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Local-scale biogeography and spatiotemporal variability in communities of mycorrhizal fungi

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Summary

Knowledge of spatiotemporal patterns in species distribution is fundamental to understanding the ecological and evolutionary processes shaping communities. The emergence of DNA-based tools has expanded the geographic and taxonomic scope of studies examining spatial and temporal distribution of mycorrhizal fungi. However, the nature of spatiotemporal patterns documented and subsequent interpretation of ecological processes can vary significantly from study to study. In order to look for general patterns we synthesize the available data across different sampling scales and mycorrhizal types. The results of this analysis shed light on the relative importance of space, time and vertical soil structure on community variability across different mycorrhizal types. Although we found no significant trend in spatiotemporal variation among mycorrhizal types, the vertical community variation was distinctly greater than the spatial and temporal variability in mycorrhizal fungal communities. Both spatial and temporal variability of communities was greater in topsoil compared with lower horizons, suggesting that greater environmental heterogeneity drives community variation on a fine scale. This further emphasizes the importance of both niche differentiation and environmental filtering in maintaining diverse fungal communities.

Introduction

Ecological communities are shaped by both deterministic factors and stochasticity (i.e. niche-neutral processes; Leibold *et al.*, 2004). Disentangling their relative contribution to community variability can shed light on the underlying ecological and evolutionary processes and enables scientists to predict the response of organisms to the environment (Vellend, 2010). Studies of how communities vary along temporal or spatial gradients (i.e. distance–decay of similarity) have been widely used to infer the relative importance of neutral and deterministic processes (Nekola & White, 1999; Gilbert & Lechowicz, 2004). Distance–decay patterns provide an insight into spatial scaling of biodiversity (Vellend, 2010), estimating total diversity (Harte *et al.*, 1999) and predicting spatial patterns from local to global scales (Nekola & White, 1999; Soininen *et al.*, 2007; Chase & Knight, 2013). Distance–decay patterns are related to spatial and temporal autocorrelation that stem from population dynamics, dispersal limitation and spatial structure of deterministic variables (Morlon *et al.*, 2008; Dray *et al.*, 2012). Understanding of the distance–decay patterns enables ecologists to identify the main dimensions of variability in communities, to generate biogeographic hypotheses and to select appropriate scale for further community-level investigation.

One of the ongoing debates in microbial ecology is whether the distribution of microorganisms is shaped by neutral processes (such as speciation, birth, death and dispersal) to the same extent as it is in macroorganisms (Bass-Becking, 1934; Green *et al.*, 2004; Martiny *et al.*, 2006; Peay *et al.*, 2010b). Although microbes were assumed to be cosmopolitan until very recently (Finlay, 2002), emerging evidence suggests that many microbes have discrete geographic ranges and do not occupy all compatible habitats (reviewed in Hanson *et al.*, 2012). Many microbial communities show strong spatial structure but it does not often correlate well with measured environmental variables (Talbot *et al.*, 2014). This unexplained variance could reflect the existence of unknown environmental drivers or dispersal-driven neutral dynamics. Although the Baas–Becking hypothesis *sensu stricto* – which states that for microbes 'everything is everywhere, but the environment selects' – has mostly

been abandoned, a number of studies continue to suggest that microbes may be more cosmopolitan and disperse more widely than macroorganisms (Queloz *et al.*, 2011; Geml *et al.*, 2012; Gibbons *et al.*, 2013; Jun Sul *et al.*, 2013; Põlme *et al.*, 2013; Tedersoo *et al.*, 2014).

Mycorrhizal fungi are an important component of the diversity and biomass of soil microbial communities in most terrestrial ecosystems and have a tremendous impact on nutrient cycling and plant productivity (Van Der Heijden *et al.*, 2006; Clemmensen *et al.*, 2013; Averill *et al.*, 2014). The prevalence of the major types of mycorrhiza, namely ectomycorrhiza (EcM), arbuscular mycorrhiza (AM), ericoid mycorrhiza (ErM) and orchid mycorrhiza (OrM), depends on plant and fungal identity and environmental conditions (Brundrett, 2002). Compared to the asexual AM Glomeromycota that produce chlamydospores, most EcM, ErM and OrM fungi have probably greater dispersal capacity due to sexual and asexual propagules of smaller size and generally aboveground spore release (Galante *et al.*, 2011). Compared with the AM fungi and largely saprotrophic OrM and ErM fungi, many species of EcM fungi have large and long-lived genetic individuals (Douhan *et al.*, 2011), and, therefore, horizontal and temporal variation in EcM fungal communities is expected to occur on larger scales. Such morphological and ontogenetic differences may potentially cause differential spatiotemporal distribution patterns, although this has never been formally tested.

Much of our knowledge about soil microbial ecology is limited to the top 5–10 cm of soil. The few studies on depth gradients have revealed biologically important vertical variation in communities of EcM and saprotrophic fungi (Dickie *et al.*, 2002; Tedersoo *et al.*, 2003; Lindahl *et al.*, 2007; Jumpponen *et al.*, 2010; Voříšková *et al.*, 2014), but cross-comparisons among studies are difficult due to differences in the spatial scale and choice of statistical methods. Fungal communities are strongly shaped by their biotic interactions (Maherali & Klironomos, 2007; Kennedy, 2010) and environmental parameters (Lekberg *et al.*, 2007; Tedersoo *et al.*, 2012, 2014) that also have a patchy distribution (Ettema & Wardle, 2002).

Here we synthesize the relative temporal and spatial (vertical and horizontal) variation in fungal communities of various mycorrhizal types to gain insight into their underlying assembly processes at the local scale. We hypothesize that: (1) due to typically more consistent and pronounced environmental changes across soil depth (Dickie & Koide, 2014), vertical variability in communities of fungi is stronger compared to horizontal and temporal variation; (2) greater soil habitat heterogeneity in the top soil layer (Cambardella *et al.*, 1994; Duan *et al.*, 2009) results in more variable communities in topsoil (Ettema & Wardle, 2002); (3) fungal communities of different mycorrhizal types display fundamental differences in their spatiotemporal patterns; and (4) species-poor communities recovered from deeper soil layers or high environmental stress periods form a nested subset of species-rich communities of topsoil or low stress periods, respectively. Although a number of ecological processes can lead to nestedness (e.g. Peay *et al.*, 2007; Montesinos-Navarro *et al.*, 2012), nestedness across an environmental gradient would indicate that species-poor communities are composed of generalists able to tolerate a wider range of environmental conditions.

Meta-analysis of spatiotemporal patterns

Re-analysis methods

On 31 August 2014, we used the Web of Science, MaarjAM (Öpik *et al.*, 2010) and PlutoF (Abarenkov *et al.*, 2010) to search for the relevant published and unpublished studies to collect all available datasets about spatial and/or temporal variation in mycorrhizal fungi. We extracted the datasets from supplementary materials or contacted the authors for missing information (Table 1). Approximately one quarter of the potentially relevant datasets were omitted due to the lack of response from the authors (6) or their consideration for further publications (3). In the 38 obtained datasets, we were able to analyse 29, 12, 2 and 1 subsets belonging to EcM, AM, OrM and ErM fungi, respectively. Horizontal, vertical and temporal variation could be addressed in 39, 17 and 13 of these subsets, respectively. Only two studies (Courty *et al.*, 2008; Voříšková *et al.*, 2014) included information about all three spatiotemporal aspects. We relied on the original separation of Operational Taxonomic Units and their assignment into mycorrhizal groups. In a few cases where mycorrhizal type was not determined in the original study, we assigned all members of Glomeromycota to AM and relied on Tedersoo & Smith (2013) about the EcM status. Because of the limited number of studies on ErM and OrM, in many cases we were only able to perform formal statistical tests on differences between mycorrhizal types using EcM and AM fungi.

In order to determine spatial or temporal variation we calculated simple Mantel correlations and correlograms between community variation and spatio-temporal gradients. For calculating community dissimilarities, we used a Hellinger-transformed Bray–Curtis index, which is robust against double absences (i.e. absences of species in both samples that are compared; Anderson *et al.*, 2011). We tested the significance of the slope of distance–decay relationships using Mantel permutation tests. In addition, the initial similarity (similarity at zero distance, Soininen *et al.*, 2007) and autocorrelation range (the distance after which similarity does not change; Robeson *et al.*, 2011) were calculated. We used one-way ANOVAs (for all studies pooled) and paired *t*-tests (for each individual study) to compare the differences in turnover rate (slope of distance decay relationship) and relative importance of spatiotemporal patterns between AM and EcM fungi and between different soil horizons (i.e. top soil vs deep layers). We used Cohen's *d* for a paired and unpaired *t*-test to calculate the effect size. The matrix size, initial similarity and total species richness were used as covariates to assess any confounding effects. All analyses were performed in vegan, ecodist and bipartite packages of R (R Development Core Team, 2007).

In order to disentangle the effect of nestedness and species replacement in community variation, we calculated these two components for each community following Baselga (2010, 2013). The partition of dissimilarity caused by nestedness in temporal and vertical gradients was determined based on the β_{SNE} index (Baselga, 2010). This measure is nonlinearly affected by the size of the dissimilarity matrix (Baselga, 2010). Nestedness was additionally tested by calculating the NODF index (which is based on overlap and decreasing fill of cells; Almeida-Neto & Ulrich, 2011).

Table 1 Spatio-temporal variation and nestedness in the communities of mycorrhizal fungi

Data set or subset	Mycorrhizal Type	NODF[1]		Rate of variation[2]		
		Vertical	Temporal	Vertical	Horizontal	Temporal
Bahram *et al*. (2011)	EcM[3]	–[4]	–	–	0.02	–
Baindard *et al*. (2013)	AM[5]	–	**24.20**[6]	–	**0.02**	**0.01**
Botnen *et al*. (2014)	EcM	–	–	–	0	–
Courty *et al*. (2008)	EcM	25.7	**18.7**	**0.04**	0.02	**0.04**
Davison *et al*. (2012)	AM	–	**46.8**	–	**0.07**	**0.01**
Dickie *et al*. (2002)	EcM	**34.43**	–	**0.57**	–	–
Genney *et al*. (2006)	EcM	**9.33**	–	**0.07**	0.01	–
Helgason *et al*. (2014)	AM	–	**39.59**	–	–	**0.01**
Higo *et al*. (2013)	AM	**49.5**	–	0.1	0.09	–
Hiiesalu *et al*. (2014)	AM	–	–	–	**0.05**	–
Horn *et al*. (2014)	AM	–	–	–	**0.12**	–
Izzo *et al*. (2005)	EcM	–	**39.9**	–	–	**0.06***
J. Oja *et al*. (unpublished)	OrM[7]	–	18.2	–	–	0
J. Vahtra *et al*. (unpublished)	OrM	–	–	–	0.00	–
Kjøller (2006); R. Kjøller (unpublished)	EcM	–	–	–	**0.05**	–
Lang *et al*. (2013)	EcM	–	–	–	0.12	–
Leckberg *et al*. (2007)	AM	–	–	–	**0.02**	–
Lindahl *et al*. (2007)	EcM	**27.76**	–	**0.41**	0.05	–
M. Bahram *et al*. (Unpublished)	EcM	–	–	–	**0.05**	–
Maherali & Klironomos, 2014)	AM	–	–	–	**0.06**	–
McGuire *et al*. (2013)	EcM	0	–	–	–	–
Montero Sommerfeld *et al*. (2013)	AM	23.7	20.9	0	**0.02**	**0.02**
P. Kohout *et al*. (Unpublished)	ErM[8]	–	–	–	**0.02**	–
Peay *et al*. (2010a)	EcM	–		–	**0.01**	–
Peay *et al*. (2010b)	EcM	–	–	–	**0.03**	–
Phosri *et al*. (2012)	EcM	–	–	–	0	–
Rosling *et al*. (2003)	EcM	**34.42**	–	**0.37**	0.06	–
Ryberg *et al*. (2009)	EcM	–	–	–	**0.06**	–
S. Mundra *et al*. (Unpublished-a)	EcM	–	–	–	**0.03**	–
S. Mundra *et al*. (Unpublished-b)	EcM	–	**27.2**	–	**0.01**	**0.01**
Talbot *et al*. (2014)	AM	**41.4**	–	**0.01**	**0.02**	–
Talbot *et al*. (2014)	EcM	**10.5**	–	**0.01**	**0.02**	–
Taylor *et al*. (2014)	AM	**50**	–	**0.1**	−0.01	0.00
Taylor *et al*. (2014)	EcM	**39.7**	–	**0.06**	0.01	−0.01
Tedersoo *et al*. (2010, Ecuador)	EcM	–	–	–	0.13	
Tedersoo *et al*. (2003)	EcM	18.5	–	**0.26**	**0.17**	–
Tedersoo *et al*. (2006)	EcM	7.79	–	**0.01**	**0.03**	–
Tedersoo *et al*. (2011, Cameron)	EcM	15.1	–	−0.01	**0.15**	–
Tedersoo *et al*. (2011, Gabon)	EcM	27.8	–	0	**0.04**	–
Tedersoo *et al*. (2011, Madagascar)	EcM	–	–	–	0.01	–
Tedersoo *et al*. (2011, Zambia)	EcM	–	–	–	−0.01	–
Voriskova *et al*. (2014)	AM	0	0	**0.73**	0	**0.2**
Voriskova *et al*. (2014)	EcM	16.75	26.87	**0.63**	0.06	**0.06**
Walker *et al*. (2005)	EcM	–	–	–	0.02	0

[1]Nestedness metric based on overlap and decreasing fill. [2]Determined as the slope of distance–decay relationship, the significance of which was determined based on Mantel test. [3]Ectomycorrhizal. [4]'–', indicates a factor was not possible to assess. [5]Arbuscular mycorrhizal. [6]Bold text indicates significant results. *, Here the slope was calculated based on β_{SNE}. [7]Orchid mycorrhizal. [8]Ericoid mycorrhizal.

Results and discussion

Horizontal variability

Of 39 data subsets (26 EcM, 11 AM, 1 ErM and 1 OrM) with horizontal distribution data, 21 (54%; including 12 EcM, 8 AM and 1 ErM) exhibited significant horizontal variability (Table 1 and Supporting Information Table S1). Communities of EcM fungi exhibit strong spatial distribution patterns with an autocorrelation range of typically 2–3 m in temperate forests (Lilleskov *et al*., 2004; Bahram *et al*., 2013). Spatial autocorrelation range, however, depends strongly on habitat type and it increases rapidly towards lower latitudes, where it often exceeds 10 m (Bahram *et al*., 2013) probably due to greater isolation of hosts, stronger dispersal limitation and, perhaps most importantly, a shift towards families with large individual mycelia (such as Suillaceae, Cortinariaceae and Bankeraceae). Larger individual mycelia might have greater interference competition (Wu *et al*., 1999) that could further affect their spatial structure (Pickles *et al*., 2012). The spatial autocorrelation range of AM fungi was slightly larger based on the few available

studies in temperate ecosystems. For example, the spatial autocorrelation range for AM fungi was 6 m (dataset of Horn *et al.*, 2014; Mantel $r = 0.295$, $P = 0.001$) and 9 m (dataset of Davison *et al.*, 2012; Mantel $r = 0.236$, $P = 0.001$) in our re-analyses. In support to this, a recent study shows that one AM fungal genetic individual can extend over 10 m (Maherali & Klironomos, 2012), which is comparable to the largest EcM fungal individuals (Douhan *et al.*, 2011). In a single dataset available for ErM (P. Kohout, M. Bahram, S. Põlme & L. Tedersoo, unpublished), the fungal community exhibited no significant spatial autocorrelation. Similar results were obtained for OrM fungal communities in 21 transects across Estonia, where significant autocorrelation was found only in four transects at < 1 m (J. Oja, J. Vahtra, L. Tedersoo & M. Bahram, unpublished).

We also calculated horizontal and temporal variation of mycorrhizal fungal communities separately for different soil horizons. These analyses revealed stronger community variation in topsoil compared with lower horizons (Mean ± SD of the slope of distance decay: 0.063 ± 0.049 vs 0.028 ± 0.025; $t = 2.42$, df = 10, $P = 0.018$, Cohen's $d = 0.73 \pm 0.68$; Table S2). In contrast with other studies, spatial autocorrelation was slightly greater in the mineral soil layer than topsoil in rain forest EcM fungal communities of Cameroon and Gabon (Tedersoo *et al.*, 2011). The generally stronger variation in topsoil can likely be ascribed to greater environmental heterogeneity (Melillo *et al.*, 1989; Duan *et al.*, 2009). Top soil is more exposed to seasonal changes of climate and localised nutrient input, as well as disturbance such as grazing by mycophagous soil fauna and fire, which could potentially affect fungal communities. Similar results of differential spatial variation among soil horizons have been reported for bacteria (Nunan *et al.*, 2003; Andreetta *et al.*, 2012) and soil fungal communities dominated by saprotrophs (Jumpponen *et al.*, 2010; Kadowaki *et al.*, 2014).

At small geographical scales (but above the size of individual mycelia), soil nutrients and aboveground vegetation (i.e. host preference) appear to be the main determinants of mycorrhizal fungal community composition (e.g. Toljander *et al.*, 2006; Lekberg *et al.*, 2007; Mummey & Rillig, 2008; Tedersoo *et al.*, 2008; Dumbrell *et al.*, 2010; Wehner *et al.*, 2014). Due to the modular nature of mycorrhizal networks – that is, certain species associate more often with each other (Chagnon *et al.*, 2012; Montesinos-Navarro *et al.*, 2012; Bahram *et al.*, 2014) – the spatial structure of fungal symbionts may follow that of plant roots (Tedersoo *et al.*, 2010) and plant species composition (Peay *et al.*, 2007). In addition, several spatially explicit studies also report strong pure spatial effects independent from obvious/measured environmental variation (e.g. Wu *et al.*, 1999; Peay *et al.*, 2007, 2010b; Dumbrell *et al.*, 2010; Tedersoo *et al.*, 2010; Tedersoo *et al.* 2012; Bahram *et al.*, 2013; Talbot *et al.*, 2014; Wehner *et al.*, 2014). Because fungal communities and abiotic factors may be independently spatially structured, the importance of environment on small-scale distribution of fungal communities may be overstated due to its confoundedness with space. In a previous study we found that a large proportion of variation in EcM fungal communities remains unexplained by environmental models, indicating a strong effect of unmeasured factors and/or great importance of stochastic processes (Bahram *et al.*, 2013).

Temporal variability

Of 13 data subsets (6 EcM, 6 AM and 1 OrM) with temporal distribution data, nine (69%; including 4 EcM and 5 AM) showed significant temporal variability (Tables 1, S1). Studies on temporal variation have addressed either seasonal or annual patterns. Voříšková *et al.* (2014) reported differential richness and shifts in fungal communities across four seasons in a temperate forest soil. Seasonal variation in EcM fungal communities is greater than horizontal spatial variation (datasets of Courty *et al.*, 2008; Voříšková *et al.*, 2014), but variation between years has relatively little importance (dataset of Izzo *et al.*, 2005). In AM fungal communities, significant temporal variation has been observed in several studies (e.g. Liu *et al.*, 2009; Dumbrell *et al.*, 2011). In addition, we found significant seasonal variation in several data subsets of AM fungi (Montero Sommerfeld *et al.*, 2013; Helgason *et al.*, 2014; Voříšková *et al.*, 2014). Several studies have reported significant seasonal temporal variation in OrM fungi inside roots (Huynh *et al.*, 2009; Kohout *et al.*, 2013; J. Oja *et al.*, unpublished). We also found no significant difference in temporal variability between root and soil fungal variation in the dataset of J. Oja *et al.*, (unpublished).

Among the re-analyzed studies, in only one temperate forest study did we observe significant nestedness of the EcM fungal community across 3 yr (dataset of Izzo: NODF = 39.9, $Z = 7.14$, $P = 0.001$); that is, species-poorer communities are subsets of species-richer communities across different years. By contrast, seasonal variation of all AM, OrM and EcM datasets on average showed weak nestedness patterns. Looking across the studies we re-examined, seasonal changes in fungal communities are ascribed to a variety of factors, including seasonal variation in litter fall, host carbon allocation belowground, release of spores and/or recruitment of newly germinated mycelium in seasons nonoptimal for vegetative growth and reproduction (Voříšková *et al.*, 2013; J. Oja *et al.*, unpublished).

Compared with horizontal and vertical gradients, temporal variation is annually a cyclic process; that is, communities across different years are nested within each other. So far, the majority of the studies have addressed temporal gradients on very short timescales, either covering seasons within a single year or in the same season across multiple years. Typically intra-annual variation is ascribed to seasonality, whereas annual variation is ascribed to succession (Visser, 1995; Jumpponen *et al.*, 2002; Nara *et al.*, 2003). However, seasonal variation may have been misinterpreted due to the confounding effects of seasonality *per se* and short-time succession in early stage successional habitats. To disentangle the stochastic and deterministic processes in temporal variation, it is necessary to replicate seasonal sampling across three or more years. In contrast to population dynamics, covariates such as soil temperature and changes in nutrients, as well as the effect of season and their interaction terms, would all sum up to represent the relative proportion of deterministic processes in temporal variation.

Vertical variability

Of the 17 data subsets (12 EcM and 5 AM) on vertical distribution, 13 (77%; including 10 EcM and 3 AM) exhibited significant vertical variability (Tables 1, S1). In support of our hypothesis, data re-analysis revealed slightly stronger vertical variation compared with spatial and temporal variation in mycorrhizal fungal communities (Fig. 1a). Based on the three studies with temporal and vertical data (Courty *et al.*, 2008; Taylor *et al.*, 2014, AM and EcM; Voříšková *et al.*, 2014, AM and EcM), vertical variation was marginally stronger than temporal variation. ($t = 1.9$, df = 5, $P = 0.058$; Cohen's $d \pm 95\%$ CI $= 0.7755 \pm 0.6632$). This was confirmed for both AM and EcM fungi in the Taylor *et al.* (2014) and Voříšková *et al.* (2014) datasets. Similarly, vertical variability was stronger than temporal variability across all studies (ANOVA $F_{1,28} = 5.45$, $P = 0.027$, Cohen's $d = 0.975 \pm 0.773$). Our re-analysis revealed that on average, vertical variation is stronger than horizontal variation ($t = 2.09$, df = 15, $P = 0.027$; Cohen's $d = 0.525 \pm 0.374$; ANOVA: $F_{1,54} = 14.28$, $P = 0.001$; Cohen's $d = 0.737 \pm 0.590$) in the communities, in spite of the fact that the vertical scale for the majority of studies was < 10 cm. The strong vertical variation of EcM communities is probably related to vertical niche partitioning among fungi (Dickie *et al.*, 2002; Tedersoo *et al.*, 2003) due to abrupt changes in organic matter quality and nutrient availability, moisture and texture (Rosling *et al.*, 2003; Lindahl *et al.*, 2007). Because host taxon is one of the main determinants of EcM fungal communities in many ecosystems (Tedersoo *et al.*, 2008; Smith *et al.*, 2009), vertical partitioning of root distribution among plant species and the relative abundance of fine roots may additionally magnify the depth effect.

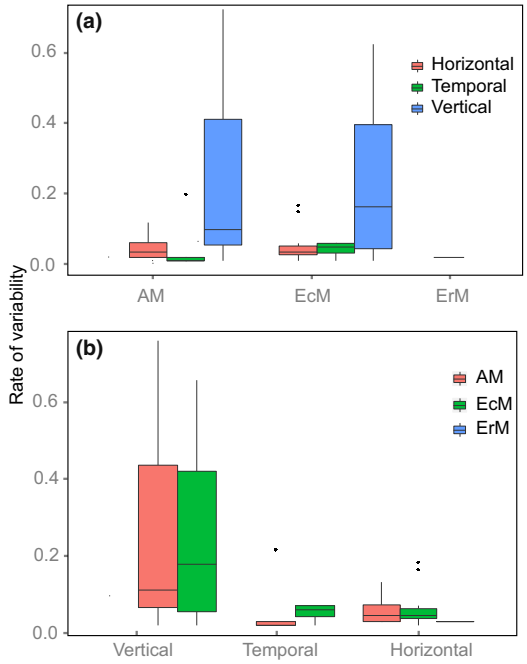

Fig. 1 Boxplot of spatio-temporal variability across (a) different dimensions and (b) different mycorrhizal types (AM, arbuscular mycorrhizal; EcM, ectomycorrhizal; ErM, ericoid mycorrhizal). The *y*-axis shows the rate of variability calculated as the slope of distance decay relationship. Note that only significant values based on Mantel test ($P < 0.05$) are displayed. '*', denotes extreme values.

In contrast to other studies, Talbot *et al.* (2014) reported relatively low vertical variation compared with horizontal variation in soil fungi inhabiting coniferous forests across North America. Given the large scale of the study compared with others in our synthesis, we re-analysed the data at the plot level to see if vertical niche partitioning was more evident at the local scale. The re-analysis suggested that the weak vertical variation is independent from geographical scale and spatial heterogeneity (Table 1). The observed discrepancy, however, may be due to the exclusion of the upper litter layers from that study, which is often where the strongest differences in fungal communities occur (Dickie *et al.*, 2002; Voříšková *et al.*, 2014). Vertical variation was also not significant in Gabon, which was ascribed to poor stratification of tropical soil and a depth gradient of 5 cm (Tedersoo *et al.*, 2011).

AM fungal communities in forests revealed strong vertical variation (datasets of Taylor *et al.*, 2014; Voříšková *et al.*, 2014), which was not evident in other ecosystems (datasets of Higo *et al.*, 2013; Montero Sommerfeld *et al.*, 2013; but see Robinson *et al.* (2009) and Jumpponen *et al.* (2010) who found significant vertical variability of saprotrophic fungal communities in grasslands). The greater vertical variation in forests compared with grasslands could be related to more pronounced vertical stratification due to greater litter input, the lack of recent tillage and less extensive mixing by earth worms and other bioengineers that are relatively uncommon in acidic forest soils. These results were supported by the original analyses of Oehl *et al.* (2005) and Tian *et al.* (2011) in grassland soils that were unavailable for re-analysis.

Contrary to our hypothesis, vertical variation in both AM and EcM fungal communities was mainly related to species replacement and not nestedness (Table 1). Compared with horizontal environmental heterogeneity, more consistent vertical variability of soil characteristics – particularly the decline of soil organic matter towards deeper layers – may lead to stronger environmental filtering. Besides, although fungal diversity is conspicuously lower in deeper soil horizons (Tedersoo *et al.*, 2003; Lindahl *et al.*, 2007), vertical niche partitioning appears to be one of the most important determinants in structuring communities of mycorrhizal fungi in forests. In-depth studies on vertical profiles of mycorrhizal fungi are typically performed in boreal and temperate forest soils with well-stratified structure. These studies report strong variability of fungal communities that may reflect their niche segregation due to interspecific interactions (Dickie *et al.*, 2002; Tedersoo *et al.*, 2003). Strong habitat heterogeneity and magnified species interactions within a fine scale across soil depth may result in greater niche segregation compared to other dimensions (Taylor *et al.*, 2014). However, it remains unclear to what extent the observed vertical variability results from environmental filtering vs niche differentiation. It would be interesting to know if lower horizon taxa could persist in the upper horizon or vice versa, and, if so, which set of taxa are dominant competitors. Addressing the vertical variation of fungal communities along a forest productivity or soil development gradient would greatly improve our knowledge about the mechanisms of vertical niche differentiation by allowing comparison of

equal magnitude vertical and horizontal gradients of soil quality to determine the underlying edaphic and microclimatic parameters.

Differences among mycorrhizal types

Contrary to our hypothesis, there was no trend in the rate of spatial variation among mycorrhizal types across data subsets ($P > 0.05$; Cohen's $d = 0.064 \pm 0.512$; Fig. 1b). Given the contrasting dispersal abilities between myorrhizal types, this finding suggests that other processes besides dispersal limitation may regulate the fungal communities in nonisland ecosystems at the local scale, and that AM and EcM fungi may have comparable dispersal rates. However, several studies focusing on horizontal distribution of mycorrhizal communities have revealed contrasting results among different groups. For example, EcM fungi exhibited stronger spatial variability compared with AM fungi in a temperate forest (Wolfe *et al.*, 2007). Based on three data subsets that included both EcM and AM fungal communities over spatial and temporal dimensions (Talbot *et al.*, 2014; Taylor *et al.*, 2014; Voříšková *et al.*, 2014), AM fungi exhibited no significantly different rate of variability compared with EcM fungi ($t = 1.138$, df = 6, $P = 0.1463$; Table 1; Cohen's $d = 0.401 \pm 0.516$). Compared to EcM and AM fungal communities, we found negligible spatial autcorrelation in OrM and ErM communities, which may reflect their small genetic individual size and limited mycelial growth in soil (Grelet *et al.*, 2010; J. Oja *et al.*, unpublished). We should note that the limited number of studies together with the different choice of molecular marker for species identification (i.e. *18S* or *ITS* rDNA) and sampling designs of the studies we re-examined make comparison of different mycorrhizal fungal groups difficult. This highlights the need for further studies with similar designs and ideally simultaneous analysis of the different mycorrhizal types.

Perspectives of spatiotemporal patterns

Unravelling the underlying processes

A few studies focusing on community assembly processes provide evidence that fungal communities are shaped by both dispersal limitation, environmental filtering and interspecific interactions at the fine scale (Wu *et al.*, 1999; Lindahl *et al.*, 2001; Lekberg *et al.*, 2007; Dumbrell *et al.*, 2010; Caruso *et al.*, 2012; Pickles *et al.*, 2012), but the relative importance of these processes remains poorly understood. A large proportion of unexplained variance inherent in microbial communities and unmeasured environmental variables leave us with a lot of uncertainty about the relative contribution of deterministic and stochastic processes on fungal community composition. Only a few studies have examined spore dispersal in a community context, indicating that distribution of spores is strongly structured horizontally (Peay & Bruns, 2014), temporally (Li, 2005; Kivlin *et al.*, 2014; Peay & Bruns, 2014) and certainly also vertically (Peay *et al.*, 2010b; Galante *et al.*, 2011; Norros *et al.*, 2012). Peay & Bruns (2014) recently showed that spore composition exhibits a strong spatial autocorrelation at the scale of 100s to 1000s of meters, leading to highly variable local spore inputs. Studies of fungal competition have shown that early arriving species tend to have a strong competitive advantage, known as a priority effect (Kennedy, 2010), which can lead to variability in community assembly trajectories (Fukami *et al.*, 2010). Priority effects are likely to be stronger when dispersal is limited as this would lead both to variability in spore arrival time and composition, and tend to reinforce local species that produce the majority of spores. As a result, spatially structured dispersal may generate fine-scale community variability and contribute to species co-existence.

The phylogenetic community structure (Stegen *et al.*, 2013) approach offers a promising alternative to investigate the relative effects of dispersal limitation and deterministic processes. If the key functional traits such as enzymatic activities are phylogenetically conserved, spatially structured environmental filtering may cause closely related species to co-occur more frequently than expected by chance, whereas competitive interactions would lead to co-occurrence of phylogenetically distant species (i.e. overdispersion) (Cavender-Bares *et al.*, 2009). The remaining variation in phylogenetic models, after deterministic processes (like environmental filtering and competition) have been taken into account, can then be explained by stochastic processes; that is, dispersal limitation coupled with drift (Stegen *et al.*, 2013). For example, AM fungi exhibited strong spatial and phylogenetic clustering at the local scale, consistent with the importance of environmental filtering (Horn *et al.*, 2014). Phylogenetic clustering of the EcM/sebacina lineage at the regional scale indicates historical effects and dispersal limitation over larger geographical scales (Tedersoo *et al.*, 2014).

Compared to horizontal gradients, vertical and temporal gradients can provide great opportunities to address the effects of deterministic vs stochastic processes due to the potentially smaller role of dispersal in shaping communities. However, disentangling the effects of niche partitioning and environmental filtering may be more challenging across these dimensions due to the lower number of intervals (up to eight horizons and eight seasons) and greater environmental variability across depth and time, respectively. Besides shifts in abiotic physical and chemical properties, carbon input, microbial biomass and root density decrease with soil depth. Seasonally, phythosynthate allocation, litter quality, temperature and moisture change substantially both in temperate and seasonal tropical ecosystems. Reduced carbon allocation, and harsh conditions in cold seasons may negatively affect fungal diversity, which partly explains community variation (Dumbrell *et al.*, 2011). Because of generally shorter generation time and greater surface-to-volume ratio compared with plants and animals, soil fungi may respond to environmental changes over smaller spatial and temporal scales. Thus, it would be most important to relate body size and longevity of fungal groups to their spatial and temporal variation to understand spatiotemporal processes. It would be also highly valuable to sample mycorrhizal fungi of different types from the same replicated study sites to be able to avoid site-specific confounding factors.

Methodological considerations

Fungal body size generates much confusion in ecology, because the network of hyphae and spores measure a few micrometres, whereas

the size of a mycelial individual may similarly vary from a few micrometers in germinating spores to tens of meters in late-successional EcM fungi to several hundred meters in saprotrophic *Armillaria* (Douhan *et al.*, 2011). Based on the size of genetic individuals, the filamentous Basidiomycota are certainly better classified as macroorganisms. These large individuals certainly live for decades if not centuries and, therefore, small-scale spatial, vertical and temporal sampling is likely to capture the same individual multiple times, which leads to both autocorrelation and overestimation of the number of genetic individuals. Although spatial autocorrelation can be easily controlled (Dormann *et al.*, 2007), temporal and vertical autocorrelation are more difficult to handle due to a limited number of factor levels and large overlap with the experimental factors. Resampling of the same individual may or may not be inherently problematic, but these issues are common to nearly all environments using either individual- or sample-based experimental design. Thus, knowledge about the maximum size of genetic individuals and spatial autocorrelation range of species enables ecologists to properly design their experiments by choosing a relevant spatiotemporal scale (Wang *et al.*, 2013).

Concluding remarks and future perspectives

Our analysis revealed a relatively strong vertical variation and absence of nested patterns in mycorrhizal fungal communities in forest soil, indicating that vertical niche differentiation among fungal guilds (Lindahl *et al.*, 2007) and fungal taxa (Dickie *et al.*, 2002) constitutes one of the key determinants in well-stratified soils. Upper soil horizons show higher spatial and temporal variability, emphasizing the importance of environmental heterogeneity in maintaining diverse fungal communities. Whether this is due to the stable moisture and temperature regime in the lower horizons, poor input of litter and limited recruitment of fungal individuals or species from spores, or the simplified community of mycorrhizal and saprotrophic fungi is an intriguing question for future research.

Our knowledge of spatiotemporal structure of mycorrhizal fungal communities is mostly limited to the horizontal dimension and EcM and AM fungi. There are only a few studies about the distribution of OrM and ErM fungi, in particular their temporal structure. Future studies focusing on vertical and temporal structure of different mycorrhizal types in the same study sites could provide useful insights into the underlying processes of their community dynamics.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Table S1 The details of the datasets that were used in our meta-anaylsis, including the detailed results of the analysis of spatio-temporal variation

Table S2 The rate of spatial variation of mycorrhizal fungal communities in different soil horizons

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