Macroecology of Microbes – Biogeography of the Glomeromycota

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1 Introduction

1.1 Why Study Glomeromycotan Biogeography?

Arbuscular mycorrhizal (AM) fungi are among the most abundant soil microorganisms, associating with 95% of plant families and occurring on all continents of the globe (Smith and Read 1997; Trappe 1987; Read 1991). All AM fungi are members of the newly created phylum Glomeromycota (Schüβler 2001). They inhabit most latitudes and terrestrial ecosystems worldwide, including both natural and human impacted systems. Despite their prevalence in the environment and importance to plant productivity, much remains unknown about patterns of diversity and the biogeography of Glomeromycotan fungi. Biogeography is defined as the study of the geographic distributions of organisms and the mechanisms that drive these distributions. Traditionally, AM fungal diversity was thought to be locally high and globally low; up to 20 species can associate with an individual plant, but less than 250 species have been described worldwide (Morton et al. 1995; Bever et al. 2001). Furthermore, international germ collections have been established in North America and Europe where researchers from around the world can send soil samples to be cultured and archived. According to these collections, many communities from around the globe appear similar, with the same morphospecies such as *Glomus intraradices* seeming to occur globally (Morton and Bentivenga 1994). Over the years, the number of morphospecies in international germ collections has remained low while the number of accessions has increased, indicating low global biodiversity for AM fungi. Furthermore, many taxonomic species such as *Glomus intraradices* and *Glomus mosseae* have been observed in a variety of geographic locations in drastically different environmental conditions. Together, these observations have contributed to the notion that AM fungal species have global distributions. However, critics claim that much of the biogeographical inferences currently made

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about AM fungi are based on information gained from biased sampling and variable methods (Fitter 2005; Johnson and Wedin 1997). Indeed, as the number of scientists working with AM fungi increases and novel regions and ecosystems are sampled, new AM fungal taxa as well as novel morphological traits have been discovered (Bever et al. 2001; Kramadibrata et al. 2000). In addition, methods used to determine AM fungal diversity and species composition are shifting from morphological to DNA-based. New techniques, new species concepts, and collaborative research efforts have invigorated studies of AM fungal biogeography. Joining conceptual frameworks and quantitative models with empirical studies will greatly advance our knowledge of Glomeromycotan biogeography.

A better understanding of Glomeromycotan biogeography is important for the following reasons:

1.1.1 Microbial Biogeography is a Frontier in Ecological Research

The biogeography of cryptic and elusive organisms, particularly microbes, is considered an emerging frontier for the advancement of biogeography (Lomolino and Heaney 2004). Much of the research on microbial biogeography can be defined by the single statement "everything is everywhere, but the environment selects", written by Lourens Gerhard Marinus Baas Becking (1934) and inspired by the work of Martinus Beijrinck (1913) (de Wit and Bouvier 2006). The Baas Becking Hypothesis states that microorganisms are not limited in their dispersal capabilities and thus have global distributions; empirical differences in the composition of microbial communities are due to environmental conditions, which promote active (i.e., observable) species and suppress latent species. In other words, all microbial life is distributed worldwide and, in a given location, most microbial species are not observable because of unfavorable environmental conditions. Baas Becking developed these concepts after decades of work comparing algae, brine shrimp, and bacterial communities among salt lakes in California and all over the world (Baas Becking 1930; Baas Becking 1934).

Although the Baas Becking Hypothesis has influenced microbial ecology for nearly 100 years, new technologies have led to a recent surge in microbial biogeography research. Currently, DNA-based techniques are advancing studies of microbial communities in natural systems, and it is now accepted that traditional morphological and culturing techniques have grossly underestimated microbial diversity (Fry 1990; Torsvik et al. 1990; Tiedje 1995). A recent review of microbial studies that primarily used DNA-based techniques showed that environmental conditions do alter microbial community composition on a variety of spatial and temporal scales, but that microorganisms may not have global distributions (Martiny et al. 2006). This suggests that microbial biogeographical patterns may be more complex than the Baas Becking Hypothesis initially predicted; everything is not everywhere *and* the environment selects. Researchers are attempting to illuminate other patterns in microbial biogeography, such as distance–decay relationships, taxa–area relationships, and local:global taxa richness ratios (Green and Bohannan

2006; Green et al. 2004; Horner-Devine et al. 2004). Mycorrhizologists could learn a great deal from recent insights in the biogeography of prokaryotes and free-living microbial eukaryotes.

1.1.2 The Wallacean Shortfall

A paucity of knowledge about the biogeography of species is referred to as the "Wallacean Shortfall", after Alfred Russel Wallace's view that the key to understanding and conserving biological diversity is through the knowledge of the geographic distributions of organisms (Lomolino 2004). As discussed above, most of the recent research on microbial biogeography has focused on bacterial, archaeal, and protozoan communities. There is little basic information about the geographic distributions of AM fungi in natural systems. Understanding how the abundances of AM fungal species vary with space will provide insights into the factors that control AM fungal diversity and improve estimates of global biodiversity. Do Glomeromycotan species exhibit random, regular, or clumped distributions at spatial scales ranging from peds to continents? Is AM fungal diversity higher in tropical regions, as is the case for macroorganisms? Is AM fungal diversity higher in more heterogeneous habitats? Is global diversity of the Glomeromycota truly low or is it underestimated due to inadequate sampling or resolution of genetic variation? Do anthropogenic activities pose a threat to AM fungal biodiversity? More observational studies of AM fungal species distributions are needed to elucidate answers to such basic, but unexplored questions.

1.1.3 Unique Properties of AM Fungi could Contribute to Biogeographic Patterns

There are reasons to believe that AM fungal biogeography should be different from that of the free-living or even other symbiotic microbes. First, AM fungi are obligate biotrophs that are tightly linked with living host plants. Because of this close relationship with plants, their biogeographical patterns could mirror those of highly mycotrophic plants or plant families. Furthermore, AM fungi associate with members of every major plant clade (Helgason and Fitter 2005). This makes them different from other symbiotic root microbes, such as nodulating rhizobia, which only associate with plants in the Fabaceae family. The strong dependence on plant hosts and general ability to colonize a wide variety of plant lineages makes AM fungi an interesting case study in microbial biogeography.

And second, the ancient Ordovician origins of AM fungi could contribute to unique biogeographical patterns created by historical processes. The earliest fossil records of AM fungi are dated prior to the breakup of Pangaea and formation of separate supercontinents and continents (Redecker et al. 2000; Simon 1993). In fact, mycorrhizal associations were thought to be integral to the establishment and diversification of land plants (Helgason and Fitter 2005; Pirozynski and Malloch

1975). Historical biogeographic factors such as continental drift could have contributed to present-day distributions of AM fungal species. In the subdiscipline of historical biogeography, the theory of continental drift and plate tectonics can be combined with phylogenetic data to make inferences about the history of speciation and biotic assembly within and among geographic regions (Riddle and Funk 2004). Applying these techniques to the study of Glomeromycotan biogeography could give insight into AM fungal phylogeography and diversification history. Therefore, a better understanding of Glomeromycotan biogeography could also provide insights into AM fungal microevolutionary and macroevolutionary processes.

1.1.4 Soil Conservation Requires a Better Understanding of AM Fungal Biogeography

The importance of conserving soil and the ecosystem functions and services it provides is increasingly recognized, as soil loss, degradation, and contamination are more prevalent in natural and managed systems (Daily et al. 1997). Mycorrhizal fungi provide many important ecosystem functions and services at multiple scales: they influence resource acquisition in individual plants, productivity and diversity in plant communities, above- and belowground herbivore interactions, nutrient cycling, soil stability, and carbon sequestration in soils (Newsham et al. 1995; van der Heijden et al. 1998; Gehring and Whitham 2002; Miller and Jastrow 2000; Rillig 2004a; Johnson et al. 2006).

Preserving the functions and services that AM fungi provide in ecosystems requires a better understanding of Glomeromycotan biogeography because individual species and isolates function differently (Hart and Klironomos 2002; Hart and Reader 2002). Different taxa have been shown to provide different growth benefits to plants (Sanders and Fitter 1992; Klironomos 2003). Certain taxonomic groups can also differ morphologically, which could have ramifications for certain ecosystem functions and services. For example, taxa in the Gigasporaceae can produce more dense hyphal networks than those in the Glomeraceae, and these differences may influence soil structure and stability (Miller and Jastrow 2002; Rillig 2004b). In order to conserve the potentially unique ecosystem functions and services that AM fungal species provide, we require a better understanding of their geographic distributions.

Conserving AM fungal diversity in soils across different geographic regions may be important if the natural distributions of certain Glomeromycotan fungi are limited. If individual AM fungal taxa have restricted native distributions then introduction of these soil microbes into new environments could result in unintentional consequences. Production of AM fungal inoculum is a growing industry in North America, with fungi being marketed for agricultural, bioremediation, and restoration industries as well as personal use in home lawns and gardens. Only a few isolates of AM fungi are used universally in these inoculum products. If everything is everywhere, then inoculation with a particular fungal isolate may not be detrimental. However, if the distribution of Glomeromycota is nonrandom,

then inoculation will introduce nonnative and possibly invasive fungal species into new environments. Invasive AM fungi have never been observed in nature. However, this may be the result of inadequate methods to characterize the species composition of AM fungal communities in ecosystems. The potential for an AM fungal species or isolate to become invasive in a foreign introduced environment has never been empirically tested. Schwartz et al. (2006) discuss the possibility of this ecological scenario using examples of ectomycorrhizal fungi that have been documented to invade new environments and cause ecosystem-level alterations (Chapela et al. 2001; Pringle and Vellinga 2006). Because we know that AM fungi influence ecosystem processes in many ways and at many different scales, it is important to determine whether AM fungal inoculum is capable of spreading beyond targeted regions and displacing native AM fungal communities. The goals of this chapter are to:

1) Examine the state of knowledge of Glomeromycotan biogeography and explore the current challenges and benefits of elucidating Glomeromycotan biogeography.
2) Present a conceptual model for the factors that control AM fungal species distributions.
3) Discuss the relevance of spatial scales for the various factors that control AM fungal species distributions.
4) Suggest modeling approaches to address AM fungal biogeographical questions.
5) Generate hypotheses and encourage new research in the area of Glomeromycotan biogeography.

2 Challenges and Benefits of Elucidating Glomeromycotan Biogeography

The scientific discipline of biogeography did not begin with the study of microbes, and therefore the fundamental concept of "species", which is central to the study of geographic ecology, does not seamlessly translate for organisms like AM fungi. The biological species concept, which defines a species according to sexual reproductive isolation, is currently the dominant paradigm for macroorganisms (Mayr 1940). Species concepts for AM fungi, prior to the use of DNA-based techniques, have been predominately morphological. Researchers use asexual spore morphology to distinguish between species and determine AM fungal diversity and community composition (Morton et al. 1995). However, applying the morphospecies concept to AM fungi has several disadvantages. First, characters with which to distinguish species are few and high intraspecific morphological variation is common (Bever and Morton 1999; Bentivenga et al. 1997). Second, spores could reflect legacy communities instead of the species that are actively forming mycorrhizae with plant hosts. And third, not all taxa readily sporulate and therefore lack structures for morphological characterization. It has become evident than many AM fungal species are cryptic in nature and cannot be cultured using current techniques (Clapp

et al. 1995). Furthermore, greenhouse pot cultures do not always reveal the complete fungal community present in the field (Stutz and Morton 1996; Fitter 2005). In a survey in southern Utah, 47 spore morphospecies were found by examining field spores, but only 12 of these species were revealed in greenhouse pot cultures after 2 successive cycles of culturing (Chaudhary 2006). Although the morphospecies concept has a role in AM fungal ecology, it can no longer be the only method used for species identification.

The genetic species concept, where species are grouped by their degree of DNA similarity, has become a dominant paradigm in microbial ecology and could be increasingly useful for Glomeromycotan fungi. An advantage of using the genetic species concept is that DNA used for comparison can be extracted from roots, indicating that it was likely forming active mycorrhizae. Furthermore, this technique does not require spore identification skills, which can be difficult to acquire, time-consuming, and highly variable among researchers. Although DNA analysis can capture more genetic variability than morphological analysis, the proportion of DNA similarity commonly used to distinguish individuals of the same species (e.g., 97%) is often criticized as being chosen arbitrarily.

Perhaps the greatest benefit in nearing a working species concept for AM fungi lies in the combination of molecular and morphological techniques. This approach could contribute to the adoption of either an evolutionary or ecological species concept, which define species by their evolutionary lineages and ecological niches (Simpson 1961; Andersson 1990). According to these species concepts, species share common lineages where lineages evolve separately from others and are under the influence of similar selection pressures. Furthermore, species have a unique role in nature with their own ecological niche in the biotic community. The major challenge to using the evolutionary or ecological species concepts is that they lack simplicity and require a deeper understanding of the biology, evolution, and ecology of AM fungi. However, this understanding will benefit not only studies of biogeography, but also all of Glomeromycotan biology.

2.1 Molecular Techniques Offer an Alternative Approach

Recent methodological advances present mycorrhizologists with new tools to tackle previously unapproachable topics. The development of molecular tools that allow for more accurate in situ species identifications and easier community level analyses have already aided investigations of AM fungal diversity (Wolfe et al. 2007; Lekberg et al. 2007). Developing and applying these techniques is extremely important given the potential limitations and biases of spore and culture based identifications. The PCR-based techniques, such as terminal restriction fragment length polymorphism (T-RFLP) analysis (Liu et al. 1997), have opened the soil “black box” to more detailed investigations beyond morphological identification colonization quantification and immuno-assays (Horton and Bruns 2001; Johnson et al. 2004; Crawford et al. 2005).

The T-RFLP technique is potentially useful for biogeographical work. T-RFLP produces a community fingerprint for a sample, using PCR with fluorescently-labeled group-specific primers and endonucleases that generate fragments that are read by a laser-sequence analyzer to yield peak profiles. These peak profiles represent the assemblage of species that are present in the sample. However, each peak does not necessarily characterize a single observational taxonomic unit (OTU). This is because of the high potential intra-isolate and intraspecific genetic variation of AM fungi (Bever and Wang 2005; Pawlowska and Taylor 2005). A series of peaks most likely characterize a single OTUs. In order to make the peak to OTU link, a database of peak profiles needs to be generated. This can be done empirically by T-RFLP of single spores or predictively by developing peak profiles through analyzing known sequences for endonuclease cleavage sites. Recently, FitzJohn and Dickie (2006) developed TRAMP-R, a package for the R statistical program that can match unknown T-RFLP profiles with database knowns.

The requirement for an additional identification step makes the technique less advantageous, especially when sequencing technology is rapidly increasing in quality and quantity and decreasing in cost for larger numbers of sequences (Rogers and Venter 2005). Although having greater numbers of sequences would allow for more accurate studies and also greatly aid efforts for greater all-fungi phylogenetic resolution (see Blackwell 2006), the T-RFLP technique will undoubtedly aid AM fungal research as alternative technologies are being developed.

2.2 Resolving AM Fungal Micro- and Macroevolutionary Processes

Past and present evolutionary events and processes affect the spatial distribution of modern taxa. Work on major fossil collections (Redecker et al. 2000) and molecular clock estimates (Simon et al. 1993) have yielded insight into the past evolutionary history of AM fungi. As mentioned in the previous section, advances in molecular techniques and analyses are helping to resolve taxonomic relations both within the Glomeromycota and amongst all fungal taxa. This greater resolution of past fungal evolutionary processes will undoubtedly enhance and direct studies of AM fungal biogeography.

In addition, the current evolutionary processes that create and regulate diversity (i.e. extinction and speciation) play a role in determining AM fungal spatial distributions. Fitness is the determinant of evolutionary success and, therefore, is extremely important to our understanding of biogeography. Estimating fitness for AM fungi can be difficult given their apparent asexuality and clonal life form, but researchers continue to develop new methodological and theoretical approaches (Pringle and Taylor 2002; Pawlowska 2005). Studies of the genomic structure of AM fungi indicate that the genetic diversity of AM fungi is complex and needs further investigation (Sanders 2002; Pawlowska and Taylor 2005; Bever and Wang 2005). However, this is no large exception to the overall difficulties of estimating

fungal population dynamics and fitness. Spore abundance can potentially estimate population size and fitness, but it is problematic to treat spores as individuals in a population when the individual is actually the much larger mycelium that most likely extends well beyond the size of the sampling unit (e.g., a soil core). Furthermore, practical and theoretical problems exist in both measuring the size of AM fungal mycelia and defining the limits of the mycelium when AM fungi have been shown to anastamose (Rosendahl and Stukenbrock 2004; de la Providencia et al. 2005).

Soil is arguably the most complex substrate on earth. The variability of the structure, chemistry, and biological assemblage in soils has yet to be fully realized in the development of a conceptual framework for ecological and evolutionary processes in soils (Crawford et al. 2005). To date, soil ecologists have retrofitted evolutionary ecology theories from aboveground macroorganisms (Martiny et al. 2006). However, this may be insufficient with respect to soil microorganisms, especially fungi. This is at least in part related to their interaction with, and the associated adaptations to, such a complex substrate, but it is also related to inherent differences in their life history and reproductive strategies. Given the high level of spatial and temporal heterogeneity in physical and biological factors, biogeographic studies of soil organisms, especially AM fungi, will benefit greatly from a model-based, exploratory approach.

2.3 A Model for Glomeromycotan Biogeography

Model building is useful for the process of formulating mechanistic hypotheses, identifying gaps in current knowledge, and eventually testing hypotheses with empirical data. Models are particularly powerful when specific predictions and assumptions are made explicit. We formulated a graphical conceptual model of the factors controlling the distribution of AM fungal species for several purposes. First, the model presents the major factors that directly and indirectly influence AM fungal species distributions. Second, the model provides an organized infrastructure in which to discuss the major mechanisms that drive species distributions. The specific prediction of this model is presence or absence of an AM fungal species in a given geographic location. And third, the model highlights hypotheses that have both been empirically tested and those where more research is needed. Mechanisms that influence species distributions vary depending on the scale of the geographic location of interest, a topic that is discussed in greater detail at the end of this chapter.

Both external forces and intrinsic properties of an organism determine the distribution of a species. In our model, factors that influence AM fungal species distributions are separated into three broad categories: abiotic external forces (rectangles), biotic external forces (octagons), and intrinsic properties (ovals) (Fig. 1). It is important to note that although few studies have directly demonstrated the effects of these three factors on species distributions, we have interpreted studies that report changes in

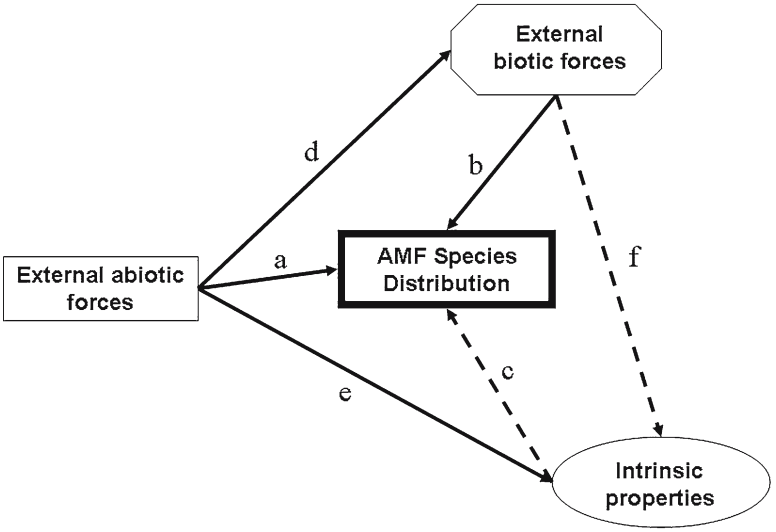

Fig. 1 Factors that influence AM fungal species distributions can be separated into three broad categories: abiotic external forces (*rectangles*), biotic external forces (*octagons*), and intrinsic properties (*ovals*). *Arrows* represent a causal influence that one factor has on either AM fungal species distributions directly (*bold box*) or on another factor. *Solid arrows* represent mechanisms that have support from published research while *dotted arrows* represent possible mechanisms that to our knowledge have never been studied

species abundances or community composition to indicate a potential for environmental effects on species distributions. Furthermore, arrows make no claim as to the strength of each causal influence or sign of the effect (positive or negative). In this way, our model is similar to an a priori model that one would formulate prior to the process of structural equation modeling (Grace 2006). Although the purpose of our model is to organize our understanding of concepts, the direction and relative strength of certain hypothesized relationships could eventually be tested with empirical data.

External abiotic forces, external biotic forces and intrinsic properties of an AM fungal species all directly influence its geographic distribution (Fig. 1). External abiotic forces, such as precipitation or edaphic characteristics, can directly influence the available habitat for a species, which affects an organism's ability to colonize and exist in a given location (Fig. 1, path a). External biotic forces, such as host plant specificity or fungal grazing, can also directly influence the ability of a species to colonize and exist in a particular geographic location (Fig. 1, path b). Paths a and b are solid, indicating that studies have demonstrated how abiotic and biotic external forces influence AM fungal community structure and composition (see discussion below). Intrinsic properties of a species, such as dispersal ability, can also directly influence its ability to colonize a location and therefore its geographic distribution (Fig. 1, path c). Other intrinsic properties such as rate of speciation or extinction can influence whether or not a species will be present in a given geographic location. In our model, path c is dashed to demonstrate the paucity of such autecological research

that addresses how intrinsic biological properties of species influence geographic distributions.

External abiotic forces, external biotic forces and intrinsic properties of species also influence AM fungal geographic distributions indirectly through their interactions with each other (Fig. 1). First, external abiotic forces could indirectly influence AM fungal species distributions by affecting organisms that generate external biotic forces (Fig. 1, path d). For example, precipitation regime could influence the host plant community, which could then influence AM fungal species distributions. Second, external abiotic forces such as climate could also indirectly influence species distributions by influencing intrinsic properties of species such as dispersal ability (Fig. 1, path e). For example, spores of the same AM fungal species may disperse differentially in a dry climate compared to a wet climate. And lastly, external biotic forces could indirectly influence geographic distributions by affecting intrinsic properties of species (Fig. 1, path f). For example, belowground herbivores such as microarthropods could preferentially graze on certain AM fungal species influencing dispersal rates.

In the following sections, we dissect the three main portions of the main model presented in Fig. 1 and discuss in detail the various abiotic and biotic external forces and intrinsic properties that could influence AM fungal species geographic distributions. Because one model with all the parts would be cumbersome to discuss we initially take a modular approach and then conclude with synthesis. Each section is organized in a manner such that direct effects of factors on AM fungal species distributions are discussed first, followed by a discussion of how factors interact to influence AM fungal geographic distributions.

2.4 Abiotic External Forces

2.4.1 Climate

Climate factors, such as precipitation and temperature, could directly influence AM fungal species distributions (Fig. 2, path a). Precipitation can alter soil moisture content, evapotranspiration rates, and plant productivity, all of which can have AM fungal community consequences. In a study of five grasslands in North America that ranged in precipitation from semi-arid to mesic (244–890 mm), Gigasporaceae spores were absent from both semi-arid sites and present in the mesic sites (Johnson et al. 2003). In a comparison of high and low rainfall sites in a wet tropical rainforest in Costa Rica, spores of *Glomus* and *Entrophospora* species were more common in the low rainfall site (Lovelock et al. 2003). In studies where precipitation was constant but soil moisture content varied, AM fungal community differences have also been observed. Across a wide soil hydrological gradient in coastal South Carolina, *Glomus etunicatum, Acaulospora laevis/koskei*, and *Scutellospora heterogama* were found to be intolerant of flood conditions while *Glomus clarum* and *Acaulospora trappei* preferred the wettest sites (Miller and Bever 1999). In a study of California tidal marshes and adjacent upland sites, AM fungal species diversity

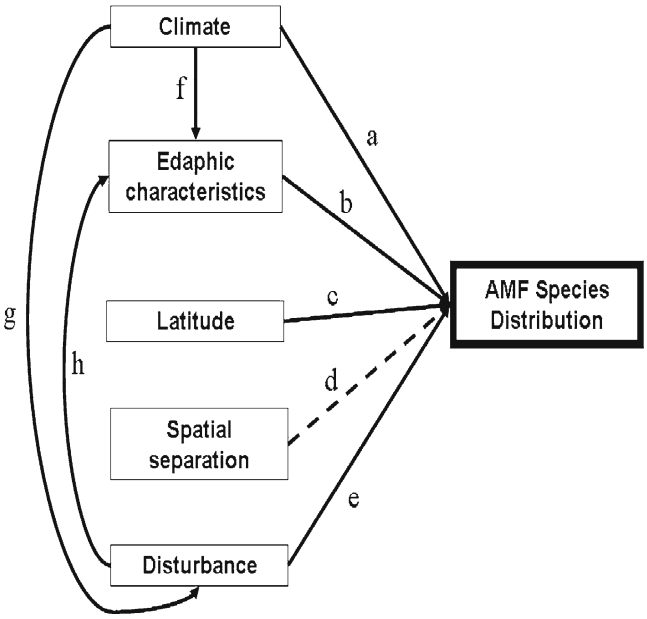

Fig. 2 Abiotic external factors (*rectangles*) that can directly and indirectly influence AMF species distributions *(bold box)*

was found to be similar across soil moisture regimes, but spore abundances differed with soil moisture (Brown and Bledsoe 1996). These field studies suggest that precipitation and soil moisture regimes could influence AM fungal species distributions.

Temperature regimes could also directly influence the geographic distributions of AM fungi as certain species can tolerate – or even thrive in – extreme air and soil temperatures. In greenhouse conditions, warmer air temperatures promoted spore abundance of *Glomus aggregatum, Gigaspora margarita*, and an unknown *Glomus* species (Redman and Johnson, unpublished data). Furthermore, air temperature is not always correlated with soil temperature. In Yellowstone National Park in the western United States, geothermal activity creates a vertical soil temperature gradient such that temperature increases with depth. Researchers have observed AM fungal colonization of plants in soils reaching temperatures of up to 48 °C (Bunn and Zabinski 2003) and extraradical hyphae in soil temperatures too high for roots to exist. Certain AM fungal species may be more tolerant to extreme soil temperatures. Extreme fluctuation of soil temperature, either seasonal or diurnal, is a common stress in nature and a potentially underestimated abiotic factor that drives AM fungal species distributions.

The degree of seasonal or diurnal fluctuation in temperature and precipitation regimes could influence AM fungal species distributions. Seasonal variation in sporulation as well as fungal abundance in roots varies by species (Gemma et al. 1989; Giavanetti 1985). Contrasting and complimentary seasonal phenologies has

been suggested as a possible mechanism that promotes diversity within AM fungal communities. In a North Carolina grassland, *Gigaspora gigantea* sporulated in the cool season while *Acaulospora colossica* sporulated in the warm season (Pringle and Bever 2002). To our knowledge, the influence of diurnal temperature or precipitation fluctuation has never been studied. The habitat heterogeneity hypothesis predicts that regions with low seasonal or diurnal climatic fluctuation should have lower AM fungal alpha or gamma diversity than regions with greater seasonal (e.g., tallgrass prairie) or diurnal (e.g., deserts) climatic fluctuation (Tews et al. 2004). A more heterogeneous habitat could mean more available niche space for species, which could promote persistence of species that disperse into a region. On the other hand, regions with less variable climates may experience less selection events and thus the persistence of a greater number of species. Seasonal and diurnal climate variability should be considered an abiotic external property that influences AM fungal geographic distributions.

2.4.2 Edaphic Characteristics

A substantial body of published literature has shown how edaphic characteristics, such as soil texture and structure, organic matter content, pH, and macronutrient and micronutrient dynamics can influence AM fungal community structure. These studies indicate that edaphic characteristics likely influence AM fungal species distributions in nature (Fig. 2, path b). Soil texture, or particle size distribution, affects many soil properties such as structure, porosity, water holding capacity, and cation exchange capacity. In an experimental garden, *Gigaspora* species preferred sandy soil, while *Entrophospora infrequens* preferred pure sandy loam and *Glomus mosseae* and *Scutellospora calospora* both preferred less sandy soils (Johnson et al. 1992). The observation that *Gigaspora* species preferentially exist in sandy soils is well documented and could be related to the fact that they generally produce large amounts of extraradical hyphae. Communities in sandy soils may shift preferentially towards *Gigaspora* for increased soil stability. Soil organic matter content could also influence AM fungal species distributions although the direct mechanism is unknown.

Most soil organisms subsist in a suitable pH range, but certain AM fungal species have been found to be tolerant to extreme soil pH (reviewed in Abbott and Robson 1991). Furthermore, soil pH affects nutrient availability and plant functioning, which could have indirect effects on AM fungal community structure. In a greenhouse experiment, two AM fungal species were affected differently by liming with $CaCO_3$ (Abbott and Robson 1985). *Glomus fasciculatum* formed mycorrhizae at a pH range of 5.3–7.5 while unidentified *Glomus* isolate WUM16 only formed mycorrhizae at pH 7.5. This evidence suggests that different AM fungal species vary in their pH ranges, which could influence AM community structure. Natural variation in soil acidity in different geographic locations could restrict AM fungal species distributions. Furthermore, human activities that alter soil pH, such as mining, could alter the natural distributions of certain AM fungi.

The influence of soil nutrients, particularly nitrogen and phosphorus, on the AM symbiosis is possibly studied the most by mycorrhizologists. The influence of nitrogen and phosphorus on AM fungal community composition has been examined. Recent work has found that AM fungal community composition shifts in response to anthropogenic nitrogen deposition and nitrogen fertilization (Egerton-Warburton and Allen 2000; Johnson et al. 2003). Furthermore, ambient soil phosphorus influences the response of AM fungi to nitrogen enrichment. Nitrogen-fertilized field plots in phosphorus-rich soil have showed a decrease in *Gigasporaceae* species while nitrogen enrichment of phosphorus-poor soil showed an increase in *Gigasporaceae* species (Egerton-Warburton et al. 2007). These studies indicate that natural variation in nitrogen and phosphorus stoichiometry could influence AM fungal species distributions. Furthermore, anthropogenic increases in N and P deposition will alter the geographic distributions of AM fungi. Many more edaphic characteristics could directly affect AM fungal species distributions, but this area of research has been previously reviewed (Abbott and Robson 1991; Lambert et al. 1980; Porter et al. 1987). Our brevity in this section should not be interpreted to indicate that edaphic properties are not an important control of AM fungal species distributions.

2.4.3 Latitude

Since the early observations of Linnaeus, Humboldt, Darwin, and Wallace that biological diversity is higher in tropical regions compared to temperate regions, ecologists have considered latitude to be a strong force that drives the distributions of many types of organisms on earth. Although there are exceptions to the rule, species richness of macro organisms generally decreases in regions closer to the poles (Hillebrand 2004). Many mechanisms have been proposed to explain the latitudinal diversity gradient including frequency of perturbation, higher productivity, higher environmental heterogeneity, and differences in speciation and extinction rates (Brown 1995). Latitude is correlated with increased surface area, climatic gradients, and solar energy inputs (Rohde 1992). The latitudinal diversity gradient has been referred to as "a pattern in search of a theory" (Rosenzweig 1992). Geographic ecologists who focus their studies on macro organisms are now primarily concerned with demonstrating which mechanisms are responsible for creating higher biodiversity in the tropics (Rohde 1992). Geographic ecologists who focus their studies on microorganisms, in particular soil microbes, must first demonstrate whether or not the latitudinal diversity gradient pattern exists for these organisms. Are soil microbes examples of or exceptions to this widespread ecological pattern?

For the most part, ecologists have yet to determine whether microorganisms exhibit the same latitudinal patterns as macroorganisms. However, some evidence suggests that the community structure of certain microbes changes along latitudinal gradients. For example, communities of gram-negative soil bacteria differed along an 800-km transect, and certain soil fungal communities differed along a southeast to northwest transect in western Canada (Staddon et al. 1998; Morrall 1974). Also,

aerobic anoxygenic phototropic bacterial communities differed along a 20,000-km marine latitudinal transect (Schwalbach and Fuhrman 2005). As studies in microbial biogeography become more prevalent, efforts should be made to not only document geographic variation in community structure, but also the mechanisms that drive biogeographical patterns (Martiny et al. 2006). This is important because studying microbial biogeography could lead to advances in the general field of biogeography. For example, recent studies have investigated speciation rate as a possible mechanism to explain higher biodiversity in the tropics. This hypothesis states that in warmer, more productive environments, metabolic rates and thus mutagenesis rates are higher creating higher rates of evolution and speciation. This hypothesis was supported by an empirical study that showed twice as much nucleotide substitution (ITS region rRNA-encoding DNA) in tropical plants compared to temperate plants (Wright et al. 2006). Furthermore, models that predict genetic divergence and speciation by metabolic rate were confirmed using contemporary and fossil data on planktonic foraminifera (Allen et al. 2006). Certain microorganisms represent a model system in which to empirically test such hypotheses because one can easily manipulate small environments, empirically measure metabolic rates, and observe genetic divergence and evolution.

Some evidence suggests that distributions of AM fungal species vary along latitudinal gradients (Fig. 2, path c), but the mechanisms that contribute to these patterns remain unknown. The issue is further complicated by the fact that AM fungi are obligate symbionts and must always be associated with host plants. Differences in AM fungal communities observed along a latitudinal gradient could be due to host specificity or other environmental variables that change along with latitude. In a latitudinal survey of AM fungal spore communities in coastal dunes along the eastern coast of the United States, plant host was held constant to control for any influence of host specificity (Koske 1987). Along this 355-km transect, AM spore species richness increased and spore community structure shifted with decreasing latitude. *Scutellospora* species such as *S. verrucosa, S. fulgida*, and *S. dipapillosa* dominated the southern half of the transect, but not the northern half. Furthermore, other latitudinal observations of AM fungi have been made such as higher *Sclerocystis* (i.e., *Glomus*), *Acaulospora*, and *Scutellospora* species diversity in the tropics and fewer *Gigaspora* species in northern Europe (Gianinazzi-Pearson and Diem 1982; Herrera-Peraza et al. 2001; Walker 1992). To our knowledge, no studies have been conducted to determine the possible mechanisms that could contribute to the differences in AM fungal community structure along a latitudinal gradient.

More research is needed in many regions of the world with latitudinal gradients of varying sizes to determine the degree to which AM fungal richness and species distributions vary by latitude. These studies are important because they will not only elucidate whether AM fungi follow the latitudinal diversity gradient so prevalent in macroorganisms, but also to increase the amount of species distribution data for tropical regions. Often the task seems daunting because many other factors are confounded with latitude such as changes in climate and host plant communities. However, advances in spatial and statistical modeling present alternatives for controlling environmental conditions, such as measuring the relative contributions of

different environmental factors. Different options and approaches are discussed below in the section on modeling.

2.4.4 Spatial Separation

In general, macroorganisms exhibit strong distance–decay relationships such that community similarity decreases with increasing distance (Nekola and White 1999). This pattern is also interpreted as spatial autocorrelation of community composition or high β–diversity (Magurran 1988). Little is known about the distance–decay relationships of microorgansisms and AM fungi are no exception (Green and Bohannan 2006). Spatial separation can influence AM fungal species distributions (Fig. 2, path d) and can be achieved in a number of ways such as long distances, geographic barriers, or simply a patch of inhospitable soil matrix. Indeed distance-decay relationships vary depending on the scale of study, with certain communities of microbes exhibiting higher β-diversity within continents than between continents (Cho and Tiedje 2000; Franklin and Mills 2003).

Vast geographic separation, such as that found between continents, can create distinct ecological provinces, or regions with biotic communities that reflect the legacy of historical events (de Candolle 1820; Martiny et al. 2006). For example, Australia is often considered a distinct province because it contains many unique animal and plant species that can be attributed to its long isolation from other continents. Tectonic history of a geographic locale can provide insight into length and degree of spatial separation that species from that location have undergone. Advances in plate tectonics have revealed that the configuration of land and sea on the earth is continually changing in time, creating new corridors and barriers to the movement of terrestrial species (Scotese 2004). Furthermore, phylogenetics allows biogeographers to track evolutionary patterns over space and time (Riddle and Funk 2004). The growing subdiscipline of phylogeography aims to understand the geographic distributions of genealogical lineages, bridging ecological and historical aspects of biogeography (Avise 2000; Riddle and Hafner 2004). Microbial biogeographers will benefit from recent advances in molecular techniques that facilitate phylogeographical studies.

The deep evolutionary origins of AM fungi predate the formation of present-day continents; such ancient vicariance events could strongly influence species distributions (Fig. 2, path d). Throughout the Mesozoic, North America and Eurasia made up the supercontinent Laurasia, while South America and Africa together were called Gondwanaland. The continents of North America and Eurasia have been separated by ocean for a shorter period of time than North America and South America. One might expect the AM fungal communities of North America and Europe to be more similar to each other than to the communities of South America or Africa. This might also suggest that global estimates of number of AM fungal species (currently less than 250) could be low since the majority of sampling has occurred in North America and Europe, two ecological provinces that separated early during the break-up of Pangaea. Using new technologies in molecular ecology,

phylogeography, and plate tectonic modeling, great advances could be made to better understand ecological provinces for AM fungi, dispersal capabilities, and the spatial dynamics of AM fungal evolution.

2.4.5 Disturbance History

Disturbances, either natural or human-caused, can directly influence AM fungal species distributions (Fig. 2, path e). A disturbance could disrupt fungal networks, destroying individuals and reducing the distribution of one or many species. The most obvious example, and perhaps the most pressing environmental problem of our time, is the reduction of habitat and associated loss of biodiversity due to human activity (Pimm et al. 1995; Wilcove et al. 1998). On the other hand, certain disturbances can increase available habitat by creating habitat heterogeneity and altering niche availability. Furthermore, in a successional framework, "late-successional" AM fungal communities may diminish while "early-successional" community distributions may increase (Connell and Slayter 1977). Many types of disturbances have the potential to create spatial patterning in species distributions.

Previous studies have shown that natural disturbances can influence the structure and composition of AM fungal communities. Fire can alter AM fungal species distributions depending on the timing, extent, and intensity of the burn (Bentivenga and Hetrick 1991; Eom et al. 1999; Dhillion and Anderson 1993). Forces that initiate primary succession, such as glacial retreat and volcanic flow, create substantial soil disturbance and also influence AM fungal distributions. After the eruption of Mount St. Helens (Washington, U.S.A.) in 1980, AM fungal communities were buried by ash and sterile tephra and were only resurrected in the presence of appropriate animal vectors (Allen 1991; Allen et al. 1987). Forces that initiate secondary succession, such as tropical storms, are generally associated with less soil disturbance and could have less of an impact on AM fungal community structure and composition than primary successional forces (Allen et al. 1998).

A substantial amount of research has shown how human disturbances and land use practices influence AM fungal communities and could therefore impact natural geographic distributions of AM fungi. Anthropogenic disturbances such as mining, grazing, and agriculture, have all been documented to influence AM fungal communities and thus have the potential to create spatial patterning in species distributions (Abbott et al. 1983; Miller 1987; Sieverding 1990; Allen 1991; Johnson and Pfleger 1992; Eom et al. 2001). It is possible that human activities have led to undocumented biodiversity losses in AM fungi, just as they have led to biodiversity losses in animal and plant species.

2.4.6 Abiotic Interactions

Thus far we have discussed how several types of abiotic external factors can directly influence AM fungal communities and species distributions. However,

these abiotic factors can also interact to affect species distributions via a myriad of different mechanisms. First, climate influences edaphic characteristics that in turn affect AMF species distributions (Fig. 2, paths f and b). For example, high mean annual precipitation can leach soils, reducing soil fertility and increasing acidity, both factors that have been shown to influence AM fungal community structure. Second, climate and disturbance can interact to influence AM fungal species distributions (Fig. 2, paths g and e). An example of this process is the differential influence of tillage on AM fungal populations between arid and mesic environments (Jasper et al. 1991). And third, disturbances can change edaphic characteristics that in turn influence AM fungal species distributions (Fig. 2, paths h and b). Disturbances such as fire and intense livestock grazing can change the structure of soil which influences AM fungal communities. Much more research has been done on direct effects of abiotic factors on AM fungal communities than indirect effects or interactions of abiotic factors. Because, in nature, many abiotic factors act in concert, more work is needed on the influence of interactive effects on AM fungal distributions.

2.5 Biotic external forces

2.5.1 Host Plant Community

Glomeromycotan fungi are obligate biotrophs – they cannot live without a plant host (Smith and Read 1997). Because they are symbiotic microorganisms, their biogeographical patterns may be different from that of free-living microbes. Other types of host-associated microbes, from human gut bacteria to leaf parasites, have been observed to exhibit patterns in distribution that are related to their hosts (Falush et al. 2003; Zhang and Blackwell 2002). In a study of nodulating rhizobia in agroecosystems at nine sites across three continents, an ITS phylogenetic analysis yielded 23 different species groups that grouped independently from site, host species, or degree of isolation (Bala et al. 2003). In other words, related rhizobial species associated with different legume species from different sites located on widely separated continents. This study illustrates that obligate, typically-generalist root symbionts can exhibit biogeographical and phylogeographical patterns that are distinct from their plant hosts.

The degree of host-specificity that an AM fungus exhibits will largely determine whether its geographic distribution will be dictated by the host plant community (Fig. 3, path a). Glomeromycotan fungi were largely thought to be generalists, but research has shown that species can exhibit host specificity (Bever et al. 2001; Sanders 2002). In other words, certain AM fungal species preferentially associate with certain plant species. Host-specificity could also occur at the population scale indicating local adaptation (Schultz et al. 2001). It follows that differences in plant community composition coupled with host-specificity could create variation in species distributions of AM fungi. In a meta-analysis of studies that used small subunit

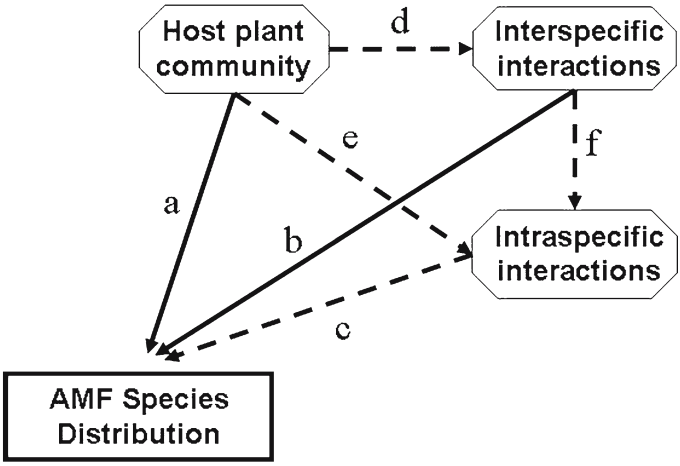

Fig. 3 Biotic factors (*octagons*) that can directly and indirectly influence AMF species distributions *(bold box)*

ribosomal DNA sequences to assess AM fungal species, taxa diversity was compared across sites and different broad vegetation types (Öpik et al. 2006). Although a number of AM fungal taxa had global distributions, 50% of the taxa were recorded from only a single site. Furthermore, AM fungi grouped by vegetation type such that taxa from a tropical forest in Panama were more genetically similar to each other than to those found in grasslands from many regions of the world. However, in a landscape-scale survey of spore communities, where the dominant plant host was always *Artemisia tridentata*, AM fungal species exhibited spatial patterns in distributions regardless of host plant (Allen et al. 1995). Authors attributed these patterns largely to latitude and contemporary environmental conditions. More studies need to be conducted to understand the spatial patterning of AM fungal species as well as the mechanisms that contribute to these patterns. Future studies in AM fungal biogeography should take into consideration the potential for AM fungal species to exhibit strong host-specificity.

Another important issue to consider in the discussion of how plant communities influence AM fungal geographic distributions is the prevalent ecological problem of invasive species. Human-introduced invasive plant species are causing dramatic changes to natural landscapes worldwide and are considered a serious threat to biodiversity (Wilcove et al. 1998). As plant communities shift toward monoculture, the distributions of fungal species could also change due to these invasions. Recent evidence suggests that plant invasions can influence other soil microbes, changing community composition and ecosystem function (Belnap and Phillips 2001; Hawkes et al. 2005; Batten et al. 2006). Some evidence has shown how human-introduced invasive species can influence AM fungal communities (Siguenza et al. 2006a, 2006b). In a recent study, AM fungal T-RFLP profiles of roots from areas dominated by native vegetation were

significantly different from areas dominated by *Centaurea maculosa*, an invasive mycorrhizal forb (Mummey and Rillig 2006). Taxa diversity was also lower in sites dominated by *Centaurea maculosa*. This study suggests that widespread plant invasions have already altered AM fungal communities and, if measures are not taken to control invasive plant species, natural distributions of AM fungal species will continue to be at risk.

2.5.2 Inter- and Intraspecific Interactions

Other organisms besides host plants could directly influence AM fungal species distributions through a variety of different mechanisms such as dispersal, mycophagy, competition, and facilitation. Interspecific interactions could restrict or expand AM fungal species distributions in many ways (Fig. 3, path b). Different types of belowground animals feed on AM fungi, either reducing distributions through consumption or increasing distributions by promoting dispersal (Allen 1991; Gange and Brown 2002). In addition, belowground animals exhibit preferential feeding for certain AM fungal species; depending on the viability of the fungi after passing through the animal's digestive system this interaction could be either beneficial or detrimental for the fungus. Aboveground animals can disperse AM fungal propagules (Gehring et al. 2002), but also compete with the fungi because both share the same plant carbon source (Gehring and Whitham 2002).

In addition to other types of organisms interacting with AM fungi to influence geographic distributions, effects from AM fungi of either different or the same species could influence distributions. Very little is known about how different AM fungal species interact with each other and even less is known about how "individuals" of the same fungal species interact with each other. Studies have shown how AM fungal species grown singly or in a mixed community interact to influence plant productivity and diversity (van der Heijden et al. 1998). However, we know of no studies that have compared the productivity or fitness of fungi grown in a mixed community compared to a fungal monoculture. Furthermore, we know of no studies that have examined the influence of intraspecific interactions on fungal productivity or fitness (Fig. 3, path c). Spatially, positive interspecific or intraspecific interactions could create a clumped distribution while negative interactions might create a regular distribution (as opposed to a random distribution) (Brown et al. 1995). Imagine positive interactions as attractive magnetic forces and negative interactions as two repellent sides of a magnet. These hypotheses suggest that spatial distributions could help elucidate the magnitude and sign of AM fungal species interactions in field conditions.

2.5.3 Biotic Interactions

Biotic factors can influence AM fungal species distributions directly and also indirectly through interactions that the host plant community, interspecific interactions, and intraspecific interactions can have on each other. As with abiotic factors, much

less research has been conducted on how biotic factors interact to indirectly influence AM fungal species distributions compared to direct effects of biotic factors on AM fungi. Nonetheless, these interactions likely exist in nature and we can speculate about several of the possible mechanisms. First, host plant community could influence interspecific interactions, which can then go on to affect species distributions (Fig. 3, paths d and b). In other words, certain interspecific interactions are dependent on the host plant community. For instance, animals that disperse AM fungal propagules may preferentially reside in certain vegetation communities. Second, host plant community could also influence intraspecific interactions, which could then go on to affect AM fungal species distributions (Fig. 3, paths e and c). Although we know of no studies that have examined this process it is feasible that intraspecific interactions could vary depending on the host plant community. A plant's ability to sustain AM fungal individuals could influence the magnitude and sign of intraspecific interactions observed between fungi of the same species. For example, highly dependent plants may sustain more AM fungi, reducing intraspecific competition and encouraging a clumped distribution. On the other hand, facultative hosts may sustain less AM fungi, enhancing intraspecific competition, contributing to a more regular distribution. And third, interspecific interactions could influence intraspecific interactions, going on to affect AM fungal species distributions (Fig. 3, paths f and c). For example, fungal grazers could keep the population size of a particular fungal species low, reducing intraspecific competition and contributing to a clumped spatial distribution. No doubt a myriad of interactions exist among AM fungi and other organisms that could influence the geographic distributions of Glomeromycotan fungi. Most of these interactions remain to be explored.

2.6 Intrinsic properties

2.6.1 Dispersal Ability

Species possess inherent properties that directly and indirectly influence their biogeographical patterns in nature (Fig. 4). The ability of a species to disperse actively through locomotion or passively via a physical or biological agent (e.g., wind, water, animal vectors) can greatly influence its geographic distribution. Microbes have traditionally been thought to have unlimited dispersal capabilities, further contributing to the concept that "everything is everywhere". However, this idea has been recently challenged as body size is not a strong predictor of dispersal capability; many large organisms (e.g., redwood trees) lack long-range dispersal abilities and microbes with active propulsion mechanisms are still unable to cross vast geographic barriers (Martiny et al. 2006). Another type of dispersal, where a species expands its range by moving outward at the boundary of its distribution, is independent of body size and could potentially lead to global distributions of microbes. However, it has been argued that range expansion would be followed by genetic divergence from the

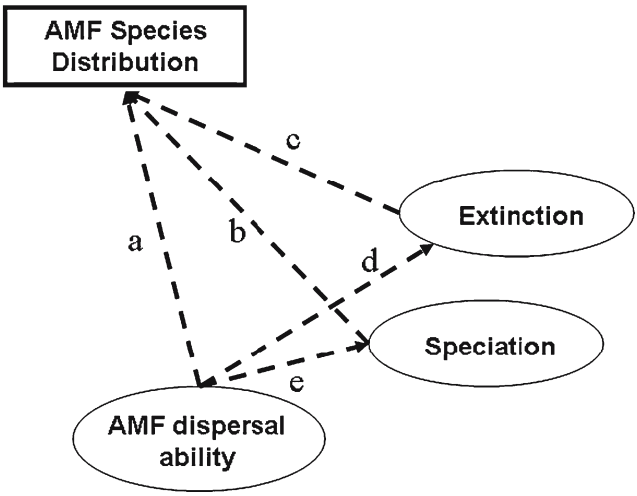

Fig. 4 Intrinsic properties of AM fungal species or isolates (*ovals*) that can directly and indirectly influence their spatial distributions *(bold box)*

source population, creating non-random biogeographical patterns (Martiny et al. 2006). Indeed, just as the dispersal capabilities of macroorganisms are species-specific, microorganisms likely vary in their inherent dispersal abilities as well.

Research has shown that Glomeromycotan fungi are able to disperse in many different ways. Physical forces such as wind and water and biological forces such as animal vectors all act as agents for the passive dispersal of AM fungi. Wind is a substantial dispersal agent in arid and semi-arid environments, moving fungi up to 2 km (Warner et al. 1987). Soil erosion of volcanic, beach, and arid environments can also release fungal propagules (Allen 1991). The influence of aboveground and belowground water movement on AM fungal dispersal is much less understood, but likely plays an important role in dispersal in mesic environments. Animal vectors, from birds to small mammals to nematodes, can disperse spores and hyphal fragments either through ingestion or by the fungi sticking to their bodies (McIlveen and Cole 1976; Ponder 1980; Rabatin and Rhodes 1982; Rothwell and Holt 1978; Allen 1991; Janos et al. 1995; Gange and Brown 2002; Gehring and Whitham 2002). Furthermore, plant hosts could facilitate the belowground range expansion of AM fungi. As hyphal networks expand in the soil matrix they encounter other root zones, initiating new infection points and spreading via "root-to-root" contact (Read et al. 1976; Allen 1991). In certain environmental conditions, hyphal growth can occur at a rate of 30 cm per year. Although research has been conducted to demonstrate several ways in which AM fungi can disperse, much remains to be investigated regarding how AM fungal taxa vary in their dispersal abilities and how this natural variability influences geographic distributions of species.

Although much remains unknown about AM fungal dispersal, inherent differences in dispersal abilities among species likely influence patterns in geographic

distributions (Fig. 4, path a). Fungi in the Glomeromycota also represent an interesting case study in microbial biogeography because the body size of fungal individuals can vary substantially. Fungal individuals comprised of intraradical structures, extraradical hyphal networks and spores can vary in size from millimeters to kilometers, a difference of six orders of magnitude. Spores of certain *Gigaspora* species can be almost 1 mm in diameter while spores of certain *Glomus* species can be smaller than 10 µm. Some morphospecies have highly variable spore sizes, such as *Glomus intraradices* with spores ranging from 40 µm to 190 µm in diameter (Schenk and Perez 1990). Furthermore, portions of the hyphal network of certain AM fungal species are totipotent, able to form new individuals from a single fragment. These observations indicate that body size or spore size alone are poor indicators of dispersal ability.

However, other life history traits indicate that species-specific differences do exist in the dispersal capabilities of AM fungi. Take for example a hypothetical comparison of the dispersal capabilities of two very different AM fungal taxa: Species A and Species B. Species A produces large spores (>500 µm) and extensive extraradical hyphal networks, but does not produce totipotent hyphal fragments. In other words, dispersal in Species A is limited to passive dispersal of spores and range extension via belowground hyphal network expansion. Furthermore, the large spores of Species A may be more likely to disperse via water and animal vectors than wind. Species B on the other hand produces small spores (<100 µm), less extensive extraradical hyphal networks, and totipotent hyphal fragments. Dispersal in Species B can occur via passive dispersal of spores, hyphal fragments and colonized root fragments. Because the spore size of Species B is small it can disperse via wind, water, and animal vectors. Species A could represent a *Gigaspora* species and Species B could represent a *Glomus* species. It is possible that observed differences in the geographic distributions of these two species could be due purely to their inherent differences in dispersal capabilities.

Life history traits of species strongly interact with environmental conditions to determine dispersal capabilities. In an environment where wind is the dominant dispersal agent, Species A might have a more clumped spatial distribution than Species B because its spores are too heavy for passive wind dispersal and it must rely on hyphal network range expansion. However, in an environment where water is the dominant dispersal agent, spores of Species A and Species B would both be dispersed creating similar spatial distributions for both species. Hypotheses regarding how life history strategies influence AM fungal species dispersal and therefore spatial distributions need further testing in a variety of different environments.

2.6.2 Speciation and Extinction

Evolutionary processes contribute to past and present geographic distributions of species (Brown and Gibson 1983). Speciation through the mechanisms of mutation, genetic drift, and natural selection can create genetic differentiation among populations, resulting in new species and a change in the original distribution. Extinction

is achieved through either a localized or complete elimination of a population, resulting in a reduced or eradicated geographic range. In general, speciation rates of microorganisms are believed to be quite high due to high mutation rates, short generation times, high population densities, and mechanisms for genetic recombination such as horizontal gene transfer (Lenski and Travisano 1994; Rainy and Travisano 1998). Microbial biogeographers suggest that high speciation rates coupled with poor dispersal would contribute to non-random biogeographical patterns; indeed certain bacteria have exhibited genetic differentiation and diversification following geographic isolation (Falush et al. 2003). However, microorganisms with high dispersal capabilities could have low speciation rates due to large amounts of gene flow. Extinction rates may also be predictable from population dynamics and dispersal capabilities. For instance, microorganisms with high dispersal capabilities and large populations likely have wide distributions and the ability to avoid complete extinction due to stochastic events. However, microbes with poor dispersal capabilities and small populations may be more prone to extinction (Martiny et al. 2006). Overall, the processes that contribute to speciation and extinction have great potential to create biogeographical patterns in microbial species distributions.

Speciation and extinction events likely influence the geographic distributions of Glomeromycotan species, but it is difficult to hypothesize in what manner or magnitude because a general lack of knowledge exists regarding AM fungal evolutionary processes. AM fungi are coenocytic, meaning their nuclei float freely within an aseptate mycelium. Spores can contain many nuclei; a single *Gigaspora* spore can contain 50,000 nuclei (Clapp et al. 2002). Modes of genetic recombination include mixing of nuclei and anastomosis (Sanders 2002). Evidence suggesting selection exists as well, demonstrating that variable traits of certain species are heritable (Bever and Morton 1999; Bentivenga et al. 1997; Feldman 1998). Because so little is known about the natural diversity and distribution of Glomeromycotan fungi it is difficult to speculate about extinction rates. We are currently in a period of accelerated extinction with an predicted loss of 15% of Central and South American plant species within the next century (Wilson 1988). Consequently, it is conceivable that AM fungal species are being lost before they have been discovered.

2.6.3 Interactions between Intrinsic Properties

Intrinsic properties of species influence AM fungal species distributions both directly and indirectly through their interactions with each other. Dispersal capabilities can interact with extinction and speciation rates to influence geographic distributions of species. For instance, species with high dispersal (e.g., Species B above) may be less likely to experience extinction events and thus have large geographic distributions (Fig. 4, paths d and c). On the other hand, species with low dispersal (e.g., Species A) may not be able to traverse geographic barriers, creating isolation and contributing to allopatric speciation and changing species distributions (Fig. 4, paths e and b). Such indirect effects that intrinsic properties could have on geographic distributions in nature could be substantial. In Fig. 4, the majority of the

pathways are dashed, indicating a serious lack of understanding of AM fungal biology, autecology, and evolutionary processes, knowledge essential to understanding the mechanisms behind Glomeromycotan biogeography.

2.7 Spatial Scaling

Observed geographic patterns greatly depend on the scale of the study and variations in distributions or spatial patterning are only meaningful if the scale of measurement is adequately defined. The models presented in this chapter highlight the external forces and intrinsic properties that influence the geographic distributions of Glomeromycotan fungal species. Each factor that can create variation in species distributions is relevant at a variety of different scales (Fig. 5). Also, distributions of soil microbes likely do not remain constant across scales. A species that exhibits a patchy distribution at the field scale may exhibit a random distribution in the core scale. Different AM fungal species can have distinct distributions as a result of life-history traits, environmental heterogeneity, host distributions or historical factors such as propagule dispersal or small-scale disturbances (Hart and Reader 2002; Ettema and Wardle 2002).

We identify seven different spatial scales that are relevant to the study of AM fungal species distributions (Fig. 6). No strict dimensions of each scale are given because the scales exist along a spatial continuum with each larger scale comprising many of the previous smaller scales. The ped, a single soil aggregate, is among the smallest natural units of soil (Singer and Munns 2002). The next largest spatial scale is the core, which is distinguished from the ped scale because a core contains

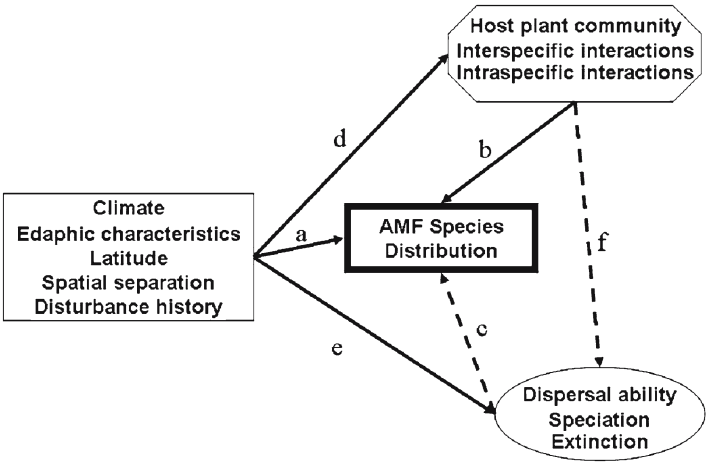

Fig. 5 Culmination of the factors that influence AM fungal species distributions: abiotic external forces (*rectangles*), biotic external forces (*octagons*), and intrinsic properties *(ovals)*

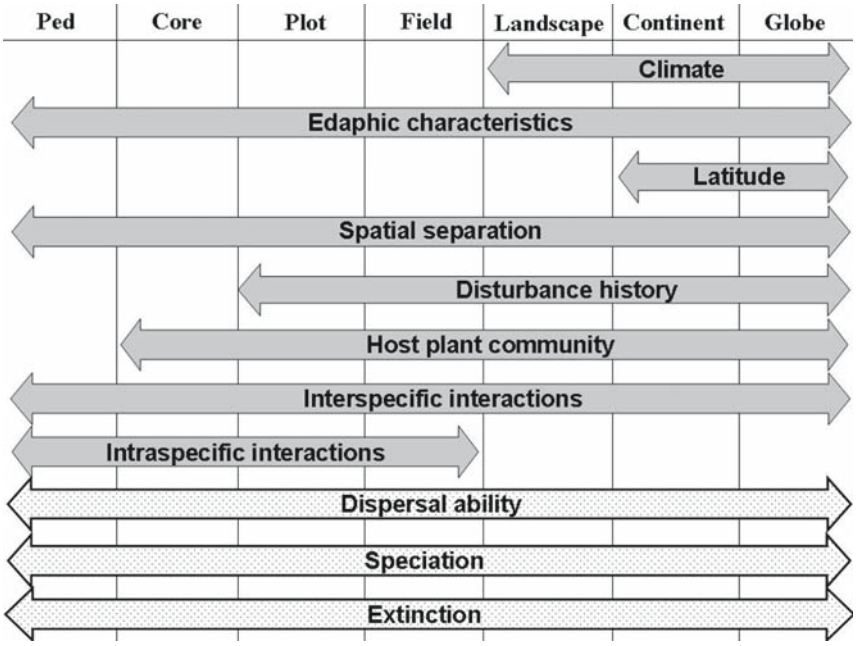

Fig. 6 The spatial scales where factors that create variation in species distributions are relevant. *Shaded arrows* indicate external abiotic and biotic forces and *dotted arrows* represent intrinsic properties of AM fungal species

many peds. It has been argued that, although scientists have been studying soil organisms for several decades, very little is known about soil structural and biological dynamics at the core and ped scales (Crawford et al. 2005). In contrast, the plot and field scales are comparatively well studied in soil ecology. Larger than the field scale are the landscape, continent, and finally global scales. Each of the major factors identified to influence geographic distributions are relevant along a gradient of these spatial scales from ped to globe.

Climatic factors, such as temperature and precipitation, likely only influence AM fungal distributions at landscape, continent, and global scales. Edaphic characteristics, such as nutrient dynamics and texture, could influence AM fungal geographic distributions on all spatial scales. For example, edaphic properties could change from the outer edges of a ped to the inner portions of a ped, influencing spatial distributions of fungi at the ped scale. Latitude likely only influences AM fungal distributions at the landscape, continent and global scales because solar radiation generally does not differ at scales smaller than the landscape scale. On the other hand, spatial separation could contribute to variation in fungal distributions at all scales; just as oceans create separation between multiple continents at the global scale, space between two soil aggregates creates separation between peds. Disturbance

history likely influences the geographic distributions of the Glomeromycota only from the plot scale to the global scale because natural and anthropogenic disturbances generally do not differ at scales smaller than the plot-level. Similarly, host plant community could affect AM fungal distributions at all spatial scales except the ped scale because plant influences on AM fungi likely do not differ within a single soil aggregate. Interspecific interactions, such as those among AM fungi of different species or between AM fungi and other organisms, could influence the distributions of Glomeromycota at all spatial scales because organisms of all sizes – from large ungulates to soil bacteria and archaea – could influence geographic distributions of AM fungal species. However, intraspecific interactions likely only influence distributions at smaller scales from the ped to the plot. By definition, interactions between individuals of the same fungal species occur in close proximity. The inherent dispersal ability of an AM fungal species is likely to be an important factor in determining patterns of distribution at all spatial scales. Different species could vary in their ability to disperse across a ped as well as across multiple continents. And, finally, although the mechanisms of speciation and extinction for Glomeromycotan fungi are poorly understood, these processes have the potential to affect geographic distributions of species at all spatial scales. The biogeographical challenge lies in identifying how species distributions vary by scale, which mechanisms are most important at various scales, and which scales are relevant for the management and conservation of Glomeromycotan fungi.

2.8 Modeling Approaches

Conservation biologists recognize the need to prioritize protection and restoration efforts, which has led to technological advances in methods for mapping and quantifying the distributions and diversity of plants and animals. Furthermore, advances in statistical modeling and mathematical theory have led to the ability to make ecological inferences at spatial scales where experimental manipulations are impractical or impossible. Advances in computing power and the development of specialized software for the capture and manipulation of geographic information systems (GIS) now make digital spatial data easily accessible and publicly available. Unfortunately, few of these technological advances have been employed for the use of determining the spatial distributions or biodiversity of microbes. Studies in microbial biogeography would particularly benefit from these modeling techniques because geographic distributions of microorganisms, especially at the smallest and largest scales, cannot be easily observed. Advanced techniques in spatial scaling represent an important frontier in microbial biogeography, becoming an essential tool in the microbial biogeographer's toolbox.

Traditional methods used to determine species distributions connect localities where a given species is present and assume that the species is uniformly distributed in that area. Researchers establish a grid, determine the presence or absence of a species in each cell of the grid (i.e., occupancy) and create a distribution map by

connecting the occupied cells. The degree to which communities located close to each other are also similar to each other, or spatial autocorrelation, can be estimated using semivariogram analysis. Semivariograms represent the average variance between two samples taken at increasing distances from one another (Schlesinger et al. 1996). However, certain methods can overestimate the interior area occupied by a species and underestimate areas inhabited outside known points (Sanchez-Cordero et al. 2004). Furthermore, biologists would agree that the probability of detection of most species is not equal to 1 and therefore methods that estimate detection probability are preferred. Modern occupancy modeling is GIS-based and incorporates information regarding detection probability to estimate abundance and occupancy of a species in the geographic range of interest (MacKenzie et al. 2006).

Another approach to estimate species distributions is ecological niche modeling which correlates occupancy data with environmental factors to predict the potential distribution of a species (Sanchez-Cordero et al. 2004). Distribution maps can be constructed using GIS-layers of environmental conditions and resources that represent relevant niche characteristics. The produced distribution maps represent the fundamental niche of a species, or the geographic region that the species could potentially occupy (Grinnell 1917; Hutchinson 1959). Distribution maps of individual species can then be summed to produce maps of biodiversity hotspots, and predicted distributions are validated with field data. Examples of methods for ecological niche modeling are GAP analysis (Scott et al. 2002), BIOCLIM (Nix 1986), and DOMAIN (Carpenter et al. 1993), which all incorporate occupancy data and environmental data such as habitat types, climatic conditions, and biophysical attributes to create potential distribution maps. Other methods that have high predictive success, such as genetic algorithm for rule-set prediction (GARP) and boosted regression trees, use evolutionary computing systems (Elith et al. 2006; Guisan et al. 2007). These techniques determine the environmental factors that best describe an ecological niche for a species through an iterative process of evaluating random subsets of data (Stockwell and Noble 1992; Stockwell and Peters 1999). Recently, GARP has had success in predicting the locations of biodiversity hotspots for plants and animals, the extent of invasive species, as well as the geography of disease transmission (Raxworthy et al. 2003; Peterson et al. 2003; Peterson 2006). To our knowledge, ecological niche modeling has never been applied to modeling geographic distributions of Glomeromycotan fungi.

Beyond mapping AM fungal species distributions, it is important to understand the dominant mechanisms that drive biogeographical patterns of species. Are observed patterns controlled more by contemporary environmental conditions or past historical events? Older methods in statistical modeling can be applied in new ways to address biogeographical questions. For example, dissimilarity matrices constructed from various types of data matrices can be compared using a Mantel test to determine whether AM fungal communities that are similar with respect to structure and composition also have similar geographic locations (i.e., autocorrelation) or environmental conditions (Mantel 1967; Martiny et al. 2006). Furthermore, analyses using partial Mantel tests can be used to parse out the amount of variation in the community that is explained by geographic distance versus other environmental

variables (Martiny et al. 2006; Smouse et al. 1986). In a similar approach, structural equation modeling could be used to simultaneously analyze several different mechanisms that generate biogeographical patterns. In structural equation modeling, a priori conceptual models presenting causal relationships between systems of interrelated variables (such as those presented in Figs. 1–5) are tested using field data. By comparing the covariance structure of data that is predicted by the model with the actual covariance structure of the data, we can test the fit of the model and fail to disprove it (Grace and Pugesek 1998; McCune and Grace 2002; Shipley 2000). At spatial scales where manipulative experiments are impossible, these methods can be used in observational studies to improve the level of inference that can be made about the dominant mechanisms behind biogeographical patterns of species.

Null models of ecological phenomena are another approach for studying ecological patterns using observational data. Null modeling involves building a mathematical model of a pattern that would result given the absence of a process of interest. An example, and potential AM fungal biogeographic application, of null modeling is co-occurrence analysis. In co-occurrence analysis, observational data of the composition of multiple communities in the form of presence absence matrices is compared to random assemblages that are generated from the original dataset using a null model algorithm. This null model algorithm is based on the principal that species with overlapping niches cannot co-exist indefinitely (Diamond 1975; Connor and Simberloff 1979; Weiher and Keddy 2001). Software combining the null model algorithm with a randomization procedure generates a standardized index of co-occurrence (Gotelli and Entsminger 2004), which provides a quantitative means of assessing the degree to which the community is structured by competition.

3 Conclusions

A better understanding of Glomeromycotan biogeography is essential for the conservation of AM fungal species and the services they provide in nearly all ecosystems worldwide. Many factors, from external abiotic and biotic forces to intrinsic properties of species, have the potential to create variation in the geographic distributions of AM fungal species. Interactions among these factors generate the many complex mechanisms that control the geographic distributions of AM fungi. Now is an exciting time to study Glomeromycotan biogeography because new approaches using molecular genetics, modeling, and mathematics are helping to reveal the many possible mechanisms that create non-random spatial patterns. As the global human population approaches 7 billion, impacts on natural ecosystems and habitat losses are increasing. Identifying hotspots of AM fungal biodiversity, regions or environmental conditions that sustain diverse communities of AM fungi, will aid in preserving the many important functions that they provide in ecosystems.

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