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The effect of anthropogenic disturbance on soil fungal communities

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

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CONTENTS

LIST OF PUBLICATIONS

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

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II. Vahter, T., Sepp, S.K., Astover, A., Helm, A., Kikas, T., **Liu, S.**, Oja, J., Öpik, M., Penu, P., Vasar, M., Veromann, E., Zobel, M., Hiiesalu, I. 2022. Landscapes, management practices and their interactions shape soil fungal diversity in arable fields – Evidence from a nationwide farmers' network. Soil Biology and Biochemistry 168:108652. https://doi.org/10.1016/J.SOILBIO.2022.108652

III. **Liu, S.**, Vasar, M., Öpik, M., Koorem, K. 2023. Disturbance induces similar shifts in arbuscular mycorrhizal fungal communities from grassland and arable field soils. Mycorrhiza 33(3), 153–164. https://doi.org/10.1007/s00572-023-01108-6

IV. **Liu, S.,** Moora, M., Vasar, M., Zobel, M., Öpik, M., Koorem, K. 2021. Arbuscular mycorrhizal fungi promote small-scale vegetation recovery in the forest understorey. Oecologia 197 (3), 685–697. https://doi.org/10.1007/s00442-021-05065-9

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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

In recent centuries, over half of the terrestrial biosphere has been transformed into anthropogenic biomes due to intensifying land-use activities and population growth (Ellis, 2011). Human activities, particularly those leading to habitat conversion, have resulted in the degradation of local biodiversity and ecosystem services (Newbold et al., 2015; Isbell et al., 2017). So far, most studies evaluating the effect of anthropogenic disturbance on biodiversity have focused on aboveground communities (Winfree et al., 2007; Pakeman, 2011; Franklin et al., 2016), while belowground communities have often been overlooked (Tibbett et al., 2020). However, a large proportion of terrestrial biodiversity resides in the soil, and soil communities play crucial roles in ecosystem functioning (Bardgett and Van Der Putten, 2014; Averill et al., 2022). Additionally, research revealed distinct responses of above- and belowground communities to land-use disturbances (Le Provost et al., 2021). Therefore, there is an urgent need to investigate the effects of anthropogenic disturbance on soil communities.

Anthropogenic activities, such as agriculture and international trade, directly influence the biotic and abiotic characteristics of natural habitats, which significantly influence soil communities (Zhang et al., 2016; Brinkmann et al., 2019; Le Provost et al., 2021). To comprehensively understand the effects of anthropogenic disturbances on soil communities, I categorize them into biotic and abiotic disturbances. Biotic disturbances, often triggered by international trade and transport of organisms, can introduce novel plant species into new ranges, and alter soil communities in the process through changes in plant community composition and organic matter quality (Reinhart and Callaway, 2006; Zhang et al., 2019). Understanding the effects of non-native species invasions on soil communities is crucial for sustaining biodiversity and ecosystem functioning. Additionally, abiotic disturbances commonly arise from conventional agricultural practices, which influence soil communities by changing soil chemical and physical properties (Abdollahi and Munkholm, 2014). With the increasing human population, it is unlikely that conventional agriculture will be entirely replaced by organic agriculture, due to its lower crop productivity (Seufert et al., 2012). Therefore, it is critical to improve the understanding of how different abiotic disturbances related to agriculture shape communities of soil organisms.

Soil fungi are key components of soil communities and play a crucial role in maintaining ecosystem services (Bahram et al., 2020; Averill et al., 2022). In addition, soil mycorrhizal fungi have been shown to provide their associated host plants with improved tolerance of abiotic and biotic stress (Begum et al., 2019; Dowarah et al., 2022). To link these ecosystem functions with soil fungal communities, fungi with different lifestyles are divided into functional guilds, including saprotrophs, ectomycorrhizal fungi, arbuscular mycorrhizal (AM) fungi, plant pathogens, and endophytes (Nguyen et al., 2016). Saprotrophic fungi play a crucial role in litter decomposition, releasing soluble plant-available nutrients into the surrounding environment (Baldrian and Valášková, 2008). Dark septate endophytes, AM and ectomycorrhizal fungi can associate with plants to assist in nutrient acquisition and reallocation among plants (Behie and Bidochka, 2014). Specifically, AM fungi can form symbiotic relationships with most terrestrial plants, facilitating the transfer of soil nutrients to plants and playing an essential role in ecosystem primary productivity (Smith and Read, 2010; Behie and Bidochka, 2014; Begum et al., 2019); ectomycorrhizal fungi establish symbioses with many tree species and transfer soil mineral nutrients to host plants through their mycelial network (van der Heijden et al., 2015; Martin et al., 2016). Additionally, symbioses between dark septate endophytic fungi and host plants can transfer nitrogen and limit metal toxicity to plants (Behie and Bidochka, 2014; Likar and Regvar, 2013). Furthermore, soil pathogenic fungi, another key component of the soil fungal community, strongly impact plant diversity and productivity due to their negative effects on plants (Maron et al., 2011). Therefore, soil fungi from different functional guilds play important roles in ecosystem functioning, and it is crucial to have detailed knowledge about how they respond to different anthropogenic disturbances.

1.1.1 The effect of biotic disturbances on soil fungal communities

Non-native plant invasion is among the most common forms of biotic disturbance caused by globalized socioeconomic activities (Kueffer, 2017), and can shift soil fungal communities due to its impact on plant communities (Reinhart and Callaway, 2006; Bunn et al., 2015). Some non-native plants have been found to have a lower abundance of pathogenic fungi than native plants, suggesting they can escape from the natural enemies in their native habitats (Mitchell and Power, 2003; Li et al., 2022). However, other non-native plants exhibit a higher abundance of pathogenic fungi than native plants due to pathogen accumulation when they grow in their new environment (Mangla et al., 2008; Luke Flory and Clay, 2013). Non-native plants have been shown to have limited effects on AM fungal abundance but strong influences on AM fungal community composition, favoring generalist AM fungi over specialists (Moora et al., 2011; Bunn et al., 2015). The abundance of endophytic fungi among native plants was found to decrease with plant invasion due to the allelopathic effects of non-native plants (Li et al., 2022). At the same time, plant invasion often increases the abundance of saprotrophic fungi, because non-native plants enhance the soil organic matter available for decomposition (Anthony et al., 2020; Li et al., 2022; Ye et al., 2023).

Most studies assessing the impact of non-native plant invasion on plant and soil communities use categorical levels based on non-native plant abundance (Anthony et al., 2020; Shen et al., 2021; Li et al., 2022). However, evaluating plant invasion using categorical levels may be too coarse to capture variation in soil fungal communities, as soil fungi exhibit heterogeneity even at very small spatial scales (Davison et al., 2016). Since plant functional traits have been identified as drivers of soil fungal community composition (Chai et al., 2019), I apply a new index that incorporates non-native plant functional traits to assess how soil fungal communities vary with plant invasion. Specifically, I use the biotic novelty index (BNI), which reflects variation in functional trait space between native and non-native plants weighted by their abundance and time of coexistence (Schittko et al., 2020), to capture changes in soil fungal communities experiencing plant invasion.

1.1.2 The effect of abiotic disturbances on soil fungal communities

Abiotic disturbances arising from agricultural activities alter soil chemical and physical properties and shape distinct responses of soil fungal functional guilds (Abdollahi and Munkholm, 2014; van der Heyde et al., 2017; Rodriguez-Ramos et al., 2021). However, these disturbances differ in the ways they operate. Therefore, dividing agricultural disturbances into chemical and mechanical disturbances can help to gain a systematic view of how soil fungi respond to disturbances (van der Heyde et al., 2017). The most common chemical disturbance in agriculture is fertilizer addition. Synthetic fertilizer application increases soil nutrient availability, leading plants to become less dependent on the nutrients provided by symbiotic partners such as endophytic and AM fungi (van der Heyde et al., 2017; Buckley et al., 2019). On the other hand, organic fertilizer has been found to increase the abundance of saprotrophic and AM fungi, as saprotrophic fungi contribute to organic matter decomposition and AM fungi help to reallocate the decomposed nutrients to plants (Yu et al., 2013; Wang et al., 2017). Herbicides and fungicides, which are also commonly applied chemical disturbances in agriculture, strongly inhibit the abundance of soil fungi (Hahn, 2014; Karlsson et al., 2014; Zaller et al., 2014), especially AM fungi by suppressing their hyphal growth (de Novais et al., 2019).

Mechanical disturbances from agricultural activities, such as tillage and clear-cutting, have significant impacts on soil fungal communities (Kohout et al., 2018; Sun et al., 2018). Conventional tillage, a common agricultural practice, decreases the abundance of mycorrhizal fungi because it directly breaks fungal hyphae in soil (Curaqueo et al., 2011; Schnoor et al., 2011; Schmidt et al., 2019). Additionally, it has been shown that saprotrophs that decompose plant residues in the soil increase under conventional tillage (Sharma-Poudyal et al., 2017), while pathogenic fungi show limited responses to tillage (Schmidt et al., 2019). However, most studies have only evaluated the response of soil fungi to single disturbance types, with little research investigating the interactive effects of different disturbance types (Rillig et al., 2019). Therefore, it is essential to explore the interactive effects of abiotic disturbances on soil fungal communities, particularly considering that common agricultural disturbances, such as herbicide, fertilizer, and tillage application, often occur simultaneously.

Considering the critical role of AM fungi in crop productivity, there is an urgent need to improve current understanding of the mechanisms that determine the response of AM fungal communities to disturbances arising from agricultural practices (Andrew Smith and Smith, 2011; Baum et al., 2015). There is no uniform pattern among recorded AM fungal responses to mechanical or chemical disturbances (Moora, 2014; van der Heyde et al., 2017). In most cases, land-use related disturbances have been shown to have negative effects on AM fungi (Xiang et al., 2015; Liu et al., 2016; Han et al., 2020), while some AM fungal taxa can flourish in disturbed habitats (De La Providencia et al., 2005; Oehl et al., 2010; Mirás-Avalos et al., 2011; Moora, 2014). These inconsistent patterns suggest that some AM fungal characteristics, taken together as life-history traits, determine AM fungal response to disturbance (van der Heyde et al., 2017). For example, fungal culturability, which indicates AM fungal ability to grow in cultures, can be considered as proxy for a ruderal life-history strategy for AM fungi (Ohsowski et al., 2014). Previous studies have demonstrated that the proportion of culturable AM fungal taxa is higher in disturbed than in natural habitats (Ohsowski et al., 2014; Garcia de Leon et al., 2018). However, this approach only focuses on a small fraction of AM fungi. As the traits of AM fungi are, to some extent, taxonomically conserved (Powell et al., 2009; Yang et al., 2017), Grime's C-S-R (Competitor, Stress tolerator, Ruderal, Grime, 1977) framework has been proposed for AM fungi at the family level to describe their life history strategy (Chagnon et al., 2013). Based on this framework, I expect AM fungi with ruderal traits (e.g., high hyphal growth rate, Powell et al., 2009), such as taxa from Glomeraceae, to become dominant after mechanical disturbance (Chagnon et al., 2013). Indeed, high abundance of Glomeraceae has been reported in mechanically disturbed habitats (De La Providencia et al., 2005; Mirás-Avalos et al., 2011). AM fungi that are efficient at resource utilization and grow slowly, such as taxa from the family Acaulosporaceae, are expected to represent a stress-tolerant life-history strategy (Chagnon et al., 2013), and might exhibit high resistance to chemical disturbances. However, to my knowledge, there is no empirical data directly contrasting the effects of chemical and mechanical disturbances on AM fungi with different life-history traits.

AM fungi are not only important for crop production but also play a critical role in promoting plant establishment under natural conditions by transferring soil nutrients to plants and increasing plant tolerance to various stresses (Porcel et al., 2012; Lenoir et al., 2016; Mathur et al., 2019). The role of AM fungi in plant establishment might be more significant under low soil nutrient conditions, as soil nutrient supply reduces the dependence of plants on nutrients provided by AM fungi (Treseder and Allen, 2002; Liu et al., 2016). At the same time, several studies have confirmed that introducing AM fungal inocula improves plant growth and the diversity of re-established vegetation in heavily degraded habitats (Asmelash et al., 2016; Vahter et al., 2020). Although AM fungi can contribute to vegetation recovery (Asmelash et al., 2016; Lenoir et al., 2016), manipulations such as introducing soil AM fungal inoculum have only been proposed for attempts to restore large-scale habitats with degraded ecosystem services. With the increasing range and intensity of human activities, semi-natural or natural habitats close to human activities also suffer from small-scale disturbances. However, knowledge about the role of AM fungi in plant recovery after small-scale disturbance is limited.

1.2 Objectives of the thesis

The main objective of this thesis is to enhance the understanding of how soil fungal communities respond to different disturbances triggered by human activities. Although previous studies have reported the effects of different disturbance types on soil fungi, knowledge about the interaction of multiple disturbances on functional guilds of soil fungi is limited. In this thesis, I categorized anthropogenic disturbances into biotic **(I)** and abiotic **(II, III, IV)** to evaluate their impact on soil fungi. Additionally, for a better understanding of how soil fungi are influenced by abiotic disturbances, I distinguished chemical and mechanical abiotic disturbances to depict the specific mechanisms underlying soil fungal responses to disturbance **(II)**. Due to the essential role of AM fungi in crop productivity, I aimed to deepen the understanding of how AM fungal families respond to large-scale mechanical and chemical agricultural disturbances **(III).** Lastly, I aimed to assess the role of AM fungi in vegetation recovery under small-scale abiotic disturbances **(IV).**

Specifically, this thesis aims to answer the following questions:

1. How does non-native plant invasion shape soil fungal communities? **(I)**
2. How do chemical and mechanical agricultural disturbances influence soil fungal communities? **(II, III)**
3. What are the impacts of chemical and mechanical disturbances on AM fungi with distinct life-history strategies? **(III)**
4. How does soil AM fungal recovery from small-scale disturbance influence vegetation recovery under different soil fertility levels? **(IV)**

I hypothesize that non-native plant invasion suppresses soil fungal diversity and the abundance of plant-associated fungi **(I)**. I expect to observe distinct responses of soil fungi to mechanical and chemical disturbances, with the combination of the two disturbances amplifying their effects **(II, III)**. Specifically, I hypothesize that the abundance of AM fungal families with the ruderal life history strategy would increase under mechanical disturbances, while families with the stress-tolerant life history strategy would persist under chemical disturbances **(III).** Additionally, I expect that the recovery of AM fungi following small-scale disturbances would increase plant diversity and biomass **(IV).**

II. MATERIALS AND METHODS

2.1 Study design and data collection

2.1.1 The effect of non-native plant invasion on soil fungal communities

In **Paper I**, fieldwork was conducted in lava flow vegetation and lowland rainforest on La Réunion island, representing early and late successional stages, to evaluate the effect of non-native plant invasion on soil fungal communities along primary succession. In the lava flow vegetation, lava flows that erupted in 1986 and 1998 were categorized as low and high invasive levels, respectively, because the younger lava flow vegetation has been heavily invaded by *Boehmeria penduliflora* Wedd. ex D.G.Long. and *Casuarina equisetifolia* L.. In the rainforest vegetation, all sample sites were in the Mare Longue Nature Reserve. The forest understory was categorized into high or low invasive levels depending on the abundance of the non-native plant *Syzygium jambos* (L.) Alston.. For each successional stage, two sites were selected under high or low invasive levels, and sampling was conducted from five plots (2 × 2m) within each site. In total, 40 plots were sampled in this study. Plant species abundance and soil samples were collected in each plot. Plant functional traits (vegetative height, stem specific density, leaf area, and specific leaf area) were recorded for the top five dominant plant species of each successional stage. For plant species whose functional traits were not measured in the field, their trait values were obtained from a dataset provided by local researchers or the TRY database (Prior, 2019; Kattge et al., 2020). Additionally, plant quantitative mycorrhizal status was included as a plant trait (Gerz et al., 2016), indicating the ability of a plant species to grow with or without mycorrhiza (Moora, 2014), for calculating the BNI of the plant community (Schittko et al., 2020).

2.1.2 The effect of abiotic disturbances on soil fungal communities

In **Paper II,** soil samples were collected from 78 crop fields distributed across the majority of agricultural areas in Estonia to evaluate the effects of different agricultural disturbances on soil fungi. Information about fertilizer and pesticide use, tillage practices, and the crops grown during the preceding five years was obtained from farmers who volunteered to participate in the study. Fertilization types were categorized into three levels: fully mineral, combined, and fully organic fertilization; the frequency of pesticide use was characterized by the number of applications per year. Since the active substances, application times, and rates of pesticides varied substantially between farmers, the generalized metric was used to assess the effect of pesticide use in a diverse agricultural settings. Tillage practices were categorized into four levels: plowing, minimum tillage, direct drilling, and a combined tillage regime. A mixed soil sample was collected from each field for molecular and agrochemical analyses.

Paper III investigated the response of AM fungal communities from meadows and arable fields to chemical and mechanical disturbances in a greenhouse experiment. Soil inoculum was collected from two locations (Sortsimäe & Tähkvere) in Estonia with the same soil type. Within each location, two sites (maximum 5 km apart) with contrasting land uses (arable field and meadow) were chosen to collect soil inoculum. Since soil inoculum collection involved mechanical disturbance of AM fungi, *Plantago lanceolata* L. was cultured for 10 weeks in each pot to re-establish AM fungal mycelial networks before applying disturbances. Mechanical disturbance was applied using a knife to vertically cut the soil and roots in the pot along a 2 cm^2 grid, while chemical disturbance was applied with two sprays of the commercially available herbicide Roundup (glyphosate) on *P. lanceolata* leaves. The experiment comprised a fully factorial combination of mechanical disturbance (cut or intact), chemical disturbance (herbicide or control), land-use history of soil (sterilized, field or meadow soil inoculum), and location of soil inoculum (Sortsimäe & Tähkvere) replicated 5 times, resulting in 120 pots. Ten days after applying the treatments, the aboveground parts of *P. lanceolata* were clipped, and *Zea mays* L. seeds were planted to the pots and grown for 10 weeks before harvesting. The root samples of *Z. mays* were used for DNA extraction to identify the AM fungi.

In **Paper IV**, a field experiment was conducted in the understory of a boreonemoral forest in central Estonia to investigate the effect of soil fungal recovery on plant recovery following small-scale disturbance under different soil fertility levels. To set up the small-scale disturbance, the experimental units, round plots with a diameter of 15 cm, were marked randomly in a uniform 50 × 50 m area with a 4 cm high metal frame (Figure 1a). To examine the role of soil fungal recovery in vegetation recovery under small-scale disturbance with different soil nutrient conditions, soil fertility was manipulated by fertilizer and sugar application. The disturbed microsite was created by filling sterilized soil, which had been sterilized using gamma irradiation and sieved to remove soil microbes and plants, back into the forest understory. Additionally, soil fungal activity was suppressed by applying the fungicide Benomyl every four weeks to inhibit the growth of soil fungi. In total, 72 experimental units were created with a full factorial combination of microsite types (intact and disturbed), soil fungal activity (natural, suppressed) and soil fertility (increased, unchanged, and decreased) (Figure 1a). During harvesting, soil samples were collected from the forest floor using a specialized soil corer (Figure 1b) and transported to the laboratory. In the laboratory, above- and below-ground parts of herbaceous plants were separated, and their dry biomass was weighed. Additionally, soil sample from each microsite was dried with silica gel for further analysis.

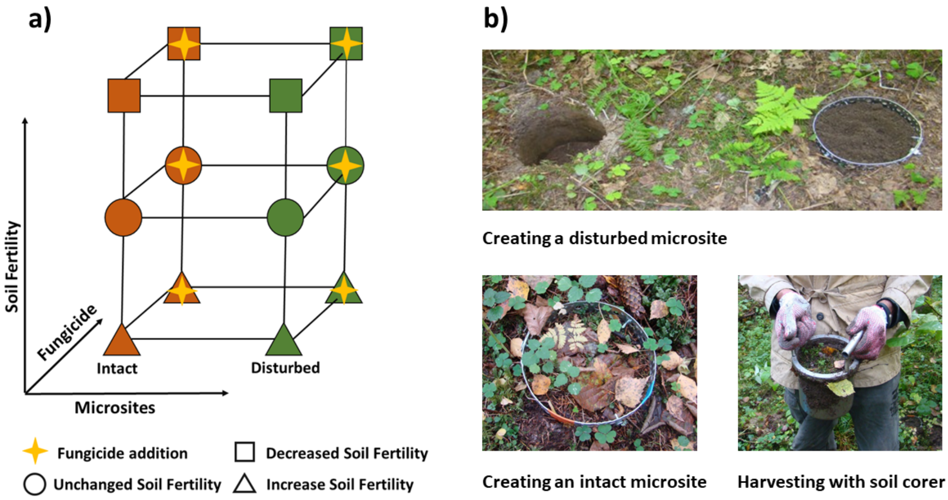

Figure 1 a) Schematic diagram to illustrate how microsite conditions were altered by manipulating three factors: microsite type (intact or disturbed), soil fungal activity (fungicide addition or natural) and soil fertility (increased, natural, decreased) in a fully factorial design. b) Examples of experimental units and harvesting. (Figure 1 in **Paper IV**)

2.2 Molecular and bioinformatics methods

For the soil samples of **Papers I, II** and **IV**, DNA was extracted from 5 g of dried soil samples with the PowerMax Soil DNA Isolation Kit (MoBio Laboratories, Inc.). For the root samples of **Paper III**, root DNA was extracted from 70 mg of dried root samples with the PowerSoil pro kit (MoBio Laboratories, Inc.). AM fungi were identified by targeting the 18S rRNA gene with the WANDA (Dumbrell et al., 2011) and AML2 (Lee et al., 2008) primer pair. Sequencing was conducted using a 2 × 300 bp paired-end read approach on an Illumina MiSeq sequencing platform at Asper Biogene (Tartu, Estonia). For identification of the general soil fungal community composition, the target marker region of the ribosomal ITS2 with degenerate primer pair fITS7:fITS7o (Ihrmark et al., 2012) and ITS4 (White et al., 1990) were amplified. The target region of 18S rRNA gene and ribosomal ITS2 region were sequenced by Novogene Company (United Kingdom) using 2 × 250 bp paired-read sequencing approach on an Illumina NovaSeq platform.

Paired-end Illumina reads were cleaned using the gDAT pipeline (Vasar et al., 2021), and demultiplexed using 8 bp barcodes, allowing one mismatch for both forward and reverse reads. Demultiplexed reads were checked for correct forward and reverse primers for each target gene, allowing one mismatch for both pairs. Both reads were selected if the average quality was ≥ 30. Filtered paired-end reads were combined with FLASH (v1.2.11, Magoč and Salzberg, 2011) using the default parameters (overlap $\geq$ 10bp, identity $\geq$ 75%). Chimeric sequences were removed with VSEARCH (v2.15.0, Rognes et al., 2016) in the reference database mode using the MaarjAM database (Öpik et al., 2010, status 2021) for the 18S rRNA gene and de novo mode for ribosomal ITS2 target marker region reads. The 18S rRNA gene reads were identified without clustering against virtual taxa (VT) in the MaarjAM database (Öpik et al., 2010) using BLAST+ searches (v2.10.1, Camacho et al., 2009) with 97% identity and 95% alignment thresholds. ITS2 target marker region reads were clustered with 97% using VSEARCH and cluster centroids were matched against taxa in the UNITE (v9.0) database using 80% alignment and 97%, 95% and 90% sequence identity thresholds for identifying up to species, genus and family level, respectively. ITS2 target marker region operational taxonomic units (OTUs) were assigned to guilds using the FungalTraits database (Põlme et al., 2020).

2.3 Statistical data analyses

In **paper I**, **II**, **III** and **IV**, the richness and diversity of plant and fungal communities were calculated using the asymptotic diversity estimation functions from the "iNEXT" package (Hsieh et al., 2016). In **paper I**, the abundance of different fungal guilds was weighted by the read number of fungal OTUs after variance-stabilizing transformation (VST) to avoid bias from unbalanced library sizes (Love et al., 2014). Generalized linear models were applied to test the effects of successional stage, plant invasion (cover of non-native plants or BNI), and their interaction on the richness and diversity of soil fungal community, as well as the abundance of each fungal guild using the "glm" function (R Core Team, 2023). If the interaction term was significant, further analysis was conducted with generalized linear models to examine the effect of plant invasion on the richness and diversity of fungi, as well as the abundance of fungal guilds within high and low successional stages. To distinguish the effect of soil properties from the effects of successional stage and plant invasion, the first principal component (hereafter: soil properties PC1, capturing 46.7% of variation in soil parameters), which was extracted from a Principal Components Analysis (PCA) on the soil properties matrix using the "princomp" function (R Core Team, 2023), was used as an additional explanatory variable in the generalized linear model described above. Permutation-based nonparametric MANOVA (perMANOVA) was applied to test the effect of successional stage, plant invasion, soil properties PC1, and the interaction of the first two factors on soil fungal communities based on Bray-Curtis dissimilarity using the "vegan" package (Oksanen et al., 2024).

In **paper II**, soil fungal taxa were classified into plant pathogenic fungi and saprotrophic fungi based on FUNguild database (Nguyen et al., 2016). Linear mixed-effects models were applied to test the effects of management practices (pesticide use frequency and fertilizer type, tillage regime) on the richness and diversity of soil fungi. Due to the correlation between pesticide use frequency and fertilizer type, they were included together in a single model (including their interaction). In order to account for the effect of soil properties on soil fungal community response to disturbances, a PCA of soil parameters was applied, and the first Principal Component (describing 38% of variation in soil parameters) was included in all the models as an additional fixed-effect term. The crop species cultured at the time of sampling was added to the models as a random-effects term. In order to account for potential spatial autocorrelation, each model was fit both in a spatial (function “lme” with a Gaussian correlation structure using Haversine distances between sampling points, Pinheiro et al., 2024) and nonspatial (function “lmer”, Bates et al., 2015) form. Model assumptions were checked visually with R package DHARMa (Hartig, 2022). The best model out of these two was selected based on Second-order Akaike Information Criterion (AICc) with R package MuMIn (Barton, 2020). P-values were calculated using either function “anova” from R package lmerTest (Kuznetsova et al., 2017) for the nonspatial models, or “anova” from R package nlme (Pinheiro et al., 2024) for the spatial models.

In **paper III**, the read number of AM fungal virtual taxa (VT) after VST was used as an estimate of VT abundance (Love et al., 2014). Culturable AM fungal VT were distinguished in each sample based on information from Garcia de Leon et al., (2018). Mean nearest taxon distance (MNTD) of AM fungal communities were estimated with “mntd” function from the “picante” package and a phylogenetic tree (Kembel et al., 2010), which was constructed based on the pairwise maximum likelihood distances of sequences using the neighbor-joining method (Schliep et al., 2016). The main effects of four categorical variables (chemical disturbance, mechanical disturbance, land-use history and location of origin of soil inoculum) and the interactions of first three variables on AM fungal richness, diversity, MNTD, abundance of AM fungal families present in more than 50% of samples and abundance of culturable AM fungi, were evaluated using ANOVA from the “car” package (Fox and Weisberg, 2019). In case of significant effects ($p<0.05$), Tukey’s HSD post hoc test was applied to evaluate differences between treatment combinations.

In paper **IV**, phylogenetic diversity (Faith, 1992) of AM fungal communities was estimated with the “pd” function (Kembel et al., 2010), based on a neighbour-joining tree, which was constructed from the pairwise maximum likelihood distances of VT sequences with the “phangorn” package (Schliep et al., 2016). The impact of soil fertility, soil fungal activity suppression, microsite type and their interactions on AM fungal richness, diversity, phylogenetic diversity, above- and belowground biomass of vascular plants, plant richness, diversity were tested using type-III ANOVA from the “car” package (Fox and Weisberg, 2019). In cases where the effect of model parameter(s) was significant in an ANOVA, a Tukey HSD post hoc test was applied with a significance level of 0.05 in order to estimate differences between the treatments.

III. RESULTS

3.1 The effect of non-native plant invasion on soil fungal communities

In **Paper I**, the cover of non-native plant species and BNI had no impact on the richness and diversity of soil fungi, as well as the abundance of different fungal guilds (Figure 2).

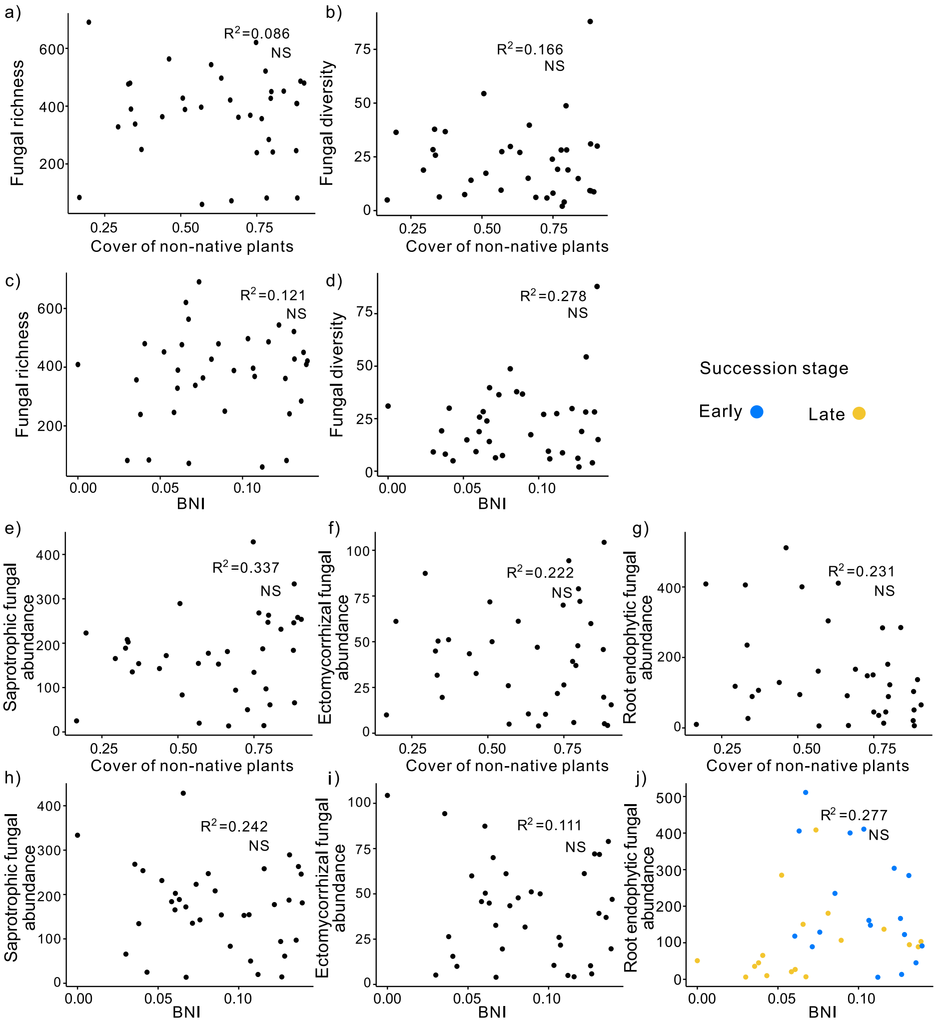

Figure 2. The effects of plant invasion (cover of non-native plants or BNI), successional stage and their interaction on fungal richness (a, c), diversity (b, d), abundance of saprotrophic (e, h), ectomycorrhizal (f, i) and root endophytic fungi (g, j). Significant categorical explanatory variables (blue – early successional stage, yellow – late successional stage) and the R^2 of each linear mixed-effects model were presented in each plot (NS – not significant). (Modified based on Figure 2, 3 and S7 in **Paper I**).

The abundance of ectomycorrhizal fungi was negatively correlated with the PC1 of soil properties ($t=-2.741$, $p=0.010$), and the abundance of root endophytic fungi was higher in early compared to late successional stage ($t=-2.449$, $p=0.020$; Figure 2). When non-native plant cover was used as fixed factor, the successional stage, rather than non-native plant cover, had a significant impact on fungal community composition ($P=0.001$, $R^2=10.1\%$). When BNI was used as the fixed factor, the interaction between BNI and successional stage had a significant influence on fungal community composition ($P=0.015$, $R^2=4.5\%$).

3.2 The effect of abiotic disturbances on soil fungal communities

In **Paper II**, total fungal richness declined with pesticide use frequency under mineral fertilization ($F=5.868$, $p<0.05$, Figure 3), increased with pesticide use frequency under organic fertilization and was unchanged when a combined fertilization regime was used ($F=9.679$, $p<0.01$; $F=0.113$, $p>0.1$, respectively; Figure 3). Total fungal diversity was unaffected by pesticide use frequency but was affected by fertilization type ($F=0.183$, $p>0.1$; $F=15.870$, $p<0.01$, respectively), resulting in higher diversity when only organic fertilizers were applied (Figure 3). In terms of different fungal guilds, the AM fungal richness decreased along pesticide use frequency ($F=5.059$, $p<0.05$; Figure 3), but no interaction was detected between fertilization and pesticide use. The diversity of AM fungi was unaffected by fertilization type and pesticide use frequency (Figure 3). Soil pathotrophic fungal richness and diversity were not significantly affected by the frequency of pesticide use or type of fertilization, while the richness of saprotrophic fungi increased with pesticide use frequency under organic fertilization ($F=6.952$, $p<0.05$, Figure 3) and their diversity was affected by fertilization type ($F=14.612$, $p<0.01$; Figure 3). The tillage regime applied in study fields did not influence the richness or diversity of any functional guild of soil fungi.

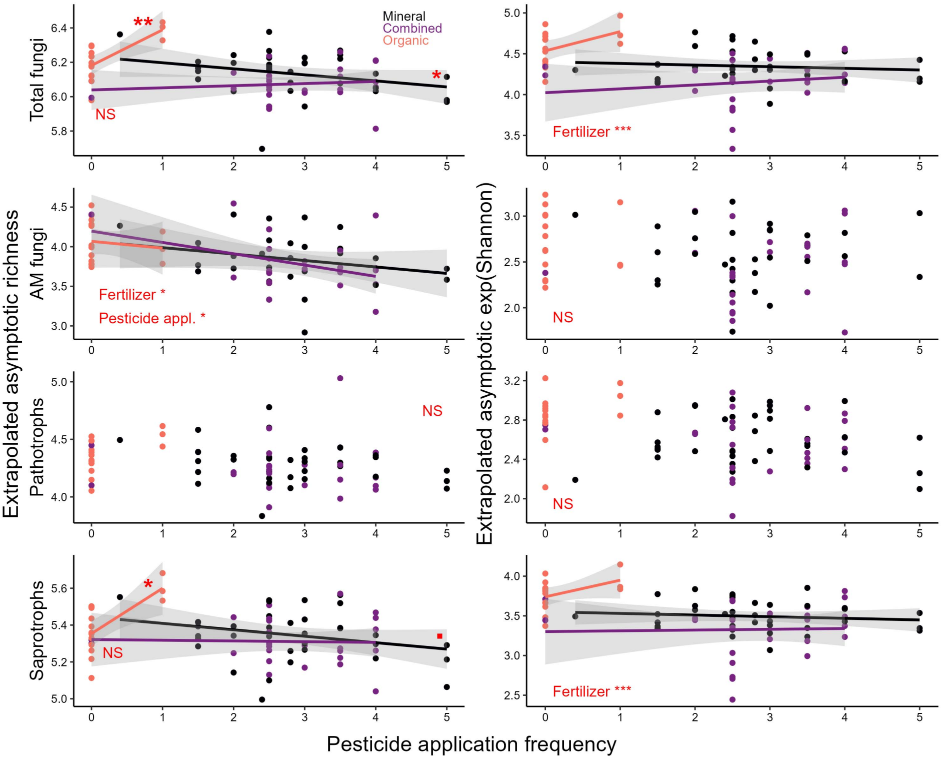

Figure 3 Effects of fertilization type and pesticide application on total, AM fungal, pathotrophic and saprotrophic soil fungal asymptotic richness and Shannon diversity. P-values from best linear mixed-effects models are presented as follows: *** – p<0.00; ** – p<0.01; * – p<0.05; NS – not significant. For significant continuous independent variables, 95% confidence intervals based on the t-distribution are shown. If there was a significant interaction between pesticide application and fertilization type, p-values for the effect of pesticide application on richness are presented for each fertilization type separately. (Modified based on Figure 4 and 5 in **Paper II**).

In **Paper III**, AM fungal richness was influenced by the interaction of herbicide addition and mechanical disturbance (F=4.49, p=0.04). AM fungal richness increased only by mechanical disturbance and was unchanged by either chemical disturbance or its combination with mechanical disturbance (Figure 4a). Chemical and mechanical disturbances had no significant effect on the diversity of AM fungal communities. MNTD of AM fungal communities was affected by the interaction between mechanical disturbance and herbicide addition (F=19.27, p<0.01). All disturbances led to significant phylogenetic clustering of AM fungal communities compared to the control, with herbicide addition having the strongest effect, and the effect of mechanical disturbance alone not differing from the effect of the combination of mechanical and chemical disturbances (Figure 4b).

The abundance of Glomeraceae was significantly influenced by the interaction of mechanical disturbance and herbicide addition (F=7.11, p=0.01). The abundance of Glomeraceae increased with herbicide addition alone while its abundance under chemical disturbance and the combination of the two disturbances did not differ from that in the control (Figure 4c). Herbicide addition decreased the abundance of Claroideoglomeraceae (F=5.03, p=0.03; Figure 4d). The abundance of culturable AM fungi was affected by the interaction between mechanical disturbance and herbicide addition (F=6.29, p=0.02). The abundance of culturable AM fungi was lowest in the control, highest in the chemical disturbance treatment, and intermediate in the presence of mechanical disturbance alone or in combination with herbicide addition (Figure 4e).

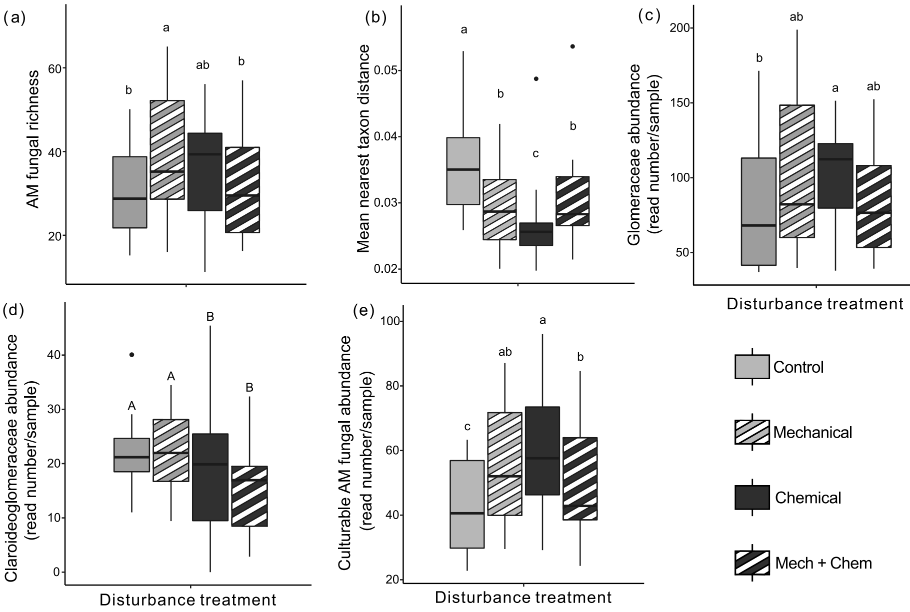

Figure 4 The effect of chemical, mechanical and the combination of chemical and mechanical disturbances on AM fungal richness (a), mean nearest taxon distance (MNTD) of AM fungal communities (b), and abundance of AM fungal families (read number/ sample): Glomeraceae (c); Claroideoglomeraceae (d) and abundance of culturable AM fungi (e). Median values (horizontal line), interquartile range (boxes), range (up to 1.5 times the interquartile range; vertical line) and outliers (dots; included in analyses) are shown. Boxes topped by the same capital letter do not differ significantly according to ANOVA (Table S3 in **Paper III**, capital letters) and Tukey's HSD test (lowercase letters) (Modified based on Figure 2, 4 and 5 in **Paper III**).

In Paper IV, the richness and phylogenetic diversity of AM fungi were significantly reduced by fungicide addition (F=9.83, p<0.01; F=6.58, p=0.01, respectively; Figure 5a, b), while not significantly influenced by soil fertility or its combinations with microsite type and soil fungal activity. The interaction between microsite type and fungal activity had a significant effect on the aboveground biomass of herbaceous plants (F=5.56, p=0.02), which was higher at intact microsites compared with disturbed microsites with fungicide addition ($p<0.05$, mean ± SE: 0.99±0.17 and 0.10±0.05, respectively). In addition, plant species richness and diversity were influenced by the interaction between microsite type and fungicide treatment (F=5.38, p=0.02; F=7.17, p=0.01, respectively). Plant species richness and diversity decreased with fungicide addition only in disturbed microsites, but not in intact microsites (Figure 5c, d). Plant species richness, diversity, and aboveground biomass of herbaceous plants were not affected by the soil fertility treatment or its combination with microsite type and fungal activity.

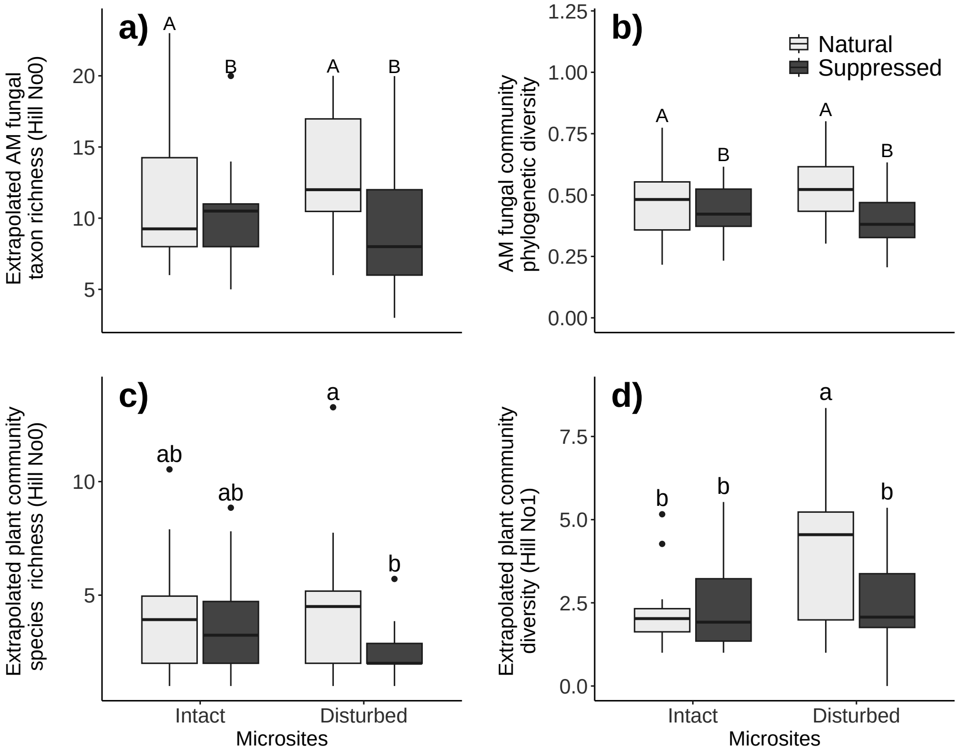

Figure 5 Effects of microsite types and fungal activity on a) extrapolated AM fungal taxon richness and b) community phylogenetic diversity; c) extrapolated plant species richness and d) Shannon diversity. The color of the boxes indicates manipulation of fungal activity (light grey: natural, dark grey: suppressed). Median values (horizontal line), interquartile range (boxes), 1.5 times inter-quartile range (vertical line; IQR) and outliers (dots) are shown. In panels a) and b), upper case letters indicate significant difference ($p \leq 0.05$) among the two types of fungal activity in the ANOVA analyses (Table 1); in panels c) and d), lower case letters indicate significant differences ($p \leq 0.05$) between the effect of microsite types and fungal activity according to Tukey HSD test. (Figure 2 in **Paper IV**)

IV. DISCUSSION

The studies conducted in this thesis evaluated the impact of different types of anthropogenic disturbances on soil fungal communities. The results showed that non-native plant invasion, a common biotic disturbance, had a limited effect on soil fungal diversity on Réunion Island. However, the Biotic Novelty Index (BNI) was a useful measure for describing variation among soil fungi experiencing plant invasion in different communities **(I)**. The results of this thesis also suggest that among abiotic disturbances, mechanical disturbances have a neutral impact on soil fungal diversity, while chemical disturbances have distinct effects on soil fungal diversity depending on the specific type of disturbance **(II, III)**. The interaction of two chemical disturbances amplified their negative effects on soil fungi, while the interaction between mechanical and chemical disturbances did not show such amplification **(II, III)**. Due to the importance of AM fungi for plant productivity, further investigation was conducted to reveal the mechanism of their response to chemical and mechanical disturbances in more detail. This thesis demonstrates that the life history traits of AM fungi and the type of disturbance simultaneously determine the response of AM fungi to disturbance **(III)**. In addition, the results demonstrate that AM fungi recover fast after small-scale disturbance and subsequently facilitate vegetative regeneration of plants in disturbed areas **(IV)**. Altogether, the research presented in this thesis advances current knowledge about the effects of disturbances on soil fungal communities, addressing the effect of multiple disturbances alone and in combination on different soil fungal guilds. This knowledge is essential for designing effective approaches for maintaining ecosystem functioning and preserving biodiversity.

4.1 Non-native plant invasion has a limited effect on soil fungal communities in Réunion

In **Paper I**, there was no significant effect of non-native plant invasion on the diversity of the soil fungal community and the abundance of fungal guilds. This phenomenon could be attributed to the low host specificity of symbiotic and pathogenic soil fungi (Davison et al., 2015; Peay et al., 2015; Spear and Broders, 2021). Therefore, this data suggests that local soil fungi can form associations with newly arrived non-native plants, which maintain the diversity and abundance of soil fungal communities. However, the fungal communities were identified from soil samples, which can contain fungal propagules that are not actively associating with non-native plants. These long-preserved propagules in the soil could mitigate the impact of non-native plant invasion on soil fungi (Nguyen et al., 2012). Additionally, the results showed that the abundance of ectomycorrhizal fungi shifted with soil chemical properties PC1, which are mostly driven by soil Ca and Mg content. While previous studies have shown that ectomycorrhizal fungal abundance is significantly correlated with soil organic carbon (Anthony et al., 2017; Marañón-Jiménez et al., 2021), the results of **Paper I** identified the importance of other soil chemical content in influencing soil fungi. Besides, the abundance of root endophytic fungi was higher in the early than in the late successional stage, which aligns with other studies indicating that the succession process is one of the drivers shaping soil fungal community (Hannula et al., 2017; Zhang et al., 2022). Thus, the results above indicate that primary succession and soil chemical content, rather than non-native plant invasion, determine the diversity of soil fungal communities on Réunion Island.

The results in **Paper I** demonstrate that the BNI, a novel index designed to account for functional trait dissimilarity and the time of coexistence between non-native and native plants in the plant community, is a useful measure in explaining soil fungal community composition (Schittko et al., 2020). BNI incorporates plant functional traits, which play a crucial role in shaping soil fungal community composition (de Vries et al., 2012; Chai et al., 2019), and using this index was more effective in evaluating the variation of soil fungal community composition under plant invasion than the abundance of non-native plants. Additionally, BNI accounts for the coexisting time between native and non-native plants, which could be important in determining the influence of non-native plants on soil fungi, as non-native plants may gradually adapt to the local soil fungi over time (Luke Flory and Clay, 2013; Schultheis et al., 2015). Therefore, these results highlight that BNI can be a useful index for evaluating variation in soil fungal community composition under non-native plant invasion. However, I primarily applied aboveground plant functional traits when calculating BNI. Incorporating belowground traits from plants might provide clearer insights into the effect of non-native plant invasion on soil fungi. Furthermore, testing the performance of BNI to evaluate non-native plant invasion on soil fungi in other regions, rather than just Réunion Island, is necessary for a comprehensive understanding.

4.2 The response of soil fungal communities to abiotic disturbances depends on the disturbance type

Soil fungal diversity showed distinct responses to chemical abiotic disturbances depending on the specific disturbance type. For instance, the results of the field survey (**II)** demonstrated that organic fertilization contributed to higher soil fungal diversity than mineral fertilizer or combined mineral and organic fertilizer, indicating different effects of fertilization types on soil fungi (Marschner et al., 2003; Treseder, 2004). Additionally, in the same study, the frequency of pesticide application significantly shaped the richness of total soil fungi and AM fungi, with higher frequency of application associated with lower richness, which supports previous research (Riedo et al., 2021). Interestingly, high-frequency pesticide application did not reduce the diversity of plant pathogenic fungi under any fertilization type, suggesting limited effects of pesticide and fertilizer application on the diversity of this guild. At the same time, in the greenhouse experiment (**III)**, there was no impact of herbicide addition on AM fungal richness. This non-significant effect may be attributed to the uniform soil inoculum used in the greenhouse experiment and the relatively short duration of the experiment, as well as the low host specificity of AM fungi (Helgason and Fitter, 2009; Davison et al., 2015).

At the same time, the results indicate that mechanical abiotic disturbances have a limited effect on soil fungal diversity. In **Paper II**, there was no significant difference in either the richness or diversity of fungi among the tillage regimes in the field survey, despite earlier evidence suggesting that reduced tillage intensity has a positive effect on fungal species richness and abundance (Treonis et al., 2010; van Groenigen et al., 2010; Säle et al., 2015). A possible explanation for this discrepancy might be that in this study, conservation tillage systems were accompanied by increased pesticide use frequency, which might have outweighed any benefits from reduced soil mechanical disturbance. In the greenhouse experiment (**Paper III)**, mechanical disturbance increased AM fungal richness but had no effect on their diversity, suggesting that mechanical disturbance may increase the inoculation of rare AM fungal species but does not enable them to become abundant. Additionally, in **Paper III**, AM fungal communities exhibited stronger phylogenetic clustering under chemical disturbance compared with mechanical disturbance. This demonstrates that mechanical and chemical disturbances could filter out different AM fungal taxa due to their distinct mechanisms, as suggested by an earlier study (Mykrä et al., 2016; van der Heyde et al., 2017).

The response of soil fungal diversity to multiple simultaneous disturbances also depends on disturbance type. In **Paper II**, the application of mineral fertilizers in combination with high-frequency pesticides amplified their negative effects on total fungal richness. This finding supports earlier research that indicated that soil fungal communities become species-poorer when exposed to more disturbances (Rillig et al., 2019). However, there were some exceptions: low frequency of pesticide application increased soil fungal richness when combined with organic fertilizers in **Paper II**, and the simultaneous application of mechanical and chemical disturbances did not have significantly different effects on the diversity of AM fungi compared with the effects of single disturbance types in **Paper III**. Although the increased soil fungal richness accompanying low pesticide frequency could be attributed to insufficient sampling, some studies have found that low concentrations of pesticides could have a positive influence on AM fungal growth and colonization of plant roots (Malty et al., 2006; Rabab and Reda, 2019). The combination of mechanical and chemical disturbances might alleviate the negative effect of chemical disturbance on the AM fungal community, as the combination of the two disturbances showed less phylogenetic clustering than chemical disturbance alone (**Paper III**). Therefore, these studies indicate that predicting the effects of multiple disturbances on the soil fungal community cannot simply be the addition of recorded effects of single disturbance types in isolation, and the effect of multiple disturbances on the soil fungal community varies with the type of disturbance.

Because the functional traits of AM fungi are to some extent phylogenetically conserved (Powell et al., 2009; Yang et al., 2017), I hypothesized that mechanical and chemical disturbance could favor AM fungal families with traits representing ruderal and stress-tolerant strategies, respectively. However, in **Paper III**, there were no clear connections between changes in the abundance of AM fungal families and their putative life-history strategies. For instance, the results demonstrated that the abundance of Glomeraceae increased after herbicide application but decreased under mechanical disturbance. This pattern is opposite to my expectation that the Glomeraceae family represents the ruderal life-history strategy and would exhibit higher abundance under mechanical disturbance due to their rapid hyphal growth (Powell et al., 2009). Fungi from the family Claroideoglomeraceae mainly form intraradical hyphae within plant roots (Varela-Cervero et al., 2016), which is thought to represent the stress-tolerant strategy (Chagnon et al., 2013). Contrary to my expectations, the abundance of Claroideoglomeraceae declined with herbicide addition. These results suggest that existing family-level generalizations may be too coarse to accurately depict the life history traits of AM fungi (Behm and Kiers, 2014). However, every disturbance type increased the abundance of culturable AM fungi, which were expected to represent ruderal life history (Ohsowski et al., 2014), indicating that life-history traits can still be helpful in interpreting AM fungal response to disturbances. Therefore, collecting data that are easier to measure and that indicate AM fungal life history traits, such as spore size and the ratio between arbuscules (nutrient exchange organs) and vesicles (lipid storage organs) of AM fungi, can significantly improve the understanding of how AM fungi respond to disturbances. (Van Der Heijden and Scheublin, 2007; Smith and Read, 2010).

4.3 AM fungal recovery after small-scale disturbances in soil plays a key role in vegetation recovery

Paper IV revealed no difference in AM fungal richness and abundance between intact and disturbed microsites without fungicide suppression, regardless of soil fertility levels. This demonstrates that AM fungi can quickly recover from small-scale disturbances. These results indicate the high resilience of AM fungi following small-scale anthropogenic disturbances, likely due to the efficient dispersal of AM fungal propagules at local scales (Fracchia et al., 2011; Davison et al., 2016; Chaudhary et al., 2020). Additionally, suppression of soil fungi reduced plant species richness, diversity, and aboveground biomass when plants were colonizing disturbed microsites. This confirms the crucial role of soil fungal recovery in vegetation restoration after small-scale disturbance. However, while I expected the role of AM fungi to be more important in low soil fertility conditions, soil fertility manipulation did not affect the dynamics of AM fungal or plant communities. Previous studies have shown an inverse relationship between the abundance of AM fungi and soil phosphorus at small scales (Koorem et al., 2014). Thus, the impact of soil fertility manipulation in this study may have been mitigated by nutrient transport through AM fungal networks inside and outside the microsites. Additionally, plant seedlings germinated from seeds in these microsites were continuously removed by weeding (Koorem et al., 2012), and most plant species in the study area are known to be vegetatively mobile (Moora et al., 2009). This suggests that the plants established in microsites mostly originated from vegetative regeneration and were able to obtain nutrients from mother plants established outside the microsites. In **Paper IV**, the biomass and diversity of plant communities were found to recover after small-scale disturbance. Therefore, these results indicate an important role of vegetative regeneration of plants in the forest understory, regardless of soil fertility levels. Moreover, plant diversity in disturbed microsites was higher than in intact microsites when soil fungi were not suppressed by fungicide, indicating the crucial role of small-scale disturbances in sustaining highly diverse habitats by providing "free sites" for vegetative reproduction (Zobel et al., 2000; Menges et al., 2017). Thus, the results demonstrate the importance of soil fungal recovery in facilitating the establishment and growth of plants via vegetative colonization from neighboring areas following small-scale disturbance.

V. CONCLUSIONS

The results of this thesis indicate that non-native plant invasion, one of the main forms of abiotic disturbance, did not have significant effect on the diversity of the soil fungal community in Réunion Island. However, the biotic novelty index (BNI) can serve as a useful measure for detecting changes in the soil fungal community under plant invasion. Mechanical abiotic disturbances had no significant impact on soil fungal diversity in the studies described in this thesis, whereas chemical abiotic disturbances affected soil fungal diversity in various ways. In addition, the simultaneous application of two chemical disturbances resulted in amplified effects on soil fungi, while the simultaneous application of chemical and mechanical disturbances did not have an interactive effect. When examining the response of AM fungi in more detail, I found that considering the life-history traits of these fungi in combination with the type of disturbance can help to gain further insights into the effects of disturbance. Finally, the results demonstrate that the rapid recovery of soil AM fungal communities under small-scale disturbances plays a crucial role in the recovery of plant communities. Specifically, the results of this thesis are as follows:

1. Soil fungal diversity and the abundance of different fungal guilds did not shift significantly with plant invasion in Réunion Island but did vary in relation to soil chemical properties and primary succession. Specifically, ectomycorrhizal fungal abundance showed a negative correlation with soil Ca and Mg content, while it had no correlation with the cover of non-native plants or the BNI. However, the interaction of the successional stage and the BNI, rather than the non-native plant cover, significantly explained the dynamics of soil fungal communities. This indicates that BNI can be an effective index for capturing soil fungal community variation under plant invasion (**I**).
2. Mechanical and chemical disturbances have distinctive influences on soil fungal communities. My studies demonstrated that mechanical disturbances had limited effects on soil fungal diversity, while soil fungi had various responses, ranging from positive to negative, to chemical disturbances, depending on the specific disturbance type. For example, pesticide application decreased soil fungal diversity, organic fertilizer increased soil fungal diversity and herbicide had a neutral effect on AM fungal diversity. Furthermore, the application of two chemical disturbances amplified their negative effects on soil fungi; by contrast, the application of mechanical disturbance even alleviated the negative effect of chemical disturbance on AM fungi when applied simultaneously **(II & III)**.
3. The abundance of AM fungal families responded differently to specific disturbances while the abundance of culturable AM fungi increased under every type of disturbance. Such results suggest that life history traits of AM fungi can provide better insight into the mechanisms behind disturbance effects. However, current knowledge about AM fungal life-history traits is sparse. For

example, in this study, AM fungal families that were expected to represent ruderal or stress-tolerant life history strategies, responded to disturbances in the opposite way than I hypothesized **(III)**.

4. The suppression of soil fungal activity with fungicide application decreased the diversity and biomass of re-established vegetation in disturbed microsites. Additionally, AM fungal diversity was found to quickly recover from pulse disturbances in species-rich habitats regardless of soil fertility levels. Therefore, these results support the idea that soil fungal recovery plays a key role in maintaining plant diversity under small-scale disturbances **(IV)**.

SUMMARY

Human activities cause significant disruptions to ecosystem services and facilitate the spread of non-native plants to new ranges, contributing to biodiversity loss. However, numerous previous studies have focused on investigating the effects of disturbances caused by human activities on aboveground communities. Therefore, our understanding of how soil communities respond to disturbances remains limited. Since soil fungi play a key role in sustaining ecosystem functions, this knowledge gap may lead to underestimating the full impact of anthropogenic disturbances on ecosystems. To address this, my thesis investigates the importance and effects of soil fungi under disturbances triggered by anthropogenic activities.

Plant invasion, the most common biotic disturbance resulting from human economic activity, is known to pose a significant threat to local plant diversity. However, the effect of plant invasion on soil fungal communities has been less studied. Previous research has indicated that saprotrophic fungi can flourish under plant invasion due to increased leaf litter input, while pathogenic fungi could be inhibited due to non-native plants escaping from their natural enemies. In this thesis, fieldwork was conducted to investigate the effect of non-native plant invasion on soil fungal community along primary succession, as soil fungal and plant diversity both vary along succession. The magnitude of plant community change in response to plant invasion was evaluated using the biotic novelty index (BNI), which incorporates plant functional traits and coexisting time between native and non-native plants. The total soil fungal diversity and abundance of different fungal guilds did not vary in relation to the BNI or the cover of non-native plants. However, the interaction of the successional stage and BNI, rather than the non-native plant cover, significantly influenced the soil fungal community **(I).** These results suggest that BNI is a better index for capturing soil fungal community variation under plant invasion compared with indices that evaluate changes in non-native plant species' presence and abundance. Thus, the BNI can contribute to understanding the responses of local soil fungal communities to vegetation changes triggered by intensifying human activities and climate change in the future.

Most common and unavoidable land-use disturbances arise from agricultural activities, which have become more extensive along with population growth in recent centuries. Therefore, it is essential to understand how different disturbances from agricultural activities influence soil fungi. In this thesis, I categorized agricultural disturbances into chemical disturbance, such as fertilizer and pesticide application, and mechanical disturbance, such as tillage. My studies demonstrated that mechanical disturbances had a limited effect on soil fungal diversity, while soil fungi exhibited various responses, ranging from positive to negative, to chemical disturbances depending on the specific type of the disturbance **(II, III).** For instance, the addition of pesticides decreased soil fungal diversity, while organic fertilizers increased it. Additionally, the interaction between two chemical disturbances amplified their negative effect on soil fungi **(II),** but the interaction

between chemical and mechanical disturbances did not show such amplification effects **(III).** These results indicate that the response of soil fungi to multiple disturbances depends on the type of disturbance but not the addition of their single-factor effects, highlighting the need for further studies to reveal the underlying mechanisms of fungal responses to multiple real-life disturbances related to human activities.

Since AM fungi can form symbiotic relationships with most crop plants and facilitate the transfer of soil nutrients to promote crop productivity, further investigation is needed to reveal the mechanisms underlying the response of AM fungi to chemical and mechanical disturbances. Previous studies have demonstrated that the life history strategies of AM fungi also influence their responses to disturbance, and these strategies are often conserved at the family level. In this thesis, I found that the abundance of different AM fungal families exhibited distinct responses to the same type of disturbance, but the abundance of culturable AM fungal taxa was higher under every disturbance **(III).** These results partly support the idea that the life history strategies of AM fungi are meaningful for understanding fungal responses to disturbance. However, the results also suggest that the family level could be too broad to capture specific life history strategies in AM fungi. For instance, the abundance of the AM fungal family expected to exhibit a ruderal life history strategy generally increased under chemical disturbance, while the abundance of the AM fungal family expected to exhibit the stress-tolerant life history strategy generally decreased under chemical disturbance. These responses of AM fungi were contrary to my hypotheses. Therefore, these results demonstrate that each AM fungal family had distinct responses to disturbance, but these responses do not align with their expected life history strategy.

AM fungi play a crucial role in plant growth and establishment in stressed habitats, and several studies have shown that the introduction of soil AM fungal inoculum facilitates vegetation recovery in disturbed habitats. Additionally, the benefits of AM fungi to plant growth and establishment are more important under low soil nutrient conditions compared with fertile habitats. Restoration management practices, including the introduction of soil inoculum, are typically applied to restore vegetation in relatively large areas with degraded ecosystem services. However, with the broadening range of human activities, the occurrence of small-scale disturbances in natural or semi-natural habitats close to human activities has increased significantly; yet this has received little attention. Therefore, evaluating the effect of soil AM fungal recovery on plant re-establishment after small-scale disturbances in habitats with different soil fertility levels is important. In this thesis I found, that AM fungal diversity can quickly recover after small-scale disturbance regardless of the soil fertility level, and the diversity and biomass of vegetation recovered after disturbances only when soil fungi did not continuously suppressed **(IV).** This highlights the crucial role of the quick recovery of soil AM fungi under small-scale disturbance in maintaining plant diversity after such disturbances.

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SUMMARY IN ESTONIAN

Inimtekkeliste häiringute mõju mullaseentele

Inimtegevus põhjustab olulisi häireid ökosüsteemi toimimises ja soodustab võõrtaimede levikut uutesse piirkondadesse, aidates seeläbi kaasa bioloogilise mitmekesisuse vähenemisele. Paljud varasemad uuringud on keskendunud sellele, kuidas inimtekkelised häiringud mõjutavad maapealseid koosluseid. Seetõttu on vähe teada, kuidas mullas olevad kooslused häiringutele reageerivad. Kuna mullas elavatel seentel on võtmeroll ökosüsteemi funktsioonide säilitamisel, võib see teadmiste lünk viia inimtekkeliste häiringute mõju alahindamiseni. Antud doktoritöö eesmärk ongi selgitada, kuidas inimtekkelised häiringud mõjutavad mullaseente kooslusi, keskendudes eraldi biootilistele ja abiootilistele häiringutele ning erinevatele mullaseente rühmadele.

Kõige levinum inimtekkeline biootiline häiring on liikide, näiteks taimede, transport väljaspoole nende looduslikku leviala. Sageli on selline tegevus ajendatud majanduslikust huvist, kuid võõrliikide kontrollimatu kasv uues levikualas ohustab märkimisväärselt kohalikku mitmekesisust. Kui võõrtaimede mõju kohalikele taimedele on suhteliselt palju uuritud, siis märksa vähem on teada taimede invasiooni mõjust mulla seenekooslustele. Varasemad uuringud on näidanud, et kõdu lagundavad seened võivad võõrtaimede sissetungi järgselt arvukamaks muutuda kuna nende taimede elutegevuse tagajärjel suureneb sageli mulda jõudva varise hulk. Samas patogeensete seente arvukus ja liigirikkus võib hoopis väheneda kuna võõrtaimedel puuduvad uues levialas neile spetsialiseerunud looduslikud vaenlased, sealhulgas ka patogeensed seened. Antud doktoritöös kasutati võõrtaimede mõju hindamiseks uudset biootilise uudsuse indeksit (BNI), mis hõlmab taimede funktsionaalseid tunnuseid kohalike ja võõrtaimede vahel hindamaks võõrtaimede mõju mullaseente kooslustele primaarsuktsessioonis. Tulemused näitasid, et uuritud Réunion i saarel erinevate seenerühmade liikide arv ning ohtrus võõrtaimede invasiooni tagajärjel ei muutunud **(I).** Küll aga näitasid tulemused, et BNI võimaldab täpsemalt kui võõrtaimede katvus kirjeldada muutuse mullaseente koosluste koosseisus erinevas suktsessiooniastmes olevates taimekooslustes **(I).**

Enamik levinumaid ja vältimatuid maakasutuse häireid tulenevad põllumajandustegevusest, mis on viimastel sajanditel rahvastiku kasvuga üha ulatuslikumaks muutunud. Seetõttu on ülimalt vajalik mõista, kuidas erinevad põllumajandustegevusest tulenevad häiringud mõjutavad mullaseeni. Käesolevas doktoritöös liigitasin põllumajanduslikud häiringud keemilisteks häiringuteks, nagu väetised ja pestitsiidid, ning mehaanilisteks häiringuteks, nagu näiteks maaharimine ja künd. Tulemused näitasid, et mehaanilistel häiretel on mulla seente mitmekesisusele üsna vähene mõju, samal ajal kui keemilised häiringud tõid mullaseentes esile erinevaid vastuseid, mis sõltuvalt häiringu tüübist ulatusid positiivsest negatiivseni **(II, III).** Näiteks pestitsiidide lisamine vähendas mullaseente mitmekesisust, samas kui orgaanilised väetised suurendasid seda. Lisaks võimendas kahe keemilise häiringu koos esinemine nende negatiivset mõju mullaseentele **(II)**, kuid keemiliste ja mehaaniliste häirete koos esinemine sellist võimendavat mõju ei toonud **(III)**. Need tulemused näitavad, et häiringute mõju mullaseentele sõltub häiringu tüübist ning mitme häiringu koosmõju on raske ette ennustada, mistõttu on sellel teemal edasised uuringud väga vajalikud.

Enamik põllukultuuridest kasvab koos krohmseentega, mis vastastikku kasulikus kooselus hõlbustavad mullas olevate toitainete transporti taimedele, saades taimelt vastutasuks süsinikühendeid. Seega on ülioluline selgitada välja, millised mehhanismid määravad krohmseente koosluste kujunemise keemiliste ja mehaaniliste häiringute korral. Varasemad uuringud on näidanud, et krohmseente elukäigustrateegiad, mis on enamasti sugukonna tasemel määratud, mõjutavad ka nende seente vastust häiringutele, ning osaliselt toetavad seda ka käesoleva doktoritöö tulemused. Nimelt, selgus, et krohmseente sugukonnad on häiringutest erinevalt mõjutatud. Samas soodustasid kõik käsitletud häiringud selliste krohmseente arvukust, mida on varem laboritingimistes kasvatatud ning mida seetõttu peetakse ruderaalseteks **(III)**. Samas viitasid selle töö tulemused ka sellele, et sugukonna tase võib olla krohmseente konkreetseid elukäigustrateegiate määramiseks liiga üldine. Näiteks kasvas keemilise häiringu korral kirjanduse põhjal ruderaalse eluloostrateegiaga ning vähenes stressi taluva eluloostrateegiaga krohmseente sugukonna arvukus. Need tulemused on aga vastuolus ootustega, et aeglase kasvuga ning stressi taluvad krohmseened taluvad keemilist stressi paremini ning viitavad vajadusele koguda rohkem andmeid krohmseente elukäigutunnuste täpsemaks hindamiseks.

Kuna krohmseentel on ülioluline roll taimede kasvus, on uuringud on näidanud, et krohmseente olemasolu suurendamise korral taastub taimkate kiiremini ning kuna krohmseened aitavad taimele toitaineid transportida, siis võib nende roll olla suurem just sellisel juhul kui toitainetesisaldus mullas on madal. Krohmseente olulisust käsitlevad uuringud on enamasti suuremahulised, kasutades krohmseente koguse muutmiseks krohmseentega rikastatud substraati. Üha ulatuslikuma inimtegevuse juures on aga märkimisväärselt suurenenud ka väikesemahuliste häiringute esinemine looduslikes või poollooduslikes kooslustes, mis on inimasustuse läheduses, krohmseente roll selliste alade taastumisel on jäänud seni tähelepanuta. Selle doktoritöö tulemused näitavad, et krohmseente kooslused taastuvad peale väikese ulatusega häiringut paari kasvuperioodi jooksul ning olenemata mullaviljakuse tasemest, on krohmseente olemasolu korral taimkatte liigirikkus ning biomass suurem kui sellistel aladel, kus krohmseened on alla surutud **(IV)**. Seega rõhutavad need tulemused krohmseente olulist rolli taimkatte taastumisel ning taimede liigirikkuse säilitamisel pärast väikesemahulisi häiringuid.

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