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BIOLOGICAE
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ELISABETH PRANGEL

# The impacts of land-use change and ecological restoration on biodiversity and ecosystem service supply in semi-natural grasslands

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# The impacts of land-use change and ecological restoration on biodiversity and ecosystem service supply in semi-natural grasslands

UNIVERSITY OF TARTU
Press

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

Dissertation was accepted for the commencement of the degree of *Doctor philosophiae* in Botany and Mycology at the University of Tartu on the 28th of August 2025 by the Scientific Council of the Institute of Ecology and Earth Sciences, University of Tartu.

Supervisor: Prof. Aveliina Helm, University of Tartu, Estonia

Opponent: Dr. Alistair G. Auffret, Swedish University of Agricultural Sciences, Sweden

Commencement: Oecologicum (J. Liivi 2, Tartu), room 127, on the 29th of October 2025 at 9.15 a.m.

Publication of this thesis is granted by the Institute of Ecology and Earth Sciences, University of Tartu.

ISSN 1024-6479 (print)
ISBN 978-9908-57-021-1 (print)
ISSN 2806-2140 (pdf)
ISBN 978-9908-57-022-8 (pdf)

University of Tartu Press
www.tyk.ee

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# LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following publications, which are referred to in the text by Roman numerals:

I. **Prangel, E**., Kasari-Toussaint, L., Neuenkamp, L., Noreika, N., Karise, R., Marja, R., ... & Helm, A. (2023). Afforestation and abandonment of semi-natural grasslands lead to biodiversity loss and a decline in ecosystem services and functions. *Journal of Applied Ecology*, 60(5), 825–836.

II. **Prangel, E.**, Reitalu, T., Kasari-Toussaint, L., Ingerpuu, N., Jüriado, … & Helm, A. (2025). Grassland restoration drives strong multitrophic biodiversity recovery, but climate extremes jeopardize drought-sensitive species. *Global Change Biology*. *31*(9), e70496.

III. **Prangel, E**., Reitalu, T., Neuenkamp, L., Kasari-Toussaint, L., Karise, R., Tiitsaar, A., ... & Helm, A. (2024). Restoration of semi-natural grasslands boosts biodiversity and re-creates hotspots for ecosystem services. *Agriculture, Ecosystems & Environment*, *374*, 109139.

IV. Lindborg, R., Hartel, T., Helm, A., **Prangel, E.**, Reitalu, T., & Ripoll-Bosch, R. (2023). Ecosystem services provided by semi-natural and intensified grasslands: Synergies, trade-offs and linkages to plant traits and functional richness. *Applied Vegetation Science*, 26(2), e12729.

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**Author's contribution** ('*' denotes a moderate contribution, '**' denotes a high contribution, '***' denotes a leading role).

| | I | II | III | IV |
|---|---|---|---|---|
| Original idea | ** | ** | ** | |
| Study design | * | ** | ** | * |
| Data collection | ** | ** | ** | * |
| Analysis and interpretation | *** | *** | *** | * |
| Manuscript writing | *** | *** | *** | ** |

# 1. INTRODUCTION

## 1.1. Ecosystem services, biodiversity, and ecosystem multifunctionality

Ecosystem services are essential goods and benefits that people can derive from nature, and the supply of these services largely depends on biodiversity (MEA 2005; IPBES 2019). Biodiversity serves as a cornerstone for sustainable and resilient ecosystem functioning. Ecosystem resilience is the capacity of an ecosystem to maintain its structure and processes over time, also in the case of environmental perturbations (Le Provost *et al.* 2023). However, we are currently experiencing an unprecedented rate of species loss and a global biodiversity crisis characterised by widespread declines in species populations and accelerated extinction rates (Barnosky *et al.* 2011). Biodiversity encompasses multiple indicators such as species richness, functional diversity, species community composition patterns, genetic and phylogenetic diversity, etc. A decline in any of these can significantly impair the supply of ecosystem services (Cadotte *et al.* 2011). As humans depend on nature and its services, restoring biodiversity and systematically monitoring the integrity of ecosystem functions and services are relevant for safeguarding human well-being and sustaining the ability of an ecosystem to withstand and recover from disturbances.

In order to better orient and quantify the vast selection of different ecosystem goods and services, there have been several efforts to classify them (MEA 2005; TEEB 2010; CICES 2013; IPBES 2019; Dasgupta 2021). One of the first groundbreaking reports in this field was the Millennium Ecosystem Assessment (MEA), released in 2005, that grouped ecosystem services into four larger categories: provisioning services (food, forage, freshwater storage, wood etc.); regulating services (carbon storage, erosion control, pollination etc.); cultural services (recreation in nature, education, cultural heritage etc.); and supporting services (nutrient cycling, habitat maintenance, soil formation etc). Later refinements merged supporting and regulating services together into one group (MEA 2005). A similar large grouping of ecosystem services was also developed by the CICES (Common International Classification of Ecosystem Services) framework (2013) – provisioning services, regulating and maintenance services, and cultural services. This is also the categorisation used in the current thesis. One of the latest global assessments on the status and trends of biodiversity and ecosystem services was released by IPBES, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, in 2019. IPBES is committed to strengthening the role of science in public decision-making on biodiversity and ecosystem services (IPBES 2019). The IPBES global report concluded that the challenges and aims raised by MEA in 2005 have not been met, and the majority of the world's ecosystem services (or nature's contributions to people, as suggested by IPBES) are still overexploited and deteriorating worldwide. IPBES assessment emphasised that in order to sustain a stable flow of ecosystem services, we need multifunctional landscapes with healthy ecosystems. Unfortunately, intensive human activities have negatively influenced a large proportion of the whole Earth's surface, with ~40% of land used in agriculture alone (World Bank 2022). Only ~25% of the Earth's land surface has remained without substantial negative impacts from human activity (IPBES 2019). According to the IPBES Land Degradation and Restoration report (2018), every year, roughly 0.08 % of land is made unsuitable for many species and destabilised for years, requiring extensive restoration efforts. For instance, about 21 million hectares of land are covered by industrial-scale palm oil monocultures (Descals *et al.* 2021), and a study by Fitzherbert *et al.* (2008) found that a mere 15% of primary forest species across multiple taxa occurred in such oil palm plantations after the conversion of the tropical forest area into the plantation (Dislich *et al.* 2017).

Large-scale monocultural and intensively managed ecosystems have lowered ecosystem multifunctionality (Schils *et al.* 2022), which refers to the capacity of the ecosystem to simultaneously sustain and supply multiple ecosystem functions and services (Manning *et al.* 2018), avoiding significant trade-offs between services. Trade-offs between ecosystem services emerge when the increase in provisioning of one or a few services is promoted at the expense of other services, driven by management choices, policy instruments, or natural environmental changes (Martinez-Harms *et al.* 2025). For instance, aiming to maximise provisioning services like production in crop fields (Foley *et al.* 2005) or production forests/plantations (Duncker *et al.* 2012; Dislich *et al.* 2017) often comes at the expense of many regulating or cultural services.

Higher species richness enhances the ecosystem's ability to provide multiple ecosystem services simultaneously in a similarly high capacity (Lefcheck *et al.* 2015). Biodiversity promotes resilience, i.e., the ecosystem's capacity to rebound, by acting as a "portfolio effect", where a diverse array of species compensates for losses caused by environmental disturbances. The more species are present, the greater is the likelihood that some can take over certain functions after other species or populations go locally (or even globally) extinct (Soliveres *et al.* 2016). A higher number of species leads to higher functional diversity as different species support ecosystem functions under varying conditions or annual differences. While species may appear functionally or taxonomically redundant, a diverse range of species is essential to sustain multiple ecosystem functions across different timeframes (de Bello *et al.* 2021).

## 1.2. Grassland ecosystems in Europe

Global grasslands cover approximately 40% of the Earth's land surface and constitute about 65% of global agricultural land (Dengler *et al.* 2020). These ecosystems serve as crucial habitats for many native species and provide an essential human food source and income. Within European agricultural systems, grasslands can be broadly categorised into two main types: semi-natural and agriculturally improved/intensified grasslands (Bengtsson *et al.* 2019; Schils *et al.* 2022). While about 17% of the land area within the European Union is grassland (Eurostat, 2025a), the intensified agricultural grasslands constitute the majority of the total grassland area, with about 13% (Eurostat, 2025b).

Semi-natural grasslands are characterised by high biodiversity and long continuity of low-intensity management, such as mowing or livestock grazing without significant fertiliser and chemical pest control input or ploughing (Dengler *et al.* 2014). These grasslands are among the most biodiverse ecosystems in Europe (Wilson *et al.* 2012), due to centuries of traditional agricultural practices suppressing interspecific competition and creating a rich structural diversity (Pärtel *et al.* 2005). The historical management style favoured high habitat connectivity and seed dispersal among grassland patches. For instance, in pasturelands, livestock was regularly moved from one pasture to another, and the grazing species alternated (cattle, horses, sheep, etc). Moving the livestock around helped zoochorous species to spread more easily within the landscape matrix, replenishing and exchanging the species constantly (Auffret 2011). Sheep, for example, have a high capacity to spread seeds through epizoochorous dispersal (Wit & Schwabe 2010; Benthien *et al.* 2016), but also within the digestive tract, like cattle and horses (Cosyns *et al.* 2005). At the same time, constant low-intensity disturbance by grazing animals suppresses the more competitive and fast-growing plant species, enabling smaller or slow-growing species to establish and reproduce due to better light conditions (Hautier *et al.* 2009). Also, constant removal of biomass by moderate grazing or hay making keeps the soil fertility moderate to low (dependent on grassland type), which, in addition, prevents biodiversity loss through competitive exclusion (higher nutrient content in soil, higher biomass production) and allows species specialised to more nutrient-poor conditions to compete with more fast-growing species (Bakker & Berendse 1999). Eutrophication of grasslands causes loss of plant species diversity (Hautier *et al.* 2009), which in turn can affect the diversity patterns of other organism groups, like different arthropods (Haddad *et al.* 2009), or also underground biodiversity like AM fungal richness (Hiiesalu *et al.* 2014).

Across Europe, there are many types of semi-natural grasslands, both pastures and meadows, from open grasslands to wooded meadows in varied environmental conditions. These ecosystems occur in a wide range of biogeographic regions, from Mediterranean dry and Central European mesic grasslands to wet or coastal grasslands and boreal and subalpine grasslands (Dengler *et al.* 2014). Different calcareous and mesic grasslands are particularly noted for high small-scale biodiversity, often supporting more than 40 vascular plant species per square metre (Wilson et al. 2012). Notably rare calcareous grasslands are alvars, mainly located in Estonia (Pärtel *et al.* 1999) and Sweden (Rosén 1982), with small fragments also found in Åland (Finland) and in the St. Petersburg district of Russia (Znamenskiy *et al.* 2006). These shallow-soiled ecosystems support a distinctive flora, including many rare and endemic species adapted to drought and nutrient-poor conditions (Zobel & Kont 1992). Many of the typical alvar grassland species have their main distribution in the south-eastern European steppe or arctic-alpine region, creating a varied assemblage of species (Van Der Maarel 1988).

In contrast, intensified grasslands generally have lower biodiversity due to the sowing of high-productivity grass species, application of fertilisers and/or agrochemicals, combined with occasional ploughing, increased grazing pressure, or frequent mowing (Schils *et al.* 2022). These grasslands are often dominated by a few competitive species, such as *Lolium perenne*, *Festuca arundinacea*, and *Dactylis glomerata*, and can also be supplemented by legumes like *Trifolium pratense or T. repens* to boost productivity (Louault *et al.* 2005; Power *et al.* 2012; French 2017). Intensified grassland systems can be further subdivided into permanent grasslands and temporary grasslands. Permanent grasslands are defined by the EU Commission as land used for growing grasses and other herbaceous forage naturally (self-seeded) or through cultivation and sowing, and the land has not been part of a crop rotation for at least 5 years (EU Commission Regulation 2004). Permanent grasslands across Europe vary, which is driven by local environmental factors and soil conditions, but also by the intensity of management (Schils *et al.* 2022). Temporary grassland is an agricultural land where forage is grown temporarily for less than 5 years. These grasslands are included in a crop rotation or frequently renovated by resowing (Søegaard *et al.* 2007). Although these different intensive grasslands are highly productive, they provide fewer regulating and cultural ecosystem services and generally support lower biodiversity compared to semi-natural grasslands (Bardgett *et al.* 2021).

## 1.3. The relationship between grasslands, ecosystem services, and biodiversity

In addition to supporting biodiversity, semi-natural grasslands provide multiple ecosystem services, such as forage production, wild food and herbs, medicinal plants, habitat maintenance, carbon sequestration and storage, nutrient cycling, pollination, natural pest control, recreational benefits, etc. (Bengtsson *et al.* 2019). Higher trade-offs between services emerge in intensified grasslands, where provisioning services are often promoted at the expense of other service categories. Schils *et al.* (2022) reported consistent trade-offs between the supply of feed (fodder for livestock) and non-feed (e.g. regulating services) ecosystem services, with higher fodder yield provided by intensified grasslands with higher nutrient input. Even though intensified grasslands express a lower capacity to provide multiple services simultaneously, they are important ecosystems in agricultural landscapes (Allan *et al.* 2015). In addition to providing animal feed, intensified grasslands can still support erosion control, pollination service, natural pest control, and provide a limited habitat for agricultural biodiversity (Aguilera Nuñez *et al.* 2024). Connecting these more temporary habitats to permanent habitats like semi-natural grasslands through green elements in the agricultural landscapes can improve landscape connectivity and dispersal of individuals, maintaining steady populations and providing services to croplands (Grass *et al.* 2019). Also, increasing the biodiversity in agriculturally improved grasslands could support a higher supply of regulating ecosystem services without significantly compromising the productivity of provisioning services (Liu *et al.* 2025). For instance, higher diversity and abundance of natural pest predator communities could consequently lead to lowered need for chemical input and improved biological pest control and pollination services. With effective biological pest control, farmers could cut down on pesticide use, lowering the costs and negative impacts on agricultural biodiversity and the environment (Janssen & van Rijn 2021; Boldorini *et al.* 2024). According to Schils *et al.* (2022), land-use change and intensification of management decrease grassland ecosystem multifunctionality, and some prominent gaps in grassland research and knowledge are connected to the lack of comparisons between permanent and temporary grasslands, which the following research is also trying to fill. It is essential to combine a multitrophic and trait-based diversity approaches to monitor species dynamics, ecosystem functioning, and ecosystem service supply in different grassland conditions and management intensities.

## 1.4. Land-use change and its impacts on grasslands

While only a century ago, the European livestock grazing predominantly occurred at moderate intensity and on semi-natural grasslands (Hartel *et al.* 2018), current grazing and fodder production have largely shifted to croplands and intensively managed grasslands (Bullock *et al.* 2011; Herzon *et al.* 2022). Consequently, semi-natural grasslands now remain as isolated remnants across European landscapes (Aune *et al.* 2018). The traditional agricultural practices that once fostered species-rich communities are now being disrupted by land-use change, agricultural intensification, land abandonment, and afforestation (Elliott *et al.* 2024). The consequences of this shift are stark. For instance, in Estonia, roughly 95% of historical semi-natural grasslands have disappeared, leaving an insufficient area to support the long-term viability of species dependent on these habitats (Helm & Toussaint 2020). Multiple studies have found that such a rapid decline in habitat area has triggered a phenomenon called "extinction debt" (Helm *et al.* 2006; Kuussaari *et al.* 2009; Spalding & Hull 2021; Silvetti *et al.* 2025) where species continue to survive in the degraded habitat, but will inevitably go extinct if the conditions fail to improve and the drivers of change are not dealt with. Extinction debt serves as an early warning sign, providing a window of opportunity to restore degraded ecosystems and avoid "paying the ecological debt" (Kuussaari *et al.* 2009). For example, Estonian calcareous grasslands still exhibit high extinction debt (Helm *et al.* 2006), while calcareous grasslands studied in Belgium showed that the debt had already been paid, and the majority of the species from the habitat had been lost (Adriaens *et al.* 2006). Restoration of such communities proves to be more complicated and costly (Kuussaari *et al.* 2009).

Habitat fragmentation exacerbates this issue by reducing grasslands' capacity to sustain ecosystem services and increasing their vulnerability to ecological disturbances and climate fluctuations. Climate change adds further pressures, the frequency and intensity of droughts and other climate extremes are expected to increase under current global trends. These changes pose growing challenges to already stressed and impoverished populations and ecosystems (Tölgyesi *et al.* 2024). However, maintaining high species richness in grasslands may help buffer the impacts of prolonged drought and mitigate the negative effects on ecosystem services (Dullau *et al.* 2023). To address these challenges, large-scale restoration efforts are essential, since protected areas of remaining habitats alone cannot secure biodiversity and sustainable ecosystem functioning (Zeng *et al.* 2023). Effective restoration must reconnect fragmented habitats, enhance ecosystem resilience, and counteract biodiversity loss. This requires both meticulous planning and long-term impact monitoring that encompass broader ecosystem dynamics, climate change impacts, and biodiversity patterns across different organism groups.

However, despite growing recognition of the importance of semi-natural grasslands for biodiversity conservation and the provision of ecosystem services (Bengtsson *et al.* 2019), significant knowledge gaps remain regarding the combined effects of land-use change and restoration on multiple taxa and the multifunctionality of these ecosystems. While multiple studies have documented declines in individual species groups or single ecosystem services following abandonment, afforestation, or intensification (Hungate *et al.* 2017; Sexton & Emery 2020; Imran *et al.* 2021; Huber *et al.* 2022), far fewer have addressed how these drivers simultaneously affect biodiversity across multiple trophic levels (Soliveres *et al.* 2016), or how such changes cascade to influence the capacity of grasslands to deliver a balanced and resilient portfolio of ecosystem services. Equally, the potential of restoration to recover both biodiversity and ecosystem multifunctionality, particularly under accelerating climate change, remains insufficiently understood, with little evidence on the potentially differing recovery trajectories of different organism groups.

Given the increasing policy focus on restoring degraded habitats, exemplified by the EU Nature Restoration Regulation and national biodiversity strategies, addressing these knowledge gaps is vital for developing restoration actions that are both effective and measurable. By combining multi-taxon biodiversity data, functional trait analyses, and ecosystem service indicators, my thesis explores how land-use change and restoration affect biodiversity, ecosystem service supply, and ecosystem multifunctionality in calcareous semi-natural grasslands called alvars. Additionally, by addressing and comparing trade-offs, synergies, and recovery pathways in both intensified and semi-natural grasslands, the findings offer a deeper scientific understanding of grassland dynamics and help to provide guidance for developing management and restoration strategies.

## 1.5. Aims of the thesis

The overarching objective of this thesis is to assess how land-use changes and ecological restoration influence the biodiversity and supply of ecosystem services in grassland ecosystems.

The specific aims of the thesis were to investigate:

1) *The impacts of land use change*. How do abandonment and afforestation of historical semi-natural alvar grasslands impact biodiversity, ecosystem service supply, and ecosystem multifunctionality (Paper **I**)?
2) *The impact of intensification through comparison of grassland types*. How do semi-natural and intensified grasslands differ in their taxonomic and functional biodiversity, and in their capacity to supply ecosystem services (Paper **IV**)?
3) *Biodiversity recovery after restoration*. How is grassland biodiversity recovering following the restoration efforts of abandoned and afforested semi-natural alvar grasslands (Paper **II**)?
4) *Effectiveness and limitations of restoration on ecosystem service supply*. Does alvar grassland restoration lead to improved supply of ecosystem services and increased ecosystem multifunctionality? Are there any constraining factors to grassland recovery (Paper **III**)?
5) *Ecosystem multifunctionality and biodiversity links*. Is there a relationship between ecosystem multifunctionality and multitrophic species richness (Paper **I, III**)?

# 2. METHODS

For papers **I–III**, I used the data collected during the LIFE+ program grassland restoration project "LIFE to Alvars" (LIFE13 NAT/EE/000082). For **paper IV**, I used a literature review, online trait databases, and available unpublished previous research data. The **paper I** focused on the pre-restoration species richness and ecosystem service supply of the Estonian semi-natural calcareous grasslands (alvars) in their different degradation phases (open grassland, overgrown grassland, afforested grassland). The main aim of the paper was to investigate how changes in land-use, like grassland afforestation and land abandonment, have affected local biodiversity, ecosystem services, and how the two are connected to one another (ecosystem multifunctionality and biodiversity relationship). The focus of **papers II** and **III** was on how large-scale restoration efforts have impacted local species richness and community composition patterns in Estonian alvar grasslands (**II**), ecosystem service supply, ecosystem multifunctionality, and the association between multitrophic species richness and ecosystem multifunctionality (**III**). **Paper IV** investigated the impact of grassland intensification on ecosystem services by comparing the differences in ecosystem service supply between a variety of semi-natural and intensified grasslands. This paper also examined the extent to which the service supply of these two broad grassland types depends on their plant species richness, composition, and functional traits.

## 2.1. Field data collection

### Study system

Estonian alvar grasslands were chosen as the model study system for papers **I–III**, since they have gone through significant degradation over the past century due to the abandonment and afforestation of less productive agricultural land unsuitable for intensification. Alvar grasslands (alvars) are semi-natural calcareous grasslands primarily found on Ordovician and Silurian limestone bedrock in northern Europe, particularly in Sweden and Estonia. Alvars, classified as a priority habitat under the European Union's Habitats Directive (6280* Nordic alvar and Precambrian calcareous flatrocks), are characterised by shallow soils (typically less than 20 cm deep) with a relatively high pH (~7). The soil type is predominantly rendzic leptosol, on monolithic limestone or limestone shingle bedrock, consisting only of a thin litter and humus layer. These shallow soils often dry out completely during the summer, while the poor drainage capacity of monolithic limestone bedrock leads to flooding in autumn and spring. The surface is also susceptible to cold damage during winter due to soil movements (Rosén 1982). The specific structure and composition of these grasslands give rise to three main vegetation types: (1) the temporarily wet *Molinetum/Sesleria* type, (2) the dry *Avenetum* type with a thicker soil layer, and (3) the arid *Festucetum* type with thin soil cover and patches of exposed bedrock (Pärtel *et al.* 1999).

### Restoration project

LIFE+ Nature grassland restoration project "LIFE to alvars" started in 2014, aiming to restore 2500 ha of degraded alvar grasslands to recover local biodiversity, ecosystem functioning, and boost the livelihood of rural areas. The degradation of alvar grasslands can mainly be attributed to land abandonment, leading to encroachment of shrubs (mostly *Juniperus communis* and *Corylus avellana*) and trees, and to afforestation with Scots pine (*Pinus sylvestris*) in the 1960s and 1970s. Restoration was carried out between 2015 and 2019. Restoration actions entailed shrub cutting, tree felling, and stump milling. The aim of the restoration was to recover semi-open grasslands with a maximum shrub cover of 30–40%, occasionally 50%, depending on local conditions and landowner preferences. Only single scattered trees were permitted. All cut woody material was burned on site or removed. Traditional low-intensity grazing regime by cattle, sheep, horses, or mixed grazing was reinstated, and grasslands were left to regenerate naturally.

## Monitoring design and site selection

An extensive monitoring scheme was set up to follow the ecological consequences of land abandonment, subsequent shrub encroachment, afforestation, and restoration of semi-natural grasslands (**I–III**). Data on biodiversity, soil, and environmental conditions were collected both **before** (2014–2016) and **after** (2019) restoration.

In total, 35 study sites were selected across western Estonia. These included **28 restoration sites**, where active restoration was implemented, and **7 non-restored comparison sites**, where no interventions took place (Fig. 1).

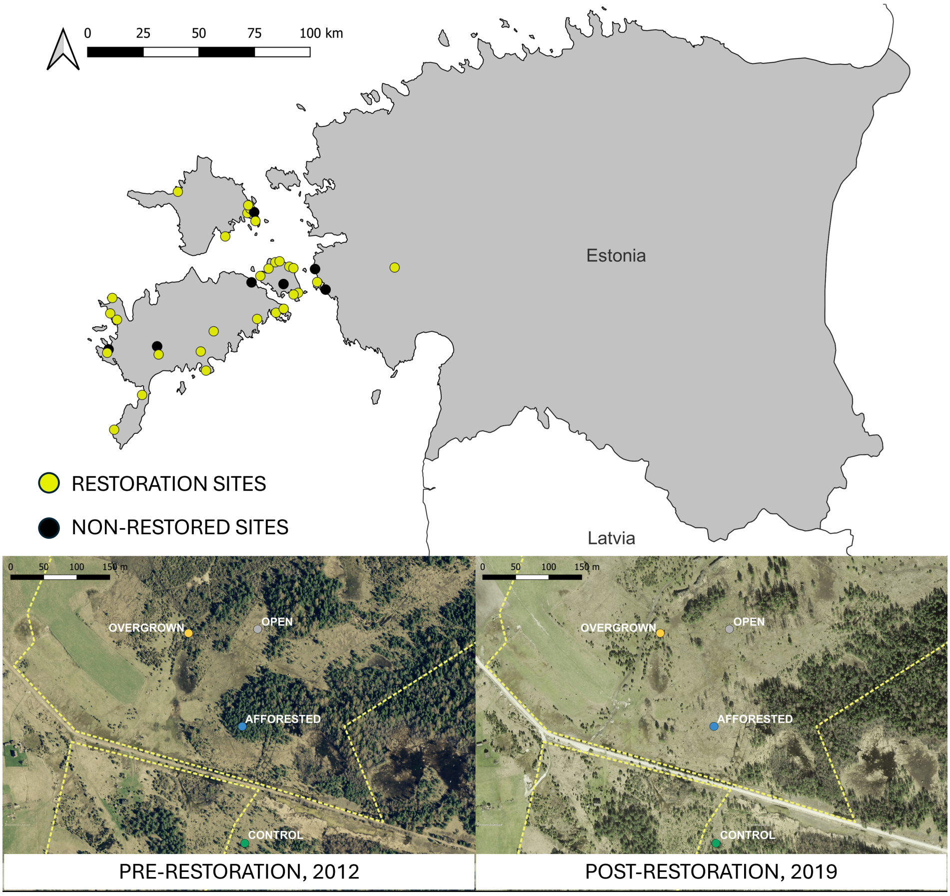

**Fig. 1.** Study areas. Top: locations of restoration and non-restored comparison sites in western Estonia. Bottom: subsite layout in the Paope restoration site before and after restoration (Geoportal, Estonian Land and Spatial Development Board). Yellow dashed polygons indicate the boundaries of *LIFE to Alvars* restoration project.

At each of the 35 study sites, three **subsites**, representing distinct stages of grassland degradation, i.e., condition classes, were identified (**Fig. 2**):

**a) Open grassland**. Alvar grasslands in the early stages of degradation: still open and relatively well-preserved, with a short herb layer and moderate shrub cover (up to 60%, primarily *Juniperus communis*), but no longer actively managed.

**b) Overgrown grassland**. Areas where former open alvars have become densely overgrown with shrubs (mainly *J. communis*) due to abandonment over the past 50–70 years, typically exceeding 60% cover.

**c) Afforested grassland**. Alvar grasslands that were planted with *Pinus sylvestris* in the 1960s–1970s, now with tree cover of at least 50%.

In the 28 restoration sites, an additional fourth subsite was included: an open **control grassland**. This additional subsite was located near the restoration site but not subject to any restoration intervention (Fig. 1). These subsites were selected to provide a nearby comparison to restored areas, offering insight into how relatively well-preserved open alvars might develop over time in the same region without restoration. They complement the information from non-restored comparison regions and serve as local non-intervention control areas. In cases where restoration sites were in close proximity, a single control subsite was shared between them.

**Fig. 2.** Example of studied grassland condition classes (subsites): open, overgrown, afforested, and control grassland.

## Biodiversity assessment before and after restoration

In each subsite, monitoring of the different taxa was carried out in close proximity to a fixed and permanently marked 1 × 1 m quadrat. The exact monitoring methods varied, depending on the specific characteristics of each organism group (Table 1). More detailed descriptions of the monitoring methods can be found in the Supplementary Information of Paper **II**.

**Table 1.** Overview of the organism groups monitored in Estonian alvar grasslands before and after restoration, with a brief summary of the monitoring methodology and used indices. Data were used in the formulation of papers **I–III**.

| Taxa | Monitoring method | Monitored indices |
|---|---|---|
| Vascular plants | Permanently marked 1 × 1 m quadrat within a 10 m radius plot | Species richness within the 10 m radius plot<br>Total and individual plant species cover % within the 1 × 1 m quadrat |
| | Plant biomass gathered from a 20 × 20 cm subplot next to a 1 × 1 m quadrat | Dry plant biomass (g/m$^2$) |
| Bryophytes & Ground lichens | Same 1 × 1 m quadrat and 10 m radius plot as for vascular plants | Species richness within the 10 m radius plot<br>Total and individual bryophyte species cover % within a 1 × 1 m quadrat |
| Epiphytic lichens | Three junipers selected within the 10 m radius plot. Where possible, the same junipers were sampled before and after restoration | Species richness on the selected junipers |
| Bumblebees | Transect walk method (Pollard 1977): individuals counted and identified on a 100 × 2 m transect near the 10 m radius plot for a maximum of 20 min (and no more than 5 minutes per flowering patch) | Abundance and species richness (identified on-site and in the lab) of bumblebees interacting with flowers |
| Butterflies | Transect walk method (Pollard 1977): individuals counted on a 250 m long transect near the 10 m radius plot during 5 min | Abundance and species richness of butterflies interacting with flowers |
| Birds | Point-count method (Bibby *et al.* 1992): 5-minute count of individuals within a 100-m radius area between 5 and 10 am. The exact location of the monitoring differed slightly from the sampling locations of other organism groups to avoid subsite overlap (birds needed larger distances between the sampling locations). | Abundance and species richness of breeding birds |
| Spiders and myriapods (millipedes, centipedes) | Pitfall trap method (Hohbein & Conway 2018): 10 traps (200 ml cups, 70 mm diameter), set for 10 days near the 10 m radius plot. | Abundance and species richness of spiders and myriapods |
| Arbuscular mycorrhizal (AM) fungi | 9 teaspoons of soil were collected from the corners of the 1 × 1 m plant quadrat | Community composition and species richness based on DNA sequences |

### Assessment of soil chemical and microbial parameters

Soil samples for determining soil organic matter content (SOM, %), pH (in KCl), and concentrations of Ca, K, Mg, and P (mg $kg^{-1}$) were collected from the topsoil layer (0–10 cm) at five randomly chosen spots within the 10 m radius plot at each subsite. Plant-available Ca, K, Mg, and P were measured following the Mehlich 3 method (Mehlich 1984). Soil organic matter content was estimated by using weight loss on ignition.

For AM fungal DNA analysis, nine teaspoons of soil were collected from the corners of the 1 × 1 m plant quadrat. DNA was extracted from 5 g of dried soil using a DNeasy® PowerMax® Soil DNA Isolation Kit (Qiagen). AM fungal sequences were amplified from soil DNA extracts using primers specific for AM fungi from the small-subunit (SSU) ribosomal RNA gene: WANDA (Dumbrell *et al.* 2011) and AML2 (Lee *et al.* 2008). Sequencing was performed on the Illumina MiSeq platform, using a 2 × 300 bp paired-end sequencing approach. All sequencing was carried out at Asper Biogene LLC (Tartu, Estonia). AM fungal sequences were matched against virtual taxa (phylogenetically defined operational taxonomic units) in the MaarjAM database (Öpik *et al.* 2010).

Soil samples for assessing bacterial activity were collected separately and sampled only before restoration. Bacterial activity was estimated based on soil microbial respiration rates (basal respiration, expressed as mg $O_2$ kg $C^{-1}$ $h^{-1}$). Oxygen consumption per gram of dry soil was calculated following the method of (Platen & Wirtz 1999). Microbial biomass carbon (MBC, mg C $g^{-1}$ dry soil) was estimated using Substrate Induced Respiration (SIR).

## 2.2. Selection of ecosystem services and their indicators

Nine ecosystem services were assessed in papers **I** and **III**: biodiversity as a service (**I**) or habitat maintenance (**III**), soil condition maintenance, soil carbon storage, pollination, pest regulation, wild food and medicinal herbs supply, forage production, wood production, and recreational and cultural heritage value (**I, III**). In paper **I**, the sum species richness of all monitored organism groups was assessed as a service ("Biodiversity"), but in paper **III**, a more specific service, "Habitat maintenance", was decided upon as a substitution. For habitat maintenance service, species richness and cover of grassland specialist plants and bryophyte species were used. In the current thesis, the supply potential of ecosystem services is evaluated rather than realised service production and consumption.

To assess the supply of these services in alvar grasslands before (**I**) and after restoration (**III**), a variety of indicator values were used as proxies (Table 2). These included environmental variables (e.g., soil properties), vegetation structure (e.g., canopy cover, biomass), diversity values (e.g., species richness), and plant functional traits (e.g., pollination syndrome). Indicator data were derived from the collected field measurements (Table 1), an online questionnaire (carried out via Google Forms), and plant functional traits (combined from different databases). Online survey materials and specific data sources for obtaining the indicator values can be found in the Supplementary information of the **I** and **III**.

**Table 2.** The ecosystem services monitored in the calcareous grasslands and the indicators used to quantify these services.

| | **SERVICES** | **Indicators for service quantification** |
|---|---|---|
| **REGULATING AND MAINTENANCE SERVICES** | Biodiversity (**I**) | – Summed species richness of vascular plants, bryophytes, lichens, bumblebees, butterflies, ground-dwelling spiders, carabids, millipedes, centipedes, and birds |
| | Habitat maintenance (**III**) | – Species richness (10m radius plot) and cover (1×1m plant quadrat) of alvar grassland specialist species (vascular plants and bryophytes) |
| | Soil condition maintenance | – Soil organic matter (SOM% from loss on ignition)<br>– Diversity of arbuscular mycorrhizal fungi (taxonomic units)<br>– Soil average depth (cm)<br>– Soil nutrient content (P, K, Mg, Ca mg kg$^{-1}$)<br>– Bacterial activity, 24h (mg $O_2$ kgC$^{-1}$ h$^{-1}$), Soil microbial biomass carbon (mgC g$^{-1}$) (indicator only used in paper **I**) |
| | Soil carbon storage | – Soil organic carbon (SOC %) = SOM%/1.9 (Pribyl 2010) |
| | Pollination | – Bumblebee and butterfly abundance<br>– Entomophilous plant cover (%) (1×1m plant quadrat)<br>– Pollinator rewards index = nectar amount (Kühn *et al.* 2004) × flowering time × entomophilous plant cover %<br>– Flower abundance (abundance on a scale 0–9 of flowering insect-pollinated plants) |
| | Pest regulation | – Ground-dwelling spider and centipede activity density (abundance × days pitfall traps in use/number of traps remained, not destroyed by wildlife or livestock) |
| **PROVISIONING SERVICES CULTURAL SERVICES** | Forage production (for animal feed) | – Forage quality index = palatability value (Kühn *et al.* 2004) × plant cover from 1×1m plant quadrat)<br>– Biomass quantity (g m$^{-3}$)<br>– Open area % available for grazing within the subsite in a 30m radius |
| | Wood production potential | – Wood production potential = Tree cover × average tree height (m) + shrub cover × average shrub height (m) of the trees in 20×20m quadrat |
| | Wild food and medicinal herbs | – Cover of local wild plants used for food, medicine, or traditional rituals (tea, oils, tinctures etc.) within the 1×1m plant quadrat |
| | Recreation and cultural heritage value | – Flower abundance within the subsite<br>– Cultural benefits evaluation survey carried out online |

--- Expressing the crossover between provisioning and cultural services categories by the wild food and herbs.

## 2.3. Literature review and databases

In paper **IV**, two methods were used to assess and compare the supply of ecosystem services in low-intensity semi-natural grasslands and agriculturally intensified grasslands. First, a non-quantitative review was conducted to analyse the synergies and trade-offs among ecosystem services in these two broad grassland types. A literature survey was carried out and complemented with additional literature known to the authors of paper **IV**. Based on the review, 12 key services were selected for comparison between the semi-natural and agriculturally intensified grasslands: biomass production for forage, supply of wild foods, habitat provision, insect pollination, biological control, carbon capture, carbon storage, erosion control, water quantity, water quality, tourism/recreation, and cultural heritage. The supply of each service was ranked based on the literature and expert opinions of the authors (**IV**) on a scale ranging from 0 to 1. To illustrate the ecosystem service supply and the potential synergies and trade-offs between the services, a flower chart diagram was used, where the petal lengths quantified the relative ecosystem service supply (Foley *et al.* 2005).

Secondly, a quantitative trait-based approach was applied, where plant functional traits were linked with ecosystem services to quantify the supply of services in these two grassland types (**IV**). For that, a literature search via Scopus and Google Scholar was conducted, identifying articles providing full vascular plant species lists with abundance values in either intensively managed or semi-natural grasslands. In addition to the published species lists, data available from previous unpublished research of the authors of paper **IV** were included. In total, 40 species lists were acquired, 16 originated from intensified and 24 from semi-natural grasslands. A selection of different grasslands within roughly similar environmental conditions was chosen, mostly including grasslands in northern and central Europe (See Supplementary information of **IV**). Since species abundance estimates varied between datasets (abundances, cover estimates, frequency of occurrence, etc.), data were scaled to a 0–1 range for comparability. Plant trait data were compiled from the TRY (Kattge *et al.* 2020), BiolFlor (Kühn *et al.* 2004), and GRoot (Guerrero-Ramírez *et al.* 2021) databases and from (Tyler *et al.* 2021).

Services associated with plant functional traits were the following:

- Forage production: average plant height (m), plant dry above-ground mass (g);
- Pollination: Insect pollination (1/0), pollinator reward, duration of flowering (months);
- Carbon storage: plant dry above-ground mass (g), root dry mass (g);
- Water retention: root mass density (g/cm), root branching density (branches per cm).

## 2.4. Data analysis

All statistical analyses were conducted using the R programming language (R Core Team 2024).

### Formulation of ecosystem services

To measure the potential supply of ecosystem services in alvar grasslands before (**I**) and after (**III**) restoration, different indicator values were used to describe a service (as mentioned above, see Table 2). Since the used indicators were with different units, all values were standardised (z-scores) prior to the analysis (**I**, **III**) using the *scale* function in R. This standardisation made the indicator values unitless and placed them on the same scale. When a service was represented by multiple indicators, the standardised indicator values were aggregated by calculating the mean, thereby obtaining a single relative score for that service per subsite. Calculating the standardised average of the multiple indicators minimised the potential correlations between different indicators describing one service. For example, scaled indicator values of pollinator abundance, insect-pollinated plant cover, flower abundance, and pollinator reward were averaged to quantify pollination service.

### Assessment of ecosystem service supply

The effects of overgrowing, afforestation (**I**), and restoration (**III**) on biodiversity, ecosystem services, and their indicator values were analysed using linear mixed effects models. For paper **I**, the *lmer* function from the *lme4* package (Bates *et al.* 2015), and for paper **III,** the *lme* function from the *nlme* package (Pinheiro *et al.* 2018) were used. The "Study site" was included as a random factor in all models. Species richness, ecosystem service values, or individual service indicators were used as response variables, and "Subsite" (Open, Overgrown, Afforested (**I**), Control) (**III**), restoration status (Before, After) (**III**), and their interaction (**III**) were included as explanatory variables. Differences between the subsites before restoration were analysed using a post-hoc test for *lmer* (Kuznetsova *et al.* 2017) for paper **I** and the differences within the subsite pairs in before-after comparisons (e.g. open subsite before vs after restoration) with post-hoc "*Estimated Marginal Means – emmeans*" by Lenth (2022) for paper **III**. In addition to comparing the differences in ecosystem service supply before and after the restoration, I also analysed the differences between the subsites after the restoration. For that, the same linear mixed effects modelling approach was used, with different ecosystem services as response variables, study site and time since restoration as random variables, and subsite (open, overgrown, afforested, control) as a fixed variable. Statistical differences between the subsites were tested with a post-hoc "Estimated Marginal Means – emmeans" test (Lenth 2022).

### Analysing the changes in taxonomic diversity

The total richness of all surveyed species groups – multitrophic species richness – including vascular plants, bryophytes, bumblebees, butterflies, spiders, myriapods, ground lichens, and AM fungi operational taxonomic units was calculated using two methods: standardised and raw richness. Birds and epiphytic lichens were excluded from the total richness because these groups were not surveyed in all subsites (**II**). In case of standardised multitrophic species richness, richness values of all species groups were divided by the maximum richness of the respective species group (Allan *et al.* 2014). This method gives more weight to the less abundant species groups (e.g., bumblebees, butterflies) compared to the more abundant species groups (vascular plants) for more balanced results. Raw multitrophic species richness was simply calculated as the sum of all detected taxa without any weight given to different species.

The change in species diversity (summed raw multitrophic species richness, standardised multitrophic species richness, and richness of individual organism groups) due to restoration (**II**) was tested using Generalized Linear Mixed Effects (GLME) models with Poisson error distribution using the package "*lme4*" (Bates et al., 2015). "Subsite" nested in "Study site" was used as a random factor, "Subsite" (Open, Overgrown, Afforested, Control), "Period" (Before restoration, After restoration), and their interaction were used as fixed explanatory variables. The contrast between the subsite pairs (e.g., Before Open vs After Open) was tested with Estimated Marginal Means (EMM) with the package "*emmeans*" (Lenth 2022). Separate GLME models and EMM tests were conducted for restoration sites and non-restored comparison sites, using the same model structure. In addition to the before-after contrast, the difference among subsites before and after restoration (e.g., After Open vs After Afforested) was tested using the EMM test (**II**). With the latter test, the assumption was that the subsites are significantly different from each other before restoration and that successful recovery of communities would lead to subsites being similar to each other in terms of ecological diversity.

To analyse the changes in community composition of the different organism groups in response to restoration (**II**), a Permutational multivariate analysis of variance (PERMANOVA) was performed using the package *vegan* (Oksanen *et al.* 2022). The contrast between the subsite pairs (e.g., Before Open vs After Open) was analysed using the package pairwiseAdonis (Martinez Arbizu 2020). To describe and visualise the change in multitrophic species community composition in before–and–after restoration comparison (**II**), a Nonmetric Multidimensional Scaling (NMDS) was used with the command *metaMDS()* for NMDS analyses from the package *vegan* (Oksanen *et al.* 2022). Bray-Curtis distance was used as a distance metric for NMDS. For vascular plants, bryophytes, and lichens, presence/absence data were used. For birds, butterflies, bumblebees, spiders, and myriapods, counts of individuals were used. For AM fungi, relative sequence abundance (% of taxon reads from the total number of sequences) was used. On the NMDS plots, group ellipses with a standard error and confidence value of

0.99 illustrated changes from before restoration to after restoration in community composition. In paper **IV**, taxonomic species richness and taxonomic Shannon diversity index (Oksanen *et al.* 2022) for both semi-natural and intensified grasslands were also calculated.

### Calculating functional diversity

Functional richness was used to analyse the difference in selected ecosystem services (forage production, carbon storage, pollination, and water retention) supply between the semi-natural and intensified grasslands (**IV**). To quantify the functional spaces for the semi-natural and intensified grassland species data, Functional richness and Rao quadratic entropy (Rao Q) were calculated. Functional richness was computed as the volume of the convex hull (defined as the smallest convex set enclosing the points) in the *n*-dimensional trait space occupied by the species (Cornwell *et al.* 2006) (**IV**).

Functional richness and Rao Q were calculated for all traits combined and with sets of traits reflecting different services (**IV**) with the help of the R package *fundiversity* (Grenié & Gruson 2022). Differences in functional richness and Rao Q values between the two grassland types were tested with a *t-test* using the Holm method for *p*-value adjustment (Holm 1979).

### Calculating ecosystem multifunctionality

The effect of overgrowing, afforestation (**I**), and restoration (**III**) on the ecosystem multifunctionality was assessed using linear mixed effects models (Bates *et al.* 2015; Pinheiro *et al.* 2018) with the study site included as a random effect (**I, III**). The model had a multifunctionality index as a response variable and the subsites (open, overgrown, afforested (**I**), control) (**III**), restoration status (before or after restoration), and their interaction as explanatory variables (**III**). To estimate the ecosystem multifunctionality, a "multiservice index" was calculated using two alternative methods (**I**) – the averaging approach (Maestre *et al.* 2012) (**I, III**) and the PCA-based multivariate approach (Meyer *et al.* 2018) (**I**). Both approaches were used for paper (**I**), and only the averaging approach was chosen for paper (**III**), since the results of the previous study paper (**I**) showed no significant differences between the approaches. The averaging approach uses the averaging of all the ecosystem service values per subsite to attain one index value per subsite. Since the averaging approach is more simplistic and robust, it was complemented with the PCA-based approach (**I**) that creates a PCA (Oksanen *et al.* 2022) for the multifunctional space and uses the PCA axis scores to calculate the multiservice index. The relationship between the multifunctionality and multitrophic species richness (raw sum) was examined using linear mixed effects models with study site included as a random effect and subsite added to take the impact of ecosystem condition into account (**I, III**).

# 3. RESULTS

## 3.1. The impacts of land-use change on grassland ecosystems

Semi-natural grasslands have high biodiversity and ecosystem multifunctionality, while grassland abandonment and afforestation on one end of the land-use change gradient and intensification on the other have significant negative effects on both (**I, IV**).

### Abandonment and afforestation

I compared three semi-natural alvar grassland condition classes – abandoned open, abandoned overgrown and afforested alvar grassland subsites – and found that open grasslands had, on average, 129 species across multiple taxa (sum of vascular plants, bryophytes, lichens, butterflies, bumblebees, spiders, carabids, myriapods, birds), while the richness decreased to 104 in overgrown grasslands and 82 in afforested grasslands (**I**). On average, the majority of the surveyed species groups had higher species richness in open subsites compared to the rest of the subsites ($p < 0.05$), except for myriapods and birds, which showed no significant difference between any of the subsites. Though in the case of the birds, there was a significant difference between all the subsites in their species composition. The alvar grassland vascular plant specialists were significantly higher in open grasslands compared to the rest of the subsites, generalist plant species richness did not differ between the open and overgrown grasslands. In case of spiders, there was no significant difference in species richness between open and afforested subsites, but there was a difference in the community composition (See **Table S2** & **S4** in Supplementary Information of **II**).

Afforested grasslands also showed more pronounced trade-offs emerging among ecosystem services compared to open and overgrown grasslands, with higher values of wood production dominating at the expense of other services (**Fig. 3. A**). Pollination, pest regulation, forage production, soil condition maintenance, wild food supply, and cultural appreciation of the landscape were all significantly lower in overgrown and/or afforested grasslands compared to open grassland subsites. In contrast, no significant difference was found in soil carbon storage capacity across the different condition classes (open, overgrown, afforested) (**I**).

There was a significant positive association between multitrophic species richness (i.e., total number of species across studied taxa) and ecosystem multifunctionality (multiservice index) across all grassland condition classes (**Fig. 3. B**), signifying that higher species richness facilitates higher ecosystem multifunctionality (**I**).

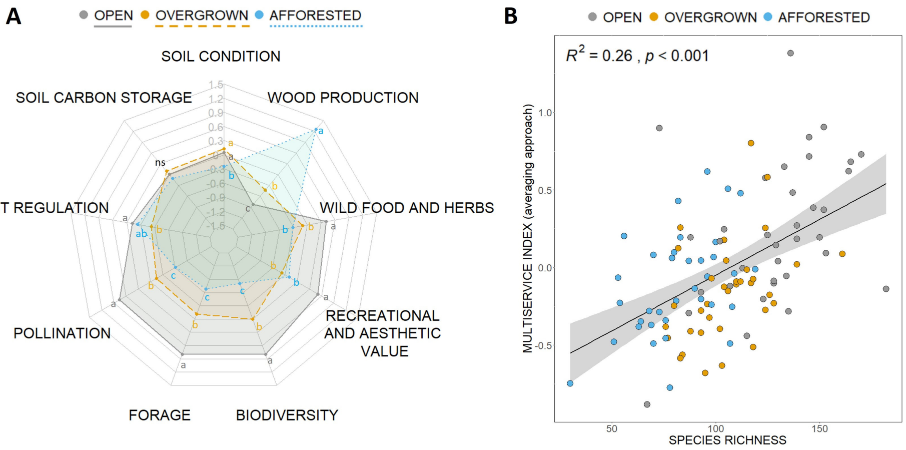

**Fig. 3. A:** A spider diagram showing the impact of abandonment and afforestation on ecosystem service supply across three alvar grassland condition classes (open, overgrown, afforested) (**I**). Each axis represents a relative score of an assessed ecosystem service, with negative values indicating lower and positive values indicating higher service supply. Different letters indicate statistically significant differences between condition classes; *ns* denotes non-significant differences. **B:** Relationship between multitrophic species richness and ecosystem multifunctionality across grassland condition classes (**I**).

## Intensification

To analyse the impact of grassland intensification on biodiversity and ecosystem service supply capacity, a selection of different semi-natural grassland and intensified grassland ecosystems in Europe were compared (average across different grassland types classified as semi-natural and intensified, see Supplementary information in **IV**). The results from the literature review showed significantly stronger service trade-offs in intensified grasslands – there was a noticeable trade-off between regulating and provisioning services in grassland ecosystems based on the management intensity (**I, IV**). Intensified grasslands have high biomass production (forage), while other ecosystem services are provided in lower capacity (**IV**). Semi-natural grasslands, on the other hand, have slightly lower forage production capacity but are good at providing habitat for biodiversity, pollination, and supporting cultural services (**I**, **IV**). Ecosystem multifunctionality in general was shown to be higher in semi-natural grasslands with low to moderate management intensity than in intensified grasslands (**IV**).

Compared to intensified grasslands, semi-natural grasslands not only had a significantly higher taxonomic diversity but also greater functional richness ($p < 0.05$) (**IV**). Functional divergence (Rao Q based on plant abundance) was also higher in semi-natural grasslands, but the differences were not statistically significant ($p \geq 0.05$) after p-value correction (**IV**). Functional richness underpinning the four assessed ecosystem services in Paper **IV** (forage, carbon storage, pollination, water retention) was significantly higher for all services ($p < 0.05$) in semi-natural than in intensified grasslands, expressing higher and likely also more stable service supply potential.

## 3.2. The impact of grassland restoration on multitrophic species richness

On average, multitrophic species richness (both standardised and raw sum) increased significantly in overgrown and afforested semi-natural alvar grasslands following restoration and reinstatement of low-intensity grazing ($p < 0.05$). On the other hand, a slight decrease in standardised multitrophic species richness in open and control subsites was recorded (**II**; **Fig. 4**). A similar negative trend was present in raw sum species richness, though marginal ($p > 0.05$). Since significant and anomalous species richness decline and community composition shift in ground-dwelling arthropods (also present in control and non-restored areas) were identified, which mainly seemed to be affecting the biodiversity results, additional analysis with the ground-dwelling arthropods (myriapods and spiders) excluded from the raw species richness was performed. Exclusion was performed to see the true impact of restoration actions, without external influencing factors, that seemed to strongly influence the ground-dwelling arthropod communities. After this exclusion, the restoration no longer had a significant impact on multitrophic species richness in open and control grasslands (See **Table 2** in **II**).

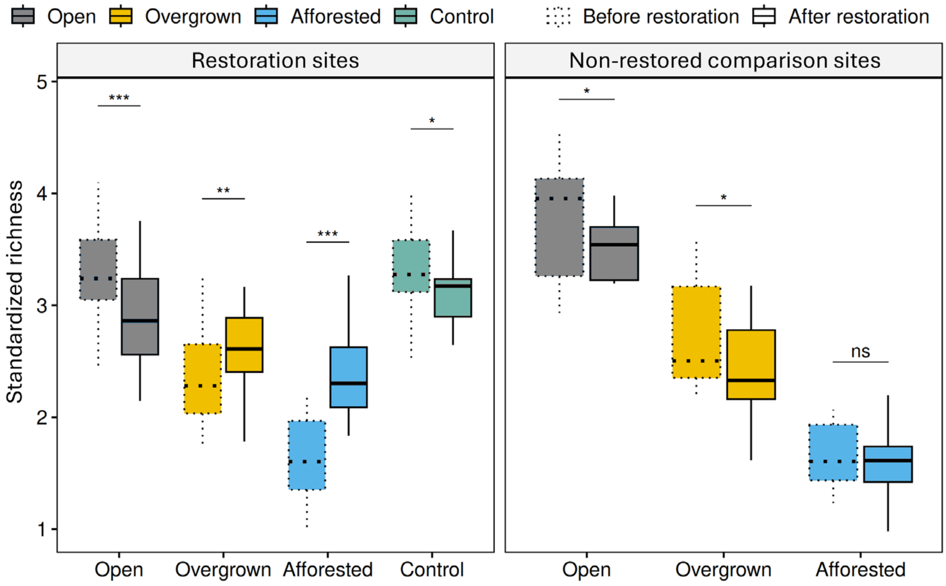

**Fig. 4.** Changes in multitrophic species richness in relation to alvar grassland restoration (**II**). The total multitrophic species richness (vascular plants, bryophytes, bumblebees, butterflies, spiders, myriapods, ground lichens, AM fungi) across all grassland condition classes **before and after restoration**. Significance levels: *** $p \leq 0.001$, ** $0.001 < p \leq 0.01$; * $0.01 < p < 0.05$, ns $p \geq 0.05$.

As presumed, the species richness post-restoration became more similar among the previously different subsites, whilst before restoration, the species richness differed significantly between the subsites (See **Table S2** in Supplementary Information of **II**). Regardless, the changes in species richness patterns and species composition are still transitional and are not happening at the same speed in all of the species groups (**II**).

The analyses revealed that the impact of restoration on multitrophic species richness varied markedly among organism groups, allowing us to distinguish three main response types (**II**):

1. **Fast responders** – organism groups that, within five years of restoration, rapidly increased in richness and/or shifted in community composition towards that of open grasslands (e.g., vascular plants, bumblebees, butterflies, birds). While vascular plants, bumblebees, and butterflies showed both an increase in species richness and a shift in community composition towards that of open grasslands, birds only had a shift in community composition with species preferring open habitats replacing species specialised to more closed canopy habitats (See **Table 2** in **II,** and **Table S3** in Supplementary Information of **II)**.

2. **Slow responders** – organism groups showing little or no measurable change in species richness and/or species composition in the short term (e.g., lichens, bryophytes, AM fungi). Ground lichens and bryophytes showed no significant difference in species richness, while AM fungi had a slight increase in taxonomic units in the afforested grasslands post-restoration, but still remained significantly lower than in open and overgrown subsites (See **Table 2** in **II,** and **Table S4** in Supplementary Information of **II)**.

3. **Disturbance-sensitive responders** – organism groups whose response patterns were shaped more by external stressors, such as prolonged drought, than by restoration actions, e.g., ground-dwelling arthropods. Ground-dwelling spiders exhibited especially drastic declines in both species richness and abundance. Additionally, to the change in species richness and abundance, the community composition of the ground-dwelling spiders was significantly different from all previous grassland condition class community composition patterns. The recovering spider community composition in all grassland condition classes became similar to one another, but shifted to an entirely new composition, not close to what it was before restoration, nor close to that of an open grassland community composition (**Fig. 5. A**).

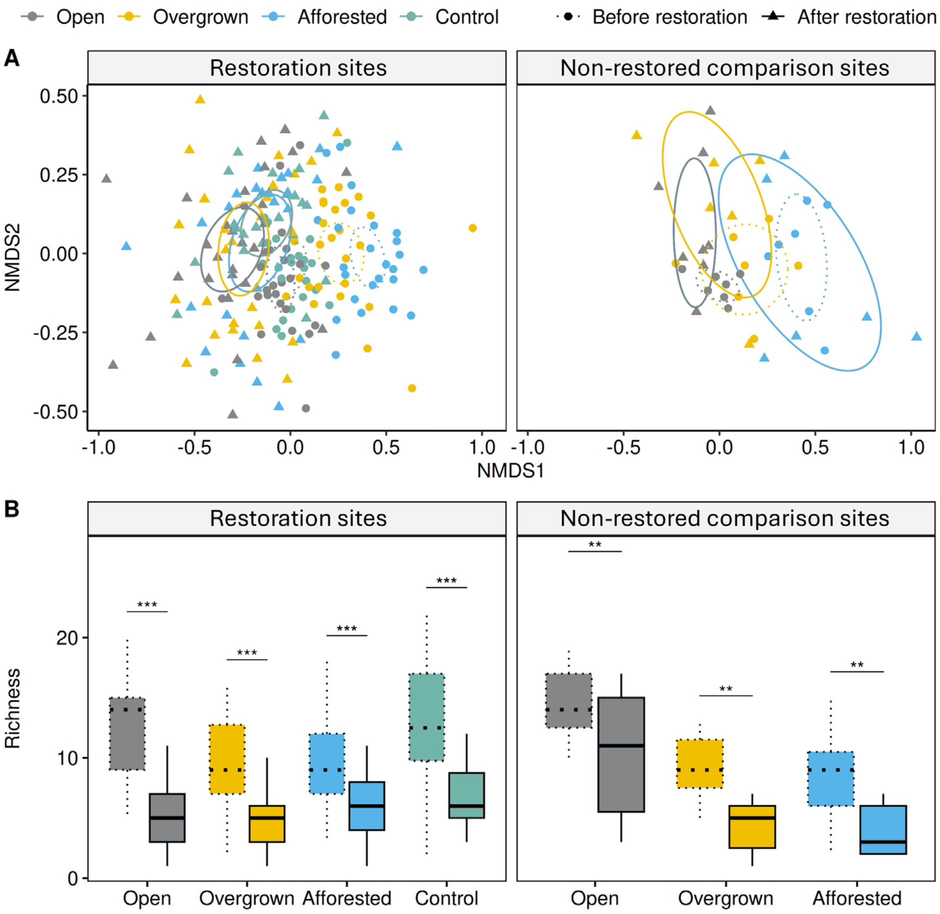

**Fig. 5. A:** Ground-dwelling spider community composition before and after restoration (**II**), visualised with nonmetric multidimensional scaling (NMDS; stress = 0.21). Ellipses represent standard errors with 99% confidence intervals. Both panels are based on the same NMDS, the restoration sites are illustrated on the left panel, and the non-restored comparison sites on the right. **B**: Ground-dwelling spider species richness before and after restoration in different condition classes. Significance levels: *** $p \leq 0.001$, ** $0.001 < p \leq 0.01$; * $0.01 < p < 0.05$, ns $p \geq 0.05$.

## 3.3. Changes in ecosystem service supply in response to grassland restoration

On average, a significant increase in multiple ecosystem services was observed in previously overgrown and afforested subsites following alvar grassland restoration and the implementation of a low-intensity grazing regime (**III**). Post-restoration, the habitat maintenance, pollination, forage production, wild food and herb supply, and cultural services all increased notably in previously overgrown and afforested grasslands in restoration sites ($p < 0.05$, see **Table 2** in **III**), showing a rapid recovery potential. There was no significant change in service supply recorded in the open and control subsites of the restoration sites, except for pest regulation service. Pest regulation, which is dependent on the condition of pest predator communities, declined sharply in all grassland condition classes (open, overgrown, afforested, control subsites), both in restoration sites and in non-restored comparison sites. In addition, while there was no significant change in forage production service in open and control subsites in the restoration sites, the service indicator – available biomass (g $m^2$) – decreased significantly. The other indicator, quality of the forage biomass, remained the same. Biomass quantity was also significantly lower in open subsites in the non-restored comparison sites, where there was no grazing impact. Soil-related services (carbon storage and soil condition maintenance) exhibited no significant reaction to restoration actions (**Fig. 6**).

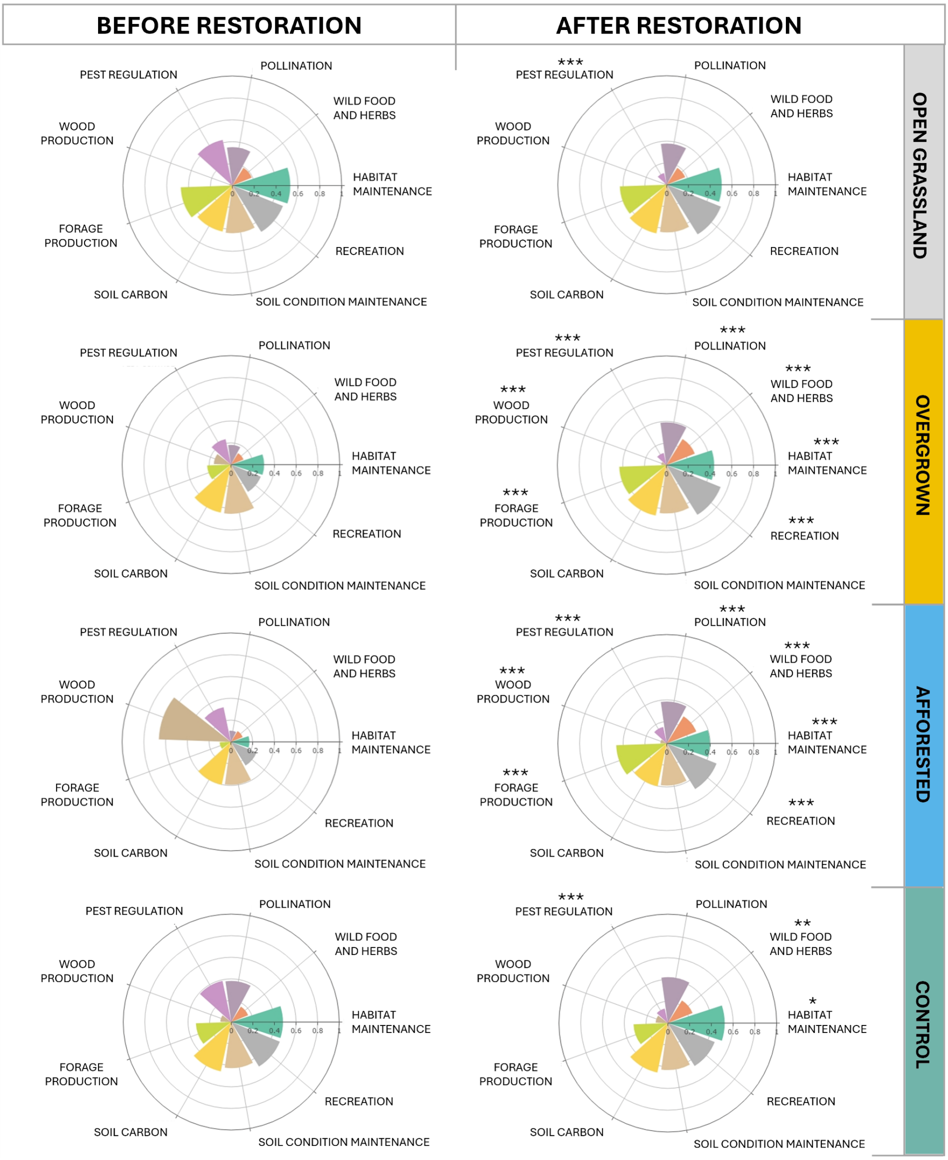

**Fig. 6.** Ecosystem service supply of all the alvar grassland condition classes in restoration sites before and after restoration (**III**). The flower diagrams represent bundles of services provided by the grassland condition class before and after restoration. The supply capacity values are indicated by the petal length of the flower diagram on a scale of 0–1 (1 being the highest value). Significance values are indicated as follows: *** $p \leq 0.001$, ** $0.001 < p \leq 0.01$; * $0.01 < p < 0.05$, showing the significant change in service supply in before-after restoration comparisons.

## 3.4. Relationship between ecosystem multifunctionality and multitrophic species richness

On average, ecosystem multifunctionality (the ecosystem's capacity to provide multiple services simultaneously in similar capacity) profited from the restoration actions, resulting in higher multifunctionality values in previously overgrown and afforested grasslands post-restoration ($p < 0.05$). A slight decrease in ecosystem multifunctionality was registered in open grasslands post-restoration (See **Fig. 6** in **III**). However, after the exclusion of drought-impacted pest predators and the pest regulation service from the analysis, open grasslands exhibited no significant difference in ecosystem multifunctionality in pre- and post-restoration comparisons (**III**).

There was also a significant positive association between multitrophic species richness and ecosystem multifunctionality after restoration ($R^2 = 0.06$, $p = 0.01$) (**III**), though the association was significantly weaker than before restoration ($R^2 = 0.31$, $p < 0.001$) and was significant only in the case of the previously afforested grasslands (**III**; **Fig. 7**).

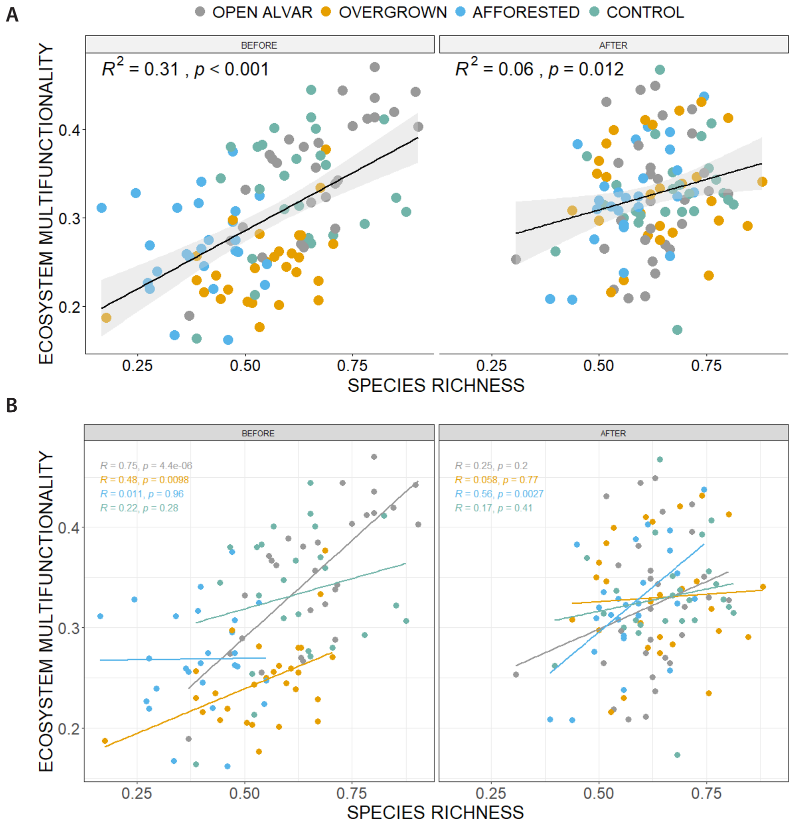

**Fig. 7**. Association between multitrophic species richness and ecosystem multifunctionality pre-restoration (left panels) and post-restoration (right panels) (**III**). **A:** The general association trend across all grassland condition classes. **B:** The associations between multifunctionality and species richness in every grassland condition class examined separately (**III**).

# 4. DISCUSSION

In this thesis, I examined how land-use change and ecological restoration impact biodiversity, ecosystem service supply, and ecosystem multifunctionality in grassland ecosystems. Across four research papers, the results demonstrate that open, traditionally managed semi-natural grasslands consistently support higher multitrophic biodiversity and higher ecosystem multifunctionality than abandoned, afforested, or intensified grasslands. Restoration of abandoned and afforested historical grasslands through shrub removal and reintroduction of low-intensity grazing can reverse the loss of multitrophic species richness and lowered ecosystem service supply (**I–IV**).

## 4.1. Biodiversity loss from land-use changes

The results of this thesis (**I–IV**) confirmed that traditionally managed semi-natural grasslands are characterised by high species richness across multiple taxa (Pärtel *et al.* 1999; Wilson *et al.* 2012; Habel *et al.* 2013). By contrast, land-use changes, whether due to abandonment, afforestation, or intensification of such grasslands, consistently reduce biodiversity, replacing species-rich assemblages with communities dominated by fewer competitive or shade-tolerant species (**I, II, IV**). These changes in diversity and community composition of plants, pollinators, natural pest predators, and soil biota also result in cascading effects on ecosystem service supply and ecosystem multifunctionality (**I**; Allan *et al.* 2015; Schils *et al.* 2022).

Intensified grasslands with high nutrient inputs, frequent biomass removal, and high biomass production-oriented species pools showed markedly lower taxonomic species richness and functional diversity estimates compared to semi-natural grasslands (**IV**). Since intensified grasslands are often more grass-dominant with fewer species in general and lacking in flowering forbs, they also lack resources for pollinators or other arthropod communities dependent on nectar or pollen as a food source (Balfour *et al.* 2025). Additionally, the intensive mowing/grazing and agrochemical use decrease the abundance and diversity of arthropods, which are a direct food source to many birds. Also, the frequent hay harvest is impacting the reproductive success of farmland birds (Buckingham *et al.* 2015). Intensification of agricultural landscapes has been found to be one of the driving forces of open habitat bird population decline across Europe (Douglas *et al.* 2023; Silva *et al.* 2023).

In afforested semi-natural alvar grasslands, multitrophic species richness was significantly lower compared to open alvar grasslands (**I**). Drastic change in light conditions due to tree growth and canopy closure eliminates many light-demanding grassland specialist plants, replacing them with a few shade-tolerant species (Wieczorkowski & Lehmann 2022). Additionally, a study by Pérez-Gómez *et al.* (2025) found that dense afforestation lowers pollinator and plant-pollinator network diversity. Canopy openness plays an important role in the abundance and diversity of flowering plants and, consequently, in the amount of pollinator rewards (nectar, pollen), as also confirmed by the results of paper **I**. All pollination indicator values (pollinator abundance, insect-pollinated plant cover, flower abundance and pollinator reward) were consistently lower in shrub-encroached and afforested alvar grasslands compared to open grasslands (**I**). But the results of papers **I** and **II** also showed that abandoned shrub-encroached alvar grasslands retain their original species pool longer than afforested or intensified grassland exhibiting "extinction debt" (Helm *et al.* 2006; Sang *et al.* 2010), meaning that loss of species can occur with a delay following the initial habitat loss or degradation, but progressive losses will continue to occur with continued habitat degradation (Kuussaari *et al.* 2009). On the positive note, as long as the species still persist, there could still be time for restoration measures, as the results of paper **II** showed rapid recovery of alvar grassland biodiversity post-restoration.

Overall, these findings align with previous research showing that land-use intensification reduces species richness across multiple taxonomic groups and shifts communities toward generalists (Gossner *et al.* 2016), and that afforestation of historical high-value grasslands leads to severe and often irreversible losses of grassland specialists (Luoto *et al.* 2003; Winberg *et al.* 2024).

## 4.2. Land-use change leads to ecosystem service decline in grassland ecosystems

Traditionally managed, historical semi-natural grasslands support various essential ecosystem services (**I**, **III**, Ford *et al.* 2012; Villoslada *et al.* 2019). In contrast, abandonment, afforestation, and intensification of grasslands consistently reduce biodiversity and lead to declines in several key ecosystem services (**I, IV**). There is a strong link between land-use change and ecosystem service supply. Grassland degradation, whether through intensification, abandonment, or afforestation, led to clear trade-offs between services, where maximising provisioning services, such as wood or forage production, often came at the expense of regulating and cultural services (**I, IV**). This corroborates previous studies on the negative impacts of drastic land-use changes in a variety of ecosystems (Power 2010; Allan *et al.* 2015; Sharma *et al.* 2019). In afforested grasslands, other services were largely traded for wood production (**I**), although timber yields (50–150 m$^3$ per hectare) were modest and are typically of low quality (Lõhmus 1984) compared to average Estonian production forests (~200–300 m$^3$ per hectare; Statistics Estonia 2024). This reflects the limitations of using such calcareous grasslands for forestry, including thin soils that are prone to summer droughts and winter frost damage (Rosén 1982, 1995).

Pollination, pest regulation, and habitat maintenance services were particularly sensitive to grassland abandonment, afforestation, and intensification, leading to declines in both pollinator and natural pest predator communities alongside overall biodiversity loss (**I, IV**). Land-use change leads to reductions in flower richness, structural vegetation complexity, habitat connectivity, and total habitat area, all of which decrease the suitability of the habitat for species providing pollination and pest regulation (Garibaldi *et al.* 2011; Goulson *et al.* 2015; Schirmel *et al.* 2015). Intensification in general affects the majority of the regulating services, with negative impacts reaching beyond the grassland ecosystem and affecting the whole landscape multifunctionality (Guo *et al.* 2023).

While alvar grassland abandonment and afforestation had notable negative impacts on services supported by mobile organisms (e.g. pollination, pest regulation), the response of soil parameters and linked ecosystem services was minimal (**I**). The comparable soil carbon content observed between afforested and open alvar grasslands indicated that afforestation of similar high-value grassland systems is unlikely to provide substantial long-term climate mitigation benefits (Tölgyesi *et al.* 2022). Although afforested areas and forests have the potential to store large amounts of carbon in both soils and aboveground biomass (Kilpeläinen & Peltola 2022), aboveground stocks may be temporary and are strongly dependent on forest management practices and the use of the harvested wood (Hurmekoski *et al.* 2022). Grasslands are also considered important and stable global carbon reservoirs, and low-intensity grassland management has been linked to slow but steady increases in soil carbon stocks (Soussana *et al.* 2004). Nonetheless, the pressure to afforest remaining grasslands has increased over recent years due to public and political appeal of tree planting as a simple nature-based climate solution. Similar to other authors, e.g., Temperton *et al.* (2019) and Tölgyesi *et al.* (2022), the current thesis results show that planting trees in biodiverse open habitats can have adverse ecological impacts, decreasing biodiversity and the supply of multiple ecosystem services (**I**). These findings also emphasise that when looking for climate and biodiversity solutions, land-use history must be incorporated into decision-making to avoid undermining existing or potentially recoverable biodiversity and ecosystem service values (**I, II, III**).

The recreational value of grasslands often depends on the abundance of flowering species, the diversity of flowers and colours (Lindemann-Matthies & Bose 2007), perceived biodiversity, and open panoramic views, making the scenery more aesthetically pleasing, etc. (Lindemann-Matthies *et al.* 2010). Since open alvar grasslands in the current study were the most flower-rich and structurally diverse habitats, they had the highest recreation potential (**I**) while also carrying a high cultural heritage value representing the historical village settlements (Eriksson 2022). As collecting wild food and other nature goods is perceived as an important tradition and a popular recreational activity within Europe, this provisioning service could additionally be connected to the cultural services category (Schulp *et al.* 2014). Open grasslands also had the highest wild food and herb supply values compared to the overgrown and afforested grasslands, which had the majority of the plants of use value available but in considerably lower abundances (**I**).

## 4.3. Post-restoration biodiversity recovery in semi-natural grasslands

Restoration of abandoned and afforested grasslands by clearing excess woody vegetation and reintroducing a traditional grazing regimen positively impacted multitrophic species richness (**II**), which in turn enhanced the supply of ecosystem services (**III**). Restoration efforts triggered a rapid response in fast-responding species groups (**II**). Within just a year, species richness of vascular plants increased notably, with gains not only noted within generalist plants, as often seen in the early succession of grasslands (Waldén & Lindborg 2016), but also in alvar grassland specialists. Such a fast recovery could have been aided by persistent seedbanks (Kalamees *et al.* 2012) and the careful selection of restoration sites with a long history of grassland persistence and fairly good landscape connectivity. These favourable conditions meant that in areas where species persisted due to past habitat continuity and good seedbanks, plant communities were relatively easy to restore, whereas sites with altered soils, different habitat conditions and land-use change intensity, and severe species loss would require more intensive interventions such as seed or hay transfer (Török *et al.* 2011; Knight & Overbeck 2021). The shift in vegetation was accompanied by other fast-responding organism groups, for instance, open-habitat bird species replaced species preferring closed canopies, leading to no net gain in species richness but significant changes in species community composition. Also, increases in bumblebee and butterfly richness in formerly overgrown areas were noted, although pollinator trends were partly shaped by drought-related declines in floral resources (Phillips *et al.* 2018).

In contrast, slow-responding organism groups such as lichens, bryophytes, and AM fungi exhibited little to no change during the short five-year monitoring period (**II**). These species require longer recovery periods, targeted interventions, and long-term monitoring in order to give us any objective feedback on grassland restoration success (Watts *et al.* 2020). While lichens exhibited no response to restoration, bryophytes specialised to open habitats began to slowly recolonise restored sites, corroborating previous findings of lichens and bryophytes exhibiting a time-lag in response to habitat change (Hämäläinen & Fahrig 2024). AM fungal diversity also improved slightly, though it remained lower than in open grasslands due to the legacy effect of the previous overgrowth and afforestation (Neuenkamp *et al.* 2018).

The trajectory of recovery was additionally strongly affected by climatic perturbations, like a prolonged drought a year before the survey. The disturbance-sensitive organism groups, like ground-dwelling spiders and myriapods (Prather et al. 2020), suffered significant declines in species richness and abundance in all of the grassland sites, also in control subsites and non-restoration comparison areas (**II**). Additionally, a slight decrease in bumblebees and vascular plant biomass could be detected in control subsites and reference sites not affected by grazing, indicating the impact of drought (**II, III**). Such additional factors can easily overshadow potential restoration benefits (or also drawbacks) and complicate decision-making on further restoration actions (Luong *et al.* 2021). While early monitoring offers critical insights into the initial effectiveness of restoration and supports adaptive management (Coon *et al.* 2021), long-term monitoring provides a comprehensive understanding of ecosystem recovery over time.

## 4.4. Grassland restoration improves ecosystem service supply and ecosystem multifunctionality

There was a rapid increase in the supply of several ecosystem services and in overall ecosystem multifunctionality following alvar grassland restoration and the implementation of a low-intensity grazing regime (**III**). The majority of the directly 'biodiversity-mediated ecosystem services' (*sensu* Isbell *et al.* 2011), such as pollination, habitat maintenance, and the supply of wild food and medicinal herbs, notably increased post-restoration compared to pre-restoration levels. Meanwhile, pest regulation, while also one of the directly biodiversity-mediated services, reacted in the opposite manner to other similar services, having significantly lowered supply capacity. This could be caused by an extreme, prolonged drought prior to monitoring rather than a direct restoration-driven outcome, since control and non-restored comparison sites exhibited similar responses. Additionally, the available plant biomass for forage was lowered that year as drought had a severe impact on plant growth and animal feed quantities. Drought results in lowered plant cover and soil moisture, which are critical conditions for ground-dwelling arthropod communities (Prather *et al.* 2020).

However, services associated with soil functioning exhibited no change. Most importantly, the soil carbon storage capacity remained consistent across grassland condition classes (open, overgrown, and afforested grassland) regardless of restoration impact (**III**). I speculate that the specifics of the alvar grasslands' soil conditions, combined with rapid vascular plant recolonisation covering open soil, could contribute to the stable soil conditions and carbon storage post-restoration (**II, III**).

## 4.5. Ecosystem multifunctionality depends on grassland biodiversity

Ecosystem multifunctionality, that is, the ability of an ecosystem to simultaneously provide different services in a similar capacity (Lefcheck *et al.* 2015), is strongly linked with the number of species and functional traits, indicating that biodiversity (taxonomic and functional) plays a significant role in the ecological functioning of grasslands (**I, III, IV**). Previous research suggests that biodiversity at multiple trophic levels is required to maintain high ecosystem multifunctionality (Hector & Bagchi 2007; Soliveres *et al.* 2016). However, it is also suggested that ecosystem multifunctionality could decrease after restoration, while grasslands are developing towards their target habitat type (DeCock *et al.* 2023). The results of paper **III** indicated that, on average, both ecosystem multifunctionality and species richness increased post-restoration, but the positive relationship between the two was not as strong as prior to the restoration (**I**, **III**). The rapid recovery of grassland species richness and composition across all of the previously different condition classes had a homogenising effect on the species pools and removed the effect of previous habitat conditions and extreme low values. Additionally, the evolving and disturbed post-restoration condition of the system could also complicate the results, still reflecting the results of the previous or transitional state, rather than the climax restored grassland condition (Deák *et al.* 2020). Long-term monitoring studies are needed to understand the recovery and full trajectory of relationships between biodiversity and ecosystem multifunctionality.

## 4.6. The future of grasslands and the impact of climate change

My findings in papers **II** and **III** reveal a rapid and largely positive initial response of both grassland biodiversity and ecosystem services to alvar grassland restoration efforts. However, this swift recovery will not be sustained over time without continued sustainable grassland management (Pärtel *et al.* 2007). Ongoing degradation and fragmentation of grasslands could make future restoration efforts more difficult and expensive. The long-term success of grassland restoration often depends on multiple factors such as the severity and duration of degradation, habitat and species characteristics, management strategies, and climatic conditions (Török *et al.* 2021). Grasslands studied in this thesis showed strong restoration potential due to the landscape context and land-use history that facilitated rapid recovery (**II**, **III**). These results can be transferable and could facilitate the restoration actions of other grassland ecosystems with similar conditions. However, my findings also indicate that there might be necessary prerequisites for successful recovery. For example, more productive, intensively managed, or significantly more degraded grasslands (e.g. grasslands transformed to croplands, intensively cultivated grasslands) in highly fragmented landscapes are less likely to exhibit similar positive responses to restoration and might require significantly more effort and resources. Challenges like seed limitation and soil legacy effects in more degraded regions require more complex restoration measures and necessitate longer monitoring periods (Török *et al.* 2011). Moreover, additional pressures like drought – exacerbated by human-induced climate change – can hinder ecosystem recovery and disrupt the link between biodiversity and ecosystem multifunctionality, further challenging habitat recovery (**III**). More species-rich grasslands with less intensive management have been found to have higher resistance and resilience to drought (Vogel *et al.* 2012), making moderately managed grasslands a valuable and sustainable ecosystem in the light of climate change. Since low-intensity semi-natural grasslands have high species richness (**I–IV**) and functional diversity (**IV**), they could be efficient at storing carbon and more resilient to potential extreme disturbance events and future climate change scenarios (Steinbeiss *et al.* 2008). Our trait-based analysis supports this, showing that plant communities in semi-natural grasslands are significantly more effective in storing soil carbon and retaining water than those in intensified grasslands, driven by traits such as higher root mass, branching density, and root architecture (**IV**). A wider range of traits with various functions could complement each other and buffer environmental perturbations, strengthening the drought resilience of the communities (Lüscher *et al.* 2022). Furthermore, regardless of the nutrient enrichment in intensified grasslands, increasing the potential carbon sequestration capacity through forage yield increase (Skinner 2013; Sollenberger *et al.* 2019), intensive grazing/mowing or ploughing can reduce the soil carbon storage in the long run (Dlamini *et al.* 2016; Krauss *et al.* 2022). The abundance-based functional divergence analysis showed no significant differences in ecosystem service supply capacity between semi-natural and intensified grasslands, reflecting that the few dominant species in intensified grasslands have the capacity to provide the different services to some extent (**IV**). However, in case of extreme disturbance (droughts, floods, etc.), semi-natural grasslands might be more resilient and better equipped to handle these perturbations due to their wider spectrum of traits and higher species complementarity (Hector & Bagchi 2007).

# 5. CONCLUSIONS

In this thesis, I explored the impact of land-use changes and restoration efforts in grassland ecosystems on the multitrophic biodiversity patterns, supply of ecosystem services, and on ecosystem multifunctionality in general. Specifically, I found that:

1. Traditionally managed historical semi-natural grasslands are biodiversity hotspots (**I, II, IV**) and capable of supplying multiple ecosystem services simultaneously exhibiting high ecosystem multifunctionality (**I, III, IV**). In contrast, land-use changes like land abandonment, afforestation (**I**), and grassland intensification (**IV**) often lead to the loss of multitrophic diversity, higher ecosystem service trade-offs, and the dominance of a few or one service. For instance, higher forage yield in intensified grasslands (**IV**) and wood production in afforested grasslands (**I**) were maximised at the expense of other services. Semi-natural grasslands exhibit a more balanced supply of a range of ecosystem services, supporting pollination, habitat maintenance, pest regulation, soil condition maintenance, carbon storage, forage production, supply of wild food, and recreational benefits simultaneously in a similar capacity (**I, IV**).

2. As expected, the restoration of abandoned and afforested alvar grasslands into open grasslands positively impacted multitrophic species richness on average, but short-term (up to 5 years post-restoration) recovery patterns follow three main trajectories: fast responders, slow responders, and disturbance-sensitive responders (**II**). Fast responders (e.g., vascular plants, insect pollinators, birds) exhibited a significant increase in species richness and/or a shift in species community composition towards open grassland assemblages already during the first five years after shrub/tree removal and reinstatement of low-intensity grazing. The slow responding groups (e.g., bryophytes, lichens, AM fungi) exhibited little to no short-term reaction to restoration, likely requiring longer timeframes for the recovery of the open habitat specialist species. Disturbance-sensitive organism groups (e.g., ground-dwelling spiders) response patterns were shaped more by external factors, such as prolonged drought, overshadowing the potential impacts of restoration actions. Ground-dwelling arthropod communities exhibited drastic declines in both species richness and abundance, and the community composition had shifted to a novel community state (**II**).

3. Alvar grassland restoration enhanced the supply of multiple biodiversity-mediated ecosystem services and increased ecosystem multifunctionality, but not all services responded equally (**III**). Post-restoration, the habitat maintenance, pollination, forage production, wild food and herb supply, and cultural services increased in previously overgrown and afforested grasslands, while soil services remained unimpacted, and pest regulation suffered significant declines compared to pre-restoration results. Since pest regulation declined

across all observed sites, including non-restored control sites, it is likely due to severe drought impacts on natural pest predator communities. Soil carbon storage remained stable, supporting grasslands' role as a long-term carbon sink (**III**).

4. Biodiversity underpins ecosystem multifunctionality, but this relationship is weaker in recently restored sites (**I, III**). Multitrophic diversity was strongly and positively linked to ecosystem multifunctionality, underscoring biodiversity's key role in sustaining ecosystem functions and services. In restored grasslands, this relationship was weaker, likely reflecting transitional, successional states and incomplete recovery. Additionally, other disturbances, like prolonged drought, can further complicate the interpretation of the results.

5. Maintaining the existence of semi-natural grasslands requires continued low-intensity management, evidence-based restoration, and consideration of land-use history (**I–IV**). Alvar grasslands still have high recovery potential (**II**, **III**). Other grassland ecosystems with similar conditions and land-use history could respond similarly to restoration efforts. However, more productive, significantly more degraded grasslands in highly fragmented landscapes likely require significantly more effort and resources. Moreover, additional pressures like drought – exacerbated by human-induced climate change – can hinder ecosystem recovery and disrupt the link between biodiversity and ecosystem multifunctionality, further challenging habitat recovery (**III**). Where possible and feasible, restoration should be implemented based on land-use history to recover degraded sites, raise landscape diversity, and increase landscape connectivity – connecting grassland habitat patches with each other and the rest of the agricultural landscapes. In restoration, long-term, multi-taxon monitoring, also accounting for environmental perturbations, is essential to detect delayed responses and support adaptive management (**II**).

# SUMMARY

In the current thesis, I investigate how changes in land-use (grassland abandonment, afforestation, and intensification) and ecological restoration affect grassland biodiversity, ecosystem service supply, and ecosystem multifunctionality. Ecosystem services are the functions and products of nature that people can obtain from ecosystems, while ecosystem multifunctionality measures the capacity of an ecosystem to supply multiple services simultaneously in similar capacity. Ecosystem services are divided into three main categories: provisioning services (e.g., wood production, food, and livestock fodder), regulating services (e.g., pollination, natural pest control), and cultural services (e.g., nature tourism). However, the condition and availability of ecosystem services have declined significantly over the last century. Already in 2005, the *Millennium Ecosystem Assessment* reported that more than half of all ecosystem services produced worldwide were overexploited and in poor condition.

Many ecosystem services depend directly on local biodiversity, and the hypothesis is that the more diverse the ecosystem, the greater the ecosystem multifunctionality. When environmental conditions change or in the case of strong disturbances, some species may go locally extinct. In ecosystems with low species richness, this means the functions those species performed will also be lost. Conversely, in diverse ecosystems, the remaining species can take over the functions of lost species, ensuring the continuity of stable ecosystem service flow and high ecosystem multifunctionality.

Semi-natural grasslands are one of Europe's most species-rich ecosystems, created by centuries of moderate human influence and traditional agricultural practices, and are thus potentially good at preserving high ecosystem service supply. Though with the intensification of agriculture at the beginning of the 20th century, the semi-natural grasslands have lost the majority of their historical spread across Europe. The remaining grassland habitat patches are highly fragmented and mostly incapable of supporting biodiversity in the long term. The main reasons for grassland loss are, on one hand, intensification (fertilisation, pesticide use, intensive mowing/grazing) and conversion to arable land, and on the other hand, the abandonment of less productive grasslands leading to overgrowth or afforestation. Changes in environmental conditions, species richness, and species composition cause changes in ecosystem functioning and in the supply of ecosystem services. To avoid further degradation, it is essential to restore and protect ecosystems, maintaining a diverse landscape structure and biodiversity at different trophic levels. In agricultural landscapes, where production depends largely on ecosystem services, it could be profitable to restore and maintain semi-natural grasslands and connect them to croplands with linear elements to increase landscape connectivity.

The aim of my doctoral thesis was to assess how abandonment and afforestation of Estonian semi-natural grasslands (alvar grasslands) on one hand (**I**) and grassland intensification on the other (**IV**), affect local biodiversity, eco-

system services, and overall ecosystem multifunctionality. In addition to factors negatively impacting grasslands, I also assessed the effectiveness of grassland restoration using semi-natural alvar grasslands as a model system, and monitored whether species richness and the supply of ecosystem services increase post-restoration (**II, III**). I used a wide selection of multitrophic species groups and ecosystem services to also assess the relationship between biodiversity and ecosystem multifunctionality.

The results of this thesis show that traditionally managed semi-natural grasslands can be described as biodiversity hotspots and capable of supporting the simultaneous supply of multiple ecosystem services, making them highly multifunctional ecosystems (**I–IV**). Intensification, abandonment and afforestation of historical grasslands lead to the decline of both biodiversity and ecosystem service supply, and trade-offs between ecosystem services emerge (**I, IV**). Typically, provisioning services are enhanced at the expense of regulating and cultural services. For example, intensification of grasslands increases the efficient production of biomass for fodder (also provisioning service) but, for instance, reduces the potential for pollination or soil carbon storage (**IV**). Similarly, afforestation of grasslands enables wood production (a provisioning service) but at the expense of many services associated with open grasslands (**III**). Afforestation has also been used to sequester more carbon as a climate change mitigation measure. However, this thesis found that species-rich semi-natural grasslands are also stable carbon sinks (**I–IV**), and for instance, the carbon storage capacity of semi-natural alvar grasslands did not differ from afforested alvar grasslands (**I**).

Despite these negative aspects, both intensively managed and semi-natural grasslands are important parts of diverse landscapes, as well as forest ecosystems (**I, IV**). Different ecosystems complement each other, and it is important to maintain diverse landscapes and find a balance that reduces trade-offs between biodiversity and production. For example, keeping livestock density below the maximum carrying capacity can increase biodiversity while simultaneously improving habitat provision and maintenance, pollinator diversity, water quality, carbon storage, and cultural services alongside agricultural production (**IV**). Moreover, afforestation of valuable historical grasslands should be avoided as a nature-based climate solution: the mitigation benefits are relatively limited, whereas biodiversity and other service losses are significant (**I**). Land-use decisions would be more optimal if based on land-use history, such as reforesting former forest land or afforesting heavily disturbed habitats like exhausted mining areas. Restoration and continuous management of semi-natural grasslands (**II, III**) and improvement of landscape connectivity support the supply of ecosystem services in agricultural landscapes.

For this reason, as part of my doctoral work, I also focused on assessing the effectiveness of restoration efforts, using results from the *LIFE to Alvars* project that restored Western Estonian alvar grasslands (**II, III**). The results showed that abandoned or afforested alvar grasslands still have significant recovery potential, but moderate and consistent management is essential to maintain ecosystem functioning and prevent encroachment by woody plants (**II**). Restoration success depends on the degradation history, local abiotic conditions, and species characteristics. On average, the multitrophic species richness increased post-restoration, though different organism groups have varied recovery rates, and restoration success can also be influenced by external factors such as prolonged drought (**II**). Given the short monitoring window assessed in this study (0.5–5 years after restoration), it was not possible to fully evaluate the recovery success of slow-recovering taxa or the long-term changes in soil processes and carbon cycling, highlighting the importance of long-term monitoring (**II**). In fragmented and/or degraded landscapes, science-based restoration is needed to improve connectivity, maintain metapopulations, and ensure sustainable functioning of the system.

In addition to the increase in multitrophic biodiversity, restoration also positively affected the supply of several ecosystem services. After restoration, previously overgrown and afforested areas showed improved capacity to provide habitat, pollination, wild food and herbs, fodder, and had a higher recreational value, while the capacity to store carbon did not change, remaining similar across all studied sites. Only two services decreased after restoration: wood production and natural pest control (**III**). Though the decline in pest regulation service was more likely caused by an extreme and prolonged drought a year before monitoring. A similar decline in natural pest enemy populations occurred in both control and unrestored comparison sites, which had no restoration interventions. In the same year, the plant biomass available for fodder also decreased (**II**, **III**) with drought strongly affecting plant growth and reducing plant cover and soil moisture, which are critical conditions for ground-dwelling arthropod communities.

The results of the doctoral thesis show that semi-natural grasslands have high value, providing habitat for diverse biota and supporting many important ecosystem services (**I–IV**). By integrating multitrophic biodiversity data, functional trait analyses, and a broad set of ecosystem service indicators, the results provide new insights into the ecological consequences of abandonment, afforestation, and intensification of grasslands, as well as highlight the recovery potential and constraints of ecosystem restoration. The findings have direct relevance for evidence-based landscape management and for designing restoration strategies that address the urgent need to halt biodiversity loss while safeguarding the sustainable supply of essential ecosystem services.

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# SUMMARY IN ESTONIAN

## Maakasutusmuutuste ja taastamise mõju liigirikkusele, ökosüsteemi hüvedele ja ökosüsteemi multifunktsionaalsusele niidukoosluste näitel

Ökosüsteemiteenused ehk ökosüsteemi hüved on looduse funktsioonid ja saadused, mida inimkond tarbib igapäevaselt. Ökosüsteemi hüved jaotatakse varustavateks (nt. puit, toit ja loomasööt), reguleerivateks (nt. tolmeldamine, looduslik kahjuritõrje) ja kultuurilisteks hüvedeks (nt. loodusturism). Ökosüsteemi hüvede seisund ja kättesaadavus on aga viimase sajandi jooksul märgatavalt kahanenud ning juba aastal 2005 ilmunud Milleniumi ökosüsteemiteenuste raportis leiti, et üle poole kogu maa ökosüsteemide poolt toodetud ökosüsteemi hüvedest on ületarbitud ning halvas seisundis. Suur osa ökosüsteemi hüvedest sõltub otseselt kohalikust elurikkusest ning mida mitmekesisem on elustik, seda kõrgem on ka ökosüsteemi multifunktsionaalsus ehk ökosüsteemi võimekus pakkuda mitmeid erinevaid ökosüsteemi hüvesid samaaegselt ja sarnasel tasemel. Keskkonnatingimuste muutumisel või tugeva häiringu olukorras võivad osad liigid lokaalselt hävida mille korral kaotame koos liikidega, ka vastavad funktsioonid, mida nad täitsid. Mitmekesise elustiku puhul on aga ülejäänud elustik suurema tõenäosusega võimeline välja surnud liigirühma funktsioonid üle võtma ning sellega tagatakse ka ökosüsteemi hüvede stabiilne kättesaadavus.

Pool-looduslikud rohumaad on Euroopa ühed liigirikkamad ökosüsteemid, mis on kujunenud sajandite või lausa aastatuhandete vältel looduse ja inimtegevuse koosmõjul. Madala intensiivsusega karjakasvatus ja rohumaade niitmine on aidanud kaasa mitmekesiste keskkonnatingimuste loomisele. Traditsiooniline majandamine tagas elupaigalaikude sidususe ja metapopulatsioonide võrgustiku säilimise, kus nt. soontaimede leviste olulisteks levitajateks olid kariloomad vastavalt läbi endozoohooria või ektozoohooria. Kariloomi liigutati ühelt karjamaalt teisele, mille käigus loomade karvkattesse või seedekulglasse jõudnud taimelevised jõudsid uude elupaika.

Põllumajanduse intensiivistumisega 20. sajandi alguses on aga kogu Euroopa pool-looduslike rohumaade ehk pärandniitude pindala ja seisund drastiliselt vähenenud, niidukooslused on küllaltki fragmenteeritud ning enamasti pole võimalised pikaajaliselt toetama elustiku mitmekesisust. Rohumaade kadumise peamisteks põhjusteks on ühest küljest rohumaade intensiivistamine (väetamine, pestitsiidide kasutamine ja intensiivne niitmine/karjatamine) ja üleskündmine põllumaadeks kui teisalt vähemproduktiivsete rohumaade maha jätmine, kinnikasvamine või metsastamine. Muutused keskkonnatingimustes ning liigirikkuses ja liikide koosseisus toovad kaasa muutusi ökosüsteemide funktsioonides ja ökosüsteemi hüvede pakkumises. Oluline on mitmekesise maastikupildi ja liigilise mitmekesisuse säilitamine erinevatel troofilistel tasemetel. Näiteks põllumajandusmaastike puhul, kus põllumajandustoodang sõltub suuresti erinevate hüvede kättesaadavusest on oluline pool-looduslike niitude ja ribaelementide olemasolu ja sidususe tõstmine.

Minu doktoritöö eesmärgiks oli hinnata kuidas muutused maakasutuses nagu poollooduslike rohumaade ehk pärandniitude kinnikasvamine ja metsastamine (**I**) ja rohumaade intensiivistamine (**IV**) mõjutab rohumaade liigirikkust, ökosüsteemi hüvesid ja kogu ökosüsteemi multifunktsionaalsust. Lisaks rohumaasid negatiivselt mõjutavatele teguritele hindasin ka pärandniitude taastamise tulemusi Eesti loopealsete näitel ning analüüsisin kas loopealsete liigirikkus ja ökosüsteemi hüvede pakkumine tõuseb taastamisjärgselt (**II, III**). Töös kasutasin võimalikult paljusid organismirühmasid ja ökosüsteemi hüvesid, et hinnata ka liigirikkuse seost ökosüsteemi multifunktsionaalsusega.

Minu doktoritöö tulemustest selgus, et traditsiooniliselt majandatud pärandniite võib kirjeldada elurikkuse tulipunktidena, mis suudavad toetada mitmete ökosüsteemi hüvede samaaegset pakkumist ehk tegemist on multifunktsionaalsete ökosüsteemidega (**I–IV**). Pärandniitude majandamisest välja jätmine, metsastamine või intensiivistamine aga toob kaasa elustiku mitmekesisuse vähenemise ning mõjub negatiivselt ökosüsteemi hüvede pakkumisele (**I, IV**). Intensiivistamine kui ka metsastamine toovad kaasa lõivsuhteid ökosüsteemi hüvede vahel, kus ühe hüve potentsiaali maksimeerimise korral toimub see teiste hüvede pakkumise arvelt (**I, IV**). Peamiselt toimub just varustavate hüvede tootmise intensiivistamine reguleerivate ja kultuuriliste hüvede arvelt. Rohumaade intensiivistamine võimaldab varustava hüve, loomasöödaks toodetava biomassi, suuremat toodangut aga näiteks väheneb tolmeldamise hüve potentsiaal või mulla süsinikuvaru (**IV**). Rohumaade metsastamine toob kaasa puidu tootmise (varustav hüve) võimaluse, kuid kaovad mitmed avatud rohumaadega seotud väärtused (**III**). Rohumaade metsastamist kasutatakse ka suurema koguse süsiniku sidumise eesmärgil kliima muutuste leevendamiks. Käesolev töö aga leidis, et mitmekesise elustikuga pärandniidud on samuti stabiilsed süsiniku sidujad (**I–IV**) ning näiteks avatud loopealsete võimekus süsinikku mulda siduda ei erinenud metsastatud loopealsete võimekusest (**I**).

Vaatamata negatiivsetele aspektidele on intensiivselt majandatud kui ka poollooduslikel rohumaadel oluline osa mitmekesises maastikupildis, rääkimata metsade olulisest rollist (**I, IV**). Erinevad ökosüsteemid täiendavaid teineteist, ning oluline on säilitada mitmekesiseid maastikke ning vajalik on leida tasakaal, mis pehmendaks elurikkuse ja tootmise vahelisi kompromisse. Näiteks kariloomade asustustiheduse hoidmine alla maksimaalse kandevõime võib tõsta liigirikkust ning samaaegselt parandada elupaikade säilimist, tolmeldajate mitmekesisust, vee kvaliteeti, süsiniku talletamist ja kultuurilisi hüvesid koos põllumajandussaaduste tootmisega (**IV**). Lisaks tuleks vältida väärtuslike ajalooliste rohumaade metsastamist looduspõhise kliimalahendusena. Sellises kontekstis on leevenduskasu pigem piiratud, samas kui elurikkuse ja teiste teenuste kulud on suured (**I**). Maakasutus otsuste tegemisel oleks optimaalsem tugineda maakasutus ajaloole ning taasmetsastada metsamaid või taastada metsastamisega tugevalt häiritud kooslusi nagu näiteks ammendatud kaevandusalad. Poollooduslike pärandniitude järjepidev hooldamine ja taastamine (**II, III**) ning maastiku sidususe parandamine aitab kaasa põllumajandusmaastike ökosüsteemi hüvedega varustatusele ja jätkusuutlikuma põllumajandusmaastiku toimimisele.

Seetõttu, pühendasin ka ühe osa oma doktoritööst rohumaade taastamistööde efektiivsuse hindamisele toetudes Lääne-Eesti loopealsete pärandniitude taastamise projekti *LIFE to Alvars* tulemustele (**II, III**). Tulemustest selgus, et mahajäetud või metsastatud loopealsetel on endiselt märkimisväärne taastumisvõime, kuid ökosüsteemi toimimise säilitamiseks ja puittaimede pealetungi vältimiseks on hädavajalik mõõdukas ja järjepidev majandamine (**II**). Taastumisedukus sõltub degradeerumise ajaloost, kohalikest abiootilistest tingimustest ja liikide iseärasustest. Tööst selgus, et keskmine liigirikkus tõusis pärast taastamist, kuid erinevad organismirühmad taastuvad erineva kiirusega ning taastumisedukust võivad mõjutada ka teised välised tingimused nagu pikk põuaperiood. Arvestades käesolevas töös hinnatud lühikest taastumisakent (0,5–5 aastat pärast taastamist), ei ole meil võimalik näiteks aeglaselt taastuvate taksonite taastumisedukust ning mulla ja süsinikuringe pikaajalisi muutusi täielikult hinnata, mis rõhutab pikaajalise seire tähtsust (**II**). Killustatud ja/või degradeerunud maastikes on vaja teaduspõhist taastamist, mis parandab ühenduvust, et hoida metapopulatsioone ja tagada süsteemi jätkusuutlik toimimine.

Lisaks üldisele liigirikkuse kasvule, mõjus taastamine positiivselt ka mitmete ökosüsteemi hüvede pakkumisele. Pärast taastamist tõusis eelnevalt kinnikasvanud ja metsastatud loopealsete võimekus pakkuda elupaika mitmekesisele elustikule, tolmeldamist, loodussaadusi, loomasööta ja suurenes ka alade rekreatiivne väärtus. Taastamisjärgselt ei muutunud ökosüsteemi süsiniku mulda salvestamise võimekus, mis säilis sarnasel tasemel kõigi uurimisalade vahel. Pärast taastamist langes ainult kahe hüve pakkumine: puidu toodang ning looduslik kahjuritõrje (**III**). Loodusliku kahjuritõrje hüve vähenemine aga tõenäoliselt polnud taastamisest tingitud, vaid languse põhjuseks oli vahetult seirele eelnenud aastal aset leidnud tugev ja pikaajaline põud. Sarnane langus looduslike kahjurivaenlaste populatsioonides toimus ka uuringu kontroll ja taastamata võrdlusaladel, kus taastamistööde mõju puudus. Lisaks vähenes sel aastal ka söödaks kättesaadav taimne biomass (**II, III**), kuna põud mõjutas tugevalt taimede kasvu. Põud vähendab taimkatet ja mullaniiskust, mis on maapinnal elavate lülijalgsete koosluste jaoks kriitilise tähtsusega tingimused.

Doktoritöö tulemused näitavad, et pärandniitudel on kõrge väärtus, pakkudes elupaika mitmekesisele elustikule ning toetades paljude oluliste ökosüsteemi hüvede pakkumist (**I–IV**). Muutused maakasutuses on aga toonud kaasa pärandniitude pindala kahanemise ja nende seisundi languse. Samas, käesolev doktoritöö näitab, et uuritud pärandniitudel (Lääne-Eesti loopealsed) on endiselt kõrge taastumispotentsiaal (**II, III**) ning sarnastes tingimustes olevatel rohumaadel võiks olla säilinud sarnane taastumispotentiaal. Intensiivsete maakasutuse muutuste ja kliimakriisi tingimustes tuleb säilitada ja majandada maastikke viisil, mis arvestab kohalikke tingimusi, elurikkust ning võimaluse korral maksimeerib ökosüsteemide multifunktsionaalsust.

# ACKNOWLEDGEMENTS

First and foremost, I would like to thank my supervisor, Aveliina Helm, for this incredible and eye-opening experience that attaining a PhD has been. I am grateful for all the opportunities, new skills, and horizons you have helped me to open. It has been a wild ride since my bachelor's, thank you for all of your support. Also, a big thank you to the rest of the workgroup, colleagues, my office roommates, and to my friends outside academia for their friendship and support: Triin, Liis, Eleonora, Bruno, Riin, Krista, Kersti, Elvi, Sigrid, Iris, Marianne, Varje, Virve, Kati, Kristiina, Maarja, Kaari, Kätlin, Jaan, Sabrina, Lena, Aurele, Slendy, and all the rest I have not listed here but deserve my gratitude. I am forever grateful to my family for always supporting and encouraging me! Thank you, Mum, Dad, Aivo, and both my grandmothers!

And last but definitely not the least, I'd like to thank my partner in crime, Nicola! Thank you for being my rock and my clarity, brightening up my gloomy days and sharing cheerful moments!

I would like to dedicate my work to you, Mum, since you never got to have the career in science you deserved! We can share this accomplishment!

***

This work was supported by the Estonian Research Council (PRG874), the European Regional Development Fund (Centre of Excellence EcolChange), the Estonian Ministry of Education and Research, Centre of Excellence for Sustainable Land Use (TK232), the European Commission LIFE+ Nature program (LIFE13NAT/EE/000082), and by the Institute of Ecology and Earth Sciences through the Science Base Funding Support (01.11.2024–31.03.2026).

# PUBLICATIONS

# CURRICULUM VITAE

**Name**: Elisabeth Prangel
**Date of birth**: 20th March 1992
**Citizenship**: Estonian
**Phone**: +372 5665 0730
**E-mail**: elisabeth.prangel@ut.ee
**ORCID**: 0000-0003-0776-5017

### Education:

| | |
|---|---|
| 2017−… | PhD studies in Botany and Ecology, University of Tartu, Estonia. |
| 2015−2017 | MSc (cum laude) in Biology, University of Tartu, Estonia. |
| 2012−2015 | BSc in Biology, University of Tartu, Estonia. |

### Employment history:

| | |
|---|---|
| 2021– | Specialist of Ecosystem Services, University of Tartu, Estonia. |
| 2017–2018 | Specialist/research assistant, University of Tartu, Estonia |
| 2016 | Apprenticeship, Estonian Environmental Board |
| 2014–2015 | Assistant, University of Life Sciences, Estonia |

### Main fields of interest:

Biodiversity, restoration ecology, ecosystem services, ecosystem multifunctionality, grasslands, land-use changes

### Publications:

Gorris, P., Bodin, Ö., Giralt, D., Hass, A. L., Reitalu, T., Cabodevilla, X., Hannappel, I., Helm, A., **Prangel, E.**, & Westphal, C. (2024). Socio-ecological perspective on European semi-natural grassland conservation and restoration: key challenges and future pathways. In *Biological Conservation* (Vol. 304, Issue March). https://doi.org/10.1016/j.biocon.2025.111038

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**Teaching & supervising:**

*Courses:*

| | |
|---|---|
| 2024 | Global Change, Nature and People (4 ECTS), University of Tartu |
| 2024 | Supervisor’s Seminar (3 ECTS), University of Tartu |
| 2021 | Practical Plant Identification (3 ECTS) |
| 2019–2021 | Field Course of Floristics (4 ECTS) |
| 2018 | Field Course of Biological Communities (3 ECTS) |

*Bachelor’s thesis supervision:*

Trepp, V. (2019). “The direct and indirect impacts of biodiversity on human physical and mental health”

Tamme, T. (2023). “The value of pollination service and its economic evaluation methods”

Leppik, R. (2025). “The history of grassland afforestation, the future and ecological impacts”

*Master’s thesis supervision:*

Pall, L. (2021). “Recovery of functional and species diversity of vascular plants on restored alvars in western Estonia”

Petron, A. (in supervision). “Impact of prolonged drought on grassland biodiversity”

## Scholarships and awards:

2022 SERE 2022, 13th European Conference on Ecological Restoration – Best poster presentation award
2018 Kristjan Jaak scholarship for short study visits abroad
2018 Dora Plus short-term mobility scholarship
2017 Smart Specialisation Scholarship for doctoral students

## Oral/poster presentations at international conferences:

**Prangel, E.,** Reitalu, T., Kasari-Toussaint, L., Helm, A. (2025). Grassland restoration increases multitrophic species richness and boosts ecosystem multifunctionality. IALE 2025 European Landscape Ecology Congress. Landscape Perspectives in a Rapidly Changing World. Oral Presentation.

**Prangel, E**., Reitalu, T., Kasari-Toussaint, L., Helm, A. (2024). Recovery of grassland functioning and biodiversity after large-scale restorations. The 66th IAVS Annual Symposium. "From local to global: vegetation patterns across spatial scales in a changing World". Oral Presentation.

**Prangel, E**., Reitalu, T., Neuenkamp, L., Kasari-Toussaint, L., Karise, R., Tiitsaar, A., Soon, V., Kupper, T., Meriste, M., Ingerpuu, N., Helm, A. (2024). Impact of grassland abandonment, degradation, and restoration on ecosystem services and multifunctionality. 14th European Conference on Ecological Restoration. "Bridging Science, Practice, and Policy of Nature Restoration". Society for Ecological Restoration Europe. Oral presentation.

**Prangel, E**., Kasari-Toussaint, L., Helm, A. (2022). Giving LIFE to grasslands – restoring biodiversity and ecosystem services. 13th European Conference on Ecological Restoration. "Restoring Nature, Reconnecting People". Society for Ecological Restoration Europe. Poster presentation.

**Prangel, E**., Bueno, C. G., Helm, A. (2021). Using species pool approach for country-wide mapping of plant-related ecosystem services. 3rd ESP Europe Conference. "Ecosystem Services Science, Policy and Practice in the face of Global Changes". Poster presentation.

**Prangel, E.** Neuenkamp, L., Helm, A. (2021). Effects of degradation and restoration on biodiversity and ecosystem services of semi-natural grasslands. 3rd ESP Europe Conference. "*Ecosystem Services Science, Policy and Practice in the face of Global Changes*". Ecosystem Services Partnership. Oral presentation.

**Prangel, E.** (2019). Restoring grasslands for increasing biodiversity and creating ecosystem service hotspots. ESP 10 World Conference. "*10 years advancing ecosystem services science, policy and practice for a sustainable future*". Ecosystem Services Partnership. Oral presentation.

**Prangel, E.** (2018). Effects of grassland habitat loss on a selection of ecosystem services. ECCB2018 conference – 5th European Congress of Conservation Biology. Society for Conservation Biology. Poster presentation.

**Other scientific activities and professional self-improvement:**

Reviewer for the following journals [n° revisions]: Agriculture, Ecosystems & Environment [1]; Restoration Ecology [3]; Urban Ecosystems [1]; Geocarto International [2]; Biological Conservation [2]; Perspectives in Plant Ecology; Evolution and Systematics [1]; Ecosystem Services [1]; Nature Communications [1]; Journal of Environmental Management [1]; npj Biodiversity [1]; Plants, People, Planet [1]; Applied vegetation Science [2]; Ecological Engineering [2]; Basic and Applied Ecology [1]; GEOSUS [1].

2025 Model-based Multivariate Analysis Summer School
2024 Conference "SERE 14th European Conference on Ecological Restoration: Bridging Science, Practice, and Policy of Nature Restoration" conference organising team member
2023 QGIS with Fundamentals of GIS training course
2023 Training School MODULE II – Flower Biology and Pollination Ecology: from concept to practice promoted by the COST Action ConservePlants – An integrated approach to conservation of threatened plants for the 21st Century
2022 Neobiota conference "12th International Conference on Biological Invasions: Biological Invasions in a Changing World" conference organising team member
2021–2025 Restoring and promoting a long-term sustainable management of Fennoscandian wooded meadows in Estonia and Latvia (WOODMEADOWLIFE), project coordinator/University of Tartu representative.
2021 Experience of European countries in financial evaluation of terrestrial ecosystem services – project coordinator. Report: Prangel, E.; Reinula, I.; Helm, A (2022). Euroopa riikide kogemus maismaaökosüsteemide teenuste rahalisel hindamisel. (1−21). Tartu Ülikool,
2021 Training course "Introduction to ecological modelling"
2019 Training course "Patterns in Vegetation Zonation: Evolution, Ecology and Human Impact"
2018 Doctoral School of Earth Sciences and Ecology complex expedition to Reunion Island
2018 Alternet Summer School – Biodiversity, ecosystem services: science and its impact on policy and society
2018 German-Estonian Summer School on Pollination Ecology

# ELULOOKIRJELDUS

**Nimi:** Elisabeth Prangel
**Sünnikuupäev:** 20.03.1992
**Kodakondsus:** Eesti
**Telefon:** +372 5665 0730
**E-post:** elisabeth.prangel@ut.ee
**ORCID:** 0000-0003-0776-5017

**Haridus:**

| | |
|---|---|
| 2020−… | Doktoriõpe, Botaanika ja ökoloogia, Tartu Ülikool, Eesti. |
| 2017−2020 | Magistrikraad (cum laude) Bioloogia, Tartu Ülikool, Eesti |
| 2012−2017 | Bakalaureusekraad Bioloogia, Tartu Ülikool, Eesti |

**Töökogemus:**

| | |
|---|---|
| 2021– | Ökosüsteemiteenuste spetialist, Tartu Ülikool. |
| 2017–2018 | Spetsialist, Tartu Ülikool |
| 2016 | Praktika, Keskkonnaamet |
| 2014–2015 | Seentekogu andmebaasi ja eksemplaride korrastaja, Eesti Maaülikool |

**Peamised uurimisteemad:**

elurikkus, taastamisökoloogia, ökosüsteemiteenused, ökosüsteemi multifunktsionaalsus, niidud, maakasutuse muutused

**Publikatsioonid:**

Gorris, P., Bodin, Ö., Giralt, D., Hass, A. L., Reitalu, T., Cabodevilla, X., Hannappel, I., Helm, A., **Prangel, E**., & Westphal, C. (2024). Socio-ecological perspective on European semi-natural grassland conservation and restoration: key challenges and future pathways. In *Biological Conservation* (Vol. 304, Issue March). https://doi.org/10.1016/j.biocon.2025.111038

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Motivans Švara, E., Ştefan, V., Sossai, E., Feldmann, R., Aguilon, D. J., Bontsutsnaja, A., E-Vojtkó, A., Kilian, I. C., Lang, P., Mõtlep, M., **Prangel, E**., Viljur, M. L., Knight, T. M., & Neuenkamp, L. (2021). Effects of different types of low-intensity management on plant-pollinator interactions in Estonian grasslands. *Ecology and Evolution*, *11*(23), 16909–16926. https://doi.org/10.1002/ece3.8325

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**Õppetöö ja juhendamised:**

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| | |
|---|---|
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| 2024 | Juhendaja seminar (3 EAP), Tartu Ülikool |
| 2021 | Taimetundmise praktikum (3 EAP), Tartu Ülikool |
| 2019–2021 | Floristika välipraktikum (4 EAP), Tartu Ülikool |
| 2018 | Koosluste välipraktikum (3 EAP), Tartu Ülikool |

*Bakalaureusetööde juhendamised:*

Trepp, V. (2019). “Elurikkuse otsesed ja kaudsed mõjud inimese füüsilisele ja vaimsele tervisele”

Tamme, T. (2023). “Tolmeldamise hüve väärtus ning selle rahalise hindamise meetodid”

Leppik, R. (2025). “Rohumaade metsastamise ajalugu, tulevik ja ökoloogilised mõjud”

*Magistritööde juhendamised:*

Pall, L. (2021). “Soontaimede funktsionaalse ja liigilise mitmekesisuse taastumine Lääne-Eesti loopealsetel”

Petron, A. (juhendamisel). “Põua mõju niidukoosluste elustikule”

## Stipendiumid ja teaduspreemiad:

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| 2018 | Kristjan Jaagu välislähetuste stipendium |
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| 2017 | Nutika spetsialiseerumise erialastipendium doktorantidele |

## Ettekanded rahvusvahelistel konverentsidel:

**Prangel, E**., Reitalu, T., Kasari-Toussaint, L., Helm, A. (2024). Recovery of grassland functioning and biodiversity after large-scale restorations. The 66th IAVS Annual Symposium. "From local to global: vegetation patterns across spatial scales in a changing World". Suuline ettekanne.

**Prangel, E**., Reitalu, T., Neuenkamp, L., Kasari-Toussaint, L., Karise, R., Tiitsaar, A., Soon, V., Kupper, T., Meriste, M., Ingerpuu, N., Helm, A. (2024). Impact of grassland abandonment, degradation, and restoration on ecosystem services and multifunctionality. 14th European Conference on Ecological Restoration. "Bridging Science, Practice, and Policy of Nature Restoration". Society for Ecological Restoration Europe. Suuline ettekanne.

**Prangel, E**., Kasari-Toussaint, L., Helm, A. (2022). Giving LIFE to grasslands – restoring biodiversity and ecosystem services. 13th European Conference on Ecological Restoration. "Restoring Nature, Reconnecting People". Society for Ecological Restoration Europe. Posterettekanne.

**Prangel, E**., Bueno, C. G., Helm, A. (2021). Using species pool approach for country-wide mapping of plant-related ecosystem services. 3rd ESP Europe Conference. "Ecosystem Services Science, Policy and Practice in the face of Global Changes". Posterettekanne.

**Prangel, E.** Neuenkamp, L., Helm, A. (2021). Effects of degradation and restoration on biodiversity and ecosystem services of semi-natural grasslands. 3rd ESP Europe Conference. "*Ecosystem Services Science, Policy and Practice in the face of Global Changes*". Ecosystem Services Partnership. Suuline ettekanne.

**Prangel, E.** (2019). Restoring grasslands for increasing biodiversity and creating ecosystem service hotspots. ESP 10 World Conference. "*10 years advancing ecosystem services science, policy and practice for a sustainable future*". Ecosystem Services Partnership. Suuline ettekanne.

**Prangel, E.** (2018). Effects of grassland habitat loss on a selection of ecosystem services. ECCB2018 conference – 5th European Congress of Conservation Biology. Society for Conservation Biology. Posterettekanne.

## Muud teadustegevused ja erialane enesetäiendus:

Retsensent ajakirjadele [retsenseerimiste arv]: Agriculture, Ecosystems & Environment [1]; Restoration Ecology [3]; Urban Ecosystems [1]; Geocarto International [2]; Biological Conservation [2]; Perspectives in Plant Ecology; Evolution and Systematics [1]; Ecosystem Services [1]; Nature Communications [1]; Journal of Environmental Management [1]; npj Biodiversity [1]; Plants, People, Planet [1]; Applied vegetation Science [2]; Ecological Engineering [2]; Basic and Applied Ecology [1]; GEOSUS [1].

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| 2023 | "Vabavara QGIS geoinformaatika alustega" koolituse läbimine |
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| 2022 | Konverentsi Neobiota korraldusmeeskonnas (12th International Conference on Biological Invasions: Biological Invasions in a Changing World) |
| 2021 | Eesti Maaülikooli ASTRA doktoriprogrammi väärtusahelapõhine biomajandus kursusel "Sissejuhatus ökoloogilisse modelleerimisse" osalemine |
| 2021 | Projekti "Euroopa riikide kogemus maismaaökosüsteemide teenuste rahalisel hindamisel" eestvedaja ja täitja. Aruanne: Prangel, E.; Reinula, I.; Helm, A (2022). Euroopa riikide kogemus maismaaökosüsteemide teenuste rahalisel hindamisel. (1−21). Tartu Ülikool, Ökoloogia ja Maateaduste Instituut. (Tartu). |
| 2021–2025 | Eesti ja Läti puisniitude elurikkuse taastamine ja looduspärandi säilitamine (WOODMEADOWLIFE), Tartu Ülikooli poolt esindaja ja projekti koordineerija. |
| 2019 | Kursus "Taimkatte kõrgusvööndilisuse seaduspärad: evolutsioon, ökoloogia ja inimmõju" |
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| 2018 | Ökosüsteemiteenuste ja elurikkuse alalise koolitus läbimine – "Alter-net Summer School-Biodiversity, ecosystem services: science and its impact on policy and society" |
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