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FROM THE COVER

Towards global patterns in the diversity and community structure of ectomycorrhizal fungi

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Abstract

Global species richness patterns of soil micro-organisms remain poorly understood compared to macro-organisms. We use a global analysis to disentangle the global determinants of diversity and community composition for ectomycorrhizal (EcM) fungi—microbial symbionts that play key roles in plant nutrition in most temperate and many tropical forest ecosystems. Host plant family has the strongest effect on the phylogenetic community composition of fungi, whereas temperature and precipitation mostly affect EcM fungal richness that peaks in the temperate and boreal forest biomes, contrasting with latitudinal patterns of macro-organisms. Tropical ecosystems experience rapid turnover of organic material and have weak soil stratification, suggesting that poor habitat conditions may contribute to the relatively low richness of EcM fungi, and perhaps other soil biota, in most tropical ecosystems. For EcM fungi, greater evolutionary age and larger total area of EcM host vegetation may also contribute to the higher diversity in temperate ecosystems. Our results provide useful biogeographic and ecological hypotheses for explaining the distribution of fungi that remain to be tested by involving next-generation sequencing techniques and relevant soil metadata.

Keywords: global analysis, latitudinal gradient of diversity, macro-ecology, soil microbes, temperature

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Introduction

The discipline of biogeography examines the distribution of regional and global biodiversity (Lomolino *et al.* 2006). Many global biogeographic patterns of marine and terrestrial macro-organisms have been attributed to historical and environmental factors that strongly covary with latitude (Hawkins *et al.* 2003; Hillebrand 2004; Ricklefs 2004; Lomolino *et al.* 2006; Kreft & Jetz 2007; Mittelbach *et al.* 2007; Tittensor *et al.* 2010). For this reason, the latitudinal gradient of diversity has

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become a cornerstone principle in ecology and biogeography since the early expeditions of Alexander von Humboldt (Lomolino *et al.* 2006).

Macro-ecological patterns of plants and vertebrates are relatively well documented owing to their size, charisma and straightforward species delimitation. In contrast, the biogeography of micro-organisms has received little attention. Rapid development of molecular identification techniques, particularly sequence analysis of ribosomal DNA (rDNA), has recently facilitated pioneering biogeography studies of microbes such as prokaryotes, protists and fungi (Fierer 2008; Taylor 2008). These molecular studies provide evidence that dispersal limitation shapes the biogeographic patterns in many microbial groups including bacteria, fungi and microeukaryotes (Taylor *et al.* 2006; Fierer 2008; Peay *et al.* 2010). By contrast, in fungal root endophytes and soil bacteria, the 'everything is everywhere, but, the environment selects' paradigm of Baas Becking (1934) receives support (Chu *et al.* 2010; Queloz *et al.* 2011) and the debate over microbial biogeography continues. For both Bacteria and Archaea, global analyses across diverse environments revealed that substrate (soil vs. water) and salinity are the principal variables that drive diversity and phylogenetic community structure (Lozupone & Knight 2007; Auguet *et al.* 2010). Richness of all major phyla of marine bacteria increases towards the equator in strong correlation with the temperature gradient (Pommier *et al.* 2007).

Among eukaryotic micro-organisms, fungi play a fundamental role in ecosystem processes through the decomposition of dead organic material and through mineral nutrition of plants via mycorrhizal symbiosis. There are many forms of mycorrhizal symbiosis, but many economically and ecologically important trees in temperate and tropical forests engage in ectomycorrhizal (EcM) interactions (Smith & Read 2008). Ectomycorrhizal fungi cover the finest root branches of the tree and provide nutrients from the soil in exchange for phytosynthetically derived carbon. These symbionts contribute up to 39% of microbial biomass and 10–35% of respiration in boreal forest soils (Smith & Read 2008; Högberg *et al.* 2010). Ectomycorrhizal fungi are estimated to comprise 20 000–25 000 species globally, which belong to >60 independently evolved lineages (Rinaldi *et al.* 2008; Tedersoo *et al.* 2010). Induced climate change, host identity and soil environments may strongly affect the diversity and community composition of EcM fungi at the local scale (Taylor 2008), but larger scale determinants of species richness and community composition remain unknown because of the paucity of molecular studies from tropical biomes. Regional to global-scale sampling of other fungal guilds such as endophytes and airborne fungi has revealed contrasting biogeographical patterns (Arnold *et al.* 2009; Amend *et al.* 2010; Herrera *et al.* 2010; Queloz *et al.* 2011), indicating that different local and global processes may drive the biodiversity of different fungal functional groups.

In this publication, we combine information from recent molecular studies to identify the main factors that influence richness and community composition of EcM fungi at the global scale. We hypothesize that the mean annual temperature and precipitation drive species richness and community composition of EcM fungi. We also address the relative importance of other geographic, biological and climatic factors in determining the alpha diversity of EcM fungi at two levels of spatial resolution (site and sample levels). We include spatial autocorrelation and differences in identification method and sample size in generalized least squares (GLS) models to account for sampling biases in the global data set.

Materials and methods

Data sources

The global analysis builds on studies that cover all continents and biomes where the EcM symbiosis occurs (Table S1, Supporting information). These data sets fulfil the following criteria: (i) only root tips are studied from soil samples (excluding studies based on soil mycelium and fruit bodies); (ii) sampling is performed in a site of 10^{-2}–10^{3} ha; (iii) the number of individual soil samples is >15; (iv) the vegetation is >10 years old; and (v) sequencing and/or restriction fragment length polymorphism (RFLP) of the nuclear rDNA internal transcribed spacer (ITS) region is used for identification of fungi. Site is defined as a compact sampling area or a transect that is located >1 km from other sampling areas. Thus, plots within 1-km distance were usually pooled to form a single site. Conversely, data sets from a few studies were divided into multiple sites to meet the above-mentioned criteria. Soil sample is defined as a single or composite sample no larger than 30 cm diameter. Data from samples that were vertically or temporally stratified, but taken within 30-cm distance, were pooled. In most studies, operational taxonomic units (OTUs) were separated based on 97.0% ITS sequence similarity and used as proxies for species-level identification. A few studies used other sequence similarity threshold values, but these were estimated to cause only minor biases because of the barcoding gap in most EcM fungal taxa (Schoch *et al.* 2012). When total species richness was not reported, sequences were assigned to OTUs using the single linkage clustering at 97.0% similarity and 70.0% coverage thresholds as

implemented in BlastClust (http://toolkit.tuebingen.mpg.de/blastclust).

Site-level species richness and the average number of species per sample were used as the primary measures of diversity. We did not attempt to extrapolate or rarefy EcM fungal diversity because species distribution data by samples were unavailable for most studies. To account for differential sampling effort, we included the number of samples and sample volume as covariates in the final analysis (see below).

For each site, available sequences were queried against the International Sequence Databases (INSD) and the fungi-specific database UNITE (Abarenkov *et al*. 2010a; http://unite.ut.ee/) by use of a massblaster tool in the PlutoF workbench (Abarenkov *et al.* 2010b). Sequences were further aligned by families as implemented in Mafft (http://mafft.cbrc.jp/alignment/server/) and subjected to maximum likelihood analyses in RAxML (*phylobench.vital-it.ch/raxml-bb/*) with default options. These procedures enabled accurate assignment of fungal sequences to EcM fungal lineages. Lineage is defined here as a rankless, strictly monophyletic taxonomic unit that represents independent evolutionary gains of the EcM symbiosis by different fungal groups (Tedersoo *et al.* 2010). The lineage-level approach was used to provide a semi-phylogenetic estimate of global trends in EcM fungal communities, because ITS sequences cannot be aligned across lineages and higher taxonomic units. Moreover, only a few individual species overlapped in the study sites, rendering direct species-to-species comparisons from different sites uninformative. Study sites (see below) and sequences were annotated for metadata and quality within a more inclusive study on all mycorrhizal fungi as described in Tedersoo *et al.* (2011). This information is publicly available via the UNITE homepage. Preliminary analyses indicated that RFLP-based studies are strongly biased towards reporting fungi that form mushroom-like fruit bodies. Thus, RFLP-based studies for which <50% of species could be assigned to EcM lineages were omitted from the community data set.

For each site, metadata on various geographical (latitude, longitude and altitude), climatic (mean annual temperature and precipitation), site (dominant host plant lineage, the number of host species sampled or present, age of vegetation, soil texture, anthropogenic disturbance) and sampling variables (volume of a root sample and all samples together, the number of samples, site area, sampling duration, molecular method and year of publication) were retrieved from original publications, cited publications or directly from the authors. Missing data for mean annual temperature and mean annual precipitation were extracted from the World Water and Climate Atlas (New *et al.* 2002). Data on soil chemistry (pH, nutrients) and density of EcM host plants were unavailable for most sites and were therefore excluded from analyses. Although edaphic variables are important at the local and regional scales (Taylor 2008), climatic and historical factors are expected to dominate on a global scale as shown for other organisms (Lomolino *et al.* 2006).

Data analysis

Spatial autocorrelation was assessed by transforming geographical coordinates into a Euclidean distance matrix according to the Earth's surface model as implemented in the rdist.earth function in the fields package of R (Furrer *et al.* 2010; R Development Core Team 2011). Full models with and without a geographical distance matrix were compared using likelihood ratio (LR) tests. In both the models of total species richness and richness per sample, the distance matrix reduced the AICc values significantly, and therefore, a spatial component was retained as Gaussian spatial correlation structure. Based on Moran's *I*, no significant spatial autocorrelation remained in the data sets.

To address the relative importance of climatic, biological and geographical factors on diversity, we built GLS models that further accounted for sample size, methodological differences and spatial autocorrelation. Sampling variables such as the number of samples, sample volume and sampling area were log transformed prior to analyses, whereas other variables were left untransformed to enable testing for nonlinear relationships. Nevertheless, the model residuals did not deviate from a normal distribution and were homoscedastic, rendering further transformations unnecessary. Total species richness and richness per sample were modelled separately by fitting linear and second-order polynomial models by use of GLS as implemented in the nlme package of R (Pinheiro *et al.* 2011). The best models were chosen based on corrected Akaike (AICc) values.

Alternative models that included different parameters had relatively similar AICc values. To obtain a conservative estimate of important variables, we applied model averaging of best models that fell into the 95% AICc confidence set of models. Beta coefficients (slopes) of individual models were weighted according to their Akaike weight across all models. Nonsignificant variables of individual models were given no weight. The averaged weight of significant variables is reported as the mean ± 95% confidence intervals of their beta coefficients. Variables were considered significant when confidence intervals excluded zero values.

To illustrate trends in the global data set, each variable in the best models was plotted against partial residuals of the dependent variable. This approach

allows evaluation of single variable effects, when all significant variables are accounted for (Kreft & Jetz 2007). Linear (or square) and LOWESS functions were fitted to illustrate trends in the partial residuals. To demonstrate the relatively species-rich sites in the global context, we constructed another set of models that accounted for the effect of significant sampling variables. Partial residuals of the best models were fitted into global maps.

To identify the relative importance of climatic, geographic and spatial variables on EcM fungal communities, we used the Adonis routine of Vegan package of R (Oksanen *et al.* 2012). Adonis represents a multivariate analysis of variance that allows simultaneous testing of multiple factors and covariates based on permutation tests. In parallel, Global Nonmetric Multidimensional Scaling (GNMDS) ordination plots were generated to demonstrate trends in fungal community composition. For both analyses, the Bray-Curtis distance measure and 1000 permutations were used. Species richness of each EcM fungal lineage represented the measure of abundance—i.e. all species contributed equally to the abundance of lineages. To assess the relative importance of spatial component on EcM fungal communities, we constructed vectors of principal coordinates of neighbour matrices (PCNM) according to Borcard & Legendre (2002). These vectors are spatial eigenfunctions that account for spatial autocorrelation at different scales. PCNM vectors were calculated based on the geographical distance matrix and sorted by coefficients of determination according to forward selection as implemented in Packfor package of R (Dray *et al.* 2009). All six significant PCNM vectors and other variables were tested for significance in Adonis. We performed a forward selection of parameters, including only significant variables in the final model. Vectors and centroids of these variables were fitted into a GNMDS plot using the function envfit.

Results

The global data set comprises local communities of EcM fungi from 69, 53 and 55 sites for total species richness, richness per sample and community composition, respectively (Table S1, Supporting information). These studies detected 6021 fungal species and include EcM fungal communities from subarctic tundra to tropical rainforest—that is, from all biomes where EcM

Table 1 Best and averaged global models for richness and community composition of ectomycorrhizal fungi

	Degrees of freedom	*t*-value/*F*-value	R^2_{adj}	*P*-value	Average beta coefficient (mean ± 95% CI)
Total species richness					
Sample size	1	4.57	n.a.	<0.001	39.61 (±17.90)
Total sample volume	1	5.27	n.a.	<0.001	26.69 (±10.99)
Mean annual temperature	1	5.36	n.a.	<0.001	10.34 (±4.34)
Mean annual temperature (polynomial)	2	−5.25	n.a.	<0.001	−0.31 (±0.13)
Mean annual precipitation	1	−4.39	n.a.	<0.001	−0.02 (±0.01)
Anthropogenic disturbance	1	−2.51	n.a.	0.015	—
Residuals	n.a.				
Species richness per soil core					
Soil texture	1	−4.47	n.a.	<0.001	−0.90 (±0.72)
Sample volume	1	2.62	n.a.	0.012	—
Anthropogenic disturbance	1	2.42	n.a.	0.020	—
Mean annual temperature	1	2.37	n.a.	0.022	—
Mean annual temperature (polynomial)	2	−3.19	n.a.	0.003	—
Residuals	n.a.				
Fungal community					
Host family	5	6.25	0.338	<0.001	n.a.
Mean annual precipitation	1	4.15	0.045	<0.001	n.a.
Mean annual temperature	1	2.84	0.031	0.006	n.a.
Anthropogenic disturbance	1	2.41	0.023	0.010	n.a.
Age	1	2.12	0.023	0.031	n.a.
Soil texture	1	2.07	0.022	0.042	n.a.
Principal coordinates of neighbour matrices spatial vectors	3	2.17	0.071	<0.001	n.a.
Residuals	41		0.443		n.a.

symbiosis is common. For each community, we recorded 19 predictor variables describing the abiotic and biotic environment, sampling methodology and geographic location (Table S2, Supporting information). Based on these variables, 31 and 85 alternative GLS models for total species richness and richness per sample, respectively, fell into the 95% AICc confidence set of models and formed the basis of model averaging.

Model averaging indicated several significant predictors of site level EcM fungal diversity at the global scale. The mean annual temperature, mean annual precipitation, sample size and sampled soil volume all had significant effects on total species richness (Table 1). The averaged model largely reflected the best model, in which increasing anthropogenic disturbance had an additional negative effect on diversity (Fig. 1; Table 1). The mean annual temperature had a broad unimodal effect on EcM fungal richness, which reached peak values between 5 and 20 °C (Fig. 1a). Distance from the equator had a significant unimodal effect on fungal richness only when three subalpine sites and climatic variables were removed from the analysis (quadratic term in GLS model accounting for sample size and sample volume: $t = -3.95$; $P < 0.001$; Fig. 2a).

At the sample level, model averaging conservatively suggested that smaller soil particles (i.e. higher clay content) positively influence species richness of EcM fungi (Table 1). Besides soil texture, the mean annual temperature, anthropogenic disturbance and increase in sample volume, all had positive effects on richness per sample in the best model (Table 1; Fig. 3). Both temperature (best GLS model: $t = -3.19$; $P = 0.003$) and latitude (quadratic term of distance from the equator in a separate GLS model partialling out the sample volume effect: $t = -3.44$; $P = 0.001$) had a unimodal effect on sample-level diversity (Figs 2b and 3a). The peaking richness in temperate regions was consistent with the site-level results.

The lineage-level analysis revealed pronounced biogeographic patterns in EcM fungal community structure. Dominant host taxon, mean annual precipitation, mean annual temperature, age of vegetation, soil texture and anthropogenic disturbance level all significantly affected the EcM fungal phylogenetic community composition at the global scale (Table 1; Fig. 4). Host family explained 33.8% of variation in the fungal community, while each of the other factors explained <5% of the variation.

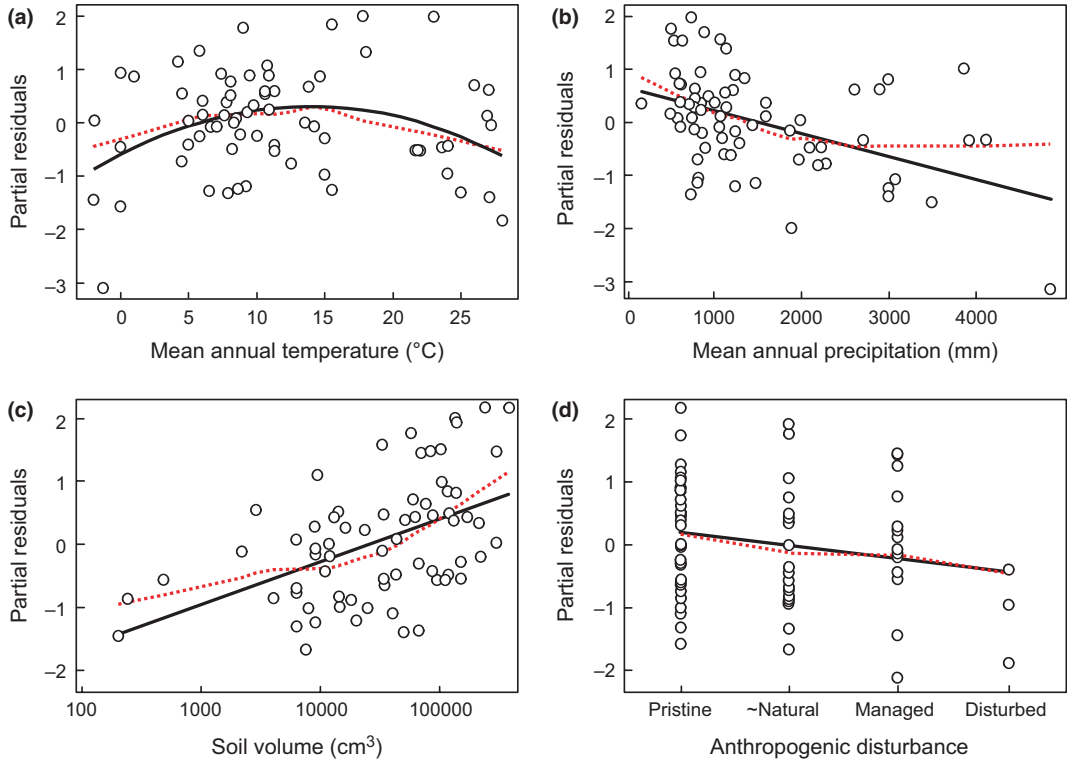

Fig. 1 Plots of partial residuals for the best model predicting the total species richness of ectomycorrhizal fungi. These plots indicate the effects of each variable when all other variables in the model are accounted for (a) mean annual temperature; (b) mean annual precipitation; (c) soil volume (non-significant in model averaging); (d) anthropogenic disturbance. Solid lines and dotted lines denote linear or polynomial regression lines and partial LOWESS curves, respectively.

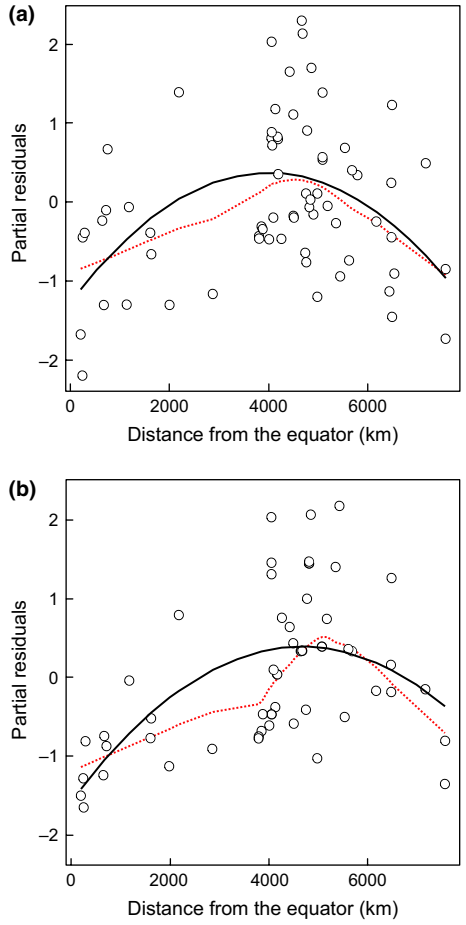

Fig. 2 Plots of partial residuals demonstrating the latitudinal diversity gradient of (a) total species richness (the effects of sample volume and sample size are partialled out; quadratic term of richness: $n = 66$; $R^2 = 0.195$; $t = -3.95$; $P < 0.001$); and (b) species richness per sample (the effect of sample volume is partialled out; quadratic term of richness: $n = 51$; $R^2 = 0.309$; $t = -3.444$; $P = 0.001$) after excluding three subalpine sites from the analyses. Solid lines and dotted lines denote linear or polynomial regression lines and partial LOWESS curves, respectively.

Discussion

Our global analysis of molecular below-ground diversity studies of EcM fungi reveals that richness of these root symbionts has a unimodal relation both with temperature and latitude, when confounding sampling and spatial variables are taken into account. Fungal richness peaks at temperate and boreal latitudes, but there is large variation among sites (Fig. 5), indicating the importance of habitat heterogeneity and local processes. The low richness in subalpine environments of temperate latitudes shows that temperature rather than distance from the equator *per se* have the strongest impact on EcM fungal richness (see Rahbek 2005 for macro-organisms). In addition, both the subarctic and lowland tropical environments have also lower phylogenetic diversity, that is, fewer lineages of EcM fungi (Bjorbækmo *et al.* 2010; Tedersoo & Nara 2010), indicating that environmental filtering may occur at both ends of the temperature gradient and it operates at both species and higher taxonomic levels. Diversity of most organisms on the planet (Hillebrand 2004), including endophytic fungi (Arnold *et al.* 2009) and marine bacteria (Pommier *et al.* 2007), is generally positively correlated with temperature. However, some ordinal-level mammalian groups such as pinnipeds and cetaceans have unimodal species richness relations to energy and latitude that is ascribed either to phylogenetically conserved metabolic constraints, a temperate evolutionary origin, or both (Buckley *et al.* 2010; Tittensor *et al.* 2010). In addition, several taxonomic groups of soil fauna such as oribatid mites, earthworms and nematodes tend to be the most diverse in temperate ecosystems, although thorough statistical proof is lacking (Lavelle *et al.* 1995; Boag & Yeates 1998; Wardle 2002; Maraun *et al.* 2007). Wet tropical ecosystems have higher soil temperature, metabolic activity and plant growth and turnover resulting in higher decomposition rates that reduce the availability of organic matter and decrease the vertical stratification of soil. In turn, these soil processes may reduce the total habitat and types of niches available to key groups of soil biota (Wardle 2002).

The negative effect of increasing precipitation on EcM fungal richness could be ascribed to stress from low oxygen availability in water-saturated soils or competition among functional guilds of soil microbes. Ectomycorrhizal vegetation, particularly the deep-rooted members of *Fagaceae*, *Myrtaceae* and *Fabaceae*, dominate many drought-prone ecosystems and may thus provide their root symbiotic fungi a competitive advantage over other soil microbes via access to deep ground water (Querejeta *et al.* 2003). Manipulative studies suggest that induced drought has a neutral effect on diversity of EcM fungi at the local scale (Richard *et al.* 2011). In contrast, overall richness of plants and animals is positively correlated with precipitation (Kreft & Jetz 2007). In many biotic interactions, host and consumer richness are causally related via niche differentiation (Qian & Ricklefs 2008; but see Hawkins & Porter 2003). Although host plant richness at the species and family levels had no significant effect on EcM fungal species richness at the global scale, co-occurrence of host tree species and families is believed to promote fungal diversity at the local scale by providing unique habitats for host-specific taxa (Ishida *et al.* 2007; Taylor 2008; Tedersoo *et al.* 2008).

Although anthropogenic disturbance had a negative effect on EcM fungal diversity at the site level, it had a

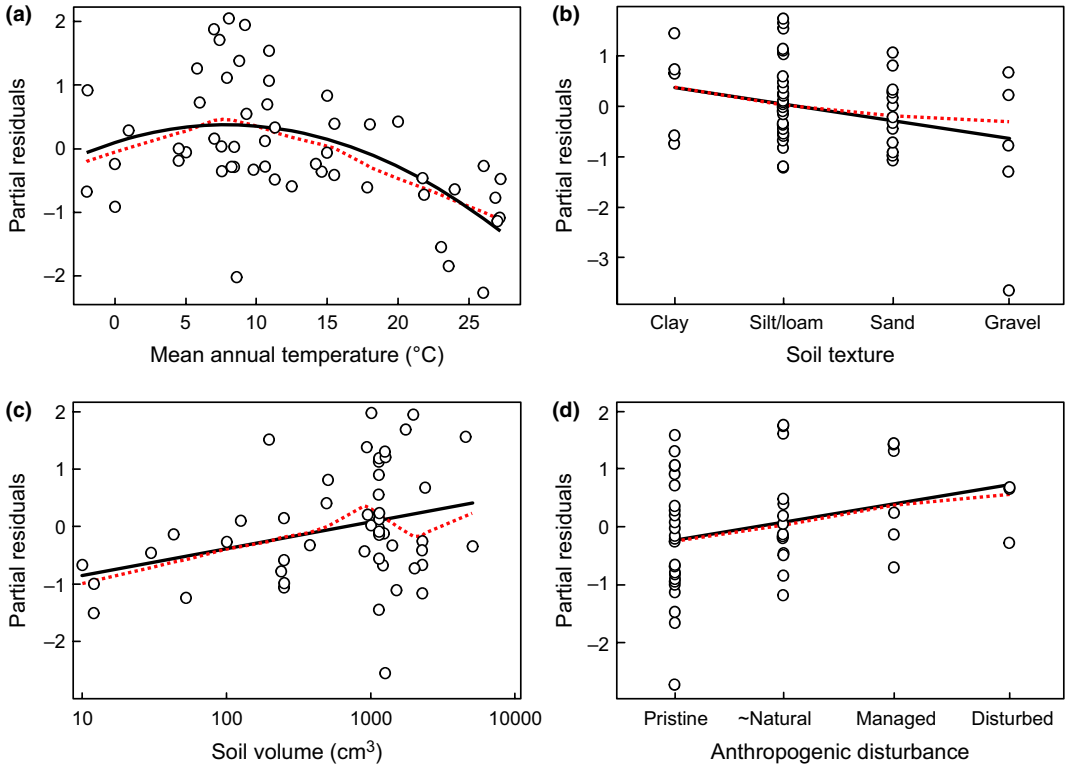

Fig. 3 Plots of partial residuals for the best model predicting the average species richness of ectomycorrhizal fungi per sample. These plots indicate the effects of each variable when all other variables in the model are accounted for (a) mean annual temperature; (b) soil texture; (c) sample volume; (d) anthropogenic disturbance. Solid lines and dotted lines denote linear or polynomial regression lines and partial LOWESS curves, respectively.

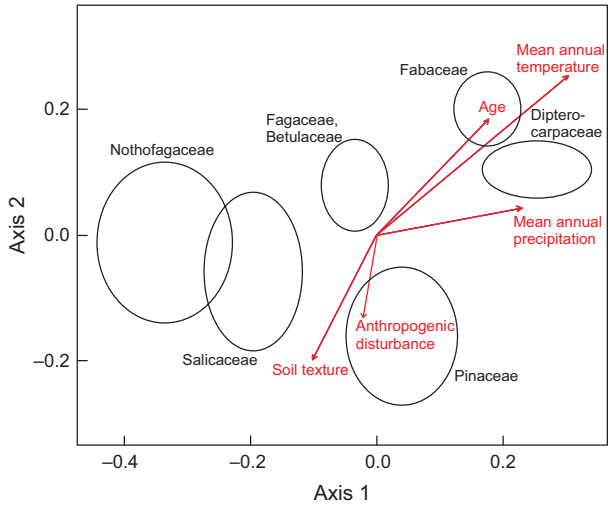

Fig. 4 Global Nonmetric Multidimensional Scaling (GNMDS) graph depicting the relative importance of variables (arrows) explaining the lineage-level community composition of ectomycorrhizal fungi at the global scale. Ellipses denote 95% confidence intervals around the mean values of the dominant host plant families. The primary axes explain 80.4% variation in the community data.

positive effect at the sample level. This result is likely due to the homogenizing effect of anthropogenic disturbance on the soil horizons and microsites that structure the natural fungal communities. Such modified habitat conditions have been shown to alter the fungal community and reduce overall richness (Taylor 2008). While homogenization reduces overall diversity by removing specialized niches, it could lead to increased fine-scale diversity by breaking up large genetic individuals and allowing the establishment of multiple small genets (Bruns *et al.* 2002) that may be less competitive, allowing for greater coexistence. Small soil particles probably complement the effect of disturbance at the sample scale by limiting the vegetative growth of roots and spread of microbes via lower porosity, which in turn may reduce competition and promote richness of soil micro-organisms (Carson *et al.* 2010). These hypotheses of disturbance and particle size effects remain to be experimentally tested over different spatial scales.

Consistent with previous fungal evolution and biogeography studies, our results suggest phylogenetic conservatism for symbiosis with particular host families in some EcM fungal lineages (Hosaka *et al.* 2008; Matheny

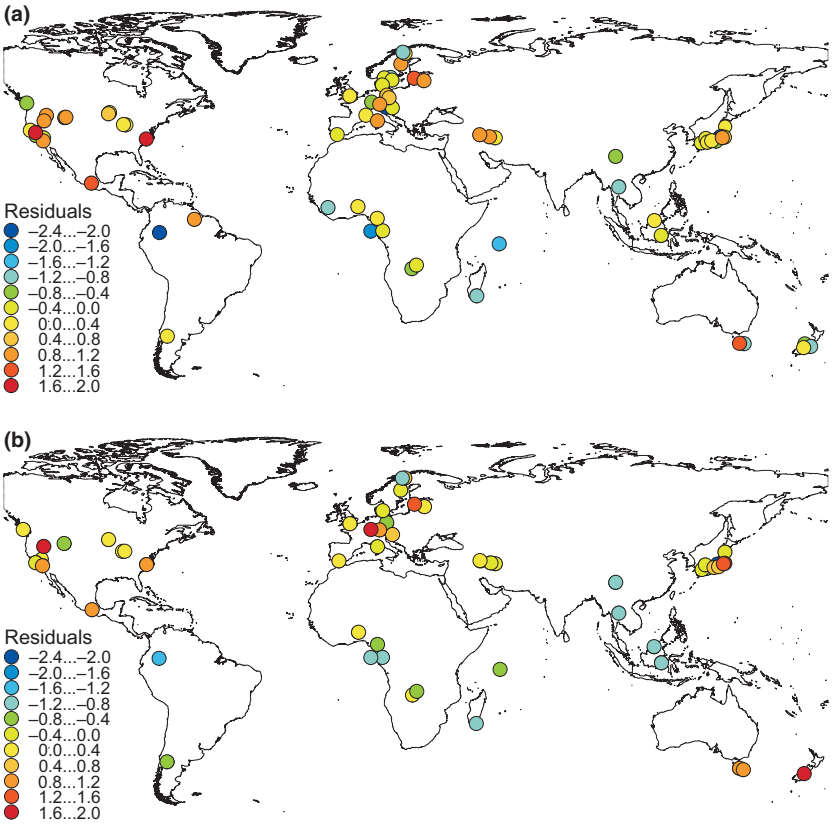

Fig. 5 Map of standardized residuals of ectomycorrhizal fungal richness that account for differences in sample size and sample volume: (a) Total species richness; (b) average species richness per sample. Circles with warmer colours indicate relatively higher species richness.

et al. 2009). Similar host effects have been found in *Frankia* actinobacterial root symbionts (Benson *et al.* 2004) and foliar endophytes (Arnold 2007), but not in the 'dark septate' *Phialocephala* root endophytes (Queloz *et al.* 2011). Phylogenetic community composition of soil bacteria depends largely on pH at the continental scale (Lauber *et al.* 2009; Chu *et al.* 2010), but there are no comparable data on fungi or other soil organisms. In steep local gradients of soil pH and mineral nutrients, these edaphic factors drive the community composition of mycorrhizal fungi but have no effect on species richness (Toljander *et al.* 2006; Dumbrell *et al.* 2010). Soil pH has a positive effect on plant diversity in regions of predominately neutral soils, but the effect is negative in regions where acidic soils dominate (Pärtel 2002), suggesting that evolutionary history has a strong influence on large-scale ecological patterns (Lomolino *et al.* 2006). Most major functional groups of macro-organisms originate in tropical regions (Wiens & Donoghue 2004; Buckley *et al.* 2010). Although paleotropical ecosystems are inferred as ancestral habitats in some species-rich groups of EcM fungi (Buyck *et al.* 2008; Matheny *et al.* 2009), the distribution of many EcM fungal lineages is restricted to the northern and/or southern temperate ecosystems (Tedersoo & Nara 2010; Tedersoo *et al.* 2010). These distribution patterns in fungi are consistent with the evolutionary history of EcM host plants. *Pinaceae*, dated to the Late Jurassic, represents the oldest known EcM plant taxon and its distribution has been restricted to the boreal to subtropical ecosystems of the Northern Hemisphere (LePage 2003). In contrast, tropical hosts in the families *Dipterocarpaceae*, *Fabaceae*, *Polygonaceae* and others are thought to have originated more recently in the Late Cretaceous or Paleogene (Bell *et al.* 2010). These data suggest that EcM fungi may have occurred over a larger area and for a much longer time period in the Northern temperate zones than in the tropics. At present, EcM host plants dominate vast areas in subarctic to temperate and Mediterranean ecosystems but are patchily distributed in tropical Africa and South America (Allen *et al.* 1995). Such fragmented habitat islands may be subject to impoverishment of species richness (Peay *et al.* 2010) and contribute to lower alpha diversity of EcM fungi in tropical ecosystems. Information about the relative abundance of EcM vegetation in tropical ecosystems throughout the geological history is limited, but it may be critical for understanding long-term evolutionary processes in EcM fungi.

Conclusions

The 'universal' latitudinal gradient of diversity that characterizes richness distribution of most terrestrial and marine macro-organisms has a unimodal form in

EcM fungi. It is striking that other soil organisms such as soil bacteria (Lauber *et al.* 2009; Chu *et al.* 2010) and soil invertebrates (Wardle 2002; Maraun *et al.* 2007) also fail to conform to the 'universal' pattern. This study also points out to the patchy or lacking information on fungal communities particularly in the tropical montane and southern temperate ecosystems and the paucity of metadata on edaphic variables in published studies that limit large-scale ecological analyses of micro-organisms (Lilleskov & Parrent 2007; Lozupone & Knight 2007; Abarenkov *et al.* 2010b). Despite these shortfalls, our results provide many ecological and biogeographic hypotheses about the patterns and their underlying mechanisms in the distribution of EcM fungi. Contrasting differentiation of soils and evolutionary history of symbiosis probably play an additional role in shaping the global distribution of EcM fungi as demonstrated for other soil organisms (Wardle 2002; Benson *et al.* 2004; Mueller *et al.* 2005). In diverse microbial groups, large-scale biogeographic analyses require combining uniform sampling design, application of next-generation sequencing technique and inclusion of edaphic variables.

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L.T., K.N. and U.K. designed the research, all authors contributed unpublished data and wrote the paper and M.B., M.T. and L.T. analysed data.

Data accessibility

Raw data of geographical, climatic and sampling variables as well as assignment to lineages are given in Table S1 (Supporting information). Sequence data of case studies are deposited in INSD previously. Taxonomic and metadata annotations of DNA sequences are publicly available via the UNITE homepage (http://unite.ut.ee/).

Supporting information

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

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

Table S2. Variables included in the global models for species richness and diversity of ectomycorrhizal fungi.

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