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A biogeographical evaluation of high-elevation myxomycete assemblages in the northern Neotropics

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ABSTRACT

This study represented an effort to apply some of the relatively well-known biogeographical and macroecological 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 States and were clearly distinct from an assemblage in Thailand.

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Introduction

The myxomycetes or myxogastrids comprise a group of amoeboid protists (Pawłowski & 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 fruit bodies containing spores and the development of a mobile multinucleate macroscopic form known as a plasmodium (see Martin & Alexopoulos 1969), which together would seem to have a positive effect on the dispersal capabilities of 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.* 2008a).

Most of the studies on the group have been carried out in temperate forests of the northern Hemisphere (Stephenson 2003). However, in recent years an increasing number of investigations have taken place in other parts of the world (e.g. Tran *et al.* 2008; Estrada-Torres *et al.* 2009; Ndiritu *et al.* 2009; Wrigley de Basanta *et al.* 2010). 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

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areas remain understudied. Even those areas such as the Neotropics, in which most recent ecological studies of tropical myxomycetes have been carried out, continue to generate important information on the global distribution and occurrence of the group.

The information generated in the context of research directed toward tropical myxomycetes has contributed greatly to our understanding of the strategies utilized by these microorganisms in a number of different ecological situations that are generally absent in temperate areas (e.g. [Schnittler & 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, despite 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 & Stephenson 2007](#)) have been carried out in a number of mountainous areas of the Neotropics.

Unfortunately, due to the impact of anthropogenic factors on mountain forests around the world (see [Bubb et al. 2004](#)), from which most high-elevation areas of the Neotropics have not escaped ([Brown & Kappelle 2001](#)), the myxomycetes occurring in these areas are threatened as much as other organisms. The 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 to provide 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 [Hughes Martiny et al. 2006](#); [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 & 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 2006–2009. For identification of species, the morphological species concept was used, following the nomenclatural 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 were 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 (FR) and non-forested zones (NFR) 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 (see [Table 1](#)). The uneven sampling in the non-Neotropical areas was mainly the product of logistic limitations (for the North American area see discussion on habitat heterogeneity and myxomycete specialization in [Stephenson & Landolt \(2009\)](#)). 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. A more detailed explanation of the study areas is provided in [Rojas et al. \(2010\)](#).

The Neotropical areas were located in Mexico, Guatemala and Costa Rica. In the first country they are located on the Trans-Mexican Volcanic Belt (also known as TMVB) and correspond to: (1) the Matlalcuéytl (=La Malinche) Volcano (hereafter abbreviated as MA, elevation of sampled plots between 3100 and 4000 m), which is located between the states of Puebla and Tlaxcala; and (2) the Cofre de Perote Volcano (PE, elevation 3400–4200 m) in the state of Veracruz. In Guatemala, the two study areas were located on the Cuchumatanes Plateau and correspond to: (3) Llanos de San Miguel (LL, elevation 3400–3500 m); and (4) La Ventoza (VE, elevation 3400–3600 m). In Costa Rica, the two study areas were part of the Talamanca Range and correspond to: (5) Cerro Buenavista or Cerro de la Muerte (CE, 3150–3450 m); and (6) Macizo del Chirripó (CH, 3150–3500 m). The two external study areas correspond to: (7) Andrews Bald (AB, elevation 1750 m), located in a high-elevation area of the Great Smoky Mountain National Park in North Carolina, United States; and (8) Doi Inthanon (DI, 1400–1700 m), the highest mountain in Thailand, located in the province of Chiang Mai.

The forests in the Neotropical areas were 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 were dominated by the tussock grasses *Festuca* and *Agrostis* in Mexico and Guatemala and by the dwarf bamboo *Chusquea* in Costa Rica. In the case of the Smoky Mountains, the sampled “bald” consisted of a non-forested area dominated by grasses, sedges and forbs; whereas the forests in Doi Inthanon were dominated by *Quercus* at higher elevations and by a *Quercus*–*Pinus* mixture at lower elevations.

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