





**MOHAMMAD BAHRAM**

Biogeography of ectomycorrhizal fungi  
across different spatial scales



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## LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following publications, which are referred in the text by their Roman numerals:

- I. **Bahram M**, Pölme S, Kõljalg U, Zarre S, Tedersoo L. 2012. Regional and local patterns of ectomycorrhizal fungal diversity and community structure along an altitudinal gradient in the Hyrcanian forests of northern Iran. *New Phytologist*, 193: 465–473.
- II. **Bahram M**, Pölme S, Kõljalg U, Tedersoo L. 2011. A single European aspen (*Populus tremula*) tree individual may potentially harbour dozens of *Cenococcum geophilum* ITS genotypes and hundreds of species of ectomycorrhizal fungi. *FEMS Microbiology Ecology*, 75: 313–320.
- III. Tedersoo L, **Bahram M**, Jairus T, Bechem E, Chinoya S, Mpumba R, Leal M, Randrianjohany E, Razafimandimbison S, Sadam A, Naadel T, Kõljalg U. 2011. Spatial structure and the effects of host and soil environments on communities of ectomycorrhizal fungi in wooded savannas and rain forests of Continental Africa and Madagascar. *Molecular Ecology*, 20: 3071–3080.
- IV. Tedersoo L, Sadam A, Zambrano M, Valencia R, **Bahram M**. 2010. Low diversity and high host preference of ectomycorrhizal fungi in Western Amazonia, a neotropical biodiversity hotspot. *ISME Journal*, 3: 465–471.
- V. Tedersoo L, **Bahram M**, Toots M, Diédhiou AG, Henkel TW, Kjølner R, Morris MH, Nara K, Nouhra E, Peay KG, Pölme S, Ryberg M, Smith ME, Kõljalg U. 2012. Towards global patterns in the diversity and community structure of ectomycorrhizal fungi. *Molecular Ecology*: in press. doi: 10.1111/j.1365–294X.2012.05602.x
- VI. **Bahram M**, Kõljalg U, Courty PE, Diédhiou AG, Kjølner R, Pölme S, Ryberg M, Veldre V, Tedersoo L. Spatial turnover in species and phylogenetic composition of ectomycorrhizal fungal communities in different ecosystems along a latitudinal gradient. Unpublished.

Author's contribution to each publication

	I	II	III	IV	V	VI
Idea and design	+	+	–	–	–	+
Sampling	+	+	–	–	+	+
Molecular analysis	+	+	+	–	+	+
Data analysis	+	+	+	+	+	+
Writing	+	+	+	+	+	+

## INTRODUCTION

Biological diversity enhances resilience, stability, productivity and ultimately functioning of ecosystems (Loreau et al. 2002). Understanding diversity patterns and structure of biological communities and the underlying processes is the cornerstone of ecology and biogeography. The processes can include both intrinsic dispersal-related traits (neutral processes) and extrinsic environmental factors (niche-based processes). The interaction of these processes differentially determines the operating factors at various spatial scales and consequently causes the scale dependence of diversity patterns (Wittaker et al. 2001; Cottenie 2005). At local scales, the balance between species formation, predation, competitive exclusion and adaptation structures the biological communities, whereas history, biogeography, range expansion, climate, evolution and extinction play important roles in structuring metacommunities at larger (i.e. regional to global) scales (Ricklefs 1987). Therefore, the underlying processes and the relative role of spatial factors differ over various geographical scales (Wiens 1989; Levin 1992). The importance of spatial scale in ecological studies is increasingly recognized (e.g. Chase & Leibold 2002; Diniz-Filho et al. 2002; Borcard et al. 2004; Rahbek 2005).

Latitudinal and altitudinal gradients are two well-known systems in ecological and biogeographical studies. These provide complementary options for understanding the relative effects of historical and contemporary (i.e. climatic, edaphic and biotic) factors on biodiversity (Rahbek 2005). Large-scale studies of biodiversity along these gradients can also provide insights into the response of communities to future climate change (Parmesan & Yohe, 2003; Harley 2011; Nogués-Bravo & Rahbek 2011). Along with elevation, temperature changes abruptly and therefore montane ecosystems provide a suitable model to address the latitudinal pattern of diversity, removing the effect of historical factors. Ecological study of biodiversity of macroorganisms along altitudinal/latitudinal gradients dates back to Alexander Von Humboldt (1807), and many studies subsequently have examined diversity patterns of macroorganisms, demonstrating that diversity generally peaks at lower latitude and altitude (Lomolino et al. 2006). In contrast, due to their minute size and limited methodology in the past, microorganisms have only recently received attention by ecologists and biogeographers because of the recent advances in molecular identification methods (Fierer & Lennon 2011). For a long time it was a common assumption that in microorganisms “everything is everywhere, but, the environment selects” (cf. Baas Becking 1934), indicating the cosmopolitan distribution of microbes. Although some exceptional groups may follow this rule and distribute randomly (e.g. root endophytes, Quéloz et al. 2011; soil Bacteria, Chu et al. 2010), there is a strong evidence that most microbial communities are spatially structured (Green et al. 2004) and show biogeographic patterns (Martiny et al. 2006). To address diversity patterns of microorganisms, a growing

number of studies have been performed along altitudinal and latitudinal gradients (e.g. Bryant et al. 2008; Amend et al. 2010; Fierer et al. 2011).

Mycorrhiza (In Greek. ‘*mykes*’, fungus; ‘*rhiza*’, root) is one of the main belowground components of terrestrial ecosystems, which is a mutualistic association that occurs between a fungus and plant roots. In a mycorrhizal association, the plant partner provides carbon for its fungal partner and receives dissolved nutrients in return (Smith & Read 2008). Ectomycorrhiza is a type of mycorrhiza, where fungal hyphae grow inbetween root epidermal/cortical cells (termed as a ‘Hartig net’) and form a dense hyphal sheath around the root tip (termed as a ‘mantle’). Traditionally, studies on ectomycorrhizal (EcM) fungi relied on their aboveground sexual structures – fruit-bodies – that do not reflect fungal communities belowground (e.g. Gardes & Bruns 1996; Dahlberg et al. 1997; Horton & Bruns 2001) because some groups do not fruit (e.g. *Cenococcum*) or form conspicuous fruit-bodies (e.g. Thelephorales, Sebaciniales). The early belowground investigation of EcM fungi was based on morphology (morphotyping; based on colour, texture, and shape of the root tips) and anatomy (anatomotyping; based on anatomy on mantel layers and emanating hyphae) of EcM root tips for species identification (Agerer 1987–2002). Aside from the potential of neglecting morphologically similar species, this method was very time consuming. The combination of morphotyping and molecular analysis of root tips presents an advanced methodology of community studies (Tedersoo et al. 2003). Molecular techniques for species-level identification mainly rely on internal transcribed spacer (ITS) region of nuclear ribosomal DNA (Gardes & Bruns 1996; Kõljalg et al. 2005).

Studies on diversity and community composition of EcM fungi have bloomed in the past decade due to the methodological advances (Taylor 2008). Recent introduction of new generation sequencing methods and high-throughput identification in fungal studies (Tedersoo et al. 2010a) has further advanced the methodology and accelerated analysis. Most of the research which has been carried out in Europe and Northern America demonstrate that EcM fungi form diverse communities and play essential roles in many temperate ecosystems (e.g. Horton and Bruns 2001; Tedersoo et al. 2006). For a long time, the common belief was that EcM is scarce in tropics; however, recent studies have reported that ectomycorrhiza is an important mutualistic type in tropical ecosystems (Peay et al. 2010; Tedersoo & Nara 2010; Smith et al. 2011).

Similarly to other soil organisms (Ettema & Wardle 2002), EcM fungi also can be both vertically (along the vertical gradient of soil profile) or horizontally structured (Lilleskov et al. 2004). Vertical spatial distribution of EcM fungi have been addressed in several studies (e.g. Dickie et al. 2002; Tedersoo et al. 2003; Lindahl et al. 2007). These studies demonstrate that depending on substrate, EcM fungi can occupy different niches along the depth gradient. In contrast to vertical distribution, only a few attempts have been made to examine horizontal spatial distribution (further referred to simply as ‘spatial distribution’) of EcM fungi. Lilleskov et al. (2004) examined the spatial structure of

EcM fungal communities in eight Northern American temperate forests and found that fungal communities are spatially autocorrelated at distance of  $< 3$  m. Spatial autocorrelation of EcM fungi can be ascribed with spatially structured environmental factors (e.g. soil nutrients; Toljander et al. 2006), species competition (Kennedy 2010), aggregation of offspring around parents (resulting from spore production or vegetative growth of mycelia), patchy occurrence of EcM fungi, soil microsites, competition, and distribution of host tree species. In addition, dispersal limitation of EcM fungi (Peay et al. 2007; Bahram et al. 2012) can also play important role in their species aggregation and spatial structure. Therefore, one can predict that spatial structure of EcM fungal communities can vary in different ecosystems. Most of the community studies have been performed at the local scale (but see Lilleskov et al. 2002; Cox et al. 2010; Ostonen et al. 2011) in temperate areas; therefore, little is known about the spatial structure of EcM fungi across different ecosystems and geographical scales.

This thesis addresses spatial structure of EcM fungal diversity and community composition from a local scale (one individual tree; II) to a global scale (V), and for the first time provides information on the belowground EcM fungal diversity in the Hyrcanian forests of Iran (I), Yasuni National Park (IV), wooded savannas and rain forests of Continental Africa and Madagascar (III). Besides, it sheds light on the altitudinal and latitudinal diversity patterns of EcM fungi (I, V, respectively).

In my thesis, the following alternative hypotheses were postulated:

- Species richness of EcM fungi declines towards higher altitude (I) and latitude (V) similar to the general diversity patterns of macroorganisms.
- Climate affects EcM fungal richness and community composition at regional and global scales (I, V).
- Spatial structure of EcM fungal communities is stronger in tropical forests, compared with temperate ecosystems, due to the patchy distribution of host trees and lower heterogeneity of putative determinants of EcM fungal community i.e. host, soil and climate (III, VI, VI).
- Species richness of EcM fungi of an individual tree is comparable to a forest site (II).
- Intraspecific ITS variation of *Cenococcum geophilum* is high even at the scale of an individual host tree (II).

## MATERIAL AND METHODS

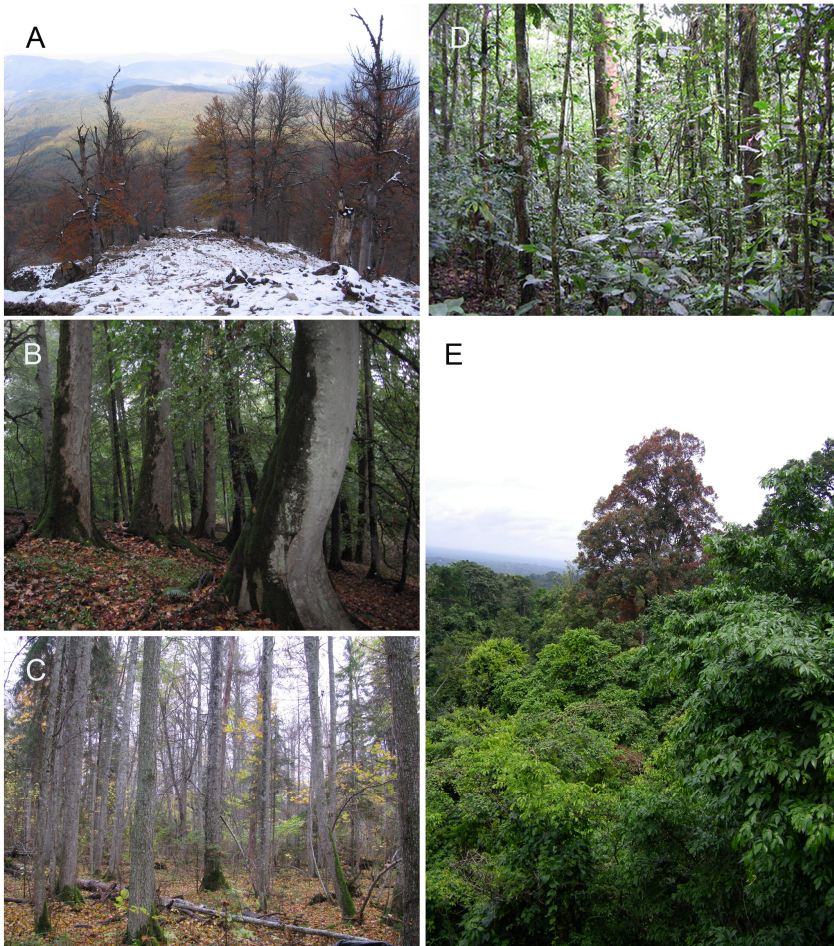
### Sampling sites and study design

Most studies were intended to test the ecological hypotheses and simultaneously document the richness of EcM fungi in poorly investigated regions. Sampling of three studies were performed in the Hyrcanian (Caspian) forests of northern Iran (I), wooded savannas and rain forests of Continental Africa and Madagascar (III) and Yasuni National Park of Ecuador (IV) (Fig.1; 2). The temperate deciduous trees such as *Fagus orientalis* Lipsky, *Carpinus betulus* L. and *Quercus castaneifolia* C.A.Mey. are the dominant plants covering the mountain slopes of the southern Caspian sea (Alborz mountain range) in northern Iran (I). In wooded savannas and rain forests of Continental Africa and Madagascar with Fabaceae and Phyllanthaceae as dominant and with some members of Dipterocarpaceae, Sarcolaenaceae or Asteropeiaceae as subdominant EcM hosts (III). Yasuni National Park, northeastern Ecuador (IV), is one of the most diverse forest sites on Earth in terms of tree species richness (including EcM hosts *Coccoloba*, 9 spp.). Depending on the ecological hypotheses and local field conditions, sampling design differed in studies I–IV (see each article for details). In addition to the poorly known regions, one study was performed in a hemiboreal mixed forest in Järvelja, southeastern Estonia (II). In this site, sampling was performed around an isolated individual aspen (*Populus tremula* (L.) Karst.) tree. The sampling design was spatially explicit and the samples were taken regularly from junctions of a grid with 2 m intervals. For metastudies (V, VI), datasets of suitable published or unpublished studies were used.



**Fig. 1.** Location map of original sampling areas represented by symbols: triangles (I), square (II), circles (III), diamond (IV).

In studies I–IV, soil samples (15 × 15 cm to 10 cm depth) were processed and prepared for molecular analysis within 48 hours at maximum. Roots were washed in tap water to remove soil and debris. Root tips were separated into morphotypes based on the morphological features of root tips, including the color, shape and presence of cystidia, extraradical hyphae and rhizomorphs. From each unique morphotype, at least two root tips per sample were transferred to CTAB extraction solution (1% cetyltrimethylammonium bromide, 100 mM Tris-HCl (pH 8.0), 1.4 M NaCl, 20 mM ethylenediaminetetraacetic acid) for molecular analysis.



**Fig. 2.** Representative views of the study sites: A) an altitudinal transect, view from the top of mountain (I); B) a *Fagus Orientalis* forest (I); C) a boreal mixed forest (the *Populus Tremula* tree is in the center) (II); D) a tropical rain forest, the Yasuni National Park (IV); and E) a tropical rain forest, Cameroon (III).

## Molecular analysis (I–IV)

One or more healthy root tips from each morphotype per sample were subjected to DNA extraction using a Qiagen DNeasy 96 Plant Kit (Qiagen, Crawley, West Sussex, UK) as recommended by the manufacturer. The primer ITSOF-T (5'-cttggtcatttagaggaagtaa-3'), in combination with reverse primers LB-W (5'-cttttcattcttcctcacgg-3'), ITS4 (5'-tcctccgcttattgatatgc-3') or ITS2 (5'-gctgcgtttctcatcgatgc-3'), was used to amplify the ITS region. For low quality sequences, which were preliminarily identified as EcM, PCR was repeated using taxon-specific primers as described in Tedersoo et al. (2008) and study III. The PCR products were run on a 1% agarose gel stained with ethidium bromide by electrophoresis and visualized under UV light. PCR products were purified using Exo-Sap enzymes (Sigma, St Louis, MO). When PCR failed to yield a reliable ITS sequence, the nuclear 28S (nuLSU) rRNA gene was amplified using primers LR0R (5'-accgctgaacttaagc-3') and TW13 (5'-ggtcctgtttcaagacg-3'). Primers ITS5 (5'-ggaagtaaaagtcgtaacaagg-3'), ITS4 and ctb6 (5'-gcatatcaataagcggagg-3') were used for sequencing of ITS and nuLSU regions. Preliminary morphological host identification of roots was confirmed based on plant plastid trnL intron sequence using TrnC (5'-cgaaatcggtagacgctacg-3') and TrnD (5'-ggggatagagggacttgaac-3') as PCR primers and TrnD as a sequencing primer. PCR instructions were adopted from Tedersoo et al. (2006), including an initial 3 min at 95 C, 35 cycles of 30 sec at 95, 30 sec at 55 C and 1 min at 72 C. Using Sequencher software (Version 4.9; GeneCodes Corp., Ann Arbor, MI), raw sequences were edited, trimmed and assembled into contigs. Molecular species were separated based on 97% ITS sequence similarity threshold and identified using MegaBLAST and BLASTn searches against the International Sequence Databases (INSD: NCBI, EMBL, DDBJ) and fungal rDNA ITS sequence database (UNITE) (Abarenkov et al. 2010a) as implemented in the PlutoF workbench (Abarenkov et al. 2010b). Unique sequences were submitted to EMBL and UNITE.

## Data analysis

Species were categorized into phylogenetic lineages according to Tedersoo et al. (2010b) to determine dominant lineages (based on species richness) in different ecosystems (I, II, III, IV), to create a phylogenetic community matrix (V) and to evaluate spatial autocorrelation within these higher-level taxonomic groups (II, VI). Bray-Curtis and Euclidean similarity indices were used to generate distance matrices for community composition and environmental factors, respectively. Fisher's Exact test followed by Benjamini-Hochberg correction was used to evaluate host or habitat (topography or soil horizon) preference of the dominant fungal species (III, IV). Multivariate analysis of variance (Adonis) was used to search for main determinants of community variation among the putative factors as implemented in Vegan package of R



(Oksanen et al. 2007; R Core Development Team 2007). Community dissimilarity between plots was visualized in Global Nonmetric Multidimensional Scaling (GNMDS) graphs. Putative factors were fitted onto GNMDS graphs using the `envfit` function in `Vegan`. In addition, Mantel test was used to examine the correlations between community variation and a focal environmental variable. Partial Mantel test was used for similar reason, but this method accounts for other variables. To account for the presence of different host trees in altitudinal plots of study I, a community distance matrix for host trees was used in Mantel test (instead of dominant host as fixed categorical variable in `Adonis`). Mantel and Partial Mantel tests were performed in the `Ecodist` package (Goslee & Urban 2007) of R.

Autocorrelation of individual species, lineages and species richness was tested by determining Moran's  $I$  and correlograms as implemented in the `Ape` package (Paradis et al. 2004) of R. To account for spatial autocorrelation in community structure and species richness, Principal Coordinates of Neighbourhood Matrix (PCNM) vectors (Borcard & Legendre 2002) were created based on spatial distance matrix using `Vegan` (I, III, V, VI). This approach allows the incorporation of proxies of geographical distance as spatial explanatory variables, which represent all the scales that can be perceived by the data, in ordination and regression analyses (Borcard et al. 1992; Borcard et al. 2004). Significant PCNM vectors were forward-selected in `Packfor` package and used in regression (I) or multivariate (III, V, VI) analyses. These vectors were used in `Adonis` to determine the effect of spatial (III) and environmental factors (V) on community variation while accounting for other variables following Oksanen (2009). This approach enables control for spatial effect while testing the effect of environmental variables. The spatial autocorrelation in species richness was controlled by the use of the spatial eigenvector mapping (SEVM) method that follows the truncation process of the PCNM method. The extracted significant eigenvector was used in model selection procedure as spatial component (I). In study V, spatial autocorrelation (which its significance was determined by Likelihood Ratio tests) in richness was controlled by including a spatial component as Gaussian spatial correlation structure, which was constructed based on range parameter and nugget of variograms. The relationship between the response and each explanatory variable was visualized to determine the type of relationship, i.e. linear, unimodal, exponential and Gaussian. In different datasets, autocorrelation range and average community dissimilarity were determined based on distance-decay curves (VI). Autocorrelation range is the distance at which community variation is dependent on geographical distance. Rarefied species accumulation curves, their  $\pm 95\%$  confidence intervals (CI), and minimum total richness estimators (ICE, Chao2 and Jackknife2) were calculated using `EstimateS` (Colwell 2006). By constructing GLS models, model comparisons and model selections were performed to test main determinants of species richness (I, V); best models were chosen based on the corrected Akaike information criterion (AICs) values as implemented in the

nlme package (Pinheiro et al. 2011) of R. For study VI, dependent variables used in model selection included species richness, autocorrelation range, average community dissimilarity and the explained proportion of community by spatial vectors. Multicollinearity between variables was checked based on the Variance Inflation Factor (VIF) values. Variables with high VIF ( $>10$ ) and thus highly correlated variables were dropped from model selection. After model averaging, the significant variables were detected based on the averaged Beta coefficient (variables were significant when their coefficient and its 95% confidence intervals excluded zero-values).

## RESULTS AND DISCUSSION

The main findings of the studies I–VI are given in bullet points and briefly discussed and interpreted thereafter.

- **Species richness of EcM fungi declines with increasing altitude (I).** The observed pattern in EcM fungi is consistent with the general altitudinal pattern of diversity in macroorganisms (Lomolino et al. 2006). Recent studies have reported contrasting altitudinal diversity patterns for macro and microorganisms, when addressing both groups simultaneously (Bryant et al. 2008; Wang et al. 2011; Fierer et al. 2011). In addition, contrasting patterns have also been observed among microbial groups. A study on a single bacterial phylum of (Acidobacteria) revealed a declining altitudinal diversity pattern (Bryant et al. 2008), whereas another study on aquatic bacteria and diatoms reported a reverse pattern (Wang et al. 2011). On the other hand, a recent study on bacteria collected from soil and leaves demonstrated no diversity pattern with increasing altitude (Fierer et al. 2011), and another study reported a hump-shape pattern for soil bacteria (Singh et al. 2011). The latter study demonstrated that even within bacteria, diversity of different phyla show contrasting relationships with altitude. Taken together, these findings indicate that different microbes may not follow a general altitudinal trend, and various factors may interplay with climate in determining microbial diversity along altitudinal gradients (Fierer et al. 2011). This suggests that biogeographical patterns of microbes may be fundamentally different from macroorganisms (V).
- **At a global scale, EcM fungal richness does not follow the general latitudinal diversity gradient (V).** Our global study on belowground diversity of EcM fungi revealed that species richness has a hump-shaped (unimodal) relationship with temperature and latitude after accounting for other variables (i.e. sampling variables and environmental factors), and it peaks in warm temperate forests while falls in tropics, which contrasts with general latitudinal pattern of diversity in macroorganisms (Lomolino et al. 2006). **At the global scale, temperature - rather than distance from the equator – was the main determinant of EcM fungal richness.** Diversity of most organisms on the planet is generally positively correlated with temperature (Hillebrand 2004). However, our analyses revealed that EcM fungal richness has a unimodal relationship with temperature. High temperature and thereby high biological activity at fine scale in tropical soil reduce the amount of organic matter that may consequently result in the impoverishment of niches for soil microbes (Wardle 2002).
- **Climate affects diversity of EcM fungi along altitudinal gradient at the local and regional scale (I).** Diversity of EcM fungi was lower at high altitude. This indicates that low temperature at high altitudes limit recruitment of rare species, which are present at lower altitude. Alternatively, high

temperature leads to greater productivity that in turn can boost fungal diversity at lower altitudes (Druebert et al. 2009). The declining pattern can be mostly ascribed to decrease in the proportion of singletons and doubletons at high altitudes. Moreover, excluding altitude, temperature was the main determinant of species richness based on the best GLS model. This finding provides additional evidence for the significant effect of temperature on species richness of EcM fungi at the global scale (V). Nevertheless, the relationship between temperature and richness was linear at the regional scale compared to the unimodal relationship at the global scale (V). This discrepancy might result from the absence of truly tropical conditions in mountain bases of the Hyrcanian forests. Similarly to our results, Bryant et al. (2008) and Wang et al. (2011; 2012) also pointed to temperature as the main explanatory factor for observed patterns of altitudinal diversity in bacteria.

- **Host plant is the key determinant of EcM fungal community composition both at the regional and global scale. It largely determines the EcM fungal community composition even in a highly heterogeneous ecosystem (i.e. an altitudinal gradient) (I). Host family was also the main determinant of EcM fungal phylogenetic community at the global scale (V).** These results were consistent with other studies performed at local scale, which demonstrated a strong host effect in structuring fungal community (Ishida et al. 2007; Tedersoo et al. 2008; Morris et al. 2009). Plants can drive belowground communities through affecting soil nutrient concentrations (e.g. litter or exudate quality or quantity) or through their specific or preferential pathogenic/mutualistic associations (Wardle 2002). Although most EcM fungal species are capable of colonizing multiple hosts (host-generalist species), some only associate with certain host species (host-specific species; Molina et al. 1992). Majority of the known host specific fungal taxa belong to *Suillus* and *Rhizopogon*, which are restricted to the Pinaceae family. Although most EcM fungi that associate with Fagales seem to be generalist, these trees might have different effects on soil nutrients which can specialize their mutualistic partners (Toljander et al. 2006; Morris et al. 2008). We found no correlation between community variation and soil variables in study I, probably because of pooling of soil samples in each plot that may have lowered the spatial resolution.
- **Climatic variables and the underlying altitude affect community composition of EcM fungi (I).** Following host, altitude was the second main determinant of community composition along the altitudinal gradient. Altitude effect can be attributable to climatic factors that had the highest correlation with altitude among the examined factors. Temperature was most strongly correlated with the community variation at local scale and precipitation had a stronger effect at regional scale. Based on our results, most EcM fungal species were present in different altitudinal ranges; however, some had a narrow range and only were present in certain altitudes. Taken together, these results suggest that while majority of EcM fungal species

may have wide temperature optima, some have low temperature breadth. **Climatic variables had also a significant effect in structuring phylogenetic community of EcM fungi at the global scale (V).** Similarly, temperature has been determined as the main determinant of the community structure of some other groups of fungi along altitudinal gradients (soil microfungi, Widden 1987; wood decomposing fungi, Meier et al. 2010).

- **EcM fungal community structure is scale dependent (II, V, VI).** The effects of host and altitude were stronger at local than regional scale (I). At larger scale (i.e. regional, continental and global scales), fungal communities diverge due to dispersal limitation (Peay et al. 2007), and spatial factors play a stronger role, blurring the effect of other factors. **Spatial processes play a significant role in structuring species community composition at the regional scale (I) and phylogenetic community at the global scale (V).** At larger scale (continental to global scale) historical factors such as geographical distribution of host plant families and long-term co-evolution between hosts and EcM fungi (Hoeksema 2010) may determine the EcM fungal community (Pritsch et al. 2010; Tedersoo et al. 2010b).
- **Diversity of EcM fungi is relatively low in one of the most biologically diverse sites on Earth, the Yasuni National Park (IV).** In spite of high richness of plant species including EcM host trees, species richness of fungi was relatively low in the Yasuni National Park. Many of the fungal species of the Nyctaginaceae family had a strong genus-level host preference or specificity. In addition, the fungal community displayed a strong spatial autocorrelation. Strong spatial structure and possibly existence of large genets can increase competitive exclusion, which in turn reduces diversity (Ricklefs et al. 1987).
- **Environmental variables (host species and soil horizon) play a negligible role in structuring EcM fungal community in Afrotropical forests, owing to the strong effect of spatial factors (III).** EcM fungal community in Afrotropical forests showed a strong spatial autocorrelation, similar to that in Yasuni National Park (IV). In a recent study, Smith et al. (2011) also pointed to a strong spatial effect, rather than host effect, in a Neotropical rainforest. Lower host specificity or preference might be beneficial for host trees to associate with mycobionts in tropical ecosystems where EcM fungal diversity is relatively lower compared to temperate ecosystems.
- **Autocorrelation range of communities was significantly larger in tropical forests, compared with temperate forests (VI).** Stronger spatial autocorrelation in the tropics can result from greater dispersal limitation of mycobionts because of patchy host distribution and larger patch sizes of soil nutrients. The habitat selectivity among fungal species and isolation of suitable host and soil patches may render EcM mycobionts dispersal limited (Peay et al. 2007). The spatial autocorrelation range of fungal communities corresponds to the patchiness of soil properties, which is stronger in tropical ecosystems. Alternatively, larger autocorrelation range can partly result from

the dominance of */russula-lactarius* lineage with relatively large genets (Lilleskov et al. 2004; Riviere et al. 2006) in tropics.

- **At the global scale, the spatial turnover of EcM fungal phylogenetic communities was stronger along the latitudinal than longitudinal gradient (VI).** This result indicates that climate and biomes, which are mostly distributed along the latitudinal gradient, play a key role in spatially structuring the fungal communities. In addition, significant autocorrelation in phylogenetic community of EcM fungi at the global scale (V, VI) lends further support for the role of dispersal limitation in their phylogeographic history (Tedersoo et al. 2010b).
- **Temperature and level of disturbance are the most important determinant of spatial autocorrelation in EcM fungal communities across different ecosystems (VI).** This further supports the significant contribution of climate in spatial structuring of EcM fungi. Lower heterogeneity of putative niche-based factors on EcM fungal community composition (i.e., host, climate and soil) and perhaps stronger relative role of neutral processes may lead to greater spatial aggregation of species. In addition, the rate of spatial turnover was greater in tropical compared to temperate ecosystems, mainly due to lower host density at small scales. Taken together, our findings suggest that spatial processes may play a stronger role in tropical ecosystems, and that neutral processes, compared to habitat heterogeneity, can have greater importance in structuring tropical EcM fungal communities.
- **Based on extrapolations, a single tree individual may potentially host hundreds of EcM fungal species that is comparable to the discovered richness in the whole forest sites (II).** We found 123 species from a single *Populus tremula* tree individual, which is comparable to all hosts taken together in other studies performed at larger areas, but making a similar sampling effort (i.e. forest site: Tedersoo et al. 2006; Courty et al. 2008; Morris et al. 2009). Besides species richness, the major components of community composition were also similar to what other studies have found from multiple hosts and larger area in temperate forests (Tedersoo et al. 2006), with */tomentella-thelephora*, */cortinarius*, */inocybe*, */russula-lactarius* and */sebacina* as the most species-rich lineages and *Cenococcum geophilum* as the most common species.
- **Dozens of genetic individuals of EcM fungi may colonize a single tree (II).** *Cenococcum geophilum* is an asexual fungus that is the most common amongst EcM mycobionts in many temperate forests (Horton & Bruns 2001). Because of asexual lifestyle, multiple ITS genotypes of *C. geophilum* can be found in small sites, providing evidence for the presence of many genetic individuals (Douhan et al. 2005). The observation of multiple genets of a single albeit dominant species allows the extrapolation that a single tree may establish EcM symbiosis simultaneously with more than one thousand fungal individuals. A better understanding of intraspecific diversity can provide insights into processes underlying community structure and functional complementarity of EcM fungi (Johnson et al. 2012).

## CONCLUSIONS

The following conclusions and working hypotheses can be inferred from my thesis:

- Spatial processes play an important role in structuring community composition of EcM fungi from local to global scales (I–VI).
- Spatial autocorrelation range of EcM fungal communities at local scales can be larger than what has been reported before (III, VI). Insights into the intraspecific variations, functional traits (e.g. enzyme activity) and interactions with other soil organisms can shed more light on underlying mechanisms of spatial distribution of EcM fungi at fine scales.
- Spatial processes may play stronger role in structuring EcM fungal communities in tropical forests, compared with temperate forests.
- Ectomycorrhizal fungi do not follow the common biogeographic patterns of macroorganisms, i.e. the latitudinal gradient of diversity (V).
- Temperature and precipitation have the strongest effect on EcM fungal diversity and community composition at the regional to global scales (II, V). The effects of temperature and probably precipitation are unimodal. The negative effect of extreme climatic conditions is attributable to environmental stress that filters out more demanding species.
- Rare species of community are more vulnerable to environmental changes (I).
- High diversity of EcM fungal species and individuals associated with an individual tree indicates that mycorrhizal networks are more inclusive than previously expected (II).
- Despite many efforts in the past decade, EcM fungi in many regions are still under investigated, particularly tropical montane and southern temperate ecosystems (V).

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## SUMMARY

Biological diversity enhances resilience, stability, productivity and ultimately functioning of ecosystems. Understanding diversity patterns and the underlying processes is the main goal of ecology and biogeography. The relative roles of niche-based and neutral processes can differ over various geographical scales, which lead to the scale dependence of diversity patterns. The diversity of macroorganisms generally increases towards the equator due to larger area, higher annual temperature and humidity as well as temporally more stable climatic conditions. Similar trend of environmental variation can also be observed with decreasing altitude. Such environmental conditions result in contrasting patterns of diversity along both latitudinal and altitudinal gradients. Research in biogeography has mostly been carried out on macroorganisms, but much less is known about microorganisms. Ectomycorrhizal (EcM) fungi are one of the key microbial groups in many forest ecosystems, supplying nutrients to their host plants and contributing to nutrient cycling. In this thesis, I examined the species richness and community structure of EcM fungi across different spatial scales. The following alternative hypotheses were postulated: 1) EcM fungal diversity decreases towards the poles and higher altitude; 2) climate is the main determinant of fungal diversity at both the regional and global scales; 3) spatial structure of EcM fungal communities is more pronounced in tropical forests, mainly due to patchy distribution of host plants; and 4) an individual host tree may support a highly diverse community of EcM fungi. The main results and conclusions are the following: 1) spatial processes are important in structuring EcM fungal communities at both local, regional and global scales; 2) the range of spatial autocorrelation in fungal communities is greater than reported previously; 3) contrary to macroorganisms, EcM fungi do not follow latitudinal pattern of diversity, which could be ascribed to the poor habitat conditions and more recent evolution of host trees in tropical ecosystems; 4) both average temperature and precipitation affect EcM fungal diversity at the regional and global scales, with extreme values causing abiotic stress and thus leading to the exclusion of rarer species; and 5) a single tree individual may potentially host hundreds of EcM fungal species that is comparable to the discovered diversity across the whole forest sites, indicating that mycorrhizal networks are highly complex on the plant perspective.

## SUMMARY IN ESTONIAN

### **Ektomükoriisat moodustavate seente biogeograafia erinevates ruumiskaalades**

Suurem organismide elurikkus soodustab koosluste produktiivsust, stabiilsust ja erinevate interaktsioonide kaudu ka funktsionaalsust. Teadaolevalt kasvab makroorganismide liigirikkus ekvaatori suunas. See on suurim aladel, kus esineb palju soojust ja niiskust ning kliima on ajalooliselt võrdlemisi stabiilne. Kuna troopilised kooslused erinevad parasvöötme kooslustest ka ajaloolis-biogeograafiliselt, rakendatakse laiuskraadi elurikkuse gradiendi uurimiseks sageli kõrgusgradienti. On leitud, et prokarüootide elurikkus ei pruugi järgida makroorganismide makroökoloogilisi mustreid. Mikro- ja makroorganismide ruumiline levik ei lange kokku ka lokaalsel skaalal, kuna makroorganismid opereerivad ruumilisel skaalal, mis erineb mikroobide omast mitme suurusjärgu võrra.

Käesolevas töös vaatlen ektomükoriisat moodustavate seente liigirikkust erinevas ruumilises skaalas ja otsin nende levikumustrite põhjuseid. Ektomükoriisaseened on majanduslikult oluliste puuliikide juursümbiondid, mis varustavad oma peremeestaimi mulla toitainetega. Need seeneliigid ei suuda ilma peremeestaimeta looduslikult kasvada. Ektomükoriisaseente määramiseks juurtelt kasutatakse viimasel 15 aastal molekulaarseid meetodeid. Nende meetodite töömahukus ja varasemalt ka maksumus on siiani oluliselt raskendanud seente ja teiste mikroorganismide makroökoloogiliste mustrite uurimist.

Oma doktoritöös testisin järgmisi alternatiivseid hüpoteese: 1) ektomükoriisaseente liigirikkus kahaneb pooluste ja suuremate kõrguste suunal; 2) kliimaatilised tingimused on peamised seente liigirikkuse mõjutajad regionaalsel ja globaalsel skaalal; 3) väikeseskaalalised ruumilised mustrid on tugevamalt eristunud troopilistes kooslustes, kuna peremeestaimed on vähearvukamad; 4) ühe puuindiviidiga seotud ektomükoriisaseente liigirikkus ja liigisisene isendite hulk võib olla väga kõrge.

Doktoritöö peamised tulemused ja järeldused on järgmised: 1) ruumilistel protsessidel on tähtis roll ektomükoriisaseente koosluste struktureerimises nii lokaalsel, regionaalsel kui ka globaalsel skaalal; 2) seenekoosluste ruumiline autokorrelatsioon võib esineda üle suurema vahemaa, kui seda on varem näidatud; 3) erinevalt makroorganismidest esineb ektomükoriisaseentel unimodaalne seos laiuskraadiga, mida tõenäoliselt põhjustavad peremeestaimede (männiliste) kõrgem evolutsiooniline vanus, peremeestaimede suurem osakaal ja mullatekkeprotsesside suurem komplekssus ning aeglus parasvöötme metsades; 4) regionaalsel ja globaalsel skaalal mõjutavad ektomükoriisaseente liigirikkust aasta keskmine temperatuur ja sademete hulk. Nende ekstreemsed väärtused põhjustavad abiootilist stressi ja läbi selle koosluste vaesumist eelkõige haruldaste liikide arvel; 5) üks puuindiviid võib ektomükoriisat moodustada samaaegselt mõnesaja seeneliigi ja kümnete sama seeneliigi indiviididega. See tõendab, et taimeindiviidid on seotud mitmekesise ning komplekse mükoriisaseente võrgustikuga. Viimase teaduslik uurimine on algsuunatud.

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## **PUBLICATIONS**

# CURRICULUM VITAE

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### Publications

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### Conference Presentations

- **Bahram M**, Zarre S, Abbasi M, Asef MR, Raidl S. Macroscopic Fungi of North Iranian Forests, South of Nowshahr. The 14th National and 2nd International Conferences of Biology. 2006, Tehran, Iran.
- **Bahram M**, Zarre S, Abbasi M, Asef MR. Two Basidiomycetes new to the flora of Iran. The 17th Iranian Plant Protection Congress. 2006, Karaj, Iran.
- **Bahram M**, Põlme S, Kõljalg U, Tedersoo L. A single European aspen (*Populus tremula*) tree harbours a diverse and horizontally randomly distributed community of ectomycorrhizal fungi in a boreal mixed forest. The Biology of Fungi (9<sup>th</sup> International Mycological Congress) 1–6 August, 2010, Edinburgh, UK.
- Ostonen I, Helmisaari H, Borken W, Kukumägi M, **Bahram M**, Tedersoo L, Lindroos AJ, Nöjd P, Uri V, Merilä P, Lohmus K. Fine root adaption strategies in European spruce forests across a climate gradient. Fifth International Symposium on Physiological Processes in Roots of Woody Plants. 8–12, August, 2010, Victoria, BC, Canada.

- **Bahram M**, Põlme S, Kõljalg U, Tedersoo L. A single European aspen (*Populus tremula*) tree individual may potentially harbour dozens of *Cenococcum geophilum* ITS genotypes and hundreds of species of ectomycorrhizal fungi. Next generation insights into geosciences and ecology 12–13, May, 2011, Tartu, Estonia.

### **Honors & Achievements**

- Ranked **2nd** in **Botany** and **11th** in **Biology** among ~ 7200 participants in the National Exam for Entering M.Sc. Programs in Biological Sciences in Iran **2004**.

### **Scholarships**

- Doctoral Studies and Internationalisation Programme DoRa: Graduate student scholarship 2008–2012
- Doctoral School of Ecology and Environmental Sciences: Graduate student scholarship 2010

### **Participation in international courses and workshops**

- Analysis of high-throughput sequencing data in microbial ecology. May, 2010. Oslo University, Norway.
- Workshop on Linking Molecular Information to Environmental Sciences. 25 October, 2010. Tallinn University, Estonia.
- Web-based Management and Analyses of the Biodiversity Data. 24–26 May, 2010, Tartu University, Estonia.
- Analysis of high-throughput sequencing data in microbial ecology. 26–28 July 2010, Tartu University, Estonia.
- Genomic methods in fungal community ecology (Fesin/Nordforsk Research Networks). 30–31 July, 2010. Edinburgh, UK.
- Preparing samples for fungal community sequencing (PhD laboratory course), 23–27 May, 2011. Uppsala University, Sweden.
- Bioinformatics using Python for Biologists. 25–29 June 2012. Instituto Gulbenkian de Ciência, Oeiras, Portugal.

# CURRICULUM VITAE

## Mohammad Bahram

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**E-mail:** Bahram@ut.ee  
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**Sünniaeg:** 23. august, 1982  
**Kodakondsus:** Iraani  
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### Haridus

2000–2004 Botaanika, Teherani Ülikool, B.Sc.  
2004–2007 Taimede ökoloogia ja süstemaatika, Teherani Ülikool, M.Sc.  
2008–2012 Botaanika ja mükoloogia, Tartu Ülikool, Ph.D.

### Publikatsioonid

- Tedersoo L, Naadel T, **Bahram M**, Pritsch K, Buegger F, Kõljalg U, Põldmaa K. 2012. Enzymatic activities and stable isotope patterns of ectomycorrhizal fungi in relation to phylogeny and exploration types in an afro-tropical rain forest. **New Phytologist**, doi: 10.1111/j.1469–8137.2012.04217.x.
- **Bahram M**, Kõljalg U, Kohout P, Mirshahvaladi S, Tedersoo L. 2012. Ectomycorrhizal fungi of exotic pine plantations in relation to native host trees in Iran: evidence of host range expansion by local symbionts to distantly related host taxa. **Mycorrhiza**, DOI: 10.1007/s00572-012-0445-z.
- Tedersoo L, **Bahram M**, Toots M, Diédhiou AG, Henkel TW, Kjoller R, Morris MH, Nara K, Nouhra E, Peay KG, Põlme S, Ryberg M, Smith ME, Kõljalg U. 2012. Towards global patterns in the diversity and community structure of ectomycorrhizal fungi. **Molecular Ecology**, doi: 10.1111/j.1365-294X.2012.05602.x.
- **Bahram M**, Põlme S, Kõljalg U, Zarre S, Tedersoo L. 2012. Regional and local patterns of ectomycorrhizal fungal diversity and community structure along an altitudinal gradient in the Hyrcanian forests of northern Iran. **New Phytologist**, 193: 465–473.
- Tedersoo L, **Bahram M**, Jairus T, Bechem E, Chinoya S, Mpumba R, Leal M, Randrianjohany E, Razafimandimbison S, Sadam A, Naadel T, Kõljalg U. 2011. Spatial structure and the effects of host and soil environments on communities of ectomycorrhizal fungi in wooded savannas and rain forests

of Continental Africa and Madagascar. **Molecular Ecology**, 20: 3071–3080.

- Ostonen I, Helmisaari H, Borken W, Tedersoo L, Kukumägi M, **Bahram M**, Lindroos AJ, Nöjd P, Uri V, Merilä P, Asi E, Lohmus K. 2011. Fine root foraging strategies in Norway spruce forests across a European climate gradient. **Global change Biology**, 17: 3620–3632.
- **Bahram M**, Põlme S, Kõljalg U, Tedersoo L. 2011. A single European aspen (*Populus tremula*) tree individual may potentially harbour dozens of *Cenococcum geophilum* ITS genotypes and hundreds of species of ectomycorrhizal fungi. **FEMS Microbiology Ecology**, 75: 313–320.
- Kohout P, Šýkorová Z, **Bahram M**, Hadincová V, Albrechtová J, Tedersoo L, Vohník M. 2011. Ericaceous dwarf shrubs affect ectomycorrhizal fungal community of the invasive *Pinus strobus* and native *Pinus sylvestris* in a pot experiment. **Mycorrhiza**, 21: 401–412.
- Tedersoo L, Nilsson RH, Abarenkov K, Jairus T, Sadam A, Saar I, **Bahram M**, Bechem E, Chuyong G, Kõljalg U. 2010. 454 Pyrosequencing and Sanger sequencing of tropical mycorrhizal fungi provide similar results but reveal substantial methodological biases. **New Phytologist**, 188: 291–301.
- Tedersoo L, Sadam A, Zambrano M, Valencia R, **Bahram M**. 2010. Low diversity and high host preference of ectomycorrhizal fungi in Western Amazonia, a neotropical biodiversity hotspot. **ISME Journal**, 3: 465–471.
- **Bahram M**, Asef MR, Raidl S. 2008. *Ramaria botryoides* a new species from Gomphales for mycoflora of Iran. **Rostaniha**, 9: 127–128.
- **Bahram M**, Asef MR, Zarre S, Abbasi M, Raidl S. 2006. Addition to the knowledge of *Amanita* in Iran. **Rostaniha**, 7: 107–120.

### Konverentsiettekanded

- **Bahram M**, Zarre S, Abbasi M, Asef MR, Raidl S. Macroscopic Fungi of North Iranian Forests, South of Nowshahr. The 14th National and 2nd International Conferences of Biology. 2006, Teheran, Iraan.
- **Bahram M**, Zarre S, Abbasi M, Asef MR. Two Basidiomycetes new to the flora of Iran. The 17th Iranian Plant Protection Congress. 2006, Karaj, Iraan.
- **Bahram M**, Põlme S, Kõljalg U, Tedersoo L. A single European aspen (*Populus tremula*) tree harbours a diverse and horizontally randomly distributed community of ectomycorrhizal fungi in a boreal mixed forest. The Biology of Fungi (9<sup>th</sup> International Mycological Congress) 1–6 August, 2010, Edinburgh, Suurbritannia.
- Ostonen I, Helmisaari H, Borken W, Kukumägi M, **Bahram M**, Tedersoo L, Lindroos AJ, Nöjd P, Uri V, Merilä P, Lohmus K. Fine root adaption strategies in European spruce forests across a climate gradient. Fifth International Symposium on Physiological Processes in Roots of Woody Plants. 8–12, August, 2010, Victoria, BC, Kanada.

- **Bahram M**, Põlme S, Kõljalg U, Tedersoo L. A single European aspen (*Populus tremula*) tree individual may potentially harbour dozens of *Cenococcum geophilum* ITS genotypes and hundreds of species of ectomycorrhizal fungi. Next generation insights into geosciences and ecology 12–13, Mai, 2011, Tartu, Eesti.

### **Teaduspreemiad ja -tunnustused**

- Teine koht botaanikas ja 11. koht bioloogias ~7200 osalejaga Rahvuslikul Magistri Sisseastumiseksamil Bioloogiateadustesse Iraanis 2004 aastal.

### **Saadud uurimistoetused**

- Doktorihõppe ja rahvusvahelistumise programm DoRa: toetatud doktorandi teadustöö finantseerimiseks aastatel 2008–2012
- Ökoloogia ja keskkonnateaduste doktorikool: toetatud doktorandi teadustöö finantseerimiseks 2010 aastal

### **Erialane enesetäiendus**

- Analysis of high-throughput sequencing data in microbial ecology. Mai, 2010. Oslo Ülikool, Norra.
- Workshop on Linking Molecular Information to Environmental Sciences. 25 Oktoober, 2010. Tallinna Ülikool, Eesti.
- Web-based Management and Analyses of the Biodiversity Data. 24-26 Mai, 2010, Tartu Ülikool, Eesti.
- Analysis of high-throughput sequencing data in microbial ecology. 26–28 Juuli 2010, Tartu Ülikool, Eesti.
- Genomic methods in fungal community ecology (Fesin/Nordforsk Research Networks). 30–31 Juuli, 2010. Edinburgh, Suurbritannia.
- Preparing samples for fungal community sequencing (PhD laboratory course), 23–27 Mai, 2011. Uppsala Ülikool, Rootsi.
- Bioinformatics using Python for Biologists. 25–29 Juuni, 2012. Instituto Gulbenkian de Ciência, Oeiras, Portugal.

## DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

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