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What drives differences in arbuscular mycorrhizal fungal communities among plant species?

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ABSTRACT

Plant species can influence communities of arbuscular mycorrhizal fungi (AMF) by hosting different AMF taxon identities and/or richness. We used presence/absence data from a recent global survey of AMF communities to assess how often AMF communities differ among plant species, and to explore whether differences result from dissimilarities in AMF taxon identity or richness. We found that AMF communities clustered among plant species in 24% of sites, and that plant species were more likely to differ in AMF taxon richness (23% of sites) than the particular taxa with which they associate (5% of sites). Overall though, the variation in both AMF richness and identity was often as great *within* as *between* plant species, suggesting that plant species identity may be less important for structuring local AMF communities than other factors, such as environmental conditions, fungal interactions or even stochastic distributions of AMF. This has implications for how we should view plant-AMF interactions and community patterns.

1. Background

Arbuscular mycorrhizal fungi (AMF) colonize the roots of about 80% of vascular plant species, and can increase uptake of some mineral nutrients, improve drought resistance and provide pathogen protection in exchange for carbon (Smith and Read, 2008). There are about 250 morphologically and up to 1000 molecularly defined AMF taxa (Kivlin et al., 2011), many of which are distributed worldwide (Davison et al., 2015). Individual plants may host anywhere from 1 to 60 taxa (Davison et al., 2015), and consistent differences in AMF richness have been observed among plant species (Lekberg et al., 2013). The underlying mechanism that drives differences in AMF richness is unclear but may involve differential resource supply by plants, because AMF richness correlates positively with fungal biomass (Antoninka et al., 2011; Lekberg et al., 2013). Plant species may also differ in the AMF taxa they host (e.g. Vandenkoornhuyse et al., 2002; Hausmann and Hawkes, 2009; Lekberg et al., 2013), possibly due to variation in phenology, root architecture or other factors that complement the distribution, colonization strategy and/or function of particular fungi (Hart and Reader, 2002; Pringle and Bever, 2002; Oehl et al., 2005; Maherali and Klironomos, 2007). Thus, plant species can differ in both AMF richness and composition (Vandenkoornhuyse et al., 2002; Hausmann and Hawkes, 2009; Meadow and Zabinski, 2012; Lekberg et al., 2013), but it is uncertain how often they do.

Differences in richness and composition are additive and contribute to the total dissimilarity (e.g. Bray-Curtis and Jaccard; Legendre, 2014 and references therein) observed among plant species. Computational approaches are now available to partition this dissimilarity, or beta diversity, into its taxon richness (here on referred to as T_{rich}) and taxon identity (here on referred to as T_{ident}) components (Podani and Schmera, 2011). We applied this method to the recent global survey of AMF (Davison et al., 2015) to quantify how often AMF communities differ among plant species, and to assess if these differences are due to dissimilarities in AMF richness (T_{rich}) or composition (T_{ident}). Determining broad scale patterns in T_{rich} and T_{ident} across plant communities is a first step to identifying

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mechanisms that may structure AMF communities (resource supply *vs.* niche complementarity for T_{rich} and T_{ident}, respectively), and to better explain and predict AMF responses to changes in plant richness. Specifically, we argue that support for T_{ident} would predict positive relationships between plant and AMF richness because plant species host different AMF taxa. Support for T_{rich}, however, could result in high AMF richness even at low plant richness if plant species that host many AMF taxa are present.

2. A global survey of AMF

We used the sample-AMF virtual taxon (VT) matrix in Table S2 in Davison et al. (2015). This dataset is unique because it reports on AMF taxa within multiple individuals of the same plant species (not pooled soil or plant samples) across 67 sites worldwide. Prior to any analyses we standardized the number of sequences to ensure plants within sites were compared at the same sequencing effort (1% of the total sequence numbers within sites, Table S1), which resulted in individual samples being characterized by an average of 143 sequences (20 sequences was the lower threshold for inclusion here and in Davison et al., 2015). This standardization reduced the number of sites that could be analyzed to 62 due to lack of replication within species (two sites were unreplicated prior to standardization), but it improved our ability to compare species as it reduced overall variability (see comparisons between rarefied and unrarefied data for first 10 sites in Table S1). Sampling effort curves for the first six sites (in alphabetic order) on standardized data indicate that AMF communities were sampled to a similar extent, and that the majority of AMF taxa occurring in the targeted plant species were identified (Fig. S1). We converted the abundance data to presence/absence data to look at turnover in the occurrence of AMF taxa rather than shifts in their relative abundance. We then calculated the Jaccard dissimilarity ($0 < d_J < 1$, with 0 being identical and 1 completely dissimilar; Jaccard, 1912) of AMF communities among plants and tested whether dissimilarities were greater among than within plant species using PERMANOVA (Anderson 2001), adonis function in the vegan package (Oksanen et al., 2015) in R, (R Development Core Team, 2010), Table S1. We considered any p-value ≤ 0.05 to be significant. PCoA plots of all sites are in Fig. S2. We used the Podani family method (Podani and Schmera, 2011; our T_{ident} = replacement) and the BAT package in R (Cardoso et al., 2015; Oksanen et al., 2015) to partition dissimilarities into T_{ident} and T_{rich}. Sub-matrices were then analyzed using PERMANOVA to identify sites where T_{ident} and T_{rich} differed significantly among species (Table S1). Fig. 1a illustrates the diversity partitioning approach for one of the 62 sampled sites. We repeated this approach among individuals (regardless of species identity) across sites to assess departures from dissimilarities explained by species (R scripts for all analyses are in Table S1). We also ran one-way ANOVAs (or Kruskal-Wallis tests when transformations failed to satisfy ANOVA assumptions) across all sites as a complementary way of assessing absolute, instead of relativized differences in AMF richness among plant species.

3. T_{ident} *versus* T_{rich}

AMF communities clustered among plant species in 24% of the sites (Fig. 1b). When the total dissimilarity was partitioned into T_{ident} and T_{rich}, differences in T_{ident} were significant in 5% of sites, whereas differences in T_{rich} were significant in 23% of the sites (Fig. 1c–d). Richness also differed among plant species in 23% of sites using ANOVAs (Table S1), and p-values from the two approaches were positively correlated ($R = 0.91$; $p < 0.001$), indicating a good correspondence between the two methods to assess differences in richness. Because T_{rich} was significant in many more sites than T_{ident}, we conclude that plant species were more likely to differ in AMF richness than to host different AMF taxa. For example, while plant species differed by an average of 15 AMF taxa in an African forest site (GAx), no difference in composition was observed. This degree of variation in AMF richness is not unique to this dataset; Öpik et al. (2009) found more than a 3-fold range in AMF richness among understory plant species in an Estonian spruce forest. We also found large differences in AMF taxon richness *among* sites. For example, all plants at site IDy hosted <10 taxa, whereas AMF taxon richness ranged between 19 and 27 taxa among plant species in site CMI. Again, similar differences have been documented previously (Lekberg et al., 2013) and could be related to differences in the availability and quality of hosts.

While the greater proportion of significant T_{rich} sites indicate that plant species were more likely to host different AMF richness than AMF taxa, it does not necessarily mean that T_{rich} was more important than T_{ident} for total AMF community dissimilarity. Comparisons of Jaccard dissimilarities reveal slightly higher overall values for T_{ident} than T_{rich} (Fig. 1b–d, Table S1), which means that differences in AMF composition contribute more to overall beta diversity than differences in richness. This is largely driven by differences among individual plants, not species however, because dissimilarities among individuals were almost as large as among species (Fig. 1c). The contribution by T_{rich} to overall dissimilarity, while smaller, is noteworthy because the *de facto* explanation for significant clustering of AMF communities is often differences in composition (e.g. Lekberg et al., 2013). We urge a greater consideration of AMF richness in future studies, not only as an additional driver of AMF communities, but also because it can influence plant diversity (van der Heijden et al., 1998) and community resistance and resilience to disturbance (Vogelsang et al., 2006; Helgason et al., 2007).

4. Do plant species identities matter for AMF communities?

AMF communities clustered among plant species in a relatively small proportion (24%) of the total number of sites. It is possible that we may have underestimated the overall (but not relative) support for both T_{ident} and T_{rich} due to the relatively small number of plant species ($n = 4$) and individuals ($n = 2–6$) sampled within sites. Future studies using a sampling scheme based on plant functional and ecological group identity (Öpik et al., 2009; Lekberg et al., 2014; Chagnon et al., 2015) rather than abundance (criterion used in Davison et al., 2015) might show greater support for both. However, the range in both AMF richness and composition *within* species was substantial and would not decrease with more replicates. For example, individuals of two South American understory species (*Embothrium coccineum* and *Lathyrus magellanicus*; site LV1) harbored an AMF richness that ranged from 1 to 25 and 4 to 21 taxa, respectively. Environmental heterogeneity can be a stronger driver for AMF communities than host plant identity (Dumbrell et al., 2010a; Davison et al., 2015), but seems an unlikely explanation for the large with-in site variation observed here as it implies frequent sample collections across strong environmental gradients. A recent, complementary analysis of the same dataset also concluded that AMF compositional variation within species is often equivalent or greater than expected by chance (Powell and Bennett, 2015). This is not unique to this dataset as extensive variation in both AMF richness and composition within plant species have been observed in other studies (van der Voorde et al., 2010). Thus, AMF distributions among co-occurring mycorrhizal plants may be either