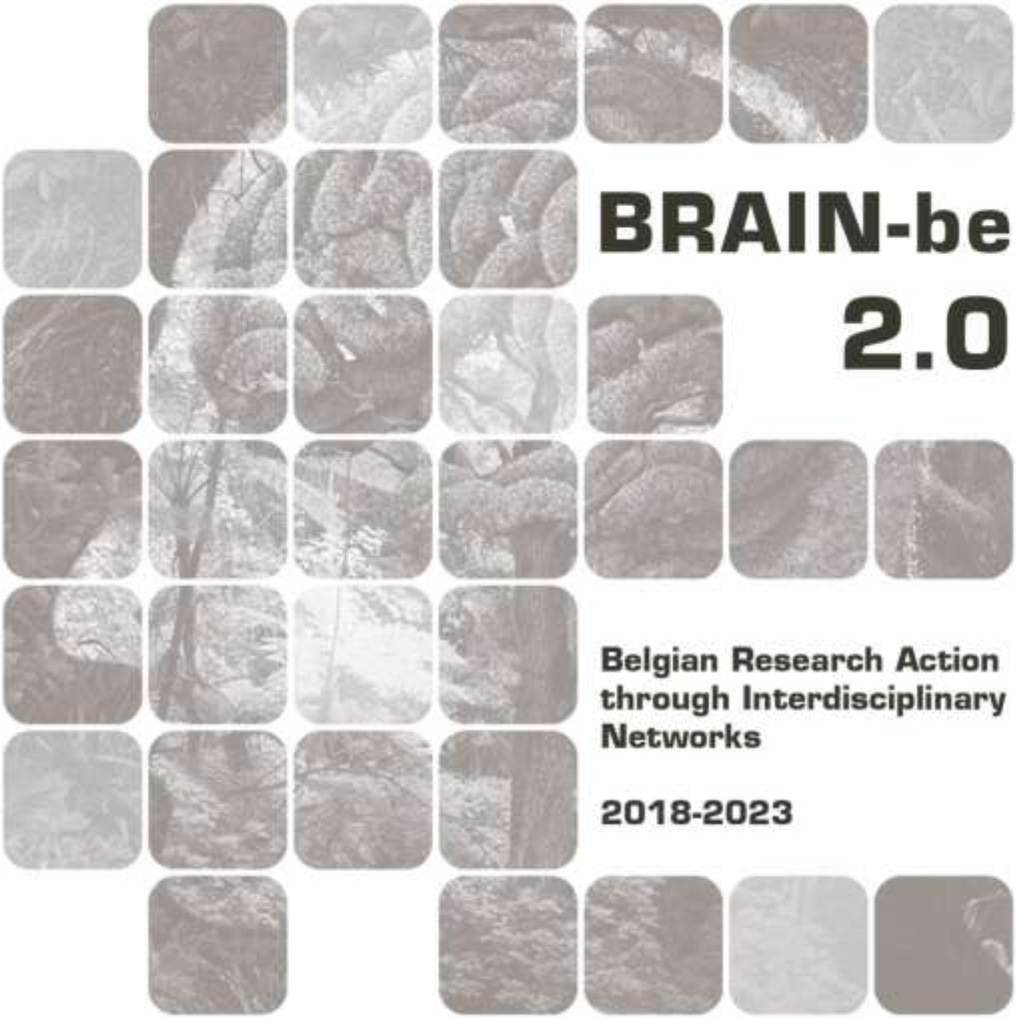

InterRest

Interactive effects of local and landscape scale restoration of semi-natural grasslands and agricultural fields on species interactions and ecosystem functions in different social-ecological systems

Hans Jacquemyn (KU Leuven) - Evan Taylor Sloan (KU Leuven)

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Belgian Research Action through Interdisciplinary Networks

2018-2023

NETWORK PROJECT

InterRest

Interactive effects of local and landscape scale restoration of semi-natural grasslands and agricultural fields on species interactions and ecosystem functions in different social-ecological systems

Contract - B2/22E/InterRest

FINAL REPORT

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ABSTRACT

Context

Calcareous grasslands were created by traditional land use in European cultural landscapes and are among the most species-rich habitat types. They host many rare and highly endangered species but are nowadays often threatened, mainly by abandonment and eutrophication. Restoration measures are therefore urgently needed. However, transnational restoration approaches are lacking, and evaluations within regional restoration schemes usually focus only on indicator species or species richness and ignore biotic interactions, ecosystem functions and the landscape context. Species interactions, in particular, are important indicators of restoration success, as they are often more sensitive to environmental changes and determine vital functions that are necessary to stabilize ecosystems. InterRest analyses and links multiple interaction networks representing different ecosystem functions (e.g. decomposition, pollination, predation) as well as social-ecological interactions.

Objectives

InterRest investigates species interactions across different trophic levels, including plant-soil, plant-pollinator, and bird-food resource interactions, in both restored and degraded calcareous grasslands that are embedded in different socio-ecological and landscape contexts in three countries (Germany, Spain and Estonia). Biodiversity and species interactions are assessed by vegetation surveys, metabarcoding of soils, bird surveys, arthropod sampling via pitfall traps and sweep netting, bird faeces sampling, transect walks for bees and pollen collection.

In addition, InterRest evaluates ecosystem functions such as soil processes, pollination and predation. To this end, we conduct decomposition experiments, measure seed set of wild plant species, and use dummy caterpillars to measure predation pressure. It is hypothesised that local restoration measures will lead to more complex and stable interactions and improved ecosystem functions compared to degraded sites. Furthermore, InterRest investigates whether landscape-scale restoration through agri-environment schemes can make local restoration efforts more effective through additive or synergistic effects.

Finally, the project investigates a range of social factors that affect the willingness and capacities of stakeholders to implement restoration at both local and landscape scales. These include farmers, nature conservation organisations, land managers and local conservation authorities. Based on stakeholder interviews and ecological data, InterRest develops social-ecological networks to better understand human-nature interdependencies. To synthesize the results of this project, meta-network and multifunctional approaches will be applied to identify conservation priorities and possible trade-offs.

Conclusions

The results obtained so far indicate that restoration through extensive management in calcareous grasslands has positive effects on biodiversity. In Estonia, plant species richness and bird abundance were higher in restored sites compared to abandoned ones, but similar effects were not observed in Germany and Spain. Long-term abandonment and intensive management both reduced wild bee species richness and abundance, either directly or indirectly through effects on floral resource availability.

The extent of calcareous grassland and AES in the surrounding landscape benefited wild bee communities, although the effectiveness of AES often depended on the amount of calcareous grasslands in the landscape. Bees collected a more diverse range of pollen in grasslands with lower shrub coverage, an indicator of sufficient management and successful restoration. Floral cover and richness were fundamental for restoring diverse interactions and supporting interaction complementarity.

Moreover, greater landscape cover of agri-environment schemes (biodiversity-friendly farming practices) promoted more redundant interactions across grasslands and buffered against grasslands becoming isolated from the regional meta-network, promoting links between regional communities. Finally,we identified five key challenges that currently hinder effective site-level management for restoration and conservation success. We provide general recommendations to strengthen management capacities and to better address these challenges locally.

Keywords

Biodiversity, calcareous grasslands, ecosystem functions, habitat restoration, interaction networks, landscape ecology

1. INTRODUCTION

Biodiversity in Europe is closely linked to cultural landscapes, where traditional agriculture led to high biodiversity through a small-scale mosaic of extensively managed land-use types (Robinson et al. 2002). However, agricultural intensification has led to widespread landscape simplification (Newbold et al. 2015) and biotic homogenization (Gámez-Virués et al. 2015; Sirami et al. 2019). To recover species-rich habitats, tailored and collaborative restoration efforts are urgently needed (Jones et al. 2018; Samways et al. 2020).

One particularly important habitat type is calcareous grasslands, which developed under extensive grazing and mowing regimes and are found across many European countries (Poschlod et al. 2002). These grasslands host plant and animal communities that especially adapted to dry, nutrient-poor soils (Kasari et al. 2016; Öckinger et al. 2006). They are among most species-rich habitats in Europe and provide niches for many endangered plants, insects and birds (Ernst et al. 2017; Gazol et al. 2012; Kormann et al. 2015).

At present, most remnants of calcareous grasslands are fragmented and embedded in intensively used agricultural landscapes, where they are threatened by ongoing land-use intensification or abandonment (WallisDeVries et al. 2002; Adriaens et al. 2006; Helm et al. 2006). The decline of traditional agropastoral practices in particular has led to shrub and tree encroachment, resulting in the homogenization of microhabitats and disrupting microorganisms-plant-animal interactions, with cascading effects on ecosystem functions (Gossner et al. 2016). At the landscape scale, habitat loss leads to increasing habitat fragmentation, with detrimental effects on biodiversity. Restoration efforts have focused on shrub and tree removal and the reintroduction of mowing or grazing regimes (Öckinger et al. 2006; Kahmen et al. 2002). In this context, “restoration” refers to the re-establishment of traditional management practices that are essential for conserving high biodiversity, including rare and endangered species, within cultural landscapes.

These restoration efforts have proven effective in enhancing species richness across multipe trophic levels (Ernst et al. 2017, Gazol et al. 2012, Kormann et al. 2015, Neff et al. 2020). However, solely evaluating recovery of certain species or species richness neglects other key aspects of ecosystem recovery (Devoto et al. 2012). First, species with different traits may respond differently to restoration management (Kormann et al. 2015). Second, species interaction networks provide better insights into communities, as they are often more sensitive to environmental change and ultimately determine ecosystem functioning (Schleuning et al. 2016; Kaiser-Bunbury et al. 2017). Therefore, these networks are important indicators for long-term ecosystem stability and resilience that cannot be captured by richness metrics alone (Tylianakis et al. 2017). Thus, network approaches are essential for restoring functional diversity and ecosystem processes (Lauhglin 2014; Engst et al. 2016). Additionally, species interactions have important impacts on ecosystem services in agricultural landscapes. For example, spill-over of beneficial organisms from calcareous grasslands are well-documented and isolation from calcareous grasslands reduces predation and pollination services (Blitzer et al. 2012).

Restoration outcomes also need to be evaluated at multiple spatial scales. Despite evidence that habitat connectivity and landscape heterogeneity can have synergistic effects on taxonomic and functional biodiversity (Gámez-Virués et al. 2015; Kormann et al. 2019) and also on the structure and stability of ecological networks (Pelissier et al. 2018; Gras et al. 2018), most terrestrial restoration programs focus on local habitats and neglect the landscape context in which the habitats are embedded (Perring et al. 2015; Lane et al. 2020). Local restoration might only be successful if calcareous grasslands are connected to other sites, enabling species recolonization. In addition, other types of extensively managed habitats may contribute to the restoration success. Agri-environment schemes (AES) have been established to increase biodiversity in agricultural landscapes and are supported by the Common Agricultural Policy in the EU. These include organic farming, flower fields or fallows. AES can play an important role in supporting the restoration of landscapes surrounding calcareous grasslands, as they generally promote biodiversity more effectively than conventionally managed fields (Batáry et al. 2015; Zingg et al. 2019). In landscapes where no other calcareous grasslands are present, AES may serve as species sources or stepping stones and therefore facilitate species richness, species interactions and ecosystem functions in restored sites. Thus, landscape-scale restoration with AES may be a crucial complement to site-level restoration. Yet, potential additive or synergistic effects of local grassland restoration combined with AES at the landscape scale have not been systematically evaluated.

Additionally, while network approaches based on interactions occurring at local spatial scales are important to determine local ecosystem functions, but may fail to capture properties of biotic interactions that emerge at larger scales (Hagen et al. 2012). To solve this, biotic interactions can be studied in novel meta-network frameworks where local communities are linked by the interactions they share (Emer et al. 2018; Librán-Embid et al. 2021). From a conservation and restoration perspective, it is essential to find and safeguard the most central (i.e. important) nodes within a meta-network (i.e. central interactions or habitats). The loss of central nodes has the most negative effects for the whole structure of the network (Martín-González et al. 2010), eventually leading to network collapse and to the disappearance of ecosystem functions at the landscape level (Emer et al. 2018).

Finally, outcomes of restoration schemes largely depend on the social-ecological context and the motivation and interest of the actors within these systems (Jellinek et al. 2019). Successful upscaling of restoration to landscapes therefore requires integrating both ecological and social dimensions (Perring et al. 2015; Isbell et al. 2017). Social–ecological networks provide a framework for analysing these complex relationships across scales (Bodin et al. 2019). By examining the structure of such networks and the alignment of ecological and social processes (social–ecological fit), we can better understand the interdependencies that either facilitate or hinder restoration success (Bodin et al. 2020; Epstein et al. 2015).

2. STATE OF THE ART AND OBJECTIVES

The major aim of InterRest is to investigate species interactions across different trophic levels including plant-soil, plant-pollinator and bird-food resource interactions, in restored and degraded calcareous grasslands that are embedded in different socio-ecological and landscape contexts in three countries (Germany, Spain and Estonia). Biodiversity and species interactions are assessed using vegetation surveys, metabarcoding of soils, bird surveys, arthropod sampling (pitfall traps and sweep netting), analysis of bird faeces, transect walks for bees and pollen collection. In addition, InterRest measures different ecosystem functions such as soil functions, pollination and predation. Specifically, we pursue the following objectives:

Objective 1

Develop an index of local restoration intensity in calcareous grasslands and assess its effect on biodiversity, species interactions across different trophic levels (plant-soil-interactions, plant-pollinator-interactions and bird-food resource-interactions) and ecosystem functions (soil, pollination and predation functions). We focus on different biodiversity dimensions, i.e. species richness, functional diversity and interaction networks of soil organisms, plants, pollinators and birds.

Objective 2

Evaluate whether local restoration of calcareous grasslands is more effective when combined with landscape restoration through AES, and whether additive/synergistic effects depend on connectivity to other calcareous grasslands. We will compare the relative importance of restoration at different spatial scales and quantify possible additive/synergistic effects to identify key drivers of restoration measures.

Objective 3

Quantify the resource use of mobile organisms (pollinators, birds) to determine the role of landscape resources under different contexts of local/landscape restoration, including the use of crops and pest species as indicators of ecosystem services and disservices. This will allow us to quantify pollination and predation functions and evaluate potential co-benefits or trade-offs with crop production.

Objective 4

Assess the interlinkages between functional diversity, species interaction networks, and ecosystem functions to identify easily quantifiable indicators for ecosystem stability and resilience. We will assess how multifunctionality can be achieved or whether there are synergies or trade-offs between different functions. The analysis of multifunctionality will give insight whether different ecosystem functions can be promoted simultaneously with local and landscape restoration.

Objective 5

Upscale species interactions (plant-pollinator, bird-food resource) to the regional scale by using meta-network approaches and assess how local and landscape restoration affect the centrality of sites This will provide guidelines for restoration prioritization and reveal properties of biotic interactions that emerge at larger spatial scales.

Objective 6

Examine the role of social–ecological networks in shaping restoration outcomes for functional diversity, species interactions, and ecosystem functions at both local and landscape scales. Using integrative socio-ecological approaches, we will analyse stakeholder structures, interdependencies, and their linkages to ecological outcomes.

3. METHODOLOGY

To achieve Objectives 1–6, we conducted intensive ecological sampling within WP1-4, focusing on biodiversity, species interactions and ecosystem functions across different taxa:

WP1 Selection of study sites and calculation of a standardized restoration index

In each of the three study regions (Germany, Spain, Estonia), 32 calcareous grasslands were selected as study sites representing a restoration gradient. Prior to site selection, all available information on management practices was compiled. Based on these data, a standardized restoration index (Objective 1) was developed across all study regions. The index was based on the following variables: (1) continuous management over the last 25 years (yes = 1, no = 0), (2) regular shrub removal (yes = 1, no = 0), (3) grazing index, and (4) woody cover.

Low to moderate intensity grazing is broadly accepted as necessary to both restore and maintain the species richness and unique community composition of calcareous grasslands (Škornik et al., 2010; van Wieren & Bakker, 2008) and to support higher pollinator richness and abundance (Lazaro et al., 2016; Weiner et al., 2011). The grazing index was used as a measure of grazing intensity and defined as:

$$G_j = \frac{\frac{\sum_{i=1}^{n} N_{ij} * M_{ij} * L_i}{12}}{A_j}$$

where N_{ij} is the number of individuals of animal species i in site j, M_{ij} is the number of months animal species i grazed in site j in 2022, L_i is the livestock unit of the animal species i and A_j is the grazed site area of site j. Livestock units for each animal species were 0.1 for goats, 0.1 for sheep, 1 for cattle, and 1.1 for horses (see Fischer et al., 2010). Woody cover was assessed by calculating the average proportion of ground covered by shrubs or trees within the five vegetation survey plots. All of the above variables other than woody cover were determined through interviews with land managers.

To create the index, sites were ordinally ranked according to the management measures (continuous management over the last 25 years, shrub removal, and grazing) and their state of abandonment as indicated by woody cover. First, a principal component analysis (PCA) was conducted on the management measures using the ‘vegan’ package (Oksanen et al., 2024). The first PCA axis (PC1) represented 41.8% of the explained variance and was positively correlated with all of the constituent variables. Sites were then ranked by their PC1 values, with the highest score set as the highest management value. Second, sites were ranked by their proportion of woody cover, with the lowest shrub cover receiving the highest rank. Lastly, the mean of both ranks was assigned to each site to create the final management-abandonment index.

WP 2 Plant-soil interactions

Task 2.1 Soil and plant data sampling

Soil and plant fieldwork was conducted in summer 2022. In each of the 96 grassland sites (32 per country), five subsites were established. At each subsite, plant diversity was characterized at three nested spatial scales (1x1 m, 2x2 m plots and 5 m radius area). From the same subsites, soil samples were collected for environmental DNA, soil chemistry, and bulk density analysis. In addition, root samples were collected from one focal plant to study its symbiotic fungi in more detail. In Germany and Estonia, the focal plant was *Centaurea jacea*, in Spain, it was *Thymus vulgaris*.

Task 2.2 Soil analysis

Basic soil chemistry analyses (pH, K and P content) of soil samples from all three countries were performed at the Centre of Estonian Rural Research and Knowledge in spring 2023. Soil organic matter content and soil bulk density were analysed at the Institute of Ecology and Earth Sciences in University of Tartu in summer and autumn 2023. Soil and root DNA was extracted in summer 2023, and the DNA samples were subsequently sent for PCR amplification and sequencing in autumn 2023.

Task 2.3. Soil decomposition experiment

In addition to previously planned soil sampling, an experiment was conducted in summer 2023 to estimate the decomposition of organic matter in our study grasslands. We used a citizen science protocol called “The teabag index”, in which standardized green tea (fast-decomposing) and rooibos tea (slow-decomposing) bags were buried at three subsites per grassland site in spring 2023 and retrieved three months later. After retrieval, the teabags were dried and weighed to calculate decomposition rates.

WP 3 Plant-pollinator interactions

Task 3.1 Plant pollinator interactions

Wild bees were recorded by transect walks in each study region during the main flight periods in 2022 and 2023 (Estonia: 23.05. – 21.08.2022; 21.05 – 16.08.23; Germany: 17.05. – 15.08.2022; 06.05 – 16.08.2023; Spain: 07.04. – 21.07.2022; 03.04. – 23.06.2023). Sampling was conducted between 9 a.m. and 5 p.m. under favorable conditions (air temperature > 15 °C, wind speed < 5 on the Beaufort scale, sunny), with few exceptions (51 out of 2216 transects) when bees were observed to be active despite suboptimal conditions. Each site was visited three times per year, except for 22 sites in Estonia that could not be sampled a third time in 2023 due to unfavorable weather conditions in late summer.

During each visit, four transects of 50 m length and 2 m width were walked for 5 minutes (excluding handling time). The number and identity of flower-visiting bees were recorded, and individuals were captured with an insect net when necessary for identification. When identification in the field was not possible, specimens were killed with ethanol or ethyl acetate and identified to species level in the laboratory. Transect placement was flexible but aimed to include flower-rich patches representative for the entire site.

Task 3.2 Pollen resource use analyses

To assess pollen resource and plant-pollinator interactions in the wider landscape, pollen samples were collected from the bodies of two Bombus species (*Bombus lapidarius* and *B. pascuorum*) in 2022 in Germany. In addition, nest blocks constructed from medium-density fiberboard were placed at each of the 32 study sites in Estonia to assess pollen resource use of the solitary bee *Osmia leaiana*. Each nest block contained 10 x 5 holes approximately 8 mm in diameter. The blocks were attached to trees or juniper shrubs at approximately 1.2 m height facing south. Between 23 June and 16 August 2022, nests were checked for occupancy by *O. leaiana*, and pollen was collected from occupied nests for metabarcoding analysis to assess floral resource use.

Pollen DNA was extracted using the Plant/Fungi DNA Isolation 96 Well Kit (Norgen Biotek). Pellets were resuspended in 200 µL of Lysis Buffer L and transferred to a 96-well plate pre-loaded with ceramic beads for mechanical homogenization using a bead mill. After homogenization, an additional

200 µL of Lysis Buffer L was added to each well, and DNA extraction was conducted following the manufacturer's protocol. PCR amplification targeted the ITS2 region using the ITS2-S2F/ITS4R primer pair (White et al., 1990; Chen et al., 2010) optimized for dual indexing (Sickel et al., 2015) on an Illumina MiSeq system (Illumina, San Diego, CA, USA). Sequencing was conducted at the Genomics Core Leuven, Belgium.

Task 3.3 Pollination function

Seeds from open-pollinated focal plants (*Centaurea jacea* in Germany and Estonia, *Lotus corniculatus* in Germany, and *Genistra scorpius* in Spain) from all study sites. In addition, a pollinator exclusion experiment was conducted with these focal plants at three study sites per region to assess the contribution of insect pollinators to seed set.

WP 4 Bird-food resource interaction

Task 4.1 Bird sampling

All field data were collected during the springs of 2022 and 2023. Between one to three bird point-counts were established in each of the 32 grasslands per region. Each point-count was conducted twice per season (spring) to cover the phenology of the different bird species within the community, between April and July, depending on latitude and seasonal progress in each region.

In addition to the point counts, acoustic monitoring was carried out between or during the two bird surveys. For this purpose, one Audiomoth recorder was placed in a central position within each grassland, near the bird count points. The recorders remained in the field for a minimum of seven consecutive days to obtain detailed information on bird acoustic diversity and persistence over time. Morning choruses were recorded following a standardized schedule in each region: consecutive 10-minute recording segments starting half an hour before sunrise and continuing for two hours after sunrise.

Task 4.2. Bird food resource sampling

All the data were collected during the springs of 2022 and 2023. In each region, available arthropod food resources were sampled using pitfall traps and sweep netting to estimate the arthropod biomass and community composition. Between one and three sampling points were established in each grassland, depending on its size. Each arthropod sampling point included three pitfall traps that remained in the field for seven consecutive days, and one sweep-netting transect. Arthropod sampling was conducted once per season, either in 2022 or 2023, depending on the region.

To study the birds' diet, faecal samples were collected during 2022 or 2023, depending on the region. A minimum number of three faecal samples per grassland were collected either by visiting natural perches commonly used by birds or by mist-netting under appropriate permits. Both arthropod and faecal samples are currently being analysed through metabarcoding to identify arthropod taxa present in both sample types.

Task 4.3 Predation function

Data for this task were collected during spring 2023. Twenty dummy caterpillars made of modeling clay were left in pairs (one brown and one green) on bushes in each grassland. The models were exposed for seven days and subsequently examined for bird beak marks to evaluate the predation pressure exerted by birds.

WP5 Actors' and stakeholders' perceptions and social-ecological networks

To achieve Objective 6, we conducted interviews with stakeholders within WP5. The first step was to identify key actors in the study regions. In total, 12 scoping interviews were conducted with these key actors, including farmers, non-governmental organizations (NGOs), and representatives of nature conservation authorities.

Based on insights from the scoping interviews, a questionnaire was developed for farmers managing calcareous grasslands. The questionnaire included questions on management practices, the economic value of the study sites, as well as farmers' motivations, challenges, and interactions with other stakeholders. In total, approximately 40 interviews were conducted with farmers associated with our study sites.

WP6 Synthesis

The synthesis phase will commence after the completion of all field and laboratory work. This work package will integrate ecological, functional, and social datasets across all study regions and will address Objectives 5 and 6. The synthesis will combine results from WP1–5 to identify key ecological and social drivers of restoration success and to provide comprehensive recommendations for biodiversity-based grassland restoration.

4. SCIENTIFIC RESULTS AND RECOMMENDATIONS

WP1 Study sites

The study was conducted in three well-studied empirical case regions in Estonia, Germany and Spain (Fig. 1). The three regions represent distinct cases of European semi-natural grassland conservation contexts. They differ in several key ecological and socio-economic contexts, including:

- Trends in nationwide coverage of semi-natural grasslands: Estonia shows a slightly increasing extent of semi-natural grasslands, whereas coverage is declining in Spain and Germany;
- Size of existing patches: Estonia hosts larger continuous grasslands patches, Germany mainly smaller fragments, and Spain a mixture of both);
- Climatic conditions: Estonia lies within the Hemi-boreal Climate Zone, Germany in the Temperate Climate Zone, and Spain in the Mediterranean Climate Zone;
- Socio-economic contexts: The three regions differ in land-use intensity, management traditions, and conservation policy frameworks.

Further details on the characteristics of the study regions are provided in Table 1.

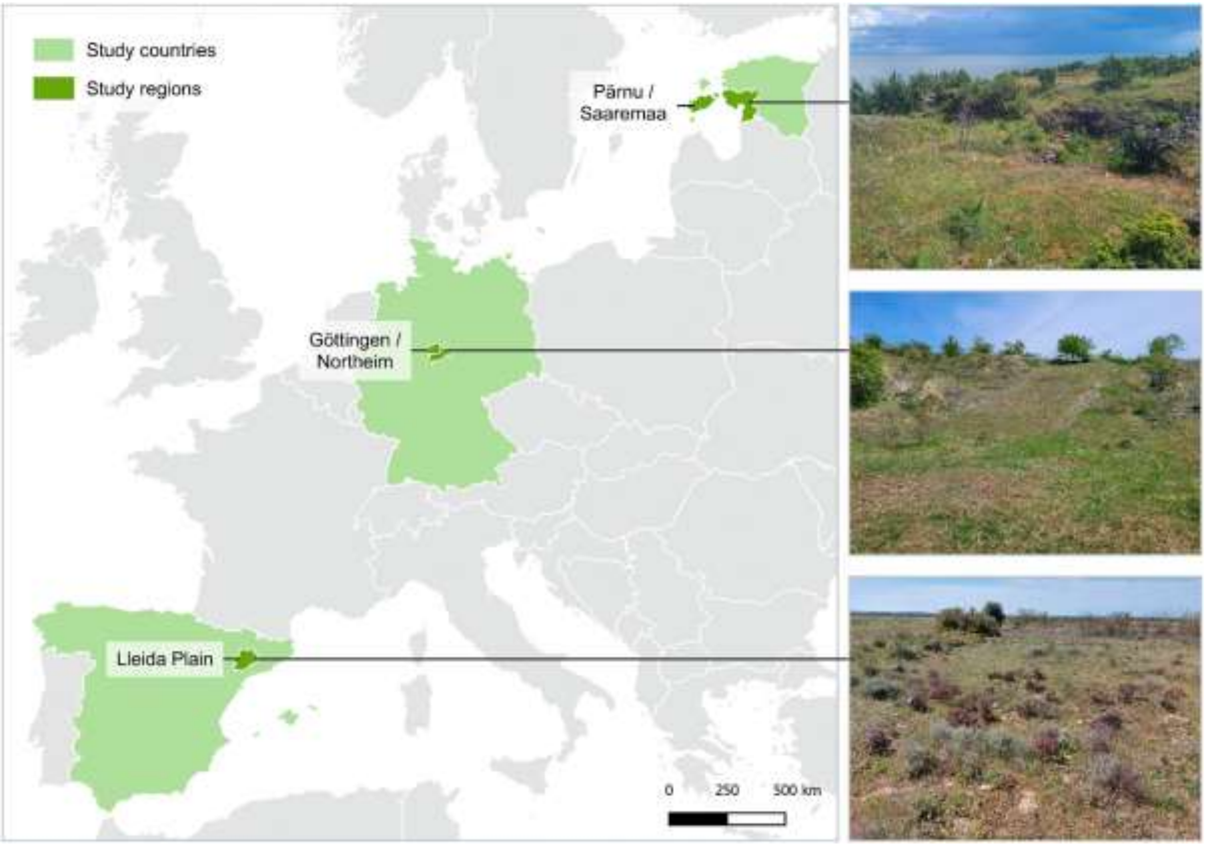

Figure 1: Map of the study regions and photos of semi-natural grassland sites in Estonia, Germany and Spain (from Gorris et al. 2025).

Table 1. Description of the semi-natural grasslands in the case study regions. Habitat codes refer to the EUNIS classification of European habitat types.

Country	Study region	Context
Estonia	Western mainland and the Baltic islands Muhu and Saaremaa	Calcareous grasslands (habitat code 6210, 6280) in Estonia are concentrated in the northern and western part of the country. The study region lies within the Hemi-boreal climate zone and features relatively large calcareous grassland patches; a single pasture often includes semi-natural grasslands of different habitat types. The study area with its 11 % semi-natural grasslands (ca. 1/3 managed) has a higher cover than the rest of Estonia. Semi-natural grasslands are embedded within a mosaic of forests and agricultural land. All managed study sites in the region are located in nature reserves. The grasslands are mainly grazed by sheep, goats, cattle, and occasionally horses. Following a large-scale decline in grassland area until the end of the 20th century, national restoration efforts during the past 15 years have led to a slow but steady increase in overall semi-natural grassland coverage, including calcareous grasslands in the study region.
Germany	Central Germany, Southern Lower Saxony in the districts Goettingen and Northeim	Calcareous grasslands (habitat code 6210) are widespread in Germany, particularly in central and southern Germany. The study region is located within temperate latitudes in the transitional zone between oceanic and continental climates. Land use in the study region is dominated by intensive crop farming with cereals, oilseed rape, maize and sugar beet as main crops, while hilltops are often covered with fertile grasslands and forest patches. Most calcareous grassland patches in the study region are smaller than 1 ha, with only a few larger sites. The grasslands are mainly grazed by horses, goats and sheep, and occasionally by cattle. Two decades ago, the coverage of calcareous grasslands in the region was estimated at 0.26%, and the small sites are widely dispersed. No recent data are available, but coverage may have declined further. With few exceptions, almost all sites have undergone successional phases in recent decades and have been restored primarily through small-scale initiatives led by local environmental NGOs.
Spain	Northern Spain, Catalonia, at low altitudes south of the Pyrenees in the Lleida Plain	Calcareous grasslands (habitat code 6210, 6220) in Spain occur across the Mediterranean, Atlantic and alpine bioregions. The study area is part of the Mediterranean Bioregion, situated south of the Pyrenees. Calcareous grasslands typically form small (ca. 0.5–20 ha) but occasionally large (up to ~1000 ha) patches, dispersed among cropped areas dominated by cereals, almonds and olive trees. Grazing is mainly by sheep and goats. Calcareous grasslands in the region follow the national trend of decreasing coverage and increasing degradation of

Country	Study region	Context
		semi-natural grassland ecosystems. Few conservation or restoration initiatives exist either nationally or within the study region.

WP 2 Plant-soil interactions

At the time of writing, results for plant–soil interactions were not yet available.

WP3 Plant-pollinator interactions

Wild bee diversity

A total of 6716 wild bee individuals were observed across the three countries: 2761 in Estonia, 2523 in Germany and 1432 in Spain. Across all transects, we identified 235 wild bee species: 86 in Estonia, 128 in Germany and 98 in Spain. Both local and landscape characteristics influenced wild bee species richness and abundance in semi-natural calcareous grasslands across three different European regions. At the local scale, wild bee richness and abundance decreased with both long-term abandonment and intensive management (Estonia, Spain), either directly or indirectly through plant community changes (Fig. 2).

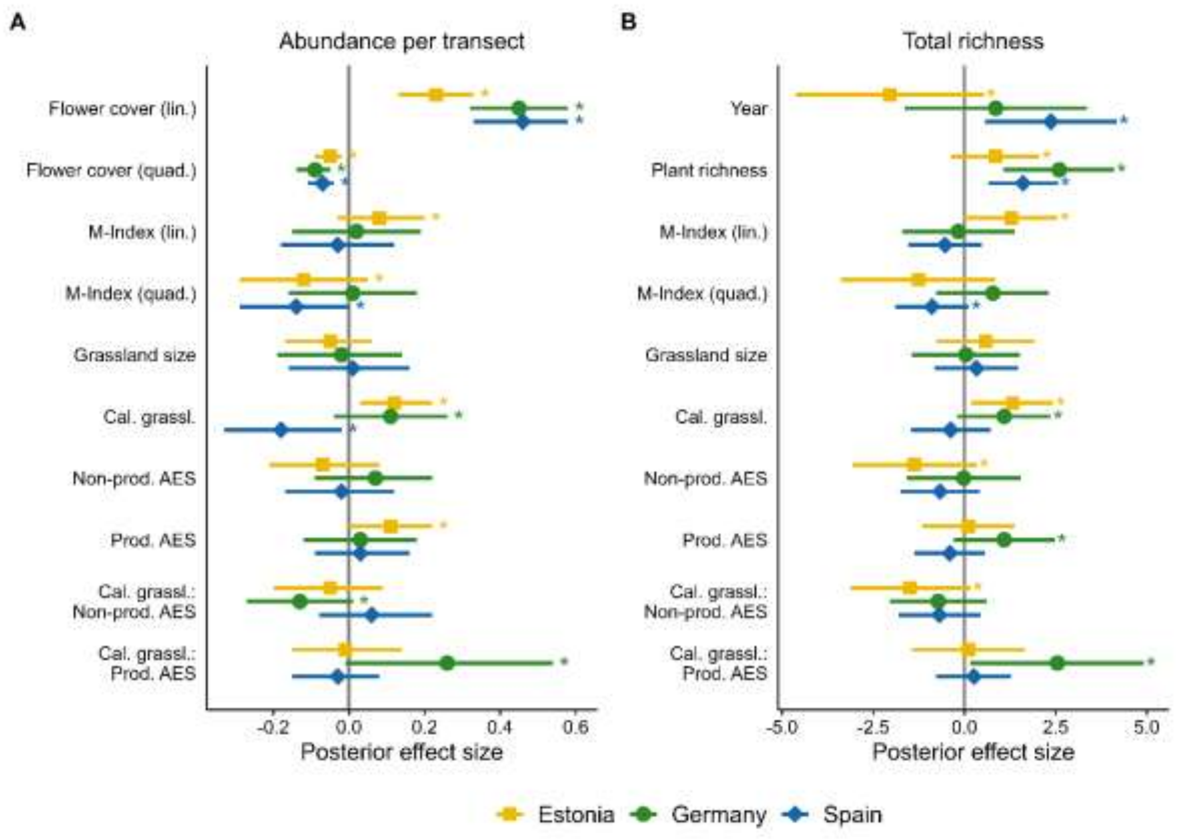

Figure 2: Estimated posterior effects from generalized linear mixed models and linear models analyzing the effects local and landscape management on wild bee abundance per transect (A) and

total species richness (B). All fixed effects (flower cover (linear), flower cover (quadratic), flowering plant richness, year, management index (linear), management index (quadratic), grassland size (ha), cover of calcareous grassland, non-productive AES, productive AES, interaction of calcareous grassland cover with both AES types, respectively) are shown. For each fixed effect, mean and 95 % credible intervals of the posterior are presented. Results are differentiated by country (from Hahnappel et al., unpubl. results).

The cover of calcareous grasslands in the surrounding landscape had clear positive effects in two of the three study regions, suggesting that connectivity between grasslands also plays a role (Fig. 3). However, the effects of agri-environment schemes (AES) often depended on the calcareous grassland cover in the landscape. Cover of productive AES was positively related to total wild bee species richness and abundance in Estonia and Germany, but in Germany this effect was observed only in combination when cover of calcareous grasslands was high. These results indicate that the conservation and restoration of calcareous grasslands should be prioritized.

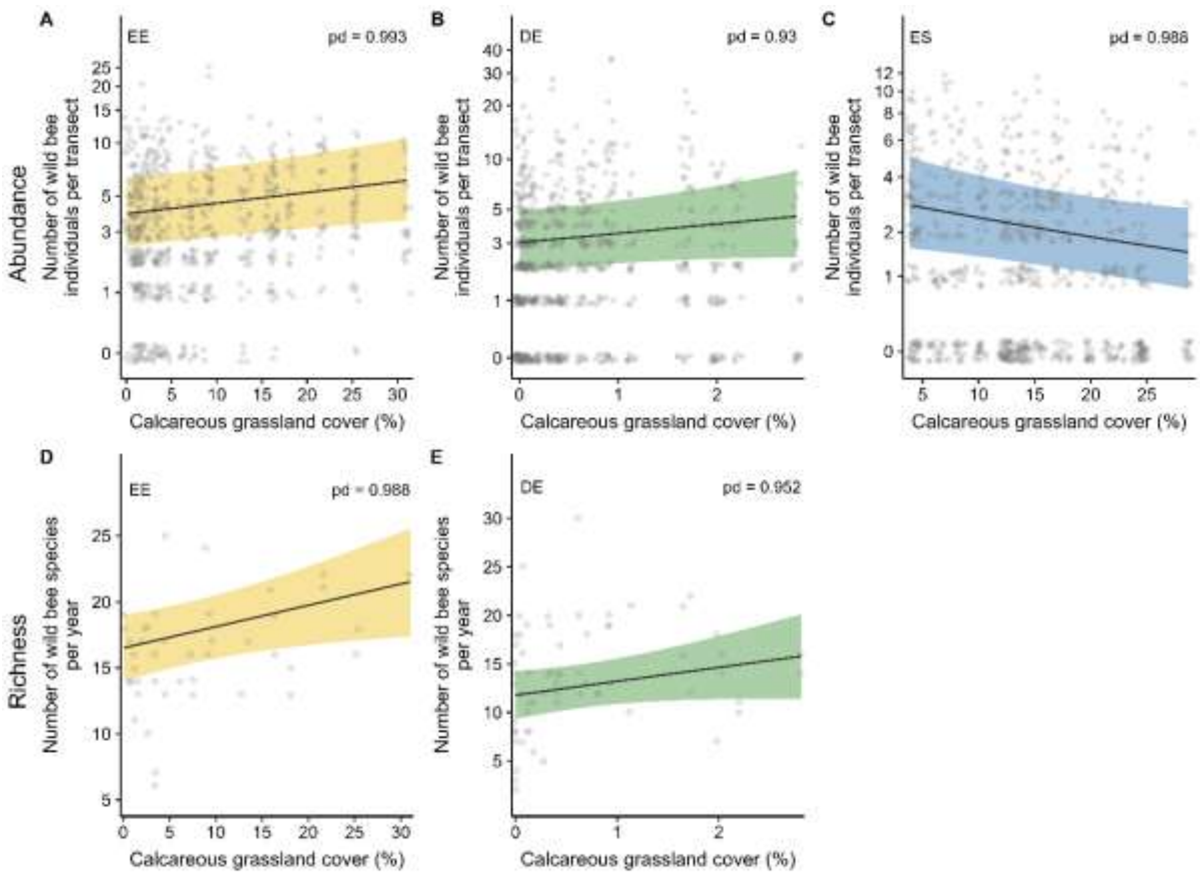

Figure 3: Effect of calcareous grassland cover within a 1 km buffer on wild bee abundance per transect (A–C) and total species richness (D–E) in Estonia (EE), Germany (DE) and Spain (ES). Mean estimated effects are shown as solid lines, while 95 % credible intervals are presented by shaded areas (from Hahnappel et al., unpublished results).

Pollen resource use

In total, 126 and 142 plant species were identified in the pollen collections of *B. lapidarius* and *B. pascuorum*, respectively. Of these, 49 (38.9%) and 67 (47.1%) were not recorded in any of the sites during the plant surveys and transect walks, suggesting that they were foraged from the surrounding landscape. Examples include *Helianthus annuus* and *Lythrum salicaria* in *B. lapidarius* and *Lathyrus heterophyllus* and *Digitalis purpurea* in *B. pascuorum*. Many of these species are known to occur in agri-environmental schemes, such as flower strips, and in agricultural fields in the surrounding landscape.

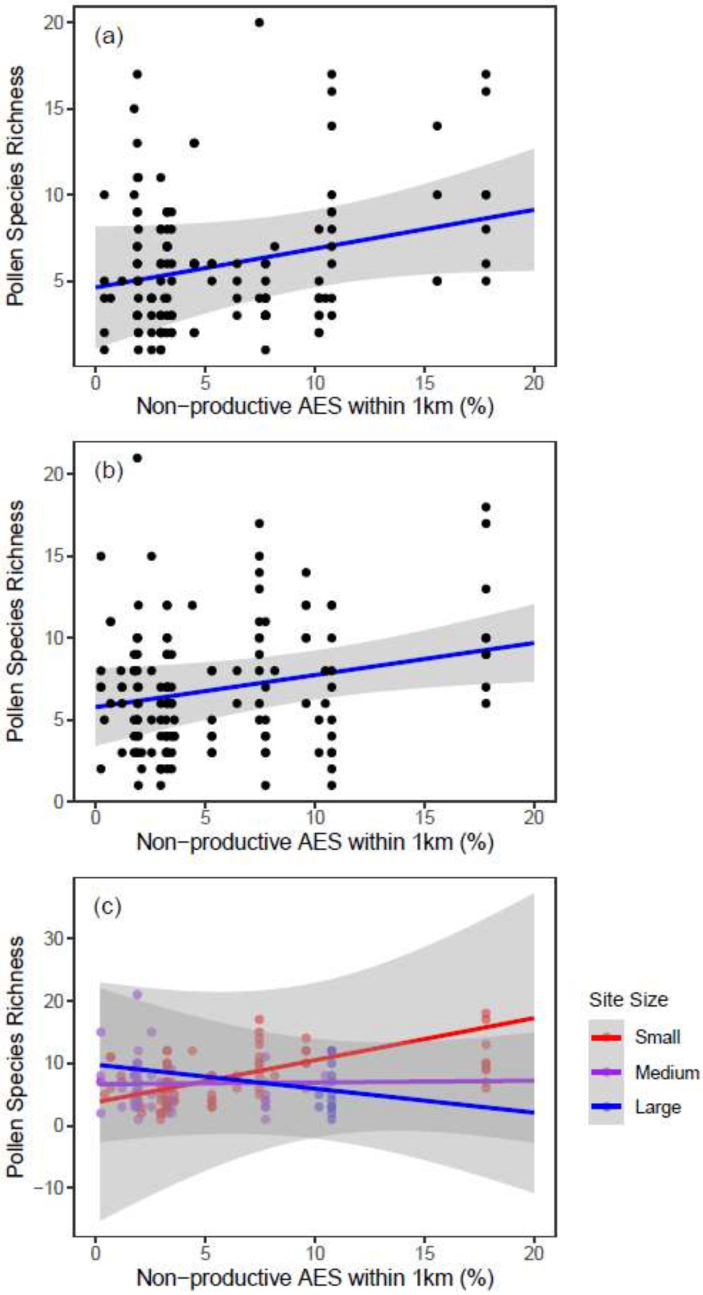

Figure 4: Effect plots assessing the influence of landscape characteristics on pollen species richness found on individual (a) *Bombus lapidarius* and (b, c) *Bombus pascuorum* samples. 3c illustrates the interaction effect between non-productive AES and site area (from Sloan et al. 2025).

The percentage of land within 1 km dedicated to non-productive AES was associated with higher pollen species richness in *B. lapidarius* (estimate = 3.34, SE = 1.64, p = 0.042; Fig. 4). For *B. pascuorum*, both the percentage of land dedicated to non-productive AES, site area, and their interaction had significant effects on pollen richness. Specifically, a higher percentage of land dedicated to non-productive AES was associated with increased pollen species richness (estimate = 7.95, SE = 2.33, p < 0.001; Fig. 4b). The negative interaction between non-productive AES within 1 km and site area (estimate = -1.89, SE = 0.729, p = 0.009; Fig. 4c) indicates that bumblebees foraged more extensively in the surrounding landscape when calcareous grasslands were small.

Besides, both local and landscape variables had significant effects on the plant species composition of pollen samples of both bumblebee species (Fig. 5). For *B. lapidarius*, the percentage of conventional agriculture and non-productive AES within 1 km, site area, and plant species richness per site had significant effects on pollen load species composition (adj-R2 = 0.069, F = 3.52, p < 0.001; Fig. 5a). For *B. pascuorum*, the percentage of conventional agriculture, productive AES, non-productive AES, and calcareous grasslands within 1 km as well as the abandonment-management index, site area, and plant species richness of each site were explanatory and significant (adj-R2 = 0.095, F = 3.16, p < 0.001; Fig. 5b).

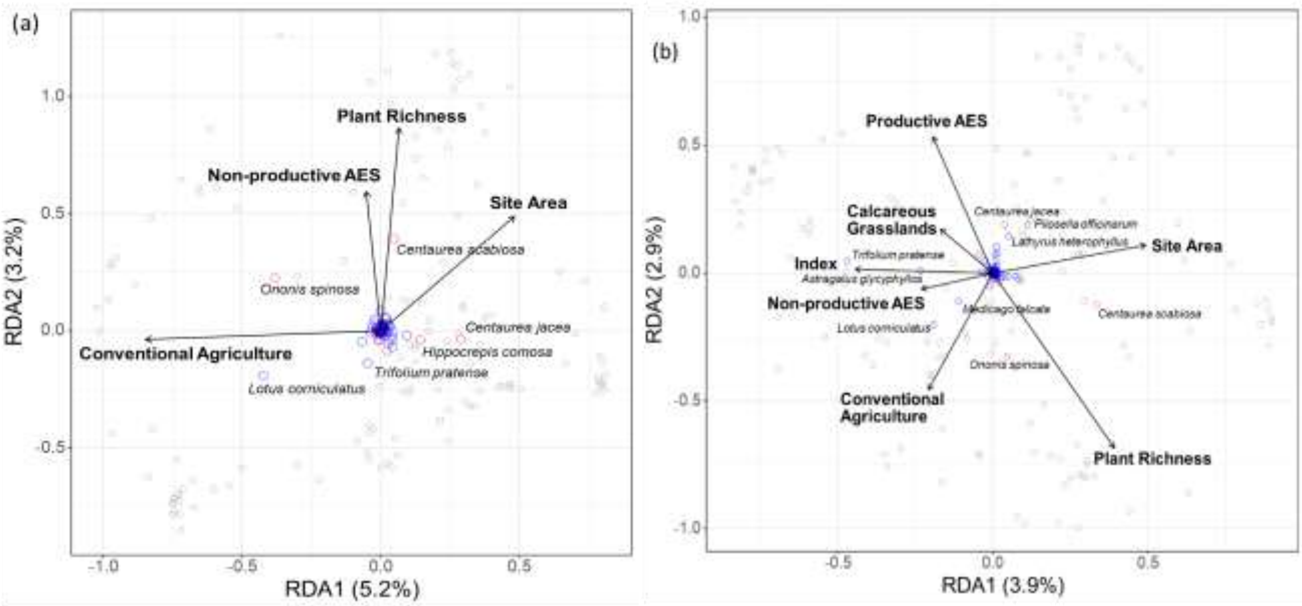

Figure 5: RDA plots showing the effect of landscape variables on the community composition of pollen samples taken from (a) *B. lapidarius* and (b) *B. pascuorum*. Samples are displayed in gray. Calcareous grassland specialist species are shown in red (Ellenberg & Leuschner, 2010), while all others are shown in blue. Labels were only added to species greater than a certain Euclidean distance from the plot origin (from Sloan et al. 2025).

These results show that changes in surrounding land use directly alter the floral resources available relative to those found within the calcareous grasslands. Variation in intrinsic site characteristics, such as management, also affects plant community composition, which may in turn affect foraging opportunities. Overall, these results indicate that local conservation management and changes in landscape composition (percentages of productive AES, conventional agriculture, and calcareous grasslands) do not increase the number of plant species from which bumblebees collect pollen, but rather lead to shifts in dietary choices according to floral availability.

In addition to bumblebees, we also examined pollen use by the solitary bee *Osmia leaiana* in Estonia. Pollen metabarcoding confirmed a strong dependence of *Osmia leaiana* on various Asteraceae to provision trap nests, with this family accounting for 94.3% of the total relative abundance of sequences across all samples (Fig. 6a). Within Asteraceae, the most abundant genera were *Crepis*, *Leontodon*, and *Pilosella*, comprising 21.1%, 19.5%, and 14.7% of total relative abundance, respectively (Fig. 6b). This included 36 species of Asteraceae across all samples. Despite the high diversity of available floral resources, Shannon diversity of pollen species in individual trap nests was generally low, indicating that individual bees provision their larvae using only a few dominant species, including *Crepis biennis*, *Leontodon hispidus*, and *Tragopogon pratensis*. These results suggest that despite a high diversity of available resources, individual bees provision their larvae with pollen from few plant species.

The results further showed that floral resource use was mainly driven directly by floral resource availability rather than being mediated through land use composition or management factors. In particular, the abundance of Cichorioideae had a significant effect on pollen community composition ($F = 2.12$, $p = 0.023$).

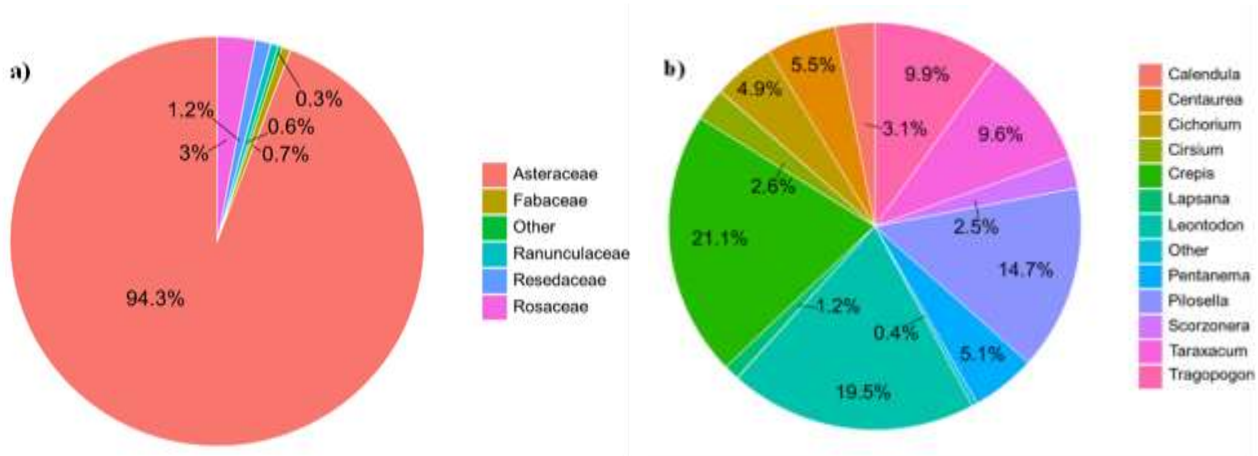

Figure 6: Pie charts illustrating the percent of total relative abundance of sequences across all samples represented by a) each plant family and b) each Asteraceae genus. Those with percentages ≥ 0.5% of total relative abundance among all samples are shown individually, while all others are grouped into the “Other” category (from Sloan et al., unpublished results).

Overall, these results show that trap nest occupancy was not affected by local management or surrounding land use in the studied grasslands. Metabarcoding of trap nest pollen provisions confirms the sepcies oligolectic foraging on Asteraceae. Among all local and landscape variables, only the species richness of Asteraceae affected the composition of pollen assemblages, suggesting that bees still select preferred floral resources and may require specific combinations of pollen to meet the dietary needs of their brood. These findings stress the importance of conserving local plant diversity within grassland habitats to support the foraging needs and reproductive success of *Osmia leaiana*, while the broader landscape composition may have limited impact.

Plant-pollinator networks and meta-networks

In a final part, we applied a meta-network approach to investigate the restoration of plant-pollinator interactions in semi-natural grasslands embedded in agricultural landscapes. Over two years, plant-wild bee interactions were recorded across 96 calcareous grasslands along restoration-abandonment gradients in three countries (Fig. 7).

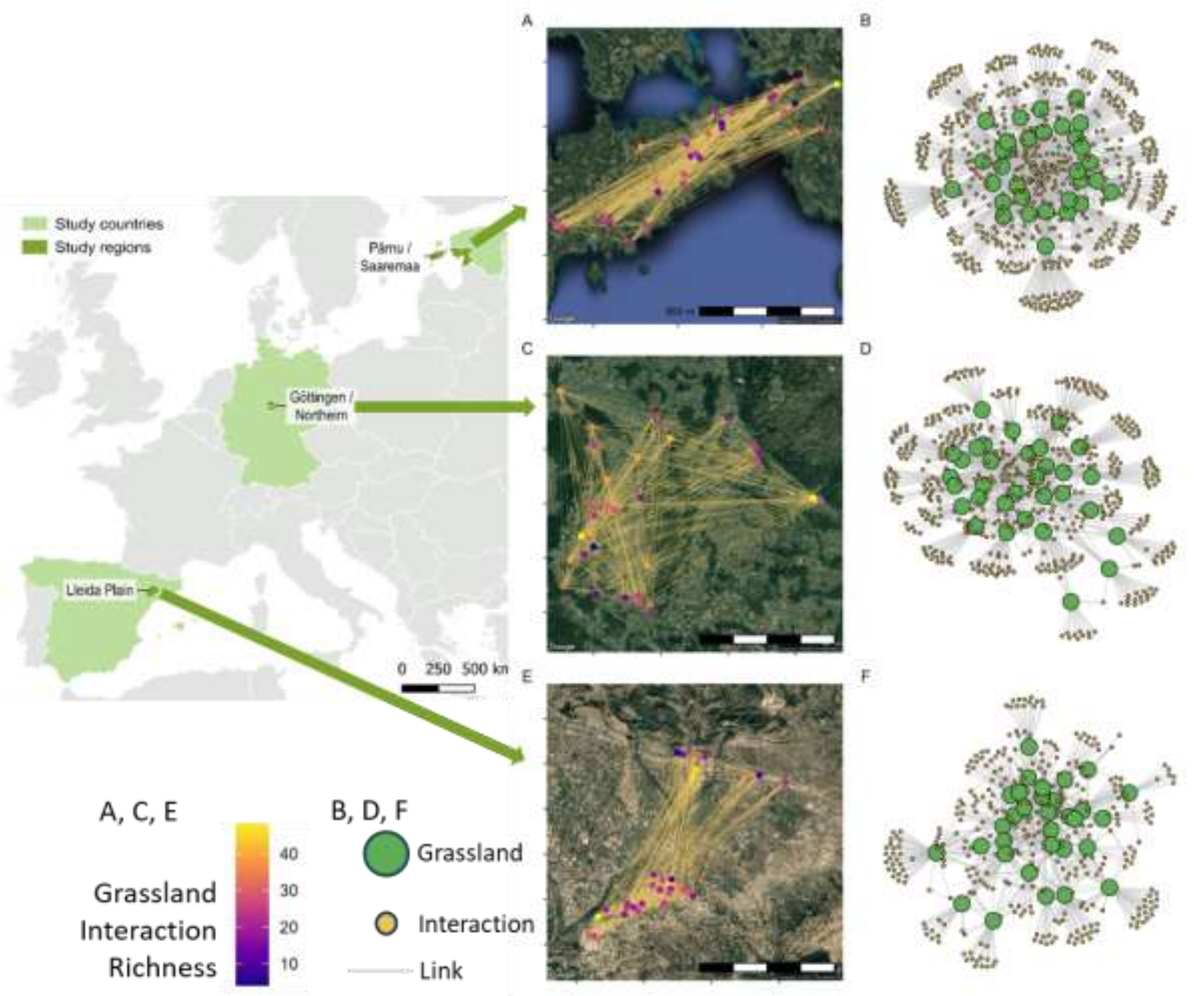

Figure 7: Map of studied regions and representation of each meta-network per country. Studied regions are marked in dark green on the European map. For each country, the representation of the plant-wild bee meta-networks structure is presented using two different projections. Panels A, C and E show the unipartite projection where the location of calcareous grasslands is presented in colored dots based on the number of interactions hold in each grassland, and yellow lines connect calcareous grasslands when they share the same plant-wild pollinator interaction, projected in the physical maps (satellite images from Google Maps, 2025). Panels B, D and F show the bipartite projection: calcareous grasslands are represented by green nodes, whereas interactions are represented by yellow nodes. Whenever an interaction is occurring uniquely in one site during the whole monitoring period (single-site interactions), the yellow node connects with one single green node (from Velada-Alonso et al., unpublished results).

Overall, the three meta-networks encompassed 5476 observed interaction events, encompassing 1385 different plant-wild bee interactions, 200 plant species, and 225 wild bee species. Single-site interactions, i.e. interactions that were only observed in one grassland per country during the entire monitoring period, represented 985 observations (70% of the total interaction richness, but 18% of the observed abundance). While meta-network size and species richness varied among countries, all networks shared similar structural properties. They were sparse (low connectance), with relatively few shared interactions overall and consistently high interaction turnover. A small number of grasslands contributed disproportionately to shared interactions (high web asymmetry), whereas most were linked to only a limited subset of others (moderate H_2'). Nestedness was low, indicating that interaction poor grasslands were not simply subsets of well-connected ones.

In general, local factors exerted a stronger influence on plant–pollinator meta-network structure than landscape-level variables (Figure 8). Among local factors, flower richness had the most pronounced effect, showing significant positive relationships with interaction richness (estimate ± standard error: 0.14 ± 0.03, $p < 0.01$), single-site interaction richness (0.26 ± 0.04, $p < 0.01$), and the proportion of single-site interactions (0.16 ± 0.05, $p < 0.01$). Flower richness was also significantly negatively associated with both grassland closeness centrality (–0.01 ± 0.005, $p = 0.05$) and apparent influence (–0.23 ± 0.09, $p = 0.01$). Similarly, flower cover had a significant positive effect on interaction richness (0.08 ± 0.03, $p < 0.01$) and single-site interaction richness (0.13 ± 0.05, $p = 0.01$).

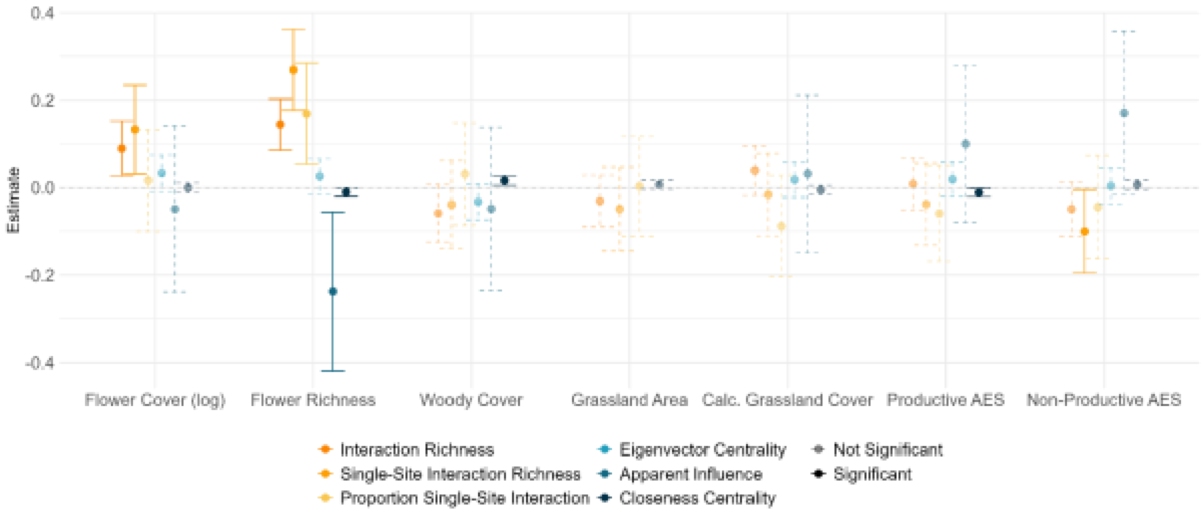

Figure 8: Effect of the flower cover, flower richness, woody cover, grassland size, landscape cover of calcareous grasslands, landscape cover of productive AES, and landscape cover of non-productive AES on the studied meta-network metrics differentiated by color (see legend). Whiskers represent 95% confidence intervals of the estimated effects. An explanatory variable is significant if whiskers do not overlap the zero dashed line (shown in bold). Non-significant effects are show with dashed and transparent lines. Country effects have been dropped for visualization purposes (from Velada-Alonso et al., unpublished results).

By contrast, woody cover was only significantly associated with higher grassland closeness centrality (0.15 ± 0.05, $p < 0.01$), denoting that increased cover of shrubs and trees promotes fewer shared interactions among few grasslands. Regarding landscape management factors, productive AES were significantly negatively linked to grassland closeness centrality (–0.011 ± 0.05, $p = 0.02$), while non-productive AES were associated with reduced single-site interaction richness (–0.1 ± 0.04, $p = 0.03$), i.e. potentially increasing the overlap of interactions among sites. None of the tested variables significantly affected eigenvector centrality, implying no detectable effects on keystone grassland status. Grassland area and cover of surrounding calcareous grasslands were not significant in any of the models. Country was significant in all tested models, indicating pronounced differences between the studied regions.

Overall, these results show that habitat quality (habitat-specialist plant richness, alongside floral cover and richness) is fundamental to restore the diversity of interactions and support interaction complementarity (Fig. 8). Additionally, landscape-scale AES can contribute to prevent the impairment of meta-network by supporting the redundancy of interactions across grasslands. Thus, both local habitat quality and a diversified biodiversity-friendly agricultural matrix will help to restore the cohesiveness of the plant-pollinator metacommunity. The meta-network approach has shown great potential for improving restoration practices by accounting for higher levels of ecological complexity. Further methodological development is needed to address limitations related to species distribution characteristics and interaction patterns to improve the restoration of calcareous grasslands.

WP4 Bird communities and predation

Bird species richness was higher in Spain (72 species) than in the other two regions (47 species in Germany and 57 species in Estonia), although the number of common species (those present at least in 5 grasslands) was the same, 24-25 species per country. However, the composition of the bird community was very different between Spain and the other two countries (Fig. 9). In Spain we recorded more species typical of open environments, while in Germany and Estonia there were more generalist species and species of closed environments (shrubs/forests).

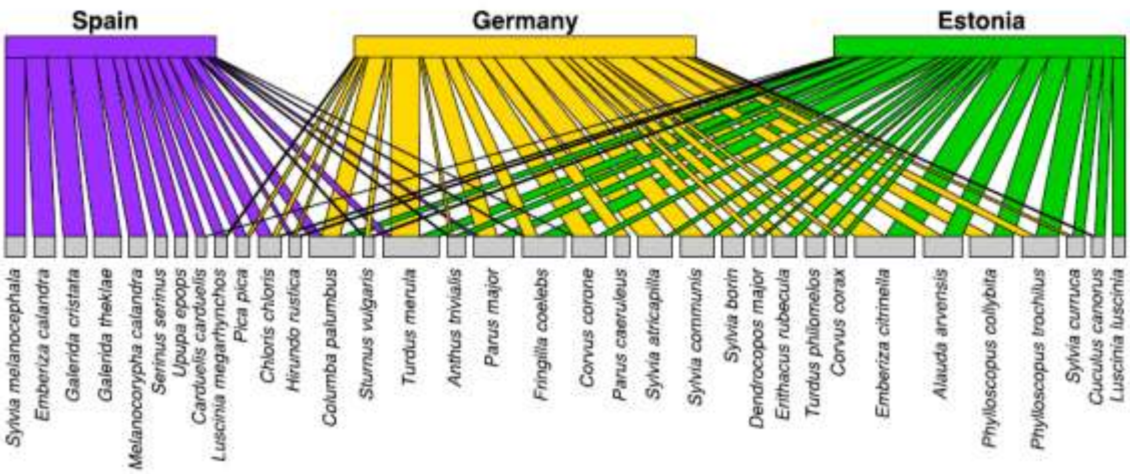

Figure 9: Network showing the occurrence of bird species in the study regions based on 2022 bird counts.

On the other hand, in Spain and Germany the number of species did not change with grassland restoration, while in Estonia the number of species increased. We also did not observe any effect of the proportion of agri-environmental schemes around the grassland on species richness. In Spain species richness was positively related to plot size and connectivity and negatively to the proportion of crops around the grassland (Objective 2). Furthermore, we observed interactions between these effects: the positive effect of connectivity was greater in small grasslands, and the negative effect of crop proportion was lower when connectivity increased. In Estonia, a positive effect of connectivity was also observed, with this effect being stronger in smaller grasslands. Grassland size and crop proportion had no clear effect on bird richness in Estonia and Germany.

The results further showed higher predation in Spain than in Germany and Estonia, as well as a positive effect of exposure height: the higher the caterpillars were placed, the higher the predation was. In line with our expectations, we also observed that bird predation was determined by predator abundance and landscape characteristics. Arthropod predation was negatively related to grassland size and positively related to management status of the grasslands. For both type of predations, the results show that fragmentation and loss of connectivity in European calcareous grasslands had negative effects on predation. In contrast, the results did not provide evidence that surrounding agri-environmental schemes were effective in compensating for the loss of predation services resulting from the reduced connectivity. Overall, we conclude that improving connectivity favours predation by insectivorous birds and arthropods, suggesting that the conservation and restoration of calcareous grasslands, in addition to greatly favouring biodiversity, can lead to an increase in key ecosystem services such as predation and pest control.

WP5 Actors' and stakeholders' perceptions and social-ecological networks

Based on the interviews, five key challenges for semi-natural grassland restoration and conservation were identified, ranging from environmental and economic to societal and political challenges. These challenges are presented in Figure 10 and summarized in Table 2.

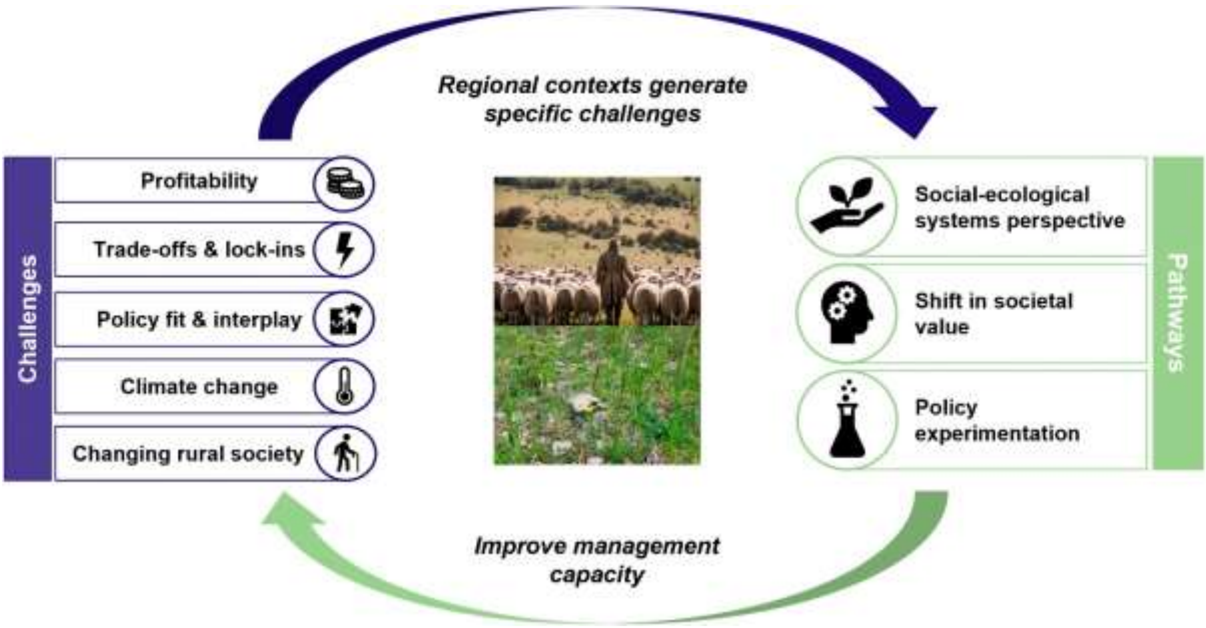

Fig. 10. General challenges that are common to restoration and conservation of European semi-natural grasslands. Regional contexts control and modify the region-specific impacts of these challenges. The three pathways help to improve semi-natural grassland management capacity, if they are regionally adapted and combined (from Gorris et al. 2025).

These challenges occur all over Europe, but are highly context-specific in their impact and require measures adapted to their local to regional socio-ecological circumstances. The following three pathways represent our general recommendations to enhance management capacities to better address these challenges locally (see Figure 10). These recommendations are, in large parts, derived from our empirical observations of some promising practices in the studied regions.

1. Adopting a *holistic social-ecological systems perspective* is an important first step to ensure semi-natural grasslands can be sustained through stabilizing and rebuilding the necessary pre-conditions for extensive farming practices locally. This requires widening the angle of the somewhat narrow site-level technical-administrative ecological view in the conservation and restoration community. Improved monetary incentives, reduced administrative barriers and a stronger focus on non-monetary benefits are needed to sustain and strengthen the engagement of the diverse set of extensive farmers presently involved in semi-natural grassland management across Europe.
2. Working towards *a wider ecosystem service-based perspective of semi-natural grasslands at the landscape scale*. This involves shifting the perspective on grasslands from being agricultural "wastelands" to not only acknowledge their conservation/biodiversity value, but also their role as key cornerstones of resilient agricultural landscapes in the context of climate change and its region-specific impacts. This will be particularly important for increasing political and public will to better support semi-natural grassland conservation and restoration and may contribute to activate more farmers as well as non-farmers to engage in the future. Furthermore, successful conservation and restoration of semi-natural grasslands is not only linked to if and how extensive farming practices are conducted in a specific site, but also to the embeddedness of a site in the wider landscape (e.g., ensure habitat connectivity).
3. *Experimental learning and policy alignment* across different levels in the political system is needed to co-create innovative solutions to adapt semi-natural grassland conservation and restoration efforts to regionally distinct socio-ecological contexts of modern landscapes. This pathway is tightly linked to finding better ways to embed traditional forms of extensive agriculture in today's rural societies and contemporary agricultural policies across Europe. Especially supporting local Communities of Practice offers a promising way to maintain local knowledge, facilitate the emergence of innovative farming practices and support local engagement. This can help to make extensive farming more attractive and feasible for younger generations and other newcomers that might be willing and eager to help preserve the cultural landscape while, at the same time, need to find ways to sustain adequate incomes through modern forms of agriculture.

Table 2 Descriptions of key challenges for grassland management and examples from the study regions in Estonia (EST), Germany (GER) and Spain (SP).

Challenge	Description	Examples
Profitability	Extensive agriculture based on grazing and hay production is key for semi-natural grassland biodiversity, but is becoming increasingly unprofitable across Europe.	Meat produced on semi-natural grasslands with low grazing intensity is more expensive [GER, SP, EST]

Challenge	**Description**	**Examples**
Trade-off and lock-in effects	Multiple interdependent use forms (food production, forestry, species conservation, infrastructure development etc.) compete with each other producing lock-in effects and sectoral trade-offs at the landscape scale.	Market share of products from goats and sheep decreases [GER, SP, EST] Grasslands are converted into arable land or forest [GER, SP, EST] Grassland conservation clashes with protection of wolves [GER]
Policy fit and interplay	Sectoral policies at multiple levels in the political system impact grassland conservation and restoration, which creates mis-fits and often fail to capitalize on potential synergies.	Regulations to obtain subsidies are not well aligned with extensive husbandry practice [GER, SP, EST] Administration produces high bureaucratic workload for farmers [GER, EST]
Climate change	The regional effects of climate change have important social, economic and ecological consequences for semi-natural grassland management.	Animals need additional food and water during draughts [GER, SP, EST] Range shifts of predators occur [EST]
Changing rural societies	Depopulation, population aging, lack of attention to its importance by society and economic marginalization in rural areas complicate extensive animal farming.	Drop-out of older extensive farmers leads to decreasing workforce and local knowledge [GER, SP, EST] Loss of local service providers (e.g., shearers, wool processors) make extensive husbandry more difficult [GER, SP, EST]

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5. DISSEMINATION AND VALORISATION

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Hannappel, I. (2024). Effects of local and landscape restoration on plant-pollinator networks in calcareous grasslands across Europe (talk). *53rd Annual Meeting of the Ecological Society of Germany, Austria, and Switzerland*. Freising, Germany.

Hannappel, I. (2024). Interactive effects of local and landscape restoration on pollinator abundance and species richness in calcareous grasslands. *14th European Conference on Ecological Restoration*. Tartu, Estonia.

Hass, A. (2024). Key challenges for restoration of species interactions and ecosystem functions in European calcareous grasslands (talk). *14th European Conference on Ecological Restoration*. Tartu, Estonia.

Velado-Alonso, E. (2024). Evaluating restoration success at the landscape level through plant-pollinator meta-networks (talk). *14th European Conference on Ecological Restoration*. Tartu, Estonia.

Cabodevilla, X. (2025). Calcareous grassland fragmentation affects the predation function provided by birds (poster). *26th Congress of la Sociedad Española de Ornitología*. Valencia, Spain.

Velado-Alonso, E. (2025). Restoration success through socio-ecological interactions. *53rd Annual Meeting of the Ecological Society of Germany, Austria and Switzerland.* Freising, Germany.

Sloan, E. (accepted). Floral resources in the surrounding landscape matrix augment plant species richness of bumblebee pollen loads in small, fragmented calcareous grasslands (poster). *British Ecological Society Annual Meeting 2025.* Edinburgh, Scotland.

6. PUBLICATIONS

Gorris, P., Bodin, Ö., Giralt, D., Hass, A. L., Reitalu, T., Cabodevilla, X., ... & Westphal, C. (2025). Social-ecological perspective on European semi-natural grassland conservation and restoration: Key challenges and future pathways. *Biological Conservation*, *304*, 111038.

Sloan, E.T., Hannappel, I., Hass, A.L., Keller, A., Librán-Embid, F., Devalez, J., Velado-Alonso, E., Reitalu, T., Westphal, C., & Jacquemyn, H. (2025). Floral resources in the surrounding landscape matrix augment plant species richness of bumblebee pollen loads in small, fragmented calcareous grasslands. *Biological Conservation, 310,* 111379.

Cabodevilla, X., Bota, G., Traba, J., Hass, A., Westphal, C., Hannappel, I., … & Giralt, D. (submitted). Habitat fragmentation and connectivity loss affects the predation ecosystem service provided by birds and arthropods in calcareous grasslands.

Sloan, E.T., Devalez, J., Keller, A., Prangel, E., Helm, A., Hass, A.L., Westphal, C., Reitalu, T., & Jacquemyn, H. (submitted). *Osmia leaiana* pollen resource use is driven by Asteraceae species richness but not local and landscape management.

Velado-Alonso, E., Hannappel, I., Librán-Embid, F., Bota, G., Cabodevilla, X., Devalez, J., … & Hass, A. (submitted). Both local habitat quality and diversified agricultural landscapes support the restoration of metacommunity cohesion in calcareous grasslands.

Hannappel, I., Westphal, C., Artola, J., Bota, G., Cabodevilla, X., Devalez, J., … & Hass, A. (submitted). Effects of local and landscape restoration on bee abundance and richness.

Gorris, P., Bodin, Ö., Hannapel, I., Hass, A.L., Westphal, C. (in progress). Of un-sung heroes in European semi-natural grassland conservation and restoration: A typology of pastoralists based on drivers of engagement and social capital derived from a German case study.

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