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RESEARCH IN CONTEXT

Evidence for phylogenetic correlation of plant–AMF assemblages?

A. Montesinos-Navarro[1,2,*], J. G. Segarra-Moragues[1], A. Valiente-Banuet[2,3] and M. Verdú[1]

[1]Centro de Investigaciones sobre Desertificación (CIDE, CSIC-UV-GV), Carretera de Moncada-Náquera Km 4.5 46113 Moncada, Valencia Spain, [2]Departamento de Ecología de la Biodiversidad, Instituto de Ecología, Universidad Nacional Autónoma de México, AP 70-275, CP 04510, México, DF, México and [3]Centro de Ciencias de la Complejidad, Ciudad Universitaria, Universidad Nacional Autónoma de México, 04510, DF, México
** For correspondence. E-mail ali.montesinos@gmail.com*

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- **Background and Aims** Specificity in biotic interactions is mediated' by functional traits inducing shifts in the community species composition. Functional traits are often evolutionarily conserved, resulting in closely related species tending to interact with similar species. This tendency may initially shape the phylogenetic composition of coexisting guilds, but other intraguild ecological processes may either blur or promote the mirroring of the phylogenetic compositions between guilds. The roles of intra- and interguild interactions in shaping the phylogenetic community composition are largely unknown, beyond the mere selectivity in the interguild interactions. Plant facilitation is a phylogenetically structured species-specific process involving interactions not only between the same guild of plants, but also between plants and other guilds such as arbuscular mycorrhizal fungi (AMF). In this study it is hypothesized that reciprocal plant–AMF interactions will leave an interdependent phylogenetic signal in the community composition of both plants and AMF.
- **Methods** A correlation was used to test for a relationship between the phylogenetic composition of plant and AMF assemblages in a patchy xeric shrubland environment shaped by plant facilitation. In addition, a null model was used to test whether this correlation can be solely explained by selectivity in plant–AMF interactions.
- **Key Results** A significant correlation was observed between the phylogenetic composition of plant and AMF assemblages. Plant phylogenetic composition in a patch was related to the predominance of plant species with high nursery quality that can influence the community assembly. AMF phylogenetic composition was related to the AMF phylogenetic diversity in each patch.
- **Conclusions** This study shows that shifts in the phylogenetic composition of plants and AMF assemblages do not occur independently. It is suggested that besides selectivity in plant–AMF interactions, inter-related succession dynamics of plants and AMF within patches could be an ecological mechanism driving community assembly. Future lines of research might explore whether interlinked above- and below-ground dynamics could be occurring across multiple guilds simultaneously.

Key words: Arbuscular mycorrhizal fungi, AMF, biotic interactions, community assemblages, facilitation, phylogenetic composition, plant guilds, vegetation patches, xeric shrubland.

INTRODUCTION

Biotic interactions between guilds are determinant forces assembling communities. It is well known that specificity in these interactions, when they occur across guilds (e.g. predators and preys, host and parasites, plants and soil micro-organisms), can induce reciprocal shifts in each assemblage, ultimately affecting the community species composition (Janzen, 1970; Connell, 1971; Packer and Clay, 2000; Dickie *et al*., 2002; Hart *et al*., 2003; Wehner *et al*., 2011).

Biotic interactions are mediated by functional traits, and most functional traits are evolutionarily conserved. Therefore, when ecologically relevant functional traits are not available, or when there is an interest in all traits, beyond single trait relationships, we can use the shared evolutionary history of species (phylogenetic relatedness) as a proxy for functional similarity. As a consequence of trait conservatism, closely related species tend to interact with similar species (i.e. phylogenetic signal in the interaction; Gómez *et al*., 2010), and this phylogenetic signal can shape the phylogenetic composition of assemblages of coexisting guilds (Sargent *et al*., 2011; Waterman *et al*., 2011). As a result of simultaneous processes of coevolution, niche differentiation and niche conservatism among closely related taxa, phylogenetic distance among host organisms may affect the communities of their mutualistic associates (Cavender-Bares *et al*., 2009). However, although most research has focused on interguild interaction selectivity, other ecological processes, such as enhanced coexistence through competitive intransitivity (Laird and Schamp, 2006), or intraguild competition among relatives within a host (Aurélien *et al*., 2013), may blur or promote the mirroring of the phylogenetic compositions between the interacting guilds. Nevertheless, less attention has been paid to these other local-scale processes that also determine the phylogenetic community structure.

The species composition of a community is the product of a plethora of ecological processes occurring in that particular community (e.g. Thonar *et al*., 2014). For a given guild, the phylogenetic species composition encapsulates the phylogenetic neighbourhood for each species within an assemblage

(Pillar and Duarte, 2010). The characterization of the phylogenetic composition at small scales allows the comparison of multiple communities where both intra- and interguild interactions can shape the final phylogenetic composition of species beyond the mere selectivity in the interguild interactions. To do so, the final phylogenetic composition of each guild can be considered across a set of natural communities (or neighbourhoods) (Pillar and Duarte, 2010) where multiple ecological processes occur simultaneously.

Patchy environments provide an appropriate framework to test for related phylogenetic composition between guild assemblages. A well-known patchy environment resulting from ecological interactions is that generated by plant–plant facilitation interactions. Facilitation is a key process for seedling establishment, which leads to an aggregated spatial distribution of species, hereafter vegetation patches (McAuliffe, 1988; Eccles *et al*., 1999; Valiente-Banuet and Verdú, 2007; Castillo *et al*., 2010). Plant facilitation is a phylogenetically structured species-specific process involving both above- (plant–plant) and below-ground [plant–arbuscular mycorrhizal fungi (AMF)] interactions (Valiente-Banuet and Verdú, 2008, 2013; Montesinos-Navarro *et al*., 2012*a*). The initial coexistence pattern of plant and AMF determined by selectivity in the interguild interactions (Montesinos-Navarro *et al*., 2012*b*) is later modified by different ecological processes and indirect interactions emerging in multispecific vegetation patches (Castillo *et al*., 2010; Beltrán *et al*., 2012; Oviedo *et al*., 2013). Accordingly, although a phylogenetic signal in plant–AMF interaction (Montesinos-Navarro *et al*., 2012*a*) suggests a mirroring between the plant and AMF phylogenetic composition, this pattern might be blurred or promoted by other ecological processes. The combination of multiple ecological processes occurring in vegetation patches can result in a local species (plant and AMF) pool (i.e. the taxa in a given patch) which might be a non-random sample of the regional species pool (i.e. the sum of taxa observed across patches). A local species pool might not be solely predicted based on the specificity of the interactions between guilds (e.g. plant–AMF) as intraguild ecological processes such as competitive exclusion or competition alleviation (Aurélien *et al*., 2013; Thonar *et al*., 2014) may be operating within a patch. These ecological processes are influenced by species traits. Regarding AMF, functional complementarity among taxa can promote plant coexistence through pathogen protection and increase of nutrient absorption rates (Van der Heijden *et al*., 1998; Hart *et al*., 2003; Powell *et al*., 2009; Wagg *et al*., 2011). Regarding plant assemblages, plant coexistence can be mediated by facilitation, where nurse plants enhance the microhabitat for the establishment of facilitated plants. Plants with high nursery quality have traits typical of early successional species such as drought tolerance, high growth rates, lower shoot:root ratio and nitrogen fixation (Valiente-Banuet *et al*., 2006; Butterfield and Briggs, 2011; Cadotte and Strauss, 2011). Interestingly, AMF are often present from the beginning of primary plant succession and show different relationships with pioneer and late-successional plant species (Kikvidze *et al*., 2010). Altogether, these findings suggest that reciprocal plant–AMF interactions are involved in the ecological mechanisms determining the community succession and therefore community phylogenetic composition.

In this study we use previous data on plant community facilitation interactions (Valiente-Banuet and Verdú, 2007, 2008) and AMF sequences (Montesinos-Navarro *et al*., 2012*b*) to assess the relevance of interguild interactions in the assembly of natural communities by using vegetation patches resulting from plant–plant facilitation. We specifically test if there is a relationship between the phylogenetic composition of plant and AMF which cannot be solely explained by the selectivity in plant–AMF interactions. We discuss possible assembly mechanisms linked to plant and AMF traits driving successional trajectories of vegetation patches.

MATERIALS AND METHODS

Study system

The study area is a xeric shrubland in the Valley of Zapotitlán (18°20N, 97°28W), central Mexico, in which the AMF regional species pool (i.e. the total sum of taxa linked to plants across patches) was obtained (Montesinos-Navarro *et al*., 2012*b*). This system is dominated by the columnar cactus *Neobuxbaumia tetetzo* (J.M. Coult.) Backeb., and other species of Asparagaceae, Fabaceae and Asteraceae. Plants are spatially aggregated in discrete vegetation patches with areas ranging from 1 to 5 m^2. Patches are surrounded by open space, but plant species can easily disperse from one patch to another. Most (97 %) of the plant species in this system require facilitation to establish (Valiente-Banuet and Verdú, 2007), leading to an absence of plants in between vegetation patches as a generalized pattern in the system. Vegetation patches are initiated by a nurse species that facilitates seedlings of other species; however, some patches may harbour only adult plants of facilitated species which are interpreted as late successional stages after the death of the nurse starting plant. From the data published in Montesinos-Navarro *et al*. (2012*b*), we selected only those vegetation patches in which complete information for all the plant species within each patch was available. A total of 17 patches were selected, sampled along two plots of 500 m^2, each capturing a representative sample of the plant species in the community and reflecting their relative abundances (Supplementary Data Table S1). In each patch, the species composition was recorded (a total of 39 plant individuals and 23 plant species), and the AMF community harboured in each plant within the patch was obtained from Montesinos-Navarro *et al*. (2012*b*) (see more details about the root sampling in Montesinos-Navarro *et al*., 2012*b*).

Phylogenetic community composition

Phylogenetic trees of plants and AMF were obtained from those published in Montesinos-Navarro *et al*. (2012*b*; GenBank accession numbers are given in Supplementary Data Table S1). The phylogenetic community composition of plants and AMF was independently characterized using analytical tools recently developed in a meta-community framework (Pillar and Duarte, 2010). Following Pillar and Duarte (2010), AMF sequences were used to calculate, after fuzzy weighting, species phylogenetic composition through an index (*P* matrix) that characterizes the phylogenetic neighbourhood for each species within each patch. Two *P* matrices were independently calculated for plant and AMF. The elements of the *P* matrix (patch × taxa) provide a characterization of the phylogenetic composition of the assemblage. *P* matrices were calculated using the SYNCSA package implemented in R (Debastiani and Pillar, 2012). As suggested by Pillar and Duarte (2010), *P* matrices can be used to explore phylogenetic patterns at the community level by using ordination techniques. The numbers of axes that capture at least 90 % of the variation in the phylogenetic community composition of plants and AMF were calculated, and a non-parametric multivariate analysis of variance (ANOVA; Anderson, 2001) was used to test if the phylogenetic composition of plants could explain the phylogenetic composition of AMF ('adonis' routine of the Vegan package of R; Oksanen *et al.*, 2013). Afterwards, we focused on the first principal component (PC1) of plants and AMF in order to be able to provide an ecological explanation for the main variation axis. Principal co-ordinate analyses (PCoAs) were conducted with Euclidean, Maximum, Manhattan and Minkowski distances. Because all four distance indices were consistent, hereafter we refer to Euclidean distance results only, equivalent to using principal component analyses (PCAs). PCAs were performed on the *P* matrix of plant and AMF independently. The magnitude of each species loading indicates the relative contribution of that species to differentiate patches along the PC1 axis (patch scores). Patch scores were calculated considering plants (plant PC1 scores) and AMF (AMF PC1 scores) independently. Accordingly, a patch score along the plant PC1 will compile information about the phylogenetic composition of the plants in that patch, and the patch score of AMF PC1 will compile information about the phylogenetic composition of the AMF assembly in the same patch. Patches harbouring species with opposite loading signs will tend to be located in opposite extremes of the PC1 axis. The relationship between plant and AMF phylogenetic composition was tested by correlating plant PC1 scores and AMF PC1 scores. A potential spatial autocorrelation was tested using a Mantel test with 9999 permutations to correlate plant PC1 and AMF PC1 with the spatial distance between patches. PCAs and correlation analyses were performed using the software R.

In order to provide an ecological interpretation of the plant PC1 axis, plant species loadings were correlated with their nursery quality, which is a proxy of multiple functional traits potentially influencing biotic interactions and community assemblages. The nursery quality of plant species (Supplementary Data Table S2) was characterized from the information available from previous studies in this system (Valiente-Banuet and Verdú, 2007, 2008). Nursery quality was estimated as the number of seedlings growing underneath a nurse which survive until the adult stage. In order to be considered as facilitation, the number of seedlings underneath a nurse needs to differ from the number expected in a random distribution, considering the proportions of the area occupied by each plant cover vs. open space (see more details on the estimation of this parameter in Valiente-Banuet and Verdú, 2007, 2008). Plant species loadings were correlated with their level of nursery quality using a non-parametric Spearman correlation, as nursery quality was not normally distributed.

Regarding AMF, in which most DNA sequences cannot be confidently assigned to known species, functional traits cannot be used. Consequently, the ecological interpretation of the AMF PC1 axis was based on its relationship with phylogenetic diversity, assuming trait conservatism (Van der Heijden *et al.*, 1998; Powell *et al.*, 2009). The mean phylogenetic diversity was characterized by the mean pairwise phylogenetic distance (MPD) among every pair of AMF sequences coexisting in a patch. The MPD of each patch was obtained as a sub-set of the matrix of phylogenetic distances between all AMF sequences in the community. The relationship between phylogenetic composition and phylogenetic diversity was assessed using a non-parametric Spearman correlation between AMF PC1 scores and MPD of AMF sequences across patches.

Finally, the relative contribution of plant MPD, nursery quality of the patch (estimated as the community-weighted mean: Lavorel *et al.*, 2008), plant and AMF phylogenetic composition (plant PC1 and AMF PC1) and the interaction between plant phylogenetic diversity and nursery quality on AMF phylogenetic diversity (AMF MPD) was estimated by means of a non-parametric ANOVA based on permutation tests using the 'adonis' function (Oksanen *et al.*, 2013). The community-weighted mean was determined using the 'functcomp' function of the PD package of R (Laliberté *et al.*, 2014).

Null model to discard patterns due to plant–AMF specificity

A significant relationship between plant and AMF phylogenetic compositions may just reflect the specificity in plant–AMF interactions described at the species level (Montesinos-Navarro *et al.*, 2012*b*). In order to discard this possibility, a matrix of 576 AMF sequences by 23 plant species present in the community was generated, with '1' for the allowed plant–AMF interactions representing the specificity in the interactions and '0' for the forbidden interactions. From the 576 allowed interactions, the same number of interactions as that observed in each patch was randomly selected, to generate 17 'theoretical patches'. In this way, the plant–AMF specificity pattern and the number of interactions per patch were maintained, but the phylogenetic composition in each patch was randomized. A correspondence between plant and AMF phylogenetic composition was tested for the set of 17 'theoretical patches' as explained above for the real phylogenetic compositions. This process was repeated 1000 times.

RESULTS

The phylogenetic composition of plants and AMF assemblages in each patch was characterized by means of plant PCA and AMF PCA, respectively. Four and two PC axes captured at least 90 % of the variation of the phylogenetic composition of plants and AMF, respectively. Plant PC1 explained 52 % and AMF PC1 88 % of the total variance of phylogenetic composition among patches (note that these two PCs come from independent PCA analyses). There was no significant spatial autocorrelation in either plant PC1 ($r = -0{\cdot}10$; P-value $= 0{\cdot}98$) or AMF PC1 ($r = 0{\cdot}06$; P-value $= 0{\cdot}15$). The phylogenetic composition of plants was not significantly correlated with the number of plant species in the vegetation patch ($r = 0{\cdot}37$; P-value $= 0{\cdot}17$). Similarly, the AMF phylogenetic composition was not significantly correlated with the number of AMF sequences found in the patch ($r = -0{\cdot}24$; P-value $= 0{\cdot}35$).

The AMF phylogenetic composition (AMF PC1) showed a linear positive relationship with AMF phylogenetic diversity (i.e. MPD) across patches (rho = 0·89; $P < 0{\cdot}001$; Fig. 1). There was a negative correlation between plant species loading in plant PC1 and the nursery quality of plant species (rho = −0·65; $P < 0{\cdot}01$, Supplementary Data Table S2). Finally, there was a significant relationship between the phylogenetic composition of plants (plant PCA) and AMF (AMF PCA) assemblages across patches. This relationship was significant when considering all PC axes accumulating at least 90 % of the total variation of plants (plant PC1–PC4) and AMF (AMF PC1–PC2) ($R^2 = 0{\cdot}49$; P-value = 0·038), and also when considering the correlation between just the first principal axes for plant (plant PC1) and AMF (AMF PC1) ($R^2 = 0{\cdot}24$; P-value = 0·04; Fig. 2). This significant relationship between plant and AMF phylogenetic compositions was not just a reflection of the specificity in plant–AMF interactions because the significant correlation between plant PC1 and AMF PC1 disappears in 903 of the 1000 randomly assembled communities in which specificity in plant–AMF interactions was preserved.

The model constructed to quantify the effect of the relationship of several plant and AMF variables on the mean phylogenetic diversity of AMF (AMF MPD) showed significant contributions of the phylogenetic composition of AMF (39 %) and plants (28 %), and of the interaction between plant phylogenetic diversity and patch nursery quality (10 %) (Table 1). In addition, there was still 18 % of non-explained variation. Plant phylogenetic diversity and nursery quality independently did not explain AMF phylogenetic diversity. A high plant phylogenetic diversity could result from distantly related species with either low or high nursery quality, and these differences can influence AMF phylogenetic diversity. Similarly, a patch with a high nursery quality community-weighted mean can harbour different plant phylogenetic diversity, which will also condition

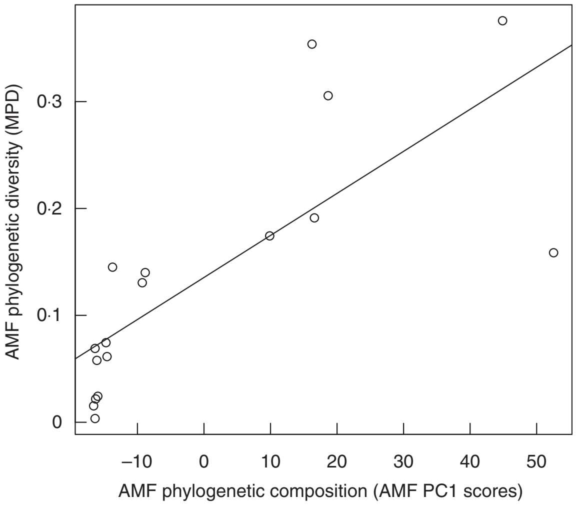

FIG. 1. Linear regression between phylogenetic diversity and phylogenetic composition of arbuscular mycorrhizal fungi (AMF) assemblages (i.e. patches). Phylogenetic diversity is measured as mean phylogenetic distance between each pairwise AMF DNA sequence present in each patch. Phylogenetic composition in each patch is characterized as the first principal component of the P matrix described by Pillar and Duarte (2010) which represents the phylogenetically weighted taxa composition of each vegetation patch.

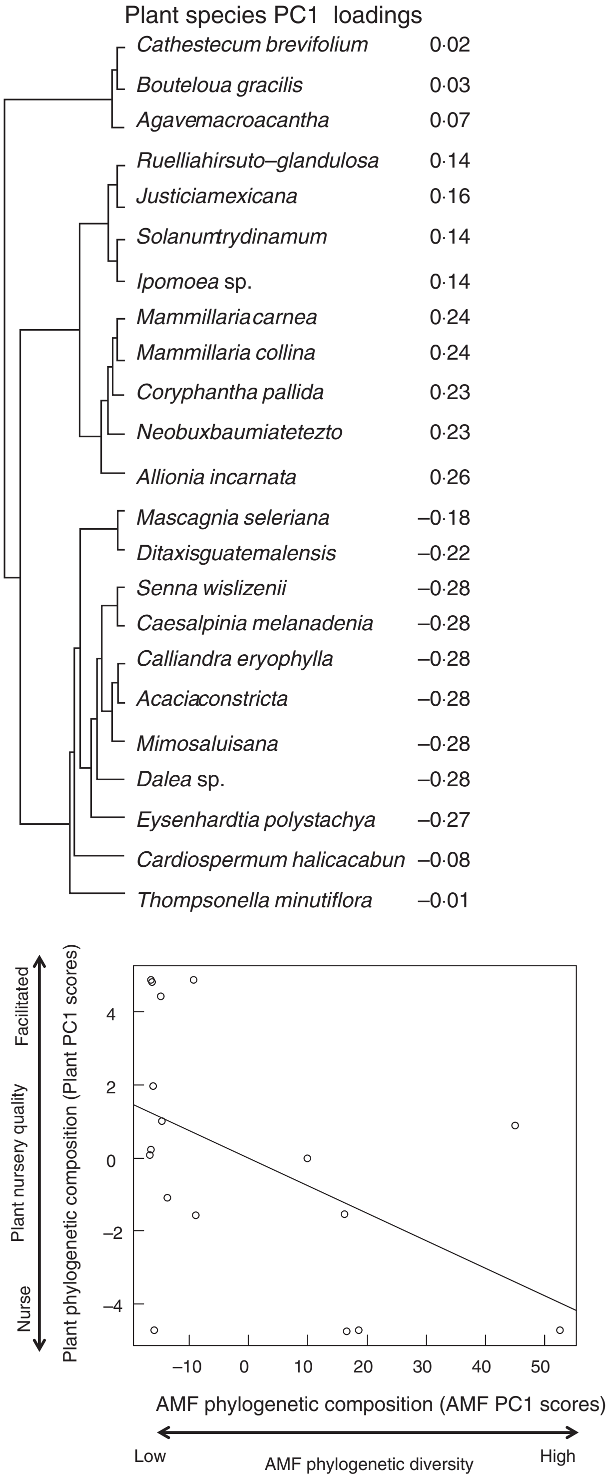

FIG. 2. Relationship between the phylogenetically weighted taxa composition of plant and arbuscular mycorrhizal fungi (AMF) across vegetation patches. The phylogenetic composition of plants and AMF in each patch is characterized as the first principal component of the P matrix described by Pillar and Duarte (2010). Plant and AMF PC1 represent the phylogenetic composition of the assemblages of the plant and AMF, respectively. Extreme values of the plant PC1 correspond to patches in which either nurse (high negative loading values) or facilitated (high positive loading values) species predominate. Extreme values of the AMF PC1 correspond to patches with low and high AMF phylogenetic diversity.

TABLE 1. *Non-parametric multiple regression to test for multiple effects on AMF phylogenetic diversity (AMF MPD)*

Source	Estimates	d.f.	F	R^2	P-value
Plant MPD	$-3{\cdot}9 \times 10^{-6}$	1	2·2	0·03	0·61
Patch nursery quality	$-2{\cdot}9 \times 10^{-2}$	1	0·0	0·00	0·98
Plant PC1	$-1{\cdot}2 \times 10^{-2}$	1	16·5	0·28	0·005
AMF PC1	$4{\cdot}0 \times 10^{-3}$	1	23·0	0·39	0·002
Plant MPD × patch nursery quality	$1{\cdot}02 \times 10^{-4}$	1	6·0	0·10	0·031
Residuals		11		0·18	
Total		16			

The model tests for the relative contribution of plant mean phylogenetic distance (plant MPD), community-weighted mean of nursery quality (patch nursery quality), plant and AMF phylogenetic composition (plant PC1 and AMF PC1) and the interaction of plant phylogenetic diversity and nursery quality.

AMF phylogenetic diversity. Accordingly, the interaction between plant phylogenetic diversity and patch nursery quality better explained the phylogenetic composition of AMF, while both effects independently were non-significant. The positive significant interaction between these two terms indicated that AMF MPD was promoted by the combination of high nurse quality and phylogenetic diversity.

DISCUSSION

This study shows a correlation between the phylogenetic compositions of two interacting guild assemblages across a patchy environment (Fig. 2). This correlation cannot be solely explained by plant–AMF specificity, and we suggest other ecological processes potentially shaping the phylogenetic composition of the vegetation patches.

Plant phylogenetic composition across patches is influenced by the predominance of plant species with the lowest nursery quality (e.g. Cactaceae, Solanaceae or Convolvulaceae), which contribute to the highest values of the plant PC1, and the predominance of plant species with the highest nursery quality (e.g. Fabaceae), which contribute to the lowest values of the plant PC1. In addition, low values of the plant PC1 correspond to high values of the AMF PC1 (Fig. 2), which in turn are patches with a high phylogenetic diversity of AMF (Fig. 1). This result, together with the significant interaction showing that the combination of plant high nursery quality and phylogenetic diversity promotes AMF MPD, suggests that patches containing predominantly diverse plant species with high nursery quality (e.g. Fabaceae) tend to have a high AMF phylogenetic diversity. In contrast, patches in which species with low nursery quality predominate such as the Cactaceae, *Mammillaria collina*, *M. carnea*, *Neobuxbaumia tetetzo* and *Coryphanta pallida*; or the Acanthaceae, *Ruellia hirsuto-glandulosa*, tend to have a low phylogenetic diversity of AMF.

Taxa composition can be crucial in plant–AMF interactions as species traits, such as nursery quality, a functional characteristic which encapsulates different traits (Valiente-Banuet *et al.*, 2006), may be influencing patterns of co-occurrence of AMF in the patch. Fabaceae have been shown to be important nurses in other systems (Barnes and Archer, 1996; Flores and Jurado, 2003; Liphadzi and Reinhardt, 2006), especially in semi-arid environments (Flores and Jurado, 2003; Bashan *et al.*, 2009; Muro-Pérez *et al.*, 2012). Their association with nitrogen-fixing bacteria has been suggested as a potential mechanism underlying colonization behaviour (Cadotte and Strauss, 2011), and a tendency to act as a nurse for other species in the community. In addition, the presence and the identity of AMF can alter the competitive interactions between plant species (Van der Heijden *et al.*, 1998; Scheublin *et al.*, 2007), and the Fabaceae tend to obtain a greater benefit from AMF than other plants (Scheublin *et al.*, 2007). Our results suggest that the capability to interact with phylogenetically distant AMF might be a potentially relevant trait in defining the nursery quality of a plant species in semi-arid plant communities, but experimental approaches will be necessary to test this hypothesis.

Interestingly, AMF can be present from the beginning of plant succession and relate differently to pioneer and late-successional plant species (Kikvidze *et al.*, 2010). This suggests that reciprocal plant–AMF interactions may be involved in ecological mechanisms of succession within a patch. The variation in phylogenetic composition of plant and AMF across patches could represent the inter-related replacement dynamics of plants and AMF within a vegetation patch over time (i.e. succession). During the successional history of a patch, it might shift from harbouring mainly species with high nursery quality, which are the only pioneer species in this system (Valiente-Banuet and Verdú, 2008), to harbouring mainly facilitated species upon the death of the species with high nursery quality. Our results are consistent with the hypothesis that this shift from the predominance of nurse to facilitated species within a patch might be coupled with a reduction in below-ground phylogenetic diversity. However, further experiments are necessary to test this hypothesis. We show that shifts in the phylogenetic composition of the two guild assemblages are not independent but there remains variation not explained by this relationship, suggesting that other indirect effects such as interactions with other guilds, not considered here, can also be influencing this dynamic. In addition, we have focused on the traits related to the PC axes that explain most of variation (PC1 of plants and AMF), but other traits related to less important sources of variation can be driving other ecological processes represented in the remaining axes. Furthermore, our results are based on the most abundant group of AMF, *Glomus*, but the consideration of other Glomeromycota could reveal new ecological processes and functions that would provide a more complete understanding of plant–AMF interactions.

In summary, we show that shifts in the phylogenetic composition of plants and AMF assemblages do not occur independently, providing indirect evidence for the potential relevance of interguild interactions in community assemblage processes. We suggest that besides selectivity in plant–AMF interactions, inter-related succession dynamics of plants and AMF within patches could be an ecological mechanism leading to the observed pattern. The consideration of other coexisting guilds in these patches and the design of experimental approaches to test for the indirect evidence provided here are necessary for a better understanding of the role of interguild biotic interactions in community assemblage. Considering the increasing feasibility of exploring the community structure of soil micro-organisms using next-generation sequencing tools, promising future lines of research might explore whether there is evidence of interlinked dynamics above- and below-ground, taking into account multiple guilds simultaneously.

SUPPLEMENTARY DATA

Supplementary data are available online at www.aob.oxfordjournals.org and consist of the following. Table S1: AMF GenBank accession number, plant host species and PC1 loading. Table S2: nursery quality score and PC1 loading for plant species.

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