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TEELE JAIRUS

Species composition and host preference among ectomycorrhizal fungi in Australian and African ecosystems

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

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

I. Tedersoo L, Jairus T, Horton BM, Abarenkov A, Suvi T, Saar I, Kõljalg U. 2008. Strong host preference of ectomycorrhizal fungi in a Tasmanian wet sclerophyll forest as revealed by DNA barcoding and taxon-specific primers. *New Phytologist* 180: 479–490.

II. Tedersoo L, Gates G, Dunk CW, Lebel T, May TW, Kõljalg U, Jairus T. 2009. Establishment of ectomycorrhizal fungal community on isolated *Nothofagus cunninghamii* seedlings regenerating on dead wood in Australian wet temperate forests: does fruit-body type matter? *Mycorrhiza* 19: 403–416.

III. Tedersoo L, Bahram M, Jairus T, Bechem E, Chinoya S, Mpumba R, Leal M, Randrianjohany E, Razafimandimbison S, Sadam A, Naadel T, Kõljalg U. 2011. Spatial structure and the effects of host and soil environments on communities of ectomycorrhizal fungi in wooded savannas and rainforests of Continental Africa and Madagascar. *Molecular Ecology*: in press. doi: 10.1111/j.1365-294X.2011.05145.x

IV. Jairus T, Mpumba R, Chinoya S, Tedersoo L. 2011. Invasion potential and host shifts of Australian and African ectomycorrhizal fungi in mixed eucalypt plantations. *New Phytologist*: in press. doi: 10.1111/j.1469-8137.2011.03775.x

Author's contribution to each paper

	I	II	III	IV
Idea and design				*
Sampling			*	*
Molecular analysis	*	*	*	*
Data analysis				*
Writing	*	*	*	*

INTRODUCTION

Mycorrhiza is a mutualistic association between plant roots and fungi. Fungi receive carbon from plants and plants get mineral nutrients in return (Smith & Read 1997). The most common mycorrhiza types are arbuscular mycorrhiza and ectomycorrhiza (EcM). About 80% of studied plant species and 92% of plant families are mycorrhizal (Wang & Qiu 2006), of which 3% form EcM (Taylor & Alexander 2005). EcM is formed mainly between woody plants and fungi from the phyla Ascomycota or Basidiomycota. In temperate regions, the majority of trees are ectomycorrhizal, whereas arbuscular mycorrhiza dominates in most tropical plants. EcM trees tend to form monodominant patches in tropical forests (Connell & Lowman 1989, Alexander & Lee 2005). The symbiosis has specific anatomical appearance: root tips of plants are covered with a fungal sheath termed as 'mantle'. In addition, fungal hyphae surround epidermal or cortical cells of root tips of plants, forming a structure termed as a 'Hartig net'.

Ectomycorrhizal trees are usually able to form symbiotic associations with several different fungal species. For example, *Pseudotsuga menziesii* hosts about 2000 species of EcM fungi throughout its range (Trappe 1977), whereas a single *Populus tremula* tree may harbor more than a hundred fungal species (Bahram et al. 2011). Most EcM fungi are able to associate with multiple hosts simultaneously, but many subdominant species show high levels of host preference or even strict specificity (Molina et al. 1992; Horton & Bruns 1998). Fungi from the genera *Suillus* and *Rhizopogon* are strongly specific to tree species from the *Pinaceae* family (Molina et al. 1992, Collier & Bidartondo 2009, Nunez et al. 2009), whereas *Alnus* spp. associate with only a limited number of fungal species (Molina et al. 1992, Tedersoo et al. 2009).

Ectomycorrhizal symbiosis has independently evolved >60 times in fungi. These monophyletic groups of fungi are referred to as 'lineages' and they correspond to section- to order-level taxa in the fungal tree of life (Tedersoo et al. 2010a). At the global scale, the most species-rich EcM fungal lineages are /tomentella-thelephora and /russula-lactarius, followed by /cortinarius, /sebacina, /clavulina, /boletus and /inocybe (Tedersoo & Nara 2010). In Australia, fruit-body surveys have revealed that the EcM lineages /cortinarius, /descolea and /russula-lactarius are the most species-rich (Claridge et al. 1999, Lu et al. 1999, Bougher & Lebel 2001, Gates et al. 2005, Ratkowsky & Gates 2005), whereas soil mycelial communities are dominated by /russula-lactarius, /tomentella-thelephora, followed by /cortinarius and /inocybe (Bastias et al. 2006, Midgley et al. 2007). In tropical forests, the lineages of /russula-lactarius, /tomentella-thelephora and /boletus dominate on root systems of host trees (Diédhiou et al. 2010, Peay et al. 2010).

Ectomycorrhizal fungal species composition and diversity in a certain site is also influenced by the presence of different forest microsites (Tedersoo et al. 2003). Some EcM plants prefer to germinate in pits, root mounds and decaying logs (Hofgaard 1993). The EcM fungal community in dead wood differs from the soil EcM fungal community (Tedersoo et al. 2003, 2008). Due to the higher moisture content and other favorable microclimatic conditions, dead wood provides a suitable substrate for proliferation of roots and growth of EcM fungi (Harvey et al. 1978). In boreal forests, dead wood-inhabiting seedlings host a limited number of EcM fungi (Iwanski & Rudawska 2007) and their community structure depends on tree species and the presence of root connections with mature host trees (Tedersoo et al. 2008). Tedersoo et al. (2008) observed that in Estonian boreal forests, isolated seedlings harbor only a few EcM fungal species that belong to the orders Atheliales and Thelephorales that predominately form resupinate fruit-bodies.

Forest plantations have become an increasingly important supply for wood during the era of rapid deforestation of primary habitats (Richardson 1998). In 2010, plantations covered about 264 million ha globally and contributed about 7% to the world's forested areas (FAO 2010). Exotic trees are preferred over native ones due to their shorter rotation period, well-studied biology and the lack of pests in new habitats. Among hundreds of tree species used, *Eucalyptus, Pinus* and *Acacia* dominate in forest plantations (Richardson 1998, West 2006). When trees are transplanted to new localities, some of them grow well, whereas others thrive only after co-introduction of their native fungi. *Eucalyptus* trees grow better with their naturally symbiotic fungi compared to fungi from other regions (Chen et al. 2007). *Eucalyptus* spp. are, nevertheless, able to grow without their naturally symbiotic fungi (Tedersoo et al. 2007) and establish symbiosis with native fungi that are available in exotic habitats (Yazid 1994, Tedersoo et al. 2007, Buyck 2008). *Pinus* spp., by contrast, are not able to grow without their naturally symbiotic fungi (Mikola 1969), and they cannot form symbiosis with local fungi in exotic tropical or southern temperate habitats (Tedersoo et al. 2007, Nunez et al. 2009, Dickie et al. 2010, Walbert et al. 2010). When *Pinus* spp. are growing with co-introduced fungi in suitable habitats, they may naturalize and become invasive in suitable climatic conditions (Nunez et al. 2009).

It is relatively easy to follow the fate of introduced large organisms such as trees and mammals in novel habitats, but the establishment and spread of microbes may easily go unnoticed. The behavior of pathogenic fungi in novel habitats is usually detected through the damage they cause. Symbiotic and commensal fungi do not cause easily detectable ecological damage and their presence remains difficult to detect. It may take a lot of time before the introduced species become naturalized or detectable. For example, the fly-agaric *Amanita muscaria*, which was co-introduced with pines, broadened its host range from northern temperate plant families to *Nothofagus* species and gained the capacity to complete its life cycle with its novel host species in New Zealand and Australia a few hundred years later (Dunk 2002, Orlovich & Cairney 2004). A species of *Laccaria,* introduced along with *Eucalyptus* from Australia, has become naturalized on root systems of some native plant species in the Iberian Peninsula (Diez 2005). In Madagascar, introduced fungi have provided a new food source for local people in *Eucalyptus* plantations (Buyck 2008). In several parts of the world, local fungal species have been found fruiting in exotic *Eucalyptus* plantations, indicating that host shifts are possible in both native and introduced fungi (Chen et al. 2007, Tedersoo et al. 2007, Buyck 2008).

In my thesis, the following main research hypotheses were tested: 1) Australian and African EcM fungal communities differ in species richness and phylogenetic community composition; 2) EcM fungi display differential host preference in African, Australian and temperate ecosystems; 3) EcM fungi are capable of shifting hosts especially when roots of native and introduced trees intermingle; and 4) EcM fungi with resupinate fruit-bodies preferentially inhabit tree roots in dead wood compared to forest floor soil.

MATERIALS AND METHODS

Study sites

In all study sites, soil cores (15x15 cm to 5 (I, II) or 10 (III, IV) cm depth) were collected from below potential host trees. In addition, fruit-bodies of all putatively EcM fungi were collected, vouchered and deposited in the herbarium of Tartu University (TU). Sampling in different studies is briefly described below (see methods of each study for detailed information).

Study I

Samples were collected from wet sclerophyll forest in Tall Trees Walk, Mt Field National Park, Tasmania (42°40.9'S; 146°42.2'E), where three 1-ha plots were established in sites, where at least three EcM host trees– *Eucalyptus regnans* F. Müll*.,* *Nothofagus cunninghamii* (Hook.) Oerst and *Pomaderris apetala* Labill. - co-occured. Sampling was performed in August, 2006.

Study II

Samples were collected from two sites. The 1-ha Yarra site is located in the cool temperate rain forest dominated by *Nothofagus cunninghamii* at Acheron Gap in the Yarra Ranges National Park (37°41'S 145°44'E, altitude 770 m), Victoria, Australia. The 600-m^2 Warra site is located in a wet sclerophyll vegetation dominated by *Eucalyptus obliqua* L'Hér a site at Warra LTER near Tahune (43°04'S; 146°40'E, altitude 155 m), Geeveston, Tasmania, Australia. Soil samples were collected from below mature *N. cunninghamii*. In addition, seedlings (1–5 years old) of *N. cunninghamii* were sampled from decaying logs of medium decay classes (III and IV sensu Christy & Mack 1984). Up to two *Nothofagus* seedlings were sampled from the same log at least 5 m distance. The absence of mature tree roots in seedlings rooting zone was confirmed by digging the wood with a sharp knife.

Study III

Four study sites were established in African ecoregions that support many EcM hosts. The Kashima site is located in an ecotone of miombo (woodland) and dambo (seasonally flooded wetland) ecosystems in Kabompo district, NW Zambia (13°19'S; 24°30'E, altitude 1080 m). Sampling was performed in a 4-ha plot in January, 2008. The Tchimbele study site is in primary lowland rainforest in Mbé National Park in Littoral province of North-Western Gabon (0°37'N; 10°24'E, altitude 400 m). Sampling was performed in a 20-ha plot in May, 2009. The Mandena site lies in a littoral forest in Toliara province of SE Madagascar (24°58'S; 47°00'E, altitude 40 m). Sampling was performed in a 2-ha plot in March, 2010. The Korup site represents a primary lowland rainforest in Korup

National Park in Southwest Province of Cameroon (5°01’N; 8°48’E, altitude 120 m). Sampling was performed in a 12-ha plot in April, 2008.

Study IV

Samples were collected from two neighbouring plantations of *Eucalyptus grandis* W. Hill ex Maiden and *Eucalyptus camaldulensis* Dehnh*,* where native trees form an understorey. The plantations are located near Tumbama village, Kabompo district, Northwestern Province of Zambia (13°28’S; 24°25’E, altitude 1077 m). Two 2-ha plots were established in these plantations in January, 2008.

Molecular analyses

Fungal and plant species were identified based on molecular methods. In all studies, the aim was to maximize the number of identified species and to optimize the DNA extraction methodology. Genomic DNA was extracted from 1–6 root tips per sample using a Qiagen MagAttract 96 DNA Plant Kit or Qiagen Dneasy 96 Plant Kit for studies III and IV, and High Pure polymerase chain reaction (PCR) Template Preparation Kit for Isolation of Nucleic Acids from Mammalian Tissue for studies I and II. Nuclear rDNA ITS and Large Subunit (LSU) regions were amplified with PCR-methodology using respective primers (Table 1). To obtain the best success from amplification, new primers were developed to target specific fungal taxa. For amplification, PuReTaq Ready-To-Go PCR kit (GE Healthcare UK Limited, Little Chalfont, Buckinghamshire, UK) was used. For each reaction, 24 µl DNA extract and 0.5 µl of each primer were added. PCR products were checked on 1% agarose gels under UV-light and purified using Exo-Sap enzymes (Sigma, St Louis, MO, USA). DNA sequencing was performed using primers ITS4 (5′-tcctccgcttattgatatgc-3′), ITS5 (5′-ggaagtaaaagtcgtaacaagg-3′) and/or LF340 (5′-tacttgtkcgctatcgg-3′) for the ITS region, and ctb6 (5′-gcatatcaataagcggagg-3′) and/or LR5 (5′-tcctgagggaaacttcg-3′) for the LSU. Sequencing was performed in Macrogen Inc. (Seoul, South Korea or Amsterdam, The Netherlands). Sequences were assembled into contigs and checked for quality with Sequencher 4.7 or 4.9 software (GeneCodes Corp., Ann Arbor, MI, USA).

DNA sequences were assigned to molecular species based on 97% similarity (excluding flanking rDNA sequences). For the lineages of /cortinarius and /laccaria, a 98% similarity was used instead (I). Species were identified by running bulk megablast queries against the International Sequence Database (INSD) and UNITE (Abarenkov et al. 2010a) as implemented in the PlutoF workbench (Abarenkov et al. 2010b). Host plant species were identified from the same DNA extract as fungi based on the plastid *trnL* region. DNA was amplified using primers trnC (5′-cgaaatcggtagacgctacg-3′) and trnD (5′-ggggatagagggacttgaac-3′) following the same protocol as for fungi. Plant DNA was sequenced using a primer trnD. Plant species were identified based on the size differences (I, II) or sequence similarity (III, IV) of the *trnL* region.

Table 1 PCR primers used in different studies

Primer	Sequence	DNA region	Target	Study	References
ITS1-F	5′-cttggtcatttagaggaagtaa-3′	ITS	Fungal	I, II	Gardes & Bruns 1993
ITS2	5’-gctgcgttcttcatcgatgc-3’	ITS	Universal	III, IV	White et al. 1990
ITS4	5’-tcctccgcttattgatatgc-3’	ITS	Universal	III, IV	White et al. 1990
ITS4B	5’-caggagacttgtacacggtccag-3’	ITS	Agaricales, Boletales	III	Gardes & Bruns 1993
ITS4–Clav	5’-ggtagtcccacctgattc-3’	ITS	/clavulina	III	Study III
ITS4–Russ	5’-agcgggtagtctcaccc-3’	ITS	/russula–lactarius	III	Study III
ITS4–Seb	5’-tcagcgggtartcctactc-3’	ITS	Sebacinales	III	Study III
ITS4–Sord	5’-cccgttccagggaactc-3’	ITS	Sordariomycetes	I, III	Study I
ITS4–Tom	5’-aactcggacgaccagaggca-3’	ITS	/tomentella–thelephora	III	Study III
ITS5	5′-ggaagtaaaagtcgtaacaagg-3′	ITS	Universal	I	White et al. 1990
ITSOF-T	5’-acttggtcatttagaggaagt-3’	ITS	Fungal	I, III, IV	Taylor & McCormick 2008
LA-W	5’ –cttttcatctttcgatcactc- 3’	ITS	Ascomycota	I, II, III	Study I
LB-Z	5’ aaaaatggcccactagaaact 3’	nLSU	Basidiomycota	I, II, III	Study I
LB-W	5’-cttttcatctttccctcacgg-3’	ITS	Basidiomycota	I, II, III, IV	Study I
LB-Y	5’-ggtccgtgtttcaagacg-3’	nLSU	Basidiomycota	I	Study I
LR0R	5’-acccgctgaacttaagc-3’	nLSU	Universal	I, II, III	Hopple & Vilgalys 1994
LR21–Cer	5’-cgactcgttgagagcacaa-3’	nLSU	Ceratobasidiaceae	III	Study III
LR3-Asc	5′-cacytactcaaatccwagcg-3′	nLSU	Ascomycota	I, II	Study I
LR3–Pez	5’-cmtcrggatcggtcgatgg-3’	nLSU	Pezizales	III	Study I
LR3–Tom	5’-ctaccgtagaaccgtctcc-3’	nLSU	/tomentella–thelephora	III	Study I
LR3-Tul	5′-bactcgcatgcaaggtgca-3′	ITS	Tulasnellales	I	Study I
LR5	5’-tcctgagggaaacttcg-3’	nLSU	Universal	III	Vilgalys & Hester 1990
LR5-F	5′-cgatcgatttgcacgtcaga-3′	nLSU	Fungal	I	Study I
LR5-Seb	5′-attcgctttaccgcacaagg-3′	ITS	Sebacinales	I	Study I
LR5-Tom	5’-ctaccgtagaaccgtctcc-3’	ITS	/tomentella–thelephora	I, III, IV	Study I
ML5	5’-ctcggaaattatcctcataag-3’	mtLSU	Fungal	II	Bruns et al. 1998
ML6	5’-cagtagaagctgcatagggtc-3’	mtLSU	Fungal	II	Bruns et al. 1998

Phylogenetic analyses

Phylogenetic analyses were prepared to identify the potential origin of EcM fungi (IV), assuming that closest relatives are likely to originate from the same continent (Hosaka et al. 2008, Matheny et al. 2009). Separate phylogenetic analyses were performed for different EcM fungal lineages (cf. Tedersoo et al. 2010a). Alignments were conducted using sequences from different study sites in Africa and all relevant INSD and UNITE sequences. The phylogenetic analyses of the /tomentella-thelephora and /russula-lactarius lineages were restricted to tropical and Southern Hemisphere isolates, because of the data set size and distinction of the northern boreal and tropical clades as seen from the other lineages. The alignments of ITS sequences were constructed using Mafft ver. 6 (Katoh & Toh 2008) and corrected manually. Unrooted Maximum Likelihood phylograms were constructed using RAxML with 200 bootstrap replicates and default options (Stamatakis et al. 2008). Rapid bootstrap values were used to estimate the robustness of branches and the potential origin of isolates. Isolates were considered to be native African if the same species were found in natural African habitats or they clustered with other African and/or SE Asian isolates with strong support (>70% BS). Conversely, taxa were regarded as Australian if they belonged to EcM lineages absent from the native vegetation of Sub-Saharan Africa, occurred in other eucalypt plantations, and/or belonged to the strongly supported Austral (incl. Australia, New Zealand, New Caledonia and Argentina) clades. Isolates that matched none of these criteria were conservatively assigned to uncertain origin.

Statistical analyses

Fisher's Exact tests were calculated to assess the occurrence of host preference (I, III, IV) and the effect of nearest host (I) on EcM fungi at the species and family levels of host trees. Species accumulation curves were calculated using a computer program EstimateS ver. 8 (Colwell 2006) to compare species richness. Moran's I was calculated to establish whether spatial factors cause biases in fungal distribution. Detrended Correspondence Analysis (DCA) using PC-ORD ver. 5.04 (McCune & Mefford 2006) was employed to reveal the effects of host species, host vicinity and plot on EcM fungal community structure (I). To address the relative importance of spatial effects on the EcM fungal communities, vectors of Principal Coordinates of Neighbor Matrices (PCNM) were constructed according to Borcard & Legendre (2002)(III). PCNM vectors were calculated based on the geographical distance matrix and ordered by coefficients of determination based on forward selection and 1,000 permutations as implemented in the Pakfor package of R (R Core Development Team 2007). All significant ($P<0.05$) PCNM vectors were included in the distance matrix for multivariate analysis. The relative effects of the PCNM vectors, host and soil horizons, were addressed based on Bray-Curtis distance measure as implemented in Adonis permutational multivariate analysis of variance function of the Vegan package of R (III). For the fourth study (IV), the relative effects of host were assessed by use of Adonis. Based on the same options, Non-metric Multidimensional Scaling (NMS) plots were constructed to visualize the relative effects of these variables on EcM fungal communities (III, IV). Vectors and centroids of each variables were fitted into the NMS plots using function envfit. Significance level of $\alpha<0.05$ was used throughout the studies. In study II, two-way ANOVA was performed to study the effects of site and substrate on species density of EcM fungi. Mann- Whitney *U* tests and Fischer's exact tests were calculated to address the differences in relative abundance of EcM fungal lineages and frequency of species, respectively, between forest floor soil and dead wood. To control false discovery rate and reduce family wise error rate arising with multiple statistical testing, obtained P values were subjected to a sharpening procedure of Benjamin-Hochberg correction (Verhoeven et al. 2005). A canonical multivariate analysis was performed to evaluate differences in fungal communities between forest floor soil and dead wood and between sites using a computer program CAP (Anderson & Willis 2003). To test whether EcM fungal taxa with resupinate and non-resupinate fruit bodies occur at similar frequency in dead wood or not, a chi-square test was used. To further address potential phylogenetical biases among EcM fungal communities among substrates, G-tests using species frequency data were performed for nine most common EcM lineages as implemented in computer program Unifrac (Lozupone et al. 2006). For this analysis, available LSU sequences from all species and ITS sequences from /cortinarius and /laccaria were aligned using Mafft 5.861 (Katoh et al. 2005) and corrected manually. Eight species lacking >250 bp LSU sequence and *Tulasnella* sp3 were removed from the analysis because of the presence of long, unstable branches and unstable position. A parsimony analysis using 100 random start generations and TBR branch swapping was run in PAUP* 4.0d81 (Swofford 2002). One of the 21,834 most parsimony trees was randomly selected as an input to Unifrac. The *P* values of *G* tests were subjected to the Benjamini-Hochberg correction.

RESULTS

In Mt. Field site, Australia (I), 123 species of EcM fungi were recovered. The majority of species (55.3%) were found only once. *Laccaria* sp. 1 and *Lactarius eucalypti* were the most frequent. The /cortinarius (28 spp.), /tomentella-thelephora (18 spp.) and /russula-lactarius (10 spp.) were the most species-rich lineages of EcM fungi. At Warra and Yarra, respectively, 86 and 25 species of EcM fungi were identified on the roots of *Nothofagus cunninghamii*. The lineage of /cortinarius dominated in both sites, followed by /clavulina and /russula-lactarius at Warra, and /descolea and /tomentella-thelephora at Yarra. In Africa, 94, 101, 46, 111 and 60 species of EcM fungi were recovered in Kashima, Tchimbele, Mandena, Korup and Tumbama, respectively. The lineages of /russula-lactarius, /tomentella-thelephora and /boletus dominated in all sites except Tumbama, where the third most species-rich lineage was /clavulina instead of /boletus. Because of differential sampling effort, the number of species is not directly comparable among sites. Species accumulation curves suggest that Australian sites comprise more species than African sites (Figure 1).

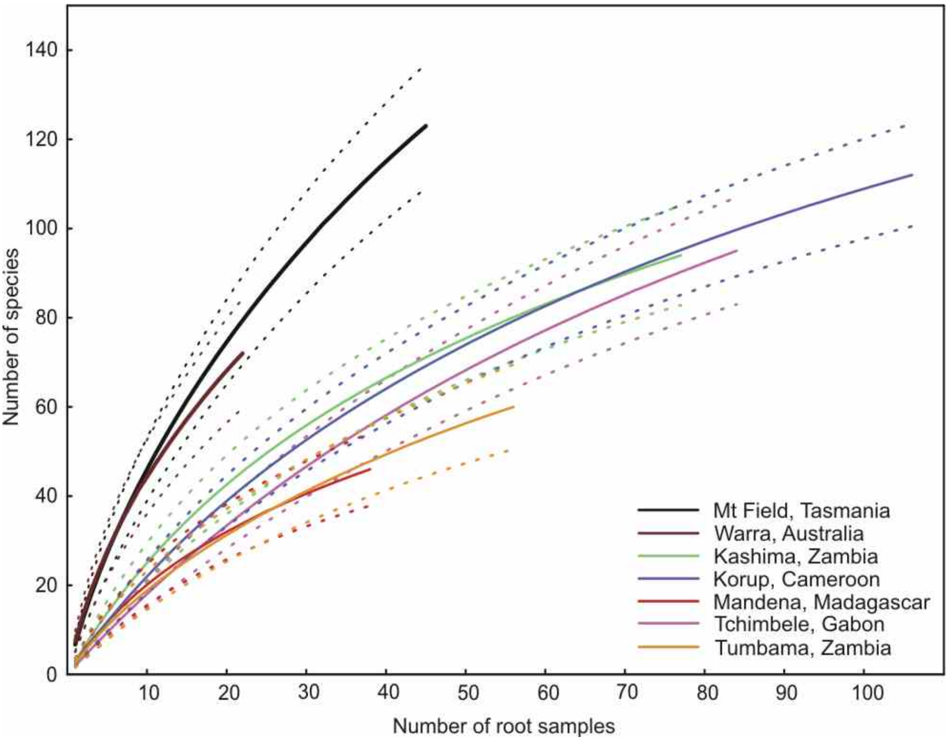

Figure 1 Rarefied species accumulation curves (solid lines) and their 95% confidence intervals (pointed lines) of ectomycorrhizal fungi at the seven study sites.

Australian EcM fungi displayed strong preference for host plants (I). Nineteen species (65.5%) were significantly affected by host plant roots in Mt Field site (Figure 2). Host species effect was stronger than host vicinity effect in 12 out of 15 cases (I). Plot had no significant effect on any species. However, host had no effect on the frequency of the EcM fungal species in Africa (III). Only in Tchimbele (III), five species showed significantly biased association towards host species, but in most cases (except one) the effect was explained by spatial autocorrelation. In the mixed eucalypt plantation in Tumbama (IV), three species of fungi with Australian origin showed host preference for their native eucalypt hosts. In all African and Australian sites, host trees did not differ in the richness of associated EcM fungi.

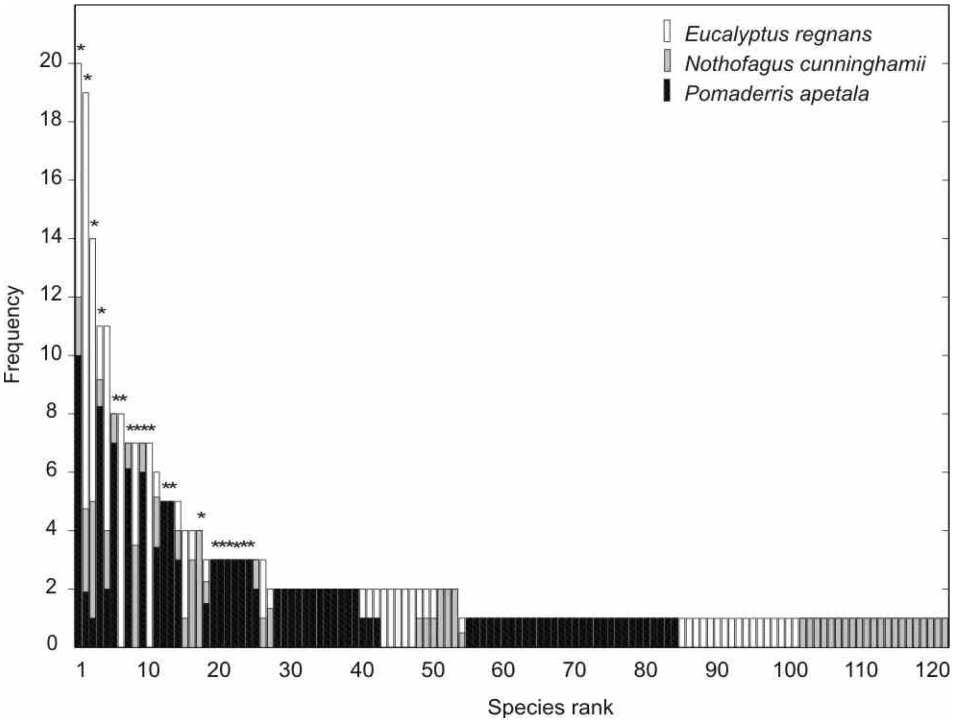

Figure 2 Ranked frequency of ectomycorrhizal fungi on three host species in study I. Differential shading demonstrates the weighted proportion of each host species. Asterisks denote statistically significant host-biased frequency according to Fisher's Exact test and sharpened Benjamini-Hochberg corrections.

In Tumbama, 28 species were associated with the introduced *Eucalyptus* spp., and 46 species with native Caesalpinioideae. Nine species of EcM fungi had potential Australian origin and eight species had uncertain origin. Fourteen species were shared between the native and exotic host trees. Majority of those species were of African origin and only three species (/terfezia-peziza depressa Z01, /tomentella-thelephora Z01, /tomentellopsis Z01) were of Australian origin. Potentially Australian species /hysterangium Z04 was found only once on native tree. Species accumulation curves for different host trees showed no difference of species diversity for native and exotic tree species neither on species nor family level (Figure 3).

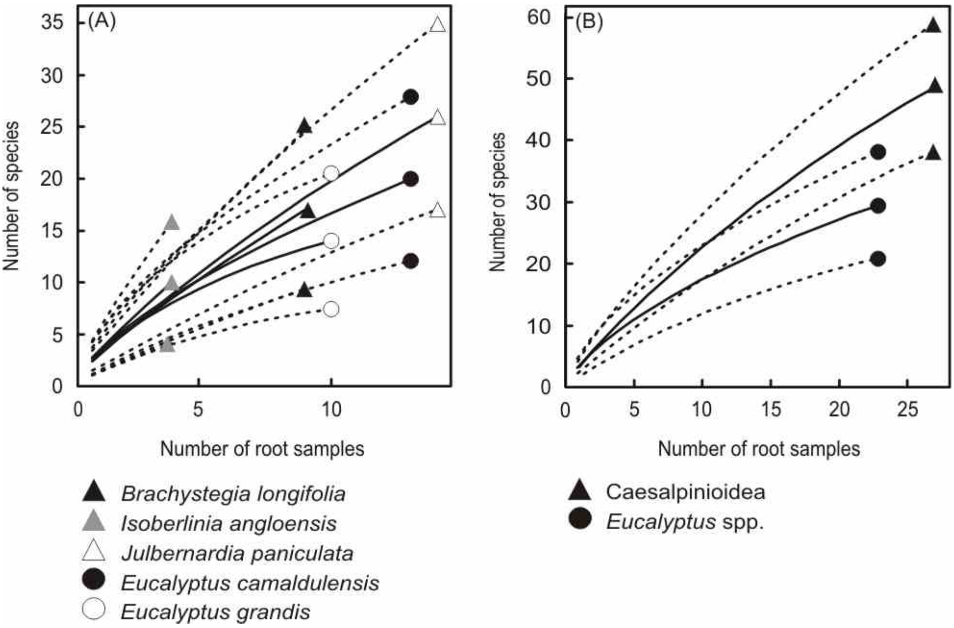

Figure 3 Rarefied species accumulation curves (solid lines) and their 95% confidence intervals (dotted lines) of ectomycorrhizal fungi on root systems as based on (a) host species; and (b) host families.

Dead wood harbored 32 species at Warra and six species in Yarra. At Warra, species density, species richness in soil and in dead wood was significantly higher than in Yarra. EcM fungal taxa with resupinate fruit-bodies were found in dead wood on 39.4% occasions, whereas taxa with no or other types of fruit bodies occurred in dead wood on 24.4% occasions. The differences in these ratios were statistically significantly different based on chi-square tests. However, lineage level tests provided no support for preferential association of resupinate fruit-body type with dead wood. Nevertheless, there were statistically significant differences in abundance of in several fungal lineages between forest floor and dead wood. In particular, /cortinarius, /russula-lactarius and /sordariales were more abundant in forest floor soil. At species level, 14 of the 21 statistically compared data displayed significant differences for substrate. In particular, /cortinarius, /descolea, /russula-lactarius and /tomentella-thelephora comprised species that were more frequent in forest floor soil than in dead wood. Species occurring most commonly in logs (*Tomentella* sp12, *Laccaria* sp7, *Cenococcum* sp., *Helotiales* sp4) were among the most frequent EcM symbionts in forest floor soil.

DISCUSSION

In a Tasmanian wet sclerophyll forest (I), EcM fungi formed a phylogenetically diverse community that comprised 123 species. Minimum species richness estimators suggested the potential species richness to range from 210 to 247 species. However, the EcM fungal diversity at Yarra (II) was relative low in the forest floor soil in *Nothofagus cunninghamii* forest patch. In different ecosystems of Africa, fungal species richness was lower compared to Australia and Northern Hemisphere in spite of generally higher sampling effort (III; Tedersoo & Nara 2010). In all Australian sites (I, II), the most species-rich and abundant EcM fungal lineages were /cortinarius, /tomentella-thelephora, /russula-lactarius, /clavulina, /descolea and /laccaria (I). All these lineages, except /descolea and /laccaria, are species-rich and abundant also in Holarctic fungal communities (Gardes & Dahlberg 1996, Horton & Bruns 1998, Tedersoo et al. 2006). The /descolea lineage is endemic to the Southern Hemisphere with an exception of a single species (Tedersoo et al. 2010a). By contrast, the /laccaria lineage is relatively species-poor (Rinaldi et al. 2008) and the species are usually relatively infrequent in mature forests of the Northern Hemisphere (Gherbi et al. 1999, Genney et al. 2006). These two lineages have not been found in African and South American tropical ecosystems (Tedersoo et al. 2010a). The most common and abundant EcM fungal lineages across all African sites included /russula-lactarius, /tomentella-thelephora and /boletus. Altogether 18 EcM fungal lineages were found from these study sites combined (III). In comparison, a single site in temperate ecosystems commonly supports more than 20 lineages (Tedersoo & Nara 2010), which indicates the relative phylogenetic poverty of African EcM communities. The community composition of EcM fungi is highly similar across different African sites, independent from ecosystem type, and resembles other tropical forests (Diédhiou et al. 2010, Peay et al. 2010). Only species of the /inocybe lineage tended to be more common in miombo woodlands of Zambia (III;IV) and Benin (N.S. Yorou & L. Tedersoo unpublished) compared to the rainforest habitats. The /russula-lactarius and /tomentella-thelephora are the dominant lineages both in Australian, African and northern temperate sites, indicating their global dominance. In particular, the /russula-lactarius lineage seems to comprise the greatest proportion of species in African ecosystems that is consistent with implications from fruit-body surveys (Buyck et al. 1996). Tropical ecosystems are inferred as potentially ancestral habitats and evolutionary centres for the /russula-lactarius lineage (Buyck et al. 2008). However, the generally lower species richness of EcM fungi in tropical regions is attributable to the poorer soil environment and evolutionary ecology of the major host plants (Tedersoo & Nara 2010).

In boreal and temperate ecosystems, host is usually one of the most important factors that affect EcM fungal species composition (Ishida et al. 2007, Morris et al. 2008). In Tasmania, 66% of the common EcM fungal species showed statistically significant host preference, although exclusive specificity was less common among the most frequent species (I). In this forest, host preference is clearly stronger than in Northern temperate ecosystems, where only few species have typically host-biased distribution (Horton & Bruns 1998, Ishida et al. 2007). Conversely, the dominant fungal species showed no host preference, independent from the plant groups and ecosystem types, in the African study sites (III). However, in NW Amazon, most of the dominant EcM fungal species displayed strong genus-level host specifity, which may be related to the inherent specificity in the *Nyctaginaceae* family (Tedersoo et al. 2010b). *Alnus* spp. in the Northern Hemisphere (Molina et al. 1992) and *Gnetum* spp. in the tropical regions (Bechem 2004) are also highly selective for their EcM symbionts, suggesting that the relative importance of host specificity is a function of the plant taxa in question rather than ecosystem types. Thus, (taxonomic) sampling effect may play a substantial role in addressing host preference and specificity patterns. Of fungi, most members of the /suillus-rhizopogon lineage are exclusively associated with certain members of the *Pinaceae* family (Molina et al. 1992). Niche partitioning via host specificity has been hypothesized to contribute to the high fungal species richness in temperate ecosystems (Ishida et al. 2007), but experimental evidence for this is lacking. High host specificity but low fungal richness in NW Amazon (Tedersoo et al. 2010b), however, contradicts these predictions on a global scale.

Host shifts rather than strict coevolution appears to be a common pattern in EcM fungi in sympatric conditions (den Bakker et al. 2004, Matheny et al. 2009). There is also limited evidence for long-distance dispersal and simultaneous host shifts in Basidiomycota (Hosaka et al. 2008, Matheny et al. 2009). We demonstrated that broadening of host range may occur spontaneously in field conditions during the establishment of exotic forestry plantations and cointroduction of mycorrhizal symbionts (IV). As expected, shifts to alien hosts were more frequent when the root systems of different host trees were overlapping. We estimated that essentially all African EcM fungal species found in Tumbama are able to colonize *Eucalyptus* spp. in vivo, because no host preference was recovered among the native fungal species (IV). Previously, Garbaye et al. (1988) demonstrated that *Eucalyptus* spp. may establish EcM symbiosis with native fungi in experimental conditions, although a few fungal species failed to form EcM in other trials (Bâ et al. 2010). In contrast to African fungi, the three most common Australian fungal species did not colonize the native trees despite their prevalence on *Eucalyptus* spp. Nevertheless, some of the alien fungi were able to complete their life cycle and form sporulating fruit-bodies. This indicates that these introduced species are adapting to the native conditions. *Eucalyptus* spp. perform better with their co-introduced fungi than with local fungi (Malajczuk et al. 1984, Chen et al. 2007). Taken together, these results suggest that adaptive coevolution between fungi and their hosts is influenced by competition among fungi in the soil habitat.

Naturalization and invasion of EcM fungi may be more common with phylogenetically closely related hosts (Selosse et al. 1998, Pringle et al. 2009).

Many invasive species need time for naturalization before they become invasive (Richardson et al. 2000). Whether or not invasive EcM fungal species may influence their new habitat is not yet predictable. In novel habitats, EcM fungi may transform soil carbon cycling (Gadgil & Gadgil 1975, Chapela et al. 2001), affect mineral nutrient dynamics (Philips & Fahey 2006), and alter surrounding vegetation (Richardson & Rejmanek 2004).

Seedlings in dead wood hosted less EcM fungal species compared to mature trees and the species composition differed from soil EcM fungal composition (II). While Tedersoo et al. (2008) found out that in northern hemisphere EcM fungi with resupinate fruit-bodies are dominating in dead wood, such relationship was also found, but not regarded as causal in the current study (II). Rather, the dominant EcM fungi in soil also dominate on root systems of seedlings in dead wood (II), except members of the /cortinarius and /russula-lactarius lineages that are considered as late successional colonizers (Last et al. 1987, Gibson & Deacon 1990). The EcM lineages of /laccaria, /descolea and /tomentella-thelephora dominated on isolated seedlings in dead wood in Australia. Of these taxa, only members of the /tomentella-thelephora lineage form resupinate fruit-bodies. In contrast to Australia, *Laccaria* spp. rarely colonize seedlings on dead wood in European boreal forests (Tedersoo et al. 2008) and they are also infrequent members of northern temperate fungal communities (Tedersoo & Nara 2010).

CONCLUSIONS

Species richness was highest in Tasmanian wet sclerophyll forests and was comparable with species richness in Holarctic region (I). In contrast, in Africa, species richness was lower, and fewer fungal lineages were present (III). Tropical EcM fungal communities are phylogenetically highly similar in different continents. There was a strong host preference among EcM fungi in a Tasmanian wet sclerophyll forest. Compared to other hosts, *Pomaderris apetala* hosted highly different EcM fungal communities (I). However, host preference was not detected among the most common fungal species in Africa (III). Based on these and previously published results, host specificity is probably related to the (taxonomic) sampling effect of hosts. Host shifts among ectomycorrhizal fungi may occur particularly commonly, when the roots of trees intermingle (IV). These host shifts may lead to naturalization and invasion of the introduced *Eucalyptus* species or spread of cointroduced EcM fungal species as detected in other ecosystems. Seedlings of *Nothofagus* associate with EcM fungi during their establishment on dead wood in Australian wet temperate forest. General commonness explains the spread of EcM fungal species in dead wood better than resupinate fruiting habit.

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SUMMARY IN ESTONIAN

Ektomükoriissete seente liigiline koosseis ja peremehe-eelistused Austraalia ja Aafrika ökosüsteemides

Mükoriisa on taimede ja seente vaheline vastastikku kasulik kooselu, mille käigus taim varustab seent suhkruga ning saab vastu mineraalaineid. Levinuimad mükoriisa tüübid on arbuskulaarne mükoriisa ja ektomükoriisa. Parasvöötme metsades on ülekaalus ektomükoriisat moodustavad puud, samas kui valdav enamus troopiliste alade puid moodustab arbuskulaarset mükoriisat. Ektomükoriissed puud moodustavad troopilistes ökosüsteemides monodominantseid kooslusi. Enamikul ektomükoriissetest puuliikidest ei ole kindlat seensümbiondi eelistust. Näiteks üks hariliku haava (*Populus tremula*) isend võib korraga moodustada mükoriisat rohkem kui saja erineva seeneliigiga. Samas lepp (*Alnus* spp.) kasvab koos vaid väheste temale omaste seentega. Lisaks peremeespuudele mõjutab ektomükoriisaseente liigilist koosseisu ka kasvukoha heterogeensus. Näiteks lagupuidu mükoriisaseente kooslus erineb mullas olevast ektomükoriisaseente kooslustest.

Seoses kasvava nõudlusega puidu järele suureneb kogu maailmas metsaistanduste pindala. Istandustes kasutatakse peamiselt kiirekasvulisi sissetoodud puuliike, millel on uues keskkonnas vähem kahjureid. Enamik istandustes kasvavaid puid on ektomükoriissed ja mitmed neist sõltuvad seensümbiontide olemasolust. Minu töö eesmärgid olid: 1) kirjeldada ektomükoriisaseente kooslusi Austraalia niisket tüüpi sklerofüllimetsas ja Aafrika valitud ökosüsteemides; 2) tuvastada ektomükoriissete seente peremehe-eelistused nendes kooslustes; 3) tuvastada, kas kohalikud ja sissetoodud seened on võimelised oma looduslikult peremeestaimelt võõrale peremeestaimele üle kanduma ja 4) võrrelda ektomükoriisaseente kooslusi lagupuidus ja mullas Austraalia lõunapöögi metsades.

Uurimustöö viidi läbi ühes Tasmaania niisket tüüpi sklerofüllimetsas, ühes Austraalia ja ühes Tasmaania lõunapöögi metsas, neljas erinevas Aafrika looduslikus ökosüsteemis ning kahes eukalüpti-istanduses Kesk-Aafrika lõunaosas, kus teise rinde moodustasid kohalikud puud. Igalt proovialalt koguti proovid sama metoodikat kasutades. Nii seene- kui ka taimeliigid määrati molekulaarsete meetodite abil. Liikide geograafilise päritolu kindlaks tegemisel kasutati võrdluseks teistest Aafrika looduslikest kasvukohtadest kogutud materjale.

Selgus, et Austraalias on ektomükoriisaseente liigiline ja fülogeneetiline mitmekesisus suurem kui Aafrikas. Kui Aafrika erinevates ökosüsteemides olid arvukamalt esindatud seened rühmadest /russula-lactarius, /tomentella-thelephora ja /boletus, siis Austraalias oli arvukaim /cortinarius, millele järgnesid /tomentella-thelephora, /russula-lactarius, /clavulina, /descolea ja /laccaria. Austraalias oli 66% ektomükoriissetest seeneliikidest peremehe spetsiifilised, samas kui Aafrika seentel peremehe-eelistust ei esinenud. Aafrikast ja

Austraaliast pärit seened olid võimelised eukalüptiistanduses mükoriisat moodustama mitteomaste peremeestaimedega.

Liigirikkus oli suurim Tasmaania niisket tüüpi sklerofüllimetsas, mis on võrreldav parasvöötme metsadega (I). Aafrikas oli nii ektomükoriissete seente liigirikkus kui ka olemasolevate seenerühmade arv väiksem (III) ning sarnanes teiste troopikas tehtud uurimuste tulemustele. Tasmaania niisket tüüpi sklerofüllimetsas eelistasid seeneliigid teatud peremeestaimi. Liigi *Pomaderris apetala* seenekooslus erines selgelt teiste puude omast (I). Aafrikas ei leitud ühelgi domineerival seeneliigil peremehe-eelistusi (III). Peremehe vahetused on ektomükoriissetel seentel suhteliselt tavalised, kui kohalike ja sissetoodud puude juured puutuvad kokku (IV). Introdutseeritud seente peremehe vahetused võivad põhjustada sissetoodud puude ja seente naturaliseerumist või bioloogilist invasiooni (IV). Lagupuidul kasvavad lõunapöögi seemikud olid sümbioosis ektomükoriisaseentega (II) ning nende seente liigilist koosseisu mõjutas antud seeneliikide ohtrus ümbritsevas mullas, mitte seente viljakeha tüüp.

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PUBLICATIONS

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Research interests

Ecology and biogeography of ectomycorrhizal fungi
Host preference of ectomycorrhizal fungi
Host shifts among native and introduced ectomycorrhizal fungi

Publications:

Tedersoo L, Bahram M, Jairus T, Bechem E, Chinoya S, Mpumba R, Leal M, Randrianjohany E, Razafimandimbison S, Sadam A, Naadel T, Kõljalg U. 2011. Spatial structure and the effects of host and soil environments on communities of ectomycorrhizal fungi in wooded savannas and rain forests of Continental Africa and Madagascar. Molecular Ecology doi: 10.1111/j.1365-294X.2011.05145.x [in print]

Jairus T, Mpumba R, Chinoya S, Tedersoo L. 2011. Invasion potential and host shifts of Australian and African ectomycorrhizal fungi in mixed eucalypt plantations. New Phytologist doi: 10.1111/j.1469-8137.2011.03775.x [in print]

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Conference presentations:

Jairus T, Chinoya S, Mpumba R, Tedersoo L. Host shifts between Australian and African ectomycorrhizal fungi. In conference "Next generation insights into geosciences and ecology", may 2011, Tartu, Estonia.

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Peremehevahetused kohalikel ja sisstoodud ektomükoriisa seentel

Publikatsioonid:

Tedersoo L, Bahram M, Jairus T, Bechem E, Chinoya S, Mpumba R, Leal M, Randrianjohany E, Razafimandimbison S, Sadam A, Naadel T, Kõljalg U. 2011. Spatial structure and the effects of host and soil environments on communities of ectomycorrhizal fungi in wooded savannas and rain forests of Continental Africa and Madagascar. Molecular Ecology doi: 10.1111/j.1365-294X.2011.05145.x [ilmumas]

Jairus T, Mpumba R, Chinoya S, Tedersoo L. 2011. Invasion potential and host shifts of Australian and African ectomycorrhizal fungi in mixed eucalypt plantations. New Phytologist doi: 10.1111/j.1469-8137.2011.03775.x [ilmumas]

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Konverentsiettekanded:

Jairus T, Chinoya S, Mpumba R, Tedersoo L. Host shifts between Australian and African ectomycorrhizal fungi. Maateaduste ja ökoloogia erialade doktorantide konverents “Next generation insights into geosciences and ecology”, mai 2011, Tartu, Eesti

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Kursus: Analyzing high throughput sequence data in microbial community ecology, 23–26 märts 2010

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