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Multiscale patterns of arbuscular mycorrhizal fungal abundance and diversity in semiarid shrublands

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ABSTRACT

The distribution of arbuscular mycorrhizal (AM) fungal abundance and diversity across multiple scales, and the factors that drive spatial patterns, remains largely unknown in arid ecosystems. We examined multiple measures of AM fungal abundance, as well as spore diversity and community composition, at microsite (1 m^2), local (1 ha), and regional (5000 ha) scales in semiarid shrublands. At the microsite scale, hyphae, spores, and glomalin-related soil protein were more abundant underneath shrub canopies, but unvegetated shrub interspaces had similar amounts of viable propagules, spore diversity, and spore community composition compared to canopies. Significant local and regional scale variation in abundance, diversity, and community composition were correlated with variation in soil organic matter, climate, and soil phosphorus concentration. We observed high alpha, beta, and gamma spore diversity and significant spatial autocorrelation of communities. This study demonstrates how multiple indicators of Glomeromycotan abundance and diversity vary differentially in natural systems and how soil and climate factors are important drivers of spatial patterns.

Introduction

Arbuscular mycorrhizal (AM) fungi (Phylum Glomeromycota) form symbioses with the majority of plants in arid ecosystems (Miller, 1979; Allen et al., 1995; Tao and Zhiwei, 2005). These obligate root symbionts improve plant host access to limited soil resources (e.g. phosphorus, nitrogen, water) in exchange for photosynthates. Many factors, such as dominant vegetation type, climate, and edaphic properties, influence the abundance and distribution of AM fungi across multiple

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spatial scales (Abbott and Robson, 1991). Abiotic factors (e.g. climate, edaphic properties), biotic factors (e.g. host plant community, interspecific interactions) and intrinsic properties of particular AM fungal species (e.g. dispersal capabilities, extinction rates) are predicted to influence AM fungal community structure at multiple scales as well (reviewed in Chaudhary et al., 2008; Fitzsimons et al., 2008; Caruso et al., 2012). Recent work examines the factors that influence Glomeromycotan distributions, focusing on biogeography at global scales, and highlights the paucity of AM fungal distributional data, particularly in arid ecosystems (Öpik et al., 2010; Turrini and Giovannetti, 2012). In many drylands, at smaller spatial scales, dominant perennial plants are distributed discontinuously within a matrix of unvegetated interspaces forming "islands of fertility" where soil nutrients and biotic activity are concentrated (Schlesinger et al., 1996). Because AM fungi are obligate plant symbionts, there is reason to think that their spatial distributions should mimic the patchiness of plants in drylands, but this hypothesis has not been thoroughly tested. Drylands comprise 41 % of terrestrial biomes (Reynolds et al., 2007); an improved understanding of Glomeromycotan abundance and diversity at multiple spatial scales will advance efforts to conserve fungal biodiversity in arid ecosystems.

Belowground, an AM fungus exists in several quantifiable forms and could exhibit different distributional patterns depending on spatial scale. Hyphae connect plant roots with the soil matrix, residing inside roots and extending into rhizosphere soil, where they absorb resources and deliver them to host plants. Hyphae can be long-lived or ephemeral (Hernandez and Allen, 2013) and also act to enmesh soil aggregates, promoting soil stability (reviewed in Rillig and Mummey, 2006). Therefore, assessments of extramatrical hyphae can indicate the potential of AM fungi to acquire resources and stabilize soil. Glomeromycota produce asexual spores which indicate reproductive output and variation in potential for dispersal and dormancy of different species. Although the community structure of AM fungi can be inferred from spore communities, it should not be assumed that the species of AM fungi inside plant roots determined using DNA-based techniques will exhibit the same patterns of occurrence as the spore communities in the surrounding soil (Bever et al., 2001; Liu et al., 2012). The phenology of AM fungi may generate distinct root and spore communities, and this may help partition fungal niches in space and time (Pringle and Bever, 2002). Relatively large AM fungal spores are rich in lipids and are likely to be an important food source for microscopic soil organisms, particularly in arid soils with low organic matter content. Living AM fungi, as well as decomposing hyphae and spores, enrich soil with organic compounds including glomalin, a highly recalcitrant glycoprotein (Rillig and Mummey, 2006). While glomalin is a putative gene product of AM fungi, glomalin-related soil protein (GRSP) is considered operationally distinct because it is the measureable quantity in soils that is deposited by a consortium of microorganisms in addition to AM fungi (Gillespie et al., 2011). Soil aggregation is strongly correlated with GRSP and its quantity in the soils reflects the potential for AM fungi to stabilize soil and store carbon. Glomeromycota propagate from spores, hyphal fragments, and colonized segments of plant roots (Jasper et al., 1989). It is extremely difficult to visually determine the viability of spores and hyphae in the soil but the mycorrhizal infection potential (MIP) bioassay offers an integrated method to measure the abundance of all viable propagules (Moorman and Reeves, 1979). Because hyphae, spores, GRSP, and MIP play different roles in the life history of AM fungi and ecosystem function, it is insightful to examine their spatial patterns individually.

Previous studies of AM fungi in arid ecosystems have shown that spore density and GRSP concentration are higher underneath shrub canopies and that hyphal density and GRSP differ across sites (Klironomos et al., 1999; Bird et al., 2002; Rillig et al., 2003). A regional scale study of Glomeromycota in *Artemisia tridentata* shrubs showed that AM spore communities varied both spatially and temporally with latitude, and that local environment likely influenced species distributional patterns (Allen et al., 1995). Previous cross-habitat comparisons have noted that the AM fungal spores of the order Glomerales (e.g. *Glomus*) tend to dominate arid environments, while the relative abundance of spores of the family Gigasporaceae (e.g. *Scutellospora*, *Gigaspora*) increase in more mesic environments (Stutz et al., 2000; Egerton-Warburton et al., 2007). No prior studies have simultaneously examined the distributions of multiple indicators of Glomeromycotan abundance, diversity and community composition, across a range of spatial scales. Our study is unique because we examine variation in four measures of AM fungal abundance as well as spore diversity and community composition across three scales ranging from 1 m^2 to 5,000 ha. We specifically test the following hypotheses:

H_1: Glomeromycota will be more abundant and diverse underneath shrub canopies compared to interspaces between shrubs.
H_2: Glomeromycota will exhibit spatial autocorrelation such that more similar communities are located closer to each other in space. In other words, AM fungal communities are expected to differ more at the regional scale than at the site scale.
H_3: Soil and climate variables will help explain variation in AM fungal distributions across multiple scales of observation.
H_4: Particular AM fungal species may be indicators of particular microsites, sites, or regions. Species in the Glomerales will be relatively less abundant, while Gigasporaceae species will be relatively more abundant, in regions with higher annual precipitation.

Materials and methods

Sampling design

The abundance, diversity, and community composition of Glomeromycota was examined at three spatial scales within the 769,000 ha Grand Staircase-Escalante National Monument in southern Utah, USA (37°24′N, 111°41′W): microsite (1 m^2), site (1 ha), and region (5 000 ha). The geologic and topographic environment of this large national monument is very heterogeneous, with 136 distinct soil types and 50 distinct ecological