Biogeographic patterns of the myxomycete biota of the Americas using a parsimony analysis of endemicity

Arturo Estrada-Torres · Diana Wrigley de Basanta · Carlos Lado

Abstract Myxomycetes are microorganisms frequently considered to be of cosmopolitan distribution, however as studies in unexplored areas have intensified, more information has become available on the patterns of distribution of these organisms, but no historical or cladistic biogeographic approaches have been applied to understand such patterns. In this study a parsimony analysis of endemicity (PAE) was used in order to generate a preliminary hypothesis on the biogeographic relationships of 13 American areas in which a well-known myxomycete biota exists. In general terms the hypotheses of the relationship between the myxomycete assemblages of areas used in this study agree with those reported for other groups of organisms. They appear to show that a historical-geographic pattern influences the distribution of myxomycetes as much as environmental factors. Three main clades were found in the analysis, with the first one including the two subantarctic localities, the second one representing the South American transition zone and the last one including all the Neotropical and Nearctic areas, but arranged into two subclades, one with the arid areas and the other with the tropical and temperate humid areas. Each clade or subclade in the cladogram is supported by the presence of several morphospecies, some of which appear to represent endemic species restricted to specific geographic areas. The results of this analysis are proposed as a working hypothesis that can perhaps be supported in the future with new data from other complementary regions of America or with more intense surveys in the areas already explored. They are inconsistent with the hypothesis of cosmopolitan distribution for these microorganisms, as they appear to indicate groups of species that are restricted to certain geographic areas, some of which may be endemic, such as those from the subantarctic forests of South America, those found exclusively in the South American arid areas or those that have been recently described from arid areas of North America.

Keywords Andean region · Distribution patterns · Myxomycetes · Nearctic · Neotropics · Ubiquity theory

A. Estrada-Torres (✉)
Centro de Investigación en Ciencias Biológicas,
Universidad Autónoma de Tlaxcala,
Apartado Postal 183,
Tlaxcala 90,000 Tlaxcala, Mexico
e-mail: arturomixo@hotmail.com

D. Wrigley de Basanta · C. Lado
Real Jardín Botánico de Madrid,
CSIC Plaza de Murillo 2,
28014, Madrid, Spain

Introduction

Myxomycetes are microorganisms that are intimately linked to the breakdown and recycling processes of plant remains. They are fundamental to the biodiversity of whole ecosystems, and as such are most important organisms. They are a major component of the total soil protozoan community (Urich et al. 2008). A recent comprehensive review paper on myxomycetes (Stephenson 2011) indicates a significant advance in the knowledge of myxomycetes since the monograph by Martin and Alexopoulos (1969) was published, but the advance has been much slower in the understanding of their patterns of distribution. Like other microbes, a large proportion of the known species of myxomycetes have been considered to be of cosmopolitan distribution (Martin and Alexopoulos 1969). Since microorganisms are so small and potentially easily dispersed, they have been considered to be different from large organisms and to follow the ubiquity hypothesis that everything is everywhere (Martiny et al. 2006; Fontaneto and Brodie 2011). This would mean that they do not follow any biogeographical patterns. Nevertheless, recent data suggest that many protists have restricted distribution and even endemisms (Cotterill et al. 2008). In the case of

myxomycetes there also appear to be some species restricted to temperate, tropical or alpine/boreal environments (Ing 1994, Stephenson and Stempen 1994). Now that more intensive surveys have been completed in various areas of the world, some of them in areas of America where there are biodiversity hotspots (Stephenson et al. 2001; Schnittler et al. 2002; Lado et al. 2003, 2007, 2011, 2012; Estrada-Torres et al. 2009; Rojas et al. 2010; Wrigley de Basanta et al. 2010b), it is possible to look for emerging patterns of distribution for these microorganisms, and look for the possible causes for their biogeography.

At present, there are around 1,000 myxomycete species (Lado 2005–2012). According to Schnittler and Mitchell (2000), who summarized the data, 446 species were estimated to be at least fairly common (known from more than 20 collections and reported from several localities), 258 to be rare (known from 2 to 20 collections and more than one locality), and 305 reported only from the type locality (in one or a few collections). This means that about 65 % of the taxa described until then were rare or very rare, and the tenet of the cosmopolitan distribution of myxomycetes should be questioned.

Several authors have recently contributed to the search for patterns of distribution in these organisms. For example Schnittler (2001) analyzed the distribution patterns of 439 species of myxomycetes, and assigned each species to one or more of the world's five major vegetation zones. Two additional factors were considered in this analysis, the humidity of the habitat where a species is usually found, and the distribution of the species according to elevation. Two important conclusions of the Schnittler study were that most myxomycete species are not cosmopolitan, since less than five species were found in all of the major vegetation and climatic zones, from the Arctic to the tropics, and that their distribution patterns can be explained by a combination of both microhabitat and macroclimate requirements.

In another study by Stephenson et al. (2008) the authors pointed out that although the spores of myxomycetes would appear to have considerable potential for long-distance dispersal, there is little question that some species are more common in some regions of the world than others. They state that the non-availability of certain microhabitats apparently impose major constraints on the occurrence of the myxomycetes species, even within a particular region. They agreed that present data on myxomycete distribution are consistent with the "moderate endemicity model" proposed by Foisner (2006), but they emphasized the importance of environmental factors on the distribution of myxomycetes. These authors however did not consider the contribution that historical-geographic factors could make to the patterns of distribution of myxomycete species.

Rojas et al. (2012) studied the myxomycete assemblages at high-elevation in three countries of the northern Neotropics, an area in North America and one in Thailand. As a result of a cluster analysis, they found that all the study areas in the Americas formed a group that is separate from the only non-American area. They found also that the species composition along the latitudinal gradient that extends from Mexico to Costa Rica shows a pattern of decreasing similarity to the temperate study area of the eastern United States. They concluded that the diversity and abundance of myxomycetes seem to be highly dependent on the characteristics of the forests in which these organisms develop, and that the distribution of the majority of myxomycete species is better explained by the particular current ecological conditions in different geographical locations than by the effect of past evolutionary and ecological events.

It appears, therefore, that only descriptive (Stephenson et al. 1993, 2000, 2008; Schnittler 2001) or hierarchical clustering methods (Rojas et al. 2012) have been used to date to try to understand the biogeographic relationships of myxomycete biota from different areas of the world, but no historical or cladistic biogeographic approaches have been applied with this aim. The use of raw distributional data and the summary of area relationship patterns in a branching diagram, using hierarchical clustering algorithms, were recognized by Porzecanski and Cracraft (2005) as one of the most common approaches to understanding the biogeographic affinities of biota. Nelson and Platnick (1981) said that "the best evidence for area relationships is congruent phylogenetic patterns among the endemic species from multiple clades". However, as happens with myxomycetes, this evidence is often lacking, especially across large spatial scales such as those characteristic of continental biota. In the case of using large spatial scales, heuristic alternatives to cladistic biogeographic methods have been suggested. One of these is the parsimony analysis of endemicity (PAE), which is a pattern-oriented method that uses a cladistic algorithm to analyze geographical patterns of distribution (Echeverry and Morrone 2010), classifying areas or localities by their shared taxa according to the most parsimonious solution. PAE was originally proposed, in a paleontological context, by Rosen (1984, 1988) with the objective of addressing the shortcomings of phenetic approaches to assess area relationships of fossil or extant organisms from different areas. Even though PAE is not regarded as a historical-biogeographic approach by some authors (Brooks and van Veller 2003; Nihei 2006), others include it within this subdivision of biogeography (Morrone and Crisci 1995; Escalante-Espinoza and Morrone 2003; Posadas et al. 2006; Echeverry and Morrone 2010), and consider that it can be used to generate a preliminary hypothesis as to the relationships between the areas studied, since "the recognition of congruent patterns of distribution among different taxonomic groups is in itself evidence that they have resulted from the same major historical events" (Echeverry and Morrone 2010). The main criticism of PAE is that ignores phylogenetic

relationships among taxa, considering only their distribution (Humphries, 1989), which is why some authors like Cracraft (1991) and Myers (1991) suggested incorporating phylogenetic information into PAE, and including natural supraspecific groups. However, compared with other approaches to cladistic biogeography, PAE can be used in cases where phylogenetic relationships of the taxa are as yet unknown (Contreras-Medina et al. 2007).

In this study, PAE has been applied in order to generate a preliminary hypothesis on the historic relationships of some American areas, in which a well-known myxomycete biota exists, as a different attempt to discuss the present ideas on myxomycete distribution patterns and to design future research to improve our knowledge on the biogeographical relationships of the myxomycete assemblages from other areas of the world.

Material and methods

A parsimony analysis of endemicity was done comparing the myxomycete assemblages of 13 geographical areas of America, from 37º28' north latitude to 54º50' south latitude (Fig. 1). Information on the areas selected, their biogeographical regions and provinces according to the schemes proposed by Udvardy (1975) and Morrone (2006), the geographic coordinates of each area and references where the information has been obtained, are summarized in Table 1.

The selection of the areas was made based on regional inventories that were deemed compatible as far as sampling effort, intensity and the inclusion of both field and moist chamber culture results was concerned. A presence/absence matrix was constructed (Table 2) considering the selected areas as units of analysis and the species as characters, coding 1 as the presence of a species identified there and 0 as its absence. The morphospecies concept, that uses differences in morphological characters to distinguish species, was used to construct the matrix. Information to distinguish species by other methods is barely emerging for this group, and therefore currently the morphospecies concept is the only reliable method. Information on a total of 371 species and 7 varieties, over 35 % of the currently accepted morphospecies, was included in the database. In addition, in order to augment the historical perspective of the information on each region (Morrone and Crisci, 1995), an analysis was performed using the data of the 48 genera found in the areas, using the same codes as above, 1 as presence of the genus and 0 as its absence. The cladograms in both analyses were rooted with a hypothetical area out-group coded with 0 for all the taxa. The analysis was performed using classical Wagner parsimony in the program NONA 2.0 (Goloboff 1993), through Winclada 1.00.08 (Nixon 2002), with heuristic searches (tree bisection and reconnection), using a maximum of 1,000 retained trees, 100 replicas and 10 initial trees per replica. Results were compared to the known biogeographic areas summarized by Morrone (2006).

Results

The parsimony analysis that included only species resulted in a most-parsimonious cladogram of 590 steps with a consistency index (CI) of 0.39 and a retention index (RI) of 0.39 (Fig. 2). At the base of the cladogram is the clade (2) that includes myxomycetes from subantarctic Chile and Argentina, both of which belong to the Andean region. It is important to note that these temperate zones are separate from the temperate zone of the northern hemisphere. Another clade (4) includes the areas of central Chile around Santiago and the Atacama (Chile) and Monte deserts (Argentina). These are also separated from the arid regions of the northern hemisphere. Two of these three areas (Atacama and Monte) belong the South American transition zone (Morrone 2006). A third clade (7) is made up of the arid areas of North America that include the Colorado Plateau (USA), the Tehuacán-Cuicatlán valley (Mexico) and the Big Bend National Park (USA). The last clade (9) encompasses five areas, three in the Neotropics (Los Tuxtlas, El Edén and Maquipucuna), one from the Mexican Transition Zone (La Malinche), and one from the Nearctic region (Great Smoky Mountains National Park, GSMNP).

A second analysis, that included species and genera, produced three equally parsimonious cladograms of 700 steps, with a consistency index of 0.39 and a retention index of 0.39, one of which had exactly the same topology as the cladogram produced including only species in Fig. 2. In the strict consensus cladogram (Fig. 3), only four clades were maintained, clade 1 including Los Tuxtlas and El Edén, the two Mexican Neotropical areas, clade 2 including Atacama and Monte deserts, clade 3 including La Malinche (Mexico) and GSMNP (USA), and clade 4 of the arid zones of North America (Colorado Plateau, Tehuacán-Cuicatlán and Big Bend). Each clade 1 to 4 is grouped in the same way as the most parsimonious tree (Fig. 2). The clades maintained in the strict consensus cladogram are those supported by the greatest number of species.

In the analysis including also genera, the relationships of the areas of the Andean region and the Neotropical region of the southern hemisphere are ambiguous in the cladogram (Fig. 3).

Discussion

In general terms the hypotheses of the relationships between areas found in this study agree with those reported for other

Fig. 1 Map of the areas included in the analysis
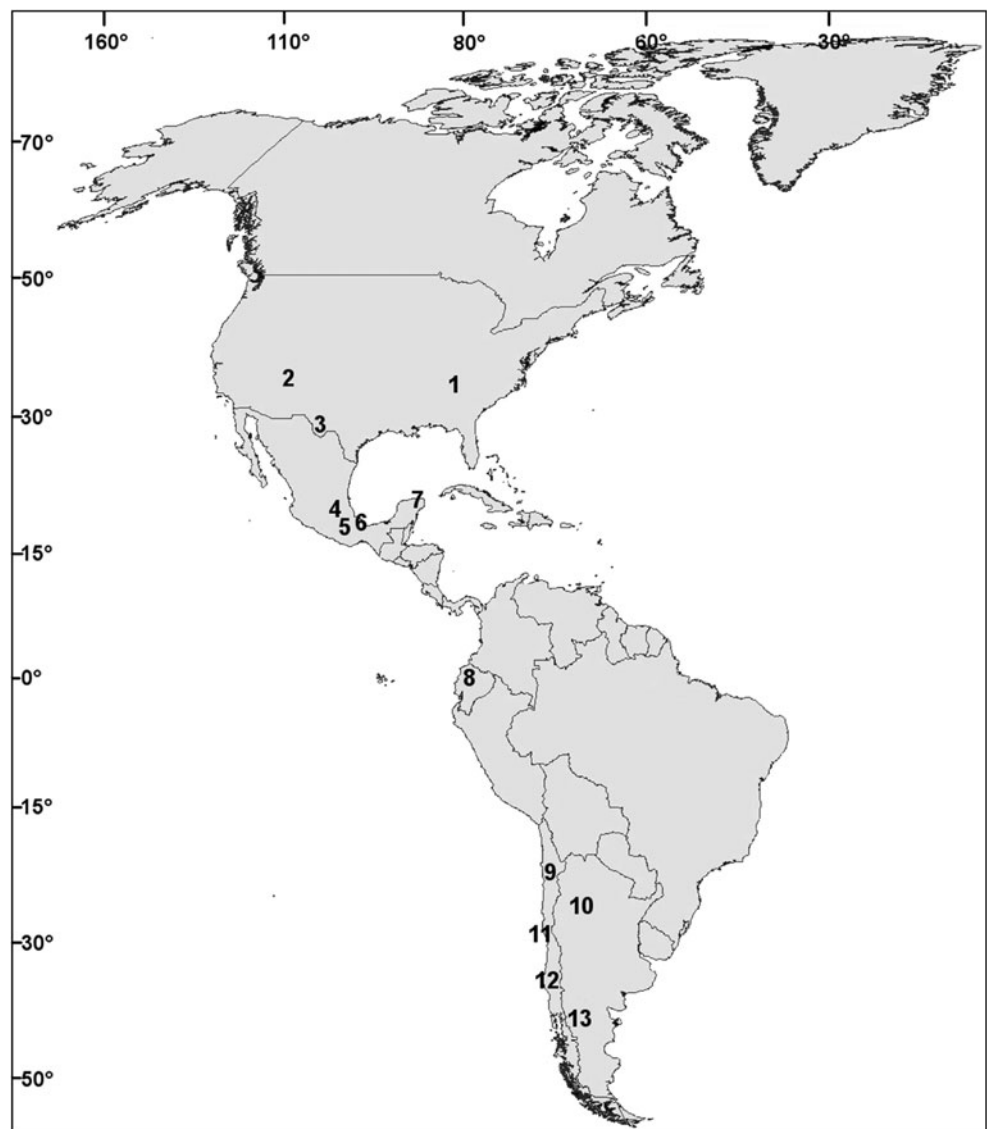
groups of organisms like plants and insects (Crisci et al., 1991), and appear to show a historical geographic pattern that influences the distribution of myxomycetes as much as the environmental factors suggested by authors such as Schnittler (2001) or Stephenson et al. (2008).

The myxomycete biota of the southern South American regions in this analysis, are mostly separated in the clado-gram from those of the North American regions (Fig. 2). Clade 2 includes the myxomycetes from the Andean region, clade 4 is composed of species from the South American transition zone. The myxomycete biota from all the prov-inces of North America is included in clade 6 with Maqui-pucuna, a Neotropical province of South America. The relationships of the areas of the Andean region and the Neotropical region of the southern hemisphere are ambigu-ous in the cladogram (Fig. 3) of the analysis including genera. A possible reason for this was that a large number of genera are of wide distribution and common to all areas.

The areas in clade 2 (Fig. 2), Maule province of subant-arctic Chile, and Magellanic Forest province of Argentina, has vegetation dominated by forests of *Araucaria* sp. and of *Nothofagus* spp. Although some myxomycete species of known broad geographical distribution are included in the myxomycete biota of these areas, the southern forests are characterized by a predominance of species in the order Trichiales, notably *Metatrichia floriformis* and *Trichia ver-rucosa*, and the presence of some species of *Diderma* such as *D. antarcticum*, *D. gracile* and *D. robustum* (Wrigley de Basanta et al. 2010b), described originally from this area, but unknown either from temperate areas of the northern hemisphere or from other austral temperate forests studied, such as those found in Australia (Mitchell 1995) and New Zealand (Stephenson 2003). The latter forests, according to Crisci et al. (1991), have a biota that is somewhat related to that of the temperate extreme South of South America. These authors based the relationship on numerous taxa such

Table 1 Summary data on selected areas included in the analysis

	Area	Region	Province	Geographic coordinates	References
1	Great Smoky Mountains National Park (USA)	Nearctic	Eastern Forests of the United States*	35º28′–35º47′ N, 83º02′–84º00′ W	Stephenson et al. 2001; Snell and Keller 2003; Adamonyte and Eliasson 2010
2	Colorado Plateau (USA)	Nearctic	Great Basin*	35º02′–37º28′ N, 105º38′–112º07′ W	Novozhilov et al. 2003
3	Big Bend National Park (USA)	Nearctic	Mexican Plateau	29º10′–29º18′ N, 102º57′–103º18′ W	Ndiritu et al. 2009
4	La Malinche National Park (Mexico)	Mexican transition zone	Transmexican Volcanic Belt	19º06′–19º20′ N, 97º55′–98º09′ W	Rodríguez-Palma et al. 2005; Rojas 2010; Rojas et al. 2010
5	Tehuacán-Cuicatlán Biosphere Reserve (Mexico)	Mexican transition zone	Transmexican Volcanic Belt	17º38′–18º52′ N, 96º55′–97º40′ W	Estrada-Torres et al. 2009
6	Los Tuxtlas Biological Station (Mexico)	Neotropical	Gulf of Mexico	18º35′ N, 95º05′ W	Lado et al. 2003
7	El Edén Ecological Reserve (Mexico)	Neotropical	Yucatán Peninsula	21º12′–21º14′ N, 87º10′–87º13′ W	Lado et al. 2003
8	Maquipucuna Biological Station (Ecuador)	Neotropical	Cauca	00º07′ N, 78º38′ W	Schnittler et al. 2002
9	Atacama Desert (Chile)	South American transition zone	Atacama	18º11′–32º01′ S, 67º45′–71º36′ W	Lado et al. 2007, 2012
10	Monte Desert (Argentina)	South American transition zone	Monte	23º02′–33º25′ S, 65º00′–69º48′ W	Lado et al. 2011
11	Central Chile (Chile)	Andean	Santiago	32º15′–34º16′ S, 70º12′–71º32′ W	Lado et al. 2012
12	Subantarctic Chile	Andean	Maule	37º47′–39º34′ S, 71º16′–73º06′ W	Lado et al. 2012
13	Subantarctic Argentina	Andean	Magellanic Forest	39º49′–54º50′ S, 67º29′–71º57′ W	Wrigley de Basanta et al. 2010b

Source: Morrone (2006) with the exception of the provinces with (*) which follow the system of Udvardy (1975).

as insects, Fungi of the genus *Cyttaria* and its host plants of the genus *Nothofagus,* and they maintain that the biota of the temperate extreme South of South America are of a more ancient origin than that of the tropical North. It is worth noting that species in the order Trichiales, such as *Metatrichia floriformis* and *Trichia verrucosa* are among the most common myxomycetes of the beech forests of Australia and New Zealand too (Stephenson 2003). Another interesting pattern in the assemblages of myxomycetes of these areas is the absence of certain other widely distributed taxa such as *Comatricha tenerrima, Cribraria violacea, Didymium squamulosum, Licea biforis* and *Physarum compressum*.

The areas studied that form clade 4 (Fig. 2) are in the South American transition zone (SAtz), an area extending along the length of the Andes that has biotic affinities with both the Neotropical and the Andean regions and is considered to be an area where ecological and historical processes have favored the evolution of a very characteristic biota (Morrone 2004). This is evident from the results of the present analysis since the myxomycete biota from Santiago province (central Chile area) considered by Morrone (2006) to be part of the Andean region, is grouped with that of the deserts of Atacama and Monte that belong to the SAtz (Table 1). The affinity between these areas has been

suggested before by Urtubey et al. (2010), for the genera of the family Asteraceae, who considered that these two provinces of the SAtz had greater affinity with the Andean region than the Neotropical region. The clades maintained in the strict consensus cladogram are those supported by the greatest number of species. The relationships between the myxomycete biota of the area of central Chile with the Atacama and Monte deserts is probably due to the prevalence of species normally found associated with arid areas such as *Badhamia melanospora, Craterium leucocephalum, Didymium dubium* and *D. wildpretii*, or the absence of other species of wide distribution in other regions, such as *Ceratiomyxa fruticulosa, Physarum viride* and *Stemonitis fusca*. Interestingly, among the myxomycetes of the SAtz are recently described species like *Didymium infundibuliforme* (Wrigley de Basanta et al. 2009) and *Licea eremophila* (Wrigley de Basanta et al. 2010a), that are associated with species of cacti and other succulents common on both sides of the Andes, but also other species that so far have only been reported from a single side of the mountain chain, and not the other, such as *D. chilense* (Lado et al. 2012), *D. operculatum* (Wrigley de Basanta et al. 2011), *Perichaena calongei* (Lado et al. 2009) and *Physarum atacamense* (Wrigley de Basanta et al. 2012a). These could possibly

Table 2 List of species included in the parsimony analysis of endemicity

Species	Areas*												
	1	2	3	4	5	6	7	8	9	10	11	12	13
Arcyria affinis Rostaf.	0	0	0	0	0	0	0	0	1	0	0	0	0
A. afroalpina Rammeloo	0	0	0	0	0	0	0	1	0	1	1	0	0
A. cinerea (Bull.) Pers.	1	1	1	1	1	1	1	1	1	1	1	1	1
A. cinerea var. *digitata* (Schwein.) Lister	0	0	0	0	0	0	1	0	0	0	0	0	0
A. denudata (L.) Wettst.	1	0	1	1	1	1	1	1	0	1	1	1	0
A. ferruginea Saut.	1	0	0	1	0	0	0	0	0	0	0	1	0
A. globosa Schwein.	0	0	0	1	0	0	0	1	0	0	0	0	0
A. incarnata (Pers. ex J.M. Gmel.) Pers.	1	0	0	1	0	0	0	0	0	0	0	1	0
A. insignis Kalchbr. & Cooke	1	0	1	0	1	0	0	0	0	0	1	1	0
A, major (G. Lister) Ing	0	0	0	0	0	0	0	1	0	0	0	0	0
A. minuta Buchet	0	0	0	0	0	0	0	0	0	1	0	0	0
A. obvelata (Oeder) Onsberg	1	0	0	1	0	1	0	0	0	0	1	1	1
A. occidentalis (T. Macbr.) G. Lister	0	0	0	1	0	0	0	0	0	0	0	0	0
A. oerstedii Rostaf.	0	0	0	1	0	0	0	0	0	0	0	0	0
A. pomiformis (Leers) Rostaf.	1	0	1	1	0	0	0	0	0	0	1	1	0
A. stipata (Schwein.) Lister	1	0	0	0	0	0	0	0	0	0	0	0	0
Badhamia affinis Rostaf.	0	1	0	1	1	0	0	0	0	1	0	0	0
B. apiculospora (Härk.) Eliasson & N. Lundq.	0	1	0	0	0	0	0	0	0	0	0	0	0
B. capsulifera (Bull.) Berk.	0	0	0	0	0	0	0	0	0	0	1	0	0
B. dubia Nann.-Bremek.	0	0	0	0	0	0	0	0	1	0	0	1	0
B. foliicola Lister	0	1	0	0	0	0	0	0	0	1	0	0	0
B. goniospora Meyl.	0	1	0	1	1	0	0	0	0	0	0	0	0
B. macrocarpa (Ces.) Rostaf.	0	1	0	0	0	0	0	0	1	1	0	0	0
B. melanospora Speg.	0	1	1	1	1	0	0	0	1	1	1	0	0
B. nitens Berk.	1	0	0	0	1	0	0	0	0	0	1	0	0
B. panicea (Fr.) Rostaf.	0	0	1	0	0	0	0	0	0	0	0	0	0
B. papaveracea Berk. & Ravenel	1	0	0	0	0	0	0	0	0	0	0	0	0
B. rugulosa T.E. Brooks & H.W. Keller	1	0	0	0	0	0	0	0	0	0	0	0	0
B. utricularis (Bull.) Berk.	0	0	0	1	1	0	0	0	0	0	1	0	0
B. versicolor Lister	0	0	0	1	1	0	0	0	0	0	0	1	0
Badhamiopsis ainoe (Yamash.) T.E. Brooks & H.W. Keller	1	1	0	0	1	0	1	0	0	0	0	0	0
Barbeyella minutissima Meyl.	1	0	0	1	0	0	0	0	0	0	0	0	0
Calomyxa metallica (Berk.) Nieuwl.	1	1	1	1	1	0	1	0	0	1	0	1	0
Ceratiomyxa fruticulosa (O.F. Müll.) T. Macbr.	1	1	1	1	1	1	1	1	0	0	0	1	1
C. fruticulosa var. *porioides* (Alb. & Schwein.) Lister	1	0	0	0	0	0	0	0	0	0	0	0	0
C. morchella A.L. Welden	0	0	0	0	0	0	0	1	0	0	0	0	0
C. sphaerosperma Boedjin	0	0	0	0	0	1	0	0	0	0	0	0	0
Clastoderma debaryanum A. Blytt.	1	0	1	1	0	0	1	0	1	0	0	0	0
C. debaryanum var. *imperatorium* Emoto	0	0	0	0	1	0	0	0	0	0	0	0	0
C. pachypus Nann.-Bremek.	1	0	0	0	0	0	0	0	0	0	0	0	0
Collaria arcyrionema (Rostaf.) Nann.-Bremek. ex Lado	1	0	0	0	1	0	0	1	0	0	0	0	0
C. lurida (Lister) Nann.-Bremek.	1	0	0	1	0	1	1	1	0	0	1	0	0
C. nigricapillitia (Nann.-Bremek. & Bozonnet) Lado	0	0	0	0	0	0	0	0	0	0	0	0	1
C. rubens (Lister) Nann.-Bremek.	0	0	0	1	0	0	0	0	0	0	1	0	0
Colloderma oculatum (C. Lippert) G. Lister	1	0	0	0	0	0	0	0	0	0	0	0	0
C. robustum Meyl.	0	0	0	1	0	0	0	0	0	0	0	0	0
Comatricha alta Preuss	0	0	0	0	0	0	0	0	0	0	1	0	1
C. elegans (Racib.) G. Lister	0	0	1	0	0	0	0	0	1	0	0	0	0

Table 2 (continued)

Species	Areas*												
	1	2	3	4	5	6	7	8	9	10	11	12	13
C. ellae Härk.	1	0	0	0	0	0	0	0	0	0	0	0	0
C. laxa Rostaf.	1	1	1	1	1	0	1	0	1	1	0	1	1
C. mirabilis R.K. Benj. & Poitras	0	0	1	0	0	0	0	0	0	0	0	0	0
C. nigra (Pers. ex J.F. Gmel.) J. Schröt.	1	1	1	1	0	0	0	0	0	0	1	1	1
C. pulchella (C. Bab.) Rostaf.	1	1	1	0	1	0	1	1	0	0	0	0	0
C. pulchelloides Nann.-Bremek.	0	0	0	0	0	0	0	0	0	1	0	0	0
C. reticulospora Ing & P.C. Holland	1	0	0	0	1	0	0	0	0	0	0	0	0
C. rigidireta Nann.-Bremek.	0	1	0	0	0	0	0	0	0	0	0	0	0
C. suksdorfii Ellis & Everh.	1	0	0	0	0	0	0	0	0	0	0	0	0
C. tenerrima (M.A. Curtis) G. Lister	1	0	1	0	1	1	1	1	0	1	1	0	0
Craterium aureum (Schumach.) Rostaf.	0	0	1	0	0	0	0	1	0	0	0	0	0
C. concinnum Rex	0	0	0	0	0	0	0	1	0	0	0	0	0
C. leucocephalum (Pers. ex J.F. Gmel.) Ditmar	0	0	0	1	1	0	1	1	1	1	1	0	0
C. minutum (Leers) Fr.	1	0	1	1	0	0	0	0	0	0	0	0	0
C. obovatum Peck	1	0	0	0	0	0	0	0	0	0	0	0	0
C. paraguayense (Speg.) G. Lister	0	0	0	0	0	1	0	0	0	0	0	0	0
Cribraria argillacea (Pers. ex J.F. Gmel.) Pers.	1	0	0	1	0	0	0	0	0	0	0	0	1
C. atrofusca G.W. Martin & Lovejoy	1	0	0	1	0	0	0	0	0	0	0	0	0
C. aurantiaca Schrad.	1	0	0	0	0	0	0	0	0	0	0	1	0
C. cancellata (Batsch.) Nann.-Bremek.	1	0	0	0	1	1	1	1	0	0	0	1	1
C. cancellata var. *fusca* (Lister) Nann.-Bremek.	0	0	0	0	0	0	1	0	0	0	0	0	0
C. confusa Nann.-Bremek. & Y. Yamam.	1	0	0	0	0	0	0	1	0	0	0	0	0
C. elegans Berk. & M.A. Curtis	1	0	0	0	0	0	0	0	0	0	0	0	0
C. ferruginea Meyl.	1	0	0	0	0	0	0	0	0	0	0	0	0
C. fragilis Lado & Estrada	0	0	0	0	1	0	0	0	0	0	0	0	0
C. intricata Schrad.	1	1	0	0	0	0	0	1	0	0	0	0	0
C. languescens Rex	1	0	0	0	0	0	1	1	0	0	0	0	0
C. lepida Meyl.	0	0	0	0	1	0	0	0	0	1	0	0	0
C. macrocarpa Schrad.	1	0	0	0	0	0	0	0	0	0	0	0	0
C. microcarpa (Schrad.) Pers.	1	0	1	0	0	0	1	0	0	0	1	1	0
C. minutissima Schwein.	1	0	0	0	0	0	0	0	0	0	0	0	0
C. mirabilis (Rostaf.) Massee	0	0	0	1	0	0	0	0	0	0	0	0	1
C. oregana H.C. Gilbert	1	0	0	1	0	0	0	0	0	0	0	0	1
C. persoonii Nann.-Bremek.	1	0	0	0	0	0	0	0	0	0	0	0	0
C. piriformis Schrad.	1	0	0	1	0	0	0	0	0	0	0	0	0
C. purpurea Schrad.	1	1	0	1	1	0	0	0	0	0	0	0	0
C. rubiginosa Fr.	0	0	0	1	0	0	0	0	0	0	0	0	0
C. rufa (Roth) Rostaf.	1	0	0	1	0	0	0	0	0	0	1	1	0
C. splendens (schrad.) Pers.	1	1	0	1	0	0	0	0	0	0	0	0	0
C. tenella Schrad.	1	0	0	0	0	0	1	1	0	0	0	0	0
C. violacea Rex	1	1	1	1	1	0	1	1	0	1	1	0	0
C. vulgaris Schrad.	1	0	0	1	0	0	0	0	0	0	0	0	0
C. zonatispora Lado, Mosquera & Beltrán-Tej.	0	0	0	0	1	0	0	0	0	0	0	0	0
Diachea arboricola H.W. Keller & Skrabal	1	0	0	0	0	0	0	0	0	0	0	0	0
D. bulbillosa (Berk. & Broome) Lister	1	0	0	0	0	1	0	0	0	0	0	0	0
D. leucopodia (Bull.) Rostaf.	1	0	0	0	0	1	0	1	0	0	0	0	0
D. silvaepluvialis M.L. Farr	1	0	0	0	0	1	0	0	0	0	0	0	0
D. splendens Peck	1	0	0	0	0	0	0	0	0	0	0	0	0

Table 2 (continued)

Species	Areas*												
	1	2	3	4	5	6	7	8	9	10	11	12	13
Diacheopsis insessa (G. Lister) Ing	1	0	0	1	0	0	0	0	0	0	0	0	0
Dianema corticatum Lister	1	1	0	0	0	0	0	0	0	1	0	0	0
D. depressum (Lister) Lister	0	0	0	0	0	0	0	0	0	0	1	0	0
D. harveyi Rex	1	1	0	0	0	0	0	0	0	0	0	0	0
D. succulenticola Lado, Estrada & D. Wrigley	0	0	0	0	0	0	0	0	1	0	0	0	0
Dictydiaethalium plumbeum (Schumach.) Rostaf.	1	0	1	0	1	0	0	0	0	1	1	0	0
Diderma acanthosporum Estrada & Lado	0	0	0	0	1	0	0	0	0	0	0	0	0
D. antarcticum (Speg.) Sturgis	0	0	0	0	0	0	0	0	0	0	0	1	0
D. asteroides (Lister & G. Lister) G. Lister	0	0	0	1	0	0	0	0	0	0	1	0	0
D. chondrioderma (de Bary & Rostaf.) G. Lister	1	0	1	1	0	1	0	0	0	0	0	0	0
D. cinereum Morgan	0	0	0	1	0	0	0	0	0	0	0	0	0
D. corrugatum T.E. Brooks & H.W. Keller	1	0	0	0	0	0	0	1	0	0	0	0	0
D. crustaceum Peck	0	0	0	0	0	0	0	0	0	1	0	0	0
D. deplanatum Fr.	1	0	0	0	0	0	0	0	0	1	0	0	1
D. effusum (Schwein.) Morgan	1	0	1	0	1	1	1	1	0	0	0	1	0
D. gracile Aramb.	0	0	0	0	0	0	0	0	0	0	0	1	0
D. hemisphaericum (Bull.) Hornem	1	0	0	1	1	1	1	1	0	1	0	0	0
D. niveum (Rostaf.) T. Macbr.	0	0	0	0	0	0	0	0	0	0	1	1	0
D. ochraceum Hoffm.	1	0	0	0	0	0	0	0	0	0	0	0	0
D. peyerimhoffii (Maire & Pinoy) H. Neubert, Nowotny & K. Baumann	0	0	0	0	0	0	0	0	0	0	0	1	0
D. radiatum (L.) Morgan	0	0	0	1	0	0	0	0	0	0	0	1	0
D. rimosum Eliasson & Nann.-Bremek.	0	0	0	0	0	1	1	0	0	0	0	0	0
D. roanense (Rex) T. Macbr.	1	0	0	0	0	0	0	0	0	0	0	0	0
D. robustum Aramb.	0	0	0	0	0	0	0	0	0	0	0	1	0
D. rugosum (Rex) T. Macbr.	1	0	0	0	0	1	1	0	0	0	0	0	0
D. sauteri (Rostaf.) T. Macbr.	0	0	0	0	0	0	1	0	0	0	0	0	0
D. spumarioides (Fr.) Fr.	0	1	0	0	0	0	1	0	0	0	0	0	0
D. subdyctiospermum (Rostaf.) G. Lister	0	0	0	0	0	1	0	0	0	0	0	0	0
D. testaceum (Schrad.) Pers.	1	0	0	1	0	0	0	0	0	0	0	0	0
D. umbilicatum Pers.	0	1	0	1	0	0	0	0	0	0	0	0	0
D. yucatanense Estrada, Lado & S.L. Stephenson	0	0	0	0	0	0	1	0	0	0	0	0	0
Didymium anellus Morgan	0	1	1	1	1	0	0	1	1	1	1	0	1
D. applanatum Nann.-Bremek.	0	0	0	0	1	0	0	0	0	0	0	0	0
D. bahiense Gottsb.	1	0	0	1	1	1	0	1	0	0	0	0	0
D. chilense Estrada, Lado & D. Wrigley	0	0	0	0	0	0	0	0	1	0	1	0	0
D. clavodecus K.D. Whitney	0	0	0	0	1	0	0	0	0	0	0	0	0
D. clavus (Alb. & Schwein.) Rabench.	1	0	0	1	1	1	0	1	0	1	1	0	0
D. comatum (Lister) Nann.-Bremek.	0	0	0	0	0	0	0	0	0	0	1	0	0
D. crustaceum Fr.	1	0	0	1	0	0	0	0	0	0	0	0	0
D. difforme (Pers.) Gray	0	1	1	1	1	1	0	1	0	0	1	1	1
D. dubium Rostaf.	0	1	1	0	1	0	0	0	1	1	1	0	0
D. eremophilum M. Blackw. & Gilb.	0	0	0	0	1	0	0	0	0	0	0	0	0
D. eximium Peck	0	0	0	0	0	0	0	0	0	0	1	0	0
D. floccosum G.W. Martin, K.S. Thind & Rehill	0	0	0	0	1	0	0	1	0	0	0	0	0
D. inconspicuum Nann.-Bremek. & D.W. Mitch.	0	1	0	0	0	0	0	0	0	0	0	0	0
D. infundibuliforme D. Wrigley, Lado & Estrada	0	0	0	0	0	0	0	0	1	1	0	0	0
D. iridis (Ditmar) Fr.	1	1	1	1	1	1	0	1	0	0	0	0	0
D. laxifilum G. Lister & J. Ross	0	0	0	0	0	0	0	0	0	0	1	0	0

Table 2 (continued)

Species	Areas*												
	1	2	3	4	5	6	7	8	9	10	11	12	13
D. leoninum Berk. & Broome	0	0	0	0	0	0	0	1	0	0	0	0	0
D. listeri Massee	0	0	0	0	0	0	0	0	0	1	0	0	0
D. megalosporum Berk. & M.A. Curtis	0	0	0	1	0	0	0	0	0	0	1	0	0
D. melanospermum (Pers.) T. Macbr.	1	0	0	1	0	0	0	0	1	0	0	0	0
D. mexicanum G. Moreno, Lizárraga & Illana	0	1	0	0	0	0	0	0	0	1	0	0	0
D. minus (Lister) Morgan	1	0	1	1	0	0	0	0	0	0	0	1	1
D. nigripes (Link) Fr.	1	0	1	1	1	1	1	1	0	0	0	1	0
D. nivicolum Meyl.	0	0	0	0	0	0	0	0	0	0	1	0	0
D. obduscens P. Karst.	0	0	0	0	0	0	0	0	0	1	0	0	0
D. ochroideum G. Lister	1	0	1	0	1	0	1	0	0	0	0	0	0
D. operculatum D. Wrigley, Lado & Estrada	0	0	0	0	0	0	0	0	1	0	0	0	0
D. orthonemata H.W. Keller & T.E. Brooks	0	0	0	0	1	0	0	0	0	0	0	0	0
D. quitense (Pat.) Torrend	0	1	0	0	0	0	0	0	0	1	1	0	0
D. serpula Fr.	0	0	0	1	0	0	0	0	0	0	0	0	0
D. squamulosum (Alb. & Schwein.) Fr.	1	1	1	1	1	1	1	1	1	1	1	0	0
D. sturgisii Hagelst.	0	0	0	0	1	0	0	0	0	0	0	0	0
D. subreticulosporum Oltra, G. Moreno & Illana	0	0	0	0	1	0	0	0	0	0	0	0	0
D. synsporon T.E. Brooks & H.W. Keller	0	0	0	0	0	0	0	0	1	0	0	0	0
D. tehuacanense Estrada, D. Wrigley & Lado	0	0	0	0	1	0	0	0	0	0	0	0	0
D. trachysporum G. Lister	0	1	0	0	0	0	0	0	0	0	0	0	0
D. umbilicatum D. Wrigley, Lado & Estrada	0	0	0	0	1	0	0	0	0	0	0	0	0
D. vaccinum (Durieu & Mont.) Buchet	0	0	0	0	1	0	0	0	1	1	1	0	0
D. verrucosporum A.L. Welden	0	1	0	1	0	0	0	0	0	0	0	0	0
D. wildpretii Mosquera, Estrada, Beltrán-Tej., D. Wrigley & Lado	0	0	0	0	1	0	0	0	1	1	1	0	0
Echinostelium apitectum K.D. Whitney	1	1	0	1	1	0	0	0	0	0	0	0	0
E. arboreum H.W. Keller & T.E. Brooks	1	1	0	0	1	0	0	0	1	1	0	0	0
E. bisporum (L.S. Olive & Stoian.) K.D. Whitney	1	0	0	0	0	0	0	0	0	0	0	0	0
E. brooksii K.D. Whitney	0	0	0	0	0	0	0	0	0	0	0	1	0
E. coelocephalum T.E. Brooks & H.W. Keller	0	1	0	0	0	0	0	0	0	0	0	0	0
E. colliculosum K.D. Whitney & H.W. Keller	0	1	1	0	1	0	0	0	1	1	0	1	0
E. corynophorum K.D. Whitney	0	1	0	0	0	0	0	0	0	0	0	0	0
E. elachiston Alexop.	0	1	0	0	0	0	0	0	0	0	0	0	0
E. fragile Nann.-Bremek.	0	1	0	0	1	0	0	0	1	0	0	0	0
E. minutum de Bary	1	1	1	1	1	1	1	1	0	1	1	1	0
Elaeomyxa cerifera (G. Lister) Hagelst.	0	0	0	1	0	0	0	0	0	0	0	0	0
E. miyazakiensis (Emoto) Hagelst.	1	0	0	0	0	0	0	0	0	0	0	0	0
Enerthenema melanospermum T. Macbr. & G.W. Martin	0	0	0	0	0	0	0	0	0	0	0	0	1
E. papillatum (Pers.) Rostaf.	1	1	0	1	1	0	0	1	0	0	0	0	0
Fuligo cinerea (Schwein.) Morgan	0	1	0	0	0	0	0	0	0	0	1	0	0
F. intermedia T. Macbr.	0	0	0	1	0	0	0	0	0	0	0	0	0
F. leviderma H. Neubert, Nowotny & K. Baumann	1	0	0	0	0	0	0	0	0	0	0	0	0
F. megaspora Sturgis	0	0	0	1	0	0	1	0	0	0	0	0	0
F. septica (L.) F.H. Wigg.	1	0	0	1	1	0	0	1	1	0	1	1	1
Hemitrichia calyculata (Speg.) M.L. Farr	1	0	0	0	1	1	1	1	0	0	1	0	0
H. clavata (Pers.) Rostaf.	1	1	0	1	0	0	0	0	0	0	0	0	0
H. leiocarpa (Cooke) Lister	0	0	0	1	0	0	0	0	0	0	0	0	1
H. minor G. Lister	0	1	1	0	1	0	0	0	1	1	0	0	0
H. pardina (Minakata) Ing	1	1	0	0	1	1	1	0	0	0	1	0	0

Table 2 (continued)

Species	1	2	3	4	5	6	7	8	9	10	11	12	13
H. serpula (Scop.) Rostaf.	1	0	0	1	0	1	1	1	0	0	0	0	0
Lamproderma arcyrioides (Sommerf.) Rostaf.	0	0	0	0	0	0	0	0	0	0	0	1	0
L. columbinum (Pers.) Rostaf.	1	0	0	1	0	0	0	0	0	0	0	0	0
L. echinosporum Meyl.	0	0	0	0	0	0	0	0	0	0	0	1	0
L. granulosum H. Neubert, Nowotny & Schnittler	1	0	0	0	0	0	0	0	0	0	0	0	0
L. gulielmae Meyl.	0	0	0	1	0	0	0	0	0	0	0	0	0
L. maculatum Kowalski	0	0	0	0	0	0	0	0	0	0	0	1	1
L. muscorum (Lév.) Hagelst.	0	0	0	0	0	1	0	1	0	0	0	0	0
L. scintillans (Berk. & Broome) Morgan	1	0	1	0	0	0	1	1	0	0	1	0	0
Leocarpus fragilis (Dicks.) Rostaf.	1	0	0	1	0	0	0	0	0	0	0	1	1
Lepidoderma chailletii Rostaf.	0	0	0	0	0	0	0	0	0	0	0	0	1
L. granuliferum (W. Phillips) R.E. Fr.	0	0	0	0	0	0	0	0	0	0	1	0	0
L. tigrinum (Schrad.) Rostaf.	1	0	0	1	0	0	0	0	0	0	0	0	0
Licea belmontiana Nann.-Bremek.	1	1	1	0	1	0	0	0	1	1	0	0	0
L. biforis Morgan	1	1	1	1	1	0	1	0	1	0	1	0	0
L. castanea G. Lister	1	1	0	1	0	0	0	0	0	0	0	0	0
L. denudescens H.W. Keller & T.E. Brooks	1	1	0	0	1	0	0	0	0	1	0	0	0
L. eremophila D. Wrigley, Lado & Estrada	0	0	0	0	0	0	0	0	1	1	0	0	0
L. inconspicua T.E. Brooks & H.W. Keller	0	1	0	0	0	0	0	0	0	0	0	0	0
L. kleistobolus G.W. Martin	1	1	1	0	1	0	0	0	0	0	1	0	0
L. microscopica D.W. Mitch.	1	0	0	0	0	0	0	0	0	0	0	0	0
L. minima Fr.	1	0	0	1	1	0	0	0	0	0	1	1	0
L. nannengae Pando & Lado	0	1	0	1	1	0	0	0	0	0	0	0	0
L. operculata (Wingate) G.W. Martin	1	0	0	0	0	1	1	1	0	0	0	0	0
L. parasitica (Zukal) G.W. Martin	1	1	0	1	0	0	0	0	0	0	0	0	0
L. pedicellata (H.C. Gilbert) H.C. Gilbert	1	1	0	0	0	0	0	0	0	0	0	0	0
L. perexigua T.E. Brooks & H.W. Keller	1	1	0	0	0	0	0	1	0	0	0	0	0
L. poculiformis Ukkola	0	0	0	0	0	1	0	0	0	0	0	0	0
L. pseudoconica T.E. Brooks & H.W. Keller	1	0	0	0	0	0	0	0	0	0	0	0	0
L. pusilla Schrad.	1	0	0	1	0	0	0	0	0	0	0	0	0
L. pygmaea (Meyl.) Ing	0	0	0	1	0	0	0	0	0	1	0	0	0
L. rufocuprea Nann.-Bremek. & Y. Yamam.	1	0	0	0	0	0	0	0	0	0	0	0	0
L. rugosa Nann.-Bremek. & Y. Yamam.	0	0	0	0	1	0	0	0	0	0	0	0	0
L. rugosa var. *fujokiana* (Y. Yamam.) D. Wrigley & Lado	0	0	0	0	1	0	0	0	0	0	0	0	0
L. sambucina D.W. Mitch.	1	1	0	0	0	0	0	0	0	1	0	0	0
L. scyphoides T.E. Brooks & H.W. Keller	1	0	0	1	0	0	0	0	0	1	0	0	0
L. succulenticola Mosquera, Lado, Estrada & Beltrán.-Tej.	0	0	0	0	1	0	0	0	1	1	0	0	0
L. tenera E. Jahn	0	1	0	0	0	0	0	0	0	0	0	0	0
L. testudinacea Nann.-Bremek.	0	1	0	1	0	0	0	0	0	0	0	0	0
L. variabilis Schrad.	0	1	0	0	0	0	0	0	0	0	0	0	1
Lindbladia tubulina Fr.	0	0	0	1	0	0	0	0	0	0	0	0	0
Lycogala conicum Pers.	0	0	0	0	0	1	0	0	0	0	0	0	0
L. epidendrum (L.) Fr.	1	0	0	1	1	0	0	1	0	1	1	1	1
L. exiguum Morgan	1	0	0	1	0	1	1	0	0	0	0	0	0
L. flavofuscum (Ehremb.) Rostaf.	0	1	0	1	0	0	0	0	0	0	0	0	0
Macbrideola andina D. Wrigley, Lado & Estrada	0	0	0	0	0	0	0	0	0	1	0	0	0
M. cornea (G. Lister & Cran) Alexop.	1	1	0	0	0	0	0	0	0	0	0	0	0

Table 2 (continued)

Species	Areas*												
	1	2	3	4	5	6	7	8	9	10	11	12	13
M. decapillata H.C. Gilbert.	1	1	0	0	0	0	0	1	0	0	0	0	0
M. declinata T.E. Brooks & H.W. Keller	0	1	0	0	0	0	0	0	0	0	0	0	0
M. martinii (Alexop. & Beneke) Alexop.	0	0	0	0	1	1	1	0	0	0	0	0	0
M. oblonga Pando & Lado	0	1	0	0	1	0	0	0	0	0	0	0	0
M. ovoidea Nann.-Bremek. & Y. Yamam.	0	0	0	0	0	0	0	0	1	0	0	0	0
M. scintillans H.C. Gilbert.	0	0	0	0	0	0	0	0	0	1	0	0	0
M. scintillans var. *verrucosa* (Nann.-Bremek. & Y. Yamam.) Y. Yamam.	0	0	0	0	0	1	1	0	0	0	0	0	0
M. synsporos (Alexop.) Alexop.	1	1	0	0	1	0	0	0	0	0	0	0	0
Metatrichia floriformis (Schwein.) Nann.-Bremek.	1	0	0	1	0	0	0	1	0	0	1	1	1
M. horrida Ing	0	0	0	0	0	1	1	0	0	0	0	0	0
M. vesparia (Batsch) Nann.-Bremek.	1	1	0	0	0	0	0	1	0	0	0	0	0
Minakatella longifila G. Lister	0	1	0	0	0	0	0	0	0	0	0	0	0
Mucilago crustacea F.H. Wigg.	0	0	0	1	0	0	0	0	0	0	0	0	0
Oligonema flavidum (Peck) Peck	1	0	0	0	0	0	0	0	0	0	0	1	0
O. schweinitzii (Berk.) G.W. Martin	1	0	0	0	0	0	0	0	0	0	0	0	0
Paradiacheopsis acanthodes (Alexop.) Nann.-Bremek.	1	0	0	0	0	0	0	0	0	0	0	0	0
P. eryhtropodia (Ing) Nann.-Bremek.	0	0	0	1	0	0	0	0	0	0	0	0	0
P. fimbriata (G. Lister & Cran) Hertel ex Nann.-Bremek.	0	1	0	1	0	0	0	1	0	0	1	0	0
P. solitaria (Nann.-Bremek.) Nann.-Bremek.	1	1	1	1	0	0	0	0	0	0	0	0	0
Perichaena calongei Lado, D. Wrigley & Estrada	0	0	0	0	0	0	0	0	1	0	0	0	0
P. chrysosperma (Curr.) Lister	1	1	1	1	1	1	1	1	1	0	0	1	0
P. corticalis (Batsch) Rostaf.	1	1	1	1	1	0	0	0	0	0	0	0	0
P. depressa Lib.	1	1	1	1	1	1	1	0	1	1	1	1	0
P. dyctionema Rammeloo	0	0	0	1	0	0	0	1	0	0	0	0	0
P. liceoides Rostaf.	0	1	0	1	0	0	0	0	0	0	0	0	0
P. luteola (Kowalski) Gilert	0	0	0	0	1	0	0	0	0	0	0	0	0
P. pedata (Lister & G. Lister) G. Lister ex E. Jahn	0	0	1	0	1	0	0	1	0	0	0	1	0
P. quadrata T. Macbr.	0	1	0	0	1	0	0	0	1	1	1	0	0
P. stipitata Lado, Estrada & D. Wrigley	0	0	0	0	1	0	0	0	0	0	0	0	0
P. vermicularis (Schwein.) Rostaf.	1	1	1	0	1	1	1	1	1	1	1	0	0
Physarella oblonga (Berk. & M.A. Curtis) Morgan	0	0	0	0	1	1	1	1	0	0	0	0	0
Physarum aeneum (Lister) R.E. Fr.	0	0	1	0	0	0	1	0	0	0	0	0	0
P. album (Bull.) Cheval.	1	0	1	1	1	1	1	1	0	0	0	1	0
P. alvoradianum Gottsb.	0	0	0	0	0	1	1	0	0	0	0	0	0
P. atacamense D. Wrigley, Lado & Estrada	0	0	0	0	0	0	0	0	1	0	0	0	0
P. auripigmentatum G.W. Martin	0	0	0	0	0	0	0	1	0	0	0	0	0
P. auriscalpium Cooke	0	0	0	0	0	0	0	0	0	1	0	0	0
P. bitectum G. Lister	0	1	1	1	1	0	0	0	0	1	0	0	0
P. bivalve Pers.	1	1	1	1	0	0	0	0	0	0	1	0	0
P. bogoriense Racib.	0	0	0	1	0	1	1	1	1	0	1	0	0
P. bruneolum (W. Phillips) Massee	0	0	0	1	1	0	0	0	0	0	1	0	0
P. carneum G. Lister & Sturgis	0	0	0	0	1	0	0	0	0	0	0	0	0
P. cinereum (Batsch) Pers.	1	1	1	1	1	1	1	1	1	0	0	1	0
P. citrinum Schumach.	0	0	0	1	0	0	0	0	0	0	0	0	0
P. clavisporum G. Moreno, A. Sánchez, A. Castillo & Illana	0	0	0	0	0	0	0	0	1	0	1	0	0
P. compressum Alb. & Schwein.	1	0	1	1	1	0	1	1	1	1	1	0	0
P. confertum T. Macbr.	1	0	0	1	0	0	0	0	0	0	1	0	0

Table 2 (continued)

Species	Areas*												
	1	2	3	4	5	6	7	8	9	10	11	12	13
P. crateriforme Petch	1	0	0	0	1	1	1	0	0	0	0	0	0
P. decipiens M.A. Curtis	1	1	0	1	1	0	0	0	1	1	0	0	0
P. didermoides (Pers.) Rostaf.	0	0	1	0	1	1	0	1	0	1	0	0	0
P. echinosporum Lister	0	0	1	1	0	0	0	0	1	0	0	0	0
P. flavicomum Berk.	1	0	1	0	0	0	1	0	0	0	0	0	0
P. galbeum Wingate	0	0	0	0	0	0	0	1	0	0	0	0	0
P. globuliferum (Bull.) Pers.	1	0	0	0	0	0	1	1	0	0	0	0	0
P. hongkongense Chao H. Chung	0	0	0	0	0	0	0	0	0	1	0	0	0
P. javanicum Racib.	0	0	0	0	0	0	0	1	0	0	0	0	0
P. lateritium (Berk. & Ravenel) Morgan	1	0	0	0	0	0	1	0	0	0	0	0	0
P. lakhanpalii Nann.-Bremek. & Y. Yamam.	0	0	1	0	0	0	0	0	0	0	0	0	0
P. leucophaeum Fr.	0	1	0	1	0	0	0	1	0	1	1	1	1
P. leucopus Link	1	0	0	0	0	0	0	0	0	0	0	0	0
P. licheniforme (Schwein.) Lado	0	0	0	0	0	0	0	0	1	1	0	0	0
P. megalosporum T. Macbr.	0	0	0	0	1	0	0	0	1	1	0	0	0
P. melleum (Berk. & Broome) Massee	1	0	0	1	1	1	1	1	0	0	0	0	0
P. murinum Lister	1	0	0	0	0	0	0	0	0	0	0	0	0
P. newtonii T. Macbr.	0	0	0	1	0	0	0	0	0	0	1	0	0
P. nicaraguense T. Macbr.	0	0	0	0	0	0	0	0	0	0	1	0	0
P. notabile T. Macbr.	0	1	1	0	1	0	0	0	1	1	0	0	1
P. nudum T. Macbr.	0	1	0	0	0	0	0	0	0	0	0	0	0
P. nucleatum Rex	1	0	0	0	0	0	1	0	0	0	1	0	0
P. oblatum T. Macbr.	0	1	0	0	1	0	0	0	0	0	0	0	0
P. ovisporum G. Lister	0	0	0	0	1	0	0	0	0	0	0	0	0
P. penetrale Rex	1	0	0	1	0	1	0	1	0	0	0	0	0
P. psittacinum Ditmar	1	0	0	0	0	0	0	0	0	0	0	1	0
P. pulcherrimum Berk. & Ravenel	1	0	0	0	0	0	0	0	0	0	0	0	0
P. pusillum (Berk. & M.A. Curtis) G. Lister	0	1	1	1	1	0	1	1	1	1	0	0	1
P. roseum Berk. & Broome	0	0	0	0	0	1	0	0	0	0	0	0	0
P. rubiginosum Fr.	0	0	0	1	1	0	0	0	0	0	0	0	0
P. serpula Morgan	0	0	1	0	0	0	0	1	0	1	0	0	0
P. schroeteri Rostaf.	1	0	0	0	0	0	0	0	0	0	0	0	0
P. spectabile Nann.-Bremek., Lado & G. Moreno	0	0	1	1	1	0	0	0	1	1	1	0	0
P. stellatum (Massee) G.W. Martin	1	0	0	0	0	1	1	1	0	0	0	0	0
P. straminipes Lister	0	0	1	0	0	0	0	0	0	0	0	0	0
P. sulphureum Alb. & Schwein.	1	0	0	0	0	0	0	0	0	0	0	0	0
P. superbum Hagelst.	1	0	0	0	0	0	0	1	0	0	0	0	0
P. synsporum S.L. Stephenson & Nann.-Bremek.	0	0	0	0	0	0	0	0	0	1	0	0	0
P. tenerum Rex	1	0	0	0	0	0	1	1	0	0	0	0	0
P. tropicale T. Macbr.	0	0	0	1	0	0	0	0	0	0	0	0	0
P. vernum Sommerf.	0	0	0	0	0	0	1	0	0	0	0	1	0
P. virescens Ditmar	0	0	0	1	0	0	0	0	0	0	0	0	0
P. viride (Bull.) Pers.	1	0	1	1	1	1	1	1	0	0	1	1	1
P. viride var. *aurantium* (Bull.) Lister	0	0	0	0	0	0	1	0	0	0	0	0	0
Protophysarum phloiogenum M. Blacw. & Alexop.	0	1	0	0	0	0	0	0	0	0	0	0	0
Prototrichia metallica (Berk.) Massee	1	0	0	1	0	0	0	0	0	0	0	0	0
Reticularia lycoperdon Bull.	1	0	0	1	0	1	0	0	0	0	0	0	0

Table 2 (continued)

Species	Areas*												
	1	2	3	4	5	6	7	8	9	10	11	12	13
R. intermedia Nann.-Bremek.	0	0	0	1	0	0	0	0	0	0	0	0	1
R. jurana Meyl.	0	0	0	1	0	0	1	0	0	0	0	1	0
R. olivacea (Ehremb.) Fr.	0	0	0	1	0	0	0	0	0	0	0	0	0
Stemonaria irregularis (Rex) Nann.-Bremek, R. Sharma & Y. Yamam.	0	0	0	0	0	0	0	0	0	1	0	0	0
S. longa (Peck) Nann.-Bremek., R. Sharma & Y. Yamam.	0	0	0	0	0	1	1	0	0	0	0	0	0
Stemonitis axifera (Bull.) T. Macbr.	1	0	0	1	1	1	1	1	0	0	1	1	1
S. flavogenita E. Jahn	1	0	0	0	0	1	1	0	0	0	0	1	0
S. herbatica Peck	0	0	1	1	0	0	0	0	0	0	0	0	0
S. inconspicua Nann.-Bremek.	0	0	0	0	0	1	0	0	0	0	0	0	0
S. lignicola Nann.-Bremek.	0	0	0	0	0	0	1	0	0	0	1	1	1
S. fusca Roth	1	0	1	1	1	1	1	1	0	0	1	1	1
S. mussoriensis G.W. Martin, K.S. Thind & Sohi	0	0	1	0	1	1	0	0	0	1	0	0	0
S. pallida Wingate	1	0	0	1	0	0	0	1	0	0	0	0	0
S. splendens Rostaf.	1	1	1	1	0	1	0	1	0	0	0	1	0
S. virginiensis Rex	1	0	0	0	0	0	0	0	0	0	0	0	0
Stemonitopsis aequalis (Peck) Y. Yamam.	1	0	0	0	0	0	0	0	0	0	0	0	0
S. gracilis (G. Lister) Nann.-Bremek.	0	0	0	0	0	0	0	0	0	1	0	0	0
S. hyperopta (Meyl.) Nann.-Bremek.	1	0	0	1	0	0	1	0	0	0	0	0	0
S. hyperopta var. *landewaldii* Bossel	0	0	0	1	0	0	0	0	0	0	0	0	0
S. microspora (Lister) Nann.-Bremek.	0	0	0	1	0	0	0	0	0	0	0	0	0
S. subcaespitosa (Peck) Nann.-Bremek.	0	0	0	1	0	0	1	0	0	0	0	0	0
S. typhina (F.H. Wigg.) Nann.-Bremek.	1	0	0	0	0	1	1	1	0	0	0	1	0
Symphitocarpus confluens (Cooke & Ellis) Ing & Nann.-Bremek.	0	0	0	1	0	0	0	0	0	0	0	0	0
S. herbaticus Ing	1	0	0	0	0	0	0	0	0	0	0	0	0
Trabrooksia applanata H.W. Keller	1	1	0	0	0	0	0	0	0	0	0	0	0
Trichia affinis de Bary	0	0	0	1	0	0	1	1	1	1	0	1	1
T. agaves (G. Moreno, Lizárraga & Illana) Mosquera, Lado, Estrada & Beltrán-Tej.	0	0	0	0	1	0	0	0	0	1	0	0	0
T. alpina (R.E. Fr.) Meyl.	0	0	0	0	0	0	0	0	0	0	0	0	1
T. botrytis (J.F. Gmel.) Pers.	1	0	0	1	0	0	0	0	0	0	0	1	0
T. contorta (Ditmar) Rostaf.	1	1	0	0	1	0	0	0	1	1	1	1	1
T. decipiens (Pers.) T. Macbr.	1	0	0	1	0	0	0	1	0	0	0	1	1
T. erecta Rex	1	0	0	1	0	0	0	0	0	0	0	0	0
T. favoginea (Batsch) Pers.	1	0	1	1	0	0	1	0	0	0	0	1	0
T. flavicoma (Lister) Ing	0	0	0	0	0	0	0	0	0	0	0	1	0
T. lutescens (Lister) Lister	0	0	0	1	0	0	0	0	0	0	0	1	1
T. persimilis P. Karst.	1	0	0	1	0	0	0	0	0	0	1	1	1
T. scabra Rostaf.	1	1	0	1	0	0	0	0	1	1	1	0	1
T. subfusca Rex	1	1	0	0	0	0	0	0	0	0	0	0	0
T. varia (Pers. ex J.F. Gmel.) Pers.	1	1	0	1	1	0	0	1	0	0	0	1	1
T. verrucosa Berk.	0	0	0	0	0	0	0	0	0	0	0	1	1
Tubifera casparyi (Rostaf.) T. Macbr.	0	0	0	1	0	0	0	0	0	0	0	0	0
T. dimorphotheca Nann.-Bremek.	1	0	0	0	0	0	0	0	0	0	0	0	0
T. ferruginosa (Batsch) J.F. Gmel.	1	0	0	1	0	0	0	0	0	0	0	1	0
T. microsperma (Berk. & M.A. Curtis) G.W. Martin	0	0	0	1	0	1	0	1	0	0	0	0	0
Willkommlangea reticulata (Alb. & Schwein.) Kuntze	1	1	1	0	1	0	1	0	0	1	0	1	1

*Area numbers refer to those in Table 1
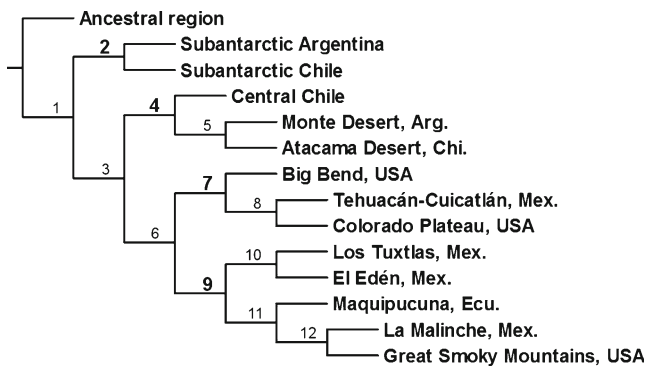
Fig. 2 The most parsimonious cladogram considering only species in the PAE analysis

indicate a group of endemic species that have evolved under the influence of specific factors in the plants on which they were found, which in turn have been influenced by the Andean uplift and its role as a geographical barrier, as suggested by Antonelli et al. (2009).

The myxomycetes from all the provinces of North America form clade 6 (Fig. 2). Also included in this clade is the assemblage of myxomycetes from Maquipucuna (Ecuador), in Cauca province, a Neotropical region (Table 1). This apparent anomaly, can be explained by the hybrid origin for the biota of South America (Crisci et al. 1991). They maintain that some organisms from tropical South America are more closely related to the biota present in North America than to that of the Andean region of South America. The relationships of this clade are sustained by species such as *Comatricha pulchella*, *Didymium iridis* and *Physarum melleum*. This clade (6) of the analysis is subdivided into two subclades, one with the arid areas (clade 7) and the other with the humid areas (clade 9) (Fig. 2). The arid area clade groups together the myxomycete biota from the provinces of Great Basin (Colorado Plateau), Mexican Plateau (Big Bend) and another plateau, the arid portion of the Transmexican Volcanic Belt, where the Tehuacán-Cuicatlán valley is located. The first is considered a cold desert and the
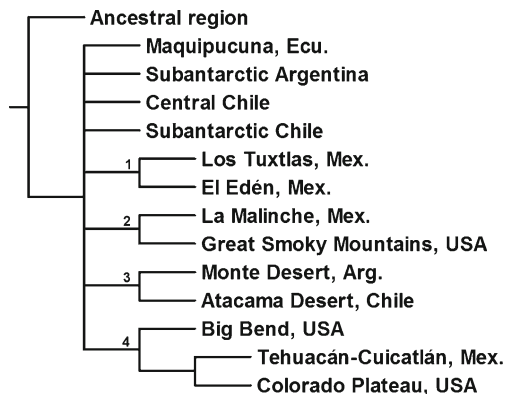
other two hot deserts on account of the main precipitation being as rain, not fog or snow as in the cold deserts. It is interesting to note, that the three areas grouped in clade 7 in this analysis were classified as part of the Madrean Region of the Holarctic realm, proposed by Takhtajan (1969). In the same way as the South American arid regions, the North American deserts in the analysis are grouped by the presence of dryland species of myxomycetes of broad distribution such as *Badhamia melanospora*, *Didymium dubium*, *Echinostelium colliculosum*, *Hemitrichia minor*, *Licea belmontiana*, *L. kleistobolus*, *Perichaena quadrata*, *Physarum notabile* and *P. spectabile*, many of which are associated with cacti and other succulents (Estrada-Torres et al. 2009; Lado et al. 2011). However, rather than being on account of the apparent ecological and floristic similarities between the North and South American arid areas (Abraham et al. 2009), the presence of these species of myxomycetes may indicate ancient lineages that were distributed over both hemispheres before the separation of the continents. The deserts of each hemisphere also exhibit differences with species that only appear in one or the other. For instance the North American deserts include many recently described species from Mexico such as *Cribraria fragilis* and *Diderma acanthosporum* (Estrada-Torres et al. 2001), *C. zonatispora* (Lado et al. 1999), *Didymium eremophilum* (Blackwell and Gilbertson 1980), *D. mexicanum* (Lizárraga et al. 1996), *D. subreticulosporum* (Lizárraga et al. 1998), *D. tehuacanense* and *Perichaena stipitata* (Estrada-Torres et al. 2009), and *D. umbilicatum* (Wrigley de Basanta et al. 2008). These species have not appeared anywhere else, despite intensive sampling in similar environments, and could constitute part of an endemic myxomycete biota of some North American deserts.

It is worth noting here that the two areas of the Transmexican Volcanic Belt (TVB) province are nested in two separate groups in clade 6 (Fig. 2). The Tehuacán-Cuicatlán area is with the dry zones (clade 7), and La Malinche area is in clade 9 of the humid zones of the northern hemisphere. Even though Tehuacán-Cuicatlán Valley has been included in the TVB (Morrone 2006), earlier studies (Villaseñor et al. 1990; Rzedowski 2006), considered it to be an independent phytogeographic province within what Rzedowski (2006) called the Mexican Xerophytic region on account of its botanical peculiarities and the high number of endemisms. In fact Villaseñor et al. (1990) determined that this area shows greater floristic affinities with the biota of other arid Mexican areas and is where typical plant species of North American arid areas such as *Aphanostephus*, *Chrysactinia* and *Zaluzania* have the limits of their North–south distribution. The myxomycete composition of the Tehuacán-Cuicatlán Valley appears to support the biogeographic relationship of the area with other North American arid zones.

Fig. 3 Strict consensus cladogram considering species and genera in the PAE

The humid area (clade 9) of the analysis includes the results from the three Neotropical provinces, Cauca, Gulf of Mexico and the Yucatán Peninsula (Table 1), with that from the Nearctic province (GSMNP) and that from the TVB province (La Malinche). Clade 9 is supported by species such as *Hemitrichia serpula*, *Licea operculata*, *Lycogala exiguum*, *Physarum penetrale* and *P. stellatum*. The apparent relationship between the myxomycete biota of the Tuxtlas area (Gulf of Mexico province) with that of El Edén (Yucatan Peninsula province) (clade 10) is supported by the presence of species frequently found in the tropics such as *Macbrideola scintillans* var. *verrucosa*, *Diderma rimosum*, *Metatrichia horrida*, *Physarum alvoradianum* and *Stemonaria longa*, some of which have a predominantly Neotropical known distribution (Lado and Wrigley de Basanta 2008). Other species of pantropical distribution that are common in Neotropical forests include, *C. sphaerosperma*, *Cribraria tenella*, *Diachea bulbillosa*, *Lycogala conicum*, *Physarella oblonga*, *Physarum aeneum*, *P. crateriforme*, *P. nicaraguense*, *P. nucleatum*, *P. roseum*, *Tubifera bombarda* and *T. microsperma*, among others (Lado and Wrigley de Basanta 2008). A possible explanation is that these could represent part of the myxomycete biota present in Gondwana, on account of this relationship between the northern tropical component of South America and other areas of the tropics (Morrone 2006; McCarthy et al. 2007).

The relationship obtained in the cladogram between the myxomycete biota from the Cauca province (Neotropical region) and the temperate areas (clade 11) is supported by the presence of species such as *Arcyria globosa*, *Collaria arcyrionema*, *Cribraria confusa*, *Diderma corrugatum*, *Physarum superbum*, *Stemonitis pallida* and *Perichaena dyctionema*, but also species more characteristic of temperate areas like *Metatrichia floriformis* and *Trichia decipiens*. One fundamental difference between the Neotropical areas of the study is that Los Tuxtlas and El Edén are lowlands (Lado et al. 2003), but the Maquipucuna area includes ecosytems from between 1,300 and 2,700 m elevation (Schnittler et al. 2002). Their separation in the cladogram is consistent with what Rojas and Stephenson (2007) and Rojas et al. (2012) have shown, that the myxomycete biota of the high-elevation forests in the Neotropics are taxonomically and ecologically closer to the assemblages associated with temperate forests than to those of tropical forests. Other authors have reached similar conclusions in different mountainous areas of the Neotropics where species normally found in temperate regions appear in higher elevation cold tropical areas (Farr, 1976). This pattern has been noted by Schnittler et al. (2002) for species such as *Fuligo septica* and *Trichia varia* in the Maquipucuna Reserve. It should be pointed out that boreal plant species of the Celastraceae (*Celastrum*), Fagaceae (*Quercus*) and Ulmaceae (*Ulmus*) families, have a similar pattern of distribution and are part of the flora of the high

mountains of the Neotropics reaching northern areas of South America like the Columbian Andes (Gentry 1995). The relationship between the biota of the Malinche mountain in Mexico and that of GSMNP of the Nearctic region has been supported by the presence of several tree genera such as *Abies*, *Alnus*, *Arbutus*, *Quercus* and *Pinus* (Sharp 1946; Miranda and Sharp 1950; Puig 1968, 1989; Rzedowski 2006) and the same relationship has even been documented for macrofungi (Guzmán 1973). In the case of the myxomycetes, there are a number of species present in both the La Malinche and the GSMNP such as *Barbeyella minutissima*, *Diacheopsis inssesa*, *Diderma testaceum*, *Didymium crustaceum*, *Lamproderma columbinum*, *Lepidoderma tigrinum*, *Licea pusilla*, *Prototrichia metallica*, *Trichia erecta*, or various species of the genus *Cribraria* like *C. atrofusca*, *C. piriformis* and *C. vulgaris*, and the genus *Elaeomyxa*, many of which could have Laurasian origins like the plants with which they are associated (Gentry 1995; Eckert and Hall 2006).

When studying the biogeographic relationships between high mountain areas of the Neotropics, Rojas et al. (2012) found the highest similarity between the myxomycete biota of Eastern North America with that of the mountains of TVB of Mexico, and the data here, comparing the mountains of GSMNP (USA) and Malinche (Mexico), confirm this affinity. Schnittler (2001) pointed out that the GSMNP is a "hotspot" of biodiversity for myxomycetes. The same conclusion was reached by Rojas et al. (2012) with reference to the forests of Mexico in terms of abundance and diversity.

The patterns suggested by the cladogram imply that historical geographic factors have affected the distribution of these microorganisms, and that very few species of myxomycetes can be considered to be of cosmopolitan distribution, since *A. cinerea* was the only species present in practically all of the areas studied, and even this morphospecies apparently includes numerous biological species, and presents serious challenges for accurate identification even for expert taxonomists. Each area included in this analysis had a particular composition of species, including species restricted to certain places, more in keeping with the "moderate endemicity model" proposed by Foisner (2006). Some of these species could represent an endemic component of the myxomycete biota of these areas (Table 3). This idea is supported also by the fact that around 50 % of all described species of myxomycetes are known only from the type locality or fewer than five localities worldwide (Stephenson 2011).

In each case, in the areas of this study, a percentage of the species reported was only found in one of the areas surveyed. A summary of the numbers of these myxomycetes of restricted distribution is given in Table 3.

The arid areas of the Monte Desert (18.1 %) and Tehuacán-Cuicatlán (17.1 %), and the temperate forest of GSMNP (20.7 %), are the ones with the greatest number of species that are exclusive to each area. On the other hand, in some

Table 3 Summary of restricted distribution of myxomycetes in the areas studied

Area	Nº Species reported	Nº Species restricted to the area	% Species restricted to the area
Great Smoky Mountains National Park	174	36	20.7
Colorado Plateau	92	13	14.1
Big Bend National Park	65	4	6.2
La Malinche National Park	142	20	14.1
Tehuacán-Cuicatlán Biosphere Reserve	105	18	17.1
Los Tuxtlas Biological Station	60	6	10.0
El Edén Ecological Reserve	75	6	8.0
Maquipucuna Biological Station	79	7	8.9
Atacama Desert	49	6	12.2
Monte Desert	72	13	18.1
Central Chile	70	8	11.4
Subantarctic Chile	42	4	9.5
Subantarctic Argentina	67	8	11.9

areas, such as Big Bend, only 6.2 % of the species are restricted to that area, or El Edén, where 8 % of the species are found only there. It is interesting to note also that in those studies that give the information, the percentage of completeness of the inventory, according to the ACE, CHAO2 or other indices, oscillates between 60 % and 92 %, meaning that between 40 % and 8 % of the species from the inventoried area were not registered in the surveys, using the strategies of sampling in each case. These data on the undetected species could signify a fraction of rare species and suppose a potential undiscovered endemic component of each ecosystem, a possibility pointed out by Foisner (2008) with reference to undersampling. In addition, the appearance of the *Diderma* species only present in the *Nothofagus* forests of subantarctic Argentina seems to indicate that they are really endemic species from this geographic area. A further example is the different species from the deserts of North and South America, and individuals only found on one side of the Andes, mentioned above.

Among the distribution patterns of American plants that have frequently attracted the attention of biogeographers are the amphitropical disjunctions, the species that typically occur North and South of the tropics but not in the intermediate tropical areas (Wen and Icker-Bond 2009). Three patterns of disjunction are recognized, according to these authors, the bipolar disjunctions, those of temperate areas and those of arid areas. Patterns of disjunction in myxomycetes have been recognized by Stephenson et al. (2008), for species like *Leocarpus fragilis*, found in temperate areas of both hemispheres but not in the tropics. In the present analysis there are various species that exhibit these patterns in both temperate areas (*Cribraria aurantiaca*, *C. mirabilis*, *C. oregana*, *Hemitrichia leiocarpa*, *Oligonema flavidum*, *Physarum psitacinum*, *Reticularia intermedia*, *Trichia decipiens*, *T. persimilis* and *T. lutescens*) and in arid areas

(*Badhamia melanospora*, *Didymium dubium*, *D. wildpretii*, *Echinostelium colliculosum*, *Hemitrichia minor*, *Licea belmontiana*, *Perichaena quadrata*, *Physarum notabile* and *P. spectabile*). Stephenson et al. (2008) attributed these patterns to long distance dispersal and in the case of plants, molecular evidence indicates that this is a probable mechanism of dispersal, but apparently mediated by birds (Wen and Icker-Bond 2009). However the areas of distribution of myxomycetes are generally broader than those of their plant counterparts and more similar to some species of widely dispersed fungi. The latter have spores of a comparable size to the myxomycetes, and are dispersed principally by wind.

Phylogeographic evidence has suggested that oceans are effective geographical barriers preventing intercontinental long distance dispersal of fungi, and that this is an infrequent phenomenon in fungal populations (James et al. 1999; Zervakis et al. 2004). An alternative explanation to long distance dispersal of myxomycete species that are widely distributed in both hemispheres is that they could be survivors of ancient lineages, possibly dating from the fragmentation of Pangea. It is proposed that the Amoebozoa, and thus the Myxomycetes, are of ancient origin, calculated as between 800 and 1,200 Ma in the middle of the Mesoproterozoic and the start of the Neoproterozoic (Wegener-Parfrey et al. 2011). There is a high probability that many myxomycetes diverged and dispersed widely from very remote times, adapting to specific climatic zones or ecological conditions, like the species from temperate zones in both hemispheres mentioned above. This would mean that the present distribution of certain morphospecies could be the distribution that those lineages had from Pangean times, some 200 Ma (Hoffman 1992), with local extinctions in certain regions or environments. This would explain some enigma in their current distribution (Wrigley de Basanta et al. 2012b). The idea of ancient origins in many morphospecies of myxomycetes appears to be supported by

the considerable genetic diversity in some widely distributed morphospecies like *D. squamulosum* (Winsett and Stephenson 2008), the presence of morphospecies made up of biological species complexes and reproductively isolated apomictic lines with restricted distribution (Clark and Haskins 2010), and by molecular evidence of the presence of cryptic species in morphospecies, such as *Fuligo septica*, *Ceratiomyxa fruticulosa* and *Lamproderma columbinum* (Fiore-Donno et al. 2005, 2009, 2011), even in relatively small geographic areas.

In summary, it seems that the myxomycete biogeographic patterns defined in this analysis, are consistent with current biogeographic regions (Morrone 2006), and that these patterns could be determined largely by the antiquity of certain lineages of myxomycetes. The definition of the subclades from the Nearctic/Neotropical grouping also appears to have an environmental component as it separates the arid areas from the humid areas. The results are also consistent with those that have been previously defined for other organisms such as groups of plants and animals. Overall the results of this analysis thus seem to show that a historical geographic pattern has influenced the distribution of myxomycetes in the American areas studied, as much as environmental factors. This could be taken as a working hypothesis that can perhaps be reconciled with independent evidence from emerging systematic and phylogenetic methods. The results are inconsistent with the hypothesis of cosmopolitan distribution for these microorganisms, as they appear to indicate groups of species that are restricted to certain geographic areas, and may be endemic, such as those from the subantarctic forests of South America, those found exclusively in the South American arid areas or those that have been recently described from North American areas.

References

Abraham E, del Valle HF, Roig F, Torres L, Ares JO, Coronato F, Godagnone R (2009) Overview of the geography of the Monte Desert biome (Argentina). J Arid Environ 73:144–153

Adamonyte G, Eliasson UH (2010) Morphological variation and taxonomic characters in *Cribraria* (Myxomycetes) from the Great Smoky Mountains National Park in eastern USA. Nov Hedwig 90:303–320

Antonelli A, Nylander JAA, Persson C, Sanmartín I (2009) Tracing the impact of the Andean uplift on Neotropical plant evolution. Proc Natl Acad Sci 106:9749–9754

Blackwell M, Gilbertson RL (1980) *Didymium eremophilum*: A new Myxomycete from the Sonoran Desert. Mycologia 72:791–797

Brooks DR, van Veller MGP (2003) Critique of parsimony analysis of endemicity as a method of historical biogeography. J Biogeogr 30:819–825

Clark J, Haskins EF (2010) Reproductive systems in myxomycetes: A review. Mycosphere 1:337–353

Contreras-Medina R, Luna-Vega I, Morrone JJ (2007) Application of parsimony analysis of endemicity to Mexican gymnosperm distributions: Grid cells, biogeographical provinces and track analysis. Biol J Linn Soc 92:405–417

Cotterill FPD, Al-Rasheid K, Foissner W (2008) Conservation of protists: Is it needed at all? Biodivers Conserv 17:427–443

Cracraft J (1991) Patterns of diversification within continental biotas: Hierarchical congruence among the areas of endemism of Australian vertebrates. Aust Syst Bot 4:211–227

Crisci JV, Cigliano MM, Morrone JJ, Roig-Juñent S (1991) Historical biogeography of southern South America. Syst Zool 40:152–171

Echeverry A, Morrone JJ (2010) Parsimony analysis of endemicity as a panbiogeographical tool: An analysis of Caribbean plant taxa. Biol J Linn Soc 101:961–976

Eckert AJ, Hall BJ (2006) Phylogeny, historical biogeography, and patterns of diversification for *Pinus* (Pinaceae): Phylogenetic tests of fossil-based hypothesis. Mol Phylogenet Evol 40:166–182

Escalante-Espinoza T, Morrone JJ (2003) ¿Para qué sirve el análisis de parsimonia de endemismos? In: Morrone JJ, Llorente J (eds) Una perspectiva latinoamericana de la biogeografía, Las Prensas de Ciencias. Facultad de Ciencias, UNAM, México DF, pp 167–172

Estrada-Torres A, Lado C, Rodríguez-Palma MM (2001) Two new species of Myxomycetes from a tropical deciduous forest of Mexico. Mycologia 93:744–750

Estrada-Torres A, Wrigley de Basanta D, Conde E, Lado C (2009) Myxomycetes associated with dryland ecosystems of the Tehuacán-Cuicatlán Valley Biosphere Reserve, Mexico. Fungal Divers 36:17–56

Farr ML (1976) Flora Neotropica Monograph 16 (Myxomycetes). New York Botanical Garden, New York

Fiore-Donno AM, Berney C, Pawlowski J, Baldauf S (2005) Higher-order phylogeny of plasmodial slime molds (Myxogastria) based on elongation factor 1-A and small subunit rRNA gene sequences. J Eucaryot Microbiol 52:201–210

Fiore-Donno AM, Nikolaev S, Nelson M, Pawlowski J, Cavalier-Smith T, Baldauf S (2009) Deep phylogeny and evolution of slime molds (Mycetozoa). Protist 161:55–70

Fiore-Donno AM, Novozhilov YK, Meyer M, Schnittler M (2011) Genetic structure of two protist species (Myxogastria, Amoebozoa) suggests asexual reproduction in sexual amoebae. PLoS One 6:e22872

Foisner W (2006) Biogeography and dispersal of micro-organisms: A review emphasizing protists. Acta Protozool 45:111–136

Foisner W (2008) Protist diversity and distribution: Some basic considerations. Biodivers Conserv 17:235–242

Fontaneto D, Brodie J (2011) Why biogeography of microorganisms? In: Fontaneto D (ed) Biogeography of microscopic organisms, The Systematics Association Special Volume 79. Cambridge University Press, Cambridge, pp 3–10

Gentry AH (1995) Patterns of diversity and floristic composition in Neotropical montane forests. In: Churchill SP, Balslev H, Forero E, Luteyn JL (eds) Biodiversity and conservation of Neotropical montane forests, Proceedings of the Neotropical Montane Forests Biodiversity and Conservation Symposium. The New York Botanical Garden, New York, pp 103–126

Goloboff P (1993) NONA, v. 2.0. Published by the author, Tucumán

Guzmán G (1973) Some distributional relationships between Mexico and United States mycofloras. Mycologia 45:1319–1330

Hoffman PF (1992) Supercontinents. In: Nierenberg WA (ed) Encyclopedia of earth system science Vol. 4. Academic, San Diego, pp 323–328

Humphries CJ (1989) Any advance on assumption 2? J Biogeogr 16:101–102

Ing B (1994) The phytosociology of myxomycetes. New Phytol 126:175–201

James TY, Porter D, Hamrick JL, Vilgalys R (1999) Evidence for restricted intercontinental gene flow in the cosmopolitan mushroom *Schyzophyllum commune*. Evol 53:1665–1677

Lado C (2005–2012) An on line nomenclatural information system of Eumycetozoa. http://www.nomen.eumycetozoa.com (24-V-2012)

Lado C, Estrada-Torres A, Stephenson SL (2007) Myxomycetes collected in the first phase of a north–south transect of Chile. Fungal Divers 25:81–101

Lado C, Estrada-Torres A, Stephenson SL, Wrigley de Basanta D, Schnittler M (2003) Biodiversity assesment of myxomycetes from two tropical forest reserves in Mexico. Fungal Divers 12:67–110

Lado C, Mosquera J, Beltrán-Tejera E (1999) *Cribraria zonatispora*, development of a new myxomycete with unique spores. Mycologia 91:157–165

Lado C, Wrigley de Basanta D (2008) A review of Neotropical myxomycetes. An Jard Bot Madr 65:211–254

Lado C, Wrigley de Basanta D, Estrada-Torres A (2011) Biodiversity of Myxomytcetes from the Monte Desert of Argentina. An Jard Bot Madr 68:61–95

Lado C, Wrigley de Basanta D, Estrada-Torres A, García Carvajal E, Aguilar M, Hernández JC (2009) Description of a new species of *Perichaena* (Myxomycetes) from arid areas of Argentina. An Jard Bot Madr 66S1:63–70

Lado C, Wrigley de Basanta D, Estrada-Torres A, Stephenson SL (2012) The biodiversity of myxomycetes in central Chile. Fungal Divers. doi:10.1007/s13225-012-0159-8

Lizárraga M, Illana C, Moreno G (1998) *Didymium subreticulosporum* (myxomycetes), a new species for America. Mycotaxon 67:313–316

Lizárraga M, Moreno G, Illana C, Castillo A (1996) Two new species of Myxomycetes from Mexico. In: Lado C, Hernández JC (eds) Abstract Volume, Second International Congress on the Systematics and Ecology of Myxomycetes, Real Jardín Botánico de Madrid, pp 56.

Martin GW, Alexopoulos CJ (1969) The Myxomycetes. Univ Iowa Press, Iowa

Martiny HJB, Bohannan BJM, Brown JH, Colwell RK, Fuhrman JA, Green JL, Horner-Devine MC, Kane M, Krumins JA, Kuske CR et al (2006) Microbial biogeography: Putting microorganisms on the map. Nat Rev Microbiol 4:102–112

McCarthy D, Ebach MC, Morrone JJ, Parenti LR (2007) An alternative Gondwana: Biota links South America, New Zealand and Australia. Biogeogr 2:2–12

Miranda F, Sharp AJ (1950) Characteristics of the vegetation in certain temperate regions of eastern Mexico. Ecol 31:313–333

Morrone JJ (2004) La Zona de Transición Sudamericana: Caracterización y relevancia evolutiva. Acta Entomol Chil 28:41–50

Morrone JJ (2006) Biogeographic areas and transition zones of Latin America and the Caribbean Islands based on panbiogeographic and cladistic analyses of the entomofauna. Annu Rev Entomol 51:467–494

Morrone JJ, Crisci JV (1995) Historical biogeography: Introduction to methods. Annu Rev Ecol Syst 26:373–401

Mitchell DW (1995) The Myxomycota of Australia. Nov Hedw 60:269–295

Myers AA (1991) How did Hawaii accumulate its biota? A test from the Amphipoda. Global Ecol Biogeogr Lett 1:24–29

Ndiritu GG, Spiegel FW, Stephenson SL (2009) Distribution and ecology of the assemblages of myxomycetes associated with major vegetation types in Big Bend National Park, USA. Fungal Ecol 2:168–183

Nelson G, Platnick N (1981) Systematics and biogeography: Cladistics and vicariance. Columbia University Press, New York

Nihei SS (2006) Misconceptions about parsimony analysis of endemicity. J Biogeogr 33:2099–2106

Nixon KC (2002) WinClada, v. 1.00.08. Published by the author, Cornell University, Ithaca, NY

Novozhilov YK, Mitchell DW, Schnittler M (2003) Myxomycete biodiversity of the Colorado Plateau. Mycol Prog 2:243–258

Porzecanski AL, Cracraft J (2005) Cladistic analysis of distributions and endemism (CADE): Using raw el of birds to unravel the biogeography of the South American aridlands. J Biogeogr 32:261–275

Posadas P, Crisci JB, Katinas L (2006) Historical biogeography: A review of its basic concepts and critical issues. J Arid Environ 66:389–403

Puig H (1968) Notas acerca de la flora y vegetación de la Sierra de Tamaulipas (México). An Esc Nac Cienc Biol Méx 17:37–49

Puig H (1989) Análisis fitogeográfico del bosque mesófilo de Gómez Farías. Biotam 1:34–53

Rodríguez-Palma MM, Estrada-Torres A, Hernández-Cuevas LV (2005) Myxomycetes (Protistas). In: Fernández FJ, López-Domínguez J (eds) Biodiversidad del Parque Nacional La Malinche (Tlaxcala, México). Coordinación General de Ecología-Tlaxcala, Gobierno del Estado de Tlaxcala, Tlaxcala, pp 25–45

Rojas C (2010) Biogeography and microhabitat distribution of myxomycetes in high-elevation of the Neotropics. PhD Dissertation, University of Arkansas

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, Estrada-Torres A, Valverde R, Morales O (2010) New records of myxomycetes from high-elevation areas of Mexico and Guatemala. Mycosphere 1:73–82

Rojas C, Stephenson SL, Valverde R, Estrada-Torres A (2012) A biogeographical evaluation of high-elevation myxomycete assemblages in the Neotropics. Fungal Ecol 5:99–113

Rosen BR (1984) Reef coral biogeography and climate through the Late Cenozoic: Just islands in the sun or a critical pattern of islands? In: Brenchley P (ed) Fossils and climate. John Wiley & Sons, London, pp 201–262

Rosen BR (1988) From fossils to earth history: Applied historical biogeography. In: Myers AA, Giller PS (eds) Analytical biogeography. Chapman & Hall, London, pp 437–481

Rzedowski J (2006) Vegetación de México. 1a. Edición Digital, Comisión Nacional para el Estudio y Uso de la Biodiversidad, México DF

Schnittler M (2001) Ecology and Biogeography of Myxomycetes. PhD Dissertation, Rat der Biologisch-Pharmazeutischen Fakultät der Friedrich-Schiller-Universität Jena

Schnittler M, Lado C, Stephenson SL (2002) Rapid assessment of a tropical myxomycete assemblage-Maquipucuna Cloud Forest Reserve, Ecuador. Fungal Divers 9:135–167

Schnittler M, Mitchell DW (2000) Species diversity in Myxomycetes based on the morphological species concept-a critical comparison. Stapfia 73:55–62

Sharp AJ (1946) Informe preliminar sobre algunos estudios fitogeográficos efectuados en México y Guatemala. Rev Soc Mex Hist Nat 7:35–44

Snell K, Keller HW (2003) Vertical distribution and assemblages of corticolous myxomycetes on five tree species in the Great Smoky Mountains National Park. Mycologia 95:565–576

Stephenson SL (2003) The Fungi of New Zealand Volume 3: Myxomycetes of New Zealand. Fungal Diversity Press, Hong Kong

Stephenson SL (2011) From morphological to molecular: Studies of myxomycetes since the publication of the Martin and Alexopoulos monograph. Fungal Divers 50:21–34

Stephenson SL, Kalyanasundaran I, Lakhanpal TN (1993) A comparative biogeographical study of myxomycetes in the mid-Appalachians of eastern North America and two regions of India. J Biogeogr 20:645–657

Stephenson SL, Novozhilov YK, Schnittler M (2000) Distribution and ecology of myxomycetes in high-latitude regions of the northern hemisphere. J Biogeogr 27:741–754

Stephenson SL, Schnittler M, Mitchell DW, Novozhilov YK (2001) Myxomycetes of the great smoky mountains national park. Mycotaxon 78:1–15

Stephenson SL, Schnittler M, Novozhilov YK (2008) Myxomycete diversity and distribution from the fossil record to the present. Biodivers Conserv 17:285–301

Stephenson SL, Stempen H (1994) Myxomycetes. A handbook of slime molds. Timber press, Portland, Oregon

Takhtajan A (1969) Flowering plants, origin and dispersal. Smithsonian Institution Press, Washington DC

Udvardy MDF (1975) A classification of the biogeographic provinces of the world. IUCN Occasional Paper No. 18. International Union for Conservation of Nature and Natural Resources, Morges, Switzerland

Urich T, Lanzén A, Qi J, Huson DH, Schleper C, Schuster SC (2008) Simultaneous assessment of soil microbial community structure and function through analysis of the meta-transcriptome. PLoS One 3(6):e2527. doi:10.1371/journal.pone.0002527

Urtubey E, Stuessy TF, Tremetsberger K, Morrone JJ (2010) The South American biogeographic Transition Zone: An analysis from Asteraceae. Taxon 59:505–509

Villaseñor JL, Dávila P, Chiang F (1990) Fitogeografía del Valle de Tehuacán. Bol Soc Bot Méx 50:135–149

Wegener-Parfrey L, Lahr DJG, Knoll AH, Katz LA (2011) Estimating the timing of early eukaryotic diversification with multigene molecular clocks. Proc Natl Acad Sci 108:13624–13629

Wen J, Icker-Bond SM (2009) Evolution of the Madrean-Tethyan disjunctions and the North and South American amphitropical disjunctions in plants. J Syst Evol 47:331–348

Winsett KE, Stephenson SL (2008) Using ITS sequences to assess intraspecific genetic relationships among geographically separated collections of the myxomycete *Didymium squamulosum*. Rev Mex Micol 27:59–65

Wrigley de Basanta D, Lado C, Estrada-Torres A (2008) Morphology and life cycle of a new species of *Didymium* (Myxomycetes) from arid areas of Mexico. Mycologia 100:921–929

Wrigley de Basanta D, Lado C, Estrada-Torres A, Stephenson SL (2009) Description and life cycle of a new *Dydimium* (Myxomycetes) from arid areas of Argentina and Chile. Mycologia 101:707–716

Wrigley de Basanta D, Lado C, Estrada-Torres A (2010a) *Licea eremophila*, a new myxomycete from arid areas of South America. Mycologia 102:1185–1192

Wrigley de Basanta D, Lado C, Estrada-Torres A, Stephenson SL (2010b) Biodiversity of myxomycetes in subantarctic forest of Patagonia and Tierra del Fuego, Argentina. Nov Hedw 90:45–79

Wrigley de Basanta D, Lado C, Estrada-Torres A (2011) Spore to spore culture of *Didymium operculatum*, a new Myxomycete from the Atacama Desert of Chile. Mycologia 103:895–903

Wrigley de Basanta D, Lado C, Estrada-Torres A (2012a) Description and life cycle of a new Physarum (Myxomycetes) from the Atacama Desert in Chile. Mycologia 104:1206–1212

Wrigley de Basanta D, Lado C, Estrada-Torres A, Stephenson SL (2012b) Biodiversity studies of Myxomycetes in Madagascar. Fungal Divers. doi:10.1007/s13225-012-0183-8

Zervakis GI, Moncalvo JM, Vilgalys R (2004) Molecular phylogeny, biogeography and speciation of the mushroom species *Pleurotus cystidiosus* and allied taxa. Microbiol 150:715–726