The distance decay of similarity in communities of ectomycorrhizal fungi in different ecosystems and scales

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Summary

1. Despite recent advances in understanding community ecology of ectomycorrhizal fungi, little is known about their spatial patterning and the underlying mechanisms driving these patterns across different ecosystems.

2. This meta-study aimed to elucidate the scale, rate and causes of spatial structure of ectomycorrhizal fungal communities in different ecosystems by analysing 16 and 55 sites at the local and global scales, respectively. We examined the distance decay of similarity relationship in species- and phylogenetic lineage-based communities in relation to sampling and environmental variables.

3. Tropical ectomycorrhizal fungal communities exhibited stronger distance-decay patterns compared to non-tropical communities. Distance from the equator and sampling area were the main determinants of the extent of distance decay in fungal communities. The rate of distance decay was negatively related to host density at the local scale. At the global scale, lineage-level community similarity decayed faster with latitude than with longitude.

4. Synthesis. Spatial processes play a stronger role and over a greater scale in structuring local communities of ectomycorrhizal fungi than previously anticipated, particularly in ecosystems with greater vegetation age and closer to the equator. Greater rate of distance decay occurs in ecosystems with lower host density that may stem from increasing dispersal and establishment limitation. The relatively strong latitude effect on distance decay of lineage-level community similarity suggests that climate affects large-scale spatial processes and may cause phylogenetic clustering of ectomycorrhizal fungi at the global scale.

Key-words: beta diversity, dispersal limitation, distance-decay curve, global analysis, island biogeography, plant–soil (below-ground) interactions, spatial autocorrelation, species-area relationship, symbiosis, variogram

Introduction

One of the primary aims of ecology and biogeography is to test hypotheses about the structure of biological diversity across space and time. The distance decay of similarity – diminishing similarity with increasing geographical distance – is one of the well-known and fundamental patterns of biodiversity (Whittaker 1975), which arises from both intrinsic processes including random and dispersal-related (i.e. neutral processes; Hubbell 2001) and niche-related processes (Cottenie 2005). The relative role of these processes determines the strength of distance decay in ecological communities and can vary between different ecosystems and organisms (Nekola & White 1999; Soininen, McDonald & Hillebrand 2007). Fitted distance-decay relationships are usually illustrated by variograms that include the following key parameters: range (i.e. extent of distance decay), still (average community dissimilarity) and nugget (randomness; Brownstein et al. 2012). Additionally, the slope of

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distance-decay relationship reflects the rate of species turnover (i.e. beta diversity) with increasing geographical distance and enables the prediction of regional species richness (gamma diversity) based on local richness (alpha diversity; Harte et al. 1999; Kraft et al. 2011). Patterns of distance decay and the underlying processes are essential for understanding the function and conservation of ecosystems (Legendre, Borcard & Peres-Neto 2005) and modelling niche-neutral effects on species distribution (Dray et al. 2012).

Ectomycorrhizal (EcM) fungi play a key role in ecosystem nutrient cycling, tree nutrition and health (Smith & Read 2008). EcM fungi are the dominant guild of soil microbes in most boreal, temperate and many tropical forests. They form diverse communities in many terrestrial ecosystems (Teder-soo et al. 2012); hundreds of species and tens of individuals may colonize a single tree individual (Bahram et al. 2011). The study of the community ecology of this group has substantially benefited from advances in molecular methods over the past decade. Several studies report that EcM fungi follow biogeographical patterns of macroorganisms such as island biogeography (Peay et al. 2007, 2012) and relationships with altitude (Bahram et al. 2012). At the global scale, however, EcM fungal richness displays an unimodal relationship with latitude (Teder-soo et al. 2012), but this effect is context-dependent (Pölme et al. 2013).

The bulk of our knowledge on distance-decay relationships is based on macroorganisms, while spatial distribution of microbes has only recently received attention owing to methodological advances (Green et al. 2004). Although microbial communities have been traditionally considered to exhibit negligible biogeographic differentiation, recent studies indicate that microbes may have a substantial distance-decay pattern (Green et al. 2004; Green & Bohannan 2006; Fierer & Jackson 2006; but see Queloz et al. 2011 for root endophytes). Yet, the underlying processes of spatial structure of microbial communities remain poorly understood.

Despite considerable progress in our understanding of alpha diversity and community composition of EcM fungi (Taylor 2008), little is known about spatial structure of EcM fungal communities in different ecosystems and the relative roles of neutral and niche processes in creating these patterns (Teder-soo et al. 2011; Peay et al. 2012). Much of our knowledge about spatial structure of EcM fungi comes from the analysis of temperate communities (Wolfe et al. 2009). In particular, Lilleskov et al. (2004) analysed spatial structure of EcM fungi in eight Northern American temperate forests dominated by conifers and found significant distance-decay relationship for half of the study sites. This and some other studies have reported significant spatial autocorrelation ranging up to 3 m in communities of temperate forests (Lilleskov et al. 2004; Pickles et al. 2012). The importance of several environmental factors such as host species (Ishida, Nara & Hogetsu 2007; Teder-soo et al. 2008), soil nutrient concentrations (Toljander et al. 2006) and climate (Ostonen et al. 2011; Bahram et al. 2012; Teder-soo et al. 2012) in structuring the EcM fungal communities have been documented over different geographical scales. All these variables, however, exhibit a strong spatial structure from fine (patches of host plants and microsites) to local (plant community) to global scales, which may, in turn, result in spatial aggregation of soil biota (Ettema & Wardle 2002).

In addition, non-random distribution of genetic individuals leads to spatial patterning of community, and thus, both the size of genetic individuals and the agglomerative distribution of individuals of the same species may account for the observed patchy growth habit of fungi in soil (Lilleskov et al. 2004; Pickles et al. 2012). Most of the fungal spores fall within 0.5 m of the fruit body, which results in greater probability of mycelium establishment in close proximity (Li 2005). Indeed, dispersal limitation is an important factor affecting distribution of EcM fungi at the local scale (Peay et al. 2007) and creating patches of EcM fungal communities in soil (Teder-soo et al. 2010). The structure and size of extraradical mycelium in soil varies greatly among taxa of EcM fungi (Agerer 2001). The size of EcM fungal genetic individuals ranges from $10^{-12}$ m$^2$ in the germinating spores to $10^7$ m$^2$ in old genets inhabiting undisturbed forests (Riviere, Natarajan & Dreyfus 2006; Douhan et al. 2011).

The relative importance of environmental and spatial variables in structuring communities may vary between different ecosystems, geographical scales and across altitude, leading to great differences in distance-decay relationships (Nekola & White 1999; Soininen, McDonald & Hillebrand 2007). At the regional scale, the stronger spatial structure of climate along latitude may lead to a stronger distance-decay pattern with latitude than with longitude (Qian, Ricklefs & White 2005). In addition to direct effects on competitive abilities, climate affects soil processes and the distribution of EcM host trees. In particular, differences in host density may potentially affect spatial distribution of EcM fungi, because crossing uninhabitable barriers requires spore dispersal. However, tropical EcM host trees are mostly distributed as monodominant stands or small groups of tree individuals among the arbucular mycorrhizal vegetation, which impedes vegetative mycelium expansion of EcM fungi between such patches. Lower host density may lead to greater importance of dispersal than niche-related processes and thus more aggregation of EcM fungi in tropical ecosystems.

In this study, we addressed the spatial distribution patterns of EcM fungal communities from local to global scales. Our main aim was to assess distance decay of community similarity in different ecosystems. We also aimed to elucidate the relative contribution of biotic and abiotic factors to distance decay at the species and phylogenetic lineage (a semiphlogenetic measure used for macroecological analyses; Teder-oo, May & Smith 2010; Teder-oo et al. 2012) levels at the local and global scales, respectively. We tested the following alternative hypotheses against the null hypotheses of random effect: (i) the extent of distance decay (i.e. spatial autocorrelation range) is relatively greater in tropical forests, because of lower host density compared with non-tropical ecosystems (Teder-oo & Nara 2010), leading to more pronounced effect of dispersal-related processes and consequently more aggregated distribution of species; (ii) the rate of
distance decay depends on phylogenetic lineage of EcM fungi – that is, lineages comprising predominately pioneer species with good dispersal abilities exhibit greater extent of distance decay; and (iii) at the global scale, the distance decay of EcM fungal lineages is greater with latitude than with longitude, following climatic patterns.

Materials and methods

DATA SOURCES

To address the relative effect of spatial variables on EcM fungal communities, we used community data sets including spatial metadata from 16 sites represented by 11 case studies that were carried out in different ecosystems (Table 1). In addition, we used the data from eight studies performed in Northern American forests (Lilleskov et al. 2004) (Table S1). These data were used only in some of the analyses due to the lack of access to raw data (species by sample table with coordinates). In all the included data sets, morphotyping in combination with internal transcribed spacer (ITS) sequence analysis was used for species identification, but different sampling protocols were used. To address the spatial turnover of lineage-level community similarity in EcM fungal communities at the global scale, we included information on the frequency of lineages from 39 additional sites (altogether 55 sites) as described in Tedersoo et al. (2012) (Table S1 and Fig. 1). We categorized the study sites into tropical (with mean annual temperature more than 18 °C) and non-tropical based on their mean annual temperature (MAT).

SPATIAL ANALYSES

Individual root samples were considered as sampling units in each study site. All samples included occurrence data of species and precise geographical locations. Singletons (i.e. species occurring only once) were removed prior to statistical analyses. Bray–Curtis dissimilarity measure was used to generate community distance matrices. For data with non-normal distribution, the absolute and log-transformed values were compared and chosen based on normality using the Kolmogorov–Smirnov test (Table S2).

To compare the spatial structure of EcM fungal communities, the extent of distance decay (i.e. spatial autocorrelation range) and rate and average community dissimilarity in different data sets were determined by generating distance-decay curves (plots of community dissimilarity vs. geographical distance). The distance-decay curves were fitted by linear, exponential, logarithmic, polynomial and Gaussian functions, and the best fit was chosen based on coefficients of determination using the KaleidaGraph software (Synergy Software, Reading, PA, USA). The significance of the relationship between community dissimilarity and geographical distance within the detected distance-decay extent was assessed by use of Mantel test for each data set. Species of EcM fungi were assigned to EcM lineages according to Tedersoo, May & Smith (2010). These lineages represent monophyletic groups of EcM fungi that have evolved EcM habit independently. To find whether EcM fungal lineages differ in their spatial structure, the above analysis was performed based on species-level community of the most diverse lineages (n > 3 species, including the /russula–lactarius, /hymenochaete–telephora, /inocybe, /cor-tinarius, /clavulinula, /boletus, /gena–humaria, /rub and /hebecina lineages), followed by Bonferroni correction for multiple tests. The spatial autocorrelation of individual frequent species (n > 2 occurrences) was examined by Moran’s I test. The Mantel and Moran’s I tests were performed in Ecodist (Goslee & Urban 2007) and Ape (Paradis, Claude & Strimmer 2004) packages of R, respectively.

Two-way analysis of variance (ANOVA) was used to compare the distance-decay extent between tropical and non-tropical sites. To compare the rate of spatial turnover across different ecosystems, the slope of distance-decay relationships over the distance-decay extent, small range (< 50 m) and maximum range (study extent) of study sites were determined for each data set. The differences between spatial ranges were tested by comparing slopes of both data sets against slopes in the randomized data sets based on 1000 permutations following Nekola & White (1999) as implemented in the Simba package of R (Jurasiński 2012).

Table 1. Original data sets that were used for the analysis of spatial turnover of species

<table>
<thead>
<tr>
<th>Site name</th>
<th>Study</th>
<th>Sampling design</th>
<th>Ecosystem type</th>
<th>Host plant</th>
<th>Mean annual precipitation</th>
<th>Mean annual temperature</th>
</tr>
</thead>
<tbody>
<tr>
<td>Benin</td>
<td>Tedersoo &amp; Yorou unpublished</td>
<td>Regular</td>
<td>Tropical rain forests</td>
<td>Fabaceae</td>
<td>1082</td>
<td>27.2</td>
</tr>
<tr>
<td>Cameroon-Korup</td>
<td>Tedersoo et al. (2011)</td>
<td>Regular</td>
<td>Tropical rain forests</td>
<td>Fabaceae</td>
<td>2900</td>
<td>26</td>
</tr>
<tr>
<td>Denmark</td>
<td>Kjøller (2006, unpublished)</td>
<td>Regular</td>
<td>Boreal mixed forest</td>
<td>Fabaceae/Betulae</td>
<td>820</td>
<td>8.2</td>
</tr>
<tr>
<td>Ecuador-Yasuni</td>
<td>Tedersoo et al. (2010)</td>
<td>Regular</td>
<td>Boreal mixed forest</td>
<td>Caryaophyllales</td>
<td>3081</td>
<td>28</td>
</tr>
<tr>
<td>Estonia-1</td>
<td>Tedersoo et al. (2003)</td>
<td>Nested</td>
<td>Boreal mixed forest</td>
<td>Pinaceae</td>
<td>620</td>
<td>4.5</td>
</tr>
<tr>
<td>Estonia-2</td>
<td>Braham et al. (2011)</td>
<td>Regular</td>
<td>Boreal mixed forest</td>
<td>Saliceae</td>
<td>620</td>
<td>4.5</td>
</tr>
<tr>
<td>France</td>
<td>Court et al. (2008)</td>
<td>Regular</td>
<td>Temperate deciduous forest</td>
<td>Fabaceae/Betulae</td>
<td>744</td>
<td>9.2</td>
</tr>
<tr>
<td>Gabon-Monts De Cristal</td>
<td>Tedersoo et al. (2011)</td>
<td>Regular</td>
<td>Tropical rain forests</td>
<td>Fabaceae</td>
<td>2100</td>
<td>23.6</td>
</tr>
<tr>
<td>Guinea</td>
<td>Diedhiou et al. (2010)</td>
<td>Regular</td>
<td>Tropical rain forests</td>
<td>Fabaceae</td>
<td>3000</td>
<td>24</td>
</tr>
<tr>
<td>Iran-Assalem</td>
<td>Braham et al. (2012)</td>
<td>Nested</td>
<td>Temperate deciduous forest</td>
<td>Fabaceae/Betulae</td>
<td>1018</td>
<td>10.6</td>
</tr>
<tr>
<td>Iran-Nowshahr</td>
<td>Braham et al. (2012)</td>
<td>Nested</td>
<td>Temperate deciduous forest</td>
<td>Fabaceae/Betulae</td>
<td>940</td>
<td>13.8</td>
</tr>
<tr>
<td>Iran-Savadkuh</td>
<td>Braham et al. (2012)</td>
<td>Nested</td>
<td>Temperate deciduous forest</td>
<td>Fabaceae/Betulae</td>
<td>873</td>
<td>14.2</td>
</tr>
<tr>
<td>Madagascar-Mandena</td>
<td>Tedersoo et al. (2011)</td>
<td>Regular</td>
<td>Tropical savanna</td>
<td>Dipterocarpaceae</td>
<td>2200</td>
<td>24</td>
</tr>
<tr>
<td>Sweden</td>
<td>Ryberg, Larsson &amp; Molau (2009)</td>
<td>Nested</td>
<td>Arctic-alpine</td>
<td>Saliceae</td>
<td>582</td>
<td>5.8</td>
</tr>
<tr>
<td>Zambia-Kashima</td>
<td>Tedersoo et al. (2011)</td>
<td>Regular</td>
<td>Tropical savanna</td>
<td>Fabaceae</td>
<td>1100</td>
<td>21.7</td>
</tr>
<tr>
<td>Thailand</td>
<td>Phosri et al. (2012)</td>
<td>Regular</td>
<td>Tropical rain forests</td>
<td>Dipterocarpaceae</td>
<td>1250</td>
<td>27.1</td>
</tr>
</tbody>
</table>
To identify the key variables that determine (i) the average community dissimilarity, (ii) the extent of distance decay and (iii) the rate of distance-decay, model selection procedure was performed based on corrected Akaike information criterion (AICc) values of General Least-Squares (GLS) models as implemented in the nlme package of R (Pinheiro et al. 2011). The extent of distance decay and average community dissimilarity data of eight additional sites in Northern American temperate ecosystems (Lilleskov et al. 2004) were also used in the model selection procedure. The following variables were included as explanatory variables in the model selection: average age of EcM trees, total extent of sampling area (estimated based on maximum distance among samples), size of individual sample, total sample volume, number of samples, number of host trees, host density (determined based on relative percentage basal area contribution of EcM to non-EcM trees in four categories (< 25%; 25–50%; 50–75%; > 75%), because precise measurements were not available in most cases), distance from the equator, MAT, mean annual precipitation (MAP), biome (tropical vs. non-tropical), total species richness per site and average species richness per sample (Table S2). The observed richness was included in the model selection, because it may be strongly correlated with measures of beta diversity (Kraft et al. 2011). Because distance from the equator and MAT were strongly correlated (Pearson $R = -0.949$; $n = 21$; $P < 0.001$), model selection was performed twice by including and excluding MAT to consider the confounding effect of these variables. To directly estimate the relative contribution of spatial and environmental variables and their shared effect, variation partitioning analysis and permutational multivariate analysis of variance (PERMANOVA) were performed by including both the vectors of principal coordinates of neighbourhood matrices (PCNM) and recorded environmental variables (Borcard, Legendre & Drapeau 1992). Variation partitioning analysis was performed in the vegan package of R.

In addition, to better account for the varying spatial scale (i.e. study area and sampling design), the slope of the distance-decay relationships (rate of distance decay) of data sets was calculated based on pairwise geographical distances in the following arbitrary spatial ranges that correspond to the sampling design in most of the studies: 0–25, 0–50, 0–100, 0–150 and 0–300 m. Significance of the slopes was examined using a permutation test. The intercept of the relationships was interpolated as initial similarity (similarity between samples at one metre distance from each other).

To examine the spatial turnover of EcM fungi at the global scale, we analysed the distance decay of similarity in lineage-level community by considering study sites as sampling units. We used abundance of species in different EcM fungal lineages for creating a lineage-level community dissimilarity matrix. This semi-phylogenetic approach allows integrating information of different sites with non-alignable sequences and non-overlapping species (Tedersoo et al. 2012). We transformed geographical coordinates using the Haversine formula (Sinnott 1984) that reflects surface distances between any points on the Earth. We used the Wisconsin double standardization method, which improves the gradient detection of dissimilarity measures (Oksanen 2011), and Bray–Curtis dissimilarity to construct the lineage-level community dissimilarity matrix. We determined the extent of distance decay by plotting lineage-level community dissimilarity as a function of geographical distance and tested the significance of distance decay in the extent of distance decay by use of Mantel test. To compare phylogenetic turnover across different ecosystems, we tested the distance decay of lineage-level community similarity between the study sites in non-tropical and tropical biomes separately. We also compared the lineage-level community turnover over latitudinal and longitudinal gradients by calculating the slope of distance-decay relationships against latitude and longitude in separate analyses.

**Results**

The community variation of 7 of 16 sites showed significant linear distance-decay relationship at the local scale based on Mantel tests (Table 2). Exponential rise to maximum was the best-fitting function according to the determination coefficient for the distance-decay relationship in 11 of 16 data sets; in 2 data sets (Madagascar and Zambia), $R^2$ of exponential fit was comparable to other functions and in 2 data sets (Benin and Thailand) and logarithmic fit was the best-fitting function. One data set (France) showed no positive distance-decay relationship; thus, it was excluded from the analyses of distance-decay extent. Based on Mantel tests, the detected extent of...
Distance decay of similarity in ectomycorrhizal communities

Table 2. Results of Mantel tests at the scale of study and distance-decay extent, average community dissimilarity, permanova and variation partitioning

<table>
<thead>
<tr>
<th>Study site range</th>
<th>Distance-decay extent</th>
<th>PERMANOVA</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mantel r</td>
<td>P</td>
</tr>
<tr>
<td>Benin</td>
<td>0.021</td>
<td>0.235</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cameroon-Korup</td>
<td>0.047</td>
<td>0.007</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Denmark</td>
<td>0.093</td>
<td>0.001</td>
</tr>
<tr>
<td>Ecuador-Yasuni</td>
<td>0.055</td>
<td>0.082</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Estonia-1</td>
<td>0.126</td>
<td>0.011</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Estonia-2</td>
<td>0.025</td>
<td>0.281</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>France</td>
<td>–0.043</td>
<td>0.904</td>
</tr>
<tr>
<td>Gabon- Monts De Cristal</td>
<td>0.082</td>
<td>0.001</td>
</tr>
<tr>
<td>Guinea</td>
<td>0.066</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Iran-Asalem</td>
<td>–0.087</td>
<td>0.93</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Iran-Nowshahr</td>
<td>0.005</td>
<td>0.418</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Iran-Savadku</td>
<td>–0.08</td>
<td>0.906</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Madagascar- Mandena</td>
<td>0.044</td>
<td>0.151</td>
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<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sweden</td>
<td>0.072</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Zambia-Kashima</td>
<td>–0.022</td>
<td>0.836</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Thailand</td>
<td>0.092</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

na: not applicable; a: variation explained by environmental factors; b: shared variation explained by spatial vectors (PCNMs) and environmental factors; c: variation explained by PCNMs.

Distance decay was statistically significant in 13 data sets and marginally significant in one data set (Estonia-2). In Madagascar, no significant distance-decay extent was detected.

The best GLS model indicated that the extent of distance decay in EcM fungal communities is significantly negatively related to the distance from the equator ($t = -4.944$, $P < 0.001$; Fig. 2) and positively related to sampling volume ($t = 3.127$, $P = 0.006$), host density ($t = 2.735$, $P = 0.014$) and age of vegetation ($t = 2.191$, $P = 0.043$). The best model explained 77.8% ($P < 0.001$) of the variation in the extent of
distance decay. By replacing distance from the equator with MAT in the model selection procedure, the best GLS model showed that differences in the slope of distance-decay relationships across sites are significantly negatively related to the density of trees at the small scale ($P < 0.01$; Fig. 5).

Across all data sets, the proportion of significant spatially autocorrelated species to all tested species did not show significant difference between tropical and non-tropical sites based on Moran’s $I$ test (mean ± SD: tropical, 42 ± 27%; non-tropical, 49 ± 29%; $P = 0.638$); the autocorrelated species mainly belonged to the lineages *Russula–lactarius* and *Tomentella–telephora* (Table S3) that are the most species-rich groups in both non-tropical and tropical sites (Tedersoo & Nara 2010). Compared to other lineages, the species-level community of the *Russula–lactarius* lineage showed stronger correlation with spatial distance in both the tropical and non-tropical sites (Table S3).

At the global scale, lineage-level community dissimilarity was significantly positively correlated with geographical distance (Mantel test: $r = 0.151$, $P = 0.001$). Distance decay was significant up to 2800 km geographical distance ($r = 0.191$, $P = 0.001$; Fig. 6). The rate of distance decay of lineage-level community similarity was remarkably higher with latitude than with longitude (Mantel test: latitude: $r = 0.223$, $P = 0.001$; longitude: $r = 0.076$, $P = 0.026$). The slope of distance-decay curve was similarly steeper across latitude than longitude (average difference in slopes = 0.123, $P = 0.001$; Fig. 7). Analysis of tropical and non-tropical sites separately revealed no significant difference between the slopes of distance decay of lineage-level community similarity in tropical sites (Mantel $r = 0.287$, $P = 0.029$) and non-tropical sites (Mantel $r = 0.223$, $P = 0.001$) (difference of slopes = 0.01, $P = 0.454$). The initial similarity between sites was higher across tropical sites (difference of slope = 0.280, $P = 0.020$).
Our results show that the extent and rate of distance decay of similarity in EcM fungal communities vary significantly across ecosystems. Among the variables included in our study, the distance from the equator and host density were the main determinants of the extents and rates of distance decay across different ecosystems, respectively. Stronger distance-decay patterns were found in communities closer to the equator, suggesting a relatively greater spatial aggregation of fungal species in tropical ecosystems. Several non-exclusive processes may explain this pattern, which will be discussed later.

First, niche differentiation by host can be typically less pronounced in tropical ecosystems (Smith et al. 2011; Tedersoo et al. 2011). Due to the relatively lower host density in tropical ecosystems (including the monodominant rain forests, where the relative basal area of EcM trees rarely exceeds 70%), dispersal limitation is likely to play a greater role in these ecosystems (Tedersoo et al. 2010). Ecosystems with low host density can be viewed as fragmented habitats for EcM fungi, because spore dispersal is required to cross the unsuitable landscape. Because of differential spore germination efficiency (Ishida et al. 2008) and wind-dispersal range (Peay et al. 2012), species of EcM fungi strongly differ in their capacity to effectively disperse and establish in fragmented landscapes (Peay et al. 2007). Host specificity (or preference) is the most important determinant of EcM fungal community composition in most studies ranging from local to global scale (Ishida, Nara & Hogetsu 2007; Tedersoo et al. 2008, 2012; Bahram et al. 2012; Pöhlke et al. 2013). In addition, host species traits such as litter quality, exudation (Wardle 2002) and fine root

Fig. 4. The rate of distance decay in ectomycorrhizal communities at the local scale (< 50 × 50 m²) for (a) non-tropical and (b) tropical forests (difference of slopes = 0.174, P = 0.001).

Fig. 5. Variation in the rate of distance decay across different scales and ecosystems. Only significant values based on permutation test (P < 0.05) are shown.
dynamics (Burton, Pregitzer & Hendrick 2000) can affect the spatial structure of soil and, in turn, EcM fungal communities at the local scale (Toljander et al. 2006). The significant effect of host coupled with low host density could result in greater fragmentation of EcM habitat and consequently stronger distance-decay patterns (Tedersoo et al. 2010).

While most of the study sites we analysed here are located in relatively homogeneous landscapes, addressing the effect of all potentially important environmental variables is impractical. We admit that stronger distance-decay patterns in tropical ecosystems may be related to the unmeasured, potentially spatially structured environmental factors that affect EcM fungal community at the local scale (Ettema & Wardle 2002). The distance decay in fungal communities may correspond to the patchiness of soil properties, which is generally more pronounced in tropical ecosystems than in boreal and temperate forests. The spatial structure of soil nutrients is related to topography and vegetation. The relatively greater autocorrelation range of soil properties in tropical forests is attributable to more stable climate over millennia and low contribution of each tree species in creating soil patches in highly diverse ecosystems (John et al. 2007; Townsend, Asner & Cleveland 2008).

Our results suggest that the dominant EcM fungal lineages may affect distance decay of fungal communities due to their contrasting spatial structure. The /russula–lactarius lineage was the most frequently spatially autocorrelated group across different sites. Lilleskov et al. (2004) also reported that members of the /russula–lactarius lineage exhibit greater than average patch size and that two species of this group display the greatest spatial autocorrelation range (> 17 m). The genet size of Russula brevipes may reach 18 m in an old forest (Bergemann & Miller 2002). Riviere, Natarajan & Dreyfus (2006) also determined relatively large genets ranging from 30 to 70 m for Russula sp. in an old-growth dipterocarp rain forest. There is evidence that species of the /russula–lactarius and / cortinarius lineages exhibit limited spore dispersal (Ishida et al. 2008; Tedersoo et al. 2009; Peay et al. 2012). The /russula–lactarius lineage is the most species-rich group in tropical sites, which may also contribute to the greater spatial range in tropical ecosystems simply due to the greater information content. The /cortinarius lineage is uncommon in tropical ecosystems while it is among the dominant groups in boreal and temperate forests. The /cortinarius lineage, however, showed no significant spatial autocorrelation in any of the sites, which could be attributable to its distribution in small, localized patches (Genny, Anderson & Alexander 2006). Among the variables included in our analysis, age of trees significantly affected the extent of distance decay, which can be related to the dominance of late successional colonizers, for example /russula–lactarius in older forests. In old forests, individuals have more stable conditions for expansion, which results in relatively large genetic individuals compared to pioneer communities. In early successional ecosystems, species with greater spore dispersal ability, higher genet turnover and thereby small genetic individuals dominate.

Significant distance decay and spatial autocorrelation were detected in the majority of data sets at the local scale, although most individual studies were designed to avoid spatial autocorrelation by increasing the distance among samples. This indicates that spatial processes, particularly dispersal limitation may play a much greater role in EcM fungal communities in non-fragmented forests than previously anticipated (Lilleskov et al. 2004). If not accounted for, the spatial structure in community composition may cause autocorrelation in model residuals and consequently higher probability of committing type I error in testing the effects of environmental variables. In addition, neglecting the effects of dispersal-related processes may lead to overlooking important patterns in communities (Cottienie 2005). This further highlights the importance of incorporating spatial processes in community studies of EcM.
fungi, for example by including a spatial component such as spatial eigenfunctions in models (Dray et al. 2012).

All meta-studies exhibit their inherent limitations, because individual studies differ in sampling design, sampling effort and measurement of environmental variables. Although our analyses accounted for the variation in sampling parameters, some important variables such as soil heterogeneity were neglected in our study due to the lack of available information. Accumulating data from more homogeneous sampling designs and host-plant community can be useful in confirming our observed patterns.

**DISTANCE DECAY AT THE SITE LEVEL**

At the global scale, distance decay in the distribution of EcM lineages was present only along latitude, but not along longitude, which resembles the continental-scale patterns in plants (Qian, Ricklefs & White 2005). This lends further support for the role of climate in structuring EcM fungal communities at regional to global scales (e.g. Tedersoo, May & Smith 2010; Bahram et al. 2012; Tedersoo et al. 2012). Being in a symbiotic relationship, fungi and plants may have co-evolved in different phylogeographic regions. In addition to this, dispersal limitation and phylogeographic history together with host and environmental factors may regulate spatial distributions of EcM fungal species at large scale (Mueller et al. 2001; Geml et al. 2008; Matheny et al. 2009), consistent with other microorganisms (Martiny et al. 2006). In particular, phylogeographic history may be a strong determinant of phylogenetic composition of EcM fungi; for instance, some lineages are almost lacking in tropical ecosystem (Tedersoo et al. 2010) and some others possess a lower rate of diversification in these ecosystems (Matheny et al. 2009; Kennedy et al. 2012).

**Conclusions**

This study demonstrates that communities of EcM fungi show a greater extent of distance decay (spatial autocorrelation range) than previously suggested. The rate of distance decay is greater in tropical compared to non-tropical ecosystems potentially owing to the typically lower host density. The strong impact of latitude, but not longitude on phylogenetic community turnover, suggests that climate has an important effect on distance decay of EcM fungal communities at the global scale, directly or indirectly by influencing soil processes and host-plant distribution. Together, our results provide new insights into the spatial structure of EcM fungal communities at various scales and raise questions regarding the underlying mechanisms.

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**References**


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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Study sites and data sets used for spatial analyses.

Table S2. Variables included in the model selection procedures.

Table S3. Species and lineages with significant spatial autocorrelation in different data sets.
Table S2. Variables included in the model selection procedures.

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References for supplementary material


Horton TR, Bruns TD. 1998. Multiple-host fungi are the most frequent and abundant ectomycorrhizal types in a mixed stand of Douglas fir (Pseudotsuga menziesii) and bishop pine (Pinus muricata). New Phytol. 139: 331–339.


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<th>Study</th>
<th>Autocorrelated species based on Moran’s I correlogram</th>
<th>Frequency of autocorrelated species</th>
<th>Autocorrelated lineages</th>
<th>Autocorrelation range</th>
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<td>Tedersoo et al. 2003</td>
<td>Inocybe_sp4, Elaphomyces_sp1, Elaphomyces_sp2, Cortinarius_sp3, Laccaria_sp1, Lactarius_sp1, Genea_sp1, Hydnotrya fallax, Sebacina_sp3, Tomentella lilacinogrisea, Tomentella_sp1, Tomentella_sp2, Tomentella_subclavigera, Tuber_sp1</td>
<td>15/16 (94%)</td>
<td>/tomentella-thelephora</td>
<td>R=0.326 P=0.040 0-3 R=0.512 P=0.005</td>
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<td>Courty et al. 2008</td>
<td>Xerocomus sp, Tomentella_punicea, Tomentella_botryoides, Cortinarius_sp4</td>
<td>4/55 (7%)</td>
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<td>Bahram et al. 2011</td>
<td>Cadophora_finlandica, Cenococcum_geophilum, Clavulina_crist, Cortinarius_sub2, Entoloma1, Genea_hispidula, Humaria_hemisphaerica, Inocybe_sub, Piloderma_olii, Russula_nigra(acrifolia), Scleroderma_areola, Tomentella_25, Tomentella_12, Tomentella_5, Tomentella_7, Tomentella_13, Tomentella_11, Tuber2</td>
<td>18/46 (39%)</td>
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<td>R=0.151 P=0.048 0-3 R=0.131 P&lt;001</td>
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<td>Ryberg et al. 2009</td>
<td>Cenococcum_geophilum, Clavulinaeae_sp.1, Hebeloma_aff. cavipes/vaccinum, Hebeloma_aff. polare/monticola, Hebeloma_aff. vinosophyllum (hiemalis), Inocybe cf. rufuloides, Russula_sp, Sebacina_epigaea, Sebacina_sp.1, Sebacina_sp.3, Thelephora_sp.1, Tomentella_aff. ramossisima, Tomentella_aff. stuposa, Tomentella_sp.12, Tomentella_sp.13, Tomentella_sp.15</td>
<td>18/27 (67%)</td>
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<td>R=0.201 P=0.006 0-6 R=0.308 P=0.006</td>
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<td>Tedersoo et al. 2011</td>
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<td>Tedersoo et al. 2011</td>
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<td>/tomentella-thelephora Y3</td>
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<td>Tedersoo &amp; Yorou, unpublished</td>
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<td>Diédhiou et al., 2010</td>
<td>21/26 (81%)</td>
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<td>Kjoller et al., 2006;</td>
<td>21/49 (43%)</td>
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Piloderma sp. 2  
Russula mairei  
Russula vesca  
Sebacinoid sp. 1  
Sebacinoid sp. 2  
Tomentella bryophila  
Tomentella sp. 6  
Tomentella subtestacea  
Tomentella terrestris  

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<th>Species</th>
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<tr>
<td>Bahram et al. 2012</td>
<td>Leccinum</td>
<td>7/26 (27%)</td>
<td>R=0.152</td>
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1 Statistical significance was based on P<0.05.
2 Number of autocorrelated species divided by number of all species examined