Chapter 10

Biogeographical patterns in myxomycetes

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Introduction

Only a very few major lineages of life, namely, the Metazoa (animals), Embryophyta (terrestrial plants), and Eumycota (some Ascomycetes and Basidiomycetes), evolved into truly multicellular, macroscopic organisms. Myxomycetes are a significant exception among protists due to their noncellular fruiting bodies, which are not formed out of a growth process but by reformation of the second vegetative stage, the plasmodium. Their mostly macroscopic fruiting bodies are the precondition to colonize habitat islands, characterized by a locally higher density of other microorganisms serving as prey, by spores (Schnittler and Tesmer, 2008). Understanding dispersal ecology and speciation patterns in the group is the key to understand and describe species distribution and diversity patterns.

Spore dispersal as a key feature for myxomycetes

Among protists, myxomycetes are unique for their multinucleate and macroscopic plasmodia but not in dispersing by spores. Stalked fruiting bodies that release airborne spores evolved independently in several protistean groups (Brown et al., 2009, 2012a,b) and even within the Amoebozoa (Brown et al., 2011; Hillmann et al., 2018). In addition to spore dispersal, these groups live as predators of other microbes and can be seen as an ecological guild [myxomycetes and myxomycete-like organisms; Schnittler et al. (2006, 2012)]. If the myxobacteria (Reichenbach, 1993) are considered, this would even include a group of prokaryotes. The two largest groups of the monophyletic Eumycetozoans (Kang et al., 2017), the dictyostelids (Swanson et al., 2002; Romeralo et al., 2010, 2011; Sheikh et al., 2018)

and the myxomycetes (Schnittler et al., 2012; Stephenson and Schnittler, 2016), form primarily stalked fruiting bodies. In the Ceratiomyxomycetes [the macroscopic *Ceratiomyxa* (Fiore-Donno et al., 2010) and the microscopic genera *Clastostelium* and *Protosporangium* (Leontyev et al., 2019)], only one to few spores are elevated on a stalk. Quite heterogeneous and paraphyletic protistean groups dispersing via spores are the protosteloid (Spiegel et al., 2004; Shadwick et al., 2009), and acrasiid amoebae (Brown et al., 2012b). Surprisingly, even the ciliate genus *Sorogena* (Bardele et al., 1991) develops stalked fruiting bodies that release spores. These cases of parallel evolution are evidence that the terrestrial lifestyle required an efficient means of dispersal, since metabolically active cells are easily transported by water but not by air due to the danger of desiccation. The obvious solution are spores, being simultaneously dormant and transport stages. Spores in the guild range from 1 to 3 μm (prokaryotic myxobacteria with a much smaller genome) over (3−)5−8 μm in dictyostelids, (4)7−12(−20) μm in myxomycetes to c. 35 μm in *Sorogena*, where the spores transport a micro- and a macronucleus as it is typical for ciliates. Spore size is the first critical parameter for dispersal, determining largely the terminal (sedimentation) velocity of spores in still air.

A comparison with the much better known ferns, where long-distance dispersal (LDD) is well established (Dassler and Farrar, 2001) in spite of a much higher average spore size (Tryon, 1970), indicates that we must assume also successful LDD for myxomycete spores. As for ferns, most myxomycetes spores are adapted to become airborne (Kamono et al., 2009). For myxomycetes, sedimentation velocities between 1 mm/s (spore size c. 7 μm) and 3 mm/s (12 μm) were reported by Tesmer and Schnittler (2007) and Schnittler et al. (2006). These values correlate well with figures calculated employing Stokes' law (predicting the terminal velocity of small spherical bodies), and if this holds true, spore size should be under strong selective pressure, since a spore of *Trichia varia* (mean diameter 13.0 μm) falls about four times faster than one of *Stemonitis axifera* (mean diameter 6.3 μm). Consequently, smaller spores should achieve higher dispersal abilities (Norros et al., 2014), at least if both downward drifts from gravity and size-sensitive deposition are taken into account.

Another critical parameter for dispersal is the starting point of a spore, determined mostly by the ability of myxomycete plasmodia to react positively phototropic as soon as the point of no return (Glöckner and Marwan, 2017) for the conversion of the plasmodial biomass into fruiting bodies is reached. As such, aerial habitats, such as the tree canopy (Schnittler et al., 2006; Snell et al., 2003) are especially effective for myxomycete dispersal. Since both trophic stages of myxomycetes (amoeboflagellates and plasmodia) require liquid water for active growth and movement, fruiting bodies often develop on substrates covered by a film of water. Taking this into consideration, the lengths of 0.5−3 mm typically achieved by the stalks of myxomycete fruiting bodies make a difference, since they elevate the spore

case above the water film, allowing the spores to dry out and become airborne. Coinciding with these considerations, stalked fruiting bodies are an ancestral character for myxomycetes (Fiore-Donno et al., 2010). Stalk length, taking away resources from the developing plasmodium, seems to be under selective pressure; widely distributed species of myxomycetes seem to develop longer stalks in tropical regions (Stephenson et al., 2004, 2008). In periodically dry environments, such as the bark surface of living trees, in addition to stalked species with a short development time, a second strategy can be seen—species developing more slowly with more robust, sessile fruiting bodies, which open in dry periods (Schnittler, 2001).

Another dispersal strategy includes animal vectors, often invertebrates. Among the Coleoptera the genera *Anisotoma* and *Agathidium* are specialized in feeding on myxomycete fruiting bodies (Blackwell et al., 1982; Wheeler, 1984). Other recorded observations of animals dispersing myxomycete spores include the Diptera (Buxton, 1954), Collembola (Chassain, 1973), acarids (Keller and Smith, 1978), tardigrades (Kylin, 1991), various earthworms (Murray et al., 1985), slugs (Keller and Snell, 2002), and nematodes (Kilgore and Keller, 2008). In addition, birds (Sutherland, 1979) as well as lizards (Townsend et al., 2005) have been observed to disperse myxomycetes. Even water may play a role in spore dispersal (Vlasenko et al., 2016): myxomycetes may fruit and produce viable spores in submerged conditions (Lindley et al., 2007).

The third parameter important for dispersal is spore ornamentation, enhancing the hydrophobicity of spores. Whereas most species of myxomycete develop colonies of stalked but separated fruiting bodies, about 10% of all species develop compound fruiting bodies, which can reach a considerable size (in *Brefeldia maxima* up to 1 m). Some of these fruiting bodies mimic puffballs [raindrop ballists (Dixon, 1963)], and like some gasteromycetes, the spores of these genera (e.g., *Lycogala*, *Reticularia*, and *Tubifera*) possess a reticulum of elevated ridges, making them extremely hydrophobic (Hoppe and Schwippert, 2014). Species with compound fruiting bodies (e.g., *Fuligo* and *Symphytocarpus*) that rely more on animal vectors seem to have less hydrophobic spores, ornamented by warts or spines. A high hydrophobicity enables spores to become airborne again, even from wet surfaces, although no quantitative data are yet available for this secondary dispersal. Only a very few species of myxomycetes possess completely smooth spores. Noteworthy are some coprophilous species that fruit on herbivore dung. Their thick-walled spores seem to be adapted to passage through the digestive tract of herbivorous animals (Eliasson and Lundqvist, 1979).

Myxomycete plasmodia usually segregate into smaller units when fruiting, with each unit converting its plasma mass into a sporocarp. Secondarily, this process can be revoked, and in the resulting compound fruiting bodies, individual sporocarps may still be discernible (pseudoaethalia) or not (aethalia). Smaller compound fruiting bodies may be fascicle-stalked

(e.g., *Arcyria cinerea* var. *digitata* and *Alwisia bombarda*), whereas large compound fruiting bodies (exceeding 2-cm diam.) are always sessile (*Fuligo* spp. and *Tubifera* spp.). The transition from segregating (solitary sporocarps) to compound fruiting bodies occurred in several lineages independently (Leontyev et al., 2015, 2019).

Height of release, spore size, and ornamentation seem to be the three decisive parameters for LDD of spores. Myxomycete spores have been detected in the air (Kamono et al., 2009), but no quantitative dispersal models have yet been developed for myxomycetes. From experiments with fungal spores (Penet et al., 2014) and pollen (Robledo-Arnuncio and Gil, 2005; Ottewell et al., 2012) of comparable sizes, we can assume successful LDD but with leptokurtic dispersal curves (having a long "tail"), which enable myxomycetes to reach distant habitat islands with a sufficiently high density of microbes. This was indirectly confirmed by surveys on remote islands, which revealed relatively diverse myxomycete assemblages [Macquarie Island, south of Tasmania (Stephenson et al., 2007); La Reunion (Adamonyte et al., 2011); Papua New Guinea (Kylin et al., 2013); Bohol Island (Macabago et al., 2017)] and the occurrence of myxomycetes in the aerial woody debris and "canopy soil" (Schnittler et al., 2006; Stephenson and Landolt, 2015). As shown by model calculations, the successful colonization of such habitat islands depends upon the reproductive system of a species (Schnittler and Tesmer, 2008). Homothallic, presumably asexual strains (Clark and Haskins, 2013) need only a single spore to colonize a new habitat, whereas heterothallic (sexual) strains require two compatible spores. However, if meiosis takes place after spore cleavage in young spores, with mating-type genes segregating into four nuclei, as discussed in Clark and Haskins (2013), this disadvantage would be revoked, since a spore should then be able to transport more than one nucleus. Gene flow between local populations seems to be high but not independent from distance. The similarity between ribotypes of *Meriderma* spp. decreases with distance (Feng et al., 2016). Effective dispersal, enabling spores to access habitat islands with high microbial density (i.e., decaying logs or accumulations of litter), is certainly a precondition the predatory lifestyle of both amoebae and plasmodia.

Myxomycete biogeography—what can we see?

Due to their comparatively conspicuous fruiting bodies, myxomycetes were "discovered" much earlier than most other protistan groups, attracting the attention of naturalists, including Linné (1753) who described some species as miniature puffballs—in an ecological sense, he was not terribly wrong. The first major monograph of the group (Rostafiński, 1875) recognized a considerable proportion of the c. 1000 morphospecies known today (Lado, 2005−2020). Therefore we can look back on a history of nearly 200 years of

records of fruiting bodies, which has resulted in a significant body of data on myxomycete distribution.

However, it should be noted that this entire body of data is based thus far on records of the fruiting bodies, not amoeboflagellates or plasmodia as the active life forms (see chapter Oleg Shchepin et al. in this volume). In this respect, we are like a gardener who wants to know the distribution of apple trees in an orchard, but he can see only the apples, not the trees. Small and nonfruiting trees under suboptimum conditions remain invisible for him. Therefore we see nothing more than the "tip of the iceberg"—myxomycete populations growing under optimum conditions that successfully produce fruiting bodies. This might be especially true for soil myxomycetes [see Stephenson et al. (2011) for a review]. Amoeboflagellates of myxomycetes were found to be the most abundant group of protists in a study based on ePCR with mRNA sequences (Urich et al., 2008), but fruiting bodies of myxomycetes on bare soil are rarely reported; accumulations of litter with a higher number of nutrients and thus microbes seem to be required for the formation of fruiting bodies. In addition, it cannot be ruled out that nonfruiting strains of myxomycetes do exist in nature, since a loss of functionality in a single gene in the complex ontogenesis of fruiting bodies may halt spore formation and thus severely interrupt dispersal abilities, similar to the loss of a stalk in the sessile *Semimorula liquescens*, where molecular data suggest a close relationship to *Echinostelium*, a genus forming long-stalked fruiting bodies (Fiore-Donno et al., 2009). There is no reason to assume that nonfruiting strains cannot persist indefinitely as populations of amoeboflagellates in soil, even if they lost the ability for LDD via spores. As such, we can expect that a species may often have a larger range than indicated by records of fruiting bodies. This has been shown to be the case for nivicolous myxomycetes, a peculiar group of soil-inhabiting myxomycetes that fruit in spring near melting snowbanks (Schnittler et al., 2015a). Fruitings are abundant only in alpine situations (Ronikier and Ronikier, 2009), which usually means mountains with a long-lasting contiguous snow cover. However, studies based on ePCR from the lowlands of Germany (Fiore-Donno et al., 2016), northwestern Russia (Shchepin et al., 2019b), and China (Gao et al., 2019) detected the sequences of several nivicolous species in areas where their fruiting bodies have never been found. As such, we must assume that a particular species of myxomycete may be more widely distributed than indicated by records of fruiting bodies alone.

However, a second line of thinking points in the opposite direction. The current species concept in myxomycetes is a morphological one, at least with respect to our data on species distribution. Another concept, although already several decades old, never found its way into diversity research, since it relies on amoeboflagellate compatibility. Early experiments, carried out mostly with cultivable members of the Physarales, demonstrated that a morphospecies may include strains that are incompatible with each other, forming separate biospecies (Collins, 1979). In addition, asexual (presumably diploid) strains may exist (Clark and Haskins, 2013). Therefore one

morphospecies may include several cryptic biospecies. Verifying this for a given morphospecies requires laborious cultivation, but only a minor fraction of all myxomycetes (mostly members of the Physarales) have been cultivated successfully from spore to spore. The different reproductive options and its consequences for species concepts are discussed in Feng et al. (2016) and Walker and Stephenson (2016).

Molecular studies may be a tool for independent verification of the morphospecies concept. In contrast to pathogenic protists, where molecular research was spurred by health arguments [e.g., *Enteroamoeba* (García et al., 2014)], myxomycetes are neither pathogenic nor of significant economic importance. Therefore molecular tools for species differentiation are still at an early stage of development, and the species concept in the group is entirely based on the morphology of the fruiting bodies. The first phylogenetic studies (Fiore-Donno et al., 2005, 2008, 2010, 2011, 2012, 2013) did not only challenge the classical taxonomic concept of the group (Leontyev et al., 2019) but also enabled researchers to develop barcoding markers. As in other protists, the 18S rRNA gene (SSU), which is usually a multicopy gene (Torres-Machorro et al., 2010), is the most promising candidate for such a barcode (Adl et al., 2014; Schnittler et al., 2017). The first studies employing barcodes [*Badhamia melanospora* (Aguilar et al., 2014) and nivicolous myxomycetes (Novozhilov et al., 2013a)] always found several ribotypes per morphospecies. This was confirmed by other studies that used additional markers, which enabled these authors to demonstrate cryptic speciation [*T. varia* (Feng and Schnittler, 2015), *Meriderma* spp. (Feng et al., 2016), and *Hemitrichia serpula* (Dagamac et al., 2017b)]. On the other hand, morphospecies are virtually always separated by their barcodes, using a 99.1% similarity threshold (Borg Dahl et al., 2018a). A first survey of wood-inhabiting, bright-spored myxomycetes (Feng and Schnittler, 2017) estimated a relation between morphospecies and ribotypes of 1:2 to 1:10, which points to a considerable amount of cryptic speciation. In other words, the current morphospecies concept is very likely underestimating diversity, despite the steep increase in newly described morphospecies within the last few decades (Schnittler and Mitchell, 2000). In addition, two studies tracing the worldwide distribution of a morphospecies based on the distribution of its ribotypes (Aguilar et al., 2014; Dagamac et al., 2017b) found ribotypes, constituting putative cryptic species, to be more limited in distribution than the morphospecies as a whole. This provides evidence for a contrasting hypothesis that many morphospecies may in fact be complexes of cryptic species showing more limited distribution patterns than the morphospecies as a whole.

Biogeographic hypotheses about myxomycete distribution

The considerations mentioned earlier need to be considered when discussing two controversial hypotheses that are used to explain biogeographic patterns in myxomycetes. Similar to the situation in other protists, the Baas Becking

model of ubiquity (Bass and Boenigk, 2011; Finlay, 2002; Finlay and Clarke, 1999) was opposed by the moderate endemicity model (Foissner, 1999). The first model argued that the ability of protists to have almost unlimited dispersal due to their small cell (spore) sizes causes them to be found everywhere (Finlay et al., 2004); geographical barriers should not limit distribution (Finlay, 2002). In this case, only habitat suitability will limit the occurrence of a protist species in a certain region. The second model claimed that some protists may be cosmopolitan, but others show geographically restricted distribution patterns (Foissner, 2006) and still others may even be endemic for a particular locality (Cotterill et al., 2008; Martiny et al., 2006). These models attenuate the tenet of "everything is everywhere" by proposing that (1) the abundances and thus the migration rates are rather low for the majority of species, (2) extinction rates are moderate, and (3) the proportion of the global species pool found locally is moderate. Indeed, for ciliates, a group usually not dispersing by spores, about 30% of the species were found to be regionally endemic (Foissner, 2008). Thus far, local endemicity has not been reported for myxomycetes, and even surveys on remote archipelagos have not revealed endemic taxa at the morphospecies level [Galapagos Islands (Eliasson and Nannenga-Bremekamp, 1983); the Hawaiian archipelago (Eliasson, 1991); Palawan Island (Pecundo et al., 2017)]. Regional endemicity may occur in some species. Possible examples include species recently described from deserts, such as *Physarum pseudonotabile* in Central Asian deserts (Novozhilov and Schnittler, 2008; Novozhilov et al., 2013b) or *Perichaena calongei*, *Didymium infundibuliforme*, and *Physarum atacamense* in South America (Lado et al., 2009; Wrigley de Basanta et al., 2009, 2012; Araujo et al., 2015). More systematic surveys are needed to determine if these species truly represent cases of regional endemicity or simply appear so due to a lack of data from other regions.

Whereas already rare dispersal events are sufficient to colonize new and remote localities, regular dispersal is necessary to ensure a minimum level of gene flow between local populations to prevent regional speciation. The first available studies employing molecular methods to investigate geographic separation among populations of myxomycetes at transcontinental scales revealed different patterns. For *Didymium difforme* [mtDNA (Winsett and Stephenson, 2011)] and *Didymium squamulosum* [ITS (Winsett and Stephenson, 2008)], no or only weak evidence for geographic separation was found. Marker resolution may be a question. A study investigating *T. varia* throughout Eurasia with three different markers [SSU, EF1A, COI (Feng and Schnittler, 2015)] found cryptic speciation but with no apparent geographic limitation for these species. However, the investigated region was limited to Eurasia. In contrast, studies of *B. melanospora* [SSU (Aguilar et al., 2014)] and *H. serpula* [SSU, EF1A (Dagamac et al., 2017b)], based on specimens collected in different parts of the world, revealed clear evidence for geographical limitation of certain genotypes. In such cases, low gene flow and/or mutations in mating-type genes

governing amoeboflagellate compatibility may facilitate the evolution of regionally endemic species.

To settle this discussion, more population genetic studies of clear-cut and widely occurring species of myxomycetes will be needed, which could determine the intensity of gene flow between local populations. This gene flow may be just strong enough to occupy all possible habitats within geological areas, allowing a morphospecies to appear cosmopolitan but not strong enough to break the dominance of locally adapted genotypes that may or may not evolve into cryptic species that become regional endemic.

Understanding which of the two models can be best applied to myxomycetes is crucial to estimate the overall diversity of the group. If all or most species are cosmopolitan in distribution, the global diversity of the group should be comparatively low. However, if indeed a significant proportion of species of myxomycetes display restricted distribution patterns and these are not simply caused by the patchiness of suitable habitats, their global diversity may be higher (Mitchell and Meisterfeld, 2005). Whereas the postulated broader distribution of amoeboflagellates in comparison to fruiting populations would support the ubiquity model, the discovery of cryptic species with a more restricted population than the respective morphospecies would comply better with the moderate endemicity model.

Two hundred years of fruiting body−based diversity research in myxomycetes

The first comprehensive monograph of the group (Rostafiński, 1875) listed a significant part of the c. 1000 species currently described for the myxomycetes (Lado, 2005−2020), although the number of species per year described as new to science seems to steadily increase. As such, for many morphospecies a considerable body of data exists, relating to collections of fruiting bodies from all over the world. However, as typical for organisms with hidden lifestyles, systematic surveys for myxomycetes have always been carried out by only a few specialists. As indicated by monographic treatments, the first studied regions were Europe (Rostafiński, 1875; Lister, 1894, 1911, 1925) and eastern North America (Massee, 1892; Hagelstein, 1944; Martin and Alexopoulos, 1969). Systematic surveys carried out within the last three decades have added a considerable number of studies of the Neotropics (Rojas et al., 2010, 2012a,b, 2013; Lado et al., 2003; Schnittler et al., 2002). Rather well studied are the deserts of western South America (Estrada-Torres et al., 2009; Wrigley de Basanta et al., 2010, 2013; Lado et al., 2011, 2013, 2014, 2016, 2017) and Central Asia (Novozhilov et al., 2006, 2009; Schnittler and Novozhilov, 2000; Novozhilov and Schnittler, 2008; Schnittler et al., 2013). Only recently have systematic studies been carried out in the Paleotropics, particularly in the southeast Asian region (Novozhilov et al., 2017a, 2019; Macabago et al., 2016, 2012, 2010; Dagamac et al., 2017a, 2015a,b, 2014,

2012, 2011, 2010; Alfaro et al., 2015; Rea-Maminta et al., 2015; Ko Ko et al., 2013, 2012, 2010a; Tran et al., 2006, 2008), whereas most parts of tropical Africa remain to be covered. Despite this geographically unevenly distributed study intensity, the available information makes it possible to compile worldwide distribution maps for particular species.

At least for the formation of fruiting bodies, temperature seems to be an important factor. Takahashi et al. (2018) studied corticolous myxomycetes associated with the bark of *Cryptomeria japonica* trees, which were sampled extensively throughout Japan. They found that myxomycete community structure varied in a manner that reflected the temperature gradient associated with latitudinal and altitudinal changes of the overall environment. Furthermore, geography-related temperature shifts affected the tree bark pH that contributed to microenvironments with specific combinations of both variables. A significant proportion of the described species of myxomycetes appears to be restricted to either temperate or tropical zones (Stephenson and Stempen, 1994). For instance, two species of *Ceratiomyxa* (*Ceratiomyxa morchella* and *Ceratiomyxa sphaerosperma*) have been found exclusively in the tropics (Rojas et al., 2008; Fig. 10.1). In contrast, the patchy but worldwide range of *Barbeyella minutissima*, a specialist of temperate coniferous forests (Schnittler et al., 2000; Stephenson et al., 2019a), corresponds mostly to the temperate zone of the planet, with some occurrences in high mountains of tropical zones (Fig. 10.2). A predictive distribution model revealed that among the 19 bioclimatic variables employed, *Annual precipitation* yielded the highest percent contribution (27.8), followed by *Precipitation of Driest*
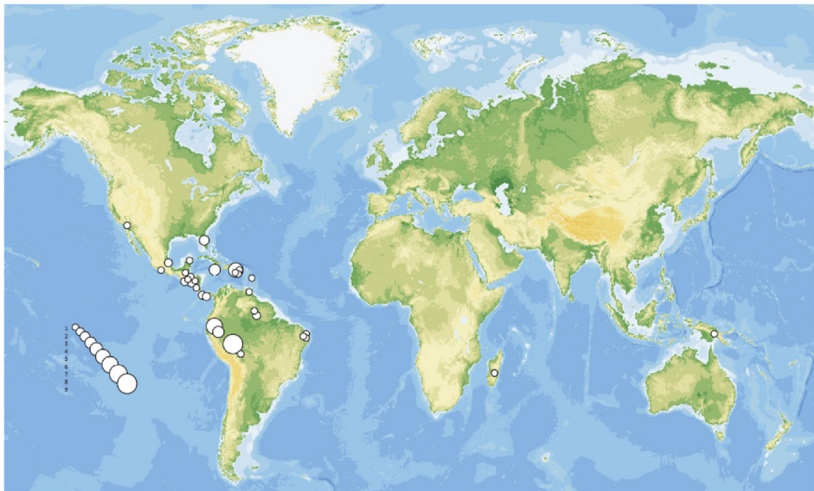
FIGURE 10.1 World distribution map for *Ceratiomyxa morchella* providing an example of a largely Neotropical species with a restricted distribution. The size of the circles indicates the number of records per investigated site.
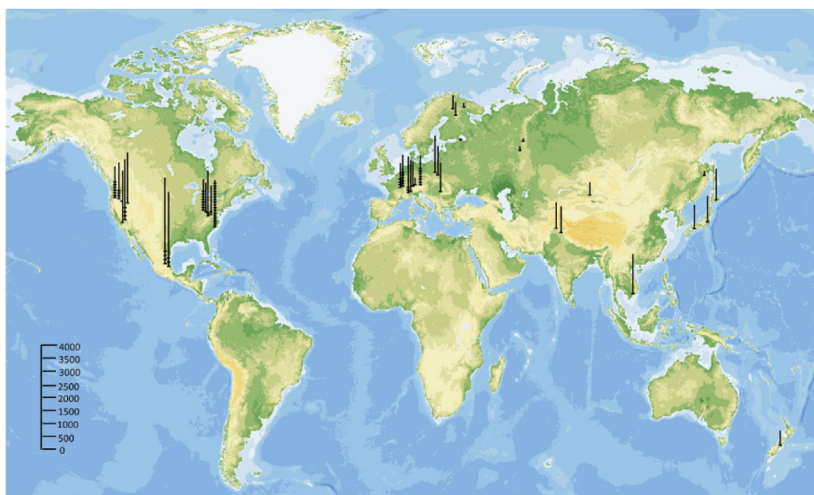
FIGURE 10.2 Needle plot showing the world distribution of *Barbeyella minutissima* from records of fruiting bodies. Each needle arises from the collecting site, its length indicates eleva- tion. *Updated from Schnittler, M., Stephenson, S.L., Novozhilov, Y.K., 2000. Ecology and world distribution of* Barbeyella minutissima *(Myxomycetes). Mycological Research 104, 1518−1523; updated after Stephenson, S.L., Novozhilov Y.K., Almadrones-Reyes, K.J., Dagamac, N.H., Schnittler, M. 2019a. New records of* Barbeyella minutissima *(Myxomycetes, Stemonitidales) with an updated distribution map. Nova Hedwigia 109 (1−2): 177−186.*

Month (23.3) and *Precipitation Seasonality* (16.0). The model suggested several areas in the Southern Hemisphere that are climatically suitable for *B. minutissima*: South America (Chile and Argentina), the eastern parts of Madagascar with a monsoon climate, and East Asia (northern highlands in the Philippines, eastern China, Taiwan, the Indonesian archipelago and Korea). However, the modeling was based on macroclimatic parameters and did not consider the presence of suitable substrates such as preferentially large, typi- cally coniferous logs with a cover of mosses and algae (Schnittler et al., 2000). The distribution data indicate that, in accordance with the ability of LDD for spores (Kamono et al., 2009; Feng et al., 2016), myxomycetes can occupy their entire potential ranges, and the collected fruiting bodies may indi- cate not all but only the most suitable habitats. As already noted in metabar- coding surveys for nivicolous myxomycetes (Borg Dahl et al., 2018b; Gao et al., 2019; Shchepin et al., 2019b), amoebal populations may occur at places where fruitings are unlikely to occur (i.e., may occupy broader ecological niches than detected with collections). These observations support the ubiquity model since all regions with suitable microhabitats seem to be covered.

On a regional scale, changes in myxomycete communities are now well documented. For example, Rojas et al. (2012b) compared the myxomycete communities associated with highland areas along a transect that extended

from North America to Central America. They showed that the similarity of species composition in these highland areas decreased with decreasing latitude (from Mexico to Costa Rica). Moreover, the similarity of species composition in these highland areas, when compared with the data available from temperate zones (in this case the United States) decreased as well. In addition, Rojas and Stephenson (2020) compared datasets from boreal, temperate, and tropical regions of North America. At the morphospecies level, the lowest similarity was observed for the boreal−tropical pair and highest for the temperate−tropical pair. Species diversity was that highest for the temperate dataset and lower for both boreal and tropical datasets. The latter may be an indication of higher fruiting propensity in temperate regions rather than an indication of intraspecific diversity, an idea that deserves further examination.

A severe problem for biogeographical studies is the apparent rarity of the fruiting bodies of many species of myxomycetes. Even surveys over several years, accumulating a large number of specimens, show a high proportion of singletons [e.g., Novozhilov et al. (2017a, 2019): Southern Vietnam, 1136 records, 107 taxa, 23% represented by singletons and Novozhilov et al. (2017b): Russian Far East, 3280 records, 161 taxa, 21% as singletons]. Schnittler and Mitchell (2000) estimated that more than half of the 446 species of myxomycetes for which data were available were represented by fewer than three collections thus far, which makes up for a significant proportion of the species known for the group, especially of the newly described species. Biogeographical studies carried in the Americas found that species abundances could be predicted on the basis of forest structure (Rojas et al., 2011), but this pattern may as well have been caused by historical geographical events (Estrada-Torres et al., 2013).

Another problem relates to the different methods used. For example, many species with minute fruiting bodies can be detected only by placing samples of substrates in moist chamber cultures (Gilbert and Martin, 1933), which have been used only in a fraction of all surveys, due to the intense amount of labor required. Whereas in forested areas most species can be observed directly in the field (Novozhilov et al., 2017b), in deserts without a high proportion of succulent plants, nearly 100% of the species present can be detected only with the moist chamber culture technique (Schnittler et al., 2015b). Most often, both approaches complement each other and are equally needed (Schnittler and Stephenson, 2000; Dagamac et al., 2017a, 2015b; Novozhilov et al., 2017a,b). Recently, it has been shown that molecular detection techniques can as well complement sporocarp-based surveys: the diversity of species with minute fruiting bodies, such as members of the genera Echinosteliales and *Echinosteliopsis*, seems to be underestimated (Shchepin et al., 2019a).

Best studied are the myxomycetes of northern temperate and boreal zones, and these seem to be among the regions with the highest morphospecies diversity. For Germany, with a long history of myxomycete research, 373 species have been recorded (Schnittler et al., 2011). For Russia, 454 species have been

recorded, and the largest share of this diversity was found in temperate and boreal regions of the country (Bortnikov et al., 2020). Japan and eastern North America, with their predominately broadleaf forests, seem to have an even higher species diversity, although precise numbers are difficult to obtain (Yamamoto, 1998). Temperate zones also have the highest diversity of corticolous and foliicolous species, which can be detected best with the moist chamber culture technique (Gilbert and Martin, 1933; Härkönen, 1981; Goad and Stephenson, 2013; Stephenson et al., 2020b).

Members of the first group, comprising c. 120 species (Mitchell, 2004) with mostly very small fruiting bodies, inhabit the bark surface of living trees and show two life strategies (Schnittler, 2001). These are (1) stalked species with a short development time and minute, usually stalked fruiting bodies with evanescent peridia (species of *Echinostelium* and *Macbrideola*) and (2) sessile species with a longer development time and robust fruiting bodies, usually covered by a thicker peridium. A special, yet species-poor ecological group found within the temperate zone are the bryophilous myxomycetes (Schnittler et al., 2010), which are adapted to moss layers in permanently humid gorges covering porous rocks or decaying logs.

In comparison, our current knowledge relating to the diversity of tropical myxomycetes seems to defy the traditional concept (as latitude increases, species richness decreases) that applies to many groups of macroorganisms. Systematic studies in tropical regions point toward a lower species richness than for temperate regions, especially for southern temperate zones. For example, the comparatively well-studied country of Costa Rica has 225 species of myxomycetes recorded (Schnittler et al., 2002; Rojas et al., 2010, 2015). Although many tropical regions are still not systematically studied, the few systematic surveys carried out in tropical forests point seem to support this same trend [e.g., Ecuador: Yasuni, 86 species (Lado et al., 2017); southern Vietnam, Cat Tien National Park, 107 species, Dalat Plateau, 105 species (Novozhilov et al., 2017a, 2019); and the Philippine archipelago, 159 species (Macabago et al., 2020; Dagamac and Dela Cruz, 2019)]. A checklist for the Neotropical zone, where myxomycetes are relatively well studied, includes a total of 431 taxa (Lado and Wrigley de Basanta, 2008). The most diverse country (323 species) is Mexico that has a high proportion of arid regions along high volcanoes with temperate and even coniferous forests. Even with this still fragmentary knowledge, we can conclude that at least the steep increase in species numbers toward tropical regions, very well known for vascular plants or insects, is not a pattern shared by myxomycetes.

The most likely reason for this discrepancy is the moisture regime. Studies along three gradients of increasing elevation and moisture revealed that in tropical regions, species richness and the proportion of moist chamber cultures positive for myxomycetes decreased with elevation [volcano Cacao, Costa Rica (Schnittler and Stephenson, 2002), the slopes of the western Andes, Maquipucuna, Ecuador (Schnittler et al., 2002); and the Dalat Plateau,

southern Vietnam, (Novozhilov et al., 2019)]. The lowest figures were always found for tropical mountains, which are characterized by continuously wet forests at the highest elevations. This is corroborated by observations that in contrast to forests of the temperate zones, the assemblage of myxomycetes associated with aerial litter is more diverse than litter from the forest floor (Alfaro et al., 2015; Stephenson et al., 2008). In addition, there are unique aerial microhabitats in the tropics such as inflorescences of large monocotyledonous forbs with a high substrate pH [especially Zingiberales, (Schnittler and Stephenson, 2002), dead lianas (Coelho and Stephenson, 2012; Ko Ko et al., 2010b; Wrigley de Basanta et al., 2008), or epiphytic liverworts (Schnittler, 2000)]. A few species such as *Physarum compressum*, *Physarum didermoides*, *Physarum javanicum*, *Physarum melleum*, or *Physarum superbum* occur very regularly in aerial microhabitats. Further investigations are needed to elucidate the reasons for the apparent lower myxomycete diversity in the wet tropics. It is possible that species may fruit less abundantly because desiccation as a trigger of fruiting body formation is absent or fruiting bodies may decompose very rapidly and thus appear to be less abundant when this is not actually the case.

Diversity and species composition of myxomycete communities from major ecosystems of the world

Tundra, forest-tundra, and subantarctic habitats

As to be expected from the scarce and less diverse cover of vegetation, zonal arctic, subarctic, and subantarctic ecosystems are rather species-poor for myxomycetes. Stephenson et al. (2000), analyzing data from c. 2000 specimens collected from the tundra and forest tundra of Alaska (Stephenson and Laursen, 1998), Iceland (Götzsche, 1990), Greenland (Götzsche, 1989), and Russian Arctic regions (Novozhilov and Schnittler, 1997; Novozhilov et al., 1999), recorded a total of 150 species, but only 33 of these were widely distributed enough to be regarded as species that are regularly associated with high-latitude regions. Lesser known are the myxomycetes of subantarctic regions (Arambarri, 1973; Arambarri and Spinedi, 1989; Stephenson et al., 2007; Wrigley de Basanta et al., 2010; Stephenson, 2011; Pinheiro Velloso et al., 2020). Two main factors are likely to limit myxomycetes distribution toward the extreme high latitudes of both hemispheres. These are substrate availability and climate. Some lineages may be better suited than others. For example, Wrigley de Basanta et al. (2010) found that members of the order Trichiales dominated in a survey of Patagonia, whereas members of the order Physarales are more common in temperate and tropical South America.

Because of the inherent resistance of the three dormant stages (microcysts, sclerotia, and spores) in the life cycle of a myxomycete, low winter temperatures would seem to be a relatively unimportant factor. Indeed, the

Taimyr Peninsula (Russia), with the most extreme winter temperatures of all the high-latitude areas intensively studied, was not only rich in species but also supported *Cribraria violacea* (Novozhilov et al., 1999), whose distribution is apparently centered in submeridional to tropical regions A possible explanation may be the rather high mean summer temperature connected with the highly continental climate, since for approximately 1 month temperatures are high enough to allow myxomycetes to complete their life cycle. Interestingly, even species developing large, compact fruiting bodies occur this far north. Examples are *Lycogala epidendrum*, *Mucilago crustacea*, and *Enteridium splendens* var. *juranum*. Two of these three species are wood inhabitants, whose distribution is limited by the presence of larger logs. In contrast, *M. crustacea* is frequently observed in pure tundra regions, emerging from thin mats of raw humus and litter, sometimes covered with bryophytes and lichens (Stephenson and Laursen, 1993). Seemingly, the latter species is not limited by the availability of a certain substrate and may accept a wide range of food organisms. Most obligate corticolous members of the Physarales and Echinosteliales are adapted to near-neutral substrates; therefore they are relatively rare in coniferous communities of forest tundra, where tree bark is more acidic [pH 4.5−3.0 (Novozhilov et al., 1999)]. A few acidophilic species [*Echinostelium brooksii* and *Paradiacheopsis fimbriata*, Taimyr Peninsula (Novozhilov et al., 1999) and *Paradiacheopsis solitaria*, Alaska (Schnittler et al., 2016)] fit into this pattern and appear to be consistent inhabitants of forest-tundra and boreal coniferous forests. As a litter-inhabiting species, *Leocarpus fragilis* spreads beyond the timberline into arctic tundra, where moist chamber cultures have revealed plasmodia of this species (Schnittler et al., 2016).

Still understudied are the communities of nivicolous myxomycetes associated with subarctic and arctic mountains. Most of the data have originated from the Scandinavian Mountains (Schinner, 1983; Johannesen and Vetlesen, 2020) and the Khibine Mountains [Kola Peninsula (Erastova et al., 2016; Novozhilov and Schnittler, 1997; Novozhilov et al., 2020)]. Only 3 of 32 species (*Diderma alpinum*, *Diderma niveum*, and *Physarum albescens*) were found to be widely distributed in the Khibine Mountains, where species richness and diversity decreases from subalpine crooked-stem birch-mountain ash forests to alpine mountain tundra (Erastova et al., 2016).

Boreal forests (taiga) and subalpine/montane coniferous forests

Taiga (coniferous boreal forests, including montane coniferous forests) represents the world's largest biome, and myxomycetes associated with this type of ecosystem are rather well studied [Alaska (Stephenson and Laursen, 1998; Stephenson, 2004; Schnittler et al., 2016); Scandinavia (Eliasson and Strid, 1976; Härkönen, 1977; Schinner, 1983; Härkönen and Varis, 2013; Johannesen and Vetlesen, 2020); Russia (Kosheleva et al., 2008; Novozhilov

and Fefelov, 2000; Schnittler and Novozhilov, 1996; Stephenson, 2004; Vlasenko and Novozhilov, 2011; Novozhilov et al., 2020; Bortnikov et al., 2020); German Alps (Schnittler and Novozhilov, 1998); Japan (Takahashi and Harakon, 2012; Takahashi and Hada, 2012; Takahashi et al., 2018)]. The most common taxa in these biomes are members of the Cribrariaceae, Trichiaceae, Physaraceae, and Stemonitidaceae on decaying conifer wood with an acidic pH, including *Arcyria denudata*, *Arcyria pomiformis*, *Comatricha elegans*, *Comatricha nigra*, *Cribraria* spp., *Enerthenema papillatum*, *Paradiacheopsis* spp., *Physarum album*, *Physarum viride*, *Licea minima, Licea variabilis*, *L. epidendrum*, *S. axifera*, *Stemonitopsis hyperopta*, and *T. varia*. In addition, a second species assemblage (*Lepidoderma tigrinum* and *Lamproderma columbinum* but especially *Colloderma oculatum* and *B. minutissima*) can be called bryophilous (Stephenson and Studlar, 1985), since they are associated with layers of bryophytes on decorticated coniferous logs (Schnittler and Novozhilov, 1996, 1998) and rocks (Schnittler et al., 2010). Food organisms may include unicellular algae, which form gelatinous layers on these substrates. This association would explain the late peak of fruiting—cool nights in late autumn characterized by an extended dewfall, thus keeping the bryophyte layer continuously wet for some weeks and thereby allowing algal growth. Moist, *Sphagnum*-rich spruce woodlands are typical for taiga forests and have a species-poor assemblage of specialized species such as *Didymium melanospermum, Physarum virescens*, *Physarum confertum*, and *Fuligo muscorum*, which typically fruit in the shelter of moss tussocks. Not a lot is known about typical myxomycete species for *Sphagnum* bogs, but at least three species (*Badhamia lilacina*, *Diderma simplex*, and *Symphytocarpus trechisporus*) seem to be specialized for this habitat and occur even in raised bogs. At higher latitudes nivicolous myxomycetes are found in low-elevation mountains (Ronikier and Ronikier, 2009; Ronikier et al., 2008; Novozhilov et al., 2020) or even in lowlands (Erastova and Novozhilov, 2015; Yatsiuk and Leontyev, 2020).

Temperate forests

Temperate deciduous forests support the most diverse and abundant myxomycete communities in the world (Ing, 1994; Novozhilov et al., 2017b; Stephenson et al., 2001; Takahashi, 2004). Especially rich seem to be broadleaf deciduous forests, occurring in climates with a summer peak in rainfall. Examples include eastern North America [Great Smoky Mountains National Park (Stephenson et al., 2001; Rojas and Stephenson, 2020)] or the Manchurian-Japanese mixed broadleaf forests of northeast Asia [Sikhote-Alin Biosphere Reserve (Novozhilov et al., 2017b) and Lazovsky State Nature Reserve (Gmoshinskiy et al., 2020)]. A number of microhabitats with specialized myxomycete assemblages have been described during the last decade, including bark and decaying twigs in the forest canopy (Schnittler et al., 2006;

Snell et al., 2003) or ravine myxomycetes (Ing, 1994), which exhibit a preference for bryophyte covers on rocks (see earlier). The latter are known from the British Islands (Ing, 1983) and Germany (Schnittler et al., 2010). Both species diversity and abundance in temperate forests tend to achieve their maximum near the wetter end of the moisture gradient (Rollins and Stephenson, 2011).

Mediterranean forests, woodlands, and scrub

Mediterranean forests and scrublands are characterized by hot and dry summers, while winters tend to be cool and moist. These two types of vegetation occur between 30 and 40 degrees northern and southern latitudes on the westward sides of continents and include five regions. These are the Mediterranean, south central and southwestern Australia, the fynbos of southern Africa, the Chilean Matorral, and the Mediterranean ecoregions of California with scrubland vegetation (chaparral). Well studied are the species-rich communities of myxomycetes around the Mediterranean Sea and Black Sea (Novozhilov, 1988; Binyamini, 1997; Härkönen, 1988; Lado, 1994; Leontyev et al., 2011), the Californian scrubland (Critchfield and Demaree, 1991; Estrada-Torres et al., 2009). Less complete information is available about southern Africa (Ndiritu et al., 2009a), the Canary Islands (Beltran et al., 2004), the Chilean Matorral (Lado et al., 2013), and scrub communities of Australia (Mitchell, 1995). High moisture gradients at small scales together with the regular fluctuations in moisture are the most likely reason for the high diversity, especially for corticolous species. Many new taxa have been described in the last few decades (Pando, 1997), and these show some similarities with communities from desert areas (Schnittler and Novozhilov, 2000). Preferred substrates for myxomycetes are *Olea europaea*, *Juniperus* spp. (Schnittler et al., 2015a), and *Quercus* spp., which support various minute species [*Echinostelium*, *Licea*, and *Macbrideola* spp. (Novozhilov, 1988; Pando and Lado, 1990; Wrigley de Basanta, 1998)]. In addition, a large supply of slowly decaying leaf litter from sclerophyllous shrubs supports many litter-inhabiting species, such as *Diderma asteroides* and *Physarum brunneolum*.

Tropical and subtropical forests

Stephenson et al. (2004) and Lado et al. (2018) summarized the body of information available on Neotropical myxomycetes and suggested that three major trends seem to exist. First, myxomycete species richness and abundance appear to be lower in tropical forests when compared to temperate forests. Second, both abundance and richness of myxomycetes decrease with increasing moisture (Schnittler and Stephenson, 2000). Third, some microhabitats with no equivalents in temperate regions support distinct assemblages of myxomycetes. Some species (e.g., *A. bombarda* and *C. sphaerosperma*)

that require high temperatures for development seem to be restricted largely if not exclusively to tropical climates.

Somewhat lagging behind are research efforts directed toward the Paleotropics, especially in Africa. A comprehensive checklist by Ndiritu et al. (2009a) listed a total of only 294 species represented by 49 genera reported from 31 African countries, most of which are anecdotal in nature. Some relatively well-studied localities in Africa and adjacent islands include Ethiopia (Dagamac et al., 2017c), Tanzania (Ukkola et al., 1996), Kenya (Ndiritu et al., 2009b), the Seychelles (Kryvomaz et al., 2020a,b), Madagascar (Wrigley de Basanta et al., 2013), and Namibia (Stephenson et al., 2019b). The survey with the highest number of species (124) reported was carried out in Madagascar, once again a region with a significant proportion of highlands and arid regions, with one species (*Perichaena madagascariensis*) reported as new to science (Wrigley de Basanta et al., 2013). Better studied areas are the southeast Asian Paleotropics, with surveys carried out in Singapore (92 species, Rosing et al., 2011), Myanmar (67 species, Ko Ko et al., 2013), Vietnam (107 species, Novozhilov et al., 2017a, 2019), Laos (44 species, Ko Ko et al., 2012), the Philippines (159 species, Macabago et al., 2020; Dagamac and Dela Cruz, 2019), and Thailand (132 species, Ko Ko et al., 2010a; Tran et al., 2008). Factors such as seasonality (Dagamac et al., 2012; Ko Ko et al., 2011), disturbance (Dagamac et al., 2017a; Rea-Maminta et al., 2015), and litter heterogeneity (Nguyen et al., 2019; Tran et al., 2006) have been investigated to explain the occurrence and distribution of myxomycetes in the region. In the last decade a number of new species have been described from the region, including *Comatricha spinispora* (Novozhilov and Mitchell, 2014), *Craterium retisporum* (Moreno et al., 2009), *Cribraria tecta* (Hooff, 2009), *Perichaena echinolophospora* (Novozhilov and Stephenson, 2015), *Diderma cattiense* (Novozhilov and Mitchell, 2014), *Diderma pseudotestaceum* (Novozhilov and Mitchell, 2014), and *Diderma dalatensis* (Novozhilov et al., 2019).

For tropical regions the moist chamber culture technique seems to provide both lower species diversity and fewer fruiting bodies per species found, following a gradient of habitat aridity from deserts (where moist chamber cultures work best) to temperate zones to tropical zones. As a consequence, the litter microhabitat, when examined by moist chamber cultures, yields considerably lower species richness than what would be expected for the same microhabitat in temperate regions (Stephenson et al., 1999).

In addition, a clear pattern of decreasing species richness with increasing elevation and moisture has been noted in several studies (field collections from Puerto Rico (Novozhilov et al., 2000), a moisture gradient along a volcano in Costa Rica (Schnittler and Stephenson, 2000), the western slopes of the Andes (Schnittler et al., 2002)], and the tropical forests of Vietnam (Novozhilov et al., 2017a, 2019; Nguyen et al., 2019). For example, in the mountain tropical forests of the Dalat Plateau (Vietnam), species richness and diversity decrease

from the middle-mountain broadleaf deciduous forest over mixed broadleaf−coniferous forest, middle-mountain open pyrogenic coniferous forest, and high-mountain cloud forest (Novozhilov et al., 2019). Only for corticolous myxomycetes is this trend reversed due to the rather high diversity of corticolous acidotolerant species on bark of *Pinus kesiya* in the pyrogenic coniferous forest. The middle-mountain broadleaf deciduous forest and mixed broadleaf−coniferous forest, being richest and as well most similar to each other, have the highest diversity in canopy trees, and many species of myxomycetes can find suitable microhabitats. In contrast, less diverse forests, such as the open pyrogenic coniferous forest and high-mountain cloud forest, have a lesser diversity in canopy trees, provide more special microhabitats (like acidic pine bark), and have more specialized myxomycete taxa. For this reason, these forests are less similar to each other.

Most likely, continuous moisture does not trigger the formation of fruiting bodies, and strong rainfall events seem to wash away amoeboflagellates and/or plasmodia. Evidence for the latter hypothesis comes from the observation that the proportion of species with phaneroplasmodia (the most robust of the types of plasmodia produced by myxomycetes) increases with increasing elevation and moisture. In addition, species richness of bark-inhabiting myxomycetes has been found to be negatively correlated with the amount of epiphyte coverage and moisture. Further support comes from aerial microhabitats, which in the tropics support a higher diversity and abundance of myxomycetes when compared to ground microhabitats. Presumably, since these microhabitats are not in contact with the forest floor, they have a better chance of drying out after rainfall events in the wet tropics.

High-elevation tropical forests have remained mostly unstudied. Studies of high-elevation *Quercus* forests in Costa Rica revealed a myxomycete community strongly differing from communities in lowland tropical forests but displaying similarities (both taxonomically and ecologically) to assemblages associated with temperate forests (Rojas and Stephenson, 2007; Rojas et al., 2010). The authors reported several species, most notably *Leocarpus fragilis*, that tend to be largely absent from tropical regions but are characteristic of temperate and boreal regions. A similar trend has been reported for mountain forests of southern Vietnam, which have a vegetation dominated by families with many temperate tree genera from the Fagaceae, Magnoliaceae, and Pinaceae, where *B. minutissima* and *L. columbinum* were present (Stephenson et al., 2019a; Novozhilov et al., 2019).

Asian Paleotropical forests seem to be richer in species of myxomycete than Neotropical forests (Dagamac et al., 2017d) and some species such as *Physarum echinosporum* (Fig. 10.3) seem to be more common in the Asian Paleotropics. The presence of conifers (*Pinus* spp.) with acidic bark and wood in the mountains of Vietnam and Thailand may contribute to this pattern. Several species (e.g., *B. minutissima*, *E. brooksii*, *Echinostelium colliculosum*, *L. columbinum*, *Licea kleistobolus*, *Lindbladia tubulina*, *Paradiacheopsis rigida*,
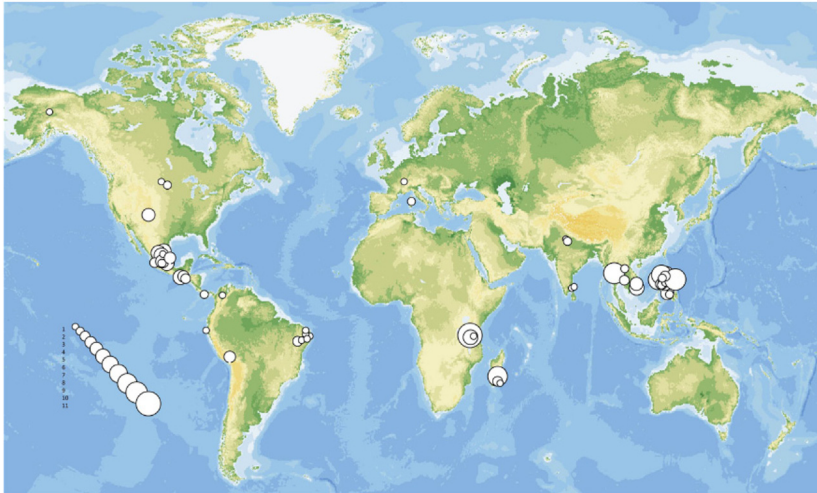
FIGURE 10.3 World distribution map for *Physarum echinosporum* providing an example of a pantropical species with a restricted distribution. The size of the circles indicates the number of records per investigated site.

and *Trichia persimilis*) that are known to be common in the temperate zones have been reported from these mountain forests (Novozhilov et al., 2019).

As noted earlier in this chapter, it has been suggested that moist tropical forests may receive too much rain to be conducive to the successful completion of the myxomycete life cycle, which appears to be best suited to alternating wet and dry periods. This hypothesis seems to be supported by reports that aerial microhabitats, in the tropics, support a greater diversity and abundance of myxomycetes when compared to ground microhabitats (as already noted but also see Chapter 8: Taxonomy and Systematics: Current Knowledge and Approaches on the Taxonomic Treatment of Myxomycetes). Specific microhabitats for tropical myxomycetes include inflorescences of monocotyledonous herbs with an extremely high pH (Schnittler et al., 2002), living leaves in the forest understory that have been overgrown with liverworts (Schnittler, 2000), and both living and decaying lianas (Wrigley de Basanta et al., 2008), once again a substrate characterized by rather high pH values.

The heterogeneity of plant species and the microhabitats provided by them seem to be crucial factors for species richness in myxomycetes, a trend observed in the Paleotropics (Tran et al., 2008; Redeña-Santos et al., 2017, 2018; Tran et al., 2008; Dagamac et al., 2015b, 2017d) as well as in Neotropics (Rojas and Stephenson, 2012). In addition, canopy openness (Rojas and Doss, 2014) may influence the ecological dynamics of myxomycete communities. Canopy gaps, especially in very moist forests, provide

microhabitats that periodically dry out, which seems to increase the fruiting propensity for myxomycetes.

Steppes and prairie

At a first glance, due to a lack of woody debris, grasslands would not seem to provide good habitats for myxomycetes, despite evidence from studies showing that amoeboflagellates are more common in grassland soils than in forest soils (Feest and Madelin, 1988). However, studies carried out in the steppe regions of Russia (Novozhilov et al., 2010, 2006), Mongolia (Novozhilov and Schnittler, 2008), Kazakhstan (Zemlyanskaya et al., 2020), and the midwestern United States (Rollins and Stephenson, 2013) reported a surprisingly high diversity of myxomycetes. Recently, Fiore-Donno et al. (2016) analyzed soil samples from a temperate grassland in Germany by ePCR and found that the most abundant OTUs belonged to the genera *Lamproderma* and *Didymium*. A special assemblage of species in grasslands often abundantly grazed by herbivores such as horses and cattle includes coprophilous species (Eliasson and Lundqvist, 1979). Typical examples include *Kelleromyxa fimicola* and *Perichaena liceoides* associated with dung and *D. squamulosum*, *Echinostelium minutum*, *Fuligo cinerea*, and *P. pseudonotabile* (Novozhilov et al., 2013b) that are associated with grass litter.

At the grassland−forest transition zone, species diversity tends to increase toward the latter. Looking at the species/genus ratio, Rollins and Stephenson (2013) found a trend of increasing taxonomic diversity moving eastward from short to tall grass prairie. In the Russian Altay (Novozhilov et al., 2010) a pronounced trend of increasing species richness was found when moving from dry steppe (6 species, $H' = 1.6$) over dark coniferous taiga and secondary mixed aspen and birch forests (99 species, $H' = 4.1$) to mixed forests (116 species, $H' = 4.2$); diversity decreased again toward the forest-steppe zone (65 species, $H' = 3.7$). Overall species dominance in the treeless dry steppe was found to be higher ($D = 0.26$) when compared to the forest steppe, where lignicolous myxomycetes occur in forest islands near streams ($D = 0.05$). As would be expected, the occurrence of woody debris causes pronounced differences between the assemblages of myxomycetes associated with open grasslands and adjacent gallery forests (Rollins and Stephenson, 2013).

Subalpine and alpine grasslands

Subalpine meadows and alpine grasslands occur above the timberline in the high mountains, mostly in regions with a temperate climate. Climatic conditions (low temperatures and heavy snow accumulation) limit the period of vegetative growth to a few months, but such areas still support rich communities of tall forbs, such as can be observed in the northwestern Caucasus

(Onipchenko, 2004) or the Southern Alps of New Zealand (Stephenson, per. obser.). This vegetation supports a rich assemblage of snowbank (nivicolous) myxomycetes, with about 100 species having been described since the pioneering studies of Meylan (see Kowalski, 1975). Nivicolous myxomycetes are best studied in the Northern Hemisphere (Borg Dahl et al., 2018b; Lado, 2004; Lado and Ronikier, 2008, 2009; Meylan, 1914; Moreno et al., 2005; Novozhilov et al., 2013a; Ronikier and Ronikier, 2009; Singer et al., 2005; Stephenson and Shadwick, 2009). Interestingly, mountain ranges of the Southern Hemisphere harbor different communities of nivicolous myxomycetes (Ronikier and Lado, 2015; Ronikier et al., 2020), and these differences seem to be present as well at the morphospecies level (Janik et al., 2020).

The soil-inhabiting nivicolous myxomycetes are not strictly alpine (Ronikier and Ronikier, 2009) but occur as well in boreal lowland forests and low-elevation mountains (Erastova and Novozhilov, 2015; Novozhilov et al., 2020; Müller, 2002; Ronikier et al., 2008; Tamayama, 2000; Yajima et al., 2006; Yatsiuk and Leontyev, 2020). As already suggested in an initial paper by Schinner et al. (1990), the prevailing conditions determine the occurrence of myxomycetes. Since amoeboflagellates are susceptible to frost, early snowfall, and a long, contiguous snow cover, providing stable temperatures around zero degrees under the snow, are crucial for the formation of fruiting bodies (Schnittler et al., 2015a; Shchepin et al., 2014). Nivicolous myxomycetes seem to be important predators in the microbial communities that exist beneath the snow (Borg Dahl et al., 2019).

Deserts and other arid areas

Since myxomycetes need water or substrates covered by a film of water for their active life stages, one might not expect these organisms to occur in deserts. However, numerous studies from arid ecosystems, often employing the moist chamber culture technique, have revealed astounding myxomycete diversity in arid regions. A series of surveys throughout Middle and Central Asia, extending from the Caspian Lowlands (Novozhilov et al., 2006), Kazakhstan (Schnittler and Novozhilov, 2000; Zemlyanskaya and Novozhilov, 2018; Zemlyanskaya et al., 2020), across the inner mountain basins of the Russian Altay (Novozhilov et al., 2010) to Mongolia (Novozhilov and Schnittler, 2008) to the Chinese province of Xinjiang (Schnittler et al., 2013), have explored the diversity of myxomycetes in winter-cold steppes and deserts. More limited data exist for Australian deserts (Davison et al., 2008; Stephenson et al., 2020a) and the southwestern United States (Evenson, 1961; Blackwell and Gilbertson, 1980, 1984; Novozhilov et al., 2003; Ndiritu et al., 2009c). A rich body of data also exists for the deserts of Central and South America [arid regions of Mexico (Estrada-Torres et al., 2009) and Chile (Lado et al., 2007)]. Published species lists from other deserts throughout the world include the Sinai Peninsula (Ramon, 1968), Morocco (Yamni and Meyer, 2008), Oman (Schnittler et al., 2015b), Saudi

Arabia (Ameen et al., 2020), Namibia (Stephenson et al., 2019b), and a few reports from the Sahara (Faurel et al., 1965).

Although the lack of moisture in desert environments undoubtedly places severe constraints on the growth and development of myxomycetes, two strategies have evolved that allow myxomycetes to use utilize the few suitable microhabitats. First, minute, usually stalked, species develop rapidly from protoplasmodia or very small aphanoplasmodia and thus can benefit from occasional rainfall events. Second, species forming sessile fruiting bodies with a hard-shelled peridium seem to be able to withstand repeated phases of drought during development (Schnittler, 2001). Eventually, the peridium dehisces to release the spores when the substrate upon which the fruiting bodies occur dries out completely. In addition, special microhabitats, most prominently succulent plants, support a distinctive assemblage of myxomycete assemblages. One prominent example is *B. melanospora* (Aguilar et al., 2014). In response to fluctuations in moisture, these species may repeatedly switch between actively feeding plasmodia and dormant sclerotia (Estrada-Torres et al., 2009). The three dormant stages (spores, microcysts, and sclerotia) are the key for myxomycete survival in deserts. Blackwell and Gilbertson (1984) reported that myxomycete sclerotia incubated at 70°C still had significant survival rates although survival differed among the species examined.

Many substrates for desert myxomycetes are characterized by a much higher pH in comparison to most substrates from other environments (Schnittler, 2001). These observations may explain the high number of apparent specialists limited to particular microhabitats or even specific life forms of vascular plants [such as the succulenticolous myxomycetes (Estrada-Torres et al., 2009)]. A remarkably high number of species have been described from material collected in deserts, and many of these are not yet known from any other type of ecosystem (Blackwell and Gilbertson, 1980; Lado et al., 2007; Mosquera et al., 2000; Novozhilov et al., 2008, 2013a; Novozhilov and Zemlyanskaya, 2006; Wrigley de Basanta et al., 2009, 2010). Interestingly, fruiting bodies of many genera common in boreal and broadleaf deciduous forests are absent or extremely rare in the arid regions of Central Asia, even in the intrazonal woody communities with a sufficient supply of coarse wood debris (Zemlyanskaya et al., 2020). Further studies using metagenomic analysis of environmental DNA may show if they are present there as populations amoebae that rarely or never fruit or if they are completely absent in the winter-cold deserts and steppes.

Coastal habitats and mangroves

Only a few studies directed toward the myxomycete communities associated with coastal habitats and mangroves have been carried out, although coastal ecosystems encompass a broad range of habitat types such as dune grass vegetation (Howard, 1948), mangrove swamps (Agra et al., 2015; Cavalcanti et al., 2014, 2016; Kohlmeyer, 1969), shingle beaches (Ing, 1967), or

marshes and coastal forests (Macabago et al., 2020; Nguyen et al., 2019; Eliasson, 1971). The most important environmental factors shaping myxomycete diversity and distribution in coastal habitats may be strong wind, sea-level oscillations (high salinity), temporarily high temperatures for coastlines in the tropics and subtropics, anaerobic soils, and the absence of forest vegetation. Ing (1994), when he reviewed myxomycete diversity in seashore communities, stated that there are no known exclusively marine myxomycetes, although species common in adjacent woodland communities have been found on dune grasses and herbaceous litter as well on driftwood accumulated on the seashore (Hagelstein, 1930). Ing (1968) noted that in areas where woodland is scarce, driftwood may be a valuable reservoir for common lignicolous species. In addition, some rare species may be common in these habitats. For example, on *Cladonia* spp. in dry slacks, the very rare *Listerella paradoxa* has been found in Scotland; elsewhere, it is known only from lichen heath on shingle or moorland. *Diacheopsis mitchellii* was described from material collected on *Cladonia* in dune systems in southeast England (Ing, 1994). Adamonyte et al. (2013) studied a great cormorant (*Phalacrocorax carbo*) colony in Lithuania, obtaining in moist chamber cultures of various kinds of substrates such rare species as *Arcyria leiocarpa*, *Badhamia apiculospora*, and *Comatricha mirabilis*. Reports of myxomycetes from mangrove belts come from Brazil (Cavalcanti et al., 2014, 2016; Agra et al., 2015; Damasceno et al., 2011). Overall diversity is low, and regular inundation by the sea appears to inhibit fruiting body development. Currently, 31 species have been recorded from mangrove forests (Cavalcanti et al., 2016); the most common are *A. cinerea*, *A. denudata*, *Collaria arcyrionema*, and *Stemonitis fusca*.

Agricultural and urban habitats

Ing (1994) noted that temperate grasslands are rather poor in myxomycetes, although *Badhamia foliicola*, *M. crustacean*, and (especially) *Physarum cinereum* often occur in residential lawns. Saunders and Saunders (1900), who examined piles of rotting straw near cornfields, reported that different species of myxomycetes tended to be associated with different parts of the pile. *F. cinerea*, *P. didermoides*, and *Physarum pusillum* were found in association with the dry outer parts of the pile, whereas *D. difforme* and *Didymium vaccinum* were consistently associated with the bottom of the pile, where water retention was greatest. Myxomycetes are not pathogenic to plants, although they occasionally cause indirect injury. This occurs when they cover and shade plant tissues and inhibit photosynthesis.

Recently, *Comatricha pulchella* and *Fuligo septica* were recorded on cultivated *Dendrobium candidum* and apparently affected the growth of this plant (Tu et al., 2016). Also, in the less explored southern Philippines (Almadrones-Reyes and Dagamac, 2018), cosmopolitan myxomycete morphospecies like

D. squamulosum, *Perichaena depressa*, and *Perichaena vermicularis* occur regularly on banana (*Musa* sp.) plantations (Buisan et al., 2019) and in rice agroecosystems (Buisan et al., 2020). Well known is the occurrence of *F. septica* on the wood chips used as organic mulch in gardening. Myxomycetes are common in parks and gardens, where they can use natural as well as artificial substrates. Ing (1994) mentioned the studies of Brãndžă (1924), where the author constructed "nurseries" (e.g., piles of branches, sawdust, leaves, manure, and waste paper) to attract myxomycetes. In this way, he recorded 33 species, including nine new to Romania. Corticolous species are not rare in parks of cities but may suffer from acid pollution (Härkönen and Vänskä, 2004; Wrigley de Basanta, 2000; Gmoshinskiy and Matveev, 2016; Hosokawa et al., 2019).

Interestingly, the low diversity of fruiting bodies as based on field observations does not agree with the abundance of amoeboflagellates and plasmodia in the soil, as shown by culturing (Feest, 1987) and ePCR (Fiore-Donno et al., 2016). Much more work is needed to correlate the occurrence of myxomycete fruiting bodies with the real diversity of these organisms in artificial habitats. Without doubt, artificial habitats can attract specialists that are rare or absent in natural vegetation. For instance, the acidotolerant corticolous *Cribraria confusa* is very common in artificial plantations and gardens on the acidic bark of *P. kesiya* and *Anacardium occidentale* but rare in natural forests (Novozhilov et al., 2017a).

Rank abundance distributions of myxomycete communities in heterogeneous vegetation, as prevailing in tropical forest ecosystems like in the Philippines and Vietnam (with many different microhabitats), seem to follow the best Zipf model (Dagamac et al., 2017d; Bernardo et al., 2018; Macabago et al., 2017; Novozhilov et al., 2019), whereas communities from artificial vegetation types (e.g., banana plantations) with only a few different microhabitats are better described with resource partitioning models—where the more abundant species can be seen as more competitive, taking the major share of the available resources (Gardener, 2014).

Heathlands

With its low and dense shrub cover warming up quickly, Ing (1994) indicated that some species of myxomycete may be associated with the litter and decaying twiglets of shrubs such as *Calluna vulgaris*. Candidate species may include *L. paradoxa* on lichens and *D. simplex* and *F. muscorum* on litter, and old stems of *Calluna* and *Erica* (Santesson, 1948).

Savannahs and semiarid grasslands

The few studies carried out in semiarid habitats include those of the Cerrado in Brazil (Maimoni-Rodella and Gottsberger, 1980), pindan vegetation of *Acacia* in Western Australia (Ing and Spooner, 1994), and the African

savannas and tropical dry forests (Dagamac et al., 2017b; Härkönen, 1981). Most common are litter-inhabiting species. Several rarely recorded species were recorded from dry forests in Ethiopia (Dagamac et al., 2017b), including *Didymium saturnus*, *Metatrichia floripara*, *Perichaena areolata*, and *Physarina echinospora*. Moreover, there is some evidence that similar to the situation with its unique flora, the East African mountain ranges may harbor a diverse and distinctive assemblage of myxomycetes. Of particular interest as substrates for myxomycetes are the hollow decaying trunks of giant tree-like lobelias. Other samples from similar habitats, placed in moist chamber cultures by Rammeloo (1975a,b), led to the description of several new species of myxomycete in the 1960s.

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Take-home messages

1. Stalked fruiting bodies are an ancestral character for myxomycetes, and spores are the key to understand their dispersal.
2. Height of release, spore size, and ornamentation seem to be the three decisive parameters for long-distance dispersal of spores in myxomycetes.
3. The global biogeography of myxomycetes should be revisited with the consideration of more molecular information in the future.
4. A number of geographical, ecological, and microhabitat associations that largely explain myxomycete biogeography are known.