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UNIVERSITY OF TARTU
Press

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Dissertation was accepted for commencement of the degree of *Doctor philosophiae* in plant ecology at the University of Tartu on March 5th, 2018 by the Scientific Council of the Institute of Ecology and Earth Sciences, University of Tartu.

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Commencement: Room 218, 40 Lai Street, Tartu, on June 6th, 2018 at 10:15 am

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 the European Social Fund

ISSN 1024-6479
ISBN 978-9949-77-703-7 (print)
ISBN 978-9949-77-704-4 (pdf)

University of Tartu Press
www.tyk.ee

CONTENT

LIST OF PUBLICATIONS

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

I. Neuenkamp L, Lewis RJ, Koorem K, Zobel K, Zobel M. 2016. Changes in dispersal and light capturing traits explain post-abandonment community change in semi-natural grasslands. Journal of Vegetation Science 27: 1222–1232.

II. García de León D, Moora M, Öpik M, Neuenkamp L, Gerz M, Jairus T, Vasar M, Bueno CG, Davison J, Zobel M. 2016. Symbiont dynamics during ecosystem succession: co-occurring plant and arbuscular mycorrhizal fungal communities, FEMS Microbiology Ecology 92: fiw097.

III. Neuenkamp L, Moora M, Öpik M, Davison J, Gerz M, Männistö M, Jairus T, Vasar M, Zobel M. 2018. The role of plant mycorrhizal type and status in modulating the relationship between plant and arbuscular mycorrhizal fungal communities. New Phytologist, DOI: 10.1111/nph.14995 (in press).

IV. Neuenkamp L, Moora M, Lind E, Gerz M, Zobel M. 2018. Composition of AM fungal communities determines the outcome of interspecific plant competition. (manuscript).

V. Neuenkamp L, Prober SM, Price JN, Zobel M, Standish RJ. 2018. Benefits of mycorrhizal inoculation to ecological restoration depend on plant functional type, restoration context and time. Fungal Ecology (pending).

Author's contribution to the publications:

I. Had main responsibility for developing the idea, collecting the resurvey data, analysing the data and preparing the manuscript.

II. Participated in collecting and analysing the data, as well as in preparing the manuscript.

III. Participated in developing the idea, and had main responsibility for collecting and analysing the data and preparing the manuscript.

IV. Participated in conducting the experiment and collecting the data, and had main responsibility for analysing the data and preparing the manuscript.

V. Participated in developing the idea, had main responsibility for collecting and analysing the data and preparing the manuscript.

I INTRODUCTION

1.1. Theoretical background

Human-induced land use change has altered nearly two-thirds of all terrestrial ecosystems (MEA, 2005) with significant consequences for biological diversity, ecosystem functioning and the provisioning of ecosystem services (TEEB, 2010; Cardinale et al., 2013). European semi-natural dry grasslands are one of the most biodiverse ecosystems globally, but they are also among the ecosystems most threatened by land use change (Habel et al., 2013). Such grasslands constitute the natural vegetation of the steppe biome of Eastern Europe (Bohn et al., 2004). However, in many other areas of Europe, where humid conditions naturally allow tree-growth, semi-natural dry grasslands have been favoured by continuous extensive land use, notably grazing by domestic animals and low intensity agriculture (Bignal & McCracken 1996, Eriksson et al. 2002). Such management practices have resulted in extremely high richness of plants and other taxa (e.g. butterflies; WallisDeVries & van Swaay, 2009) at small spatial scales (<100m^2) (Wilson et al., 2012; Dengler et al., 2012). Almost 20% of Europe's endemic vascular plants are restricted to grasslands, which is twice as many as those restricted to forests, despite the latter covering a much larger area (Hobohm & Bruchmann, 2009). However, socio-economic shifts during the last century have led to a dual process of agricultural intensification (e.g. Strijker 2005) and land use abandonment (e.g. Ceballos et al. 2010) that has affected a large proportion of European semi-natural dry grasslands and poses a considerable threat to grassland biodiversity.

Abandonment of semi-natural dry grasslands has predominantly occurred in grasslands where agriculture intensification would not be profitable. After cessation of management, regeneration succession of semi-natural dry grasslands typically leads to gradual shrub and tree encroachment, reducing the area of grassland habitat (Poschlod et al., 2005), altering light and soil conditions in remaining grassland patches, and consequently influencing plant species richness (Gazol et al., 2012). In particular, dense woody cover is associated with the loss of typical grassland species dependent on traditional land management, which in turn reduces plant species richness (Rejmanek & Rosen, 1988; Pärtel et al., 1999). Since many typically grassland species are rare, the potential for local extinctions due to land use change is a major concern in grassland conservation (e.g. Saar et al., 2012; Ödman & Olsson, 2014). Some mechanisms shaping the responses of grassland plant communities to land use abandonment have been identified during recent decades (e.g Hautier et al., 2009, Öckinger et al., 2010; Ozinga et al., 2009). However, detailed knowledge of such mechanisms represents a necessary baseline for designing conservation and restoration strategies that can effectively reduce biodiversity loss and species extinctions in grassland ecosystems.

One approach to understanding plant community responses to environmental change is to conceptualize plant community composition as the outcome of multiple ecosystem processes simultaneously filtering plants according to their functional traits (Weiher & Keddy, 1995). Observed plant composition represents the cumulative action of these filters, i.e. of the most relevant ecosystem processes (Schamp & Aarssen, 2009). Environmental change thus affects plant community composition by altering ecological filtering processes, and assessing plant trait responses to environmental change can inform about shifts in the most relevant ecosystem processes (Mayfield et al., 2010). The filters can be thought of as belonging to three broad categories: dispersal filters (can a species disperse to a certain habitat?); environmental filters (can a species tolerate certain abiotic environmental conditions e.g. light conditions, soil fertility, etc.) and biotic filters (can a species survive in the presence of certain biotic interactions?) (White & Jentsch, 2004; Mayfield & Levine, 2010).

Previous studies have shown that shifts in dispersal (Ozinga et al., 2009; May et al., 2013) and environmental filters (especially light conditions) (Gazol et al., 2012; Bernhard-Verdier et al., 2012) influence the directions of compositional changes in grassland vegetation following land use abandonment. The complex vegetation structure and lack of grazing in abandoned grasslands can hinder long distance dispersal of grassland species by wind or grazing animals, while reduced light availability under dense vegetation limits the establishment of light-demanding grassland species (Pärtel et al., 1999; Saar et al., 2012). These observations indicate that successful conservation or restoration of typical grassland communities requires maintenance or re-establishment of low woody cover levels and continuous grazing management (Kiehl et al., 2010, Habel et al., 2013). Since grazing management is labour and cost-intensive, and the relative contribution to shifts in grassland communities of altered dispersal compared with altered light conditions is often unclear, grazing management is not always included in conservation plans for semi-natural dry grasslands (Römermann et al., 2009; Tälle et al., 2015). An assessment of the relative importance of shifts in light and dispersal conditions for shaping compositional changes in abandoned semi-natural grasslands can thus help to clarify the potential contribution of grazing management to successful grassland conservation and restoration.

Grassland conservation through suppression of woody cover and regular grazing management may also benefit grassland biodiversity by influencing several biotic filters believed to drive compositional changes in grassland communities. In particular, regular biomass removal and the creation of niches for plant regeneration in patches of bare soil may equalize plant-plant competition (Grime et al., 1987). In addition, increased plant diversity can itself provide nectar sources for pollinators (Lazaro et al., 2016; Orford et al., 2016) and the movement corridors of grazing animals can enhance the dispersal efficiency of other organisms (Ozinga et al., 2009; Albert et al., 2015; Tälle et al., 2015).

In addition to biotic filters involving interactions between plants and aboveground organisms – e.g., pollinators and aboveground herbivores – there is an increasing body of research suggesting that interactions between plants and soil biota also play a central role in structuring plant communities (van der Putten et al., 2013). This suggests that variations in soil communities might influence plant community development and ecosystem functioning (Kardol et al., 2006; Mace et al., 2012) and are thus an important factor to consider for biodiversity conservation and restoration in terrestrial ecosystems (Carbajo et al., 2011; Wubs et al., 2016). However, knowledge about the role of soil biota in determining plant biodiversity and ecosystem functioning is only now emerging (Bever et al., 2010; Delgado-Baquerizo et al. 2016), as is an understanding of how to integrate soil biota into conservation and restoration practices (Harris, 2009; Kardol & Wardle, 2011, Wubs et al., 2016).

Among soil biota, mycorrhizal fungi may be of particular relevance for attempts to conserve and restore terrestrial ecosystems (Kardol & Wardle, 2010), since about 80–90% of all land plants host these obligate symbionts (Brundrett et al., 2009). In exchange for plant-assimilated carbon, mycorrhizal fungi increase plant nutrient supply (Smith & Read, 2008), enhance plant resistance to pathogens (Jung et al., 2012; Laliberté et al., 2015) and alleviate the effects of environmental stress (Augé et al., 2015, Gehring et al., 2017). Through these mechanisms, mycorrhizal fungi can influence plant performance and, by mediating plant-plant interactions (Hart et al., 2003; Moora & Zobel, 2010; Lin et al. 2015; Peay, 2018), affect plant diversity and community structure (van der Heijden et al., 1998; Klironomos et al., 2011, Teste et al., 2017). Moreover, mycorrhizal fungi can improve soil physical characteristics, since their extraradical hyphae and production of glomalin promotes soil aggregate stability and resistance to soil erosion (Rillig et al., 2002).

While there are multiple potential benefits to plants arising from the mycorrhizal association, recent meta-analyses have demonstrated that mycorrhizal effects on plants are context-dependent, i.e. they vary with host plant and mycorrhizal fungal identity, and with biotic and abiotic environmental conditions (Hoeksema et al., 2010; Lin et al., 2015; Bunn et al., 2015). These analyses showed soil nutrient availability (mainly N and P) and plant functional characteristics, reflecting plant reliance on mycorrhizal fungi for nutrient uptake, to be important factors regulating the benefits that mycorrhizal inoculation provides to plant growth. Plant characteristics that determine the degree to which plants are involved in the mycorrhizal symbiosis (e.g. for nutrient uptake) also appear useful candidates for explaining mycorrhizal effects on plant-plant interactions and plant community structure (Janos, 2007; Hempel et al., 2013; Moora, 2014; Menzel et al., 2016, 2017; Bueno et al., 2017; Gerz et al., 2018). For example, plant mycorrhizal type (e.g. arbuscular mycorrhiza (AM), ectomycorrhiza (EcM)) determines the role of mycorrhizal symbiosis in nutrient cycling (Philipps et al., 2013) and could potentially impact plant community structure (Bennett et al., 2017, Jo et al., 2018). Mycorrhizal status reflects how frequent mycorrhizal symbiosis occurs in plant species; plant species are either always

(obligately) or sometimes (facultatively) mycorrhizal (Trappe, 1987; Smith & Read, 2008). Mycorrhizal status is therefore indicative of the degree to which plant species rely on the mycorrhizal symbiosis (Smith & Read, 2008; Moora, 2014). Changes in environmental conditions can induce shifts in the dominant mycorrhizal type and status within plant communities (Hempel et al., 2013; Bueno et al., 2017), which in turn, can lead to shifts in local fungal communities (Lekberg et al., 2012; Gazol et al., 2016). Thus, shifts in dominant plant mycorrhizal type and status probably influence how strongly plant community structure is linked to the presence and composition of local mycorrhizal fungal communities.

One shortcoming of most previous attempts to investigate the context-dependency of mycorrhizal effects is that they were conducted under controlled conditions (i.e. with pot experiments). This limits inferences that can be drawn about the situations determining the benefits of mycorrhizal fungi in nature (Hoeksema et al., 2010; Bunn et al., 2015; Lin et al., 2015; but see Maltz & Treseder, 2015). Pot experiments may show that plant performance increases following mycorrhizal inoculation (Hoeksema et al., 2010), but they do not clarify whether or not addition of mycorrhizal fungi in the field is beneficial, as mycorrhizal fungi might already be present in local soils or able to disperse to them (Kulmatiski & Beard, 2011). In a similar manner, evidence from pot experiments that mycorrhizas have positive effects on plant diversity is of limited relevance to understanding the ways in which mycorrhizal fungi influence plant communities in nature. This is because such results do not inform about the relative importance of mycorrhizal fungi compared with other environmental factors determining plant community composition (e.g. soil fertility, light availability, dispersal limitation) (Klironomos et al., 2011). Consequently, predicting the effectiveness of inoculation with mycorrhizal fungi in biodiversity conservation and ecosystem restoration requires thorough testing under field conditions.

Notwithstanding the need for field experiments in mycorrhizal research, controlled microcosm experiments are useful for detecting the potential mechanisms regulating interactions between plant and mycorrhizal fungal communities. For example, competition experiments have revealed that equalizing inter-specific plant competitive abilities could be one mechanism through which mycorrhizal fungi influence plant diversity (Hart et al., 2003; Lin et al., 2015), and that mycorrhizal effects vary with fungal taxon identity (Scheublin et al., 2007; Stanescu & Maherali, 2017) and fungal richness (Vogelsang et al., 2006; Wagg et al., 2011). However, most such experiments have the shortcoming that the employed inocula contained low numbers of fungal taxa, whereas plants are frequently colonized by several mycorrhizal fungal taxa simultaneously in nature. Moreover, experiments have frequently focused on competition between plants that have very different reliance on the mycorrhizal symbiosis (Moora & Zobel, 2010), but in many ecosystems most plants are mycorrhizal. Consequently, the results of such experiments can provide information about the 'coarse scale' effects of mycorrhizal fungi on plant-plant interactions (sensu

Hart et al., 2003), i.e. presence vs absence of fungi, functional differences between fungi. Inferences to be drawn from such approaches about the role of mycorrhizal fungi for plant-plant interactions in nature are thus arguably limited to early successional ecosystems, i.e. to conditions where dispersal limitation of mycorrhizal fungi, and thus of suitable fungal inoculum, might disadvantage strongly mycotrophic plant species (Hart et al., 2003; Moora & Zobel, 2010). In order to understand the role of mycorrhizal fungi for plant-plant interactions in more successionally advanced ecosystems, experiments using natural fungal inocula would be strongly preferable (Moora & Zobel, 2010). This is because in more mature ecosystems, mycorrhizal fungi are abundant and most plants are mycorrhizal. Therefore, the 'fine-scale effects' of mycorrhizal fungi (sensu Hart et al., 2003), such as the roles of fungal diversity and composition, are more likely to shape plant-plant interactions.

1.2. Objectives of the thesis

This thesis aims to address these knowledge gaps and, in doing so, to determine the potential of mycorrhizal fungi as a tool for improving strategies of biodiversity conservation and ecosystem restoration. The thesis uses abandoned semi-natural dry grasslands – a target of many conservation and restoration efforts in Europe (Kiehl et al., 2010; Habel et al., 2013) – as a model of land use change. It explores the main plant- and mycorrhizal fungal-related filters determining plant responses to land use change. Among mycorrhizal fungal filters, the thesis focusses on effects of arbuscular mycorrhizal fungi (AM; phylum Mucoromycota, subphylum Glomeromycotina; Spatafora et al., 2016), which form the dominant type of mycorrhizal symbiosis associated with grassland plants (Gerz et al., 2016) and indeed with terrestrial plants globally (involving 80% of plant species; Smith & Read, 2008). The thesis includes five papers:

Paper I: The objective of paper I was to assess the main plant-related ecological filters driving compositional changes in grassland plant communities after land use abandonment, disentangling the relative importance of light and dispersal limitation. To meet this objective paper I used a plant functional trait approach, considering plant traits reflecting adaptation to reduced light availability and dispersal strategies as determinants of differences between the plant composition of continuously managed and abandoned grasslands.

Paper II and III: Using an observational study design, papers II and III tested whether compositional changes in plant and AM fungal communities in semi-natural grasslands are correlated. The rationale behind this approach is that re-introduction of local AM fungal communities during grassland restoration could represent a useful tool for promoting the re-establishment of typical grassland communities, including rare target plant species (e.g. Torrez et al., 2016). In addition, papers II and III tested in greater detail which abiotic and biotic factors shape the strength of the plant-AM fungal relationship. Paper II

focussed on the potential role of dispersal limitation of plants and AM fungi (Zobel & Öpik, 2014; Horn et al., 2017). Paper III addressed the role of soil nutrient availability (Zobel & Öpik, 2014; Horn et al., 2017) and plant functional characteristics describing plant involvement in the AM symbiosis (e.g. mycorrhizal type or status) (Moora, 2014; Gerz et al., 2016; Gazol et al., 2016).

Paper IV: Paper IV tested whether, in addition to the plant functional characteristics examined in paper III, the differential effects of AM fungal composition on plant-plant interactions is a factor regulating the plant-AM fungal relationship (Hart et al., 2003; Moora & Zobel, 2010). For this, paper IV used a greenhouse experiment comparing the effects of two natural AM fungal communities originating from different grassland habitats studied in paper III on the interaction of grassland species native to the study region of paper III.

Paper V: The objective of paper V was to summarize published field evidence revealing effects of mycorrhizal inoculation on plant growth and plant diversity in ecosystem restoration and to investigate the context-dependency of effects. For this, paper V used meta-analysis of 34 experimental studies reporting responses to mycorrhizal inoculation for one or both of plant growth and diversity, and estimated variation in inoculation effects on these response variables in relation to relevant explanatory factors (Hoeksema et al., 2010; Lin et al., 2015; Bunn et al. 2015).

II MATERIAL AND METHODS

2.1. Relevance of light and dispersal limitation for plant composition in grasslands

2.1.1. Study design and data collection

Paper I assessed the relevance of light and dispersal limitation as drivers of compositional shifts in grassland plant communities in response to land use abandonment, with a particular focus on shifts in the functional structure of plant communities. The taxonomic and functional community structure of the same semi-natural dry grasslands in Estonia was compared between two points in time: 1975, when traditional grazing prevailed (baseline data), and 2013, when management had ceased for at least 30 years (revisitation data). The study area is approximately 1.5 km^2 of calcareous semi-natural dry grassland, located in Western Estonia (latitude: 58.642N, longitude: 23.516E). Under continuous grazing management, this area was open, with juniper (*Juniperus communis, L.*) cover of ca. 30% and pine (*Pinus sylvestris, L.*) cover of < 1%. The maintenance of these grasslands depends on active management, particularly grazing by domestic animals and cutting of shrubs and trees, but these practices ceased in the 1980s (Rosen 1982, Pärtel et al., 1999), leading to widespread overgrowth by juniper and pine (ca. 40–100% cover) in the semi-natural dry grasslands of this region. The dataset of paper I comprised plant composition data collected in 1975 by M. Zobel and K. Zobel (baseline data) from 93 plots of $4m^2$ located randomly within five study sites (Fig. 1 in I) and measurements of the same plots in 2013 (revisitation data) using the same sampling methodology. The functional structure of plant communities was described by assigning plant functional traits known to respond to changes in dispersal conditions and reduced light availability ('response traits' sensu Lavorel & Garnier, 2002) to all species recorded during the baseline and resurvey (Table 1).

2.1.2. Data analysis

The functional structure of plant communities was measured by estimating the distribution of plant functional traits within plant communities. Two metrics were calculated for each trait: (1) the community-weighted mean (CWM) i.e. the mean of the trait values weighted by the relative abundances of species (Garnier et al., 2004), and (2) functional diversity (FD), calculated as the mean species pairwise distance (MPD) in trait values weighted by species abundances (de Bello et al., 2016). CWM summarizes shifts in community composition resulting from selection processes for certain functions/functional traits (Ricotta & Moretti, 2011). MPD reflects shifts in patterns of trait similarity i.e. trait convergence or divergence, which can be related to ecological filters structuring the plant community (Cornwell & Ackerly, 2009). Successional changes in mean traits and FD were assessed from shifts in CWM values and MPD between the baseline and resurvey data.

Table 1: Response traits used in the analyses. All trait information was retrieved from the Leda trait database (Kleyer et al. 2008). (According to Table 1 in paper I)

Trait	Data type	Attributes	Indicative for ecological process
leaf dry matter content ($mg\ g^{-1}$)	continuous		shade tolerance (Kitajiima et al., 2010)
specific leaf area ($mm^2\ mg^{-1}$)	continuous		shade in general (Gommers et al., 2013)
clonal mobility	binary	0,1; no clonal mobility, clonal mobility	shade avoidance (Stuefer et al., 1994; Zobel et al., 2010)
vegetation height (m)	continuous		shade avoidance (Gommers et al., 2013)
seed mass (mg)	continuous		zoochory by ungulates (Albert et al., 2015)
release height (m)	continuous		
epizoochorous dispersal	binary	0, 1; no epizoochorous dispersal, epizoochorous dispersal	epizoochory, long distance dispersal (Albert et al., 2015)
endozoochorous dispersal	binary	0, 1; no endozoochorous dispersal, endozoochorus dispersal	endozoochory, long-distance dispersal (Albert et al., 2015)
bird dispersal	bird	0, 1; no bird dispersal, bird dispersal	endozoochory, ornithochory, long-distance dispersal (Albert et al., 2015)
simple wind dispersal (without special adaptions)	binary	0, 1; no wind dispersal, wind dispersal (without the help of diaspore appendages)	anemochory (Tamme et al., 2013)
specialised wind dispersal	binary	0, 1; non wind dispersal, wind dispersal (with the help of diaspore appendages)	anemo-, epizoochory, long distance dispersal (LDD) (Tamme et al., 2013; Albert et al. 2015)

To assess the proportion of variation in taxonomic community composition explained by dispersal and light related traits in different surveys, partial redundancy analysis (pRDA) was performed. Thus, the variation explained by the sub-models comprising traits related either to dispersal (release height, seed mass, dispersal syndrome), or light availability (plant height, clonal mobility, specific-leaf area (SLA), leaf dry matter content (LDMC)) was compared to the full model comprising all traits. The same approach was used to further compare the contribution of different aspects of dispersal and light-capturing strategies for explaining variation within their respective group of traits related to dispersal and light availability. Variation among sites was accounted for by including site as a conditioning variable in all pRDA.

2.2. Covariation of plant and AM fungal communities in grasslands

2.2.1. Sampling design and data collection

Papers II and III used two spatial gradients, each representing three consecutive stages of regeneration succession in semi-natural dry grasslands, as model systems to investigate patterns of covariation between plant and AM fungal communities. These model systems are of the same grassland type as studied in paper I, with a similar land use history. Paper II assessed shifts in covariation strength between plant-AM fungal communities along an early successional gradient – regeneration succession in a former gravel pit – and paper III considered a later successional gradient – regeneration succession of mature grasslands after cessation of management.

To address the role of plant and AM fungal dispersal limitation as potential factors regulating the strength of covariation between communities, the study sites of paper II were located along two early successional gradients on two Western Estonian islands (Muhu, Saaremaa), with moderate distances (distance 1–40 km) between successional stages, assuming that dispersal limitation could occur between successional stages. To assess local factors determining the strength of plant and AM fungal covariation, such as soil nutrient availability and plant involvement in the AM symbiosis, the study sites of paper III were situated in one grassland area (2 km^2) in Western Estonia (latitude: 58.624N, longitude: 23.542E). In this study site, patches with varying degrees of overgrowth (transitional grasslands (TR) and young pine forests (FO)) surrounded open grassland (GR) patches.

Plant and AM fungal communities in paper II were sampled from six sites – one site per successional stage and island, with ten plots per site (n=60) – and in paper III from 25 sites within the studied grassland, each containing three plots, i.e. one plot per successional stage (n=75). For each plot (1x1 m) the identity and cover of plant species in the field layer were determined and the relative abundance of plants forming AM symbiosis (AM plants) was calculated to

provide an estimate of the proportional cover of these species in the community. Moreover, the relative abundance of AM plants with different mycorrhizal status (AM status: a plant, either obligately or facultatively forming the AM symbiosis, Moora, 2014) was estimated. Data on mycorrhizal status were obtained from the MycoFlor database (Hempel et al., 2013).

To describe the AM fungal communities present in plant roots and soil, a 10x10x10 cm soil core was collected from the centre of each plot; plant roots and soil were separated and dried for molecular analysis. In paper III two additional soil subsamples were taken from each plot for analysis of soil geochemical properties and for measuring the concentration of the AM fungal neutral lipid fatty acid marker (NLFA 16ω:5), which provides an estimate of AM fungal abundance in soil (Mårtensson et al., 2012). AM fungal communities in soil and plant roots were characterised based on the DNA extracted from dried soil (Gazol et al., 2016) and mixed root samples (Hiiesalu et al., 2014; Saks et al. 2014). Glomeromycotina gene sequences (SSU rRNA) were amplified with the primers NS31 and AML2 (Simon et al., 1992; Lee et al., 2008) and identified using pyrosequencing as described in Davison et al. (2012) and Öpik et al. (2013). To assign taxonomic information to the quality-filtered (Davison et al., 2012; Vasar et al., 2017) sequences, the similarity of sequences to published Glomeromycotina sequences in the Maarj*AM* database (Öpik et al., 2010) was assessed (Blast+ search; Camacho et al., 2009). The Maarj*AM* database classifies the central part of Glomeromycotina SSU rRNA gene sequences into phylogenetically delimited sequence clusters – virtual taxa (VT, cf. Öpik et al., 2009), which roughly correspond to species-level taxa (Öpik et al., 2013). Sequences were assigned to VT if sequence similarity was ≥97% and quality criteria for sequence alignment were met (see paper II, III).

2.2.2. Data analysis

To investigate successional dynamics in plant and AM fungal communities in both papers (II, III), shifts in plant and AM fungal (VT) species richness (the number of VT per sample), and plant and AM fungal species composition among successional stages were tested using linear mixed models and ordination techniques (NMDS). The species matrix for the ordination analyses contained relative plant and AM fungal abundances in each plot. Relative AM fungal species (VT) abundance was calculated as the proportion of reads from individual VT compared to the total number of reads in a sample (Kohout et al., 2014; Leff et al., 2015).

In both papers (II, III), correlation (i.e. a scaled measure covariance) between plant and AM fungal communities was assessed using multivariate correlation analyses (procrustean randomization tests; PROTEST, Peres-Neto & Jackson, 2001). The assumption is that strong interdependence of two communities is reflected in strong correlation between the compositions of both communities. In a further step, partial PROTEST was performed in paper III to assess

correlation between plant and AM fungal communities while accounting for the effects of variation in soil conditions on both communities. The residuals from Procrustes correlation serve as an estimate of variation in correlation strength: high residuals indicate weak correlation, and vice versa (Lisboa et al., 2014). In paper III, the partial Procrustes residuals were used to relate variation in correlation strength to successional stage, AM fungal abundance (NLFA 16ω:5) and the relative abundances of AM, obligate and facultative AM plants.

In paper II, the potential role of dispersal and microsite limitation for plant and AM fungal communities during grassland succession was compared by estimating the completeness of plant and AM fungal communities. Community completeness was calculated as the ratio between plant and AM fungal species present in a plot and the number of species present in the local species pool (sensu Zobel, 2016; all species recorded in the grassland plots of one island). Low completeness was assumed to indicate either strong dispersal or microsite limitation.

2.3. Relevance of AM fungal composition for mediating plant-plant interactions

2.3.1. Experimental design and data collection

Paper IV used the dry semi-natural grasslands studied in paper III as a model system to test the effect of differences in AM fungal composition on plant-plant interactions with a full-factorial greenhouse experiment. The AM fungal communities present in the soil of open grasslands and young pine forests, which differed significantly in species richness and composition (paper III), served as natural inocula in the experiment. The experiment tested the effect of inoculum type on the growth response of two focal forb species (*Leontodon hispidus, L.; Plantago lanceolata, L.*) to competition with a competitor grass species (*Festuca rubra, L.*). Experimental plants were native to the study region, but differed in their habitat preference: *P. lanceolata* grew more frequently in open grasslands, *L. hispidus* in young pine forests and *F. rubra* was equally frequent in both habitat types.

Seedlings for all experimental plants were pre-germinated for five weeks from sterilized seeds collected from the study region (*P. lanceolata*, *L. hispidus*) or locally produced seeds (*F. rubra*). Inocula were produced from mixtures of field soil and sterile sand to equalize soil chemical properties between inocula. The five-week old seedlings of *P. lanceolata* and *L. hispidus* were transplanted into pots (one seedling per pot), and grown for 15 weeks either alone or in mixture with four individuals of *F. rubra.* The pots differed in soil inocula: grassland inoculum containing 1/3 of live grassland soil, 1/3 of sterilized forest soil and 1/3 of sterile sand; forest inoculum containing live forest soil (1/3), sterilized grassland soil (1/3) and sterile sand (1/3); and a non-mycorrhizal control soil containing only sterilized soils (2/3) and sand (1/3). Each forb

species-competition-soil combination was replicated 10 times (n=120) and 40ml of microbial wash mixed from grassland and forest soils was added to each pot to control for potential differences in soil bacteria and non-AM fungal communities among treatments (Koide & Li, 1989). After 15 weeks, plant biomass from each pot was harvested, divided into root and shoot fractions for each species, dried at 55°C for 24h and weighed.

AM fungal root colonization was estimated for five root subsamples of both forb species (*P. lanceolata*, *L. hispidus*) from each treatment combination, (n=30 samples per species) to assess whether inoculation was successful and whether changes in plant biomass were linked to changes in AM fungal abundance in plant roots. Preparation of roots and estimation of root colonization followed the methods described by Koske & Gemma (1989) and McGonigle et al. (1990). No root colonization was recorded in the roots of *L. hispidus* and *P. lanceolata* growing in non-mycorrhizal control soils, and thus colonization results are reported only for the grassland and forest inoculum treatments.

2.3.2. Data analysis

Plant growth responses to competition and inoculation were calculated as estimates of relative plant growth in competition compared with growth without competition (RIIc), and relative plant growth when inoculated compared with growth in non-mycorrhizal control soils (RIIi), respectively. Thus, RIIc and RIIi were calculated for plant biomass according to Armas et al. (2004; Relative-Interaction Index, RII):

$$RII = [biomass_{treatment} - mean(biomass_{control})]/[biomass_{treatment} + mean(biomass_{control})],$$

where $biomass_{treatment}$ is the biomass of the focal plant grown in the experimental treatment (i.e. in mixture with *F. rubra* – RIIc; with inoculum – RIIi), and $biomass_{control}$ is the biomass of the same species growing in control conditions (i.e. without *F. rubra* – RIIc; in non-mycorrhizal control soils – RIIi). Values of RII are symmetrical around zero, and bound between –1 and 1. Positive values indicate a beneficial effect of the interaction with *F. rubra* (RIIc) or with added AM fungi (RIIi) on plant biomass, and negative values indicate a detrimental effect. The difference between inoculation effects (RIIi) on the focal forb species compared to *F. rubra* when grown in mixture with each other ($dRIIi_{mixture}$) served as an estimate of the competitive benefit the focal species received from inoculation compared to the competitor species. Positive values indicate that inoculation benefits were larger for the focal than the competitor species, suggesting less competitive pressure on the focal species, and negative values indicate that inoculation benefits were smaller for the focal than the competitor species, suggesting amplified competition (for the focal species) (Moora & Zobel, 2010).

Linear models were used to test for significant differences in interaction parameters (RIIc, RIIi, dRIIi $_{mixture}$) among different types of inoculum (grassland, forest, control), focal plant species (*P. lanceolata*, *L. hispidus*) or depending on the combination of inoculum type and focal species. Interaction indices and linear models were calculated for root, shoot and total biomass (i.e. shoot + root biomass). The same approach as described above for plant growth was applied to test for a response to inoculation and competition in the percentage of root colonization in the focal species.

2.4. Relevance of mycorrhizal fungi for ecosystem restoration

2.4.1. Study design and data collection

Paper V used meta-analysis to summarize the context-dependency of plant responses to mycorrhizal inoculation in field-based restoration projects. The relevant studies for the meta-analysis were selected based on a literature search in the ISI Web of Science database (1900–2016) using the keywords mycorrhiza* AND (restoration OR reclamation OR rehabilitation). This search identified 34 studies suitable for the meta-analysis testing the effect of mycorrhizal inoculation on plant growth (biomass, height) and/or plant species richness under field conditions in a restoration context. If a study reported results from multiple comparisons (e.g. from different host plants, inoculation treatments or study sites), information about all comparisons was collected. Comparisons were pooled into five datasets. Three 'global datasets' were constructed to assess the general effect of inoculation on plant growth and plant richness in response to different explanatory factors, one for each response variable (plant biomass, height and richness). If studies reported data on inoculation effects for multiple points in time, only data on inoculation effects from the last harvest were included into the global datasets. For plant growth, two 'time datasets' were also compiled using all studies from the global biomass and height datasets that reported inoculation effects over multiple time points (up to 36 months). There were too few suitable studies (n=1) to construct a 'time dataset' for plant richness.

For each comparison, data on plant response to inoculation was extracted from text, tables and figures. Moreover, data on potential factors influencing mycorrhizal effects on plant performance were recorded from each publication i.e. data on plant functional group, soil conditions (pH, soil total N, available P), disturbance history, inoculum complexity, control treatment and time since restoration (Hoeksema et al., 2010; Bunn et al., 2015; Lin et al., 2015; Maltz and Treseder, 2015). See Table 2 for details.

Table 2: Explanatory factors used to assess the context dependency of inoculation effects on plant biomass, height and richness (Table 2 in paper V).

Explanatory factors	Categories/ units	Proportion of comparisons where data was available (%) for plant biomass (global dataset, time dataset)	Proportion of comparisons where data was available (%) for plant height (global dataset, time dataset)	Proportion of comparisons where data was available (%) for plant richness
Time (since inoculation)	number of months	–, 100	–, 100	——
Plant functional group	C3-grass, C4-grass, non-N-fixing forb, forb-grass mix, non-N-fixing woody, N-fixing woody	100, 100	100, 100	100
Habitat conditions				
pH	1–14 (min = 4.4; max = 10.2)	67, 100	87, 100	44
soil total N	g kg^{-1} (min = 0; max = 12)	60, 100	67, 100	11
soil available P	mg kg^{-1} (min = 0; max = 61)	63, 91	87, 91	44
Disturbance history [a]	soil severely altered, soil not altered	100, 100	100, 100	100
Inoculum complexity [b]	single, mix, mix-whole soil, whole soil inoculum	100, 100	100, 100	100
Control treatment [c]	no inoculum, sterile soil, sterile soil & microbial wash	100, 100	100, 100	100

[a] Categories of disturbance history reflect the degree of soil disturbance. "Soil severely altered" included studies in which disturbance activities removed or severely altered the topsoil (e.g. mining, road construction, tree logging with bulldozers, agriculture), assuming that mycorrhizal fungal communities had been severely altered by these activities. Otherwise, studies were categorized as "soil not altered"

[b] Categories of inoculum complexity were chosen as follows: Single inoculum is an inoculum containing a single fungal taxon originating from commercial inoculum or natural soil applied as a tablet, water-mixture or solution of water and nurse plant roots. A mix inoculum is a mixture of 2–10 fungal taxa originating from commercial inoculum or natural soil applied as a tablet, water-mixture or solution of water and nurse plant roots. Mix-whole soil inoculum refers to studies comparing effects of inoculation with a fungal mix to whole soil inocula using the same control for both treatments. Thus, comparisons are not statistically independent and effect sizes were calculated as the average effect of both types of inocula. Whole soil inoculum consists of soil collected from reference sites, expected to contain the complete biotic soil community i.e. organisms including but not exclusively mycorrhizal fungi. All studies comparing fungal mixtures to whole soil inocula used AM fungi. For AM fungi, inoculation effects stemming from whole soil inocula can be related to mycorrhizal fungal effects, if they are compared to a control, which has received a microbial filtrate (wash) containing the majority of soil organisms of the experimental soil, except AM fungi (pore size 50 µm; Koide and Li, 1989). This method works effectively for AM fungi due to their relatively large spores compared to the majority of other soil microbial communities (e.g. bacteria and non-AM fungi) (Uibopuu et al., 2012). For plant biomass 100% of all comparisons using whole soil inoculum and 50% of all comparisons using the "mix-whole soil" type of inoculum soil applied a microbial wash to control treatments, 50% applied no specific control treatment (no inoculum). For plant height, 100% of the comparisons using whole soil inoculum or the "mix-whole soil" type inoculum applied microbial wash to control treatments.

[c] No inoculum refers to the type of control treatment where no specific mycorrhizal control treatment was applied, but plants where grown in untreated soil at the restoration site. Sterile soil refers to the type of control treatment where control plants were grown in field soil that had been sterilized by radiation or autoclaving. Sterile soil plus microbial wash refers to the type of control treatment where a microbial filtrate (wash) containing the majority of soil organisms of the experimental soil, except mycorrhizal fungi, was added to the sterilised control soil.

2.4.2. Data analysis

The natural logarithm of the response ratio (ln(R) = ln(inoculated/non-inoculated)) was used to estimate the effect sizes of plant responses to mycorrhizal inoculation. A positive response ratio indicates a beneficial effect of inoculation, and a negative response ratio a detrimental effect. Effect sizes were calculated for each comparison, except for comparisons from the same study that shared the same control. For these comparisons combined effect sizes and sample variances were calculated, to guarantee the independence of experimental comparisons in the datasets (Borenstein, 2009).

The significance of mycorrhizal inoculation effects, as well as the effects of explanatory variables on plant biomass, height and richness were tested with mixed-effects models (Viechtnbauer, 2010). These models estimated inoculation effects as mean effect sizes weighted by sample variances (Viechtbauer, 2010), and inoculation effects were considered significant if weighted mean values and their 95% confidence intervals (CI) significantly differed from zero (Borenstein, 2009). In models testing for changes through time of plant responses to inoculation (within studies), time after inoculation (in months) was included as a fixed factor. To test the interactive effects of time and other explanatory variables, the interaction term of both variables was included as a fixed factor. All models included study as a random factor, in order to adjust effect size estimates for methodological differences between studies. Potential publication bias was assessed by visually checking each dataset via funnel plots and testing for asymmetry with Eggers' regression test (Borenstein, 2009). There was no indication of publication bias.

2.5. Statistical software

All statistical analyses performed in paper I–V were carried out using R (ver. 3.1.0; R Core Team 2014) in the RSTUDIO environment (ver. 0.98.932).

III RESULTS

3.1. Relevance of light and dispersal limitation for plant composition in grasslands

Closed vegetation structure, with reduced light availability, and altered dispersal conditions were the main drivers of shifts in plant functional structure in semi-natural grasslands experiencing land use abandonment. Compositional shifts in grassland communities were characterised by an increase in the proportion of plant species with either larger or coarser leaves (higher SLA or higher LDMC), which are adaptations to low light availability, and an increase in the proportion of species with clonal growth forms, which are able to escape low light availability (Fig.3 in I). Abandonment also led to a higher proportion of species adapted to the changed dispersal conditions of the closed vegetation, e.g. species relying on bird-dispersal instead of wind and epizoochorus dispersal in the fur of grazing animals (Fig.3 in I). Shifts in traits related to wind dispersal were somewhat weaker than for those for traits related to animal dispersal, yet a decrease in species specially adapted to wind dispersal over long distances became apparent in the most overgrown sites (Fig. S8 in I). Consequently, small sedges and forbs declined the most in response to land use abandonment and their decline likely led to a reduction in small-scale species richness. The majority of these species have high light requirements, rely on wind or epizoochorus dispersal in the fur of animals, and are typical of dry semi-natural grasslands in the study region (e.g. *Carex caryophyllea L., Thymus serpyllum L., Antennaria dioica L.)*.

Variance partitioning showed that the proportion of variation in plant composition explained by plant traits related to light availability and dispersal explained increased from 31% in grazed grasslands to 37% in abandoned grasslands (Fig. 1a). This increase reflected an increase in variation attributed to both light or dispersal traits and a concomitant decrease in variation attributed to differences between study sites. Dispersal traits explained a larger proportion of variation in plant community composition than light traits both in grazed and abandoned grasslands. Yet, the increase in variation explained by light traits following grassland abandonment exceeded the increase in variation explained by dispersal traits, suggesting that the importance of light relative to dispersal traits increased following land use abandonment in the studied grasslands (ratio between explained variation (%) of dispersal vs. light traits: grazing = 1.8, $\text{abandonment}_{2013}$= 1.5; Fig 1a).

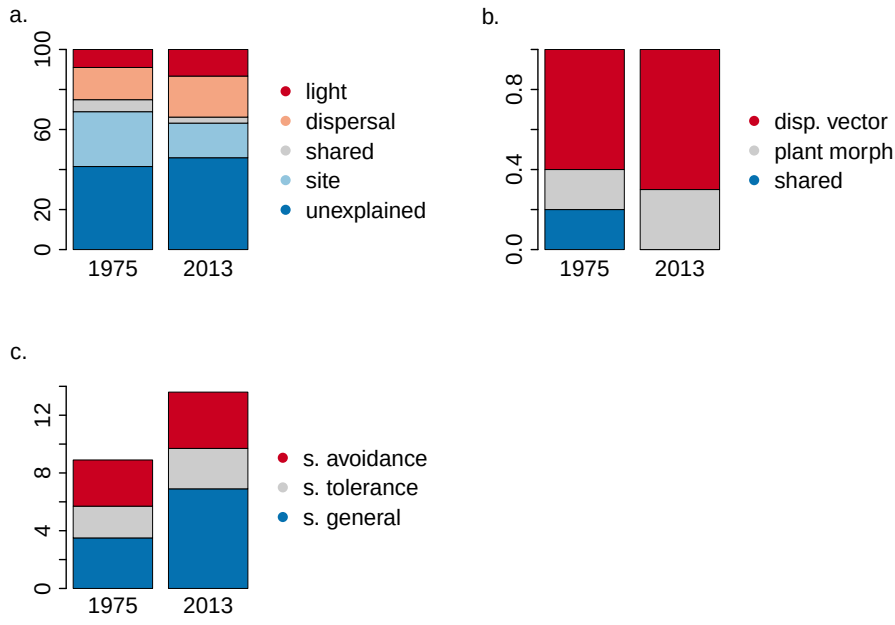

Fig.1: Variation in plant community composition of semi-natural dry grasslands explained by groups of dispersal traits and light traits. Grassland communities were measured prior to (1975) and following (2013) land use abandonment. Estimates of explained variance are based on partial RDA with trait groups as fixed and site differences as conditioned factors. (**a)** Proportions of variation in community composition explained by dispersal and light traits, their intersection as well as site differences in different years (1975, 2013). (**b)** Proportion of variation in community composition explained by different aspects of dispersal strategies (dispersal syndrome, plant morphology). (**c)** Proportion of variation in community composition explained by light traits reflecting different strategies to cope with reduced light availability (shade avoidance (s. avoidance), shade tolerance (s. tolerance) and shade in general (s. general)) as well as by their interaction in different years (1975, 2013). Dispersal traits ('dispersal') included the traits of dispersal vector (disp. vector): epizoochorous, endozoochorous and bird dispersal, special and simple wind dispersal; and plant morphology (plant morph.): release-height and seed mass. Light traits ('light') included clonal mobility (CM), vegetation height (VH), specific leaf area (SLA) and leaf dry matter content (LDMC). CM and VH were representatives of the 'shade avoidance' strategy, LDMC represented 'shade tolerance' and SLA shade in general ('shade general'). Modified after Fig. 5 in I.

3.2. Covariation of plant and AM fungal communities in grasslands

Multivariate correlation analysis revealed significant correlation of plant and AM fungal community composition across early (regeneration of disused gravel pits, II: $r_{\text{plant-soil AM fungi}}=0.44$; $r_{\text{plant-root AM fungi}}=0.31$) and late (regeneration succession after cessation of grazing management, III: $r_{\text{plant-soil AM fungi}}=0.44$; $r_{\text{plant-root AM fungi}}=0.40$) stages of grassland succession. The residuals of Procrustes correlation remained stable during the early stages of grassland succession (II), but significantly decreased during later stages (III) (Fig 3 in II, Fig S5 in III). Residuals increased most during the transition from open or partially overgrown grasslands to young pine forest. These results suggest that plant and AM fungal communities were correlated equally strongly during regeneration of grassland vegetation from gravel pits (bare soil), but the strength of correlation decreased following shrub and tree encroachment into mature grasslands, which occurred due to cessation of management.

Further analysis of the abiotic and biotic factors influencing the strength of correlation between plant and AM fungal communities during the later stages of grassland succession (III) revealed that the strength of correlation weakened when models controlled for variations in soil properties (Δr: 10–12%), but the correlation remained significant (Fig. 2 in III). This suggests that variation in soil properties had only a moderate effect on the correlation of plant and AM fungal communities. At the same time, the composition of plant AM status in the grassland communities significantly influenced the strength of correlation between plant and AM fungal communities. Procrustes residuals decreased with the increasing abundance of obligate AM plants and vice versa for the abundance of facultative AM plants (Fig. 2a, b). These findings suggest that plant and AM fungal communities were strongly correlated when the abundance of obligate AM plants was high, but the relationship weakened with increasing abundance of facultative AM plants. The abundance of AM plants in the grassland communities and the biomass of AM fungi (NLFA 16ω:5) did not influence the strength of correlation between plant and AM fungal communities (Fig. 2c, d).

Analysis of the completeness of plant and AM fungal communities during the regeneration of disused gravel pits (II) demonstrated that for both plants and AM fungi the proportion of local species pools realized in the studied local grassland communities increased during succession (Fig 3). These results suggest that over time increasing numbers of plant and AM fungal species successfully disperse to and establish in grassland sites from surrounding grassland habitats. At the same time, the completeness of AM fungal communities exceeded that of plant communities in all successional stages (Fig. 3). This finding indicates that the proportion of the local taxon pool that was realised in the studied grasslands was larger among AM fungi than plants (Fig 3), potentially reflecting a faster arrival of AM fungi than plants to the study sites than.

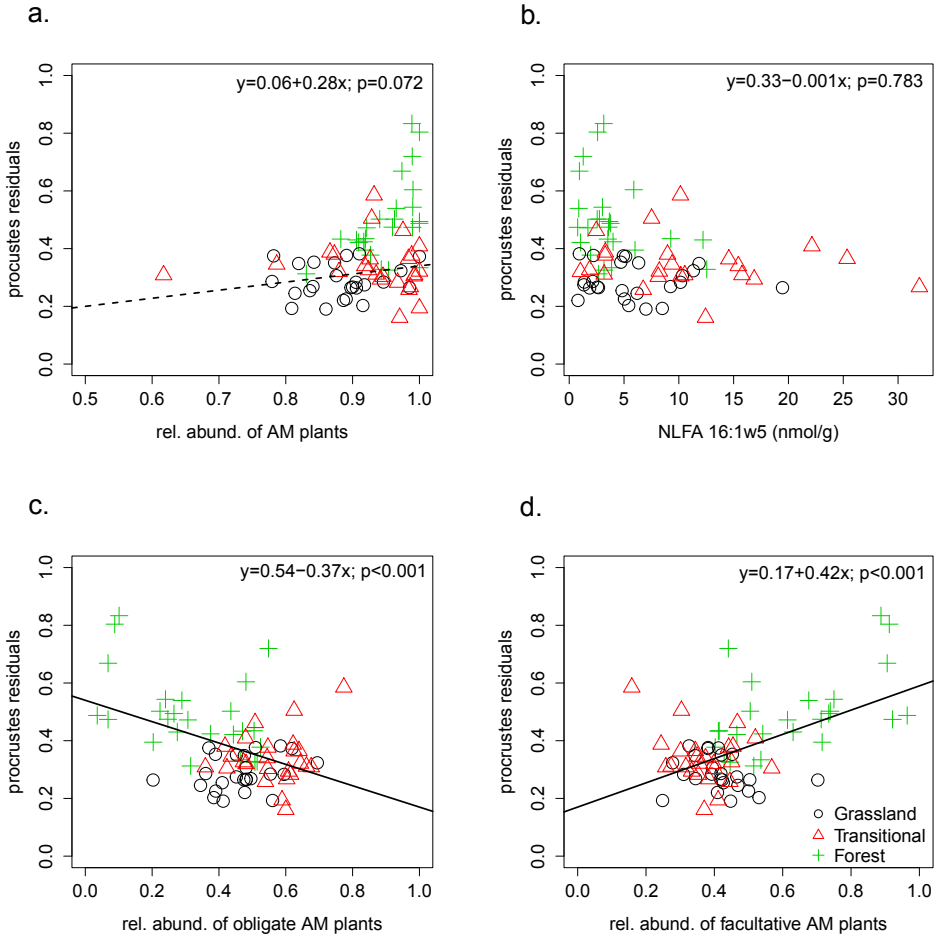

Fig. 2: Relationships between the strength of plant-soil AM fungal correlation and the relative abundance of AM **(a)**, obligate AM **(c)** and facultative AM **(d)** plants in the ground layer and AM fungal abundance (NLFA 16:1ω5) **(b)**. Data for NLFA 16:1ω5 are shown with outliers omitted (see Table S5 in IV for relationships considering all data). The strength of co-variation was measured as the residuals from Procrustes correlation, i.e. low values of Procrustes residuals indicate strong correlation. Regression lines, equations and p-values for the fixed effect are shown on each plot based on linear mixed-effects model-estimated regression parameters. Regression lines of significant ($p<0.05$, solid line) and marginally non-significant relationships ($p<0.1$; dashed line) are shown. Copy of Fig. 3 in III.

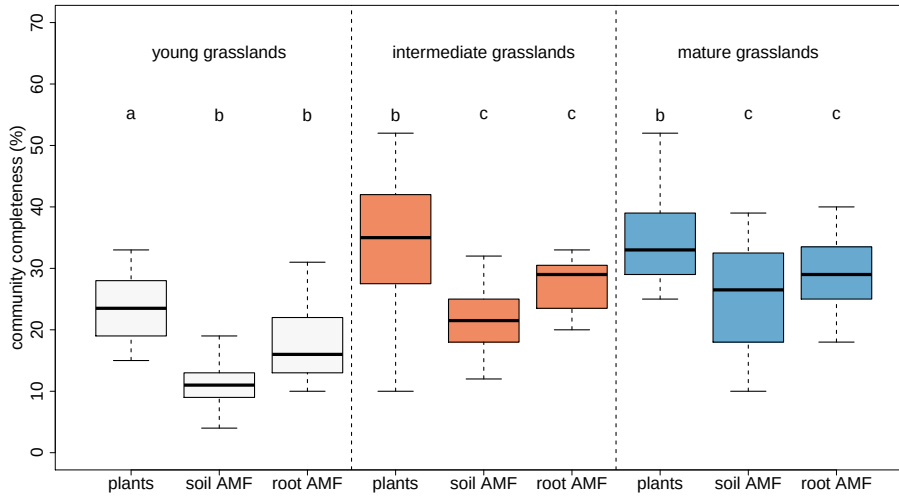

Fig. 3: The proportions (%) of taxa present in each plot relative to the total number of taxa observed for all successional stages on each island (local taxon pool) for plants, AM fungi in soil (soil AMF) and AM fungi in roots (root AMF). Community completeness is a relative measure that was calculated for each taxon and habitat (soil or root) separately. Box whiskers extend to the 95% confidence intervals around the median (black line). Modified after Fig 4 in II.

3.3. Relevance of AM fungal composition for mediating plant-plant interactions

The results of greenhouse experiments showed that inoculation with both AM fungal inocula (grassland inoculum, forest inoculum) led to abundant colonization of the roots of all experimental plants. Hyphae and arbuscules were most abundant in forb roots, with an average root length colonization of 80% by hyphae, and 40% by arbuscules. There was negligible variation in percentage root colonization in response to competition and inoculation (Table S1, Table S2 in IV). There was, however, significant variation in plant biomass detectable in response to the competition and inoculation treatment. Since results showed similar trends for root, shoot and total biomass, only the results for total biomass are presented. See paper IV for a detailed presentation of other fractions of biomass. For ease of reading total biomass is hereafter referred to as plant biomass.

Competition with four *F. rubra* individuals significantly reduced the biomass of the focal forb plants (RIIc<0; Fig.4, Table 3). Inoculation with AM fungi increased forb biomass both when grown alone and in mixture with *F. rubra* (Fig. 4, Table 3). The opposite pattern was true for *F. rubra,* whose biomass decreased in response to inoculation (Table 3), leading to an overall greater inoculation benefit for both forbs compared with *F. rubra* (dRIIi>0; Table 3). The beneficial effects of inoculation with AM fungi on plant responses to competition varied with the type of inoculum (grassland or forest).

For both forb species, the growth response to competition was stronger when inoculated with the grassland inoculum (Fig. 1 in IV). Larger growth benefits from the grassland inoculum were related to the fact that the forb species and *F. rubra* showed opposite growth responses to inoculum type. When grown in mixture with *F. rubra*, the growth response of both forb species was highest with the grassland inoculum, lower with the forest inoculum and lowest in the non-mycorrhizal control soil (Table 3a). *F. rubra* showed exactly the opposite trend, exhibiting highest growth in non-mycorrhizal control soil and lowest growth with the grassland inoculum (Table 3b). Consequently, the grassland inoculum promoted forb growth over the growth of *F. rubra*, relatively more than the forest inoculum (dRIIi, Table 3d). Yet, since the growth response of *F. rubra* to inoculation differed less between inoculum types, differences between the average dRIIi for the grassland compared with the forest inoculum were marginally non-significant (Table 3b, d).

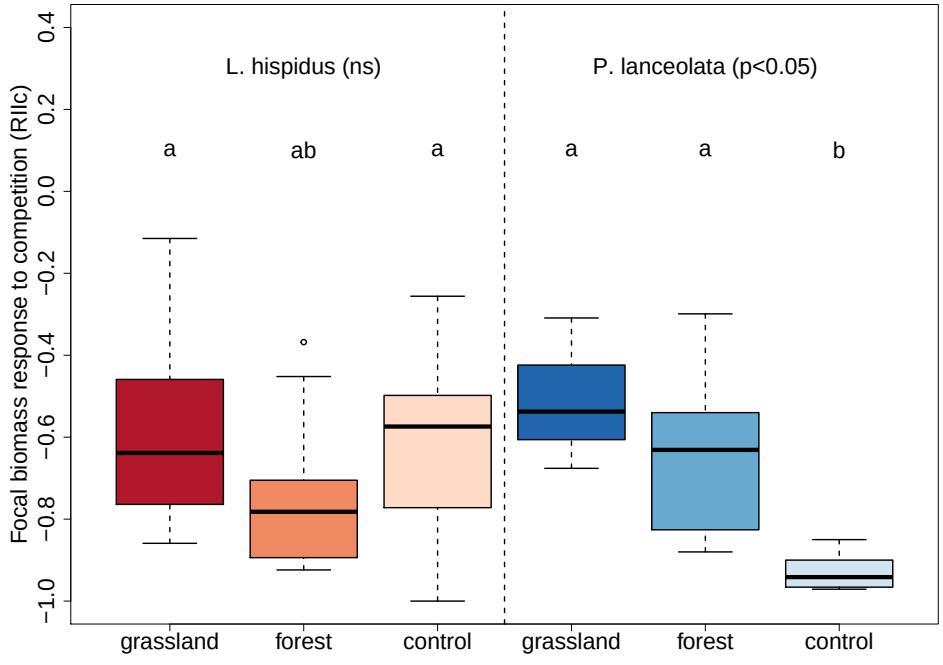

Fig. 4: Differences in relative biomass response of focal species to competition in relation to focal species identity (*L. hispidus*, *P. lanceolata*) and type of inoculum. Different letters indicate significant differences according to linear models ($p<0.05$). Box whiskers extend to the 95% confidence intervals around the median (black line). grassland = grassland inoculum; forest = young pine forest inoculum; control = non-mycorrhizal control. Copy of Fig. 2 in IV.

Table 3: Results of linear models assessing the factors influencing different measures of plant response to competition. The measures were **(a)** total biomass of focal species (*L. hispidus*, *P. lanceolata*) and **(b)** competitor species (*F. rubra*) when grown in mixture with each other; (c) total biomass growth response of focal species to competition (RIIc) and **(d)** the difference in growth response to inoculation of focal species and *F. rubra* when grown in mixture with each other ($dRIIi_{mixture}$). Growth response parameters were calculated based on total plant biomass (root + shoot biomass), see Table S3-S5 in V for separate results of root and shoot biomass. Explanatory factors tested were focal species (*L. hispidus*, *P. lanceolata*), type of inoculum (grassland inoculum, forest inoculum) and the interaction of both factors. For RIIc, values >0 indicate an increase and values <0 a decrease of plant biomass in response to competition. For, $dRIIi_{mixture}$ values >0 indicate a larger and values <0 a smaller growth benefit from inoculation to focal species compared to *F. rubra*. If factor levels significantly ($p<0.5$) or marginally non-significantly ($p<0.1$) differed from each other, group means (± SE) are displayed, with different letters indicating significant differences ($p<0.05$). Copy of Table 2 in IV.

Types of plant growth response (total biomass, g)	explanatory factor	estimate	SE	DF	p-value	Post Hoc Test (TUKEY)
a) Bio-mass$_{focal,\ mixture}$	**mean value**	**0.8**	**0.1**	**0**	**<0.001**	
	focal species			1	0.083	*L. hispidus*^{a} = 0.6±0.2 *P. lanceolata*^{a} = 1.0±0.2
	type of inoculum			**2**	**<0.001**	grassland^{a} = 1.5±0.2 forest^{b}= 0.9±0.2 control^{c} = 0.03±0.01
	focal species × type of inoculum			5	0.229	
b) Bio-mass$_{comp,\ mixture}$	**mean value**	**6.3**	**0.5**	**0**	**<0.001**	
	focal species			1	0.435	
	type of inoculum			**2**	**<0.001**	grassland^{a} = 4.6±0.3 forest^{a}= 5.1±0.4 control^{b} = 9.1±1.2
	focal species × type of inoculum			5	0.187	
c) RIIc$_{focal}$	**mean value**	**–0.67**	**0.03**	**0**	**<0.001**	
	focal species			1	0.375	
	type of inoculum			**2**	**0.004**	grassland^{a} = –0.56±0.04 forest^{b}= –0.69±0.04 control^{b} = –0.77±0.05
	focal species × type of inoculum			**5**	**<0.001**	*L. hispidus*: grassland^{a} –0.59±0.07; forest^{a} –0.74±0.06; control^{a} –0.61±0.06 *P. lanceolata*: grassland^{a} –0.52±0.04; forest^{a} –0.65±0.06; control^{b} –0.93±0.01
d) $dRIIi_{mixture}$	**mean value**	**1.16**	**0.03**	**0**	**<0.001**	
	focal species			**1**	**0.022**	*L. hispidus*^{a} = 1.20±0.03 *P. lanceolata*^{b} = 1.31±0.04
	type of inoculum			1	0.088	grassland^{a} = 1.29±0.03 forest^{a}= 1.21±0.04
	focal species × type of inoculum			**3**	0.075	*L. hispidus*: grassland^{a} 1.20±0.04; forest^{a} 1.20±0.05 *P. lanceolata*: grassland^{a} 1.39±0.02; forest^{b} 1.23±0.06

Both forb species showed similar growth responses to competition, but they differed in how competition responses were modulated by inoculation (Table 3c). The growth responses to inoculation of both species were positive and of similar magnitude when grown alone (Table S4 in V). When grown in mixture with *F. rubra*, only the biomass of *P. lanceolata* significantly increased in response to inoculation, while the biomass production of *L. hispidus* did not differ between inoculated and non-inoculated conditions. (Fig. 4). Both forb species tended to receive larger growth benefits from the grassland compared to the forest inoculum, but this difference in growth benefit was only significant for *P. lanceolata* (Table 3d; Fig. 4).

3.4. Relevance of mycorrhizal fungi for ecosystem restoration

A meta-analysis of 34 restoration experiments showed that mycorrhizal inoculation led to a significant increase in plant growth and plant richness: on average a 1.7 fold increase in plant biomass and a 1.3 fold increase in plant height and richness. Inoculation effects were dependent on the nutrient-uptake strategies of the host plant and the soil conditions of the restoration site. Growth benefits from inoculation were largest for those plants with high nutrient demand (N-fixing woody plants) and inefficient nutrient-uptake (C4-grasses) and those growing in soils with low N or P availability (Fig 5; Fig. 3 in V). Inoculation complexity and the type of control treatment used did not significantly influence measured inoculation effects.

Time-series analyses demonstrated that the positive effects of inoculation on plant growth could increase within timeframes of up to three years, in particular for N-fixing woody species (Fig. 4a, b in V). These analyses also indicated that the benefits from inoculation are greater in restoration sites where soil has been severely disturbed prior to restoration (e.g. due to mining, road-construction) compared to restoration sites with undisturbed soils (Fig 4c in V). These results suggest that disturbance history, through alteration of the soil mycorrhizal fungal community, may be another factor influencing the success of restoration efforts.

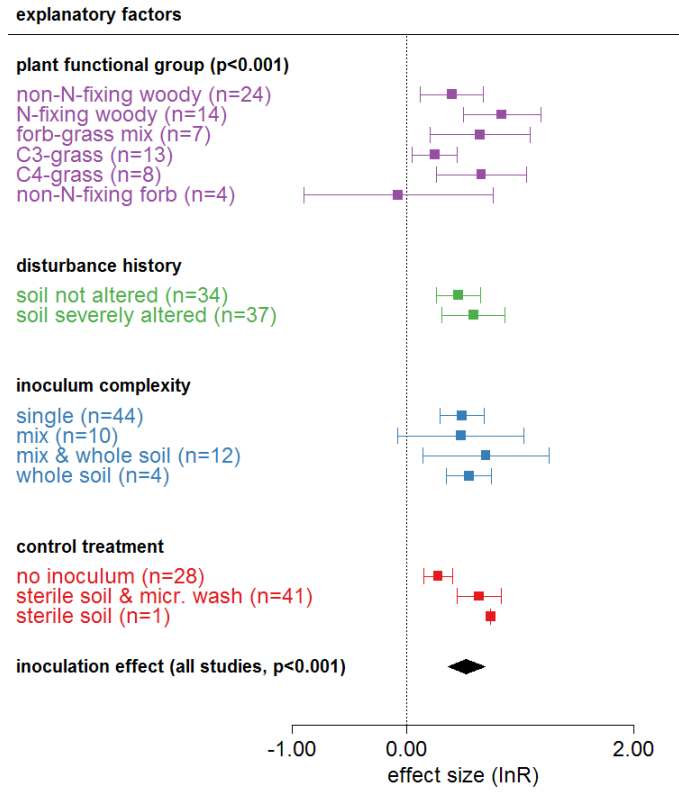

Fig. 5: Plant biomass response to inoculation in the global dataset (n=70), and levels of categorical explanatory factors 'plant functional group', 'disturbance history', 'inoculum complexity' and 'control treatment'. Symbols are means (closed squares, centre of the diamond) ± 95% confidence intervals (error bars, right/left tip of the diamond). Differences among factor levels were estimated using random-effects models. Effect size is the natural logarithm of the response ratio where positive values equate to a benefit of inoculation on plant biomass. Copy of Fig. 2 in V.

IV DISCUSSION

4.1. Maintenance of dispersal conditions through grazing as a prerequisite for successful grassland conservation and restoration

Land use abandonment resulted in significant shifts in the dispersal and light capturing strategies of the dominant plants in semi-natural grasslands. Although animal-mediated dispersal remained the dominant dispersal strategy, land use abandonment was characterised by a decrease in the importance of wind-mediated and a shift in the importance of different types of animal-mediated dispersal strategies. These changes probably reflected the lack of grazing animals as dispersal vectors in abandoned semi-natural grasslands (Ozinga et al., 2009). Although the total abundance of animal-dispersed (endo- and epizoochorous) species decreased, this change was not general, as evidenced by the increased abundance of bird-dispersed species, which suggests that land use abandonment favoured bird-dispersed species over mammal-dispersed species (MacArthur & Levins, 1967; Purves & Dushoff, 2005). Reduced light availability in abandoned grasslands increased the abundance of shade-tolerant berry-producing forest species with large seeds and high specific leaf area (SLA; Metcalfe & Grubb, 1995; Wilson et al., 1999), which are dispersed by birds. Moreover, the decreased representation of species adapted to long distance dispersal by wind – manifested by small seed size and appendages that keep seeds airborne (Tamme et al., 2013) – indicates that the denser vegetation structure of abandoned grasslands might limit wind-mediated seed dispersal between sites (Weiher & Keddy, 1995; Damschen et al., 2014).

Corroborating earlier studies, abandonment of semi-natural grasslands also promoted species adapted to low-light conditions, with increased abundance of species that are strong competitors for light (i.e. avoid shade) or are able to tolerate shade (Lavorel & Garnier 2002, Bernard-Vernier et al. 2012, Gommers et al. 2013). While there was a clear increase in the abundance of bird-dispersed species at the expense of species favouring other types of animal dispersal, plant responses to abandonment were more diverse in terms of the strategies used to improve light capture, indicating that multiple processes (related to reduced light availability) shaped community assembly (Spasojevic & Suding, 2012). Species that increased in abundance after land use abandonment maximised light acquisition through three strategies: i) tall and fast growth (Franklin et al. 2008), which was reflected in the high abundance of tall plants and plants with high SLA (Poorter & Remkes 1990, Westoby 1998); ii) rapid occupation of open habitat patches (Zobel et al. 2010, Johansson et al. 2011), which was reflected in the high abundance of clonal plants; and iii) maximised photosynthesis (Givinsih 1988, Wilson et al. 1999) and leaf protection (Kitajiima et al. 2010, Moles et al. 2013) to increase shade tolerate, which was reflected by increases in SLA and LDMC in densely overgrown sites.

Overall, the importance of dispersal relative to light traits in explaining compositional shifts decreased with abandonment. These results indicate that dispersal was limited in abandoned grasslands due to the denser vegetation structure and the lack of domestic grazing animals as dispersal vectors, which played an important role in grazed semi-natural grasslands. At the same time, shifts in the relative importance of light traits highlight the increased relevance of adaption to reduced light availability for plant species survival and thus plant community composition in abandoned semi-natural grasslands. Several typical grassland species share characteristics opposite to those promoted by the altered dispersal and light conditions in abandoned semi-natural grasslands, i.e. low height, high light requirements and adaptation to wind and epizoochorous dispersal (Laasimer, 1965; Saar et al, 2012), and are thus likely to be most susceptible to land use abandonment. In summary, it appears that successful grassland conservation needs to incorporate both restoration of light and dispersal conditions. Such goals can be achieved by reducing the woody cover to a maximum of 40% and by re-establishing a regular grazing regime. The former would restore the typical light conditions (Rosen & van der Maarel, 2000), and the latter would restore the dispersal conditions (Ozinga et al. 2009) by increasing habitat connectivity and provisioning of suitable microsites for plant species establishment (Bakker et al., 2006; Albert et al., 2015).

4.2. The relevance of symbiont availability for successful grassland conservation and restoration

The analysis of drivers of plant composition in semi-natural grasslands in study II–IV revealed that besides interactions between plants and grazing animals, interactions between plants and their associated AM fungal communities shape plant community composition. Strong correlation between plant and AM fungal communities during early and mature stages of semi-natural grassland succession suggests that shifts in richness and community composition of one symbiont could induce shifts in the community of the other, corroborating findings from mesocosm experiments (van der Heijden et al., 1998; Vogelsang et al., 2006; Klironomos et al., 2011). Thus, re-establishment of typical grassland plant communities might be enhanced by considering local AM fungal communities in parallel (e.g. Torrez et al., 2016). A significant shift in the abundance, diversity and composition of local AM fungal communities in young pine forests indicates a need to consider re-introduction of AM fungal communities from appropriate target communities in order to achieve successful restoration of heavily overgrown grasslands (cf. Kardol et al., 2006; Wubs et al., 2016).

Abundance of AM fungi (NLFA) in young pine forests was low, which may reflect limited wind-dispersal of AM fungi in the dense vegetation structure of young pine forests, a situation similar to that mentioned before for grassland plants (Damschen et al., 2014). However, community completeness of all measured AM fungal communities was high, suggesting that local environmental

conditions rather than dispersal limitation drove the spatial distribution of AM fungi at the studied scales (see also Lekberg et al., 2012; Davison et al., 2015). Another factor limiting symbiont abundance in young pine forests might have been the shift in the dominant mycorrhizal type from AM to EcM, which is typical of regeneration succession in European semi-natural grasslands (Prévosto et al., 2011; Gerz et al., 2016) i.e. an EcM tree layer forms over an AM plant dominated field layer. This shift might lead to suppression of AM by the EcM fungi associated with the relatively large root systems of pine trees, and subsequently to a reduction in AM fungal abundance in young pine forests (c.f. Gazol et al., 2016). Yet, AM fungal abundance in the soil (NLFA) was a weak predictor of correlation strength between plant and AM fungal communities, suggesting that fine-scale effects (sensu Hart et al., 2003; i.e. shifts in the diversity and composition of AM fungi) may be more relevant drivers of plant community recovery in restored grassland (Moora & Zobel, 2010).

Plant and AM fungal community diversity and composition was similar in most of the early and later stages of grassland succession, when plant-AM fungal correlation was strong. However, in both symbiont communities diversity significantly declined and composition shifted at the transition to pine forest, and correlation between plant and AM fungal communities weakened. Differences between grassland and forests in terms of AM fungal diversity and composition have been reported before (Moora et al., 2014; Davison et al., 2015). However, the results of this thesis provide evidence that differences in AM fungal community composition influenced plant-plant coexistence, which may have translated into differences in plant community structure (see also Scheublin et al., 2007; Wagg et al, 2011).

Experimental results from study IV showed that AM fungal communities from open grasslands could balance competition between grassland plants. This was probably one factor contributing to the strong linkage between plant and AM fungal communities in open grasslands and enabling the observed high small-scale plant diversity, which is typical of semi-natural grassland (van der Heijden et al., 1998). The positive effects of native grassland inocula on plant species richness observed in the meta-analysis also support this interpretation. Weaker effects on plant-plant interactions of the AM fungal community from young forests might then explain the weaker linkage of plant and AM fungal communities in young pine forests and perhaps in part the lower plant diversity observed in this habitat type. These findings underline the need to coordinate reintroduction of plants and their associated AM fungal communities from appropriate target systems during grassland restoration, in order to promote re-establishment of the plant-AM fungal interaction patterns and thus the plant community structure that is typical of the grassland under restoration (Kardol et al., 2006; Harris, 2009; Wubs et al., 2016).

The importance of AM fungal re-introduction in grassland restoration is likely to depend on the functional composition of the target and degraded plant communities. In study III, the strength of the plant-AM fungal relationship varied according to the dominant plant mycorrhizal status in the plant communities

measured, suggesting that plant reliance on mycorrhizal symbiosis could be another factor regulating how tightly plant and AM fungal communities are related (Brundrett et al. 2002). The importance of plant functional traits for mediating the plant-AM fungal relationship has mostly been observed in controlled greenhouse experiments with low numbers of plant and AM fungal species (Hoeksema et al., 2010; Wagg et al., 2011; Lin et al., 2015; but see Wubs et al., 2016), but these results provide evidence for this effect occurring in nature.

High abundance of obligate AM plants in semi-natural grasslands was associated with a strong correlation between plant and AM fungal communities, while a high abundance of facultatively AM plants was associated with weak correlation. Shifts in plant AM status largely reflected a shift from legumes to grasses, with high legume abundance in open and partially overgrown grasslands, and high grass abundance in young pine forests. High reliance on the mycorrhizal symbiosis by legumes, which is probably due to high nutrient demand (in particular P for N-fixation; Azcon et al., 1991, Wagg et al., 2011), might have been one mechanism that led to the strong association between plant and AM fungal communities in open grasslands. By contrast, the grass species that were abundant in the young forests (C3-grasses) were frequently facultatively AM plants (Hempel et al., 2013), i.e. they form mycorrhiza but not always, and are able to perform well when fungal abundance is low. Weak reliance of C3-grasses on mycorrhizal symbiosis is frequently attributed to their fibrous and well-branched root systems that allow efficient nutrient uptake (Hetrick et al., 1990; Maherali et al., 2014). In summary, the relationship between plant and AM fungal communities is likely to be strong if the majority of plant species rely obligately on AM symbiosis, and weak if the majority of plant species rely facultatively on AM symbiosis. The weak mycorrhizal response of the grass *F. rubra* to inoculation in the competition experiments supports this conclusion. Consequently, the relative abundance of obligate AM plants in a grassland community might serve as a first indication of how important a consideration of the AM symbiosis should be in the conservation of a particular semi-natural grassland.

4.3. Nutrient limitation as a regulator of mycorrhizal benefits to ecosystem restoration across ecosystems

The meta-analysis of restoration experiments conducted in study V confirms the potential of mycorrhizal inoculation to benefit ecosystem restoration across different habitat types globally. Addition of mycorrhizal fungi to restoration sites promoted plant growth and plant richness, and effects of mycorrhizal inoculation remained stable or even increased over timeframes of 3 years. However, the strength of these effects was strongly context-dependent, corroborating results reported from controlled conditions (Hoeksema et al., 2010). The most important factor regulating mycorrhizal benefits to plant growth was nutrient availability,

which is consistent with the well-known role of mycorrhizal fungi in facilitating plant nutrient uptake (Koide, 1991; Schwartz & Hoeksema, 1998; Smith & Read, 2008). Growth responses to mycorrhizal inoculation were greatest for N-fixing plants, C4 grasses and in soils with low N and P concentration. The strong growth responses of N-fixing plants and C4 grasses probably reflect high nutrient demand (mostly P) for maintaining N-fixation (Mortimer et al., 2008; Wagg et al., 2011), and inefficient nutrient uptake due to the coarse root systems of C4 grasses, respectively (Hetrick et al., 1990; Wilson & Hartnett, 1998). The stronger plant growth response to mycorrhizal inoculation in low N and P soils is consistent with the theory that plant benefits from trading C for fungal-derived nutrients are greatest under low nutrient-availability (Koide, 1991; Schwartz and Hoeksema, 1998; Jones and Smith, 2004). With regard to drivers of plant-AM fungal covariation in semi-natural grasslands, these results support the notion that differences in the nutrient uptake strategies of plants may have mediated plant reliance on mycorrhizal symbiosis and thus the relationship between plant and AM fungal communities.

Plant growth responses to inoculation did not vary significantly in relation to inoculum complexity (i.e. the number of fungal taxa contained in the inoculum), perhaps reflecting the low host specificity of the AM fungi used as inoculant in most restoration experiments (Smith & Read, 2008). However, whole soil inocula (native fungal communities from the soil of intact reference ecosystems) tended to promote plant growth more than other types of inocula. The high efficiency of whole soil inocula might be due to the adaptation of native fungal communities to the soil properties at the restoration site or due to the complementary functions provided by the high fungal diversity of whole soil inocula (van der Heijden et al., 1998; Hart & Klironomos, 2003). In concert with earlier studies reporting similar findings (Barea et al., 2011; Maltz & Treseder, 2015) and in light of the differential response of plant-plant interactions to variations in AM fungal composition discussed above, these results highlight the effectiveness of whole soil inocula for promoting plant growth and probably plant diversity in ecosystem restoration.

Inoculation benefits were stronger in soils that had been severely disturbed prior to restoration (e.g. due to mining or road-construction) compared with non-altered soils, emphasizing the importance of soil legacies as regulators of restoration outcomes (Prach & Hobbs, 2008; Standish et al., 2009). Severe soil disturbance can reduce the abundance of mycorrhizal fungi and alter their community composition, hampering the natural recovery of mycorrhizal fungal communities (Moora et al., 2014; Lekberg & Koide, 2005). Our results demonstrate that in these cases mycorrhizal inoculation can alleviate symbiont limitation, thereby assisting recovery of mycorrhizal fungal communities at restoration sites and promoting subsequent revegetation of disturbed soils by annual and perennial species (Barea et al., 2011). However, effects of disturbance history on plant responses to inoculation were weaker than effects of nutrient availability. This may reflect the wide range of disturbance histories included within the category “severely disturbed soils”, which probably induced

differential plant responses to inoculation. Further research should attempt to distinguish those types of disturbance for which mycorrhizal inoculation is particularly beneficial in assisting ecosystem recovery.

In addition to promotion of plant growth, the results of the meta-analysis showed that mycorrhizal inoculation can increase plant richness and the similarity in composition of restored and intact/historic reference plant communities (Fischer et al., 2013; Koziol and Bever, 2016; Torrez et al., 2016). These findings corroborate predictions from mesocosm experiments (van der Heijden et al., 1998) and demonstrate the high potential of mycorrhizal inoculation for promoting restoration of diverse communities towards the state of intact/historic reference sites. The outcomes of previous plant-competition experiments (Moora & Zobel, 2010) and the one conducted in study IV suggest that positive inoculation effects on plant richness could result from the equalizing effect of mycorrhizal fungi on the competitive abilities of dominant and subordinate plants (Grime et al., 1987). Mycorrhizal inoculation may thus help to meet the aim of restoring diverse communities from sown target species, which currently challenges many restoration practitioners (e.g. Grman et al., 2015), by facilitating establishment and persistence of rare, often less competitive plant species. Conclusions about a positive influence of mycorrhizal inoculation on plant richness in ecosystem restoration were based on a small number of studies, so further research is required to precisely establish the potential of mycorrhizal inoculation to restore plant diversity and composition in a wide range of ecosystem types and environmental conditions.

V CONCLUSIONS

Widespread human-induced degradation of terrestrial ecosystems poses an acute threat to biodiversity and ecosystem functioning (MEA, 2005). As such, there is an urgent need to optimize existing strategies and develop new approaches to effectively conserve and restore ecosystem diversity and function (Martin et al., 2016). On one hand, research assessing the effectiveness of existing conservation and restoration measures can provide conservation practitioners with scientific, evidence-based arguments to underpin requests for political and financial support in taking action. This may be especially relevant for conservation and restoration measures that incur additional costs and labour requirements in the long-term (e.g. regular grazing management of semi-natural grasslands; Tälle et al., 2015). On the other hand, it is crucial to investigate the potential of new and lesser-known conservation and restoration strategies (e.g. inoculation with soil biota, such as mycorrhizal fungi; Kardol & Wardle, 2010; Wubs et al., 2016). The results of this thesis contribute in both of these ways to the improvement of science-based biodiversity conservation and ecosystem restoration.

The results of this thesis confirm the relevance of integrating regular grazing management into semi-natural grassland conservation and restoration planning. This integration would help to maintain the abundance of typical and often rare grassland species, whose life-history strategies are adapted to and thus dependent on regular grazing by ungulates. With regard to mycorrhizal fungi, the results provide evidence for a strong relationship between plant and AM fungal communities in grasslands, with mediation of plant-plant interactions by AM fungal communities being one mechanism linking plant and AM fungal communities in grasslands. The recorded strong linkages between plant and AM fungal communities suggest that AM fungal communities should be considered in grassland conservation and restoration planning. Significant changes to AM fungal diversity and composition in young pine forests indicate that re-introduction of AM fungal communities from appropriate target systems could benefit grassland restoration in very overgrown sites. Moreover, application of AM fungal inoculum in grassland restoration might be especially beneficial if the abundance of obligate AM plant species is high in the target grassland community, since the compositions of local plant and AM fungal communities were most tightly correlated in such grassland types.

Some of the results in this thesis suggest plant-mycorrhizal fungal relationships are relevant to understanding the suitability of inoculation with mycorrhizal fungi in a range of degraded ecosystem types besides grasslands. Benefits from mycorrhizal fungi to revegetation success and re-establishment of whole plant communities can be expected to be greatest under conditions of nutrient limitation. This means that the benefits for ecosystem restoration from mycorrhizal inoculation will be greatest in ecosystems with low soil nutrient availability (N and P), and high abundance of plants with strong reliance on mycorrhizal symbiosis (e.g. obligate AM plants), due to high nutrient-demand (e.g. N-fixing species) or low nutrient-uptake efficiency (e.g. C4 grasses with coarse root systems).

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SUMMARY IN ESTONIAN

Taimekoosluse ja arbuskulaarmükoriisse seenekoosluse dünaamika rohumaadel muutuva maakasutuse tingimustes

Alatest 1992. aastast, kui allkirjastati bioloogilise mitmekesisuse konventsioon ning seeläbi tõsteti globaalses skaalas esile elurikkuse vähenemise problemaatika, on välja töötatud erinevaid elurikkuse kaitse strateegiaid. Samas elurikkuse langus jätkub seniajani, olles ühelt poolt tingitud nö. poliitilise tahte puudumisest ning teiselt poolt seotud piisava informatsiooni puudumisega elurikkuse muutumist põhjustavate mehhanismide osas. Eriti vähe on andmeid mikroskoopiliste mullaorganismide mitmekesisuse ja funktsionaalse struktuuri kohta. Samas on nende liikide määramine ja funktsiooni uurimine aina lihtsam tänu kiirelt arenevatele molekulaarsetele meetoditele.

Pool-looduslikud rohumaad kujutavad endast Euroopa liigirikkamaid taimekooslusi, mille elurikkus sõltub nii ajaloolisest kui ka tänapäevasest inimtegevusest. Lisaks taimede kõrgele liigirikkusele on pool-looduslikud rohumaad oluliseks elupaigaks ka paljudele teistele liigirühmadele (nt. liblikad ja linnud) ning pakuvad mitmeid ökosüsteemi hüvesid (nt. kultuurilised ja tolmeldamise hüved). Kuna Euroopa pool-looduslikud rohumaad on kujunenud kestva ja mõõduka niitmise ja/või karjatamise tulemusel, siis on taolise maakasutuse jätkumine vajalik nende säilimiseks. Alates 20.sajandi keskpaigast on kogu Euroopas linnastumise, põllumajanduse intensiivistumise ja traditsioonilise majandamise lakkamise tõttu pool-looduslike rohumaade pindala ja kvaliteet oluliselt vähenenud. Majandamata rohumaad võsastuvad, seal suureneb puittaimede katvus, mis omakorda vähendab tänu valgus- ja mullatingimuste muutmisele rohurinde taimede liigirikkust. Kinnikasvanud rohumaade taastamiseks on vaja puittaimede katvust vähendada ja rohumaid regulaarselt karjatada ja/või niita. Karjatamine soodustab niidutaimede seemnete levimist ning seetõttu leevendab ka koosluste fragmenteerumise mõju.

Lisaks mulla- ja valgustingimuste ja seemnete levimistingimuste muutumisele maakasutuse käigus mõjutavad taimekoosluste mitmekesisust ja koosseisu ka muutused mullaelustikus. Viimaste hulgas on olulisel kohal arbuskulaarmükoriisa (AM) seened, mis moodustavad sümbioosi umbes 80–90%-ga maismaa taimeliikidest. Mükoriisaseened saavad peremeestaimelt süsivesikuid ning vastutasuks varustavad taimi toitainetega (eriti fosfori ja lämmastikuga) ning kaitsevad taimi patogeenide eest. AM seened mõjutavad taimede kasvu ja viljakust ning selle kaudu ka taimede omavahelisi interaktsioone ning lõppkokkuvõttes taimeliikide kooseksisteerimist. Kuigi AM seente võimalik mõju taimekooslustele on üldteada, on empiirilisi andmeid taimekoosluste ja AM seenekoosluste kovariatsiooni kohta väga vähe. Seetõttu pole selge, kas rohumaade kasutusrežiimi muutumine mõjutab ka seenekooslusi ning kas muutused taime- ja seenekoosluses on paralleelsed?

Käesolevas töös esitati järgmised küsimused:
i) Kuidas muutub pool-looduslike rohumaade taimekooslus maakasutuse muutumisel? ii) Kuidas mõjutab maakasutuse muutus AM seenekooslust? iii) Kuidas sõltub taime- ja seenekoosluse kovariatsioon keskkonnatingimustest? iv) Millist rolli mängivad AM seened taimekoosuste taastamisel?

Kinnikasvanud ja karjatatava rohumaa võrdlus näitas, et taimekoosluse muutudes muutus erineva valgusnõudluse ja levimisstrateegiaga taimeliikide esindatus. Kinnikasvamisel suurenes varjutaluvate ja/või klonaalselt kasvavate liikide osakaal ning tõusis lindlevijate taimeliikide arv. Valgusnõudlike, madalate ja tuul- ning loomlevijate (v.a. linnud) taimeliikide osakaal langes. Rohumaade taimekoosluste taastamisel tuleb silmas pidada, et valgustingimuste ja levimistingimuste taastamine on oluline osa kogu protsessist.

AM seente ja taimekoosluse liigilise koosseisu võrdlev analüüs näitas, et nii taime- kui ka AM seenekoosluste koosseis muutus rohumaa kinnikasvamisel oluliselt. Liigirikkuse langus oli eriti märgatav mändidega tihedalt kinni kasvanud rohumaadel. Taime- ja AM seenkoosluste kovariatsioon oli oluline, s.t. muutustega ühe koosluse koosseisus kaasnesid vältimatult muutused ka teise koosluse koosseisus. Seega võib AM seente lisamine kinnikasvanud ning vaesunud elurikkusega rohumaade taastamisel kasuks tulla. Samas näitab varaste suktsessiooniastmete analüüs, et AM seentel on hea levimisvõime. Seega võib AM seente diaspooride lisamine rohumaade taastamisel olla oluline olukorras, kus taastamisala ümbruskonnas ei ole heas seisukorras olevaid rohumaid või AM seente eoste levik on takistatud ümbritseva tiheda taimestiku poolt. AM seente olemasolu on eriti oluline obligatoorselt mükoriissetele taimeliikidele, mille hulka kuuluvad paljud liblikõielised.

Taimekoosluste taastamiseksperimentide metaanalüüsi tulemused näitasid, et mükoriisaseente lisamine mõjutas taimekasvu ja liigirikkust üldiselt positiivselt, kuid mõju suurus varieerus, olles kõige suurem toitainete (eriti lämmastiku ja fosfori) defitsiidi tingimustes või tingimustes, kus mükoriisaseente ohtrus oli väga madal. Näiteks sõltusid mükoriisast rohkem liblikõielised taimed, mis vajavad N-fikseerimise toetamiseks suhteliselt rohkem fosforit. Analüüs näitas, et mükoriisa positiivne efekt ei ilmne ainult isendi ja liigi tasemel, vaid on märgatav ka koosluse tasemel, suurendades muuhulgas taastatava taimekoosluse sarnasust häiringuteta referentsökosüsteemiga.

Käesoleva doktoritöö tulemused näitavad mükoriisaseente positiivset mõju taimekoosluste liigirikkusele. Samuti näitavad tulemused, et mükoriisaseente kasutamine taimekoosluste taastamisel on võimalik ja vajalik. Edaspidised uuringud saavad anda vastuse küsimusele, millise seeneinokulumi kasutamine taastamiskatsetes on nii majanduslikult kui ökoloogiliselt efektiivseim.

ACKNOWLEDGEMENTS

In deeply thank my supervisor, Martin Zobel, for encouraging me to start my PhD studies and for his endless help, guidance, support and patience during the PhD studies. My gratitude goes also to Nobert Hölzel, who supervised my earlier studies, for establishing the contact to Martin Zobel and the Department of Botany in Tartu. My research stay in Tartu during my MSc studies was the moment, when I got inspired to continue my studies with a PhD program.

I had the pleasure to be part of the most welcoming and supporting Plant Ecology Laboratory and the Department of Botany. The warm and friendly atmosphere, with plenty of room for scientific discussions and outdoor activities, excursions and get-togethers, made coming to work something to look forward to and made feeling at home in Tartu very easy. I thank everyone for creating such a nice atmosphere! My special thank goes to my friends and colleagues Guille, David, Maret, Kadri, Inga, Teele, Mari, Maarja, Martti, Aveliina, Tsipe, Robert, Jaak-Albert, Rob, John, Carlos, Jon, Lars, Jodi, Nacho, Sabrina, Liis, Kersti, Madli, Aurèle, Elisabeth and Marge for shared field-work adventures, scientific advice, as well as countless, desperately needed coffee- and chocolate breaks.

Moreover, I thank Jodi, Rachel Standish and Suzanne Prober for three exciting months of collaboration in Perth and exploring the Australian nature – this was a great experience! I had also the chance learning laboratory methods to identify microbial communities under the guidance of Minna Männistö – thank you for this possibility! I learned a lot and was able to experience the arctic winter, which I – unbelievable but true – enjoyed.

The years of PhD studies seemed sometimes endless, but spending so many years in Tartu gave me the chance to learn the Estonian language, which help tremendously to integrate into the everyday life in Tartu. Learning a language is tough and starting using it is even tougher – thank you, Mari, Laura, Ülle, Teele, Illi, Kaili and Mare for having the patience and encouraging me to try speaking this so different and at the same time so beautiful language!

Finally, I want to thank my family and friends back home, who always supported me, although it might have remained slightly mysterious to them why I chose to live so far abroad and what I was doing exactly all the time. Every single of your visits I appreciated a lot and gave me a feeling of being at home.

***

The research included in this thesis was funded by the Estonian Research Council [IUT 20–28 and PUTJD78], the Estonian Science Foundation [9050, 9157] and the European Regional Development Fund (Centre of Excellence EcolChange and DoRA Programme Activity 6). Moreover research was supported by the Academy of Finland (252323) and a Murdoch University Research and Development Grant awarded to RJ Standish.

PUBLICATIONS

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Education:

2012–present	University of Tartu, Estonia, PhD candidate in plant ecology and ecophysiology
2009–2012	University of Münster, Germany, MSc in Landscape Ecology
2006–2009	University of Münster, Germany, BSc in Landscape Ecology
1996–2005	Schweizer-Allee Gymnasium, Dortmund, Germany
1992–1996	Aplerbecker-Mark Primary School, Dortmund, Germany

Institution and position held:

2012–present	University of Tartu, Institute of Ecology and Earth Sciences, Department of Botany, research specialist and fieldwork assistant
2012	German Research Foundation (DFG), vegetation survey in the Swabian Alb for the Project "Biodiversity Exploratories"
2009	University of Münster, Institute of Geostatistics, field course assistant "Basics of GPS mapping", BSc level
2008 and 2010	University of Münster, Institute of Landscape Ecology, field course assistant "Vegetation recording in forest ecosystems", BSc level
2005–2006	Max-Wittmann special needs school, Dortmund, Germany, assistant teacher

Supervision

2014	Supervision of Tuuliki Koppel's BSc Thesis "The role of arbuscular mycorrhizal in grassland restoration". (co-supervision with Martin Zobel, University of Tartu)
2016	Supervision of Helen Vaaks BSc Thesis „Urban biodiversity – the potential of urban grasslands for biodiversity conservation". (co-supervision with Martin Zobel, University of Tartu)
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Languages German (mother tongue), English (very good), Estonian (good), French (basics)

Major research interests:
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Science publications:
Published:

Neuenkamp L, Moora M, Öpik M, Davison J, Gerz M, Männistö M, Jairus T, Vasar M, Zobel M. 2018. The role of plant mycorrhizal type and status in modulating the relationship between plant and arbuscular mycorrhizal fungal communities. New Phytologist (in press).

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Neuenkamp L, Kopka A, Herzig B. 2009. Farbstandards für Kompensationsflächenpools. Natur in NRW 4/09.

Submitted/in preparation:

Neuenkamp L, Prober SM, Price JN, Zobel M, Standish RJ. 2018. Benefits of mycorrhizal inoculation to ecological restoration depend on plant functional type, restoration context and time. Fungal Ecology

Garcia de Leon D, **Neuenkamp L**, Moora M, Öpik M, Davison J, Pena-Veneqas CP, Vasar M, Jairus T, Zobel M. 2018. Arbuscular mycorrhizal

fungal communities in tropical rainforest are resilient to slash and burn agriculture. Journal of Tropical Ecology.

Neuenkamp L, Moora M, Lind E, Gerz M, Zobel M. 2018. Composition of AM fungal communities determines the outcome of interspecific plant competition.

Popular science publications:

Tamme R, **Neuenkamp L**. 2017. Taimede dieedil hoidmiseks kulub igal aastal 500 kilogrammi suhkrut. Novaator (20.7.2017): http://novaator.err.ee/608404/taimede-dieedil-hoidmiseks-kulub-igal-aastal-500-kilogrammi-suhkrut.

Conference presentations:

Neuenkamp L, Price JN, Prober SM, Moora M, Öpik M, Männistö M, Davison J, Zobel M., Standish RJ. Mycorrhizal fungi – tiny organisms that can shape ecosystems. (oral presentation) Doctoral Student Conference of the Departments of Botany and Zoology, University of Tartu 12.–13.01.2018 in Mooste, Estonia.

Neuenkamp L, Price JN, Prober SM, Moora M, Öpik M, Männistö M, Davison J, Zobel M., Standish RJ. They matter! Mycorrhizal fungi in ecosystem restoration. (oral presentation) 9th International Conference on Mycorrhiza (ICOM) 01.–05.08.2017 in Prague, Czech Republic.

Neuenkamp L, Gerz M, Männistö, M, Davison D, Moora M, Öpik M, Zobel M. Can plant traits explain the plant-AM fungal relationship? (oral presentation) Doctoral Student Conference of the Department of Botany, University of Tartu 17.–18.11.2016 in Jäneda, Estonia.

Neuenkamp L, Price JN, Prober SM, Moora M, Öpik M, Männistö M, Davison J, Zobel M., Standish RJ. Arbuscular mycorrhizal fungi and ecosystem restoration: A local and global perspective. (oral presentation) Annual Symposium of the International Society of Vegetation Science (IAVS) 19–24.07.2015 in Brno, Czech Republic.

Neuenkamp L, Gerz M, Koorem K, Männistö, M, Davison D, Moora M, Öpik M, Zobel M. Response of AMF diversity to land use change in a grassland ecosystem. (poster presentation) 1st Global Soil Biodiversity Initiative Conference. "Assessing soil biodiversity and role in ecosystem services". 02.–05.12.2014 in Dijon, France.

Neuenkamp L, Gerz M, Koorem K, Männistö, M, Davison D, Moora M, Öpik M, Zobel M. AMF and plant communities in three successional stages of calcareous grassland: How they vary and covary? (oral presentation) Doctoral Student Conference of the Department of Botany, University of Tartu 13.–14.11.2014 in Jäneda, Estonia.

Neuenkamp L, Lewis RJ, Zobel M. 30 years of succession in an Estonian calcareous grassland: how does time and land use history shape plant community functional composition? (oral presentation) Annual Symposium of

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Neuenkamp L, Gerz M, Moora M, Öpik M, Männistö M, Davison J, Vasar M, Jairus T, Zobel M. Arbuscular mycorrhizal fungi: key to successful grassland restoration? (oral presentation) Conference of the Society for Ecological Restoration (SER) 3.–8.08.2014 in Oulu, Finland.

Neuenkamp L, Gerz M, Moora M, Öpik M, Männistö M, Davison J, Vasar M, Jairus T, Zobel M. Arbuscular mycorrhizal fungi: key to successful grassland restoration? (Poster presentation) 33rd New Phytologist Symposium "Networks of Power and Influence: ecology and evolution of symbioses between plants and mycorrhizal fungi" 14.–16.05.2014 in Zürich, Switzerland.

Neuenkamp L, Metsoja JA, Zobel M, Hölzel N. The impact of management on biodiversity-productivity relations in Estonian floodplain meadows (oral presentation). Conference of the Society for Ecological Restoration (SER) 9.–14.09.2012 in Ceske Budejovice, Czech Republic.

Kopka, A., Greiwe A, **Neuenkamp L**, Schulte A. 2009.Entwicklung eines Standards für Geodaten für das webbasierte Kompensationsflächenmanagement. Angewandte Geoinformatik 2010 – Beiträge zum 22. AGIT-Symposium Salzburg. Herausgeber: Strobl J, Blaschke T, Griesebner G: 113–118.

Scholarships and Awards:

Award for best BSc study results among the Natural Sciences at the University of Münster, Germany (2009); price was a scholarship for the MSc degree studies in Landscape Ecology at the University of Münster, Germany.

Prize for the third best poster presentation at the the 33rd New Phytologist Symposium 14.–16. 5. 2014 in Zürich, Switzerland. Title of the poster: „Arbuscular mycorrhizal fungi: key to successful grassland restoration?".

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Prize for the second best oral presentation at the doctoral student conference of the Institue of Botany (University Tartu), 17.–18. November 2016 in Kubja, Estonia. Title of the presentation: "Can Plant traits Explain the plant-AM fungal relationship?".

Courses attended:

2013 Participation in the SER summer school on Mediterranean Ecosystem Restoration 13.–18.05.2013 held by the University of Avignon, France (organizer: Elise Buisson).

2016 Participation in the statistics course "Species traits: a functional approach to biodiversity, from organisms to ecosystems (6th edition)" held 29.05–03.06.2016 at the University of South Bohemia, Ceske Budejovice, Czech

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Neuenkamp L, Moora M, Öpik M, Davison J, Gerz M, Männistö M, Jairus T, Vasar M, Zobel M. 2018. The role of plant mycorrhizal type and status in modulating the relationship between plant and arbuscular mycorrhizal fungal communities. New Phytologist (ilmumas).

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Neuenkamp L, Kopka A, Herzig B. 2009. Farbstandards für Kompensationsflächenpools. Natur in NRW 4/09.

Käsikirjad:

Neuenkamp L, Prober SM, Price JN, Zobel M, Standish RJ. 2018. Benefits of mycorrhizal inoculation to ecological restoration depend on plant functional type, restoration context and time. Fungal Ecology

Garcia de Leon D, **Neuenkamp L**, Moora M, Öpik M, Davison J, Pena-Veneqas CP, Vasar M, Jairus T, Zobel M. 2018. Arbuscular mycorrhizal

fungal communities in tropical rainforest are resilient to slash and burn agriculture. Journal of Tropical Ecology.

Neuenkamp L, Moora M, Lind E, Gerz M, Zobel M. 2018. Composition of AM fungal communities determines the outcome of interspecific plant competition.

Populaarteaduslik artiklid:

Tamme R, **Neuenkamp L**. 2017. Taimede dieedil hoidmiseks kulub igal aastal 500 kilogrammi suhkrut. Novaator (20.7.2017): http://novaator.err.ee/608404/taimede-dieedil-hoidmiseks-kulub-igal-aastal-500-kilogrammi-suhkrut.

Konverentsiettekanded:

Neuenkamp L, Price JN, Prober SM, Moora M, Öpik M, Männistö M, Davison J, Zobel M., Standish RJ. Mycorrhizal fungi – tiny organisms that can shape ecosystems. Tartu ülikooli botaanika ja zooloogia osakonna doktorantide konverents, 12.–13.01.2018, Mooste, Eesti. (suuline ettekanne)

Neuenkamp L, Price JN, Prober SM, Moora M, Öpik M, Männistö M, Davison J, Zobel M., Standish RJ. They matter! Mycorrhizal fungi in ecosystem restoration. Mükoriisa 9. rahvusvaheline konverents (ICOM), 01.–05.08.2017, Praha, Tšehhi. (suuline ettekanne).

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(IAVS) aastakonverents, 01–05.09.2014, Perth, Austraalia. (suuline ettekanne)

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Teaduspreemiad ja stipendiumid:

2009 Magistriõppestipendium maastikuökoloogia erialal, Münsteri ülikool, Saksamaa. Stipendium oli auhinnaks maastikuökoloogia bakalaureusõppe parimate tulemuste eest

2014 Poste ettekannete konkurss, 33. New Phytologist sümpoosion, 14.–16. 5. 2014, Zürich, Šveits. Kolmas koht.

2014 Suuliste ettekannete konkurss, Tartu ülikooli botaanika osakonna doktorantide konverents, 13.–14.11.2014, Jäneda, Eesti. Esimene koht.

2016 Suuliste ettekannete konkurss, Tartu ülikooli botaanika osakonna doktorantide konverents, 17.–18.11.2016, Kubja, Eesti. Teine koht.

Kursused ja suveülikoolid:

2013 Suveülikool „Vahemere ökosüsteemide taastamine.", 13.–18.05.2013, Avignon, Prantsusmaa. Korraldaja: Elise Buisson (Avignoni Ülikool), Taastamisökoloogia Selts (SER).

2016 Kursus "Species traits: a functional approach to biodiversity, from organisms to ecosystems (6th edition).", 29.05–03.06.2016, Ceske Budejovice, Tšehhi. Korraldajad: Francesco de Bello (Lõuna-Boheemia Ülikool), Eric Garnier, Bill Shipley ja Alison Munson.

2016 Teaduskommunikatsiooni kursus "Teaduskommunikatsioon – MI1820", 01.09–31.10.2016, Tartu Maaülikool, Eesti. Korraldaja: Kristi Parro.

Muu teaduslik tegevus:

Retsenseerinud artikleid ajakirjades: Journal of Vegetation Science, Plant and Soil, FEMS, Plant Ecology & Diversity, Proceedings of the Royal Society B: Biological Sciences, Ecological Engineering, Basic and Applied Ecology, Environmental Microbiology, Nordic Journal of Botany, Plant Ecology, Fungal Ecology

Teadusprojekti "Urban grassland management: a questionnaire study across Europe" kaasjuhtimine (koos V. Klausi, J. Lampineni ja M. Tuomiga); alates 06.2016

Liige teadusühingutes: Floristisch-soziologische Arbeitsgemeinschaft e.V. (Flor-Soz) (alates 2011); British Ecological Society (BES) (alates 2015); Pärandkoosluste Kaitse Ühing (PKÜ) (alates 2016)

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