Chapter 12
Spatial Heterogeneity in Mycorrhizal Populations and Communities: Scales and Mechanisms

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Abstract The importance of a spatial context in understanding the ecology and evolution of organisms has become increasingly clear. Although there is a growing awareness of the importance of mycorrhizal fungi in many communities and ecosystems, much of this understanding is based on a spatially homogenized view of these soil fungi. This homogenized approach may limit our understanding of how these organisms interact with plants and other biota in the field. As an attempt to advance a spatial framework for understanding mycorrhizal ecology, we review our current understanding of the spatial structure of communities and populations of ectomycorrhizal and arbuscular mycorrhizal fungi at the scale of landscapes, communities, and individual host root systems. A variety of potential mechanisms such as disturbance, abiotic and biotic dispersal of mycorrhizal propagules, and biotic interactions may be responsible for generating and maintaining this spatial variation of populations and communities, but the links between observed spatial patterns and mechanisms have yet to be formed. Future work assessing the potential functional significance of spatial variation of mycorrhizal fungi for plant communities and ecosystem function, as well as measuring spatial variation in mycorrhizal function, will continue to advance our understanding of the spatial template for mycorrhizal–plant interactions in the field.

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C. Azcón-Aguilar et al. (eds.), *Mycorrhizas - Functional Processes and Ecological Impact*, 167
DOI: 10/1007-978-3-540-87978-7_12, © Springer-Verlag Berlin Heidelberg 2009

12.1 Introduction

Recent empirical and theoretical research on a variety of organisms has illustrated that spatial scale is important when researchers investigate the dynamics and structure of populations (e.g., Campbell and Dooley 1992; Schweizer et al. 2007), the composition of communities (Turnbull et al. 2007), and the functioning of ecosystems (Maestre et al. 2005). When studying large organisms in the aboveground, much of this spatial structure is intuitive to the investigator through simple observations in the field. But for small organisms that inhabit the belowground, the spatial dynamics of populations and communities are elusive. An understanding of how soil organisms are structured over space can have practical implications for sampling design in studies of soil populations and communities (Klironomos et al. 1999; Lilleskov et al. 2004; see also Chapter 11 by Pickles et al.), but can also inform basic questions about modes of dispersal, how species diversity is maintained at local and regional scales, and how aboveground communities interact with belowground communities (Ettema and Wardle 2002).

Mycorrhizal fungi are one group of soil organisms that should display clear spatial patterns and processes. Mycorrhizal fungi are symbionts that obtain part or all of their carbon from living plant hosts. Furthermore, plant populations and communities that associate with such fungi have their own spatial structure and distributions. We should expect that this extrinsic force of aboveground spatial structure, in addition to spatial variation of soil properties (e.g., organic matter, moisture, pH, nutrient availability) that directly influence fungal growth, should result in distinct spatial organization of mycorrhizal fungi. Other intrinsic properties of mycorrhizal populations and communities such as varying modes of dispersal, differences in rates of growth and types of mycelia, and interactions among different individuals and species could also lead to spatial patterns of mycorrhizal fungi. Thus, soils represent heterogeneous environments where any differences in fundamental or realized niches among genetically different mycorrhizal fungi are expected to result in complex interactions among genetically different mycorrhizal fungi, their host species as well as intrinsic and extrinsic factors. Such interactions are expected to alter growth and local fitness of distinct mycorrhizal fungi thereby creating spatially structured populations and communities.

Unfortunately, many of our studies of mycorrhizal populations and communities (intentionally or not) ignore spatial structure. In field studies, spatial variability is often considered a sampling inconvenience when assessing responses of mycorrhizal fungi to experimental treatments (see also Chapter 11 by Pickles et al.). In greenhouse studies or laboratory studies where the functioning of mycorrhizal fungi is assessed, soils or inoculum are often thoroughly homogenized by mixing to limit spatial variation. Clearly, these steps are necessary to obtain clean data on basic properties and functions of mycorrhizal communities. But to achieve biological relevance in the field, we need to understand the spatial template on which mycorrhizal populations and communities interact with each other, their hosts, and their environment.

In this paper, we review our current understanding of the spatial ecology of mycorrhizal fungi, with a focus on the groups of fungi that form arbuscular mycorrhizal (AM) and ectomycorrhizal (EM) associations. We first establish the scales relevant to the functioning of mycorrhizal fungi. We then review potential mechanisms that could determine spatial structure of EM and AM fungal populations and communities, and highlight studies that have found spatial variation at various scales. We conclude with a proposal of promising future research directions, including how a spatial context for mycorrhizal associations could be useful in ecological restoration. This review is not meant to be comprehensive – there is still a considerable amount of research to be done before we can truly understand spatial dynamics of mycorrhizal fungal populations and communities. Our goal is to provide a spatial framework for considering the ecology and evolution of mycorrhizal populations and communities that may provoke thought, discussion, and further research – and that will push the study of mycorrhizal ecology and evolution towards greater relevance to the natural world.

12.2 Defining Relevant Spatial Scales for Mycorrhizal Fungi

With any discussion of spatial pattern and process, it is important to identify the spatial scales relevant to the organisms of interest. We believe four scales are most relevant for our discussion of spatial pattern and process of mycorrhizal populations and communities: (1) across landscapes, (2) within plant communities/ecosystems, (3) within an individual host root system, and (4) within an individual mycelium. Kilometers would be the physical distance for landscape scale patterns and processes, meters for the plant community or ecosystem scale, millimeters to centimeters for the host root scale, micrometers to centimeters for individual mycelia. In addition to identifying the appropriate scales, it is important to consider the potential mechanisms that might lead to spatial structure of mycorrhizal fungal populations and communities. Both intrinsic and extrinsic factors can lead to spatial patterns and processes in mycorrhizal communities. Intrinsic factors are inherent characteristics of the biology of the organisms (e.g., mode of dispersal), whereas extrinsic factors are properties of the environment inhabited by the organisms (e.g., soil moisture or pH).

At what spatial scale studies should be conducted will depend on the research questions. Any microevolutionary change occurs at the population level and will generally be investigated at smaller scales than studies aiming to describe and understand the mechanisms that shape communities or species distributions among geographic locations. Clearly, genetic change within any species results as the action of the evolutionary forces, mutation (and recombination), selection, genetic drift, and gene flow (migration among populations). These basic forces represent the underlying mechanisms that are responsible for the make-up of all populations. Their relative importance and role in structuring the spatial distribution of mycorrhizal fungi, however, is still poorly understood.

12.3 Spatial Ecology of Mycorrhizal Populations

12.3.1 Size and Spatial Distribution of Genetic Individuals

A basic tenet of the spatial ecology of any taxonomic group is an understanding of the size of individuals and their distribution over space. For mycorrhizal fungi, we could consider genetic individuals (genets) or physiological individuals (ramets). Because EM fungi often produce conspicuous fruiting bodies that are easy to map over space, many studies have employed molecular markers to determine the size and orientation of EM fungal genets in forests. Studies across a range of ecosystems and a variety of EM fungal species have shown that sizes of genets can range from 1 (Baar et al. 1994; Gryta et al. 1997; Gherbi et al. 1999) to 300 m^2 (Bonello et al. 1998). Intrinsic factors that influence genet size and spatial distribution include dispersal mode and frequency (e.g., asexual via hyphae or sexual via basidiospores) (Redecker et al. 2001), mycelial persistence (Guidot et al. 2004; Bergemann et al. 2006), and life history strategy (e.g., early versus late successional stage colonizers) (Deacon et al. 1983; Dahlberg and Stenlid 1990). Extrinsic factors such as small-scale disturbances and land-use history can also affect genet size and persistence, as was shown for *Hebeloma cylindrosporum*, where forest disturbance due to human activity negatively correlated with genet size (Guidot et al. 2002). For those EM fungi that do not produce conspicuous fruit bodies or do so infrequently, other sampling methods are necessary to determine the spatial distribution of genetic individuals. For example, Kretzer et al. (2004) sampled tuberculate mycorrhiza in addition to fruiting bodies for two co-occurring *Rhizopogon* species to determine their genet sizes and distributions.

In contrast, there are few studies to date that have measured the size of genetic individuals of AM fungi. In fact, the coenocytic hyphae and multinucleate spores of AM fungi complicate the study of "individuals" as findings suggest co-occurrence of genetically different nuclei within the same cytoplasm (Kuhn et al. 2001; Hijri and Sanders 2005). Investigation of spatial structure at this very lowest level within spores and mycelia is extremely challenging as it necessitates the development of nuclei-specific genetic markers. Working in an undisturbed coastal perennial grassland in Denmark, Rosendahl and Stukenbrock (2004) found 11 *Glomus* phylotypes that had a patchy distribution. Based on the distribution of phylotypes, the authors suggested the occurrence of a single *Glomus* individual with a mycelium covering at least 10 m in length, while the other less dominant phylotypes observed were smaller individual mycelia.

12.3.2 Spatial Distribution of Genetic Variation with Mycorrhizal Populations

In addition to understanding the distribution of individuals over space, it is useful to understand how genetic variation is spatially structured within mycorrhizal populations. Gene flow is an important intrinsic factor that affects how genetic variation is

distributed over local spatial scales in mycorrhizal populations (Redecker et al. 2001). For mycorrhizal fungi, gene flow between individuals is influenced by modes and rates of propagule dispersal. Whether a species fruits aboveground (epigeous) or belowground (hypogeous) has a profound effect on the maximum distance between individuals at which gene flow can still occur. The epigeous species *Russula brevipes* exhibited strong genetic differentiation between populations located in the west coast of California and the Rocky mountains of Colorado 1,5002002 km apart (Bergemann and Miller), but not at smaller spatial scales (approximately 1 km apart) (Bergemann et al. 2006). In contrast, studies of hypogeous EM fungal species in the genera *Rhizopogon*, *Cenococcum*, and *Tuber* have shown much greater population differentiation at smaller spatial scales (LoBuglio and Taylor 2002; Murat et al. 2004; Grubisha et al. 2007). That difference between population genetic structure of epigeous and hypogeous fungal species reflects a contrast in dispersal modes, whereby epigeous fruiters producing airborne spores can disperse far greater distances than hypogeous species whose dispersal agents are often small mammals with much smaller home ranges (Maser et al. 1978; Meyer et al. 2005), but see Carriconde et al. (2008) for a recent example of strong genetic differentiation at fine-scales (<140m) in a wind-dispersed epigeous species.

In addition to effects on genet size, the degree to which species disperse as spores or conidia versus vegetative spread also influences the spatial distribution of genetic diversity within a population. For example, Kretzer et al. (2005) studied the population structure of two co-occurring congeneric EM fungi, *Rhizopogon vinicolor* and *R. vesiculosus*, in three 50 × 100 m forest plots in the pacific northwestern United States. Genets of *R. vesiculosus* were much more clustered within a plot than *R. vinicolor* genets, suggesting a much greater degree of clonal expansion in *R. vesiculosus*. Similarly, Gryta et al. (2006) studied co-occurring *Tricholoma populinum* and *T. scalpturatum* populations and also found differences in the spatial distribution and size of genets between taxa, revealing that one species, *T. scalpturatum*, relied more heavily upon spore dispersal for genet establishment than *T. populinum*, which exhibited greater vegetative expansion.

All mycorrhizal fungi "disperse," at least locally, through vegetative growth of hyphae, and this can result in the formation of large mycelial networks (Giovannetti et al. 2004). While many EM fungi do produce fruiting bodies, dispersal of AM fungi is likely to be more limited. Quantification of dispersal of different AM genotypes has not been achieved to date. Extrinsic factors such as variation in local environmental conditions over space, either biotic or abiotic, may create spatial structure in mycorrhizal populations by creating spatial variation in selection pressures on AM fungi, although data for this are lacking. Strong gradients in nutrient availability or other abiotic factors as well as the distribution of plant species might select for certain genotypes of mycorrhizal species in different soil patches thereby creating patchy mycorrhizal populations (Koch 2006; Croll et al. 2008).

Several studies have assessed the influence of extrinsic factors on the spatial structure of genetic variation in EM fungi populations. In a study of four EM fungal species along a zinc pollution gradient in Belgium, Colpaert et al. (2004) showed a greater number of zinc tolerant genotypes in plots less than 2 km from the pollution source than in plots situated 7–15 km away for *Suillus luteus*, *S. bovinus*, and *R. luteolus*. However, subsequent work by Muller et al. (2004) found high genetic diversity within polluted

sites and high levels of gene flow between zinc polluted and unpolluted sites. These results suggest that zinc tolerant subpopulations in polluted plots were not established by a single founder event, and that admixture between zinc tolerant and zinc sensitive individuals between subpopulations separated by 5–15 km is common, a result further supported by the presence of zinc tolerant genotypes in non-polluted plots (Colpaert et al. 2004). Comparing genetic diversity of *T. populinum* and *T. scalpturatum* populations in 20 × 10 m forest plots subjected to frequent flooding or not, Gryta et al. (2006) discovered that the genetic diversity of both species was greater within the regularly flooded plot than in the undisturbed plot 50 km away, despite the intrinsic differences between these species in dispersal mode discussed in the previous section.

The studies that have measured genetic variation within populations of AM fungi have mostly focused on the scale of plant communities. In a 90 × 110 m agricultural plot in Switzerland, Koch et al. (2004) showed genetic and phenotypic variation in the common AM fungal species *Glomus intraradices*. There was no link between the genetic variation observed and tillage treatments in this field, but variation was observed between different plots distributed over space. Subsequent work showed that the different genotypes had varying effects on the growth of host plants (Koch et al. 2006), which suggests that there could be spatial variation in AM fungal function in the field associated with the spatial variation in the different genotypes. In another agricultural system, Stukenbrock and Rosendahl (2005) also found spatial structuring within fields of organic and conventional agriculture of several genotypes of *Glomus* spp. The factors that influence co-existence and the spatial distribution of different genotypes in natural communities have yet to be identified. It is possible that genotypes differ in their growth requirements and that complex genotype × environment interactions promote genetically diverse populations. Strong competition among closely related genotypes or species may also be a mechanism creating patchy distributions. AM fungal hyphae from the same spore or isolate frequently fuse to form new cytoplasmatic connections (Giovannetti et al. 1999, 2004; Avio et al. 2006), which may enhance local fitness and persistence of genotypes and species.

12.4 Scaling Spatial Ecology of Mycorrhizal Communities

Just as individual species of mycorrhizal fungi can be structured over space, multispecies communities of mycorrhizal fungi can also have a distinct spatial structure. We have organized our discussion of the spatial ecology of mycorrhizal communities by scale, from across landscapes to within communities to within host root systems.

12.4.1 Spatial Variation in Mycorrhizal Communities Across Landscapes

A variety of mechanisms could contribute to landscape-level spatial patterns of mycorrhizal communities. Clearly, there are many gradients in both abiotic and biotic factors that could influence the composition of mycorrhizal communities,

including soil type and the type of plant community. In North American temperate forests with similar vegetation and climate types, the species composition of AM fungi was similar but relative abundance of different species was different, perhaps due to differences in local soil conditions (Klironomos et al. 1993). EM fungal communities have also been shown to be related to soil factors and dominant tree composition (Kernaghan et al. 2003).

Changes in biotic and abiotic factors as ecosystems develop may result in a heterogeneous distribution of AM fungi across sites of different successional ages. AM fungal spore data have given conflicting results with either no changes in AM fungal composition, changes only in the abundance of species, or differences in species diversity (Benjamin et al. 1989; Johnson et al. 1991; Koske and Gemma 1997). Along an old-field to forest chronosequence, AM fungal species abundances became more even, due to the reduction of spores of a single species in older sites (Johnson et al. 1991). In developing sand dune plantings, AM fungal species changed in both their presence and abundance (Koske and Gemma 1997); however, these differences may be due to the import of AM fungi on planting stock or differential sporulation. In both cases, certain AM fungal species appeared to be early successional while others dominated later in succession, and this variation was tied to host plants and soil nutrients. Recent molecular methods indicate that spore data may not give a complete picture of variation in AM fungal diversity over sites of different age; however, spatial differences were still present in AM fungal communities across a primary volcanic succession at Mt. Fuji (Wu et al. 2007). Simultaneous changes in plants, environment, and AM fungi during ecosystem succession make it difficult to isolate cause and effect from these surveys. Human changes in land use for agriculture, industry, and residential development provide "natural" experiments that shift specific factors such as plant and habitat diversity which determine local AM fungal community composition (Cousins et al. 2003; Li et al. 2007).

Large-scale anthropogenic or natural disturbances also play a role in the spatial structure of mycorrhizal communities across landscapes. Many studies of EM fungi have shown that logging activities can alter abundance and community composition (Jones et al. 2003). For example, Twieg et al. (2007) sampled the EM communities from 5-, 26-, 65- and 100-year-old Douglas fir (*Pseudotsuga menziesii*) and paper birch (*Betula papyrifera*) forest stands recovering from either stand replacing forest fire, or clearcut logging (see also Chapter 13 by Simard). EM fungal diversity was significantly lower in all 5-year-old Douglas fir stands than in the older age class stands, but no differences in diversity were detected between different aged birch stands, likely due to the ability of paper birch to stump resprout. EM fungal community composition also differed among different aged stands. For example, the frequencies of *Russula* and *Piloderma* species increased in Douglas fir plots with time since disturbance, while other species, such as *Rhizopogon* species were more prevalent in the 5-year-old burned or logged plots. Since replicate stands were a minimum of 800 m apart, these results illustrate how disturbances such as clearcutting and fire can generate a mosaic of spatially-structured EM fungal communities across the landscape, over which additional factors, such as the distribution of host tree species or distance from remaining adult trees (Cline et al. 2005), can create additional, fine-scale spatial patterns.

In tropical forests in Panama, Mangan et al. (2004) suggested that the diversity of AM fungi in these systems could be influenced by forest fragmentation. Fragmentation of these forest systems occurred after major flooding around hilltop forests after the construction of the Panama Canal. AM fungal communities on the mainland sites in this study were more similar to each other over a distance of greater than 5 km than to sites on a nearby island that was less than 1 km away despite minimal differences across sites in topography and soil characteristics.

The composition of the regional species pool is an intrinsic property of mycorrhizal communities that could also explain landscape level spatial variation in abundance and composition. Lekberg et al. (2007) recently addressed this process with a study of 10 fields located 1 to 25 Km from each other in Zimbabwe. They found that although local soil characteristics explain some of the regional variation in species composition of AM fungi in the different fields, distance between sites also explained a significant portion of dissimilarity between sites, potentially due to dispersal limitation.

12.4.2 Spatial Variation in Mycorrhizal Communities Within Plant Communities

Nested within larger landscape-scale variation in mycorrhizal communities is variation within plant communities. Most of the work on spatial heterogeneity of mycorrhizal communities has focused on this spatial scale. One extrinsic factor that could lead to spatial structure in mycorrhizal communities is the spatial distribution of compatible plant hosts within a plant community. Numerous studies have shown that both EM and AM fungi show varying levels of host-specificity or host preference for different plant species (Molina and Trappe 1982; Bever et al. 1996; Massicotte et al. 1999; Vandenkoornhuyse et al. 2003). As the structure of aboveground plant communities can be spatially structured (Miller et al. 2002; Seabloom et al. 2005), the spatial distribution of individual plants aboveground could lead to small-scale spatial structure of mycorrhizal communities belowground.

At a coarser scale of resolution, the local diversity of the plant community may influence the composition of the mycorrhizal communities. Experimental studies have shown that plant community composition can affect the composition of mycorrhizal communities at a m^2 scale (Burrows and Pfleger 2002), so variation in plant community composition within a site could drive composition of the mycorrhizal community. In an old-field ecosystem in North Carolina, Schultz (1996) found that distinct morphospecies of AM fungi had different patch sizes throughout the site, and the species richness of the AM fungal community was positively associated with plant species richness. Landis et al. (2004) also found that AM fungal richness was positively correlated with plant species richness and soil N content in oak savannas, while Pringle and Bever (2002) found high spatial heterogeneity in the community composition of AM fungi at a scale of several meters at this same site. Boerner et al. (1996) found that the abundance of AM fungal propagules in a series of plant communities was spatially heterogeneous within several meters, and that patches of low

abundance of AM fungi at some sites were associated with high densities of non-mycorrhizal plant species.

Lilleskov et al. (2004) examined EM fungal communities from eight forest stands and found that the EM fungal communities exhibited a high degree of fine-scale spatial heterogeneity, with the greatest degree of spatial autocorrelation detected at distances 2.6 m apart. In an old-growth conifer forest in California, Izzo et al. (2005) examined how the spatial structure of EM fungal communities changed over time. Soil samples collected over three successive years also showed higher EM fungal community similarity at spatial scales <4 m apart. At even finer spatial scales (<20 cm), the EM fungal community was temporally dynamic and similarity indices at this spatial scale were lower than that exhibited at the overall plot level, suggesting a high degree of species turnover possibly due to root senescence. In a study of EM fungal communities associated with eight co-occurring tree species in Japanese mixed hardwood–conifer forests, Ishida et al. (2007) found that many EM fungal species exhibited a high degree of host specificity, and that the degree of host overlap was positively correlated with phylogenetic relatedness between tree species. Although this study did not examine these results in a spatially-explicit context, the spatial distribution of potential host tree species will likely determine the spatial distribution of host specific EM fungi, as well as help to maintain high levels of EM fungal community diversity.

In addition to spatial variation in the local plant community, the soil environment can also be spatially variable in abiotic properties within a plant community at relatively small spatial scales (Robertson et al. 1997; Boerner et al. 1998). This small-scale environmental heterogeneity might also lead to the spatial structuring of mycorrhizal communities. In a study of maquis and salt marsh plant communities in Portugal, the spatial distribution of spores of AM fungi was closely linked with environmental variables and proximity to individual plants (Carvalho et al. 2003). Klironomos et al. (1999) also found similar patchiness of AM fungal spores in relation to the dominant shrub present in a southern California chaparral ecosystem. Few other studies have attempted to link spatial patterns of mycorrhizal fungi in the field with local environmental conditions, making it difficult to know the relative contribution of environment or plant on the spatial structure of mycorrhizal communities. A study by Toljander et al. (2006) examined the EM fungal community along a 90-m natural nutrient concentration gradient in northern Sweden, and found both EM fungal species richness increased and community structure varied along the gradient. Although host tree species was not responsible for this pattern, the high degree of spatial autocorrelation between soil N content and base cation concentration along this gradient makes it difficult to discern which of the soil chemical characteristics contributes most significantly to the observed community changes. In addition to differences in soil chemical properties, preference for specific substrates within the soil can also lead to spatial partitioning in EM fungal communities. Tedersoo et al. (2003) examined the spatial distribution of EM fungal species in soil and woody debris, and discovered that EM fungal species in the Thelephoroid clade, Athelioid clade, and the Sebacinales, showed a greater affinity for coarse woody substrates, whereas other EM fungi in the Agaricales and the Ascomycota were more abundant in the mineral soil.

Another potential mechanism leading to patchy distributions of mycorrhizal communities over space is the dispersal of mycorrhizal propagules. A variety of organisms have been shown to move viable spores of mycorrhizal fungi at scales ranging from cm to km (e.g., Maser et al. 1978; Meyer et al. 2005; Ashkannejhad and Horton 2006). Differential dispersal of mycorrhizal species by dispersal agents may lead to patchiness of species distributions in the field as dispersed propagules establish and spread. The relative abundance of dispersal agents should also affect the spatial heterogeneity of mycorrhizal fungi within an ecosystem. For example, in soils with a high abundance of earthworms and other macrofauna that may consume propagules of AM fungi, increased dispersal are expected to reduce patchiness within AM fungal communities. Although many dispersal agents have been identified, their exact role in contributing to the spatial structure of mycorrhizal communities remains unclear.

12.4.3 Spatial Variation in Mycorrhizal Communities Within Root Systems

Just as there is variation in mycorrhizal community structure between neighboring plant root systems, there can be spatial variation in the abundance and composition of mycorrhizal communities within the root systems of individual plants. This variation can occur in the rhizosphere, where hyphae and spores extend into the soil immediately adjacent to root systems, or can occur where the fungi colonize the roots of the host plants.

At the scale of individual roots, it would be expected that one of the major driving factors influencing the spatial distribution of mycorrhizal fungi would be interactions within and among mycorrhizal species. For both EM and AM fungi, there is evidence that, when the fungi are colonizing host plant root systems, competitive (Pearson et al. 1993; Kennedy et al. 2007) or facilitative (van Tuinen et al. 1998) interactions can occur between different mycorrhizal species. Just as interactions between species can create spatial structure in other communities (Seabloom et al. 2005), these interactions might lead to the formation of spatial patterns within roots. Spatial structure of mycorrhizal fungi within a root system may increase the total diversity of mycorrhizal fungal species within a root as species are spatially segregated and competition is minimized. To date, the role of this mechanism in creating within root spatial patterns of mycorrhizal fungi has not been explicitly tested. Recent work by Maherali and Klironomos (2007) showed that the number of co-existing AM fungal species grown on individual *Plantago lanceolata* also depends on the initial phylogenetic composition of the fungi. Their results suggest that conservation of similar traits among closely related AM species acts as a mechanism that promotes co-existence of phylogenetically diverse communities due to functional complementarity among taxa.

Alteration of mycorrhizal communities by neighboring plants could be an extrinsic factor that could lead to spatial variation in mycorrhizal abundance and

composition within a root system. Using terminal restriction fragment length polymorphism (T-RFLP), Mummey et al. (2005) showed that AM fungal communities within the roots of the grass species *Dactylis glomerata* that had been growing next to the invasive exotic plant *Centaurea maculosa* were different in composition compared to roots growing without neighboring *C. maculosa* roots. Although the exact mechanisms to explain this observation remain untested, alteration of the local rooting environment through resource uptake or exudation of secondary compound by the roots of one species could change the environment surrounding a root and could select for certain AM fungal species.

Differences in the physiology or function of different types of roots within a root system may also play a role in fine-scale spatial structure of mycorrhizal communities. This phenomenon has been recognized for several decades in EM fungal communities, where late-stage fungi are found on roots closest to the trunk of the tree and early stage fungi are found on roots furthest from the base of the tree (Ford et al. 1980; Mason et al. 1982). This pattern has also been observed in AM fungal systems. In a study examining the molecular diversity of AMF in three nitrogen-fixing forbs, different AM fungal communities were present in root nodules than in roots without root nodules (Scheublin et al. 2004). The authors suggested that different AM fungi may have preferences for these spatially segregated locations within the root system because of variation in the availability of nitrogen or interactions between AM fungi and *Rhizobium* spp. within the root system.

12.4.4 Vertical Spatial Variation in Mycorrhizal Communities

Although the focus of this review so far has been on horizontal spatial variation in mycorrhizal communities, some studies have documented vertical spatial variation in both AM and EM fungal communities through soil profiles. Oehl et al. (2005) described the vertical distribution of AM fungi in various managed systems in the Upper Rhine Valley. In addition to finding a general decline in the species richness of AM fungi moving down the soil profile, these authors found that different AM fungi had different rates of sporulation at the various depths within the soil profiles of the sampled sites, with some species being only found in lower portions of the profiles. Similar patterns have been observed for EM fungal communities. Dickie et al. (2002) found that different EM fungal species showed preferences for different soil profile layers and that EM fungal species richness decreased with increasing soil depth. Mycorrhizas and their associated extraradical mycelium are not always found in the same soil profile (Genney et al. 2006). Furthermore, Moyersoen et al. (1998) did not find a vertical separation of AM and EM in a rainforest ecosystem, although such a vertical trend was found in the roots of the dual mycorrhizal tree, *Populus tremuloides* (Neville et al. 2002). Lindahl et al. (2007) also found a similar vertical partitioning between EM and saprotrophic fungi in the soil horizons. Vertical niche partitioning is thought to be one way by which the high species diversity of mycorrhizal fungi can be maintained at small spatial scales (Bruns 1995).

12.5 Knowledge Gaps and Future Directions

12.5.1 Linking Mechanisms with Patterns

At a variety of spatial scales, many mechanisms have been proposed as determinants of spatial structure in mycorrhizal populations and communities, but few direct links have been made between observed spatial patterns in the field and specific mechanisms. Probably the best way to attempt to make these links would be to complement observations in the field with experimental manipulations. For example, some authors have suggested that dispersal limitation of mycorrhizal fungi might lead to the spatial structure of mycorrhizal communities in the field (Mangan et al. 2004). Following the approach that plant community ecologists have used (Foster 2001), one could first map out the mycorrhizal community composition of a particular site, locate areas of low mycorrhizal fungal species richness, and add spores of various species to these sites. Follow-up studies could determine if the addition of mycorrhizal propagules increases the richness of the mycorrhizal community, or if other local factors such as local environment or host plant availability influence mycorrhizal community composition in low richness patches.

Other mechanistic explanations for creation of spatial structure of mycorrhizal fungi in the field rely on differential dispersal and spread of mycorrhizal fungi in the field. Although many dispersal agents of mycorrhizal propagules have been identified, few studies to date have successfully tracked the establishment and spread of mycorrhizal propagules within a site in relation to dispersal agents. Several studies have monitored the spread and establishment of EM fungi that have been intentionally inoculated into a site (Schwartz et al. 2006), but few studies have examined the process of natural establishment of mycorrhizal propagules. By continuing to develop molecular markers to track specific isolates of mycorrhizal fungi in the field, especially for AM fungi, we might be able to better understand the movement, growth, and interactions of mycorrhizal in natural settings. This approach might be especially important considering the widespread and unregulated transport of mycorrhizal inoculum throughout the world for commercial purposes. Because such practices have potentially positive or negative consequences (Schwartz et al. 2006), any intentional movement of non-native microbes should be considered with more care than is currently the case.

As with many aspects of the mycorrhizal symbiosis, it remains unclear whether the plants or the fungi are in control of the observed spatial structure of plant–mycorrhizal interactions or if there are processes that lead to feedbacks between the plants and fungi. Can the spatial patterns of mycorrhizal fungi influence the spatial patterns and processes in aboveground plant communities, or are the plant communities driving the spatial patterns in mycorrhizal communities? Do the processes that influence the spatial structure of plant communities happen at the same scale as processes that influence the spatial structure of mycorrhizal communities?

For the most part in our discussion, mycorrhizal “species” have been treated as if they are clearly defined entities. For EM fungi, their biology and genetics are

generally better understood than for AM fungi. The comparatively low number of known AM fungal "species" (relative to that of known EM fungal species) is likely a gross underestimation (see also Chapter 10 by Morton). Even though most AM fungal species appear to be generalists, it is still unclear whether AM fungal individuals are generalists, as opposed to assemblies of more specialized genotypes. How are intraspecific functional and genetic diversity (Koch et al. 2004; Munkvold et al. 2004) linked and at what spatial scale? More work is needed to obtain a better understanding of the genetics of AM fungi, and to address at what spatial scale genetic diversity or species/taxa identity is relevant for the survival of AM individuals and their function and distribution across terrestrial ecosystems. In plant ecology, there are studies that have assessed the effect of individual plant species on the local community diversity (e.g., Wiegand et al. 2007). This approach may also be applicable for mycorrhizal fungi and could provide an alternative way to studying spatial patterns in natural communities.

12.5.2 Linking Spatial Patterns with Functional Significance

Although many studies have measured some form of spatial heterogeneity of mycorrhizal fungi in the field, there have been few attempts to assess whether spatial variation in composition of mycorrhizal communities translates into spatial variation in the function of mycorrhizal fungi. Spatial structure in mycorrhizal populations and communities could have important functional significance from a variety of perspectives. From a fungal biology/ecology perspective, understanding the patterns of spatial segregation between mycorrhizal species could help understand interactions between mycorrhizal fungi and controls of mycorrhizal diversity at all the spatial scales considered in this review. From a plant and ecosystem ecology perspective, considering the spatial structure of mycorrhizal fungi in the field could help further clarify the potential role of mycorrhizal fungi in aboveground and belowground properties and processes. Spatial variation in the function of mycorrhizal fungi in the field has been repeatedly proposed to have important community and ecosystem effects (Streitwolf-Engel et al. 2001; Lovelock and Miller 2002; Thiet and Boerner 2007), yet attempts to measure this functional variation are lacking potentially as a result of the methodological limitations of measuring mycorrhizal function in the field (Read 2002).

One potential method for measuring functional variation of mycorrhizal communities in the field is through rotated cores (Johnson et al. 2001). These cores provide a method of severing experimental plants from the hyphal network of mycorrhizal fungi within a plant community from which the potential function of the mycorrhizal community can be inferred by comparing a rotated core to a non-rotated core. By placing rotated cores into the field in a spatially explicit manner, it might be possible to estimate small-scale spatial variation in AM fungal function for individual plants or for ecosystem processes such as nutrient uptake and decomposition.

Another emerging method for addressing functional variation in mycorrhizal communities over space involves using molecular approaches to assess spatial patterns of expression of functional genes. For example, Luis et al. (2005) used primers that targeted laccase genes in basidiomycetes and showed that most dominant laccase sequences were probably associated with extraradical hyphae of EM fungi in small patches. At an even smaller scale of within a mycelium, work in mesocosms has also found spatial variation in gene expression in *Paxillus involutus* using cDNA microarrays (Wright et al. 2005).

It is also possible to investigate spatial patterns by making use of frequently occurring natural gradients in nature. Establishing pure fungal cultures of specific target species or taxa along such gradients and the analysis of their functional and genetic diversity might provide exciting insight into how species and communities are formed. Transplant experiments and subsequent genetic analyses of mycorrhizal communities in such systems may be a way to investigate to what degree mycorrhizal fungi are locally adapted.

12.5.3 Development of Spatially-explicit Models

Recent efforts have been made to model the interactions between mycorrhizal fungi and plants using theoretical approaches. For example, recent studies have modeled mechanisms leading to the coexistence of both plants and fungi (Johnson et al. 2006). While these models have provided useful frameworks for considering the dynamics of mycorrhizal interactions, they have generally not explicitly incorporated spatial structure. Given that a spatially-explicit approach can influence the outcome of models (Tilman and Kareiva 1997), attempts to parameterize these models with the empirical work discussed above could potentially improve their ability to predict outcomes of ecological interactions of mycorrhizal fungi. Coupling empirical estimates of spatial variation of plants and mycorrhizal fungi with theoretical models exploring the significance of this spatial heterogeneity may further advance our understanding of the ecology of mycorrhizal–plant interactions.

12.6 Conclusion

Mycorrhizal associations are, by their nature, multispecies assemblages. In addition, the associated fungi are biotrophs (many are obligate biotrophs), and they inhabit the cryptic soil environment, making it very challenging to study their ecology, even when we ignore the effects of space. Nonetheless, it will not be possible to understand the structure and dynamics of individual species and of multispecies communities unless we do take a spatial approach. This review illustrates that mycorrhizal ecologists have recognized the importance of understanding the

effects of spatially-explicit processes on mycorrhizal populations and communities. However, it is also clear that this area of ecology is at its infancy, and there is much work yet to be done.

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