Brief research history and status of myxomycete conservation in the Neotropics

Carlos Rojas[1] & Robin Doss[2]

[1] Instituto de Investigaciones en Ingeniería y Escuela de Biología, Universidad de Costa Rica, San Pedro de Montes de Oca 11501-2060, Costa Rica. rojas_carlos@outlook.com
[2] Escuela de Biología, Universidad de Costa Rica, San Pedro de Montes de Oca 11501-2060, Costa Rica. robin.g.doss@gmail.com

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ABSTRACT. As it is the case of most disciplines, biological groups and regions in the world; the historical path of research on myxomycetes in the Neotropical region has been written on the basis of a series of milestones, iconic researchers and emblematic pieces of work. In this short review, a highlight-based version of such history is provided by focusing on the effort carried out in different countries within the region. Due to historical and logistic limitations, the picture explaining the biogeography and ecological dynamics of myxomycetes for the Neotropics is still very incomplete. As such, it has been difficult to incorporate myxomycetes in the conservation agenda of organizations in the region. In spite of the latter, modern research techniques seem to represent the tool to bring our knowledge on myxomycete biology to a level of complex analysis over the environmental interactions of the group.

RESUMEN. Como sucede con la mayoría de disciplinas, grupos biológicos y regiones en el mundo; el camino histórico de la investigación con mixomicetes en la región Neotropical ha sido escrito con base en una serie de hitos, investigadores icónicos y trabajos emblemáticos. En esta corta revisión, una versión de esa historia basada en eventos importantes y con un enfoque en el esfuerzo llevado a cabo en los diferentes países, es ofrecida. Debido a limitaciones históricas y logísticas, la imagen de la biogeografía y la dinámica ecológica de los mixomicetes en el Neotrópico todavía no es clara. De esta forma, ha sido difícil incorporar a los mixomicetes en la agenda de conservación de organizaciones en la región. A pesar de lo anterior, algunas técnicas modernas de investigación parecen representar la herramienta para llevar nuestro conocimiento sobre la biología de mixomicetes a un nivel de análisis complejo de la interacción de este grupo con el ambiente.

KEY WORDS. Biogeography, ecosystem dynamics, mycetozoans, myxogastrids, restoration ecology, sustainability.

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 & Burki 2009). Even though myxomycetes have been studied since the seventeenth century (Stephenson *et al*. 2008), investigation of their applied ecology is still underrepresented. In recent years there has been an increasing number of publications on a series of ecological aspects of myxomycetes (e.g. Stephenson *et al.* 2004, Win Ko Ko *et al*. 2011, Rojas *et al.* 2011a). However, their management status is still in a conceptual stage until a more robust body of data including the biogeography, natural history and level of ecosystem interaction of the group is obtained.

For tropical myxomycetes, the Neotropical region is perhaps the area of the world for which there has been the greatest number of investigations. In a distributional review in the Neotropics, Lado & Wrigley de Basanta (2008) reported 431 species and 558 publications on myxomycetes for the entire region. Later publications have increased both the number of species and published investigations (e.g., Estrada-Torres *et al.* 2009, Rojas *et al.* 2010c). Such a research effort does not have a counterpart in the other tropical areas of the world where studies are far less common. Given this situation, the Neotropics represent an excellent candidate region for a preliminary analysis of the distribution of myxomycetes and the intrinsic interactions facilitated by their occurrence.

Myxomycete research in the Neotropical region. The Neotropics, or New World Tropics, *are sensu stricto* the region that occurs between the Tropic of Cancer and the Tropic of Capricorn of 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 of 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 application implies an operational definition that can be used for a number of practical purposes, including biogeographical, palaeoecological and climate change research. As a consequence, the analysis of conservation efforts is part of the mechanistic approach facilitated by such definition. In this way, the term Neotropics or Neotropic/Neotropical region has a broader scope and more practical meaning in the sense of Olson et al. (2001) and will be used herein to define the region of analysis.

Research on myxomycetes has been carried out in the Neotropical region for more than 100 years. According to Lado & Wrigley de Basanta (2008), the first known reports of a myxomycete in the Neotropical area were from Chile and Peru in 1828 and 1829, respectively (Bertero 1828, Rudolphi 1829). Even though research efforts at that time were limited, the collection of Myxomycetes in the Neotropics has continued since then. In a similar way to the history of other types of scientific research in the New World, European researchers took the lead in Neotropical myxomycete research. A former French soldier from the army of Napoleon Bonaparte, 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 military service and dedicating himself to the study of cryptogams in South America. Similarly, another French mycologist, Joseph Henri Léveillé, was responsible for the first reports of myxomycetes in Colombia (Léveillé 1863).

In spite of these isolated efforts, it was not until the decade of 1880 that more serious surveys were carried out in the southern Neotropics. Interestingly, according to the former hypothesis that myxomycetes were fungi, the majority of those surveys were conducted by trained mycologists. A number of recognized researchers 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 & Gaillard 1888). 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 findings.

From that moment on, myxomycete research in the Neotropics began to take place more systematically in the northern countries of Latin America, while it became established 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 & Sydow 1902). With the establishment of Panama and the completion of the Panama Canal by the United States in 1914, a period of biological exploration in the following decades included the study of myxomycetes in the Panamanian isthmus as well (Standley 1927, 1933).

By this point in time, the incipient study of fungi and myxomycete occurrence and distribution in the Neotropics had already taken researchers to virtually all major areas within the region. 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, El Salvador, Guatemala, French Guiana, Haiti and Honduras (see Lado & 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 & Haynes 1999) and 2013 for El Salvador (Rojas *et al.* unpublished data currently submitted for publication).

In spite of this, information on myxomycetes from the Neotropical region was by some means available for the majority of the countries by the decade of 1970. For that reason, Marie Leonore Farr, an American myxomycologist generated a monograph for Neotropical myxomycetes at the end of that period (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 following decade, recognized myxomycete studies 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 & Oliveira 1985, Cavalcanti & Pôrto 1985), Elly Nannenga-Bremekamp from the National Botanic Garden of Belgium (e.g., Eliasson & Nannenga-Bremekamp 1983, Nannenga-Bremekamp 1989) and Gastón Guzmán from the Xalapa Institute of Ecology in Mexico (e.g., Guzmán & Guzmán-Dávalos 1981, Guzman & Villareal 1984), respectively.

During the past 20 years, the research effort in the Neotropics has had different objectives in different areas. For example, the country that has received most of the effort in relation to occurrence of myxomycetes is Mexico. Lado & Wrigley de Basanta (2008) calculated that approximately 72% of all the published articles about myxomycetes from Mexico have been produced since 1990. In addition to this type of research in Mexico, the first complex ecological studies took place during the late part of this time period as well. However, most of the ecological analyses on Neotropical myxomycetes have occurred in Costa Rica (e.g., Schnittler & Stephenson 2000, Schnittler 2001, Schnittler & Stephenson 2002, Rojas & Stephenson 2007, 2008, Rojas *et al.* 2010b), Ecuador (e.g., Schnittler 2001, Schnittler & Stephenson 2002, Schnittler *et al*. 2002, Stephenson *et al.* 2004) and Puerto Rico (e.g., Novozhilov *et al.* 2000, Schnittler & Stephenson 2002, Wrigley de Basanta *et al.* 2008).

The southern section of the Neotropics has received significant attention in the last decade. In addition to the already mentioned studies in Ecuador, some projects in Chile (e.g., Lado *et al.* 2007, Wrigley de Basanta *et al.* 2009), Paraguay (McHugh 2009) and Argentina (e.g., Crespo & Lugo 2003, Wrigley de Basanta *et al.* 2009, 2010, Lado *et al.* 2011) have been carried out. Also, a series of regional studies in Brazil (e.g., Maimoni-Rodella & Cavalcanti 2006, Cavalcanti *et al.* 2009, Costa *et al.* 2009, Alves *et al.* 2010) have generated important information on the distribution of myxomycetes in that country. The southwestern Amazon forests of Peru have also been the focus of recent research (Rojas *et al.* 2011b) and Colombian myxomycetes are currently under study (Rojas *et al*. 2012).

In the northern section, recent studies include those of Estrada-Torres *et al.* (2009) in Mexico, Rojas et al. (2010c) in Mexico and Guatemala, Rojas *et al*. (2010a) in Costa Rica and Rojas *et al*. (2011a, 2011c) in all three aforementioned countries. For the Caribbean, Camino *et al.* (2008) have contributed to the knowledge of myxomycetes from Cuba and Wrigley de Basanta *et al.* (2008) have collected recent data from Puerto Rico. In spite of these efforts, most Central American and Caribbean countries still require an activation of myxomycete research (see gaps of information in Lado & Wrigley de Basanta 2008).

Conservation status. In terms of conservation, myxomycetes have not been included in the majority of programs anywhere in the world. In a way, the apparently mild ecological level of interaction with other groups of organisms, at least based on modern evidence (see Stephenson 2011 for current stage of knowledge), has caused this group to be relegated to a secondary plane. Due to the present lack of knowledge on actual intra-ecosystem interactions for most microbial groups of organisms (see Baveye 2009), the latter may simply be a product of conservative execution of biological research in terrestrial ecosystems. In spite of this, a group such as the myxomycetes has inherent constraints (i.e. undocumented complete life cycle) that have not allowed for a faster accumulation of knowledge about the ecological interactions shaping the distribution and biogeography of the group on the planet.

At the moment, most of the ecological research on myxomycetes carried out worldwide has relied on the presence of fruiting bodies for the construction of diversity related datasets (see GBIF at www.gbif.org). In fact, historical information is practically based solely on these elusive structures since fruiting bodies are the form of the organisms that has been maintained in herbaria collections. The problem with such a traditional approach is that most of the current distributional information about myxomycetes is based only on the reproductive stage of these organisms (Rollins & Stephenson 2011). Even though this limitation in the study of myxomycetes is understandable from a historical perspective, this should not be neglected on the construction of hypotheses about the ecological dynamics of the group (see Rojas & Stephenson 2012). This is particularly true in complex ecosystems such as tropical forests where a myriad of factors interact to shape the dynamics among organisms and the environment.

For myxomycetes, vegetative stages have not traditionally been used for taxonomic purposes since the morphology and ultrastructure of amoeboid and plasmodial stages may not provide the desired level of resolution for this task (see discussion on Rollins & Stephenson 2011 and details about the biology of the group on Gray & Alexopoulos 1968). Alternatively, genetic, biochemical and molecular tools have been demonstrated to provide the required information, even at intraspecific levels, for species of myxomycetes (Chen et al. 2012, Fiore-Donno *et al.* 2012). The limitation to increasing knowledge at the latter level resides in the fact that culturing has not been successful for all species of myxomycetes (see Herrera *et al*. 2011) and in most cases the isolation of forms is difficult since the culturing of only a handful of species has been mastered due to their systematical use (i.e., *Physarum polycephalum*) in laboratory studies.

In spite of the latter constraints, modern techniques such as environmental DNA sampling, fatty acid methyl ester and phospholipid-linked fatty acid analyses, metabolic pathway detection, community fingerprinting and fluorescent in-situ hybridization promise to support myxomycete –and microbial– ecologists in the construction of more robust hypotheses about the dynamics of microscopic assemblages and their relation with ecosystem processes. Some of these techniques have already provided interesting and relevant information about the biology of myxomycetes (i.e. environmental DNA sampling and fatty acid analyses; see Stephenson *et al.* 2011, Herrera et *al.* 2011), but most current publications on myxomycete ecology do not incorporate such techniques as they involve higher research costs, specialized infrastructure and additional training. Unfortunately, these limitations seems to be more common in developing countries where academic institutions tend to have more limited budgets and a narrower selection of programs than their counterparts in developed countries.

These limitations are the typical case in Latin America, the region located in the heart of the Neotropics. Unfortunately, in the last 50 years, this region has also been plagued with political instability, corruption, armed conflicts and drug trafficking (e.g., Elliott 2012). All these problems have shaped the region into one of the most dangerous areas worldwide (see Seguridad, Justicia y Paz at www.seguridadjusticiaypaz.org.mx). One visible effect of this problematic has been the lack of political viability to develop serious legislation and action towards the conservation of natural resources, including biodiversity.

Interestingly, when conservation initiatives have been developed, the majority have focused on macroscopic organisms –namely animals and plants– and marine resources (e.g., Hecnar 2009). Fungi as well as insects, protists, bacteria and other microorganisms –ironically the most abundant groups on the planet– have traditionally been excluded in these initiatives; in spite of their incredibly important role in maintaining the dynamics of nearly all ecosystems (see Cotterill *et al*. 2008).

Given this general situation, myxomycetes have not been traditionally incorporated into conservation efforts in the Neotropics. In the last years, however, the group has been proposed to be included into the IUCN *red list index for microfungi* by the independent UK-based foundation Cybertruffle (www.cybertruffle.org.uk), which seeks to disseminate information about fungi and allies. This proposal considers the coordination of the effort by a Cuban myxomycetologist, thus making the Neotropical region one of the first candidates for conducting myxomycete research for conservation purposes. In spite of the latter and to the best of our knowledge, this proposal is not currently being executed. As such, we consider that there are no active myxomycete conservation efforts being carried out anywhere in the world.

From the ecological point of view, the lack of conservation efforts in relation with myxomycetes in the Neotropical region may have a simple explanation. As it was described in previous sections, the ecology of myxomycetes in this region has only been studied for just over a decade and most efforts have ignored the vegetative stages. The obvious product of these historical limitations is that a very incomplete picture of the biogeography of Neotropical myxomycetes is currently available. It is clear that with only the moderately complete baseline data available; a true conservation program focusing on the protection of the ecosystem services facilitated by the group and the ecological dynamics of their functional diversity is far from being implemented. Moreover, if a more classical, biodiversity-based conservation program is sought out, a rather complete inventory of the species present in an area is required before an adequate categorization of their status is performed. Thus far, for the Neotropical region the countries with the highest number of myxomycetes species are Mexico and Brazil (see Lado & Wrigley de Basanta 2008), but the only country with a comprehensive ecological analysis of the occurrence of species in relation with forest types is Costa Rica (Rojas *et al*. 2010a, 2010b). In spite of this, none of these Neotropical countries actually counts on a robust-enough database to assess myxomycete distribution within their territories.

Given the state of knowledge on myxomycete distribution in the Neotropical region and the historical limitations on the study of the group, it is clear that their conservation status is still uncertain and that guidelines for future programs are yet to be determined. In any case, it is important that the process of discussion to analyze and implement the idea of myxomycete conservation moves forward through an international concerted process of objective scientific examination. Such an approach would at least alleviate the natural human tendency –so common in conservation practices– to construct biased experimental designs, fit experimental data to preconceived ideas on biological systems and use science as a method to implement socio-political agendas (see Clark & May 2002). In spite of the latter, it seems that if there is a tropical area of the world, for which myxomycete conservation programs can be started once the required baseline information is in place, such area would be the Neotropics.

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