Preserving mobile insects in semi-natural grasslands

Minding the matrix

Weber, Julia

2026

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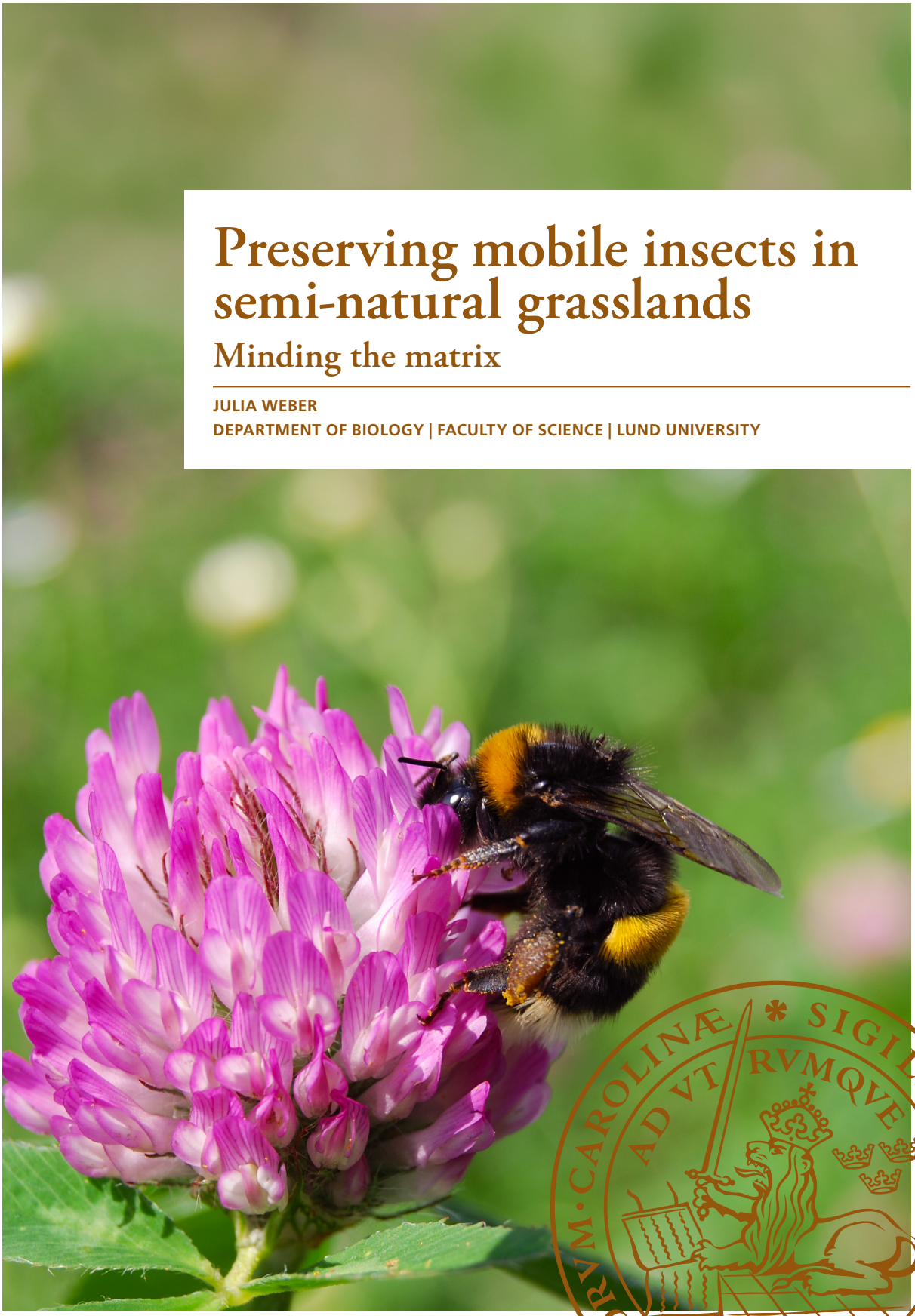

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Julia Weber

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DOCTORAL DISSERTATION

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Key words: Landscape complementation, farmland biodiversity, conservation, leys, bumblebees, butterflies, legumes, clover, semi-natural grasslands, remote sensing, machine learning, PPI

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MADE IN SWEDEN

Till pappa
Jochen Weber
1949–2022

Jag önskar att jag hade fått dela livet med dig lite längre.
Jag älskar dig och jag saknar dig.

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Abstract

Declines of insect pollinator diversity in farmlands have neither been halted nor reversed despite large efforts to change the negative trend. One driver of this is agricultural intensification, which has resulted in landscape simplification by loss of non-crop habitats, and increased use of inorganic fertilizers and synthetic pesticides. Consequently, the presence of grazing animals in agricultural landscapes have decreased, leading to loss of semi-natural grasslands which are of great value for pollinating insects. Remaining grasslands may be under heavy grazing pressure, resulting in a rapid seasonal depletion of floral resources. Given that increasing the quality and quantity of grasslands is often costly and slow to yield results, there is a growing need to expand conservation efforts beyond grasslands to include the surrounding agricultural landscape – the matrix – to gain a more effective conservation strategy for grassland pollinators. The matrix can provide complementary or supplementary floral resources for pollinating insects through for example mass-flowering crops. However, they often fail to sustain pollinators throughout the season, leading to hunger gaps during critical life stages. Leys, which are perennial grasslands grown for fodder production and increased soil quality, often include legumes which could offer floral resources for grassland pollinators. However, flower availability in leys may be depleted due to frequent harvesting or intensive grazing. This thesis aims to investigate if flower-rich leys in the matrix is an efficient measure of improving the conservation value of grasslands for pollinators. Using field data and satellite-based predictive modelling to map legume availability across landscapes, I investigate how resources from leys support bumblebee and butterfly populations in grasslands and in smaller habitats in the matrix, and experimentally test how mowing regimes affect bumblebee populations. From the four chapters of this thesis, three main findings can be highlighted: i) while legume-rich conventional leys provide floral resources despite being regularly mowed and grazed, organic leys provide a more consistent flower resource, ii) variation in the extent of flower-rich leys and the area of semi-natural grasslands in the surrounding landscape, when combined with measures increasing the value of smaller habitats such as field borders, influence species richness and abundance of both bumblebees and butterflies in agricultural landscapes, and iii) legume flower cover in leys can be reliably predicted from remotely sensed phenology and productivity data combined with management and soil variables. The results and conclusions of this thesis fill a knowledge gap of which holds potential in increasing the conservation value of grasslands for farmland pollinator populations.

Populärvetenskaplig sammanfattning

Trots många bevarandeinsatser fortsätter surret i jordbrukslandskapet att tystna. Den biologiska mångfalden associerad med jordbrukslandskap minskar över hela världen, inte minst i Europa. Även om många åtgärder har implementerats för att gynna både växter och djur vänder inte den negativa trenden. En anledning till att den biologiska mångfalden minskar är att jordbruket har blivit allt intensivare, vilket har lett till att komplexiteten i landskapet – såsom fältkanter och andra delar av landskapet som nyttjas av vilda växter och djur – har minskat. Dessutom ökar produktionen i jordbruket då användning av konstgödsel och olika växtskyddsmedel ger allt större skördar. Detta leder ofta till övergödning och att rester av bekämpningsmedel sprider sig i naturen, vilket gör att många arter som tidigare gynnades av människans markanvändning inte längre kan överleva. Om den biologiska mångfalden i jordbruket minskar kan de negativa effekterna av till exempel klimatförändringarna bli allt värre, då de olika biologiska funktioner som mångfalden av arter ger försvinner. Människan är beroende av många av dessa biologiska funktioner, till exempel är vår matproduktion direkt beroende av insekter såsom vilda bin och fjärilar, då många av våra grödor är beroende av deras pollinering. För att pollinerande insekter ska överleva i jordbrukslandskapet behöver deras behov för överlevnad och reproduktion uppfyllas. Humlor behöver till exempel boplatser till sina kolonier, medan fjärilar behöver lägga sina ägg på särskilda värdväxter för att kunna fortplanta sig. Gemensamt för både humlor och fjärilar är att de är beroende av betesmarker.

När behovet av naturlig gödning från till exempel betande djur har minskat, har även behovet av betesmarker sjunkit. Mängden betesmarker i Sverige har minskat från cirka 1,4 miljoner hektar vid 1800-talets slut, till drygt 400 000 hektar idag. Även om de betesmarker som finns kvar idag kan ha ett högt värde för biologisk mångfald, kan de ofta bli hårt betade vilket leder till färre blommor senare under sommaren. Dessa blommor är pollinerande insekter såsom humlor och fjärilar beroende av för föda, särskilt under den senare delen av sommaren då de ska fortplanta sig. Mycket forskning har fokuserat på hur man kan öka kvaliteten och kvantiteten av betesmarker i jordbrukslandskapet. Även om det finns stora värden i att bevara och återskapa betesmarker i sig, kan sådana åtgärder både vara kostsamma och tidskrävande, och det kan ta tid innan några positiva effekter kan mätas. Det kan därför vara nödvändigt för forskningen att även fokusera på potentiella

bevarandeåtgärder i det omkringliggande jordbrukslandskapet runt betesmarker för att vända den negativa trenden av biologisk mångfald.

Ett sätt att gynna pollinerande insekter i betesmarker i jordbrukslandskapet är att odla blommande växter som kan ge extra födoresurser när mängden blommor i betesmarker är låg. Vall är den vanligaste grödan i Sverige, och är odling av olika gräsblandningar för att producera foder och bete för djur. Rödklöver, vitklöver och foderlusern är baljväxter som ofta används i vallodling för att öka proteininnehållet i fodret och för att binda kväve till marken. Det är sedan tidigare känt att både humlor och fjärilar födosöker på blommande klöver, och det finns forskning som visar att humlekolonier gynnas av fröodling av rödklöver som blommar i stora mängder under sensommaren. Vall med insådda baljväxter har således potentialen att vara en landskapstäckande födokälla för pollinerande insekter. Men eftersom vallar regelbundet skördas eller betas har deras faktiska värde för den biologiska mångfalden länge varit oklart. Min avhandling ämnar undersöka om baljväxtrika vallar kan gynna humlor och fjärilar i jordbrukslandskapet i allmänhet, och i betesmarker i synnerhet. Dessutom undersöker jag om effekten varierar beroende på om vallen brukas ekologiskt eller konventionellt, eller om den betas eller skördas.

Baserat på flera fältstudier visar resultaten i avhandlingen att sättet som vallar brukas på spelar en avgörande roll. Ett viktigt resultat är att baljväxter i både konventionella och ekologiska vallar blommar i stor utsträckning trots att de skördas eller betas. Det som skiljer ekologiska och konventionella vallar åt är att ekologisk vall har en stabilare tillgång på blommor under säsongen jämfört med konventionella vallar, vilket bidrar till att tillgången av blommor över tid blir högre. Dessutom visar jag att landskap som har ekologiska vallar och samtidigt blomtäta fältkanter, har både högre antal och artrikedom av humlor och fjärilar.

Genom att kombinera fältdata på förekomst av baljväxter i vallar med bland annat satellitdata visar jag även att man med en fjärranalysmodell kan förutsäga med hög precision hur stor sannolikhet det är att landskap innehåller baljväxtrika vallar. Detta kan bli ett värdefullt verktyg för framtida forskningsstudier som ämnar att studera interaktionen mellan pollinerande insekter och blomrika vallar ytterligare.

Då vallar redan har ett ekonomiskt och agronomiskt syfte i jordbruket visar den här avhandlingen att rätt brukade vallar kan vara ett kostnadseffektivt och användbart verktyg för att bevara pollinerande insekter. Min avhandling visar att vi inte nödvändigtvis behöver ta jordbruksmark ur produktion för att vända den nedåtgående trenden av biologisk mångfald i jordbrukslandskapet.

List of chapters

Chapter I

Weber, J., Carrié, R., Ekroos, J., & Smith, H. G. (2026). Seasonal effect of organic farming on legume-rich ley fields and their potential to enhance landscape-scale floral resources for pollinating insects. *Manuscript submitted for publication.*

Chapter II

Mai, N., Weber, J., Carrié, R., Kümmerle, T. & Smith, H. G. (2026). Satellite derived phenology and productivity indices predict legume flower cover in rotational grasslands at the local and landscape scale. *Manuscript.*

Chapter III

Weber, J., Ekroos, J., Carrié, R. & Smith, H. G. (2026). Availability of ley fields influences species richness and abundance of butterflies and bumblebees in grasslands of intensively farmed landscapes. *Manuscript.*

Chapter IV

Weber, J., Carrié, R., Persson, A. S., Ekroos, J. & Smith, H. G. (2026). Sparing of flower-rich leys from mowing does not favour bumblebee colony growth and reproduction in semi-natural grasslands. *Manuscript.*

Additional published papers not included in the thesis

Lindström, Å., Alerstam, T., Andersson, A., Bäckman, J., Bahlenberg, P., Bom, R., Ekblom, R., Klaassen, R. H. G., Korniluk, M., Sjöberg, S., & Weber, J. (2021). Extreme altitude changes between night and day during marathon flights of great snipes. *Current Biology*, *31*(15), 3433–3439.e3433. https://doi.org/10.1016/j.cub.2021.05.047.

Author contributions

Chapter I

All authors contributed to the conceptualisation of the study. JW and RC designed the methodology. JW performed the data collection and analysis, with input from HGS and JE. JW wrote the first manuscript draft and all authors contributed with revisions and comments.

Chapter II

HGS and TK conceptualised the study. All authors designed the methodology. JW and NM performed the data collection. NM performed the analysis with input from HGS, RC, and JW. NM wrote the first manuscript draft and all authors contributed with revisions and comments.

Chapter III

All authors contributed to the conceptualisation of the study. JW, RC and JE designed the methodology. JW performed the data collection and analysis with input from HGS and JE. JW wrote the first manuscript draft and all authors contributed with revisions and comments.

Chapter IV

JW and RC conceptualised the study. JW and ASP designed the methodology. JW performed the data collection with input from ASP. JW performed the analysis with input from HGS, JE and RC. JW wrote the first manuscript draft and all authors contributed with revisions and comments.

Authors: Julia Weber (JW), Romain Carrié (RC), Henrik G. Smith (HGS), Johan Ekroos (JE), Natalja Mai (NM), Tobias Kümmerle (TK), Anna Sofie Persson (ASP).

Abbreviations

SNG	Semi-natural grasslands
SR	Species richness
EU	European Union
GLMM	Generalized mixed model
LME	Linear mixed effects model
HR-VPP	High-Resolution Vegetation Phenology and Productivity
CLMS	Copernicus Land Monitoring Service
VPPs	Vegetation Phenology Parameters
STs	Seasonal Trajectories
PPI	Plant Phenology Index
SGU	Sveriges geologiska institut, Geologial Survey of Sweden
SLU	Sveriges lantbruksuniversitet, Swedish University of Agriculture
IACS	Integrated Administrative and Control System database
SVMs	Support Vector Machines
LFCC	Legume Flower Cover Class
SMOTE	Synthetic Minority Oversampling Technique
TP	True Positives
FP	False Positives
TN	True Negatives
FN	False Negatives

Introduction

Biodiversity declines in agricultural landscapes

Long-term declines of biodiversity associated with farmland in the European Union (EU) have neither been halted nor reversed despite large resources allocated to this in the Common Agricultural Policy (CAP; Kleijn *et al.*, 2011; Pe'er *et al.*, 2014). A major driver of farmland biodiversity declines is agricultural intensification (Figure 1; Habel, Ulrich, *et al.*, 2019; Stoate *et al.*, 2001; Tsang *et al.*, 2025), that have resulted in landscape simplification by loss of non-crop habitat and increased management intensity of arable fields (Emmerson *et al.*, 2016; Raven & Wagner, 2021). Additionally, the use of inorganic fertilizers (Habel, Trusch, *et al.*, 2019; Wagner, 2020) and synthetic pesticides (Goulson *et al.*, 2015; Nicholson *et al.*, 2024; Rundlöf *et al.*, 2022) has reduced biodiversity across all agricultural landscapes (Newbold *et al.*, 2015).

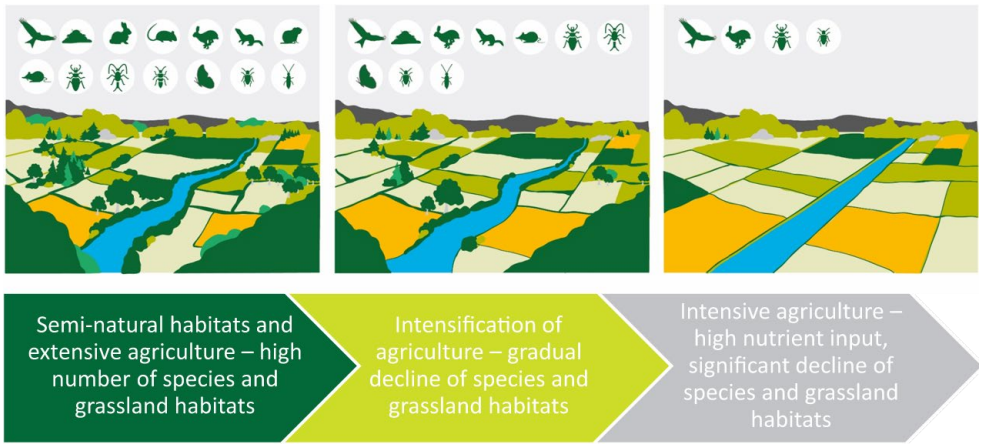

Figure 1. Illustration of agricultural intensification.
The process of agricultural intensification from species-rich landscapes to simplified landscapes with high agricultural intensity, with only a few remnant species left. Figure originally published by European Court of Auditors (2020).

The availability of inorganic fertilizers has also reduced the reliance on animal husbandry for crop fertilization in productive agricultural landscapes, at the expense

of livestock manure (Crews & Peoples, 2004). This has resulted in intensively managed agricultural landscapes that have become depleted of grazing animals (Cousins *et al.*, 2015; Ustaoglu & Collier, 2018). Over time, this has resulted in loss of semi-natural grasslands (SNGs), that are critical to many species of conservation concern (Eriksson, 2021; Nieto *et al.*, 2014; SLU Artdatabanken, 2020; van Swaay *et al.*, 2012), through a combination of intensification of use and abandonment (Pazúr *et al.*, 2024). Consequently, wild species associated with SNGs have declined (Auffret *et al.*, 2018; Kuussaari *et al.*, 2007; Török & Dengler, 2018).

Not only the loss of grasslands, but also changes in their management may contribute to biodiversity declines. SNGs remaining in contemporary landscapes have undergone significant changes in management. Whereas many of these grasslands were traditionally used for hay production, they are today nearly invariably grazed, and with high stocking rates for economic reasons or to fulfil conditions for environmental support (Figure 2; Cousins *et al.*, 2015; Eriksson & Cousins, 2014; Jakobsson *et al.*, 2024). The most common grazing regime of SNGs today significantly alters their floral composition, such that they typically contain a high richness of flowering plants early in the season, but becomes increasingly sparse as the season progresses due to increasing grazing pressure (Harris *et al.*, 2024; Timberlake *et al.*, 2019).

Figure 2. Semi-natural grasslands under different management practices.
(Left) A mowed semi-natural grassland in Ammarnäs (Lappland region in northern Sweden) illustrating traditional management practices, allowing for a high diversity of flowering plants. (Right) A semi-natural grassland under intensive grazing pressure, which corresponds to how grasslands most commonly are managed in modern times. Photo taken by Åke Lindström (left) and the author (right).

Restoring biodiversity in agricultural landscapes

To counteract contemporary biodiversity declines, agri-environment schemes (AES) have been implemented in the EU. AES typically reduces overall land-use intensity within fields, but such measures may mostly target species of low conservation concern (Ekroos *et al.*, 2014; Smith *et al.*, 2010). However, even if SNG are targeted by AES for their high biodiversity values (Smith *et al.*, 2016), there is controversy whether the measures lead to increased biodiversity (e.g. Berg *et al.*, 2019). Additionally, SNGs were traditionally managed mainly by cutting herbs and grasses for hay production, whereas in modern times, most SNGs are managed by fairly intensive grazing (see example in Figure 2), which may result in deteriorated habitat quality for species of conservation concern, for example because of lack of forage resources for flower-visiting insects (Öckinger & Smith, 2007). Current management within AES has been developed to hinder grassland encroachment and to benefit plant diversity, but may consequently lead to loss of other organisms such as farmland birds and pollinators.

Much research on the role of grassland for biodiversity conservation has focussed on how the quality and quantity of SNGs and their connectivity affect associated species. While increasing SNG habitat quality and quantity can effectively protect biodiversity in fragmented landscapes (e.g. Prangel *et al.*, 2024; Török *et al.*, 2021), it comes at a vast variation in both effectiveness and costs (Knight & Overbeck, 2021; Török *et al.*, 2011). Consequently, lack of uptake of conservation measures and their impact on biodiversity might be too weak to counteract current biodiversity declines. While the value of conservation actions in SNGs, such as improved grazing regimes, should not be overlooked, more focus could be given to conservation actions in the landscape surrounding them to gain additional benefits for biodiversity.

Pollinating insects in semi-natural grasslands

Wild pollinating insects such as bees and butterflies have declined in species richness and abundance across the EU (European Commission: Directorate-General for *et al.*, 2026; European Commission: Directorate-General for *et al.*, 2025). While multiple drivers have been identified for these losses, such as agricultural intensification and climate change (Raven & Wagner, 2021), loss of SNGs has been suggested to be a significant reason for these pollinator declines (Habel, Ulrich*, et al.*, 2019; Nath *et al.*, 2023; Potts *et al.*, 2016).

While island biogeography theory in general and metapopulation theory in particular provide strong theoretical constructs to protect networks of SNG patch-dependent species (e.g. Krauss *et al.*, 2003; Lindgren & Cousins, 2017), additional

ecological processes may be at least as important for the persistence of mobile grassland insects. Particularly relevant is when the surrounding landscape provides supplementary or complementary resources required by the organism (Dunning *et al.*, 1992; Smith *et al.*, 2014). That is, mobile organisms relying on SNGs may to a varying degree be dependent on additional resources found in the surrounding landscape. This may particularly be the case when flower resources in grasslands are low due to intensive grazing (cf. Davidson *et al.*, 2020; Lázaro *et al.*, 2016)

Many pollinator species inhabiting SNGs interact with the wider landscape through foraging movements and dispersal. Thus, changes in the landscape matrix surrounding SNGs can also affect their value for pollinators (Gallé *et al.*, 2022). The "matrix" can be described as the part of the landscape where a species cannot successfully reproduce sufficiently well to maintain their populations in contrast to in the organism's main habitat (Fletcher *et al.*, 2024), or would exist in much lower densities if the main habitat did not exist (Dunning *et al.*, 1992). Additionally, the matrix can provide supplementary or complementary resources, such as flower resources, for grassland pollinators at different temporal scales. Agricultural intensification has resulted in loss of flower resources in the matrix surrounding SNGs, such as through loss of incidental habitats (Ihse, 1995; Street *et al.*, 2010), arable weeds (Tyler *et al.*, 2020), or flower-rich leys, as suggested by Bommarco *et al.* (2012). Thus, in a more intensively farmed landscape, the landscape matrix might offer less complementary resources for pollinator populations (cf. Dunning *et al.*, 1992; Smith *et al.*, 2014).

Conservation efforts in the matrix

While flower resources are generally scarce in the intensively farmed matrix surrounding SNGs, it can occasionally contain abundant flower resources for pollinators. Mass-flowering crops can provide nectar and pollen to flower-visiting insects in grasslands (Riggi *et al.*, 2024). However, such crops are often temporary and may fail to provide resources at critical time periods (Nicholson *et al.*, 2021) and does not cover the entire season of the pollinator's activity (Odoux *et al.*, 2014), and the impact on pollinator populations has shown to be limited (Jönsson *et al.*, 2015; Shaw *et al.*, 2020; Westphal *et al.*, 2009). However, this may be due to the degree of implementation and phenology of flower strips, and there is evidence that at least bumblebee populations benefit from the presence of more extensive late-flowering habitats such as clover-seed production fields (Rundlöf *et al.*, 2014). This could indicate that crops blooming later in the season – such as leys containing clover and other legumes – could potentially increase the availability of important foraging resources for grassland-dwelling pollinating insects at critical time periods (as suggested by Harris & Ratnieks, 2022; Risberg, 2004; Risberg & Pettersson, 2005), possibly favouring populations at the time of reproduction.

However, it is important to emphasize that the marginal value of additional flower-rich habitats in the matrix for pollinating insects in SNGs may depend on several factors. For example, the quality of the SNG itself could affect the need of added floral resources, since local habitat quality can mask for more subtle landscape-level effects if not accounted for (Clough *et al.*, 2014). Additionally, effects might vary depending on the amount of SNGs in the landscape, as more SNGs allows to higher landscape-level pollinator populations, which can be an important pre-requisite for any positive effects of complementary flower resources in the matrix (Bishop *et al.*, 2025)., Finally, ecological traits such as mobility and foraging specialisation of targeted organisms can affect their ability to effectively utilize complementary resources in the landscape (Ekroos *et al.*, 2010; Öckinger & Smith, 2007).

Figure 3. A ley field being mowed.
A field of grass ley being mowed, with a semi-natural grassland in the background. Photo taken by Josefin Winberg (2022).

Leys as a conservation measure

Leys are temporal grasslands (Figure 3) used in crop rotations to produce fodder for livestock (Allen *et al.*, 2011), to increase soil fertility (Reeves, 1997), and reduce weed infestation (Martin *et al.*, 2020). While sometimes purely grass-based, leys often include legumes (Van Eekeren *et al.*, 2023) such as *Trifolium repens*, *Trifolium pratense* and *Medicago sativa* to increase fibre and protein content for livestock (Mortenson *et al.*, 2004), while simultaneously promoting nitrogen

fixation and producing more protein with less added nitrogen through fertilisation (Suter *et al.*, 2015). Additionally, *T. repens, T. pratense* and *M. sativa* are frequently visited by wild pollinators such as bumblebees and butterflies (Chaguthi & Dyola, 2018; Dupont *et al.*, 2011; Harris & Ratnieks, 2024; Hederström, Johansson*, et al.*, 2024; Messellem *et al.*, 2025), and pollen from all legume species have been found in pollen loads of two species of bumblebees; *Bombus lapidarius* and *Bombus pascourum* (Sloan *et al.*, 2025). This suggests that such leys, when properly seeded and managed, could create complementary foraging opportunities for pollinators and other flower-visiting insects in SNGs, allowing them to bridge hunger gaps when floral resources in grasslands are low (cf. Carrié *et al.*, 2018; Schellhorn *et al.*, 2015). Because of their agronomic value, maintaining leys could be a cost-efficient way to provide flower resources during periods when they are scarce in SNGs (cf. Risberg, 2004), as they may provide flower resources as a co-benefit.

The amount of flower resources provided by legumes in leys may depend on their management. Flower availability depends on the seed-mixes used (Beye *et al.*, 2022) and intense cutting regimes may result in leys being harvested before blooming (Cong *et al.*, 2020; Risberg, 2004). Because of the importance of nitrogen fixation in organic farming, where the use of mineral nitrogen fertilizers is banned, leys may intentionally contain more legumes than in conventional farming (Risberg, 2004). Whether the ley is used for grazing or not, may also affect the provision of flower resources, since grazing can dramatically reduce flower abundance (Carrié *et al.*, 2018; Lázaro *et al.*, 2016). Hence, both the amount and species richness of legumes in leys may affect their ability to provide complementary resources to flower-visiting insects in SNGs, However, there are still uncertainties regarding the extent to which leys provide significant amounts of floral resources for pollinating insects since they are harvested multiple times during the growing period, which could reduce flower abundance (as suggested by Milberg *et al.*, 2024). Consequently, the effect of ley management on the variation in flower availability in landscapes remains unclear.

Thesis aims and scope

This thesis aims to investigate if flower-rich leys in the matrix surrounding SNGs is an efficient measure of improving the conservation value of grasslands and the pollinator populations dependent on them. To distinguish effects of the availability of SNGs and resources in the wider landscape (matrix), I have used a multifactorial space-for-time substitution study system that enables the evaluation of independent effects of availability of SNGs and the structure of the surrounding landscapes (Figure 4).

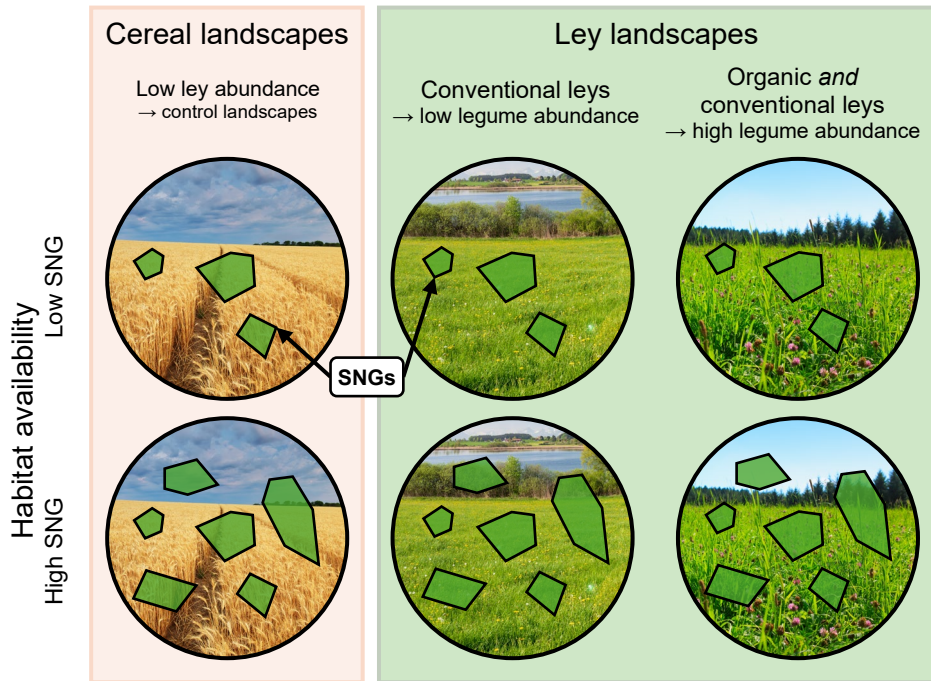

Figure 4. Study design system.
The fundamental study design system consisting of landscapes (shown as circles) within six categories, each centering around a focal semi-natural grassland (central green polygon). The categories are defined by contrasts in habitat availability (either high or low SNG; y-axis) and matrix properties (x-axis). Habitat availability is illustrated by green polygons within each landscape circle. Matrix properties (illustrated by different circle backgrounds) consist of either cereal landscapes or two types of ley landscapes. Ley landscapes consists of either only conventional leys (and other crops) and are hypothesised to have low ley legume abundance, or organic and conventional leys which are hypothesised to have high ley legume abundance.

In **chapter I**, I studied if availability of flower resources for flower-visiting insects in leys was different between organic and conventional management at field and landscape scales, and if this was modified by grazing. Using the data collected for my first chapter, a predictive model was trained in **chapter II** to map legume flower cover in leys across landscapes using high-resolution satellite-derived vegetation phenology, combined with information on productivity and management (organic or conventional). Having gained insight on floral resources provided by leys within and across landscape matrices in the first two chapters, I investigated if and how species richness and abundance of two important pollinator groups; bumblebees and butterflies in SNGs were affected by the quality of the surrounding matrix in terms of availability of flower-rich leys (**chapter III**). Finally, I experimentally alter mowing regimes in ley strips in the study landscapes in **chapter IV**, to understand how mowing practices affects pollinator populations and their reproductive success. Overall, the different chapters in this thesis aims to guide the reader between agronomy and ecology, from single ley fields to landscapes and from individual flowers to pollinator responses.

The research questions, aims and expectations for each of the chapters are described below:

Chapter I

Can I establish field- and landscape-level effects of ley management on the availability of flowering legume resources in leys across the season?

Chapter I aims to investigate the contribution of organic and conventional ley management to flower resources for flower-visiting insects at field and landscape scales, and how this was modified by grazing. I investigated whether there was a difference in legume flower abundance in ley fields depending on farming practices (organic or conventional) and ley harvest type (harvested for fodder or grazed). I also considered how farming practices affected the seasonal variation in flower resources. Blooming was expected to be lowest early in the season, and to some extent increase as the season progresses because of plant development and increased flowering availability. Additionally, I expected to see increased flowering abundance in organic ley fields compared to conventional ley fields, and that this difference could be influenced by seasonal effects.

Chapter II

Can legume blooming counts be used to train a predictive model to successfully map legume abundance in leys based on remote sensed data?

Building on the data and knowledge obtained from chapter I, chapter II aimed to develop a predictive model to map legume flower availability in leys which can be applied over large spatial and temporal extents. This was achieved in collaboration with geographers, where we predicted legume flower cover in individual leys. The prediction used a combination of optical satellite remote sensing data capturing biomass production and phenology of ley vegetation, combined with other variables related to farming practices, and soil characteristics that could influence legume flower cover. We expected that legume flower cover in leys can be reliably predicted from a combination of remotely sensed biomass production and phenology information, indicators of farm management and soil characteristics.

Chapter III

Does increased availability of flower-rich ley fields increase species richness and abundance of butterflies and bumblebees in SNGs? Do these effects vary over the season and are they mediated by amount of SNG in the landscape?

In this chapter, I investigate if and how species richness and abundance of two important pollinator groups; bumblebees and butterflies, in open, semi-natural habitats are affected by the quality of the surrounding matrix in terms of availability of flower-rich leys. I also investigate whether flower resources from leys in the wider landscape mostly benefit generalist species, and if they target grassland specialist species. I expected to find effects of additional floral resources in the form of leys on both bumblebee and butterfly species richness, as population-level effects of more floral resources in the matrix over time should translate into higher species richness compared to landscapes with fewer floral resources. Additionally, I expected higher abundance in focal SNGs in landscapes with leys, assuming that leys provide more floral resources on a landscape scale compared to landscapes without leys.

Chapter IV

Does mowing exclusion of ley strips benefit pollinator populations in focal SNGs?

Bridging on from chapter III, chapter IV takes an experimental approach aiming to investigate if provisioning of additional floral resources for pollinators from leys, in

landscapes where leys are already grown, would benefit pollinator populations in SNGs that may be devoid of such resources caused by intense grazing. This was done using an experimental setup where I excluded mowing from strips of legume rich leys during mid-summer, and measured responses in commercial colonies of *Bombus terrestris*. I expected that in landscapes where ley strips had been left unmowed, bumblebee colonies in SNGs would acquire a greater weight gain, compared to control landscapes where leys were managed and mowed as usual.

Methods

Study area and data collection

To address my research questions, I combined a space-for-time substitution study and an experimental study in which I investigated effects of leys in the matrix on the species richness, abundance, fitness and resource utilization of bumblebees and butterflies in SNGs. The field studies were carried out in the agricultural landscape of Scania, southern Sweden (Figure 5). This area is suitable for these studies given its strong variation in the structure of agricultural landscape, including the availability of SNGs and leys, within relatively small distances (Persson *et al.*, 2010).

Study design 1

A landscape-scale space-for-time substitution design was the foundation for **chapter I, II and III**. Based on land-use data obtained from the Integrated Administrative and Control System database (IACS) provided by the Swedish Board of Agriculture, 24 SNGs were matched in triplicates based on the matrix properties surrounding them within a radius of 1 km (illustrated in Figure 4 and Figure 5). The three grasslands in a triplet were surrounded by either a) conventional cereal farming, b) conventional mixed farming (crops and leys), or c) organic mixed farming (crops and leys). Since organic farming typically includes legumes in leys (Risberg, 2004), and also provides more stable cultivated and wild flowering resources (Carrié *et al.*, 2018), I used this as a proxy for identifying leys that should contain more legumes compared to their conventional counterpart. To distinguish between matrix effects from leys and the availability of additional SNGs and resources in the wider landscape, 12 of the 24 landscapes had a low proportion of SNG in the surrounding landscape, and 12 had a high proportion of SNG in the surrounding landscape. In addition to the site selection based on land-use data obtained from IACS, all fields in all landscapes were also ground truthed to control for any changes not visible in the land-use data. When ground truthing leys, they were also identified as either grass-legume leys or grass leys by assessing the presence or absence of legume leaves in each ley field. Legume leys were defined as those containing either *Trifolium repens*, *T. pratense* and/or *Medicago sativa*, the

three most common legume species sown in leys in Sweden as specified by seed mix producers (Swedish Agro, Varaslättens lagerhus, Lantmännen, Klöver Ess Agri, Vallberga Lantmän). Data on legume presence was used to develop a predictive model to map legume flower availability in leys, as presented in **chapter II**. In each landscape, I sampled butterfly, bumblebee and floral diversity and abundance during 2020 and 2021 in the focal grassland and in an uncultivated field border along a cereal field. Each site was sampled three times each year and survey rounds were separated by 4-12 days. In each sampling site, flower and insect surveys were conducted on one transect of 100 m (Figure 6). This data was analysed in **chapter III**.

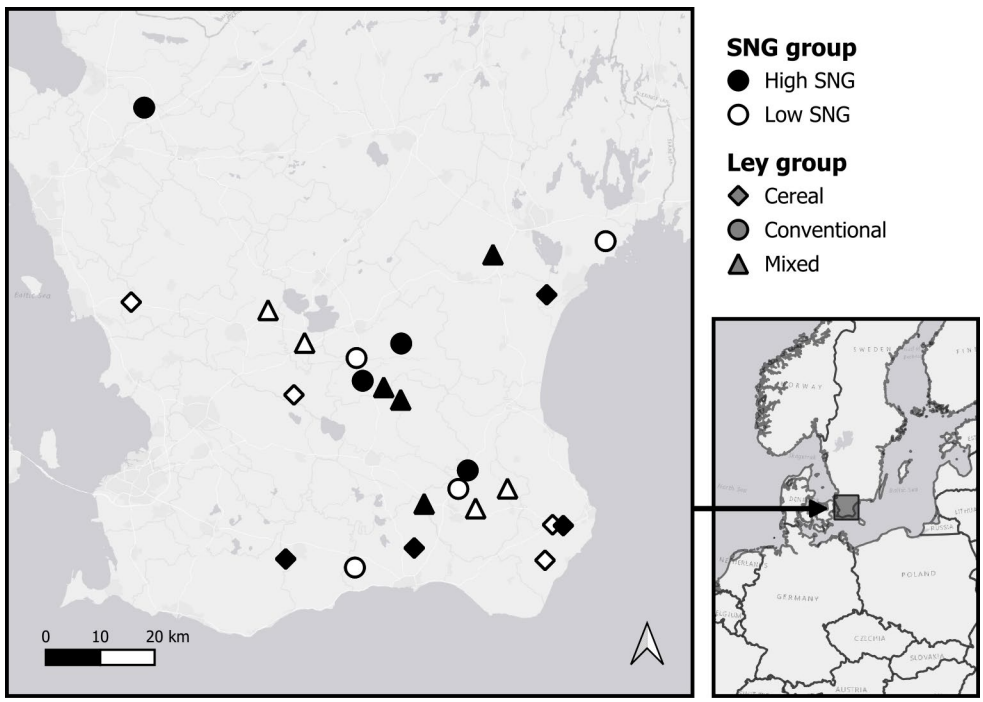

Figure 5. Map of study area in Scania, southern Sweden.
The figure showing the study locations in Scania, southern Sweden, that were included in chapter III. Most of these landscapes were also used in field designs for chapter I, II and IV. The map shows the multifactorial space-for-time substitution study system with two different SNG groups that corresponds to differences in SNG abundance within each landscape, and three different ley groups that describe matrix properties in each group. Cereal landscapes were dominated by cereal production, conventional ley landscapes contained conventionally managed leys as well as other crops, and mixed ley landscapes contained a mix of conventional and organic leys as well as other crops.

Figure 6. Photos from field work in 2021 and 2022.
Top left: Field assistant Alice Hennig weighing bumblebee colonies placed next to a semi-natural grassland during fieldwork 2022. This data was analysed in chapter IV. Photo by the author.
Top right: The author doing a transect walk in 2021 where she catches and identifies bumblebees and butterflies, as well as identifying flowering plants, to collect data on species richness and abundance. This data was analysed in chapter III. Photo by Alice Hennig.
Bottom left: Data on legume flower abundance analysed in chapter I and II was estimated using 50 x 50 cm wooden squares placed in ley fields during fieldwork 2021. Photo by Michelle Pozzini.
Bottom right: A ley field in 2022 that shows one part being mowed and one part being excluded from mowing during mid-summer, which was part of the experiment conducted for chapter IV. Photo by the author.

In 2021, flower abundance in all grass-legume leys in all landscapes was sampled (whether mowed or grazed) four times during the season, between late May to early

August. Flower sampling was done using two 50 cm × 50 cm quadrats (Figure 6) placed >3 m from the field edge, at least 100 m (if possible) apart. I counted flowers in two haphazardly placed quadrats per ley field, regardless of field size, without considering flower density when placing the quadrats. All blooming flower heads of *T. repens, T. pratense* and *M. sativa* were counted within the quadrats (Figure 6). When legume flowers were counted, data on mowing and grazing management of the ley field was also collected. The data obtained from these flower counts was analysed in **chapter I.**

Study design 2

The second study design was set up in 2022 for the experimental study in **chapter IV**. In this experiment, 12 focal SNGs were selected in otherwise intensively farmed landscapes, with most of them also being used in study design 1 (Figure 5). In six of the landscapes, I established flowering leys by persuading farmers to leave a total of one ha of legume rich ley unmowed in each landscape during July (Figure 6). In the remaining six landscapes, all leys were left to be traditionally mowed throughout the study. In close vicinity to each focal grassland, I established four commercial colonies of *Bombus terrestris*. Colony development was measured by weighing each colony seven times between establishment in late June and termination in late July (Figure 6). Colony development was estimated by calculating the proportional weight gain by each colony. After the termination of the experiment, I dissected each colony to count the number of opened and closed queen cocoons.

Additional data collection

To obtain averaged seasonal productivity and phenology information per ley in 2020 and 2021 used in **chapter II**, High-Resolution Vegetation Phenology and Productivity (HR-VPP) dataset was used, provided by the Copernicus Land Monitoring Service (CLMS), the Earth Observation component of the European Union space program. The dataset is derived from optical satellite imagery with a spatial resolution of 10 x 10 m and a revisit time of 5 days. The HR-VPP data consists of Vegetation Phenology Parameters (VPPs) derived from the Seasonal Trajectories (STs) of the Plant Phenology Index (PPI) on an annual basis, after the end of the growing season. The PPI is a physically-based vegetation index and provides reliable performance for deriving STs and phenological, as well as productivity parameters (Jin & Eklundh, 2014). Subsequently, phenological and productivity parameters were aggregated to the field level, resulting in averaged seasonal productivity and phenology information per ley in 2020 and 2021 respectively.

Data on ley age and farming type (organic or conventional) for each ley field was obtained through the IACS database and through the Swedish certification KRAV. To acquire data on soil clay content, the "Digital Soil Map of Sweden" provided by the Geologial Survey of Sweden (SGU) and the Swedish University of Agriculture (SLU) was used.

Data analysis

All statistical tests for **chapter I, III and IV**, and data extraction and balancing for **chapter II** were done in R v. 4.4.1 (R Core Team, 2024) or later versions, as stated in each chapter. All illustrations of data and model results was done using the package ggplot2 (Wickham, 2016).

Chapter I

In chapter I, I tested whether legume flower abundance in leys differed depending on farming practice both on a field and landscape level using generalized mixed models (GLMM) with negative binomial error distribution. When analysing field-scale blooming from legumes, I analysed legume flower abundance per field in leys containing legumes (expressed as the number of blooming flowers in the two sampling squares on a continuous scale) in relation to farming type (organic *vs.* conventional), ley management type (mowing or grazing) and survey round (1/2/3/4). I also included interactions between survey round and farming type, and survey round and ley type. To avoid the issue of excess zeros at the field level, I analysed leys with legumes separately from the grass leys. To account for non-independence of data collected in the same landscape, I used field identity within landscape identity as a random effect. For the landscape-level analysis, the sum of all blooming flower heads from grass-legume leys in each landscape was used as the response variable (assuming zero flowers in grass-leys). Survey round, ley area (in ha), % conventional ley of total ley area (as an inverted measurement of % organic leys to account for zeroes in dataset), and % grazed ley of total ley area was used as predictors. Continuous predictors were $\log_e$-transformed to linearize relationships. In the landscape analysis, I controlled for non-independence of data by using landscape identity as a random factor. To test the effect of individual parameters, I used Type II Wald chi-square tests, and for factors with more than two categories, post-hoc analyses were done using Tukey-contrasts.

Chapter II

In chapter II, I used Support Vector Machines (SVMs) to perform a multiclass and binary class prediction of legume flower cover in leys. SVMs are suitable for classification tasks in ecological studies because of their flexibility and robustness. Additionally, they have proved to be relatively robust to overfitting, and can effectively handle high-dimensional data, i.e., data that contains numerous variables. To train each SVM, I split every dataset containing legume flower cover class (LFCC) information into a training dataset containing 70% of the total data and a test dataset containing 30% of the data. Datasets containing LFCC information were split with similar class distributions in training and test dataset, using a stratified sampling approach to conserve the original area distribution of each individual class.

SVMs solve a classification problem by finding a hyperplane that maximizes the margins between classes while minimizing the classification error, using the structural risk minimization concept. Hyperplanes provide linear decision boundaries between data points of different classes. However, many real-life observations are not linearly separable into different classes. Therefore, SVMs are often expanded using the "kernel trick", which involves mapping data into a higher dimensional space using a non-linear kernel function. Each SVM training was done using a linear, radial, and polynomial kernel. For the linear kernel, "cost" was additionally tuned, which controls the penalty associated with misclassification. For the radial kernel, both "cost" and "sigma" was tuned, where sigma represents the width parameter of the radial function, which is used to calculate the similarity between two data points. When SVMs were trained using a polynomial kernel, the hyperparameters "cost", "scale", and "degree" was tuned where scale influences how much importance is given to each feature in the input space. Degree in the polynomial function refers to the highest power of the variable in the polynomial expression, determining the complexity of the hyperplane of the SVM with a higher degree creating a more complex hyperplane.

To estimate model performance within the training process, and choose suitable hyperparameters, I used k-fold cross-validation. This meant that the training dataset was randomly divided into k folds, of which k-1 folds were considered for training and the remaining fold for validating the model performance, i.e. testing the model within the training process. Since the training data was very imbalanced, by containing 170% more legume-poor leys (354), compared to legume-rich leys (131), the Synthetic Minority Oversampling Technique (SMOTE) was applied. SMOTE generates new synthetic samples for minority classes by interpolating between existing observations and their nearest neighbours. This procedure resulted in a more balanced training dataset with 354 legume-poor leys and 354 legume-rich leys.

To evaluate the predictive performance, each SVM was trained to solve a classification task. This was done using evaluation metrics based on True Positives (TP): instances where the model correctly predicts the positive class, False Positives (FP): instances where the model incorrectly predicts the positive class, True Negatives (TN): instances where the model correctly predicts the negative class, and False Negatives (FN): instances where the model incorrectly predicts the negative class. In a multi-class classification task, the "positive" class is the class whose predictability is trying to be evaluated, while the "negative" class is composed of all the other classes that are not considered the "positive" class.

I considered Accuracy as a first evaluation metrics for the SVMs, which describes how many times an SVM made a correct prediction, i.e. how capable the model is of predicting TP and TN across the entire dataset. Accuracy ranges from 0 to 1, with 1 meaning that the SVM is predicting everything correctly. Since the accuracy metric can only be reliable if the dataset is class-balanced, it was combined with other evaluation metrics that can expose issues in predicting minority classes.

Chapter III

In this chapter, I analysed species richness and abundance of bumblebees and butterflies in separate models for each sampling site: focal SNG or cereal field border. Analyses of species richness were based on data pooled over the season, whereas abundance was analysed with data separated by sampling round. I used GLMMs, in which I accounted for non-independence of data by using year within landscape identity as random factors. I inspected distributions and homogeneity of variance of residuals to select the appropriate error structure for each model. I specified models on species richness based on a gaussian error distribution and square root transforming the dependent variable. For models on bumblebee species richness in focal grasslands and butterfly species richness in cereal field borders I specified a Poisson error distribution. When analysing abundance in focal grasslands, the models were fitted using negative binomial error distributions, whereas in cereal field borders a Poisson error distribution was fitted instead. Model terms were "ley group" (factor with three levels), "SNG group" (factor with two levels), "year" (factor with two levels) and "transect flower abundance" (continuous variable). When data was analysed separated by sampling round, "sampling round" (factor with three levels) was also included. Interactions between ley group and transect flower abundance, SNG group and transect flower abundance, ley group and SNG group, sampling round and ley group, and sampling round and SNG group were tested, and were only included in the final analyses if they were statistically significant.

Chapter IV

Regarding the experimental data for chapter IV, I measured and analysed colony development as proportional weight gain, whereas colony fitness was measured and analysed using $\log_e$(total number of new daughter queen cocoons). I fitted linear mixed effects models (LMEs) and I accounted for non-independence of data by using landscape identity as a random factor. I tested the effect of individual parameters using Type II Wald chi-square tests. Model terms for all models were "treatment" (factor with two levels; mowed *vs* ummowed), "SNG area" (in hectares; continuous numerical variable) and "legume rich ley area" (in hectares; continuous numerical variable). I included interactions between the following model terms: treatment and SNG area, and treatment and legume rich ley area. Interactions were only included in the final models if significant.

Results and discussion

Legume flower abundance in leys

Although prior studies have confirmed that leys provide nectar and pollen for pollinators, such studies primarily analysed a mix of wild and sown flowers (Carrié *et al.*, 2018) or focused specifically on clover seed-production leys (Rundlöf *et al.*, 2014). Currently, there appears to be no research that examines the timing of legume blooms within leys across replicated organic and conventional farming systems. **Chapter I** provides valuable insight into temporal variation in legume blooming within leys, both at the field level and upscaled to landscape level. The results show that organic ley fields are more likely to be grass-legume leys (90.5%) compared to conventional leys (47.2%) ($\chi 2 = 25.8$, df = 1, N = 451, $p<0.001$; see supplementary material to chapter I).

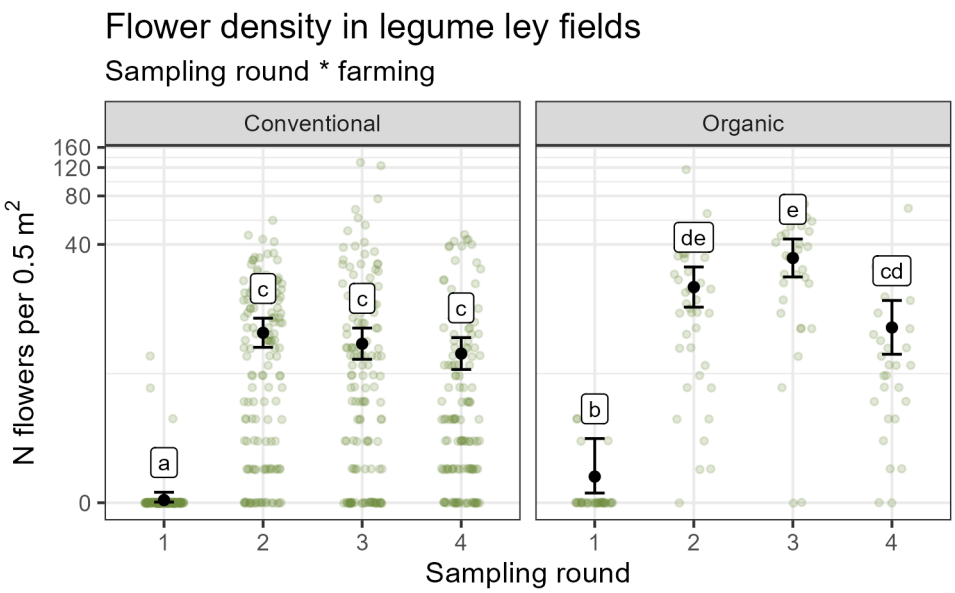

Figure 7. Effect plot on flower density in legume ley fields.
Density of legume flowers (number per two sampling squares) in different types of leys in relation to management type (organic vs conventional). Black dots show fitted effect values drawn from the model, with error bars showing 95% confidence intervals. Letters above black dots denotes Tukey-contrasts. Green dots show raw data points.

Additionally, organic leys were found to have significantly higher legume flower abundance in sampling round 2 and 3 compared to conventional ley fields (Figure 7), which could not be explained by variation in legume species composition. When results were upscaled to the landscape level, a clear positive effect of ley area on total ley legume flower abundance was observed (Figure 8A). However, the lower contribution of leys at the landscape scale, when the relative proportion of conventional management was larger, was of appreciable size (Figure 8B). Ultimately, **chapter I** shows that leys do provide floral resources despite being harvested by mowing or grazing. Importantly, organic leys in particular seem to be a more consistent flower resource, both because of their increased probability of containing legumes and because they are less likely to have zero blooming throughout the season.

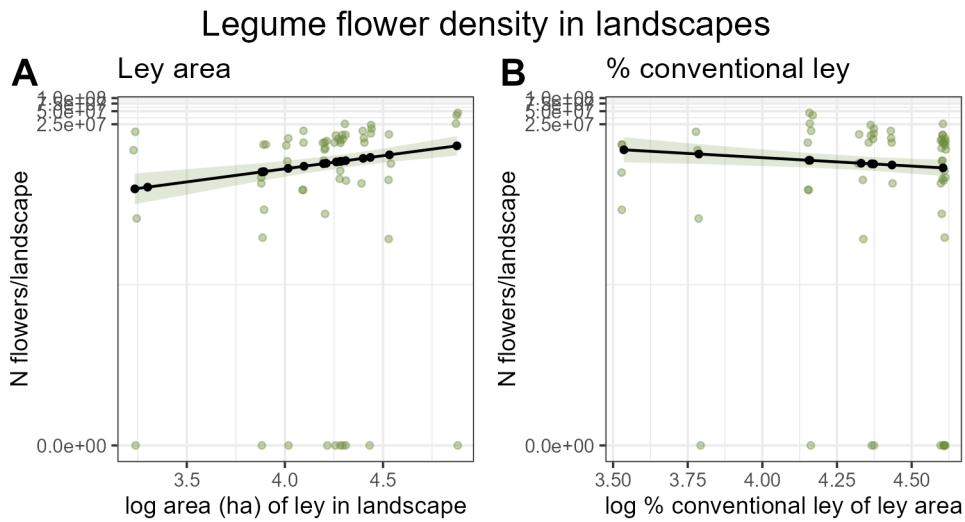

Figure 8. Effect plots on legume flower density in landscapes.
Flower abundance (estimated number of flowers summed over all leys) per landscape in relation to ley area (A) and proportion of leys under conventional management (B). Black dots show fitted effect values drawn from the model. Green dots show raw data points. Shaded green areas show 95% confidence intervals.

Evidence suggests that organic farming (Austin *et al.*, 2019) in general, and organic leys in particular (Carrié *et al.*, 2018) support pollinator communities by offering a consistent supply of floral resources. The factors driving this increased availability on organic farms are explored in detail in **chapter I**. However, the total effect of legume-rich leys depends on the landscape contrasts, such as to what extent legume-rich leys provide additional floral resources in relation to other habitats such as SNGs (c.f. Kleijn *et al.*, 2011).

Subsequently, **chapter II** demonstrates that legume flower cover in leys could be successfully predicted on a landscape level using a combination of optical satellite remote sensing data capturing biomass production and phenology, with variables describing farming practices, and soil characteristics. The results show that on a landscape scale, predicted and observed share of legume-rich, as well as legume-poor leys of 2020 and 2021 were highly correlated (r=0.92 p <0.001 and r=0.91, p<0.001; Figure 9). These findings suggests that the model is suitable to monitor legume-rich leys and their impact on e.g. biodiversity over a large spatial extent and in different production contexts. Implementing such a model in future research could greatly improve our abilities to design large-scale studies across entire landscapes to understand effects of gradients of legume densities on pollinating insects as well as other mobile organisms.

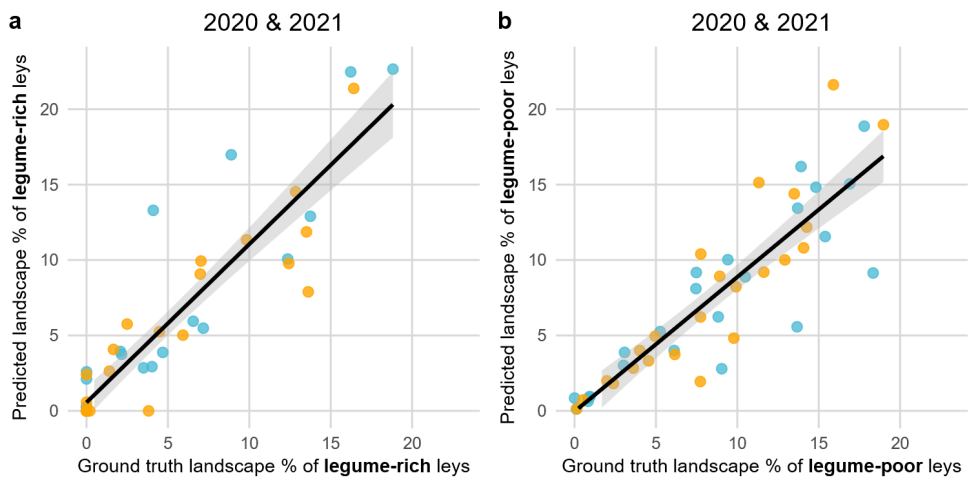

Figure 9. Correlation between ground-truth landscape share and predicted landscape share. Correlation between ground-truth landscape share (x-axis) and predicted landscape share on the y-axis for a) legume-rich leys in 2020 and 2021 (r=0.92, p-value: <0.001), and b) legume-poor leys in 2020 and 2021 w (r= 0.91, p-value: <0.001). Blue dots indicate 24 landscapes from 2020 with a total of 207 legume-poor leys and 86 legume-rich leys, and orange dots indicate 24 landscapes from 2021 with a total of 300 legume-poor leys and 102 legume-rich leys. Shaded areas represent the 95% confidence intervals of the regression line.

Pollinator responses from leys in the matrix

While studies on how ley fields in particular provide benefits for pollinators are relatively scarce (see e.g. Carrié *et al.*, 2018), several studies show that clover seed production fields can provide moderate to positive effects for pollinators (Rundlöf *et al.*, 2014; Teixeira *et al.*, 2025). Sown grass-legume mix grasslands, managed for pollinator benefits, have been shown to provide moderately positive effects on

bumblebee, butterfly and solitary bee abundance within the grasslands (Brandl *et al.*, 2022). **Chapter III** investigates how the availability of ley fields influences species richness and abundance of two important pollinator taxa: bumblebees and butterflies. The results in **chapter III** indicate that the species richness of bumblebees in SNGs is significantly influenced by the surrounding agricultural landscape, but not according to our predictions that the availability of leys in the matrix would allow for a higher species richness. Instead, I found that cereal-dominated landscapes supported higher local richness compared to landscapes with leys (Figure 9). This may be caused by attraction effects that shape pollinator communities within grasslands (Olsson *et al.*, 2015) and the wider landscape (Holzschuh *et al.*, 2016), which could mask broader population trends (Kleijn *et al.*, 2011). For instance, grasslands in resource-poor landscapes may exhibit deceptively high densities of bumblebees and butterflies simply because these areas function as a primary attraction for foraging insects in an otherwise barren landscape.

Despite that the effects of matrix properties on bumblebees and butterflies in focal grasslands were relatively weak, I found significant responses on species richness and abundance of pollinators found in cereal field borders in the surrounding landscape. **Chapter III** presents that species richness of bumblebees was higher in cereal field borders in flower-rich ley landscapes (mixed ley) compared to grass-dominated ley landscapes (conventional ley), and higher in landscapes with a high abundance of SNGs compared to landscapes with low SNG abundance, but only if local flower abundance was high (Figure 9B; Figure 9C). These findings suggest that while supplemental floral resources might be a viable conservation tool for bumblebees, its success depends on the presence of non-crop habitats that provide essential nesting and foraging sites (Biegerl *et al.*, 2025; Carrié *et al.*, 2018). This reinforces previous research that bumblebee persistence in agricultural landscapes requires high-quality habitat at both local and landscape scales (Clake *et al.*, 2022; Maurer *et al.*, 2020; Westrich, 1996). Furthermore, ensuring a permeable agricultural matrix which allows for movement between diverse and adjacent habitat types is critical for bumblebees to gain benefit from complementary resources in the matrix (Clake *et al.*, 2022).

Synthesising the results in **chapter III** suggests that in landscapes with low availability of primary habitats, the presence of flower-rich leys allows for pollinators to use the landscape more broadly. This could possibly be because the organic leys provided flower resources more consistently across the season than conventional leys, as observed in **chapter I**, which corresponds to results from other studies showing that organic farming, regardless of crop type, benefit aggregated pollinator diversity and richness across landscapes (Carrié *et al.*, 2018; Ockermüller *et al.*, 2025).

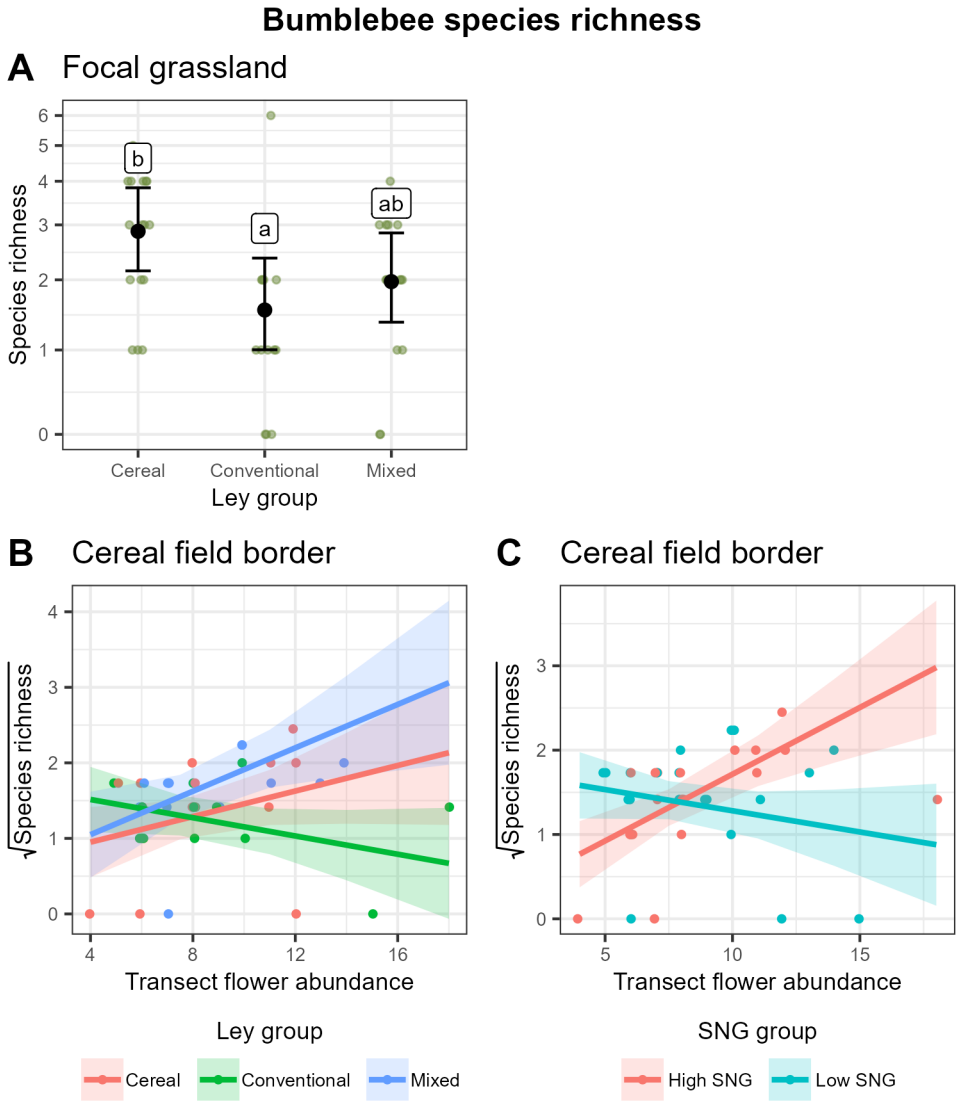

Figure 10. Bumblebee species richness in focal grasslands and cereal field borders. Bumblebee species richness in landscapes within a 1 km radius from a focal grassland in A. focal grassland by landscape ley group, B. cereal field border by transect flower abundance and ley group, and C. cereal field border by transect flower abundance and SNG group. Black dots in plot A show fitted effect values drawn from the model, with error bars showing 95% confidence intervals. Letters above black dots denotes Tukey-contrasts. Green dots show raw data points. In plot B and C, coloured dots show raw data points whereas solid lines show fitted values drawn from the model. Shaded areas show 95% confidence intervals of the fitted values. Cereal = low availability of ley fields, conventional = high availability of conventional ley fields, mixed = high availability of organic and conventional ley fields. SNG group show proportion of SNG in the landscape.

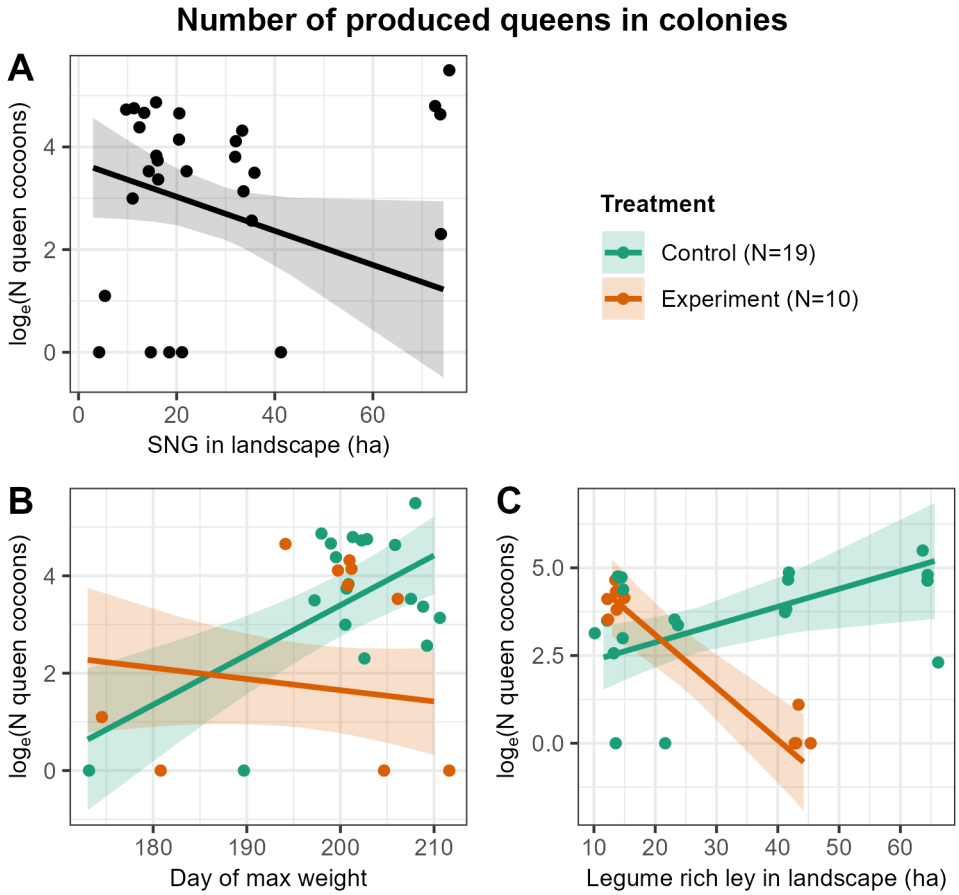

Figure 11. Number of produced queens in colonies.
Number of produced queens, calculated as number of open and closed queen cocoons in terminated colonies, by (A) area of SNG in the landscapes, (B) treatment type and Julian day number when the highest weight was recorded for each colony, and (C) treatment type and hectare of legume rich ley in the landscapes. Solid dots show original data jittered on the x-axis by value 2 to avoid overlap. Solid lines show fitted values drawn from the statistical model, with shaded areas showing ± 95% confidence intervals. Colonies with waxmoth infestation scores ≥ 4 were excluded from the analysis.

With the insight gained from chapter III, I investigated the potential effects that retaining parts of leys unmowed can pose on pollinator populations in **chapter IV**. In this chapter, I present findings on responses in commercial *Bombus terrestris* colonies on the availability of unmowed ley strips in the surrounding landscape. The findings show that bumblebee colony development is not benefitted by the availability of unmowed ley strips in the landscape. Instead, responses on colonies placed in the experimental landscapes where parts of leys were left unmowed were negative. Colonies exposed to the treatment produced significantly fewer new daughter queens with increasing area of legume-rich ley in the surrounding

landscape compared to colonies in control landscapes (Figure 11). Interestingly, reproduction in colonies placed in control landscapes responded positively (as expected) to the amount of legume rich leys in the surrounding matrix (Figure 11).

Figure 12. Photo of an unmowed ley strip.
Photo of an unmowed ley strip which was part of the experimental setup in chapter IV. Photo taken by the author (2022).

There was a drastic contrast between the flower-rich, unmowed ley strips and the surrounding mowed fields in experimental landscapes (Figure 12). This discrepancy might have caused concentration effects, attracting pollinators from the wider landscape. Given that bumblebees are highly mobile (Walther-Hellwig & Frankl, 2000) and tend to aggregate at high-quality forage sites within agricultural matrices (Heard *et al.*, 2007), both experimental and wild populations may have converged on these unmowed areas (cf. Holzschuh *et al.*, 2016; Riggi *et al.*, 2024). Consequently, high density of individuals could lead to competition in floral resources, potentially limiting the expected population-level benefits of the unmowed ley strips. Additionally, the increased aggregation of pollinators within the unmowed ley strips may facilitate the transmission of pathogens (Graystock *et al.*, 2015). There is evidence suggesting that bumblebee colonies in landscapes with wildflower plantings can experience reduced weight gain and elevated *Nosema* spore loads in workers (Angelella *et al.*, 2025). It is possible that the concentration effects observed in our flowering ley strips increased pathogen exposure, which potentially could explain why colony weights decreased in the experiment. Furthermore, as the specific composition of a floral community can dictate pathogen

acquisition rates (Adler *et al.*, 2020), the role of ley-specific plant species in disease dynamics remains a critical area for future studies, to ensure that flowering leys, when used as conservation measures, do not inadvertently function as ecological traps through disease hotspots.

The potential of leys as a floral resource for pollinators

The findings in this thesis strongly suggests that while conventional leys do provide floral resources, as shown in **chapter I**, **chapter III** shows that organic management of leys greatly enhances the positive effects on both flower availability and pollinator responses. However, I cannot recommend organic farming as a conservation measure for pollinating insects without addressing what implications this might have on farmers. This is further discussed in **chapter I**. While organic farming obviously provides positive outcomes for biodiversity in agricultural landscapes, it comes at a cost for farmers through for example yield loss compared to conventional farming (Seufert & Ramankutty, 2017), that may or may not be compensated by policy payments (cf. Reumaux *et al.*, 2026). Possible explanations for increased legume blooming in organic farming are mostly related to the difference in yield, and associated growth rate and harvest time between the farming systems (Seufert & Ramankutty, 2017; Smith *et al.*, 2019). Interestingly, regional statistics from our study area in Skåne county shows that the difference in yield per hectare between organic and conventional leys grown for fodder production is relatively low. Nationwide, the organic yield from leys was 86% of the conventional yield in 2021, and in Skåne county, the organic yield was equally large (99%) as the conventional yield (Swedish Board of Agriculture, 2023b).

When the field study for **chapter I** was conducted, 41% of all arable land was used to grow ley nationwide, and 22% of arable land in Scania 2021 (Swedish Board of Agriculture, 2023a, 2023c), corresponding to $1{,}05 * 10^6$ and $9{,}6 * 10^4$ hectares respectively. While I cannot isolate what promotes blooming within organic farming systems, **chapter I** concludes that organic farming indeed increases flowers that are available for flower-visiting insects in agricultural landscapes, and **chapter III** show that the availability of such leys modifies species richness and abundance of bumblebees and butterflies. What is clear is that, with extensive ley farming on a landscape level, both organic and conventional, indeed do provide extensive flower resources. Given that ley is the most common crop grown in Sweden (Swedish Board of Agriculture, 2023a, 2023c), it holds great potential as a floral resource for pollinators such as bees and butterflies given that management actions that promotes floral abundance can be identified.

Conclusions and final remarks

To halt the decline in biodiversity associated with agricultural landscapes, both biodiversity in general and pollinating insects in particular, conservation measures and management recommendations must be based on evidence. In this thesis, I demonstrate that floral resources from leys differ depending on management practices, and that flower availability can be efficiently mapped using remote sensing data combined with variables related to farming practices and soil characteristics. Increased availability of flower-rich leys has effects on how pollinators such as bumblebees and butterflies are distributed in the landscape. When combined with measures increasing the value of smaller habitats in the matrix such as field borders, leys can benefit pollinator populations in agricultural landscapes. However, the effect of partially delayed mowing of ley fields on pollinator populations is still somewhat unclear. Below, I highlight and synthesise the most important findings from the chapters in this thesis to give clarity in how leys could be used as a conservation measure for pollinating insects.

In **chapter I**, I highlight the critical role of both conventional and organic ley production in enhancing landscape-scale floral availability. Notably, even a small proportion of organic leys within a landscape can significantly increase landscape blooming abundance. Combined with the potential population-level benefits of flower-rich leys on pollinators described in **chapter III,** results suggest that legume-rich leys may add complementary and supplementary floral resources in the agricultural matrix for pollinators inhabiting SNGs (cf. Hederström, Ekroos*, et al.*, 2024). Furthermore, the small yield gap between organic and conventional leys in the study area highlights the opportunity that organic management practices could potentially be leveraged to increase benefits for pollinators without compromising agricultural output.

Chapter II evaluated the predictability of legume floral cover across expansive spatial and temporal scales. This did not only give valuable understanding of landscape characteristics in **chapter III**, but can possibly guide future studies on how such resources influence pollinator communities within SNGs. I demonstrate that remote sensing data combined with data on soil characteristics, and farming management practices, can effectively train a SVM that provide coarse-level predictions of ley floral resources. These findings in **chapter II** underscore the importance of integrating remote sensing into ecological monitoring to assess habitat quality at landscape scales. Refining these predictive frameworks will be

essential for future research aimed at mapping floral availability, ultimately providing the high-resolution data needed to reconcile agricultural practices with biodiversity conservation.

While **chapter III** could not present a uniform, positive response on grassland bumblebee and butterfly species richness and abundance by increased floral resources from leys in the arable matrix, findings suggests that leys serve as complementary foraging habitat and allow for pollinators to move between habitat patches in the matrix. Importantly, the efficacy of both leys and additional primary habitats in the matrix was moderated by local resource density. These results emphasise that conservation strategies must address landscape-scale matrix resources and local habitat quality simultaneously to effectively conserve pollinator communities in agricultural landscapes.

This thesis highlights the potential of leys in general, and legume-rich leys in particular, to provide flower resources for pollinating insects at landscape scales. It fills a knowledge gap of which holds potential in increasing the conservation value of SNGs for farmland pollinator populations. Finally, I hope that this thesis can provide insight and strength to future management recommendations for optimising the conservation of grassland specialists and inform under which circumstances additional floral resources on arable land benefits flower-visiting insects in focal grasslands.

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Can biodiversity declines in semi-natural grasslands be halted by minding the matrix?

Biodiversity in agricultural landscapes is declining. Species connected to semi-natural grasslands, such as flowering plants and the pollinating insects relying on them, are of particular concern. In this thesis, Julia Weber discusses how leys – grasses and legumes grown for fodder production – in the agricultural matrix can benefit pollinating insects in semi-natural grasslands. She fills a knowledge gap of which holds potential in increasing the conservation value of semi-natural grasslands for pollinating insects.

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