cases except in Costa Rica, with an average of only 4.75 ranks per study area. Similarly, the relative abundance of the first ranks is lower in this same country, where the starting values for each study area are lower than one.

When assemblages of species were compared to one other using cluster analysis, the two methods for the calculation of the distances among groups produced different arrangements of study areas (Fig. 3). In both cases, all study areas corresponding to a particular country grouped together. However, when Euclidean distances were used, all the Mexican study areas formed a separate cluster when compared with the others. In the first instance, species assemblages from Andrews Bald and Doi Inthanon also group with the other Neotropical areas, and in the second instance, these two assemblages fall in the Costa Rican group. In contrast, when Bray-Curtis distance measures were used to evaluate the relationship of species assemblages in the study areas, a different result was obtained. In this case, the myxomycete assemblage from Doi Inthanon falls apart from any of the other groups, and the assemblage from Andrews Bald shows a higher degree of similarity with those from Mexico and Guatemala. In the second case, the assemblages from Costa Rica form a different cluster than the one composed of the latter study areas.

When the models of species distribution were evaluated, a series of different patterns was apparent. The most frequently encountered species recorded from moist

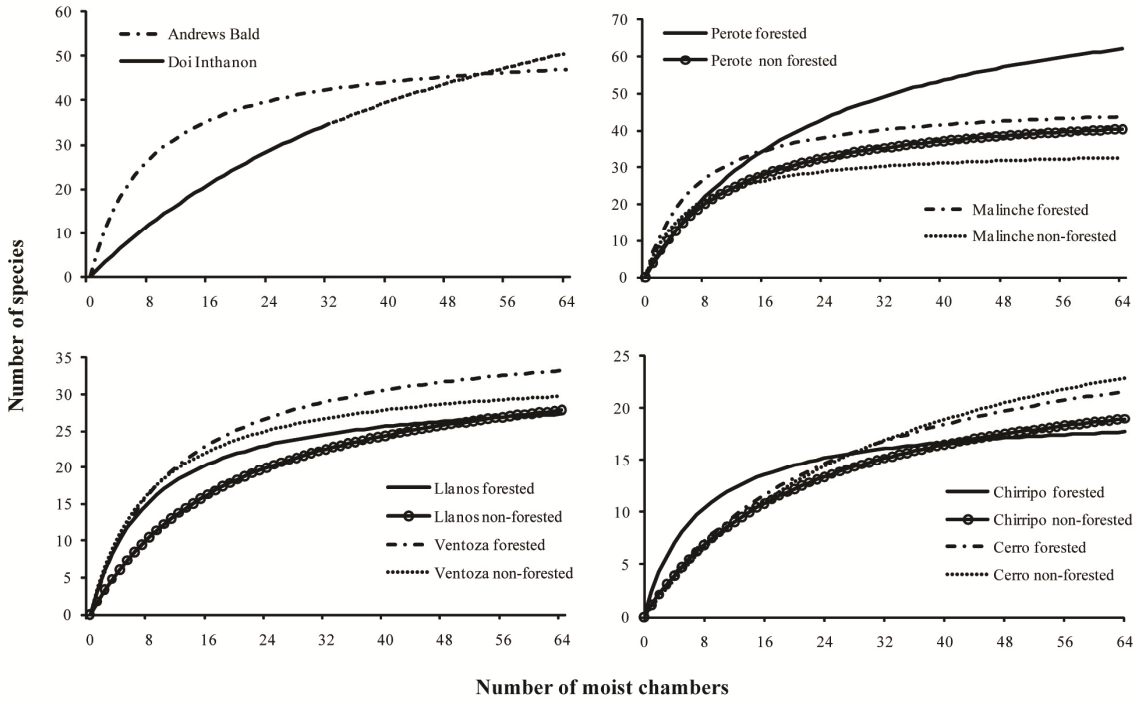

Figure 1. Species accumulation curves generated for each study area using the rarefaction values for the abundance-based coverage estimator (ACE).

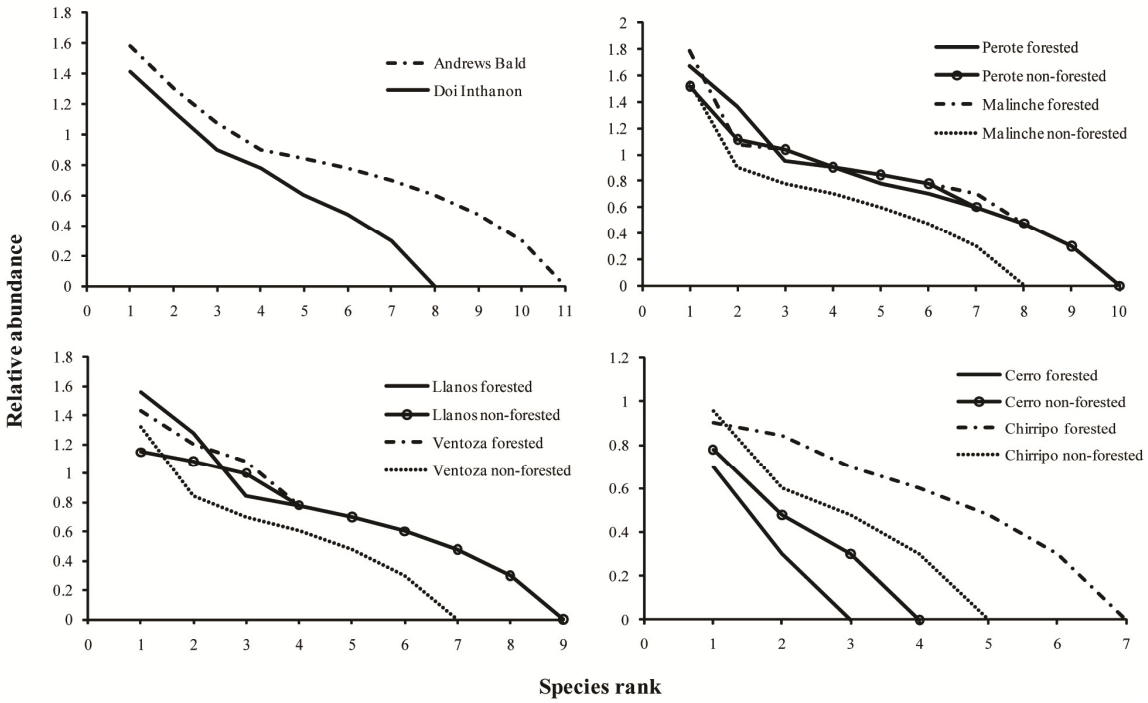

Figure 2. Rank abundance plots generated for each study areas based on records obtained from moist chamber cultures.

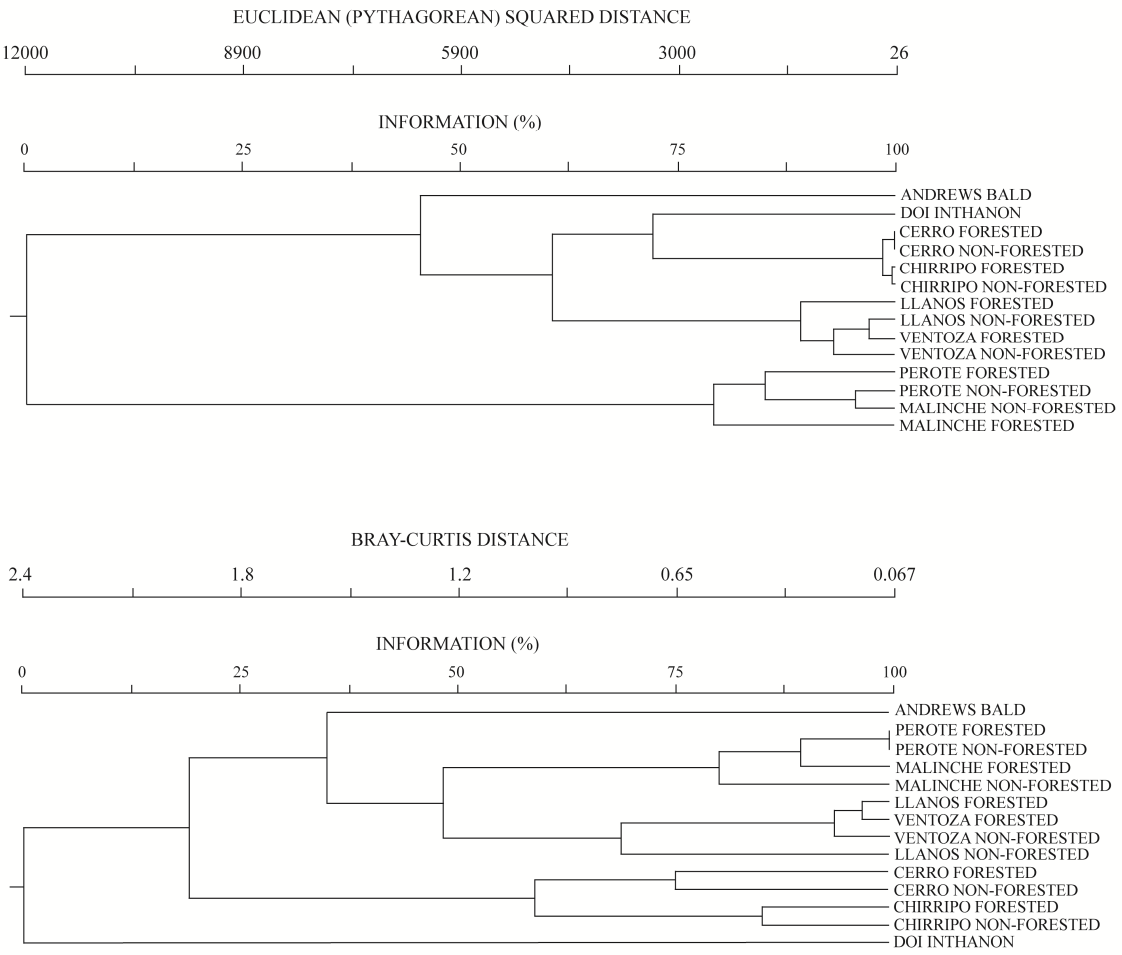

Figure 3. Arrangement of species assemblages from the different study areas by means of cluster analyses performed using the Ward's method (above) and the Sorensen's method (below).

chamber cultures were not present in all study areas and showed uneven abundance values (Table 1). All goodness of fit Chi-square tests performed using the numerical values for species abundances across study areas yielded significant differences (not shown, $P < 0.01$ in all cases). In a similar manner, the substrate-specificity evaluation showed that myxomycetes exhibit a preferential use of some of the evaluated substrates in the study areas (F (3, 356) = 4.34, P = 0.005, R^2=0.05). The results from this analysis show that aerial litter is more frequently used than either ground litter (Tukey, P = 0.032) and bark (Tukey, P = 0.0052). When substrate use is evaluated for each country separately, significant differences were found only for Costa Rica (F (3, 68) = 3.43, P = 0.02, R^2=0.13). As in the previous case, myxomycetes were found more frequently on aerial litter than on ground litter (Tukey, P = 0.03) and bark (Tukey, P = 0.03).

The Principal Component Analysis showed that about 72% of the variation in the dataset is explained by the first three components, which are light exposure, height above the ground and substrate moisture. The ordination of the 16 field-collected most abundant species is presented in Fig. 4. Average values for both temperature and relative humidity in the experimental plots in Costa Rica are also provided for the core of species around the center of the ordination and the three outlier species. The specific analyses performed with the microenvironmental information recorded in the field indicate that there are differences in temperature (F (21,58) = 5.71, P = 0.0001, R^2 = 0.67) and atmospheric moisture (F (21,58) = 5.60, P = 0.0001, R^2 = 0. 66) associated with the different species. One of the outlier species (*Arcyria cinerea*) in the PCA ordination was collected from significantly warmer microenvironments than the other species (Tukey, P = 0.001). In contrast, *Ceratiomyxa fruticulosa*, one of the species in the core group, was collected in

Table 1. The ten most frequently encountered species of myxomycetes (top to bottom) and their distribution by abundance class across the countries, study areas and vegetation type-based study sites evaluated in this study. For abbreviations see Materials and methods.

Species	**Species code**	**Country / Study area / Vegetation type**													
		US	**TH**	**MX**				**GT**				**CR**			
		AB	**DI**	**PE**		**MA**		**LL**		**VE**		**CE**		**CH**	
		NF	**F**	**F**	**NF**	**F**	**NF**	**F**	**NF**	**F**	**NF**	**F**	**NF**	**F**	**NF**
Didymium difforme	DDYdif	O	R	A	A	A	A	C	O	C	O				
Stemonitis fusca	STEfus	C		C	C	O	C	A	C	A	A	O	O	C	O
Arcyria cinerea	ARCcin	A	O	O	O	O		C	C	O	O	R	R	O	O
Didymium iridis.	DDYiri	O	C	O		O	O	O	C	C	C			O	R
Didymium squamulosum	DDYsqu		O	O	O	C	R	C	O	R	O		O	O	R
Comatricha nigra	COMnig	C		A	R	O	O	R		O	O	R	R	O	R
Physarum compressum	PHYcom			C	C	C	R	O	O	O	R	R	R	O	C
Perichaena depressa	PERdep		R	O	C	C	O	O	O	O	O			R	R

Table 1. Continued.

Physarum bivalve	PHYbiv	C		O	C	R	O		R	R	R	R			
Didymium bahiense	DDYbah			O		O	R	O		C	R	R	R		R

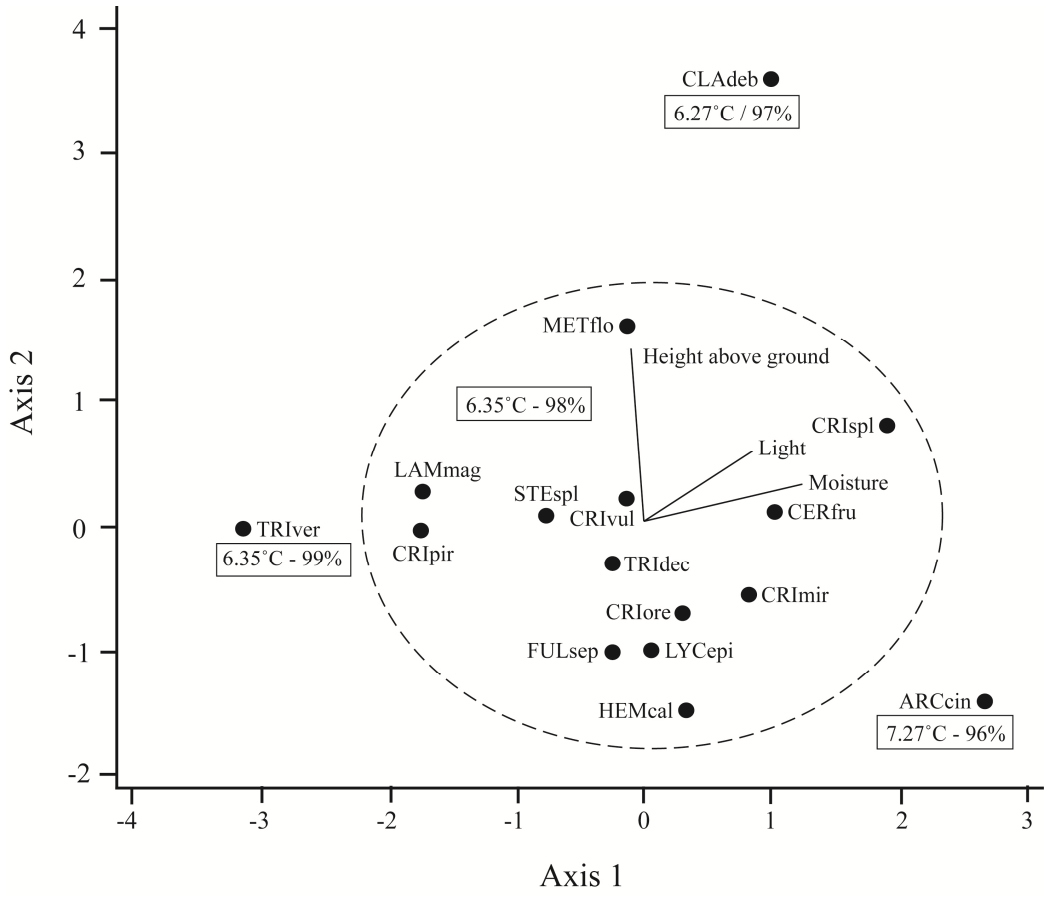

Figure 4. Principal Component Analysis (PCA) ordination of the 16 most abundant field-collected species in all study areas that shows the three most important microenvironmental components as internal axes. A central core of species is defined by the dashed line and three outliers can be identified. For both these and the central core of species, temperature and relative humidity values are provided in boxes. These measurements correspond to the values obtained for all species found in the Cerro de la Muerte study area.

significantly dryer microenvironments than the other species (Tukey, $P = 0.05$).

The lowest values for niche breadth were obtained for *A. cinerea*, *Clastoderma debaryanum* and *Cribraria oregana*, whereas the highest values were obtained for *Cr. mirabilis* and *Stemonitis splendens* (Table 2). In a similar way, *Cr. mirabilis* and *Fuligo septica* show high values of niche overlap with the other abundant species ($M = 0.88$ for both species; $SD = 0.13$ and 0.14, respectively), whereas the lowest average values of overlap were obtained for *Cl. debaryanum* and *A. cinerea* ($M = 0.60$ and 0.62, $SD = 0.11$ and 0.14, respectively). The difference in niche overlap values between *Cr. mirabilis* and *Cl. debaryanum* is significant but moderately weak (F (1,13) = 5.13, P =0.04, $R^2 = 0.28$).

The values obtained for θ and m, the two neutral parameters evaluated, show that considerable variation exists among the different study areas (Table 3). The highest value for theta was obtained for the forests at Cofre de Perote, whereas the oak-dominated forest of Macizo del Chirripó had the lowest value. In a similar way, the highest value for m was obtained for the non-forested area of La Malinche, whereas the forested area at Llanos de San Miguel was characterized by the lowest value for the same parameter. The correlation analyses performed show a significant linear correlation between the m values and both species richness and species abundances in the study areas (for species richness F (2,11) = 4.08, $P = 0.04$, $R^2 = 0.42$; for species abundance F (2,11) = 6.13, $P = 0.01$, $R^2 = 0.52$). However, in both cases the significant relationship corresponds to a second-degree polynomial correlation with a low point associated with the intermediate values of m.

When the two niche-based models were evaluated, all the linear correlation values were high (Table 3) and there was no overall pattern of model dominance. The broken

stick model is better than the geometric series model in explaining abundance distribution in eight of the study areas, whereas the latter provides a better explanation of abundance distribution for the remaining six areas. For six of the seven non-forested areas, the broken stick model showed the highest correlation values of the model pair, whereas for five of the seven forested areas, the geometric series model provides a better fit for the observed distributions.

Discussion

The numbers of records and species recorded from each of the study areas during this investigation are similar to those reported in previous studies. Using a comparable sampling scheme, Rojas and Stephenson (2007) found an average of 24 species of myxomycetes per study site in a high-elevation forest in Costa Rica, whereas during the present investigation the average was 23 species per study site (not shown previously). It is evident that both the numbers of records and species are associated with the sampling effort and that the overall higher numbers recovered from moist chamber cultures most likely respond to the more systematic approach that is followed when using this method. However, field collections and moist chamber cultures are complementary approaches for the study of myxomycetes (see Stephenson 2004b), and in both cases their ecological use is meaningful when information at different levels is required.

Table 2. Niche breadth and overlap values for the 16 most abundant species obtained from field collections in the study areas.

Species code	Niche breadth	Species code															
		A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P
A	1.99	1	0.74	0.43	0.64	0.95	0.53	0.79	0.72	0.63	0.77	0.51	0.62	0.50	0.53	0.65	0.41
B	3.03		1	0.75	0.92	0.80	0.87	0.95	0.98	0.93	0.97	0.86	0.91	0.82	0.85	0.94	0.79
C	2.04			1	0.55	0.47	0.65	0.56	0.55	0.53	0.52	0.68	0.59	0.88	0.65	0.57	0.68
D	3.46				1	0.71	0.99	0.87	0.94	0.98	0.89	0.98	0.99	0.97	0.97	0.97	0.94
E	2.17					1	0.61	0.85	0.78	0.70	0.83	0.59	0.68	0.57	0.61	0.72	0.48
F	3.21						1	0.93	0.93	0.93	0.92	0.98	0.94	0.80	0.95	0.95	0.92
G	2.83							1	0.94	0.87	0.97	0.80	0.86	0.82	0.82	0.89	0.72
H	3.11								1	0.94	0.96	0.89	0.93	0.89	0.88	0.96	0.83
I	3.38									1	0.99	0.97	0.98	0.93	0.95	0.98	0.94
J	2.93										1	0.82	0.88	0.81	0.82	0.91	0.74

Table 2. Continued.

K	3.16	1	0.92	0.82	0.94	0.93	0.94
L	3.43		1	0.75	0.97	0.97	0.97
M	2.54			1	0.79	0.73	0.81
N	3.46				1	0.99	0.88
O	3.27					1	0.83
P	2.94						1

Codes used for species names: A = *Arcyria cinerea*, B = *Ceratiomyxa fruticulosa*, C = *Clastoderma debaryanum*, D = *Cribraria mirabilis*, E = Cribraria oregana, F = *Cribraria piriformis*, G = *Cribraria splendens*, H = *Cribraria vulgaris*, I = *Fuligo septica*, J = *Hemitrichia calyculata*, K = *Lamproderma magniretispora*, L = Lycogala epidendrum, M = Metatrichia *floriformis*, N = *Stemonitis splendens*, O = *Trichia decipiens* and P = *Trichia verrucosa*

Table 3. Values for the estimators θ and m according to the neutral theory and regression analysis values obtained for the two abundance models being evaluated as arranged by study area. For abbreviations see Materials and methods.

Study areas	**Neutral model**		**Abundance models**	
	θ value	***m* value**	**BS R^2**	**GS *FI***
Andrews Bald (non-forested)	3.28×10^9	0.07680	0.949	0.933
Doi Inthanon (forested)	1.47×10^9	0.08207	0.944	0.973
Cofre de Perote forested	5.51×10^9	0.08174	0.873	0.936
Cofre de Perote non-forested	819.369	0.08774	0.990	0.939
La Malinche forested	16.8282	0.62407	0.960	0.850
La Malinche non forested	12.1712	0.67336	0.982	0.857
Llanos de San Miguel forested	46.5926	0.07616	0.809	0.882
Llanos de San Miguel non-forested	22.7779	0.19478	0.982	0.908
La Ventoza forested	52.9382	0.09188	0.963	0.972
La Ventoza non-forested	4.41×10^8	0.12803	0.991	0.953
Cerro Buenavista forested	21.0169	0.57973	0.956	0.978
Cerro Buenavista non-forested	21.5408	0.48517	0.978	0.982
Macizo del Chirripó forested	12.8708	0.28590	0.991	0.890
Macizo del Chirripó non-forested	16.5278	0.33027	0.986	0.957

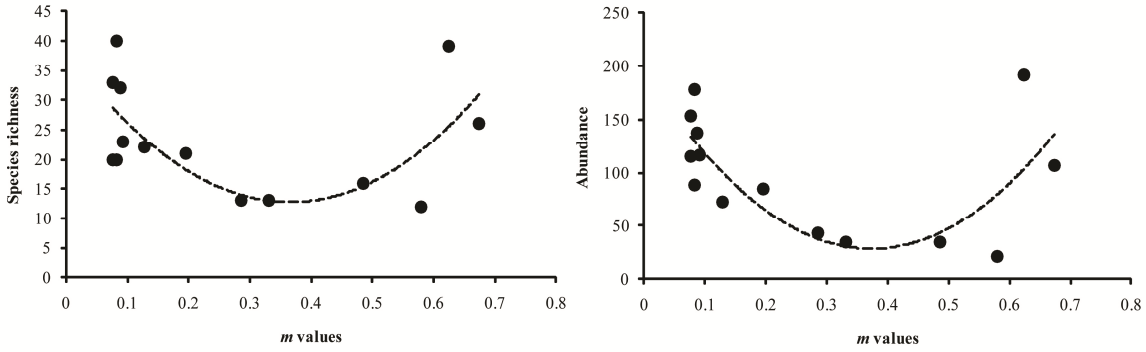

Figure 5. Simple correlation analysis plots of the neutral parameter *m* evaluated in relation to both species richness and species abundance recorded for the study areas. In both cases correlations are polynomial of second degree. Degree of statistical significance is provided in the results.

The rarefaction curves generated indicate that for most areas the sampling effort was sufficient. It is clear that a higher number of samples probably would have yielded a higher number of species. However, this is difficult to assess, as a large body of evidence showing that myxomycetes are randomly distributed in tropical forests is still lacking. The latter is one of the assumptions of rarefaction analyses, and if myxomycetes in the high-elevation forested areas that have been studied are not randomly distributed, then this type of technique might have overestimated the actual species richness in the study areas (see Magurran 2004). In any case, the technique is still useful for comparing the species richness for different sampling efforts among study areas. When this is done, it is not surprising that the data set for Doi Inthanon shows that more effort would have been necessary in this study area to recover most of the taxa present.

Notably—and this is perhaps the value of the information from this study area—the species richness at Doi Inthanon based on a smaller sample size is still higher than the species richness of all areas in Costa Rica and comparable to the species richness found in the study areas in Guatemala. In fact, the rank-abundance plot for this study area shows what is presumably a less preemptive assemblage than in the case for Costa Rica and a pattern that is very similar to Guatemala as well. The species composition and distribution of the myxomycete assemblage at Doi Inthanon are somewhat different than those found in these two Neotropical countries (Rojas et al., unpublished data), but such a difference in species richness and distribution is probably associated with a number of external factors as well.

When the species richness and the rank-abundance plots of all the study areas are analyzed in detail, it seems that the high-elevation forests of Costa Rica provide the least

favorable conditions for myxomycetes. A similar observation was reported for the myxomycetes associated with twigs when the assemblages associated with samples from different geographical locations of the world were compared (see Stephenson et al. 2008b). In contrast, forests in Mexico seem to favor the occurrence of the group in terms of both overall diversity and abundance. When only open areas are considered, Andrews Bald seems to support the most species-rich assemblage. Recent studies have shown that Mexico is a region with a comparatively high number of myxomycetes present (e.g., Wrigley de Basanta et al. 2008, Estrada-Torres et al. 2009). However, other studies carried out in temperate forests of Eastern North America have shown complex and species-rich assemblages as well (Stephenson 1988, Stephenson et al. 2001).

Whether or not temperate areas truly support the highest diversity of myxomycetes, which is the prevailing view of myxomycete distribution, is a question that still requires more study in tropical and boreal areas of the world. However, the pattern shown by the data generated in the present study seems to indicate that both the diversity and abundance of myxomycetes are highly dependent on the characteristics of the forests with which these organisms are associated. Such a pattern of different levels of microenvironmental preference in myxomycetes has been reported for temperate (e.g., Stephenson 1988) and tropical areas (e.g., Schnittler 2001, Schnittler and Stephenson 2002, Rojas et al. 2009).

It is remarkable to note that the relationships that existed among the study areas differed depending on the particular algorithm used when the cluster analysis was carried out. This is not surprising and has been well documented for the Euclidean and Bray-Curtis distance measure protocols in the past (e.g., Ludwig and Reynolds 1988).

However, in the analysis provided herein, irrespective of the distance measure used, the study areas of the three Neotropical countries grouped together. This is somewhat remarkable when considering that Euclidean distance-based analyses are less sensitive and tend to split groups by emphasizing outliers (McCune and Grace 2002). The differences in the relationships that exist among the study areas when the two methods used in the analysis are observed relies on the position of the groups and the two non-Neotropical areas. In the case of the Bray-Curtis distance-based analysis, the arrangement of study areas seems to have more biogeographical significance.

All the study areas in the Americas form a group that is separate from Doi Inthanon, the only non-American area. In addition, the relative positions of the Neotropical areas suggest that the species composition of the assemblages of species that exist along the latitudinal gradient that extends from Mexico to Costa Rica show a pattern of decreasing similarity to the temperate study area at Andrews Bald. In contrast, a previous study carried out by Rojas and Stephenson (2007) suggested that there was some affinity between myxomycete assemblages in high-elevation areas in Costa Rica and temperate areas in North America. Moreover, the grouping of Mexican and Guatemalan areas suggests that these areas have some aspects in common. This may be related to a combination of the patterns of microenvironmental preference exhibited by particular species and the fact that the plant composition and forest structure for high-elevation areas of these two countries is very similar (see Islebe and Velazquez 1994).

In the same way, the difference in abundance for the ten most frequently encountered species among study areas suggest that the distribution of these taxa depends on more factors than just the intrinsic characteristics of each species. This observation

supports other distributional analyses of myxomycetes carried out recently (e.g., Stephenson et al. 2008a). Although most of the species considered in the present study have known broad distribution ranges, it is very likely that they show ecological differentiation of some type. Even at the substrate preference level, as analyzed herein, some differences could be detected among the species making this group of abundant taxa. The preferential use of aerial substrates in the Neotropics, especially in Costa Rica, is one of those patterns. However, this apparent preference of myxomycetes for aerial substrates, which was already documented for tropical areas (see Stephenson et al. 2004b, Stephenson et al. 2008a) may also be a simple response to particular environmental factors such as high levels of moisture.

For example, the higher moisture content of ground substrates in these study areas, a condition that is apparently not suitable for the production of fruiting bodies (see Black et al. 2004), very likely influences the apparent substrate preference. In a previous study in the highland oak forests of Costa Rica, Rojas and Stephenson (2007) reported a negative correlation between the number of fruiting bodies present in the field and the precipitation registered for the area in which their study was carried out. Rollins (2008) observed a similar pattern along a gradient of decreasing precipitation in the grasslands of North America. At the same time, the use of aerial litter by myxomycetes may also be related to the availability of this substrate type in the study areas. In habitats where aerial substrates are limited, there tends to be a low incidence of myxomycetes on this type of substrate (e.g., Estrada-Torres et al. 2009).

Unfortunately, studies of environmental variables of this type and their effect upon the compositional and abundance dynamics of assemblages of myxomycetes are

still at a relatively early stage. However, the results obtained from the microhabitat-centered PCA analysis demonstrate the functionality of this approach when it is used in combination with environmental data collected *in situ*. In this case, the effect of distance from the ground on the average temperature and moisture of particular microhabitats and its subsequent effect on the species of myxomycetes occurring under the different environmental conditions is apparent from the results provided herein. However, the two of the outlier species in the ordination did not show any deviation from the central tendency values when the individual parameters measures *in situ* were tested. This may represent an indication of a combined parameter-based response from myxomycetes, which would actually more accurately resemble a natural pattern. For example, in one recent study, Rojas and Stephenson (2007) showed that the combined effect of some microenvironmental variables on the presence of myxomycetes in a high-elevation forest in Costa Rica was stronger than the individual effect of a particular variable when the two types of analyses were carried out. Similar observations have been reported for other types of biological systems (e.g., Schnittler et al. 2006).

Some species showed an apparent preference for a particular set of conditions when the *in situ* environmental parameters are analyzed. For example, our results indicate that *Arcyria cinerea* was generally associated with warmer microenvironments than any of the other common species, whereas *Ceratiomyxa fruticulosa* was found more frequently in comparatively dryer microenvironments. Both are myxomycetes generally regarded as being widely distributed species (see Martin and Alexopoulos 1969), which would, in theory, have a higher probability of showing broad preferences for such parameters. In the case of *A. cinerea,* this is not supported by the narrow niche shown in

the results. However, the apparent restricted ecological distribution of *C. fruticulosa* is supported by the results of niche breadth analysis and by other observations made in Neotropical lowland forests (e.g., Rojas et al. 2008). Previous studies have shown that both species are more frequently recovered in field surveys carried out in mid-elevation localities where a combination of moderate rainfall and warm temperatures is present (see Tran et al. 2006, Stephenson and Landolt 2009). It seems that the more moist and relatively colder high-elevation study sites surveyed in the present study influence their occurrence in a different way.

In any case, the different levels of niche overlap among the various species and the significant differences that exist between extremes seem to be an indication of specialization. The body of data available supporting this observation has increased considerably over the past decade for tropical areas, and includes evidence for certain species at different ecological levels such as microhabitats (Wrigley de Basanta et al. 2008), ecosystems (Estrada-Torres et al. 2009) and forest types (Rojas et al. 2009). The data obtained in the present study show that species such as *Clastoderma debaryanum* and *Cribraria mirabilis*, commonly associated with more temperate environments, do sometimes occur in temperate-like environments in the Neotropics. This conforms to previous observations for other species made in high-elevation areas of Costa Rica (Rojas et al. 2009) and, to a lesser extent, similar areas in Guatemala (see Estrada-Torres et al. 2000).

When the neutral parameters were analyzed, it seems evident that the assemblages of species associated with the high-elevation areas evaluated in the present study do not support the neutrality concept for myxomycetes. There was no clear pattern of the

influence of these parameters on the dynamics of the assemblages studied under the assumptions of the UNT (see Hubbell 2001). This is not a surprising finding, since it is widely recognized that "neutral" communities may occur only in theory (see Doncaster 2009). Regardless of such an observation, the results obtained for this analysis indicate that some ecological aspects related to myxomycete assemblages undoubtedly deserve further study. For example, both θ and m values showed a significant correlation with species richness. In fact, in the latter case, our results also revealed a significant correlation with species abundance.

In theory, high values for θ should be associated with high speciation rates and larger metacommunity sizes. In the example presented herein, assemblages of species in the various study areas ("communities") are assumed to belong to the same "metacommunity" according to the neutral theory. Therefore, θ values would indicate that speciation rates in the different areas show some variation. However, in real terms it does not make very much sense that comparable study areas have the dramatically different θ values observed in the results we obtained. What these do seem to indicate is that such high values may correspond to species assemblages in study areas with different conditions, which in this case may be the result of a number of factors.

One element to consider in this analysis is that all study areas with high θ values seem to have a stronger human influence. For instance, the natural character of the non-forested areas (balds) in the Great Smoky Mountains is still a matter of debate (Jenkins 2007), and the extent of human influence on the vegetation of Doi Inthanon, Cofre de Perote and the Cuchumatanes area has been well documented (e.g., Steinberg and Taylor 2008 for the latter). Although levels of disturbance were not assessed in the study areas

and the observations made are highly speculative, one possible implication of this neutral parameter-based approach is that similar areas with different levels of disturbance might be expected to show different degrees of species richness. In this sense, recent empirical evidence suggests that for myxomycetes, this pattern seems to be case for at least some natural systems (e.g., Tran et al. 2008, Ndiritu 2009).

In a similar fashion, the significant polynomial correlations obtained when the parameter *m* was analyzed seem to suggest that the dynamics that occur within and among assemblages of species in the various study areas are determined by more than one factor. This is not surprising in the context of biogeographical analysis, since similar patterns have been suggested by the data sets obtained in other studies of myxomycetes (e.g., Stephenson et al. 1993). The high values of species richness and abundance associated with low values of the migration parameter established in the neutral theory suggest that species occurring in areas with strong limitations on dispersal show evidence of coexistence. This can be associated with the capacity of particular groups of sympatric myxomycetes to exhibit microhabitat preference, as it has been observed in the genus *Ceratiomyxa* (Rojas et al. 2008) and also suggested for tropical myxomycetes in general on the basis of data obtained in other recent studies (e.g., Stephenson et al. 2004b, Rojas et al. 2009).

The correlation values obtained in the evaluation of both niche-based species abundance models were consistently high. Even though the approach followed does not provide enough evidence to favor one model over the other, it would not be surprising that myxomycetes actually use more than one ecological strategy, depending upon the conditions that exist for a particular system. The results presented herein suggest, for

example, that the taxonomic composition of assemblages of species in non-forested areas are best explained by the broken stick model, an explanation that assumes a low degree of niche preemption. In contrast, non-forested areas in the northern Neotropics tend to provide more severe environments than neighboring forested areas (see Brown and Kappelle 2001), and one would assume that a higher degree of species displacement would occur in the former. On the other hand, the higher correlation values of species assemblages in forested areas with the geometric series model would appear to indicate that inter-specific competition is stronger in this type of situation. Evidence for tropical forests is not conclusive, as one could argue that the use of non-traditional substrates such as inflorescences (Schnittler and Stephenson 2002) and lianas (Wrigley de Basanta et al. 2008) has the potential to broaden spatial niches for tropical myxomycetes or, conversely, be an indication of niche separation in particular species.

Whatever the case, these interpretations do not seem to support the species richness values obtained in most of the study sites, which show that non-forested areas supported fewer species than forested ones across the entire region being subjected to study. However, in a recent comprehensive analysis of the ecology of myxomycetes in Costa Rica, Rojas et al. (2009) found that most species seem to show macro- and microenvironmental associations of some kind. In this context, the contrasting results of the niche-based species abundance analysis seem to be an indication of a response to multiple factors as well.

In summary, it appears that the patterns of myxomycete occurrence indicate that this group exhibits variable degrees of ecological association in the high-elevation areas studied. These preferences have been not only detected but actually documented for

particular species in this and other studies. If the revived concept of Fenchel and Finlay (2004) applies to microorganisms such as myxomycetes, it would be highly unrealistic that a consistent pattern of microenvironmental preferences would be documented at different ecological levels for the localities examined in both the present study and other investigations carried out in other parts of the world. In a similar way, the UNT proposed by Hubbell (2001) seems to be unrealistic in explaining the patterns of biodiversity and distribution of myxomycetes in the high-elevation areas studied. However, this approach still offers the possibility of revealing possible patterns of ecological association that can determine the direction of future research. In this sense, it is very likely that niche-based models still offer the best arguments to explain biogeographical patterns in high-elevation Neotropical assemblages of myxomycetes. The data presented herein seem to indicate the latter. For this reason, even though the magnitude and direction of a number of environmental variables can have on the dynamics of myxomycete assemblages and particular species is still a subject that requires additional study, it is clearly evident that different myxomycete species are not ecologically equivalent.

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Chapter 8

A review of Costa Rican myxomycetes

Abstract: No comprehensive review of the taxonomic composition of the assemblage of myxomycetes known from Costa Rica has been done since 1975. As a result of a series of studies carried out in the country during the last decade, considerable additional data now exist, and this review provides an update on this group of organisms. Collecting carried out in Costa Rica since 1975, a review of the published literature, and an examination of herbarium specimens were used to generate an annotated list consisting of a total of 208 species in 36 different genera. This includes 62 species not previously reported from Costa Rica. The relative abundance of the different orders follows the expected distribution for the Neotropics, with the order Physarales being the most abundant. The data also show that the distribution of species is highly heterogenous. This suggests that most myxomycetes in Costa Rica are highly specialized for certain microhabitats that are defined by particular macro- and microenvironmental factors.

Keywords: Central America, mycetozoans, Neotropics, species list

Introduction

The myxomycetes (plasmodial slime molds or myxogastrids) are a group of ameboid protists (Adl et al. 2005) known to occur in all terrestrial ecosystems examined to date. As a group within the Amebozoa (Pawlowski and Burki 2009), myxomycetes have a unicellular amoeboid or flagellated vegetative stage in which they resemble other

amoebae. In contrast, however, their life cycle also includes the particular capacity to produce both unicellular multinucleate structures known as plasmodia and fungus-like fructifications that contain meiotic spores (Stephenson and Stempen 1994).

This combination of morphologically different stages gives myxomycetes a high theoretical capacity for dispersal and colonization (Schnittler and Tesmer 2008). However, it seems that the ability of myxomycetes to actually do this depends largely on individual requirements of the species involved and pre-existing ecological conditions. For example, recent studies in the Neotropics have indicated that a particular species seems to be associated with a microhabitat defined by a series of discrete ecological parameters and that these microhabitats vary among taxa (e.g., Schnittler and Stephenson 2002, Rojas and Stephenson 2007, Wrigley de Basanta et al. 2008). Because of this, myxomycetes are not homogeneously distributed with respect to either macro- or microenvironmental factors. If this is in fact a biological pattern, then different geo-climatic areas would potentially support different myxomycete assemblages. For the Neotropics, this seems to be the case (e.g., Stephenson et al. 2004).

Costa Rica is a good example of an area in which previous studies have also shown that the distribution of species of myxomycetes seems to be ecosystem-related (e.g., Schnittler and Stephenson 2000). However, the lack of a long-term dataset of myxomycetes and information on their distribution patterns across various environments in this country has reinforced the speculative distributional ranges usually cited for particular species. This problem, also common in other areas of the Neotropics, represents an obstacle that must be taken in consideration when attempting to elucidate the actual distributions of particular species of myxomycetes. As an effort to standardize

the degree of knowledge about Neotropical myxomycete taxa, Lado and Wrigley de Basanta (2008) compiled a large set of records from the literature in order to generate an updated list of myxomycete species and their distribution in the Neotropics. The last occasion when a similar task had been carried out was in 1976, when Marie L. Farr published her monograph on Neotropical myxomycetes (Farr 1976). Unfortunately, due the limitations of the research methodology used in both instances, it is very likely that a number of non-published records, including collections in small herbaria, were left out of the list as part of the effort involved in each of these projects.

When the latter point is considered along with the additional fact that the last comprehensive study dealing with myxomycetes in Costa Rica was carried out 34 years ago (Alexopoulos and Sáenz 1975), it seems worthwhile to evaluate the progress that has been made in the country since then. For this reason, the study presented herein was designed with two main objectives. The first was to review the list of myxomycete species reported from or known to occur in Costa Rica and the second was to provide basic ecological information for each taxon. For example, myxomycetes seem to have an important role in the soil environment (Novozhilov et al. 2000) but developing a good understanding of their ecology and interspecific relationships is not possible without having a good taxonomic baseline already in place.

Materials and methods

The information presented in this paper was generated at different times during the period of 1905 to 2009. The specimens considered were collected by a number of different individuals using different methodologies. However, the methods used to

compile information for this paper have been carefully selected. For example, the nomenclatural treatment used for all myxomycete species is that of Lado (2005-2010) except for *Stemonitis smithii* and the genus *Tubifera*, for which the treatment of Martin and Alexopoulos (1969) has been used. Synonyms are provided for species that were reported previously for Costa Rica under a different name. Following Lado (2005-2010), synonyms are specified with the symbols ≡ and = when accepted names are based upon the same type or upon different type specimens, respectively. All identifications of noted particular specimens are based on the morphological species concept (see Clark 2004 for a discussion of shortfalls and problems).

Compilation of the annotated checklist

The information presented in this paper was compiled from a number of sources, with the more important to these being (1) Hennings 1902, (2) Welden 1954, (3) Alexopoulos and Sáenz 1975, (4) Farr 1976, (5) Schnittler and Stephenson 2000, (6) Moore and Stephenson 2003, (7) Rojas and Stephenson 2007, (8) Rojas and Stephenson 2008, (9) Rojas et al. 2008, (10) Lado and Wrigley de Basanta 2008 and (11) Moreno et al. 2009. The number preceding each of these published reports represents the code used in the annotations for each taxon.

All species names were obtained from the sources mentioned above and used to create a preliminary list of Costa Rican myxomycetes in a manner similar to what has been used in a recent previous publication (i.e. Lado and Wrigley de Basanta 2008). However, in addition to published records, myxomycete collections in five herbaria were examined. These herbaria (acronyms given in parentheses) were the Museo Nacional de

Costa Rica (CR), the Universidad de Costa Rica (USJ), the University of Arkansas (UARK), the United States National Fungus Collection (BPI) and the Botanische Staatssammlung München (M). The selection of these five herbaria was based on the fact that they were designated as the primary repositories for specimens obtained during the course of important research projects carried out in the country, including seven that were described in the publications listed above. With the exception of most collections deposited in BPI, all the collections in the other the herbaria were examined directly. In addition, as an extra source of information, the electronic portal of the Global Biodiversity Information Facility (GBIF) was used to validate some of the records. Locations of all collecting areas represented in this survey are indicated in Figure 1.

All species reported herein are supported by either deposited vouchers at the studied herbaria or listed previously published reports. However, four doubtful species for which no vouchers or published reports were found are included, although their occurrence in Costa Rica remains uncertain.

Field work

On different occasions during the period 1994-2009, the three authors carried out field work in Costa Rica. During this time, a combination of field and laboratory techniques were used. For the former, specimens were collected directly in different vegetation zones in the country using the opportunistic sampling method described by Cannon and Sutton (2004). Upon being collected, specimens were returned to the laboratory, dried at room temperature, glued to a paper strip, and placed in pasteboard boxes using the protocol described by Stephenson and Stempen (1994).

For the laboratory component, samples of different types of dead plant material were collected in the field and used to prepare several series of moist chamber cultures. The latter consisted of plastic disposable Petri dishes (15 cm) lined with filter paper. Sample material was placed on the filter paper and soaked in distilled water for 24 hrs, after which excess water was poured off. Examination of cultures was carried out at different times for a period not longer than four months. Substrates used to obtain myxomycetes in this manner included ground litter, aerial litter (as described in Stephenson et al. 2004), wood and bark, twigs, flowers and inflorescences, fruits and dung.

Classification of species

In order to evaluate the occurrence of myxomycetes according to forest type and substrate, a frequency-based classification of records was carried out on the main database following Stephenson et al. (1993). In this classification, the frequency of occurrence of each one of the species in relation to the different forest types and substrates was evaluated in relation to the total number of records with available information for each factor. In this manner, species with occurrences higher than 1.5% the total number of records were considered as abundant, those between 1.5-0.5% as common, between 0.5-0.15% as occasional and less than 0.15% as rare. Only the values for the abundant and common categories were used to determine forest type and substrate preference. For those species in which the number of records for the country is very low, all available information was used.

Forest types and substrates

To determine forest type and substrates a careful examination of records following the methodology detailed in Rojas et al. (2009) was performed. For the first one, all geographical coordinates were first checked for consistency and accuracy. Forest types were assigned to collections by performing a GIS analysis using ARCMap, version 9.2 and the Holdridge Life Zone system (Holdridge et al. 1971).

With this system, forests are classified according to environmental criteria such as elevation, biotemperature and evapotranspiration values. When arranged in a gradient of precipitation from highest to lowest, the forest types in which myxomycetes were found in Costa Rica correspond to premontane rain forest (PRF), lower montane rain forest (LMRF), montane rain forest-transition to lower montane (MRFTLW), montane rain forest (MRF), subalpine rain paramo (SRP), premontane wet forest-transition to perhumid (PWFTp), lowland wet forest (LWF), lowland wet forest-transition to premontane (LWFTP), premontane wet forest (PWF), premontane wet forest-transition to lowland (PWFTL), lower montane wet forest (LMWF), lowland moist forest (LMF), premontane moist forest-transition to lowland (PMFTL), premontane moist forest (PMF), lowland moist forest-transition to premontane (LMFTP), lower montane moist forest (LMMF), lowland moist forest-transition to dry forest (LMFTd) and lowland dry forest (LDF). The letter codes assigned to each forest type are used in the annotations for each species.

For substrates, a series of 10 categories was first created upon the original recorded substrates available in the main database and individual records were re-arranged into these newly created categories. From nonwoody to increasingly woody, the

substrate categories correspond to dung (DU), flowers and inflorescences (FI), living plants (LP), living cryptogams, (LC), ground litter (GL), aerial litter (AL), lianas (LI), fruits (FR), twigs (TW) and dead bark and wood (DBW). In a manner similar to that described in the last section, the letter codes assigned to each substrate category were used for the annotations of species.

Annotations and format of the list of species

The list of species is arranged alphabetically and for each taxon a number of annotations have been included. In all cases, after the species name and protologue, the forest and substrate types from which the species was predominantly recorded are provided using the letter codes explained earlier. This is followed by the publications listed above where the species was mentioned, which are provided as a series of numbers that correspond to the number codes for these information sources. After this, the codes for the herbaria where vouchers are deposited and other Neotropical countries where the species was recorded are provided as well. Species names that represent new records for Costa Rica are preceded by an asterisk, whereas those that are also new for the Neotropical region are preceded by two consecutive asterisks. For the four doubtful species, a question mark precedes the taxonomic name as well.

Data analysis

As a way to evaluate the taxonomic richness of the studied area, the taxonomic diversity index *sensu* Stephenson et al. (1993) was calculated by determining the ratio between the numbers of species and the number of genera found. This index is useful to

estimate the intrageneric diversity of a given area, in the frame of biogeographical studies.

Similarly, in order to estimate the maximum number of species expected, species richness indicators were calculated using the program SPADE (Chao and Shen, 2003). The values corresponding to the ACE estimator recommended by Chao et al. (2006) were selected after running a simulation using the multinomial predictive model. Following this calculation, the completeness of the survey was estimated from the relationship that existed between the number of species found in the database created and the expected value obtained with SPADE.

In addition, two Pearson's Chi square tests of Goodness of Fit were performed to evaluate statistical differences in both the number of species found in the 10 forest types with the highest number of species and the number of species found in the three substrates with the highest species richness. A Monte Carlo simulation was used to evaluate possible problems in the species richness values used during the Chi-Square tests. The program PAST, version 1.92 (Hammer et al. 2001) was used for these calculations.

Results

The final database of all myxomycete collections in the country encompassed 4990 records. These records were derived from a representative sample of forest types and localities throughout Costa Rica (including Cocos Island, Fig. 1). Altogether, the database contained 208 species in 36 different genera and 62 species not previously reported for this country as well as 7 species not previously reported for the Neotropics.

Three more taxa are presumed to occur in the country but their presence is still uncertain. These numbers generate an overall taxonomic diversity index value of 5.80. An appreciable proportion (e.g., > 65%) of the species in the country correspond to the dark-spored clade, the group that included the two genera (*Physarum* and *Didymium*) with highest species richness (Fig. 2).

The ACE value for the maximum number of species to be expected, based on the entire dataset, was 253 species, with a 95% confidence interval between 232-291 species. According to this value, about 83% of the species of myxomycetes that would be expected to occur in Costa Rica are reported herein. The forest types with the most species present were montane rain forest, premontane wet forest, lowland moist forest and premontane moist forest, whereas some of the transitional forest types showed the lowest values of species richness (Fig. 3). The data suggest that there are differences in the number of species present in the ten most represented forest types ($\chi^2 = 19.33$, d.f. = 9, $p < 0.05$; Monte Carlo $p < 0.05$).

Similarly, dead bark and wood and the two types of litter studied were the substrates with the highest number of species, whereas dung, lianas and fruits fell towards the other extreme of the distribution (Fig. 4). For the three substrates characterized by the most species of myxomycetes, it seems that the one represented by dead bark and wood is the one that supports the largest myxomycete community ($\chi^2 = 29.68$, d.f. = 2, $p < 0.0001$; Monte Carlo $p < 0.0001$).

The most common species in the dataset were *Arcyria cinerea*, *Physarum compressum*, *Didymium iridis* and *Didymium squamulosum*. The annotated list of all species documented for Costa Rica is provided below.

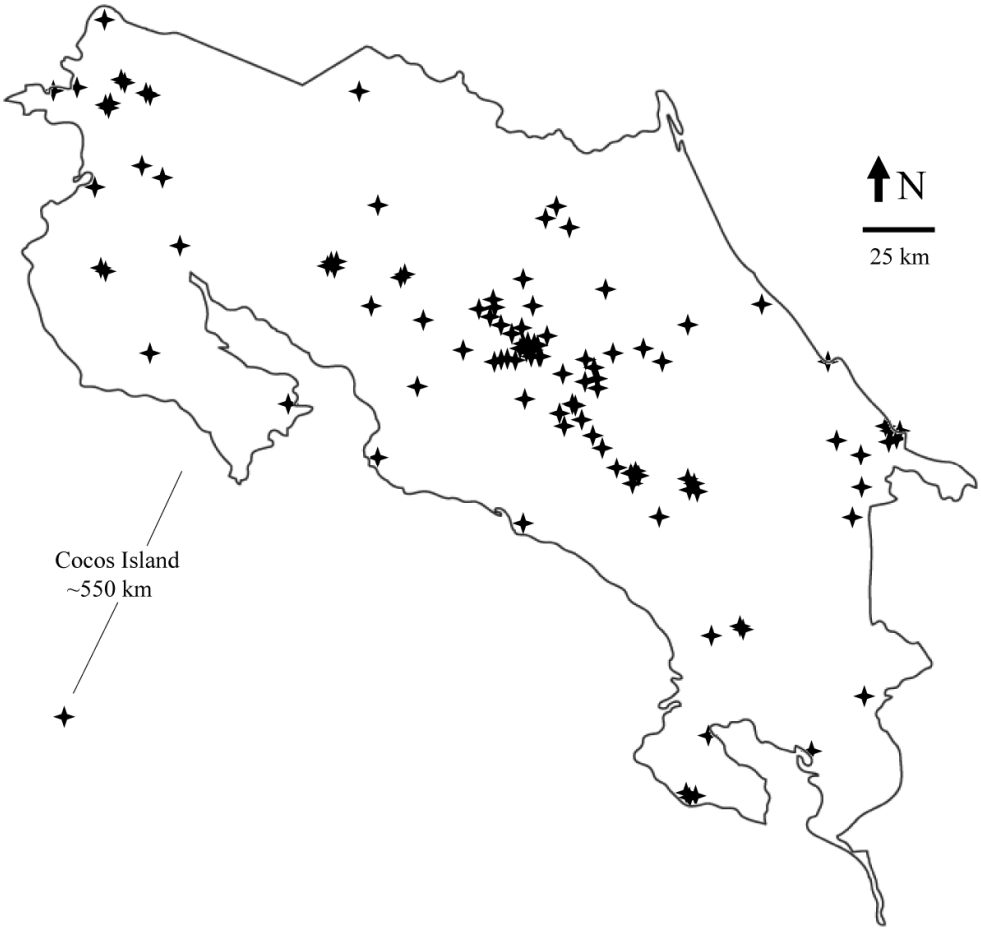

Figure 1. Map of Costa Rica showing collecting locations for the records considered in the present study.

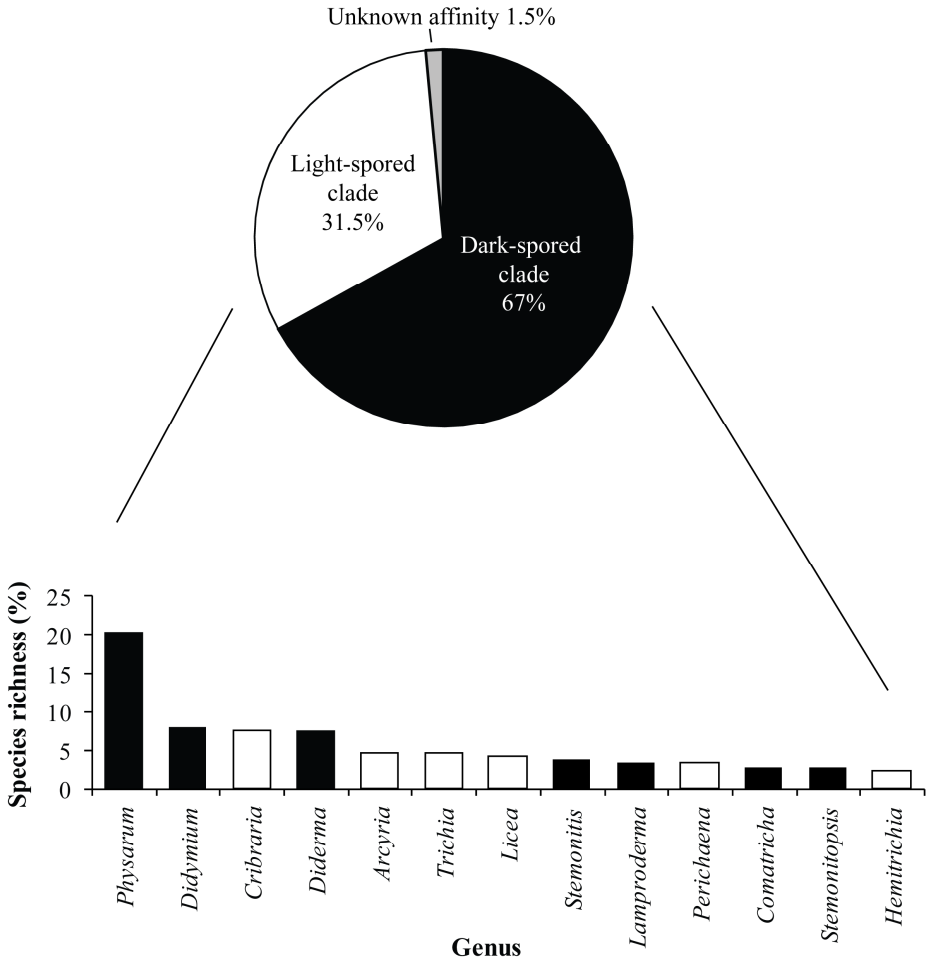

Figure 2. Taxonomic composition of the assemblage of myxomycetes reported from Costa Rica. Distribution by clades with phylogenetic affinity (above) and genera (below), with highest species richness sorted by decreasing values from left to right. Bar colors correspond to the tones provided for clades in which genera are arranged (see Fiore-Donno *et al.* 2005 and Fiore-Donno *et al.* 2010).

List of Costa Rican Myxomycetes

Arcyria afroalpina Rammeloo, Bull. Jard. Bot. Belg. 51(1/2):229 (1981)

Primarily found in LTRF, on ground and aerial litter. Reported in 5, 8 and 9. Vouchers deposited in UARK. Also reported from Mexico, Cuba, Puerto Rico and Ecuador.

Arcyria cinerea (Bull.) Pers., Syn. Meth. Fung. 184 (1801)

Present in almost all ecosystems, common in LTRF, primarily on DBW and GL. Reported in 2, 3, 4, 5, 7, 8 and 10. Vouchers deposited in USJ, CR, UARK and M. Ubiquitous in the Neotropics.

Arcyria denudata (L.) Wettst., Verh. Zool.-Bot. Ges. Wien 35:Abh. 535 (1886)

Present in almost all ecosystems, common in PWFTp and PWFTL, primarily on DBW and GL. Reported in 2, 3, 4, 7 and 10. Vouchers deposited in USJ, UARK and M. Ubiquitous in the Neotropics.

Arcyria incarnata (Pers. ex J.F.Gmel.) Pers., Observ. Mycol. 1:58 (1796)

Primarily found in PMFTL and PMF, on DBW. Reported in 3, 4 and 10. Vouchers deposited in USJ and UARK. Ubiquitous in the Neotropics.

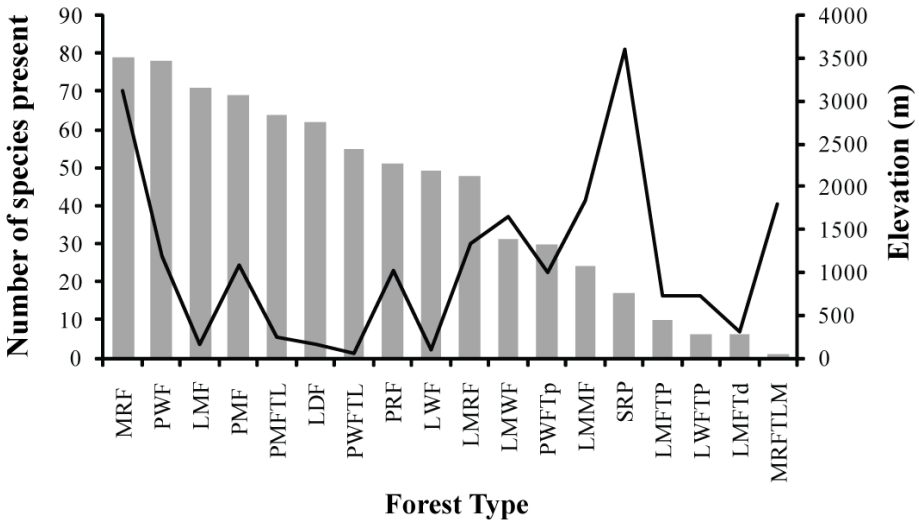

Figure 3. Number of species of myxomycetes found (gray bars) and elevation (black line) arranged according to the different forest types found in Costa Rica. For abbreviations see Materials and Methods.

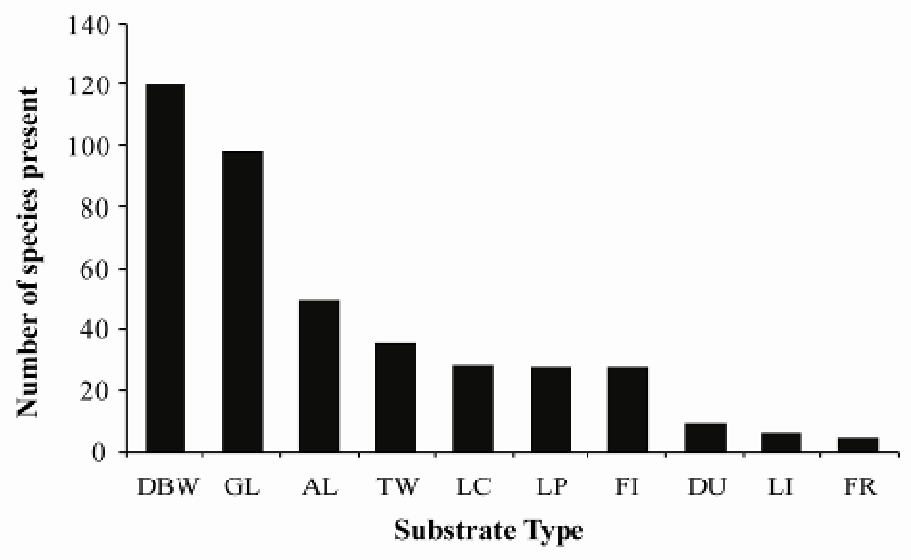

Figure 4. Number of species of myxomycetes found in the different substrate types evaluated in the present study. For abbreviations see Materials and Methods.

Arcyria insignis Kalchbr. & Cooke, in Kalchbr., Grevillea 10: 143 (1882)

Primarily found in LMF, LTDF, PWF, PMF and LMWF, on DBW, GL, AL, LP and FI. Reported in 3, 4 and 10. Vouchers deposited in USJ, BPI, UARK and M. Widespread in the Neotropics (see 10).

Arcyria magna Rex, Proc. Acad. Nat. Sci. Philadelphia 45:364 (1893)

Primarily found in PMF, on DBW. Reported in 3, 4 and 10. Vouchers deposited in USJ, BPI and UARK. Also reported from Mexico, Panama, Cuba, Dominica and Brazil.

Arcyria minuta Buchet, in Patouillard, Mém. Acad. Malgache 6:42 (1927)

Known only from Cocos Island (LWF) and Villa Mills (MRF). Found in DBW. Reported in 8 and 10. Vouchers deposited in UARK and M. Also reported from Mexico, Panama, Brazil and Argentina.

Arcyria obvelata (Oeder) Onsberg, Mycologia 70(6):1286 (1979)

= *Arcyria nutans* (Bull.) Grev., Fl. Edin. 455 (1824)

Primarily found in PMFTL, on DBW. Reported in 4 and 10. Vouchers deposited in UARK. Widespread in the Neotropics (see 10).

? *Arcyria oerstedii* Rostaf., Sluzowce Monogr. 278 (1875)

Possibly found in LMF, on DBW. Reported in 4. No vouchers known (see comments of this species in 4). Also reported from Mexico, Panama, Cuba, Venezuela, Brazil, Paraguay and Argentina.

* *Arcyria pomiformis* (Leers) Rostaf., Sluzowce Monogr. 271 (1875)

Primarily found in PMF, on DBW. First published report for Costa Rica. Vouchers deposited in UARK and M. Also reported from Mexico, Panama, Jamaica, Puerto Rico, Colombia, Venezuela, Brazil, Ecuador and Argentina.

Badhamia cinerascens G.W.Martin, J. Wash. Acad. Sci. 22(5):88 (1932)

Only one collection made in LMF, on DBW. Reported in 3 and 10. No vouchers known. Also reported from Colombia and Argentina.

* *Badhamia utricularis* (Bull.) Berk., Trans. Linn. Soc. London 21:153 (1853)

Primarily found in MRF, on DBW. First published report for Costa Rica. Vouchers deposited in M. Also reported from Mexico and Bolivia.

* *Barbeyella minutissima* Meyl., Bull. Soc. Bot. Genève 6:89 (1914)

Only found in MRF, on DBW. First published report for Costa Rica. Vouchers deposited in UARK. Also reported from Mexico.

Ceratiomyxa fruticulosa (O.F.Müll.) T.Macbr., N. Amer. Slime-Moulds 18 (1899)

Primarily found in PWFTL and PMFTL, on DBW. Reported in 2, 3, 4, 5, 7, 9 and 10. Vouchers deposited in USJ, BPI, UARK and M. Ubiquitous in the Neotropics. See Rojas et al. (2008) for a detailed discussion of the ecological requirements of the species of *Ceratiomyxa*.

Ceratiomyxa morchella A.L.Welden, Mycologia 46(1):94 (1954)

Primarily found in PWFTL, PMFTL and PWF, on DBW. Reported in 3, 4, 9 and 10. Vouchers deposited in USJ, BPI, UARK and M. Also reported from Mexico, Honduras, Panama, Ecuador, Peru, Jamaica, Puerto Rico, Venezuela and Suriname.

This appears to be a tropical lowland species.

Ceratiomyxa sphaerosperma Boedijn, Misc. Zool. Sumatr. 24:1 (1927)

This species has been found only in PWFTL, on DBW and GL. Reported in 2, 3, 4, 9 and 10. Vouchers deposited in USJ and UARK. Widespread in the Neotropics (see 10).

Clastoderma debaryanum A.Blytt, Bot. Zeitung (Berlin) 38:343 (1880)

Found in LWF, LDF, PWF and MRF, on DBD, TW and AL. Reported in 3, 4, 5, 7, 8 and 10. Vouchers deposited in USJ, BPI, UARK and M. Widespread in the Neotropics (see 10).

Clastoderma pachypus Nann.-Bremek., Proc. Kon. Ned. Akad. Wetensch., C. 71(1):44 (1968)

Primarily found in LDF and PRF, on AL. Reported in 8 and 10. Vouchers deposited in UARK and M. Also reported from Mexico and Brazil.

Collaria arcyrionema (Rostaf.) Nann.-Bremek. ex Lado, Ruizia 9:26 (1991)

≡ *Lamproderma arcyrionema* Rostaf., Sluzowce Monogr. 208 (1874)

Primarily found in LMF, LWF and PWF, on GL and AL. Reported in 3, 4, 5, 7 and 10. Vouchers deposited in USJ, BPI, UARK and M. Widespread in the Neotropics (see 10).

Collaria lurida (Lister) Nann.-Bremek., Nederlandse Myxomyceten (Zutphen) 236 (1975)

≡ *Comatricha lurida* Lister, Monogr. Mycetozoa 119 (1894)

Primarily found in LMF, LWF and PWF, on GL. Reported in 8 and 10. Vouchers deposited in UARK. Also reported from Mexico, Cuba, Puerto Rico and Colombia.

Collaria rubens (Lister) Nann.-Bremek., Nederlandse Myxomyceten (Zutphen) 236 (1975)

≡ *Comatricha rubens* Lister, Monogr. Mycetozoa 123 (1894)

Primarily found in LMF and PRF, on GL. Reported in 5 and 10. Vouchers deposited in UARK. Also reported from Mexico, Ecuador and Argentina.

Comatricha elegans (Racib.) G.Lister, Guide Brit. Mycetozoa, ed. 3 31 (1909)

Primarily found in LMWF and LMF, on DBW and AL. Reported in 3, 4, 8 and 10. Vouchers deposited in BPI and UARK. Also reported from Mexico, Cuba, Jamaica, Haiti, Puerto Rico, Colombia, Ecuador, Venezuela, Trinidad, Brazil, Chile and Argentina.

Comatricha laxa Rostaf., Sluzowce Monogr. 201 (1874)

Primarily found in LMF and PRF, on GL and AL. Reported in 8 and 10. Vouchers deposited in UARK. Also reported from Mexico, Guatemala, Panama, Cuba, Puerto Rico, Venezuela, Brazil and Chile.

** *Comatricha laxifila* R.K.Chopra & T.N.Lakh., in Chopra, Nannenga-Bremekamp & Lakhanpal, Proc. Kon. Ned. Akad. Wetensch. 95(1):44 (1992)
This species has been found only in LDF, on DBW. First published report for Costa Rica. Vouchers deposited in UARK. Not yet reported for the Neotropical region (see 10).

Comatricha nigra (Pers. ex J.F.Gmel.) J.Schröt., Krypt.-Fl. Schlesien Pilze Schles. 3(1):118 (1885)
Primarily found in LWF, PRF and MRF, on DBW, TW, GL and AL. Reported in 8 and 10. Vouchers deposited in UARK and M. Widespread in the Neotropics (see 10).

Comatricha pulchella (C.Bab.) Rostaf., Sluzowce Monogr. Suppl. 27 (1876)
Primarily found in LWF, PRF and MRF, on DBW, AL and LC. Reported in 7, 8 and 10. Vouchers deposited in USJ, UARK and M. Also reported from Mexico, Panama, Puerto Rico, Venezuela, Brazil, Ecuador, Bolivia, Uruguay and Argentina.

Comatricha tenerrima (M.A.Curtis) G.Lister, Guide Brit. Mycetozoa, ed. 4 39 (1919)
Primarily found in LWF, PRF and MRF, on TW, GL, AL, LC and FI. Reported in 3, 4, 7, 8 and 10. Vouchers deposited in USJ, BPI and UARK. Also reported from Mexico, Belize, Cuba, Jamaica, Puerto Rico, Venezuela, Brazil, Ecuador, Peru and Argentina.

Craterium aureum Morgan, J. Cincinnati Soc. Nat.Hist. 16:27 (1893)

Primarily found in LWF and PMF, on AL and LP. Reported in 8 and 10. Vouchers deposited in USJ and UARK. Also reported from Mexico, Jamaica, Puerto Rico, Dominican Republic, Colombia, Venezuela, Brazil, Ecuador, Peru and Argentina.

Craterium concinnum Rex, Proc. Acad. Nat. Sci. Philadelphia 45:370 (1893)

Primarily found in MRF and SRP, on GL, AL and FI. Reported in 5 and 10. Vouchers deposited in UARK and M. Also reported from Cuba, Jamaica, Colombia and Ecuador.

Craterium leucocephalum (Pers. ex J.F.Gmel.) Ditmar, in Sturm, Deutschl. Fl. Pilze 1(1):21 (1813)

Primarily found in LMF, PMF and LMMF, on GL. Reported in 3, 4, 5 and 10. Vouchers deposited in USJ, BPI, UARK and M. Widespread in the Neotropics (see 10).

* *Craterium paraguayense* (Speg.) G.Lister, in Lister, Monogr. Mycetozoa, ed. 2 95 (1911)

Primarily found in PWF, LMFTP and LMWF, on GL and LP. First published report for Costa Rica. Vouchers deposited in USJ, UARK and M. Also reported from Panama, Colombia, Venezuela, French Guiana, Brazil, Ecuador, Paraguay and Argentina.

* *Cribraria aurantiaca* Schrad., Nov. Gen. Pl. 5 (1797)

These species has been found only in MRF, on GL. First published report for Costa Rica. Vouchers deposited in M. Also reported from Mexico, Panama, Venezuela, Jamaica, Brazil, Chile and Argentina.

Cribraria cancellata (Batsch) Nann.-Bremek., Nederlandse Myxomyceten (Zutphen) 92 (1975)

≡ *Dictydium cancellatum* (Batsch) T.Macbr., N. Amer. Slime-Moulds 172 (1899)

Primarily found in PWFTL, LDF, PRF and PMF, on DBW. Reported in 2, 3, 4 and 10. Vouchers deposited in USJ, BPI, UARK and M. Ubiquitous in the Neotropics (see 10).

* *Cribraria confusa* Nann.-Bremek. & Y.Yamam., Proc. Kon. Ned. Akad. Wetensch., C. 86(2):212 (1983)

This species has been found only in LDF, on DBW. First published report for Costa Rica. Vouchers deposited in M. Also reported from Mexico, Belize and Ecuador.

* *Cribraria costata* Dhillon & Nann.-Bremek., Proc. Kon. Ned. Akad. Wetensch., C. 81(2):141 (1978)

These species has been found only in MRF, on DBW, GL and DU. First published report for Costa Rica. Vouchers deposited in M. Also reported from French Guiana.

Cribraria intricata Schrad., Nov. Gen. Pl. 7 (1797)

Primarily found in PMFTL and MRF, on DBW. Reported in 3, 4, 7, 8 and 10. Vouchers deposited in USJ, BPI, UARK and M. Widespread in the Neotropics (see 10).

Cribraria languescens Rex, Proc. Acad. Nat. Sci. Philadelphia 43:394 (1891)

Primarily found in PMFTL, LMF, LDF and MRFTLW, on DBW. Reported in 3, 4 and 10. Vouchers deposited in USJ, BPI, UARK and M. Widespread in the Neotropics (see 10).

* *Cribraria macrocarpa* Schrad., Nov. Gen. Pl. 8 (1797)

This species has been found only in MRF, on DBW. First published report for Costa Rica. Vouchers deposited in M. Also reported from Mexico, Colombia and Chile.

Cribraria microcarpa (Schrad.) Pers., Syn. Meth. Fung. 190 (1801)

Primarily found in LWF, PRF and PMF, on DBW, GL and AL. Reported in 3, 4, 5, 8 and 10. Vouchers deposited in USJ, UARK and M. Widespread in the Neotropics (see 10).

Cribraria minutissima Schwein., Trans. Amer. Philos. Soc. 4:260 (1832)

Only one collection made in LMFTP, on DBW. Reported in 3 and 10. No vouchers known. Also reported from Mexico, Jamaica, Guadeloupe, Dominica, Trinidad, Brazil and Uruguay.

Cribraria mirabilis (Rostaf.) Massee, Monogr. Myxogastr. 60 (1892)

Primarily found in MRF, on DBW. Reported in 7 and 10. Vouchers deposited in USJ and UARK. Also reported from Mexico, Brazil and Chile.

Cribraria piriformis Schrad., Nov. Gen. Pl. 4 (1797)

Primarily found in MRF, on DBW. Reported in 7 and 10. Vouchers deposited in USJ and UARK. Also reported from Mexico, Guatemala, Panama, Brazil and Chile.

* *Cribraria purpurea* Schrad., Nov. Gen. Pl. 8 (1797)

Primarily found in LMRF, on DBW. First published report for Costa Rica. Vouchers deposited in UARK. Also reported from Mexico and Venezuela.

Cribraria splendens (Schrad.) Pers., Syn. Meth. Fung. 191 (1801)

Primarily found in PWFTL, PMF and LMWF, on DBW. Reported in 3, 4 and 10. Vouchers deposited in USJ. Also reported from Mexico, Jamaica, Virgin Islands, Venezuela, Brazil and Chile.

Cribraria tenella Schrad., Nov. Gen. Pl. 6 (1797)

Primarily found in PWFTL, PMF and LMRF, on DBW. Reported in 3, 4 and 10. Vouchers deposited in USJ, UARK and M. Widespread in the Neotropics (see 10).

Cribraria violacea Rex, Proc. Acad. Nat. Sci. Philadelphia 43:393 (1891)

Primarily found in LDF and LMF, on DBW and GL. Reported in 3, 5, 8 and 10. Vouchers deposited in USJ, UARK and M. Widespread in the Neotropics (see 10).

Cribraria vulgaris Schrad., Nov. Gen. Pl. 6 (1797)

Primarily found in MRF, on DBA and LC. Reported in 4, 5, 7 and 10. Vouchers deposited in USJ, BPI and UARK. Also reported from Argentina.

Diachea bulbillosa (Berk. & Broome) Lister, in Penzig, Myxomyc. Fl. Buitenzorg 45 (1898)

Primarily found in LDF and LMRF, on GL and LP. Reported in 3, 4 and 10. Vouchers deposited in USJ, UARK and M. Also reported from Panama, Cuba, Jamaica, Puerto Rico, Dominica, Grenada, Colombia, Venezuela and Ecuador.

Diachea leucopodia (Bull.) Rostaf., Sluzowce Monogr. 190 (1874)

Primarily found in LWF, LWFTP and LMMF, on GL. Reported in 1, 3, 4, 5, 8 and 10. Vouchers deposited in USJ, BPI, UARK and M. Cosmopolitan.

Diacheopsis sp. Meyl., Bull. Soc. Vaud. Sci. Nat. 57:149 (1930)

This genus is reported from one collection found in MRF, on DBW. Reported in 7. Vouchers deposited in UARK. In the Neotropics the genus is only reported from Mexico and Costa Rica.

Dictydiaethalium plumbeum (Schumach.) Rostaf., in Lister, Monogr. Mycetozoa 157 (1894)

Primarily found in PWFTL and MRF, on LP. Reported in 3, 4 and 10. Vouchers deposited in USJ. Also reported from Mexico, Nicaragua, Panama, Dominican Republic, Puerto Rico, Colombia, Venezuela, Brazil, Chile and Argentina.

Diderma chondrioderma (de Bary & Rostaf.) G.Lister, in Lister, Monogr. Mycetozoa, ed. 3 258 (1925)

Primarily found in PWF and MRF, on DBW and LC. Reported in 2, 3, 7 and 10. Vouchers deposited in USJ, BPI and UARK. Also reported from Mexico, Belize, Jamaica, Puerto Rico, Dominica, Brazil and Ecuador.

Diderma corrugatum T.E.Brooks & H.W.Keller, in Brooks, Keller & Chassain, Mycologia 69(1):180 (1977)

Primarily found in LDF and PMFTL, on DBW and LI. Reported in 5 and 10. Vouchers deposited in UARK and M. Also reported from Cuba, Brazil and Ecuador.

Diderma deplanatum Fr., Syst. Mycol. 3:110 (1829)

Primarily found in LDF, on DBW. Reported in 5 and 10. Vouchers deposited in UARK and M. Also reported from Mexico and Brazil.

Diderma effusum (Schwein.) Morgan, J. Cincinnati Soc. Nat.Hist. 16:155 (1894)

Primarily found in LMF, LDF, PMF, LMRF, on TW, GL, LC and FI. Reported in 3, 4, 5, 8 and 10. Vouchers deposited in USJ, BPI, UARK and M. Widespread in the Neotropics (see 10).

* *Diderma globosum* Pers., Neues Mag. Bot. 1:89 (1794)

This species has been found only in PWFTp, on DBW. First published report for Costa Rica. Vouchers deposited in M. Also reported from Venezuela, Ecuador, Peru and Argentina.

Diderma hemisphaericum (Bull.) Hornem., Fl. Dan. 33:13 (1829)

Primarily found in LWF, LDF, PWF and LMRF, on GL and AL. Reported in 3, 4, 5, 8 and 10. Vouchers deposited in USJ, BPI, UARK and M. Widespread in the Neotropics (see 10).

** *Diderma indicum* K.S.Thind & H.S.Sehgal, Mycologia 56(4):564 (1964)

Primarily found in PMF, on LP. First published report for Costa Rica. Vouchers deposited in USJ. Apparently not yet reported for the Neotropical region (see 10).

* *Diderma montanum* (Meyl.) Meyl., Annuaire Conserv. Jard. Bot. Genève 15-16:311 (1913)

This species has been found only in MRF, on GL. First published report for Costa Rica. Vouchers deposited in M. Also reported from Venezuela.

Diderma niveum (Rostaf.) T.Macbr., N. Amer. Slime-Moulds 100 (1899)

Possibly found in MRF, on TW. Reported in 4 and 10. No vouchers reported (see information on this species in 4). Also reported from Mexico, Colombia, Chile and Argentina.

* *Diderma ochraceum* Hoffm., Deutschl. Fl. 2:pl. 9, fig. 2b (1795)

This species has been found only in MRF, on LC. First published report for Costa Rica. Vouchers deposited in UARK. Also reported from Mexico.

Diderma rugosum (Rex) T.Macbr., N. Amer. Slime-Moulds 105 (1899)

This species has been found only in LWF, on GL. First published report for Costa Rica. Vouchers deposited in UARK. Also reported from Mexico, Panama, Jamaica, Antigua and Trinidad.

* *Diderma saundersii* (Berk. & Broome ex Massee) Lado, Cuad. Trab. Fl. Micol. Iber. 35 (2001)

This species has been found only in PWFTL, on GL. First published report for Costa Rica. Vouchers deposited in UARK. Also reported from Mexico and Ecuador.

Diderma sauteri (Rostaf.) T.Macbr., N. Amer. Slime-Moulds 103 (1899)

This species has been found only in PMF, on GL. Reported in 3 and 10. Vouchers deposited in UARK. Also reported from Mexico and Venezuela.

* *Diderma subdictyospermum* (Rostaf.) G.Lister, in Lister, Monogr. Mycetozoa, ed. 2 101 (1911)

This species has been found only in PWF, on GL. First published report for Costa Rica. Vouchers deposited in UARK. Also reported from Mexico and Venezuela.

* *Diderma subincarnatum* Kowalski, Mycologia 59(1):169 (1967)

This species has been found only in PWFTL, apparently on GL. First published report for Costa Rica. Vouchers deposited at BPI. Also reported from Mexico and Chile.

Diderma testaceum (Schrad.) Pers., Syn. Meth. Fung. 167 (1801)

Primarily found in LWF, PRF and MRF, on GL, AL and FI. Reported in 3, 4, 5 and 10. Vouchers deposited in USJ, BPI, UARK and M. Also reported from Mxico, Cuba, Jamaica, Dominican Republic, Guadeloupe, Brazil and Chile.

* *Didymium anellus* Morgan, J. Cincinnati Soc. Nat.Hist. 16:148 (1894)

Primarily found in LMF and PWF, on AL. First published report for Costa Rica. Vouchers deposited in UARK. Also reported from Mexico, Jamaica, Puerto Rico, Trinidad, Colombia and Brazil, Ecuador, Chile and Argentina.

* *Didymium bahiense* Gottsb., Nova Hedwigia 15:365 (1968)

Primarily found in PWF, LMRF and MRF, on GL and AL. First published report for Costa Rica. Vouchers deposited in UARK and M. Also reported from Mexico, Colombia, Venezuela, Ecuador and Brazil.

Didymium clavus (Alb. & Schwein.) Rabenh., Deutschl. Krypt.-Fl. 1:280 (1844)

Primarily found in PWF, LMRF and MRF, on GL, AL and FI. Reported in 2, 3, 4, 5 and 10. Vouchers deposited in USJ, BPI, UARK and M. Widespread in the Neotropics (see 10.)

* *Didymium comatum* (Lister) Nann.-Bremek., Proc. Kon. Ned. Akad. Wetensch., C. 69(3):361 (1966)

Primarily found in PWF and LMRF, on GL. First published report for Costa Rica. Vouchers deposited in UARK and M. Also reported from the Antillean Windward Islands.

Didymium crustaceum Fr., Syst. Mycol. 3:124 (1829)

Primarily found in PMF, on DBW. Reported in 3, 4 and 10. Vouchers deposited in USJ. Also reported from Mexico, Cuba, Dominica and Bolivia.

Didymium difforme (Pers.) Gray, Nat. Arr. Brit. Pl. 1:571 (1821)

Primarily found in LMF, LWFTP, PRF and SRP, on GL and AL. Reported in 3, 4, 5 and 10. Vouchers deposited in USJ, BPI, UARK and M. Widespread in the Neotropics (see 10).

Didymium dubium Rostaf., Sluzowce Monogr. 152 (1874)

Primarily found in LMWF and MRF, on DBA, FR and GL. Reported in 7 and 10. Vouchers deposited in USJ and M. Also reported from Mexico, Colombia, Venezuela and Argentina.

* *Didymium floccosum* G.W.Martin, K.S.Thind & Rehill, Mycologia 51(2):160 (1959)

Primarily found in LDF, on GL. First published report for Costa Rica. Vouchers deposited in UARK. Also reported from Venezuela, Ecuador and Argentina.

Didymium iridis (Ditmar) Fr., Syst. Mycol. 3:120 (1829)

Primarily found in LWF, LMF, PWF, PWFTp and LMRF, on GL, AL, LC, FR and FI. Reported in 3, 4, 5, 8 and 10. Vouchers deposited in USJ, BPI, UARK and M. Probably ubiquitous in the Neotropics.

* *Didymium laxifilum* G.Lister & J.Ross, in G.Lister, Essex Naturalist 27(10):264 (1945)

Primarily found in PMF, substrate not reported. First published report for Costa Rica. Vouchers deposited at USJ. Also reported from Mexico.

* *Didymium listeri* Massee, Monogr. Myxogastr. 244 (1892)

Primarily found in PWF and LMRF, on GL. First published report for Costa Rica. Vouchers deposited at UARK. Also reported from from Mexico and Ecuador.

Didymium minus (Lister) Morgan, J. Cincinnati Soc. Nat.Hist. 16:145 (1894)

Primarily found in LWF, LDF, PMF and SRP, on DBW, GL, AL and LC. Reported in 3, 4, 8 and 10. Vouchers deposited at USJ, BPI, UARK and M. Also reported from Mexico, Jamaica, Antigua, Dominica, Ecuador, Colombia, Brazil, Uruguay, Chile and Argentina.

Didymium nigripes (Link) Fr., Syst. Mycol. 3:119 (1829)

Primarily found in LWF, LDF, PMF, LMRF, MRF and SRP, on DBW, GL, AL, LP and FI. Reported in 3, 4 and 10. Vouchers deposited at USJ, BPI, UARK and M. Widespread in the Neotropics (see 10).

Didymium ochroideum G.Lister, J. Bot. 69:297 (1931)

Primarily found in LMF, LDF, PRF and LMRF, on GL, AL and FR. Reported in 5 and 10. Vouchers deposited at UARK and M. Also reported from Mexico, Brazil and Ecuador.

Didymium ovoideum Nann.-Bremek., Acta Bot. Neerl. 7:780 (1958)

Primarily found in LDF and PWF, on GL. Reported in 5. No vouchers known (see information on this species in 5). Also reported from Mexico.

Didymium squamulosum (Alb. & Schwein.) Fr., Symb. Gasteromyc. 19 (1818)

Present in almost all ecosystems, more common in LWF, PWF and LMRF, primarily on GL, AL, LC, FI and DBW. Reported in 2, 3, 4, 5, 7, 8 and 10. Vouchers deposited at USJ, BPI, UARK and M. Ubiquitous in the Neotropics.

* *Didymium sturgisii* Hagelst., Mycologia 29(4):397 (1937)

This species has been found only in LMF, on GL. First published report for Costa Rica. Vouchers deposited at M. Also reported from Mexico.

* ? *Echinostelium apitectum* K.D.Whitney, Mycologia 72(5):954 (1980)

This species has been found only in LDF, on DBW. First published report for Costa Rica. No vouchers known, but the species seems to have been observed in the country. Also reported from Mexico and Ecuador.

Echinostelium bisporum (L.S.Olive & Stoian.) K.D.Whitney & L.S.Olive, in Whitney, Bennett & Olive, Mycologia 74(4):680 (1982)
This species has been found only in LWF, on GL. Reported in 6 and 10. No vouchers known but observed in cultures prepared for the isolation of protosteloid amoebae. Also reported from Cuba.

Echinostelium minutum de Bary, in Rostafinski, Sluzowce Monogr. 215 (1874)
Primarily found in LDF, LMF, PWF and PRF, on DBW and AL. Reported in 5, 8 and 10. Vouchers deposited at UARK and M. Widespread in the Neotropics (see 10).

* *Enerthenema papillatum* (Pers.) Rostaf., Sluzowce Monogr. Suppl. 28 (1876)
This species has been found only in MRF, on TW. First published report for Costa Rica. Vouchers deposited at UARK. Also reported from Mexico, Brazil, Ecuador, Chile and Argentina.

Fuligo cinerea (Schwein.) Morgan, J. Cincinnati Soc. Nat.Hist. 19:33 (1896)
This species has been found only in LDF, on DBW. Reported in 5 and 10. No vouchers known (see information on this species in 5). Also reported from Mexico, Cuba, Jamaica, Dominica, Barbados, Brazil and Argentina.

* *Fuligo intermedia* T.Macbr., N. Amer. Slime-Moulds, ed.2 30 (1922)

This species has been found only in PMF, on DBW. First published report for Costa Rica. Vouchers deposited at BPI. Also reported from Mexico.

Fuligo megaspora Sturgis, Colorado Coll. Stud. Sci. Ser. 12:443 (1913)

Primarily found in LMFTP and PWFTL, on LP. Reported in 3, 4 and 10. Vouchers deposited at USJ, BPI and UARK. Also reported from Mexico, Guatemala, Brazil and Argentina.

Fuligo septica (L.) F.H.Wigg., Prim. Fl.Holsat. 112 (1780)

Primarily found in PMF, PWF and LMF, on GL and DBW. Reported in 2, 3, 4 and 10. Vouchers deposited at USJ, CR, BPI, UARK and M. Widespread in the Neotropics.

Hemitrichia calyculata (Speg.) M.L.Farr, Mycologia 66(5):887 (1974)

= *Hemiarcyria stipitata* Massee, J. Roy. Microscop. Soc. London 1889(1):354 (1889)

= *Arcyria stipitata* (Massee) Massee, Monogr. Myxogastr. 163 (1892)

Present in almost all ecosystems, more common in LMF, PWFTL, PWF and MRF, primarily on DBW, GL and LP. Reported in 2, 3, 4, 7 and 10. Vouchers deposited at USJ, BPI, UARK and M. Apparently ubiquitous in the Neotropics (see 10).

Hemitrichia leiocarpa (Cooke) Lister, Monogr. Mycetozoa 177 (1894)

≡ *Arcyria leiocarpa* (Cooke) Massee, Monogr. Myxogastr. 167 (1892)

Primarily found in LWF and MRF, on DBW and TW. Reported in 3, 7 and 10. Vouchers deposited at USJ and M. Also reported from Mexico, Belize, Panama, Cuba, Colombia, Grenada and Brazil.

Hemitrichia minor G.Lister, J. Bot. 49:62 (1911)

= *Perichaena minor* (G.Lister) Hagelst., Mycologia 35(2):130 (1943)

Primarily found in LDF, LMF, PWF, PRF, PMF and LMRF, on DBW, GL and AL. Reported in 5, 8 and 10. Vouchers deposited at UARK. Also reported from Mexico, Belize, Panama, Dominica, Brazil and Chile.

Hemitrichia pardina (Minakata) Ing, Myxomycetes Britain and Ireland 132 (1999)

≡ *Perichaena minor* var. *pardina* (Minakata) Hagelst., Mycologia 35(1):131 (1943)

Primarily found in LMF and PMF, on GL, AL and LP. Reported in 10. Vouchers deposited at UARK and M. Also reported from Mexico, Cuba, Puerto Rico, Brazil and Ecuador.

Hemitrichia serpula (Scop.) Rostaf. ex Lister, Monogr. Mycetozoa 179 (1894)

Present in almost all ecosystems, more common in LDF and MRF, primarily DBW, GL and LP. Reported in 3, 4, 7, 8 and 10. Vouchers deposited at USJ, BPI, UARK and M. Widespread in the Neotropics (see 10).

* *Lamproderma arcyrioides* (Sommerf.) Rostaf., Sluzowce Monogr. 206 (1874)

Primarily found in MRF, on GL. First published report for Costa Rica. Vouchers deposited at BPI and M. Also reported from Mexico, Jamaica, Dominican Republic, Puerto Rico, Brazil and Argentina.

Lamproderma columbinum (Pers.) Rostaf., in Fuckel, Jahrb. Nassauischen Vereins Naturk. 27-28:69 (1873)

Primarily found in MRF, on DBW and LC. Reported in 7 and 10. Vouchers deposited at USJ and UARK. Also reported from Mexico.

** *Lamproderma cribrarioides* (Fr.) R.E.Fr., Svensk Bot. Tidskr. 4:259 (1911)

Primarily found in MRF, on DBW. Reported in 7 and 10. Vouchers deposited at UARK. Not reported from other country in the Neotropics.

Lamproderma echinulatum (Berk.) Rostaf., Sluzowce Monogr. Suppl. 25 (1876)

Primarily found in MRF, on DBW and LC. Reported in 7 and 10. Vouchers deposited at USJ. Also reported from Mexico.

** *Lamproderma magniretispora* G. Moreno, C. Rojas, S.L. Stephenson & H. Singer Mycological Progress 8(3):215 (2009)

This species has been found only in MRF, on DBW. Reported in 11. Vouchers deposited at UARK. Not reported from other country in the Neotropics.

Lamproderma muscorum (Lév.) Hagelst., Mycologia 27(1):88 (1935)

Primarily found in LMRF, on DBW. Reported in 3 and 10. Vouchers deposited at BPI. Also reported from Mexico, Colombia, Venezuela and Brazil.

** *Lamproderma sauteri* Rostaf., Sluzowce Monogr. 205 (1874)

Primarily found in MRF, on DBW. Reported in 7 and 10. Vouchers deposited at UARK. Not reported from other country in the Neotropics.

Lamproderma scintillans (Berk. & Broome) Morgan, J. Cincinnati Soc. Nat.Hist. 16:131 (1894)

Primarily found in LMF, LDF, PWF and LMRF, on GL, AL and LC. Reported in 3, 4, 5, 8 and 10. Vouchers deposited at USJ, BPI, UARK and M. Also reported from Mexico, Panama, Cuba, Jamaica, Haiti, Puerto Rico, Antigua, Dominica, Colombia, Venezuela, Brazil, Ecuador and Bolivia.

Leocarpus fragilis (Dicks.) Rostaf., Sluzowce Monogr. 132 (1874)

Primarily found in MRF and SRP, on DBW and TW. Reported in 7 and 10. Vouchers deposited at USJ, UARK and M. Also reported from Mexico, Colombia, Brazil, Chile and Argentina.

* *Lepidoderma trevelyanii* (Grev.) Poulain & Mar.Mey., in Poulain, Meyer & Bozonnet, Bull. Mycol. Bot. Dauphiné-Savoie 165:10 (2002)

This species has been found only in PWF, on DBW. First published report for the Costa Rica. Vouchers deposited at UARK. Also reported from Chile and Argentina.

Licea biforis Morgan, J. Cincinnati Soc. Nat.Hist. 15:131 (1893)

This species has been found only in PMF, on GL. Reported in 5. No vouchers known. Also reported from Mexico, Belize, Cuba, Jamaica, Colombia, Brazil, Ecuador and Chile.

* *Licea denudescens* H.W.Keller & T.E.Brooks, Mycologia 69(5):668 (1977)

This species has been found only only in PWF, on DBW. First published report for the Costa Rica. Vouchers deposited at M. Also reported from Mexico, Belize and Brazil.

* *Licea erecta* K.S.Thind & Dhillon, Mycologia 59(3):463 (1967)

This species has been found only in LMRF, on DBW. First published report for the Costa Rica. Vouchers deposited at UARK. Also reported from Belize, Cuba and Brazil.

* *Licea minima* Fr., Syst. Mycol. 3:199 (1829)

Primarily found in MRF and SRP, on DBW, GL and FI. First published report for the Costa Rica. Vouchers deposited at UARK and M. Also reported from Mexico, Panama and Uruguay.

Licea operculata (Wingate) G.W.Martin, Mycologia 34(6):702 (1942)

Primarily found in LDF, LMF and PWF, on DBW and AL. Reported in 5 and 10. Vouchers deposited at UARK. Also reported from Mexico, Panama, Puerto Rico, Dominica, Venezuela, Brazil, Ecuador, Peru and Uruguay.

* *Licea pedicellata* (H.C.Gilbert) H.C.Gilbert, in Martin, Mycologia 34(6):702 (1942)

This species has been found only in LDF, on DBW. First published report for the Costa Rica. Vouchers deposited at UARK. Also reported from Mexico, Panama, Puerto Rico, Grenada, Brazil and Ecuador.

Licea perexigua T.E.Brooks & H.W.Keller, in Keller & Brooks, Mycologia 69(4):674 (1977)

This species has been found only in LDF, on DBW. Reported in 5 and 10. Vouchers deposited at UARK. Also reported from Mexico, Belize and Ecuador.

* *Licea pusilla* Schrad., Nov. Gen. Pl. 19 (1797)

This species has been found only in SRP, on DBW. First published report for Costa Rica. Vouchers deposited at UARK. Also reported from Mexico, Panama and Jamaica.

** *Licea testudinacea* Nann.-Bremek., Acta Bot. Neerl. 14:141 (1965)

Primarily found in MRF and SRP, on DBW. First published report for Costa Rica

Vouchers deposited at UARK. Not reported from other country in the Neotropics.

* *Lycogala conicum* Pers., Syn. Meth. Fung. 159 (1801)

Primarily found in PWFTL, PMFTL and PMF, on DBW. First published report for the Costa Rica. Vouchers deposited at USJ and UARK. Also reported from Mexico, Nicaragua, Panama, Cuba, Jamaica, Guadeloupe and Brazil.

Lycogala epidendrum (L.) Fr., Syst. Mycol. 4:80 (1829)

Present in almost all ecosystems, more common in MRF, LMWF and PWFTL, on DBW, GL and LC. Reported in 3, 4, 5, 7 and 10. Vouchers deposited at USJ, CR, BPI, UARK, M. Widespread in the Neotropics (see 10).

Lycogala exiguum Morgan, J. Cincinnati Soc. Nat.Hist. 15:134 (1893)

Primarily found in PMFTL, LDF and PWF, on DBW and GL. Reported in 3 and 10. Vouchers deposited at USJ, BPI, UARK and M. Also reported from Mexico, Panama, Cuba, Jamaica, Puerto Rico, Guadeloupe, Martinique, Dominica, Colombia, Venezuela, Guyana, French Guiana, Brazil and Ecuador.

Macbrideola cornea (G.Lister & Cran) Alexop., Mycologia 59(1):112 (1967)

Primarily found in LDF, on DBW. Reported in 5 and 10. Vouchers deposited at UARK. Also reported from Mexico and Ecuador.

Macbrideola decapillata H.C.Gilbert, Stud. Nat.Hist. Iowa Univ. 16:158 (1934)

This species apparently has been found only in lowlands (unknown forest type) on DBW. Reported in 4 and 10. No vouchers known. Also reported from Mexico and Ecuador.

Macbrideola martinii (Alexop. & Beneke) Alexop., Mycologia 59(1):114 (1967)

Primarily found in LDF, LMRF and LMWF, on DBW, LI and GL. Reported in 5 and 10. Vouchers deposited at UARK. Also reported from Mexico, Belize, Jamaica, Dominica, Brazil and Ecuador.

Macbrideola scintillans H.C.Gilbert, Stud. Nat.Hist. Iowa Univ. 16:156 (1934)

Primarily found in LDF and LMRF, on DBW. Reported in 5 and 10. Vouchers deposited at UARK and M. Also reported from Mexico and Belize.

Metatrichia floriformis (Schwein.) Nann.-Bremek., Proc. Kon. Ned. Akad. Wetensch., C. 88(1):127 (1985)

≡ *Trichia floriformis* (Schwein.) G.Lister, J. Bot. 57:110 (1919)

Primarily found in MRF, LMRF, PMF, PWF, LDF and LMF, on DBW, LI, LC and DU. Reported in 3, 4, 7 and 10. Vouchers deposited at USJ, BPI, UARK and M. Also reported from Mexico, Jamaica, Puerto Rico, Venezuela, Brazil, Ecuador, Chile and Argentina.

Metatrichia vesparia (Batsch) Nann.-Bremek. ex G.W.Martin & Alexop., Myxomycetes 143 (1969)

Primarily found in LDF, LMF, PWF, and PMF, on DBW, GL and LP. Reported in 3, 4, 5 and 10. Vouchers deposited at USJ, BPI, UARK and M. Widespread in the Neotropics (see 10).

* *Paradiacheopsis acanthodes* (Alexop.) Nann.-Bremek., in Nannenga-Bremekamp & Yamamoto, Proc. Kon. Ned. Akad. Wetensch., C. 89(2):236 (1986)

This species has only been found only in LDF, on DBW. Reported in 5 as *Paradiacheopsis* cf. *acanthodes*. Vouchers deposited at UARK. Not reported from any other country in the Neotropics.

Paradiacheopsis longipes Hoof & Nann.-Bremek., Proc. Kon. Ned. Akad. Wetensch. 99(1-2):51 (1996)

Primarily found in PMF, on GL. Reported in 5 and 10. No vouchers known. Not reported from any other country in the Neotropics.

Paradiacheopsis rigida (Brândza) Nann.-Bremek., in Martin & Alexopoulos, Myxomycetes 231 (1969)

This species has been found only in MRF, on DBW. First published report for Costa Rica. Vouchers deposited at UARK. Also reported from Belize.

Perichaena chrysosperma (Curr.) Lister, Monogr. Mycetozoa 196 (1894)

Primarily found in LWF, LMF, PMF and LMRF, on DBW, TW, GL and AL. Reported in 3, 4, 5, 8 and 10. Vouchers deposited at USJ, UARK and M. Widespread in the Neotropics (see 10).

Perichaena corticalis (Batsch) Rostaf., Sluzowce Monogr. 293 (1875)

Primarily found in LDF and LMF, on AL. Reported in 5 and 10. Vouchers deposited at UARK. Also reported from Mexico, Panama, Cuba, Dominican Republic, Ecuador, Brazil, Chile and Argentina.

Perichaena depressa Lib., Pl. Crypt. Arduenna 378 (1837)

Primarily found in LMF, LDF, LWF and MRF, on DBW, TW and AL. Reported in 3, 5, 7, 8 and 10. Vouchers deposited at USJ, UARK and M. Widespread in the Neotropics (see 10).

* *Perichaena dictyonema* Rammeloo, Bull. Jard. Bot. Belg. 51(1/2):230 (1981)

Primarily found in LWF, LDF and PWFTL, on GL and FI. First published report for Costa Rica. Vouchers deposited at UARK and M. Also reported from Puerto Rico and Ecuador.

* *Perichaena microspora* Penz. & Lister, in Penzig, Myxomyc. Fl. Buitenzorg 76 (1898)

This species has been found only in LDF, on GL. First published report for Costa Rica. Vouchers deposited at UARK and M. Also reported from Cuba and Brazil.

Perichaena pedata (Lister & G.Lister) Lister ex E.Jahn, Ber. Deutsch. Bot. Ges. 36:667 (1919)

Primarily found in LMF, PRF and SRP, on DBW and GL. Reported in 5, 8 and 10. Vouchers deposited at UARK and M. Also reported from Mexico and Ecuador.

Perichaena vermicularis (Schwein.) Rostaf., Sluzowce Monogr. Suppl. 34 (1876)

Primarily found in LMF, LWF and LDF, on DBW, GL, AL and LP. Reported in 5 and 10. Vouchers deposited at USJ, UARK and M. Also reported from Mexico, Panama, Cuba, Brazil, Brazil, Ecuador, Peru, Bolivia, Chile and Argentina.

Physarella oblonga (Berk. & M.A.Curtis) Morgan, J. Cincinnati Soc. Nat.Hist. 19:7 (1896)

Primarily found in PWFTL and PMF, on DBW and GL. Reported in 3, 4 and 10. Vouchers deposited at USJ, BPI, UARK and M. Widespread in the Neotropics (see 10).

Physarum album (Bull.) Chevall., Fl. Gén. Env. Paris 1:336 (1826)

= *Physarum nutans* Pers., Ann. Bot.(Usteri) 15:6 (1795)

Primarily found in PMFTL, LMF, LMMF and MRF, on dead DBW and GL. Reported in 3, 4 and 10. Vouchers deposited at USJ, BPI, UARK and M. Widespread in the Neotropics (see 10).

* *Physarum auriscalpium* Cooke, Ann. Lyceum Nat.Hist. New York 11:384 (1877)

= *Physarum limonium* Nann.-Bremek., Proc. Kon. Ned. Akad. Wetensch., C. 69(3):357 (1966)

This species has been found only in PWFTL, on FI. First published report for Costa Rica. Vouchers deposited at UARK. Also reported from Mexico, Belize, Panama, Puerto Rico, Guadeloupe, Dominica, Venezuela and Brazil.

Physarum bitectum G.Lister, in Lister, Monogr. Mycetozoa, ed. 2 78 (1911)

Primarily found in PWF and MRF, on DBW. Reported in 3, 4 and 10. Vouchers deposited at USJ, BPI and UARK. Also reported from Mexico, Jamaica, Puerto Rico, Colombia and Venezuela.

Physarum bivalve Pers., Ann. Bot. (Usteri) 15:5 (1795)

Primarily found in MRF, SRP and LMF, on DBW and GL. Reported in 3, 4 and 10. Vouchers deposited at USJ, BPI, UARK and M. Also reported from Mexico, Panama, Cuba, Haiti, Antigua, Colombia, Venezuela, French Guiana, Peru, Ecuador, Brazil, Chile and Argentina.

Physarum bogoriense Racib., Hedwigia 37:52 (1898)

Primarily found in LMF, PWF, PMF and LMRF, on GL, LP and DBW. Reported in 3, 4 and 10. Vouchers deposited at USJ, BPI and UARK. Widespread in the Neotropics (see 10).

Physarum brunneolum (W.Phillips) Massee, Monogr. Myxogastr. 280 (1892)

This species has been found only in MRF, on DBW. Reported in 7 and 10. Vouchers deposited at USJ. Also reported from Mexico, Colombia and Chile.

Physarum cinereum (W.Phillips) Massee, Monogr. Myxogastr. 280 (1892)

Primarily found in LMF, PWF, MRF and SRP, on GL, LP and DBW. Reported in 3, 4, 5 and 10. Vouchers deposited at USJ, BPI, UARK and M. Widespread in the Neotropics (see 10).

Physarum citrinum Schumach., Enum. Pl. 2:201 (1803)

Primarily found in PWFTL, LMF and PWF, on LC. Reported in 3, 4 and 10. Vouchers deposited at USJ and UARK. Also reported from Mexico, Colombia, Venezuela, Guadeloupe, Chile and Argentina.

Physarum compressum Alb. & Schwein., Consp. Fung. Lusat. 97 (1805)

Present in almost all ecosystems, more common in LWF, LMF and PWF, on FI, GL and AL. Reported in 3, 4, 5, 8 and 10. Vouchers deposited at USJ, CR, BPI, UARK and M. Widespread in the Neotropics.

Physarum contextum (Pers.) Pers., Syn. Meth. Fung. 168 (1801)

This species has been found only in MRF, on LC. Reported in 7 and 10. Vouchers deposited at USJ. Also reported from Mexico, Nicaragua and Argentina.

Physarum crateriforme Petch, Ann. Roy. Bot Gard. (Peradeniya) 4:304 (1909)

Primarily found in LDF, on DBW. Reported in 5 and 10. Vouchers deposited at UARK. Also reported from Mexico, Belize, Cuba, Puerto Rico, Antigua, Saint Lucia, Brazil and Ecuador.

Physarum decipiens M.A.Curtis, Amer. J. Sci. Arts 6:352 (1848)

Primarily found in LMF and PMF, on DBW and LP. Reported in 2, 3 and 10. Vouchers deposited at USJ, and BPI. Also reported from Mexico, Brazil, Peru and Bolivia.

Physarum dictyosporum G.W.Martin, Brittonia 14:183 (1962)

This species has een found only in LDF, on GL. Reported in 3 and 4. Vouchers deposited at BPI. Also reported from Mexico and Colombia.

Physarum didermoides (Pers.) Rostaf., Sluzowce Monogr. 97 (1874)

Primarily found in LWF and LMF, on FI and GL. Reported in 2, 3, 4, 5 and 10. Vouchers deposited at USJ, BPI, UARK and M. Widespread in the Neotropics (see 10).

* *Physarum echinosporum* Lister, J. Bot. 37:147 (1899)

Primarily found in LMF and MRF, on TW. First published report for Costa Rica. Vouchers deposited at USJ. Also reported from Panama, Jamaica, Antigua, Dominica, Brazil, Ecuador, Uruguay and Chile.

* *Physarum flavicomum* Berk., London J. Bot. 4:66 (1845)

Primarily found in LDF, PWF and LMMF, on DBW and GL. First published report for Costa Rica. Vouchers deposited at BPI, UARK and M. Also reported from Mexico, Belize, Antigua, Trinidad, Colombia, Brazil and Chile.

Physarum flavidum (Peck) Peck, Annual Rep. New York State Mus. 31:55 (1879)

This species has been found only in MRF, on LC. Reported in 3, 4 and 10. Vouchers deposited at BPI. Not reported from any other country in the Neotropics.

Physarum globuliferum (Bull.) Pers., Syn. Meth. Fung. 175 (1801)

Primarily found in LMF, LDF, PMF and MRF, on DBW and GL. Reported in 3, 4, 5 and 10. Vouchers deposited at USJ, BPI, UARK and M. Widespread in the Neotropics (see 10).

* *Physarum gyrosum* Rostaf., Sluzowce Monogr. 111 (1874)

Primarily found in LDF and PMFTL, on LP. First published report for Costa Rica. Vouchers deposited at USJ and UARK. Also reported from Mexico, Colombia, Brazil and Uruguay.

Physarum javanicum Racib., Hedwigia 37:53 (1898)

Primarily found in LWF, LMF and LMRF, on DBW, GL and AL. Reported in 3, 4, 8 and 10. Vouchers deposited at BPI, UARK and M. Also reported from Mexico, Cuba, Jamaica, Puerto Rico, Colombia, Venezuela, Trinidad, French Guiana, Brazil and Ecuador.

* *Physarum leucophaeum* Fr., Symb. Gasteromyc. 24 (1818)

This species has been found only in PWFTL, on GL. First published report for Costa Rica. Vouchers deposited at BPI and UARK. Also reported from Mexico, Cuba, Jamaica, Dominican Republic, Antigua, Guadeloupe, Dominica, Ecuador, Brazil, Chile and Argentina.

Physarum leucopus Link, Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesammten Naturk. 3:27 (1809)

Primarily found in PMF and MRF, on DBW. Reported in 3, 7 and 10. Vouchers deposited at USJ and BPI. Also reported from Mexico, Guatemala, Panama, Jamaica, Colombia, Brazil, Paraguay and Argentina.

Physarum melleum (Berk. & Broome) Massee, Monogr. Myxogastr. 278 (1892)
Primarily found in LWF and LMF, on GL, LP and DBW. Reported in 3, 4, 5, 7, 8 and 10. Vouchers deposited at USJ, BPI, UARK and M. Widespread in the Neotropics.

Physarum murinum Lister, Monogr. Mycetozoa 41 (1894)
This species has been found only in LWF, on DBW. Reported in 3, 4 and 10. Vouchers deposited at BPI. Also reported from Mexico.

* *Physarum mutabile* (Rostaf.) G.Lister, in Lister, Monogr. Mycetozoa, ed. 2 53 (1911)
This species has been found only in PMF, on DBW. First published report for Costa Rica. Vouchers deposited at USJ. Also reported from Mexico, Venezuela, Brazil and Argentina.

Physarum nicaraguense T.Macbr., Bull. Iowa Univ. Lab. Nat.Hist. 2:382 (1893)
Primarily found in LMF and PMF, on LP. Reported in 3, 4 and 10. Vouchers deposited at USJ and BPI. Also reported from Mexico, Belize, Nicaragua, Jamaica, Haiti, Puerto Rico, Trinidad and Brazil.

Physarum notabile T.Macbr., N. Amer. Slime-Moulds, ed.2 80 (1922)

Primarily found in LWF, LMF, PWF and LMMF, on FI, GL and AL. Reported in 3, 4, 5 and 10. Vouchers deposited at USJ, BPI and UARK. Also reported from Mexico, Jamaica, Dominica, Brazil, Bolivia and Argentina.

Physarum nucleatum Rex, Proc. Acad. Nat. Sci. Philadelphia 43:389 (1891)
Primarily found in LMF and PMFTL, on DBW and AL. Reported in 3, 4 and 10. Vouchers deposited at USJ, BPI, UARK and M. Also reported from Mexico, Nicaragua, Cuba, Jamaica, Puerto Rico, Dominica, Trinidad, Venezuela, French Guiana, Brazil, Ecuador and Argentina.

* *Physarum oblatum* T.Macbr., Bull. Iowa Univ. Lab. Nat.Hist. 2:384 (1893)
Primarily found in LMF and LMRF, on FI. First published report for Costa Rica. Vouchers deposited at BPI and UARK. Also reported from Mexico, Belize, Panama, Jamaica, Dominica, Colombia, Venezuela, Brazil and Ecuador.

* *Physarum penetrale* Rex, Proc. Acad. Nat. Sci. Philadelphia 43:389 (1891)
Primarily found in PWF, PRF and LMRF, on DBW and TW. First published report for Costa Rica. Vouchers deposited at UARK and M. Also reported from Mexico, Panama, Jamaica, Dominica, Venezuela, French Guiana, Brazil and Chile.

* *Physarum pezizoideum* (Jungh.) Pavill. & Lagarde, Bull. Soc. Mycol. France 19:87 (1903)

Primarily found in PWFTL, on DBW. First published report for Costa Rica. Vouchers deposited at UARK. Also reported from Mexico, Cuba, Brazil and Argentina.

Physarum polycephalum Schwein., Schriften Naturf. Ges. Leipzig 1:63 (1822)
Primarily found in LWF, PWF and PMF, on TW and GL. Reported in 3, 4 and 10. Vouchers deposited at USJ, BPI and UARK. Widespread in the Neotropics (see 10).

Physarum pulcherripes Peck, Bull. Buffalo Soc. Nat. Sci. 1:64 (1873)
Primarily found in LWF and LMF, on GL. Reported in 3, 4 and 10. Vouchers deposited at USJ, BPI and UARK. Also reported from Mexico, Panama, Jamaica, Dominica, Trinidad and Venezuela.

Physarum pusillum (Berk. & M.A.Curtis) G.Lister, in Lister, Monogr. Mycetozoa, ed. 2 64 (1911)
Present in almost all ecosystems, more common in LWF, PWFTL and MRF, on GL, AL, DBW, LP and FI. Reported in 5, 8 and 10. Vouchers deposited at USJ, UARK and M. Widespread in the Neotropics (see 10).

Physarum rigidum (G.Lister) G.Lister, in Lister, Monogr. Mycetozoa, ed. 3 36 (1925)
Primarily found in PWF and PMF, on DBW. Reported in 3, 4 and 10. Vouchers deposited at USJ and BPI. Also reported from Jamaica, Puerto Rico, Trinidad, Brazil, Uruguay and Argentina.

* *Physarum robustum* (Lister) Nann.-Bremek., Proc. Kon. Ned. Akad. Wetensch., C. 76(5):484 (1973)

This species has been found only in MRF, on DBW. First published report for Costa Rica. Vouchers deposited at UARK. Also reported from Mexico.

* *Physarum roseum* Berk. & Broome, J. Linn. Soc., Bot. 14:84 (1873)

Primarily found in LDF and PMFTL, on DBW. Reported in 5 as doubtful. Vouchers deposited at USJ and UARK. Also reported from Mexico, Jamaica, Dominica, Brazil and Paraguay.

Physarum serpula Morgan, J. Cincinnati Soc. Nat.Hist. 19:29 (1896)

Primarily found in LMF and LWF, on TW, GL and LP. Reported in 8 and 10. Vouchers deposited at USJ, UARK and M. Also reported from Mexico, Panama, Cuba, Jamaica, Trinidad, Brazil, Ecuador and Argentina.

Physarum stellatum (Massee) G.W.Martin, Mycologia 39(4):461 (1947)

Primarily found in LMF, LDF, PWF, PRF, LMWF and MRF, on DBW and TW. Reported in 3, 4, 5 and 10. Vouchers deposited at USJ, BPI, UARK and M. Widespread in the Neotropics (see 10).

* *Physarum straminipes* Lister, J. Bot. 36:163 (1898)

This species has been found only in PMF, on GL and LP. Reported in 5 as doubtful. Vouchers deposited at UARK. Also reported from Mexico and Chile.

Physarum superbum Hagelst., Mycologia 32(3):385 (1940)

Primarily found in LMF and LWF, on GL and FI. Reported in 8 and 10. Vouchers deposited at USJ, UARK and M. Also reported from Mexico, Haiti, Puerto Rico, Venezuela, Ecuador and Peru.

Physarum tenerum Rex, Proc. Acad. Nat. Sci. Philadelphia 42:192 (1890)

Primarily found in LMF, PWF, LMWF, on DBW. Reported in 2, 3, 4 and 10. Vouchers deposited at USJ, UARK and M. Widespread in the Neotropics (see 10).

Physarum viride (Bull.) Pers., Ann. Bot. (Usteri) 15:6 (1795)

Primarily found in PWFTL, PWF and LMWF, on DBW and GL. Reported in 1, 3, 4 and 10. Vouchers deposited at USJ, BPI, UARK and M. Cosmopolitan.

* *Reticularia jurana* Meyl., Bull. Soc. Vaud. Sci. Nat. 44:297 (1908)

This species has been found only in PWFTp, on GL. First published report for Costa Rica. Vouchers deposited at M. Also reported from Mexico, Panama, Dominican Republic, Jamaica, Puerto Rico, Brazil, Ecuador, Uruguay, Chile and Argentina.

* ? *Reticularia splendens* Morgan, J. Cincinnati Soc. Nat.Hist. 15:137 (1893)

This species has been found only in PWF, on DBW. First published report for the country. No vouchers reported, but the species seems to have been observed in the country. Also reported from Mexico, Panama and Chile.

* *Stemonaria gracilis* Nann.-Bremek. & Y.Yamam., in Nannenga-Bremekamp, Yamamoto & Sharma, Proc. Kon. Ned. Akad. Wetensch., C. 87(4):461 (1984)
This species has been found only in LMF, on GL. First published report for the country. Vouchers deposited at M. Also reported from Peru.

Stemonaria longa (Peck) Nann.-Bremek., R.Sharma & Y.Yamam., in Nannenga-Bremekamp, Yamamoto & Sharma, Proc. Kon. Ned. Akad. Wetensch., C. 87(4):453 (1984)
Primarily found in LWF, LMF, PWF and PMF, on DBW and LP. First published report for Costa Rica. Vouchers deposited at USJ, UARK and M. Widespread in the Neotropics (see 10).

Stemonitis axifera (Bull.) T.Macbr., N. Amer. Slime-Moulds 120 (1899)
= *Stemonitis ferruginea* Ehrenb., Sylv. Myc. Berol. 25 (1818)
Primarily found in PMFTL, LDF, PWF, LMWF and MRF, on DBW and GL. Reported in 1, 3, 4 and 10. Vouchers deposited at USJ, UARK and M. Probably ubiquitous in the Neotropics.

Stemonitis flavogenita E.Jahn, Verh. Bot. Vereins Prov. Branderburg 45:165 (1904)
Primarily found in LWF and MRF, on TW and AL. Reported in 3, 4, 8 and 10. Vouchers deposited at BPI and UARK. Also reported from Mexico, Guatemala, Panama, Cuba, Jamaica, Puerto Rico, Venezuela, Trinidad, Ecuador, Brazil and Argentina.

* *Stemonitis foliicola* Ing, Trans. Brit. Mycol. Soc. 50(4):555 (1967)

This species has been found only in PWFTL, on GL. First published report for Costa Rica. Vouchers deposited at UARK. Also reported from Peru.

Stemonitis fusca Roth, Bot. Mag.(Römer & Usteri) 1(2):26 (1787)

Present in almost all ecosystems, more common in LWF, PMF and MRF, on DBW, TW, GL and AL. Reported in 3, 4, 5, 7, 8 and 10. Vouchers deposited at USJ, BPI, UARK and M. Widespread in the Neotropics (see 10).

Stemonitis herbatica Peck, Annual Rep. New York State Mus. 26:75 (1874)

Primarily found in LWF, LMF, PWF and PMF, on DBW and LP. Reported in 3 and 10. Vouchers deposited at BPI and UARK. Also reported from Mexico, Belize, Guatemala, Bahamas, Cuba, Jamaica, Dominican Republic, Puerto Rico, Antigua, Guadeloupe, Martinique, Dominica, Venezuela, Brazil, Ecuador and Argentina.

* *Stemonitis pallida* Wingate, in Macbride, N. Amer. Slime-Moulds 123 (1899)

This species has been found only in PRF, on DBW. First published report for Costa Rica. Vouchers deposited at UARK. Also reported from Mexico, Panama, Cuba, Jamaica, Puerto Rico, Trinidad, Venezuela, French Guiana, Brazil, Ecuador and Argentina.

Stemonitis smithii T.Macbr., Bull. Iowa Univ. Lab. Nat.Hist. 2:381 (1893)

Primarily found in PMFTL, PMF and MRF, on DBW and LC. Reported in 7. Vouchers deposited at USJ and UARK. Also reported from Mexico, Nicaragua, Panama, Jamaica, Puerto Rico, Antigua, Dominica, Venezuela, Trinidad, Peru, Brazil, Chile and Argentina.

Stemonitis splendens Rostaf., Sluzowce Monogr. 195 (1874)

Primarily found in PMFTL, PWF, PMF and MRF, on DBW, GL and AL. Reported in 3, 4 and 10. Vouchers deposited at USJ, BPI, UARK and M. Widespread in the Neotropics (see 10).

Stemonitopsis aequalis (Peck) Y.Yamam., Myxomycete Biota Japan 625 (1998)

This species has been found only in LWF, on GL. Reported in 3 and 10. Vouchers deposited at BPI. Also reported from Panama, Jamaica, Dominica and Brazil.

** *Stemonitopsis amoena* (Nann.-Bremek.) Nann.-Bremek., Nederlandse Myxomyceten (Zutphen) 205 (1975)

Primarily found in LMF, on LP and FI. First published report for Costa Rica. Vouchers deposited at USJ and M. Not reported from other country in the Neotropics.

* *Stemonitopsis gracilis* (G.Lister) Nann.-Bremek., Nederlandse Myxomyceten (Zutphen) 210 (1975)

Primarily found in PRF, on DBW. First published report for Costa Rica. Vouchers deposited at UARK. Also reported from Mexico, Cuba and Brazil.

Stemonitopsis hyperopta (Meyl.) Nann.-Bremek., Nederlandse Myxomyceten (Zutphen) 206 (1975)

Primarily found in LWF, PMFTL and PRF, on TW. Reported in 6 and 10. Vouchers deposited at USJ, UARK and M. Also reported from Mexico, Guatemala, Panama, Jamaica, Puerto Rico, Dominica, Brazil, Chile and Argentina.

Stemonitopsis subcaespitosa (Peck) Nann.-Bremek., Nederlandse Myxomyceten (Zutphen) 211 (1975)

Primarily found in PWFTL and PMFTL, on DBW. Reported in 3, 4 and 10. Vouchers deposited at USJ, BPI and UARK. Also reported from Mexico, Dominica, Venezuela, Brazil and Argentina.

Stemonitopsis typhina (F.H.Wigg.) Nann.-Bremek., Nederlandse Myxomyceten (Zutphen) 209 (1975)

≡ *Comatricha typhoides* (Bull.) Rostaf., in Lister, Monogr. Mycetozoa 120 (1894)

Primarily found in LMF, PMFTL, PRF, PMF and MRF, on DBW and GL. Reported in 3, 4, 5 and 10. Vouchers deposited at BPI, UARK and M. Widespread in the Neotropics (see 10).

Symphytocarpus herbaticus Ing, in Ing & Nannenga-Bremekamp, Proc. Kon. Ned. Akad. Wetensch., C. 70(2):229 (1967)

Primarily found in PWFTL, PWF and LMFTP, on DBW and GL. Reported in 3 and 4. Vouchers deposited at USJ and UARK. Also reported from Mexico, Guatemala, Jamaica,

Dominican Republic, Puerto Rico, Antigua, Guadeloupe, Martinique, Dominica, Venezuela and Argentina.

* *Trichia affinis* de Bary, in Fuckel, Jahrb. Nassauischen Vereins Naturk. 23-24:336 (1870)

Primarily found in PMFTL and PWF, on DBW. First published report for Costa Rica. Vouchers deposited at UARK. Also reported from Mexico, Panama, Cuba, Trinidad, Ecuador and Chile.

Trichia botrytis (J.F.Gmel.) Pers., Neues Mag. Bot. 1:89 (1794)

Primarily found in PWFTL and MRF, on DBW, TW and LC. Reported in 7 and 10. Vouchers deposited at USJ and UARK. Also reported from Mexico, Jamaica, Dominican Republic, Brazil, Chile, and Argentina.

* *Trichia contorta* (Ditmar) Rostaf., Sluzowce Monogr. 259 (1875)

Primarily found in LMRF and SRP, on DBW. First published report for Costa Rica. Vouchers deposited at M. Also reported from Mexico, Brazil and Chile.

Trichia decipiens (Pers.) T.Macbr., N. Amer. Slime-Moulds 218 (1899)

Primarily found in LMWF and MRF, on DBW, GL and AL. Reported in 3, 4, 7 and 10. Vouchers deposited at USJ, BPI, UARK and M. Also reported from Mexico, Guatemala, Cuba, Jamaica, Puerto Rico, Venezuela, Brazil, Ecuador, Chile and Argentina.

Trichia favoginea (Batsch) Pers., Neues Mag. Bot. 1:90 (1794)

Primarily found in LMWF and MRF, on DBW, GL and AL. Reported in 3, 4 7 and 10. Vouchers deposited at USJ, BPI, UARK and M. Widespread in the Neotropics (see 10).

* ? *Trichia flavicoma* (Lister) Ing, Trans. Brit. Mycol. Soc. 50(4):558 (1967)

This species has been found only in LDF, on DBW. First published report for Costa Rica. No vouchers known, but the species seems to have been observed in the country. Also reported from Mexico and Dominican Republic.

Trichia persimilis P.Karst., Not. Sällsk. Fauna Fl. Fenn. Förh 9:353 (1868)

Primarily found in LMWF and MRF, on DBW, GL and DU. First published report for Costa Rica. Vouchers deposited at M. Also reported from Mexico, Panama, Peru and Chile.

Trichia scabra Rostaf., Sluzowce Monogr. 258 (1875)

Primarily found in MRF, on DBW and GL. Reported in 3, 4 and 10. Vouchers deposited at BPI, UARK and M. Also reported from Mexico, Jamaica, Colombia, Venezuela, Brazil, Ecuador and Argentina.

Trichia varia (Pers. ex J.F.Gmel.) Pers., Neues Mag. Bot. 1:90 (1794)

Primarily found in PWFTL, on DBW. Reported in 3, 4 and 10. Vouchers deposited at USJ, BPI and UARK. Also reported from Mexico, Cuba, Jamaica, Venezuela, Ecuador, Chile, Paraguay and Argentina.

Trichia verrucosa Berk., in Hooker, Fl. Tasman. 2(9):269 (1859)

This species has been found only in MRF, on DBW and GL. Reported in 3, 4, 7 and 10. Vouchers deposited at USJ, UARK and M. Also reported from Mexico, Cuba, Jamaica, Dominica, Colombia, Brazil, Chile and Argentina.

Tubifera bombarda (Berk. & Broome) G.W.Martin, Brittonia 13:110 (1961)

Primarily found in LWF and PWF, on GL. Reported in 3, 4, 8 and 10. Vouchers deposited at USJ, BPI and M. Also reported from Jamaica, Puerto Rico, Venezuela, French Guiana and Brazil. Several of the specimens collected in Costa Rica lack any evidence of the bristle-like pseudocapillitium so characteristic of this species and may represent a distinct taxon.

* *Tubifera casparyi* (Rostaf.) T.Macbr., N. Amer. Slime-Moulds 157 (1899)

This species has been found only in PWFTL, on LC. First published report for Costa Rica. Vouchers deposited at UARK. Also reported from Mexico and Argentina.

Tubifera ferruginosa (Batsch) J.F.Gmel., Syst. Nat. 2:1472 (1792)

Primarily found in MRF, PRF and PMF, on DBW. Reported in 3, 4 and 10. Vouchers deposited at USJ, BPI, UARK and M. Also reported from Mexico, Panama, Jamaica, Dominican Republic, Puerto Rico, Guadeloupe, Dominica, French Guiana, Brazil, Ecuador, Chile and Argentina.

Tubifera microsperma (Berk. & M.A.Curtis) G.W.Martin, Mycologia 39(4):461 (1947) Primarily found in PWFTp, LMF, LMFTP and LMRF, on DBW. Reported in 3, 4 and 10. Vouchers deposited at USJ, BPI, UARK and M. Widespread in the Neotropics (see 10).

Wilkomlangea reticulata (Alb. & Schwein.) Kuntze, Revis. Gen. Pl. 2:875 (1891) ≡ *Cienkowskia reticulata* (Alb. & Schwein.) Rostaf., Sluzowce Monogr. 91 (1874) Primarily found in MRF, on DBW. Reported in 3, 4 and 10. No vouchers known. Also reported from Mexico, Belize, Panama, Venezuela, Brazil, Peru, Uruguay and Argentina.

Discussion

The comprehensive database of myxomycete collections compiled for this paper is largely the product of field studies carried out in Costa Rica during the past decade (see Rojas et al. 2009). It is not surprising that a high percentage of the species reported herein have not been included in recent publications. For example, about ten years ago Schnittler and Stephenson (2000) increased the number of species known for this country to 126, and just recently Lado and Wrigley de Basanta (2008) reported a total of 143 species in their recent literature review. However, field surveys carried out during the past decade in areas of the country traditionally understudied have yielded a number of species not previously known for these areas. In fact, if the four doubtful species are considered, the total number of myxomycetes for Costa Rica would increase to 212 species.

This number should be higher if the diversity prediction using ACE values is correct. The completeness of the survey is calculated as more than 80% using this

indicator. However, it is important to remember that variations in the calculation of the maximum number of species occur when different algorithms are used (see Magurran 2004). As such, the estimation provided herein is not intended as an "exact" calculation. For comparison, Schnittler and Stephenson (2000) calculated that between 70-80% of the myxomycetes on bark and litter in different forest types in Costa Rica were recovered in their study by using a different estimator. Similarly, Schnittler et al. (2002) calculated the completeness of a rapid assessment project in a cloud forest in Ecuador of about 92%. However, the values from those projects may reflect the limitations of the research carried out. With only a limited number of populations of amoebae forming fructifications at a given time, and the well-known fact that many species, especially those forming large fructifications, rarely occur in moist chamber cultures, these surveys represent only "snapshots" of biological systems and do not necessarily reflect the total species assemblage of a particular area. Almost always such rapid assessments underestimate the species richness of an area as a product of their temporally limited research effort. Given this situation, it is still difficult to determine if the completeness of myxomycete surveys accurately reflect a biological pattern. However, it is very likely that the number of species of myxomycetes reported for Costa Rica in this paper reflects the majority of the taxa actually present in the country.

In any case, one aspect that should be taken in consideration is the taxonomic treatment that authors have used to report myxomycetes from Costa Rica. Until recently, most taxonomic treatments primarily followed Martin and Alexopoulos (1969). However, in recent years the treatments of Lado (2001, 2005-2010) have been incorporated into the publications related to Costa Rican myxomycetes. Due this discrepancy, the synonymies

of the names reported herein have been included. In any case, species such as *Stemonitis smithii* T. Macbr. and *Cribraria oregana* H.C. Gilbert have been treated separately. In the first instance, this species is not reported in Lado and Wrigley de Basanta (2008) since, according to the treatment of Lado (2005-2010), the taxon in question should be included in *Stemonitis axifera* (Bull.) T.Macbr. For the purpose of the present paper, *S. smithii* has been considered a separate taxon. In the case of *C. oregana*, this species was reported in Lado and Wrigley de Basanta (2008); however, no vouchers or reports of this species were found during the course of this investigation. For that reason, this taxon was not included in the current list.

One aspect of interest is the high value for the taxonomic diversity index. For comparison, the value obtained by Stephenson et al. (1993) from an analysis of the data given by Alexopoulos and Sáenz (1976), also in Costa Rica, was only 3.93. This type of data shows the importance of nearly exhaustive surveys, since it is obvious that this aspect can invariably modify the value of taxonomic diversity depending upon how exhaustive an area has been examined. The high value of intrageneric diversity obtained herein can also be used to infer ecological aspects of the community under study. Given the high taxonomic diversity value obtained in this study, it is not surprising that *Physarum* and *Didymium*, the two genera with the highest numbers of species were the ones with a higher presence across substrates and forest types (not previously shown). This might indicate these genera utilize a wide range of resources, which is possible when species use different resources in different ways.

In this sense, the differences in species richness and species assemblages (see Rojas et al. 2009) noted for different forest types and substrates might reflect a

contrasting pattern of specialization in resource use. This seems to be a common phenomenon in tropical myxomycetes, for which evidence has been provided recently by several authors (e.g., Schnittler 2001, Schnittler and Stephenson 2002; Rojas et al. 2008; Wrigley de Basanta et al. 2008; Estrada-Torres et al. 2009). These data suggest that the complex mosaic of microenvironments found in tropical forests provides myxomycetes with a number of exploitable niches that seem to have driven particular species to a degree of specialization that is not found in other types of ecosystems. In spite of this apparent pattern, the data provided in this paper are not conclusive for the majority of the species due the low number of records for an accurate ecological analysis.

It is clear however, that some of the most common species of myxomycetes in Costa Rica are present in a large number of forest types and substrates. In almost every survey carried out in this country, species such as *Arcyria cinerea*, *Hemitrichia calyculata*, *Didymium squamulosum* and *Physarum compressum* were reported. This contrasts with the situation that exists for species that belong to such genera as *Lamproderma* and *Trichia*, for which high-elevation forests and dead bark and wood seem to be the preferred combination of forest type and substrate for example. Of course, this is definitely an artifact of the sampling techniques and effort used by different collectors in different forest types as well as of the combination of different environmental characteristics influencing fructification patterns in the field and in laboratory conditions. However, it is an observation that might indicate that there are genera more specialized for colder, more temperate-like environments such as the oak-dominated high-elevation forests of Costa Rica.

In summary, myxomycetes are more common in Costa Rica than previously realized. The high diversity of species reported certainly suggests that patterns of species distribution should be analyzed in the context of research carried out in other areas of the world. Even in well studied areas, patterns of species distribution need to be reconsidered in the context of forest structure (e.g., Keller et al. 2004; Schnittler et al. 2006). In most tropical countries, the prerequisite baseline data are not yet available to encourage researchers to conduct such type of studies. For that reason, basic information about myxomycete assemblages from different parts of the world is still required.

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Chapter 9

New records of myxomycetes from high-elevation areas of Mexico and Guatemala

Abstract: Surveys of four high-elevation study areas in central Mexico and northwestern Guatemala were carried out to obtain baseline information on the species of myxomycetes present. All study areas were sampled in 2006 and 2007. Both specimens that had fruited in the field and those obtained from moist chamber cultures in the laboratory were considered. The myxomycetes recorded included seven species that represented new records for Mexico and 35 that were new for Guatemala. Five of these were new records for the Neotropics. A list of these species and information on the microhabitats in which they occurred is provided. This relatively limited study clearly demonstrates that high-elevation areas in the Neotropics are still under sampled for myxomycetes. For most countries in the region, there are still information gaps relating to distribution patterns of myxomycetes. In the context of biodiversity conservation, it is important to continue studying groups of organisms such as myxomycetes in the rapidly changing Neotropical ecosystems.

Keywords: Cuchumatanes, Cofre de Perote, La Malinche, myxogastria, species distribution

Introduction

The myxomycetes or myxogastrids are a group of ameboid protists (Adl et al. 2005) with the particular ability to produce fruiting bodies that resemble microscopic

fungi (Stephenson et al. 2008a). These organisms are known to occur in virtually all terrestrial ecosystems (Stephenson 2003). However, most studies have been directed towards temperate forests of the Northern Hemisphere (Stephenson et al. 2004).

In spite of this situation, tropical areas of the world have received a moderate level of study. For example, the Neotropical region has been the subject of more than 550 scientific articles on myxomycetes (see Lado and Wrigley de Basanta 2008). As expected, as new studies occur in the region, more and more species of myxomycetes continue to be added to the known myxobiota (e.g., Rojas and Stephenson 2007; Estrada-Torres et al. 2009). In fact, several new species have been recently described from understudied ecosystems in the region (e.g., Moreno et al. 2009; Wrigley de Basanta et al. 2009), and it is very likely that this trend will continue for some time.

One of the reasons why new species continue to be discovered is the nature of the Neotropical region, in which the ecological complexity of regional ecosystems provides a large number of microenvironments and high species diversity (see Kricher 1999). However, niche differentiation in myxomycetes also seems to play a role in explaining this pattern (see Rojas et al. 2009). In this way, the wide variety of conditions that allow for the existence of multiple microenvironments and the capacity of myxomycetes to use a number of different resources would favour the occurrence of different species in this type of situation. As with other groups, this pattern seems to be determined by a combination of global and local factors (Stephenson et al. 2008a).

In the ecosystems that occur at high elevations in the Neotropical region, myxomycetes have not been studied extensively. This is still true in spite of the baseline information that has been obtained for the myxomycete assemblages present in some of

these areas, especially in countries such as Mexico, Costa Rica and Ecuador (e.g., Schnittler et al. 2002; Rodríguez-Palma et al. 2005; Rojas and Stephenson 2007). As a result of this, most high-elevation Neotropical ecosystems continue to be understudied for myxomycetes.

The lack of information on the biota of high-elevation ecosystems is an important aspect of the conservation that needs to be addressed. High-elevation ecosystems in the Neotropics are extremely important as water reservoirs and natural erosion controllers (Brown and Kappelle 2001). Moreover, these ecosystems represent biodiversity treasures and the landscapes associated with them are visually appealing (Aldrich et al. 2000). The study of microscopic organisms such as myxomycetes is important for understanding the dynamics of these forests.

However, major differences in what is known exist from place to place within the Neotropical region. In Mexico, for example, researchers have generated more than 130 publications and have used this to advance the argument that this country has the richest myxobiota in the entire Neotropics (see Lado and Wrigley de Basanta 2008). In Guatemala, on the other hand, few studies of myxomycetes have been carried out, and only two publications (Farr 1976; Estrada-Torres et al. 2000) have reported these organisms for the entire territory.

In spite of this situation, it is very likely that additional study of some of the poorly known ecosystems in both countries would continue to provide important ecological information about the assemblages present. For that reason, the present study was designed to generate baseline information on the myxomycetes of high-elevation areas of Mexico and Guatemala. In both cases, these data are important for setting the

stage for future studies of myxomycetes, especially with respect to monitoring changes in the community dynamics of microorganisms in relation to predicted global climate change.

Methods

This study was carried out between the years 2006 and 2007. All species names follow the nomeclatural treatment of Lado (2005-2010) except for *Perichaena liceoides*, for which the original protologue is provided. The morphological concept of species was used in all cases.

Study areas

Four study areas in the northern section of the Neotropics were used in the surveys carried out (Fig 1). In each of the study areas, two study sites corresponding to forested and non-forested conditions were selected. In each of these study sites, two collecting plots were established. Collectively, this effort produced a total of 16 plots arranged in 8 different study sites. All sampling was confined to *high-elevation areas*, defined in this study as those areas occurring at elevations >3000 m.

In Mexico, the two study areas correspond to (A) the Matlalcueyetl (=La Malinche) Volcano (hereafter abbreviated as Malinche, collecting plots located between 19˚14'–19˚16' N and 97˚59'–98˚02' W, 3100–4050 m), which is located between the states of Puebla and Tlaxcala and (B) the Cofre de Perote Volcano (Perote, collecting plots located between 19˚29'–19˚31' N and 97˚09'–97˚10' W, 3400–4200 m) in the state of Veracruz. In these two cases, the forests surveyed are located below the treeline (Fig 2) and are dominated by *Pinus hartwegii* Lindl. and *Abies religiosa* (Kunth.) Schltdl. &

Cham, whereas non-forested areas at the highest elevations are dominated by the tussock grasses *Festuca tolucensis* Kunth and *Calamagrostis tolucensis* (Kunth) Trin. ex Steud.

In Guatemala, the two study areas were located on the Cuchumatanes Plateau and correspond to (C) Llanos de San Miguel (Llanos, collecting plots located at 15˚30' N and 91˚29' W, 3400–3500 m) and (D) La Ventoza (Ventoza, collecting plots located at 15˚27' N and 91˚32' W, 3400–3600 m). In these areas, the forests surveyed are dominated by *Juniperus standleyi* Steyerm. or *Pinus hartwegii* Lindl. and non-forested sites are dominated by the tussock grass *Agrostis tolucensis* Kunth or *Agave hurteri* Trel.

Sampling method

All the study areas were sampled within two consecutive periods between June and July of 2006 and 2007. Both specimens that had fruited in the field and those obtained from moist chamber cultures in the laboratory were considered.

In the latter case, a series of samples of dead plant material corresponding to ground litter, aerial litter, bark and twigs was collected from each of the plots. These samples were taken to the laboratory, where they were used to prepare moist chamber cultures using the protocol described by Stephenson and Stempen (1994).

With this method, each sample was placed in a Petri dish previously lined with filter paper and pH-neutral water was added the dish until it covered all the sample material. After approximately 24 h, the pH of the substrate was measured using a pH meter and then the excess water was poured off. The reason for measuring this parameter is that a number of previous studies have determined pH to be an important factor in determining microenvironmental preferences in myxomycetes.

After this process, all moist chamber cultures were kept at room conditions for approximately 10 weeks. During this period, they were examined for the presence of myxomycete fruiting bodies every week. Extra water was added to the culture as necessary in order to maintain a humid microenvironment. When fruiting bodies were detected, these were extracted from the moist chamber culture and placed in a pasteboard box for identification and storage. All collections made in this manner were deposited in the mycological herbarium of the University of Arkansas (UARKM).

In addition to the specimens obtained from moist chamber cultures, collections were obtained in the field using the opportunistic protocol described by Cannon and Sutton (2004). With this method, myxomycetes were searched for in the areas corresponding to the collecting plots. When fruiting bodies were found, pH was measured in the area surrounding the fruiting body with a portable pH meter. After this, the fruiting bodies were collected, returned to the laboratory and processed in the same manner as described previously for identification and storage of specimens from moist chamber cultures.The information represented by all of the specimens collected was used to construct a database, and this was used for the annotations of individual species.

Species list and annotations

The list of species provided in this paper includes only those taxa for which no previous records were known for the areas surveyed. As such, this list does not reflect the actual species diversity found in each study area and each country. The latter data have been summarized in a separate manuscript (Rojas et al. unpublished data).

The starting point used to compile the list was the recent review of myxomycetes for the Neotropics (Lado and Wrigley de Basanta 2008). The list of new records for the study areas considered in the present study is presented in alphabetical order by genus and then species. In all cases, the species name is followed by the authors. After this, an indication of the origin of the particular record (FC for field collections and MC for moist chamber cultures) is given, along with the number of collections and the year in which these were obtained. The country and study area (in parenthesis), forest type, substrate types and range of pH values recorded for all specimens of the species in question are provided as well. Those species that represent new records for the Neotropical region are indicated.

For the annotations, forest types were coded as following: (A) non-forested areas dominated by *Agrostis tolucencis*, (B) non-forested areas dominated by *Festuca tolucensis*, (C) *Abies religiosa*-dominated forest, (D) *Pinus hartwegii*-dominated forest and (E) *Juniperus standleyi*-dominated forest. In a similar manner, substrate types were abbreviated as following: ground litter (GL), aerial litter (AL), twigs (TW), bark (BA) and decaying wood (DW). When a particular species was associated with more than one forest and/or substrate type, the abbreviations for the latter are listed in order of their frequency for that particular species.

In countries where the species was previously observed, study areas where specimens were collected are only mentioned and no detailed data are provided. The number of specimens recorded and the other data given in each instance corresponds only to the country for which the species is a new record. All new records from Mexico are

denoted with one asterisk before the name, two asterisks are used for new records for Guatemala, and new records for the two countries by three asterisks.

Results

A total of 82 species were recorded from the various study areas. Seven of these represented new records for Mexico and 35 were new records for Guatemala. In addition, five new records for the Neotropical region were found. For Mexico, one specimen that could only be identified to the genus level also represented a new record.

Approximately 55% of the records of species new to the areas studied were collected in forested plots, whereas the remaining 45% were collected in non-forested plots. About 27% of the total number of collections was recorded from the *Pinus hartwegii*-dominated forests, whereas about 24% and 5% were from the *Juniperus standleyi* and the *Abies religiosa*-dominated forests, respectively. When the substrates of the new records were evaluated, approximately 48% were associated with aerial litter, 21% with twigs, 17% with ground litter and 14% with bark.

The annotated list of all new species documented from the study areas is provided below.

List of new myxomycetes for Mexico and Guatemala

***** *Amaurochaete* Rostaf. (a specimen that could be identified only to genus)
MC, 1 collection, 2007. Mexico (Malinche), in C, on TW, pH = 4.6.

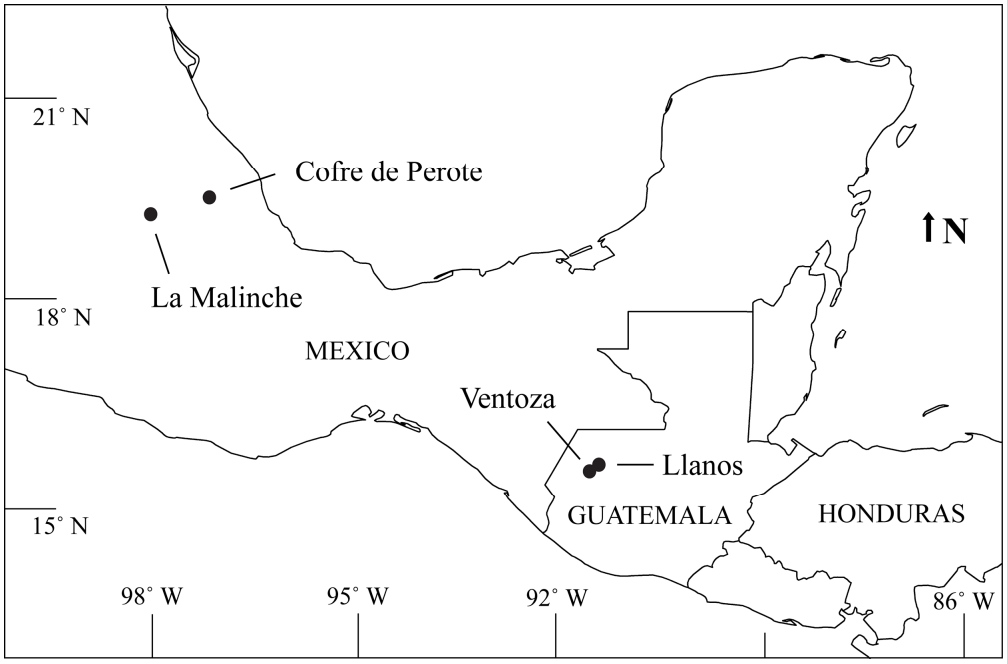

Fig 1 – Map of central-southern Mexico and the northern section of Central America showing the geographic location of the four study areas considered in the present study. For complete names see the "study areas" section in Methods.

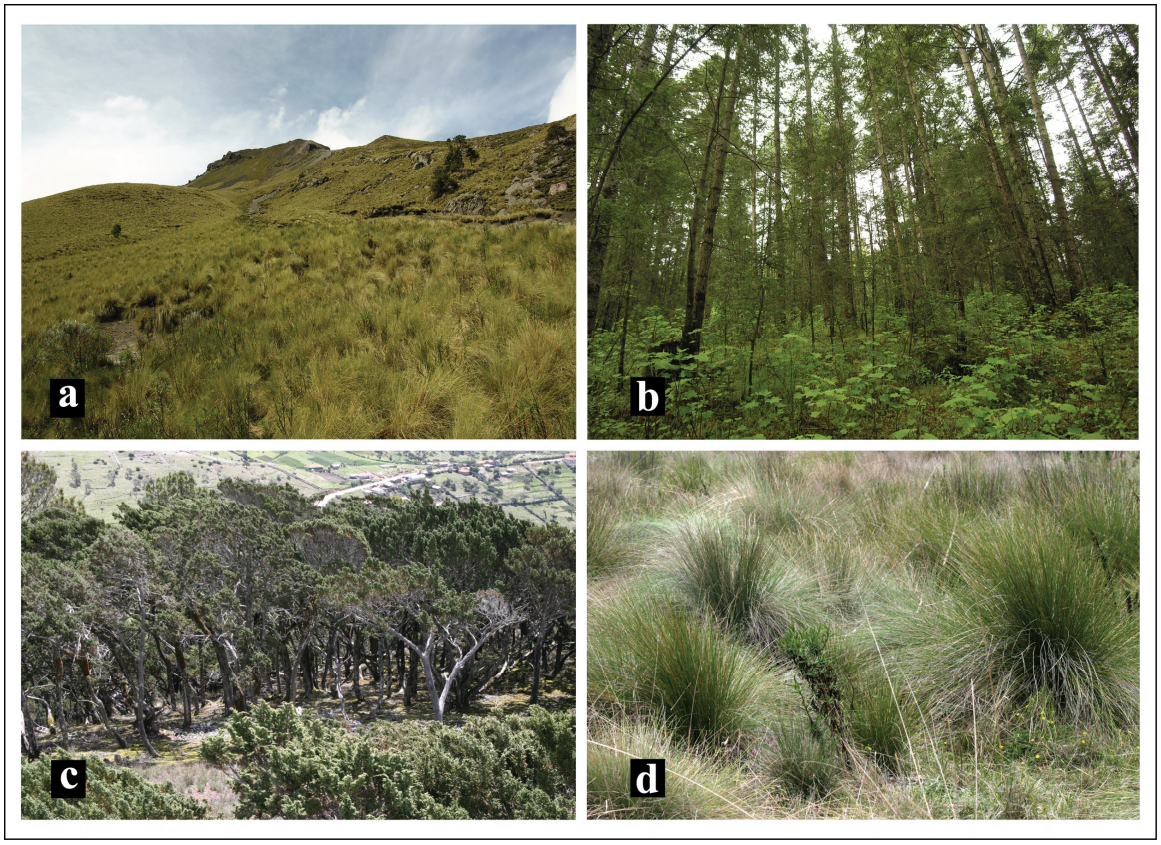

Fig 2 – Some of the study areas surveyed in the investigation: (a) non-forested area dominated by *Festuca tolucensis* close to the summit in the La Malinche Volcano; (b) *Abies religiosa*-dominated forest in the Cofre de Perote volcano; (c) *Juniperus standleyi*-dominated forest in the Ventoza study area; (d) detail of the tussock grass *Agrostis tolucencis* dominating the landscape in the Llanos de San Miguel

** *Arcyria afroalpina* Rammeloo

MC, 3 collections, 2006. Guatemala (Llanos), in D, on AL and BA, pH range = 5.8–6.2.

* *Arcyria occidentalis* (T.Macbr.) G.Lister

FC, 1 collection, 2007. Mexico (Malinche), in C, on DW, pH = 4.6. New record for the Neotropics.

** *Badhamia melanospora* Speg.

MC, 1 collection, 2006. Mexico (Malinche and Perote) and Guatemala (Ventoza), in E, on AL, pH = 5.7.

** *Ceratiomyxa fruticulosa* (O.F.Müll.) T.Macbr.

FC, 11 collections, 2007. Guatemala (Llanos and Ventoza), in D, E and A, on DW, pH range = 3.2–8.1.

** *Comatricha nigra* (Pers. ex J.F.Gmel.) J.Schröt.

MC, 10 collections, 2006 and 2007. Mexico (Malinche and Perote) and Guatemala (Llanos and Ventoza), in E, D and A, on TW and BA, pH range = 4.0–5.2.

* *Comatricha rigidireta* Nann.-Bremek.

MC, 1 collection, 2006. Mexico (Perote), in D, on BA, pH = 4.8. New record for the Neotropics.

** *Cribraria languescens* Rex

FC, 1 collection, 2007. Guatemala (Llanos), in D, on DW, pH = 3.7.

** *Cribraria minutissima* Schwein.

FC, 1 collection, 2007. Guatemala (Llanos), D, on DW, pH = 3.7.

** *Cribraria oregana* H.C.Gilbert

FC, 6 collections, 2007. Guatemala (Llanos and Ventoza), in D, on DW, pH range = 3.9–4.5.

** *Cribraria vulgaris* Schrad.

FC, 2 collections, 2007. Guatemala (Llanos), in D, on DW, pH range = 3.7–3.8.

** *Diachea leucopodia* (Alb. & Schwein.) Fr.

MC, 1 collection, 2006. Mexico (Perote) and Guatemala (Llanos), in A, on AL, pH = 5.0.

** *Didymium anellus* Morgan

MC, 21 collections, 2006 and 2007. Mexico (Malinche and Perote) and Guatemala (Llanos and Ventoza), in E, D and A, on AL and GL, pH range = 4.1–6.2.

** *Didymium bahiense* Gottsb.

MC, 18 collections, 2006 and 2007. Mexico (Malinche and Perote) and Guatemala (Llanos and Ventoza), in E, D and A, on AL, GL and TW, pH range = 3.9–6.8.

** *Didymium clavus* (Alb. & Schwein.) Rabenh.

MC, 5 collections, 2006. Mexico (Malinche and Perote) and Guatemala (Llanos and Ventoza), in E and A, on AL, pH range = 3.5–6.1.

** *Didymium difforme* (Pers.) Gray

MC, 28 collections, 2006 and 2007. Mexico (Malinche and Cofre) and Guatemala (Llanos and Ventoza), in E, D and A, on AL, GL and TW, pH range = 4.8–7.5

** *Didymium dubium* Rostaf.

MC, 5 collections, 2006 and 2007. Mexico (Perote) and Guatemala (Llanos and Ventoza), in A, on GL and AL, pH range = 5.2–5.8.

** *Didymium iridis* (Ditmar) Fr.

MC, 43 collections, 2006 and 2007. Mexico (Malinche and Cofre) and Guatemala (Llanos and Ventoza), in E, D and A, on AL, GL, TW and BA, pH range = 3.8–6.8.

** *Didymium minus* (Lister) Morgan

MC, 9 collections, 2006 and 2007. Mexico (Malinche and Perote) and Guatemala (Llanos and Ventoza), in E and A, on AL, pH range = 4.4–6.2.

** *Didymium squamulosum* (Alb. & Schwein.) Fr.

MC, 29 collections, 2006 and 2007. Mexico (Malinche and Perote) and Guatemala (Llanos and Ventoza), in both E, D and A, on AL and GL, pH range = 4.5–6.6.

** *Echinostelium minutum* de Bary

MC, 6 collections, 2006 and 2007. Mexico (Malinche and Perote) and Guatemala (Llanos and Ventoza), in E and D, on BA and TW, pH range = 3.3–4.8.

** *Fuligo septica* (L.) F.H.Wigg.

FC, 4 collections, 2007. Guatemala (Llanos), in D and A, on DW, pH range = 3.5–6.6.

** *Lamproderma scintillans* (Berk. & Broome) Morgan

MC, 2 collections, 2006. Mexico (Perote) and Guatemala (Llanos and Ventoza), in A, on AL, pH range = 4.6–6.1.

** *Licea belmontiana* Nann.-Bremek.

MC, 5 collections, 2006. Guatemala (Llanos and Ventoza), in E, D and A, on TW and BA, pH range = 3.7–4.9.

* *Licea deplanata* Kowalski

MC, 2 collections, 2006. Mexico (Perote), in B, on TW, pH range = 4.5–5.8. New record for the Neotropics.

** *Licea minima* Fr.

MC, 8 collections, 2006 and 2007. Mexico (Malinche) and Guatemala (Llanos and Ventoza), in E, D and A, on BA and TW, pH range = 3.6–4.7.

** *Licea pusilla* Schrad.

MC, 1 collection, 2007. Guatemala (Llanos), in D, on GL, pH = 4.8.

*** *Licea testudinacea* Nann.-Bremek.

MC, 6 collections, 2007. Mexico (Malinche) and Guatemala (Ventoza), in C, D and A, on BA and TW, pH range = 3.7–6.0. New record for the Neotropics.

** *Lycogala epidendrum* (L.) Fr.

FC, 4 collections, 2007. Guatemala (Llanos and Ventoza), in E and A, on DW, pH range = 4.7–7.0.

* *Paradiacheopsis solitaria* (Nann.-Bremek.) Nann.-Bremek.

MC, 1 collection, 2006. Mexico (Malinche), in D, on BA, pH = 4.9. New record for the Neotropics.

** *Perichaena chrysosperma* (Curr.) Lister

MC, 2 collections, 2006. Mexico (Malinche and Perote) and Guatemala (Llanos), in A, on GL, pH range = 4.5–5.6.

** *Perichaena corticalis* (Batsch) Rostaf.

MC, 2 collections, 2006. Mexico (Malinche and Perote) and Guatemala (Llanos), in A, on GL, pH = 5.6.

** *Perichaena depressa* Lib.

MC, 21 collections, 2006 and 2007. Mexico (Malinche and Perote) and Guatemala (Llanos and Ventoza), in E, D and A, on AL, GL, TW and BA, pH range = 3.5–7.1.

* *Perichaena dictyonema* Rammeloo

MC, 2 collections, 2006. Mexico (Malinche), in C, on AL, pH range = 6.6–7.3.

* *Perichaena liceoides* Rostaf., Sluzowce Monogr. 295 (1875)

MC, 12 collections, 2006 and 2007. Mexico (Malinche and Perote), in C, D and B, on AL and GL, pH range = 4.8–7.9.

** *Physarum bivalve* Pers.

MC, 4 collections, 2007. Mexico (Malinche and Perote) and Guatemala (Llanos and Ventoza), in D and A, on AL and BA, pH range = 4.8–5.8.

** *Physarum echinosporum* Lister

MC, 5 collections, 2006 and 2007. Mexico (Malinche and Perote) and Guatemala (Llanos), in D and A, on AL, BA, TW and GL, pH range = 4.1–6.1.

** *Physarum pusillum* (Berk. & M.A.Curtis) G.Lister

MC, 1 collection, 2006. Mexico (Malinche and Perote) and Guatemala (Ventoza), in D, on AL, pH = 5.5.

** *Stemonitis fusca* Roth

MC, 94 collections, 2006 and 2007. Mexico (Malinche and Perote) and Guatemala (Llanos and Ventoza), in E, D and A, on TW, AL, BA and GL, pH range = 3.7–6.0.

** *Trichia botrytis (*J.F.Gmel.) Pers.

MC, 2 collections, 2006. Mexico (Malinche) and Guatemala (Llanos and Ventoza), in E and D, on GL, pH range = 4.9–5.3.

** *Trichia contorta* (Ditmar) Rostaf.

MC, 3 collections, 2006. Mexico (Malinche) and Guatemala (Llanos and Ventoza), in A, on GL and TW, pH range = 4.0–5.3.

** *Trichia subfusca* Rex

MC, 3 collections, 2006 and 2007. Mexico (Malinche) and Guatemala (Llanos and Ventoza), in E and D, on GL, pH range = 4.2–4.4.

Discussion

The number of new records of myxomycetes obtained in the present study is probably not surprising. This is especially true when it is considered that the myxobiota

of Guatemala is very much understudied. However, even though there have been a number of investigations in Mexico, the present study reports eight new myxomycete species for that country.

The latter is not an unimportant result. As is true for many other countries, high-elevation areas in Mexico have not received as much attention as lowland areas (see Lado and Wrigley de Basanta 2008). Both La Malinche and Cofre de Perote are exceptions to the latter and have been studied in the past (e.g., Guzmán and Villareal 1984; Rodríguez-Palma et al. 2005). However, in both cases the effort was centered on forested areas, leaving the grass-dominated communities that occur beyond the treeline understudied. In the case of La Malinche, for example, most previous studies have been carried out in the *Abies religiosa* forest (Rodríguez-Palma et al. 2005).

For Guatemala, the situation is very different. It is clear that the 26 species of myxomycetes known for this country before the present study (see Lado and Wrigley de Basanta 2008) do not reflect the diversity of forms that would be expected to occur in this area. However, no studies have been carried out in most parts of this country. In this sense it is not surprising that the present study increased by 135% the number of known species for Guatemala. Both the investigation carried out by Estrada-Torres et al. (2000) and the present study were centered on the Cuchumatanes Plateau, the highest mountain range in the country. For this reason, it is very likely that future studies will increase the number of myxomycetes known for Guatemala, especially those directed towards areas that still remain unexplored.

In any case, about half of the collections that represent new records for both countries were obtained from the less studied non-forested areas. This result suggests that

such areas may provide a number of new records for other countries in the Neotropics. A comprehensive examination of the species present in high-elevation non-forested areas of Costa Rica (Rojas et al., unpublished data) provides evidence for such a hypothesis. In the present study, non-forested ecosystems had not been sampled in any of the study areas (see Guzmán and Villareal 1984; Estrada-Torres et al. 2000; Rodríguez-Palma et al. 2005)

The fact that the forest type accounting for the lowest number of new records is the *Abies religiosa* forest lends support for the hypothesis that most myxomycetes in understudied ecosystems have not yet been documented. This is due in part to the fact that most myxomycetes seem to display patterns of occurrence that can be related to macro- and microenvironmental characteristics of the habitat (see Stephenson et al. 2008a), which accounts for the particular species assemblages associated with different types of forest. This phenomenon undoubtedly accounts for the fact that about half of the new records were recovered from the less studied *Juniperus standleyi* and *Pinus hartwegii* forests.

For the moist chamber culture component of the present study, most of the new records were associated with either aerial litter or woody twigs. The presence of certain myxomycetes for these substrates is not surprising, since both have been previously documented as supporting distinctive assemblages of species (see Stephenson et al. 2004, 2008b). As such, it is remarkable to observe that such substrates yielded a large number of new records during the present study. At least for aerial litter, the results seem to support the hypothesis that this is an important substrate for myxomycetes in tropical forests (see Black et al. 2004).

In the present study, aerial litter also yielded all of the species of *Didymium*. This is not surprising since this genus is frequently encountered in myxomycete surveys carried out in tropical areas (e.g., Schnittler and Stephenson 2000; Tran et al. 2006). In contrast, the presence of species of the genus *Licea* primarily on bark and twigs seems to indicate an apparent specificity of members of that genus for those substrates. This phenomenon has been reported previously (see Ing 1994). Evidently, both vegetative and reproductive structures in myxomycetes can reach and grow on virtually any surface in the forest. However, the presence of a number of species primarily associated with, or even restricted solely to particular substrates, seems to be an indication of the specificity that some myxomycetes apparently show for particular food resources and/or substrate features, as well as the importance of those factors on the dynamics of myxomycete communities.

Even though the range of pH values recorded in the present was wide, most myxomycetes were recorded from substrates that are relatively acidic. One of the more unexpected results is that some of the species found to tolerate these acidic conditions (e.g., *Badmahia melanospora*, *Perichaena corticalis*, *Physarum pusillum* and *Stemonitis fusca*) have been associated with more basic pH values in other studies (e.g., Estrada-Torres et al. 2009). However, this result is not totally surprising, since other studies have shown that particular species of myxomycetes in high elevations ecosystems tend to occur on substrates with lower pH values than is the case in lowlands (see Schnittler and Stephenson 2000; Rojas and Stephenson 2008).

In any case, most of the species reported herein are common and have broad distribution ranges within the Neotropical region (see Lado and Wrigley de Basanta

2008). However, some species such as *Arcyria occidentalis*, *Comatricha rigidireta*, *Licea deplanata*, *L. testudinacea* and *Paradiacheopsis solitaria*, all of which are new records for the Neotropics, are obviously still not yet documented for other countries in the region. It is perhaps noteworthy that all of these species produce small fruiting bodies and thus may have been overlooked in previous studies that did not use the moist chamber culture method. It is important to mention that the use of this technique usually yields species that are not found under natural conditions. Since most records of myxomycetes from Latin America have been obtained in the field, it is still impossible to say whether or not the new records truly represent rare taxa in the Neotropics or simply reflect the relatively few studies that have been carried out in suitable habitats, or that have used both collecting techniques.

One obvious result from the present study and other recent investigations carried out in the high-elevation areas of the Neotropics (e.g., Rojas and Stephenson 2007) is that myxomycetes do occur, sometimes in abundance, in these areas. Within the context of conservation, it is important to know the composition of species present in different areas of similar characteristics in order to assess the effect of possible changes in the dynamics of these assemblages. Rapid-assessment projects such as the one described herein are relevant in this sense, since they provide baseline information that can be used for the monitoring of species assemblages in threatened ecosystems.

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Chapter 10

Conclusions

The studies of myxomycete assemblages associated with high-elevation areas of the Neotropics included in this investigation generated important information regarding the ecology of this group of terrestrial protists. When the data from low elevations, oceanic islands or different biogeographical provinces were considered in the analysis, it seemed apparent that myxomycete assemblages at high elevations show similar responses to a number of macroenvironmental factors. These responses seem likely to influence the patterns of abundance of the group in the study areas that were considered. In contrast, the different composition of species assemblages at high elevations seemed to be the product of a multifactorial response exhibited by particular species to the factors that define the microenvironments in which they are found.

The results obtained in the analysis presented in Chapter 2 showed that by using a probabilistic approach, myxomycete assemblages in Costa Rica do not seem to be randomly distributed across the country. The abundant species in the study showed significant relationships with particular forest types and substrates. This observation can be interpreted as evidence of the habitat specialization exhibited by myxomycetes in tropical areas, which seems to show that species are not randomly distributed across different ecosystems within the same geographic area. In a similar way, the other results presented in this chapter supported the same argument. Some species were shown to have a clear elevational distribution in Costa Rican forests. This is not considered to be the product of elevation *per se*, but is rather more likely to be evidence that those species

were associated with different forest types and forest structures or plant species occurring at particular elevations. Overall, in spite of some constraints inherent to the analyses carried out for this chapter, the value of the *data mining* process in combination with data collected directly from the field, also showed that these complementary approaches are valuable to generate meaningful information for biological analysis.

In contrast to the latter, the analysis presented in Chapter 3 corresponds to a rapid assessment project carried out in only one of the study areas in Costa Rica. Both the spatial and temporal scales were highly reduced in this analysis, but the level of resolution was improved with the sampling effort. In this case, it was clear that a survey with increased effort in the high-elevation oak forests of Costa Rica was adequate to observe the presence of species that had not been reported for that country at the time of the study. In this manner, the similarity of the assemblage of species found in the study area when compared to previously observed myxomycete assemblages in temperate areas provided an indication of a biogeographical pattern associated with true temperate and temperate-like forests. Due to this apparent pattern, the analysis of spatial niches—considered herein as the multidimensional set of parameters defining the microenvironment in which the different species occur—was very useful to characterize the microhabitats of particular species. For this reason, the results of this chapter supported the utilization of a similar methodology in subsequent analyses of myxomycete assemblages in other forest types. The relationship found to exist between precipitation levels and the abundance of myxomycetes in the forest evaluated also suggested that climatic factors are important for the natural history of the group in the areas area being considered.

When the dynamics of myxomycete communities were evaluated in the context of isolation provided by the oceanic island evaluated in Chapter 4, it seemed that some of the macroecological patterns previously observed for high elevations were also supported by the results from this contrasting ecosystem. In this case, the effectiveness of rapid-assessment projects to rapidly characterize the myxobiota of a particular area was observed again. In this case, data supporting the observation that myxomycete diversity and abundance decrease with increasing elevation in tropical areas was evident from the results presented in this chapter. In this case, even an indication of the importance of some characteristics of the microenvironment could be defined.

One example was the higher occurrence of myxomycetes on aerial litter at lower elevations, which switched to more records on ground litter at the highest elevation. This observation provided an indication that apparent substrate specificity may be also associated with substrate availability and macroenvironmental factors. In addition, the species composition of the assemblages found on Cocos Island was very noteworthy from a biogeographical perspective, since the majority of the species have broad distribution ranges in the Neotropical region.

This result suggested that frequently encountered myxomycetes in Neotropical areas may not show limitations in their dispersal capabilities and that immigration events in isolated territories may occur more frequently than in the case of macroscopic organisms. Moreover, it is likely that due the limited numbers of plant species, forest types and microhabitats in this island; myxomycetes coexist in the system by means of resource specialization.

The data presented in Chapter 5 shows that such strategies are possible in mycetozoans and likely to occur in myxomycetes. In this chapter it seemed evident that the most cosmopolitan macroscopic species of the genus *Ceratiomyxa* shows a wider resource utilization pattern than the other two macroscopic species, which are more regionally distributed. The results presented in this chapter also suggested that in areas where all the three species occur sympatrically, the two species with the narrower distribution seemed to have different resource utilization patterns. The quick characterization of the microenvironment for each species also constituted important evidence for future studies of a similar nature in either the same Neotropical region or across biogeographical areas. In the present dissertation, the high-elevation areas of the Neotropics constituted the other reference point.

The comprehensive analysis presented in Chapter 6 provides a summary of these results. The data obtained during this part of the project indicated that myxomycetes show a pattern of decreasing species richness with decreasing latitude, and this was apparently influenced by the structure of the forest in which the species occurred. Moreover, the highly variable similarity values among assemblages in the Neotropical areas and those from other biogeographical provinces suggest that the distribution of myxomycetes was not neutral at that spatial scale.

The pattern of resemblance of Neotropical myxomycete assemblages with the assemblage studied in the temperate area seemed to indicate that temperate-related myxomycete species were more likely to be found in less tropical areas. This observation did not seem surprising during the general analysis. However due the lack of available information on the biogeography of myxomycetes in these areas before the present

dissertation, these data represented a good starting point to generate hypotheses about the global distribution of these organisms.

As a complementary approach, the results provided in Chapter 7 are potentially useful as well. For example, the indication that the myxomycete assemblage studied in Southeast Asia was different from those studied in the Americas represented a milestone in the context of limited research recently explained for tropical myxomycetes. In a similar way, the effective combination of *in-situ* measurements of microenvironmental parameters and multivariate analysis of similar factors to generate meaningful data, suggested that a potential characterization of the microenvironment in which myxomycetes occur is possible at that level of analysis.

The evaluation of the structure of the myxomycete assemblages studied in relation with large-scale models of distribution suggested that this approach can be used with this group. However, it is likely that revised models centered on microorganisms will represent better tools to study the distribution of myxomycete in the future. In any case, the information presented in this chapter shows that most of the results obtained appeared not to support neutral models of species distribution and seemed, in contrast, to be better explained by niche-based models. These results were important for the integration of the knowledge on myxomycetes into ecosystem biology in the high-elevation areas considered in this dissertation. However, a good point of reference regarding the taxonomic identity of the myxomycetes present in those areas should have been established before a complete integration could be carried out.

For this reason, a complete review of the myxomycetes occurring in Costa Rica is provided in Chapter 8. In this analysis, the importance of the consideration of previous

research is evident. Before this dissertation project started, a total of 126 species of myxomycetes were known to occur in Costa Rica. With the field work carried out in the context of this project, the review of historical material and the collaboration of contemporaneous researchers, the catalog of myxomycetes known for Costa Rica increased to more than 200 species. The composition of species seemed to conform to previous studies, but the development of this review represents a point of reference for future studies in the region. In the same context, Chapter 9 provides valuable taxonomic information on the species present in Mexico and Guatemala. The report of a number of new species for both countries represents a valuable result of this dissertation. Overall, these recently mentioned reviews represent the quality of the effort carried out in the high-elevation areas of those countries and provide potentially useful information for the management of the surveyed areas.

In spite of all the effort carried out during this project, it is clear that a number of other research questions could not be investigated in the framework of this dissertation. During this time, however, some questions and possible strategies to address future research have been identified with the objective of continuing this line of research. Even though the biogeographical and ecological studies presented contain a number of methodological limitations and possibly errors, this dissertation represents an exhaustive survey of high-elevation areas of the northern Neotropics.

The high-elevation non-Neotropical or lowland Neotropical areas surveyed for comparison in most of the chapters also represent one component of the effort carried out during this study. As such, the value of the data generated during this investigation is valid not only in terms of the information provided for the study of myxomycete ecology

and global distribution of terrestrial protists but also in relation to the study of rapidly changing ecosystems. In the present case, the latter were represented by the lowland Neotropical forests and evidently, the high-elevation areas of the northern Neotropics and other areas of the world. For this reason, the empirical data generated also represents baseline information on the biogeography and ecology of a group of microorganisms that can potentially be used for the protection and management of the various study areas.

Appendix 1

Complete list of species and numbers of records from all high-elevation study areas considered in this investigation

The main database created for an analysis of high-elevation assemblages of myxomycetes of this dissertation contains records obtained directly in the field and also those extracted from moist chamber cultures. For this reason, the different analyses used in the investigation were carried out with due consideration of the main objective of the particular chapter involved and the methods used to obtain the records. Due to this approach, the total list of actual species found in each study area is incomplete in the various chapters. A complete list of myxomycete species for future reference is provided in Table 1 of this appendix.

Except for two species (*Perichaena liceoides* and *Stemonitis smithii*), the taxonomic treatment used throughout this dissertation follows the reference given below. For these two species, the original protologues are provided.

Lado C. 2005-2010. An on-line nomenclatural information system of Eumycetozoa. http://www.nomen.eumycetozoa.com (available through a link given on the Eumycetozoan Project web site (http://slimemold.uark.edu).

Protologues:

Perichaena liceoides Rostaf., Sluzowce Monogr. 295 (1875)

Stemonitis smithii T.Macbr., Bull. Iowa Univ. Lab. Nat.Hist. 2:381 (1893)

Table 1. Complete list of species and number of records from all high-elevation study areas considered in this dissertation arranged according to total abundance values. Abbreviations are provided at the end of the list.

COUNTRY	**US**	**TH**	**MX**				**GU**				**CR**				**TOTAL**
Study area	**AB**	**DI**	**CP**		**LM**		**LL**		**LV**		**CM**		**CH**		
Vegetation type	**NF**	**F**	**F**	**NF**	**F**	**NF**	**F**	**NF**	**F**	**NF**	**F**	**NF**	**F**	**NF**	
Didymium difforme (Pers.) Gray	5	2	47	33	61	35	7	6	12	3					211
Stemonitis fusca Roth	7		9	13	6	8	36	10	27	21	5	6	8	4	160
Arcyria cinerea (Bull.) Pers.	38	6	4	4	7		7	12	4	3	2	1	4	4	96
Didymium iridis (Ditmar) Fr.	3	8	5		5	3	6	14	16	7			5	1	73
Didymium squamulosum (Alb. & Schwein.) Fr.		4	5	6	8	2	19	3	2	5		3	5	1	63
Comatricha nigra (Pers. ex J.F.Gmel.) J.Schröt.	8		23	2	3	6	2		4	4	1	2	3	1	59

Table 1. Continued.

Physarum compressum Alb. & Schwein.			8	8	11	1	6	3	4	2	1	2	3	9	58
Perichaena depressa Lib.		2	6	8	12	4	6	5	5	5			2	2	57
Physarum bivalve Pers.	20		5	7	2	3		1	2	1	2				43
Lycogala epidendrum (L.) Fr.			2	1	3	1	1	2	1		5	2	9	5	32
Didymium bahiense Gottsb.			3		5	1	5		12	1	2	1		1	31
Badhamia melanospora Speg.			8	11	3	4			1						27
Cribraria microcarpa (Schrad.) Pers.		26													26
Didymium anellus Morgan	1			1	2	1	4	6	6	5					26
Didymium clavus (Alb. & Schwein.) Rabenh.			6	6	2		3			2	1	2	1	3	26
Licea minima Fr.	4				7		2		4	2	2	3	1		25

Table 1. Continued.

Physarum echinosporum Lister			1	4	3	8	2	3			2				23
Diderma hemisphaericum (Bull.) Hornem.		14	1	2							2	2			21
Physarum pusillum (Berk. & M.A.Curtis) G.Lister	2	1	1	2	3				1				7	4	21
Ceratiomyxa fruticulosa (O.F.Müll.) T.Macbr.			1		4		2	6	3		1		1		18
Perichaena corticalis (Batsch) Rostaf.			2	3	5	4		1						2	17
Diderma effusum (Schwein.) Morgan	12		1	2											15
Didymium minus (Lister) Morgan				4	1			8	1			1			15

Table 1. Continued.

Echinostelium minutum Raper	1	3	1	2	2		2		4				15
Lamproderma scintillans (Berk. & Broome) Morgan	8		2	2				1		1			14
Perichaena chrysosperma (Curr.) Lister			6			5		2					13
Perichaena liceoides Rostaf.			2	4	5	1							12
Physarum didermoides (Pers.) Rostaf.			4	1	3	2	2						12
Licea testudinacea Nann.-Bremek.					3				2	1	3	2	11
Comatricha elegans (Racib.) G.Lister	4		1		5								10

Table 1. Continued.

Metatrichia floriformis (Schwein.) Nann.-Bremek.							5		5		10
Perichaena vermicularis (Schwein.) Rostaf.	1		3	1	1	2				2	10
Leocarpus fragilis (Dicks.) Rostaf.							3		6		9
Paradiacheopsis fimbriata (G.Lister & Cran) Hertel ex Nann.-Bremek.			8		1						9
Arcyria pomiformis (Leers) Rostaf.				1	7						8
Comatricha pulchella (C.Bab.) Rostaf.	4		1					3			8

Table 1. Continued.

Cribraria minutissima Schwein.		8										8
Licea operculata (Wingate) G.W.Martin	6	2										8
Physarum Pers. sp.	1	1	1		2	3						8
Fuligo septica (L.) F.H.Wigg.			1	1	1		1	3				7
Perichaena Fr. sp.			1		2	3			1			7
Physarum viride (Bull.) Pers.	4		1							2		7
Trichia decipiens (Pers.) T.Macbr.					4					3		7
Clastoderma debaryanum A.Blytt	1	2								2	1	6
Comatricha Preuss sp.	2		1	1	1			1				6
Cribraria oregana H.C.Gilbert							3		3			6

Table 1. Continued.

Didymium dubium Rostaf.			1				4		1				6
Fuligo cinerea (Bull.) Pers.	3			2	1								6
Hemitrichia calyculata (Speg.) M.L.Farr		2	1	1						1		1	6
Physarum cinereum Morgan	3		1	2									6
Stemonitis splendens Rostaf.				4						1	1		6
Trichia contorta (Ditmar) Rostaf.				1	3		1		1				6
Trichia favoginea (Batsch) Pers.										4		2	6
Trichia subfusca Rex	2			1				3					6
Cribraria vulgaris Schrad.			1	1		1		1		1			5
Didymium nigripes (Link) Fr.						1		1			2	1	5

Table 1. Continued.

Licea belmontiana Nann.-Bremek.					1	3	1				5
Tubifera ferruginosa (Batsch) J.F.Gmel.				1						4	5
Arcyria afroalpina Rammeloo		2			2						4
Calomyxa Nieuwl. sp.			1	3							4
Cribriaria mirabilis (Rostaf.) Massee				1				2	1		4
Licea Schrad. sp.	1	2		1							4
Stemonitis flavogenita E.Jahn	3					1					4
Trichia botrytis (J.F.Gmel.) Pers.				2	1	1					4
Comatricha laxa Rostaf.	1	1					1				3

Table 1. Continued.

Hemitrichia serpula (Scop.) Rostaf. ex Lister					1		2		3
Lamproderma magniretispora Moreno, Rojas, Stephenson & Singer						3			3
Physarum album (Bull.) Chevall.	1		1	1					3
Physarum melleum (Berk. & Broome) Massee			1				2		3
Badhamia affinis Rostaf.	2								2
Badhamia macrocarpa (Ces.) Rostaf.	1	1							2
Comatricha tenerrima (M.A.Curtis) G.Lister			1					1	2

Table 1. Continued.

Cribraria piriformis Schrad.						2	2
Cribraria splendens (Schrad.) Pers		2					2
Diachea leucopodia (Bull.) Rostaf.	1			1			2
Dianema Rex sp.				2			2
Diderma chondrioderma (de Bary & Rostaf.) G.Lister		1				1	2
Didymium Schrad. sp.				1	1		2
Licea deplanata Kowalski		2					2
Licea pusilla Schrad.			1			1	2
Paradiacheopsis rigida (Brândza) Nann.-Bremek.	1					1	2

Table 1. Continued.

Perichaena dictyonema Rammeloo			2					2
Physarum straminipes Lister		1			1			2
Stemonitis herbatica Peck			1	1				2
Stemonitis mussooriensis G.W.Martin, K.S.Thind & Sohi	1					1		2
Trichia scabra Rostaf.			1		1			2
Trichia verrucosa Berk.							2	2
Wilkommlangea reticulata (Alb. & Schwein.) Kuntze		2						2
Amaurochaete Rostaf. sp.				1				1
Arcyria occidentalis (T.Macbr.) G.Lister			1					1

Table 1. Continued

Badhamia utricularis (Bull.) Berk.		1			1
Barbeyella minutissima Meyl.				1	1
Collaria arcyrionema (Rostaf.) Nann.-Bremek. ex Lado	1				1
Comatricha rigidireta Nann.-Bremek.	1				1
Craterium aureum (Schumach.) Rostaf.	1				1
Cribraria intricata Schrad.				1	1
Cribraria languescens Rex			1		1
Cribraria minutissma Meyl.			1		1
Diderma Pers. sp.	1				1

Table 1. Continued.

Diderma testaceum (Schrad.) Pers.	1						1
Didymium vaccinum (Durieu & Mont.) Buchet		1					1
Echinostelium apitectum K.D.Whitney		1					1
Enerthenema papillatum (Pers.) Rostaf.						1	1
Lamproderma Rostaf. sp.	1						1
Lepidoderma de Bary sp.			1				1
Licea variabilis Schrad.				1			1
Macbrideola cornea (G.Lister & Cran) Alexop.	1						1

Table 1. Continued.

Paradiacheopsis solitaria (Nann.-Bremek.) Nann.-Bremek.			1			1
Physarum robustum (Lister) Nann.-Bremek.					1	1
Physarum superbum Hagelst.	1					1
Reticularia lycoperdon Bull.			1			1
Reticularia splendens Morgan				1		1
Stemonitis axifera (Bull.) T.Macbr.			1			1
Stemonitis smithii T.Macbr.	1					1
Symphytocarpus flaccidus (Lister) Ing & Nann.-Bremek.	1					1

Table 1. Continued.

Record abundance	153	88	184	139	220	110	126	96	125	72	62	36	75	40	1526
Species richness	33	20	45	33	55	29	28	23	23	22	31	17	24	14	115

Abbreviations used in the list of species

Countries: US = United States, TH = Thailand, MX = Mexico, GU = Guatemala and CR = Costa Rica.

Study areas: AB = Andrews Bald, DI = Doi Inthanon, CP = Cofre de Perote, LM = La Malinche, LL = Llanos de San Miguel, LV = La Ventoza, CM = Cerro de la Muerte and CH = Chirripo. For complete names and details of the study areas see Chapter 1.

Vegetation type: NF = non-forested, F = forested.

Appendix 2

Metadata of the study areas considered in this investigation

The complexity of the field work involved in this investigation does not permit a quick evaluation of the location and basic information relating to the different study areas. For this reason a metadata file was compiled. To access the file, please use the attached compact disk. You can easily open the file using the computer program Google Earth*. A series of images of the study areas and maps showing the relative abundance of the ten most common species for both forested and non-forested areas are also included in the same disk.

* Google Earth is a registered name of Google Inc., Mountain View, California.