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ORIGINAL ARTICLE

Metadata-mining of 18S rDNA sequences reveals that "everything is not everywhere" for glomeromycotan fungi

Haishui Yang[1] · **Yajun Dai**[1] · **Mingmin Xu**[2] · **Qian Zhang**[3] · **Xinmin Bian**[1] · **Jianjun Tang**[4] · **Xin Chen**[4]

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Abstract In microbial ecology, the "everything is everywhere" hypothesis has long been controversial. In the present study, we performed data-mining for 18S rDNA sequences of glomeromycotan fungi in order to test this hypothesis. 18S rDNA sequences targeted using AM1–NS31 fragments were retrieved from GenBank, with a total of 1768 sequences collected from 34 sites worldwide. In total, 229, 330 and 518 operational taxonomic units (OTUs) were defined based on 97, 98 and 99 % similarity, respectively. The 97 % OTUs showed a limited geographical range of glomeromycotan fungi. Among the OTUs, 58.1 % were endemic, and 17.9 % and 9.2 % were found in two and three sites, respectively. The most widespread OTU was shared by 17 sites. Phylogenetic structure analysis demonstrated that most local communities (26 of 34) were clustered. OTUs with larger host breadth had wider geographic ranges. A significant distance–decay relationship was revealed that was independent of habitat. Cluster analysis showed that fungal composition was not related to habitat, while Fast UniFrac analysis indicated that the distribution of Glomeromycota was affected by temperature. Taken together, these results suggest that glomeromycotan fungi were not randomly distributed under natural conditions; rather, they were affected by host plants, dispersal ability and temperature. Thus, the distribution of glomeromycotan fungi argues against the hypothesis that "everything is everywhere."

Keywords Arbuscular mycorrhizal fungi · Community · Distribution · Host · Dispersal · Temperature

Introduction

A species' distribution pattern and the mechanism(s) underling it is central to the study of biodiversity in ecology (Martiny et al. 2006). Unlike macrobiota, however, relatively little is

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✉ Haishui Yang
yanghaishui@njau.edu.cn

✉ Xin Chen
chen-tang@zju.edu.cn

Yajun Dai
2013101010@njau.edu.cn

Mingmin Xu
2013116030@njau.edu.cn

Qian Zhang
east.qzhang@gmail.com

Xinmin Bian
yanghaishui@gmail.com

[1] Key Laboratory of Crop Physiology, Ecology and Production Management, Ministry of Agriculture, Nanjing Agricultural University, Nanjing 210095, People's Republic of China

[2] College of Life Sciences, Nanjing Agricultural University, No.1, Weigang Road, Nanjing 210095, China

[3] Research Institute of Forestry, Chinese Academy of Forestry, Beijing 210095, China

[4] College of Life Sciences, Zhejiang University, Hangzhou 310058, People's Republic of China

known about the geographic distribution of microorganisms. Since the beginning of the twentieth century, it has been assumed that microbes disperse randomly and globally, summarized as "everything is everywhere," and referred to as the EisE hypothesis (Martiny et al. 2006). For the past several decades, however, there has been growing controversy around the EisE hypothesis, with examples of free-living and non-free-living microorganisms that both support and refute it. Positive evidence has included free-living microbes such as ciliates, diatoms, protists and bacterioplankton (Finlay et al. 1999; Darling et al. 2000; Glockner et al. 2000; Heino et al. 2010), as well as the non-free-living Usnea fungi that exhibit bipolar distribution (Wirtz et al. 2008). Increasing evidence against the hypothesis has been found with the use of new molecular study methods. For example, microbial prokaryotes and eukaryotes showed typical species–area and distance–decay relationships (Green et al. 2004; Bell et al. 2005; Noguez et al. 2005), and cyanobacteria, rhizobia and ectomycorrhizal fungi were found to be restricted by their hosts (Usher et al. 2004; Dickie and Reich 2005; Steenkamp et al. 2008). However, we do not know whether arbuscular mycorrhizal fungi (AMF), a group of soil functional microbes with ecological importance, have distribution patterns that support the EisE hypothesis.

AMF belong to the phylum Glomeromycota, and form obligate symbioses with most terrestrial plants (Smith and Read 2008). These fungi rely entirely on host plants to complete their life cycles. But unlike other non-free-living microorganisms, such as rhizobia in Fabaceae and ectomycorrhizal fungi in Pinaceae, Glomeromycota are widely distributed among plants. For vascular plants, including angiosperms, gymnosperms and pteridophytes, studies have found that AMF have high colonization potential, with *Glomus* spp. dominating AMF communities in roots (Vandenkoornhuyse et al. 2003; Russell and Bulman 2005; Wubet et al. 2006; West et al. 2009). AMF communities have also been reported in bryophytes, although the AMF species were mainly from the *Glomus* genus (Russell and Bulman 2005). In basal liverworts in particular, mycorrhizal symbionts were restricted to *Glomus* group Ab (Ligrone et al. 2007). In addition, while Brassicaceae were once considered as not associating with AMF, molecular study showed colonization of *Thlaspi* species in Brassicaceae by *Glomus* fungi at a low frequency (Regvar et al. 2003). Some achlorophyllous plants even obtained carbon by tapping into mycorrhizal networks of glomeromycotan fungi (Bidartondo et al. 2002).

Glomeromycota also have a wide geographic distribution, having been reported in almost all terrestrial habitats. Extensive studies have reported their occurrence in tropical, temperate and boreal forests (Helgason et al. 2002; Husband et al. 2002; Öpik et al. 2008), grassland and savannah (Li et al. 2010b), farmland, and other anthropogenic conditions (Helgason et al. 1998). Glomeromycotan fungi even occur in some severely stressful environments, including desert (Wu et al. 2007), Tibetan alpine (Liu et al. 2012), low-arctic (Pietikainen et al. 2007), salt marsh (Wilde et al. 2009), lake (Baar et al. 2011) and mangrove habitats (Wang et al. 2011). Indeed, it may appear that Glomeromycota have a random distribution pattern around the globe.

However, fossil evidence suggests that Glomerales originated during the Ordovician around 460 million years ago (Chaudhary et al. 2008), when the continental plates did not break up, and combined as the supercontinent of Pangaea (Scotese 2004). With geological evolution, historical factors may have affected the distribution of glomeromycotan fungi. Recent molecular studies suggest that they were host-preferential to some extent (Vandenkoornhuyse et al. 2002; Li et al. 2010b), and thus factors affecting large-scale plant distribution, such as temperature and precipitation, could influence distribution of the fungi as well (Koske 1987; Lugo et al. 2008). Research has shown that the propagules of some glomeromycotan fungal species can only be dispersed several meters under natural conditions, indicating that geographic isolation might affect distribution (Chaudhary et al. 2008). For the cosmopolitan *Glomus mosseae*, genetic evidence has suggested that its global distribution was mediated only recently by human agricultural activities (Rosendahl et al. 2009). Taken as a whole, these findings indicate that glomeromycotan fungi might have a unique large-scale distribution pattern that is distinct from that of all other non-free-living microorganisms.

In this study, we hypothesized that the distribution of Glomeromycota argued against the EisE hypothesis. To test this hypothesis, we performed a meta-analysis of 18S rDNA sequences amplified with AM1-NS31 primers from 34 clone libraries. By examining the taxonomic and phylogenetic similarities in different sites, we explored the global distribution patterns of glomeromycotan fungi. We posited that the fungi were not randomly and globally distributed, but were highly endemic. We also hypothesized that the distribution pattern was related to host, geographical isolation, historical factors and climate.

Methods

Data source

In AMF molecular diversity studies, the most widely used primer pair is the AM1-NS31. In our analysis, we included only AM1-NS31 DNA sequences in order to maintain the lowest possible sequencing error rate among the various studies. The AM1 primer was originally designed and published by Helgason et al. (1998), and we performed a search in the Web of Science and extracted all literature in which this paper was cited. In total, 31 studies using AM1-NS31 for identifying AMF communities were selected for our analysis. The

samples in these studies were collected from 34 sites (Table S1), and the details of each site, including host, latitude, longitude, continent and climate, were retrieved from the original papers. With the accession numbers published in these papers, we extracted 1768 glomeromycotan fungal DNA sequences from GenBank.

Data analysis

Sequence handling and OTU definition

Sequences were aligned with Clustal X (Drummond et al. 2010), and alignments were uploaded into Geneious Basic 5.0.3 (Drummond et al. 2010) and edited manually to remove ambiguous nucleotides and leading and trailing gaps. FASTA-formatted alignments were exported and classified into operational taxonomic units (OTUs) based on 97, 98, and 99 % similarity. This was done in Mothur v.1.10 (Schloss et al. 2009) using the "hcluster" command by setting cutoff values of 0.03, 0.02 and 0.01.

Phylogenetic analysis

Representative sequences were selected for each 97 % OTU using the "get.oturep" command in Mothur v.1.10 (Schloss et al. 2009). All representatives were aligned in Clustal X (Drummond et al. 2010) and exported in the PHYLIP format for phylogenetic analysis. A maximum-likelihood phylogenetic tree was constructed using the "GTRCAT" model with 1000 bootstrap replications, performed in RAxML version 7.0 (Stamatakis 2006).

Local community composition and structure

We assessed local community composition by calculating the proportion of shared 97 % OTUs among sampling sites. OTUs occurring in only one site were referred to as endemic OTUs, and the endemic ratio was used to infer fungal distribution to support or refute the EisE hypothesis. We also introduced two new indicators to reflect phylogenetic information in community structure: net relatedness index (NRI) and net taxon index (NTI) (Faith 1992; Webb 2000). Both indices were calculated using Phylocom version 3.40 software with 97 % OTUs. Based on the maximum phylogenetic tree, NRI was calculated with $[-(\mathrm{MPD}-\mathrm{MPD}_{\mathrm{null}})/\mathrm{SD}(\mathrm{MPD}_{\mathrm{null}})]$, where MPD is the mean pairwise phylogenetic distance between species in a community, $\mathrm{MPD}_{\mathrm{null}}$ is the mean MPD for 1000 random communities, and SD ($\mathrm{MPD}_{\mathrm{null}}$) is the standard deviation. NTI was calculated with $[-(\mathrm{MNTD}-\mathrm{MNTD}_{\mathrm{null}})/\mathrm{SD}(\mathrm{MNTD}_{\mathrm{null}})]$, where MNTD is the mean nearest pairwise phylogenetic distance between species in a local community, $\mathrm{MNTD}_{\mathrm{null}}$ is the mean MNTD for 1000 random communities, and SD ($\mathrm{MNTD}_{\mathrm{null}}$) is the standard deviation. NRI reflects the phylogenetic "clumpedness" of taxa over the whole local phylogeny. Positive NRI represents the clumpedness of local communities, while negative NRI represents overdispersion. NTI is used to test the extent to which taxa are clustered in a local community, with positive and negative NTI indicating clustered and dispersed taxa, respectively. Thus NRI and NTI indirectly reflect the distribution pattern of taxa in local communities. If NRI and NTI for most local communities are positive, a high degree of endemism is suggested, providing indirect evidence to dispute the EisE hypothesis in glomeromycotan fungi.

Effects of hosts and historical factors

The distribution of Glomeromycota may be closely related to that of their host plants, given the obligate symbiotic nature of the relationship. Here we analyzed the relationship between host breadth and geographic range of 97 % OTUs. Host breadth was calculated as the occurrence of each OTU across host species, while geographic range was defined by the occurrence of each OTU among common sites. Linear regression analysis was performed using SPSS version 16.0 software (SPSS Inc., Chicago, IL, USA).

The effects of historical factors are reflected by the distribution of glomeromycotan fungi across continents. We calculated the occurrence of 97 % OTUs among the continents of Europe, Asia, North America, Latin America and Africa. If most OTUs occurred in only one continent, it indicated the potential effects of historical factors on fungal distribution.

Effects of habitat and dispersal ability

The distribution of glomeromycotan fungi across habitats indicates the effects of habitat filtering, which was reflected in cluster analysis of molecular taxonomic and phylogenetic similarity. We classified habitats as follows: forest, grassland, scrubland, successional habitats, and habitats under anthropogenic disturbance. For taxonomic similarity, cluster analysis was performed with the Bray–Curtis method based on 97 % OTU composition using PAST [PAlaeontological STatistics] software version 1.91 (Hammer et al. 2001). For phylogenetic similarity, we performed cluster analysis with UniFrac distance (Lozupone and Knight 2005), which is calculated as the percentage of branch length leading to descendants from only one of the environments represented in the phylogenetic tree, and reflects differences among phylogenetic lineages adapted to live in one environment versus the others.

Distance–decay analysis was performed to test the effects of dispersal ability on the distribution of glomeromycotan fungi. Distance–decay relationships were assessed based on 97, 98 and 99 % sequence similarity with log (x + 1)-transformed data. Bootstrapping of linear regression was performed with 10,000 permutations to test whether the slope of the similarity–distance relationship was significantly different from zero (Horner-Devine et al. 2004). Similarity between local fungal communities was calculated using the Bray–Curtis method, and geographical distance was calculated with latitude and longitude in decimal degrees. Calculations were conducted using PAST version 1.91 software (Hammer et al. 2001). In addition, to distinguish the effect of dispersal ability from that of habitat, a two-tailed partial Mantel test was performed with 10,000 permutations in the XLSTAT 7.5 software program (Addinsoft, Paris, France). The dissimilarity of habitats between local communities was calculated with Euclidean distance based on categorical composition of habitats using PAST version 1.91 (Hammer et al. 2001).

Effects of climate

On a large geographic scale, climate may be a factor affecting the distribution of glomeromycotan fungi. In this analysis, we assessed the effects of precipitation and temperature on Glomeromycota distribution. Precipitation in our sampling sites was classified into five types, according to the Köppen-Geiger climate classification (Kottek et al. 2006): desert, steppe, fully humid, summer dry, and monsoonal. Temperature was classified into four types: hot summer, warm summer, hot arid and cold arid (Table S1). Three-dimensional principal coordinates analysis (3D-PCoA) was performed with Fast UniFrac to determine precipitation and temperature effects based on fungal phylogeny. Fast UniFrac, a new version of UniFrac specifically designed to handle very large datasets (Lozupone et al. 2006), provides tools with which to compare microbial communities using phylogenetic information.

Results

Community composition and structure analysis

Based on sequence similarity of 97, 98 and 99 %, all 1768 sequences were assigned into 229, 330 and 518 OTUs, with an average of 14, 16 and 21 OTUs per site, respectively (Table 1). For the 97 % OTUs, no OTU was found in all 34 sites. Most OTUs, 133 of 229, were found in one site, accounting for 58.1 %, while 17.9 % and 9.2 % of the OTUs were shared by two and three sites, respectively. The most widely distributed OTU was found in 17 sites, and shared 100 % similarity with *Glomus intraradices* (accession number: FJ009602) according to BLAST (Figs. 1 and 2a). Most endemic OTUs were less abundant, with 93 % represented by only 1 to 4 sequences per site, and only 7 % represented by 4 to 50 sequences per site (Fig. 2b).

Of the total 34 local glomeromycotan communities, 26 had positive NRI values, while the other eight had negative NRI values (Table 1). The average NRI was positive. Thirty-two glomeromycotan fungal communities had positive NTI values, while only two communities were negative. The average NTI value was also positive.

Effects of hosts and historical factors

Linear regression analysis showed that glomeromycotan fungal geographic range was positively correlated with host breadth ($P<0.001$). OTUs with higher host specificity were found to have narrower geographic distribution. This host effect explained 77 % of geographic variation in glomeromycotan fungal composition (Fig. 3).

Most OTUs were specific to one continent, accounting for 74 %, while 19 % of the OTUs were shared by two continents. The proportions shared by three and four continents were very low, at 5 and 1 %, respectively (Fig. 4).

Effects of habitat and dispersal ability

The effects of habitat were assessed at both the molecular taxonomic and phylogenetic levels. At a molecular taxonomic level, no habitat filtering effects were evident in glomeromycotan communities (Fig. 5a), with communities of one type of habitat scattered across different clades of the clustering dendrogram. Among nine forest communities, clustering occurred only in UK03 and UK04 and in PA01 and JP02, while others were scattered. Of the eight grassland glomeromycotan communities, six were scattered. Six glomeromycotan communities in successional habitats also showed little clustering tendency. Nine glomeromycotan communities in habitats under anthropogenic interference were scattered, and two scrubland communities (SP01 and SP02) also did not cluster together.

A similar lack of habitat filtering effect was shown at a phylogenetic level (Fig. 5b). Eight forest glomeromycotan communities clustered separately from each other. Six grassland communities clustered separately, with only two savannah habitat communities, MA01 and UG01, clustering together. Of seven successional type glomeromycotan communities, three (PH01, PO01 and PO02) were clustered together. However, five of eight anthropogenic communities were clustered together, as well as two shrubland communities (SP01 and SP02).

Table 1 OTU characteristics at increasing similarity levels and the phylogenetic structure of glomeromycotan fungi

Sample ID*	Sequence number	97 % similarity			98 % similarity	99 % similarity	NRI	NTI
		Observed OTUs	Endemic OTUs	Endemic fraction	Observed OTUs	Observed OTUs		
UK01	11	5	0	0	6	7	2.03	2.059
UK02	69	18	5	0.28	18	18	0.65	0.6285
UK03	22	15	2	0.13	17	17	0.72	0.4326
UK04	13	5	2	0.40	6	6	−0.25	0.5178
UK05	15	14	7	0.5	15	16	−0.40	1.0417
UK06	64	11	2	0.18	14	17	1.62	2.5677
ES01	66	13	4	0.13	37	43	1.89	3.3745
ES02	112	12	3	0.16	22	30	1.82	3.2969
AU01	179	14	10	0.27	44	61	3.18	3.4451
FR01	64	6	3	0.50	6	9	−0.95	1.1007
GE01	55	14	5	0.17	32	39	0.75	2.0145
IT01	32	16	1	0.06	17	20	−0.93	0.7535
NE01	10	4	3	0.75	6	7	0.12	0.6804
PO01	32	6	3	0.5	8	14	0.28	1.2775
PO02	24	8	3	0.38	8	12	−0.47	1.2307
SP01	114	12	7	0.64	17	25	1.28	2.288
SP02	23	6	0	0.00	9	10	1.76	1.657
SW01	81	9	0	0.00	11	11	1.40	1.3644
CH01	20	8	1	0.13	11	11	1.92	1.5303
CH02	27	9	4	0.44	7	8	0.50	0.5839
JP01	24	18	0	0.00	7	8	2.93	2.5573
JP02	101	12	8	0.67	15	28	0.40	1.4651
PH01	33	16	3	0.60	5	6	0.30	−0.2135
US01	17	15	5	0.33	16	16	1.90	1.2412
US02	179	10	3	0.30	15	29	2.27	2.5441
US03	28	12	1	0.03	13	16	1.38	1.9191
US04	16	12	1	0.08	12	15	1.36	2.1799
US05	35	18	12	0.67	22	31	−2.16	−0.8997
CA01	53	18	4	0.22	22	35	2.19	2.5452
ME01	56	20	2	0.22	12	16	−0.27	0.4409
PA01	61	29	11	0.40	38	46	1.09	1.407
UG01	48	19	7	0.37	20	28	1.35	2.2719
MA01	20	15	1	0.13	9	11	1.06	1.6964
CAM01	42	21	11	0.73	18	19	−0.21	0.573
Average	52	13	4		16	21	0.90	2.059
All sites	1768	229	133		330	518	–	–

*Abbreviations in sample IDs represent country names: UK United Kingdom, ES Estonia, AU Austria, FR France, GE Germany, IT Italy, NE Netherlands, PO Portugal, SP Spain, SW Switzerland, CH China, JP Japan, PH Philippines, US United States of America, CA Canada, ME Mexico, PA Panama, UG Uganda, CAM Cameroon

OTU operational taxonomic unit, *NRI* net related index, *NTI* net taxon index

Bootstrapping of linear regression between glomeromycotan fungal community similarity and geographic distance showed significant distance–decay curves for all taxonomic resolution levels (Fig. 6). The partial Mantel test showed a negative correlation between glomeromycotan fungal compositional similarity and geographic distance when habitat was fixed (r= −0.231, P=0.001 for 97 % similarity; r=0.227, P= 0.001 for 98 % similarity; r=−0.200, P=0.001 for 99 % similarity) (Table 2). When geographic distance was controlled, habitat was not related to fungal community similarity (Table 2).

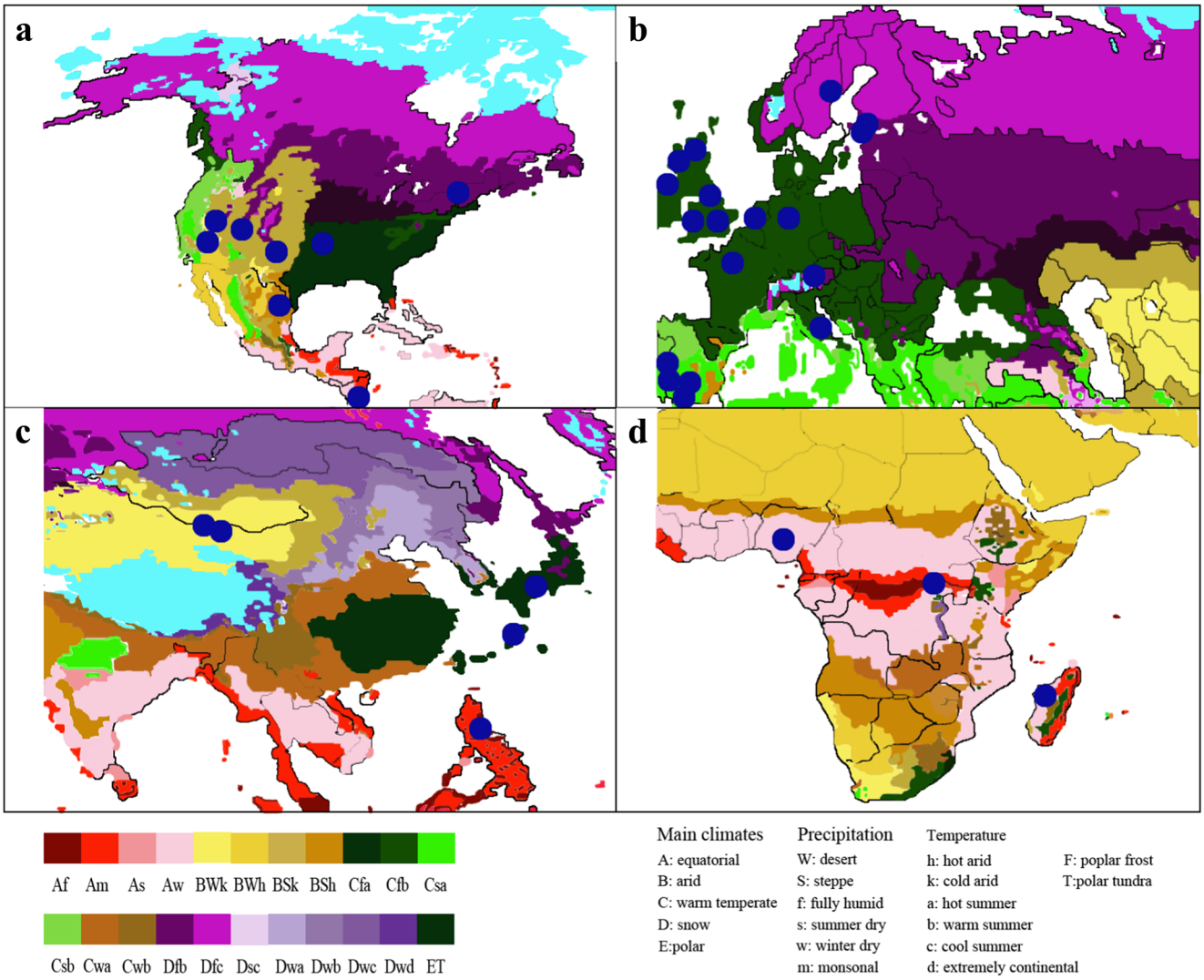

Fig. 1 Geographic origins of 34 samples: **a** North America; **b** Europe; **c** Asia; **d** Africa. This figure is generated from a modification of the map by Kottek et al. (2006)

Climate effects

3D-PCoA analysis showed differences between glomeromycotan communities from hot arid and cold arid regions (Fig. 7a). Fungal communities in hot summer regions were also distinct from those in warm summer regions (Fig. 7b). However, 3D-PcoA analysis showed that communities were scattered randomly among the five precipitation types (Fig. S1).

Discussion

The current study found that the distribution of Glomeromycota did not support the EisE hypothesis, as results showed a high degree of endemism and nonrandom distribution. Although fungi were found to occur in each continent, they possessed highly endemic species, with distribution significantly limited by geographic distance, but showing little affect of habitat type. The cosmopolitan distribution at a higher taxonomic level may be caused by historical factors, while the endemic distribution at a species level might result from host-mediated factors and dispersal ability.

Glomeromycotan fungi are widely distributed around the globe, occurring in almost all habitats (Chaudhary et al. 2008; Smith and Read 2008). Our study showed the appearance of Glomeromycota in all sampled continents. This pattern may have ancient origins. Fossil evidence suggests that glomeromycotan fungi originated during the Ordovician, about 460 million years ago (Mya) (Redecker et al. 2000). At that time, the land

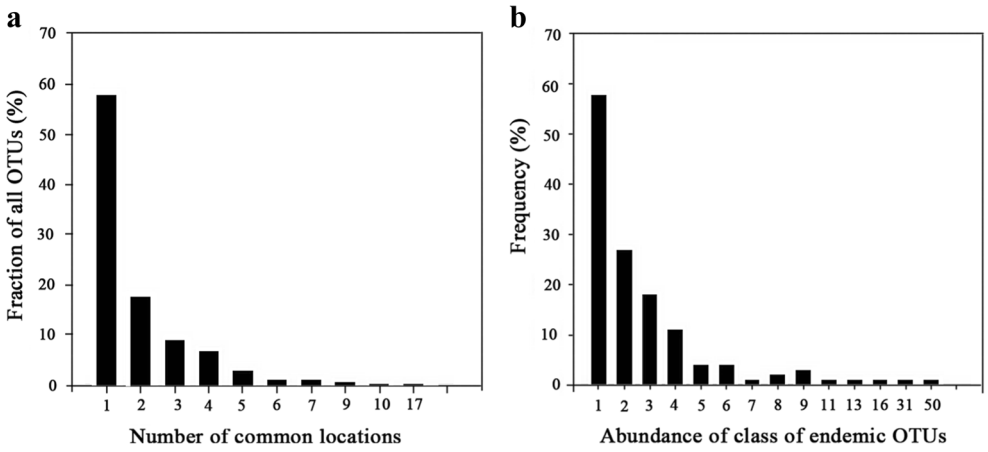

Fig. 2 Occurrence of 97 % OTUs among sampling sites (**a**) and abundance of endemic OTUs (**b**)

was formed as a continuous plate, named "Pangaea" (Scotese 2004), which remained until the Triassic ushered in the Mesozoic Era (251–199.6 Mya), when Pangaea separated into Gondwana and Laurasia. During the period between the Ordovician and the Triassic, early plants that formed symbiotic relationships with glomeromycotan fungi began to colonize and live in the land (Wang et al. 2010). However, at this time, plant coverage and diversity was low, with strong winds and a dry climate (Pirozynski and Malloch 1975), thus permitting the long-range dispersal of fungi across the whole supercontinent, mediated by physical agents (Chaudhary et al. 2008).

With geological evolution, Gondwana was fragmented into the Afrotropic, Oceania, Indo-Malay and Neotropic ecozones at the Early Cretaceous (145.5–65.5 Mya); Laurasia separated into the Palearctic and Nearctic at 55 Mya. From that point, the continents were isolated by oceans, and distribution of glomeromycotan fungal species across these tectonic plates became much less common, especially around 60 Mya, with the explosive appearance of angiosperms on the planet (Fiz-Palacios et al. 2011). The increasing vegetation coverage reduced the capacity for wind erosion of surface soil. Thus long-range dispersal mediated by physical agents (i.e., wind) became infrequent, and host plants and geographic limitation may have affected the dispersal of fungal species (Chaudhary et al. 2008).

Host plants have potentially strong selectivity for glomeromycotan fungal species (Yang et al. 2012). Recent studies showed that co-existing plants were associated with distinctive fungal communities (Vandenkoornhuyse et al. 2002; Li et al. 2010a; Gosling et al. 2013). Our study found that Glomeromycota species distribution might be limited by host plants: a low host range in fungal species was associated with a low geographic range (Fig. 3). As the tectonic plates were

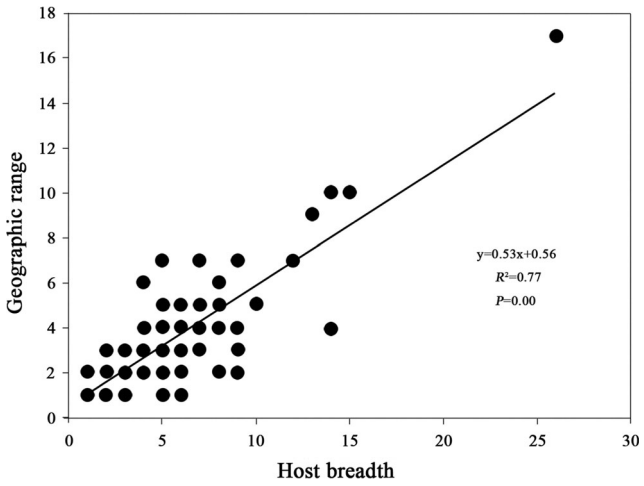

Fig. 3 Effects of host plant on glomeromycotan fungal distribution: a positive linear relationship exists between host breadth and geographic range of 97 % OTUs

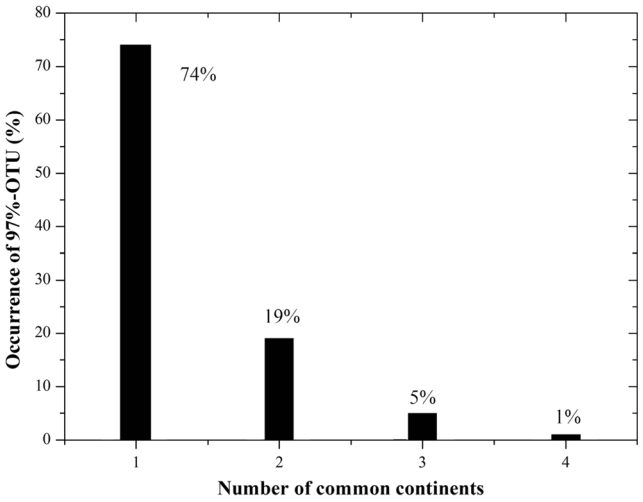

Fig. 4 Effects of historical factors on glomeromycotan fungal distribution: occurrence of 97 % OTUs among different continents

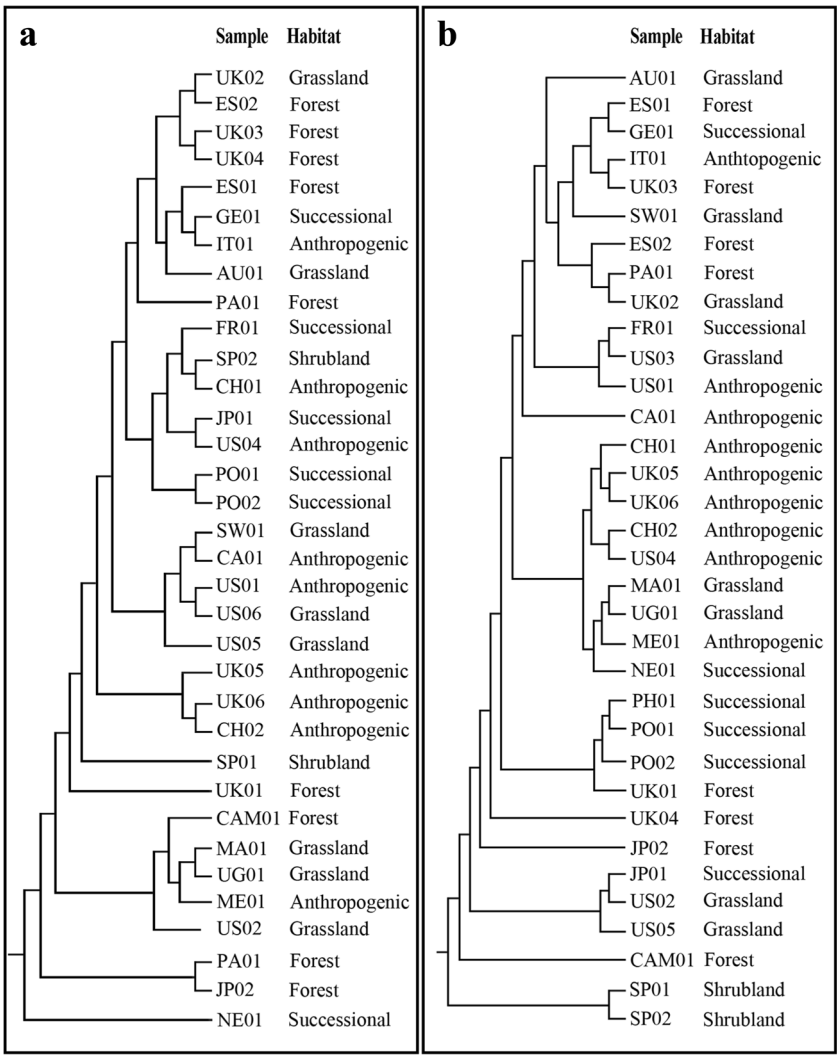

Fig. 5 Effects of habitat filtering on glomeromycotan fungal distribution: cluster analysis of 97 % OTU composition in different habitats based on molecular taxonomic level (**a**) and phylogenetic level (**b**)

isolated by oceans, and with the evolution of climate and geology, plant community composition became distinctive and formed distinct distribution patterns. Because of the obligate nature of mycorrhiza, some

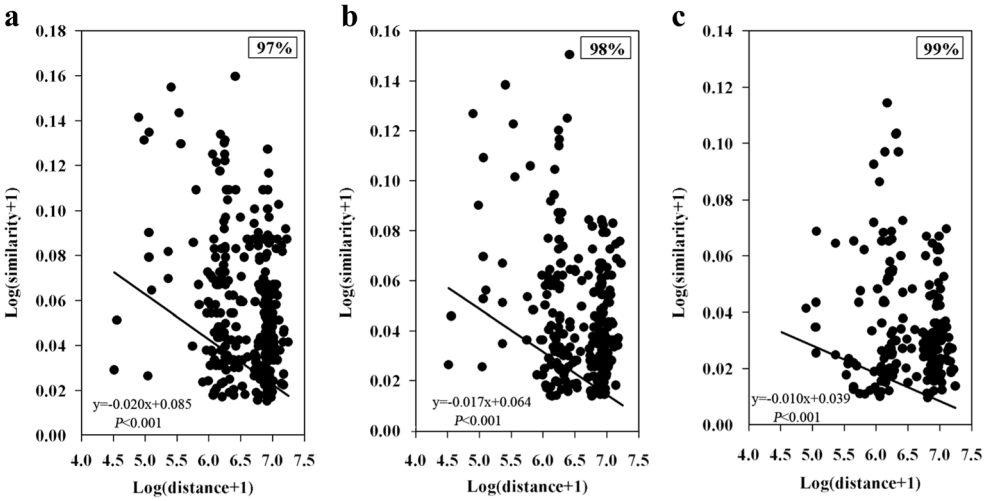

Fig. 6 Effects of dispersal limitation on glomeromycotan fungal distribution: distance–decay curves are shown between 97 % OTU composition similarity and geographic distance at different taxonomic resolution levels

Table 2 Relationships between geographic distance and similarity of AMF community composition

Sequence similarity for OTUs	Partial Mantel test				Bootstrapping of linear regression		
	$r(S{\cdot}D){\cdot}H$	P	$r(S{\cdot}H){\cdot}D$	P	Coefficient	t	P
97 %	−0.231	0.001	−0.044	0.304	−0.020	−9.272	<0.0001
98 %	−0.227	0.001	−0.034	0.338	−0.017	−9.928	<0.0001
99 %	−0.200	0.001	−0.071	0.160	−0.010	−7.777	<0.0001

The partial Mantel statistic $r(S{\cdot}D){\cdot}H$ estimates the correlation between S (community similarity) and D (geographic distance) while controlling for the effect of H (habitat type). Conversely, $r(S{\cdot}H){\cdot}D$ estimates the correlation between S and H while controlling for D. P values are also presented to indicate whether partial Mantel regression coefficients were significantly different from zero following 10,000 permutations

glomeromycotan fungal species may have found compatible hosts and co-evolved to the present, while others, unfortunately, did not and became extinct. Thus, host selectivity might be a strong driving force for the high degree of endemism of glomeromycotan fungal species (Yang et al. 2012).

Our study suggests that geographic distance is another possible factor determining the highly endemic nature of glomeromycotan fungi, as this could act as a limiting factor for dispersal and lead to allopatric speciation. Glomeromycota are soil-borne microbes that reproduce asexually via spores, and are dispersed mainly through widespread hyphal networks (Smith and Read 2008). Although they possess extensive hyphal networks in the soil, their spread is still limited to a local scale. Thus, geographic isolation would prohibit genetic communication of glomeromycotan species among different sites. Researchers have speculated that asexuality among AMF may be an ecological adaptation that inevitably limits dispersal (Rosendahl 2008). Lekberg et al. (2007) indicated that regional dispersal dynamics may play an important role in structuring AMF biogeography. Although several glomeromycotan species (such as *G. mosseae* and *G. intraradices*) are known to have ubiquitous distribution, their global distribution is considered a recent phenomenon caused by human agricultural activity (Rosendahl et al. 2009). In this study, only one OTU was widely distributed (occurring in 17 of 34 sites), and shared 100 % similarity with *G. intraradices* from the BLAST search.

We also found that temperature (but not precipitation) was a factor affecting the distribution of glomeromycotan fungal species on a global scale. Temperature may influence fungal communities both directly and indirectly (Helgason et al. 1998; Heinemeyer et al. 2004). Temperature has been found to directly influence fungal growth (Heinemeyer et al. 2004). Koske (1987) found that temperature was a controlling factor in the distribution of AMF communities. Gai et al. (2009) demonstrated that temperature may be the most important factor influencing the distribution of glomeromycotan fungi in the grasslands of the Tibetan Plateau. Temperature may also exert indirect effects on fungal distribution through host plants. On a global scale, plant distribution patterns are directly correlated with temperature, which may drive the formation of different glomeromycotan fungal communities.

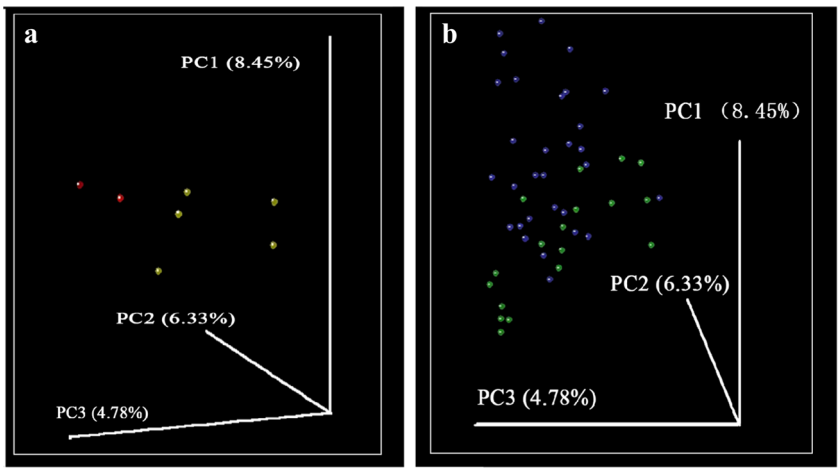

Fig. 7 Effects of climate on glomeromycotan fungal distribution: 97 % OTU composition in different climatic zones: **a** cold arid vs. hot arid; **b** hot summer vs. warm summer

Conclusion

This study showed that Glomeromycota were highly endemic and that their distribution was not random, and may be affected by host plants, dispersal ability, historical factors and temperature. However, neither habitat nor precipitation was significantly associated with distribution on a global scale. These findings suggest that the distribution of glomeromycotan fungi argues against the EisE hypothesis.

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