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TANEL VAHTER

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UNIVERSITY OF TARTU
Press

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Dissertation was accepted for the commencement of the degree of *Doctor philosophiae* in plant ecology at the University of Tartu on 18.06.2021 by the Scientific Council of the Institute of Ecology and Earth Sciences. University of Tartu.

Supervisor:	Prof. Maarja Öpik, University of Tartu, Estonia
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Commencement:	Online via Zoom and Council hall of the University of Tartu, 18 Ülikooli Street, Tartu, on 17 August 2021 at 15:00.

Publication of this thesis is granted by the Institute of Ecology and Earth Sciences, University of Tartu and by the Doctoral School of Earth Sciences and Ecology created under the auspices of European Social Fund.

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ISSN 1024-6479
ISBN 978-9949-03-644-8 (print)
ISBN 978-9949-03-645-5 (pdf)

University of Tartu Press
www.tyk.ee

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LIST OF PUBLICATIONS

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

- **I.** **Vahter T**, Sepp SK, Astover A, Helm A, Kikas T, Liu S, Oja J, Öpik M, Penu P, Vasar M, Veromann E, Zobel M, Hiiesalu I. Impoverished landscapes amplify negative effects of intensive agriculture on soil fungi. *Manuscript*
- **II.** Hoeffner K, Beylich A, Chabbi A, Cluzeau D, Dascalu D, Graefe U, Guzmán G, Hallaire V, Hanisch J, Landa BB, Linsler D, Menasseri S, Öpik M, Potthoff M, Sandor M, Scheu S, Schmelz MR, Engell I, Schrader S, **Vahter T**, Banse M, Nicolai A, Plaas E, Runge T, Roslin T, Decau ML, Sepp SK, Arias-Giraldo LF, Busnot S, Roucaute M, Pérès G. 2021. Legacy effects of temporary grassland in annual crop rotation on soil ecosystem services. *Science of The Total Environment* **780**: 146140.
- **III.** García de León D, **Vahter T**, Zobel M, Koppel M, Edesi L, Davison J, Al-Quraishy S, Hozzein WN, Moora M, Oja J, Vasar M, Öpik M. 2020. Different wheat cultivars exhibit variable responses to inoculation with arbuscular mycorrhizal fungi from organic and conventional farms. *PloS ONE* **15**: e0233878.
- **IV.** **Vahter T,** Bueno CG, Davison J, Herodes K, Hiiesalu I, Kasari-Toussaint L, Oja J, Olsson PA, Sepp SK, 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**: 1741–1751.

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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**
I	***	***	**	***
II	**	*	*	*
III	–	–	**	*
IV	***	***	***	***

I. INTRODUCTION

1.1. Background

We are living in the era of a managed planet with almost 40% of terrestrial land used for agriculture (Foley *et al*., 2011). At the same time, the loss of species and habitats poses as great a danger to life on Earth as climate change (IPBES, 2019). Although humans are almost entirely dependent on the capacity of soils for production of food (FAO, 2015a), the United Nations report on "The Status of World's Soil Resources" (FAO, 2015b) concludes that the majority of world soil resources are in either fair, poor or very poor condition not only in terms of soil physicochemical parameters but also biodiversity. Considering also the decreasing area of agricultural land per capita globally (FAOSTAT, 2017), there is an urgent need for more sustainable agricultural management to ensure both food safety and functional ecosystems (Tilman *et al.*, 2011). In addition to providing food for a growing human population, soils in agroecosystems provide numerous vital ecosystem services, including water and soil conservation, nutrient cycling and pathogen suppression (Pretty, 2018). The provisioning of these services is, however, heavily reliant on the biotic component of soils (Delgado-Baquerizo *et al.*, 2016). Although there is unequivocal evidence that the functions and services of ecosystems are impaired by biodiversity loss (Cardinale *et al*., 2012), there is a distinct gap in terms of available soil biodiversity information relevant for policy-making at both national and local scales (Bardgett and Putten, 2014; Bender *et al.*, 2016; Guerra *et al*., 2021).

Fungi are a key constituent of soil biota, representing a wide array of trophic modes and functions (Peay *et al*., 2016). In agriculture, fungi can be a vital asset for their role in decomposing crop residues, acquiring nutrients for plants through the mycorrhizal pathway but also for the way in which they engineer soil physicochemical properties (Gianiazzi *et al*., 2010; Lange, 2014). On the other hand, fungi also comprise some of the most economically important plant pathogens, many of them soil-dwelling. An important part of most plants microbiomes are mycorrhizal fungi (Smith and Read, 2008). Globally, arbuscular mycorrhiza (AM) is considered to be the predominant type of mycorrhizal associations (Brundrett and Tedersoo, 2018), formed by fungi in the subphylum Glomeromycotina (Spatafora *et al*., 2016) and most plants. In AM symbiosis, fungi provide their plant partners with limiting nutrients such as phosphorus and nitrogen (Smith and Read, 2008) and enhance their resistance to biotic and abiotic stresses (Pozo et al., 2015; Sikes *et al*., 2010). In exchange for these benefits, some of the photosynthetic carbon produced by plants is allocated to the fungal symbionts (Keymer *et al*., 2017).

1.1.1. Effects of agricultural land-use practices on AM fungi

Arable field management has a major influence on soil fungi. One of the key impacts of agricultural management on soil fungi arises from the use of external inputs, such as fertilizers (Marschner *et al.*, 2003; Treseder, 2004) and pesticides (Druille *et al.*, 2013; Helander *et al.*, 2018; Riedo *et al.*, 2021), affecting both the physical and chemical soil environment but also soil biota. Additionally, soil tillage regimes (Bowles *et al.*, 2017), crop diversity (Garland *et al.*, 2021; Guzman *et al.*, 2021) and specific soil properties of a field (Zarei *et al.*, 2010) have been identified as important factors for shaping soil fungal communities in arable lands. While many of these aspects have been extensively studied in experimental systems, we are still lacking regional-scale surveys focusing on the impacts of management practices in production farmlands (but see Riedo *et al.*, 2021). This means that not only is there little knowledge about the status of soil biodiversity in food production, but the lack of empirical data also makes it difficult to promote more biodiversity friendly and sustainable agricultural approaches such as organic or conservation agriculture.

Conservation agriculture promotes the maintenance of a permanent soil cover, minimum soil disturbance, and diversification of plant species, aiming to reduce soil loss and increase soil carbon content but also support soil biodiversity (Hobbs *et al*., 2008). Therefore, one of the key components of conservation agriculture is the introduction of temporary grasslands to annual crop rotations. Temporary grasslands help decrease soil disturbance and increase both soil cover and plant diversity in the rotations (Lemaire et al., 2015; Martin *et al*., 2020). Temporary grasslands may also enhance a number of ecosystem services including soil structure maintenance, water regulation, pathogen regulation and biodiversity conservation (Schwartz *et al*., 2003; van Eekeren *et al*., 2008; Christensen *et al*., 2009; Postma-Blaauw *et al*., 2010; Conant *et al*., 2017; Loaiza Puerta *et al*., 2018; Sirimarco *et al*., 2018; Martin *et al*., 2020).

In addition to the immediate positive effects during the time a field is under temporary grassland, there are effects reaching far beyond the grassland stage and into the crop periods that follow. The strength of grassland legacy effects for successive crops in a rotation system is, however, uncertain and likely to depend on many aspects. These include the duration of the grassland phase, management of the grassland, management of the following crops and specific edaphic conditions of the field (van Eekeren *et al*., 2008; Christensen *et al*., 2009; Carter and Blair, 2012; Crotty *et al*., 2016; Panettieri *et al*., 2017). Compared to an annual crop rotation without grassland, van Eekeren *et al*. (2008) observed that after three years of crops, there were still benefits to the physical properties and biodiversity of soil in having a preceding three-year grassland period. As a possible consequence of grassland legacies on soil properties, Christensen *et al*. (2009) observed that grassland introduction into an annual crop rotation increased the yield and quality of the grain in the following crops.

Not only do the preceding crops affect the performance of crops that follow, but they may also affect the AM fungal communities in the soil (Miller, 2000;

Karasawa *et al.*, 2002, Beirruti *et al.*, 2018). This can have important implications for both the nutrient economy in a crop rotation and also the soil AM fungal biodiversity. It is thought that because of the wide distribution of AM fungal interactions, the capability of modern crop species to interact with AM fungi was likely inherited from their ancient progenitors (Martin-Robles *et al.*, 2018; Sawers *et al.*, 2018). Wheat (*Triticum* spp.) is a major food crop that is widely grown around the world under diverse climatic conditions, with a total of more than 700 million tons produced annually (FAOSTAT, 2021). It is classified as a facultatively mycorrhizal plant species with the strength of association depending on the variety (Hetrick and Wilson, 1993). Under experimental conditions, AM fungi have been shown to enhance wheat growth and nutrition (Graham and Abbot, 2000; Zhu *et al.*, 2001). Suppression of AM fungi, however, has been linked with yield reductions (Owen and Clewett, 2010). Importantly, different wheat varieties can associate with distinct AM fungal communities (Mao *et al.*, 2014), which might lead to differential responses in inoculation experiments, both in terms of root colonisation and nutrient exchange, but also crop yield (van Geel *et al.*, 2016; Thirkell *et al.*, 2020; Elliott *et al.*, 2020). It has also been suggested, that these differential responses of wheat varieties to inoculation might be connected to the time when the variety was first released (Hetrick and Wilson, 1993). The study conducted by Hetrick and Wilson (1993) on 20 wheat varieties demonstrated that the varieties released before 1950 consistently benefited from AM fungal inoculation, while the response of newer varieties was more varied. They hypothesized that these differences in the responses of wheat to inoculation might be a product of changing agricultural and plant breeding practices, which may have favoured varieties that can effectively exploit the highly fertilized modern agricultural systems relying less on AM fungi for nutrition. This idea has been corroborated by a meta-analysis from Zhang *et al.* (2019) who also found that there was a tendency for recent wheat varieties to exhibit decreased responses to AM fungi in terms of yield. However, this hypothesis has also been met with opposing results – a meta analysis by Lehmann *et al.* (2010) found no evidence of newer wheat genotypes having lost their ability to interact with AM fungi. Therefore, it is possible that domestication could have had variable effects on crop traits, in some cases including the disruption of symbiosis (Porter and Sachs, 2020).

The benefit from AM fungal symbiosis may be especially important in agroecosystems which rely more on natural processes rather than synthetic inputs for both nutrients and pest control (Thirkell *et al.*, 2017). While it has beed demonstrated by numerous studies, that the AM fungal communities in organic and conventionally managed soils are different (Verbruggen *et al.*, 2010; Dai *et al.*, 2014; Moora *et al.*, 2014; Banerjee *et al.*, 2019), the effects these AM fungal communities have on the growth and yield of cereals is largely unclear. For instance, in an experiment with maize, Verbruggen *et al.* (2012) did not find a positive plant-growth effect of AM fungal inoculum originating from organic farming, while Gottshall *et al.* (2017) reported a positive effect of organic-field inoculum on wheat growth. Here, it is also important to note that most inoculation experiments with wheat have used AM fungal strains originating from cultures (van Geel *et al.*, 2016). These cultured taxa could exhibit specific traits compared with the uncultured AM fungal taxa they commonly share habitat with in the field (van der Heijden *et al.*, 2008; Ohsowski *et al.*, 2014).

1.1.2. Landscape contribution to AM fungal biodiversity

A large proportion of European biodiversity depends on the habitats provided by low-intensity farming practices, yet this resource is declining as European agriculture is intensifying and these seminatural habitats are becoming increasingly fragmented (Krauss *et al.*, 2010; Sutcliffe *et al.*, 2014). It has been stressed that in fragmented landscapes, dispersal of organisms is often disrupted, leading to failure in spontaneous recovery of species richness but also failure to establish and maintain genetically diverse populations (Aavik and Helm, 2018).

There is little known about how the surrounding landscape and uncropped landscape elements within and around agricultural fields contribute to soil fungal diversity (Grilli *et al.*, 2017). Environmental heterogeneity has been found to be a major factor determining the turnover of AM fungal communities at the landscape scale (Gast *et al.*, 2011) but Williams and Hedlund (2013; 2014) on the other hand found no such effect on microbial community composition, inferred from soil microbial fatty acid profiles. In addition, Boeraeve *et al.* (2019) found that in forest ecosystems, it is rather the habitat area and abiotic factors that shape AM fungal communities, not landscape context. Still, seminatural grasslands and uncropped landscape elements such as field margins, hedgerows or small forested patches within the fields may be sources of fungal propagules, especially considering the wide array of their insect vectors that can move between the surrounding landscape and the fields (Aguilera *et al.*, 2020; Albrecht *et al.*, 2020; Gallé *et al.*, 2020). Although fungi exhibit a range of dispersal modes and can disperse over long distances (Chaudhary *et al.*, 2020; Paz *et al.*, 2021), the diluting effects of distance and a reduced probability of establishment in a disturbed environment can limit successful dispersal even at a distance of tens of meters (Norros *et al.*, 2012). A diverse landscape potentially offers many habitats for different fungal species, acting as a source of propagules to an otherwise biodiversity sink of agricultural fields (Holyoak *et al.*, 2005; Runge *et al.*, 2006). In Europe, the formerly commonplace semi-natural grasslands are estimated to have lost 90% and in some regions even more of their former area during the last century (Wallis de Vries *et al.* 2002). In Estonia, there were close to a million hectares of semi-natural grasslands in the 1930's while today, only about 35 000 hectares are managed (Helm and Toussaint, 2020). This is likely to have ecologically significant effects, given the fact that semi-natural grasslands can harbour a very high diversity of AM fungi (Sepp *et al.*, 2018; Neuenkamp *et al.*, 2018), and thus may serve as important diversity banks and sources of soil biota for agricultural systems.

Temperate grasslands are threatened most by changes in land use – typically conversion into agricultural land or abandonment (Hoekstra *et al.*, 2005). Even though the restoration of indigenous grasslands is a well-established priority in developed countries, conflicting economic interests over grasslands imply that alternative habitats need to be considered alongside restoration schemes to offset the loss of grassland areas (Kasari *et al.*, 2016). Potential alternative habitats include abandoned agricultural land (Fagan *et al.*, 2008), urban brownfields (Rebele and Lehmann, 2002) and post-mining landscapes (e.g Kirmer *et al.*, 2012; Swab *et al.*, 2017). With up to 800,000 km^2 of land impacted by mining activity globally (Cherlet *et al.*, 2018), post-mining areas could represent an important addition to offset grassland habitat loss both locally and globally.

Creation of grassland plant communities in degraded landscapes has remained problematic, with conventional restoration techniques often yielding low plant diversity compared with unrestored areas following natural succession (Tischew and Kirmer, 2007). This may be due to particular practices, including fertilization or propagation of species unsuited to the habitat conditions (Tischew and Kirmer 2007). Moreover, incomplete approaches that focus on plants but neglect plant-associated microbiomes have been identified as a factor explaining restoration failure (Koziol and Bever, 2017). Given the extreme abiotic conditions often present in post-mining areas, AM fungi may be critical for plant survival and vegetation establishment. Potential benefits of inoculation with diverse communities of native AM fungi have been proposed in a number of grassland restoration studies (e.g. Koziol *et al.*, 2018; Middleton and Bever, 2012; Wubs *et al.*, 2016). Addition of mycorrhizal fungal inoculum may indeed facilitate rapid establishment of vegetation (Neuenkamp *et al.*, 2019). However, mine restoration experiments have most often employed a narrow selection of AM fungi, and examples of using native AM fungal communities alongside their native host plants and tracking their co-development are lacking.

1.2. Objectives of the thesis

The general knowledge gap addressed in this thesis is the status of soil AM fungal biodiversity in agroecosystems as an outcome of farmland management. By definition, agroecosystems do not stand isolated from natural ones. With interlinked nutrient, water and energy cycles in addition to the movement of organisms between the systems, it is clear that focusing solely on arable fields, although also crucial, will not provide long term sustainable solutions for biodiversity loss and food security. Despite this perspective, we often lack information about how farmland biodiversity develops, making management decisions in our landscapes extremely difficult. This thesis aims to advance the understanding of how AM fungi are faring in food production systems but also to assess some possible means for fostering AM fungal biodiversity as a land management option.

The main objective of this thesis was **to gain information on the status of soil AM fungal biodiversity in anthropogenic ecosystems, with an emphasis on arable fields, and identify the main sources of impact**. To achieve this goal, we utilized a large scale farmers network in Estonia and used soil eDNA metabarcoding, in tandem with metadata collected from the farmers, to assess the impacts of common agricultural practices and landscape configuration on soil AM fungi (**Paper I**). In addition, as it is widely considered a beneficial practice for biodiversity, we explored the effects of temporary grasslands in crop rotations and their impact on soil AM fungi (**Paper II**). We also experimented with the crops themselves, using modern and heirloom varieties of wheat: inoculating them with soil from both organic and conventional farming systems, and assessing the plant responses under greenhouse conditions (**Paper III**). These studies allow us to decipher the effects of some common agricultural practices on AM fungi, effectively creating a selection of interventions needed to sustain diverse and functional soils for food production. In addition to field management, landscape biodiversity and the condition of ecosystems surrounding arable fields can be an important factor for soil fungal diversity and the functions they provide (**Paper I**). Therefore, we also experimented with the creation of diverse vegetation assemblages in biodiversity-poor landscapes by using native AM fungal inoculations as a possible means to ameliorate some of the effects of intensive landscape management on AM fungi (**Paper IV**).

Specifically, the main research questions in this thesis were:

1. What are the diversity patterns of soil fungi in Estonian arable fields in relation to how they are managed? (**I**)
2. Does landscape configuration, specifically the proportion of non productive landscape elements, affect fungal diversity in arable soils? (**I**)
3. How does the inclusion of temporary grasslands in a crop rotation affect soil fungal diversity and what proportion of grassland is needed in a crop rotation to achieve a positive influence on soil fungi? (**II**)
4. How does the choice of crop variety affect the benefits of AM fungal symbiosis in conventional and organic management systems? (**III**)
5. Could low diversity landscapes benefit from inoculations with native AM fungi to restore species rich vegetation assemblages? (**IV**)

II. MATERIALS AND METHODS

2.1. Effects of agriculture and landscape configuration on soil fungi

2.1.1. Study design and data collection

Paper I was designed to assess the richness and diversity of soil fungi in common agricultural systems under cereal cropping. Our aim was to encompass the regionally most widely used practices for fertilization, soil tillage and pesticide use, but also include variables such as soil chemistry and landscape configuration. The study used a purposely established network of farmers for choosing the study fields in Estonia. For this, we advertised the opportunity to take part in a broad-scale study of soil fungi by publishing outreach articles in national media. The criteria for a field to be used in the study were that it had to be actively used for cereal cropping and should not be in a transition period from conventional to organic (or *vice versa*) management. Another condition for participating in the study was the provisioning of metadata by the farmer, including the types of fertilizers used, soil tillage technology and frequency of pesticide use. A total of 78 fields fulfilled these criteria and were included in this study (Figure 1).

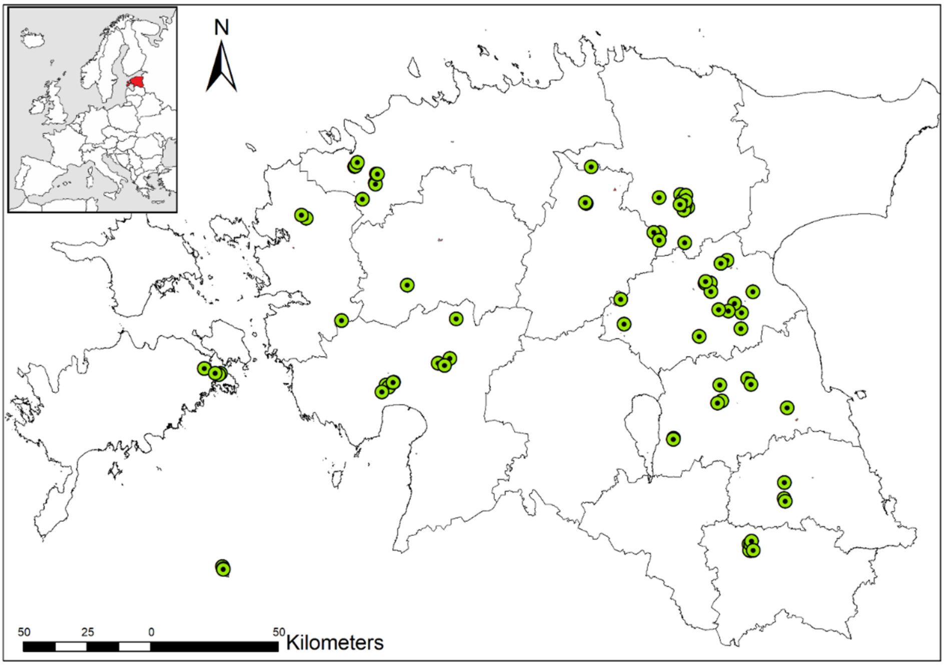

Figure 1 Location of study sites in Estonia.

All soil samples were collected from the fields at the final stages of crop maturity during an 8-week period from August to September in 2019. Twenty individual soil samples from a representative area of the field were collected, pooled and analysed for fungi using molecular techniques (see section 2.4). Soil chemical parameters were determined from the same samples in a certified laboratory. Landscape configuration was assessed by quantifying the percentage of uncropped landscape element cover of a given field, adding buffer zones cartographically around the elements. As there are no published references about the relative importance of different landscape elements to fungal dispersal, we used literature notes on arthropod movements as a proxy for setting the buffer distances (Aguilera *et al.*, 2020; Albrecht *et al.*, 2020; Gallé *et al.*, 2020). While not ideal, this approach allowed us to also take into consideration the effect of landscape elements situated outside the field margins. For instance, proximity to diverse seminatural grasslands would have been unaccounted for if only area of the landscape elements within a field would have been used.

In **Paper II**, we assessed the effects of temporary grasslands on soil biota and ecosystem services in an intensive farming system, in comparison with continuous cropping practices. Specifically, we focused on the effects of continuous cropping, and of 3 and 6 years of grassland in an annual crop rotation and assessed the resulting AM fungal richness, diversity and community composition in the soil. Additionally, collaborating groups also studied soil bacterial, total fungal, springtail, enchytraeid and earthworm biodiversity dynamics. Furthermore, soil structure maintenance (aggregate stability), water regulation (saturated hydraulic conductivity), disease suppression (soil suppressiveness to *Verticillium dahliae*) and forage production were assessed as ecosystem services related to soil biota. The experiment was held at the Agro-Ecosystems, Biogeochemical Cycles and Biodiversity long-term observatory on environmental research (SOERE ACBB), managed by the French National Institute of Agricultural Research and Environment (INRAE), located in Lusignan, France (46°25′12.91″ N; 0°07′29.35″ E).

Specifically, we compared three treatments: (i) a fertilized annual crop rotation with grain maize, winter wheat and winter barley (AC), (ii) a three-year-old grassland preceded by three years of crop (3G, i.e. 50% of grassland in the crop rotation), and (iii) a three-year old grassland preceded by three years of crop and six years of grassland (6G, i.e. 75% of grassland in the crop rotation). The grasslands were sown with perennial ryegrass (*Lolium perenne* cv. Milca), tall fescue (*Festuca arundinacea* cv. Soni) and cocksfoot (*Dactylis glomerata* cv. Ludac). The three treatments were replicated in four random plots of 4000 m^2 each. Soil sampling took place in spring, before tillage and the sowing of crops. For the grassland plots, samples were taken during the grassland phases. For each plot, four soil samples were collected and analysed using molecular techniques (see chapter 2.4).

2.1.2. Data analyses

To test the effects of management practices and landscape elements on the diversity of soil fungi in **Paper I**, we fitted linear mixed models, with management practices (fertilizer type, frequency of pesticide use, tillage regime) or landscape element influence as fixed-effect terms, and crop species at the time of sampling and soil parameters (pH, P, K, organic C) as random-effect terms. We also tested the validity of the set landscape element buffer distances by either decreasing or increasing all possible influence distances cartographically by 50% and re-analysing the main effect of landscape elements. The addition of soil taxonomy (and the associated categorical variable for soil texture), did not improve the model fit in our study and was therefore excluded from subsequent analyses. Linear mixed models for testing the interactions of the fixed-effect terms were fit using backward elimination of non-significant terms. As dependent variables, we used Hill numbers of order 0 and 1 (richness and Shannon diversity [exp(H)], respectively) that were extrapolated to the asymptote to estimate the diversity at complete sampling coverage. Effects of soil chemical parameters on soil fungal diversity were tested by fitting linear models with asymptotically extrapolated diversity values as the dependent variable, and soil parameters as the independent variables.

For **Paper II**, in addition to AM fungal species richness, we further calculated Pielou's evenness (J′) as follows: $J' = H' / \ln N$, where N represents the total number of species and H′ represents the Shannon Wiener diversity index. For the abundance of AM fungi, we used the number of reads as a coarse proxy. Similarly to Paper I, we used linear mixed-effects models followed by Tukey tests for post hoc pairwise comparisons to inspect for effects of the three treatments and blocks on the abundance and diversity of AM fungi. Because the individual samples within a plot are not independent, we specified a nested design in the random effect of the model. To compare the community structure of AM fungi between the treatments a data matrix of pairwise compositional distances among samples was calculated using Bray-Curtis dissimilarity. Non-metric multi-dimensional scaling was used to visualise the distance matrix. The null hypothesis of no difference among crop rotation treatments in AM fungal communities was inspected by PERMANOVA, run on the Bray Curtis distance matrix.

2.2. Responses of modern and heirloom wheat varieties to AM fungi of organic and conventional farming origin

2.2.1. Experiment design and data collection

Paper III used AM fungal inoculations with live soil from organic and conventional farming to assess the reliance on mycorrhizal symbiosis of six heirloom and modern wheat varieties in a greenhouse environment. The soil for the inoculation experiment was collected from four arable fields in April 2017 – two fields under conventional management and two under certified organic management. As we were not interested in the spatial variation of the soil community but rather in maximizing the suite of species present, the soils of organic and conventional management fields were pooled respectively. All sites had been cultivated with spring barley in the year prior to soil collection. The spring wheat varieties used in the experiment were Diamant, Pikker, Tähti, Runar, Arabella and Sorbas. The older varieties, Diamant – released in 1929 – and Pikker – released in 1959, represent plant breeding at a time when the use of mineral fertilizers was minimal and pesticides were not used. In contrast, the most recent varieties, Arabella – released in 2012 – and Sorbas – released in 2016, were developed under conditions of intensive fertilizer and pesticide use.

The substrates for the experiments were prepared by mixing the organic and conventional soils but one being sterilized by gamma irradiation and the other serving as live inoculum. A mixed live soil microbial wash was added to all pots to restore the resident soil microbial community without re-adding AM fungi. Each combination of soil inoculum treatment (two) and spring wheat variety (six) was replicated 10 times, producing a total of 120 pots. The experiment was conducted in a greenhouse with a day length of 16 h at temperature regime 20˚C day/12˚C night. The plants were watered when necessary. Fertilizers and pesticides were not used. The experiment was harvested after 16 weeks of growth.

At the end of the experiment, the height of each plant individual was measured. Thereafter, grains, shoots and roots were harvested separately, dried at 70˚C for 48 h and weighed. The fine roots of harvested plants were stained with trypan blue and the percentage of mycorrhizal fungal colonization was estimated using the magnified grid-line intersection method (Koske, 1989). The fine roots of three randomly harvested plants within each treatment combination were retained for further molecular analysis. Soil chemical parameters (N, P, K, Ca, Mg, Cu, Mn, B, pH) were determined in a certified laboratory.

2.2.2. Data analyses

The proportional grain weight – a ratio between grain weight and the sum of all other biomass fractions – was used as a coarse proxy of crop yield. We also calculated the inoculation responsiveness (IR) on standardized data following Gottshall *et al.* (2018) by subtracting the average plant-trait value with conventionally managed field inoculum from the average plant trait value with inoculum from organically managed fields. Differences among the inoculation responsiveness of varieties could not be statistically tested because this proxy was based on average values (i.e. there is no within-variety variability per plant trait).

The effect of inoculum source on plant traits, AM fungal richness and read abundance, variety identity and their interactions were tested with linear models. Because AM-fungal-sample taxon-accumulation curves showed no relationship between the number of sequences obtained and the taxon richness, we performed fungal richness analyses on unrarefied richness data. The significance of terms was measured with F tests and Tukey post hoc tests.

To compare AM fungal communities between treatments and varieties, Bray Curtis dissimilarity of relative abundances was used as the measure of the distance between communities. Non-metric multidimensional scaling was used to visualize the separation of communities. To test for differences in community composition, we used PERMANOVA analysis. For PERMANOVAs testing the effect of soil origin, 999 permutations were run. Due to the limited amount of data, all possible permutations of variety comparisons within and across soil origins were done.

2.3. Native AM fungal inoculation for creating diverse vegetation assemblages

2.3.1. Experiment design and data collection

In order to test the efficacy of AM fungal inoculation to restore species-rich vegetation assemblages in impoverished landscapes, we used barren post-mining landscapes as a restoration model system in **Paper IV**. The three experimental sites all represent inactive, post-mining oil shale quarries in Estonia. All the sites had been levelled for afforestation five years prior to the start of our experiment, but effectively had no herbaceous plant cover. Native soil inoculum for the experiment was tailor made in a greenhouse, using trap culturing methodology. Target community soil was collected from a mine spoil area restored more than half a century ago and which exhibited a diverse grassland plant community. Plant seeds for trap culturing AM fungi and the subsequent field experiment were compiled from hand-collected seeds of *Achillea millefolium*, *Anthemis tinctoria*, *Campanula persicifolia*, *Medicago lupulina*, *Plantago media*, *Plantago lanceolata*, *Prunella vulgaris*, *Thymus serpyllum*, *Trifolium arvense* and *Trifolium aureum* (0.3 g/m^2 of each species) originating from Estonian grasslands, but also a commercially grown native mix of *Festuca rubra*, *Lolium perenne*, *Poa pratensis* and *Trifolium repens* (2.75, 1.5, 0.5, 0.25 g/m^2 respectively). Trap cultures were prepared by mixing the live soil with sieved sand and peat substrate at a ratio of 2/7/1, sowing the seed mixture and maintaining the 4 L pots for 18 weeks. Then the above-ground plant material was removed and one 4 L container used as inoculum for each 4 m^2 plot in the field.

In spring 2017, 24 plots of 2 m × 2 m (with 1 m buffer between plots) were established in a uniform grid, at each of the three sites. Plots were randomly allocated to the four treatments of the full-factorial design: no biota added control, soil inoculum only, plant seeds only and soil inoculum with plant seeds, with six replicates per treatment at each site. Live soil inoculum was applied at a concentration of 1 L/m^2, and seeds were evenly sown at a density of 32 g of seed mixture per plot. Control plots and seeded plots that were not inoculated received the same amount of mock inoculum that did not undergo the trap-culturing stage and hence were not expected to contain AM fungal propagules. After applying the treatments, plots were raked to mix the seeds and inoculum with the local quarry substrate. Finally, all plots were mulched with a thin layer of straw to improve moisture conditions for seed germination and to prevent wind and water carrying away seeds or inoculum.

Soil for molecular identification of AM fungi and fatty-acid profiling was sampled in August 2018 from the central 1 m^2 of each plot. Soil for fatty-acid analyses was pooled per treatment within each site because of practical constraints. Fatty acids were extracted according to van Aarle and Olsson (2003) and analysed using gas chromatography and flame ionization detection (FID), as described by Frostegård *et al.* (1993). Vegetation relevés were described in parallel with soil collection. In each plot, a 1 m × 1 m square was placed in the centre of the larger 2 m × 2 m plot. All vascular plant species within the square were recorded and their abundance was estimated as percentage cover (Peet and Roberts, 2013).

2.3.2. Data analyses

To assess the effects of inoculum and seed addition on the richness, diversity and abundance of plants and AM fungi, we used generalized linear models with the addition of fungi or seeds and the site as a fixed effect. We did not rarefy the molecular dataset because we found no confounding relationships between the number of sequences obtained and the taxon richness. As a measure of AM fungal and plant diversity we used the asymptotic Shannon entropy index, or Hill number order $q = 1$, also known as the effective number of species (Joust, 2006). To compare fungal and plant communities between treatments, Bray–Curtis dissimilarity of relative abundances was used as a measure of distance between communities. Non-metric multidimensional scaling was used to visualize the separation of communities. PERMANOVA was used to test for the significance of differences in community composition. For assessing the plant community reliance on AM fungi, and therefore the effect inoculations could have on the development of vegetation, we also used the community mycorrhization index (MI; Gerz *et al.*, 2016; Moora, 2014). MI was used to evaluate the prevalence of mycorrhizal symbiosis in the recorded plant communities as MI shows the frequency of mycorrhizal species, weighted by species abundances. MI is expressed as (Moora *et al.*, 2014):

$$lnMI = ln\frac{community\ weighted\ proportion\ of\ mycorrhizal\ plants}{community\ weighted\ proportion\ of\ non\text{-}mycorrhizal\ plants}$$

Data about the mycorrhizal status of plant species were derived from Bueno *et al.* (2017) and a further literature search. Only plant taxa that could be identified to species level were included this analysis. Generalized linear models were used, as described previously, to assess differences in community MI between different treatments.

2.4. Molecular and bioinformatic analyses

In **Papers I, II and IV**, DNA was extracted from one 5-g subsample of dried soil using a PowerMax Soil DNA Isolation Kit following Gazol *et al.* (2016). In **Paper III**, DNA was extracted from 70 mg of roots by using a DNeasy Plant Mini Kit, following Saks *et al.* (2014). In **all papers**, AM fungal sequences were amplified from DNA extracts using AM-fungal-specific primers for the small-subunit (SSU) ribosomal RNA gene: WANDA (Dumbrell *et al.*, 2011) and AML2 (Lee *et al.*, 2008). A first PCR was conducted with amplicon specific primers linked to Illumina Nextera XT sequencing adapters. A second PCR was performed with Nextera XT index adapters. After the second PCR, samples were purified and the resulting mix sequenced on the Illumina MiSeq platform, using a 2 × 300 bp paired-read sequencing approach. In **Paper I**, the total soil fungal community was identified by also sequencing the ITS2 region with the forward primer mixture of fITS7 and fITS7o (Ihrmark *et al.*, 2012; Kohout *et al.*, 2014), and the reverse primer ITS4 (White *et al.*, 1990). Sequencing was done on the Illumina MiSeq platform, using a 2 × 250 bp paired-end sequencing approach. All sequencing was carried out at Asper Biogene (Tartu, Estonia).

The bioinformatic workflow has been consistent in the studies this thesis comprises and follows the steps described by Vasar *et al.* (2021). Briefly, Illumina paired-end raw AM fungal reads were demultiplexed by checking double barcodes, allowing one mismatch for both reads. Reads were retained if they carried the correct primer sequences (allowing one mismatch for each) and had an average quality of at least 30 (after removal of primer and barcode sequences). Orphan reads were removed. Paired-end reads were combined with FLASH (v1.2.10, Magoč and Salzberg, 2011), using the default parameters – overlap at least 10 bp and overlap identity at least 75%. Putative chimeric sequences were identified and removed using VSEARCH (v2.14.1, Rognes *et al.*, 2016) with the default parameters in reference database mode. In the cleaning and quality filtering stage, ITS reads were additionally trimmed at 220 bases for forward and 180 bases for reverse reads, as suggested by Lekberg et al. (2018). Before the chimera removal step, sequences from the fungal ITS were preclustered with 97% identity into Operational Taxonomic Units (OTUs) using VSEARCH to reduce computational complexity and time. Cluster information was stored to allow mapping clusters back to individual reads.

AM fungal sequences (SSU) were matched against virtual taxa (VT; phylogenetically defined taxonomic units) in the MaarjAM database (Öpik *et al.*, 2010) while total fungal sequences (ITS2) were assigned to taxa according to the species hypothesis (SH) in the UNITE database (Nilsson *et al.*, 2018). Furthermore, in **Paper I**, subsets of plant pathogenic fungi and saprotrophic fungi were extracted from the total fungal (ITS2) dataset, based on the FUNguild database (Nguyen *et al.*, 2016), retaining only assignments with confidence levels of “Probable” and “Highly Probable”. A fungal taxon was considered to be a plant pathogen when the FUNguild “Guild” field contained “Plant Pathogen”, and saprotrophic when the “Trophic Mode” field contained “saprotroph”.

III. RESULTS

3.1. Effects of agriculture and landscape configuration on soil fungi

3.1.1. Soil fungal diversity in arable fields of Estonia

In total, 2572 fungal taxa were recorded from the study fields, comprising 2432 species hypotheses from the ITS dataset and 140 virtual taxa from the AM fungal dataset. The type of fertilizers used, average frequency of annual pesticide use and proportion of uncropped landscape elements in the field were all significant factors for soil fungi (Table 1). More specifically, both richness and diversity of total soil fungi were highest when organic fertilizers were used, whereas under mineral fertilization, richness and diversity were generally lower. Interestingly, the use of a combined fertilization regime, which most often meant occasional application of slurry manure, resulted in the lowest richness and diversity of soil fungi at our study sites. AM fungal diversity was generally less affected by the type of fertilization, although richness was reduced by combined fertilization. We also found that the average number of times that pesticides were applied to a field affected the richness and diversity of most fungal groups. With increasing frequency of pesticide use, fungal richness and diversity generally decreased. For AM fungi, only the richness was negatively affected by pesticide use. Counter-intuitively, the richness of plant pathogenic fungi was unaffected by pesticide use but the Shannon diversity decreased by this. The proportion of a field influenced by landscape elements exhibited a significant effect on the richness of soil total fungi, but also the richness and diversity of plant pathogens and saprotrophs. The assigned areas of influence for uncropped landscape elements were indicative of fungal dispersal, as similar results were obtained when buffer distances were reduced by 50% but significance was lost when they were increased by 50%. AM fungi were seemingly unaffected by landscape configuration in our study fields, whereas the richness of other functional groups was significantly increased when a higher proportion of a field was influenced by the landscape elements. Additionally, we found no effect of different tillage practices on soil fungi, but tillage practices were not independent of pesticide use. We observed an increased frequency of pesticide use when conservation tillage practices were applied.

There was a significant tripartite interaction between fertilization type, frequency of pesticide use and field area influenced by uncropped landscape elements for soil AM fungal species richness ($F = 5.527$, $p = 0.006$). For total soil fungi, fertilization type and landscape elements exhibited a significant interaction, which affected total fungal species richness ($F = 9.073$, $p < 0.001$), but not diversity. The interaction between fertilizer type and frequency of pesticide use was most pronounced for the richness of saprotrophic fungi ($F = 6.984$, $p = 0.002$) and the diversity of total ($F = 3.666$, $p = 0.031$) and saprotrophic fungi ($F = 4.146$, $p = 0.023$).

Table 1 Main effects of management on asymptotic estimates of soil fungal richness and Shannon diversity at full sampling coverage. ANOVA test results of linear mixed-effects models with soil variables and crop species as random factors are shown. Degrees of freedom (*df*), *F*-statistics and *p* values are reported. Significance at 0.001***, 0.01** and 0.05* levels shown. Symbol • indicates marginal significance at 0.1 level. *ns* – not significant.

			Uncropped-landscape-element influence	Fertilization type	Pesticide-use frequency	Tillage type
Richness	All fungi (ITS)	*df*	1	2	1	3
		F	8.987	11.867	11.830	0.989
		p	**	***	***	*ns*
	AM fungi (SSU)	*df*	1	2	1	3
		F	1.597	3.300	11.689	0.291
		p	*ns*	*	**	*ns*
	Plant pathogens (ITS)	*df*	1	2	1	3
		F	4.427	1.415	1.567	0.893
		p	*	*ns*	*ns*	*ns*
	Saprotrophic fungi (ITS)	*df*	1	2	1	3
		F	7.810	2.526	3.025	2.356
		p	**	•	•	•
Shannon diversity	All fungi (ITS)	*df*	1	2	1	3
		F	3.150	17.363	10.126	0.893
		p	•	***	**	*ns*
	AM fungi (SSU)	*df*	1	2	1	3
		F	0.190	2.665	1.401	0.682
		p	*ns*	•	*ns*	*ns*
	Plant pathogens (ITS)	*df*	1	2	1	3
		F	4.419	7.516	7.448	1.086
		p	*	***	**	*ns*
	Saprotrophic fungi (ITS)	*df*	1	2	1	3
		F	5.029	17.007	14.404	1.605
		p	*	***	***	*ns*

3.1.2. Temporary grasslands in crop rotations as a practice to support soil biodiversity

The duration of the temporary grassland period in a crop rotation affected both the soil organisms and related ecosystem services. In the case of AM fungi, however, the positive effect of having temporary grassland in a crop rotation was only significant for species richness when a high (75%) proportion of grassland was utilized ($X^2 = 7.51$, p = 0.023; Table 2).

Table 2 Mean values ± standard errors of bacterial and total fungal richness and evenness indexes; AM fungal sampled-based abundance (sequence number per sample), richness and evenness indexes, and microbial biomass by experimental treatment (n = 24). Annual crops only (AC), grassland with medium percentage (50 %) of grassland in the rotation (3G) and grassland with high percentage (75 %) of grassland in the rotation (6G). Different letters denote significant differences between treatments with a > b (Tukey HSD test). χ^2 – values and associated P – values are indicated.

		Treatments					Blocks	
		AC	3G	6G	χ^2	P	χ^2	P
Bacteria	Richness	$60.9^a \pm 3.9$	$51.0^a \pm 4.4$	$56.7^a \pm 4.5$	3.91	0.142	0.02	0.881
	Evenness	$0.95^a \pm 0.00$	$0.95^a \pm 0.01$	$0.95^a \pm 0.00$	0.53	0.769	0.10	0.752
Total fungi	Richness	$181.2^a \pm 9.9$	$146.3^a \pm 5.3$	$164.1^a \pm 6.9$	5.22	**0.074**	1.42	0.234
	Evenness	$0.78^a \pm 0.01$	$0.75^a \pm 0.02$	$0.75^a \pm 0.02$	2.02	0.364	0.35	0.555
AM fungi	Abundance	$529.2^b \pm 143.7$	$1274.9^a \pm 163.3$	$1030.6^{ab} \pm 198.2$	12.86	**0.002**	7.82	**0.050**
	Richness	$9.4^b \pm 1.3$	$10.8^{ab} \pm 0.7$	$13.1^a \pm 0.9$	7.51	**0.023**	12.04	**0.007**
	Evenness	$0.60^{ab} \pm 0.04$	$0.49^b \pm 0.04$	$0.64^a \pm 0.03$	10.35	**0.006**	3.25	0.355
Microbial biomass	0 – 10 cm	$144.5^b \pm 7.5$	$171.7^{ab} \pm 5.9$	$206.2^a \pm 18.5$	6.13	**0.034**	0.56	0.661
	10 – 20 cm	$120.2^b \pm 3.1$	$168.9^a \pm 2.5$	$181.1^a \pm 10.1$	29.24	< **0.001**	1.63	0.279
	20 – 30 cm	$114.9^b \pm 10.1$	$131.2^b \pm 10.0$	$160.8^a \pm 18.1$	11.63	**0.009**	10.15	**0.009**

Conversely, the abundance of AM fungi was highest under a moderate (50%) proportion of grassland in the crop rotation and did not increase thereafter ($X^2 = 12,86$, $p = 0.002$). The evenness of the AM fungal communities was highest under continuous cropping and with a high proportion of grassland in a rotation ($X^2 = 10.35$, $p = 0.006$). Soil total fungal and bacterial richness and evenness showed a limited response to temporary grasslands, but soil microbial biomass increased in all soil depths (Table 2).

The soil AM fungal communities showed a clear distinction between crop rotations (Figure 2, block b). Specifically, annual crops (AC) and those with temporary grasslands included (3G and 6G) hosted a divergent community of AM fungi, while the duration of the grassland period in the rotation had less of an effect. Community differences in other organism groups were generally less pronounced. The studied ecosystem services gave mixed responses to the introduction of temporary grasslands. Provisioning of services such as soil-pathogen regulation decreased, while water regulation was unaffected by the introduction of temporary grasslands to the rotation. Soil-structure maintenance was positively impacted by temporary grasslands. Forage production was unaffected by the duration of the temporary grassland phase.

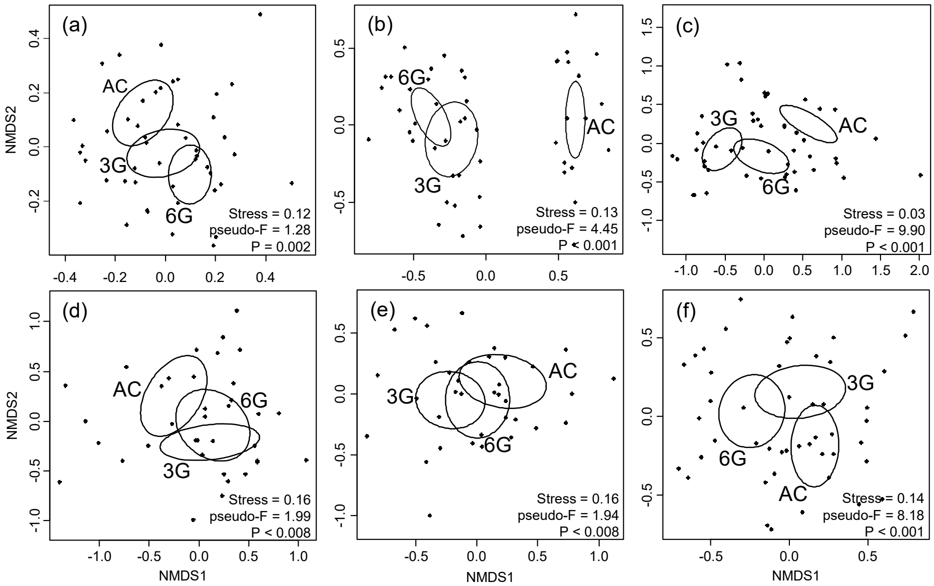

Figure 2 Non-metric multidimensional scaling ordinations showing differences, based on Bray-Curtis dissimilarity among bacterial (a), total fungal (b), AM fungal (c), springtail (d), enchytraeid (e) and earthworm (f) communities (i.e. the composition of OTUs or species) in experimental crop-rotation treatments. Individual points represent samples and the ellipses represent the bidirectional 95% confidence intervals of treatments. Significant dissimilarities between treatments were assessed by PERMANOVA. Pseudo *F*-values and associated *p*-values are indicated. Experimental crop-rotation treatments: annual crops only (AC), grassland period with a medium (50%) duration in the crop-rotation (3G) and grassland period with a high (75%) duration in the rotation (6G).

3.2. Responses of modern and heirloom wheat varieties to AM fungi of organic and conventional farming origin

In general, there was a trend for wheat varieties to be shorter ($F_{5,104} = 80.3$, $P < 0.01$) and produce less roots ($F_{5,104} = 4.83$, $P < 0.01$) but more grain ($F_{5,104} = 7.33$, $P < 0.01$), depending on the years since release. The response of wheat to inoculation with organic or conventional farming derived soil (IR) varied between the varieties, although in general, plants that received organic soil inoculum grew taller ($F_{1,104} = 21.8$, $P < 0.01$) and had larger root systems ($F_{1,104} = 4.0$, $P = 0.05$). The variety Pikker, released in 1959, showed the most positive response to inoculation with soil from organic farming, leading to taller plants, and higher root, shoot, grain and proportional grain weight, in comparison to soil inoculum from conventional farming (Figure 3). By contrast, Arabella, one of the newer varieties, which was released in 2012, performed better when inoculated with soil biota from conventional farming.

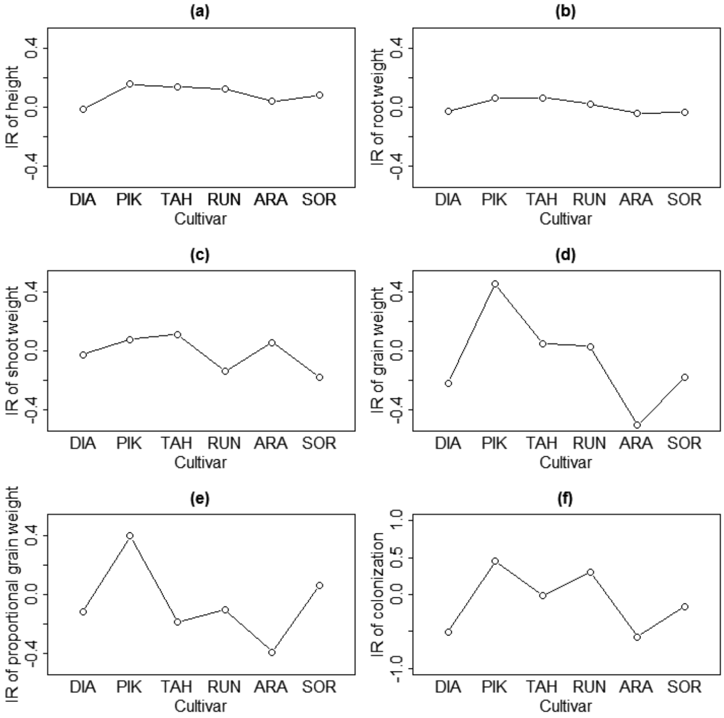

Figure 3 Average inoculation responsiveness (IR) of wheat variety traits, showing the differences in the effects of organic and conventional inocula on: (a) plant height, (b) root weight, (c) shoot weight, (d) grain weight, (e) proportional grain weight, and (f) root colonization. Higher IR values show a stronger positive effect of organic inoculum. DIA: Diamant 1929, PIK: Pikker 1959, TAH: Tähti 1972, RUN: Runar 1972, ARA: Arabella 2012, SOR: Sorbas 2016.

The five most dominant VTs in the dataset made up 96% of all sequences and were members of the genus *Glomus* (VT388 – 40%), the *Glomus/Rhizophagus irregularis* species complex (VT113 – 30%, VT115 – 21%, VT114 – 4%) and the genus *Funneliformis* (VT67, related to *Funneliformis coronatum* – 1.5%). AM fungal communities in the roots of wheat plants differed significantly when grown in organic or conventional field soils (PERMANOVA $R^2 = 0.23$; $p < 0.01$). There was no significant difference in the AM fungal richness or read abundance across all varieties. The two varieties that exhibited the greatest difference in measured plant traits between organic or conventional field soils – Pikker and Arabella – also tended to exhibit diverging AM fungal community compositions when grown in different soils (Figure 4), but did not differ significantly in the number of AM fungal taxa present, nor their read abundance.

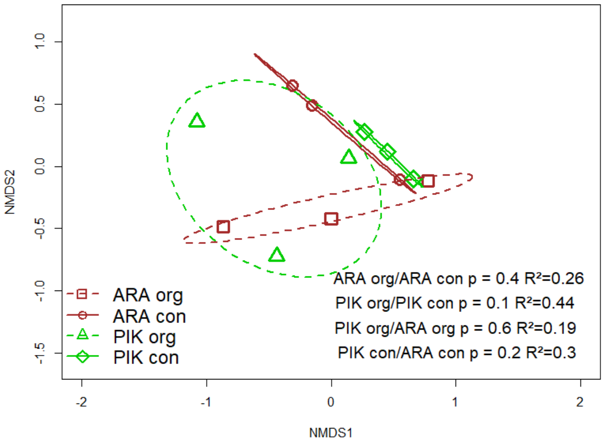

Figure 4 Non-metric multidimensional scaling ordinations showing differences, based on Bray Curtis dissimilarity, for the wheat varieties Arabella (ARA) and Pikker (PIK) when grown in either soil from organic (org) or conventional (con) farming. Each point represents the community associated with roots of one wheat plant. Ellipses show one standard error around treatment centroids. PERMANOVA *p*-values and effect sizes shown.

3.3. Native AM fungal inoculation for creating diverse vegetation assemblages

The year after experiment establishment, we recorded a total of 49 plant species growing in the experimental plots. All the species were native to Estonia and at least one plant species was recorded in every plot. The maximum number of species per square metre of plot was 16, which was found on one of the plots that had received both plant seeds and soil inoculum. Mean plant species richness differed between the treatments, with control plots the most species poor, followed by those that received only soil inoculum and then seeded plots (Figure 5). The highest mean plant species richness was recorded in those plots that received both soil inoculum and plant seeds. The pattern was also similar for the extrapolated asymptotic Shannon entropy of plants. Plant community mycorrhization was also significantly affected by the addition of soil biota, with plant communities in plots that received soil inoculum exhibiting a higher relative reliance on AM fungal symbiosis. There was, however, no clear distinction in the plant community composition between seeded plots that did or did not receive soil inoculum. The seeding itself was therefore the main factor in determining plant community composition. From the 14 plant species seeded, nine were present in the second year of the experiment. The species that were seeded but not detected afterwards were *Campanula persicifolia, Poa pratensis, Thymus serpyllum, Trifolium arvense* and *T. aureum*.

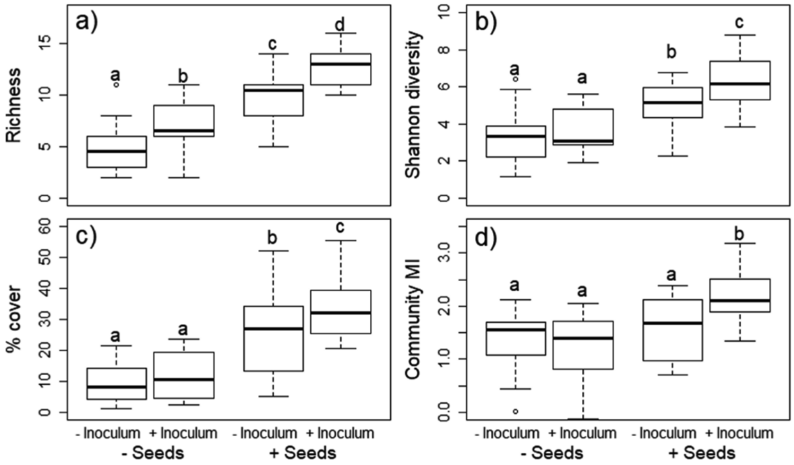

Figure 5 a) Mean plant species richness per 1×1 m plot, b) plant extrapolated asymptotic Shannon entropy, c) % plant cover, and d) mean plant community mycorrhization index (MI) in the second year of the experiment. Letters indicate significant differences between treatments according to post-hoc general linear hypothesis tests, using Tukey pairwise differences.

Following soil molecular analyses, we found a total of 44 AM fungal virtual taxa from the experimental plots. Similarly to the plant communities, the highest richness of AM fungal virtual taxa was found in plots that received both soil inoculum and plant seeds (Figure 6). The plots that received soil inoculum and seeds also harboured a more diverse community of AM fungi and had higher AM fungal biomass, as shown by the AM fungal fatty-acid biomarker concentrations. The AM fungal communities were, however, not distinct between inoculated and uninoculated plots, which was also evident from the high number of shared virtual taxa (22 of 44 VTs) between all treatments.

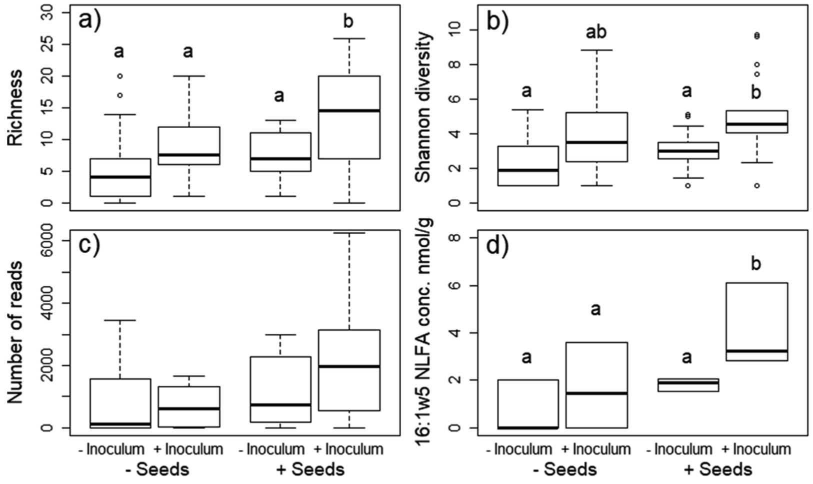

Figure 6 a) AM fungal species richness per soil sample, b) AM fungal extrapolated asymptotic Shannon entropy, c) AM fungal reads per sample (*ns*) and d) AM fungal fatty-acid biomarker concentrations in the second year of the experiment. Letters indicate significant differences between treatments according to post hoc general linear hypothesis tests using Tukey pairwise differences (missing letters denote that no significant differences were found).

IV. DISCUSSION

4.1. State of soil fungal biodiversity in Estonian arable lands

The first step in problem-solving is defining the issue. Few countries in the world have the luxury of up-to-date soil biodiversity data from arable lands and Estonia is no exception. While the scientific community has worked rigorously to provide a mechanistic understanding of the processes taking place in soil, there is an inherent risk in extrapolating knowledge from controlled experiments to real farming. While in science we are often required to make such extrapolations given a lack of local field data, personal experience has shown that the first question from a farmer being informed about the possible impacts of agricultural practices on soil biodiversity is often: "*How do you know what is happening in my field?*".

It is these questions that motivated the work behind **Paper I** – what are the main factors behind soil biodiversity degradation in farming systems, is it actually happening in Estonia and are the reasons for it the ones we would expect from what is published so far? What we found from the 78 fields in Estonia was a mixture of the expected and unexpected. There were rather large differences between the number of fungal species we found in the fields. In the case of total fungi, some field soils would harbour twice the amount of species the poorest ones did. For AM fungi, the diversity gap was even greater, with a sixfold difference between the fields in either end of the diversity spectrum. In a geographically small area with no transitions between biomes or climate zones, it is difficult to attribute these differences to the environment alone, especially considering that the contrasting fields were sometimes very close to each other. Of course, our analysis does not explain all the variance, but the information farmers gave us about the management of their fields did give many insights into what factors might be acting upon fungi in these soils. We observed clear effects of fertilization modes and intensity of pesticide use, but surprisingly not of tillage. We also found that the proportion of field area influenced by uncropped landscape elements was an important factor for both the species richness and Shannon diversity of most fungal groups. Moreover, there were significant interactions between the management practices in shaping soil fungal biodiversity with some factor combinations leading to a greater decline than expected from the sum of their parts.

The influence of fertilization modes on soil fungi has been shown convincingly by numerous past studies (e.g. Marschner *et al.*, 2003; Treseder, 2004). Surprisingly, combined fertilization, which in our study system most often meant occasional fertilization with cow or pig slurry from big farms, generally resulted in lower fungal diversity when compared to fully organic or even mineral fertilization. A plausible explanation for this might be the lower organic matter content of slurries, which does not provide the same benefits to soil biota as solid animal or green manures (Bittman *et al.*, 2005; Walsh *et al.*, 2012; Wentzel and Joergensen, 2016). Additionally, intermittent application of organic nutrients might provide an unstable habitat for the fungi and promote low-diversity successional communities (Bardgett and Caruso, 2020).

Total fungal richness and Shannon diversity were significantly reduced when pesticides were used more frequently. Pesticide use also decreased the species richness of AM fungi but did not change the Shannon diversity, suggesting an impact on rarer species of the community. Similarly, Riedo *et al.* (2021) showed the negative effects of pesticides on root AM fungal colonization and biomass in soil by using the number of pesticide residues found in soil as a predictor. A possible mechanism behind the reduction of AM fungal richness is the suppression of weeds, affecting the more specialized AM fungi associated with them (Schreiner *et al*., 2001; Lekberg *et al*., 2017). Counterintuitively, pesticides did not reduce the species richness of plant pathogenic fungi but did reduce their Shannon diversity. This means that with frequent pesticide use, the relative abundances of some pathogenic taxa can increase (Elsas *et al*., 2012). This could result in a negative feedback loop, where the use of pesticides causes a selective increase of dominance in the soil pathogen community (Garnault *et al.,* 2021), leading to possible disease outbreak and subsequently, even more frequent use of pesticides. Although there is evidence that reduced tillage intensity can have a positive effect on both fungal species richness (Säle *et al*., 2015, Bowles *et al*., 2016) and abundance (Groenigen *et al*., 2010; Treonis *et al*., 2010), we saw no appreciable differences in either the richness or diversity of fungi in relation to tillage in our study sites. In our study, the application of conservation tillage technology was often accompanied by an increase in pesticide use, which might outweigh any benefits from reduced soil disturbance.

The positive influence of uncropped landscape elements was significant for the species richness and diversity of most fungal groups. A diverse landscape offers many opportunities for different fungal species, acting as a source of propagules to what is otherwise a biodiversity sink of agricultural fields (Holyoak *et al*., 2005; Runge *et al*., 2006). In the study fields, the landscape elements area of influence was positively associated with total fungal richness and diversity, as well as plant pathogenic and saprotrophic fungal richness and diversity, while AM fungi were unaffected. The reason for this might be the comparatively low host-specificity (Sepp *et al*., 2019) and small species pool of AM fungi (Pärtel *et al*., 2017). In contrast, it is possible that the agricultural landscape is a habitat to AM fungi that are inherently more resilient to disturbances and dispersal from adjacent landscape elements would repleat the arable soil fungal community with a similar suite of species that is already present. We also observed interactions between landscape, fertilization type and pesticide-use frequency. A significant tripartite interaction was found for AM fungal richness, which means that impoverished landscapes amplify the negative effect of pesticide-use and detrimental fertilization regimes.

4.2. Consideration of AM fungi in crop rotations

Being obligate symbionts, AM fungi are influenced by the plant hosts available to them. Therefore, agricultural practices such as use of bare fallow periods and chemical weed suppression, and the selection of cash and cover crops will have an impact on AM fungi. When planning crop rotations, there are many incentives in play. The farmers experience, local conditions, availability of machinery, commodity market prices and local regulations are only some of the factors behind planning and designing a crop rotation for a given field. In addition, rarely does a crop rotation decision involve only one field. With varying sowing and harvesting times, different needs for plant protection and fertilization, and also if the farmer produces meat or dairy products, the selection of crops in a rotation is an arduous task – a task not made easier by the fact that the decisions made will have an effect on a farmer's livelihood for many years. This means that any new information will be heavily scrutinized before being put into practice. Nevertheless, in **Papers II** and **III**, we show that in addition to the agrotechnology involved, the design of the rotation and the identity of varieties are also factors to consider in making these decisions.

From the literature, the effect of grasslands on biodiversity conservation for successive crops varies among studies. For example, Postma-Blaauw *et al.* (2010) noted a rather short-term grassland legacy effect from one to three years for a broad range of soil biota, while Crème *et al.* (2018) found that microbial biomass still benefited from the previous grassland after three years of crops. In our study, the effect of temporary grassland in the crop rotation had a positive effect on AM fungal richness and evenness, and there was an added benefit in further increasing the proportion of grassland in the crop rotation. The increase in AM fungal richness in treatments with increased grassland permanence could be due to more plant residues and higher host diversity but also lower levels of soil disturbance (Oehl *et al.*, 2003; Vályi *et al.*, 2015). We also observed a shift in AM fungal community composition when a temporary grassland was introduced. This could be linked to the speed of development of crop specialist species vs grassland species: as soon as grassland is introduced, the annual-cropping-associated AM fungi decrease in abundance, but conversely, the return of those fungi adapted to lower disturbance grasslands presumably takes much longer (Vályi *et al.*, 2015; French *et al.*, 2017). As bacterial, fungal and earthworm communities were not affected by the grassland period duration, our findings emphasize that the benefit of extending the grassland duration in the crop rotation to enhance biodiversity does not apply to all organisms in a similar manner.

Nevertheless, grassland introduction did promote a range of services and the effects may last for almost a decade, depending on the organism group and related functions. Thus, to evaluate the effect of agricultural practices on soil properties, it would be informative to also consider legacy effects of past land use. From a policy point of view, temporary grasslands in Europe need to be cultivated and re-seeded at least every five years due to cross-compliance obligations in the European Common Agricultural Policy (CAP). Of course, temporary grasslands are not a long-term fix, but they do offer possibilities for biota in intensively managed landscapes which could otherwise be subject to continuous cropping. Therefore, greater flexibility in farmers' decision-making would be needed in order to benefit from temporary grasslands in a more holistic manner. Instead of imposing the permanent preservation of formerly temporary grasslands, policy could rather promote increasing the proportion of grasslands in rotations.

In **Paper III**, our results indicated differential responses of wheat varieties to AM fungi from organic or conventionally managed soil. It is already known that wheat varieties exhibit different responses to mycorrhizal fungal inoculation (Graham and Abott, 2000; Zhu *et al.*, 2001; Thirkell *et al.*, 2020; Elliott *et al.*, 2020). Even though some studies have found that older varieties respond to AM fungal inoculation in a more positive manner, others provide mixed results (Zhang *et al.*, 2019; van Geel *et al.*, 2016; Lehmann *et al.*, 2012). In our experiment, we found some support for older varieties responding differently than recent ones. Specifically, one of the oldest varieties in this study, Pikker, responded more positively to inoculation with organic field soil than other varieties, while one of the most recent varieties studied, Arabella, responded more positively to inoculum from conventionally managed soils. Still, although AM fungal communities in organic and conventional soils differed, our experiment did not demonstrate a general unidirectional effect of inoculum source on wheat growth and yield, which is consistent with earlier studies (Verbruggen *et al.*, 2012). This means that even though we can observe some differences in the nature of AM fungal associations between the varieties, the cause of this variation is still elusive. We might hypothesize that similarly to production agriculture, plant breeding has taken a shift towards increased external inputs and may have inadvertently reduced plant reliance on symbiotic fungi, but grain weight is not the only trait crops are bred for. With newer varieties also being much shorter and possessing greater resistance to specific pests, it is also possible that these traits have come at the cost of altering the plant mycobiome. On a positive note, this also indicates the possibility that crops could be bred to take better advantage of mutualistic relationships, for instance, needing less fertilization (Sawers *et al.*, 2018, Cobb *et al.*, 2021). This of course would require the rules of variety registration to also accept metrics of success other than yield; one suggestion would be nutrient use efficiency.

4.3. Creating sources of biodiversity through restoration of below-ground interactions

In **Paper I** we show that diverse landscapes may act as sources of biodiversity for anthropogenic ecosystems, which might otherwise lose fungal taxa. In **Paper II** we also show that the development of diversity takes time and a temporary fix does not necessarily translate into sustained biodiversity in the long term. Biodiversity functions at landscape scale, which is why it is important to foster the diversity of habitats in all landscapes, including agricultural ones. In addition to the intrinsic value of nature, biodiversity in agricultural landscapes is the provider of many essential ecosystem services such as pest control and pollination, or as a source of beneficial soil fungi (Gianiazzi *et al*., 2010; Bengtsson *et al*., 2019).

We examined the effect of simultaneously introducing native grassland AM fungi and plant seeds on the development of diverse plant communities in former oil shale quarries in Estonia (**Paper IV**). We observed a clear effect of AM fungal and plant propagule introductions, with co-introduction of plants and symbiotic fungi increasing the diversity and abundance of both groups more than the introduction of either group alone. These results corroborate experimental evidence that using native microbial species in vegetation restorations is beneficial (Koziol *et al*., 2018; Davidson *et al*., 2016) and support the idea that native AM fungi provide more suitable partners for native plants (Moora *et al*., 2004; Maltz and Treseder, 2015).

Although we show that the addition of soil inoculum had an effect on both plants and AM fungi, the use of soil inoculum alone did not lead to significant differences in comparison to the control. This may be explained by the obligate nature of AM fungi, which cannot sustain growth or complete their life cycle in the absence of a plant host (Pepe *et al*., 2018). By contrast, plant seed addition increased plant richness and diversity regardless of soil inoculation. This indicates that the availability of plant seeds, rather than seedling establishment, limits vegetation recovery at these sites. Inoculation and seeding independently increased the richness, diversity and abundance of plants and AM fungi, resulting in an additive rather than interactive effect. This demonstrates that both plant and AM fungal propagules were, to some extent, available at the sites, but their proliferation was limited by a lack of appropriate partners (Garcia de Leon *et al*., 2016). Alternatively, it is possible that while some plant and AM fungal propagules are dispersing to the sites, their quantity is not sufficient for vegetation establishment. In both cases, this suggests that both plants and fungi face a degree of symbiont limitation in biodiversity poor conditions, which can be ameliorated using parallel reintroductions.

We also observed substantial similarities in the AM fungal taxon lists and community composition among treatments, while plant communities were similar between the inoculated and uninoculated treatments, but differed between seeded and unseeded treatments. The large overlap between AM fungal communities in inoculated and uninoculated plots might reflect the fact that the inoculum source was a re-vegetated mine spoil not far from the restoration sites. While plant and AM fungal communities responded somewhat differently to the treatments, linkage in the responses of the partner groups was apparent in the plant community mycorrhization index: mycorrhizal plants were more abundant in the inoculated and seeded plots. These results strengthen existing evidence that AM fungi are important for the development of plant communities and that plant and fungal communities can co-vary (Neuenkamp *et al*., 2018), as long as there is a source of propagules for both.

CONCLUSIONS

The main conclusions reached in this thesis were:

- Soil fungal biodiversity in Estonian arable fields is affected by farming practices, with fertilization type, frequency of pesticide use and proportion of uncropped landscape elements within and around fields being the most influential factors we studied. **(I)**
- The effect of reduced tillage intensity was negligible for soil fungal biodiversity, which could be due to a generally higher frequency of pesticide use when conservation tillage methods were applied. **(I)**
- The effects of field management practices can interact with each other, possibly amplifying the pure effects of detrimental practices when used in combination. **(I)**
- The inclusion of temporary grassland in crop rotations increases soil AM fungal richness and evenness. **(II)**
- Due to legacy effects, increasing the proportion of grassland in a crop rotation could provide an added benefit to soil AM fungal biodiversity. **(II)**
- The inclusion of temporary grasslands into a crop rotation has varying effects on the response of other soil organism groups and is not uniform. **(II)**
- The crop variety can affect plant-fungal mutualistic interactions. **(III)**
- Our evidence suggests that some older wheat varieties may be better adapted to AM fungal communities from organically managed fields, whereas more recent varieties can perform better with AM fungal communities from intensive management, but this response was not uniformly aligned with variety age. **(III)**
- The land managers' actions have great influence on soil fungal communities, which identifes them as the key stakeholders for conserving and improving soil fungal biodiversity in food production. **(I–III)**
- Inoculation with native AM fungi in tandem with sowing of native plants could be used to effectively restore species rich vegetation in degraded landscapes such as post-mining areas. **(IV)**
- A holistic approach, encompassing crop rotation cycles with respective management needs and also landscapes, would need to be considered in future studies to develop (soil) biodiversity friendly and sustainable agriculture. **(I–IV)**

SUMMARY

The aims of this thesis were to gain information about how agricultural land use affects soil fungi and what are the main sources of impact. To achieve these goals, we conducted a national scale observational study in Estonian arable fields, using soil eDNA metabarcoding to link land use practices to fungal diversity in soil. We found that the way fields are managed has a significant impact on soil fungi. We showed that the **loss of soil biodiversity is indeed happening in Estonia**, but also that not all agricultural practices were as detrimental or positive as we thought based on earlier evidence. We showed that the type of fertilizer used has a clear impact on soil fungi, with organic fertilization arguably the best option for promoting soil fungal biodiversity. Still, we also learned that there is a difference in how fertilizers are used as the occasional application of slurry manure can be more detrimental to soil fungi than using only mineral nutrients. We also found a connection between the frequency of pesticide use and soil fungal biodiversity, leading to more impoverished fungal communities with every additional application. The relatively strong, adverse effect of pesticides was also the likely reason we did not observe a positive contribution of conservation tillage practices to soil biodiversity. Therefore, when the incentive is there, **the first thing a farmer could consider to advance towards more sustainable soil management is the use of organic fertilizers and cutting down on pesticide use as much as possible.** This is easier said than done, but also speaks in favour of more diverse farming. With the supply of organic fertilizers being a clear bottleneck in Estonia, diversified production of grains, meat and dairy products would be at least part of the solution. Unfortunately, what we mostly see is rather the consolidation of smaller farms with diverse production outputs into large specialized industrial agro-companies.

As AM fungi are obligate symbionts, the plant partner should, expectedly, also be a major contributor to AM fungal diversity in arable systems. To explore this further, we utilized a crop rotation experiment which also included temporary grasslands and studied the direct and legacy effects of the grassland periods on soil AM fungi. Indeed, we found that **the inclusion of temporary grasslands, albeit species poor ones, into an intensive crop rotation had positive effects for AM fungi**, as well as other soil organisms and related ecosystem services. Here again, it has to be stressed that temporary grasslands are economically viable only when the forage produced can be used at the farm or sold at competitive prices; this is yet another factor speaking in favour of the diversification of farm production. Furthermore, by experimenting with different wheat varieties and AM fungal inoculum sources, we also found that the **symbiotic interactions depend on the variety of crops cultivated**, with different varieties getting more or less of the AM fungal benefit. As this has everything to do with plant breeding, we should bear in mind that classical breeding techniques would usually yield a new variety after a minimum of ten years of selective breeding. If we want AM fungal friendly crop varieties by 2030, which is the turning point for new green deals and development strategies, we might already be too late.

Importantly, in the Estonian arable field soil survey, we also demonstrated that soil fungi do not live in an enclosed soil environment. Similarly to other biota, soil fungi move and disperse through a landscape, neglecting arbitrary borders between fields, grasslands or pristine natural ecosystems. Taking into consideration the likely biodiversity source-sink relationships in agricultural landscapes, it is up to us to make sure there are sources of biodiversity still available in the future. Once a biodiversity source is lost, restoration can become a difficult, lengthy and expensive endeavour. Nevertheless, in an inoculation experiment conducted in depleted quarries we observed that **it is possible to make use of the tight-knit relationship between AM fungi and plants to establish species-rich vegetation at a fast pace in places where it has been lost**. By inoculating native plants with compatible AM fungi, we take, to an extent, the chance element out of dispersal and bring the two partners together where they are needed most. While the development of true diversity, one that comprises not only plants and AM fungi, invariably takes time, proactive restoration of diverse habitats in impoverished landscapes might just buy us the time we need to start turning society to a more sustainable direction.

These findings highlight the fact that the **land managers have a great role to play in the development of soil biodiversity**. Nevertheless, seldom are things so clear-cut in ecology. With many interconnected variables acting upon soil organisms at once, oftentimes driven by economical, practical and even habitual considerations, the informed management of soil fungi in arable systems is not a linear inflow of knowledge towards more sustainable farming. It is rather a soup of information, with bits and pieces boiling up from the bottom as the heat is increased. When popping the lid, we are only looking at a snapshot in time, with some new pieces of information and some re-discovered old ones floating on top, surrounded by the broth of common knowledge we perceive as static in the torrent of research outcomes. Luckily, we all know that usually there is some good stuff at the bottom that is still waiting for discovery. This perspective, although very human, is nonetheless fraught with dangers. For instance, fertilization of crops has been studied using scientific methods for more than a century – a clear indication that **farming, much like everything humans do, is not static but in constant development**. This means there is a constant need for change and adaptation, not only in the way we grow our food, but also in the way we conduct the science needed to shape food production for the challenges ahead. As biodiversity has only recently become the focus of these challenges, it can also mean that **some aspects of farming, heavily researched for tackling other challenges, would need to be given a second look from the perspective of biodiversity and ecosystem functioning**. For example: conservation tillage – carbon smart, climate smart, money smart, but according to our findings, not very biodiversity smart, with the increased pesticide applications needed to control weeds effectively cancelling out the positive effects from reduced mechanical disturbance.

The future of farming and the future of the science behind the development of profitable, sustainable and biodiversity-smart food production will therefore need to focus on the construction of bridges – bridges that will span from one discipline to another, providing contextual solutions that do not limit themselves to single practices or taxonomies. I will be the first to admit that although AM fungi are an integral group of soil organisms, **agricultural policy should be based on information on all relevant soil organisms, not just AM fungi.** We have found that it is rather the rule than an exception that different groups of organisms, or even functional groups within fungi, can react differently to anthropogenic impacts. Therefore, it is necessary that the scientific community make as much effort as possible to create these bridges between disciplines in science and policymaking and with the people that grow our food.

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SUMMARY IN ESTONIAN

Krohmseente tähtsus kestlikus põllumajanduses

Valdav enamik toidust, mida toodame ja igapäevaselt tarbime, pärineb ühel või teisel moel mullast. Vaatamata mulla kesksele rollile meie elus, on selle seisundile ja elustikule liialt vähe tähelepanu pööratud. Üks peamine põhjus seisneb selles, et meil puudub laiapõhjaline ja usaldusväärne informatsioon sellest, kuidas inimene mulda ja selle elustikku mõjutab. Suureks takistuseks muldade uurimisel on paradoksaalselt olnud seal esinevate liikide tohutu arvukus ja mitmekesisus. Peotäies mullas võib elada tuhandeid liike ja miljoneid indiviide, valdav enamik neist mikroskoopilised ning meile tundmatud. Nii nagu maapealsetes vaadeldavates ökosüsteemides, toimuvad ka mullas kõik ökosüsteemide dünaamikale omased protsessid nagu konkurents, kisklus, parasitism ja mutualism. Nagu teisedki ökosüsteemid, ei ole mulla ökosüsteem oma toimimises kuidagi eraldatud teistest teda ümbritsevatest protsessidest. Mulda mõjutavad paljud elusorganismid, kes seda kasutavad substraadi ja toiduallikana ning ka inimesed läbi oma maakasutuse. Ligi 40% maakera maismaapinnast on põllumajanduslikus kasutuses. Samal ajal on elupaikade ja elurikkuse kadumist peetud vähemalt sama suureks ohuks elule maal kui kliimamuutusi. Seetõttu on oluline, et kõik inimese kasutatavad ökosüsteemid, sh põllumajanduslikud, oleksid elurikkust ja seeläbi ökosüsteemide toimimist soodustavad.

Mullaelustikus on olulisel kohal seened. Seened on mullaökosüsteemi insenerid, efektiivsed orgaanilise aine lagundajad ja süsinikuvaru tekitajad, aga ka majanduslikult olulised taimekahjustajad. Seened on ka mükoriisa ehk seenjuure moodustajad, võimaldades taimedel omastada toiteaineid ja pakkudes kaitset mitmesuguse stressi eest. Vastutasuks saavad mükoriisaseened taimedelt süsinikuühendeid, mida nad eluks vajavad, kuid ise toota ei suuda. Ühed levinumad mükoriisa moodustajad on arbuskulaar-mükoriisaseened (AM), olles partneriks valdavale osale maismaataimedele. AM seened moodustavad sümbioosi ka enamike oluliste põllukultuuridega, mistõttu võlgneme inimestena tänu oma toidu eest ka palja silmaga nähtamatutele mullas elavatele seentele. Kuigi mullas elavad seened on olulised nii inimesele, kui ökosüsteemide toimimisele laiemalt, teame me vähe nii seente elurikkusest põllumajanduslikes ökosüsteemides kui ka teguritest, mis neid enim mõjutavad. See muudab mullakasutust puudutavate otsuste tegemise keeruliseks nii põllumajandustootjate kui seaduseloojate jaoks.

Käesoleva doktoritöö üheks peamiseks eesmärgiks oli saada ülevaade Eesti põllumajandusmaade mullaseente elurikkusest ning selgitada välja, millised tegurid seda enim mõjutavad. Selleks kasutasime Eesti tootjate külvikorras olevaid põlde, mille muldadest määrasime DNA-triipkoodi põhjal kõik seal elavad seened. Kogusime ka tootjatelt infot põllul kasutatavate majandamispraktikate kohta ja määrasime kartograafiliselt maastikuelementide mõjualas oleva põllumaa osakaalu. Töö tulemusena leidsime, et seente elurikkuse erinevus võib Eesti erineva majandamisega põllumuldades olla kahekordne, AM seente puhul isegi kuuekordne. Olulisemateks teguriteks mulla seene-elurikkuse kujunemisel olid kasutatavate väetiste tüüp, pestitsiidide kasutamise sagedus ja maastikuelementide mõju.

Positiivset mõju mullaseentele avaldas orgaaniliste väetiste kasutamine, samas kui mineraalsete väetiste kasutamisega kaasnes madalam seente mitmekesisus. Kõige madalama seente elurikkusega olid aga kombineeritud väetamisega põllud, kus vaheldumisi kasutatakse nii mineraalseid kui orgaanilisi väetisi, viimaseid peamiselt vedelsõnnikuna. Kuna orgaaniliste toiteainete lagundamiseks on vaja suurt hulka erinevaid mulla mikroorganisme, sh seeni, on nende toime mineraalsete väetistega võrreldes pikaajalisem ning lisaks taimedele toituvad sellest mulla mikroorganismid, parandades mullaviljakust, struktuuri ja erosioonikindlust. Seega on orgaaniliste väetiste kasutamise ja elurikkuse omavaheline positiivne seos ootuspärane. Mineraalsetes väetistes sisalduvad toiteained on enamasti taimedele juba kättesaadavas vormis. Seetõttu ei panusta mineraalväetiste kasutamine oluliselt mulla toiduvõrgustikku, mistõttu väheneb ka mullaseente elurikkus. Vahelduva väetusrežiimi juures võib olla orgaaniliste väetiste lagundamiseks vajaliku seenekoosluse areng pärsitud, kuna igal ajal ei pruugi olla neile vajalikke toitaineid. Seetõttu võib kombineeritud väetamise puhul väheneda ka orgaanilise väetise kasutamise efektiivsus. Kuna orgaanilistel väetistel on selge ja positiivne mõju mullaelustikule ning paljudele teistele mulla omadustele, tuleks teha lisapingutusi, et tänasest veelgi suurem osa põllumassiive orgaanilisi väetisi saaksid. Siinkohal ei peeta silmas vaid loomasõnnikuga väetamist, vaid laiemat käsitlust orgaanilistest toiteainete allikatest, sh kompost ja toidujäätmed, makro- ja mikrovetikad, järvemuda jm orgaanilise aine allikad.

Pestitsiidide kasutamise intensiivsus, mida hinnati läbi pestitsiidide kasutamise sageduse, vähendas oluliselt mullaseente elurikkust. Kõnekas on asjaolu, et tulemused olid statistiliselt olulised vaatamata sellele, et ei uuritud täpselt, millist preparaati ning kui palju kasutati. See tähendab, et kuigi mõned preparaadid võivad olla teistest ohutumad, on nende mõju siiski kumulatiivne ning leida tuleks võimalusi pestitsiidide kasutamist vähendada. Selle saavutamiseks on oluline nii integreeritud taimekaitse senisest täielikum rakendamine kui ka edasiminekud sordiaretuses ja bioloogilises tõrjes. Vastupidiselt ootustele ei olnud mullaharimise intensiivsus läbiviidud uuringus mullaseente elurikkuse oluline mõjutaja. Nii künnipõhistel kui vähendatud intensiivsusega mullaharimises olevatel põldudel oli seente elurikkus sarnane. Selle põhjuseks võib olla tendents, kus mullaharimise intensiivsuse vähendamisel kasutasid tootjad ka rohkem pestitsiide. Kuna pestitsiidide kasutamise sagedus oli mullaseente elurikkusega negatiivses seoses, võib pestitsiidide sagenev kasutamine samaaegselt mullahäiringute vähendamisega pärssida viimasest tulenevat positiivset mõju.

Lisaks leidsime ka olulised seosed maastikuelementide mõjualade katvuse ja mullaseente elurikkuse vahel. Mida suurem proportsioon põllupinnast asub piisavalt lähedal mõnele maastikuelemendile, seda mitmekesisem on sellisel põllul ka seenekooslus. Mitmekesine maastik pakub palju elupaiku erinevatele seeneliikidele, mistõttu on nad ka elurikkuse allikaks põllumuldadele, mis majandamise käigus liike kaotavad. Seetõttu tuleb olemasolevaid maastikuelemente igal juhul säilitada ning neid ka juurde luua. Lisaks väetiste tüübile, pestitsiidide kasutamise sagedusele ja maastikuelementide mõjule, tuvastasime nende faktorite vahel ka olulised interaktsioonid. Nii on näiteks surve AM seente mitmekesisusele mineraalsete väetiste, pestitsiidide ja vaesunud maastike koosmõjul suurem kui faktorite negatiivsete mõjude summa oodata lubaks. Seetõttu on oluline põllumajandustootmise keskkonnamõju vähendamisel lisaks põllul tehtavatele tegevustele arvestada ka maastiku mitmekesisusega ning leida viise selle suurendamiseks.

Osana doktoritööst uurisime ka lühiajaliste rohumaade mõju mulla seeneelustikule ja selle poolt pakutavatele ökosüsteemihüvedele. Leidsime, et kolmeaastasel püsirohumaal on juba oluline positiivne mõju AM seente ohtrusele, samas kui kuueaastase lühiajalise rohumaa puhul on kõrgemad nii AM seente liigirikkus kui ohtrus. Samas eksperimendis uuritud mullaselgrootutele aga sarnast positiivset tulemust ei leitud. Tõenäoliselt on suuremate organismide elurikkuse kujunemine ka aeglasem protsess, kuna nende levimine pole sama efektiivne kui mikroskoopiliste AM seente puhul. Küll aga oli lühiajalise rohumaa osakaalu suurendamisel külvikorras positiivne mõju mulla struktuurile. Kuna näiteks AM seente liigirikkus oli usutavalt suurem alles kuueaastase rohumaa järel, viitab see vajadusele võimaldada tootja jaoks suuremat paindlikkust lühiajaliste rohumaade rajamisel. Tänased põllumajanduse reeglid näevad ette, et lühiajalise rohumaa kestvus ei tohi ületada viit aastat, mistõttu ei pruugi lühiajalistest rohumaadest tulenev kasu elurikkusele veel realiseeruda.

Lisaks külvikorra ülesehitusele, uurisime ka kultuurtaimede suhteid AM seentega. Teaduskirjanduses on viiteid sellest, et kultuurtaimede AM seentest saadav kasu on ajas vähenenud.. On arvatud, et see võib olla tingitud sordiaretuse käigus kaduma läinud vajadusest AM seentega sümbioosi luua, kuna sarnaselt tootmispõldudega, on ka sordiaretuses tõusnud väetiste ja taimekaitsevahendite kasutamise foon. Seega võivad taimed olla aretuse käigus kohastunud pigem toiteaineterikaste tingimustega, kus AM seentest saadav kasu on väike ja motivatsioon sümbioosi loomiseks madal. Sümbioos AM seentega võib olla aga eriti oluline näiteks maheviljeluses, kus sünteetilisi väetisi kasutada pole lubatud ning mulla toiteainete sisaldust hoida keerulisem. Oma töös võtsime luubi alla globaalselt ühe olulisema toidukultuuri – nisu – erinevate sortide suhted AM seentega tava- ja maheviljeluse muldades. Kasvatasime kuut viimase sajandi jooksul aretatud nisusorti koos AM seentega, mis pärinesid tava- või maheviljelusest ning uurisime nii taimede kasvu kui ka seentega loodud suhteid. Leidsime, et erinevalt varasemalt kirjeldatust, ei esinenud eri ajal aretatud nisusortidel ühesuunalist nihet mükoriissuse vähenemise suunas. Küll aga leidsime, et mõne sordi puhul võib mõju olla siiski oluline. Nii oli näiteks ühe vanema, 1959. aastal Eestis aretatud sordi Pikker kasvuvastus oluliselt parem mahemullast pärit AM seentele kui tavamajandamisest pärit seentele. Samas, üks uuemaid nisusorte Arabella (2012, Poola), kasvas paremini just tavamajandamisega mullast pärit AM seentega. Ka mõlema nisusordi juurtest DNA põhjal määratud AM seente kooslused olid mõnevõrra erinevad. Seetõttu võib arvata, et antud juhul sobisid vanemale sordile pigem AM seened maheviljelusest, uuemale aga tavaviljelusest pärit seened. Kuna uuemad sordid ei ole ainult saagikamad, aga ka lühemad ja üldiselt ka haiguskindlamad, ei saa väita, et toiteainete fooni suurenemise ja mükoriissuse vähenemise vahel oleks selge seos. Sordiaretus ei keskendu teadupärast ainult saagikusele, vaid olulised on ka tunnused nagu näiteks vastupanu haigustele ja lamandumisele. Et need tulemused näitasid olulisi erinevusi nisusortide mükoriisast saadavast kasust, tähendab see võimalust aretada AM seentest rohkem kasu saavaid sorte. Uue sordi aretus traditsiooniliste aretusmeetoditega võtab aga vähemalt kümme aastat. Seega, kui tahaksime järgmise Eesti Põllumajanduse ja Kalanduse arengukava välja töötamisel soodustada mükoriisast enam kasu saavaid uusi sorte, on sellise aretusega alustamiseks sobilik aeg.

Doktoritöö esimeses osas näitasime, et mitmekesised maastikud võivad oluliselt täiendada inimmõjuliste, sh põllumajanduslike ökosüsteemide mulla AM seente elurikkust. Lühiajaliste rohumaade uuringus leidsime ka seda, et elurikkuse kujunemine võtab aega ning lühiajalised lahendused ei pruugi olla jätkusuutlikud. Suur osa inimeste jaoks olulistest elurikkuse funktsioonidest, näiteks tolmeldamine ja looduslik kahjuritõrje, avalduvad maastiku skaalas. Seetõttu on oluline elurikkust toetada kõikides maastikes, sh põllumajanduslikes. Suur osa Euroopa elurikkusest elab madala majandamisintensiivsusega pool-looduslikel põllumajandusmaadel, mille kadumine viimase sajandi jooksul on olnud ülimalt kiire. Nii on ligi miljonist hektarist pool-looduslikest rohumaadest 1930-ndate Eestis täna majandamises kõigest umbes 35 000 hektarit (3,5%). Käesoleva töö kontekstis on see eriti murettekitav ka seetõttu, et pool-looduslikel rohumaadel on väga suur AM seente elurikkus, mis võiks panustada ka intensiivselt majandatavate põllumaade mullaelurikkuse täiendamisse. Kuigi ajalooliste pool-looduslike niitude säilitamine ja taastamine on selge prioriteet, on nende elupaikade kadu olnud niivõrd drastiline, et lisaks väheste säilinud pool-looduslike niitude taastamisele tuleb kaaluda ka alternatiivsete elupaikade rajamist. Käesolevas doktoritöös kasutasime mudelsüsteemina kohalikult väga olulise keskkonnamõjuga kaevandamisjärgseid põlevkivikarjääre ning eksperimenteerisime liigirikka taimekoosluse taastamisega, kasutades selleks pärismaiseid AM seente kooslusi. Selleks paljundasime looduslike niidumuldade AM seeni nn püüniskultuurides. Püünisteks on taimed, mille seemned olid pärit heas seisus pool-looduslikelt niitudelt. Püüniskultuurides tekitatakse taimede jaoks kunstlikult toiteainetevaene kasvukeskkond, mistõttu on neil vajadus mullas olevate AM seentega sümbioos moodustada. Selliselt kasvatatud kultuurides on AM seente leviste tihedus tunduvalt kõrgem kui mullas looduslikult tavapärane on, mistõttu on võimalik saadud mulda kasutada omamoodi juuretisena AM seente külvamiseks taastamisalale. Kolmes Eesti põlevkivikarjääris läbi viidud katse näitas, et nii taimede kui ka AM seente liigirikkus ja mitmekesisus oli oluliselt suurem, kui lisaks taimede seemnetele külvati ka neile sobilikke AM seeni. Liigirikaste niitude rajamine mükoriisaseente abiga on seega arvestatav alternatiiv karjääride metsastamisele ja seda võimalust tuleks kaaluda. Arvestades niiduliikide kehva käekäiku nii Eestis kui mujal maailmas ja nii ökoloogiliselt, majanduslikult, kui ka ühiskondlikult koormaks olevaid ulatuslikke karjäärialasid, võiks liigirikaste niidukoosluste rajamine olla positiivne lahendus nii keskkonnakaitselisest, kui ka majanduslikust ja sotsiaalsest perspektiivist lähtudes. Ühtlasi näitab eksperimendi edukus ka seda, et antud metoodikat kasutades on võimalik liigirikkaid niidukooslusi rajada ka kohtadesse, kus need on hävinenud, sh põllumaadele, tööstusaladele ja linnakeskkonda.

Kokkuvõttes toob antud doktoritöö esile, et Eesti põllumuldades on sarnased AM seente elurikkuse vähenemise trendid nagu mujal Euroopas ning selle peamisteks põhjusteks on intensiivse majandamisega kaasnevad tegurid nagu sünteetiliste väetiste ja pestitsiidide kasutamine, aga ka lihtsustuvad maastikud, kus vähenev elurikkus ei suuda enam põllumuldade elustikku täiendada. Leidsime, et lühiajalised rohumaad võivad olla efektiivne viis mullaelustiku toetamiseks külvikorras, kuid mõju suurendamiseks võiksid need olla ka pikaajalisemad kui seadused täna võimaldavad. Tuvastasime, et ka taimede aretustöö on oluline aspekt kultuursortide mükoriissuse kujunemisel ning seda tuleks tuleviku sordiaretuses lisaks teistele tunnustele silmas pidada. Lisaks näitasid meie eksperimendid, et isegi kui AM seente elurikkuse tugipunktideks olevad liigirikkad taimekooslused on maastikust kadunud, on neist aladest võimalik AM seente külvide abil luua alternatiivsed elupaigad olulistele niiduliikidele.

ACKNOWLEDGEMENTS

Thank you, Maarja, for involving me into all aspects of what it is to be a scientist. I am grateful to have been able to take part in several projects and studies during the course of my PhD studies, many of which have made it possible to meet great people from all around the world. I am also thankful for the relatively hands off approach to supervising, focusing on the important rather than micromanagement. Although at some points, my eagerness to start new things has backfired in terms of timely output, I feel the scientific freedom has made my PhD studies something that I will look back on with warm feelings and a sense of gratitude.

I would also like to thank the senior staff at the Plant Ecology, Macroecology and Landscape Biodiversity working groups. Although senior by academic status, you are a youthful group of people that I have enjoyed being with for purposes that stretch way beyond the science we do. It has been very reassuring to have you all around. To bring the academic family together, I also thank all of my junior colleagues who have become my friends during this time of moving to another city and a new environment. It is not easy to make friends in general, let alone in adulthood, but I feel that I have gained many.

I take this opportunity to also thank my family and friends. Many of you still probably feel that pursuing a career on soil fungi that most people have never seen is a pretty weird thing to do, but I am thankful for all the support I have received throughout the years. My special acknowledgments, however, go to the closest people in my life, Inga and my children Viiu and Ville. I have had some of the most stimulating scientific discussions with you Inga, some close calls regarding professional burnout but many special moments I will remember forever. Thank you for all the encouragement and support. Viiu and Ville, although at the moment more concerned with the amount of jam on the porridge and their bodily functions, have taught me that the work I do is only one aspect of life. I will try and never forget it.

Lastly, I would like to thank all of my collaborators who have made this thesis possible. I'm sure we will be tackling many more research questions and bottles of great wine in the future.

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The research comprising this thesis was supported by grants from The Estonian Environmental Investment Center (grant no. 15499), the Estonian Research Council ((IUT 20-28, PUT 1170, PUT1589, PUT1170, PRG1065, PRG874) and the European Regional Development Fund (Centre of Excellence EcolChange TK131) and ERA-NET Cofund BiodivERsA3 (SoilMan).

PUBLICATIONS

CURRICULUM VITAE

Name: Tanel Vahter
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Education:

2016–...	University of Tartu, Institute of Ecology and Earth Sciences, PhD studies in botany and ecology
2014–2016	Tallinn University, MSc in landscape ecology (*cum laude*)
2011–2014	Tallinn University, BSc in geoecology
1998–2010	Tallinn 32nd Secondary School

Töökohad ja ametid:

2020–...	Mullainfo OÜ, CEO
2016–...	University of Tartu, Faculty of Science and Technology, Institute of Ecology and Earth Sciences, Specialist in Plant Ecology
2014–2016	Agricultural Research Centre, chief specialist, lab of agrochemistry

Teaching:

2021	Ayesh Piyara Wipulasena Aleihela Yamannalage masters thesis “Development of a high-throughput method for soil fatty acid derivatization and analysis” supervisor (co-supervisor Koit Herodes, University of Tartu)
2021	Manju Kasaju masters thesis “Effect of soil sample preparation on fatty acid biomarker content” supervisor (co-supervisor Koit Herodes, University of Tartu)
2020	Epp-Maria Lillipuu masters thesis “Arbuskulaar-mükoriisseid seeni sisaldavad inokulaadid põllumajanduses” supervisor (co-supervisor Inga Hiiesalu, University of Tartu).

Has contributed to the teaching of the following courses:

LOOM.01.031	Mycorrhizal studies
LTOM.01.006	Ecosystem functioning and protection
LTOM.00.001	Seminar in Biology and Biodiversity Conservation
LOOM.03.081	Reclamation of Mining Areas

Scientific publications:

Hoeffner K, Beylich A, Chabbi A, Cluzeau D, Dascalu D, Graefe U, Guzmán G, Hallaire V, Hanisch J, Landa BB, Linsler D, Menasseri S, Öpik M, Potthoff M, Sandor M, Scheu S, Schmelz MR, Engell I, Schrader S, **Vahter T**, Banse M, Nicolai A, Plaas E, Runge T, Roslin T, Decau ML, Sepp SK, Arias-Giraldo LF, Busnot S, Roucaute M, Pérès G. 2021. Legacy effects of temporary grassland in annual crop rotation on soil ecosystem services. *Science of The Total Environment* **780**: 146140.

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Vahter T, Nõges M. 2017. Comparing a simple arbuscular mycorrhizal fungal inoculum with commercial products for enhancing plant growth. *Agraarteadus* **28**: 94–105.

Research grants:

RITA2/95 – "Development of a fatty acid biomarker based soil health indicator for use in arable farming systems" (09.06.2021 – 09.12.2022), Tanel Vahter, University of Tartu, Faculty of Science and Technology, Institute of Ecology and Earth Sciences.

Honours & awards:

2020	Dora Plus T1.1 short term mobility grant
2018	Dora Plus T1.1 short term mobility grant
2018	International Association of Vegetation Science (IAVS) Travel grant for participation at IAVS 2018. annual symposium in Montana USA.
2018	Third place in "Quarrie Life" European region project competition – student supervisor
2017	COST Action FP1305, Short term Scientific Mission "Linking abundance of arbuscular mycorrhizal fungi in soil with plant performance and diversity" to University of Lund, travel grant recipient.
2016	Third place in Tallinn University masters thesis competition.
2015	Tallinn University student research grant "Agricultural usage of arbuscular mycorrhiza fungi"

Presentations:

04.08.2017	Poster presentation at the International Conference on Mycorrhiza in Prague “Manipulating below ground diversity for above ground diversity: the application of arbuscular mycorrhizal fungi in vegetation restoration”
26.10.2017	Poster presentation at the Nature Based Solutions conference in Tallinn “Manipulating below ground diversity for above ground diversity: the application of arbuscular mycorrhizal fungi in vegetation restoration”
15.11.2017	Seminar presentation at Lund University ecology house “Manipulating below ground diversity for above ground diversity: the application of arbuscular mycorrhizal fungi in vegetation restoration”
05.12.2017	Poster presentation at the international Soil Day conference at the Estonian University of Life sciences “Manipulating below ground diversity for above ground diversity: the application of arbuscular mycorrhizal fungi in vegetation restoration”
27.07.2018	Oral presentation at the IAVS Annual Symposium in Montana “Manipulating below ground diversity for above ground diversity: the application of arbuscular mycorrhizal fungi in vegetation restoration”
08.02.2018	Oral presentation at NEFOM (North-European Forest Mycologysts Meeting) in Uppsala SLU “Manipulating below ground diversity for above ground diversity: the application of arbuscular mycorrhizal fungi in vegetation restoration”
21.04.2018	Oral presentation at the summerschool of Theoretical Biology “Põllumajandus – vivaarium või ökosüsteem”
04.05.2018	Poster presentation at the conference Biotic Interactions and Biodiversity Patterns Across Scales, Tartu “Manipulating below ground diversity for above ground diversity: the application of arbuscular mycorrhizal fungi in vegetation restoration”
24.05.2019	Oral presentation at EBOR: Ecological history and long-term dynamics of the Boreal forest ecosystem consortium meeting at Laelatu “Application of arbuscular mycorrhizal fungi in vegetation restoration: restoring the belowground for aboveground diversity”
25.10.2019	Oral presentation at ESP 10 conference in Hannover “Agricultural practices in soil biodiversity management – better practice does not always make perfect”
05.11.2019	Oral presentation at the Biodiversa project SoilMan consortium meeting at Laelatu “Estonian survey of soil fungal diversity in agricultural soils”
05.11.2019	Oral presentation at the Estonian State Forest Management Centers Environmental Protection conference in Pärnu “Krohmseente kasutamine liigirikka taimkatte taastamiseks ammendatud karjäärides”.

15.11.2019	Oral and poster presentation at the Above- and Belowground Biodiversity for Sustainable Ecosystems conference in Zürich “Tillage and arbuscular mycorrhizal fungi – better practice does not always make perfect”.
23.11.2019	Poster presentation at the DarkDivNet network meeting “Tillage and arbuscular mycorrhizal fungi – better practice does not always make perfect”
05.12.2019	Poster presentation at the international Soil Day conference at the Estonian University of Life sciences “Tillage and arbuscular mycorrhizal fungi – better practice does not always make perfect”
07.12.2019	Oral presentation at the annual conference of the Estonian Mycological Society “Krohmseente kasutamine liigirikka taimkatte taastamiseks ammendatud karjäärides”.
21.01.2020	Oral presentation at the Estonian Ministry of Rural Affairs Biodiversity Day “Mulla elurikkus põllumajanduses: mustast kastist majandamisotsusteni”.
31.10.2020	Seminar presentation at the Institute of Ecology, Tallinn University “Mükoriisaseened karjääride ökoloogilises taastamises – maa-alune elurikkus maapealse elurikkuse hüvanguks”.
03.12.2020	Oral presentation at the international Soil Day conference at the Estonian University of Life sciences “Eesti põllumuldade seeneelustiku seisund. Tulemusi üleriigilisest uuringust” Virtually
12.12.2020	Oral presentation at the annual conference of the Estonian Mycological Society “Eesti põllumuldade seeneelustiku seisund. Tulemusi üleriigilisest uuringust” Virtually

Courses

2020–	Methods of consultancy. Estonian University of Life Sciences.
2018–	PhD course in “Sample Preparation for High-Throughput Sequencing” in Uppsala 12-16. February
2017–	WRB (world reference base) soil classification summer school in Kaunas, Lithuania, July 2017

R&D related managerial and administrative work

2019−2021	Board member of Estonian Soil Science Society
2018−...	International Association of Vegetation Science (IAVS) member
2014−...	Estonian Soil Science Society member
2013−...	Estonian Geographical Society member
2018	Participation in the development of the Estonian Agricultural and Fisheries Development Plan 2030
2019…	Participation in the Ministry of Rural Affairs’ Soil Policy Working Group

Science outreach

Publications:

Vahter T. 2020. Riigipööre mullaökosüsteemis. *Schola Biotheoretica* XLVI (23−32). Sulemees.

Vahter T. 2018. Põllumajandus – vivaarium või ökosüsteem? *Schola Biotheoretica XIV* (145−151). Eesti Looduseuurijate Selts (Sulemees).

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Vahter T. 2017. Tibu või krokodill ehk krohmseente inokulaatidest keskkonnas. *Schola Biotheoretica XLIII* (163−172). Eesti Looduseuurijate Selts (Sulemees).

Vahter T. 2015. Põlengute mõjudest muldadele Kurtna maastikukaitseala näitel. *Sügisball. Noorgeograafide sügissümpoosioni artiklite kogumik* (78−92). Tallinna Ülikooli Kirjastus.

Articles in the media:

20.05.2021	„Eelnõu nagu 1950. aastatest." Väärtuslikul põllumaal soovitakse piirata elurikkuse soodustamist. Eesti Päevaleht
19.11.2020.	Liigirikkamad põllumullad on Lääne-Eestis ja vaesemad Pandivere ümbruses. Postimees – Maaelu
16.09.2020.	Põllumajanduslike biopreparaatide kasutamisel tasub olla kriitiline ja ettevaatlik. Põllumajandus.ee
14.09.2020.	Põllumehed ostavad kasuliku seenelisandi pähe sageli kasutut toodet. ERR Novaator.
07.2020	Artikkel "Krohmseened taimedes" ajakirjas Horisont
19.05.2020.	Mikroseened aitavad karjääri muuta roheliseks niiduks. ERR Novaator
08.09.2019.	Glüfosaat põllul, asteroid taevas. Vikerraadio teadussaade Labor
24.01.2019.	Teadlased hakkavad uurima põllumulla seeneelustikku. Postimees – Maaelu
24.10.2018.	Lubjakivikarjääridest on võimalik seeneniidistiku abil taas rohumaad luua. ERR Novaator
21.01.2017.	Teadlased üritavad alvarite liigirikkust taastada seente abil. Saarte Hääl

Videos:

11.11.2020.	Kuidas hoida Eestimaa mullad viljakana ka aastal 2035? Tartu Ülikool https://www.youtube.com/watch?v=YD1xWRbfIQE&ab_channel=Tartu%C3%9Clikool
04.11.2019.	Elukeskkonna taastamine karjäärides. Osoon https://etv.err.ee/999507/elukeskkonna-taastamine-karjaarides
15.01.2018.	Mükoriisaseened – taimeabilised põllumajandusest keskkonnakaitseni. Liftikõne Koostööfestivalil "Õigel Ajal Õiges Kohas" https://www.youtube.com/watch?v=G3rAZAgvJNY&ab_channel=TalTechMEKTORY

Other activities:

Manuscript reviews for journals: Molecular Ecology; Mycorrhiza; New Phytologist; Plants, People, Planet; Environmental Microbiology; Pedobiologia; Applied Soil Ecology; FEMS Microbiology Ecology; Ecological Engineering, Biology and Fertility of Soils; Science of the Total Environment

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Haridustee:

2016–...	Tartu Ülikool, doktoriõpe (botaanika ja ökoloogia)
2014–2016	Tallinna Ülikool, magistriõpe (maastike ökoloogia), *cum laude*
2011–2014	Tallinna Ülikool, bakalaureuseõpe (geoökoloogia)
1998–2010	Tallinna 32. Keskkool

Töökohad ja ametid:

2020–...	Mullainfo OÜ, tegevjuht
2016–...	Tartu Ülikool, Loodus- ja täppisteaduste valdkond, ökoloogia ja maateaduste instituut, taimeökoloogia spetsialist
2014–2016	Põllumajandusuuringute Keskus, agrokeemia laboratoorium, peaspetsialist

Õppetöö:

2021	Ayesh Piyara Wipulasena Aleihela Yamannalage magistritöö “Development of a high-throughput method for soil fatty acid derivatization and analysis” juhendamine (kaasjuhendaja Koit Herodes, Tartu Ülikool)
2021	Manju Kasaju magistritöö “Effect of soil sample preparation on fatty acid biomarker content” juhendamine (kaasjuhendaja Koit Herodes, Tartu Ülikool)
2020	Epp-Maria Lillipuu magistritöö “Arbuskulaar-mükoriisseid seeni sisaldavad inokulaadid põllumajanduses” juhendamine (kaasjuhendaja Inga Hiiesalu, Tartu Ülikool).

Osalenud järgmiste kursuste õpetamisel:

LOOM.01.031	Mükoriisaõpetus
LTOM.01.006	Ökosüsteemide toimimine ja kaitse
LTOM.00.001	Bioloogia ning elustiku kaitse erialaseminar
LOOM.03.081	Kaevandusalade rekultiveerimine

Teadusartiklid:

Hoeffner K, Beylich A, Chabbi A, Cluzeau D, Dascalu D, Graefe U, Guzmán G, Hallaire V, Hanisch J, Landa BB, Linsler D, Menasseri S, Öpik M, Potthoff M, Sandor M, Scheu S, Schmelz MR, Engell I, Schrader S, **Vahter T**, Banse M, Nicolai A, Plaas E, Runge T, Roslin T, Decau ML, Sepp SK, Arias-Giraldo LF, Busnot S, Roucaute M, Pérès G. 2021. Legacy effects of temporary grassland in annual crop rotation on soil ecosystem services. *Science of The Total Environment* **780**: 146140.

Davison J, Moora M, Semchenko M, Adenan SB, Ahmed T, Akhmetzhanova AA, Alatalo JM, Al-Quraishy S, Andriyanova E, Anslan S, … **Vahter T**, … Öpik M. 2021. Temperature and pH define the realised niche space of arbuscular mycorrhizal fungi. *New Phytologist.*

Põlme S, Abarenkov K, Nilsson RH, Lindahl BD, Clemmensen KE, Kauserud H, Nguyen N, Kjøller R, Bates ST, Baldrian P, Frøslev TG, … **Vahter T**, … Tedersoo L. 2020. FungalTraits: a user-friendly traits database of fungi and fungus-like stramenopiles. *Fungal Diversity* **105**: 1–16.

García de León D, **Vahter T**, Zobel M, Koppel M, Edesi L, Davison J, Al-Quraishy S, Hozzein WN, Moora M, Oja J, Vasar M, Öpik M. 2020. Different wheat cultivars exhibit variable responses to inoculation with arbuscular mycorrhizal fungi from organic and conventional farms. *PloS ONE* **15**: e0233878.

Vahter T, Bueno CG, Davison J, Herodes K, Hiiesalu I, Kasari-Toussaint L, Oja J, Olsson PA, Sepp SK, 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**: 1741–1751.

Davison J, García de León D, Zobel M, Moora M, Bueno CG, Barceló M, Gerz M, León D, Meng Y, Pillar VD, Sepp, SK,…**Vahter T**,…Öpik M. 2020. Plant functional groups associate with distinct arbuscular mycorrhizal fungal communities. *New Phytologist* **226**: 1117–1128.

Vahter T, Nõges M. 2017. Comparing a simple arbuscular mycorrhizal fungal inoculum with commercial products for enhancing plant growth. *Agraarteadus* **28**: 94–105.

Teadusgrandid:

RITA2/95	„Biomarker-rasvhapetel põhineva põllumuldade bioloogilise seisundi indikaatori väljatöötamine" (09.06.2021 – 09.12.2022), Tanel Vahter, Tartu Ülikool, Loodus- ja täppisteaduste valdkond, ökoloogia ja maateaduste instituut.

Stipendiumid ja tunnustused:

2020	Dora Pluss T1.1 lühiajalise õpirände stipendiaat
2018	Dora Pluss T1.1 lühiajalise õpirände stipendiaat
2018	International Association of Vegetation Science (IAVS) reisigrant IAVS 2018. aasta sümpoosionil osalemiseks, Montana USA.
2018	Projektis "Quarrie Life" 3. koht üle-Euroopalisel projektikonkursil – tudengite juhendaja
2017	COST Action FP1305, Short term Scientific Mission "Linking abundance of arbuscular mycorrhizal fungi in soil with plant performance and diversity" Lundi Ülikooli, toetuse saaja.

2016 Tallinna Ülikooli üliõpilaste 2015/2016 õppeaasta teadustööde konkursil terve ja jätkusuutliku eluviisi valdkonnas magistritööde kategoorias 3. koht

2015 Tallinna Ülikooli tudengiteaduse uuringugrant teemal “Agricultural usage of arbuscular mycorrhiza fungi”

Esinemised erialakogunemistel:

04.08.2017 Posterettekanne International Conference on Mycorrhiza Prahas teemal “Manipulating below ground diversity for above ground diversity: the application of arbuscular mycorrhizal fungi in vegetation restoration”

26.10.2017 Posterettekanne Nature Based Solutions konverentsil Tallinnas teemal “Manipulating below ground diversity for above ground diversity: the application of arbuscular mycorrhizal fungi in vegetation restoration“

15.11.2017 Seminar Lundi Ülikooli ökoloogiamajas teemal “Manipulating below ground diversity for above ground diversity: the application of arbuscular mycorrhizal fungi in vegetation restoration”

05.12.2017 Posterettekanne Mullapäeval Eesti Maaülikoolis teemal “Manipulating below ground diversity for above ground diversity: the application of arbuscular mycorrhizal fungi in vegetation restoration“

27.07.2018 Suuline ettekanne IAVS Annual Symposionil Montanas 22–27 juulil “Manipulating below ground diversity for above ground diversity: the application of arbuscular mycorrhizal fungi in vegetation restoration”

08.02.2018 Suuline ettekanne NEFOM (North-European Forest Mycologysts Meeting) kohtumisel Uppsalas SLU-s teemal “Manipulating below ground diversity for above ground diversity: the application of arbuscular mycorrhizal fungi in vegetation restoration”

21.04.2018 Suuline ettekanne Teoreetilise Bioloogia kevadkoolis teemal “Põllumajandus – vivaarium või ökosüsteem”

04.05.2018 Posterettekanne sümpoosionil Biotic interactions and biodiversity patterns across scales, Tartus, teemal “Manipulating below ground diversity for above ground diversity: the application of arbuscular mycorrhizal fungi in vegetation restoration”

24.05.2019 Suuline ettekanne EBOR: Ecological history and long-term dynamics of the Boreal forest ecosystem konsortsiumi kohtumisel Laelatul, ettekandega “Application of arbuscular mycorrhizal fungi in vegetation restoration: restoring the belowground for aboveground diversity”

25.10.2019 Suuline ettekanne ESP 10 konverentsil Hannoveris teemal “Agricultural practices in soil biodiversity management – better practice does not always make perfect”

05.11.2019	Suuline ettekanne Biodiversa projekti SoilMan konsortsiumi kohtumisel Laelatul teemal “Estonian survey of soil fungal diversity in agricultural soils”
05.11.2019	Suuline ettekanne RMK looduskaitsekonverentsil Pärnus teemal “Krohmseente kasutamine liigirikka taimkatte taastamiseks ammendatud karjäärides”.
15.11.2019	Suuline ja posterettekanne Above- and Belowground Biodiversity for Sustainable Ecosystems kohtumisel Zürichis teemal “Tillage and arbuscular mycorrhizal fungi – better practice does not always make perfect”.
23.11.2019	Posterettekanne DarkDivNet võrgustiku kohtumisel teemal “Tillage and arbuscular mycorrhizal fungi – better practice does not always make perfect”
05.12.2019	Posterettekanne Maaülikoolis peetud Mullapäeval teemal “Tillage and arbuscular mycorrhizal fungi – better practice does not always make perfect”
07.12.2019	Suuline ettekanne Eesti Mükoloogiaühingu aastakonverentsil detsembris 2019, teemal “Krohmseente kasutamine liigirikka taimkatte taastamiseks ammendatud karjäärides”.
21.01.2020	Suuline ettekanne Maaeluministeeriumi korraldatud Elurikkuse Teemapäeval ettekandega “Mulla elurikkus põllumajanduses: mustast kastist majandamisotsusteni”.
31.10.2020	Tanel Vahter – Mükoriisaseened karjääride ökoloogilises taastamises Maa-alune elurikkus maapealse elurikkuse hüvanguks. Ettekanne Tallinna Ülikooli Ökoloogia Keskuses.
03.12.2020	Ettekanne üleilmse Mullapäeva konverentsil Eesti Maaülikoolis “Eesti põllumuldade seeneelustiku seisund – tulemusi üleriigilisest uuringust” Virtuaalselt.
12.12.2020	Ettekanne Eesti Mükoloogiaühingu aastakonverentsil “Eesti põllumuldade seeneelustiku seisund – tulemusi üleriigilisest uuringust” Virtuaalselt.

Kursused

2020–	Nõustamismetoodika konsulendile. Eesti Maaülikool.
2018–	Mullaelustiku DNA põhise määramise intensiivkursus. Uppsala Ülikool.
2017–	WRB (*world reference base*) süsteemis muldade klassifitseerimise suvekool. Kaunas, Leedu.

Teadusorganisatsiooniline ja -administratiivne tegevus

2019−2021	Eesti Mullateaduse Seltsi juhatuse liige
2018−...	International Association of Vegetation Science (IAVS) liige
2014−...	Eesti Mullateaduste Seltsi liige
2013−...	Eesti Geograafia Seltsi liige

Töö komisjonis

2018	Osalemine valdkondlikes töörühmades Eesti Põllumajanduse Arengukava 2030 välja töötamisel
2019…	Osalemine Maaeluministeeriumi "Mullapoliitika kujundamise töögrupi" töös Tartu Ülikooli esindajana.
2020	Osalemine Keskkonnaameti kokku kutsutud ökoloogide, ametnike ning põllumeeste esindusorganisatsioonide liikmete töögrupis, mille eesmärgiks on kaardistada ühised eesmärgid ning viisid nendeni jõudmiseks.

Teaduse populariseerimine:

Artiklid kogumikes:

Vahter T. 2020. Riigipööre mullaökosüsteemis. *Schola Biotheoretica* XLVI (23−32). Sulemees.

Vahter T. 2018. Põllumajandus – vivaarium või ökosüsteem? *Schola Biotheoretica XIV* (145−151). Eesti Looduseuurijate Selts (Sulemees).

Hiiesalu I, **Vahter T. 2018.** Elurikkuse kaitse põllumajanduse ökoloogilise intensiivistamise abil. *Schola Biotheoretica XLIV* (151−159). Eesti Looduseuurijate Selts (Sulemees).

Vahter T. 2017. Tibu või krokodill ehk krohmseente inokulaatidest keskkonnas. *Schola Biotheoretica XLIII* (163−172). Eesti Looduseuurijate Selts (Sulemees).

Vahter T. 2015. Põlengute mõjudest muldadele Kurtna maastikukaitseala näitel. *Sügisball. Noorgeograafide sügissümpoosioni artiklite kogumik* (78−92). Tallinna Ülikooli Kirjastus.

Artiklid meedias:

20.05.2021	„Eelnõu nagu 1950. aastatest." Väärtuslikul põllumaal soovitakse piirata elurikkuse soodustamist. Eesti Päevaleht
19.11.2020.	Liigirikkamad põllumullad on Lääne-Eestis ja vaesemad Pandivere ümbruses. Postimees – Maaelu
16.09.2020.	Põllumajanduslike biopreparaatide kasutamisel tasub olla kriitiline ja ettevaatlik. Põllumajandus.ee
14.09.2020.	Põllumehed ostavad kasuliku seenelisandi pähe sageli kasutut toodet. ERR Novaator.
07.2020	Artikkel "Krohmseened taimedes" ajakirjas Horisont
19.05.2020.	Mikroseened aitavad karjääri muuta roheliseks niiduks. ERR Novaator
08.09.2019.	Glüfosaat põllul, asteroid taevas. Vikerraadio teadussaade Labor
24.01.2019.	Teadlased hakkavad uurima põllumulla seeneelustikku. Postimees – Maaelu
24.10.2018.	Lubjakivikarjääridest on võimalik seeneniidistiku abil taas rohumaad luua. ERR Novaator
21.01.2017.	Teadlased üritavad alvarite liigirikkust taastada seente abil. Saarte Hääl

Videod:

11.11.2020	Kuidas hoida Eestimaa mullad viljakana ka aastal 2035? Tartu Ülikool https://www.youtube.com/watch?v=YD1xWRbfIQE&ab_channel=Tartu%C3%9Clikool
04.11.2019	Elukeskkonna taastamine karjäärides. Osoon https://etv.err.ee/999507/elukeskkonna-taastamine-karjaarides
15.01.2018	Mükoriisaseened – taimeabilised põllumajandusest keskkonnakaitseni. Liftikõne Koostööfestivalil "Õigel Ajal Õiges Kohas" https://www.youtube.com/watch?v=G3rAZAgvJNY&ab_channel=TalTechMEKTORY

Muu:

22.03.2017	Osalemine TÜ lahtiste uste päeval taastamise pildimänguga
31.03.2017	Ettekanne Tallinna 32. Keskkoolis teemal "Muld ja keskkond, teadus ja teadlane"
20.04.2017	Osalemine Tallinna Pae Gümnaasiumi teaduspäeval krohmseente töötoa läbiviimisel
14–16.06.2017	Kohtumine rahvusvaheliste teadusajakirjanikega Muhus. Intervjuud läbiviidavate katsete teemal loopealsetel.
02.11.2017	Esinemine Tartu Ülikooli demopäeval lühiettekandega teemal "Mükoriisaseened taimekasvu soodustava abivahendina – rakendusi looduskaitsest põllumajanduseni"
28.11.2017	Esinemine ülikoolide ja ettevõtete koostööfestivalil Õigel Ajal Õiges Kohas, Mektorys Tallinnas teemal "Mükoriisaseened taimekasvu soodustava abivahendina – rakendusi looduskaitsest põllumajanduseni"
01.02.2018	Osalemine töötoaga "Geenidest maastikuni" 9. klasside Tartu Ülikooli avatud uste päeval.
28.02.2018	Osalemine töötoaga "Geenidest maastikuni" 12. klasside Tartu Ülikooli avatud uste päeval.
26.–27.05.2018	Laelatu kevadakadeemia "Inimene ja keskkond Eestis 20 a pärast" paneeldiskussioonis osalemine Laelatu Bioloogiajaamas. Projektikonkursi QuarryLife Tartu bakalaureusetudengitest koosneva meeskonna kaasjuhendamine – muld-inokulatsiooni ja looduslike seemnete külvi planeerimise, läbiviimise ja monitoorimise juhendamine. Tulenev artikkel: https://novaator.err.ee/871576/lubjakivikarjaaridest-on-voimalik- seeneniidistiku-abil-taas-rohumaad-luua
13.06.2018	Osalemine Tartu Loodusfestivalil botaanika osakonda tutvustava väljapanekuga.
28.08.2018	"Elurikkus ja igaühe looduskaitse" (seminar). Sagadi looduskoolis peetud seminar põhikooli loodusainete õpetajatele.

28.09–24.10.2018 Teadlaste öö 2018 raames koostatud näitus TÜ botaanikaaia õppeklassis “Botaanikud pole kuivikud ehk taimeteadus üle maade ja läbi aegade”.

09.08.2019 Paide Arvamusfestivali teadusala panelist teemal “Laastav või taastav põllumajandus”

13.09.2019 Koolitusseminar Anija Vallavalitsuse ja valla koolide õpetajatele teemal “Elurikkus ja igaühe looduskaitse”

10.10.2019 Tartu Ülikooli keemia instituudi analüütilise keemia õppetooli seminar teemal “Application of arbuscular mycorrhizal fungi in vegetation restoration: Restoring the belowground for above-ground diversity”

16.10.2019 Keskkonnaagentuuri korraldatud Keskkonnateadlikuse foorumi panelist teemal “Kas keskkonnale on võimalik lisada hinnasilti?”

06.11.2019 Tartu Ülikooli Loodusmuuseumi loodusõhtu teemal “Põllumajandus – loodus või majandusteadus?”

05.12.2019 Panelist Maaülikoolis peetaval Mullapäeva konverentsil mullakaitse teemal.

04.02.2020 Lihaveisekasvatajate Seltsi infopäeval antud loeng teemal “Mulla elurikkus kellele ja milleks?”

11.02.2020 Ettekanne Keskkonnaametis teemal “Eesti põllumuldade bioloogilisest seisundist”

Muu teaduslik tegevus:

Retsenseerinud ajakirjadele: Molecular Ecology; Mycorrhiza; New Phytologist; Plants, People, Planet; Environmental Microbiology; Pedobiologia; Applied Soil Ecology; FEMS Microbiology Ecology; Ecological Engineering, Biology and Fertility of Soils; Science of the Total Environment

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47. **Tarmo Annilo**. Studies on mammalian ribosomal protein S7. Tartu, 1998, 77 p.
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