

**SERGEI PÕLME**

Biogeography and ecology of *Alnus*-  
associated ectomycorrhizal fungi –  
from regional to global scale





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REGIONAL TO GLOBAL SCALE



Department of Botany, Institute of Ecology and Earth Sciences, Faculty of Science and Technology, University of Tartu, Estonia

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Supervisors: Dr. Leho Tedersoo, University of Tartu, Estonia  
Prof. Urmas Kõljalg, University of Tartu, Estonia

Opponent: Dr. Rasmus Kjølner, University of Copenhagen, Denmark

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## I. LIST OF ORIGINAL PUBLICATIONS

This thesis is based by following papers that are referred in the text by Roman numerals:

- I. **Tedersoo L, Suvi T, Jairus T, Ostonen I, Põlme S. 2009.** Revisiting ectomycorrhizal fungi of the genus *Alnus*: differential host specificity, diversity and determinants of the fungal community. *New Phytologist* **182**: 727-735.
- II. **Pritsch K, Becerra A, Põlme S, Tedersoo L, Schloter M, Agerer R. 2010.** Description and identification of *Alnus acuminata* ectomycorrhizae from Argentinean alder stands. *Mycologia* **102**: 1263-1273.
- III. **Põlme S, Bahram M, Yamanaka T, Nara K, Dai YC, Grebenc T, Kraigher H, Toivonen M, Wang PH, Matsuda Y, Naadel T, Kennedy G. P, Kõljalg U, Tedersoo L. 2013.** Biogeography of ectomycorrhizal fungi associated with alders (*Alnus* spp.) in relation to biotic and abiotic variables at the global scale. *New Phytologist* (Accepted).

### Authors contribution to each publication

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

## 2. INTRODUCTION

Ecological and biogeographical processes drive the structure and diversity of natural communities. A range of factors, including both abiotic and biotic variables, shape the distribution of organisms through their inherent ecological tolerances and differential competitive abilities. Micro- and macroorganisms are often involved in symbiotic associations that may constrain the distribution of one or both of the partners. Due to methodological restrictions, microbial biogeography has long relied on theoretical arguments over empirical data. Rapid developments of molecular tools in the recent decades have, however, enabled us to shed light in microbial biogeography and diversity at the global scale. Accumulating evidence suggests that microbes do exhibit biogeographic patterns, but these do not necessary coincide with the patterns observed in macroorganisms (patterns such as latitudinal or altitudinal gradient in diversity; Bryant *et al.*, 2008; Fierer *et al.*, 2011, Quélez *et al.*, 2011; Bahram *et al.*, 2012). Furthermore, microbial divisions and kingdoms strongly differ in their ecology and dispersal and could be subject to different ecological factors.

Mycorrhizal fungi are widespread soil-inhabiting microorganisms that display a number of mutualistic benefits from associations with most terrestrial plants (Smith & Read, 2008). Among mycorrhizal types, ectomycorrhizal (EcM) symbiosis, which appears in many ecologically and economically important trees, represents potentially one of the most prominent and ecologically crucial mutualistic associations in terrestrial habitats. It has been estimated that total EcM fungal richness could be at least 20 000 species (Rinaldi *et al.*, 2008). Current evidence suggests that species richness of EcM fungi appears to have a unimodal relationship with latitudinal gradient (Tedersoo & Nara, 2009; Tedersoo *et al.*, 2012) and it declines along the altitudinal gradient (Bahram *et al.*, 2012). The first of these patterns is different from the widely observed pattern of greater species richness in tropical rather than temperate zones (Hillebrand, 2004). Similarly to macroorganisms, both of these diversity gradients were largely ascribed to climatic variables, particularly the mean annual temperature and precipitation. The unimodal relationship between EcM fungal richness and latitudinal gradient could be partly ascribed to temperate origin of EcM— the distribution of many EcM fungal lineages is restricted to the temperate ecosystems, which is consistent with the evolutionary history of host plants (Tedersoo & Nara, 2009; Tedersoo *et al.*, 2010; Tedersoo *et al.*, 2012). For example, the origin of the oldest known ectomycorrhizal plant family, Pinaceae, is temperate (Hibbett & Matheny, 2009). In addition to evolutionary history, high biological activity in tropical soil reduces the amount of organic matter that may result the impoverishment of niches for soil microorganisms, potentially reducing EcM fungal diversity (Wardle, 2002).

The EcM community structure is affected by a number of biotic and abiotic factors such as climate (O'Dell *et al.*, 1999), successional stage (Nara *et al.*, 2003), interspecific interactions of EcM (Koide *et al.*, 2005), edaphic factors (Aponte *et al.*, 2010) and dispersal limitation at various scales (Peay *et al.*,

2007; Peay *et al.*, 2010). Studies examining autocorrelation at local scales have demonstrated that most of the EcM taxa show patchiness up to 3 meters (Lilleskov *et al.*, 2006; Bahram *et al.*, 2010). Host species identity has also been increasingly shown to influence the structure and richness of EcM fungal assemblages at a range of taxonomic levels, as large proportion of EcM fungi exhibit host preference (Ishida *et al.*, 2007; Morris *et al.*, 2008; Tedersoo *et al.*, 2008; Bahram *et al.*, 2012). However, it often remains unknown whether the host effect is related to phylogenetic distance among them or driven by random processes independent of evolutionary links, i.e. the effect of a species *per se*. For example effects of host tree on EcM communities may be mediated by indirect factors such as differences in leaf litter, carbon production or modification of soil properties (Conn & Dighton, 2000; Dickie *et al.*, 2006; Aponte *et al.*, 2010). Such taxonomic sampling effect is ubiquitous in ecology and largely accounts for increase in biodiversity and function of soil animals and fungi with raising richness of host or substrate (Cardinale *et al.*, 2006). *Alnus* and its mycobionts could serve as a suitable model system to address host effect.

Much of the early work about host effects on EcM assemblages focused on the genus *Alnus* (Molina, 1979; Molina, 1981). EcM fungal communities of other boreal and temperate ecosystems are more diverse compared to *Alnus*, which associates with greater proportion of host specific fungi (Kennedy & Hill, 2010). Around 50–60 species of EcM fungi are documented as ectomycorrhizal symbionts of *Alnus* world-wide (Pritsch *et al.*, 1997; Kennedy & Hill, 2010; Rochet *et al.*, 2011) and at least the basidiomycetes are strongly specific to their host tree genus (Molina *et al.*, 1992; but see Kennedy *et al.*, 2011). Based on a representative collection of fruit-body specimens, Rochet *et al.* (2011) argued that a few EcM fungal MOTUs (molecular operational taxonomic unit) partition hosts at the subgenus level in France. Hereafter the EcM fungal MOTUs are treated as species level taxa. While most of the *Alnus*-associated fungal MOTUs have been recorded only once, a few of the most common species are distributed both in Europe and North and South America (Becerra *et al.*, 2005; Kennedy & Hill, 2010; Kennedy *et al.*, 2011). Together with EcM fungi, *Alnus* forms tetrapartite association involving arbuscular mycorrhizal fungi (AM) and actinorrhizal bacteria. However, infection of AM is usually scant in mature trees (S. Pöhlme *et al.*, unpublished) and EcM fungi are thought to play a major role in scavenging soil nutrients (Chatarpaul *et al.*, 1989; Yamanaka *et al.*, 2003). For *Alnus*, both fungal and actinobacterial root symbionts are obligatory and beneficial for obtaining atmospheric nitrogen and soil mineral nutrients, respectively (Yamanaka *et al.*, 2003; Benson & Dawson, 2007). Although *Frankia* actinobacteria are always present in healthy *Alnus* stands, actinorrhizal symbiosis is facultative for the actinobacteria that are ubiquitous free-living soil organisms (Benson & Dawson, 2007; Chaia *et al.*, 2010).

First known fossil records of *Alnus* dates back to late Tertiary (Chen & Li, 2004) and origin of genus is considered to be East Asia where the highest level



of endemism occurs (Navarro *et al.*, 2003). Donoghue and Smith (2004) compared continental disjunction patterns of major plant clades and concluded that Beringia has been primary path between Old and New world. Fossil records support the hypothesis that *Alnus* has spread from Eurasia multiple times using both the Beringian and North Atlantic land bridges (Furlow, 1979). Today, *Alnus* comprises approximately 28–44 species that are widely distributed in the boreal and temperate zone of the Northern hemisphere and extends rapidly further south along with the Andes in South America (Chen & Li, 2004). Such wide geographical range of host-symbiont association could potentially provide a good model system for addressing biogeography, co-evolution and host specificity of microbial taxa (Yamanaka *et al.*, 2003; Anderson *et al.*, 2009; Pokharel *et al.*, 2011; Rochet *et al.*, 2011).

## 2.1. Aims and hypothesis

In this thesis, I focus on *Alnus*-associated ectomycorrhizal fungi because of their manageable richness, wide geographical distribution and similar habitat in wet soils. This thesis aims to disentangle the relative effects of ecological and climatic factors on the community structure and species richness of *Alnus*-associated EcM fungi at the regional and global scale. The following hypotheses were postulated:

- 1) since *Alnus* mycota seems to be distinct in broad geographical area despite environmental and spatial variation, we hypothesized that *Alnus* species and their phylogenetic relationships account for the strongest predictor of EcM fungal community composition at the intrageneric level at the global scale (**III**);
- 2) based on results of global metastudy (Tedersoo *et al.*, 2012), we hypothesized that *Alnus* EcM fungal species richness is largely determined by mean annual temperature and precipitation at the global scale (**III**);
- 3) since edaphic variables have crucial importance in microbial ecology we hypothesized that at regional scale, soil conditions, particularly pH and limiting phosphorus, drive the EcM community structure and species richness rather than geographical and genetic variables (**I**);
- 4) global biogeography of *Alnus* EcM communities reflects ancient migration routes of host (**III**).

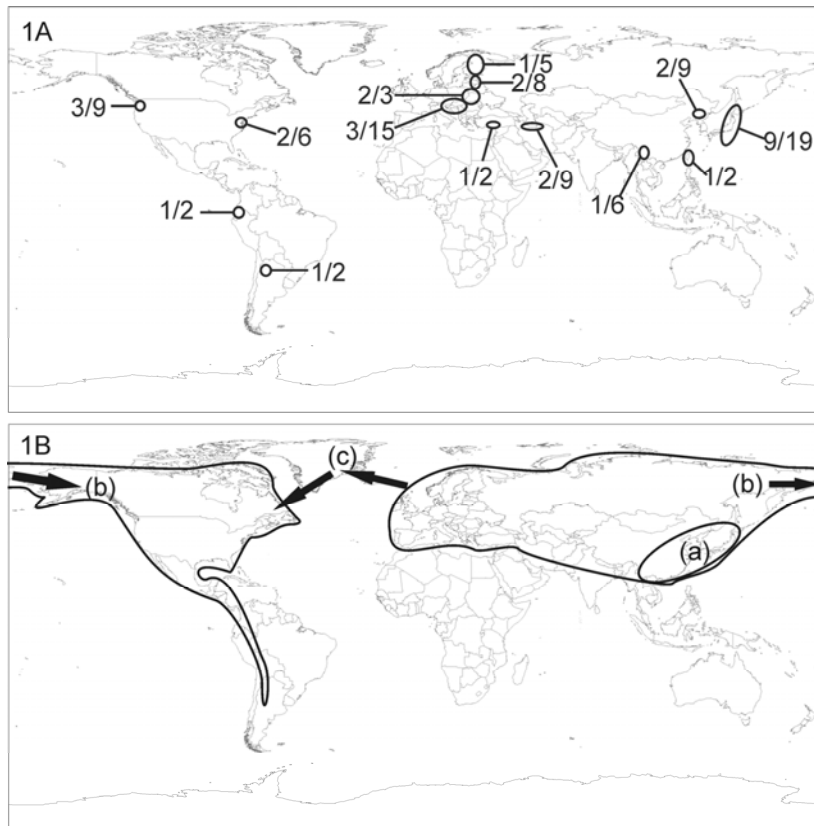
In addition, our aims were to

- 6) describe the morphological and anatomical features of EcM types in poorly investigated Argentinean *Alnus* forests (**II**);
- 7) investigate EcM mycota of Estonian *Alnus* communities (**I**).

### 3. MATERIAL AND METHODS

#### 3.1. Sampling design

Study sites in *Alnus* habitats were arbitrary selected to meet certain criteria of each study. Each study site harbored at least six host trees situated at minimum 10 meters apart to secure statistical independence between individual samples (Lilleskov *et al.*, 2006). From around each individual tree, one soil core (15\*15 cm to 10 cm depth) including *Alnus* roots were collected with a spade or a sharp knife. In studies **I** and **II**, study sites were larger and more than six soil cores per plot were sampled (see details from particular articles). In total we sampled 97 study sites of *Alnus* habitats (Fig. 1) from all continents where *Alnus* is distributed, except Africa where a single species (*A. glutinosa*) inhabits a narrow area in Northwest part of continent. Out of ca. 28–44 valid species our sampling covered 22 *Alnus* species from all three subgenera — *Alnobetula*, *Clethropsis* and *Alnus* (Navarro *et al.*, 2003).



**Figure 1.** 1A) map of study sites indicating number of host species/number of sites studied in the region; 1B) approximate *Alnus* distribution in the present day; a) hypothetical origin of the genus; b) possible migration route via Bering land bridge; c) possible migration route via North Atlantic land bridge.

Soil samples including *Alnus* roots were stored in the plastic bags until processed within 48 hours after collection. Tree roots were separated from soil and carefully cleaned under tap water. Ectomycorrhizal morphotypes were distinguished under stereomicroscope based on colour and roughness of mantle, presence of emanating hyphae and rhizomorphs (Fig. 2), except for study **II** where the more specific comparative anatomical protocol of Agerer (1991) was followed. All different morphotypes from each study site were stored in CTAB buffer (1% cetyltrimethylammonium bromide, 100 mM Tris-HCL (pH 8.0), 1.4 M NaCl, 20 mM ethylenediaminetetraacetic acid) and subjected to further molecular analyses. In order to analyse soil properties at each site, ca 50 g of rhizosphere soil was pooled from the six soil core samples (**I**, **III**). Concentrations of total soil nitrogen (N), exchangeable phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg) and soil pH were measured. In addition to soil properties we evaluated host age at each site, using available data of habitats or advice of local experts. Geographical coordinates and altitude were recorded using a GPS Garmin 60CSx (Garmin International Inc., Olathe, KS, USA).

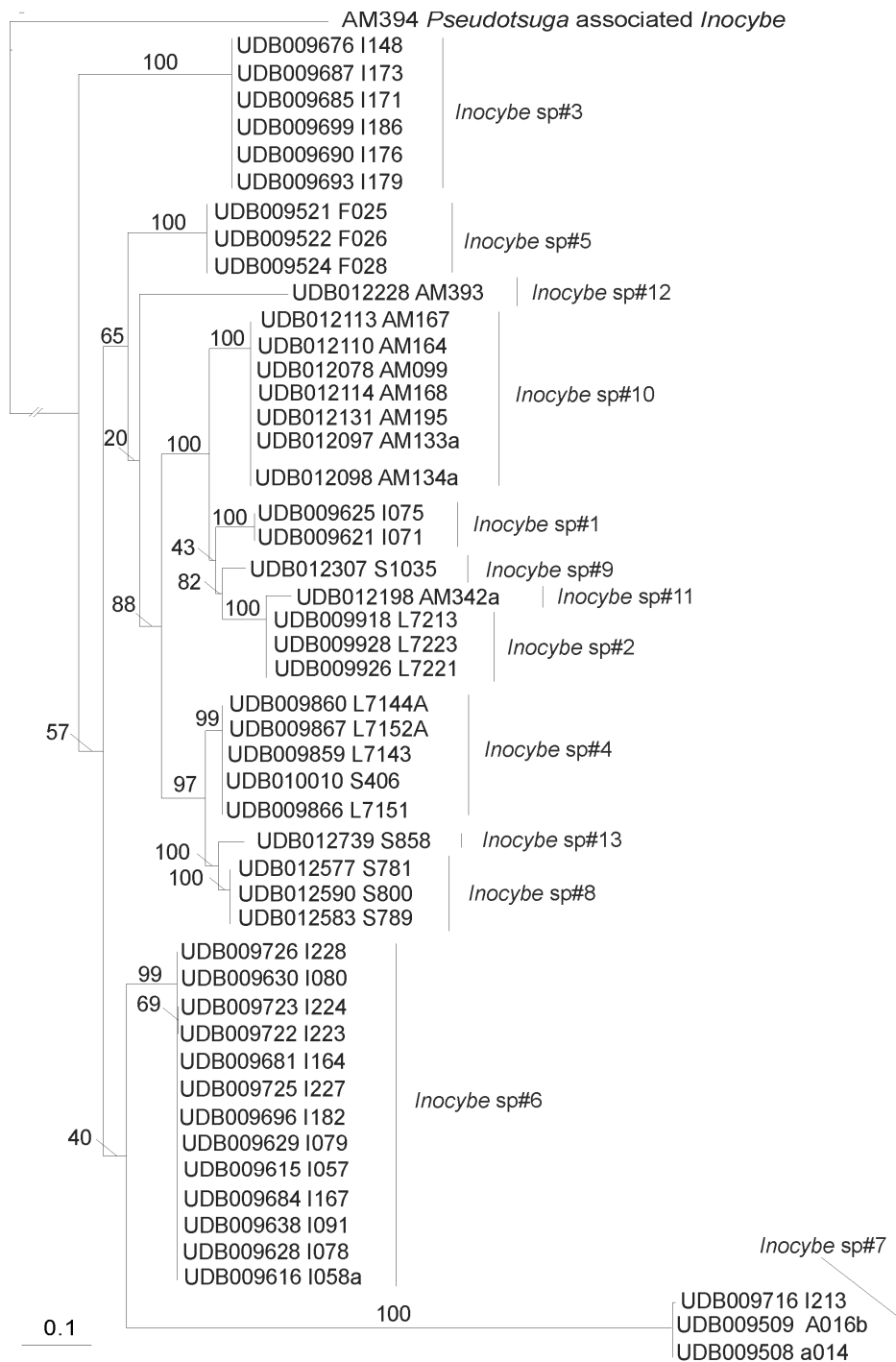


**Figure 2.** Selection of ectomycorrhizal root tips associated with *Alnus glutinosa*: a) *Cortinarius alnetorum*; b) *Inocybe* sp. (white); c) *Tomentella aff. ellisii*; d) *Lactarius* sp.

## 3.2. Molecular analysis

At least one mycorrhizal root tip from each morphotype per soil core was subjected to DNA extraction. Fungal genomic DNA was extracted using QIAGEN DNeasy 96 Plant Kit for study **I** and **III**, or QIAGEN DNeasy Plant Mini kit for study **II** following the manufacturer's instructions in both cases. Fungal rDNA Internal Transcribed Spacer (ITS) region was amplified with a forward primer ITSOF-T (5'- acttggtcatttagaggaagt -3') in combination with reverse primers LB-W (5'- ctttcatctttccctcacgg -3') or TW13 (5'- ggtccgtgtttcaagacg -3') or primers ITS1F (5'- ctgggtcatttagaggaagta-3') and ITS4B (5'- caggagactgtacacgggtccag-3') (Gardes & Burns, 1993) in study **II**. Detailed PCR protocols are described in particular articles. Primers TrnC (5'- cgaaatcggtagacgctacg -3') and TrnD (5'- ggggatagagggacttgaac -3') were used to amplify plant plastid trnL region from mycorrhizas in study **I** and **III**, in order to confirm host identity of rare fungal species (occurring once or twice). PCR products were separated by electrophoresis through a 1.5% agarose gel in 0.5 × TBE buffer (45 mM Tris Base, 45 mM Boric Acid, 1 mM EDTA (pH 8.0)), visualized under UV light and purified using Exo-Sap enzymes (Sigma, St. Louis, MO, USA) in **I** and **III**, or a QIAquick PCR purification kit (QIAGEN, Hilden, Germany) in study **II**.

Sequencing of fungal DNA was performed with primers ITS5 (5'-ggaagtaaaagtcgtaacaagg -3') and ITS4 (5'- tcctccgcttattgatatgc -3') in **I** and **III** or ITS1F and ITS4B (**II**). In studies **I** and **III**, sequences were assembled, checked, trimmed and manually corrected using Sequencher 4.10.1 software (GeneCodes Corp., Ann Arbor, MI, USA). Sequences were confirmed to belong to EcM lineages (cf. Tedersoo *et al.*, 2010) or *Alnus* host trees by the use of blastN searches against the International Sequence Databases (INSD) or UNITE (Abarenkov *et al.*, 2010). In study **III**, for each fungal lineage the ITS sequence of suitable outgroup taxa was downloaded from INSD and aligned automatically using MAFFT 6 (Kato & Toh, 2008). In study **II**, the alignments were performed with ClustalW (<http://www.ebi.ac.uk/clustalw/>). In study **I**, 97% ITS region identity was used as a barcoding threshold except in the genus *Alnicola*, where molecular species were identified based on a neighbour-joining tree comprising both the generated root tip and previously deposited vouchered fruit-body sequences downloaded from the INSD. In study **III**, Maximum Likelihood (ML) and fast bootstrap analyses were performed applying default settings in RAxML (Stamatakis *et al.*, 2008) as implemented in the Cypres web portal in order to create phylograms of all *Alnus*-associated fungal genera. These phylograms were used to distinguish fungal MOTUs based on combination of branch length and bootstrap support values (Fig. 3). In study **II**, a Neighbour joining analysis was performed in 4.0d81 PAUP (Swofford, 2002), to demonstrate the phylogenetic affinities of *Alnus*-associating *Tomentella* spp.



**Figure 3.** Delimitation of *Inocybe* species based on ITS phylogram.

### 3.3. Data analyses

MOTU occurrence data of soil core samples in each study site were pooled and each site was treated as a single sampling unit. Bray-Curtis dissimilarity metric was used to calculate community distance matrices (III). All soil nutrient concentrations were logarithm-transformed prior to analyses (I, III). In addition, EcM colonization and soil nutrient proportions were arcsine-square-root transformed and species richness was square-root-transformed (I).

Estimates of the mean annual temperature and precipitation were retrieved from a high-resolution database of Earth's surface climate (Hijmans *et al.*, 2005) using the software ArcGIS 9.3 (ESRI, Redlands, CA, USA). The effect of geographical and phylogenetic distances derived from geographical distance matrix and host phylogeny respectively, were taken into account using Principal Coordinates of Neighbour Matrices (PCNM) — eigenvectors that are used to transform distances to rectangular data that suitable for constrained ordination or regression (Borcard & Legendre, 2002). Significant PCNM vectors ( $\alpha=0.05$ ) were forward-selected in the Packfor package of R (Dray *et al.*, 2007) and used in the multivariate analyses (III).

#### 3.3.1. Community structure

To address the relative importance of climatic, edaphic, spatial and biological factors on community structure of EcM fungi as based on the frequency of MOTUs in study III, we used a permutational multivariate analysis of variance as implemented in the Adonis routine of the Vegan package of R (Oksanen *et al.*, 2007). Adonis is a nonparametric modification of multivariate ANOVA. Adonis enables to include multiple factors, covariates and their interactions in the model. Statistical significance was tested against 999 null permutations (III). In study I, the main variables accounting for changes in the EcM fungal community structure were tested for significance implementing the computer program DISTLM forward 1.3 (McArdle & Anderson, 2001) using 9999 permutations. DISTLM forward does a multivariate multiple regression based on forward selection of predictor variables, either individually or in sets, with tests by permutation. All individual variables were tested (i) separately or (ii) grouped by site, soil, host and micro-biotope before the analysis.

#### 3.3.2. Species richness

In study III, the effects of edaphic factors and climate on species richness of EcM fungi were addressed by use of the Generalized Least Squares analysis (GLS) as implemented in the nlme package of R 2.12.1 (Pinheiro *et al.*, 2008). In study I, the effects of site, host species, micro-biotope and soil nutrient variables on species richness per sample (i.e. species density) and EcM

colonization were studied using a mixed ANOVA with plot as a random factor nested within site and site nested within host species.

### **3.3.3. Biogeography**

In order to evaluate similarity of fungal communities between biogeographic regions (III), statistical support of similarity in the area cladograms was tested in the Pvcust package of R (Suzuki & Shimodaira, 2006). Pvcust calculates probability values (*p*-values) for each cluster using bootstrap resampling techniques with 1000 repetitions.

## 4. RESULTS AND DISCUSSION

Phylogenetic relations among hosts accounted for strongest predictor of EcM community structure at global scale (III), while at regional scale edaphic variables, particularly soil organic matter and pH were the main determinants of community structure among two sister species (I). Ecological processes are often scale dependent (Schneider, 2001), which is also relevant in case of *Alnus* mycobiont communities. *Alnus* is considered to possess strongest host-genus specificity among EcM trees (Molina, 1981). It is suggested that host specificity is most pronounced at the level of *Alnus* subgenus, but not between sister species (Rochet *et al.*, 2011). This is supported by results of study I where redundancy analysis revealed marginal difference between *A. glutinosa* and *A. incana* EcM communities. However, when accounting for host evolutionary history as measured by multi-level phylogenetic relationships among 22 *Alnus* species at the global scale, host explains 43% of EcM community structure, being the most influential factor (III). Based on Estonian material, *Alnus* exhibits strong reciprocal specificity with the associated mycobionts especially with basidiomycetes (I), which was generally supported at the global scale (III).

Highly similar EcM morphotypes resulted in different sequences referring to cryptic radiation of closely related species (I, II, III). Host promiscuity and speciation via shifts to phylogenetically distant hosts rather than co-speciation seems to be more frequent in other groups of EcM fungi (e.g. den Bakker *et al.*, 2004; Suvi *et al.*, 2010; but see Wu *et al.*, 2000). However, different *Alnus*-associated lineages are not closely related indicating frequent host shifts after the divergence of *Alnus* and *Betula* (I). The important role of host structuring mycobiont community has been increasingly shown in numerous studies (Ishida *et al.*, 2007), but according to the best of our knowledge this is the first time when intrageneric host effect, measured by multi-level phylogenetic relationships, is tested at global scale.

**Spatial structure explained roughly 10% of EcM community composition at global and regional scales (I, III).** Biological similarity typically decreases with geographical distance, known as distance decay. Distance decay has important role in ecology (Nekola & White, 2004) and is often regarded as self-evident. However, studies of ectomycorrhizal communities have controversial results – for example Queloz and colleagues (2010) demonstrated that the similarity of species assemblages of the *Phialocephala fortinii* s.l.–*Acephala applanata* species complex did not decrease with increasing geographical distance. Members of this complex are, however asexual root endophytes and their species context obscure, which may have blurred particular results. We demonstrated that in case of *Alnus* mycobionts, distance decay is evident, but by far less influential than host phylogeny (III).

Soil calcium accounted for the strongest predictor of richness of *Alnus*-associated EcM species at global scale (III) exhibiting positive effect, while soil humidity was most important at local scale (I). To best of our knowledge, study III is the first study, simultaneously accounting for edaphic variables with



unified methodology and addressing ectomycorrhizal ecology at global scale. Therefore, this unexpected outcome contrasts with the conclusions of metastudy conducted by Tedersoo and colleagues (2012), who demonstrated that global patterns of EcM species richness can be largely ascribed to mean annual temperature and precipitation. Biotic calcium availability is often a limiting factor shaping ecosystem structure and function (Beier *et al.*, 2012) as calcium deficits may have pervasive impacts at multiple scales from organisms to ecosystems (Likens *et al.*, 1998; DeHayes *et al.*, 1999; Hamburg *et al.*, 2003). The effect of liming in manipulative field studies supports our finding — calcium affected the overall fungal richness in forests of *Picea* and *Fagus* (Rineau & Garbaye, 2009). Aponte and colleagues (2010) accounted for natural calcium gradient and demonstrated that greater soil calcium concentration favours generalist EcM species over specialists. However, direct causal relationship between *Alnus*-associated EcM diversity and calcium concentration remains conjectural. Possibly, elevated levels of available soil calcium could enhance the role of EcM symbiosis in mineral nutrition of plants, which in turn broadens the niche for co-existence of more species. Arnott (1995) suggested that ubiquity of Ca-oxalate crystals in fungal hyphae may provide selective advantage to the organism. It has been shown that calcium uptake is limiting for many key functions of plants (McLaughlin & Wimmer, 1999) and improved physical condition of host plants may thereby enhance richness of EcM fungi (Swaty *et al.*, 2004). In addition, *Alnus* and its EcM fungi might have elevated requirements of soil calcium since the presumed origin of host genus is Southeast Asia (Navarro *et al.*, 2003), where limestone rich habitats are abundant. Moreover, unexpected results of study III might be influenced by specific ecological traits of *Alnus* genus. For example, *Alnus* species are absent from tropical lowland forests, which shortens the temperature gradient by ca 25%, just from the critical point above 20 °C, where EcM fungal richness has been suggested to decline (Tedersoo *et al.*, 2012). Association with actinobacteria, pioneer or riparian habitats and extreme reciprocal specificity makes *Alnus* distinct host genera, which might strongly contribute to symbiont diversity. In particular, low within site species richness may cause low resolution blurring global patterns.

While the effect of temperature was negligible, study III did confirm the negative relationship between mean annual precipitation and species richness at global scale (Tedersoo *et al.*, 2012), whereas plot humidity was most important determinant of richness at regional scale (I). For example, dry sites harboured three times more singletons than waterlogged sites at regional scale (I). It is suggested that anaerobic conditions in water saturated soils may cause low oxygen stress and/or competition among functional guilds of soil microbes (Tedersoo *et al.*, 2012). Since enhanced water uptake is regarded as one of the main benefits for host plant from EcM (Marschner & Dell, 1994) with increased drought tolerance (Parke *et al.*, 1983), water saturated soils may also reduce mycorrhizal dependence of host plants, potentially reducing EcM diversity and biomass.

The total richness of 146 species found worldwide (I, II, III) is substantially higher than previous records from *Alnus* EcM studies and can be ascribed to greater sampling effort in terms of both geographical area and number of host species. In addition to dominant fungal species that were relatively widespread and abundant across most of study sites and host species, our data indicates numerous rare species found only once or twice that had restricted geographical range and host associations. This could be partly matter of sampling intensity as for many taxa, especially microbes, asymptote may never be reached (Gotelli *et al.*, 2001). However there are studies that demonstrate that even severely under-sampled communities are able to detect valid diversity patterns and gradients (Kuczynski *et al.*, 2010). According to extrapolation of rarefaction curve, the number of *Alnus*-associated EcM fungal species is substantially greater and certain isolated locations or rare host species may harbour several potentially endemic taxa (Rochet *et al.*, 2011).

All studied species of *Alnus* seem to exhibit narrow specificity towards highly specific fungal taxa. Thus, high specificity seems to be a common phenomenon of all *Alnus* species, which distinguishes this genus from other members of the Betulaceae family. Such great, uniform specificity seems to be unique to *Alnus* among EcM plant genera. There is some evidence that the level of specificity may be quite variable among the tropical genera *Pisonia* (Nyctaginaceae; Suvi *et al.*, 2010) and *Gnetum* (Gnetaceae; Tedersoo & Pölme, 2012).

In accordance with earlier studies, *Alnus*-associated EcM fungal communities were relatively uniform at the global scale (I, II, III). Most abundant and species-rich phylogenetic lineages of EcM fungi included /tomentella-thelephora (comprising 32 MOTUs in 95% of sites), /hebeloma-alnicola (22 MOTUs in 67% of sites), /cortinarius (24 MOTUs in 52% of sites), /russula-lactarius (15 MOTUs in 43% of sites), /inocybe (13 MOTUs in 21% of sites) and /genea-humaria (6 MOTUs in 21% of sites). Despite resemblance of *Alnus*-associated EcM communities at global scale, relative abundance of fungal lineages were strongly shifted in certain regions. For example /genea-humaria was dominant lineage in Iran, but only occasionally present in other regions. In addition, the /inocybe lineage was also relatively common in Iran compared with the other regions. Similarly, sampling *Alnus* communities in Mexico mountain forests ascertained high abundance of /clavulina and /sebacina species (Kennedy *et al.*, 2011), which were rarely present *Alnus* symbionts in the rest of the study areas. Causes of these discrepancies remain unknown as community composition of other hosts in Iran and Mexico provides no evidence to the hypothesis that certain regional environmental conditions favour the abundance of particular EcM fungal lineages (Morris *et al.*, 2009; Bahram *et al.*, 2012). Moreover, it is not the case of unique host association as South America fungal communities of the same host do not resemble to Central American communities in terms of abundance of particular fungal lineages.

Remarkably, several *Alnus*-associated mycobionts that shared 100% ITS similarity occurred both in Europe, Asia and America (I, II, III), which is the

greatest natural range of EcM fungal species besides the asexual *Cenococcum geophilum* complex. Symbiont migration follows migration routes of host (Murat *et al.*, 2004) or may occur via long distance dispersal events (Moyersoen *et al.*, 2003). Considering strong reciprocal specificity characteristic to *Alnus* mycobionts, presence of the same EcM species in such large geographical distance is probably a result of host-symbiont co-migration. In specific biological interactions such as *Alnus* and its EcM fungi, competition among species and environmental filtering may be less strong than in communities that are saturated with species.

Comparison between fungal community similarities of different regions suggested that the host and mycobiont have co-migrated at different spatial and temporal scales (III). For example, the relative similarity of EcM community in Eastern Asia compared with Northwest America is consistent with the hypothesis that many temperate forest plant groups moved out of Asia to the new World mostly via Beringian land bridge during the last 30 Myr (Donoghue & Smith, 2004). Last glacial maximum depleted dramatically biota of Northern and Central Europe and most of the species survived in Southern refugia. After retraction of ice shield Northern Europe was re-colonized by the descendants of Southern refugia (Hewitt, 1999) resulting in high similarity between these regions.

Both, the wide distribution of symbiont species and biogeographic similarity between South and North Europe, and Asian regions with Northwest America provides evidence for strong co-migration between the mycobiont and host.

## 5. CONCLUSIONS

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

- Intrageneric phylogenetic relationship among *Alnus* species is the main driver of EcM community structure at the global scale, while sister species support similar fungal communities at regional scale. Cryptic radiation of EcM fungal species within the host genus seems to be more prominent compared to other host genera (I–III).
- Geographical and edaphic variables have a minor effect on *Alnus*-associated EcM fungal community compared to host identity at the global scale (III), while the complex of soil variables and geographical (site) effect drives the community composition at the local and regional scales (I).
- The positive effect of soil calcium on *Alnus*-associated EcM fungal species richness contrasts with the general unimodal relationship between EcM fungal species richness and mean annual temperature (latitude). This finding also refers to the potential importance of local predictors including edaphic variables at the global scale. However, I anticipate that this contrasting pattern may result from the peculiar ecology (wet and pioneer habitats, association with actinobacteria and narrow range of EcM fungi) of the genus *Alnus* (III).
- The mean annual precipitation has a negative effect on *Alnus*-associated EcM fungal species richness at the global scale (III). Similarly, soil humidity accounts for the strongest predictor of species richness at the local scale (I).
- Although *Alnus* mycobiont communities are relatively uniform at global scale, there are certain discrepancies in particular biogeographic regions (III).
- Comparison of fungal community similarity supports the hypothesis of Beringia being the primary migration route of *Alnus* between Eurasia and America. The mycota of Northern Europe is highly similar to that of Southern Europe due to the recent origin of northern biota from southern refugia (III).

## 6. SUMMARY

Discipline of biogeography addresses distribution and abundance of organisms at various geographical scales. Traditionally, biogeographic research has focused on macroorganisms due to their size and straightforward species delimitation. Therefore, ecological patterns of macroorganisms are well documented, while relevant microbial data is controversial and give rise to wide debates. Microbial biogeography patterns do not necessary coincide with patterns observed in macroorganisms. Moreover, microbial taxa and ecological guilds could be subject to different ecological factors.

Ectomycorrhizal (EcM) fungi that form mutualistic relationships with many ecologically and economically important host trees are typically regarded as microorganisms. Current metadata suggests that host identity has a key role in fungal community structure. In contrast to most macroorganisms, EcM fungal species richness exhibits unimodal relationship with latitude, which is largely ascribed to favourable climate in temperate regions as well as the evolutionary origin of major host taxa. However, to date there are no studies with unified methodology addressing EcM fungal ecology within a particular host genus at global scale. In this thesis, I aimed to disentangle ecology and biogeography of *Alnus*-associated EcM fungi in different spatial scales. *Alnus* has a wide geographical distribution range and manageable richness of fungal symbionts, which we considered favourable for addressing differences in richness and inferring biogeographic patterns. I postulated the following alternative hypothesis: 1) host species and their phylogenetic relationships account for the strongest predictor of EcM fungal community composition at the intrageneric level at the global scale; 2) at regional scale, soil conditions such as pH and phosphorus concentration drive the EcM community structure rather than geographical and host genetic distance; 3) at global scale, *Alnus*-associated EcM fungal species richness is largely determined by the mean annual temperature and precipitation; 4) global biogeography of *Alnus* EcM communities reflects ancient migration routes of the host.

The main results and conclusions are the following: 1) phylogenetic relations among hosts account for strongest predictor of EcM community structure, while geographical and edaphic variables have a relatively low impact at the global scale; 2) at the regional scale edaphic variables were the dominant determinants of EcM fungal community structure; 3) soil calcium accounted for the key determinant of *Alnus*-associated EcM fungal species richness at the global scale, while soil humidity was the most influential at the local and regional scales; 4) Beringia is likely to be primary migration route of *Alnus* from Eurasia to America rather than North Atlantic land bridge; 5) high similarity between North and South Europe probably results from recent post-glacial recolonisation.

## 7. SUMMARY IN ESTONIAN

### Lepa juurtel ektomükoriisat moodustavate seente biogeograafia ja ökoloogia.

Ökoloogia uurib organismide vahelisi interaktsioone, levikumustreid ja nende sõltuvust keskkonnast. Biogeograafia uurib taksonite ja ökosüteemide levikut ja sellest tulenevaid protsesse nii ajas kui ruumis. Traditsiooniliselt on ökoloogia ja biogeograafia peamisteks uurimisobjektideks olnud makroorganismid. Osaliselt kindlasti nende näiliselt lihtsama määramise ja leitavuse tõttu. Mikroorganismide makroökoloogia uurimine on hoogustunud alles viimase paarikümne aasta jooksul tänu molekulaarsete meetodite kiirele arengule. Alates 1990-test aastatest kasutatakse bioloogilistes proovides (muld, vesi, õhk, organismide koed jm.) esinevate bakterite ja seente määramiseks DNA nukleotiidseid järjestusi. Bakterite puhul kasutatakse liikide määramiseks peamiselt rDNA SSU nukleotiidseid järjestusi ja seente puhul rDNA ITS lõikude järjestusi. Viimane on oluliselt varieeruvam ja võimaldab seeni määrata liigi tasemel. Enne molekulaarsete meetodite kasutusele võtmist sai mikroorganisme määrata kas kaudselt või ainult neid liike, mida oli võimalik puhaskultuuri eraldada. Uute meetodite abil selgus, et paljud makroorganismidele omased ökoloogilised mustrid mikroorganismide puhul ei kehti. Lisaks on tulemused tihti vasturääkivad ja hästi toetatud konsensus mikroorganismide makroökoloogia ja biogeograafia osas puudub. Veelgi enam, erinevatele mikroorganismide taksonitele ei pruugi kehtida ühtsed ja universaalsed "reeglid" kuna bakterite, seente ja protistide nõuded kasvukeskkonnale on väga varieeruvad. Tõenäoliselt ei ole mõistlik mikroorganisme biogeograafias ja ökoloogias vaadelda ühtse rühmana.

Ektomükoriisa on seenjuure vorm, kus peremeestaim saab seene vahendusel kasvuks vajalikke mineraalaineid ja vett. Seen omakorda saab taimelt fotosünteesi käigus fikseeritud süsivesikuid. Senised uurimisandmed näitavad, et ektomükoriisat moodustavate seente liigirikkus on kõrgeim parasvöötmes, vastupidiselt makroorganismide üldlevinud mustrile. Viimase kohaselt on suurim liigirikkus ekvatoriaalses vöötmes ja pooluste suunas liikudes see langeb. Ometi puudub siiani ühtse meetodikaga läbi viidud globaalne uuring, mis käsitleb ektomükoriisat moodustavate seente makroökoloogiat. Oma doktoritöös uurisin ma ühtse meetodikaga perekond *Alnus* (lepp) juurtel ektomükoriisat moodustavaid seeni globaalses ja regionaalses skaalas. Lepp on levinud eelkõige põhjapoolkeral ja selle liigitekke tšenter asub tõenäoliselt Kagu-Aasias. Sealt on lepp levinud edasi Euroopasse ja kunagi Beringi väina kohal olnud maismaasilla kaudu Põhja-Ameerikasse. Alternatiivina on välja pakutud ka võimalikku levikut Põhja Atlandi kaudu soojemate kliimaperioodide jooksul. Sõltuvalt klassifikatsioonist eristatakse selles perekonnas tänapäeval 28–44 liiki. Lepa liigid omavad vastastikku kasulikku kooselu väga erinevate mikroorganismidega. Nende juurtel esinevad nii õhulämmastikku fikseerivad bakterid, ektomükoriisat moodustavad seened ja vähemal määral ka arbuskulaarset mükoriisat moodustavad seened. Ektomükoriisat moodustavad seened esinevad kõigil lepa liikidel

ja teadaolevalt esinevad mitmed seenetaksonid ainult lepa juurtel. See on erinev enamikest teistest ektomükoriisat moodustavatest puu perekondadest, kus sellist spetsialiseerumist esineb harva. Ligikaudu viimase kolme miljoni aasta jooksul on lepp kiiresti laiendanud oma levilat Lõuna-Ameerikas, kasutades Kesk-Ameerika ja Andide mäestikke levikukoridorina läbi troopiliste laiuskraadide. Selline kirjeldatud laialt levinud peremees-sümbiondi kooslus on sobiv mudel globaalseks biogeograafia ja ökoloogia uurimiseks. Minu doktoritöö peamised testitavad hüpoteesid olid alljärgnevad: 1) globaalses skaalas mõjutab lepa seenekoosluse struktuuri enim peremeesliikide fülogeneetiline distant; 2) regionaalses skaalas mõjutab lepa juurtel ektomükoriisat moodustavate seente koosluse struktuuri mulla koostis, eriti pH ja fosfor; 3) globaalses skaalas on lepaga seotud ektomükoriisa seente liigiline mitmekesisus määratud aasta keskmise temperatuuri ja sademete hulga poolt; 4) lepaga seotud ektomükoriisa seente biogeograafia peegeldab peremehe globaalseid levikuteid.

Käesolev doktoritöö võimaldab teha mimeid uudseid järeldusi ja kinnitada olemasolevaid hüpoteese. Globaalses skaalas mõjutavad peremeesliikide fülogeneetilised distantid 43% ulatuses lepaga seotud ektomükoriisete seente koosluse struktuuri. Ruumiline paiknevus mõjutab seenekoosluse struktuuri 10% ulatuses ning mulla pH-l ja aasta keskmisel temperatuuril on marginaalne mõju. Seevastu regionaalses skaalas, määravad mulla pH ja orgaanilise aine sisaldus, enim seenekoosluse struktuuri. Varasemad uuringud on leidnud, et peamised mõjutegurid, mis määravad ektomükoriisete seente liigirikkust globaalses skaalas, on aasta keskmine temperatuur ja sademete hulk. Täpsemalt on tuvastatud ektomükoriisa liigirikkuse unimodaalne seos temperatuuriga ja negatiivne seos sademete hulga. Meie uuringust selgus üllatuslikult, et lepaga seotud ektomükoriisete seente liigirikkus on enim mõjutatud ja positiivses seoses mulla kaltsiumisisaldusega. Samas leidis kinnitust negatiivne seos ektomükoriisa liigirikkuse ja sademete hulga vahel. Meile teadaolevalt oli see esimene uuring, mis ühtse meetodikaga adresseeris ektomükoriisa biogeograafiat globaalses skaalas ja võttis ühtlasi arvesse ka mulla omadusi. Sarnaselt globaalsele muustrile, oli ka regionaalses skaalas liigirikkus negatiivses seoses mulla veesisaldusega. Mõned lepaga seotud mükobiondid, kes esinevad Ameerikas, Euroopas ja Aasias, jagavad omavahel 100% sarnasust ITS järjetustes. Võrreldes lepaga seotud seenekoosluste liigist ja arvulist koosseisu erinevate mandrite ja piirkondade vahel selgus, et tõenäoliselt on Beringia maismaasild olnud põhiline lepa levikutee Euraasia ja Ameerika vahel. Põhja ja Lõuna Euroopa seenekooslused osutusid väga sarnaseks, mis tõenäoliselt tuleb jääaja järgsest lepa ja tema juursümbiontide levikust põhja suunas lõunapoolsetest refuugiumidest.

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## CURRICULUM VITAE

**Name:** Sergei Põlme  
**Date of birth:** 27.05.1982  
**Citizenship:** Estonian  
**Address:** Institute of Ecology and Earth Sciences, 14a Ravila St, 50411,  
Tartu, Estonia  
**Phone:** +372 5594 5041  
**E-mail:** sergei.polme@gmail.com  
**Current position:** University of Tartu Natural History Museum, curator

### Education

2008– PhD studies in Botany and Ecology, University of Tartu  
2006–2008 MSc in Biology, University of Tartu  
2002–2006 BSc in Biology, University of Tartu  
1989–2001 Secondary Education, Pärnu Ülejõe Gümnaasium

### Language

**skills:** Estonian (mother tongue), English (good), Russian (basic)

### Publications

**Tedersoo L, Suvi T, Jairus T, Ostonen I, Põlme S. 2009.** Revisiting ectomycorrhizal fungi of the genus *Alnus*: differential host specificity, diversity and determinants of the fungal community. *New Phytologist* 182: 727–735.

**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.

**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

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**Phosri C, Põlme S, Taylor A.F.S, Kõljalg U, Suwannasai N, Tedersoo L. 2012.** Diversity and community composition of ectomycorrhizal fungi in a dry deciduous dipterocarp forest in Thailand. *Biodiversity and Conservation* 8: 1–12.

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**Arula T, Kotta J, Lankov A, Simm M, Põlme S. 2012.** Diet composition and feeding activity of larval spring-spawning herring: Importance of environmental variability. *Journal of Sea Research* 68: 33–40.



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**Nimi:** Sergei Põlme  
**Sünniaeg:** 27.05.1982  
**Kodakondsus:** Eesti  
**Aadress:** Ökoloogia ja Maateaduste Instituut, 14a Ravila St, 50411, Tartu, Eesti  
**Telefon:** +37255945041  
**E-mail:** sergei.polme@gmail.com  
**Praegune töökoht:** Tartu Ülikooli Loodusmuuseum, kuraator

### Hariduskäik:

2008– Botaanika osakond, Ökoloogia ja Maateaduste Instituut, Tartu Ülikool, doktorant  
2006–2008 MSc bioloogias, Tartu Ülikool  
2002–2006 BSc bioloogias, Tartu Ülikool  
1989–2001 Pärnu Ülejõe Gümnaasium

**Keelteoskus:** eesti (emakeel), inglise (heal tasemel), vene (suhtlustasandil)

### Publikatsioonid:

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