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# Soil eukaryotic community responses to land use and host identity

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

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# LIST OF PUBLICATIONS

**This thesis is based on the following publications denoted in the text by bold Roman numerals:**

I. Sepp, S.-K., Davison, J., Moora, M., Neuenkamp, L., Oja, J., Roslin, T., Vasar, M., Öpik, M., Zobel, M. (2020). Woody encroachment in grassland elicits complex changes in the functional structure of above- and below-ground biota. Ecosphere (pending)

II. Sepp, S.-K., Jairus, T., Vasar, M., Zobel, M., & Öpik, M. (2018). Effects of land use on arbuscular mycorrhizal fungal communities in Estonia. Mycorrhiza, 28(3), 259–268. https://doi.org/10.1007/s00572-018-0822-3

III. García de León, D., Davison, J., Moora, M., Öpik, M., Feng, H., Hiiesalu, I., Jairus, T., Koorem, K., Liu, Y., Phosri, C., Sepp, S., Vasar, M., & Zobel, M. (2018). Anthropogenic disturbance equalizes diversity levels in arbuscular mycorrhizal fungal communities. Global Change Biology, 24(6), 2649–2659. https://doi.org/10.1111/gcb.14131

IV. Sepp, S.-K., Davison, J., Jairus, T., Vasar, M., Moora, M., Zobel, M., & Öpik, M. (2019). Non-random association patterns in a plant–mycorrhizal fungal network reveal host–symbiont specificity. Molecular Ecology, 28(2), 365–378. https://doi.org/10.1111/mec.14924



Author's contributions to the publications:

Was responsible for ***, contributed substantially **, contributed *

| | Designing the study | Carrying out the experiment | Analysing the data | Preparing the manuscript |
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| I | | | *** | *** |
| II | ** | *** | *** | *** |
| III | | | * | * |
| IV | ** | *** | *** | *** |

# I INTRODUCTION

## 1.1. Background

Knowledge on belowground diversity and its dynamics has lagged behind for decades, compared to understanding of aboveground biodiversity (Bardgett & van der Putten, 2014). Yet, awareness of the importance of soil biota in ecosystem functioning has risen at a quickening pace (Wall *et al.*, 2012). Belowground organisms are responsible for a vast array of ecosystem functions, including plant productivity, organic matter decomposition, nutrient cycling, climate regulation and pathogen control (van der Heijden *et al.*, 2015; Delgado-Baquerizo *et al.*, 2016, 2020). The piecemeal data on soil biodiversity, however, still precludes use of this major reserve of biodiversity and function (Orgiazzi *et al.*, 2016) in global assessments and policymaking (Cameron *et al.*, 2018).

Advances in molecular methods have provided the basis for overcoming some of the limitations of biodiversity research belowground (Lindahl *et al.*, 2013; Hart *et al.*, 2015), allowing ecologists to infer patterns of the structure and function of soil (micro-)biota (e.g., Davison *et al.*, 2015; Bahram *et al.*, 2018). It must be noted, however, that these rapid advances come at a cost of being prone to bias at nearly every step of the process, such as storage and extraction methods, primer choice (Garlapati *et al.*, 2019; Beng & Corlett, 2020), as well as dependence on the reference data available for accurate species identification (Lücking *et al.*, 2020).

### 1.1.1. Impact of land use

Growth of the human population has altered a significant proportion of all terrestrial ecosystems, with an estimate of roughly 50 million $km^2$ of soils (Goldewijk *et al.*, 2011) being under anthropogenic use (e.g., crop and livestock production). Current and future sustainability of human societies is unconditionally linked to the health, functions, and the very existence of soils worldwide (Sanderman *et al.*, 2017). Fact is that current human dominance of soil resources has several negative consequences, ranging from accelerated erosion and compaction to loss of biodiversity and soil organic matter and depletion of nutrients (Keesstra *et al.*, 2016). Nevertheless, impact of land use on different parts of soil biodiversity is poorly quantified (Creamer *et al.*, 2016), and as such, generalisations about soil functional changes or losses resulting from anthropogenic change are difficult to make.

Biodiversity studies typically consider the responses of single trophic groups to environmental change. There are mostly methodological reasons for this, as it is much more difficult to study different taxonomic groups together than to deal with one group. At the same time, the response of a given trophic group may depend on the abundance and diversity of other trophic groups (Soliveres *et al.*, 2016). Thanks to the methodological developments of recent years, it is now possible to use environmental DNA metabarcoding to study large fractions of the entire biotic community (Calderón-Sanou *et al.*, 2020) and to address associations

(i.e., multivariate correlation; Peres-Neto & Jackson, 2001) among different taxonomic and functional groups (Prober *et al.*, 2015; Tedersoo *et al.*, 2016; Janssen *et al.*, 2018; Neuenkamp *et al.*, 2018; Wubs *et al.*, 2019; Zinger *et al.*, 2019). Such a multitaxon approach makes it possible to identify which groups exhibit high turnover along the spatial and temporal gradients of interest and thus provides indirect information about changes to ecosystem function. Multitaxon studies are needed in order to understand which organisms show highest turnover and potentially drive changes in total community structure along different ecological gradients.

Interactions between plants and soil microbes have a great importance for determining plant fitness and community dynamics, and subsequently whole ecosystem processes (Semchenko *et al.*, 2018). In respect to these soil organisms, much attention has been focused towards functionally important functional groups such as arbuscular mycorrhizal (AM) fungi from the phylum Glomeromycota (Tedersoo *et al.*, 2018). With approximately three quarters of terrestrial plant species (Brundrett & Tedersoo, 2018) providing photoassimilated carbon to these obligately symbiotic organisms in exchange for nutrients foraged from the soil matrix (Smith & Read, 2008) and increased resistance to biotic and abiotic stresses (Sikes *et al.*, 2010) the amount of effort is unsurprising. Further, AM fungi contribute to ecosystem characteristics such as soil aggregation (Rillig *et al.*, 2015) and carbon and nitrogen cycling (Hodge & Storer, 2015; Treseder, 2016). Knowledge of AM fungal diversity is important to understanding of plant diversity patterns and community function (Zobel & Öpik, 2014; Kokkoris *et al.*, 2020), and in turn infer the role of the symbiosis in ecosystems.

The type and intensity of land use are important drivers of local biodiversity (Newbold *et al.*, 2015). With respect to AM fungi, intensification of land use has been demonstrated to result in a decrease in AM fungal molecular richness in roots (Helgason *et al.*, 1998) or in soil (Lumini *et al.*, 2010; Verbruggen *et al.*, 2012; Xiang *et al.*, 2014). Other studies have shown either an increase in root AM fungal molecular richness (Vályi *et al.*, 2015) or no changes in soil AM fungal molecular richness (Dai *et al.*, 2013) under intensive land use. However, no studies have examined if these discrepancies between studies might be influenced by initial diversity of ecosystems, which is becoming equalized by disturbance. It has been suggested that anthropogenic activity on community diversity and composition operates via facilitation of disturbance-tolerant, generalist taxa. Indeed, such patterns have been recorded among soil fungi at the regional scale (Mueller *et al.*, 2016).

Current information about the effect of land use on AM fungal communities is based mostly on comparisons of different agricultural practices (e.g., Jansa *et al.*, 2003; Lumini *et al.*, 2011; Manoharan *et al.*, 2017). Moreover, while these studies suggest that agricultural intensification can lead to decreases in AM fungal diversity and changes in community composition, they do not explicitly compare anthropogenic sites with analogous natural habitat. In order to identify large-scale variation in the effects of anthropogenic disturbance on AM fungal communities, it is necessary to compare natural and anthropogenic ecosystems in

otherwise analogous habitat conditions across a geographically broad range of locations. Further, there is much less information about the effects of e.g., seminatural land use or forestry management on AM fungal communities (but see Koorem *et al.*, 2017).

Particular AM fungal taxa may be favoured or inhibited by specific abiotic conditions such as soil pH (Dumbrell *et al.*, 2010), nitrogen and phosphorus availability (Camenzind *et al.*, 2014; Liu *et al.*, 2015), and soil texture (Lekberg *et al.*, 2007). The effects of land use on diversity and composition of AM fungi may result from different mechanisms. In open treeless ecosystems such as arable fields and cultivated grasslands, change in AM fungal community composition can be caused by different responses of fungal taxa to the combination of mechanical disturbance and nutrient addition (Säle *et al.*, 2015). AM fungal community composition in plant roots also may depend on light conditions; individual AM fungi can benefit or suffer from increased light availability to the host plant (Öpik *et al.*, 2009; Liu *et al.*, 2015; Koorem *et al.*, 2017). Land use changes associated either with the removal of upper vegetation layers (forest clearcutting) or the introduction of an upper canopy (shrub and tree encroachment) may affect AM fungal communities by increased or decreased carbon supply from plants to the fungi under changed light conditions.

### 1.1.2. Host preference in AM fungi

Generally, AM fungi have been shown to exhibit low host specificity (e.g., compared to root endophytes; Abrego *et al.*, 2020). Due to the relatively low number of fungal species (*ca* 288 described or *ca* 1700 putative species (Öpik & Davison, 2016); and relatively high number of mycorrhizal plant species (estimates up to 90% of the ca 308 000 known vascular plant species; Fitter & Moyersoen, 1996; Christenhusz & Byng, 2016), individual AM fungal species must associate with many different host plants, a fact that has been demonstrated in an analysis of a global scale dataset by Lekberg and Waller (2016). However, when viewed at the scale of a single community, AM fungi have been found to associate non-randomly with different plant species (Davison *et al.*, 2011, 2016; Bainard *et al.*, 2014).

It is possible that host – AM fungal preferences might manifest at the level of plant functional groups, rather than individual plant species. It has been shown that ecological groups of plant species associate with a specific set of AM fungal species (Öpik *et al.*, 2009; Davison *et al.*, 2011; Koorem *et al.*, 2017), with some evidence that plant adaptation to certain environmental conditions is related to the ability to selectively form functional symbiosis with AM fungi (Osborne *et al.*, 2018). At a finer taxonomic scale, the composition of AM fungal communities in the roots of plant individuals appears to depend on plant functional traits (Kotilínek *et al.*, 2017). These lines of evidence suggest that the ecological properties of plants can substantially shape AM fungal community composition (Geml & Wagner, 2018), and thus possibly the function of the fungal microbiome assembled in the roots (van der Heijden & Hartmann, 2016).

## 1.2. Objectives of the thesis

The main objective of the thesis was to **assess the effect of anthropogenic influence on soil microbial communities**. Toward that goal, we used eDNA metabarcoding from soil (**Papers I, II, III**) and roots (**Paper II**) to study the responses of mainly the arbuscular mycorrhizal fungal, but also other co-existing soil eukaryotic groups to land use change. Most of the work was carried out on understudied seminatural ecosystems to fill the knowledge gaps in these kinds of habitat types, but we also aimed to generalize, and thus addressed AM fungal communities in anthropogenic vs natural settings at a global scale.

A secondary aim was, drawing from the previous results, to **establish the occurrence of possible host-symbiont preference in the AM fungal – plant interaction network**, as host preference is one of the key areas of research needed to interpret results from metabarcoding, and to guide the application of plant symbiotic partners.

In particular, the papers comprising the thesis focused on the following:

**Paper I:** The paper studied the effect of management dependent presence or absence of woody vegetation on associations between different taxonomic and functional groups of soil biota in a wooded meadow. We used eDNA metabarcoding to address several taxonomic and functional groups in parallel, considering eukaryotes (in particular soil micro- and mesofauna), fungi and more specifically arbuscular mycorrhizal (AM) fungi. We aimed to infer the role of woody plants as ecosystem engineers (sensu Jones *et al.*, 1994, 1996) in driving the diversity and composition of the wider biotic community, notably aboveground vegetation and soil biota. In addition, we sought to assess the effectiveness of soil metabarcoding in describing the plant communities in comparison with conventional vegetation plots.

**Papers II, III:** Papers II and III were, in general, targeted towards describing the effect of land use on AM fungal communities. Toward that goal, Paper II studied the response of AM fungi to different land use types, including both 'pulse' (e.g., forest clearcutting) and 'press' (e.g. seminatural grassland management) type (Bender *et al.*, 1984) of human impacts. Paper III took a more global view on the impact of humans and looked at the effect of land-use-induced anthropogenic disturbance on the diversity and composition of AM fungal communities using a global set of paired anthropogenic (disturbed) and natural (undisturbed) plots.

In Paper II, as an additional aim, we compared the AM fungal communities of plant roots and surrounding soil to assess the effect of host plant in the formation of the observed AM fungal set.

**Paper IV:** We aimed to establish whether plant species exhibit specificity towards their fungal symbionts, and whether such specificity depends on plant traits. We accomplished this by exhaustively sampling a local plant – AM fungal network and describing the host effect of the plant species as well as looking at the bipartite network level characteristics of the system.

# II MATERIALS AND METHODS

## 2.1. Complex changes in biota as response to woody encroachment

### 2.1.1. Study design and data collection

**Paper I** assessed the compound effects of woody encroachment on the composition and diversity of grassland soil biota and aboveground vegetation. The study compared wooded and open patches in a wooded meadow habitat where the environmental conditions were homogeneous throughout the study area, and sampling plots differed by presence or absence of woody vegetation. The meadow of 153 ha has been a hayfield since at least the beginning of the 18th century, but probably for centuries earlier (Kukk & Kull, 1997; Kukk, 2004). The mowed area began to decrease in the 1940s, and currently only about 15 ha is used as a hayfield and mown annually. According to information from local landowners, currently wooded patches developed around large tree individuals during the 1940s and further expanded during the 1960s and 1970s.

Sampling was conducted in plots of 30 × 30 m, in each of which nine regularly spaced soil samples were collected. Two plots were located in open parts and two in wooded parts of the meadow. For each sampling point, we also described a 1 × 1 m vegetation subplot where all vascular plant species in the ground-layer community were recorded and their abundance was estimated as percentage cover (Peet & Roberts, 2013). The study encompassed the aboveground vegetation, general fungi, arbuscular mycorrhizal (AM) fungi, soil animals and plant DNA fragments present in soil.

### 2.1.2. Data analysis

The general soil fungal and soil animal data were split into functional and dietary groups, respectively, to draw conclusions about the patterns of more particular soil organism groups. Animal taxa were grouped based on dietary traits according to expert opinion, namely fungivores, bacterivores, litter feeders, root feeders, macro plant feeders, algal/lichen feeders, predators and parasitic animals. Fungal taxa were further classified into eight functional groups, based on the FUNguild database (Nguyen *et al.*, 2016), namely animal pathogens, plant/fungal pathogens (including parasites), saprotrophs (i.e., fungi whose main autecological niche is saprotrophy) and fungal decomposers (i.e., fungi that fill the decomposition niche in a community – including saprotrophs, but also certain mycorrhizal fungi; Lindahl & Tunlid, 2015), AM fungi, EcM fungi, fungal endophytes (but excluding fungi with recorded pathotrophic mode), and other symbiotrophs (mostly ecto- and orchid mycorrhizal, and lichenized fungi). Only FUNguild assignments with confidence levels of Probable and Highly Probable were

retained, whereas remaining fungal taxa were considered as undefined fungi. To compare soil biotic community richness, plant community richness, and compositional differences between the two habitat types, we fitted linear mixed models (LMM) and used permutational multivariate ANOVAs (PERMANOVA). LMMs (function lmer() from R package lme4; Bates *et al.*, 2015) used sample taxon richness as the dependent variable, habitat as an independent variable and plot as a random factor; the results of richness models were validated by parallel analyses with Chao extrapolated Shannon diversity (Chao *et al.*, 2014) as the dependent variable. We tested the effect of habitat on the composition of soil biotic communities using PERMANOVA with 999 permutations (function *adonis()* from R package vegan), assuming a nested data structure of plots within habitat types. For a coarse-scale overview of the biotic changes associated with woody plant encroachment, we performed a $\chi 2$ test (function *Chisq.test()* in R) on the cumulative sequence count table of the groups of soil biota (fungal functional groups, animal dietary groups, and plants) in either habitat type. The standardized residuals (standardized by residual cell variance) of individual cells were then used to infer the relative effect of each group of soil animals on the difference between the two habitat types. Pairwise correlation (i.e. a scaled measure of covariance) among groups of soil organisms and the plant community were assessed using Procrustean randomization tests (Peres-Neto & Jackson, 2001), using the functions *procrustes()* and *protest()* from the vegan package.

## 2.2. Effects of land use on AM fungal communities at small and large scales

### 2.2.1. Study design and data collection

The study in **Paper II** incorporated six regional habitat types from 12 sites in Estonia: semi-natural grazed dry calcareous grassland, overgrown ungrazed calcareous grassland, semi-natural wooded meadow (haymaking once per year), farmyard lawn, boreonemoral mixed forest, and clear-cut sites of boreonemoral forest. We identified AM fungi in the roots of a single plant species to avoid the effects of host species identity on root AM fungal community composition (Jansa *et al.*, 2008; Dumbrell *et al.*, 2010). Five randomly chosen individuals of *Prunella vulgaris* – a herbaceous plant species that occurs in a wide array of grassland and forest ecosystems – were excavated from each site. From the soil surrounding the roots of each focal plant individual, 5 g soil samples were collected for identification of the AM fungi available to the focal plant in soil.

For **Paper III**, 16 sites were included worldwide with two plots sampled per site: a natural grassland (unwooded sites), forest or shrubland (both considered wooded sites), and a corresponding anthropogenic homologue. The anthropogenic plot was located nearby (<10 km apart) and represented either an intensively managed arable land, cultivated lawn, heavily overgrazed pasture, roadside or wasteland (Table S1). Each plot represented an area with similar vegetation in

terms of vegetation height and the identity of dominant plant species. In all cases, disturbance had completely altered the natural plant community with virtually no plant species from the undisturbed community present.

### 2.2.2. Data analysis

In **Paper II**, We used linear mixed effects model to compare mean sample AM fungal richness and diversity among different habitat types. To account for the non-independence between samples from the same site, we included site in the models as a random factor, thereby effectively nesting samples within site. For comparisons of AM fungal community composition among habitat types, non-metric multidimensional scaling (NMDS) of Bray-Curtis distances was used to visualize the separation of communities. To test for significant differences among communities, we used nested two-way PERMANOVA with sample type and site nested within habitat as explanatory variables. For pairwise differences between habitat community compositions, we ran PERMANOVA for all possible habitat pairs and used Bonferroni correction to set significance levels for p-values. UniFrac distance (Lozupone & Knight, 2005) also was used to test for differences in phylogenetic community composition among samples.

To compare the difference in the dispersion of AM fungal communities in soil and root samples in **Paper II**, we calculated beta diversity in two complementary ways. First, by taking the group average distance from the centroid of all samples of that type (either root or soil). The alternative included calculating the mean distance to the centroid for the two sample types within individual sites and testing the differences in within-site dispersion (for both root and soil samples) among habitat types.

In **Paper III**, The effects of disturbance (natural, anthropogenic), ecosystem type (wooded, unwooded) and their interaction on alpha (AM fungal taxon richness and Chao extrapolated diversity (Chao *et al.*, 2014)) and beta diversity estimates were assessed using linear mixed models). Soil pH and soil phosphorus concentration (mg/kg) were included as covariates and a random effect structure of plot nested within site was incorporated. The proportion of cultured taxa in samples was modelled using a generalized linear mixed model (GLMM) with a binomial error structure and the same random and fixed effect structures as for the LMMs. Permutation multivariate analyses of variance (PERMANOVA) based on the single matching coefficient distance to centroid ($dCen_{sm}$) were conducted to assess the effects of ecosystem type, disturbance and their interaction, soil pH and soil phosphorus concentration on AM fungal taxonomic composition.

Beta diversity in **Paper III** was estimated within plot and within disturbance category (across sites). Following the recommendations of Anderson *et al.* (2011), we (i) estimated variation among communities with a measure of multivariate dispersion (*dCen*; the distance of each sample from a group centroid in multi-variate space (Anderson *et al.*, 2006)), based on dissimilarities derived using the simple matching coefficient ($dCen_{sm}$); and (ii) explored relationships between

community structure and environmental variables (including ecosystem type, disturbance and soil chemistry) using nonmetric multidimensional scaling (NMDS) based on $dCen_{sm}$.

## 2.3. Specificity patterns in a plant-mycorrhizal network

### 2.3.1. Study design and data collection

In **Paper IV**, the study was carried out in a phytocoenotically and edaphically homogenous plot in a semi-natural dry calcareous (alvar) grassland. Sampling was carried out as two temporal snapshots during one year: in the first half of July, and in the first half of September. On both occasions, the entire root system of up to five individuals of each plant species present in the *ca* 1000 $m^2$ plot (45 × 25 m) was excavated and subsequently sequenced for AM fungi. In total, 35 plant species (including two non-mycorrhizal species) were sampled (33 in July; 30 in September), and 224 samples were collected. The plant species belonged to 19 families, including 2 monocot and 15 eudicot families.

The local plant community was described with the help of 10 1 × 1 m vegetation plots from a separate study at the same site, conducted in the same year as the current study (García de León *et al.*, 2016). Percentage plant cover was estimated visually for each species in each plot. The local frequency of a plant species was calculated as the proportion of plots in which it was present; its local abundance was calculated as the sum of its cover values in all plots. The local abundance measure was taken to represent a coarse overview of the relative dominance of different plant species in the study habitat. We classified two plant functional groups for further analyses, namely grasses and forbs. Plant mycorrhizal status was defined as the frequency of occurrence of mycorrhizal symbiosis of said plant species in literature records (Gerz *et al.*, 2018). Mycorrhizal status was assigned on the basis of the data set in Gerz *et al.*,(2016), using two approaches: (a) mycorrhizal status as a categorical variable: plant species that have been consistently described as colonized by AM fungi in reporting literature are considered obligately mycorrhizal (OM); species sometimes reported as being colonized by AM fungi and sometimes not are considered facultatively mycorrhizal (FM); and (b) mycorrhizal status as a continuous variable (mycorrhizal status coefficient): calculated as the proportion of empirical observations of AM fungal colonization among all reports of mycorrhizal status for the particular plant species (Gerz *et al.*, 2016); larger values indicate a more obligatory state of AM formation.

### 2.3.2. Data analysis

To test which plant characteristics were related to AM fungal richness in root samples, we used linear mixed-effects models. The explanatory variables were plant mycorrhizal status, plant mycorrhizal coefficient, plant functional group, plant local abundance and plant local frequency, as well as the time of sampling. The response variable was the number of AM fungal virtual taxa in a plant root sample. To account for the non-independence of samples from the same species, we included plant species as a random factor. We used PERMANOVA analyses of Morisita-Horn distances to test the effects of plant species, time of sampling, plant mycorrhizal status, plant mycorrhizal coefficient, plant functional group, plant local abundance or plant local frequency on AM fungal community composition in root samples.

For calculating the plant-AM fungal network parameters, we used the aggregated species-level matrix with cells containing mean AM fungal taxon relative abundance per plant species across both seasons, and chose network indices that were able to incorporate abundance data. To test whether the observed network exhibited non-random patterns, we used a null model approach. In short, we compared the network characteristic value calculated from the real life data matrix to a pool of values from 999 matrices that were generated by randomly reshuffling the original data frame (using a conservative *quasiswapcount* algorithm). If the real value lied outside the 95% confidence interval of the distribution of the random values, the observed network was said to differ significantly from random, i.e., some biological factor is influencing the pattern.

## 2.4. Molecular and bioinformatics methods

For the soil sampling in **Papers I**, **II** and **III**, DNA was extracted from each individual 5 g sample of dried soil with the MoBio PowerMax Soil DNA Isolation Kit (MoBio Laboratories, Carlsbad, USA). For **Papers II** and **IV**, plant root sampling comprised randomly subsampling the root system of the target individual's root system up to a maximum of 75 mg (depending on availability of material), and extracting the DNA using the PowerSoil®-htp 96 Well Soil DNA Isolation Kit (MO BIO Laboratories, Inc., Carlsbad, CA, USA).

AM fungal DNA from the small-subunit (SSU) ribosomal RNA gene V4 region was amplified using the AM fungal specific primer pair WANDA (Dumbrell *et al.*, 2011) and AML2 (Lee *et al.*, 2008) for **Paper I**, and NS31 (Simon *et al.*, 1992) and AML2 for **Papers II**, **III** and **IV**. In **Paper I**, the following other amplicons and primer pairs were used: general fungi – ITS2 region with degenerate primer pair fITS7 and fITS7o (forward) and ITS4 (reverse primer; White *et al.*, 1990; Ihrmark *et al.*, 2012; Kohout *et al.*, 2014); plants – chloroplast trnL region with primers trnL(UAA)g and trnL(UAA)h (Taberlet *et al.* 2007); general eukaryotic community – 18S SSU rRNA gene V4 region with primers F574 and R952 (Hadziavdic *et al.* 2014). Sequencing was performed on

Illumina MiSeq platform for **Paper I** and 454 Life Sciences platform for **Papers II**, **III** and **IV**.

The bioinformatics workflow for all included papers has followed the steps described in Vasar *et al*. (2017). In short, sequence reads go through barcode and primer verification and removal, and quality filtering; Illumina-generated paired-end reads are combined. Chimeric sequences are omitted. The sequences are then submitted to a BLAST+ (Camacho *et al.*, 2009) search against the respective databases: Maarj*AM* (Öpik *et al.*, 2010) for AM fungi **(Papers I – IV**), UNITE (Nilsson *et al.*, 2018) for all fungi (**Paper I**), and GenBank (Clark *et al.*, 2016) for plants and general eukaryotic sequences (**Paper I**). In the Maarj*AM* database, SSU marker gene data from AM fungi is used to define phylogenetically determined species estimates called virtual taxa, henceforth referred to as VT. The resulting taxon identifications are subsequently collected into sample × taxon community matrices, which is the basis of all subsequent statistical analyses.

# III RESULTS

## 3.1. Complex changes in biota as response to woody encroachment

### 3.1.1. Changes in the belowground biota

Thirteen out of eighteen studied organism groups exhibited different mean richness per sample between the two studied habitat types, notably woody and open patches (Table 1). In all cases, mean sample richness was higher in open patches, except for EcM fungi, which exhibited significantly higher richness in wooded patches. In addition to the differences observed among plant communities (presented above), the two habitats hosted different communities of general soil fungi (ITS2; PERMANOVA $R^2 = 0.2$, $p = 0.002$) and soil animals (SSU V4; PERMANOVA $R^2 = 0.13$, $p = 0.002$), with the soil fungal communities of wooded habitat being distinct between the two sampling plots. With the exceptions of litter and macro plant -feeding soil animals, all soil organism groups included differed highly significantly in their community compositions between the two habitat types (Table 1), with habitat accounting for 9% (bacterivorous animals) to 44% (plants) of compositional variation. Out of 171 tested pairwise compositional correlations between communities of the groups included in the study (Procrustes Protest analysis), 99 indicated significant correlation at the sample level among different organism groups. Notable significant results included correlations between community compositions of plants and all fungi (ITS2 general fungal amplicon; $r = 0.9$, $p = 0.003$), plants and all soil animals ($r = 0.7$, $p = 0.003$), plants and AM fungi (AM-fungal specific amplicon; $r = 0.6$, $p = 0.003$), and all fungi and all soil animals ($r = 0.8$, $p = 0.003$). In terms of habitat-wise differences at the organism group level, there was a marked effect of habitat type on the relative abundance (based on sequence count) of different soil organism groups (contingency table $\chi^2 = 2.39 \times 10^4$, df = 17, p-value < 0.001; Fig. 1), with AM, EcM, other symbiotrophic fungi and fungal decomposers contributing most to the $\chi^2$ score.

**Table 1** Differences in mean taxon richness per sample and community composition of different organism groups in wooded and open habitat patches in **Paper I**, derived from eDNA metabarcoding. Animal groups comprise mostly micro- and meso-scale soil animals. Animals were classified by dietary traits; fungi by functional group. $R^2$ values and p-values for testing the difference in mean sample richness (linear mixed-effects models, LMM), and difference in community composition (Permutational multivariate ANOVA, PERMANOVA) between open and wooded habitat patches are presented. (Table 1 in Paper I).

| Organism group | Mean sample richness in* open patches | Mean sample richness* in wooded patches | LMM $R^{2\dagger}$ | LMM p-value‡ | PERMANOVA $R^2$ | PERMANOVA p-value‡ |
|---|---|---|---|---|---|---|
| Plants (DNA based) | 19.9 ±1.4 | 13.7 ±0.8 | 0.44 | **0.022** | 0.44 | **0.002** |
| AM fungi | 30.1 ±1.5 | 21.8 ±2 | 0.37 | 0.054 | 0.19 | **0.013** |
| EcM fungi | 17.6 ±1.1 | 36.2 ±1.5 | 0.82 | **< 0.001** | 0.1 | **0.002** |
| Plant/fungal pathogenic fungi | 15.7 ±0.8 | 10.4 ±0.9 | 0.58 | 0.064 | 0.2 | **0.002** |
| Animal pathogenic fungi | 6.4 ±0.5 | 3.1 ±0.3 | 0.53 | **< 0.001** | 0.25 | **0.007** |
| Saprotrophic fungi | 38.8 ±1.6 | 24.9 ±2.3 | 0.66 | 0.054 | 0.18 | **0.002** |
| Decomposer fungi (incl. mycorrhizal) | 68.5 ±2 | 47.1 ±2.8 | 0.7 | **0.018** | 0.17 | **0.002** |
| Other symbiotrophic fungi | 5.9 ±0.6 | 2.7 ±0.3 | 0.56 | **0.03** | 0.14 | **0.003** |
| Endophytic fungi | 11.8 ±0.7 | 8.7 ±0.7 | 0.61 | 0.236 | 0.19 | **0.002** |
| Undefined fungi | 173.9 ±5.4 | 104.7 ±5.4 | 0.8 | **< 0.001** | 0.17 | **0.002** |
| Fungivorous animals | 34.2 ±1.1 | 24.6 ±1.3 | 0.61 | **0.008** | 0.13 | **0.002** |
| Bacterivorous animals | 27.6 ±1.4 | 23.7 ±0.9 | 0.32 | 0.155 | 0.09 | **0.002** |
| Litter feeding animals | 20.5 ±1 | 13.4 ±1.1 | 0.59 | **0.034** | 0.12 | 0.248 |
| Root feeding animals | 17.6 ±0.7 | 11.7 ±0.6 | 0.62 | **< 0.001** | 0.21 | **0.002** |
| Macro plant feeding animals | 5.1 ±0.4 | 3.2 ±0.3 | 0.28 | **< 0.001** | 0.08 | 0.108 |
| Algal/lichen feeding animals | 12 ±0.5 | 9 ±0.4 | 0.38 | **< 0.001** | 0.1 | **0.003** |
| Predators | 22.9 ±1 | 15.9 ±0.7 | 0.5 | **< 0.001** | 0.1 | **0.002** |
| Parasitic animals | 6.4 ±0.3 | 4.7 ±0.4 | 0.31 | **0.03** | 0.13 | **0.007** |
| All fungi (ITS primer) | 288.2 ±8.2 | 196.1 ±8.2 | 0.75 | **< 0.001** | 0.19 | **0.002** |
| All animals | 72.6 ±2.1 | 53.3 ±2.1 | 0.65 | **< 0.001** | 0.13 | **0.002** |

* Mean taxon/OTU richness per sample ± standard error is reported

† Pseudo-R-squared values for Mixed-Effect models conditional on random effects (plot) are presented

‡ P-values for multiple comparisons are controlled for false discovery rate (FDR).

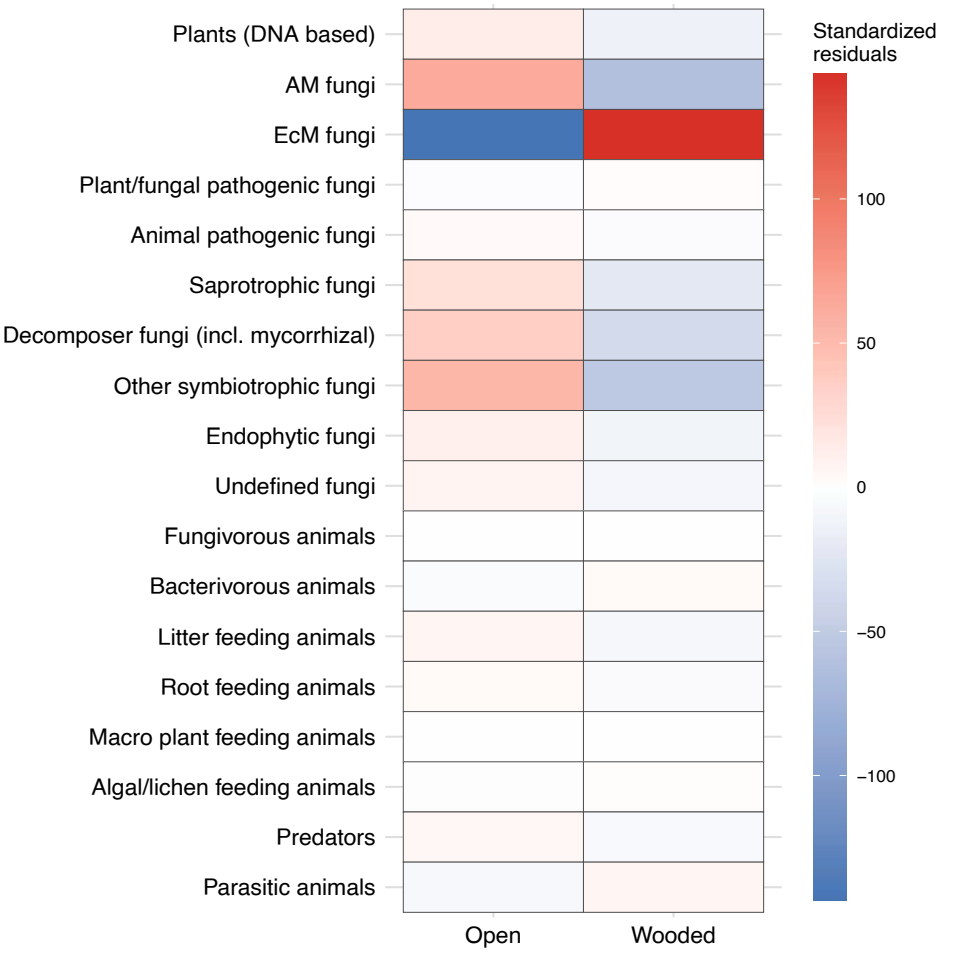


**Figure 1** The relative contribution of each studied functional group to the community compositional difference between wooded and open habitats in **Paper I**. Contribution of each functional group and habitat combination to the overall $\chi 2$ score in a contingency table of cumulative organism group frequency (sequence counts of the organism groups among all samples from each habitat) are presented. Red colors indicate positive association with a habitat type; blue colors indicate negative association. Color intensity indicates the size of the standardized residual between expected and observed frequency (sequence counts). Plants, fungi, and soil micro- and mesofauna were addressed. (Figure 3 in Paper I).

### 3.1.2. Coincidence of plant community patterns above- and below ground

Vegetation plots indicated differences between wooded and open patches in mean plant species richness per sample (open: 28.7±1 SE and wooded: 10.2±0.5 SE species; LMM $p < 0.001$) and in plant community composition (PERMANOVA $R^2 = 0.5$, $p < 0.001$). Using plant DNA sequences from soil, a similar pattern was detected, with wooded and open patches differing in mean sample richness (open: 19.9±1.4 SE and wooded: 13.7±0.8 SE; LMM $p = 0.022$) and community composition (PERMANOVA $R^2 = 0.44$, $p = 0.002$). A strong association between plant communities detected by vegetation survey and from plant DNA in the soil was also revealed by Procrustes analysis ($r = 0.879$; $p < 0.001$).

## 3.2. Effects of land use on AM fungal communities at small and large scales

In **Paper II**, no clear pattern was observed in cumulative VT number per site among the habitat types representing different land uses. Likewise, mean VT richness per sample did not differ among habitat types either in soil ($F_{5, 48} = 0.45$, $p = 0.8$) or in root samples ($F_{5, 31} = 1.92$, $p = 0.23$). Mean extrapolated diversity (*exp*H′) per sample likewise showed no significant effect of habitat type (soil: $F_{5, 48} = 0.36$, $p = 0.86$; roots: $F_{5, 31} = 0.91$, $p = 0.53$; Fig. 2). However, mean VT richness per sample was significantly greater in soil samples than in root samples ($F = 75.46$, $df = 90$, $p < 0.001$), with a mean sample VT richness of 26 (±0.97 SE) and 16 (±0.89 SE) respectively. Ninety VT, representing a large majority of sequences (158 752 sequences), were detected in both sample types, 30 VT were found only in soil samples (1151 sequences) and 5 VT were found only in root samples (31 sequences).

In **Paper III**, ecosystem type (naturally wooded vs. unwooded) influenced AM fungal richness (Figure 2a), and Chao extrapolated diversity per sample (Figure 2b). Specifically, unwooded sites exhibited higher alpha diversity per sample than wooded sites. Disturbance did not have a unidirectional effect on AM fungal richness (Figure 2a), Chao extrapolated diversity per sample (Figure 2b) or on any measure of beta diversity (Figure 2c) per plot. In sites where mean natural AM fungal diversity was low, disturbance increased mean richness (Figure 2e), Chao extrapolated diversity (Figure 2f) and beta diversity per plot (Figure 2g); while it decreased mean diversity estimates per plot in sites where mean natural diversity was high. Disturbance also generally increased the proportion of cultured taxa in **Paper III** (Figure 2d,h).

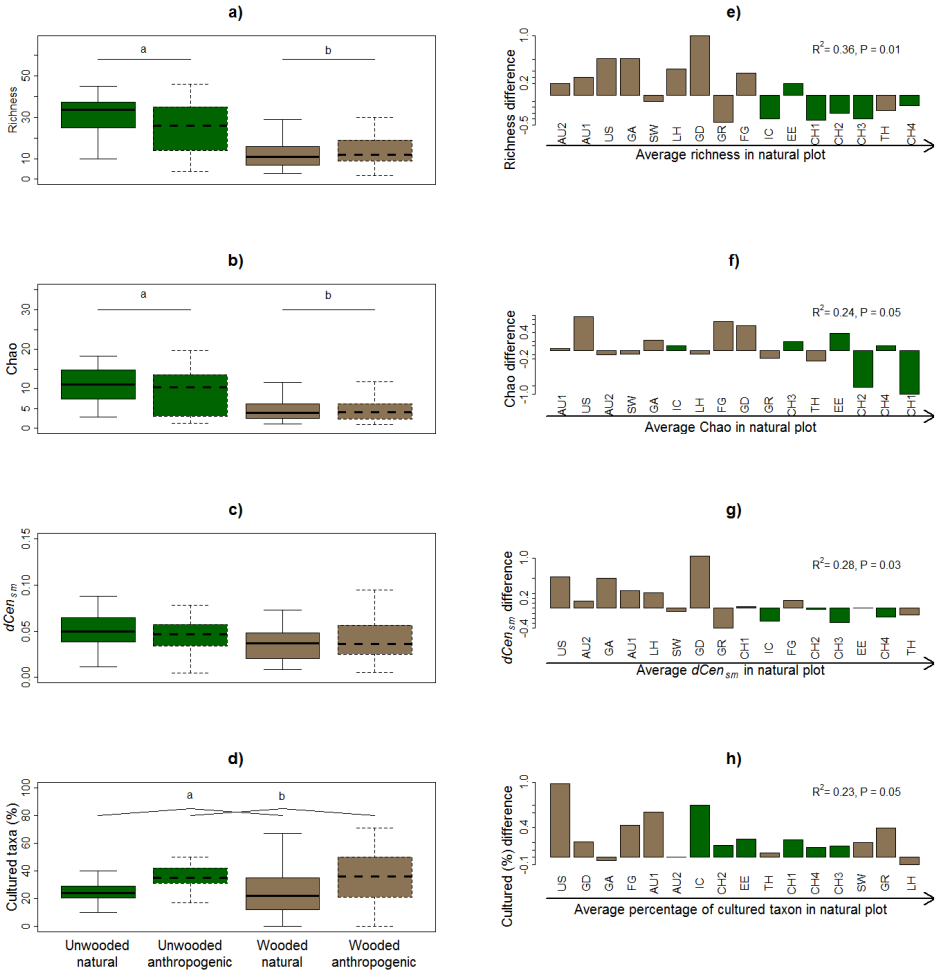


**Figure 2** Effect of disturbance on arbuscular mycorrhizal fungal diversity estimates in **Paper III**: Richness (a), Chao extrapolated diversity (b), beta diversity (c; $dCen_{sm}$), and proportion of cultured taxa per sample (d) for unwooded and wooded sites. Within-site standardized differences in diversity between anthropogenic and natural plots (*y*-axis) vs. natural plot diversity (*x*-axis) for richness (e), Chao extrapolated diversity (f), beta diversity (g) and the proportion of cultured taxa (h). Letters within panels (a–d) ($n$ = 177) indicate significant differences between ecosystem and disturbance categories identified in models (Table S4). Thick lines represent medians; boxes indicate interquartile ranges; and whiskers show maximum and minimum values per sample. Bars (sites) within panels e–h ($n$ = 32) are arranged in rank order. Differences above zero indicate positive effects of disturbance on diversity; differences below zero indicate negative effects of disturbance. AU1: Australia 1; AU2: Australia 2; CH1: China 1; CH2: China 2; CH3: China 3; CH4: China 4; EE: Estonia; GD: Guadeloupe; FG: French Guiana; GA: Gabon; GR: Greece; IC: Iceland; LH: Lithuania; SW: Sweden; TH: Thailand; US: United States. R-squared describes Pearson correlation between diversity in the natural plot and the diversity difference (i.e. the result of subtracting diversity in the natural plot from diversity in anthropogenic plot). (Figure 2 in Paper III).

Community composition (reported as results of PERMANOVA tests here and throughout the paragraph) of AM fungi in **Paper II** differed among habitat types (F = 6.7, *df* = 5, p = 0.001) and sample types (F = 21.1, *df* = 1, p = 0.001), with a significant interaction between the two factors (F = 1.4, *df* = 5, p = 0.028). The habitat effect remained when separately analysing soil samples (F = 5.6, *df* = 5, p = 0.001) and root samples (F = 2.5, *df* = 5, p = 0.001). Phylogenetic community composition was also significantly different among habitat types (F = 14.6, *df* = 5, p = 0.001) and sample types (F = 50.9, *df* = 1, p = 0.001), with a significant interaction between habitat and sample type (F = 2.6, *df* = 5, p = 0.001). In **Paper III**, ecosystem type ($R^2$ = 18%, $p < 0.01$), disturbance ($R^2$ = 5% $p < 0.01$), their interaction ($R^2$ = 4%, $p = 0.01$) and pH ($R^2$ = 6%, $p = 0.04$) influenced AM fungal taxonomic composition.

Beta diversity analyses in **Paper II** showed more dispersion between soil samples than root samples both when using simple taxon abundances (F = 19.0, *df* = 1, $p_{perm} < 0.001$; Figure 3), and when accounting for both taxon abundances and phylogenetic diversity (F = 17.5, *df* = 1, $p_{perm} < 0.001$). The within-site beta diversity was marginally significantly different among habitats (F = 4.2, *df* = 5, p = 0.0547) when sample type and site were included in the model. In **Paper III**, beta diversity within plot, measured using $dCen_{sm}$, did not differ significantly between wooded and unwooded sites; however, alternative beta diversity metrics indicated higher beta diversity per sample in wooded sites.

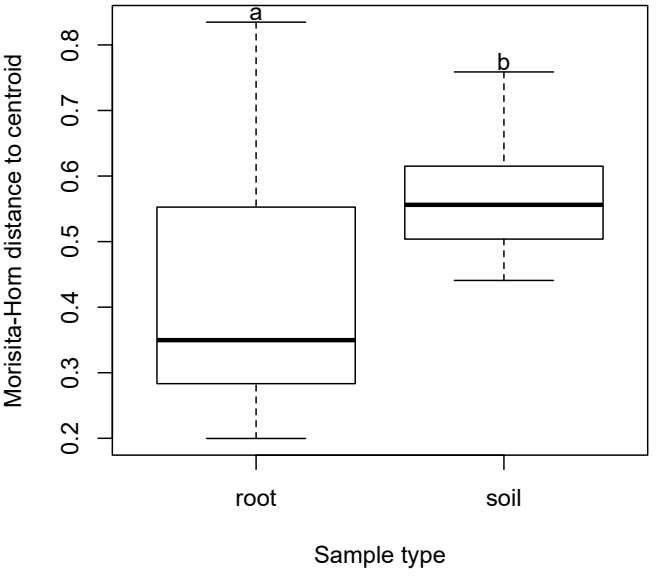


**Figure 3** Mean sample distances from beta diversity centroid for soil and root samples in **Paper II**, using Morisita-Horn distance. Mean values (middle line), 1st and 3rd quartiles (boxes), 1.5 times inter-quartile range (whiskers) and outliers (dots) are shown. Boxes topped by the same letter do not differ significantly at $p \leq 0.05$ by ANOVA. (Figure 4 in Paper II).

## 3.3. Specificity patterns in a plant-mycorrhizal network

In the network study in **Paper IV**, 98 AM fungal VT were detected from 33 plant species in summer and 97 VT from 30 plant species in autumn. Mean AM fungal VT richness per sample was significantly affected by plant species ($F_{23,191} = 4.63$, $p < 0.001$). Furthermore, mean AM fungal VT richness was affected by plant functional group ($F_{1,28} = 7.32$, $p = 0.011$) and the local abundance of plant species ($F_{1,28} = 7.645$, $p < 0.001$), with grasses and locally more abundant plant species having more AM fungal VT per sample respectively (Fig. 4 a, f). Plant mycorrhizal status coefficient was positively related to mean sample AM fungal richness ($F_{1,28} = 6.094$, $p = 0.02$ Fig. 4c). Plant species had the strongest effect on the taxon composition of AM fungal communities in root samples; sampling time and plant functional group also exhibited a marginally significant effect on AM fungal community composition, but explained little variance.

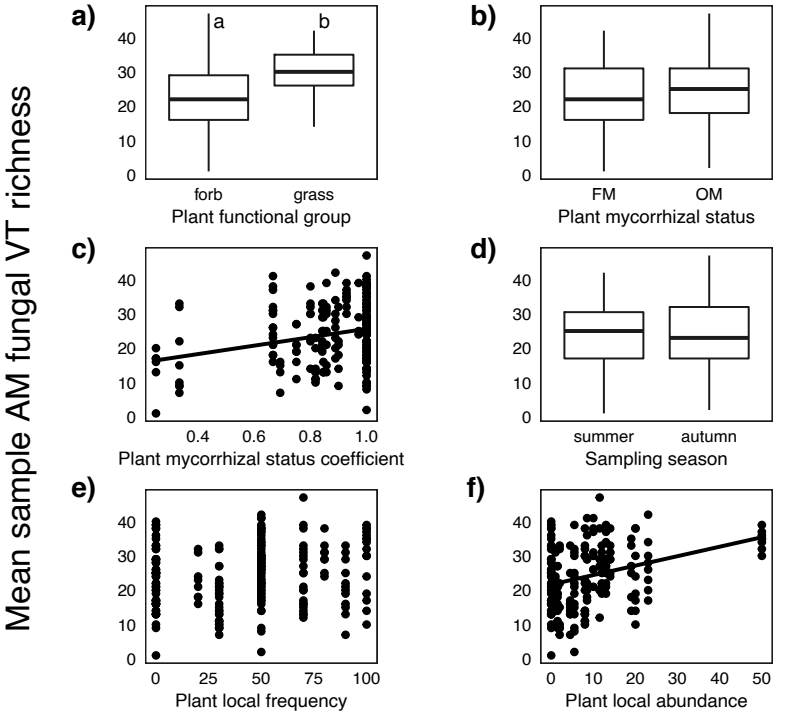


**Figure 4** Richness of arbuscular mycorrhizal (AM) fungal VT per sample among plant functional groups, plants of different mycorrhizal status, sampling times, and in relation to plant species frequency and abundance in **Paper IV**. Differing letters in boxplots and trend lines in scatterplots indicate a significant effect (linear mixed models with plant species as random factor). In boxplots, mean values (middle line), 1st and 3rd quartiles (boxes) and up to 1.5 times inter-quartile range (whiskers) are shown. Zero values for plant local frequency and local richness indicate that these plants were not identified in other plant quadrats on which these measures were based, but were present in our plot. (Figure 2 in Paper IV).

The modularity of the plant-AM fungal interaction network, which included all plant species in both sampling times, was 0.18, which is higher than expected by chance ($p < 0.001$). Five modules of plant-AM fungal interactions could be distinguished, with one exhibiting highly significant within-module phylogenetic clustering of AM fungal taxa (mean pairwise distance = 0.103, $z = –2.359$, $p = 0.005$, plant species in module = 6). Network connectance (connectance = 0.521; $p < 0.001$), nestedness (nestedness temperature = 27, $p < 0.001$) and links per species (i.e. average number of symbiotic partners of a species; (links per species = 12.9, $p < 0.001$) were significantly lower than expected by chance. The overall specialization index in the entire network (H2') was also significantly higher than expected at random (H2' = 0.16, $df = 998$, $p < 0.001$). When compared to random distributions of AM fungal taxa among plant species, all but one plant species demonstrated a higher-than random level of symbiont specialization (d').

Plant species-level specialization index (d') was significantly affected by plant local abundance ($F_{1,28} = 6.43$, $p = 0.017$), with locally less abundant species being more specialized (Fig. 5j) Forbs also showed a tendency to be more specialized than grasses (Fig. 5f), but the trend was marginally non-significant ($F_{1,28} = 3.621$, $p = 0.067$). When using the quantitative mycorrhizal status coefficient, more obligatorily mycorrhizal plants were less specialized ($F_{1,28} = 6.332$, $p = 0.018$; Fig. 5h).

Among the plant – AM fungal networks split by plant functional group, grasses had a greater average number of links (plant – AM fungal connections) per plant species than forbs (forbs – 50.6, grasses – 63.6), with the difference being larger than expected by chance ($p < 0.001$). Moreover, the network of forbs and AM fungi had a higher modularity than the network of grasses and AM fungi (forbs – 0.20, grasses – 0.14), the difference being larger than expected by chance ($p < 0.001$, Fig. S9 in **Paper IV**). There was a trend for grasses to be less specialized than forbs ($F_{1,28} = 3.62$, $p = 0.067$).

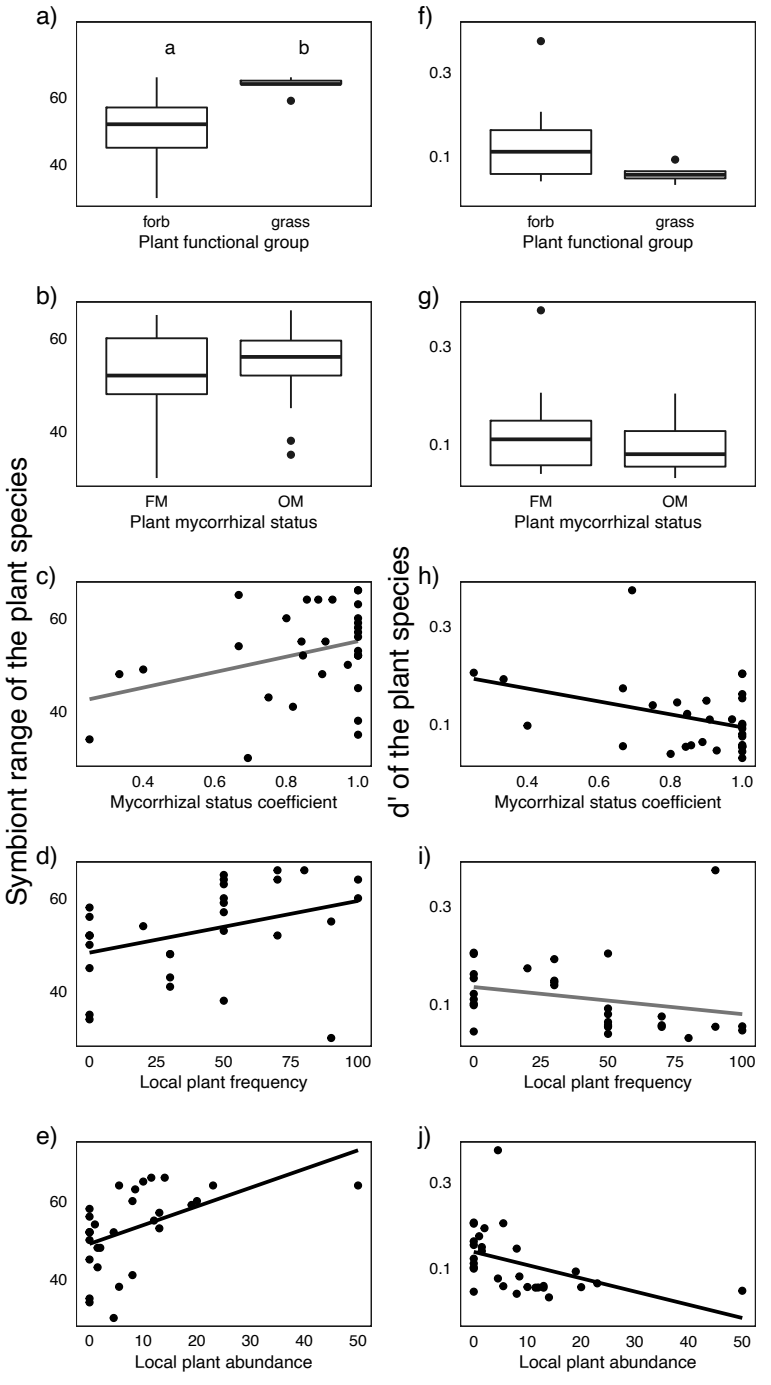


**Figure 5** Plant-AM fungal interaction network parameters in **Paper IV**: plant species symbiont range (or "degree") (a–e) and plant species d' (level of specialization) (f–j) in relation to plant functional group, mycorrhizal status, frequency and abundance. Differing letters in boxplots and black lines in scatterplots indicate a significant effect; grey lines indicate a marginally non-significant effect (linear models). In boxplots, mean values (middle line), 1st and 3rd quartiles (boxes) and up to 1.5 times inter-quartile range (whiskers) are shown. (Figure 3 in Paper IV).

# IV DISCUSSION

The research conducted in this thesis primarily sought to determine the impact of land use intensity and mode on communities of different soil-dwelling eukaryotic organism groups. This was achieved by carrying out studies varying in scale, land use type, and the soil biotic components targeted. We show that land use affects soil eukaryotic communities at global and local scales, but not always in an expected manner (i.e., decreased diversity with increased human disturbance), emphasizing the need for in-depth studies encompassing several aspects of biodiversity. In addition, the thesis sheds light on a pressing issue in the field of plant symbiotic microbiota – whether the microbial communities assembled in plants are results of stochastic processes or are they derived from possible functional or ecological properties of the involved organisms.

## 4.1. Soil biota undergoes complex and correlated changes in response to woody plant presence

In **Paper I**, we showed that the presence of wooded patches in an otherwise homogeneous open grassland ecosystem impacts the diversity and composition of the wider eukaryotic community. Moreover, a majority of the soil eukaryotic organism groups exhibited significant correlation in community structure, either with the plant community, or with other groups. The functional structure of the biotic community, as characterized by the proportion of DNA sequences attributed to different functional groups, differed significantly between open and wooded grassland patches, to which symbiotic fungi (AM, EcM and other symbiotrophic fungi) contributed the most. Current evidence concerning correlated patterns of richness among different taxonomic groups is inconsistent (Wolters *et al.*, 2006; Gossner *et al.*, 2016; Banerjee *et al.*, 2018; Noreika *et al.*, 2019; Delgado-Baquerizo *et al.*, 2019). Our results confirm some of the previously established patterns in terms of decreasing plant diversity related to woody plant encroachment in European grasslands (Poschlod & WallisDeVries, 2002; Dengler *et al.*, 2014), and demonstrate analogous patterns among other soil biota – higher diversity of fungi (on average *ca* 65% higher richness per sample, excluding EcM fungi) and soil animals (on average *ca* 40% higher) in open than wooded grassland patches. The strength of this pattern is emphasized in our study system by the fact that the reverse diversity pattern – higher diversity in wooded than in open grassland patches – emerged only among EcM fungi, which reflects the presence of their host plant species (Schwob *et al.*, 2017) in wooded patches.

Widespread impacts of woody plant encroachment were evidenced by simultaneous responses in multiple groups in **Paper I**. Among others, we recorded significant pairwise correlations between community matrices of plants and fungi, plants and soil animals. The compositions of all fungal functional groups were significantly correlated with the plant community. Where most animal

dietary groups likewise correlated significantly with plant community, some of them – such as fungi- and bacterivorous, parasitic, and litter-feeding animals – were less tightly interlinked with the vegetation. Such dampening of knock-on effects between trophic layers may perhaps be explained by patterns of generality of specific trophic associations. At the community level, the differences in responses to woody encroachment were observed between kingdoms: where fungi exhibited clear responses, animals revealed less distinct patterns, with plants in between. Such differential patterns among animals and fungi may be attributable to the trophic wiring of the system, with plants and fungi being more intimately depending on each other, but soil animals being characterized by omnivorous or generalist feeding associations (see Digel *et al.*, 2014).

We further demonstrated the applicability of metabarcoding plant-derived eDNA from soil in identifying plant diversity. There was a significant correlation between plant richness, and significant correlations between compositional patterns of plant communities, described either with the help of conventional vegetation plots, or by plant metabarcoding.

On the other hand, in **Paper I**, the methodological caveats of molecular species delimitation became very clear in the comparison of several different organism groups. The specific resolution achieved for a group of organisms (such as soil animals) varies with a wealth of methodological choices (including storage and extraction methods, primer choice etc.; Garlapati *et al.*, 2019; Beng & Corlett, 2020). Beyond the constraints of molecular techniques and sufficiency of sampling, the outcome data are highly dependent on the reference data available for accurate species identification – differences in reference database quality might also partly explain why some patterns are visibly more pronounced. Thus, results based on molecular identification of species must always be taken with a grain of salt, and the importance of clear descriptions of the methods must be stressed.

## 4.2. Land use modifies the AM fungal communities

AM fungal taxon richness per sample did not differ significantly among habitat types in the regional study in **Paper II**. These results are in concordance with some earlier findings in which similar AM fungal diversity levels were observed irrespective of land use intensity (Morris *et al.*, 2013; Simons *et al.*, 2017). On the other hand, in the same climatic region, Moora *et al.* (2014) found that AM fungal taxon richness differed among habitats of different land use type and intensity. The lack of discernible patterns of AM fungal richness in this study may reflect the relatively low disturbance in the natural and seminatural vs disturbed or abandoned habitat types. Whereas we expected to observe greater AM fungal richness in open than in forested habitats as reported in Moora *et al.* (2014), we detected no clear trend with respect to habitat openness, corroborating some earlier observations of no difference between AM fungal richness (e.g., Koorem *et al.*, 2017). Thus, local factors such as subtle differences in soil conditions, may affect AM fungal taxon richness patterns more than regional

scale drivers related to habitat types or disturbance regimes. However, AM fungal community composition was significantly different among most habitat types in both root and soil samples. The results are similar to previous works (Moora *et al.*, 2014; Vályi *et al.*, 2015; Rodriguez-Echeverria *et al.*, 2017) which showed that habitat type and land use intensity drives compositional change of AM fungal communities.

We also hypothesized that the effect of land use in **Paper II** depends on differences in habitat openness, leading to opposite changes for increased (clear-cutting) or decreased (shrub encroachment) light availability in the field layer, however, the direction of change was not as distinct as we expected. AM fungal communities in boreonemoral forests were somewhat different from those in nearby clear-cut areas, whereas shrub encroachment following abandonment of former calcareous grasslands resulted in only a slight change in soil AM fungal community composition. Yet, the contrast among habitats with improved (clear-cut) or deteriorated (overgrown grassland) light conditions was not particularly evident. As for calcareous grasslands, vascular plant communities change after abandonment as well (Neuenkamp *et al.*, 2016), but these changes typically concern relative abundances of species rather than the overall composition (species list) of communities. Changes in AM fungal communities thus are in accordance with rather small changes in plant community composition in abandoned calcareous grasslands.

In the global survey of **Paper III**, there was no unidirectional effect of anthropogenic disturbance on AM fungal alpha or beta diversity. However, disturbance increased diversity in sites with naturally low diversity and decreased diversity in sites with naturally high diversity, that is, disturbance had the effect of equalizing levels of diversity over large scales. A similar pattern has been shown with plant communities where species-rich plant communities may impoverish following disturbance (Gibson *et al.*, 2011) and naturally species-poor plant communities may gain species after disturbance (Widenfalk & Weslien, 2009). The equalizing of diversity levels by disturbance, however, has not been claimed to be a general trend yet.

An equalizing effect of disturbance on levels of AM fungal alpha diversity is also consistent with findings on other microbes (ectomycorrhizal fungi, archaea and bacteria; Epp Schmidt *et al.*, 2017) that reported biotic homogenization resulting from biodiversity loss in some communities, but not others. As suggested by Epp Schmidt *et al.* (2017), a mechanism analogous to that influencing plants (i.e., the exclusion of an important number of late successional specialist species from naturally rich communities, which is compensated in naturally poor communities by the arrival of new pioneer species) may also influence the AM fungal communities.

The functional structure of AM fungal communities showed a more pronounced directional change in response to disturbance, in terms of both community composition and the proportion of cultured AM fungal taxa increasing in anthropogenic communities. Higher proportions of cultured AM fungi in anthropogenic habitats can be the result of ruderal traits in these fungi (Chagnon *et al.*,

2013). Traits including fast growth rate, efficient hyphal fusion and short-life cycles (van der Heijden *et al.*, 2008; Chagnon *et al.*, 2013; Ohsowski *et al.*, 2014) may enable cultured AM fungi to be relatively resistant to soil disturbance and to have the capacity to re-establish functional hyphal networks and symbiotic interactions with host plants.

The results of **Paper II** and **III** indicate that it is not sufficient to focus solely on levels of AM fungal diversity, because these may decrease or increase following land-use-related disturbance, depending on the local ecological context. Focus must also be placed on understanding and potentially preserving the functional structure of AM fungal communities experiencing anthropogenic disturbance.

## 4.3. Host-symbiont preference in plant-AM fungal networks

In **Paper II**, we found that the AM fungal community composition seemed to be more similar among different habitats in root samples of the single focal plant species than in soil samples. This could indicate that even the single host plant, common among all studied habitats, may behave as an additional filter sensu Davison *et al.* (2016) between the local AM fungal taxon pool (in soil) and the realized taxon pool in plant roots. Further, root AM fungal communities were also more similar than soil communities in terms of phylogenetic beta diversity. Because phylogenetic similarity could be considered a proxy of functional similarity (Chagnon *et al.*, 2013), lower phylogenetic beta diversity in the roots may yet again indicate a host plant filter, by which a plant species selects its AM fungal partners according to function. The pattern dampening effect of the host plant could be explained by its plasticity, which may buffer or amplify certain changes in habitat conditions. In particular, the focal plant species (*Prunella vulgaris*) individuals exhibit large performance plasticity in response to changes in growing conditions (cf. Uibopuu *et al.*, 2012). The ability to buffer local conditions may be facilitated due to intraspecific variation of the host plant (Johnson *et al.*, 2012), especially given the wide range of habitat conditions sampled in the current study.

Network analysis is a powerful approach for addressing ecological interactions between functionally different partners (Bascompte & Jordano, 2007), and it has already demonstrated its value in disentangling the characteristics of plant – AM fungal relationships (Öpik & Moora, 2012; Chagnon, 2016). Drawing on the hints to host preference in **Paper II**, the network level study on **Paper IV** confirmed that the network of interacting plants and AM fungi in the studied grassland ecosystem exhibited a significantly higher level of specialization than would be expected from null models. Further, nestedness in the network was demonstrated to be higher than expected at random. A bipartite interaction network is nested when interactions are organized such that specialists (for example, plants that interact with few AM fungi) interact with subsets of the species with

whom generalists (for example, plants that associate with many AM fungi) interact (Staniczenko *et al.*, 2013). Tylianakis *et al.* (2018) showed that nestedness in AM interaction networks is caused by non-random symbiont attachment, preferentially to more central (species with shorter indirect links to others within the same trophic level) plant or AM fungal species. The environmental conditions in the dry calcareous grassland ecosystem studied, where soil moisture, for instance, can change rapidly from one extreme to the other (Lundholm & Larson, 2003), may place considerable stress on plant-AM fungal networks. It has been suggested that nested network structure can contribute to network persistence because the core of interactions then occurs between generalists and is therefore stable enough to allow the remaining, more specialized symbiotic community to remain viable even in the presence of disturbance (Bascompte *et al.*, 2003). Bastolla *et al.* (2009) demonstrated that a highly nested interaction network allows for the maximum number of species to coexist, given a certain number of interactions. It has further been shown that a new species entering a community will experience the lowest competitive load if it attaches to generalist species (Bastolla *et al.*, 2009). This naturally leads to a nested network and could be one of the mechanisms facilitating high species richness at the current study site.

# 5. CONCLUSIONS

Taking into account the fact that soil biodiversity globally is at risk and largely influenced by human activities (Geisen *et al.*, 2019), a better understanding of the diversity, but also interactions of soil organisms, is essential to balance the needs of the human society with the very basic requirements of a functioning ecosystem. In that regard, research comprising this thesis explored the effect of land use at both local and global scales, and took into consideration various groups of soil organisms.

Changes, even seemingly minute, in land use that result from human management decisions induce an array of changes in the belowground. The presence or absence of woody vegetation in the aboveground translate to complex and correlated changes of soil-dwelling animals and fungi. Moreover, the intensity of the reaction to the presence of an 'ecosystem engineer' is largest among fungi with a symbiotic lifestyle, thus suggesting that these groups of organisms are key elements of the change in biotic community and the resulting ecosystem function in this system. The results indicate that a multitrophic perspective is needed to distinguish the organisms that are, on the one hand, most affected by management decisions, and on the other hand, drive the subsequent cascading changes in the ecosystem.

Further, change of land use mode or intensity does not always translate into discernible and clear changes in the diversity of some organism groups, in this case arbuscular mycorrhizal fungi. However, land use rather consistently affects the compositional structure of the biotic community, and thus potentially the function of the belowground sphere, highlighting the need to take into account multiple facets of the biotic component of ecosystems when assessing the effect of human impact. What is more, results from the global study demonstrate that contrasting mechanisms of diversity might dominate at different ends of the diversity gradient. This implies that it does not always suffice to take the (non-) existence of intuitively clear patterns of, for example, diversity as is, but a more detailed view can reveal ecologically significant motifs.

At a finer scale, the study demonstrates patterns of host preference in a ubiquitous symbiotic interaction such as the arbuscular mycorrhiza, indicating the need for biodiversity research to take into account not only the focal group of organisms, but also the co-existing biota, with whom multipartite interactions drive the assembly of communities.

The rapidly evolving environmental DNA metabarcoding approach used throughout the study should and is becoming a common tool in community ecology, given the challenges of traditional morphology-based species detection and identification across the entire tree of life. Having said that, a good morphological basis is essential for development of ecologically meaningful metabarcoding standards in most organisms, meriting integrated approaches combining traditional and DNA-based methods. Further, metabarcoding should never be taken at face value, because depending on the organism group, blind trust in sequences and databases might lead the field even further astray. Therefore, there is a dire need of good standards in both the technical details and reference datasets in order to generate true and comparable results.

# SUMMARY

Soil and the organisms that dwell in it are inextricably linked with the functioning of terrestrial ecosystems. Alas, compared to the aboveground, research on soil organisms has lagged behind for decades due to the methodological constraints on detecting and identifying species in the belowground. This, in turn, has impeded reaching information about one of the largest biodiversity reserves into climatic models and onto the desks of decision makers. Luckily, developments in DNA-based metabarcoding techniques mean that this much needed information is now being accumulated by ecologists with an ever hastening pace. Nevertheless, much of the knowledge pertaining diversity patterns of underground organisms is still missing or inconclusive.

To a large extent, ecosystem processes are influenced by interactions between primary producers – in terrestrial habitats, plants – and interacting soil organisms. Although soil biota is diverse, much of the research conducted focuses only on particular branches on the tree of life. In nature, however, interactions that drive ecosystem processes are often multipartite and the responses of one group of organisms to a change in environment might depend on the behavior of others. Exactly these kinds of issues can be solved with more affordable molecular methods that enable barcoding of large portions of soil biodiversity and study correlations of multiple organism groups.

On the other hand, generalizations are still being hindered by the lack of information about specific organisms or organism groups. For example, knowledge of the responses of arbuscular mycorrhizal (AM) fungi, a ubiquitous group of microscopic soil organisms that form symbiosis with most of the terrestrial plants, to human influence has long been centered on agroecosystems with natural and seminatural habitats being left in the background. In addition to knowledge gaps in community ecology or macroecology of AM fungi in the soil, processes governing the assembly of AM fungi in plant roots are unknown. For example, do members of this species-poor, but omnipresent fungal group colonize plant roots randomly, or are there any species-species preferences between host and symbiont?

The research presented in this thesis mainly revolves around responses of soil eukaryotic communities to land use change. We showed that, at coarse taxonomic scales, different soil organism groups (e.g., mycorrhizal fungi, root-feeding animals, etc.) respond to habitat change in a correlated manner, in terms of both diversity and community composition. From the perspective of a narrower group of organisms – the AM fungi – we demonstrated a homogenizing effect of human disturbance on diversity of this group of soil fungi. In naturally poor habitats, human influence enriches the AM fungal community through addition of disturbance tolerant taxa, and in naturally rich habitats, human disturbance removes a part of species, expectedly late successional ones. At a local scale, we similarly showed that even intuitively detrimental habitat change does not directly translate to species loss or gain, but more to the change in the species composition. Thus,

function derived from the set of species present, not the number of species present (i.e., richness), might drive ecosystem responses to anthropogenic change.

We also studied host preference in plant–AM fungal interactions. We demonstrated that a single host plant species tends to select a similar set of fungal partners from the soil species pool, irrespective of habitat type. Furthermore, we explored the patterns governing plant–AM networks and demonstrated that fungal assemblies in roots of different plant species do not result from stochastic processes, but instead exhibit host/symbiont preference and follow structures that promote resilience of said networks.

We show significant changes of soil biota in response to land use change. Given that human impact influences and endangers soil biodiversity at a global scale, knowledge of the direction and mechanisms of the effects is necessary to balance the ever-growing needs of humanity and the need for retaining the integrity of ecosystems.

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# SUMMARY IN ESTONIAN

## Eukarüootse mullaelustiku seos maakasutuse muutuse ning peremeestaime identiteediga

Võrreldes maapinnal elavate organismidega, on mikroskoopilise mullaelustiku uurimine aastakümneid, mõnes aspektis aastasadu, ajale jalgu jäänud. Muld ning selles elavad organismid on aga ökosüsteemide lahutamatu osa. Mullaelustiku funktsioonid on näiteks orgaanilise aine lagundamine, toitainetsükli käigushoidmine ning taimestiku produktiivsuse tagamine. Kahjuks tähendab mullaorganismide uurimise keerukus seda, et vähesedki teadaolevad andmed on tihtipeale vastukäivad ning kliimamudelitesse ning otsusetegijate laudadele on teadmised mullaelust visad jõudma.

Samas on viimastel aastakümnetel kättesaadavamaks muutunud molekulaarsed meetodid maa-aluse elu uurimiseks. Tänu organismide triipkoodistamisele ehk DNA-järjestuste põhisele määramisele suudavad ökoloogid tuvastada ka silmale nähtamatuid organisme ning süüvida ühe suurima elurikkuse varamu – mulla – mitmekesisuse ning ka funktsioonide mustritesse.

Ökosüsteemides toimuvaid protsesse mõjutavad maismaal valdavalt primaarprodutsentide – taimede – ning nendega otse või kaudsemalt seotud mullaorganismide vahelised suhted. Kuigi on selge, et mullaelustik on liigirikas ning selle kujunemisel on oluline roll enamike suurte organismirühmade esindajatel, võetakse uuringute fookusesse sageli vaid üks kindel rühm. Põhjused on arusaadavad – mitme asjaga korraga tegelemine hajutab paratamatult fookust ning mitme rühma esindajate määramine käib n-ö tavaökoloogile tihtipeale üle jõu. Looduses toimivad interaktsioonid aga mitme osapoole vahel ning ühe taksonoomilise rühma vastus keskkonnamuutusele võib sõltuda lisaks iseomastele tunnustele ka teiste organismirühmade käitumisest. Eelmainitud molekulaarsed meetodid on sellistes olukordades suureks abiks. Just viimastel aastatel toimunud sekveneerimistehnoloogiate oluline täiustumine ning odavnemine võimaldavad suhteliselt mõistlike kulutustega triipkoodistada suurt osa elurikkusest. See annab võimaluse uurida lisaks üksikutele organismirühmadele ka elurikkuse erinevate komponentide koosvarieerumist ja seeläbi hinnata, kas kooslustes toimuvad muutused on samasuunalised. Taolised teadmised on olulised muuhulgas ka selleks, et mõista, millised elusolendid on inimtegevusest enim mõjutatud, ning teades erinevate organismidega seotud ökosüsteemi funktsioone, suudame hinnata, millised ökosüsteemi protsessid tõenäoliselt enim muutuvad.

Doktoritöö üheks eesmärgiks oli uurida, kuidas käitub mulla eukarüootne mikroelustik sõltuvalt puisniidu majandamisest. Puisniidud on liigirikkad puu- ja põõsagruppidega heinamaad, mis Eestis esinevad peamiselt läänepoolsetes maakondades ja läänesaartel, ning kus puittaimede esinemine sõltub inimese majandamisotsusest. Selleks määrati Laelatu puisniidul DNA-triipkoodi põhjal nii mullaseened, mullaloomad, spetsiifilisemalt AM (arbuskulaarmükoriissed) seened ning ka mullas leiduv taimne DNA. Uurimuse tulemusena tuvastati puittaimede

roll ökosüsteemi inseneridena puisniidul – puittaimede esinemine või puudumine muidu homogeenses keskkonnas tingis enamiku uuritavate organismirühmade mitmekesisuse ning koosluse liiglise muutuse. Kõikide uuritud rühmade puhul, välja arvatud ektomükoriisaseened, oli elurikkus kõrgem puittaimedeta ehk avatud kasvukohas, kinnitades ka varasemate, üksikutele organismirühmadele keskendunud tööde tulemusi. Ektomükoriisaseente puhul ilmnenud vastupidist mustrit võib põhjendada peremeestaimede (puittaimede) olemasolu ning ohtrusega kasvukohas. Lisaks olid enamike rühmade vahelised muutused korrelatsioonis kas omavahel või taimkatte muutusega. Avatud ning puittaimedega proovilappide eluskoosluse funktsionaalne struktuur erines olulisel määral, kusjuures enim mõjutasid erinevust sümbiootilise eluviisiga seened (näiteks AM seened ja ektomükoriisaseened). Korrelatsioon taimekooslusega esines kõikidel seenerühmadel, kuid mitmel loomarühmal, näiteks seen- ja bakteritoidulistel loomadel, parasiitsetel mullaloomadel ning kõdutoidulistel, ei ilmnenud olulist koosluse koosseisu sõltuvust taimkattest. Seda võib seletada erineva mullaelustiku spetsiifilisusega sümbioosse partneri või toidulaua suhtes – mullaloomad on üldjuhul troofilistes suhetes vähem valivad kui näiteks sümbioosse eluviisiga seened.

Teisalt uuriti, kas mullas leiduva taimset päritolu DNA põhjal on võimalik tuvastada maapealse taimkatte tegelikke mustreid. See teadmine on oluline näiteks globaalsete uurimuste teostamisel, kus traditsioonilise taimkattekirjelduse tegemiseks puudub ekspertiis. Ilmnes, et mullast DNA-triipkoodi põhiselt tuvastatud taimekoosluste muster korreleerus traditsioonilistel taimkatteruutudel tuvastatud mustriga. Küll aga ei olnud võimalik DNA-põhiselt taimeliike täpselt tuvastada, selle põhjuseks on üldiste referentsandmebaaside puudulikkus ning kõikuv kvaliteet. Seega võib DNA-põhise analüüsiga tuvastada küll ökoloogiliselt olulise mustri, kuid täpse taimkatte liiginimekirja koostamiseks ei ole need meetodid veel piisavalt arenenud.

Samas ei ole vähemtähtsad ka kindlate organismirühmade täpsemad alusuuringud, sest, nagu öeldud, on teadmised varjatud mullaelustikust endiselt lünklikud ning mõnel puhul vasturääkivad. Üheks enim levinud taimede ning mikroorganismide suhteks on arbuskulaarne mükoriisa, kus n-ö üht otsa pidi taimejuurtes ning teist otsa pidi mullas elavad krohmseente hõimkonna mikroseened varustavad taime mullas leiduvate toitainetega ning saavad taimelt fotosünteesi käigus fikseeritud energiarikkaid süsinikuühendeid. Lisaks nn toitainekaubandusele pakub umbes kahe kolmandiku maismaataimedega sümbioosis elav seenerühm taimedele muuhulgas kaitset patogeenide ja põua eest ning kujundab seeneniidistikust erituvate valkudega mulla struktuuri. On ilmne, et AM seenekooslused mõjutavad otseselt taimkatet ning sellest johtuvaid ökosüsteemide protsesse.

Lõpuni pole aga selge näiteks see, kuidas mõjutavad inimtekkelised häiringud ökosüsteemides, so muutused maakasutuse režiimis ning intensiivsuses, AM seenekooslusi. On leitud, et maakasutuse intensiivistumine põhjustab AM seente elurikkuse langust nii taimejuurtes kui mullas, kuid ka vastupidist – inimtekkelised häiringud võivad AM seente liigirikkust hoopis tõsta. Samas ei ole seni uuritud, kuidas inimmõju järgsed protsessid sõltuvad süsteemi algsest seisundist.

Piisavat tähelepanu ei ole saanud ka maakasutuse intensiivsuse skaala keskmes asetsevad ökosüsteemid. Kui taimesümbiontide uuringute lõviosa on keskendunud just põllumajandusmaadele ning väga intensiivsele ökosüsteemi inimesepoolsele ümberkujundamisele, siis palju vähem on teada mulla mikroelustiku käitumisest poollooduslikes kooslustes (nt alvarid, puisniidud). Üheks käesoleva töö põhiliseks eesmärgiks oligi uurida inimtekkeliste muutuste mõju AM seente kooslustele nii kohalikul kui ka globaalsel skaalal.

Globaalsel skaalal tehtud uuringus leiti, et inimtekkeline häiring ei mõjuta AM seente elurikkust kindlasuunaliselt – mõju suund sõltub ökosüsteemi esialgsest elurikkusest. Selgus, et inimtegevusel oli elurikkust ühtlustav mõju – AM seente osas liigirikkamates looduslikes paikades oli inimtegevusel elurikkust vähendav ning looduslikult vaesemates paikades suurendav mõju. Tõenäoliselt võib olla tegemist elurikkuse gradiendi eri otstes domineerivate erisuunaliste mehhanismidega: liigirikastes elupaikades mõjutab häiring negatiivselt hilissuktsessioonilisi elupaigaspetsiifilisi liike, samas kui liigivaestes elupaikades soodustab häiring vabade elupaikade loomisega uute pioneerliikide saabumist. Samuti leiti, et inimtekkelised häiringud mõjutavad funktsionaalselt erinevaid AM seeneliike erinevalt. Nimelt oli inimmõjuga proovialade AM seenekooslustes rohkem kultuuris kasvatatavaid AM seeneliike, mida võib seletada nende liikide tõenäoliselt ruderaalse elukäigustrateegiaga – kultuuris kasvatatavad seeneliigid on kiirekasvulised ja lühikese elutsükliga, mis soodustab nende esinemist ja populatsiooni taasloomist ka häiritud elupaikades.

Lokaalsel skaalal uuriti AM seenekoosluste muutust Eesti looduslikel ja poolloodusliкel aladel, kaasates nii majandatud (nt püsivalt hooldatud alvar, puisniit) või looduslikus seisundis (salumets) ning ka „häiritud“ (nt kinnikasvanud alvar, õuemuru, lageraielank) kasvukohti. Leiti, et vastupidiselt hüpoteesile ei erinenud häiritud ja häirimata kasvukohad AM seente liigirikkuse poolest. Selline tulemus võib olla tingitud piisavalt vähesest häiringust – isegi lageraie on võrreldes tavalise põllumajandusmaaga mullaelustikule tõenäoliselt tunduvalt vähem häiriv. Samas leiti, et AM seenekoosluse koosseis erines oluliselt kasvukohatüüpide lõikes.

Eelmainitud lokaalskaala uuringus võeti proove nii taimejuurtest kui ka neid ümbritsevast mullast, kusjuures juureproove võeti ainult ühe kõigis käsitletud kasvukohtades kasvanud generalistliku taimeliigi – hariliku käbiheina – isenditelt. Kui sarnane kasvukohtade vaheline ökoloogiline muster oli tuvastatav nii juure- kui mullaproovidest, ilmnes, et ühe taimeliigi juurtes elavad AM seenekooslused on eri kasvukohtade vahel sarnasemad, kui mullast leitavad AM seenekooslused, seda nii taksonoomiliselt kui fülogeneetiliselt. Kuna seenekoosluse fülogeneetilist koosseisu võiks osalt tõlgendada ka funktsionaalsete tunnuste näitajana, võib oletada, et uuringu fookuses olnud peremeestaimeliik võib valida oma sümbioosseid partnereid vastavalt nende funktsioonidele.

Potentsiaalset peremeestaime- või seenpartneri eelistuse temaatikat laiendati analüüsiga, kus võeti vaatluse alla terviklik taimede ning AM seente vaheline interaktsioonivõrgustik *ca* 0,1 ha suurusel alvari proovialal. Võrreldes sümbioossete partnerite identiteete ja ohtrusi kõikide koosluses esinevatel taimeliikidel,

ilmnes, et taimeliigi juurtest leitav AM seenekooslus ei olnud juhuslik, vaid peegeldab osade partnerite eelistamist teistele. Samuti tuvastati, et antud koosluses esines interaktsioonide pesastumine, see tähendab, et partneri valikul rohkem spetsialiseerunud liigid moodustasid interaktsioone liikidega, kellega elasid sümbioosis ka partneri valikul generalistlikumad liigid. Selline struktuur on oluline kogu võrgustiku stabiilsuse tagamiseks, kuna interaktsioonide enamik leiab aset generalistlike liikide vahel, tagades nii ilmselt uuritud koosluse (alvar) vastupidavuse muutliku niiskusrežiimi poolt põhjustatud stressile.

Doktoritöös läbiviidud uuringute tulemusena ilmnes korduvaid olulisi mullaelustiku muutusi sõltuvalt maakasutusrežiimist. Arvestades, et inimtegevus ohustab mulla elurikkust globaalsel skaalal, on teadmised inimmõju ulatusest erinevatele mullaorganismide rühmadele olulised, et tasakaalustada inimkonna järjest kasvavaid vajadusi ning vajadust säilitada ökosüsteemide terviklikkust ja põhifunktsioone.

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# PUBLICATIONS

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**Institutions and positions:**

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**Teaching work:**

2020 Supervision of Simone Sui's BSc thesis "Arbuscular mycorrhiza and its role in plant stress tolerance" (co-supervision with Maarja Öpik, University of Tartu).

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LOOM.01.031 Mycorrhizal-Study Associations
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**Research interests:**

Community ecology of soil organisms, with focus on arbuscular mycorrhizal fungi; network ecology; host preferences in plant-fungal interactions; land use; co-variation of soil organisms.

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Davison, J., León, D. G. de, Zobel, M., Moora, M., Bueno, C. G., Barceló, M., Gerz, M., León, D., Meng, Y., Pillar, V. D., **Sepp, S.-K.**, Soudzilovaskaia, N. A., Tedersoo, L., Vaessen, S., Vahter, T., Winck, B., & Öpik, M. (2020). Plant functional groups associate with distinct arbuscular mycorrhizal fungal communities. New Phytologist, 226(4), 1117–1128. https://doi.org/10.1111/nph.16423

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**Science outreach:**

**Publications:**

**Sepp S.-K.** (2017). Krohmseened ja inimmõju [Glomeromycota and human impact]. Laanisto, Lauri; Öpik, Maarja; Vanatoa, Alo; Tammaru, Toomas; Tinn, Oive; Kull, Kalevi (eds.). Schola Biotheoretica XLIII (157−161). Tartu: Sulemees Publishers.

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**Sepp S.-K.**, Moora M., Zobel M., Öpik M. A whole-system study reveals non-random association patterns in a plant-fungal interaction network (poster presentation). 3rd Symposium on Ecological Networks and 3rd Symposium on Molecular Analysis of Trophic Interactions; 11.–15.09.2017 in Uppsala, Sweden.

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**Sepp S.-K.**, Öpik M, Zobel M. Do plants care? – Hints of specificity in plant-arbuscular mycorrhizal interactions (oral presentation). 2nd Nordc-Baltic Ecology Seminar (Biotic interactions and biodiversity patterns across scales); 4.05.2018 in Tartu, Estonia.

**Sepp S.-K.**, Öpik M., Zobel M. Does the fungus matter? – Non-random association in an arbuscular mycorrhizal network (oral presentation). Doctoral Student Conference of the Department of Botany, University of Tartu; 6.–7.12.2018 in Kubija, Estonia.

**Sepp S.-K.**, Neuenkamp L, Vasar M, Oja J, Öpik M, Zobel M. Trees as ecosystem engineers: A glimpse into the depths below (oral presentation). 3rd Nordic-Baltic Ecology Seminar; 19.–23.08.2019 in Svanvik, Norway.

**Sepp S.-K.**, Neuenkamp L, Vasar M, Oja J, Öpik M, Zobel M. Trees as ecosystem engineers of soil biota: A multi-taxon sequencing approach (oral presentation). Yearly integration seminar of plant ecologists from University of Tartu and Estonian University of Life Sciences; 11.–12.10.2019 in Märdi, Estonia.

**Sepp S.-K.**, Neuenkamp L, Vasar M, Oja J, Öpik M, Zobel M. Hand in hand in the dark: A multi-taxon approach to studying vegetation and soil biota (poster presentation). DarkDivNet2019 workshop; 20.–23.11.2019 in Tartu, Estonia.

**Sepp S.-K.**, Öpik M, Zobel M. Impact of land use on arbuscular mycorrhizal fungi (oral presentation). Granö Research and Networking Workshop (Biological interactions from microbes to ecosystems); 23.–29.08.2020 in Tartu, Estonia.

**Courses attended:**

2018 Participation in the statistics course "Applied biostatistics in biological sciences using R" (2 ECTS), held 29.10.–02.11.2018 at Estonian University of Life Sciences, Tartu, Estonia (organized by the Doctoral School of Earth Sciences and Ecology; lecturers: Christian Ritz, Assoc. professor, University of Copenhagen, Denmark; Daniel Gerhard, Senior lecturer, University of Canterbury, New Zealand)

**Other activities:**

Manuscript reviewer for: Genomics, Proteomics & Bioinformatics; Molecular Ecology; Revista de Biología Tropical; Soil Biology & Biochemistry; Functional Ecology; Journal of Ecology; Mycorrhiza; New Phytologist

Co-organizer of 2nd Nordc-Baltic Ecology Seminar (Biotic interactions and biodiversity patterns across scales); 4.05.2018 in Tartu, Estonia.

Co-organizer of Centre of Excellence EcolChange PhD Conference 2019 EcolChange in World of Synergies. 12.11.2019 in Voore, Estonia.

Co-organizer of the international Granö Research and Networking Workshop (Biological interactions from microbes to ecosystems); 23.–29.08.2020 in Tartu, Estonia.

# ELULOOKIRJELDUS

Nimi: Siim-Kaarel Sepp
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**Haridustee:**

2015–... Tartu Ülikool, doktoriõpe (botaanika ja ökoloogia)
2013–2015 Tartu Ülikool, magistriõpe (taime-ja seeneteadus), *cum laude*
2008–2013 Tartu Ülikool, bakalaureuseõpe (bioloogia)
1996–2008 Miina Härma Gümnaasium

**Töökohad ja ametid:**

2015–... Tartu Ülikool, Loodus- ja täppisteaduste valdkond, ökoloogia ja maateaduste instituut, spetsialist

**Õppetöö:**

2020 Simone Sui bakalaureusetöö „Arbuskulaarse mükoriisa roll taimede stressitaluvuses“ juhendamine (kaasjuhendaja Maarja Öpik, Tartu Ülikool).

Osalenud järgmiste kursuste õpetamisel:
LOOM.01.031 Mükoriisaõpetus
LTOM.01.006 Ökosüsteemide toimimine ja kaitse
LOOM.01.126 Floristika välipraktika
LOOM.01.114 Erialapraktika taime- ja seeneteaduses

**Uurimisvaldkonnad:**

Mullaorganismide koosluseökoloogia, rõhuasetused arbuskulaarmükoriissetele seentele; võrgustikuökoloogia; peremehe-eelistus taim-seen interaktsioonides; maakasutus; mullaorganismide kovariatsioon.

**Teadusartiklid:**

**Avaldatud:**

Davison, J., León, D. G. de, Zobel, M., Moora, M., Bueno, C. G., Barceló, M., Gerz, M., León, D., Meng, Y., Pillar, V. D., **Sepp, S.-K.**, Soudzilovaskaia, N. A., Tedersoo, L., Vaessen, S., Vahter, T., Winck, B., & Öpik, M. (2020). Plant functional groups associate with distinct arbuscular mycorrhizal fungal communities. New Phytologist, 226(4), 1117–1128. https://doi.org/10.1111/nph.16423

Vahter, T., Bueno, C. G., Davison, J., Herodes, K., Hiiesalu, I., Kasari-Toussaint, L., Oja, J., Olsson, P. A., **Sepp, S.-K.**, Zobel, M., Vasar, M., & Öpik, M. (2020). Co-introduction of native mycorrhizal fungi and plant seeds accelerates restoration of post-mining landscapes. Journal of Applied Ecology, 57(9), 1741–1751. https://doi.org/10.1111/1365-2664.13663

**Sepp, S.-K**., Davison, J., Jairus, T., Vasar, M., Moora, M., Zobel, M., & Öpik, M. (2019). Non-random association patterns in a plant–mycorrhizal fungal network reveal host–symbiont specificity. Molecular Ecology, 28(2), 365–378. https://doi.org/10.1111/mec.14924

**Sepp, S.-K.**, Jairus, T., Vasar, M., Zobel, M., & Öpik, M. (2018). Effects of land use on arbuscular mycorrhizal fungal communities in Estonia. Mycorrhiza, 28(3), 259–268. https://doi.org/10.1007/s00572-018-0822-3

García de León, D., Davison, J., Moora, M., Öpik, M., Feng, H., Hiiesalu, I., Jairus, T., Koorem, K., Liu, Y., Phosri, C., **Sepp, S.**, Vasar, M., & Zobel, M. (2018). Anthropogenic disturbance equalizes diversity levels in arbuscular mycorrhizal fungal communities. Global Change Biology, 24(6), 2649–2659. https://doi.org/10.1111/gcb.14131

Lekberg, Y., Vasar, M., Bullington, L. S., **Sepp, S.-K.**, Antunes, P. M., Bunn, R., Larkin, B. G., & Öpik, M. (2018). More bang for the buck? Can arbuscular mycorrhizal fungal communities be characterized adequately alongside other fungi using general fungal primers? New Phytologist, 220(4), 971–976. https://doi.org/10.1111/nph.15035

**Käsikirjad:**

**Sepp, S.-K.**, Davison, J., Moora, M., Neuenkamp, L., Oja, J., Roslin, T., Vasar, M., Öpik, M., & Zobel, M. (2020). Woody encroachment in grassland elicits complex changes in the functional structure of above- and belowground biota. Ecography (saadetud ajakirja)

Põlme, S., Abarenkov, K., Nilsson, R. H., Lindahl, B., Clemmensen, K., Kauserud, H., Kjoller, R., Baldrian, P., Frøslev, T. G., Adojaan, K., Vizzini, A., Suija, A., Pfister, D., Baral, H.-O., Järv, H., Madrid, H., Nordén, J., Liu, J.-K., …, **Sepp, S.-K.**, … Tedersoo, L. (2020). FungalTraits: A user-friendly traits database of fungi and fungus-like stramenopiles. Fungal Diversity (saadetud ajakirja)

Davison, J., Moora, M., Semchenko, M., Adenan, S. B., Ahmed, T., Alatalo, J., Al-Quraishy, S., Andriyanova, E., Anslan, S., Bahram, M., Batbaatar, A., Brown, C., Bueno, C. G., Cahill, J., Cantero, J. J., Casper, B., Cherosov, M., Coelho, A., …, **Sepp, S.-K.**, … Öpik, M. (2020). Temperature and pH define the realized niche space of arbuscular mycorrhizal fungi. New Phytologist (saadetud ajakirja)

Rasmussen, P. U., Abrego, N., Roslin, T., Öpik, M., **Sepp, S.-K.**, Huotari, T., Andersson, A. F., Hugerth, L. W., & Tack, A. J. M. (2020). Elevation and plant species shape arbuscular mycorrhizal fungal communities in the Arctic. New Phytologist (saadetud ajakirja)

Hoeffner, K., Arias-Giraldo, L. F., Banse, M., Beylich, A., Chabbi, A., Cluzeau, D., Dascalu, D., Decau, M.-L., Graefe, U., Guzmán, G., Hallaire, V., Hanisch, J., Landa, B. B., Linsler, D., Menasseri, S., Nicolaï, A., Öpik, M., Plaas, E., …, **Sepp, S.-K.**, … Pérès, G. (2020). Legacy effects on soil ecosystem services of temporary grassland during annual crop rotation on soil ecosystem services. Science of the Total Environment (pending)

Vahter, T., Mignon, S., Peres, G., Potthoff, M., Landa, B., **Sepp, S-K.**, Bengtsson, J., & Öpik, M. AM fungal diversity patterns under reduced tillage agriculture are context dependent. Käsikirjana

**Teaduse populariseerimine:**

**Artiklid:**

**Sepp S.-K.** (2017). Krohmseened ja inimmõju. Laanisto, Lauri; Öpik, Maarja; Vanatoa, Alo; Tammaru, Toomas; Tinn, Oive; Kull, Kalevi (Toim.). Schola Biotheoretica XLIII (157−161). Tartu: Sulemees Publishers.

**Muud populaarteaduslikud tegevused:**

Botaanika osakonna esindamine Loodusfestivali Linnalooduse päeval 15.06.2019.

Botaanika osakonna esindamine Tartu Ülikooli lahtiste uste päevadel aastatel 2018 ja 2019.

**Sepp S.-K.** Krohmseente (Glomeromycotina) mitmekesisusest Eesti kasvukohtades. Suuline ettekanne Eesti Mükoloogiaühingu aastakoosolekul; 9.12.2017 Jõgeva.

**Konverentsiettekanded:**

**Sepp S.-K.,** Öpik M. Land use effects on arbuscular mycorrhizal fungal diversity (posterettekanne). Briti Ökoloogiaühingu aastakonverents BES 2016; 11.–14.12.2016 Liverpool, Suurbritannia.

**Sepp S.-K.**, Öpik M, Jairus T, Zobel M. Land use effects on AM fungal communities (suuline ettekanne). Konverents Woody Root 7; 26.–29.06.2017 Tartu.

**Sepp S.-K.**, Moora M., Zobel M., Öpik M. A whole-system study reveals non-random association patterns in a plant-fungal interaction network (posterettekanne). 3. Ökoloogiliste võrgustike sümpoosion ning 3. Troofiliste interaktsioonide molekulaarse analüüsi sümpoosion; 11.–15.09.2017 Uppsala, Rootsi.

**Sepp S.-K.**, Moora M., Zobel M., Öpik M. A whole-system study reveals non-random association patterns in a plant-fungal interaction network (posterettekanne). XIII Eesti ökoloogiakoverents; 20.04.2018 Tartu.

**Sepp S.-K.**, Öpik M, Zobel M. Do plants care? – Hints of specificity in plant-arbuscular mycorrhizal interactions (suuline ettekanne). 2. Põhja- ja Baltimaade ökoloogiaseminar; 4.05.2018 Tartu.

**Sepp S.-K.**, Öpik M., Zobel M. Does the fungus matter? – Non-random association in an arbuscular mycorrhizal network (suuline ettekanne). Tartu ülikooli botaanika osakonna doktorantide konverents; 6.–7.12.2018 Kubija.

**Sepp S.-K.**, Neuenkamp L, Vasar M, Oja J, Öpik M, Zobel M. Trees as ecosystem engineers: A glimpse into the depths below (suuline ettekanne). 3. Põhja- ja Baltimaade ökoloogiaseminar; 19.–23.08.2019 Svanvik, Norra.

**Sepp S.-K.**, Neuenkamp L, Vasar M, Oja J, Öpik M, Zobel M. Trees as ecosystem engineers of soil biota: A multi-taxon sequencing approach (suuline ettekanne). TÜ ja EMÜ ökoloogide iga-aastane koostööseminar; 11.–12.10.2019 Märdi.

**Sepp S.-K.**, Neuenkamp L, Vasar M, Oja J, Öpik M, Zobel M. Hand in hand in the dark: A multi-taxon approach to studying vegetation and soil biota (posterettekanne). Koostöövõrgustiku DarkDivNet2019 õpikoda; 20.–23.11.2019 Tartu.

**Sepp S.-K.**, Öpik M, Zobel M. Impact of land use on arbuscular mycorrhizal fungi (suuline ettekae). Granö keskuse teadusliku võrgustumise õpikoda; 23.–29.08.2020 Tartu.

**Kursused**

2018 Osalemine statistikakursusel „Rakenduslik biostatistika kasutades R-i“ (2 EAP), 29.10.–02.11.2018 Eesti Maaülikoolis (korraldajaks Maateaduste ja ökoloogia doktorikool; õppejõud: Christian Ritz, Assoc. professor, University of Copenhagen, Denmark; Daniel Gerhard, Senior lecturer, University of Canterbury, New Zealand)

**Muu teaduslik tegevus:**

Retsenseerinud artikleid ajakirjades: Genomics, Proteomics & Bioinformatics; Molecular Ecology; Revista de Biología Tropical; Soil Biology & Biochemistry; Functional Ecology; Journal of Ecology; Mycorrhiza; New Phytologist

2. Põhja- ja Baltmaade ökoloogiaseminari kaaskorraldaja; 4.05.2018 Tartu.

Teaduse tippkeskuse EcolChange 2019. aasta doktorantide konverentsi World of Synergies kaaskorraldaja. 12.11.2019 Voore.

Granö keskuse teadusliku võrgustumise rahvusvahelise õpikoja Biological interactions from microbes to ecosystems kaaskorralaja. 23.–29.08.2020 Tartu.

# DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

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