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EVELI OTSING

Tree species effects on fungal richness and community structure

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UNIVERSITY OF TARTU
Press

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

Dissertation was accepted for the commencement of the degree of *Doctor philosophiae* in Botany and Mycology at the University of Tartu on October 5th, 2020 by the Scientific Council of the Institute of Ecology and Earth Sciences, University of Tartu.

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Commencement: Room 218, 40 Lai Street, Tartu, on December 3rd, 2020 at 12.15 p.m.

Publication of this thesis is granted by the Institute of Ecology and Earth Sciences, University of Tartu.

ISSN 1024-6479
ISBN 978-9949-03-491-8 (print)
ISBN 978-9949-03-492-5 (pdf)

Tartu University Press
www.tyk.ee

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LIST OF ORIGINAL PUBLICATIONS

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

I. **Otsing E**, Barantal S, Anslan S, Koricheva J, Tedersoo L. 2018. Litter species richness and composition effects on fungal richness and community structure in decomposing foliar and root litter. *Soil Biology and Biochemistry* 125: 328–339.

II. Tedersoo L, Anslan S, Bahram M, Drenkhan R, Pritsch K, Buegger F, Padari A, Doust NH, Mikryukov V, Gohar D, Amiri R, Hiiesalu I, Lutter R, Rosenvald R, Rähn E, Adamson K, Drenkhan T, Tullus H, Jürimaa K, Sibul I, **Otsing E**, Põlme S, Metslaid M, Loit K, Agan A, Puusepp R, Varik I, Kõljalg U, Abarenkov K. 2020. Regional-scale in-depth analysis of soil fungal diversity reveals strong pH and plant species effects in Northern Europe. *Frontiers in Microbiology* 11: 1953.

III. **Otsing E**, Anslan S, Ambrosio E, Koricheva J, Tedersoo L. Tree species richness and neighbourhood effects on ectomycorrhizal fungal richness and community structure in boreal forest. Unpublished.

IV. Tedersoo L, Bahram M, Põlme S, Koljalg U, Yorou NS, Wijesundera R, Ruiz LV, Vasco-Palacios AM, Thu PQ, Suija A, Smith ME, Sharp C, Saluveer E, Saitta A, Rosas M, Riit T, Ratkowsky D, Pritsch K, Põldmaa K, Piepenbring M, Phosri C, Peterson M, Parts K, Pärtel K, **Otsing E**, Nouhra E, Njouonkou AL, Nilsson RH, Morgado LN, Mayor J, May TW, Majuakim L, Lodge DJ, Lee SS, Larsson KH, Kohout P, Hosaka K, Hiiesalu I, Henkel TW, Harend H, Guo LD, Greslebin A, Grelet G, Geml J, Gates G, Dunstan W, Dunk C, Drenkhan R, Dearnaley J, De Kesel A, Dang T, Chen X, Buegger F, Brearley FQ, Bonito G, Anslan S, Abell S, Abarenkov K. 2014. Global diversity and geography of soil fungi. *Science* 346: 1078–1089.

Author's contribution to each publication:

I Participated in conceiving the study idea and design, performed sampling, molecular and statistical analysis, wrote the manuscript with contributions from coauthors

II Participated in performing sampling and molecular analysis

III Participated in conceiving the study idea and design, performed statistical analysis, wrote the manuscript with contributions from coauthors

IV Participated in performing sampling and molecular analysis

INTRODUCTION

Fungi play important roles in forest ecosystems as mutualists, saprotrophs and pathogens. Fungal communities are drivers of soil organic matter decomposition and nutrient cycling (Swift et al., 1979), as well as the mediation of plant nutrition and productivity via mycorrhizal symbiosis (van der Heijden *et al.*, 1998; Read & Perez-Moreno, 2003). One of the fundamental aspects in above- and belowground relationships is to understand the extent to which plant species diversity influences fungal diversity and *vice versa* (Wardle *et al.*, 2004). Plant diversity influences soil microbes through species identity (Nguyen *et al.*, 2016b; Chen *et al.*, 2019). Plant species identity along with species-specific genetic traits prompts differences in litter quality (Conn & Dighton, 2000; Aponte *et al.*, 2010, 2013), microclimate under the tree canopy (Joly *et al.*, 2017), root parameters (Comas & Eissenstat, 2009), root exudates (Zhalnina *et al.*, 2018), mycorrhizal type (Tedersoo & Bahram, 2019), etc. The strength of feedbacks between above- and belowground biodiversity depends on the group of soil biota (Wardle, 2006). Plant diversity effects on diversity of free-living biota are driven by chemical differences among plant-derived litter types, while the diversity of root-associated biota is influenced by genetic differences among plant species (Wardle, 2006; Nguyen *et al.*, 2016b). Mycorrhizal fungi can regulate plant communities via soil feedback (Aponte *et al.*, 2013). Interactions between plants and fungi play an important role in ecosystem functioning. However, the effects of plant diversity on microbial communities in forest ecosystems are not well understood.

Mycorrhizal symbiosis has a fundamental role in the nutrient cycling and plant nutrition through the acquisition of phosphorus and nitrogen under limiting conditions (Read & Perez-Moreno, 2003). Plants allocate a substantial proportion of carbon belowground to mycorrhizal fungal symbionts. Fungal tissues potentially represent a large carbon input into soil organic matter pools (Langley & Hungate, 2003; Clemmensen *et al.*, 2015). Decomposition exhibits a major control over carbon and nutrient cycling in forest ecosystems (Berg, 2000; Hättenschwiler, 2005). Climate, soil organisms and plant litter are the main factors affecting decomposition (Cadisch & Giller, 1997; Krishna & Mohan, 2017; See *et al.*, 2019). The quality of soil organic matter is strongly influenced by the chemical and physical properties of the input plant litter (Hättenschwiler, 2005; Cassart et al., 2020). In forest ecosystems, litter from different plant species becomes usually mixed (Staelens *et al.*, 2003; Ťupek *et al.*, 2015). This leads to an issue of how mixing the litter from different tree species influences decomposers. Previous studies have suggested that more heterogeneous plant litter mixture promotes greater resource partitioning and niche specialists, hence supporting higher microbial diversity (Hooper *et al.*, 2000; Chapman & Newman, 2010; Santonja *et al.*, 2017). Decomposers may be specialized to break down litter from the plant with which they are associated (Strickland *et al.*, 2009). As a result, plant litter is often decomposed more rapidly in the vicinity of the plant from which it originates, termed as the 'home-field advantage effect' (Ayres

et al., 2009; Veen *et al.*, 2015). It has been demonstrated that EcM fungi may have preference for certain litter species (i.e., plant species represented in litter) (Conn & Dighton, 2000; Aponte *et al.*, 2010, 2013).

Litter species composition has usually stronger effects on decomposition than litter species richness *per se* (Wu *et al.*, 2013; Cuchietti *et al.*, 2014; Santonja *et al.*, 2017). For example, decomposer communities are influenced by leaf litter origin from broadleaf or coniferous trees (Prescott & Grayston, 2013; Nagati *et al.*, 2018) and deciduous or evergreen trees (Aponte *et al.*, 2010, 2013). Compared with broadleaved and deciduous trees, litter of coniferous and evergreen trees has higher lignin content but lower nitrogen content, rendering these types of litter more difficult to decompose (Prescott *et al.*, 2000; Aponte *et al.*, 2012). Besides leaf litter that is deposited aboveground, plant root litter is an important source of carbon input to forest soils (Rasse *et al.*, 2005; Fan & Guo, 2010). Root litter seems to contribute even more to the carbon pools in soils than aboveground litter due to higher content of lignin that is chemically more recalcitrant (Rasse *et al.*, 2005). Similarly to leaf litter, root litter is mixed in the stands of several tree species (Brassard, 2010). Li *et al.* (2018) found no differences in the composition of the root fungal community between the levels of root litter richness. However, the effect of root litter mixing on fungal richness and community composition still remains unknown.

The tree species diversity effect on root-associated and plant pathogenic fungi is expected to be stronger compared to the effect on free-living decomposer fungi. Decomposers are more generalist than root-associated fungi in their associations with plant-derived resources, predicting stronger links and feedbacks between plant and root-associated fungal diversity (Wardle, 2006). Tree species identity affects EcM fungal species richness and community composition (Ishida *et al.*, 2007; Tedersoo *et al.*, 2012; Bogar & Kennedy, 2013), as many species of EcM fungi exhibit host preference or specificity at different taxonomic levels (Ishida *et al.*, 2007; Bahram *et al.*, 2012; Kennedy *et al.*, 2015; Molina & Horton, 2015). Due to host specificity, forest stands with more plant species should be able to support higher richness of root-associated fungi (Kernaghan *et al.*, 2003; Wardle, 2006; Ishida *et al.*, 2007; Tedersoo *et al.*, 2016; Nguyen *et al.*, 2016b). The influence of tree species identity on EcM fungi is associated with tree phylogeny. Stands with more phylogenetically distant hosts harbour higher richness of fungi and more dissimilar fungal communities comparing to stands with closely related host trees (Ishida *et al.*, 2007; Smith *et al.*, 2009; Põlme *et al.*, 2013; Tedersoo *et al.*, 2013; Nguyen *et al.*, 2016b).

Tree species identity is one of the most important factors controlling EcM fungal richness and community composition in forest ecosystems, but the importance of tree species combinations on EcM fungal communities in mixed stands has received limited attention. In mixed-species stands, root-associated fungi can be shared among different tree species (Simard *et al.*, 1997; Horton & Bruns, 1998). Many previous studies have found that tree species composition affects EcM fungal richness and community composition in mixed stands through a neighbourhood effect (Haskins & Gehring, 2004; Bahram *et al.*, 2011; Jairus

et al., 2011; Bogar & Kennedy, 2013; Santolamazza-Carbone *et al.*, 2019). This effect can be related to the unique properties created by heterospecific neighbours that are not found in single-species stands (Cavard *et al.*, 2011). The neighbour effects on EcM fungal communities are found to be indirectly mediated by litter quality and associated soil properties as well as temperature and moisture (Conn & Dighton, 2000; Brandtberg *et al.*, 2000; Légaré *et al.*, 2005; Aponte *et al.*, 2010, 2013). Therefore, at a stand scale, different tree species create spatial heterogeneity of soil conditions that can lead to niche partitioning and increase in biodiversity (Conn & Dighton, 2000; Buée *et al.*, 2007).

This thesis addresses fungal diversity in relation to plant litter and host plant diversity and tree neighbourhood effects. I postulated the following main research hypotheses (in bold), referring to particular studies (Roman numerals):

1) **Litter species richness enhances fungal richness (I).** More diverse plant litter is expected to promote niche specialists and hence support higher microbial diversity.
2) **Composition of saprotrophs, plant pathogens and EcM fungi is mainly driven by litter species composition (I).** We expected to detect shifts in fungal community composition related to variation in litter and soil nutrient availability.
3) **The relative proportion of host-specific EcM fungi is greater in the litter of their intimate host plant (I).** We predicted that the relative proportion of host-specific EcM fungi is greater in their host plant litter than in the other plant species litter due to their evolutionary history of being exposed to the host plant litter with certain litter quality; in particular, we expected that alder-specific fungi occur in relatively greater abundance in alder litter, because of their high host-specificity.
4) **Diversity of biotrophic fungal groups responds strongest to dominant vegetation, whereas free-living groups are more affected by abiotic variables (II).** Soil fungal groups that are directly associated with plants (e.g. mycorrhizal fungi, plant pathogens) show higher degree of specificity while saprotrophs are more generalist.
5) **EcM fungal richness increases with increasing number of tree species at different spatial scales (II, III, IV).** At least partly due to host specificity, forest stands with more plant species should be able to support higher richness of root-associated fungi.
6) **Tree species identity determines EcM fungal richness (II, III) and composition (III).** Host species identity is expected to influence the richness and structure of EcM fungal assemblages as many species of EcM fungi exhibit host preference or specificity.
7) **EcM fungal richness and community composition associated with individual tree species vary depending on neighbourhood context (III).** EcM fungal community associated with a certain host species is expected to differ in mixtures compared with pure stands as influenced by the co-occurring tree species.

MATERIAL AND METHODS

Sampling sites and study design

To test the hypotheses, our research team and collaborators carried out field experiments and observational studies, and identified fungal species with molecular methods. To study foliar and root litter richness and composition effects on fungal richness and community structure, a litter decomposition experiment was set up in the Satakunta forest diversity experimental area in Southwest Finland (https://treedivnet.ugent.be/) **(I)**. For studying the effects of tree species richness and composition on EcM fungal richness and community structure, root samples were collected from the exploratory sites established as part of the FunDivEUROPE platform in North Karelia, Finland (www.fundiveurope.eu) **(III)**. Altogether 1251 composite soil samples were collected within the period of 2011 to 2018 from the northern Baltic region (Estonia and North Latvia) to determine the biotic and abiotic factors underlying the diversity of soil fungi at regional scale **(II)**. To study the influence of biotic and abiotic factors on soil fungal diversity at global scale, composite soil samples were collected from natural communities of 365 sites across the world **(IV)**.

For the litter decomposition experiment in study **I**, we selected two five-species mixture plots (20 × 20 meters) of silver birch (*Betula pendula* Roth), black alder (*Alnus glutinosa* L. Gaertn.), Siberian larch (*Larix sibirica* Ledeb.), Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* L. Karst.) planted in 1999 (Figure 1A). Within each of the two plots, we randomly selected five individual focal trees of each species, except the non-native larch, and placed litter bags under these trees on the soil surface. Each focal tree (treated as "block") received eight bags of single-species foliar and root litters, two bags of two-species (the same random combination for both foliar and root litters), two four-species foliar and root litter mixtures and two extra bags of single-species foliar and root litter that matched the tree identity, altogether 560 litter bags. All roots were dried at 65 °C for 48 hours to kill EcM fungi, whereas leaves were dried at room temperature to better mimic natural conditions. One gram of dried litter was weighed into each bag, with litter species mixes pooled in equal proportion. Litter bags were harvested after 12 months of decomposition **(I)**.

The North Karelia exploratory platform in Finland is composed of 28 plots (30 × 30 meters) of monocultures, two- and three-species mixtures of silver birch (*Betula pendula* Roth.), Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* L. Karst.) established in 2010 (Figure 1B,C,D,E) **(III)**. There are four replicate plots of monocultures and each of the tree species combinations (birch, pine, spruce, birch–pine, birch–spruce, pine–spruce, birch–pine–spruce). Fine root samples were collected from all 28 plots by sampling four trees per species per plot, resulting in 192 samples. Coarse roots were traced from the tree trunk; smaller root branches attached to these were dug out and 15 cm root

length including most intact fine roots and mycorrhizas were collected. Roots were carefully cleaned from adhering soil with water. Each mycorrhizal root sample was cut to equal length fragments and from each sample, ten fragments were randomly selected and washed again with water. These root samples were placed on a tissue paper to remove the excess water and then placed into tubes containing CTAB buffer (1% cetyltrimethylammonium bromide, 100 mM Tris–HCl (pH 8.0), 1.4M NaCl, 20 mM EDTA) for molecular analyses **(III)**.

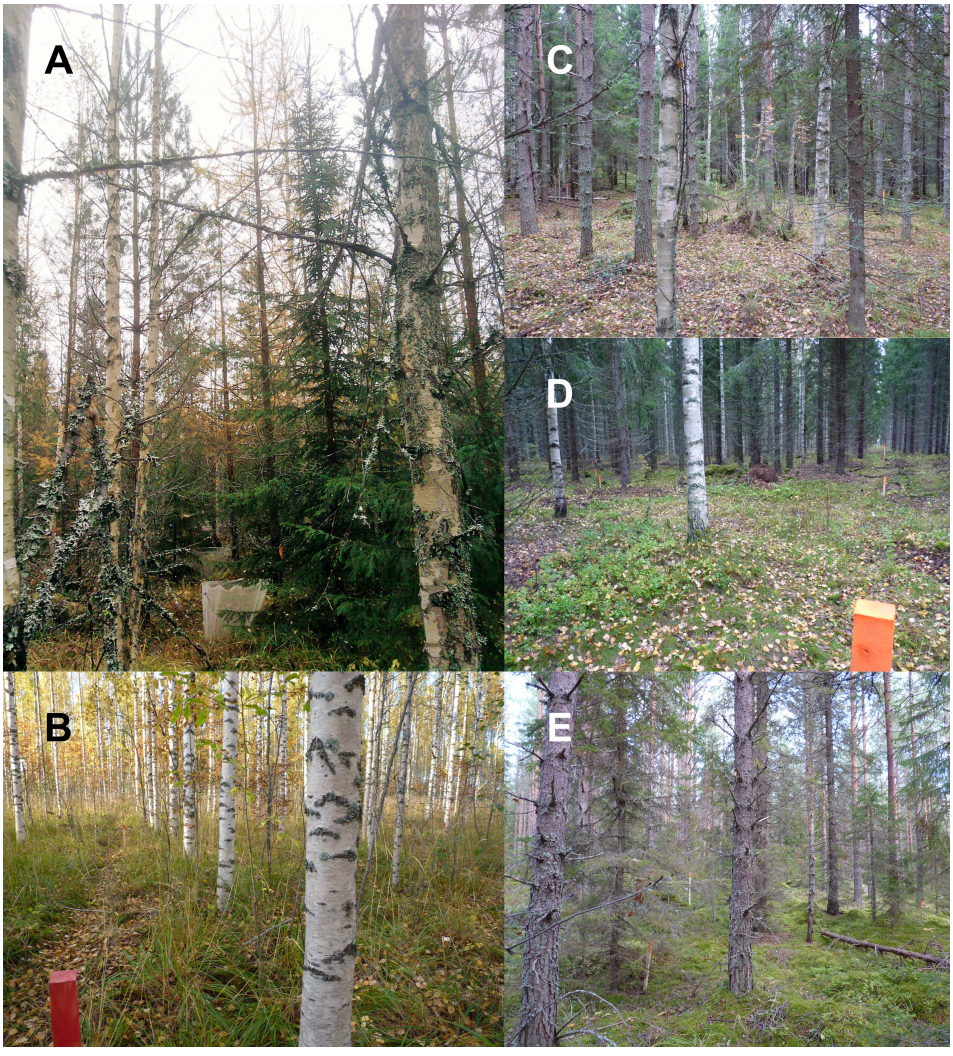

Figure 1. Satakunta experimental area plot of five-species mixture (A), study **I**, and North Karelia exploratory region plots of birch monoculture (B), birch–pine–spruce (C), birch–spruce (D) and pine–spruce (E) mixtures, study **III**. Photos by E. Otsing (A) and Timo Domisch (B, C, D, E).

In the regional and global soil sampling studies **(II, IV)**, the composite soil samples consisted of 40 pooled soil cores and were collected from mostly 2500-m^2, circular plots. In a plot, we randomly selected 20 trees located at least eight meters apart **(II, IV)**. From two opposing sides of each tree, 1–1.5 meters from each tree trunk, loose debris was removed from the forest floor and soil cores (5 cm in diameter and 5 cm in depth) were collected using a sterilized PVC tube **(II, IV)** or sharp knife **(II)**. About 10 grams of soil from the margins of each core was placed into a zip-lock plastic bag, with the interior of the soil core placed back into the hole **(II, IV)**. Coarse roots and stones were removed, and the soil was air-dried at <40 °C **(II, IV)**. Soil cores almost always included fine roots and comprised both the organic layer and top mineral soil **(II, IV)**. During sampling, all woody plant and dominant herb species were recorded and the relative basal area was estimated using direct measurements or visual estimates **(II)**.

Molecular analysis

DNA was extracted from homogenized leaf and root litter samples **(I)**, root samples **(III)** or soil samples **(II, IV)** using PowerSoil DNA Isolation Kit (MoBio/Qiagen, Carlsbad, CA, USA) following the manufacturer's protocols. We extracted DNA from 0.20 grams of litter **(I)**, 2.0 grams of soil **(II, IV)** and approximately 0.20 grams of root samples **(III)**. Only for studies **II** and **IV**, DNA extracts were further purified using FavorPrep™ Genomic DNA Clean-Up Kit (Favorgen, Vienna, Austria). In study **I,** DNA extracts were subjected to polymerase chain reaction (PCR) with a mixture of five forward primers ITS3ngsMixTag1-5 (consensus: CTAGACTCGTCANCGATGAAGAACGYRG) and a degenerate reverse primer ITS4ngsUni (CCTCCSCTTANTDATATGC). In study **II**, DNA was amplified with the universal eukaryotic primers ITS9mun (TGTACACACCGCCCGTCG) and ITS4ngsUni. In study **III**, PCR was carried out using a mixture of five forward primers ITS3ngsMixTag1-5 and a degenerate reverse primer ITS4ngs (TCCTSCGCTTATTGATATGC). In study **IV,** PCR was performed using a mixture of six forward primers ITS3ngsMixTag 1-5,10 and a degenerate reverse primer ITS4ngs. All forward primer mixtures were equimolar **(I, III, IV)**. The reverse primers (in study **II,** also forward primers) were tagged with unique 10–12 base pairs long identifiers **(I–IV)**. PCR protocols are described in detail in studies **I–IV**. We included both negative and positive controls in PCR and sequencing runs in all studies. Amplicons were subjected to adaptor ligation and Illumina MiSeq sequencing (2 × 300 paired-end) in the Estonian Genome Center (Tartu, Estonia) **(I)** or in NERC Biomolecular Analysis Facility (Liverpool, UK) **(III)**. In study **II**, PCR products were sequenced on PacBio Sequel II instrument using SMRT cell 1M in University of Oslo. In study **IV**, amplicons were subjected to 454 adaptor ligation, emulsion PCR, and 454 pyrosequencing by using the GS-FLX+ technology and Titanium chemistry as implemented by Beckman Coulter Genomics (Danvers, MA).

Data analysis

Bioinformatic analyses for the high throughput sequencing data were performed using PipeCraft 1.0 platform (Anslan *et al.*, 2017) **(I, II, III)** or mothur **(IV)**. Detailed options for data processing are given in papers **I–IV**. The internal transcribed spacer (ITS2) reads were assigned to operational taxonomic units (OTUs) by clustering at 97% sequence similarity threshold **(I, III),** 98% threshold (**II**) or 90.0% and 95.0-99.0% sequence similarity thresholds **(IV)**. All OTUs represented by a single sequence (singletons) were removed **(I–IV)**. The most abundant **(I–III)** or the longest **(IV)** sequence of each cluster was selected as a representative for BLASTn sequence similarity search against both International Nucleotide Sequence Databases collaboration (INSDc; http://www.insdc.org) and UNITE (Nilsson *et al.*, 2019; https://unite.ut.ee/) databases. BLASTn searches were run against reference sequences of fungi in 1%-distance species hypotheses (SH) that include third-party taxonomic and metadata updates (Kõljalg *et al.*, 2013; Nilsson *et al.*, 2014) as implemented in the PlutoF workbench (Abarenkov *et al.*, 2010) **(I–IV)**. We used BLASTn output values of taxonomic assignment to remove remaining potential artefacts and positive and negative controls to account for tag switching errors and contaminants. We relied on 98% (or 97%), 90%, 85%, 80% and 75% sequence identity as a criterion for assigning OTUs to species, genus, family, order or class level, respectively **(I–IV)**. Each fungal genus, family or order was assigned to functional categories based on study IV itself (**IV**) or FUNGuild (Nguyen *et al.*, 2016a) **(I, III)**. In study **II**, the newly built FungalTraits database (Põlme et al. unpublished; used beta version available at DOI:10.15156/BIO/807446) was used to assign OTUs to guilds and EcM fungi further to lineages and exploration types. Taxa were considered to be EcM if they matched to any sequences belonging to EcM fungal lineages and exhibited sequence blast score/sequence length above the predetermined lineage-specific thresholds (Tedersoo & Smith, 2013, 2017) **(I–IV)**.

For richness modelling, we calculated the standardized residuals of OTU richness in relation to the square-root of the number of obtained sequences to account for differences in sequencing depth **(I, III, IV)**. For study **II**, all OTU richness measures were converted to residuals based on the average values of raw residuals taken from regression analyses of OTU richness vs. square root-transformed sequencing depth and log-transformed sequencing depth. In study **I**, we tested the effects of litter species richness and composition, focal tree species identity, plot (fixed factors) and block (random factor; nested in tree species and plot), and mass loss (covariate) on standardized residuals of OTU richness in foliar and root litter samples. In study **III**, we tested the effects of tree species richness, composition (fixed factors) and identity (nested in plot), and plot (random factors) on standardized residuals of OTU richness in root samples. General linear models (GLM) (Type I SS) for standardized residuals of OTU richness were calculated in STATISTICA 12 (StatSoft Inc., Tulsa, OK, USA) **(I, III)**. Using one-way and two-way analysis of variance (ANOVA), we

performed Tukey's post hoc tests to distinguish statistically significantly different groups, using the R package agricolae (De Mendiburu, 2014) **(I, III)**. We used the random forest machine learning algorithm to generate non-linear models for all richness variables using combined features of random forest (Liaw & Wiener, 2002) and VSURF (Genuer *et al*., 2019) packages in R. Model evaluation was performed using 999 trees **(II)**. Because these analyses provided no information about the type of fit or determination coefficient, we tested these pre-selected best predictors by fitting quadratic functions and general linear modelling for each dependent variable as implemented in STATISTICA 13 (TIBCO Software Inc., NY, USA) **(II)**. In study **IV**, candidate predictors were preselected from multiple linear and polynomial regression analyses based on coefficients of determination and forward selection criteria to determine the best predictors of global fungal diversity. The most parsimonious models were determined according to the corrected Akaike information criterion (AICc). Components of the best models were forward-selected to determine their relative importance as implemented in the packfor package (Dray *et al*., 2009) **(IV)**. We used piecewise structural equation modeling, implemented in piecewiseSEM package (Lefcheck, 2016) **(II),** and Structural Equation Modeling (SEM) in Amos version 22 (SPSS Software, Chicago, IL) **(IV)** to characterize direct and indirect relationships between OTU richness and the potential predictors **(II)**.

As implemented in PRIMER v6 (Clarke and Gorley, 2006) and PERMANOVA+ (Anderson *et al.*, 2008), permutational multivariate analysis of variance (PERMANOVA) with 999 permutations was used to test differences in fungal community composition **(I, III)**. With previously described nested designs, we tested the effects of litter species richness and composition, focal tree species identity, plot and block, and mass loss on fungal community structure in foliar and root litter samples **(I).** The effects of tree species richness, composition and identity, and plot were tested on EcM fungal community structure in root samples with previously described nested designs **(III)**. The Bray-Curtis dissimilarity metric was applied on the Hellinger transformed sequence abundance data **(I, II, III)**. Euclidean distance was used to generate environmental distance matrices **(I, III)**. Hellinger transformation with Euclidean distance and a multistage model selection procedure, implemented in the DISTLM function of PERMANOVA+, were used for fungal community composition modelling **(IV)**. Statistical significance level was considered at $\alpha = 0.05$ **(I–IV)** or 0.001 **(II)**. To visualize the effects of different factors on fungal community composition, non-metric multidimensional scaling (NMDS) were performed on abundance data in vegan package (Oksanen *et al.*, 2017) **(I–IV).** Potential non-linear effects were estimated using General Dissimilarity Modelling (GDM) (Manion *et al*., 2018) **(II)**.

RESULTS AND DISCUSSION

Partly in agreement with hypothesis 1, fungal richness increased with increasing number of plant species represented in foliar litter (*litter species richness*), but the effect was weak and context-dependent in root litter (I). In foliar litter mixture, plant species richness was one of the two strongest predictors for total fungal, saprotroph and plant pathogen richness, but none of the tested factors affected EcM fungal richness. Plant species composition of litter had a significant additional effect on richness of all fungi, plant pathogens and saprotrophs in foliar litter but not in root litter. Three out of the seven foliar litter mixtures had significantly higher observed fungal richness compared with the expected fungal richness based on single-species litter (two-species mixtures alder–birch and birch–spruce and the four-species mixture alder–birch–pine–spruce). Root litter species richness and composition showed significant but weak effects on richness of saprotrophs, plant pathogens and EcM fungi. Although significant synergistic effects of root litter mixtures on total fungal richness were detected (the two-species mixtures alder–birch and birch–spruce), the overall richness effect was non-significant, because of the lack of synergistic four-species effect. Overall, these results are consistent with several studies, which reported enhanced fungal richness or diversity with increasing foliar litter species richness (Kubartová *et al.*, 2009; Chapman & Newman, 2010; Santonja *et al.*, 2017), suggesting promotion of fine-scale resource heterogeneity in litter mixtures (Chapman & Newman, 2010). The patterns of root litter richness effects can partly be explained by 1) the initial root heating treatment impact for endophytes and pathogens or 2) the paucity of specialist fungi for fine root decomposition as roots naturally decompose in the soil matrix (Šťursová *et al.*, 2012) and roots of all species were colonized by EcM fungi (Langley & Hungate, 2003; Fernandez *et al.*, 2016). This study is inconclusive with regard to the litter species richness effects on fungal richness associated with roots.

Consistent with hypothesis 2, community composition of saprotrophic and plant pathogenic fungi in foliar litter was strongly affected by litter species composition, but its effect on EcM fungal composition was negligible (I). In root litter, litter species composition influenced significantly community composition of saprotrophic and plant pathogenic fungi, but this effect was much weaker than in foliar litter (I). Several studies have also reported that foliar litter of different tree species developed distinct microbial communities, particularly when conifers and broadleaved trees were compared (Aneja *et al.*, 2006; Chapman & Newman, 2010; Urbanová *et al.*, 2015). Furthermore, mixing different litter species altered microbial community composition (Kubartová *et al.*, 2009; Chapman & Newman, 2010). Several studies have analyzed succession of fungal communities on decomposing root litter of one single tree species (Kohout *et al.*, 2018; Herzog *et al.*, 2019), but studies reporting root litter mixing effects on fungal communities are scarce (Li *et al.*, 2018). In root litter, the species composition effect was much weaker, which could be

related to our heating treatment or lower specificity of soil-borne root decomposers. However, root litter of broadleaved trees differed from root litter of conifers in their fungal composition, indicating the effect of litter chemistry or the confounding phylogeny effect (Betulaceae *vs.* Pinaceae) (Silver & Miya, 2001; Prescott, 2010; Guerrero-Ramírez *et al.*, 2016). After one year of decomposition, many of the typical leaf pathogenic fungi were present, indicating that a part of the decomposer community most probably originated from living tissues. Saprotrophs are influenced directly by chemical differences among plant-derived substrate types (Wardle, 2006). While saprotrophic fungi are the primary decomposers of fresh litter (Cooke & Rayner, 1984; Talbot *et al.*, 2013), some plant pathogens (Baker & Bateman, 1978; Osono, 2007) are also potentially important in the initial stages of decomposition, as they often express saprotrophic activity after leaf senescence. Considering that plant pathogens have strong preferences for host species, litter species composition may affect plant pathogen community composition with strong patterns between coniferous and broadleaf litter types (Zhou & Hyde, 2001; Arnold, 2007; Prescott & Grayston, 2013).

We found no support to hypothesis 3 as host-specific EcM fungi showed no evidence for preferring the litter of their intimate host (I). With respect to host-specific EcM fungal taxa, alder-specific fungal taxa contributed most to the relative OTU and sequence abundance both in foliar and in root litter, but they showed no evidence of preference for alder litter. It cannot be excluded that fresh litter might be an unsuitable substrate for EcM fungi to test this effect. Nonetheless, our results suggest that the growth of EcM fungal hyphae into fresh litter is rather opportunistic and unspecific. Aponte *et al.* (2010, 2013) found that two coexisting tree species, through variability in their litter quality, generate species-specific changes in the soil abiotic properties, thus creating selective environmental conditions that shape EcM fungal communities with potential positive feedbacks. The calcium content in litter and soil, together with soil pH, are among the most influential variables for mediating indirect host species effects on EcM fungal communities (Aponte *et al.*, 2010).

Partly consistent with hypothesis 4, biotrophic groups responded more strongly to host plant effects than free-living groups – tree species had respectively 27% and 52% stronger effects on composition of plant pathogens and EcM fungi compared with saprotrophs, but both biotrophic and free-living groups were more affected by soil pH (II). Most overstorey tree species had an effect on community composition of EcM fungi, but only a few had significant influence on other fungal guilds. Community structure of saprotrophs, pathogens and EcM fungi was most strongly influenced by soil pH, which explained 11.4%, 6.4% and 5.3% of variation, respectively. Plant species did not affect the diversity of soil saprotrophs, but had a weak effect on litter (explained 3.1% of variation) and wood (4.4% variation) saprotrophs and leaf pathogens (4.4% variation). Soil pH (unimodal relationship) and plant richness (positive effect) had strongest effects on total fungal richness. Soil pH was the most important predictor of richness for most fungal functional and taxonomic

groups. EcM fungal richness was most strongly related to soil calcium concentration, followed by relative abundance of *Betula* sp., *Corylus avellana*, EcM plants taken together and soil pH. Leaf pathogens prevailed at weakly acidic to neutral soils and their richness was negatively related to proportion of EcM plants, particularly to *Picea abies*. Litter saprotrophs prevailed at near-neutral pH and their richness responded negatively to proportion of EcM plants, in particular to *Picea abies,* with synergistic effects between pH and tree composition. The strong negative effect of EcM plant proportion is attributable to reduced soil pH and potential competition between EcM and saprotrophic fungi for nutrients bound in soil organic material (Fernandez & Kennedy, 2016; Sterkenburg *et al.*, 2018). The EcM conifers *Picea abies* and *Pinus sylvestris* are associated with strongest effects on diversity and composition of most fungal groups, with part of these effects attributable to soil acidification by exuding organic acids and shedding recalcitrant litter (Prescott *et al.*, 2000; Cornelissen *et al.*, 2001; Tedersoo & Bahram, 2019). Therefore, both of these conifers are important tree species in North European forest ecosystems by generating habitats suitable for the specialist host-associated and acidophilic fungal communities and adding much to the landscape-scale soil microbial diversity. Taken together, the positive effects of tree diversity on overall fungal richness represent a combined niche effect of soil properties and intimate associations.

Individual studies provided context-dependent support to hypothesis 5. At regional scale, evidence for a positive relationship between tree species richness and EcM fungal richness was not found (III), while the results were mixed in study II. At global scale, host plant richness had a positive impact on EcM fungal richness (IV). Based on study **II,** we detected significant positive correlation between EcM fungal richness and host richness ($r=0.46$, $P<0.05$). However, EcM tree species richness effect on EcM fungal richness was non-significant in best models explaining richness of fungi, or in Structural Equation Models **(II)**. In addition to modelling in study **III**, we summed the number of EcM fungal OTUs separately for each tree species within a plot and compared it between plots of monocultures, two- and three-species mixtures. Tree species richness had non-significant effect on EcM OTU richness in birch ($F_{2,13}=2.08$; $P=0.165$), pine ($F_{2,13}=0.18$; $P=0.834$) and spruce root samples ($F_{2,13}=0.60$; $P=0.564$) **(III)**. In the global soil-based assessment, richness of EcM fungi responded positively to the relative proportion and species richness of EcM plants (explaining 18.3 and 8.5% of variance, respectively) as well as to soil pH (13.0%) **(IV)**. The results from study **III** are consistent with previous research reporting no significant effect of increasing plant species richness on EcM fungal species richness at the local scale (Tedersoo *et al.*, 2016; Nguyen *et al.*, 2016b) and global scale (Tedersoo *et al.*, 2012). However, the 28 plots of the exploratory region were located in an area of 150 km by 150 km; such regional-scale assessment, relatively small sample size and the presence of confounding edaphic, geographic and climatic factors may have blurred the richness-to-richness relationships **(III)**. In contrast, positive correlation between plant and EcM fungal diversity has been observed at local scale in

several studies (Kernaghan *et al.*, 2003; Tedersoo *et al.*, 2016). Variation in EcM fungal richness explained by host richness in study **IV** indicates either niche differentiation of fungi in forests of mixed hosts or sampling effects (forests with higher host diversity are more likely to include plant species that harbour high fungal diversity). Also, it is suggested that soil microbial richness should be positively affected by plant richness due to greater environmental heterogeneity (Bruns, 1995; Wardle, 2006; Dickie, 2007) as each plant species creates consistent patterns in the chemical composition of litter and root exudates (Gobran *et al.*, 1998; Aponte *et al.*, 2010; Waring *et al.*, 2015; Zhalnina *et al.*, 2018). However, on the smaller scale, other factors such as tree species identity may have a stronger influence on EcM fungal richness than tree species richness *per se* (Tedersoo *et al.*, 2010, 2016; Nguyen *et al.*, 2016b; Nagati *et al.*, 2018; Chen *et al.*, 2019). Despite a well-established background and evidence for positive relationships of plant and microbial richness, these effects remain elusive and point to the importance of the study system, geographic scale and ability to disentangle diversity effects from sampling effect and various confounding variables.

Partly consistent with hypothesis 6, tree species identity was one of the most important factors affecting EcM fungal composition, but it had no effect on EcM fungal richness (III). However, EcM fungal richness in study II was significantly influenced by tree species identity. Based on study **II,** we detected significant effect of tree species identity on EcM fungal richness ($F_{5,90}$=5.78; P<0.001). Post-hoc tests revealed that *Betula pendula* and *Quercus robur* were associated with significantly higher EcM fungal richness compared with *Pinus sylvestris* (Figure 2) **(II)**. In study **III**, pine had lower EcM fungal richness than birch, but it was non-significant. Pine and spruce shared more EcM fungal OTUs than pairwise combinations with birch **(III)**. The ordination graphs showed less distance (i.e. higher community similarity) between EcM fungal communities of pine and spruce than between both of the conifers and birch (Figure 3A) **(III)**. These results are in line with other studies, which have demonstrated that the identity of plant species affect community composition of EcM fungi at local and global scales (Dickie, 2007; Ishida *et al.*, 2007; Tedersoo *et al.*, 2012; Bogar & Kennedy, 2013). Multiple studies have shown that host tree species is the most important factor shaping the community composition of EcM fungi (e.g. Dickie, 2007; Bogar & Kennedy, 2013). Similarly to our results, Nagati *et al.* (2018) found that EcM fungal community composition was more influenced by dominant tree species than variation in tree species richness. Different tree species with different EcM fungal communities indicates to some degree of specificity and/or preference in plant-fungi interactions (Santolamazza-Carbone *et al.*, 2019). Host specificity and/or preference have an important role in driving EcM community composition and are often phylogenetically conserved at subgenus, genus and family levels (Kernaghan *et al.*, 2003; Ishida *et al.*, 2007; Põlme *et al.*, 2013; Tedersoo *et al.*, 2013; Molina & Horton, 2015).

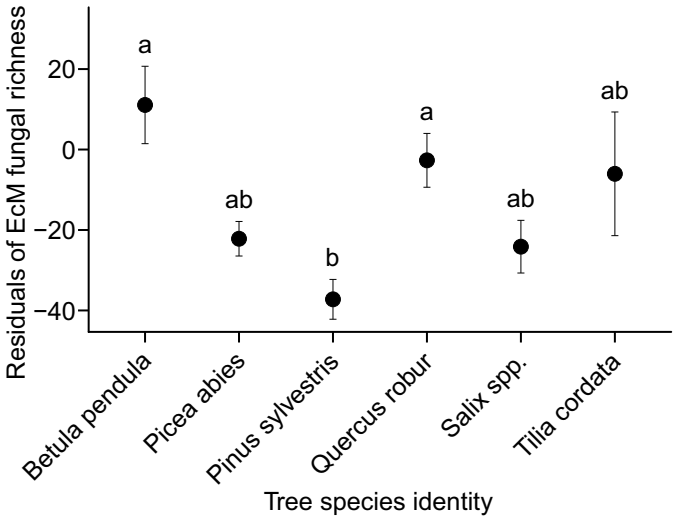

Figure 2. Relationships between tree species identity and residuals of EcM fungal richness based on study **II**. For this analysis, we chose plots comprising a single EcM tree species. Circles and whiskers represent means and standard errors, respectively. Different letters denote significant differences (P<0.05) among hosts.

EcM fungal richness associated with either birch, pine and spruce did not depend on tree neighbourhood context, i.e. species composition of co-occurring trees. EcM fungal community composition of spruce (but not that of pine and birch) was significantly influenced by tree species composition, which is only partly consistent with hypothesis 7 (III). The NMDS ordination indicated that EcM fungal community structure of spruce differed the most in birch–spruce mixture compared to spruce monoculture (Figure 3B). Similarly to our results, Hubert & Gehring (2008) found that richness of EcM fungi was not influenced by a neighbouring heterospecific EcM host. However, that study revealed that the EcM fungal community structure of ponderosa pine *(Pinus ponderosa)* was affected by the neighbouring pinyon pine (*Pinus edulis*), but pinyon pine EcM community structure was insensitive to the presence of ponderosa pine neighbours. Bahram *et al.* (2011) also showed neighbouring tree species effects on EcM community composition of *Populus tremula*. Heterospecific neighbouring plants can create community shifts compared with monocultures through different mechanisms. Priority effects among *Alnus*- and *Betula*-associated EcM fungi allowed the established *Alnus* neighbourhood to control the structure of the *Betula* EcM fungal community possibly by providing sufficient supply of photosynthate for EcM fungi and facilitate the colonization of *Betula*, which the fungi typically do not associate with (Bogar & Kennedy, 2013). Also, the influence of host neighbourhood can be associated with improved soil properties (Brandtberg *et al.*, 2000; Légaré *et al.*, 2005). Aponte *et al.* (2010) found that litter and topsoil under the canopy of winter-deciduous oak

Quercus canariensis were richer in calcium and the soils were less acidic than those under the evergreen oak *Quercus suber*, suggesting that the conditions may be either favouring or limiting certain fungal species. Pine (*Pinus sylvestris*) and spruce (*Picea abies*) litter is rich in phenolic compounds that results in accumulation of recalcitrant organic layer (Strack *et al.*, 1989; Kuiters, 1990). However, birch–spruce stands with different quality litter inputs and improved soil physical and chemical properties create spatial heterogeneity that may influence EcM fungal communities (Brandtberg *et al.*, 2000; Dickie, 2007; Aponte *et al.*, 2013). Mixed birch and spruce stands in forestry has been suggested as the admixture of broad-leaved species can lead to higher microbial activity, lower accumulation of organic matter on the forest floor and increase in soil pH resulting in higher total yields and better quality of both species' timber compared with pure stands (Brandtberg *et al.*, 2000; Schua *et al.*, 2015).

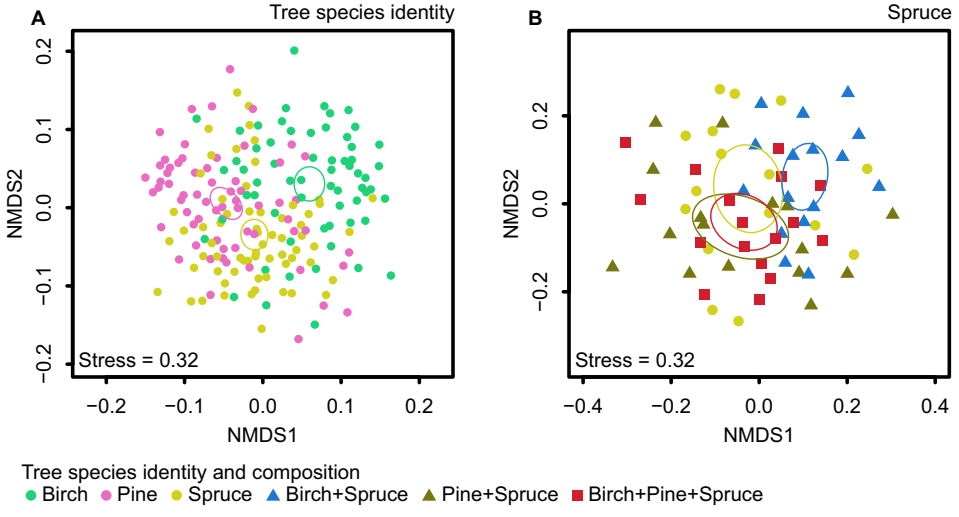

Figure 3. NMDS ordination plots visualizing the relative importance of (A) tree species identity and (B) tree species composition effects for spruce in explaining the community structure of EcM fungi in root samples. Ellipses denote 95% confidence intervals for the different groups. Figure adapted from Fig. 6 in study **III**.

CONCLUSIONS

The following main conclusions and working hypothesis can be inferred from this thesis:

- Foliar litter mixtures with higher richness (number of plant species represented in litter mixtures) harbour higher fungal diversity, suggesting that the presence of higher fine-scale resource heterogeneity promotes niche specialists in diverse litter mixtures **(I)**.
- Root litter richness effect on fungal diversity is context-dependent and remains inconclusive **(I)**.
- Foliar litter composition has a strong influence on community composition of saprotrophic and plant pathogenic fungi. In root litter, litter composition effect on community composition of saprotrophic and plant pathogenic fungi is weaker **(I)**.
- Litter species composition can have a weak impact on EcM fungal community composition in foliar litter, but it may have no such effect in root litter **(I)**.
- Host-specific EcM fungi are not relatively more abundant in their host plant's litter **(I)**, but this issue warrants further research.
- At global scale, host plant richness and EcM fungal richness show a positive relationship **(IV)**. At regional and local scale, there is controversial evidence that EcM fungal richness is influenced by tree species richness **(II, III)**.
- EcM fungal richness varies among different tree species, which may be partly related to the hosts' genetic features and litter properties such as pH **(II)**.
- Tree species identity plays an important role in structuring the communities of plant pathogens **(II)** and EcM fungi **(II, III)**.
- Tree neighbourhood context (i.e., species composition of co-occurring trees) does not influence EcM fungal richness of either birch, pine or spruce **(III)**.
- EcM fungal communities associated with spruce differ in birch–spruce mixture compared with pure stands, suggesting that birch neighbourhood in mixed stands may improve soil properties that have a direct effect on EcM fungal communities **(III)**.
- Based on all studies (**I–IV**), the species richness effect of plants on fungi is generally positive, but largely depends on the context, i.e. the influence of particular plant species (taxonomic sampling effect) and the various confounding factors, which may or may not be accounted for in many studies.

SUMMARY

Fungi make strong contributions to the carbon and nutrient cycles of forest ecosystems. Saprotrophs are the main drivers of organic matter decomposition. Mycorrhizal fungi supply nutrients to their host plants and contribute to nutrient cycling. Mycorrhizal fungi and plant pathogens regulate plant productivity via plant-soil feedback. Tree species are expected to affect fungal communities through direct biotic interactions and quality of input litter. Interactions between plants and fungi play important roles in the ecosystem functioning, but still little is known about the functional significance of tree species diversity on fungal richness. In forest ecosystems, litter from co-occurring tree species usually becomes mixed, leading to a question of how mixing the litter from different tree species affects decomposers. Tree species mixtures are associated with greater fine-scale environmental and resource heterogeneity that could promote higher biodiversity in forest stands. In addition to foliar litter, root litter is another major carbon source in forest soils. Compared with foliar litter, root litter has higher lignin content and it decomposes more slowly, playing an important role in carbon accumulation and long term storage in forest soils. Similarly to foliar litter, root litter becomes mixed in the stands of several tree species. However, the effects of root litter mixing on fungal communities still remain mostly unknown. Tree species diversity may affect biotrophic ectomycorrhizal fungi and plant pathogens more strongly compared to free-living saprotrophs. Richness and community composition of biotrophic fungi are most strongly controlled by tree species identity, but tree species richness and composition may also have roles in determining richness and composition of ectomycorrhizal fungi and plant pathogens in mixed stands.

This thesis addresses diversity of fungi in relation to tree litter and host tree diversity and tree neighbourhood effects. The following main hypotheses were postulated: 1) fungal richness increases with increasing litter richness; 2) litter composition affects the community composition of saprotrophs, plant pathogens and EcM fungi; 3) the relative proportion of host-specific EcM fungi is higher in their host plant litter; 4) diversity of biotrophic EcM fungi and plant pathogens is related to dominant vegetation, whereas free-living saprotrophs are more affected by abiotic factors; 5) tree species richness increases EcM fungal richness at different spatial scales; 6) tree species identity affects richness and composition of EcM fungi; 7) EcM fungal richness and community composition depend on tree neighbourhood context. To study the effects of tree species, we analysed root and soil samples and decomposed foliar and root litter samples. Litter and root samples were collected from tree diversity experimental areas in Finland. For larger-scale field surveys, we collected soil samples from Estonia and North Latvia, and worldwide. We used high-throughput sequencing methods to identify fungal taxa present in the collected samples.

The main results and conclusions are the following: 1) fungal diversity increases with increasing foliar litter richness. This suggests that litter mixtures

provide more microhabitats for the niche specialists. Fungal diversity in root litter is only weakly affected by litter richness; 2) foliar litter composition determines community composition of saprotrophic and plant pathogenic fungi, but in root litter, litter composition effect on saprotrophic and plant pathogenic fungi is weaker. EcM fungal community composition in foliar litter can be weakly affected by litter composition; 3) host-specific fungi may not prefer the litter of their host plant; 4) EcM fungal richness is related to plant richness at global scale. At regional scale, positive correlation between plant richness and fungal richness can be present, but this effect may not be directly causal; 5) tree species identity can determine EcM fungal richness. Tree species identity has also an important effect on community composition of EcM fungi and plant pathogens; 6) EcM fungal richness of birch, pine or spruce does not depend on neighbouring tree species. EcM fungal community of spruce differs in mixed stands of birch and spruce compared with spruce monocultures. This suggests that birch neighbourhood in mixed stands may improve soil properties that can influence EcM fungal communities; 7) taken together, tree species richness has usually a positive effect on fungal diversity, but the direct influence depends on the effect of particular plant species and the confounding factors. This thesis provides new insights into the effects of root litter mixing on fungal communities. Also, it improves the knowledge of neighbourhood effects on root-associated EcM fungal communities and stresses the importance of mixed tree species stands in forestry. Future research should incorporate larger plant species gradients in order to study the relationship between plant species richness on fungal richness. However, care must be taken by accounting taxonomic sampling effects, which can mask the effect of tree species richness *per se*.

SUMMARY IN ESTONIAN

Puuliikide mõju seente liigirikkusele ja liigilisele koosseisule

Seened on metsaökosüsteemis olulised süsiniku ja toitainete ringes. Saprotroofid on looduses peamised orgaanilise aine lagundajad. Mükoriisat ehk seenjuurt moodustavad seened aitavad taimedel omastada mineraalaineid ja seeläbi suurendavad nende produktiivsust. Mükoriisaseentel ja patogeenidel on oluline mõju taimekooslustele ka taimede- ja mulla-vahelise tagasiside kaudu. Taimede ja seente interaktsioonidel on ökosüsteemi funktsioneerimises tähtis osa, mistõttu maapealse ja mulla bioloogilise mitmekesisuse seoste mõistmine on olnud kaasaegsetes ökoloogilistes uuringutes oluline teema. Siiani pole hästi teada, mil määral puude liigirikkus ja koosseis mõjutavad seente liigirikkust ja kooslust. Puuliigid mõjutavad eeldatavalt seenekooslusi läbi otseste bioloogiliste interaktsioonide ja varise kvaliteedi. Metsaökosüsteemides seguneb kooskasvavate taimeliikide erineva keemilise koostisega lehevaris. Kas ja kuidas selline varisesegu mõjutab seal ja mullas elavaid mikroorganisme on jätkuvalt oluline uurimisteema. Juurevaris on lehevarise kõrval samuti oluline metsamulla süsinikuallikas, mis sarnaselt lehevarisele seguneb mitme puuliigiga puistutes. Juurevarise segunemise mõjusid on lehevarisega võrreldes märksa vähem uuritud. Mükoriissete seente liigirikkust ja liigilist koosseisu mõjutab kõige enam nendega interakteeruv puuliik, kuid puude liigirikkusel ja koosseisul võib samuti olla roll ektomükoriissete seente liigirikkuse ja koosseisu kujunemisel segapuistutes. Oma doktoritöös käsitlen seente elurikkust seoses taimede varise ja peremeestaimede mitmekesisuse ning puude naabruse mõjuga. Doktoritöö peamised hüpoteesid on järgmised: 1) seente liigirikkus varises on seda suurem, mida suurem arv puuliike on esindatud; 2) varise koosseis mõjutab oluliselt saprotroofide, taimepatogeenide ja ektomükoriisaseente liigilist koosseisu; 3) peremehe-spetsiifiliste ektomükoriisaseente suhteline osakaal on suurem just nende peremeestaime varises; 4) biotroofsete ektomükoriisaseente ja taimepatogeenide mitmekesisus on seotud peapuuliigi ja puude liigirikkusega, samas kui saprotroofe mõjutavad rohkem abiootilised tegurid; 5) ektomükoriisaseente liigirikkus suureneb puuliikide arvu suurenemisega erinevatel ruumiskaaladel; 6) puuliik määrab ektomükoriisaseente liigirikkuse ja liigilise koosseisu; 7) ühe puuliigi ektomükoriissete seente liigirikkus ja liigiline koosseis sõltuvad naabruses kasvavatest puuliikidest.

Hüpoteeside testimiseks viisin koos uurimisrühmaga läbi välieksperimendid ja vaatlusuuringud ning määrasin molekulaarsete meetoditega seeneliigid. Puuliikide mõju tuvastamiseks analüüsisime seenekooslusi lehe- ja juurevarise proovides ning juure- ja mullaproovides. Varise segamise mõju uurimiseks viisime läbi lagunemiskatsed Satakunta metsade elurikkuse uuringualal Edela-Soomes, mis on osa ülemaailmsest puuliikide mitmekesisuse eksperimentaaluuringute võrgustikust *TreeDivNet* (https://treedivnet.ugent.be/). Selleks, et uurida puude mitmekesisuse mõju ektomükoriissete seente kooslustele, kogusime juureproovid Põhja-Karjalas asuvast uuringuregioonist (vt Foto 1, lk 11). See on osa

projektist *FunDivEUROPE* (www.fundiveurope.eu), mille eesmärk on uurida puuliikide mitmekesisuse mõju ökosüsteemile Euroopa küpsetes metsades, keskendudes iga metsaregiooni puhul sellele omastele puuliikidele monokultuurides ja segapuistutes. Mullaseente elurikkust mõjutavate biootiliste ja abiootiliste tegurite määramiseks regionaalsel skaalal korjasime Eestist ja Põhja-Lätist 1251 mullaproovi ning globaalsel skaalal kogusime 365 mullaproovi. Sealhulgas Euroopast 86, Aasiast 77, Aafrikast 36, Põhja-Ameerikast 27, Lõuna-Ameerikast 59 ja Austraaliast 80 proovi. Seentaksonite määramiseks eraldasime kogutud proovidest DNA ja kasutasime mass-sekveneerimise meetodit. Seeneliikide määramiseks kasutasime rRNA geene siduvat ITS markerit. Saadud DNA-järjestused on talletatud ja avaandmetena kättesaadavad rahvusvahelistes geenipankades (INSDC, UNITE).

Minu doktoritöö peamised tulemused ja järeldused on järgmised: 1) seente liigirikkus lagunevas lehevarises on seda suurem, mida rohkem on selles erinevate puuliikide lehti. See viitab asjaolule, et väikeseskaalaline ressursside heterogeensus varisesegus tagab rohkem nišše, mis võimaldab koos eksisteerida suuremal arvul seeneliikidel. Juurte liigirikkuse mõju seente liigirikkusele sõltub kontekstist ja on ebaselge; 2) lehevarise koosseisul on tugev mõju saprotroofide ja taimepatogeenide liigilisele koosseisule. Juurevarise koosseis mõjutab saprotroofide ja taimepatogeenide liigilist koosseisu, kuid mõju on nõrgem kui lehevarises. Lehevarises võib varise koosseisul olla nõrk mõju ektomükoriisaseente liigilisele koosseisule, kuid juurevarises ei pruugi sellel mõju olla; 3) peremehespetsiifiliste ektomükoriisaseente ohtrus ei pruugi peremeestaime varises suurem olla; 4) globaalsel skaalal on peremeestaimede liigirikkuse ja ektomükoriisaseente liigirikkuse vahel positiivne seos. Regionaalsel tasemel on positiivne korrelatsioon enamasti tuvastatav, ent see ei pruugi olla otsene põhjuslik seos; 5) ektomükoriisaseente liigirikkus võib puuliikide lõikes erineda. Puuliigil on oluline roll taimepatogeenide ja ektomükoriisaseente koosluste struktureerimisel; 6) ektomükoriissete seente liigirikkus kasel, männil või kuusel ei sõltu naabruses kasvavatest puuliikidest. Ektomükoriisaseente liigiline koosseis kuusel võib kase ja kuuse segametsas erineda kuuse monokultuuriga võrreldes, osutades sellele, et kase naabrus kase–kuuse puistudes võib olla seotud paranenud mullaomadustega, mis võivad mõjutada ektomükoriissete seente kooslusi; 7) taimede liigirikkuse mõju seente elurikkusele on kõigi nelja töö põhjal pigem positiivne, ent sõltub suuresti kontekstist – liikide valikust ja segavatest tunnustest, millega paljudes uuringutes ei arvestata.

ACKNOWLEDGEMENTS

First of all, I thank deeply my supervisor Leho Tedersoo for the guidance and patience since my bachelor studies. I acknowledge all the co-authors of the papers included in this thesis. I am thankful to my colleagues for all the assistance and support: Sten Anslan, Mari Pent, Kati Küngas, Ahto Agan, Rasmus Puusepp, Ingrid Liiv, Indrek Hiiesalu, Mohammad Bahram, Sergei Põlme, Jane Oja, Heidi Tamm and many others. Last but not least, I am grateful to my family and friends for all the support and understanding.

Financial support was provided by Estonian Science Foundation (grants 9286, 1399PUT, 171PUT, PRG632, PSG136, MOBERC10, MOBERC13, MOBERC21, IUT20-30), Environmental Investment Centre (KIK12322), State Forest Management Centre (T160148), University of Estonian Life Sciences (P180024MIME, P200029MIME), Norway-Baltic financial mechanism (EMP265, EMP442), Frontiers in Biodiversity Research, European Research Council and the UK Natural Environment Research Council (grant number NE/K014285/1). The laboratory work was supported by the UK Natural Environment Research Council Biomolecular Analysis Facility at the University of Liverpool.

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