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Arbuscular mycorrhizal fungi associated with a single agronomic plant host across the landscape: The structure of an assemblage

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ABSTRACT

Arbuscular mycorrhizal (AM) fungi (phylum Glomeromycota) are important components of natural and managed ecosystems. We explored the AM fungal assemblage in a selection of maize fields across a landscape in eastern New York State and characterized their diversity, dominance, and species abundance distribution. In this managed agroecosystem, we could investigate environment-influenced composition and diversity patterns unencumbered by immediate host species effects. We found that AM fungal taxon abundances were distributed lognormally, which suggests that the fungal community structure is shaped in a complex manner by many interacting niche-related factors rather than by only a single factor of disturbance associated with agricultural management. In addition to species abundance distribution, the focal assemblage shared with natural AM fungal communities a pattern of very strong dominance of certain taxa. To quantify this pattern, we developed two new indices "overdominance" and "inequitability". Contrary to expectations based on observations of natural AM fungal communities, we found that most of the individual field communities were dominated by taxa from within a narrow phylogenetic range. At the landscape scale, we did not find an inverse relationship between the levels of taxonomic richness and phylogenetic relatedness expected in complex communities shaped by competitive exclusion.

1. Introduction

The arbuscular mycorrhizal (AM) fungi (phylum Glomeromycota) are important components of both natural and managed ecosystems. Symbiotic association with these fungi alters nutrient acquisition strategies and carbon budgets of plants (Smith and Read, 2008). While AM fungi make nutrients more available to plants in nutrient limiting conditions, thus buffering the impact of fluctuations in nutrient pool size, plants may also preferentially acquire nutrients through the fungal pathway even when no increase in nutrient status or absorption is observed (Smith et al., 2009). In turn, the fungi acquire substantial fractions of the plants' photosynthate pool, up to and including amounts that may limit plant growth (Johnson et al., 1997). Association with AM fungi impacts plant–pathogen interactions, reducing the severity of several root and foliar diseases, but exacerbating the effects of others (Borowicz, 2001; Hol and Cook, 2005). These fungi may mediate plant–plant interactions as well, from moderating the effects of competition (Scheublin et al., 2007; van der Heijden, 2004) to facilitating the invasion of exotics (Carey et al., 2004). The nature and outcome of these many interactions with their host communities differs depending on the identities of the fungi involved. The AM fungi also impact the abiotic components of ecosystems, contributing to both soil aggregate stability and soil organic matter (Jastrow and Miller, 1998), and the ability of soils to provide key ecosystem services (Gianinazzi et al., 2010).

While understanding about the role of AM fungi in shaping plant community composition is beginning to emerge (O'Connor et al., 2002; van der Heijden et al., 1998; van der Heijden et al., 2003), less is known of the forces that affect the diversity of AM fungal communities. In macroorganisms, insight into processes that influence the composition and diversity of an assemblage can be derived from species abundance distributions, SADs (Magurran, 2004). An SAD summarizes information on species richness (number of species) and abundance (number of individuals observed of each species) in a community (McGill et al., 2007). A collection of models is available, which describe and explain relative abundances of species in an assemblage in terms of niche occupancy. The general form of the SAD for natural AM fungal communities is uncertain, and may fit either the lognormal or broken stick model (Dumbrell et al., 2010a; Unterseher et al., 2011). The lognormal distribution of species abundance is

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commonly found in large, equilibrium assemblages of macroorganisms (Magurran, 2004). A mathematical interpretation of this statistical model suggests that numerous ecological processes are responsible for determining the number of individuals per species in an assemblage (Magurran, 2004). The lognormal model is interpreted biologically to imply hierarchical partitioning, along several axes, of niche space (Sugihara, 1980) or of habitat (Kolasa and Strayer, 1988). In contrast, the broken stick distribution of species abundance suggests that niche space is partitioned by uniformly dividing a single resource-related axis (MacArthur, 1957; Sugihara, 1980). Even though the form of SAD for natural AM fungal communities is uncertain, all these communities appear to be very strongly dominated by taxa that are not together from any discernible, frequently dominant clade (Dumbrell et al., 2010a).

While stochastic neutral processes, like dispersal limitation, have some role in shaping the structure of natural AM fungal communities, the primary mechanism regulating these communities is niche partitioning (Dumbrell et al., 2010b). However, in the case of AM fungi, niche space is remarkably complex. AM fungi are obligate biotrophs that depend on their plant hosts for energy. Consequently, their niche space is affected by the attributes of the plant hosts as well as by the properties of the physical environment (Dumbrell et al., 2010b). In particular, the identities of the plant species have an impact on the reproductive success of AM fungi (Bever et al., 1996), even though these fungi have historically been considered as generalists in the ability to colonize receptive hosts regardless of species (Smith and Read, 2008).

One possible approach to explain relative abundances of AM fungal species in an assemblage in terms of niche apportionment is by isolating the effects of selective pressures generated by the host plant community from other pressures. Managed agroecosystems with their simplified pool of AM host plants offer a study system where this separation can be readily accomplished. Indeed, research characterizing the AM fungal communities in agricultural settings has concluded that they are very low in diversity (Daniell et al., 2001; Helgason et al., 1998), which is consistent with low complexity of niche space. However, most of these investigations were focused on AM fungal diversity in individual agronomic fields, in which niche space may be overly simplified and thus lead to underestimation of AM fungal diversity.

The question of AM fungal diversity in natural and managed systems has been typically addressed by using taxon-based diversity approaches that do not consider the phylogenetic relatedness of the taxa involved. However, the recent observation that the extent of phylogenetic clustering in the AM fungal community affects species richness (Maherali and Klironomos, 2007) underscores the significance of considering phylogeny in studies of diversity. Communities that are overdispersed phylogenetically are expected to be more species-rich than communities that are phylogenetically clustered. The mechanism likely responsible for this pattern is competitive exclusion, which prevents closely related and functionally similar species from co-occurring.

The goal of the present study was to elucidate the type of mechanisms, other than host species identity and host community structure, that influence the diversity of AM fungal assemblage. We addressed this goal by assessing AM fungal taxon abundance distributions in a landscape-wide assemblage of AM fungi in an agronomic system with a single plant host species (maize, *Zea mays*). We also examined patterns regarding: (i) low taxonomic diversity of AM fungi in agronomic systems, (ii) overdominance and idiosyncrasy in AM fungal communities, and (iii) the relationships between taxonomic and phylogenetic diversity measures.

2. Materials & methods

2.1. Sampling

To assess sampling effort needed to characterize AM fungal diversity in New York State maize fields, we collected soil samples from an experimental maize field at the Willsboro Research Farm in Willsboro, NY, on a Kingsbury clay loam soil, 44°22′N; 73°23′W (Field A) in October 2008. This site is described further in Moebius et al. (2007). Twenty samples were taken at regularly spaced intervals along four transects. In the spring of 2009, additional samples were taken from seven active, conventionally managed fields, which were in maize cultivation for multiple seasons. No differentiation was made between cultivars of maize. Detailed site histories, including crops several seasons prior, or historical tillage intensity were not available. Fields were located in Flying Point, NY, on a Haven Loam, 40°53′56.0″N, 72°21′34.5″W (Field B), and a Bridgehampton Silt Loam, 40°53′47.5″N, 72°21′28.7″W (Field C); in Jamesport, NY, on a Riverhead Sandy Loam, 40°56′44.4″N, 72°35′47.9″W (Field D); in Queens County, NY, on a Riverhead Sandy Loam, 40°44′55.0″N, 73°43′22.7″W (Field E); in Dutchess County, NY, near Wappinger's Falls, on Hoosic Gravelly Loam, 41°38′7.2″N, 73°48′54.6″W (Field F), and 41°38′2.7″N, 73°48′49.1″W (Field G); and in Colombia County, NY, near Red Hook, on a Blasdell Channery Loam, 41°59′44.8″N, 73°37′8.1″W (Field H). The samples were collected using a modification of the methods used by the Cornell Soil Health Team (Gugino et al., 2009), keeping individual samples from within a field separate rather than compositing them. Ten samples from each field were taken as follows: five pin flags were placed at ~20 m intervals in a "relaxed W" arrangement across the field, starting 20 m from a corner of the field, and with the angle described by the line between flags decreasing by 30° at each turn starting from a 120° angle. Two samples were taken near each pin flag, 2 m apart, along a line perpendicular to the line leading to the next pin flag. In this way, for each sample, one other sample was taken 2 m distant, and a series of distances were represented between samples in a field. Samples were collected by removing the top 2 cm of soil and excavating ~4 L of maize rhizosphere soil, which was placed immediately in a zip-lock freezer bag, and cooled under ice until placed in a 4 °C cooler for storage.

2.2. Trap culturing

To capture the diversity of AM fungi present in maize fields, we established trap cultures for each individual field sampling point, using maize plants of cultivar Mandan Red (Seeds of Change, Rancho Dominguez, CA) to bait AM fungi and support their sporulation under shared conditions of a climate controlled greenhouse. In arable agronomic systems characterized by regular disturbance, trap culturing allows the use of spores as an integrative measure of AM fungal community composition (Oehl et al., 2003). Spores formed in trap cultures are expected to more accurately represent the AM fungal community than spores directly extracted from field samples (Johnson, 1993; Oehl et al., 2004) because the latter are often degraded or damaged (Douds and Millner, 1999) and thus unsuitable for diversity estimation. Results from trap culturing depend on the greenhouse host species used (Jansa et al., 2002). Therefore, the use of maize as a trap culture host to recover fungi that associate with maize plants in the field was expected to enable faithful reconstruction of the field AM fungal communities.

The greenhouse pot cultures were established by mixing 0.5 L of field soil with 0.75 L of washed, autoclaved, pool filter sand (crushed sandstone), placing the mix in a standard 5½ inch black plastic greenhouse pot, and covering the mix surface with 0.25 L of