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REGULAR ARTICLE

Resource availability differentially drives community assemblages of plants and their root-associated arbuscular mycorrhizal fungi

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Abstract
Background and aims Understanding the role of resource availability in structuring biotic communities is of importance in community ecology. This study investigates how light and soil nutrient availability drive assemblages of both plants and their root-associated arbuscular mycorrhizal fungi (AMF).
Methods We conducted a 4-year light [full light or shade] and soil fertility [unfertilized or fertilized with $(NH_4)_2HPO_4$] interactive manipulations in an alpine meadow ecosystem. Species and phylogenetic compositions of plant and AMF communities were simultaneously measured, and the primary ecological processes structuring both communities were inferred from the community phylogenetic analysis.
Results Reducing light and/or increasing soil fertility significantly reduced species richness and changed community compositions of both plant and AMF. Plant community phylogenetic structure shifted from random in untreated control to overdispersion in other treatments, whereas AMF communities were phylogenetically clustered and random in unfertilized and fertilized plots, respectively. These results suggest that plant communities in treated plots were mainly determined by competitive exclusion, and that AMF communities in unfertilized and fertilized plots were determined by

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environmental filtering and random process, respectively.

Conclusions We observed strong effects of light and soil nutrient availability on both plant and AMF communities, and our findings highlight that the primary ecological processes that drive plant and AMF assemblages should be highly dependent on the level of resource availability.

Keywords Soil fungi · Phylogenetic structure · Community assembly · Light intensity · Soil fertility · Alpine meadow

Introduction

Understanding how resource availability governs biotic communities is a crucial step toward predictive community ecology. Numerous observational and experimental studies have shown strong effects of the resource availability on species diversity and species compositions of plant communities (e.g. Tilman 1986; Wassen et al. 2005; Liu et al. 2012; Borer et al. 2014), but relative little is known about the effects of resource availability on belowground communities in rhizosphere soils, where diverse microorganisms interact with plants and play key roles in biogeochemical cycles (Wardle et al. 2004; Philippot et al. 2013).

Arbuscular mycorrhizal fungi (AMF, phylum Glomeromycota), which can form mutualistic associations with the roots of most terrestrial plants, are especially significant in rhizosphere because they can increase soil resource capture (especially phosphorus [P], and possibly nitrogen [N]) as well as improve the stress tolerance of their hosts in return for plant photosynthates (Smith and Read 2008; Hodge et al. 2010). The resource-trade relationship between AMF and plants suggests that AMF community might be very sensitive to changing resource availability (Johnson 2010), and that any factors affecting plant nutrients and photosynthetic rate would also change the abundance and species composition of AMF community (Johnson 2010). Some spore-based and DNA-based field studies have reported negative effects of increasing N and/or P availability on the abundance and diversity of AMF community (Egerton-Warburton et al. 2007; Alguacil et al. 2010; Liu et al. 2012; Camenzind et al. 2014), whereas others have shown no effect or positive effect (Antoninka et al. 2011; Van Diepen et al. 2011). More recently, Shi et al. (2014a) conducted a mesocosm experiment with planting a single plant species and found that the AMF richness inside roots was decreased dramatically by synchronous fertilization and shade treatment but not by fertilization or shade alone. Such inconsistent observations suggest that the response of AMF community to changing resource availability might be highly dependent on the absolute and relative resource demands of both plants and AMF (Treseder and Allen 2002; Johnson 2010). On the other hand, many field studies have shown strong host preference of AMF (Helgason et al. 2002; Mao et al. 2014; Veresoglou and Rillig 2014), indicating that the changes in plant species composition induced by changing resource availability could also exert strong impacts on AMF community (Liu et al. 2012).

Even though the communities of both plants and their associated AMF would be shifted synchronously by changing resource availability, exploring the underlying ecological processes that drive these shifts remains a challenge. Several competition-based hypotheses have been proposed to explain the shifts in community structure of both plant (Rajaniemi 2002; Lamb et al. 2009) and AMF (Johnson 2010), but which are difficult to be tested in fields. The phylogenetic analysis of community structure, which merges phylogenetic relatedness between species with the studies of community ecology, can efficiently determine the relative importance of the deterministic (e.g. environmental filtering or competitive exclusion) and stochastic processes in driving community assembly (Webb et al. 2002; Cavender-Bares et al. 2009). Under the assumption of phylogenetic niche conservatism (the niche-related traits are similar among closely related lineages), in theory, the environmental filtering and competitive exclusion should generate patterns of phylogenetical clustering and overdispersion, respectively (Webb et al. 2002). This method was widely used in the studies of plant community (Dinnage 2009; Yang et al. 2012; Parmentier et al. 2014), but in recent years it has been increasingly used to analyze the communities of mycorrhizal fungi (Kivlin et al. 2011; Lim and Berbee 2013; Horn et al. 2014; Rincón et al. 2014; Saks et al. 2014; Shi et al. 2014b) and other microbes (Pontarp et al. 2012; Wang et al. 2013). Since the functional traits of AMF have been shown to be conserved (Powell et al. 2009; Maherali and Klironomos 2012), the ecological processes driving AMF assemblages can be efficiently inferred from the community phylogenetic structure (e.g. Shi et al.

2014b). To our knowledge, however, no study has used the method of phylogenetic analysis to elucidate how the resource availability affects communities of both plant and AMF.

Light intensity and soil fertility are especially important in regulating plant and AMF communities. In theory, reducing light intensity will generate light and carbon limitations for plants and AMF, respectively (Tilman 1986; Johnson 2010). Enrichment of soil nutrients will enhance the light competitions of plants (Newman 1973; Hautier et al. 2009), and it may also enhance the carbon competition of AMF because plant carbon allocation to AMF will be reduced when plants are not limited by soil nutrients (Johnson 2010). Thus, we predicted that reducing light availability and increasing soil fertility would significantly change the community structure and reduce the species richness of both plant and AMF due to the enhanced resource competition. To test this hypothesis, we conducted a 4-year interactive treatments with reducing light intensity (shade) and increasing soil fertility (fertilization with N and P) in an alpine meadow ecosystem. We measured simultaneously the species and phylogenetic compositions of plant and AMF communities, and the primary ecological processes driving assembly of both communities were inferred from the community phylogenetic analysis. In particular, the objectives of this study were to answer the following questions: 1) how do the assemblages of plant and AMF respond to shade, fertilization and their interaction? 2) whether the competitive exclusion is the primary process driving the shifts of both communities; and 3) which resource is the most important factor in governing plant or AMF communities?

Materials and methods

Study site and experimental design

This experiment was carried out on a flat field in the Walaka experimental site (34°00′N, 102°00′E; 3,500 m above sea level) of the Research Station of Alpine Meadow and Wetland Ecosystems of Lanzhou University in the eastern Qinghai-Tibetan Plateau of China. This experimental site is a typical alpine meadow with dominant plants of Cyperaceae and Poaceae, where the mean annual temperature is 1.2 °C, the mean annual frost period is about 270 days, the mean annual precipitation is 620 mm, and the mean annual cloud-free solar radiation is about 2,580 h. The growing season in this region is from May to September. The biodiversity in this experimental site is relatively high, with an average of 20–35 vascular plant species per 0.25 m^2 (Yang et al. 2012) and a total of 38 AMF phylotypes identified in 100 root samples from a 0.15 ha field (Liu et al. 2012).

Experimental treatments began in May 2008, with a split-plot design with two soil fertility levels (ambient soil and fertilization) nested within two treatments of light manipulation (full light and shade). Fertilization treatment was generated with 45 g of $(NH_4)_2HPO_4$ fertilizer applied in every May (the corresponding N and P inputs were about 9.5 g N and 10.6 g P m^{-2} yr^{-1}). For the shade treatment, a 1.3-m height canopied black-nylon mesh, which was permeable to air and water, was used to block *c*. 70 % of photosynthetically active radiation (PAR) during the growth season. In total, four treatments consisting of control, shade, fertilization, and synchronous shade and fertilization (hereafter referred to as S + F treatment), were established in this study. Each treatment had eight replicated plots (2×2 m), with 1-m buffer strips between plots. Five replicated plots in each treatment were randomly selected in this study, for a total of 20 plots. Before sampling, the midday PAR at the heights of 0, 10 and 40 cm above ground in each plot were measured in a summer sunny day (the midday PAR above plant level in this day was 6,508 μmol photons m^{-2} s^{-1}).

Sampling and analyses of vegetation and soil properties

In each plot, a 0.25 m^2 quadrat was randomly selected to measure the plant species richness and abundance at the end of August 2011. Species abundance was calculated on the basis of the number of individuals or ramets. All individual plants in each quadrat were clipped to the soil surface and used to measure the shoot biomass after dried at 80 °C for 48 h. Dry plant materials were ground to a fine powder for the determination of the shoot nutrient contents. Concurrent with the vegetation investigation, in each plot, five soil cores with depth of 0–25 cm and diameter of 3.8 cm were randomly collected and mixed as one sample. All soil samples were stored in an ice box and transported back to the laboratory. Fine live roots were carefully separated from each soil sample, washed cleanly and used for DNA extraction and the determination of AM colonization. The remaining soils were air-dried, sieved with a 1-mm mesh and used for soil chemical analysis and extraction of AMF spore

and extraradical hyphae. In total, 20 root samples and 20 soil samples were collected in this study. Soil characteristics (including soil moisture, pH, total N, organic C, available P and available N) and the shoot N and P concentrations were analyzed using the methods described by Liu et al. (2012).

Analyses of AM colonization, spore density and extraradical hyphae

Roots were stained with trypan blue according to the method described by Brundrett et al. (1994), and the percent root length AM colonization, arbuscular colonization and vesicular colonization were quantified using magnified intersection method (McGonigle et al. 1990). Spores of AMF in each soil sample were separated from 25 g dry soil by wet sieving and sucrose centrifugation (Brundrett et al. 1994), and the spore density was counted using a dissecting microscope. Extraradical hyphae of AMF in each soil sample were extracted and stained with trypan blue followed the protocols of Brundrett et al. (1994) and Miller et al. (1995). Hyphal length was measured using a line intersection method and used to calculate the hyphal length density (Brundrett et al. 1994).

Analysis of AMF communities inside roots

Molecular analysis of AMF communities inside roots was the same as the method of Liu et al. (2012). Briefly, partial 18S rRNA gene sequences of AMF were amplified from the extracted root DNA via a nested PCR method, using GeoA2-Geo11 (Schwarzott and Schüßler 2001) and NS31-AML2 (Simon et al. 1992; Lee et al. 2008) as the first and second primer combinations, respectively. The second PCR products were purified and used to construct clone libraries (20 in total), and then the inserted DNA fragments were re-amplified (48 putative positive clones per clone library) and screened using restriction fragment length polymorphism (RFLP) with restriction enzymes *Hin*fI and *Hin*1II. One representative clone of each RFLP type in each treatment was sequenced, for a total of 136 sequences. The remaining clones were classified by RFLP typing. All DNA sequences were edited and compared with published sequences using the online BLAST search tool (http://blast.ncbi.nlm.nih.gov; accessed 20 March 2014). The non-AMF and possibly chimeric sequences were eliminated from the dataset, and only the remaining 114 AMF sequences were analyzed further. In total, 751 AMF clones were identified from 902 positive clones (*c*. 83 %).

All AMF sequences obtained in this study were used to BLAST against the online Maarj*AM* database (http://maarjam.botany.ut.ee; accessed 20 March 2014), which has collected most 18S rRNA gene sequences of AMF from published environmental sequences and morphologically described taxa, and phylogenetically defined sequence group as molecular virtual taxon (VT; similar with phylotype or species) with sequence identity ≥97 % (Öpik et al. 2010). The VT taxonomy of AMF is increasingly used as a reference for identification of environmental sequences (Öpik et al. 2014). If possible, each obtained sequence was grouped into a corresponding VT according to the sequence identity (≥97 %), query coverage (≥97 %) and BLAST bit score, and the sequence with identity low than 97 % was regarded as an unnamed new VT. To further confirm the VT delimitation of our AMF sequences, we aligned our sequences and the representative sequences of VTs in Maarj*AM* database using ClusterW and constructed a maximum likelihood (ML) tree using Mega 5.0 with Tamura 3-parameter model and 1000 bootstrap replications (Tamura et al. 2011). Those sequences with ambiguous VT delimitation (i.e. one sequence could be grouped into more than one VT after BLAST search) were corrected according to the sequence identity, bootstrap values and the topology of phylogenetic tree.

To elucidate the phylogenetic relationships between our VTs and the published AMF sequences, one representative sequence from each VT (these sequences have been deposited in Genbank database under the accession numbers KJ817383-KJ817409), the most closely related sequences from GenBank and the representative sequences of major genera of Glomeromycota (http://schuessler.userweb.mwn.de/amphylo) were used to construct a ML phylogenetic tree according to the method described above. Each VT obtained in this study was grouped into corresponding genus and family of Glomeromycota according to the phylogenetic tree. The community composition of AMF inside roots was calculated on the basis of the clone numbers of each VT in a root sample. The VT or genus or family richness of AMF in each sample was calculated, and the sampling effort curves of VT richness were computed using EstimateS 8.0 (Colwell 2006).

Statistical analysis

Before analysis, all measured variables were tested for normality and those obviously non-normal variables were $\log_{10}(x+1)$ transformed. We used two-way ANOVA to test the effects of shade, fertilization and their interaction on each variable, and the significant differences of each variable among treatments were determined using Tukey's honestly significant difference (HSD) test at the 95 % confidence level. To assess the responses of plant and AMF to the resource availability (light, N and P) that would be highly changed by our treatments, we first generated proxies of light, N and P availability by principal component analysis (PCA) using the scores of the first principle component (PC1) of data matrices which included light intensities at different heights above ground (note: since we did not measure the PAR values above plant level in each plot, we used 6508 and 1952 μmol photons m^{-2} s^{-1} [100 and 30 % full light PAR] to represent the light intensities above plant level in shaded and unshaded plots, respectively) or soil available N and shoot N or soil available P and shoot P (hereafter referred to as light or N or P availability score). Using the PC1 scores of a particular data matrix to define the resource availability was used previously (Liu et al. 2012). Linear regression analyses were performed using the plant or AM fungal variables against the scores of light, N and P availability. All above statistical analyses were performed using SPSS 13.0 (SPSS Inc. IL, USA), with the exception that linear regression was done using R 2.15.2 (R Core Team 2012).

The dissimilarities of plant or AMF species compositions among samples were computed by non-metric multidimensional scaling (NMDS) with Bray-Curtis distance using 'metaMDS' function of the R package 'Vegan' (Oksanen 2013). This statistical method can depict community composition in multi-dimensions, and the variance of samples is maximized on the first dimension (Oksanen 2013). The treatments were fitted as centroids onto the ordination plots using 'ordiellipse' function from the 'Vegan' package (Oksanen 2013). To explore the relationships between resource availability and community compositions of plant or AMF, the PC1 scores of light, N and P availability were fitted as vectors onto the NMDS plots using 'envfit' function from the 'Vegan' package (Oksanen 2013).

The phylogenetic patterns of both plant and AMF communities were analyzed using the R package 'Picante' (Kembel et al. 2010). Before analysis, we first calculated the phylogenetic distances of all detected plant species (Table S1) or AMF VTs. Plant phylogenetic tree was created using the 'Phylomatic' program (Webb and Donoghue 2005) in association with the 'R20100701' version of the Angiosperm Phylogeny Group III supertree (http://www.mobot.org/mobot/research/apweb), and branch lengths for the tree were calculated using the 'Bladj' program included with Phylocom 4.2 (Webb et al. 2008). The AMF phylogenetic tree was calculated using Mega 5.0 according to the method described above (Tamura et al. 2011). The mean nearest taxon distance (MNTD), a commonly used measure of community phylogenetic structure (Kraft et al. 2007; Kembel 2009), was employed to quantify the relatedness of co-occurring plant species or AMF VTs. Based on the MNTD, we calculated the inter-community MNTD (betaMNTD) using 'comdistnt' function (Kembel et al. 2010), and again, we performed NMDS and vector fitting (see details described above) using the data of betaMNTD. This statistical method was used by others (Stegen et al. 2012; Wang et al. 2013), and it can clearly depict the phylogenetic difference in community composition between a given pair of samples in a two dimensional plot (Wang et al. 2013). In addition, to evaluate the degree of non-random phylogenetic structure of our communities, we calculated the nearest taxon index (NTI) using 'ses.mntd' function (NTI is equivalent to −1 times the output of 'ses.mntd'; Kembel et al. 2010), in which observed MNTD was compared with the null distribution of MNTD generated by the 1000 randomizations of 'phylogeny. pool' null model, and the MNTD for each taxon was weighted by its abundance. NTI is a standardized measure of the phylogenetic distance to the nearest taxon for each taxon in the sample (Webb et al. 2002), and through which we could infer the importance of niche-based and neutral processes in driving community assembly (Kembel 2009). In general, a mean NTI across all samples that is significantly different from zero indicates phylogenetic clustering (NTI>0; species more closely related than expected) or overdispersion (NTI<0; species more distantly related than expected) (Kembel 2009). The significant difference between NTI and null expectation of zero was tested using two-tailed *T* test at the 95 % confidence level.

To determine how the effects of shade and fertilization on AMF community mediated through the changes of plant variables, we used Amos 5.0 (SPSS Inc., IL,

USA) to construct and test a structural equation model (SEM; Grace 2006). In this model, we chose shoot biomass (represents the plant productivity), shoot N:P ratio (represents the plant nutritional status) and plant species richness (represents the range of host niche for AMF; Hiiesalu et al. 2014) as three plant variables that would potentially influence AMF community. The shade and fertilization were fitted as 100 or 30 % light intensity and 0 or 45 g fertilizer every year, respectively. The species or phylogenetic compositions of AMF community were represented by the scores of the first NMDS dimensions. We tested how well the models fitted our data using the maximum likelihood Chi-square goodness-of-fit test and Bollen-Stine bootstrap test (Grace 2006).

Results

Relationships between treatments with light, N and P availability

Light intensity varied among 0, 10 and 40 cm layers (F_2 = 38.2; P<0.001), but all were highly affected by shade, fertilization and their interactions (all P≤0.002). On average, the light intensities (0–40 cm heights above ground) under shade, fertilization and S + F treatments were 24.5, 36.4 and 18.3 % of that in control, respectively. Our treatments changed significantly the available soil N and P, whereas other soil characters (total N, organic C, pH, etc.) were similar among treatments (Table S2). Shade improved soil available N (F_1 = 62.1; P<0.001), whilst fertilization dramatically increased soil available P (F_1=191.8; P<0.001) and decreased soil N:P ratio (F_1 = 196.1; P<0.001). In comparison with the control, our treatments significantly increased the concentrations of both shoot N and P, but decreased shoot N:P ratio (Table 1). PCA ordinations showed that the variations of light (83.0 %), N (86.6 %) and P (88.6 %) availability could be well explained by the PC1 of light, N and P matrices, respectively. In addition, the loading values of PC1 of all matrices are positive (Fig. S1), suggesting that the PC1 scores increased with the increasing availability of each resource.

Effects of treatments on plant community

Forty-nine plant species within 18 families were found in this study (Table S1). Most species, particularly the sedges and leguminous species, were extinct in plots with S + F treatment (Table S1). Both shade and fertilization dramatically decreased the individual density and the plant richness at the levels of species, genus and family (all P<0.001), meanwhile the shoot biomass was reduced and increased by shade and fertilization, respectively (Table 1). All above variables, but not the family richness (F_1 = 0.7; P=0.417), were also significantly affected by shade and fertilization interaction (all P<0.05). In addition, plant species richness was correlated negatively with the scores of both N and P availability and positively with light availability (Fig. 1a).

NMDS ordinations of plant communities revealed that both the species and phylogenetic compositions were highly changed by treatments (Fig. 2a,b); however, plant species composition was more sensitive to treatments than the phylogenetic composition, because the phylogenetic compositions were similar under shade and fertilization treatments (Fig. 2a,b). Resource availability, especially the light, was very important in governing the species (light: R^2 = 0.83, P<0.001; N: R^2 = 0.68, P<0.001; P: R^2 = 0.72, P<0.001) and phylogenetic (light: R^2 = 0.82, P<0.001; N: R^2 = 0.58, P<0.001; P: R^2 = 0.53, P=0.003) compositions of plant communities (Fig. 2a,b).

Our treatments reduced significantly the NTI of plant community compared with the untreated control (Fig. 3a). However, regression analyses showed that light availability, but not the N and P availability, was correlated significantly with the NTI of plant community (Fig. 1b). In addition, NTI of plant community in control did not differ from zero, whereas that in other treatments were similar and significantly lower than zero (Fig. 3a). These results suggest that plant community in control plots was phylogenetically random, and the communities under other three treatments were phylogenetically overdispersed.

Effects of treatments on AMF abundance inside and outside roots

The percentage of root length AM colonization was significantly affected by fertilization and shade × fertilization interaction (Table 1), and both arbuscular and vesicular colonization responded remarkably to fertilization (Table 1). Under fertilized condition, however, all colonization variables were dramatically decreased by shade (Table 1). In contrast to the significant variation of hyphal abundance inside roots, we did not observe

Table 1 Plant and AMF variables in different treatments and the results of two-way ANOVA for the effects of shade, fertilization and their interaction

	Plant variables					AMF variables					
	Species richness	Shoot Biomass (g 0.25 m^{-2})	Shoot N (mg g^{-1})	Shoot P (mg g^{-1})	Shoot N:P ratio	RLC (%)	AC (%)	VC (%)	Extraradical hyphae (m g^{-1} soil)	Spore density (spores 25 g^{-1} soil)	VT richness
Control	28.2±0.9a	122.4±10.1b	6.7±0.4c	0.3±0.04c	24.2±3.8a	32.4±6.5x	4.5±0.7x	5.7±1.2x	27.4±8.4	27.0±2.5	8.4±0.5x
Shade (S)	13.0±0.3c	61.5±2.9c	9.2±1.1c	1.0±0.2b	10.4±2.3b	38.0±9.8x	6.0±3.0x	5.2±1.9x	18.6±3.7	43.2±14.3	7.8±1.2xy
Fertilization (F)	16.4±1.2b	180.1±9.7a	13.0±0.4b	1.4±0.1b	9.4±0.9b	35.5±2.9x	3.0±1.2x	4.0±1.2x	21.8±5.4	27.6±4.3	8.2±2.6xy
S + F	8.4±0.4d	80.2±7.0c	18.7±0.6a	2.7±0.2a	7.2±0.7b	8.8±2.3y	0.3±0.2y	0.8±0.5y	15.7±2.8	23.8±3.8	4.6±0.5y
Summary of ANOVA											
Effect of S	***F*=228.1**	***F*=102.6**	***F* =35.2**	***F*=40.8**	***F*=12.0**	*F*=3.0	*F*=0.1	*F*=2.0	*F*=1.8	*F*=0.6	***F*=5.5**
	***P*<0.001**	***P*<0.001**	***P*<0.001**	***P*<0.001**	***P*=0.003**	*P*=0.104	*P*=0.705	*P*=0.174	*P*=0.196	*P*=0.440	***P*=0.032**
Effect of F	***F*=114.0**	***F*=23.2**	***F*=128.6**	***F*=84.5**	***F*=15.3**	***F*=4.5**	***F*=4.9**	***F*=5.3**	*F*=0.6	*F*=1.4	*F*=3.6
	***P*<0.001**	***P*<0.001**	***P*<0.001**	***P*<0.001**	***P*=0.001**	***P*=0.049**	***P*=0.042**	***P*=0.034**	*P*=0.454	*P*=0.247	*P*=0.076
Effect of S × F	***F*=22.0**	***F*=6.1**	***F*=5.5**	*F*=3.3	***F*=6.4**	***F*=6.9**	*F*=1.7	*F*=1.1	*F*=0.1	*F*=1.6	*F*=2.8
	***P*<0.001**	***P*=0.025**	***P*=0.032**	*P*=0.09	***P*=0.022**	***P*=0.018**	*P*=0.212	*P*=0.315	*P*=0.814	*P*=0.220	*P*=0.113

Data are means ± SE (n =5). Significant differences among treatments within each variable were determined using Tukey's HSD test ($P \leq 0.05$) and indicated by dissimilar letters. Significant effects are in bold

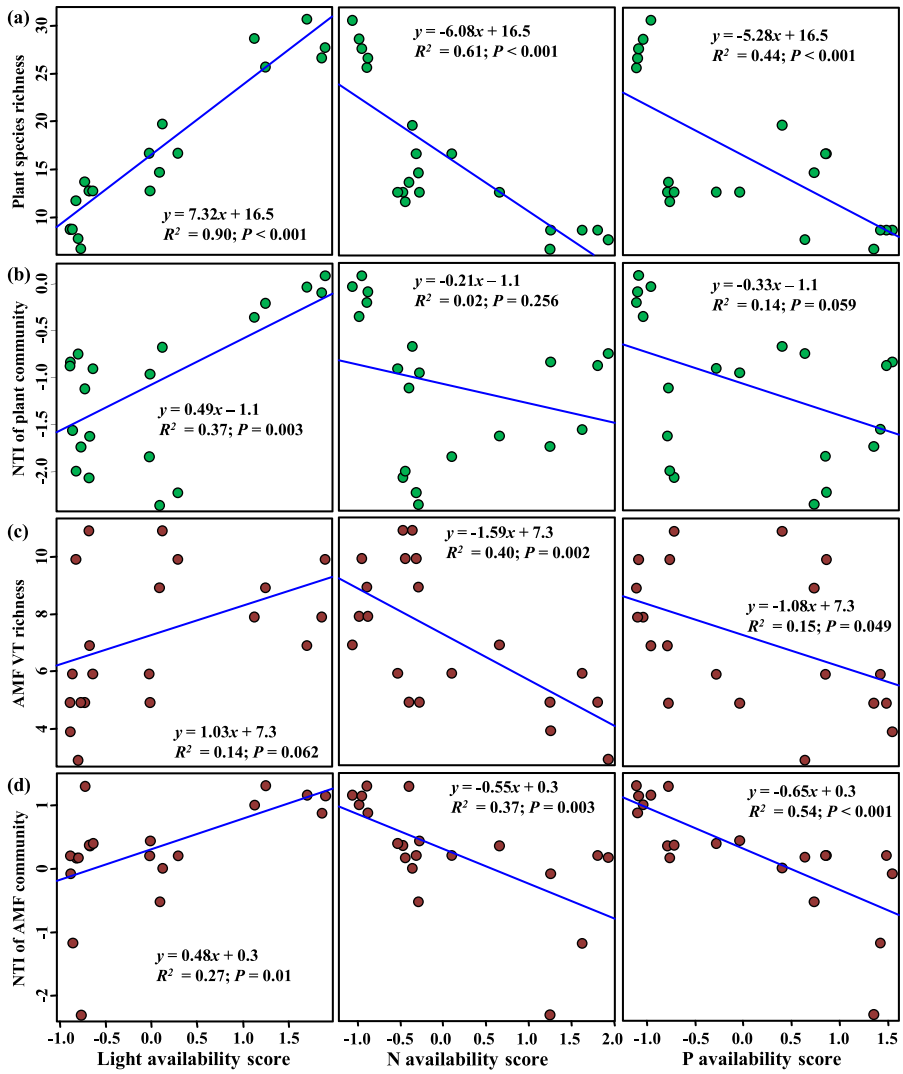

Fig. 1 Linear regressions of plant species richness (**a**), nearest taxon index (NTI) of plant community (**b**), virtual taxon (VT) richness of AMF (**c**) and NTI of AMF community (**d**) versus the scores of light, nitrogen (N) and phosphorus (P) availability. The light, N and P availability scores were derived from the first principal components of a light intensity matrix, a N matrix and a P matrix, respectively (see Materials and methods). The light, N and P availability scores increase with increasing light or N or P availability (see Fig. S1)

statistically significant effects of treatments on the abundance of extraradical hyphae and spores in soils (Table 1). Using above variables against the scores of N, P and light availability showed that only the three colonization variables were correlated negatively with both N and P availability (all $P<0.05$).

Effects of treatments on AMF community

Sampling effort curves indicate that the majority of AMF VTs inside roots were captured in each treatment (Fig. S2). A total of 27 AMF VTs, including 25 named and two new VTs, was identified in this study. These VTs are belonging to nine genera within four families: Glomeraceae (21 VTs within *Glomus*, *Rhizophagus*, *Funneliformis*, *Septoglomus* and two new genus-like clades), Claroideoglomeraceae (3 VTs within *Claroideoglomus*), Diversisporaceae (2 VTs within *Diversispora*) and Gigasporaceae (1 VT within *Scutellospora*) (Fig. S3). Taken as a whole, the VT166 (related to an unknown *Glomus* sequence; 21.3 % of all AMF clones), which was extremely inhibited by

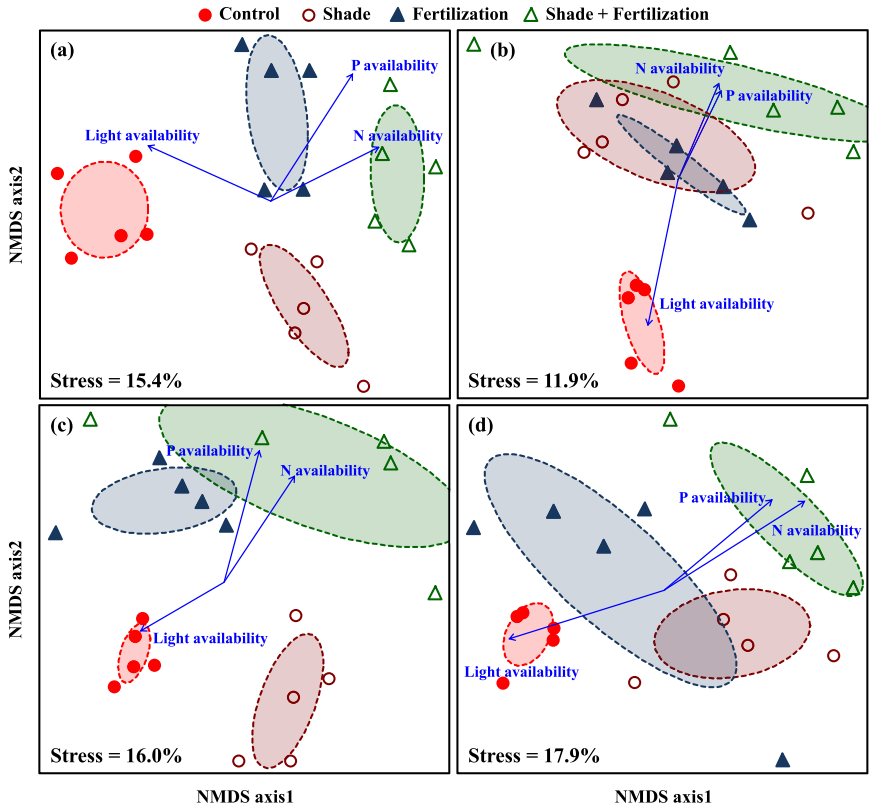

Fig. 2 Non-metric multidimensional scaling (NMDS) patterns of community dissimilarities among treatments using the data of plant species composition (**a**), plant betaMNTD (**b**), AMF virtual taxon (VT) composition (**c**) and AMF betaMNTD (d). *Ellipses* with different colors indicate 95 % confidence ellipses for centroids of each treatment. The PC1 scores of light, N and P matrices that represent light, N and P availability (see Fig. S1) are fitted as vectors onto each ordination plot

fertilization (F_1 = 88.7; P<0.001), was the most dominant in our samples, followed by VT113 (related to *Rhizophagus intraradices*; 21 %). Half of VTs responded significantly to our treatments (Fig. S3), with some VTs being specific to particular treatments (e.g. VT143 only detected in treatment with shade) or levels of resource (e.g. VT83 and VT166 preferred to full light and low-fertility conditions, respectively).

Our treatments did not change AMF richness at the levels of VT, genus and family (all P>0.05), but there was an interactive effect of shade and fertilization on the family richness of AMF (F_1 = 6.2; P=0.024). Nonetheless, the VT richness was correlated negatively with the scores of both N and P availability (Fig. 1c). In addition, NMDS ordinations revealed that both the species and phylogenetic compositions of AMF community varied among treatments (Fig. 2c,d), and both were significantly correlated with the scores of all resource availability, especially the N availability (for species composition: R^2 = 0.74, P<0.001; for phylogenetic composition: R^2 = 0.76, P<0.001).

The NTI of AMF community was affected significantly by shade (F_1 = 5.4; P=0.034) and fertilization (F_1 = 15.5; P=0.001), and it was correlated positively with light availability and negatively with both N and P availability (Fig. 1d). Moreover, the NTI of AMF community in control and shade treatments were significantly higher than zero, whereas it did not differ from zero in the other two treatments (Fig. 3b). These results indicate that AMF communities in unfertilized plots were phylogenetically clustered and in fertilized plots were phylogenetically random.

SEM fitting

Our SEM represented the experimental variables well (Chi-square = 8.34, P=0.501; Bollen-Stine bootstrap, P=0.742), and clearly elucidated the plant-mediated

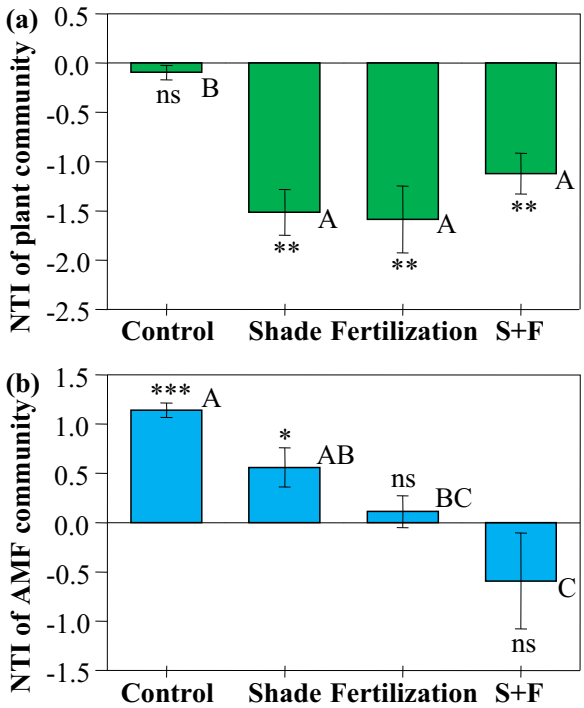

Fig. 3 The nearest taxon index (NTI, mean ± SE) of plant (**a**) and AMF (**b**) communities varied in treatments. *Asterisk* indicates that the NTI is significantly different from zero (ns, non-significant; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$). Significant differences of NTI between columns are indicated with different capital *letters* after Tukey's HSD test ($P \leq 0.05$). S + F, synchronous shade and fertilization treatment

influences of shade and fertilization on AMF community. The parameters included in this model explained 55 % and 63 % of the variance in the species and phylogenetic compositions of AMF community, respectively (Fig. 4). All plant variables were affected strongly by both shade and fertilization, especially the effects of shade on shoot biomass (λ=0.86) and plant species richness (λ=0.77). All pathways from plant variables to AMF community were significant (all λ>0.05; Fig. 4), but the species composition was affected mainly by shoot biomass (λ=−0.51) and the phylogenetic composition mainly by plant species richness (λ=−0.64). Taken as a whole, the total effects of shade on both species (λ=−0.71) and phylogenetic (λ=−0.64) compositions of AMF community were stronger than that of fertilization (for species composition: λ=0.04; for phylogenetic composition: λ=0.41).

Discussion

Our field experiment with simultaneous analysis of plant and AMF communities revealed that the species richness of both communities respond negatively to reducing light and/or increasing soil nutrient availability (Fig. 1), and that the community structure of both plant and AMF were highly sensitive to the changes of light and soil nutrient availability (Fig. 2). These findings support our research hypothesis and highlight the importance of light and soil nutrient availability in determining the assemblages of both plant and AMF.

In our study, plant species richness declined dramatically with reducing light intensity and/or increasing soil fertility (Table 1), corroborating the findings in other ecosystems (e.g. Edelkraut and Güsewell 2006; Reich 2009; Dickson and Foster 2011). It has been suggested that both shade and fertilization induced decline of plant richness is mainly attributed to the enhanced light

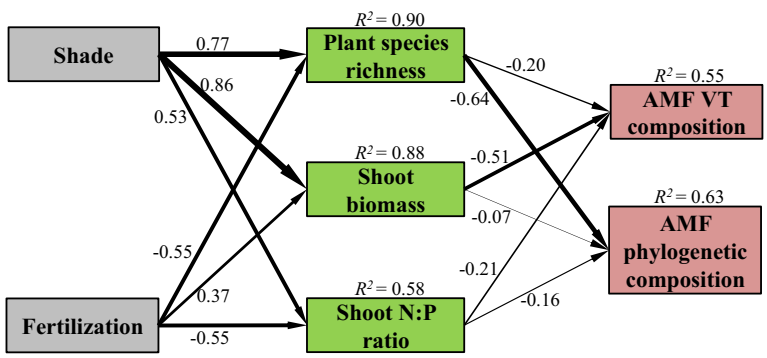

Fig. 4 A structural equation model showing the causal influences of treatments (shade and fertilization), plant species richness, shoot biomass and shoot N:P ratio on the species and phylogenetic compositions of AMF community inside roots. The width of *arrows* indicates the strength of the causal effect. The *numbers* above the *arrows* indicate path coefficients (λ), and all pathways in this model are significant (all λ>0.05). R^2 values represent the proportion of variance explained for each variable

limitation and light competition (Hautier et al. 2009; Borer et al. 2014). This mechanism appears to be operating in our case, because the light availability for the whole plant community was largely reduced by both shade and fertilization treatments (Fig. S1c). Furthermore, the height of the winning plant species, *Elymus nutans* (Poaceae), which can strongly compete light with other plants via the advantageous traits of high plant height, high specific leaf area and high foliar N concentration (Hu et al. 2011), was significantly increased by both shade and fertilization (data not shown), indicating that the light competition in the plant communities was enhanced by our treatments. The competition-based explanation is also supported by our finding that plant phylogenetic pattern shifted from random in control to overdispersion in other treatments (Fig. 3), from which we could infer that plant communities in treated plots were mainly determined by the competitive exclusion (Webb et al. 2002).

In contrast to the large loss of plant species in all treated plots, we found that only S + F treatment reduced VT richness of AMF inside roots (Table 1). This result partially accords with our first expectation, but it is consistent with a mesocosm experiment with similar experimental design, in which AMF richness colonizing roots of *Ligularia virgaurea* was reduced significantly by synchronous shade and fertilization treatment, but not by treatments with shade or fertilization alone (Shi et al. 2014a). In theory, both shade and fertilization (synchronous N and P inputs) will reduce carbon supply to AMF (Johnson 2010), resulting in reduction of AM colonization and AMF richness (Hodge and Fitter 2010; Liu et al. 2012). In our case, however, neither shade nor fertilization reduced the AM colonization as well as the spore density and extraradical hyphal abundance (Table 1), indicating that our shade or fertilization treatments did not reduce plant carbohydrate supply to AMF. This speculation is supported by a ^{13}C tracing experiment, in which shade or P fertilization did not reduce recently assimilated plant carbon allocation to AMF structures inside roots (Olsson et al. 2010). On the contrary, our S + F treatment caused the AM colonization to decline by four-fold (Table 1), suggesting that the carbohydrate supply to AMF might be highly reduced under this treatment. It has been reported that the competition for host carbohydrates among AMF species could be sufficiently strong to exclude some AMF taxa from host roots (Hepper et al. 1988). Thus, the reduced AMF richness under S + F treatment can be partially explained by the enhanced carbohydrate competition among AMF species. However, it is also possible that the decline of AMF richness in this study might be mediated by the large loss of plant species, because AMF richness is usually positively correlated with plant species richness in natural ecosystems (Landis et al. 2004; Hiiesalu et al. 2014). More ingenious experiments are encouraged to quantify how changing light intensity and/or soil fertility affect the carbon supply to AMF as well as the pattern and strength of competition among AMF taxa.

Even though plant and AMF richness responded differently to our treatments, the species and phylogenetic compositions of both communities varied significantly among treatments (Fig. 2). These results are in line with other studies showing significant impacts of shade and/or fertilization on plant and/or AMF species compositions (Heinemeyer et al. 2004; Liu et al. 2012; Camenzind et al. 2014; Shi et al. 2014a), and provide new evidence on the relationships between resource availability and phylogenetic structure of both plant and AMF communities. The changes of plant community should be mainly attributed to the enhanced competition for light and/or soil nutrients that were caused directly by both shade and fertilization, because resource competition is a major process controlling the structure of plant communities (Tilman 1986). However, our SEM analysis showed that the effects of both shade and fertilization on AMF community were mainly mediated by the shifts in the plant species richness and shoot biomass (Fig. 4). These findings corroborate other studies showing that AMF community structure is highly dependent on the plant carbohydrate supply and the plant species composition (Johnson et al. 2005; Johnson 2010; Liu et al. 2012), and also suggest that, in our case, the treatment-induced changes in biotic (host) niche and plant productivity might be the major factors that caused the shifts of AMF community composition. It is interesting that AMF phylogenetic composition was influenced strongly by the plant species richness but weakly by the shoot biomass (Fig. 4), suggesting that the host niches may be more important than plant carbohydrate supply in determining the AMF phylogenetic structure. In addition, we found that the total effect of fertilization on AMF phylogenetic composition was stronger than that on species composition, indicating that the species phylogenetic relatedness within a AMF community might be more sensitive to changing soil nutrient availability. Given that the community phylogenetic

composition contains more information compared with the species composition (Webb et al. 2002), exploring the dynamics of community phylogenetic structure under changing environments should be encouraged in future researches, because it will facilitate our understanding in predicting ecosystem processes and impacts of global change (Cavender-Bares et al. 2009).

The important finding in our study is that changing light and soil nutrient availability would change the ecological processes driving assemblages of both plant and AMF (Fig. 3). In our experimental system, plant communities randomly assembled in control plots, but after treatments the competitive exclusion became as a dominant process in shaping plant communities. By contrast, the phylogenetic pattern of AMF community shifted from phylogenetic clustering in unfertilized plots (control and shade) to phylogenetic random in fertilized plots (fertilization and S + F treatment), indicating that AMF communities in unfertilized and fertilized plots were mainly determined by environmental filtering and random process, respectively. The phylogenetic patterns of AMF communities in natural ecosystems are largely unknown, but several recent studies showed that AMF communities inside roots were frequently phylogenetically clustered (Horn et al. 2014; Saks et al. 2014; Shi et al. 2014b). Competitive exclusion can also produce phylogenetically clustered pattern even when the functional traits are evolutionally conserved (Mayfield and Levine 2010), but in our case, the shift of phylogenetic pattern might be associated with the P availability, because the major difference between unfertilized and fertilized plots was the P availability. It has been shown that the AMF function of providing P to their host plants is phylogenetically conserved (Powell et al. 2009), and that different AMF phylogenetic groups would prefer to colonize roots under different P availability (Alguacil et al. 2010; Camenzind et al. 2014). Consequently, it is possible that plants under low P availability would like to select (environmental filtering) functionally similar AMF (e.g. high P-uptake efficiency), which might be also phylogenetically closely related, from the local species pool. This is also supported by our finding that the NTI of AMF community was correlated negatively with the score of P availability (Fig. 1d). Further studies are required to address whether the most important process driving AMF assemblage would shift from environmental filtering to stochastic process and finally to competitive exclusion along low to high P availability gradient.

Our experimental design cannot directly distinguish the effects of light and soil nutrient availability, because the light, N and P availability were synchronously changed by both shade and fertilization treatments. However, our statistical analyses successfully quantify the correlations between the availability of each resource with both plant and AMF communities (Figs. 1 and 2). In our study, the light availability, rather than the N or P availability, was the most correlated factor with plant variables, suggesting that light availability might be more important in determining plant community. On the contrary, effects of N and P availability on AMF community seem to be stronger than that of light, because our AMF community composition as well as the AMF richness and NTI were more correlated with the scores of both N and P availability. This might be the fact because the core function of AMF is to enhance soil nutrient uptake of their hosts (Hodge et al. 2010), and P or N limitation of plants is very important in maintaining stable AM associations (Johnson et al. 2010). Regardless of whichever resource is the most important for plant or AMF, our results clearly showed that the negative effects of shade and fertilization on both plant and AMF were additive, corroborating other observations (Dickson and Foster 2011; Shi et al. 2014a) and suggesting that more attentions should be paid to assess the effects of synchronous changes in light and nutrient availability on both partners of mycorrhizal symbionts.

In summary, our 4-year field experiment reveals that reducing light and/or increasing soil nutrient availability would significantly reduce the species richness and change the community structure of both plant and their root-associated AMF. The changes of plant community were strongly linked to the ecological process shift towards dominance by competitive exclusion, whereas the changes of AMF community were largely mediated by the shifts in plant species richness and shoot biomass that were caused by both shade and fertilization. To our knowledge, this is the first study that tested the resource-mediated changes of two associated communities at the levels of both species and phylogenetic compositions. Given the key roles of plant and AMF communities in natural ecosystems, it is essential to evaluate the ecosystem consequence of changing communities caused by reducing light and/or increasing soil nutrient availability, and this knowledge will help us to fully predict the ecological impacts of global change such as nutrient deposition and atmospheric haze.

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