

Restoring biodiversity and ecosystem services on managed grasslands

J. P. Reinier de Vries

Propositions

1. The depletion of earth's ecosystems will continue as long as societies value ownership above public matters. (this thesis)

2. Biodiversity research increasingly undervalues taxonomic expertise. (this thesis)

3. Multidisciplinary science requires multidisciplinary education.

4. Environmental stewardship is not learnt behind desks.

5. A sustainable future begins with liability.

6. Fish will only recognize the environmental crisis once their pond dries out.

Propositions belonging to the thesis, entitled

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Restoring biodiversity and ecosystem services on managed grasslands

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Restoring biodiversity and ecosystem services on managed grasslands

J. P. Reinier de Vries

Thesis

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To my father and to the JNM,
for showing me that the world is full of life



ONE

Introduction

Consequences of agricultural land use change

Agricultural innovation during the 20th century has transformed landscapes across the globe at an unprecedented scale. Developments of machinery, irrigation, synthetic fertilizer and more productive crop varieties have boosted agricultural productivity and promoted food security (Godfray et al., 2010; Willett et al., 2019). This 'green revolution' has improved human welfare substantially. It also reshaped the economic conditions under which farmers grow and sell their products. Surging productivity and the globalization of food markets led to tightening economic margins on agricultural products, which pushed farmers to increase their production efficiency and scale (Emmerson et al., 2016; Zimmermann & Heckelei, 2012). While the most efficient farms expanded, many small-scale farmers quit. In industrialized regions in particular, farming intensified heavily and became reliant on external inputs such as fertilizer, fuel and pesticide products. Furthermore, fields grew larger and more monotonous, and farming became increasingly focused at animal protein production (Foley et al., 2011).

The optimization of farmland's provisioning function – food production – has come at the cost of the environment (IPBES, 2019; Rockström et al., 2025). Modern intensive farming creates highly simplified landscapes with very little space for natural vegetation. Furthermore, its use of external inputs causes various forms of environmental pollution including greenhouse gas emissions, soil and water contamination, and nutrient enrichment. These environmental costs are so severe that agriculture has become the primary driver of global environmental change: The food system alone causes the transgression of planetary boundaries in terms of climate change, land and freshwater use, nutrient cycling and biosphere integrity (Rockström et al., 2025; Sakschewski et al., 2025; Steffen et al., 2015). Of all the indicators that define these boundaries, the current loss of biodiversity is the one that exceeds its reference levels most drastically (Newbold et al., 2016; Sakschewski et al., 2025). Biodiversity loss on land is caused by the culmination of multiple drivers and several of these, such as pollution, invasive species introductions and climate change, are indirectly linked to agriculture. But the most widespread and impactful driver of biodiversity loss, habitat destruction, is a direct effect of agricultural expansion and intensification (IPBES, 2019; Jaureguiberry et al., 2022).

We do not fully oversee the consequences of this deterioration of natural life for the functioning of earth's ecosystems, nor for human well-being in the future, but it is clear that these consequences are fundamental (IPBES, 2019; Sakschewski et al., 2025). Human societies rely on a wide range of provisioning, regulating and cultural services that are sustained by earth's biodiversity and ecosystems (Cardinale et al., 2012; Dasgupta, 2021; Folke et al., 2021). For example, the decline of biodiversity-

based ecosystem services increasingly threatens agricultural productivity and food security itself (Deguines et al., 2014; Rockström et al., 2025). Moreover, a growing number of organizations advocate that biodiversity and ecosystems have intrinsic value beyond their utility to humans (IPBES, 2019).

Safeguarding earth's biodiversity and ecosystems requires a combination of approaches to conserve remaining natural habitats and to restore degraded habitats (Suding et al., 2015). Agriculture fuels the loss of natural habitats and habitat elements, but can also facilitate ecosystem restoration. The redesign of farming systems therefore ranks among the most urgent environmental challenges. Essentially, future agriculture must safeguard food security while preserving and restoring nature on land.

The degradation of managed grassland habitats

The ecological impacts of agriculture are for an important part linked to grassland ecosystems. Grasslands cover 40% of earth's land surface and roughly half of this area is ecologically degraded (Bardgett et al., 2021; Petermann & Buzhdygan, 2021). Biodiversity declines in grasslands exceed other biomes at the global level (Newbold et al., 2015, 2016). Grasslands also make up two-thirds of the world's agricultural area (Bardgett et al., 2021). This high share may seem controversial from a global nutrition perspective, because managed grasslands produce fodder for livestock instead of direct human nutrition (Foley et al., 2011; Springmann et al., 2018). However, many grasslands cover areas that are unsuitable for arable farming. Furthermore, they support a wide range of ecosystem services next to livestock keeping, including climate and water regulation, clean water supply, nutrient retention, erosion control, biodiversity preservation and cultural services (Bardgett et al., 2021; Bengtsson et al., 2019).

The human influence on grasslands dates back millennia. Natural grasslands occur in areas where the growth of woody vegetation is restricted, either by soil and climate conditions or by disturbances such as herbivory and wildfire (Bond, 2021). These natural disturbances have been widely suppressed by humans, and nutrient inputs in recent decades have further lifted natural restrictions to succession. As a result, human management is now the prevailing restriction to succession in regions where abiotic conditions would allow succession towards wooded habitats (Bråthen et al., 2021; Petermann & Buzhdygan, 2021; Shipley et al., 2024). These managed grasslands are strongly influenced by alterations of human management regimes. For centuries, large areas of 'semi-natural' grassland were used for extensive grazing or haymaking with little or no fertilization (Shipley et al., 2024). This type of management maintains nutrient-limited conditions, moderate disturbance levels and small-scale habitat heterogeneity, which allows many different plant species to

co-exist (Borer et al., 2014; Johansen et al., 2019). Species-rich herbaceous vegetations in turn support a high diversity of arthropods and higher trophic groups (Fig. 1.1). Nowadays, such extensive management practices have widely been abandoned or intensified. The intensification of grassland management, through nutrient enrichment and increased harvesting and grazing regimes, usually leads to dominance of the fastest-growing and most disturbance-tolerant plant species. Therefore, intensively used grasslands tend to have homogenized swards that support far fewer plant species, ecological niches and biodiversity-based ecosystem services (Bengtsson et al., 2019; Gossner et al., 2016; Harpole et al., 2016).

Semi-natural grassland habitats support a large part of the biodiversity of Europe (Dengler et al., 2014; Habel et al., 2013). But in large parts of the continent, these habitats are now confined to small nature reserves in landscapes dominated by intensively used farmland. Despite their protected status, most semi-natural grassland remnants experience ongoing biodiversity declines due to habitat fragmentation and the influx of nutrients from their surroundings (Habel et al., 2019; Klaus et al., 2018). It comes as no surprise that grassland plants and animals, such as wild bees, butterflies, bugs and grasshoppers, have all shown drastic declines across Europe (Dvořák et al., 2022; Eichenberg et al., 2021; Ekroos et al., 2020; Gossner et al., 2016; Seibold et al., 2019; Warren et al., 2021).

European agricultural policies have long promoted intensification of agricultural management, without accounting for the broader implications of ecosystem degradation for society (Emmerson et al., 2016). This approach is widely criticized for falling short in safeguarding societal interests beyond food production. In response, more recent policies such as agri-environment schemes (in place since 1992) try to incentivize biodiversity-friendly management on farmland (Batáry et al., 2015). Extensified management schemes on grasslands are one of the most widely applied restoration measures for farmland biodiversity. By prescribing restrictions to fertilization, stocking density and first mowing dates, these schemes aim to mimic the traditional use of semi-natural grasslands. Although such schemes have helped to restore grassland ecosystems locally, they have not reversed the overall trends of degrading biodiversity and ecosystem service delivery (Batáry et al., 2015; Kleijn et al., 2011; Kleijn & Sutherland, 2003; Pe'er et al., 2017). Hence, Europe's grassland systems remain far from a resilient, ecologically restored state that safeguards their biodiversity, ecosystem functions, and diverse contributions to human well-being on the long term.



Figure 1.1 Example grasslands of different land use intensity levels. First row, left to right: Extensive grassland rich in forb species; *Orchis purpurea* flowering in May; *Bombus hortorum* feeding on *Crepis biennis* and the rare *Bombus sylvarum* feeding on *Lotus corniculatus* (both flowers occur in low- to medium-extensive grasslands); young cattle on a grass-dominated, medium-extensive field. Second row, right to left: Organic silage field with sown-in wildflowers; conventional silage production with sown-in legumes (*Trifolium repens* and *T. pratense*); conventional field shortly after mowing. All pictures were taken in South-Limburg, the Netherlands (photo credit: Reinier de Vries).

Limitations to grassland ecosystem restoration

Scientists and public organizations call for a much wider application of ecological approaches to farming, but such approaches remain poorly adopted by farmers. The reluctance of farmers is often due to socio-economic constraints such as social acceptability and economic uncertainty (Kleijn et al., 2019; Scherfranz et al., 2025). Nevertheless, most agro-ecological studies do not take these constraints into account. Many studies have highlighted that management for biodiversity can improve ecosystem service delivery, and some also showed positive effects on yield (e.g. Dainese et al., 2019; Pywell et al., 2015; Schaub et al., 2020), but very few have quantified opportunity costs and profitability. But when opportunity costs outweigh its benefits, management for biodiversity will still not pay off for farmers (Scheper et al., 2023; Woodcock et al., 2025). This prevents more large-scale application of such management. Effects on farmer income are therefore crucial to consider in the development of ecological restoration programs.

Furthermore, our understanding of the effects of land use intensification on biodiversity still has important caveats. Biodiversity assessments have historically been dominated by vascular plants and larger vertebrate animals, whereas little attention was paid to invertebrates (Dirzo et al., 2014; Wagner, 2020). This

changed only recently when studies revealed drastic declines of invertebrate populations (Cardoso et al., 2020; Hallmann et al., 2017; Wagner et al., 2021). However, research on invertebrates is still dominated by only a few groups of charismatic species, such as butterflies (Papilionoidea), and well-known ecosystem service providers, such as wild bees (that are pollinators) and carabid beetles (that are natural enemies of pests). We still know little about the effects of land use change on other invertebrate groups, which together represent the majority of species in grasslands and other habitats (Wagner, 2020). Most studies on invertebrates are not only limited in their taxonomic scope, but also lack broad spatial coverage and robust reference data (Cardinale et al., 2018; Cooke et al., 2025). Studies that lack comparison to an undisturbed reference situation may underestimate the effects of environmental changes or overstate the effectiveness of restoration measures. Invertebrate studies face a very poor availability of historical reference data, but this caveat can partly be compensated by studying spatial gradients of changes such as land use intensification (Blüthgen et al., 2022). Thorough inventories across multiple invertebrate groups and locations, particularly locations that reflect the main drivers of biodiversity change, are therefore eminently needed.

The implementation of ecological restoration practices faces additional knowledge gaps, particularly when aiming to support understudied invertebrate taxa. Many restoration programs prescribe management practices without investigating local biodiversity outcomes. Therefore, the effects of these practices cannot be evaluated, nor can they be adjusted to local circumstances (Kleijn et al., 2011). Unfortunately, thorough multi-taxa biodiversity inventories are so time-consuming that they can impossibly be conducted across all restoration schemes. Habitat quality indicators may provide a solution to this constraint because they show potential for efficient data collection across large areas, while still reflecting fine-scale (even within-field) biodiversity patterns (Cavender-Bares et al., 2022). To be widely applicable, such indicators should predict biodiversity patterns across a wide range of taxa and disturbance levels (Manning et al., 2015). Generalizable indicators can enable important improvements to current restoration programs. For example, they can facilitate the adaptation of restoration practices at a field-specific basis. Grassland managers could for instance tailor mowing dates to local characteristics, such as productivity and floral composition, instead of following a fixed prescription. Such adaptations may enhance local restoration outcomes, as well as spatial heterogeneity and resource continuity at landscape scales (Bishop et al., 2024; Johansen et al., 2019). By allowing more flexibility in management, they may even improve the compatibility of restoration practices with farming (Herzon et al., 2018). Locally tailored restoration schemes can therefore help to overcome various limitations of current approaches to the ecological restoration of grassland habitats.

Box 1: Grasslands in South Limburg

The studies presented in this thesis were conducted within a study area of approximately 10 by 10 kilometers. This study area is situated in the valley of the river Geul in the region South-Limburg, which forms the southeastern tip of the Netherlands. This region is unique within the Netherlands due to its soils and terrain, which originated from the uplift of a plateau that now lays between 100 and 312 meter above sea level. This plateau consists of lime-rich parent material, which was covered by eolian loess deposits during the most recent glacial periods. Thereafter, the plateau was incised by water runoff through the Geul valley and many smaller tributaries (Fig. 1.2). Most of the current landscape is therefore characterized by loess soils, while light clay deposits are found on the bottom of the valley. At specific locations on the valley's slopes, the lime-rich parent material reaches near the surface and creates alkaline circumstances (Willems, 2001; Wösten et al., 2013).

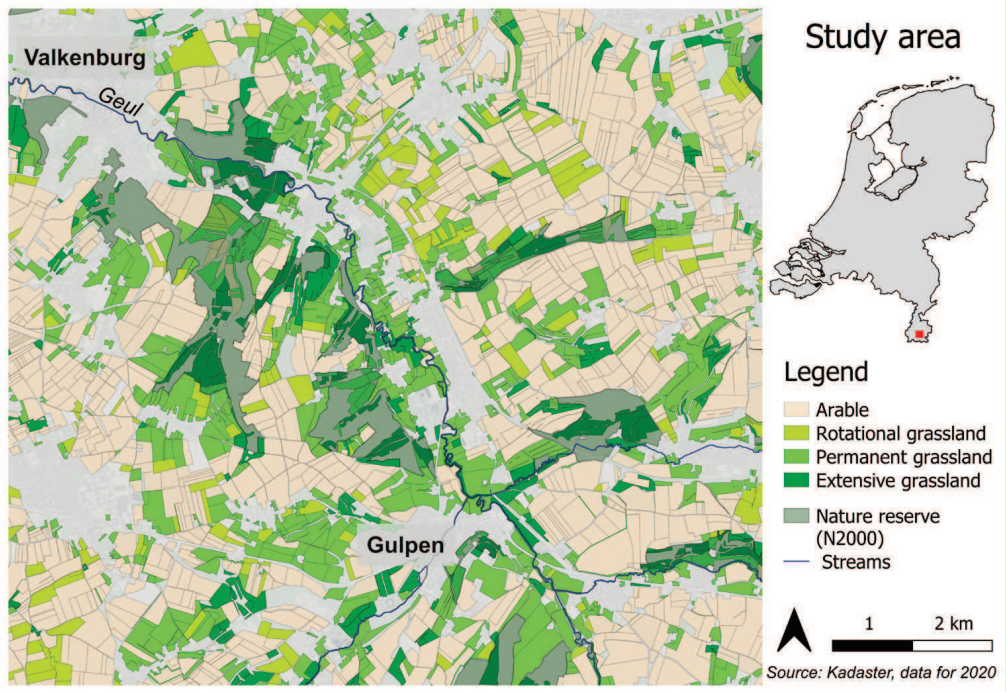


Figure 1.2 Map of the study region around the towns Valkenburg and Gulpen in the southeast of the Netherlands. The region's rural landscape supports a mosaic of arable fields and grasslands along a gradient of land use intensity levels. Permanent and rotational grasslands are usually managed intensively, but small percentages are extensified within organic or agri-environment schemes. These schemes are not distinguished on this map. The depicted extensive grasslands have a nature conservation status. Most of these areas fall under the Natura-2000 network of nature reserves.

Owing to the fertility of its loess soils, three-quarters of the rural land in South Limburg is used for farming including croplands, orchards and grasslands. Grasslands represent just over half of this agricultural land regionally. South Limburg has a fine-grained agricultural landscape with relatively small fields (± 2 ha on average) but usually high land use intensities (Van der Meulen, 2025). At the same time, the valley of the river Geul supports one of the largest Natura-2000 areas in the Netherlands, which protects forests, alluvial habitats and species-rich grasslands. Therefore, grasslands within our study area show vast differences in land use intensity. Agricultural grasslands, including both permanent grasslands and temporary grasslands in crop rotations, are dominant (± 60% resp. 20% of grasslands in the study area). Most of these grasslands are part of conventional dairy farms and are managed intensively, with five harvests per year, intensive grazing schemes, and high nutrient inputs (± 250-330 kg effective nitrogen per hectare per year). This type of management is widespread in the Netherlands but represents one of the highest land use intensity levels on grasslands in Europe and worldwide (Eurostat, 2025). A minor part of agricultural grasslands —approximately 10% of the above-mentioned area— is managed more extensively by organic farms, beef producers and agri-environment schemes. The remaining ± 20% of grasslands in the study area is used extensively to promote nature restoration. Most of these grasslands are used as unfertilized hay meadows with two cuts per year, or as extensively grazed pastures (<2 livestock units per hectare). Specific locations, where historic extensive management and phosphorus buffering of alkaline soils have maintained nutrient-poor conditions, still support species-rich grassland vegetations that have largely disappeared in the rest of the Netherlands. These sites are typically mown once per year or grazed by sheep (Willems, 2001).

The gradient of land use intensity on grasslands in this study area occurs under broadly similar abiotic conditions, all of which in principle allow intensive conventional management. The actual land use intensity is therefore dependent on decisions of land owners aiming for agricultural production or nature restoration. Mowing, grazing and mixed management schemes occur at all intensity levels. Furthermore, the different land use types are spatially intermixed across the study area, with no strong clustering of similar intensity levels (Fig. 1.2). These characteristics allowed us to compare the effects of land use intensification across grasslands within one study region. We selected study sites across the widest possible land use intensity gradient, ranging from very low intensity to land use intensity levels that are among the world's highest on grasslands.

Aims and outline

This thesis aims to investigate critical constraints to the restoration of biodiversity and ecosystem service delivery on managed grasslands, considering that the intensification of human land use has been the principal driver of their widespread degradation. This thesis presents four field studies that seek to understand the implications of land use intensification in grasslands from an environmental economics perspective (**chapter 2:** what does intensification mean for farmers and society?) and from an ecological perspective (**chapter 3:** what does intensification mean for biodiversity?). Furthermore, this thesis investigates strategies to restore grassland biodiversity, specifically testing broadly applicable habitat quality indicators (**chapter 4**) and adaptation of restoration practices to local conditions (**chapter 5**).

Throughout this thesis, land use intensity is quantified by means of productivity of the sampled grasslands. Productivity provides a quantitative measure that comprises multiple management aspects, such as fertilization and harvesting intensity, and facilitates comparison across different management types (e.g. mown or grazed, fertilized or unfertilized). The data presented in this thesis were obtained in a study region situated in the south of the Netherlands (see Box 1). The grasslands in this region represent a broad land use intensity gradient, ranging from relatively well-preserved reference grasslands to monocultural grasslands that are among the world's most intensively used. In fact, this gradient roughly reflects the range of land use intensity levels that can be found in managed grasslands in other temperate regions across the world (Bardgett et al., 2021). This study system can therefore inform on the implications of the land use intensification trend that occurred in temperate grasslands globally.

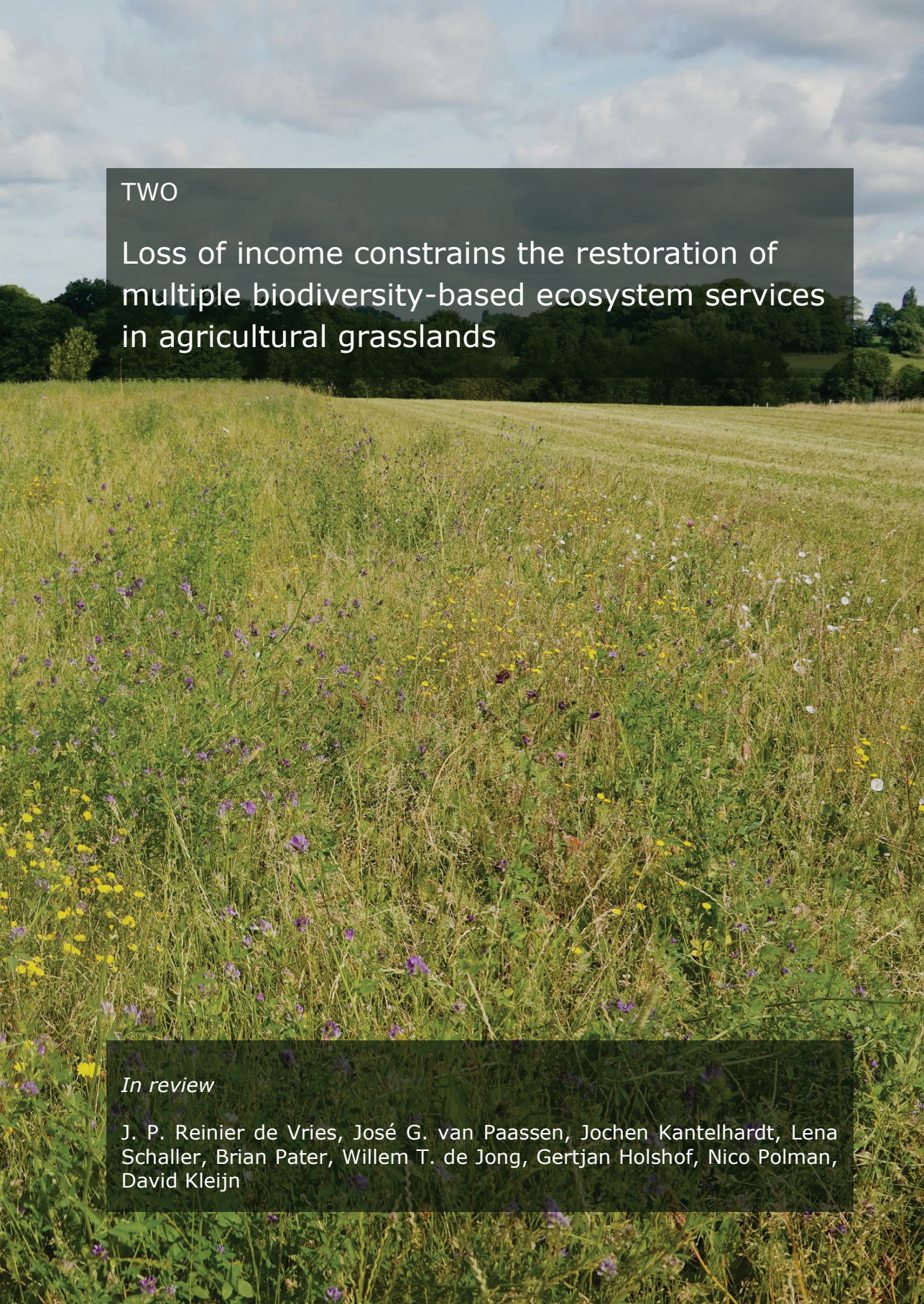
Chapter 2 evaluates whether the restoration of biodiversity-based ecosystem services in grasslands induces win-wins or trade-offs between farming and society. The contributions of multiple ecosystem services to grassland productivity are compared with the effect of fertilization. Next, each grassland's contribution to the income of farmers is assessed by calculating field-level gross margins, and is compared to the delivery of ecosystem services of societal importance.

Chapter 3 investigates the effects of land use intensification on arthropod biodiversity, using data collected by sweep-net sampling in a space-for-time design. Changes in overall abundance and species richness along the land use intensity gradient are quantified for a broad range of arthropod groups. Subsequently, more detailed insight into the effects of land use intensification on arthropod communities is obtained through a novel approach that quantifies the distributions of individual species along the land use intensity gradient.

Thorough inventories of multiple arthropod groups are extremely labour-intensive and limited in spatial coverage. Therefore, **chapter 4** explores the potential of flower species richness and total flower cover to serve as broadly applicable indicators of grassland biodiversity. The relations of these two metrics with plant and arthropod species richness are investigated across multiple taxonomic groups, across a broad land use intensity gradient and across three months (April, June and July).

Given the importance of flowers for grassland biodiversity, **chapter 5** tests experimentally if the effect of reduced mowing —a broadly promoted biodiversity restoration strategy— on the flowering of grassland forbs is dependent on the local productivity level. Effects on aggregated flower cover and species richness, on cover and richness recovery rates, and on the flowering trends of individual forb species across the growing season are compared across four mowing regimes.

Finally, **chapter 6** integrates the main insights from these studies in a general discussion. This discussion focuses first on the research priorities that emerge from the results of this thesis, and then discusses how the content of this thesis could be used in practice to restore grassland ecosystems more effectively.



TWO

Loss of income constrains the restoration of multiple biodiversity-based ecosystem services in agricultural grasslands

In review

J. P. Reinier de Vries, José G. van Paassen, Jochen Kantelhardt, Lena Schaller, Brian Pater, Willem T. de Jong, Gertjan Holshof, Nico Polman, David Kleijn

Abstract

Biodiversity loss and ecosystem degradation impair the delivery of multiple ecosystem services to both farming and society. Despite increasing evidence that biodiversity-based ecosystem services support agricultural production, farmers are reluctant to manage for biodiversity. This has been attributed to the economic costs of enhancing biodiversity, which may outweigh its benefits to farmers, but this has rarely been examined under real-world conditions. Here, we evaluated whether restoring grassland ecosystem services induces win-wins or trade-offs between farming and society. We found that increasing legume cover enhanced productivity and could improve profitability whilst reducing environmental impacts. However, no other biodiversity-based ecosystem service contributed to grassland productivity, which was maximized by increasing management intensity. Biodiversity, nutrient retention and carbon sequestration strongly traded off with farmer income. These results imply that most biodiversity-based ecosystem services should be considered public goods critical to society. Restoring these services requires societal support that makes biodiversity management economically rewarding.

Introduction

Agriculture is one of the most important drivers of global environmental change (IPBES, 2019; Willett et al., 2019). Intensification of farming practices has boosted productivity across agricultural systems, but leads to widespread deterioration of water and climate regulation, ecosystem resilience and biodiversity (Foley et al., 2011; Rockström et al., 2017). This is cause for concern, not only because ecosystems and biodiversity have intrinsic value but also because they sustain human well-being through numerous regulating, provisioning and cultural ecosystem services (Cardinale et al., 2012). Several biodiversity-based ecosystem services contribute directly to agricultural production, and scientific evidence is accumulating that their deterioration is increasingly constraining our ability to enhance or maintain agricultural productivity and therefore food security (Bardgett et al., 2021; Deguines et al., 2014; Isbell et al., 2013). Scientists and public organizations therefore call for farming strategies that restore ecosystem services to support agricultural productivity (IPBES, 2019; Kremen & Merenlender, 2018; Rockström et al., 2017; Willett et al., 2019), but few farmers embrace this approach (Kleijn et al., 2019).

The reluctance of farmers to adopt ecosystem restoration practices may be linked to the economic consequences of such management. Many ecological studies highlight yield benefits of ecosystem service enhancement (Lehmann et al., 2020; Pywell et al., 2015; Schaub et al., 2020), but the associated management costs and opportunity costs that farmers face when other production factors—such as inputs or area—are constrained by restoration measures, are rarely considered (Bardgett et al., 2021; Kleijn et al., 2019). In a recent study, Scheper et al. (2023) showed that, although biodiversity measures produced benefits for both biodiversity and yield, the costs of enhancing biodiversity outweighed the economic gains for farmers. However, this study evaluated only the benefits of pollination services to farmers, while biodiversity-friendly farming can promote a broad range of ecosystem services simultaneously (Cardinale et al., 2012; Petermann & Buzhdygan, 2021). Considering the benefits of multiple ecosystem services to farming could tip the balance between costs and benefits if the combined benefits of these services would outweigh the production costs associated with enhancing biodiversity (including management and opportunity costs), and therefore impose a positive relationship between biodiversity and farmer income (Fig. 2.1A,C). But if costs to production outweigh the ecosystem service benefits to farming from a certain biodiversity increase, they impose a trade-off between biodiversity and farmer income (Fig. 2.1B).

Here we examine the contributions of multiple ecosystem services to productivity, and consequently, agricultural income to farmers, in real-world grassland systems. We focus on grasslands because they are the most widespread farming system globally, covering a quarter of earth's land and two-thirds of its agricultural area (FAO, 2022). At the same time, they can support significant biodiversity levels and

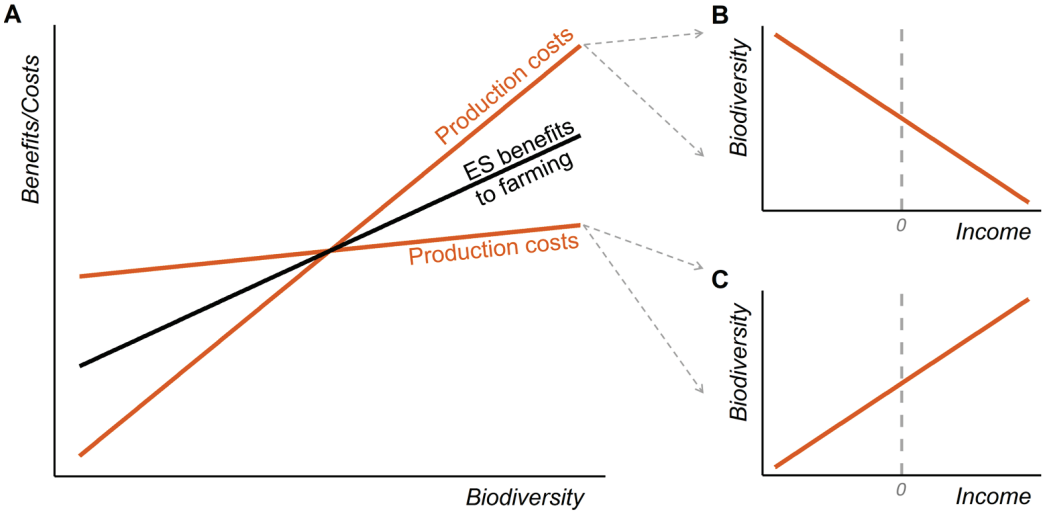


Figure 2.1 A conceptualization of the importance of the relationships between biodiversity and *both* production costs (i.e. management and opportunity costs) and benefits for the economically most profitable farming strategy (A). When enhancing biodiversity results in a more rapid increase of production costs than of ecosystem service benefits to farming, farmer income is maximal at low biodiversity (B) even though ecosystem service benefits may outweigh production costs at intermediate biodiversity levels. When production costs increase more slowly with biodiversity than ecosystem service benefits, the optimal economic solution is to maximize biodiversity (C). For simplicity, we assume linear relationships.

regulating services, but are widely affected by ecosystem degradation (Bardgett et al., 2021; Ekroos et al., 2020; Seibold et al., 2019).There is good evidence that grassland productivity is supported by a number of interrelated biotic and abiotic factors and ecological processes, that are moderated by biodiversity. For example, a vast body of experiments has demonstrated that plant diversity promotes biomass production and yield stability (Binder et al., 2018; Cardinale et al., 2012; Finger & Buchmann, 2015; Schaub et al., 2020), especially when enhancing symbiotic relations between grasses and legumes (Ashworth et al., 2018; Finn et al., 2013). Furthermore, several biodiversity-mediated soil functions promote grassland productivity: nutrient release from organic matter decay by the soil microbiome enhances plant growth (Tsiafouli et al., 2015); earthworms further stimulate plant growth through their influence on biotic and abiotic soil properties (Van Groenigen et al., 2014); and soil organic matter improves soil structure and water holding capacity, thus increasing drought resilience (Lehmann et al., 2020; Liu et al., 2019). Grassland ecosystems may also have wider societal benefits. For example, species-rich grasslands support high biodiversity levels and sustain refuge habitats for many rare and threatened species (Petermann & Buzhdygan, 2021; Warren et al., 2021). They are also aesthetically appealing to people, supporting recreation and well-being (Lindemann-Matthies et al., 2010; Nowak-Olejnik et al., 2020). Plant diversity and soil organic matter reduce nutrient leaching to ground- and surface waters (De Vries et al., 2012; Leimer et al., 2016) and promote soil carbon sequestration (De

Deyn et al., 2011; Yang et al., 2019). Since grasslands account for a third of global terrestrial carbon stocks, they contribute substantially to global climate change mitigation (Bai & Cotrufo, 2022). In sum, because biodiversity has been found to support both productivity and the delivery of wider societal benefits, managing for biodiversity-based ecosystem services on grasslands could produce win-win's for farmer income and society (Binder et al., 2018; Fischer et al., 2017; Schaub et al., 2020).

Currently, most grassland farmers seek to maximize productivity through intensive use of external inputs such as fertilizers (Drinkwater & Snapp, 2007; Emmerson et al., 2016), rather than aiming to maximize ecosystem service delivery. There is clear evidence that the intensity of grassland management is negatively related to on-field biodiversity (Beckmann et al., 2019; Ekroos et al., 2020; Harpole et al., 2016; Schulz et al., 2024) and amplifies nutrient losses to the environment (Klaus et al., 2018), both of which contribute to the deterioration of grassland ecosystems and biodiversity (Gossner et al., 2016; Wagner et al., 2021). The effects of management intensity on ecosystem services supporting grassland productivity are however less clear. For example, plant diversity declines may prevent high-input systems from reaching maximum productivity (Isbell et al., 2013; Schaub et al., 2020), but the positive effects of legumes on productivity seem to persist under high nutrient inputs (Ashworth et al., 2018; Finn et al., 2013). Soil biodiversity appears robust to grassland intensification (Le Provost et al., 2021), but fertilization can nevertheless reduce biodiversity-moderated organic matter decay (Riggs & Hobbie, 2016). Furthermore, fertilization can accelerate soil carbon accumulation (Poeplau et al., 2018; Seabloom et al., 2021), but the associated practices of biomass removal, plant diversity decline and soil disturbance may inhibit carbon sequestration (Bai & Cotrufo, 2022; Yang et al., 2019). Whether restoring ecosystem services actually provides opportunities for win-wins for farmers and society is therefore determined both by the contributions of multiple ecosystem services to productivity, and by their exact relationships with management intensity and farmer income.

We examined the delivery of multiple biodiversity-based ecosystem services along a grassland intensification gradient in the Netherlands, one of the most intensively farmed countries in the world. Grasslands in the Netherlands are predominantly used for intensive dairy farming. However, the establishment of protected areas and the implementation of agri-environment schemes in our study region has resulted in a fine-grained mosaic of grasslands exposed to comparable environmental and socio-economic conditions, but with differing management intensities. Management ranged from unfertilized, low-productivity grasslands to heavily fertilized, sown monocultures that were cut up to six times per year. This allowed us to study the relationship between ecosystem service delivery and farmer income across the widest possible range of management intensity, and produce important insights into the drivers and consequences of the land use intensification trend observed in grasslands globally. We first analysed which ecosystem services contribute to

grassland productivity, and second, how multiple ecosystem services relate to farmer income. We quantified plant and bee species richness, legume cover, nitrate (NO_3^-) and phosphate (PO_4^{3-}) leaching, soil carbon content, decay rate and earthworm abundance and species richness as indicators of ecosystem service delivery. Grassland productivity and farmer income were assessed from data on forage yields and management costs at field level, which were obtained from farmer interviews and national agricultural statistics.

Materials and Methods

2.2.1 Site selection

We selected 41 grasslands in an area of approximately 70 km^2 in the southeast of the Netherlands (Fig. 7A.1). Land use in this area is characterized by intensive conventional arable and dairy farming, organic mixed farming and conservation management in one of the largest Dutch Natura2000 protected areas (*Geuldal*). The study area has broadly similar climate and soil conditions (loamy and light clay soils: Wösten et al., 2013) and low hills (70-170 m a.s.l.) which create local variation in hydrology and soil depth. We surveyed grasslands that have been used agriculturally in the past and could support intensive management for livestock farming. Therefore, the current management intensity gradient reflects the varying objectives of land owners for agricultural production or ecological restoration. From high to low intensity, grasslands were used for conventional dairy, organic dairy or beef cattle farming, and managed under agri-environment schemes (i.e. hay production) or nature conservation schemes for hay meadows and species-rich grasslands. Management intensity ranged from 1-6 cuts a year and nitrogen inputs ranged from 0-332 $kg \cdot ha^{-1} \cdot year^{-1}$ of effective nitrogen (Table 7A.1). Twenty-two of the sites were mown, nine were grazed and ten had mixed management for at least two years prior to sampling. The sampled grasslands were on average 711 (± 239) m apart from their nearest neighbour and we confirmed there was no spatial autocorrelation in management intensity.

2.2.2 Ecosystem services

Ecosystem service delivery was assessed by field measurements of biodiversity, nutrient leaching, carbon storage and soil quality indicators that were undertaken in each grassland. Biodiversity lays the basis for the delivery of multiple ecosystem services (IPBES, 2019). We measured plant, bee and earthworm species richness, representing diverse and functionally important groups in grasslands that have been widely used as biodiversity indicator groups (Van Groenigen et al., 2014; Westphal et al., 2008). Plant species richness was measured between May 29th – June 17th in ten quadrants of 50*50 cm, distributed evenly along a 150 m transect running from edge to centre of the field, and crossing heterogeneities (e.g. elevation differences) within the field when present. For each species the percentual coverage was estimated, from which the combined cover of leguminous species (Fabaceae) was

extracted as an indicator of nitrogen fixation by legumes. Bee species richness was measured along the same transects within a width of 1 m during three 15-minute surveys, held in May, June and July 2021 under favourable weather conditions (i.e. on dry, sunny days with temperatures >15°C and wind speeds <3 Bft) (Westphal et al., 2008). Specimens that could not be species-identified in the field were collected to be identified in the lab. To minimize disturbance, soil measurements were collected at three locations separate from the transect (one near the field's edge, two in the centre). Nutrient leaching was measured during a six-month period (early May – early October) by ion-exchange resin bags capturing leaching nitrate (NO_3^-) and phosphate (PO_4^{3-}) ions (Klaus et al., 2018). Bags contained 21 g of a mixed-bed cation-anion exchange resin and were placed at 20-25 cm depth: Below the rooting depth of most grassland species, ions at this depth were thought to indicate nutrient losses from the grassland topsoil to the groundwater, which is a dis-service causing water quality deterioration (Nijssen et al., 2017). After bag retrieval, ions were extracted by an acid solution (80 ml, 2M NaCl, 0.1M HCl) and measured in milligram per kilogram resin [$mg \cdot kg^{-1}$] using a segmented flow analyser. Soil carbon content, indicating carbon storage, was measured from soil cores collected during April 27th – May 6th at 5-10 cm depth and extracted by dry combustion (Dumas method). Earthworm species richness and abundance were measured in 30*30*20 cm soil volumes, which were manually collected and sorted in the field allowing species identification in the lab. Organic matter decomposition was measured by tea bag decay, for which at each location two pairs of red and green tea bags were buried at 8 cm depth over a 90-day period (July – October), whereafter dry weight losses were used to calculate the decay rate (Keuskamp et al., 2013). Earthworm abundance and the decay rate respectively indicate soil structure enhancement and nutrient release, both reflecting soil quality (Lehmann et al., 2020).

2.2.3 Management and productivity

Key determinants of production costs and benefits, fertilization inputs, silage or hay yields (number of cuts and dry weights) and grazing intensity (livestock units) per hectare, were investigated via questionnaires with farmers. To avoid influences from year-specific conditions and fluctuations, farmers were asked specifically to indicate average management and yield characteristics. We then calculated annual inputs and outputs using national agricultural statistics. First, fertilization inputs coming from artificial and organic (slurry and manure) products and from excretion by grazing livestock, were multiplied by nitrogen working coefficients per input type (Blanken et al., 2021; Remmelink et al., 2020) to derive the total input of effective nitrogen [kg $N_{eff} \cdot ha^{-1} \cdot yr^{-1}$]. Livestock excretion per hectare was derived from grazing intensity [$hours \cdot ha^{-1} \cdot yr^{-1}$] using animal-specific slurry excretion coefficients for dairy or beef cattle, yearlings or sheep (Blanken et al., 2021; Remmelink et al., 2020). Second, productivity was determined by combining harvested (dry weight during collection) and grazed yields. Grazed yield weights were derived from grazing intensity by using animal-specific grazing or feed requirements, corrected for

grazing efficiency and residue losses (Blanken et al., 2021; Remmelink et al., 2020). By this we quantified yield as derived from the fields under current management, but excluded storage and feeding losses as well as potential long-term effects of grazing on grass growth. Subsequently, productivity was assessed in terms of metabolic energy (ME) [GJ·ha^{-1}·yr^{-1}] and digestible protein [kg DP·ha^{-1}·yr^{-1}], which are commonly used measures of fodder nutrition value (Polman et al., 2021; Schippers et al., 2012). Therefore, dry-weight yields were multiplied with standardized estimates of the metabolic energy and protein contents of conventional dairy cattle silage (first cut or the following cuts), organic dairy and beef cattle silage, good-quality hay or poor-quality hay, as well as for fresh grass grazed by conventional dairy cattle (rotation grazing), organic dairy and beef cattle, or extensive continuous grazing (Blanken et al., 2021; CVB, 2022; Remmelink et al., 2020; Schippers et al., 2012). Good- and poor-quality hay were distinguished by mowing date (before or after June 20th, respectively) (Schippers et al., 2012) and poor-quality hay yields were corrected by fill unit (1.2) to account for the decreased nutrition intake from this forage (Andrieu et al., 1988). Further detail on our productivity assessment is provided in the supplementary information, Table 7A.1 and the supplementary text.

2.2.4 Field-level gross margin

We assessed the contribution of grassland to the income of farmers by means of calculating field-level gross margins [€·ha^{-1}·yr^{-1}], subtracting variable costs (fertilizing and harvesting) from yield revenues for each field. By this approach we assessed the intermediate outputs of forage production but excluded animal protein production by livestock keeping, which would induce additional opportunity costs but also revenues from product diversification (for example, beef farms may make higher revenues from low-quality fodder than dairy farms). In reality, livestock farmers are both the producers and consumers of grassland forage, and their uptake of biodiversity-friendly management depends on its compatibility at farm level. An intermediate output approach excludes these effects but allows comparison at field level. Furthermore, to compare private benefits with public good delivery, we excluded current compensation payments for biodiversity measures, such as agri-environment schemes, from the assessment of field-level gross margin.

Yield revenue was derived using standardized prices of €24,61 per GJ metabolic energy for feed value and €0,97 per kg for protein (Remmelink et al., 2020). Fertilizer product costs were assumed to be €0,76 per kg N_{eff} for artificial fertilizer, but zero for slurry, since slurry prices fluctuate strongly but grassland farmers typically use their own slurry. Fertilizing costs were determined by assuming standard equipment (pneumatic spreader for artificial fertilizer, assuming a standard quantity of 50 kg N_{eff}·ha^{-1} per round; slurry injector for all organic fertilizer inputs). Furthermore, harvesting costs were determined assuming standard equipment (disk mower, circle swirl and collector, and bale wrapper producing 400-kg bales) for all yields, thus including grazed quantities. Grazed forage was regarded

as silage or hay if the energy content was above resp. below 5.87 $GJ \cdot kg^{-1}$. The number of hay cuts was indicated by land owners (i.e. 1-2 times), but for all silage yields as well as hay grazing the number of cuts was simulated assuming yields of 2500 $kg \cdot ha^{-1}$ per cut; by this we could incorporate grazing and avoid effects of individual management decisions. For both fertilizing and harvesting operations, standard costs were based on contractor cost price estimates obtained from Remmelink et al. (2020) which include machinery investment, maintenance and depreciation, labour, fuel and lubricants and business risk (5% surcharge), but not VAT or real-world customer rates. Further detail on the assessment of gross margin is provided in Table 7A.1 and the supplementary text (Appendix 7A).

2.2.5 Data analyses

To allow field-level comparisons, species observations per quadrat (plants), survey (bees) or soil core (earthworms) were combined to derive observed species richness, earthworm abundance and percentual legume cover estimates (Table 7A.2). Replicated measurements of decay rate (n=6), nutrient losses (n=3) and soil carbon content (n=3) were averaged at site level, after excluding two erroneous decay rate measurements and one exceptional soil carbon measurement from a peaty location. One site however experienced topsoil disturbance from sod reseeding in late summer, hence topsoil measurements obtained later (i.e. of decay rate and earthworms) were excluded. First, on the remaining sites (n=40) we used multiple linear regression and an information theoretic approach (Grueber et al., 2011; Harrison et al., 2018) in R 4.3.2 (R core team, 2023) to analyse how fertilization and ecosystem services related to grassland productivity. We selected plant species richness, legume cover, decay rate, earthworm abundance and soil carbon content as indicators of ecosystem services that have been shown to contribute to grassland productivity. Furthermore we included the quadratic term of fertilization as initial analyses indicated a saturating relationship with productivity (Drinkwater & Snapp, 2007). Predictors were z-standardized and tested for multicollinearity by the Variance Inflation Factor (VIF: threshold = 0.5), which was avoided by excluding plant richness as a model predictor. The global model thus included six predictors but given the limited sample size, we restricted the model set to all possible combinations of maximum four predictors and the intercept-only model. These 42 models were derived using the R-package *MuMIn* (Bartoń, 2023) and ranked by their Akaike Information Criterion for small sample sizes (AIC_c) (Table 7A.3). Candidate models within $\Delta AIC_c < 4$ were selected to construct an averaged model, using Akaike model weights (ω_m) to determine full-model parameter estimates accounting for model selection uncertainty (Harrison et al., 2018). Relative predictor importance (ω_p) was based on standardized effect sizes (Schielzeth, 2010). The complete and best-performing models were validated by plotting their standardized residuals versus fitted values, all global model predictors and spatial coordinates, and versus land use characteristics not in the model (hay or silage, mowing or grazing) (Zuur & Ieno, 2016), using R-package *DHARMa* (Hartig, 2022).

Next, generalized linear models were used to analyse how multiple ecosystem service indicators related to the field-level gross margin. Following structured data exploration, nitrate loss and legume cover were square-root transformed to avoid right skew, and species richness was modelled in the Generalized Poisson distribution accounting for overdispersion, using R-package *glmmTMB* (Brooks et al., 2017). Non-linear functional forms (Paul et al., 2020) were evaluated for each service by the statistical support for quadratic and cubic terms ($\Delta AIC_c > 2$). Model residual patterns were validated and related to land use characteristics and pH, and were handled by excluding one outlier for phosphate loss (which was based on only two field measurements) and by including longitude as a model predictor for soil carbon. Subsequently, model performance was assessed by pseudo-R^2 for generalized linear models (Nakagawa & Schielzeth, 2013) and partial R^2 for soil carbon (Jaeger et al., 2017). Finally, we used the validated models to predict multiple ecosystem service delivery at three gross margin levels of 50, 700 and 1350 euro per acre per year. These values approximate the 10th, 50th and 90th quantiles of the collected data and illustrate real-world cases of low, medium and high productivity grasslands.

Results

2.3.1 Linking ecosystem service delivery and management to grassland productivity

Grassland productivity ranged from 4 to 91 GJ·ha^{-1}·year^{-1} (corresponding to dry weights of 1.2-14.5 tonnes·ha^{-1}·year^{-1}, which is representative for Dutch livestock grasslands (Remmelink et al., 2020), and the model set revealed a strong relation with fertilization ($\Delta AIC_c = 70$ between the best models with and without fertilization: see Table 7A.3 for the full model set). The candidate models within $\Delta AIC_c < 4$ also included the quadratic term, indicating diminishing returns from fertilization at high input levels. Furthermore, these models consistently showed a positive relation between legume cover and productivity (Table 2.1). At high-input grasslands (>250 kg N·ha^{-1}·yr^{-1}), increasing the legume cover allowed to maintain productivity while reducing nutrient inputs by about a third (Fig. 2.2A). The relative contribution of legumes in low-intensity grasslands was even more important. On the other hand, we found no consistent support for relations between productivity and organic matter decay, earthworm abundance or soil carbon (Table 2.1).

2.3.2 Relating ecosystem service delivery to farmer income

The gross margin of forage production at field level, which is an intermediate output in livestock production systems, ranged from 18 to 1711 €·ha^{-1}·year^{-1} (Fig. 2.2B). Extensification of agricultural production led to cost savings, notably from reduced fertilization, but gross margins were mainly driven by yield revenues and therefore closely followed management intensity. Generalized linear models revealed strong relations between gross margin and the indicators of grassland biodiversity, nutrient retention and carbon storage (Fig. 2.3, Table 7A.4). Gross margin was negatively

Table 2.1 Candidate models relating ecosystem services to grassland productivity (GJ·ha^{-1}·yr^{-1})

	Models						
Predictor	1	2	3	4	coeff.	95% CI	ω_p
Fertilization	1.28	1.23	1.21	1.21	1.24	**1.03 to 1.46**	1
Fertilization^2	-0.27	-0.26	-0.27	-0.26	-0.27	**-0.46 to -0.07**	1
Legume cover	0.24	0.22	0.20	0.22	0.22	**0.09 to 0.36**	1
Decay rate	-0.10				-0.04	-0.17 to 0.08	0.42
Soil carbon			-0.04		-0.01	-0.06 to 0.05	0.11
Earthworm abundance				0.03	0.00	-0.04 to 0.05	0.11
(Intercept)	*0.26*	*0.26*	*0.26*	*0.25*	0.26	0.04 to 0.48	
ΔAIC_c	0.00	0.34	2.61	2.79			
Weight (ω_m)	0.42	0.36	0.11	0.11			

Candidate models ranked in order of ΔAIC_c (difference in Akaike Information Criterion for small sample size) and selected within ΔAIC_c < 4. Explanatory variables were z-standardized and the maximum number of predictors per model was limited to 4. Akaike model weights (ω_m) give the probability of each model being the best given the candidate set of six models. For each predictor, coefficients are given for each model (Models 1-4) and for the averaged model (coeff.), with 95% confidence intervals (marked bold if not overlapping zero) and relative parameter importance (ω_p).

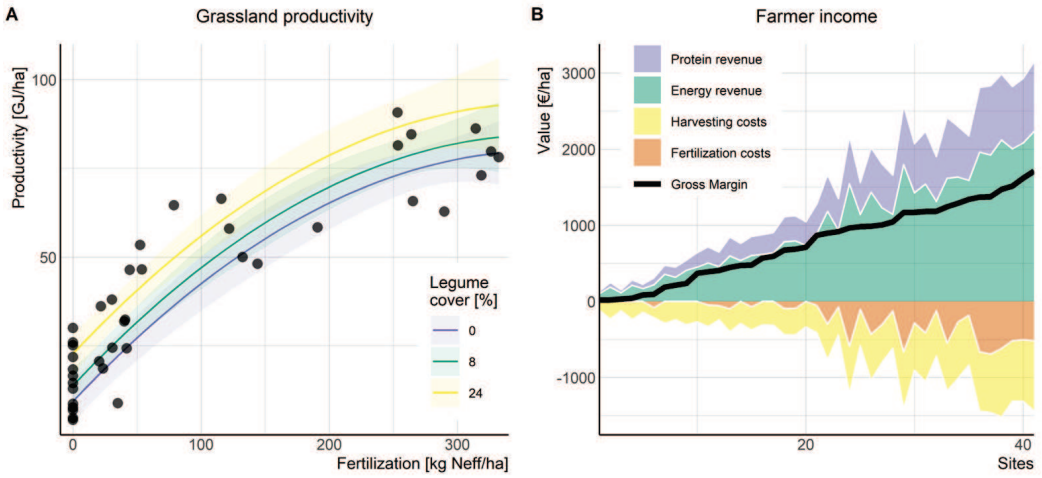


Figure 2.2 A: Model inference showed that grassland productivity in terms of net energy content (n=40) was strongly positively related to fertilization as well as to legume cover, but not to soil ecosystem services. Using the averaged model, productivity was predicted at three legume covers (0, 8 and 24%, i.e. the 10th, 50th and 90th quantiles measured in the field) reflecting a 14 GJ production increase. Moreover, the model indicates that fertilization effects stabilize at high input levels (± >250 kg N_{eff}·ha^{-1}·yr^{-1}). B: By estimating yield revenues from the produced energy and protein contents, as well as management costs from harvesting and fertilization, we calculated the gross margin reflecting farmer income for each grassland. Sites are sorted by gross margin.

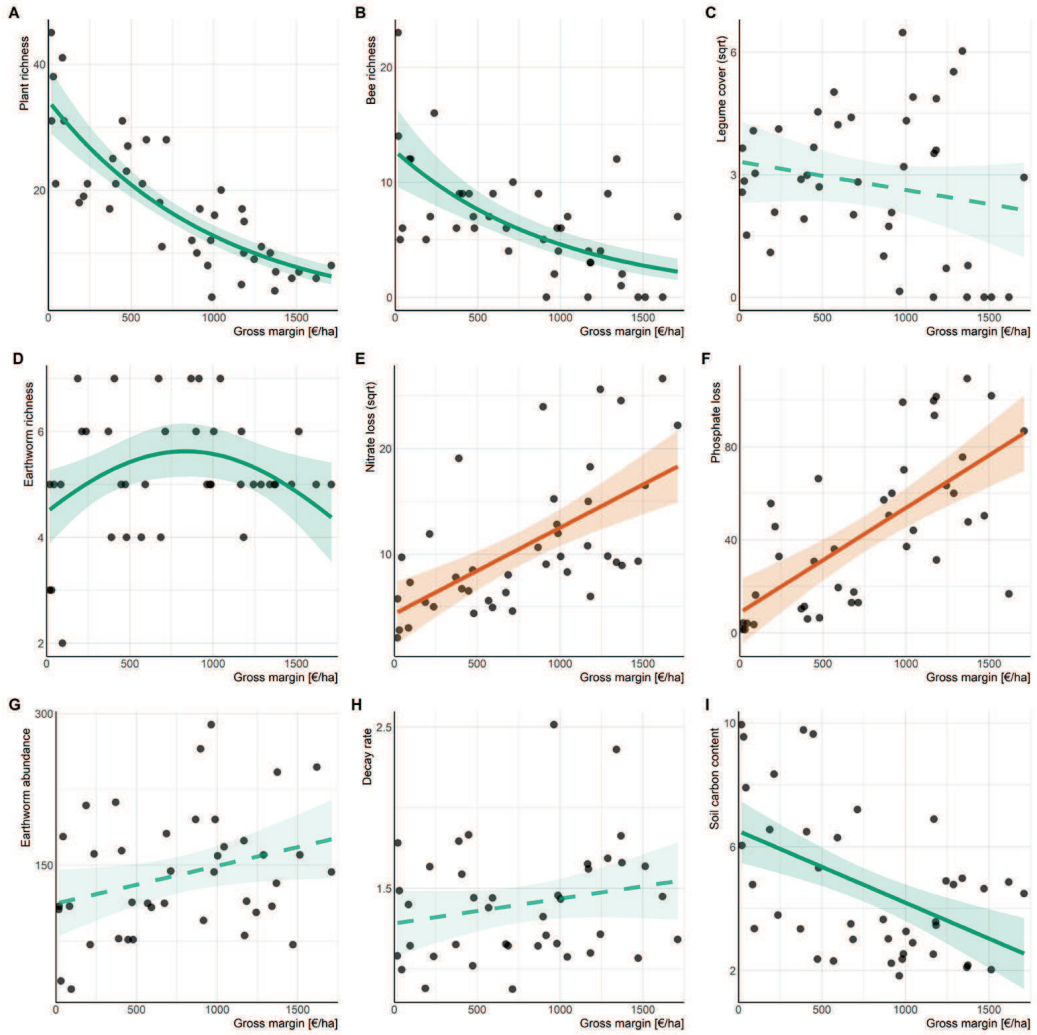


Figure 2.3 Results of generalized linear models showing how ecosystem service indicators relate to farmer income as indicated by gross margin. Panels show indicators of biodiversity (A-D: plant and bee richness, legume cover and earthworm richness), nutrient leaching (E-F: nitrate and phosphate losses) and soil quality (G-H: earthworm abundance and decay rate) and soil carbon storage (I). In red, nutrient leaching represents a disservice causing environmental harm. Legume cover and nitrate loss were square-root transformed. Significant relations are shown with solid lines. Ribbons indicate standard errors (SE).

related to plant species richness (R^2=0.82; p<0.001), bee species richness (R^2=0.64; p<0.001) and soil carbon content (R^2=0.31; p=0.002), while the disservices nitrate loss (R^2=0.38; p<0.001) and phosphate loss (R^2=0.46; p<0.001) increased with gross margin. Legume cover as well as decay rate and earthworm abundance – both reflecting soil quality – were not significantly related to gross margin. Non-linear relations (Paul et al., 2020) were evaluated for each

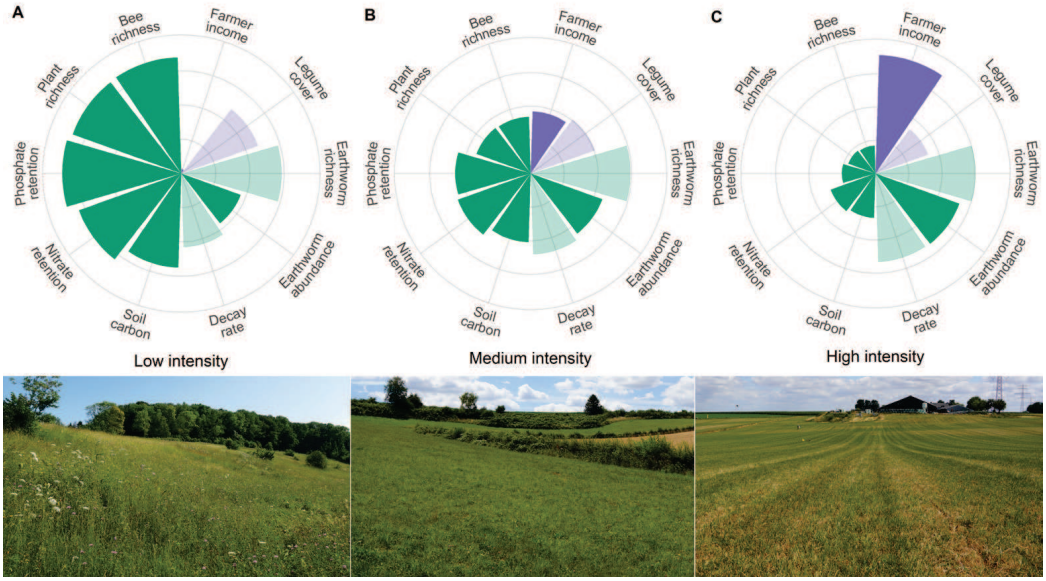


Figure 2.4 Private benefits (purple) and public goods (green) trade off along the grassland management intensity gradient. Ecosystem services can either provide private benefits (legume cover: Fig. 2.2) or sustain public goods (all other) and were predicted for low, medium and high intensity scenarios represented by farmer income (i.e. gross margin) levels of 50, 700 and 1350 €·ha^{-1}·year^{-1}, using generalized linear models (Fig. 2.3). Scales represent the standardized range of each variable (zero to 95th quantile), with unsignificant variables in faded colours. Nitrate- and phosphate retention are derived as the reciprocal of nutrient losses measured, and square-root transformed values are shown for both nitrate retention and legume cover. From low to high intensity, gross margin increases trade off with public good delivery from biodiversity (plant and bee richness), nutrient retention and soil carbon sequestration, while soil functions are not affected. The photographs show three grassland examples (photo credit: Reinier de Vries).

indicator but were only supported for earthworm species richness (ΔAIC_c = 2.5), which peaked at intermediate gross margins (R^2=0.03; p=0.02).

The abovementioned generalized linear models were used to predict ecosystem service delivery at low, medium and high gross margins of 50, 700 and 1350 €·ha^{-1} (Fig. 2.4). The first scenario resembles the most extensively managed grasslands which are characterized by high biodiversity, carbon sequestration and nutrient retention, but contribute minimally to farmer income (Fig 2.4A). Moderately extensive management results in more productive hay grasslands which can often be encountered on farmland under agri-environment schemes (Fig 2.4B): Compared to the first scenario, soil carbon content was 25% lower while plant and bee richness were 50% lower, but earthworm richness was 20% higher. The third scenario resembles high-intensity grasslands typical for conventional dairy farming in the Netherlands, which contribute strongly to farmer income, but biodiversity and soil carbon sequestration are reduced by 70% and 50% respectively compared to the first scenario, while nitrate- and phosphate losses are 9 resp. 6 times higher (Fig. 2.4C).

Discussion

2.4.1 Ecosystem service contributions to grassland productivity

We analysed the relations of fertilization and five biodiversity-based ecosystem services with grassland productivity, and found that next to fertilization, only legume cover was positively related to productivity. These results obtained under real-world conditions support the positive effects of nitrogen fixation by legumes on total biomass that were observed in experimental settings (Ashworth et al., 2018; Finn et al., 2013). Our analyses suggest that the contribution of legumes to production persisted even in very intensive systems (Finn et al., 2013). Note however that due to data limitations, we did not model interactions between legume cover and fertilization, even though studies have shown that really high fertilizer application rates can suppress nitrogen fixation by legumes and cause displacement of legumes by grasses (Kristensen et al., 2022; Zetterlind et al., 2025). Therefore, optimizing nitrogen fixation by legumes may in practice require a limited reduction of fertilization. The positive effect of fertilization on productivity also diminished at the highest input levels. These results suggest that a limited reduction of fertilizer inputs (e.g. to 200 kg $N \cdot ha^{-1} \cdot yr^{-1}$) in combination with increased legume cover, can help farmers maintain productivity at lower input costs. The partial replacement of fertilizer use by a biodiversity-based ecosystem service is an illustration of the ecological replacement hypothesis (Kleijn et al., 2019), and represents a win-win outcome for farmers and the environment (by means of reduced nutrient loading).

However, this win-win outcome occurred only on the most intensively used grasslands. Of the other investigated ecosystem services, organic matter decay (supporting nutrient cycling), earthworm abundance and soil carbon content (both improving soil structure) did not contribute significantly to productivity, and plant richness correlated negatively with fertilization. This is contrasting the results of controlled experimental studies that repeatedly showed positive effects of these soil services and plant diversity on productivity (Cardinale et al., 2012; Lehmann et al., 2020; Schaub et al., 2020; Van Groenigen et al., 2014). The lack of clear relations in our study indicates that in real-world settings, the contributions of these ecosystem services to grassland yield may be obscured by factors such as nutrient availability, species composition or management. For example, positive effects of plant diversity were found to dissipate when nutrient inputs increase or when the most productive species are selected (Cardinale et al., 2007; Roscher et al., 2016; Zetterlind et al., 2025). Furthermore, biodiversity-based ecosystem services were found to be more important in arable production systems that depend on pollination or pest control (e.g. Dainese et al., 2019). However, Scheper et al. (2023) showed that even substantial biodiversity benefits to crop yields may not compensate production losses in grasslands.

2.4.2 Ecosystem service declines with gross margin

We related nine ecosystem service indicators to gross margin (indicating farmer income) and found clear negative relations with grassland biodiversity, nutrient retention and carbon storage. These results can be explained by the strong association of gross margin with grassland management intensity. Previous studies have also shown that plant and bee species richness in grasslands decline strongly with increasing land-use intensity (Beckmann et al., 2019; Ekroos et al., 2020). Furthermore, our results indicate that plant and bee richness declines are most pronounced at the low end of the gross margin spectrum. This suggests that it is most cost-effective to support biodiversity in low-intensity grasslands (i.e. highest biodiversity gains per profit lost) (Kleijn et al., 2009). The lack of relationships of gross margin with earthworm abundance and (soil biota-mediated) decay rate and the unimodal relationship with earthworm species richness suggest that soil functions are more robust to intensification of grasslands management. This matches with findings by Le Provost et al. (2021), who found strong negative relations with grassland intensity for aboveground biodiversity, but not for belowground biodiversity. Furthermore, the sharp increase in nutrient losses with grassland intensity most likely results directly from fertilization (Klaus et al., 2018). Fertilization has also been found to increase carbon accumulation rates (Poeplau et al., 2018; Seabloom et al., 2021). However, our results reflect that long-term soil carbon stocking in the examined intensive grasslands was likely disrupted by biomass removal and increased disturbance, which can cause rapid losses of sequestered carbon (Bai & Cotrufo, 2022).

We applied an intermediate output approach to gross margin so that we could directly compare field measurements of ecosystem service delivery to private benefits for farmers. This approach determines the plot-level benefits, using fixed market prices for energy and protein units, but has the limitation that the costs and benefits of animal production at the farm level were not taken into account. However, the consideration of animal husbandry may increase both the generated income and the opportunity costs of extensification at farm level, and may differ between dairy and beef producers (Corporaal & Van Os, 2002; Remmelink et al., 2020). Beef farms have generally lower protein requirements but also make lower revenues than dairy farms (Blanken et al., 2021), while both compete for the same resources (such as land). The intermediate outputs for dairy farms are therefore used as a benchmark in this study. This approach does provide a robust indicator of field-level management effects on farmer income, which reflects the main question addressed in this study. Animal husbandry should however be taken into account when evaluating the attractiveness to farmers of compensation schemes for biodiversity or ecosystem service delivery.

Furthermore, financial support for biodiversity-friendly management such as price premiums (e.g. for organic products), compensatory payments of agri-environmental schemes or budgets for nature restoration were not incorporated in

the calculation of gross margin. These payments sustain the continuation of more extensive management practices in our study area. However, they are in fact payments for public good delivery, while we were interested in a generalizable comparison of private benefits and public good delivery across a range of management intensities.

2.4.3 Distinguishing between private benefits and public goods

Our results indicate that nitrogen fixation by legumes was the only ecosystem service that delivered private benefits to farmers in the form of improved income. All other investigated ecosystem services did not contribute to farmer income and should, within the context of a commercial farm, be considered as public goods that are predominantly important to society (Bengtsson et al., 2019; Dasgupta, 2021). These public goods include biodiversity preservation, soil health, nutrient retention to maintain water quality, and carbon sequestration to foster climate change mitigation and promote water retention. Although these assets may be relevant to farmers as well, they do not provide exclusive and marketable returns for their investments. Food supply is of crucial societal importance, but is a marketable service and in the case of livestock farming, current production levels are economically driven and arguably exceed societally desirable levels (Springmann et al., 2018; Willett et al., 2019). Our study clearly illustrates the strong trade-offs between private benefits to farmers and public good delivery along the management intensity gradient (Fig. 2.4). These trade-offs were most pronounced for biodiversity preservation, nutrient retention and carbon sequestration, while soil health indicators persisted under high land-use intensity. Enhancing ecosystem services therefore produces considerable benefits to society through parallel recovery of biodiversity, water quality and climate change mitigation, but it does not pay off for a farmer.

This trade-off explains why only a small proportion of farmers integrate ecosystem service restoration in their farm management, and why these farmers generally need governmental subsidies to be able to do so. The lack of unsubsidized extensive grasslands reflects that grassland extensification and the associated delivery of public goods are critically depending on the willingness of society to compensate farmers for the associated loss of income from agricultural production. Currently, market shares of higher-priced nature-friendly products remain marginal in most countries (Möhring et al., 2025), and financial support from other stakeholders such as the tourism sector remains exceptional. Moreover, global trade rules do not allow governments to pay farmers for biodiversity management more than income forgone (WTO, 1994). This in turn means that management for biodiversity and public good delivery cannot commercially compete with agronomic production as an earning model for farmers. In this setting, biodiversity restoration on farms depends on intrinsically motivated farmers and will remain a marginal affair.

2.4.4 Implications

The Netherlands is currently amongst the most intensively farmed countries in the world (Eurostat, 2025). In other regions, farming intensity is sometimes constrained by environmental conditions such as terrain and climate, but more often are farmers limited by economic drivers such as investments and market access (Foley et al., 2011; Springmann et al., 2018). Farming systems across the globe are increasingly connected through global trade (Nocera & Koslowsky, 2011) and as a result, management intensifies in grasslands and other agricultural systems all over the world (FAO, 2022; Springmann et al., 2018). As grassland management in other parts of the world becomes more similar to conventional grassland management in the Netherlands, more widespread ecosystem degradation and growing friction between farmer and societal interests can be expected (Bardgett et al., 2021; Vermunt et al., 2022). The surveyed grasslands in our study represent the entire range of land-use intensification from no-input, semi-natural grasslands to high-input monocultures that are being cut six times a year. As such they provide a relevant model system to illustrate the effects of grassland intensification on ecosystem service delivery and farmer income.

Our study shows that grassland management intensity drives the optimization of farmer income but deteriorates the delivery of multiple public goods. This might seem an intuitive outcome but, as far as we know, this is one of the first studies that provides quantitative evidence for this. So far, a few studies have modelled trade-offs between public good delivery and economic returns (Polasky et al., 2011; Schulz et al., 2024) and many studies have just pointed out the benefits of managing for biodiversity, without considering the associated costs to farming (Binder et al., 2018; Isbell et al., 2013; Pywell et al., 2015; Schaub et al., 2020). But it is unrealistic to assume that farmers will invest in public goods if the consequences are that their production costs increase. Restoration of ecosystems on farmland therefore requires the taxation of negative impacts or financial rewarding of public good delivery by society (Polasky et al., 2011; Vermunt et al., 2022). Rewards to farmers could target either product prices or private (e.g. tourism-driven) or public payment schemes for public ecosystem services, but should rival both the short-term benefits and long-term stability offered by marketable goods to be effective. In doing so, society can avoid current and future costs of ecosystem service deterioration, that are predicted to exceedingly outweigh investments in public good delivery (Dasgupta, 2021). This makes safeguarding public goods the most important argument for biodiversity and ecosystem service restoration.

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THREE

Land use intensification transforms grassland arthropod communities: a few winners expand but most species disappear

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Abstract

Arthropod declines pose existential threats to terrestrial ecosystems but remain poorly understood. In human-dominated habitats such as managed grasslands, arthropod communities are thought to decline as a result of land-use intensification. However, studies that link land-use intensity to arthropod species richness, abundance and composition have found mixed results. These inconsistencies may stem from differences in the investigated intensification levels or arthropod communities, as different species may show different responses to land-use change. We show that effects of land-use intensification on arthropod communities can be understood better by examining the distributions of individual species along land-use intensity gradients. We sampled multiple arthropod groups along a wide gradient of grassland productivity as a proxy for land-use intensity. Species richness halved from low to high productivity levels, but overall abundance remained stable because increasing Diptera numbers counteracted strong declines in other orders. Dissimilarity metrics failed to reveal a substantial change in species composition that was shown in individual species' distributions. While low-productivity grasslands supported many species that were confined to narrow productivity ranges, high-productivity grasslands were dominated by a few widely occurring species. Overall, 56% of all species declined or disappeared as land-use intensified at low-to-medium intensity levels ('losers'); 35% preferred intermediate intensities, and only 9% profited from high-intensity management. These 'winners' probably sustain overall abundance levels in high-productivity grasslands. Such large changes in species composition could have significant consequences for ecosystem functioning, necessitating further experimental studies. The uneven distribution of biodiversity losses implies that ecological restoration should focus on low-intensity grasslands.

Introduction

Arthropod populations in human-dominated landscapes have significantly declined in the recent past (Benton et al., 2002; Hallmann et al., 2017; Van Klink et al., 2020; Wagner, 2020). As the most abundant and diverse faunal life form (Stork et al., 2015), arthropods are central to trophic networks and ecosystem functions such as nutrient cycling and pollination (Cardinale et al., 2012; IPBES, 2019; Potts et al., 2016). Therefore, the revelation of drastic arthropod declines has been cause for alarm (Cardoso et al., 2020; Goulson, 2019). Many studies have attributed these declines to ongoing land-use intensification, causing habitat loss, declines of critical resources (e.g. through plant diversity decline), increased disturbances and landscape simplification (Gossner et al., 2016; Harpole et al., 2016; Raven & Wagner, 2021; Seibold et al., 2019). Yet, most arthropods are challenging to survey and systematic long-term monitoring schemes exist for only a few arthropod groups (Van Swaay et al., 2025; Warren et al., 2021). Hardly any multi-decadal records of other arthropods exist, and those available may reflect already degraded reference situations or sampling locations that are not representative of environmental changes in the wider landscape (Cooke et al., 2025; Montgomery et al., 2020; Wagner et al., 2021). As a result, the effects of land-use intensification remain poorly understood for a wide range of different arthropod groups.

Studying arthropod diversity along spatial gradients in land-use intensity provides a way to accelerate our understanding of intensification-driven changes to arthropod assemblages (Cooke et al., 2025; Wagner, 2020). Alternative to time series, biodiversity patterns along spatial gradients are more readily obtained and can provide more direct accounts of the drivers of biodiversity change (Blüthgen et al., 2022; Cardinale et al., 2018). Gradient studies may include ecologically degraded locations that are rarely part of existing long-term studies (Wagner et al., 2021), and can be considered proxies for changes over time, such as the shift from traditional extensive land management to modern intensive agriculture that occurred over the past century in Europe and other temperate regions (Bardgett et al., 2021; Emmerson et al., 2016). Global syntheses have indicated that land-use intensification is especially impacting biodiversity in grassland habitats (Newbold et al., 2015, 2016). While extensively used grasslands are known hotspots of arthropod diversity in temperate regions (Bardgett et al., 2021; Habel et al., 2019), steep declines of species richness with land-use intensity were shown among several groups of grassland arthropods, such as wild bees (Ekroos et al., 2020), Araneae, Hemiptera, Coleoptera and Orthoptera (Allan et al., 2014; Simons et al., 2015).

However, there have also been many studies that found no relation between land-use intensity and species richness (Beckmann et al., 2019). This might be due to non-linearity along the full land-use intensity gradient, as species richness losses were shown to be most profound under intensification at low intensity levels that might be missed by studies in more intensively used landscapes (Allan et al., 2014; Kleijn et al., 2009, 2011). The lack of relationships with species richness may also

be influenced by the limitations of using species richness as the main response variable, notably because it does not capture changes in species composition (Chase & Knight, 2013; Hillebrand et al., 2018; Kuczynski et al., 2023). More detailed quantitative data of arthropod communities can uncover changes in species assemblages or arthropod abundances. These metrics are increasingly assessed in biodiversity studies, but also show contrasting results. Land-use intensification has been linked to biotic homogenization (i.e. increasing similarity of species assemblages between sites) across multiple taxonomic groups in European grasslands, amplifying biodiversity decline at landscape scales (Chisté et al., 2018; Gossner et al., 2016). But metrics of community dissimilarity have also revealed widespread patterns of biotic differentiation in response to land-use change (Dornelas et al., 2023; Keck et al., 2025). Furthermore, abundances of grassland arthropods have shown stronger declines than species numbers (Seibold et al., 2019; Van Strien et al., 2019), but have also been found to increase with land-use intensity (Kleijn et al., 2010; Silva-Monteiro et al., 2022). This suggest that there are also arthropods that can cope with or even profit from land-use intensification.

The contrasting results of these different studies relating changes in arthropod communities to land-use intensification might result from changes in species composition that the most commonly used community indicators failed to capture. To date, most studies aggregate the responses of many different arthropod species or entire groups into common metrics of species richness, total abundance or community dissimilarity (Cooke et al., 2025). But while species richness does not reflect changes at community and population levels (Hillebrand et al., 2018), total abundance may be largely driven by a few abundant arthropod species (Shortall et al., 2009). Furthermore, dissimilarity (beta-diversity) metrics aggregate differences that arise from the turnover of unique species (Legendre, 2014), but also from stochastic drift (e.g. dispersal outside species' reproductive habitats) and from increased fragmentation of species distributions (Araújo et al., 2022; Chase et al., 2019; Wayman et al., 2024; Zhou et al., 2022). In reality, arthropods exhibit vast ecological differences, and the effects of land-use intensification probably differ widely between arthropod groups and species. Certain species may profit from the decline of other species or from increased resource availability in intensively managed systems, e.g. when feeding on plant matter or manure (Simons et al., 2014; Simons & Weisser, 2017), and the prevalence of such species may differ between arthropod groups (Powell et al., 2024; Simons et al., 2014). It is critical to understand which species lose and which species win under changing environmental conditions (Boyes et al., 2019; Dornelas et al., 2023; Wagner, 2020). Hence, land-use intensification-driven shifts in arthropod communities can probably be better understood by assessing the responses of individual species.

In this study, we quantified the changes in grassland arthropod communities along a land-use intensity gradient in the Netherlands. Ranging from low-productive unfertilized hay meadows to highly productive and heavily fertilized silage fields, this gradient reflected the entire range of grassland management intensities within

one study region and arguably covers the variation in grassland management intensity throughout much of northwestern and central Europe. We asked whether the relationships between land-use intensity and arthropod abundance, species richness and community dissimilarity differ between the main above-ground arthropod orders. Furthermore, we asked whether responses of arthropod communities to land-use intensification can be better understood by examining the responses of individual species than by examining aggregate indices such as species richness or beta diversity. We addressed this question by analyzing the distributions of individual species along the sampled land-use intensity gradient.

Methods

3.2.1 Study sites

Data were collected in a study area situated in the valley of the river Geul in the south of the Netherlands (between 50°48'09"N, 5°49'46"E and 50°53'30"N, 5°56'24"E) (Fig. 7B.1). This area is a regional hotspot of grassland biodiversity, supporting various grassland types on fine clay and loess soils with locally more lime-rich conditions (Willems, 2001; Wösten et al., 2013). Here, differences in land-use intensity are mainly the result of management targeting either nature conservation, biodiversity-friendly agriculture, or optimizing agricultural production. We selected 41 grasslands that represented the widest possible gradient in land use intensity (see Table 7B.1 for specifications). Study sites included i) unfertilized nutrient-poor semi-natural grasslands that were mown once per year; ii) hay meadows in protected areas and iii) hay meadows under agri-environment schemes, both of which were cut twice a year or had limited grazing rates (<2 $LSU \cdot ha^{-1}$) and no fertilizer inputs; iv) pastures used for grazing or fodder production for suckler cows or organic dairy cows, with intermediate fertilizer inputs (50-150 kg $N_{eff} \cdot ha^{-1} \cdot yr^{-1}$); and v) conventional dairy cow fodder production grasslands with up to six cuts per year and high fertilizer inputs (up to 330 kg $N_{eff} \cdot ha^{-1} \cdot yr^{-1}$). This gradient represents the entire range in grassland management intensity that is present in large parts of temperate Europe where historically, grassland habitats evolved as semi-natural systems maintained by extensive human management (mowing or grazing), which has been steadily replaced by high-input management for maximum productivity (Emmerson et al., 2016; Habel et al., 2013). The sampling sites were on average 778 ± 428 m apart and showed no spatial pattern in productivity (Fig. 7B.1). We quantified annual productivity in terms of net metabolic energy for livestock [$GJ \cdot ha^{-1} \cdot yr^{-1}$] as an indicator of land use intensity that reflects both biomass production and forage quality, facilitating the direct comparison of different management regimes. Annual biomass production (dry yield in tons) was collected through interviews with farmers and land owners, and was multiplied by the standard energy content values of different forage types (4.1 $GJ \cdot t^{-1}$ for low-quality hay; 5.2 for high-quality hay; 5.9 for extensive grazing; 6.2 for conventional silage; 6.4 for conventional silage, first cut; 6.6 for conventional grazing) (CVB, 2022; Schippers et al., 2012).

3.2.2 Arthropod sampling

We used sweep-net sampling to collect a broad range of arthropod groups along a 150-meter transect in each grassland. Transects were pre-defined and ran from edge to center of the grasslands. We conducted 70 1-m-wide single-sweeps per part of 50 m in June and July, but 160 in May, because we expected that this would produce a roughly similar total arthropod abundance in each month. Sweep-netting is a suitable method for representative field-scale sampling of vegetation-dwelling arthropods, including herbivores and predators, but underestimates the presence of fast-flying pollinators (Simons et al., 2014; Spafford & Lortie, 2013). Therefore, additional counts of bees (Anthophila) and hoverflies (Syrphidae) were obtained along the same transect during 15-minute pollinator walks (5 minutes per 50 m), surveying a width of 1 m (Scheper et al., 2015a). Pollinator surveys were done on the same day but prior to sweep-netting to minimize disturbance. Both methods were conducted between 10:00 and 17:30 and under suitable weather conditions (temperature >15 °C, wind <3 Bft, sunshine >50%) (Westphal et al., 2008). Pollinators were counted in the field and collected only when they could not be identified to species level on the wing, while sweep-net samples were collected in zip-lock bags and stored frozen. Afterwards, (sub)order-level abundance counts were obtained for adult Diptera, Auchenorrhyncha, Heteroptera, Hymenoptera, Coleoptera, Araneae and Orthoptera (other arthropod orders occurred in low numbers but were included in total abundance counts, while Sternorrhyncha, Thysanoptera, Acari and Collembola were not included in the counts). Pollinator counts were combined with the sweep-net data to complement the assessments of both pollinator groups, primarily regarding species diversity. Count data represented over 80% of all individuals of both bees and hoverflies, but only 6% and 1.4% of the total abundance of Hymenoptera and Diptera recorded.

Furthermore, we obtained species identities for all specimens belonging to Heteroptera, Araneae and Orthoptera, and for subgroups of Hymenoptera (Anthophila, Formicidae), Coleoptera (Cantharidae, Chrysomelidae, Coccinellidae, Elateridae) and Diptera (Asilidae, Bibionidae, Conopidae, Opomyzidae, Platystomatidae, Rhagionidae, Sciomyzidae, Stratiomyidae, Syrphidae, Tabanidae, Tephritidae, Tipulidae, Ulidiidae). Species were identified with help of the citizen science platform Waarneming.nl and relevant identification keys (references are given in Table 7B.2). In a few cases, identification was limited to genus or species-pair level. The selection of subgroups for species identification aimed to cover a broad range of taxonomic and ecological groups, while the inclusion of additional species groups was mainly constrained by lack of suitable identification keys or taxonomic expertise.

3.2.3 Data analyses

The individual samples (nine per site, referring to the three transect sections over three rounds) were summed (abundance data) or aggregated (species identity data)

to obtain site-level estimates of abundance and species richness, with abundances being corrected for the increased sweep-netting effort in May and for one missing sample. We checked sampling completeness with the Jacknife-1 estimator of total richness, which was derived using R-packages *BiodiversityR* and *vegan* (Kindt & Coe, 2005; Oksanen et al., 2024). Sampling completeness ranged between 60-80% and showed no trend with productivity. This indicates that more species-rich communities were sampled roughly as complete as simpler communities, and we therefore used the original data in our analyses. Abundance counts over all arthropods and of the seven (sub)orders, and observed richness over all identified groups and of Diptera, Heteroptera, Anthophila, Coleoptera, Araneae, Orthoptera and Formicidae, were related to productivity (metabolic energy) as a single explanatory variable. We used generalized linear models with generalized Poisson or negative binomial distributions to account for overdispersion, using R-package *glmmTMB* (Brooks et al., 2017). Non-linear relations were evaluated by the statistical support for quadratic and cubic model terms, which were kept if notably improving the model ($\Delta AIC_c > 2$), using R-package *MuMIn* (Bartoń, 2023). Model residual patterns were validated using R-package *DHARMa* (Hartig, 2022). Non-normal residual patterns were prevented by the selected distributions and residuals were not correlated with land use factors outside the model (silage or hay production, mowing or grazing, grass-to-forb ratio), hence no additional covariates or random effects were included in the models.

We investigated community dissimilarity (beta-diversity) within classes of low productivity (4-21 $GJ \cdot ha^{-1} \cdot yr^{-1}$: 14 sites), medium productivity (21-48 $GJ \cdot ha^{-1} \cdot yr^{-1}$: 13 sites) and high productivity (48-91 $GJ \cdot ha^{-1} \cdot yr^{-1}$: 14 sites). Beta-diversity was quantified by Jaccard's dissimilarity index and was partitioned into components of replacement (true niche differentiation) and richness or abundance differences (loss or gain) (Legendre, 2014), following both abundance-based (Bray-Curtis) and incidence-based approaches, using R-package *BAT* (Cardoso et al., 2015). We derived all possible unique comparisons of pairs of sites within one productivity class. The dissimilarity levels of adjacent classes were compared with Dunn's tests, using Bonferroni's adjustment of p-values and a threshold of p=0.01 to account for the large number of comparisons, using R-package *rstatix* (Kassambara, 2023).

To better understand how the relationships between land-use intensity and arthropod abundance, species richness and community dissimilarity were shaped by the responses of individual species, we performed additional analyses based on the center points of the distributions of individual species along the land-use intensity gradient. In line with Chisté et al. (2016), we calculated these center points as abundance-weighted means, i.e. the mean productivity (P_{mean}) over all sites (i-n) for a particular species (j) weighted by its abundance at each site (x_{ij}), using the following formula:

$$P_{mean}(j) = \frac{\sum_{i=1}^{n} x_{ij} \cdot P_i}{\sum_{i=1}^{n} x_{ij}}$$

Next, we excluded singletons (i.e. species with single observations over all samples), and classified all remaining species based on whether their center point was located at low, medium or high productivity (using the same classes as the community dissimilarity analysis). The species that were centered at low productivity levels were regarded as species 'losing' under land use intensification (their numbers decreased as land use intensified), while species centered at medium productivity levels were regarded as 'intermediate' and species centered at high productivity levels were regarded as 'winning' (their numbers increased as land use intensified). We then calculated the percentage of losing, intermediate and winning species in each taxonomic group. These percentages were compared to a simulation of 10.000 randomized distributions of species along the productivity gradient (i.e. assuming no consistent effect of productivity on species distributions). Randomized distributions were constructed by randomly rearranging the recorded counts of each species over all 41 sampling sites, thus maintaining each species' original counts. Subsequently, we recalculated each species' center point and derived the randomized percentages of losing, intermediate and winning species (i.e. the percentage of center points falling in each productivity class). The density curves of the 10.000 randomized percentages then allowed us to statistically test for differences with the measured percentages of losing, intermediate or winning species at the community level.

Finally, we assessed how the measured and randomized percentages of losing, intermediate and winning species changed with the distribution width of species. For this the percentages of losing, intermediate and winning species were calculated for subsets of species that had been recorded at an increasing minimum number of sites (range from 1 to 33, as above this number, too few species (<14) remained to reliably estimate percentages). We used saturation curves to model how the percentages of losing, intermediate and winning species changed while increasing the minimum number of occurrences, and assessed the differences between the measured and randomized data. All data analyses were performed in R 4.5 (R core team, 2025) and can be found in a Zenodo repository (De Vries et al., 2025).

Results

3.3.1 Abundance versus species richness

We collected nearly 170,000 specimens in total and identified 27,200 individuals (16%) to species level, representing 520 species. Over all orders, total abundance did not change significantly with productivity, whereas observed species richness across all identified subgroups declined exponentially ($p = 0.01$) (Fig. 3.1A,C; Table 7B.3). Total richness did not change markedly in the medium-to-high productivity range (± 45-90 $GJ \cdot ha^{-1} \cdot yr^{-1}$), but was approximately halved from the lowest to medium productivity levels. Richness declines were found for all subgroups except Coleoptera (no trend; $p < 0.01$ for all other subgroups) and were exponential for Heteroptera and Araneae (Fig. 3.1D, Fig. 7B.2B). Abundance declined significantly

with productivity for Auchenorrhyncha (unimodal), Heteroptera (exponential), Araneae (cubic), Coleoptera and Orthoptera, but Hymenoptera abundance remained stable, and Diptera abundance increased significantly with productivity ($p < 0.01$) (Fig. 3.1B, Fig. 7B.2A, Table 7B.3). Being the most numerous group (46% of all specimens), the increase in Diptera was almost as large as the decline in abundance of all other orders combined. However, only subgroups of Diptera and Hymenoptera were identified to species level and the abundance of these subgroups did not follow the whole-order trends but declined with productivity (exponential for the identified Diptera) (Table 7B.3).

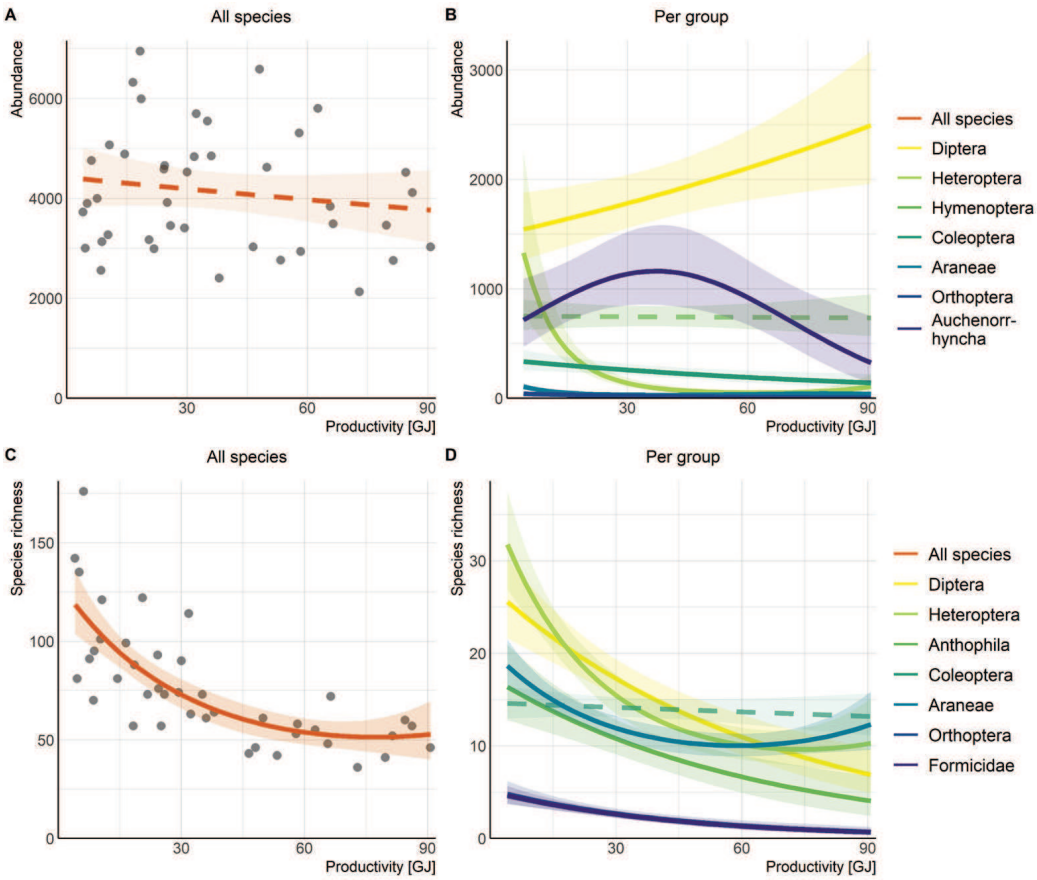


Figure 3.1. Relations of arthropod abundance and observed species richness with grassland productivity [GJ·ha^{-1}·year^{-1}]. Significant relations are shown in solid lines with 95% confidence intervals (ribbons). Total arthropod abundance was not related to productivity (A), but different (sub)orders showed contrasting relations including an increase of Diptera abundance (B). Total observed species richness was derived over subgroups within each order that were identified to species level, and declined exponentially with productivity (C). This decline is reflected in all analyzed groups except Coleoptera (D).

3.3.2 Community dissimilarity

Species assemblages of different grasslands differed markedly, particularly when differences in abundance were taken into account. Total abundance-based beta-diversity estimates over all species and for most groups were above 0.8, while incidence-based beta-diversity estimates were mostly between 0.6 and 0.8 (Table 7B.4; class averages). However, dissimilarities between sites were generally high in both low-, medium- and high-productivity classes (4-21, 21-48 and 48-91 $GJ \cdot ha^{-1} \cdot yr^{-1}$, respectively). The majority of the beta-diversity differences between adjacent productivity classes were not significant and when differences were significant, they did not show a consistent increase or decrease with grassland productivity (Table 7B.4; class comparisons). Over all species, replacement averaged 0.5 in both abundance-based and incidence-based approaches, and was more important than richness or abundance differences (average 0.17 resp. 0.35). At group level, abundance-based dissimilarities were dominated by abundance differences in Anthophila, Heteroptera, Formicidae and Orthoptera (the last two groups being rather species-poor), while incidence-based dissimilarities were mostly driven by species replacement. Neither replacement nor richness or abundance differences showed a consistent trend with grassland productivity.

3.3.3 Distributions along the land-use intensity gradient

Most species had the center of their distribution in low productivity grasslands (Fig. 3.2), meaning that they are declining under land use intensification from low to medium intensity levels. These 'losing' species represented 56% of the 380 species that were observed with two or more individuals, whereas 35% were intermediate species (centered at medium productivity) and 9% were winning species (centered at high productivity). These percentages contrast markedly with the randomized species distributions that assumed no relation with productivity, in which on average 62% (95%-Confidence Interval ±6) of all species were classified as intermediate species, while winning species represented 22% (±5) and losing species represented 16% (CI ±5) of all species (Fig. 3.3A-B). The observed percentage of losing species was 1.8 times higher than this mean randomized percentage for Coleoptera (29% of species), 3.6 times higher for all species, and nearly five times higher for Hemiptera, Formicidae and Orthoptera (each >70% of species) ($p<0.0001$ for all groups). On the other hand, for all groups except Coleoptera the empirically observed percentage of winning species was 2-6 times lower than what would have been expected based on randomized distributions ($p<0.0001$ for all other groups) (Fig. 3.3B).

Furthermore, most losing species were entirely restricted to low productivity levels or were only incidentally recorded at higher productivity levels (Fig. 3.2: reflected by a lack of points in the upper-right area for each subgroup). For 110 species (29% of all species excluding singletons) more than 90% of the specimens were observed at low-productivity sites, and for 242 species (64%) this was the case for sites of

low to medium productivity. 57 species (15%) were recorded proportionately (i.e. at least 33% of specimens) at high-productivity sites. High-productivity sites were dominated by species that were recorded widely across the productivity gradient (Fig. 3.2: reflected by a broad spread of points in the lower area for each subgroup) and supported very few range-restricted species: Only five species were restricted to high productivity sites and these all had fewer than five observations. These patterns are quantitatively illustrated in Fig. 3.3C which shows how the percentages of losing, intermediate and winning species change over subsets of increasingly widely occurring species. Randomized distributions indicate that with an increasing number of occurrences, it can be expected that the percentage of intermediate species increases towards 100% as losing and winning species are filtered out (dashed lines: dots reflect 100 randomizations). The observed percentage of losing species indeed drops sharply when more narrow-ranged species are excluded (losing species represented two-thirds of the species found at <5 sites). However, counter to expectations based on randomized distributions, the observed percentage of winning species increases among more widely occurring species (solid yellow line crosses the dashed line) and is significantly higher than randomized percentages for species occurring at >10 sites ($p = 0.02$). 20% of the species occurring at >20 sites (41 species, i.e. 11% of the total) were classified as winning species.

Discussion

We found that with increasing land use intensity, arthropod species richness in grasslands declined but overall arthropod abundance remained stable. The stable abundance over all arthropods was mainly driven by an increase in Diptera numbers that counteracted abundance declines in most other orders. The distributions of individual species revealed large shifts in arthropod communities with increasing land-use intensity. At the landscape scale, arthropod biodiversity was strongly centered in low-productivity grasslands. High-productivity grasslands were dominated by a small set of widely distributed species which partly profit from increasing productivity. A few winning species thus probably sustained the overall arthropod abundance at high-intensity grasslands while many losing species caused biodiversity levels to be very low.

3.4.1 Contrasting responses of species richness and abundance

The exponential decline of arthropod species richness with increasing productivity aligns with other studies on grassland plants (Kleijn et al., 2009) and arthropods (Allan et al., 2014). In line with previous large-scale studies on grassland arthropods (Allan et al., 2014; Ekroos et al., 2020; Simons et al., 2015), we measured richness declines across multiple arthropod groups, with the exception of Coleoptera. Although they are often used as indicator groups, this lack of trend for Coleoptera does match with other studies on Coleoptera richness (Batáry et al., 2007; Mei et al., 2024). The sampled Coleoptera families include many generalist feeders and

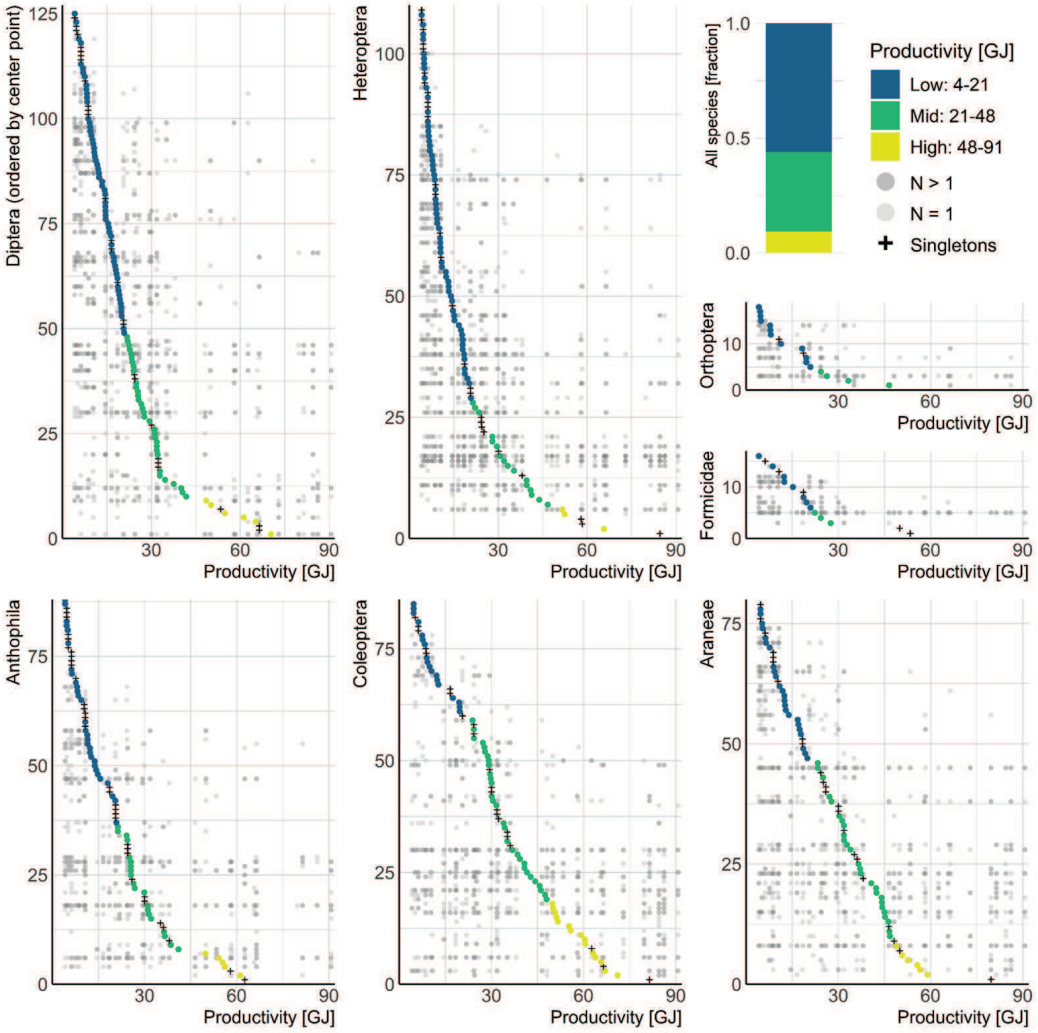
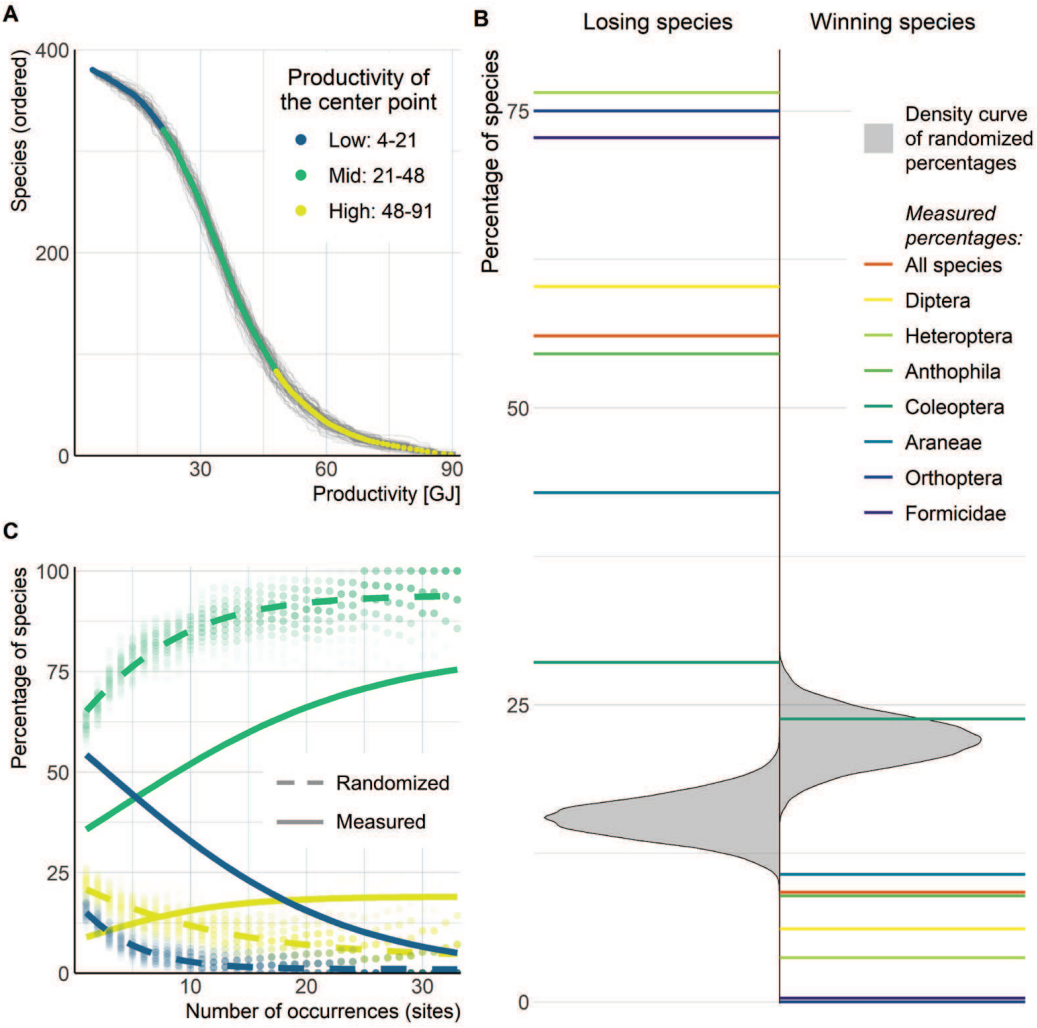


Figure 3.2. Species distributions along the land use intensity gradient expressed in terms of grassland productivity [GJ·ha^{-1}·yr^{-1}]. The center point of each species' distribution was calculated as the productivity at which the abundance-weighted mean of all specimens occurred (colored dots). Species are ordered on the y-axis from high to low by increasing center points, with singletons (i.e. one record over all sites) indicated as crosses. Non-singleton species were classified by center point into low, middle and high productivity classes (representing losing, intermediate and winning species, colored in blue, green and yellow respectively; classes represent 14, 13 and 14 sites respectively): The bar plot shows the fraction of species centered in each productivity class over all species. Grey dots show all sites where a species was recorded (single records in light grey, higher numbers in dark grey).

Figure 3.3. The measured percentages of losing, intermediate and winning species (i.e. species centered at low, medium or high productivity levels respectively) compared to randomized simulations that assume no consistent effect of land-use intensity on species distributions. A: We randomized the distributions of species on the productivity gradient



(Figure 3.3 continued) by randomly rearranging the recorded counts for each species (n=380 excluding singletons) over all 41 sampling sites, and re-calculating their center points (i.e. the abundance-weighted mean productivity for each species). Ordered by productivity, the randomized center points show an S-shaped curve as most species are classified as intermediate species (green), while small percentages are classified as losing or winning species (blue resp. yellow). B: These randomized percentages were derived 10.000 times and plotted as density curves for losing species (left side of the graph) and winning species (right side of the graph). Compared to these randomized simulations, the measured percentages of losing and winning species differed significantly for nearly all taxonomic groups (plotted as horizontal lines). C: The percentages of losing, intermediate and winning species (blue, green resp. yellow) changed among more widely occurring species (i.e. species recorded at an increasingly high minimum number of sites). However, the changes in measured percentages (solid lines) contrast with the change of the randomized distributions (100 iterations, shown with opaque dots and dashed lines). Randomized simulations project that without the influence of land-use intensity, the percentage of intermediate species would approach 100% among the most widely distributed species while the percentages of losing and winning species would decrease towards zero.

appear less sensitive to land use intensity than other arthropod groups in terms of species richness. Our results suggest that Heteroptera richness is most sensitive to land use intensity. The recorded richness declines are probably mainly driven by processes that erode niche diversity, such as declines of floral diversity or microhabitat variation (Joern & Laws, 2013; Woodcock et al., 2009). The selected sampling methods provided a broad and ecologically diverse representation of vegetation-dwelling arthropods, but did not target soil- and surface-dwelling arthropods. Hence, while our results hold within the realm of the species considered, this study can be expanded by comparisons with different area-based collection methods (e.g. suction sampling) and by the inclusion of species identity data of yet more arthropod groups. Such studies can make important contributions to our understanding of poorly studied groups that nevertheless play central roles in many ecosystems.

The abundance declines with increasing productivity that were observed in most orders were offset by the increase in abundance of a single order: true flies (Diptera). This positive relation between productivity and Diptera abundance aligns with the findings of Silva-Monteiro et al. (2022) who measured an increase of total arthropod abundance with productivity in a cross-continental study of wet grasslands, where Diptera represented 80% of all specimens. The increase of Diptera numbers with grassland productivity is probably driven by families that live from decaying organic matter (Powell et al., 2024). Likewise, the steep exponential decline of Heteroptera numbers most likely reflects the reliance of many species on specific forbs that are often restricted to low-productivity grasslands, while the unimodal trend of Auchenorrhyncha in this study was partly driven by high numbers occurring in humid grasslands at low-to-medium productivity levels. These different relations of separate arthropod orders with land-use intensity can largely explain the contrasting relations of overall arthropod species richness and abundance.

3.4.2 Shifts in species composition

Our results confirm that species richness patterns underestimate biodiversity declines with land use intensification because they ignore effects on species numbers and community composition (Chase & Knight, 2013; Gossner et al., 2016; Hillebrand et al., 2018). Species richness in low-productivity grasslands was approximately twice as large as in high-productivity grasslands, but compared to high-productivity grasslands six times more species had their distributional center-point in low-productivity grasslands (Fig. 3.2). This implies that on top of significant richness losses, also the number of unique species and the population size of many species declined with productivity. However, our analyses of dissimilarity (beta-diversity) and replacement in species assemblages did not reveal these patterns. This is probably because these metrics aggregate all differences between sites without considering where individual species were observed. Although many studies have interpreted dissimilarity metrics as measures of biotic homogenization or differentiation (Dornelas et al., 2023; Gossner et al., 2016; Keck et al., 2025), other

mechanisms can also play a role in determining them. For example, we found an increasing dissimilarity of Anthophila assemblages from medium- to high productivity levels, most likely because species showed more fragmented distributions across high-productivity grasslands (Fig. 3.2 & Table 7B.4: see also Araújo et al., 2022 and Wayman et al., 2024); a pattern that seems to reflect the dependence of a common set of species on the grass-clover mixtures that are found in some of the high-productivity grasslands in this area. Furthermore, stochastic effects such as spillover to unsuitable habitats (reflected by single records far from species' prevailing productivity ranges: see Fig. 3.2) can enhance dissimilarity, especially among species-poor communities (Zhou et al., 2022). The lack of consistent patterns in our results suggests that the traditionally used measures of dissimilarity do not comprehensively capture the changes in species communities resulting from contrasting land use (Wayman et al., 2024).

The center point analyses provided more comprehensive results with which the consequences of land-use change for species communities can be evaluated. Center points of species distributions on the productivity gradient indicate whether individual species are declining or increasing in abundance, i.e. losing or winning, under land use intensification. Some previous studies did not record a clear dominance of either losing or winning species in time series, which they related to variation in the responses of species to environmental change (Dornelas et al., 2019; Outhwaite et al., 2020). We found that as land use intensifies, there are many more arthropod species that decline ('lose') than there are that increase ('win'). This finding aligns closely with several studies of single arthropod groups in managed grasslands, such as grasshoppers (Chisté et al., 2016), Auchenorrhyncha (Chisté et al., 2018), ants (Heuss et al., 2019) and moths (Mangels et al., 2017). Chisté et al. (2016) and Heuss et al. (2019) recorded largely analogous relations with land-use intensity for the Orthoptera and Formicidae species that overlap with our study, but each of these studies also recorded six additional losing species, and intermediate distributions were found for six out of the eight Formicidae species that were losing in our study. These differences probably reflect that land-use intensity levels in our area were higher than in the German regions where these studies were conducted, which may have resulted in more negative distribution patterns for the same species, but also in regional extinction of the most sensitive species. Therefore, center point studies from different regions should be compared by the absolute values derived per species and not by relative shares of winners and losers.

Different from the approach used by Chisté et al. (2016), we compared the actual and randomized species distributions at the community level, rather than testing whether individual species increased or declined with intensification. This allowed us to incorporate the many species that were only observed a few times (n>2). Across all sampled groups, we recorded much more losers and (with one exception) fewer winners than would be expected based on random distributions, even when for that group species richness showed no relation with productivity. Moreover, 'losers' (56% of all species) represent only the species that declined in the transition

from low to medium intensity levels. In our results, 'intermediate' species include species that declined as land use changed from medium to high productivity levels, as well as species that were recorded proportionately across a wide productivity range. Only 15% of all species occurred proportionately at high-intensity grasslands, which implies that the percentage of declining species increased even to 85% under the conversion to high land-use intensity levels.

3.4.3 From narrow to broad niches

Most losing species were fully or largely restricted to a narrow range of low productivity levels, whereas in each taxonomic group, a subset of intermediate and winning species occurred widely along the productivity gradient (see Fig. 3.2 & 3.3C). This pattern resembles the prevailing species abundance distribution of communities in nature with many rare species and a few common species (McGill et al., 2007). But rather than 'natural rarity', species distributions on the productivity gradient reflect their sensitivity or tolerance to land-use intensification. Species with narrow niches on the productivity gradient were often numerous in low-productivity grasslands but were progressively lost at higher productivity levels, whereas species that appear tolerant to land use intensification became increasingly dominant (see also Simons et al., 2015). This pattern results in the often-observed biotic homogenization in intensively used systems (McKinney & Lockwood, 1999; Newbold et al., 2018). Narrowly distributed species may be harder to sample, but not including them may lead to unfounded conclusions. For instance, Simons & Weisser (2017) concluded that further intensification of current German grassland landscapes is possible without biodiversity loss in arthropod communities, but their analysis was mainly based on the 25% of species that were most widespread along gradients of productivity. Obtained at a highly comparable productivity gradient, our results indicate that these species were probably the most tolerant to land-use intensification.

The winning species in our study did not include any species that were only abundant at high-productivity grasslands. Most of these species tolerated a wide range of productivity levels. They represented only 9% of all species but 20% of the most widely occurring species. Most winning species seemed to profit from land-use intensification because of increased food availability. Such species include mobile generalist feeders such as the honey bee *Apis mellifera* (Hymenoptera; recorded at 33 sites, centered at 54 $GJ \cdot ha^{-1}$), aphid feeders such as *Tytthaspis sedecimpunctata* (Coleoptera; recorded at 31 sites, centered at 51 $GJ \cdot ha^{-1}$), and species feeding on roots and organic matter such as *Agriotes gallicus* (Coleoptera; recorded at 31 sites, centered at 64 $GJ \cdot ha^{-1}$) and *Geomyza tripunctata* (Diptera; recorded at 21 sites, centered at 70 $GJ \cdot ha^{-1}$). These winning species were not necessarily generalists, but tended to be well-adapted to the specific niches and high disturbance levels that characterize intensively used grasslands (Boyes et al., 2019; McKinney & Lockwood, 1999).

The presence of a small set of well-adapted species that increase in abundance with increasing productivity levels could explain the persistence of overall arthropod abundance at high land-use intensity levels. However, arthropod communities in the more intensively used grasslands were increasingly dominated by families of Diptera and Hymenoptera that were not identified to species level. These families mainly include small and poorly known species whose larvae live as decomposers (Diptera) or parasitoids (both Diptera and Hymenoptera). As hardly any research exists on patterns in species composition of these families, it remains unknown if their numeric dominance at intensively used grasslands results from a few winning species or also from increased species diversity. While parasitoids would probably follow the patterns of their hosts, decomposer diversity may indeed persist under intensified land-use (Le Provost et al., 2021). However, the Dipteran taxa with decomposer larvae that were identified to species level (26 species belonging to 7 families) showed similar diversity losses as other arthropod groups: most species were largely confined to lower productivity levels whereas five species were winning as land-use intensified (Fig. 7B.3). This aligns with other studies that found high turnover and strong numeric dominance of single Diptera species in intensively used systems (Powell et al., 2024; Shortall et al., 2009). It is therefore likely that also among families that remained unidentified in this study, a small set of species maintained high overall abundance levels under intensified grassland management.

3.4.4 Implications

Our findings suggest that when species from different taxonomic or ecological guilds are pooled together, abundance responses can differ markedly from diversity responses. We showed that land-use intensification on grasslands is related to consistent losses in diversity but not abundance. This means that local grassland intensification cannot explain the severe losses of overall arthropod abundance that were recorded over decadal timescales (Seibold et al., 2019; Van Klink et al., 2020). It is even possible that extensified management results in declining arthropod abundance in certain contexts, such as when Diptera are dominant (Silva-Monteiro et al., 2022). The absence of clear relations between land-use intensity and overall arthropod abundance at site level suggests that landscape-scale effects, such as loss of semi-natural habitat (Seibold et al., 2019), changes in cropping patterns (Litovska et al., 2025), increased frequency of climatic extremes (Boggs, 2016; Sohlström et al., 2022), or increased loading of harmful chemicals such as insecticides (Mancini et al., 2020), might be important drivers of the recorded arthropod declines over time. Moreover, declines of arthropod biomass (Hallmann et al., 2017) may be amplified by losses of large-bodied species and individuals in arthropod communities (Martínez-Núñez et al., 2024; Oliveira et al., 2016).

We also show that species richness and dissimilarity metrics underestimate the actual losses of arthropod biodiversity because species identities are not considered. The most profound consequence of land use intensification is the progressive loss of species across all arthropod groups that are sensitive to land-use intensification,

most of which have a distribution that is confined to a narrow range of low productivity levels. Arthropod abundance seems more resilient to intensification because of a small subset of widespread winners that compensate for losses in the majority of species (Newbold et al., 2018). Further research is needed to better understand abundance changes across arthropods with differing ecologies, and the consequences of these changes for ecosystem functioning (Cooke et al., 2025; Wagner, 2020). Winning species can probably sustain certain ecosystem processes such as food provision for generalist insectivores, but may not support more specialized trophic interactions (Holland et al., 2006). Furthermore, winning species may also amplify dis-services such as crop damage as they often include important pest species (Zhang et al., 2007). While severe species losses are expected to erode ecosystem service provisioning, we can only assess which ecosystem services are at stake when knowing which arthropods lose or profit under environmental change (Cardinale et al., 2012; Cooke et al., 2025).

Arthropod species losses were most pronounced in grasslands at the low-to-medium productivity range. This finding implies that biodiversity conservation will be most effective at lower land-use intensity levels, which aligns with other studies (Allan et al., 2014; Kleijn et al., 2009, 2011; Kleijn & Sutherland, 2003). Low-intensity grasslands play critical roles in preserving many arthropod species (Habel et al., 2013; Van Swaay et al., 2025; WallisDeVries et al., 2002) and we show here that losing such grasslands affects the large majority of species across multiple taxa. However, low-intensity grasslands have become rare or absent in modern agricultural landscapes where productivity levels above 50 $GJ \cdot ha^{-1} \cdot yr^{-1}$ have become the norm (Bardgett et al., 2021; Emmerson et al., 2016). Grass-dominated hay meadows that are common in agri-environment schemes and nature reserves, both aimed at biodiversity restoration, typically still reach medium productivities of 20-40 $GJ \cdot ha^{-1} \cdot yr^{-1}$ (Schippers et al., 2012). Although more species tolerate these productivity levels than those of high-intensity grasslands, their value for biodiversity conservation is incomparable low-productive, forb-dominated grasslands (Habel et al., 2013, 2019). Restoration of more low-intensity grassland habitats will therefore be crucial to halt and reverse the widespread biodiversity loss of grassland arthropods.

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FOUR

Flower richness is an effective indicator of grassland arthropod biodiversity

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Abstract

To curb biodiversity loss, reliable and scalable indicators that represent a broad range of species groups are urgently needed. Habitat quality metrics may provide more broadly representative and more efficiently measurable biodiversity indicators than single species groups. However, few studies have critically evaluated the applicability of habitat quality indicators across multiple arthropod groups. Flowers may reflect multiple aspects of habitat quality in grasslands. Therefore, we test if flower species richness and flower cover can indicate local species richness of plants and multiple arthropod groups in grasslands. Flower, plant and arthropod data were collected along transects in April, June and July in 41 Dutch grasslands, ranging from low to high land-use intensity levels. Flower richness showed consistent linear relations with plant and arthropod species richness, and closely resembled both the seasonal increase of arthropod richness and the exponential declines of plant and arthropod richness with increasing land-use intensity. By contrast, flower cover decreased over the sampling period and showed more variable relations with plant and arthropod richness, which were strongly driven by a few dominant flowering species. Flower richness qualifies as a broadly representative biodiversity indicator in grasslands that can efficiently be surveyed at site level, and is directly relatable to local land use practices. Flower richness measurements can therefore steer biodiversity restoration efforts such as result-based agri-environmental schemes on farmland, in which there is increasing emphasis on improving habitat quality.

Introduction

Measuring biodiversity is complex, time-consuming and hindered by numerous factors that limit the detectability of wild species. These constraints severely impede our understanding of biodiversity patterns in space and time and therefore, our ability to curb biodiversity loss. Mounting evidence shows that biodiversity is in peril in ecosystems across the world (IPBES, 2019; Jaureguiberry et al., 2022; Newbold et al., 2015, 2016). But while the larger and charismatic species are relatively well-known, biodiversity losses amongst the smaller organisms that form the majority of earth's biodiversity are rather poorly understood (Dirzo et al., 2014; Van Klink et al., 2020; Wagner, 2020). Efforts to halt and reverse biodiversity losses depend on biodiversity measurements that are detailed enough to capture the fine scales of species' ecological requirements, but efficient enough to be collected across large areas and frequent time intervals. Therefore, there is a pressing need of reliable, readily quantifiable and scalable indicators that represent biodiversity patterns across a wide range of species groups (Pereira et al., 2013; Turner, 2014).

Grassland habitats form a system in which anthropogenically driven biodiversity losses have been especially severe (Bardgett et al., 2021; Newbold et al., 2016; Seibold et al., 2019). Vascular plants and arthropods form their most abundant and diverse lifeforms, and reach some of their highest levels of local species richness in temperate grasslands (Dengler et al., 2014; Habel et al., 2013; Wilson et al., 2012). Vascular plant richness has most widely been used to indicate grassland biodiversity and restoration results (Elmiger et al., 2023). However, previous studies have shown that plant species richness does not necessarily reflect biodiversity patterns of other taxa (Billeter et al., 2008; Manning et al., 2015; Vessby et al., 2002). Plant species richness is typically determined on small areas (such as 1 m2 quadrat surveys) and requires expert knowledge (Tasser et al., 2019), especially for grasses (Poaceae and related families). Surveys on arthropod groups are even more heavily constrained by the scarcity of expert knowledge, as well as by ecological factors such as species' short lifespans, large population fluctuations and dependencies on weather conditions (Cooke et al., 2025; Wagner, 2020). Therefore, most field studies are limited to single 'indicator groups' that are relatively well known or readily sampled, such as butterflies or carabid beetles (Augenstein et al., 2012; Gerlach et al., 2013; Van Swaay et al., 2025). Many papers use such groups as indicators of overall arthropod diversity and claim that these arthropod groups are good indicators of biodiversity in general. However, other studies have shown that single arthropod groups can be poor indicators of wider arthropod diversity (Billeter et al., 2008; Fleishman & Murphy, 2009; Segre et al., 2023; Vessby et al., 2002). Critical evaluations of indicators that may be good proxies for wider (arthropod) biodiversity in grasslands remain scarce.

The challenges that come with measuring plant and arthropod biodiversity create a need for simple habitat quality metrics that depict biodiversity patterns. Such metrics should be strong predictors of biodiversity across multiple species groups,

should remain indicative under changing circumstances and conditions such as land-use intensity (Manning et al., 2015), and should be readily measurable at field level across wide geographical areas and frequent time intervals (Kleijn et al., 2020). Metrics that can be quantified with the help of citizen scientists or by remote sensing show particular potential for upscaling in space and time (Cavender-Bares et al., 2022; Dickinson et al., 2010). In grasslands, flower metrics hold promise to be used as generalizable biodiversity indicators. They can be readily quantified at field level and show potential for automated data collection by remote sensing techniques (Elvekjaer et al., 2024; Gonzales et al., 2022; Torresani et al., 2023). Flower metrics appear indicative of several pollinator groups such as butterflies, hoverflies and bees, and outperform single species groups as indicators (Kral-O'Brien et al., 2021; Segre et al., 2023). While correlations of flower metrics with plants and flower-visiting insects may be anticipated, it is perhaps more surprising that carnivorous groups such as spiders have also been related to flower metrics (Mei et al., 2021; Rowe et al., 2021). This may indicate that flower metrics do not only reflect direct ecological interdependencies such as consumer-resource relationships, but also indirect drivers such as vegetation structure or productivity (Joern & Laws, 2013; Manning et al., 2015; Woodcock et al., 2007). Moreover, flower metrics show strong seasonal variation that can reflect seasonal shifts in local arthropod richness (Bishop et al., 2024; Gonzales et al., 2022). Indicators that capture seasonal trends may be especially useful for arthropod groups with short life spans, multiple generations or strong turnover in community composition during the growing season. The applicability of flower metrics as biodiversity indicators in grasslands has however not been tested across multiple taxonomic groups.

Here, we test if flower cover and flower species richness are indicative of local species richness patterns of plants and a wide range of arthropod groups in managed grasslands. Focusing on a study area in the Netherlands that hosts grasslands along a wide gradient of land-use intensity, we test whether these flower metrics are robust biodiversity indicators across varying land-use intensity levels and across the growing season from April to July.

Methods

4.2.1 Study design

This study was performed in the valley of the river Geul in the south of the Netherlands (50°53'30N, 5°49'47E; 50°48'09N, 5°56'25E), which has a small-scaled heterogeneous landscape and represents a national biodiversity hotspot. Grasslands form a major land-use type in this region and show a high variety in land-use intensity, owing to management decisions aimed at either agricultural production, biodiversity-friendly agriculture or nature conservation. We selected 41 grasslands of at least three years old that covered the maximum width of this land-use intensity gradient. Including nutrient-poor semi-natural grasslands, hay meadows, agri-environmental schemes, organic pastures and monocultural high-

input grasslands, this gradient represents most of the managed grassland types that can be found in northwestern and central Europe (Bardgett et al., 2021). In each grassland, a transect measuring 150 by 1 meter was set up from edge to center of the field. Transects were laid across heterogeneities within the field, such as differences in elevation, to cover this variation during sampling.

4.2.2 Data collection

Flower and arthropod surveys were conducted in three rounds: from 18-4 to 2-5 (hereafter 'April'), 30-5 to 17-6 (hereafter 'June') and 5-7 to 15-7 (hereafter 'July') in 2022. To ensure the comparability of flower and arthropod metrics for each site, both were collected on the same day or at maximum two days apart in case of adverse weather conditions. In the flower surveys, we counted the number of open flowers within the 150 m2 transect for each flowering forb species, with the exception of wind-pollinated species such as *Rumex* spp., following Scheper et al. (2015). In most cases we managed to count the exact number of individual flowers, but when flower abundance was particularly high we counted per groups of 10 flowers. Composite flowers such as Apiaceae and *Trifolium* were counted per head and then multiplied by the estimated average number of open flowers per head. The flower area per species was subsequently estimated by multiplying the flower counts by the average surface area per individual flower in cm2, and total flower cover on the transect was derived as the sum of flower area estimates for all recorded species.

Arthropod communities were surveyed by sweep-net sampling complemented with pollinator transect walks. Contrary to passive collection methods such as pitfall or Malaise traps, these two methods are area-based and directly relatable to flower measurements on the sampled transect. Sweep-net sampling targets a broad range of vegetation-dwelling arthropod groups while pollinator transects target fast-flying pollinators that may be missed with sweep-netting (Simons et al., 2014; Spafford & Lortie, 2013). Both survey methods were conducted on dry days with low wind speeds (< 3 Bft), low cloud cover (<50%) and temperatures above 15 °C, and between 10:00 and 17:30 (Westphal et al., 2008). Pollinator transect walks were performed prior to sweep-net sampling and flower surveys to minimize disturbance. Following Westphal et al. (2008), we counted all bees (Anthophila) and hoverflies (Syrphidae) that were observed on the 150 m2 transect up to 1 m in front of the observer, while slowly walking along the transect for 15 minutes per survey (excluding catching and handling time). Specimens were only collected if they could not be identified with certainty in the field. Subsequently, on each 50-m subsection of the transect we conducted 70 single-sweeps of approximately 1 m wide in June and July, but 160 in April, because we expected lower arthropod abundances in this month and therefore roughly comparable total arthropod counts in each month. Sweep-net samples were collected in ziplock bags and stored frozen upon identification in the lab. We identified all specimens belonging to Anthophila, Araneae, Formicidae, Heteroptera and Orthoptera and to selected families of

Coleoptera (Cantharidae, Chrysomelidae, Coccinellidae and Elateridae; hereafter 'Coleoptera') and Diptera (Asilidae, Bibionidae, Conopidae, Opomyzidae, Platystomatidae, Rhagionidae, Sciomyzidae, Stratiomyidae, Syrphidae, Tabanidae, Tephritidae, Tipulidae and Ulidiidae; hereafter 'Diptera'). These seven subgroups represent a wide range of taxonomic and ecological groups within the limits of the identification materials and taxonomic expertise that were available to us. Species lists and identification references per family are given in Tables 7B.2 and 7C.4-6.

We furthermore obtained measurements of plant species richness and productivity for each field. Plant species richness was surveyed in May (14th-31st) in 10 quadrants of 50*50 cm that were spread evenly along the 150-m transect. For each quadrant the percentual coverage of each species present was estimated and corrected to total 100%. Productivity was assessed by the annual production of net metabolic energy per hectare in Gigajoule [$GJ \cdot ha^{-1} \cdot yr^{-1}$]. This metric accounts both for biomass production, which was collected through interviews with land owners, and for forage quality (energy content), which was estimated from standard energy content values per forage type (CVB, 2022; De Vries et al., 2026).

4.2.3 Data analyses

Species richness of flowers and arthropods was measured as the number of observed species per transect per round. Both flower metrics (flower cover and flower richness) could be compared with arthropod richness for each month separately, but to allow comparison with plant richness, flower cover was averaged over three months and total flower richness was derived after the three species lists were pooled together. Flower cover measurements were square root transformed to prevent right-skew due to the high cover of single flowering species. Next, metrics were z-standardized to facilitate model comparisons and the construction of multiple linear models.

The relations of both flower metrics with plant richness, overall arthropod richness and the richness of seven arthropod subgroups were first analyzed using single linear models. Orthoptera were only modelled in July because of their low numbers in earlier months (>60% zero records). Since ecological relations are often non-linear, we evaluated the statistical support for quadratic or cubic terms with Akaike's information criterion for small sample sizes (AIC_c: the tested exponential terms were rejected if $\Delta AIC_c < 2$, indicating low model improvement) and model residual patterns, using R-package *MuMIn* (Bartoń, 2023). Following the results of single linear models in which relations with flower richness were stronger than with flower cover, the linear terms of both flower metrics were combined in multiple linear models to assess the added value of flower cover as a second predictor next to flower richness. The contribution of both metrics to the models' explanatory power was measured by their effect on adjusted R-squared (ΔR^2_{adj}). Finally, we analyzed how flower cover and flower richness in each month related to grassland productivity [$GJ \cdot ha^{-1} \cdot yr^{-1}$], a proxy for land-use intensity. These relations were

analyzed using linear models in which exponential terms were included if statistically supported ($\Delta AIC_c > 2$). All analyses were done in R 4.5.0 (R core team, 2025), model predictions were derived from the R-package *glmmTMB* (Brooks et al., 2017) and residual patterns were validated with R-package *DHARMa* (Hartig, 2022).

Results

4.3.1 Relations of flower metrics with plant and arthropod species richness

We recorded 520 arthropod species, 141 plant species and 122 flowering species (species lists are provided in the repository material). All flowering species were native to the study area. Species richness of plants and of all arthropods combined was significantly related with both flower species richness and flower cover, but relations were consistently stronger for flower richness ($p < 0.0001$) than for flower cover ($p < 0.01$) (Fig. 4.1, Table 7C.1). Plant species richness increased linearly with flower richness (slope = 0.89; $R^2_{adj} = 0.78$), but was unimodally related to flower cover ($R^2_{adj} = 0.24$). Overall arthropod species richness showed a similar rate of increase with flower richness in April, June and July, explaining more than half of the variation in species richness (slopes range 0.75-0.85; R^2_{adj} ranges 0.55-0.72). The relation between flower cover and overall arthropod richness was unimodal in April ($R^2_{adj} = 0.25$) and turned linear in June and July, but became steeper from June (slope = 0.49; $R^2_{adj} = 0.22$) to July (slope = 0.69; $R^2_{adj} = 0.46$). Furthermore, the measured increase in overall arthropod richness from April to July was closely resembled by increasing flower richness levels (Fig. 4.1C: range in values on the X-axis increases), but not by flower cover which showed an overall decline over time (Fig. 4.1D: range in values on the X-axis decreases). Arthropod richness of all measured subgroups except Coleoptera increased significantly and linearly with flower richness in each of the three months ($p < 0.01$ for Araneae in April and June, <0.001 for all other subgroups) (Fig. 4.2, Table 7C.1). Significant relations with flower cover were found for Diptera (unimodal) and Anthophila in April, for Heteroptera and Anthophila in June, and for all groups except Coleoptera in July. Only for Anthophila (bees) in June the correlation with flower cover was stronger than with species richness (both <0.001).

Pearson correlations between flower cover and flower richness were relatively weak in April, June and over the whole season (0.32-0.38), but strong in July (0.63). Added as a second explanatory variable next to flower richness, flower cover did not improve explanatory power (R^2_{adj}) for the model explaining plant species richness. Flower cover did contribute significantly to explanatory power of the two-predictor models explaining the species richness of all arthropod species, Anthophila and Heteroptera in both June and July ($p < 0.05$) (Fig. 4.3, Table 7C.2). But compared to the models based on flower richness alone, flower cover only led to a substantial improvement of explanatory power for Anthophila in June (partial R^2_{adj} for flower cover = 0.26; <0.1 in all other models). For most arthropod groups, explanatory power was highest in July (>0.5 for all groups except Coleoptera).

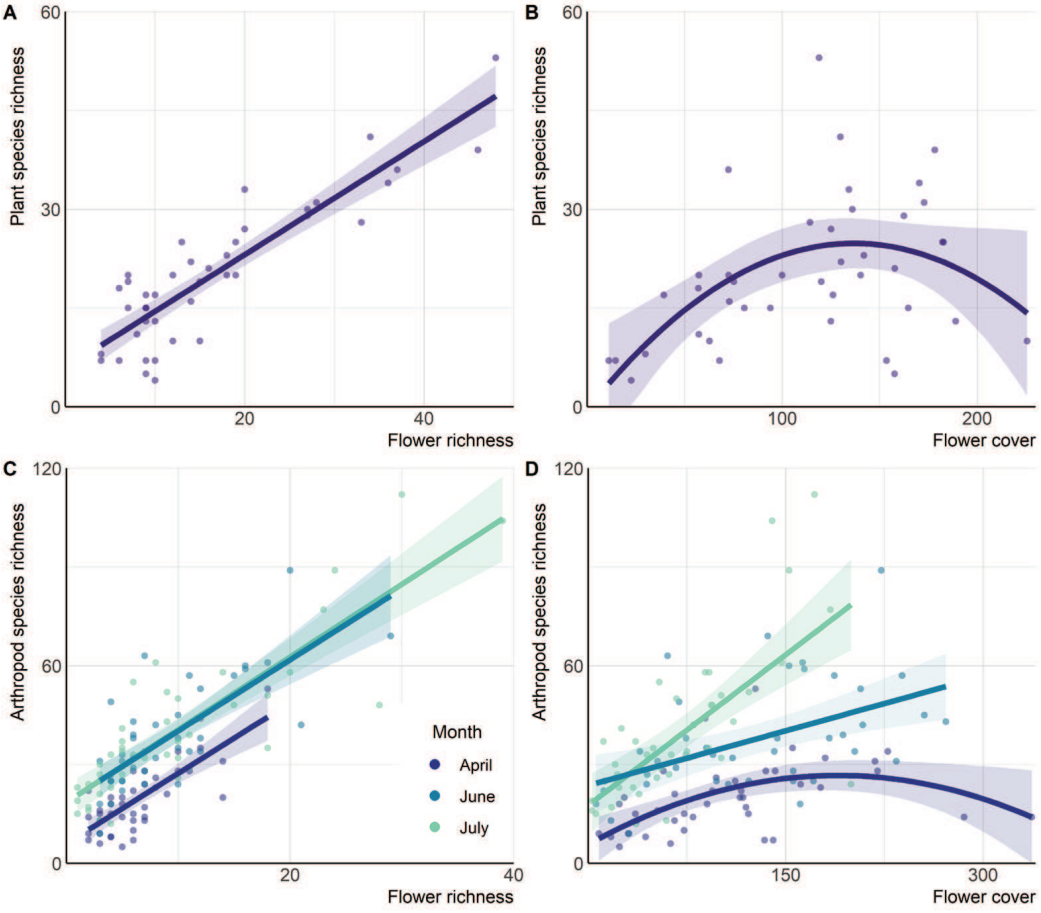

Figure 4.1. relations of plant species richness (A-B) and overall arthropod species richness (C-D) with flower species richness or flower cover (square root transformed) in grasslands. Arthropod richness was measured in April, June and July and was related to the corresponding measurements of both flower metrics separately, whereas plant richness was related to the aggregated flower richness or averaged flower cover over these three months. Relations are shown with 95% confidence intervals.

4.3.2 Relations of flower metrics with grassland productivity

Flower richness showed a relatively weak linear decline with grassland productivity in April (R^2_{adj} = 0.15, $p < 0.01$) but showed much stronger declines in June and July (R^2_{adj} = 0.65, $p < 0.0001$; Fig. 4.4, Table 7C.3). In these two months, flower richness decreased sharply with increasing productivity at the low productivity range, but remained relatively stable at low richness levels across the high productivity range. The steady increase in flower species richness over time across the three-month study period was exclusively observed in low-productivity grasslands (<30 GJ·ha^{-1}·year^{-1}). The relations between flower richness and arthropod richness were similar at low, medium and high productivity levels, but plant richness at high-productivity grasslands was lower than at less productive

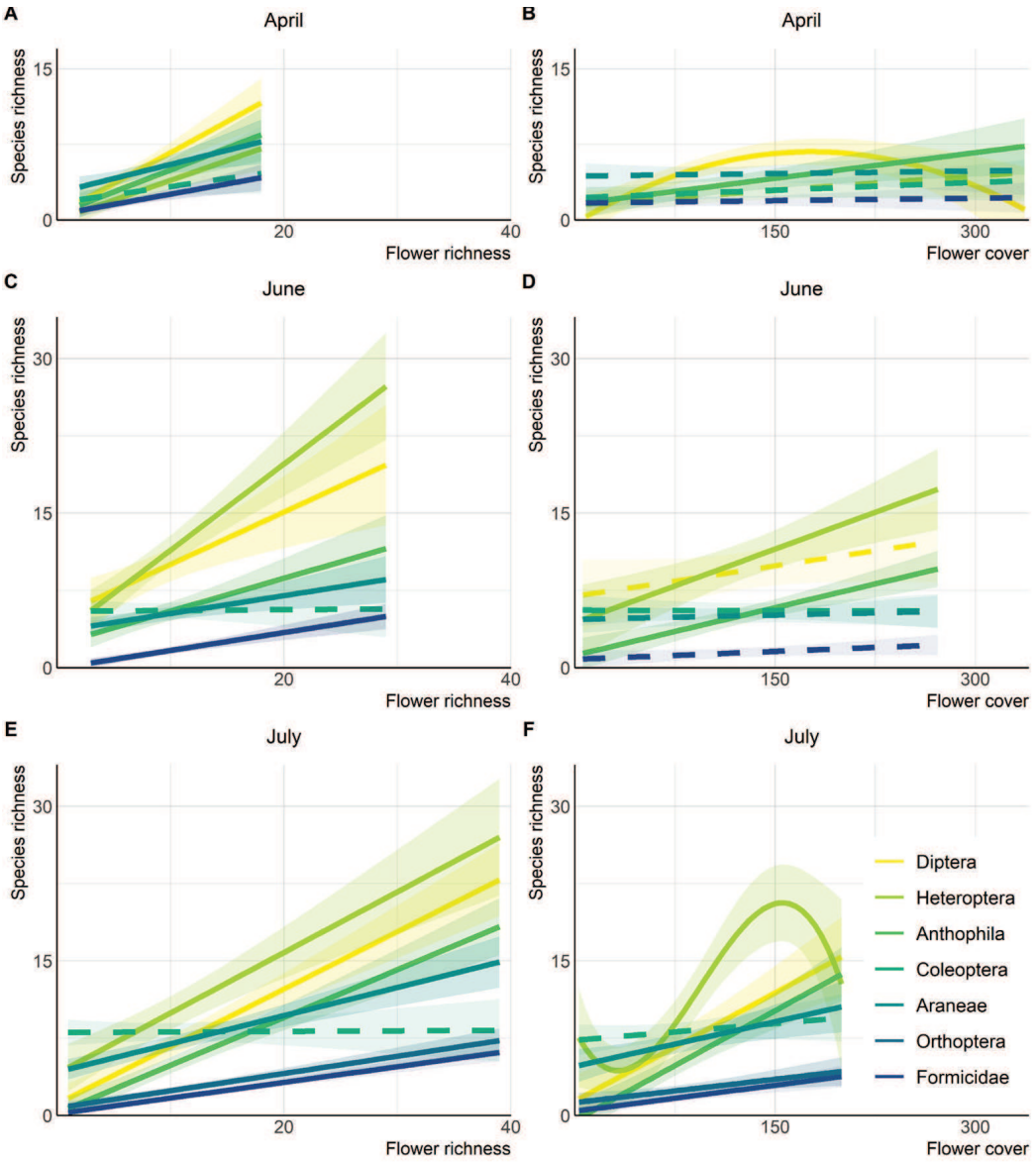

Figure 4.2. Relations between arthropod species richness per subgroup and flower richness (right) or flower cover (left: square root transformed) in April (A-B), June (C-D) and July (E-F). Significant relations ($P<0.05$) are shown with solid lines with 95% confidence intervals, unsignificant relations are shown with dashed lines. Exponential terms were included when statistically supported.

grasslands with the same flower richness levels (Fig. 7C.1). This difference mainly resulted from a loss of grass species. Relations of flower richness with plant and arthropod richness were also similar at fields that were predominantly mown or grazed (Fig. 7C.2). Flower cover showed a high variability across the productivity gradient, especially at high productivity levels (>45 GJ·ha^{-1}·year^{-1}) which supported

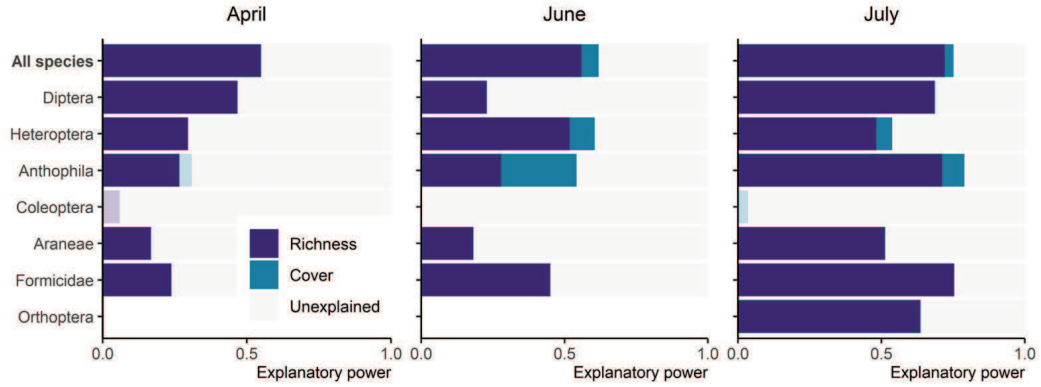

Figure 4.3. Arthropod richness in April, June and July across all sampled species (first row) and per arthropod subgroup explained by flower richness and flower cover. Explanatory power (partial R^2_{adj}) indicates the variation in arthropod richness explained when subsequently including flower richness and flower cover in multiple linear models. Negative values of partial R^2_{adj} are not shown. Unsignificant relations are shown in faded colors.

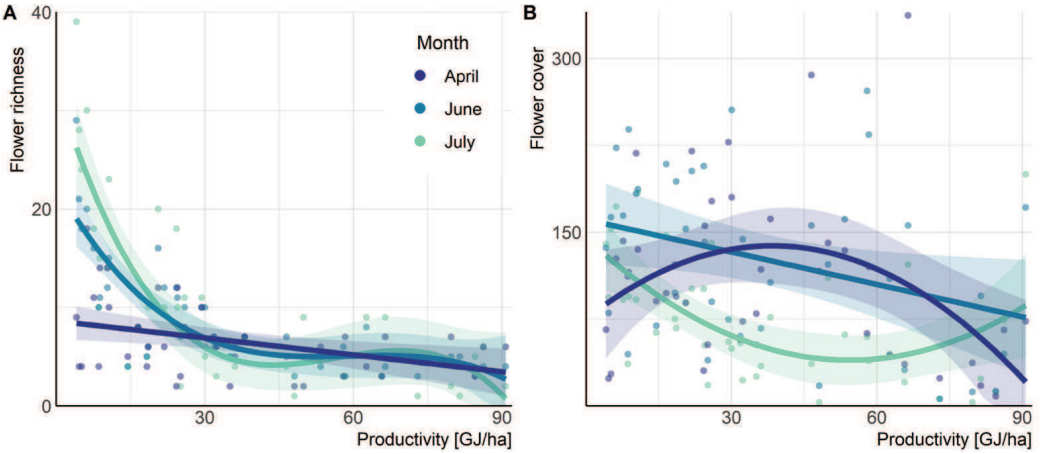

Figure 4.4. Changes in flower species richness and flower cover (square root transformed) and along the sampled productivity gradient in April, June and July. Flower richness in June and July was best explained in cubic terms and flower cover in April and July was best explained in exponential terms, other models show linear relations.

both the lowest as the highest cover levels in each month (Fig. 4.4, Table 7C.3). These peaks in high-productivity grasslands were largely driven by Taraxacum agg. in April and Trifolium repens in June and July. Flower cover showed a significant unimodal pattern in April (when cover peaked at medium productivity levels) and declined significantly with productivity in June and July (linear terms; $p < 0.05$), with the decline being unimodal in July (with a dip in cover at intermediate productivity levels). Productivity explained 9-27% of the variation in flower cover.

Discussion

Flower richness indicated species richness of plants and a broad range of arthropod groups, and did so in simple linear terms. Relations of flower richness with arthropod richness stayed approximately constant over time from April to July but increased in explanatory power, as both flowers and arthropods increased in richness. This richness increase was concentrated at low-productivity habitats. Relations of flower cover with species richness were mostly positive but also showed unimodal patterns, which were mainly driven by peaks of single flowering species in high-productivity grasslands. Only for Anthophila in June, flower cover substantially improved the explanatory power of flower metrics.

4.4.1 Representativeness

The strong linear relations of flower richness with species richness of almost all examined plant and arthropod groups probably reflect multiple ecological connections. The relation with plant richness follows inherently from the dominance of flowering forbs in grassland species assemblages (Bråthen et al., 2021). Plant richness in turn promotes niche differentiation and stability in arthropod communities (Haddad et al., 2009, 2011; Joern & Laws, 2013). Higher plant richness increases the structural complexity of arthropods' physical habitats (Stein et al., 2014), and flower richness in particular is linked to open vegetation swards (Eskelinen et al., 2022) which provide suitable microclimatic conditions to many arthropod species (Woodcock et al., 2007). Flower richness is also directly linked to resource provisioning for flower-visiting insects (e.g. Anthophila and many Diptera families) and many specialized herbivores (e.g. Heteroptera) (Bernays & Graham, 1988; Blumgart et al., 2023; Scheper et al., 2014; Segre et al., 2023). Furthermore, relations with flower richness may reflect shared environmental drivers such as climatic conditions and land-use intensity. When land use intensifies, both increased competition for light, increased mowing frequencies and increased grazing pressure may suppress flower richness (Borer et al., 2014). Flower and arthropod richness both increased from April to July and this increase was concentrated in low-productivity grasslands, which reflects the concentration of both plant and arthropod biodiversity in these habitats (De Vries et al., 2026; Kleijn et al., 2009). Yet, the relations of plant and arthropod richness with flower richness did not substantially weaken with increasing land-use intensity. By serving as a surrogate for multiple aspects of arthropod habitat quality that is applicable across a wide range of land-use intensity levels, flower richness qualifies as a broadly representative biodiversity indicator in grasslands.

Flower cover generally showed much weaker and more variable relations with plant and arthropod species richness. Consistent positive relations were only found for bees (Anthophila), which aligns with other studies on pollinators (e.g. Bishop et al., 2024; Cole et al., 2017; Scheper et al., 2015), while positive relations with other arthropod groups were largely confounded with the relations with flower richness.

The relations of bees with flower cover reflect their direct consumer-resource relationship with flowering plants (Potts et al., 2003), that is less strong and consistent in the other sampled groups. The variability of relations between flower cover and plant or arthropod richness was influenced by the mass flowering of single plant species, notably of *Taraxacum* agg. and *T. repens* in high-productivity grasslands. Each of these species represented more than 20% of the total flower cover over three months and the ten most common species (8.2% of all flowering species) contributed 86% to the total flower cover. Strong effects of a few dominant species on total abundance were also observed in arthropods (De Vries et al., 2026) and explain why flower cover showed no consistent decrease with land-use intensity, nor an increase over time. Total flower cover is therefore not useful as a general biodiversity indicator.

The consistency in the relations of flower richness with plant and arthropod richness found here stands in contrast to the limited levels of representativeness that have been found for single arthropod indicator groups (Billeter et al., 2008; Fleishman & Murphy, 2009; Gerlach et al., 2013; Segre et al., 2023; Vessby et al., 2002), and to the finding that associations between plant and arthropod taxa weaken with increasing land-use intensity (Manning et al., 2015). Plants have been found to be more robust biodiversity indicators when analyzed in terms of species composition (Schaffers et al., 2008; Tobisch et al., 2023), but this does not provide an efficient method for large-scale application. Detailed inventories of species composition and population trends remain crucial to monitor habitats of high nature value and species of conservation concern (Busch et al., 2019; De Vries et al., 2026; Van Swaay et al., 2025). Our results show that flower richness surveys across larger areas can complement such inventories. It should however be noted that non-native flowers, which were not recorded in this study, may weaken the associations of arthropod richness with flower richness substantially (Burghardt et al., 2010; Tartaglia & Aronson, 2024). Therefore, non-native species may need to be excluded when flower richness is used as a biodiversity indicator.

Moreover, flower richness can account for seasonal changes in habitat quality, which are particularly relevant for arthropods because of their short life cycles and high seasonal turnover in community composition (Obrist & Duelli, 2010; Schellhorn et al., 2015). Previous studies have reported progressive declines of floral resources during the growing season in more intensively used habitats, which cause resource limitation for bees (Bishop et al., 2024; Neumüller et al., 2020) and might also reflect wider patterns of increasing disturbance at seasonal timescales. Using flower richness as a biodiversity indicator, our results imply that low-productivity grasslands become increasingly important biodiversity refuges during the growing season, while local richness in high-productivity grasslands may even decline after early spring.

4.4.2 Applications

Powerful biodiversity indicators should combine broad and reliable representativeness with simplicity of assessment and interpretation (Elmiger et al., 2023). In this respect, flower metrics stand out as intuitive and relatively easily surveyed indicators. Flowers are typically more easily detected and identified than non-flowering plants or arthropods, and can nowadays be identified reliably by non-experts using automated identification tools (Joly et al., 2014; Mäder et al., 2021). This provides opportunities to upscale biodiversity monitoring through citizen science strategies (Dickinson et al., 2010). Moreover, remote sensing techniques show potential for upscaling flower measurements across entire landscapes (Cavender-Bares et al., 2022; Gonzales et al., 2022). For instance, previous studies have used remote cameras to measure flowering phenology (Mann et al., 2022) and drone imagery to measure grassland flower cover as a predictor of bee diversity (Torresani et al., 2023; Chieffallo et al., 2025). It is still challenging to measure flower richness or composition over larger areas with remote sensing techniques (Elvekjaer et al., 2024; Sun et al., 2018), but further developments in this field can be anticipated. While more general vegetation metrics such as NDVI or structural heterogeneity are already widely used in remote sensing campaigns, measures of flower richness would provide more detailed and directly interpretable ecological insights in grassland habitats (Cavender-Bares et al., 2022; Gonzales et al., 2022).

4.4.3 Implications

For optimal usefulness in conservation, biodiversity indicators should ideally be directly relatable to local land use practices (Elmiger et al., 2023). Flower richness can be quantified objectively at field scale and is sensitive to within-field conditions and management decisions. This makes flower richness a promising key performance indicator (KPI) to assess biodiversity values in e.g. agri-environmental schemes (AES) (Elvekjaer et al., 2024; Kleijn et al., 2020). Practitioners can locally improve native flower richness in multiple ways, but given its sensitivity to grassland productivity, result-based rewards may be needed to prevent trade-offs with farmers' income (chapter 2). Result-based payments can help farmers to derive income from their biodiversity achievements and are seen as a promising way to improve the effectiveness of agri-environmental schemes. However, these schemes are critically dependent on biodiversity measurements that indicate what results have been achieved (Hasler et al., 2022; Herzon et al., 2018). It is increasingly recognized that such measurements should quantify habitat quality rather than the abundance of a particular species group (Fijen et al., 2025; Tobisch et al., 2023). As a biodiversity indicator, flower richness can complement detailed biodiversity inventories that are limited in scale. Flower richness provides a robust representation of many species groups by simple linear terms, that persists across different levels of land-use intensity and even reflects seasonal changes of habitat quality. As flower richness can be readily assessed by both practitioners and the general public and can be targeted through objective and scalable monitoring, standardized surveys and result-based reward schemes can potentially be enrolled over large spatial extents in cost-effective ways.

Acknowledgments

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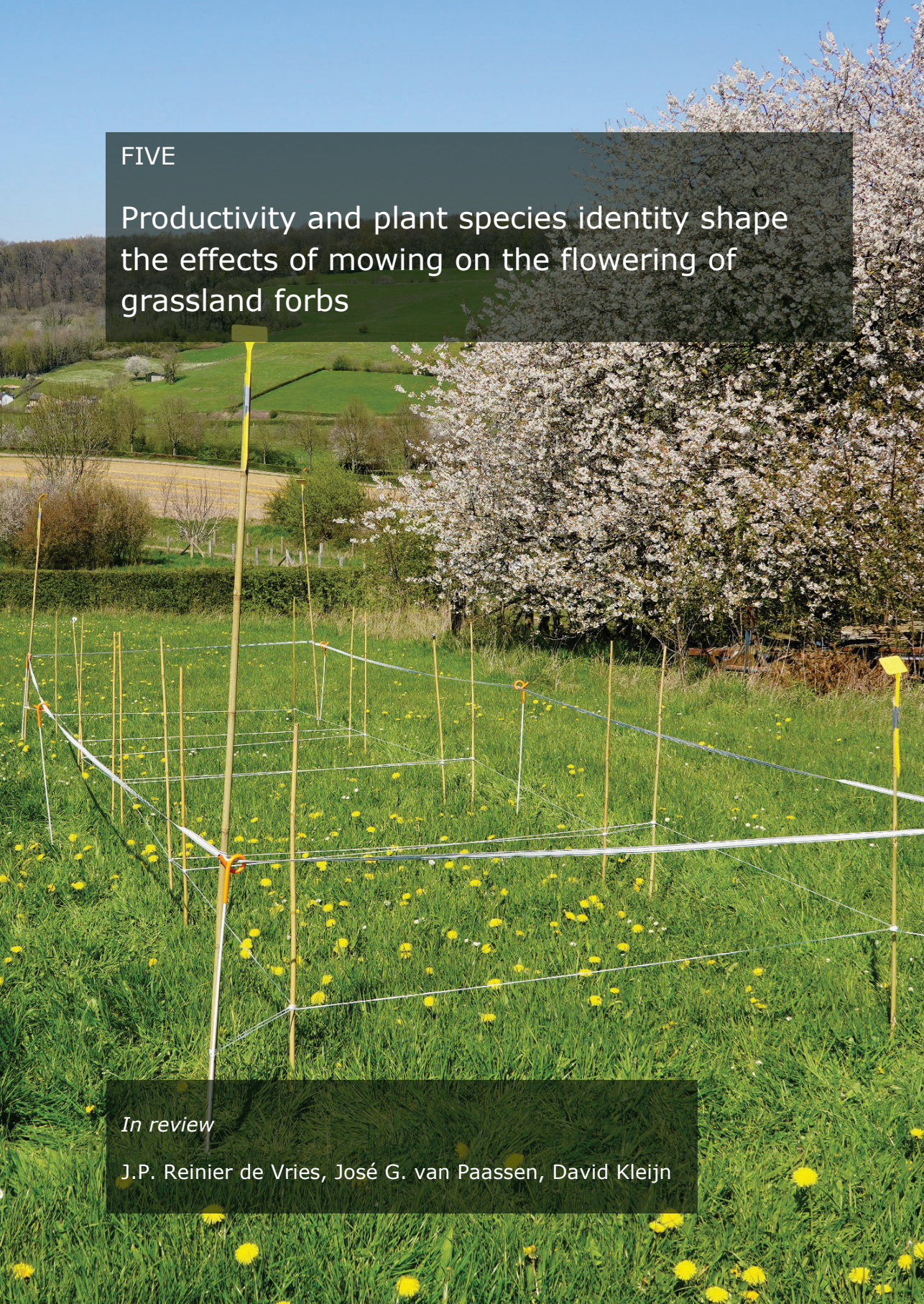

FIVE

Productivity and plant species identity shape the effects of mowing on the flowering of grassland forbs

In review

J.P. Reinier de Vries, José G. van Paassen, David Kleijn

Abstract

1. Flower-rich grasslands have become increasingly rare in intensively used landscapes. Restoration of these grasslands is a key strategy to halt biodiversity loss. Many restoration schemes propose reduced mowing regimes to prevent losses of flowers, but mowing can also facilitate reflowering by alleviating light competition from dominant species. However, it remains unclear which conditions determine whether reduced mowing can promote or suppress grassland flowers.
2. Here we examine how the effect of reduced mowing on grassland flowers is moderated by grassland productivity. On 12 fields along a productivity gradient, we established four plots with different mowing regimes (three to zero cuts during the main growing season). In each plot and for each forb species, we measured flower cover over time in three- to five-day intervals. We then analyzed the effects of mowing and productivity on flower richness and flower cover across the main growing season, on their recovery after mowing, and on the flowering of individual forb species.
3. Reducing the mowing frequency increased full-season flower cover at low-productivity sites, but this effect disappeared with increasing productivity. Full-season summed daily flower richness increased with both reduced mowing and lower productivity. The effects of mowing on flower cover and richness were strong and productivity-dependent in late spring, but disappeared in summer.
4. After mowing, flower cover recovered more rapidly at lower productivity levels and higher mowing frequencies, while recovery rates of flower richness only increased with mowing frequency at lower productivity levels. Whether flowers recovered after mowing differed strongly between species. Half of all observed species recovered fully after a single spring cut, but only a few species recovered fully under more frequent mowing regimes.
5. *Synthesis and applications.* Reduced mowing only promotes flowering in low- to medium-productive grasslands. Here, mowing regimes can be tailored to the phenology of local forb assemblages. Rest periods and uncut refuges can preserve late-phenological species that will not reflower after mowing, while spring cuts can enhance reflowering of spring flowers like *Trifolium pratense* from July onwards. Frequent mowing benefits only a few species but from May onwards, only these species persist in high-productivity grasslands.

Introduction

Many temperate semi-natural grasslands are characterized by an abundance of flowers during significant parts of the growing season. Flowering forbs can make up most of the cover and biomass of grassland vegetation and reach exceptionally high species richness at small spatial scales (Dengler et al., 2014; Petermann & Buzhdygan, 2021; Wilson et al., 2012). Such grasslands provide key resources to a wide range of flower-visiting arthropods (Ebeling et al., 2011; Öckinger & Smith, 2007; Schuldt et al., 2019). The species richness of flowering plants in grasslands is a good indicator of the diversity of a wide range of arthropod groups, including groups that are not directly using flowers as resources but depend on e.g. structural or microclimatic characteristics that correlate with flower richness (Joern & Laws, 2013; Woodcock et al., 2007; chapter 4). However, both flowering forbs and arthropods in grasslands have declined sharply over the last 50 to 100 years (Eichenberg et al., 2021; Newbold et al., 2016; Seibold et al., 2019; Wesche et al., 2012). Declines of flowering plants can cause resource deficits for arthropod species, which can induce cascading declines across multiple trophic levels (Scheper et al., 2014; Simons et al., 2014). The resulting biodiversity losses may in turn threaten the ecological functioning of grasslands and the delivery of ecosystem services (Cardinale et al., 2012; Dainese et al., 2019). Therefore, sustaining a high flower richness is a crucial element of grassland conservation and restoration.

In managed grasslands, biodiversity declines are predominantly driven by nutrient enrichment (Harpole et al., 2016) in combination with increased mowing frequencies or grazing intensities (Berger et al., 2024; Gossner et al., 2016; van Klink et al., 2019). Particularly strong biodiversity losses are associated with the widespread conversion of extensively managed hay meadows: In many regions, meadows that used to be cut once or twice per year are now being cut four to six times per year, with associated high fertilizer application rates (Bardgett et al., 2021; Gossner et al., 2016; Shipley et al., 2024). More frequent mowing negatively affects the seed set and reproduction of the majority of forb species (Busch et al., 2019), increases direct mortality of arthropods (Humbert et al., 2009, 2012; Steidle et al., 2022) and interrupts the availability of the habitat structures, microclimatic niches, host plants and floral resources that many species require (Dahlström et al., 2008; Gardiner & Hassall, 2009; Johansen et al., 2019; van Klink et al., 2019). Reduced-mowing regimes are therefore one of the most frequently used measures for biodiversity restoration in agri-environment schemes, nature restoration programs and public campaigns, and generally prohibit mowing in (parts of the) grasslands during certain periods of the year (Buri et al., 2014; Garbuzov et al., 2015; Shipley et al., 2024).

However, defoliation by mowing or grazing is an inherent part of the processes that shape and maintain semi-natural grasslands. Without defoliation, most grassland species will disappear because of grass and shrub encroachment (Bardgett et al., 2021; Marini et al., 2009). Regular defoliation allows large numbers of flowering

species to co-exist because such intermediate levels of disturbance create open swards, prevent dominance of tall-growing species and maintain nutrient-limited conditions (Borer et al., 2014; Socher et al., 2013). Cessation of mowing in meadows usually erodes biodiversity and experiments have shown that this decline is mainly driven by increasing competition for light, particularly when nutrient availability and productivity are high (Eskelinen et al., 2022; Hautier et al., 2009). Indeed, in more productive sites, earlier and more frequent mowing is required to maintain floral species richness (Kleijn & Scheper, 2025).

In modern agricultural landscapes, the cover and diversity of wildflowers often drops in May, resulting in markedly lower flowering in late spring and summer —when most arthropod populations peak (Bishop et al., 2024; Timberlake et al., 2019). Continuous flowering from early spring to late summer is important as it sustains flower-visiting insects with specialized or complex life cycles (Ogilvie & Forrest, 2017; Persson & Smith, 2013; Timberlake et al., 2019), supports food web stability (Ebeling et al., 2011), and indicates sustained structural and microclimatic heterogeneity (Joern & Laws, 2013). Measures for biodiversity and flower-visiting insects in particular should therefore aim to prolong flowering periods and enhance flowering later in the season (Glenny et al., 2023; Soley & Wilsey, 2025). Flowering periods can be prolonged by promoting species that flower sequentially (Soley & Wilsey, 2025) and also by mowing early in the growing season, which can initiate reflowering during summer (Johansen et al., 2019; Meissen et al., 2020; Noordijk et al., 2009).

It is often argued that management for grassland biodiversity should promote heterogeneous or phased mowing regimes to sustain landscape-wide continuity of flowers across the growing season (Bonari et al., 2017; Johansen et al., 2019; Shipley et al., 2024). However, it remains unclear how site conditions and species composition influence the contrasting effects of mowing on flowering forbs. Mowing obviously causes a loss of flowers in the short term (Hemmings et al., 2022), but without mowing, flower cover and diversity may also decline because of increased competition for light or because plants divert resources from flowering to seed set. Early-season mowing can enhance flowering later in the season, but whether plants are actually able to produce new flowers after mowing is dependent on a number of factors, such as life history strategies of plants (e.g. determinate versus indeterminate growth strategies) and whether essential resources such as nutrients are available for regrowth (Hofmann & Isselstein, 2005; Noordijk et al., 2009; Prigge et al., 2024). The effects of different mowing regimes on flowering during the growing season may therefore differ markedly between species and between low- and high-productive grasslands (Fig. 5.1). A better understanding of the complex interactions that ultimately determine flower cover and diversity in grasslands requires detailed knowledge of species' flowering phenology and their responses to mowing at different productivity levels. To date, few studies have quantified the flowering of different forb species over time (e.g. Hemmings et al., 2022; Noordijk et al., 2009; Timberlake et al., 2019) and none have experimentally

linked this to changes in mowing regime across a range of productivity levels.

In this study, we tested how mowing frequency affected flower species richness and flower cover from late April to mid-August in twelve grasslands of different productivity levels. All sites were situated on loamy soils in the south of the Netherlands, but ranged in management intensity from unfertilized hay meadows to intensively used fodder production fields. We asked 1) whether less mowing promotes flower richness and cover at all productivity levels, 2) how flower recovery after mowing changes with productivity and mowing regime, and 3) how flower recovery after mowing differs among individual flowering species. We expected that 1) the positive effect of reduced mowing on flower richness and flower cover diminishes at higher productivities and may become negative in high-productivity grasslands, where flowering forbs are rapidly suppressed by dominant grass species. Furthermore, we expected that 2) the rate of flower recovery after mowing increases with site productivity as higher nutrient availability enhances plant (re)growth, and that 3) rapidly reflowering species are more prevalent in more productive grasslands with higher mowing frequencies, enhancing the recovery of flowers in these sites.

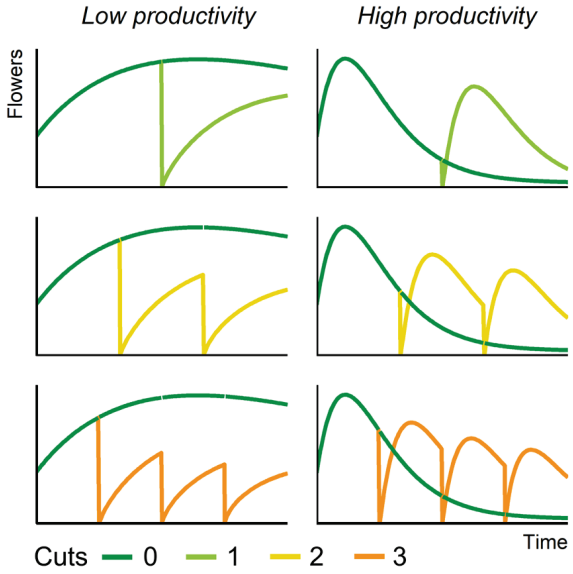

Figure 5.1 Hypothetical curves of flower richness or cover during the main growing season (± April-August) under different mowing regimes in low- and high-productivity grasslands. Mowing during the main growing season (1-3 cuts) creates a sawtooth-like flower curve as it causes complete flower losses that are followed by a flower recovery phase. Net effects of mowing across the growing season are given by the area between the flower curve for a given mowing regime and the flower curve under unmown conditions (dark green). The curves drawn here assume a gradual increase of flowers during spring at low productivity levels, but a rapid increase followed by progressive suppression of flowers at high productivity levels. The curves also assume that flower recovery after mowing follows the same trajectories but with recovery rates of 90% of the flower growth prior to each cut. These assumptions result in net losses of flowers due to mowing at low productivity levels, but net increases at high productivity levels.

Methods

5.2.1 Study design

We selected twelve mown grasslands that ranged in land-use intensity from unfertilized hay meadows that were cut twice per year, to intensively fertilized fodder production grasslands that were mown five times per year (Fig. 5.2A, Table 7D.1). This range of management intensity reflects the main grassland types that can be found across large parts of the West- and Central European lowland. Since the study sites were all situated on loess soils within one study area, differences in species composition were predominantly driven by management intensity (i.e. fertilization rate and mowing frequency). At each site, we set up a block of four plots of 2*2 meter, with a 50 cm buffer between the plots and a 25 cm buffer around the experiment (Fig. 5.2B). The plots were set up with bamboo sticks (1.2 m or 2.5 m in tall swards) and nylon rope and were clearly marked so that site managers knew to avoid them. The experiment was maintained for a 117-day period lasting from April 20th until August 15th 2023, corresponding to the main activity period of

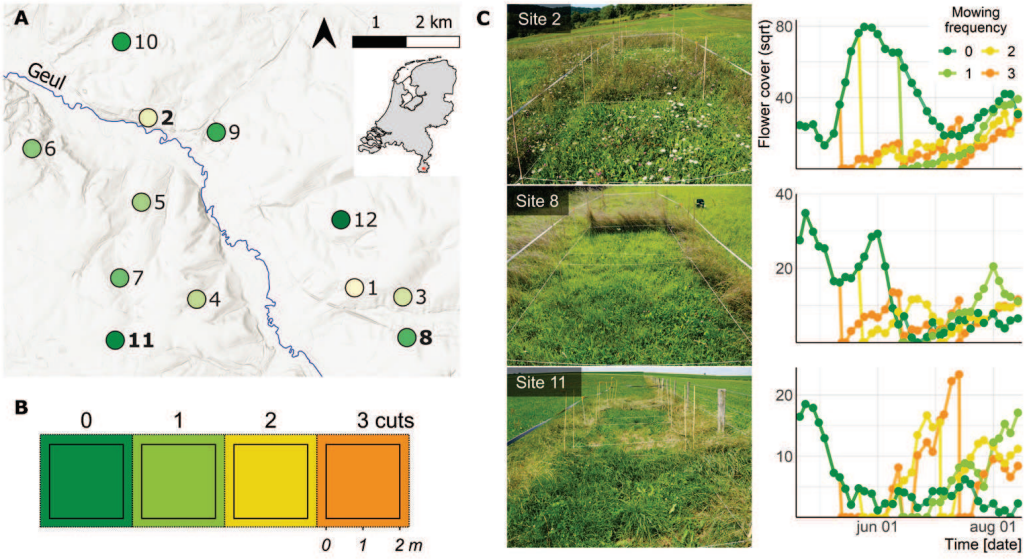

Figure 5.2 Setup and examples of the experimental fields. Panel A: Twelve sampling sites were located in a study area of approximately 6 by 8 km in the very south of the Netherlands (sites are ordered by productivity level). Panel B: At each site, we set up a block of four plots, each measuring 2*2 m with 25-cm buffer. Four mowing regimes with zero, one, two or three cuts between April 20th and August 15th were randomly allocated within each site. Panel C: Examples of experimental plots at sites with low productivity (site 2: 340 $g.m^{-2}$), medium productivity (site 8: 590 $g.m^{-2}$) and high productivity (site 11: 900 $g.m^{-2}$), with the corresponding curves of flower cover per plot measured during the experiment. Flower cover was summed over all flowering forbs and square root transformed. Data obtained prior to mowing were averaged at site level for visual reasons (see Fig. S1 for the unaveraged curves). Pictures were taken on August 14th (Site 2 & 8) and July 5th (Site 11) (photo credit: Reinier de Vries).

most grassland arthropods. During this period, dry weather in May-June induced a local precipitation deficit that peaked at ±120 mm in July, but shrunk to below-average levels (to ±60 mm) in August (KNMI, n.d.). As fertilization during this period was prevented by the plot setup, fertilizer inputs (which were applied in the form of artificial fertilizer and slurry injection) were mimicked by the application of organic fertilizer pellets (Culterra NPK 10-4-6). Application dates and effective nitrogen contents were matched with the farmers' fertilization to the specific field (Table 7D.1).

Four mowing treatments that represented the typical range of grassland defoliation regimes in the study area were randomly allocated over the four plots at each site: three cuts during the sampling period (13-14 May, 13-14 June and 14-15 July) with a 30-day regrowth period, which resembles intensive management with five cuts during the entire year; two cuts (24-25 May and 4-5 July) with a 40-day regrowth period, resembling moderately intensive management with four cuts per year; one cut (14-15 June) with a 60-day regrowth period, resembling fairly extensive management with two cuts per year (typically in June and September); and an unmown plot which reflects extensive management of grasslands mown only once a year (typically in late summer after our experiment). We mowed the plots and a 25-cm buffer zone with a brush cutter at ± 7 cm height and removed the cuttings right after mowing.

5.2.2 *Data collection*

Biomass samples were collected from randomly allocated 50*50 cm quadrants upon each mowing operation, as well as from all plots at the end of the experiment (14-15 August). Dry weights were measured after drying the samples for 48 hours at 70 °C. Productivity [$g \cdot m^{-2}$] was determined at the site level and was quantified by taking the average dry weight of the samples collected upon the first cut in each of the three plots that were mown during the experiment (i.e. on 13-14 May, 24-25 May and 14-15 June). The remaining samples were excluded because they were affected by prior mowing (follow-up cuts) or by the die-off and decay of overshoot vegetation (samples from the unmown plots collected in August). Flower surveys were conducted in every plot at intervals of three to five days during the entire duration of the experiment (34 surveys in total). Following Scheper et al. (2015), we obtained exact counts of the number of flowers for each flowering forb species, with the exception of exclusively wind-pollinated species such as *Rumex* spp. Composite flowers such as *Trifolium* and Apiaceae species were counted per head and multiplied by the estimated average number of open flowers per head. Subsequently, flower counts were multiplied by the average surface area per individual flower [cm^2] to estimate the flower area per species. For each survey we calculated plot-level flower species richness (the observed number of species) and flower cover (flower area summed over all species), which are commonly used flower metrics in ecological studies (Doublet et al., 2022; Hyjazie & Sargent, 2022; Scheper et al., 2015; chapter 4).

5.2.3 Data analyses

First, we constructed curves of flower species richness or flower cover over time by connecting the subsequent field surveys (34 points per plot), which are hereafter referred to as flower curves (see Fig. 5.2C and 7D.1). Days of mowing operations were included in the flower curves as zeroes. For each plot, the area under the flower curve (AUC) was used to determine the summed daily flower richness [species·day] or flower cover [cm^2·day] over the full season (April 20th - August 15th), and separately for late spring (May 25th - July 6th) and summer (July 6th - August 15th). These AUC metrics account for differences in the time intervals between subsequent surveys. Late spring and summer both represent periods of flower decline in agricultural landscapes (Bishop et al., 2024) and make up approximately one third of the sampling period (corresponding to the two-cuts mowing regime). The remaining third of the sampling period (April 20th – May 25th) was not analyzed separately because it largely fell before the first mowing dates, hence no effect of mowing could be expected. Next, the recovery rates of flower richness [species·day^{-1}] and flower cover [cm^2·day^{-1}] after mowing were estimated as the slope of the flower curve over a 21-day interval after each cut. This interval includes data of seven flower surveys and avoids the saturating part of flower curves after initial recovery, so that recovery could be calculated as a linear coefficient with intercept (0,0) (i.e. zero flowering right after mowing).

Second, we used linear mixed models to analyze the interactive effects of productivity (P) and mowing frequency (M) on summed daily flower richness and flower cover. Flower cover was square root transformed to limit right-skew induced by the mass-flowering of single species. Both response variables were analyzed over the full season, late spring and summer, producing six equivalent models (n=48 for each; i.e. one data point per plot per field). Each model treated M as an ordered factor (0-3 cuts) and included site as a random factor (12 levels) because mowing treatments were nested within site. To examine the responses of flower recovery, we also ran two similar linear mixed models testing the interactive effects of M and P on the recovery of flower richness and flower cover after mowing. Both recovery models (n=72, corresponding to the total number of cuts across all plots and treatments) included M as a three-level ordered factor (1-3 cuts) and included two random terms (RT), accounting for site (12 levels) and the mowing round (3 levels). For each response variable (V), we fitted four nested sub-models (V~P*M+(1|RT), V~P+M+(1|RT), V~P+(1|RT), V~1+(1|RT)) using maximum likelihood estimation with the R-package *lme4* (Bates et al., 2015). Statistical support for the individual model terms was evaluated with likelihood ratio tests and their relative importance was evaluated by ΔAIC_c and partial R^2, using R-package *MuMIn* (Bartoń, 2023). The importance of random effects was evaluated by conditional R^2 (Nakagawa & Schielzeth, 2013). Model assumptions and residual diagnostics were evaluated for each full model with the R-package *performance* (Lüdecke et al., 2021) which did not indicate problems. All analyses were performed using R 4.5 (R core team, 2025).

Last, to investigate the importance of species identity for reflowering potential we constructed flower curves for each individual species for which enough records were available (>10 records and >200 individual flower heads in total). Species-specific flower curves were drawn by averaging flower cover over the yet unmown plots across all sites and thereafter over each mowing regime separately. The surveys prior to mowing were averaged over all treatment plots that had not yet been mown because the treatments only differed after the first cut. Subsequently, mean flower cover [cm^2] was square root transformed to improve comparability among different species. The extent of flower recovery after mowing (i.e. the species' capability of producing new flowers) was quantified for each mowing regime by dividing the AUC after the first cut (the recovery phase) with the AUC of the unmown plots over the same period. To assess which factors influence flower recovery after mowing, we determined for each species the mean date and productivity at which it flowered (both weighted by the number of flowers), as well as the range of productivity levels at which it was recorded (see also De Vries et al., 2026).

Results

5.3.1 Effects of mowing on summed daily flower richness & flower cover

Measured across the full main growing season (April 20th and August 15th), summed daily flower richness increased when productivity and mowing frequency decreased, with a marginally insignificant interaction between both terms ($p = 0.053$; Table 7D.1, Fig. 5.3A). In late spring, the positive effect of reduced mowing on summed daily flower richness disappeared when productivity increased (significant interaction: Table 7D.1, Fig. 5.3B). The biggest difference in late spring occurred between the unmown and the one-cut plots, while differences ceased between more frequent mowing treatments. In summer, summed daily flower richness decreased with productivity but was not related to mowing frequency (Fig. 5.3C).

Mowing frequency significantly moderated the overall negative effect of productivity on flower cover over the full season and late spring (significant interactions: Table 7D.1, Fig. 5.3D). Flower cover in both periods increased with reduced mowing at low productivity levels, but this increase diminished with rising productivity and even became slightly negative at the highest productivity levels. In low-productivity sites, late-spring flower cover was much higher in the 0-1 cut plots, that were not mown or mown halfway this period, than in the 2-3 cut plots that had already been mown (Fig. 5.3E). In summer, flower cover had declined even at most unmown low-productive sites (Fig. 5.3F). Flower cover in this period declined with productivity but showed no relation with mowing frequency. Flower cover was less strongly affected by productivity than summed daily flower richness in each period (partial $R^2_m = 0.26$-0.46 for summed daily flower richness, 0.24-0.34 for flower cover: Table 7D.1). The recovery rate of flower richness after mowing was significantly moderated by productivity and mowing frequency (significant interaction: Table

Table 5.1. Linear mixed models relating flower responses to productivity and mowing frequency

Term	X^2	p-value	R^2_m	R^2_c
Full-season summed daily flower richness			*0.43*	*0.93*
Productivity	6.49	0.011	0.38	
Mowing	14.65	0.0021	0.03	
Interaction	7.71	0.053	0.01	
Late spring summed daily flower richness			*0.57*	*0.92*
Productivity	9.45	0.0021	0.46	
Mowing	23.81	2.7E-05	0.08	
Interaction	12.82	0.0051	0.03	
Summer summed daily flower richness			*0.28*	*0.90*
Productivity	3.95	0.047	0.26	
Mowing	4.30	0.231	0.01	
Interaction	2.84	0.42	0.01	
Full-season flower cover			*0.43*	*0.84*
Productivity	6.70	0.0097	0.34	
Mowing	9.53	0.023	0.05	
Interaction	10.52	0.015	0.04	
Late spring flower cover			*0.44*	*0.64*
Productivity	7.12	0.0076	0.24	
Mowing	9.70	0.021	0.11	
Interaction	10.19	0.017	0.09	
Summer flower cover			*0.28*	*0.83*
Productivity	3.97	0.046	0.24	
Mowing	3.11	0.37	0.01	
Interaction	6.75	0.080	0.03	
Recovery flower richness			*0.39*	*0.70*
Productivity	7.63	0.0057	0.31	
Mowing	11.91	0.0026	0.08	
Interaction	6.03	0.049	0.02	
Recovery flower cover			*0.27*	*0.72*
Productivity	3.85	0.050	0.19	
Mowing	12.83	0.0016	0.07	
Interaction	2.45	0.29	0.01	

Summed daily flower richness, flower cover (square root transformed) or recovery after mowing were related to productivity [$g \cdot m^{-2}$] and mowing frequency (0-3 cuts for richness & cover; 1-3 cuts for recovery) across 12 sites. Flower richness and cover were measured over the full sampling season (20-4 to 15-8), late spring (25-5 to 6-7) and summer (6-7 to 15-8). Recovery was defined as the linear increase of flower richness or cover during 21 days after mowing. R^2_m indicates the predictive power of the fixed model components, R^2_c includes the random terms (site for richness and cover, site + mowing round for recovery).

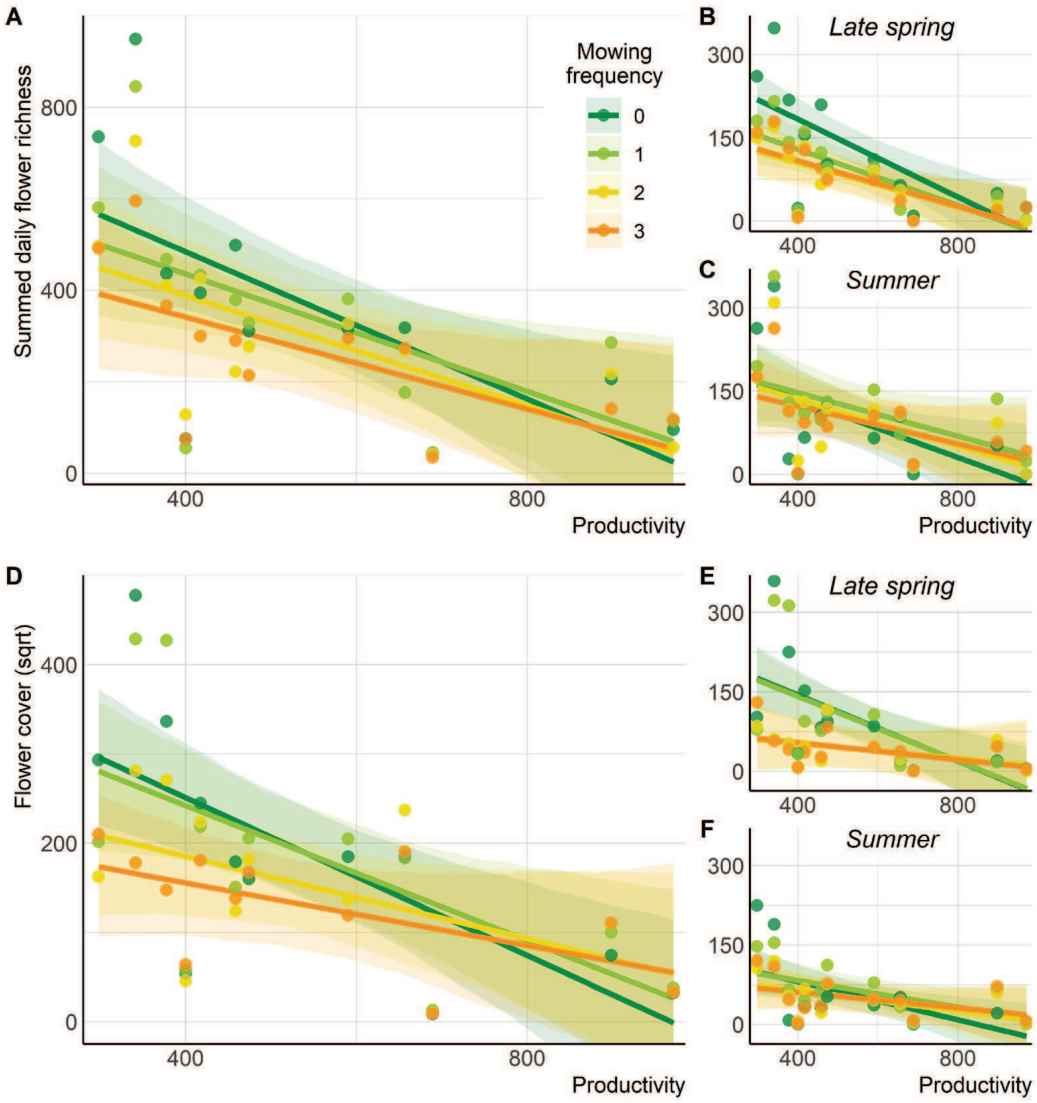

Figure 5.3 Summed daily flower richness [species·day] (A-C) and flower cover [cm^2·day] (D-F) in relation to productivity [$g \cdot cm^{-2}$] and mowing frequency (0-3 cuts between 20-4 and 15-8) in mown grasslands. Both flower variables were determined over the full season (A & D) and over late spring (25-5 to 6-7: B & E) and summer (6-7 to 15-8; C & F) by the area under the flower curve (see Fig. 5.1). Flower cover was square root transformed.

7D.1, Fig. 5.4A). The recovery rate increased when productivity declined and at low productivity levels, recovery increased further when the mowing frequency rose from one to 2-3 cuts. The recovery rate of flower cover was rather poorly explained by the model (R^2_m = 0.27) but also showed a decline with productivity and increase with mowing frequency (no significant interaction: Table 5.1, Fig. 5.4B). Again, the recovery rate was increased on the plots that were mown 2-3 times compared to plots that were mown once by June 13th-15th. The second cut of the three-cuts

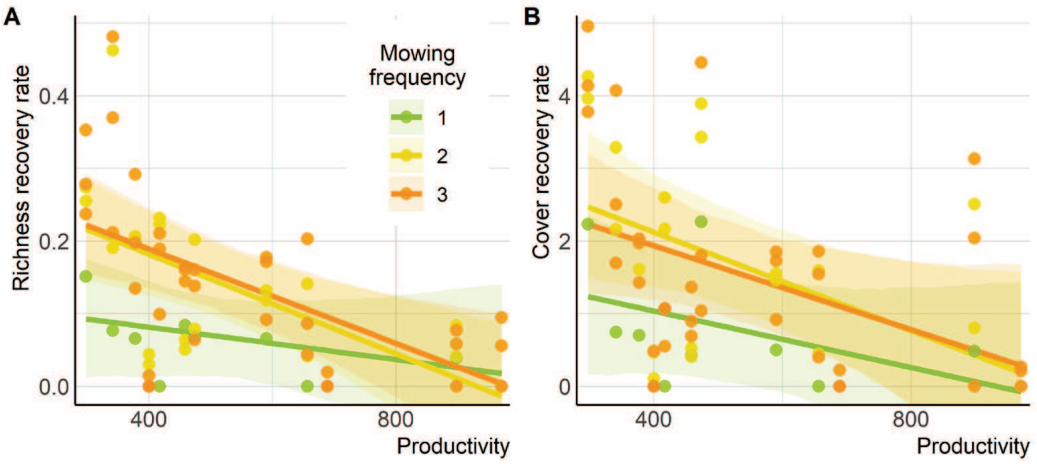

Figure 5.4 Recovery rates after mowing for flower richness [species·day^{-1}] and flower cover [cm^2·day^{-1}] in relation to productivity [g·cm^{-2}] and mowing frequency. Recovery was defined as the linear increase of flower richness or flower cover during 21 days after mowing. The number of recovery estimates per site corresponds to the number of cuts (1-3) and was modelled as a second random effect, next to site.

regime was also conducted on June 13th-15th, but the recovery rates after this cut showed a similar difference from the one-cut regime (Fig. 7D.2) and were not different from the other two cuts of the three-cuts regime.

5.3.2 Effects of mowing on individual flowering species

We recorded a total of 60 different flowering species across all sites. Three-quarters of all species were centered at below-average productivity levels and 29 species were found only at these sites, whereas 12 species (20%) were found exclusively at sites of above-average productivity (Table 7D.2). In early spring, late spring and summer, total flower cover over all sites was dominated (58-67%) by different pairs of species (*Taraxacum* agg. and *Rhinantus alectorolophus*, *R. alectorolophus* and *Leucanthemum vulgare*, *Daucus carota* and *Trifolium repens* respectively). For 34 species data availability was sufficient for species-level analyses. These analyses highlighted the large differences between species, which can be broadly divided in groups of species that fully or partly reflowered after mowing and species that recovered poorly (Table 7D.2, Fig. 5.5). Poorly recovering are species for which reflowering after mowing did not exceed 5% of their flower cover on unmown plots over the same period, partly recovering species reached 5-100% of their flower cover on unmown plots, and for fully recovering species reflowering after mowing exceeded their flower cover on unmown plots.

Poorly recovering species were strongly affected when mowing occurred during or prior to their main flowering peaks. The biggest losses of flower cover were found for *R. alectorolophus*, *L. vulgare* and *Centaurea jacea*, that all flowered in later spring or summer. On the other hand, poorly recovering species that flowered early

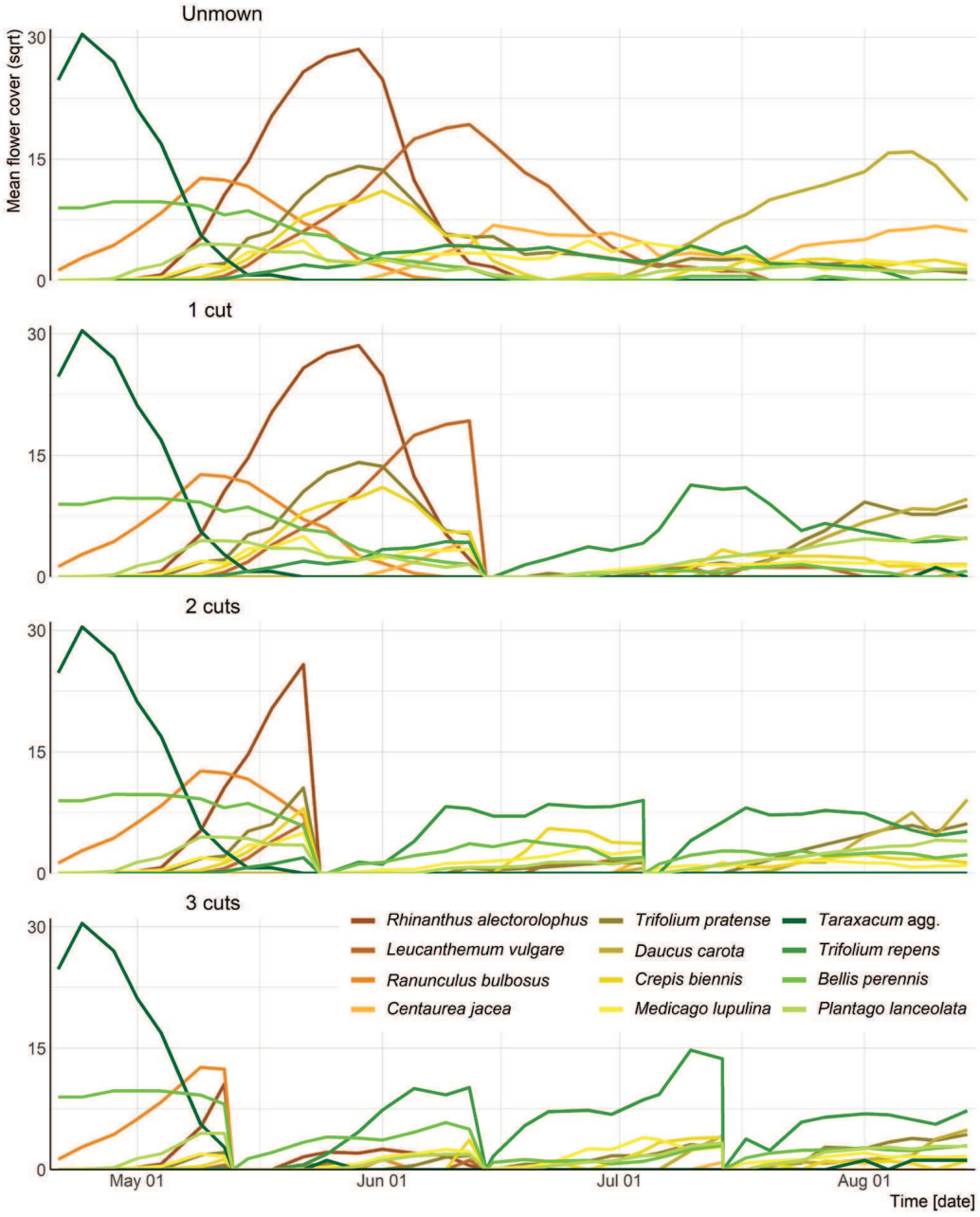

Figure 5.5 Flower curves of the twelve most important flowering species, which all contributed >1% to the total flower cover over all sampled grasslands. To assist the visual comparison of species and mowing regimes, flower cover was averaged over all unmown plots prior to mowing, and subsequently over each mowing regime separately. Mean flower cover [cm^2] was square root transformed. Species are colored by abundance (darker colors represent a higher share of total flower cover) and by the extend of flower recovery after mowing (see Table S2): poorly recovering species are colored orange (recovery <5% of flowering on unmown plots), partly recovering species are colored yellow (recovery 5-100%), and fully recovering are colored green (recovery >100%).

and therefore had largely finished flowering by the time that the first plots were mown (e.g. *Ranunculus*, *Vicia* and *Veronica* species) experienced relatively small total flower losses under the tested mowing regimes. Poorly recovering species with a relatively late flowering phenology (± centered past June 1st) were all confined to low-productivity grasslands. Early flowering was common among species characteristic of high-productivity grasslands, such as *Taraxacum* agg.

The flower cover of well-recovering species in plots that were cut once in June often matched their flower cover in unmown plots, but more frequent mowing allowed only partial recovery for most species. Among partly recovering species, late-flowering species such as *D. carota*, *Medicago lupulina* and *Lotus corniculatus* showed the largest decrease in flower cover relative to unmown plots. However, for some species with flowering peaks in spring (e.g. *Crepis biennis*, *Plantago lanceolata* and most notably *Trifolium pratense*), mowing resulted in prolonged flowering periods and increased flower cover during summer. Only *T. repens*, *Bellis perennis* and *Capsella bursa-pastoris* substantially increased flowering under more frequent mowing regimes. *T. repens* and *B. perennis* represented 64% and 10% of the total flower recovery under the most frequent mowing regime.

Discussion

Mowing of herbaceous vegetation is often seen as undesirable because it removes flowers and therefore negatively affects arthropod communities. But in temperate managed grasslands, mowing is an integral part of the disturbances that prevent these habitats from turning into forests. This study examined the effects of mowing frequency on the flowering of grassland forbs and tested whether these effects depend on productivity. Measured across the main growing season (mid-April to mid-August), flower cover increased when the frequency of mowing was reduced in low-productivity grasslands, but not in grasslands of higher productivity. Summed daily flower richness increased with decreasing mowing frequencies and productivity. The effects of mowing on summed daily flower richness and flower cover were the largest in late spring but disappeared in summer. Forbs reflowered faster after mowing at higher cutting frequencies and at lower productivity levels, but at high productivity the recovery of flower richness did no longer increase with mowing frequency. The potential for recovery after mowing varied strongly between species and only a few species recovered fully under frequent mowing regimes.

5.4.1 Effects of mowing on flower richness and flower cover

Our results indicate that if highly productive grasslands are not mown, both flower richness and flower cover decline rapidly after early spring, which means that reducing the mowing frequency does not enhance flowering in these habitats. This is most likely due to the increase of competition for light with increasing productivity, which benefits fast-growing grasses at the expense of flowering forb species (Borer et al., 2014; Harpole et al., 2016; Rodríguez-Rojo et al., 2017).

Intensively managed high-productivity grasslands supported only a limited number of forb species that mostly flower early in spring, before the first cut (April to early May: see Table 7D.2 and Busch et al., 2019). *Taraxacum* agg. was the most important early spring species in this study (Fig. 5.5). Contrastingly, low-productive grasslands typically support a wide range of forb species that flower consecutively (Doležal et al., 2019). These sites can therefore stay rich in flowers across the entire growing season from April to August, with peaks in flower cover corresponding to the phenology of locally dominant forbs. Our results show clearly that early mowing in these grasslands has strong negative impacts on flower cover and flower richness. The shift in forb species composition with productivity most likely explains the productivity-dependency of the effect of reduced mowing on flower cover and, although less pronounced, summed daily flower richness.

We found the biggest effects of mowing on flower cover and richness, with the strongest productivity dependency, during late spring (May 25th - July 6th). This is not surprising since the first cuts of our mowing treatments also fell shortly before or during late spring (i.e. on May 13th, May 25th and June 15th), and the biggest loss of flowers can be expected shortly after mowing. Moreover, the strong interaction between mowing frequency and productivity follows logically from the shift in flowering phenology with productivity. On unmown plots, late spring overlapped with major flowering peaks in low-productive sites and with secondary flowering peaks in medium-productive sites, whereas highly productive sites had already largely lost their flowers (Fig. 7D.1). The loss of flowers in high-productivity grasslands and the widespread mowing of medium-productive hay meadows by the onset of June can explain the decline of landscape-wide flower availability in June (Bishop et al., 2024). Landscape-wide flower availability generally remains low during summer as the regrowth of flowers after mowing is rarely comparable to flowering prior to mowing. But also at unmown plots, the summed daily flower richness and flower cover dropped during summer (July 6th - August 15th) in all but the two least productive sites in this study. The progressive suppression of flowering forbs by grasses under unmown conditions and the gradual recovery of flowers after mowing can explain the lack of effects of mowing on both flower richness and flower cover during summer.

5.4.2 *Effects of mowing on flower recovery*

Productivity also influenced how fast grassland flowers returned after mowing. We had expected that flower recovery would accelerate at higher productivity levels because a higher nutrient availability would facilitate faster regrowth, but our results indicate that flowers return faster in low-productivity grasslands than in high-productivity grasslands (Fig. 5.4). Due to the reduction of recovery rates with productivity, flower cover and richness still declined with productivity in summer when all flowers on mown plots represent regrowth. Reflowering could thus not nearly make up for the strong declines of flower cover and especially flower richness with productivity. This is not surprising given the general lack of flowers in the

grass-dominated swards of high-productivity grasslands, which are usually mown four to five times per year.

A plausible explanation for both the decrease of flower recovery rates with productivity and their increase with mowing frequency (in interaction for the recovery of flower richness) is the effect of competition for light on sward structure. Increased productivity and reduced mowing both allowed the development of tall, dense swards where forb species were either outcompeted or growing taller. When such swards are mown, a larger proportion of a plant's biomass is removed and it may need more time to recover. Contrastingly, low productivity levels and frequent mowing suppress competition for light and therefore allow low-statured forbs to develop close to the ground. These forbs are left largely intact by mowing and can start flowering again within days after mowing. Alternatively, the recorded increase of flower recovery rates with mowing frequency could have been influenced by water stress because the cut in June—after which recovery was the slowest—coincided with dry weather conditions (Klimešová et al., 2010; KNMI, n.d.). However, these dry conditions should then also have impacted flower recovery of the three-cuts regime, which was mown simultaneously. This was not the case (see Fig. 7D.2), which indicates that weather conditions had a minor influence on flower recovery in this experiment.

5.4.3 Effects of mowing on individual species

The trends in flower cover of individual species support our expectation that floristic composition strongly determines the productivity-dependent effects of mowing on grassland flowers. In line with the results of Busch et al. (2019), most of the forb species that we observed showed a limited ability to recover after mowing and occurred predominantly at lower productivity levels, where mowing typically occurs maximum twice per year. Species with a late phenology and poor ability to recover after mowing were even fully confined to low-productivity grasslands. Contrastingly, the species found at high-productivity sites either flowered early or showed a rapid recovery after mowing. *Trifolium repens* was the species that reflowered most rapidly and abundantly under frequent mowing regimes, and the presence this species essentially determined whether frequent mowing of high-productivity sites led to net increases of flower cover (see Fig. 5.5 and Fig. 7D.1). But although *T. repens* strongly dominated the flowering at high-productivity sites after mowing, in absolute terms it was still more abundant and more rapidly reflowering in lower-productivity grasslands.

The extensive mowing regime with a single cut in June allowed substantially more species to reflower fully after mowing (i.e. flower cover after mowing equaled the flower cover at unmown plots over the same period). The slower flower recovery under this mowing regime was compensated by the longer recovery period after mowing. This mowing regime even enhanced the flower cover of several species during summer, especially of *T. pratense* which is an important resource for

bumblebees (Goulson et al., 2005; Rundlöf et al., 2014). At the end of our experiment, the flower cover of other Fabaceae, *Plantago lanceolata* and *D. carota* on the single-cut plots exceeded their cover on the unmown plots while these species were still recovering, which suggests a further increase after the experiment during late August and September (see Fig. 5.5). This pattern aligns with the results of Johansen et al. (2019) who found that from August onwards, flowering on hay meadows that were mown in June exceeded the flowering of hay meadows that were mown later or left uncut. Furthermore, these results suggest that advancing the timing of the spring cut could enhance flower recovery rates in hay meadows where species like *T. pratense*, *P. lanceolata* and *D. carota* are dominant, since earlier mowing would reduce light competition and seed set. Future studies should examine whether advanced spring cuttings (e.g. between mid-May and early June) can enhance flowering in summer and after mid-August, and which forb species determine this.

5.4.4 Multi-year changes

Our single-year experiment did not account for adaptation of the grassland forb community to new mowing regimes over multiple years, but plant communities will inevitably change following changes in defoliation regimes. Kleijn & Scheper (2025) have shown that over multiple years, frequent mowing (3-4 cuts per year, which resembles two cuts between April and August) promotes the species richness of vegetations dominated by two or three tall forb species. Such changes could occur in one or two years in medium-productive grasslands that are currently mown twice per year, providing that seed resources are available. However, frequent mowing is already standard in highly productive grasslands, yet they remain poor in forb species and dominated by swiftly regrowing grasses. Reducing productivity is indispensable to suppress dominant species and enhance flower richness in these grasslands (chapter 4).

5.4.5 Practical implications

This study indicates that to optimize flowering in meadows or grassland-like habitat elements such as road verges, mowing regimes should be adapted to the phenology of the local forb species. Since most forb species are disadvantaged under strong competition for light, the potential benefits of reduced mowing dissipate when productivity increases. Resultantly, mowing reduction initiatives such as No Mow May can have no or even adverse effects on flowers in highly productive sites. Flower cover can be enhanced in such sites by promotion of the few forbs that thrive under frequent mowing, notably *T. repens*. This is a low-cost intervention that could be applied across large areas and can even pay off for farmers, because *T. repens* is a nitrogen-fixing species that can partly replace fertilization (Harris & Ratnieks, 2022; chapter 2). Increasing the cover of *T. repens* can improve floral resource availability in late spring and summer for a limited set of pollinators, such as common bumblebees. However, promoting a single forb species in highly disturbed

habitats is unlikely to provide wider biodiversity benefits (Beye et al., 2022; Rakosy et al., 2022).

At lower productivity levels, there is substantially more potential to enhance flowering throughout the growing season by adjusting current mowing regimes. Most grasslands of low-to-medium productivity, such as agri-environment schemes, are currently mown integrally at fixed times in June and September (Humbert et al., 2012). This study indicates that if site managers would like to promote flowers, they should avoid integral mowing during the main flowering peaks of poorly recovering species. By maintaining uncut refuges or delaying the first cut until late summer in low-productivity sites, they can preserve flower-rich habitats in June and July and support late-flowering species such as *Centaurea spp*. (Buri et al., 2014; Révész et al., 2025). At the same time, (partial) mowing in spring can promote reflowering in summer if the right forb species are present. Spring cuttings can be especially beneficial at medium-productive sites where they can prevent domination of grasses and potentially enhance forb species richness in the long term (Kleijn & Scheper, 2025). Moreover, advancing spring cuttings can benefit farmers by improving the quality of hay yields, which can potentially compensate for areas left uncut during summer (Boob et al., 2019). Variation in mowing regimes, with first cutting dates ranging from late May to late September, reflects the practices that traditionally shaped Europe's biodiversity-rich grassland landscapes (Johansen et al., 2019). Most grassland biodiversity and wildflowers are nowadays sustained by agri-environmental schemes and nature conservation schemes (De Vries et al., 2026; chapter 4). Through regional coordination, such schemes can restore spatial variation in extensive mowing regimes at the landscape level, which can support the flowering of multiple forb species throughout the growing season.

Acknowledgments

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Discussion

Grassland ecosystems support critical biodiversity and ecosystem services, but their degradation is widespread and ongoing. Since many grasslands are shaped by human management, land use intensification is often the principal driver of degradation in grassland ecosystems. This thesis investigated constraints and opportunities for the restoration of temperate managed grassland ecosystems (Fig. 6.1). Two chapters investigated the implications of land use intensification for grassland biodiversity and ecosystem service delivery, and whether their restoration contributes to or trades off with the income of farmers. Next, two chapters examined the potential of habitat quality indicators and site-level management adjustment to improve the effectiveness of grassland restoration schemes. In chapter 2, grassland productivity was found be primarily driven by management intensity with only a minor contribution of biodiversity-based ecosystem services. Farmer income, which depends on productivity, therefore traded off strongly with the delivery of wider ecosystem services, that are primarily of public concern. This implies that societal support for public good delivery is critical to the restoration of grassland ecosystems. Chapter 3 explored the effects of land use intensification on grassland arthropods in further depth, and found declines of species richness but not of overall arthropod abundance. A novel approach to analyse the responses of individual species revealed that up to 85% of all species declined when land use intensified, but a small set of widespread species profited from increasing productivity. This suggests that a low number of species can keep up total arthropod numbers in intensively used habitats. Moreover, by explicitly considering species identity, these analyses revealed stronger impacts on biodiversity than traditional richness and diversity metrics did. Unfortunately, thorough biodiversity inventories that reveal responses of individual species are extremely laborious. Chapter 4 showed that flower richness can be used to rapidly assess the quality of grassland habitats for a wide range of arthropod groups and across multiple land use types. Flower richness can therefore be used to evaluate effects of restoration measures such as biodiversity-friendly management. Chapter 5 tested how reduced mowing regimes influenced the flowering of grassland forbs at different productivity levels. Reduced mowing promoted flowers only at lower productivity levels and not at high productivity levels, whereas spring mowing could enhance reflowering in late summer. Flowering across the growing season can therefore be optimized by tailoring mowing regimes to local productivity levels and forb species composition. Overall, this thesis showed that managed grasslands hold much potential to restore biodiverse ecosystems and the public goods that they deliver, but that restoration success requires a drastic reduction of current agricultural land use intensity. This thesis presented both socio-economic and management approaches to improve restoration outcomes.

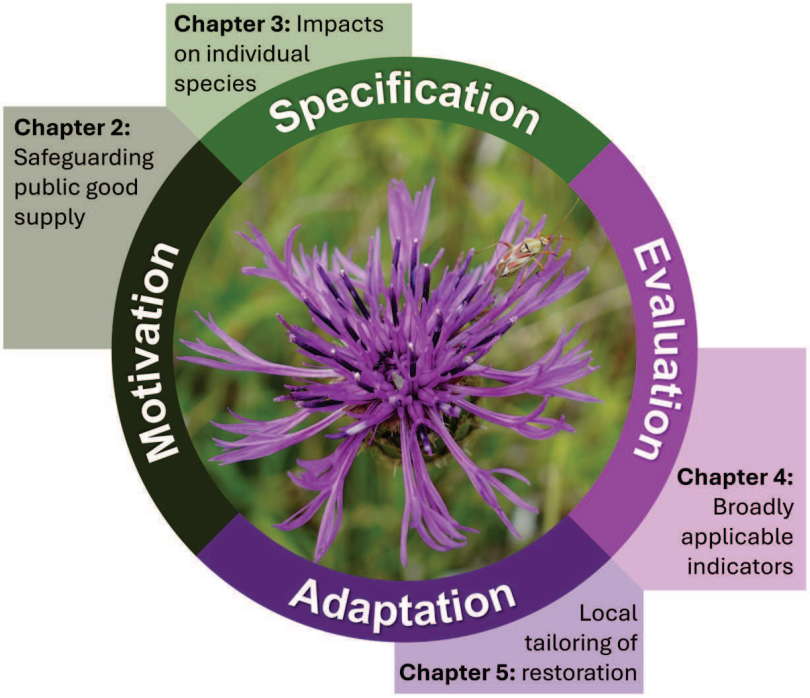

Figure 6.1 This thesis addresses the implications of land use intensification for grassland ecosystems (chapter 2-3) and explores approaches to improve restoration management (chapter 4-5). Chapter 2 showed that safeguarding public goods forms the main motivation for ecosystem restoration. Chapter 3 specified how land use intensification drives species loss. Chapter 4 showed that habitat quality indicators can be used to evaluate restoration efforts efficiently, and chapter 5 showed how this enables adaptation of restoration strategies to site-specific conditions. Photo: A *Centaurea scabiosa* flower is visited by three insect orders: a true bug (Hemiptera), a beetle (Coleoptera) and ants (Hymenoptera) (photo credit: Reinier de Vries).

The multidimensional importance of grassland ecosystems

Grassland ecosystems support a high percentage of Europe's species diversity, including disproportionally many threatened species and regional endemics. This biodiversity is to a large extend dependent on managed grassland habitats (Dengler et al., 2014; Van Swaay et al., 2025). This thesis confirmed this and recorded regionally important levels of plant and arthropod diversity on managed grasslands (chapters 3-4). Moreover, chapter 2 underscores that managed grasslands can sustain multiple ecosystem functions that are at the basis of environmental stability at global and regional levels, such as carbon sequestration, nutrient retention, water retention and erosion control (Bardgett et al., 2021; Bengtsson et al., 2019). Grassland management is therefore important to restore globally breached boundaries of climatic stability, land and freshwater use, nutrient cycling and biosphere integrity (Rockström et al., 2025; Sakschewski et al., 2025). The role of grasslands in sustaining biodiversity and ecosystem functioning is especially important in regions with a high share of agricultural land.

However, the expansion of highly intensive land use strategies has eroded the capacity of managed grasslands to sustain this multitude of ecological functions. By optimizing one particular function, livestock keeping, grassland management became a driver of widespread ecosystem degradation. The prevailing narrow focus of grassland management on maximizing the production of livestock products is therefore increasingly controversial (Rockström et al., 2025). All chapters of this thesis highlighted that intensified grassland management causes local biodiversity declines, driven by habitat and resource loss. This aligns with many previous studies (for example: Eichenberg et al., 2021; Ekroos et al., 2020; Gossner et al., 2016; Newbold et al., 2016). Chapter 2 showed that in parallel to this local biodiversity loss, intensively used grasslands fall short in sustaining ecosystem services of public importance, and instead cause nutrient spillover to surrounding landscapes (Bardgett et al., 2021; Nijssen et al., 2017). Resultantly, land use intensification on grasslands poses increasing threats to human well-being in the future.

Ecosystem restoration is a public obligation

More and more publications and organisations call for the re-establishment of more extensive farming strategies that provide a wider range of services to society. Among these is a large number of agro-ecological studies that emphasize the benefits of biodiversity-based ecosystem services for agricultural production, such as productivity gains due to complementarity effects among plant species, pest control by natural enemies, and crop pollination (Albrecht et al., 2020; Dainese et al., 2019; Schaub et al., 2020). It is often suggested that such services can create 'win-win outcomes' for biodiversity and agricultural production (Bommarco et al., 2013; Fischer et al., 2017; Pywell et al., 2015). But why then, have agricultural sectors consistently moved away from management that fosters ecosystem services? And why are farmers so reluctant to adopt the ecological restoration strategies that researchers and public organisations propose?

Agro-ecological approaches to farming have to compete with the highly effective use of external inputs. Plant growth can be boosted with fertilizers, pests can be controlled with pesticides, and pollinator colonies can be hired and placed, right at the specific location and time where their services are needed. These inputs cost money, but ecological solutions also come with maintenance costs and opportunity costs that arise from associated constraints to agricultural management. In chapter 2, this thesis showed that under current economic conditions, the opportunity costs of reducing management intensity (notably of restricting fertilization) strongly outweigh the contributions of biodiversity-based ecosystem services to the productivity of agricultural grasslands. Few consumers are motivated to compensate productivity losses by paying higher prices for biodiversity-friendly products. Resultantly, the opportunity costs of management for biodiversity induce a strong trade-off between the income of farmers and the restoration of public goods. This trade-off deters most farmers and erodes the economic perspective of the few farmers who are still intrinsically motivated to do so.

Agro-ecology should therefore reconsider its narrative focusing on ecosystem's contributions to agricultural production. While these contributions are often not decisive to farmers, **safeguarding public goods** provides a much stronger rationale for ecosystem restoration. This perspective also shifts responsibilities. Currently, by emphasizing the importance of ecosystems for agricultural production rather than for public goods, it is implied that farmers are primarily responsible for the restoration of farmland ecosystems. Conversely, acknowledging that public goods form the primary motivation for ecosystem restoration also means that society should provide alternative means of income to farmers. Farmers can only invest in public goods if they provide a stable source of income, rivalling the economic margins of marketable agricultural products. Revenues for public goods can be provided by public means or by companies as part of sustainability reporting. Such revenues would create numerous opportunities for farmers to develop new business models. This can halt the ongoing loss of smaller farms and may temper frictions between farmers and society, which arose in recent years in large parts of Europe (van der Ploeg, 2020). Moreover, investments in public good restoration are likely to prevent considerably higher societal costs that result from their degradation (Dasgupta, 2021). For example, restored grasslands can act as sources of clean water and prevent higher costs for purification of polluted water. The restoration of grassland ecosystems *can* therefore earn itself back from a long-term societal perspective.

Understanding biodiversity responses to land use intensification

This thesis found stronger trade-offs with farmer income for plant and bee richness than for other public goods (chapter 2), indicating that biodiversity conservation is least compatible with modern farming. This result aligns with previous studies that quantified effects of agricultural intensification on multiple functions of European managed grasslands, of which biodiversity conservation was deteriorated most severely (Le Provost et al., 2023; Schils et al., 2022). Even global assessments indicate that the impact of agriculture on biodiversity is causing one of the strongest transgressions of planetary boundaries, with fundamental consequences for future human well-being (IPBES, 2019; Jaureguiberry et al., 2022; Rockström et al., 2025). It is thus crucial to understand thoroughly how agricultural practices affect biodiversity, which taxa and communities are most affected, and what determines restoration success. In European grasslands, plants and arthropods were found to be the most deteriorated taxa when agricultural land use intensified (Gossner et al., 2016; Le Provost et al., 2021). However, our understanding of biodiversity change still has important deficiencies, particularly with respect to arthropods. Chapters 3 and 4 of this thesis aim to improve our understanding of the effects of land use intensification on grassland biodiversity and arthropods in particular. Both chapters build upon previous studies that showed that spatial gradients can provide detailed insights about specific drivers of biodiversity change (Blüthgen et al., 2022; Cooke et al., 2025; Wagner, 2020). Chapter 3 addresses the need of rigorous inventories to overcome shortcomings that persist in most current biodiversity assessments,

while chapter 4 addresses the need of scalable approaches to assess local biodiversity levels more widely.

At first, chapter 3 revealed shortcomings of the most widely used biodiversity metrics, species richness (alpha-diversity) and dissimilarity of communities (beta-diversity). Many studies use (abundance-based) dissimilarity metrics such as turnover to overcome the well-known limitations of simple species richness comparisons, which ignore changes in population size and community composition (Chase & Knight, 2013; Hillebrand et al., 2018; Kuczynski et al., 2023). Dissimilarity metrics have shown that land use intensification can homogenize biotic communities (e.g. Gossner et al., 2016), but they often show weak or inconsistent trends that are difficult to interpret (Dornelas et al., 2023; Keck et al., 2025). Uncertainty arises because it is usually impossible to differentiate between contrasting ecological processes that can create dissimilarity. In chapter 3, the uncertain outcomes of dissimilarity analyses were compared with a **species-level approach** to measure biodiversity change. This approach improved interpretability substantially and revealed that across all sampled arthropod groups, land use intensification retained a subset of widespread species while filtering out (much) larger numbers of species that do not tolerate intensification. This filtering caused more drastic biodiversity losses than that was shown by standard alpha- and beta-diversity analyses, since arthropod communities homogenized with increasing land-use intensity (Clavel et al., 2011; McKinney & Lockwood, 1999). Species-level analyses can also show which species are most vulnerable to decline or extinction (Chisté et al., 2016), which remains poorly known for many arthropod groups. However, declines of individual species are only picked up by rigorous inventories of species populations, which are sparsely available for most arthropod groups. Consequently, hardly any meta-analyses have assessed species-level responses to land use change (but see Newbold et al., 2018). It is plausible that many studies that conducted less sensitive analyses have actually underestimated biodiversity loss.

Second, the effects of drivers of biodiversity change are often non-linear. Both for species richness (chapters 2 and 3) and distributions of individual species (chapter 3), the biggest impacts of land use intensification occurred at low-to-medium intensity levels, compared to the medium-to-high intensity range that is most common in modern agricultural landscapes. Previous studies on grassland plant and arthropod richness have found similar exponential declines with land use intensity (Allan et al., 2014; Beckmann et al., 2019; Kleijn et al., 2009). However, **reference habitats** such as formally protected grasslands have often already experienced certain degrees of land use intensification and habitat degradation (Dengler et al., 2014). Exponential relationships amplify the risk that studies underestimate biodiversity change because they rely on reference habitats that have already undergone biodiversity loss. When undegraded reference habitats and historic reference data are both lacking (as in most intensively farmed regions respectively for most arthropod groups), assessments of biodiversity change are impaired to an unknown degree (Wagner, 2020). This thesis has explicitly tested non-linear

relationships and surveyed the widest available gradient of land use intensity in managed grasslands. This gradient included some of the best-preserved semi-natural grasslands that exist in the Netherlands, where species-rich vegetation types were successfully maintained and restored (Willems, 2001). This allowed thorough assessments of biodiversity change at low-to-medium land use intensity levels.

At the same time, the Netherlands has experienced severe degrees of regional species extinction over multiple decades (Van Strien et al., 2016, 2019). It is impossible to reconstruct how this has affected species assemblages for most arthropod groups, but historic butterfly data suggest that baseline shifts may be severe (Van Strien et al., 2019). Regional extinctions are likely to reduce the 'tail' of losing species in regional species assemblages, as presented in chapter 3. Therefore, similar standardized data collected in comparable landscapes that experienced less environmental degradation may provide a way to estimate baseline shifts. When landscapes are closely comparable, species can be expected to occur at similar land use intensity levels, and the presence of additional losing species in less degraded regions may reflect local extinction rates in more degraded regions —especially if historic records of these species exist. In chapter 3, we provisionally compared our data with studies from a less intensively farmed region in central Germany (Chisté et al., 2016; Heuss et al., 2019), which indeed recorded losing species that disappeared in our study area. The sampled groups (Orthoptera and Formicidae) were too species-poor to allow estimation of regional extinction rates in our study area. However, such estimates could potentially account for baseline shifts in regions where reference habitats experienced historic biodiversity loss.

By analyzing simplified responses such as species richness and by sampling incomplete environmental gradients or already degraded reference habitats, many ecological studies probably underestimate the biodiversity losses caused by drivers such as land use intensification. Scientists should consider these risks carefully even when they cannot avoid them. This is particularly important in heavily altered systems such as modern agricultural landscapes. However, many agro-ecological studies do not include any reference habitats as positive control. It is relatively easy to establish significant richness increases in comparison to strongly impoverished conventional agricultural fields (i.e. negative control), from which perspective simple restoration measures in simplified and intensively used agricultural landscapes appear effective (Marja et al., 2019; Scheper et al., 2013). But without positive control, it is impossible to judge to what extend restoration measures succeed in restoring local ecosystems and species assemblages. This thesis showed that most arthropod species depend on lower productivity levels than those typical for restoration schemes in agricultural landscapes. This thesis is therefore a plea for rigorous biodiversity inventories of multiple arthropod groups across a wide range of locations, explicitly including the best available reference habitats, and enabling comparison with other landscapes.

Unfortunately, rigorous arthropod surveys and species-level analyses depend on laborious counting and identification work. Genetic sequencing can only relieve this burden when it becomes feasible to reliably assess population sizes, and even then, data collection will be subject to field constraints such as capacity and weather conditions. These constraints restrict the spatial coverage and temporal resolution of biodiversity data severely. Thorough biodiversity inventories should therefore be paired with more rapid and large-scale assessments of generalizable biodiversity indicators. **Habitat quality indicators** are promising candidates for such assessments because they can often be measured more efficiently than biodiversity itself and because habitat deterioration is the most important direct cause of biodiversity loss (Jaureguiberry et al., 2022). Chapter 4 of this thesis showed that in grassland habitats, flower richness can be used as a broadly representative indicator of habitat quality for plants and arthropods. Flower richness reflected the species richness of multiple taxonomic groups across a wide land use intensity range and even reflected seasonal changes in arthropod richness. Nevertheless, general indicators are unlikely to accurately reflect the distribution of individual species. Habitat quality metrics like flower richness should therefore complement detailed inventories of threatened species and habitats.

Informing restoration management

Restoration of extensive grassland management practices, e.g. by restricting fertilization and harvesting frequencies, forms one of the most widely implemented ecological restoration measures in agricultural landscapes. Such measures have been supported by the European Union since 1992 as agri-environment schemes (Batáry et al., 2015). The high diversity of grassland species and the relatively large area and long duration of restoration measures create a high potential for grassland restoration schemes to support biodiversity and ecological processes. However, most restoration schemes establish medium-productive grasslands that support more species than intensive agricultural grasslands, but are still too productive for most plant and arthropod species (chapters 3-5). Previous studies have shown that the effects of Europe's agri-environment schemes are variable and not enough to curb the ongoing ecological degradation of agricultural landscapes (Batáry et al., 2015; Kleijn et al., 2011; Pe'er et al., 2022). Improving the effectiveness of restoration schemes is thus urgent. It is expected that their effects can improve if restoration measures would be based on local evidence instead of general one-size-fits-all approaches, but this requires structural monitoring of biodiversity outcomes (Herzon et al., 2018; Pe'er et al., 2022). This thesis discusses the potential of using habitat quality indicators as biodiversity evaluation tools (chapter 4) and tests whether they can direct site-specific adjustments of restoration practices (chapter 5).

Chapter 4 showed that using habitat quality indicators as **evaluation tools** can help resolve a critical constraint to improved restoration management: knowing what biodiversity outcomes are actually achieved at which locations. While it is

unfeasible to monitor the width of grassland species frequently across large areas, habitat quality indicators such as flower richness can be assessed at a considerably greater spatial extent and temporal resolution (chapter 4). Using innovations such as participatory data collection, image recognition and remote sensing, flower surveys could potentially even be enrolled across all grassland restoration schemes (Dickinson et al., 2010; Gonzales et al., 2022; Mäder et al., 2021). This means that they can be used to assess restoration success, tailor management decisions, and provide rewards for achieved results. Habitat quality indicators can therefore make critical contributions to new policy approaches that seek to introduce result-based payments, which should motivate farmers to improve restoration outcomes (Herzon et al., 2018). For example, flower richness could form a Key Performance Indicator (KPI) for the evaluation of restoration outcomes in grasslands (Kleijn et al., 2020). KPI's should measure the quality of restored habitats in order to improve current agri-environment schemes, that only assess the area of restored habitats (Fijen et al., 2025; Herzon et al., 2018). Since flower richness can be quantified from individual fields up to entire regions, they can facilitate habitat quality assessments at varying scales and inform decisions of individual farmers, cooperatives and governments.

Lacking effective evaluation tools, current agri-environment schemes prescribe general measures that may not be optimally suited to local conditions (Batáry et al., 2015) and may suppress habitat heterogeneity at the landscape level (Johansen et al., 2019). Habitat quality indicators can be used to **tailor restoration management** to local conditions and to enhance habitat heterogeneity. Chapter 5 of this thesis tested if restoration practices can be adjusted to promote flowers in individual fields. Indeed, the effect of a widely applied one-size-fits-all approach, delayed mowing, differed considerably among fields that differed in productivity level and floral composition. Similar to chapter 3, the responses of individual species provided most insight about the effects of mowing. To promote flowering in grasslands, management regimes can best be tailored to the phenology of locally prevailing forb species. First cuts should preferably be timed after peak bloom of the most abundant species. Furthermore, the potential of local species to recover after mowing determines whether spring cuts can enhance reflowering in summer, or whether uncut refuges are needed to preserve poorly recovering species with a late phenology (chapter 5). Due to this variation between species, phased mowing regimes are desired in fields with a high diversity of forb species. Spatial variation in mowing regimes can also help preserve landscape-scale floral resources during the entire growing season (Bishop et al., 2024). Locally tailored management can thus improve restoration outcomes from local to landscape scales. While this study focused on mown grasslands, flowers can also guide local adjustments of restoration management in grazed systems (chapter 4), while other habitat quality indicators may facilitate similar adaptive management approaches in other habitat types.

However, the most important determinant of local flower richness was not the mowing regime but the productivity level of grasslands (chapter 5). The effect of

productivity on flower richness increased towards summer (chapter 4), when arthropod activity peaks while floral resources in agricultural landscapes decline (Bishop et al., 2024). Furthermore, like most arthropod species (chapter 3), also most forb species were centered at or even confined to low-productivity habitats (chapter 5). Reduced mowing was only effective in lower-productivity grasslands where it did not lead to a strong dominance of more competitive plants, but frequent mowing in high-productivity grasslands supported only a few forb species. **Reducing productivity** thus remains the main prerequisite for ecosystem restoration in grasslands that are degraded by land use intensification (all chapters). In intensively farmed regions where even protected grasslands face chronic nutrient enrichment, this is a strenuous challenge that requires landscape-scale solutions (Nijssen et al., 2017). On top of that, species-rich grassland systems do not recover easily once they are lost, even when favourable conditions are restored (Buisson et al., 2022; Nerlekar & Veldman, 2020). Environmental policies should therefore not only facilitate ecosystem restoration at degraded sites, but prioritize the preservation of remaining grasslands of high nature value.

Rural landscapes that support grassland ecosystems and human well-being

If we are to safeguard ecosystems and their vital contributions to human well-being, intensively farmed rural landscapes must change drastically, but these landscapes must sustain food security at the same time (IPBES, 2019; Kremen & Merenlender, 2018). Global food demands keep increasing (Godfray et al., 2010) and calls for regional self-sufficiency in food production have increased recently in response to geopolitical tension (Mangnus & Candel, 2025). However, many modern agricultural landscapes are for large parts used for intensive livestock farming while falling short in producing more critical components of healthy human diets. In such cases, reduced animal stocks and more diverse crop growth are needed to improve food security (Foley et al., 2011; Rockström et al., 2025; Springmann et al., 2018). Nevertheless, managed grasslands can play a central role in sustainable food production systems by combining more sustainable forms of livestock farming with the delivery of ecosystem services to agriculture, and by safeguarding public goods that are important to society. This requires reforms of current practices that drive the degradation of ecosystems and the public goods they deliver (Fig. 6.2).

Using grasslands sustainably involves regulation of inputs in order to prevent external environmental costs that deteriorate public goods (Fig. 6.2). Local productivity losses due to such regulations can however be partly mitigated by innovations, such as utilizing nitrogen-fixing legumes in grassland swards (chapter 2). Recent studies indicate that combinations of fast-growing grasses, forbs and legumes can even be as productive as current high-input grasslands when receiving substantially lower fertilization (O'Malley et al., 2025; Zetterlind et al., 2025). Regulation may also lead to increased prices of agricultural end products, which may in turn preserve the income of farmers. The diversification of grassland swards with legumes and other disturbance-tolerant forbs can improve soil health, reduce

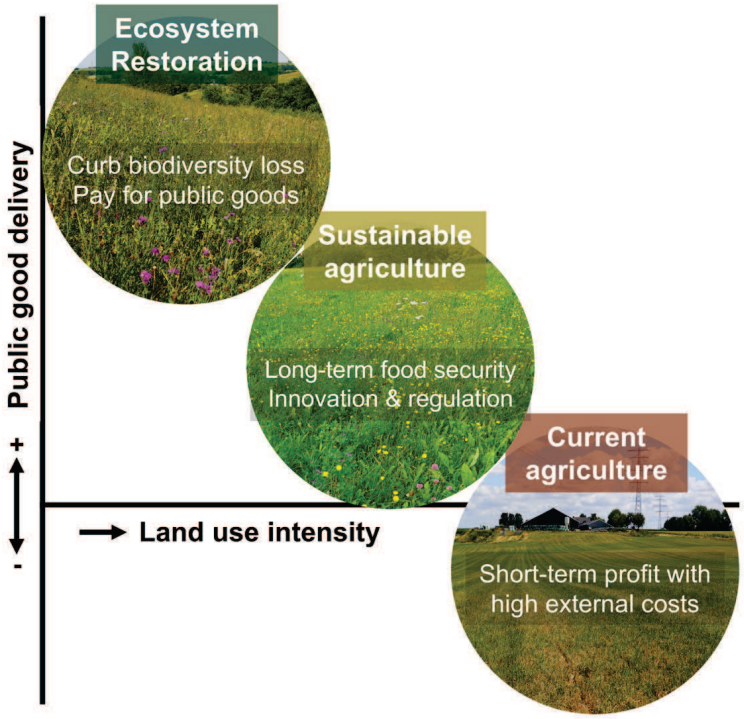

Figure 6.2 The trade-off between land use intensity and public good delivery on grasslands can be addressed by heterogeneous management strategies. Current intensive farming endorses short-term profits but does not acknowledge its own soaring external environmental costs. This disrupts the supply of public goods to society. Sustainable farming practices must secure long-term food supply while preventing further harm to public goods, e.g. by regulating input levels. Ecosystem services, management innovation and price corrections in response to new regulation may largely preserve the income that farmers make by agricultural production. However, a more drastic extensification of current land use is necessary to curb biodiversity loss and restore all public goods that are sustained by healthy ecosystems. To sustain such management for ecosystem restoration alongside sustainable agriculture, the delivery of these public goods to society should provide alternative means of income to farmers (photo credit: Reinier de Vries).

drought stress and enhance the water retention capacity of agricultural grasslands (Grange et al., 2021; Lehmann et al., 2020; Liu et al., 2019). These forbs can also provide floral resources to arthropod species that tolerate rather intensive management regimes (chapter 3 to 5). Such species are often the main providers of ecosystem services like crop pollination (Kleijn et al., 2015). But while a limited extensification that involves input regulation and sown-in forbs may already enhance the supply of ecosystem services to agriculture, much more drastic extensification of current land use is required to curb biodiversity loss. This thesis showed that restoring high-quality habitats is not only the most cost-efficient way to support biodiversity (Kleijn et al., 2009; chapter 2), but is indispensable for the majority of grassland species (chapters 3 and 5). High-quality habitats also provide the strongest support for public goods such as carbon sequestration, nutrient retention and water resources (chapter 2).

Ecologists have long argued over conservation paradigms that seek to combine agricultural land use and biodiversity restoration ('land-sharing') or to maximize agricultural productivity so that other land can be set aside for nature ('land-sparing') (Tscharntke et al., 2012). These approaches may actually be largely complementary. On the one hand, set-aside areas are crucial to maintain and restore biodiversity because a large part of all species survives only in habitats that have no agricultural function, including semi-natural grasslands in Western Europe (chapter 3). Semi-natural habitat elements are also crucial for biodiversity in strongly altered agricultural landscapes (Martínez-Núñez et al., 2022), but biodiversity-friendly agricultural practices can be applied much more widely in such landscapes. Interventions over large areas are necessary to sustain viable populations of widespread species and the ecosystem services they provide (Bishop et al., 2025). Recent studies embrace this complementarity by promoting diversification of land use practices in multifunctional landscapes (Le Provost et al., 2023; Manning et al., 2018). It is however critical to not just optimize multifunctionality scores of single landscapes (for example, Neyret et al., 2023), but to ensure that healthy diets, ecosystem functions and biodiversity are *all* sustained at relevant regional scales. To restore favourable conditions for biodiversity and ecosystem service delivery, various restoration strategies must be integrated in landscape planning (Kleijn et al., 2020). Scientists should therefore determine which land use types and expanses are needed to fulfil specific functions. For example, Bishop et al. (2025) and Fijen et al. (2025) quantified what area and quality of semi-natural habitats are needed to support pollinator populations. Integrative restoration approaches in intensively used regions should prioritize biodiversity preservation as this function is least compatible with modern farming, while restoring biodiversity will foster multiple other functions in parallel (chapter 2).

The multiple functions of rural landscapes are fulfilled most effectively when land use practices are planned at locations that hold most potential to improve their associated functions, or where specific functions are most needed. In many cases, preferrable conditions for growing food crops—fertile soils where yields are higher with lower input levels—do not overlap with sites where ecosystem restoration has most potential (Bakker et al., 2021). Such sites include wet, nutrient-poor or alkaline soils that often already support permanent grasslands, hence restoration actions would not compromise production for direct human consumption. When adequately located, restored ecosystems can support location-dependent functions such as flood prevention and clean water supply. Furthermore, new nature and agri-environment schemes with long durations and strict extensification criteria, such as cessation of fertilization, can extend and connect existing nature reserves (Smart et al., 2014). This is needed to counteract the fragmentation of natural habitats in many intensively used landscapes (Diekötter et al., 2008). Long-term agri-environment schemes should also be planned as buffers that reduce the drift of agricultural inputs into nature reserves. On the other hand, more flexible agri-environment schemes and forb-rich production grasslands are probably most

effective in structurally simple agricultural landscapes where they create bigger ecological contrasts (Scheper et al., 2013), and where there is a high demand for ecosystem services like pollination, pest control and erosion prevention. Linear landscape elements such as field margins, hedges, stream banks and road verges can connect such fields with semi-natural source habitats (Kleijn et al., 2020), provided that the management of such elements is adjusted to support biodiversity (chapter 5). Combining these principles at the landscape scale results in a zonation of different land use practices, including different types of grasslands and grassland-like habitats (Fig. 6.3).

Landscape-level zonation can only be implemented fairly when ecological restoration practices provide a stable income to farmers, rivalling the revenues of intensive livestock farming. Nature restoration can be economically viable in locations where it supports strong economic interests such as tourism and drinking water extraction. For example, some of the largest species-rich grassland restoration sites in our study region were initiated by drinking water producers (Op den Kamp & Ovaa, 2019). Cooperation among regional stakeholders, for instance in the tourism sector, can enhance support for such restoration projects. Furthermore, land use change can be fostered by agronomic stakeholders such as retailers and banks when they are held accountable, for instance by consumers, for the indirect consequences of their operations (Kleijn et al., 2020). However, payments for public goods are necessary to initiate restoration projects that do not support marketable interests (chapter 2). The optimization of multiple public goods justifies payment increases for projects with more positive biodiversity outcomes, which can motivate farmers to enhance restoration outcomes even when this amplifies productivity setbacks (Pe'er et al., 2022). Moreover, result-based payments will encourage land owners to establish restoration schemes at the most suitable locations, which will help optimize the allocation of restoration schemes in rural landscapes. In this way, farmers and other landowners and stakeholders can restore semi-natural habitats, biodiversity and public good delivery in balance with other critical functions that our rural landscapes provide.



Figure 6.3 Illustration of a rural landscape where grasslands that vary in land use intensity are allocated such that they facilitate food production, ecosystem functions and biodiversity. Towards the left, sustainable production grasslands with sown-in legumes and other forbs, partly forming grassland strips between arable fields, sustain ecosystem services such as pollination and erosion control. Alongside linear landscape elements such as hedges and road verges, they form connections with set-aside habitats such as water retention sites and nature reserves. In the centre, extensified pastures and meadows support a wider array of species and ecosystem functions, and form a buffer around the semi-natural grassland on the right. Here, management aims to optimize biodiversity and other public goods. In more productive grasslands, rotational mowing and grazing practices help sustain the flowering of disturbance-tolerant forbs during the growing season. In less productive habitats such as hay meadows and road verges, phased mowing and uncut refuges foster a wider variety of forb species. The foreground shows typical forb and arthropod species of higher (left) to lower (right) productivity levels. Note that species on the left are usually widespread and found at lower productivity too (credit: Reinier de Vries).



SEVEN

Supplementary materials

7.1 Appendix A

Supplement to chapter 2, "Loss of income constrains the restoration of multiple biodiversity-based ecosystem services in agricultural grasslands"

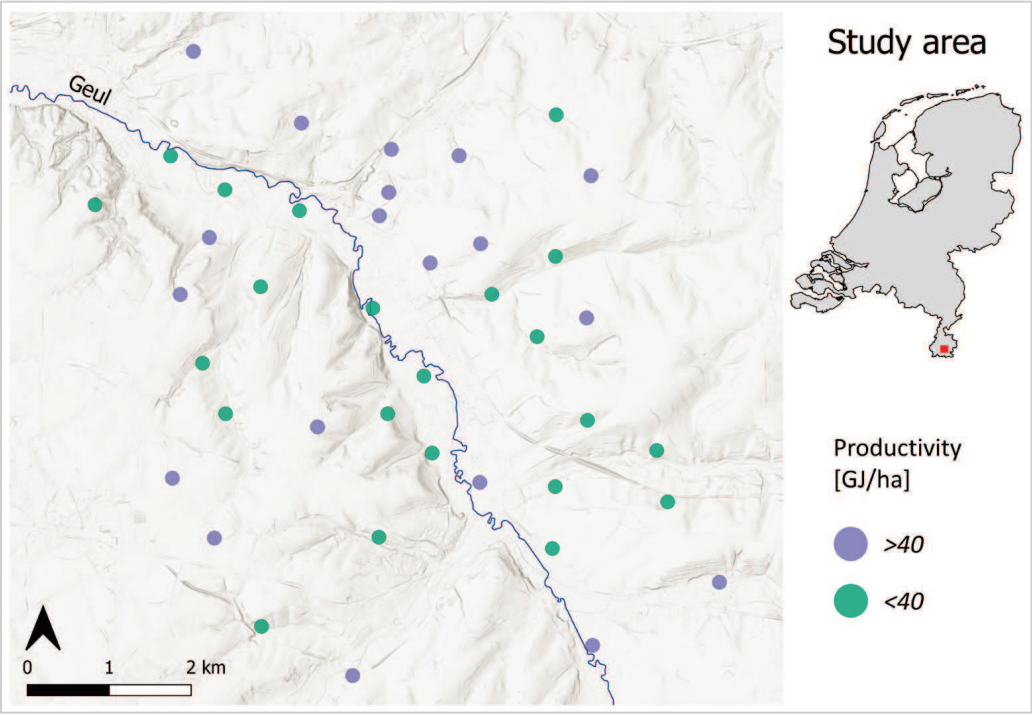

Figure 7A.1 This study was performed on 41 grasslands in a study area of approximately eight by eight kilometres, situated around the river Geul in the south of the Netherlands. The sampled grasslands are indicated by dots and coloured by annual productivity in terms of energy for livestock (GJ·ha^{-1}).

Table 7A.1 Parameters determining the gross margin (farmer income) per ha per year

Yield	Dominant use		Fertilization (kg N_{eff})	Dry yield (tons)	Energy (GJ)	Protein (kg)	Harvesting costs (€)	Fertilizing costs (€)	Gross margin (€)
1	silage	mown	253	14500.00	90.71	943	921.40	514.30	1710.80
2	silage	mown	264	13500.00	84.56	878	809.20	502.90	1619.88
3	silage	mown	254	13000.00	81.45	845	794.60	514.49	1514.86
4	silage	mown	314	13750.00	86.21	894	899.50	617.16	1471.88
5	silage	grazed	332	12116.79	78.15	939	768.81	690.23	1374.72
6	silage	mown	326	12523.58	79.72	877	780.69	662.69	1369.05
7	silage	mown	79	11000.00	64.59	605	653.20	181.60	1341.55
8	silage	mown	116	11312.50	66.43	687	745.33	266.98	1288.62
9	silage	grazed	265	10106.77	65.73	824	627.12	545.61	1244.13
10	hay	grazed	52	9091.67	53.39	606	597.48	120.63	1183.86
11	silage	grazed	190	10667.59	62.64	717	643.49	411.00	1182.21
12	silage	grazed	122	9873.00	57.97	666	620.29	281.00	1171.43
13	silage	mown	319	11450.99	72.98	806	749.37	660.67	1167.54
14	hay	grazed	54	8305.88	46.49	532	491.53	123.96	1044.56
15	silage	grazed	132	8508.48	49.96	596	497.45	305.26	1004.49
16	silage	mown	191	9300.00	58.34	605	603.56	429.92	988.53
17	silage	mown	44	7902.33	46.40	435	479.75	102.15	981.58
18	silage	mown	290	10000.00	62.80	650	624.00	587.72	964.08
19	hay	mown	30	6890.58	38.04	430	367.21	69.96	915.97
20	silage	mown	144	7650.00	48.12	497	472.38	295.88	898.24
21	hay	mown	22	6641.22	36.10	402	359.92	50.37	867.79
22	hay	mown	0	5798.87	30.04	319	335.33	0.00	713.40
23	hay	grazed	41	6240.67	32.33	343	348.23	93.67	686.73
24	hay	grazed	40	6146.11	31.84	338	345.47	92.25	673.81
25	hay	mown	0	5004.48	25.93	275	312.13	0.00	592.93
26	hay	mown	0	4848.65	25.12	267	307.58	0.00	569.30
27	hay	grazed	31	4727.78	24.50	260	304.05	70.96	480.01
28	hay	mown	0	4214.62	21.84	232	289.07	0.00	473.15
29	hay	grazed	42	4686.60	24.28	258	302.85	96.70	448.03
30	hay	grazed	23	3593.11	18.62	198	187.92	53.93	407.96
31	hay	grazed	20	3975.00	20.60	219	282.08	47.23	389.63
32	hay	mown	0	3542.86	18.36	195	269.45	0.00	371.27
33	hay	mown	0	4791.40	16.55	140	305.91	0.00	236.92
34	hay	mown	0	2500.00	12.95	138	239.00	0.00	213.13
35	hay	mown	0	4200.00	14.51	123	288.64	0.00	187.19
36	hay	grazed	35	1705.91	8.84	94	132.81	80.70	95.00
37	hay	mown	0	2000.00	6.91	58	141.40	0.00	85.18
38	hay	mown	0	2500.00	8.64	73	239.00	0.00	44.23
39	hay	mown	0	1350.00	4.66	39	122.42	0.00	30.52
40	hay	mown	0	2213.13	7.64	65	230.62	0.00	20.11
41	hay	mown	0	1200.00	4.14	35	118.04	0.00	17.91

Grassland management parameters determining forage production and agronomic profit. Fertilization was measured in kg effective nitrogen (Neff), yields were measured in dry weight (tons), energy content (Gigajoule) and protein content (kg digestible protein). Sites are sorted by gross margin (n=41).

Table 7A.2 Ecosystem service indicators per field

Field	Legume cover	Plant species richness	Bee species richness	Earthworm sp. richness	Earthworm abundance	Decay rate (x100)	Nitrate loss	Phosphate loss	Soil carbon	Soil pH
1	8.6	8	7	5	143	1.2	491.9	86.7	4.5	6.7
2	0.0	6	0	5	247	1.4	708.1	16.7	4.9	5.8
3	0.0	7	0	6	160	1.6	272.0	101.9	2.0	6.7
4	0.0	6	0	5	71	1.1	86.7	50.3	4.6	6.5
5	0.6	7	2	5	242	1.7	79.5	47.6	2.2	6.6
6	0.0	4	1	5	132	1.8	601.7	109.2	2.1	6.7
7	36.3	10	12	5	109	2.4	84.7	75.5	5.0	7.3
8	30.5	11	9	5	160	1.7	95.8	60.0	4.8	7.4
9	0.5	9	4	5	103	1.2	655.3	63.2	4.9	6.1
10	23.6	15	3	4	114	1.1	35.7	31.3	3.5	6.5
11	12.9	10	3	4	180	NA	333.2	101.5	3.6	6.4
12	12.4	17	4	6	80	1.6	224.3	93.5	6.9	7.0
13	0.0	5	0	5	174	1.6	116.0	99.7	2.5	6.7
14	24.0	20	7	7	168	1.1	68.7	44.0	2.9	6.4
15	18.7	16	6	6	159	1.4	95.2	37.0	3.3	6.2
16	10.2	3	4	5	195	1.5	142.6	70.0	2.5	6.8
17	42.0	12	6	5	143	1.2	163.7	99.1	2.4	7.2
18	0.0	8	2	5	289	2.5	231.5	157.7	1.8	7.5
19	4.3	17	0	7	95	1.2	81.4	59.9	2.2	6.0
20	3.0	10	5	6	265	1.3	573.4	50.4	3.0	6.3
21	1.0	12	9	7	195	1.1	112.9	57.1	3.6	5.9
22	7.9	28	10	6	144	0.9	21.1	12.9	7.2	7.2
23	4.1	11	4	4	181	1.1	64.2	17.5	3.0	5.7
24	19.4	18	6	7	112	1.2	40.3	12.9	3.5	5.8
25	17.8	28	9	5	108	1.4	24.3	19.4	6.3	7.5
26	25.2	21	7	4	112	1.4	31.1	35.9	2.3	5.8
27	7.3	27	6	4	76	1.4	19.1	6.4	5.3	7.7
28	20.6	23	7	5	113	1.0	71.8	66.3	2.4	7.2
29	13.4	31	9	5	76	1.8	42.3	30.6	9.6	7.3
30	8.9	21	9	7	164	1.6	44.9	5.9	6.5	6.2
31	3.7	25	9	4	77	1.8	363.3	11.2	9.8	7.1
32	8.3	17	6	6	212	1.2	60.7	10.3	3.3	6.1
33	17.0	21	16	6	161	1.1	25.0	32.8	3.8	6.2
34	4.3	19	7	6	71	1.6	141.3	45.6	8.3	7.6
35	1.2	18	5	7	209	0.9	29.4	55.6	6.6	6.6
36	9.2	31	12	2	27	1.1	53.3	16.2	3.3	5.5
37	16.6	41	12	5	109	1.4	9.0	3.5	4.8	7.4
38	2.3	21	6	5	178	1.0	93.7	4.1	7.9	7.8
39	8.1	38	5	3	35	1.5	7.8	1.3	9.5	7.1
40	13.3	31	14	5	109	1.8	33.2	4.2	6.0	7.7
41	6.6	45	23	3	106	1.1	4.2	1.5	9.9	7.9

Grassland ecosystem service indicators collected through field measurements and aggregated at field level. Replicate measurements were summed (species richness and abundance) or averaged (other). Sites (n=41) are sorted by gross margin in correspondence with Table 7A.1.

Table 7A.3 Model set relating productivity to fertilization and ecosystem service indicators

Models	*(Intercept)*	Fertilization	Fertilization^2	Legume cover	Decay rate	Soil carbon	Earthworm abundance	R^2_{adj}	ΔAIC_c	weight
1	0.26	1.28	-0.27	0.24	-0.10			0.96	0.00	0.38
2	0.26	1.23	-0.26	0.22				0.95	0.34	0.32
3	0.26	1.21	-0.27	0.20		-0.04		0.95	2.61	0.10
4	0.25	1.21	-0.26	0.22			0.03	0.95	2.79	0.09
5	6.E-17	1.01		0.29				0.92	5.49	0.02
6	7.E-17	1.05		0.31	-0.09			0.93	5.80	0.02
7	6.E-17	0.99		0.30			0.05	0.92	7.43	0.01
8	7.E-17	0.98		0.28		-0.04		0.92	7.75	0.01
9	7.E-17	1.03		0.31	-0.09		0.05	0.93	7.95	0.01
10	0.38	1.26	-0.39					0.91	8.30	0.01
11	0.36	1.20	-0.37			-0.11		0.92	8.35	0.01
12	7.E-17	1.04		0.30	-0.09	-0.01		0.93	8.54	0.01
13	0.39	1.29	-0.40		-0.06			0.91	9.91	3.E-03
14	6.E-17	0.98		0.29		-0.02	0.04	0.92	10.12	2.E-03
15	0.37	1.23	-0.38		-0.04	-0.10		0.92	10.63	2.E-03
16	0.36	1.21	-0.37			-0.12	-0.03	0.92	10.88	2.E-03
17	0.38	1.26	-0.39				5.E-03	0.91	10.92	2.E-03
18	0.39	1.29	-0.40		-0.06		6.E-04	0.91	12.69	7.E-04
19	6.E-17	0.83				-0.14		0.86	19.38	2.E-05
20	5.E-17	0.89						0.85	20.07	2.E-05
21	7.E-17	0.84				-0.15	-0.03	0.86	21.88	7.E-06
22	6.E-17	0.84			-0.01	-0.14		0.86	21.98	6.E-06
23	5.E-17	0.90			-0.04			0.85	22.31	5.E-06
24	5.E-17	0.88					0.02	0.85	22.47	5.E-06
25	7.E-17	0.84			-0.01	-0.15	-0.03	0.86	24.64	2.E-06
26	5.E-17	0.90			-0.04		0.02	0.85	24.87	2.E-06
27	6.E-17				0.29	-0.50		0.35	70.07	2.E-16
28	5.E-17			-0.18	0.29	-0.52		0.38	70.80	2.E-16
29	4.E-17				0.28	-0.44	0.13	0.36	71.91	9.E-17
30	8.E-17					-0.49		0.26	72.20	8.E-17
31	7.E-17			-0.17		-0.51		0.29	73.14	5.E-17
32	5.E-17			-0.16	0.28	-0.49	0.07	0.38	73.36	4.E-17
33	6.E-17					-0.42	0.16	0.28	73.61	4.E-17
34	6.E-17			-0.14		-0.46	0.11	0.30	75.30	2.E-17
35	-2.E-17				0.25		0.32	0.19	77.80	5.E-18
36	-7.E-18						0.34	0.13	77.98	4.E-18
37	-2.E-18				0.28			0.08	78.40	4.E-18
38	-2.E-17			-0.04	0.25		0.31	0.20	78.40	4.E-18
39	-7.E-18			-0.03			0.34	0.13	80.41	1.E-18
40	2.E-17							0.00	80.49	1.E-18
41	-6.E-18			-0.12	0.28			0	80.68	1.E-18
42	1.E-17			-0.11				0.01	82.54	5.E-19

Full model set ranked in order of ΔAIC_c (difference in Akaike Information Criterion for small sample size), with z-standardized variables and at maximum four predictors per model. Adjusted R^2, ΔAIC_c and model weights are given for each model.

Table 7A.4 GLMs relating multiple ecosystem services to gross margin

Ecosystem service indicator	Intercept	Slope	SE	p-value	R-squared
Plant richness	3.53	-9.88E-04	9.74E-05	<2e-16	0.82
Bee richness	2.54	-1.02E-03	1.66E-04	9.7E-10	0.64
Legume cover (sqrt)	3.32	-6.92E-04	5.60E-04	0.22	0.04
Earthworm richness	1.65	0.104	0.200	0.61	0.03
Earthworm richness^2		-0.467	0.199	0.02	
Nitrate loss (sqrt)	4.34	8.16E-03	1.64E-03	1.4E-05	0.38
Phosphate loss	8.69	4.51E-02	7.84E-03	1.3E-06	0.46
Earthworm abundance	111.89	3.72E-02	1.86E-02	0.05	0.09
Decay rate	1.28	1.54E-04	1.14E-04	0.19	0.04
Soil carbon content	6.51	-2.32E-03	5.57E-04	0.002	0.31

Generalized linear models (Generalized Poisson for richness, else Gaussian) related ecosystem services to gross margin. Legume cover and Nitrate loss where square root-transformed, and n=40 for earthworm richness and abundance and decay rate (else 41).

Supplementary text

Determining productivity, management costs and the gross margin

Parameters were obtained per hectare per year in all cases. The farmer interviews specifically asked for average, 'normal-year' conditions to avoid deviation due to year-specific conditions or management choices as far as possible.

We assumed standard operations and equipment for fertilization and silage- or hay cutting, and based cost estimates on standard contractor rates. These rates include machinery investment, maintenance and depreciation, labour, fuel and lubricants and business risk (5% surcharge), but not VAT or real-world customer rates; hence they provide an estimate of cost prices for a farmer. The calculations explained here are documented in Zenodo: 10.5281/zenodo.12820208.

Input variables:

- Fertilization from artificial fertilizer, slurry and manure inputs in product quantities was derived from farmer interviews.
- Cut harvests; the (approximate) dry weight and mowing dates of all silage and hay cuts were derived from farmer interviews. Based on date and field management, we distinguished the first and following silage cuts, silage cuts in alternative management (i.e. organic or beef cattle, in contrast to conventional dairy), and hay cuts preceding and following the 20th of June.
- Grazing was assessed through farmer interviews by duration (months) and density (animals per hectare) of dairy cows, suckler cows, yearlings and sheep.

Fertilization inputs:

- Livestock excretion was derived from grazing intensity (duration * density) by using animal-specific slurry excretion coefficients for dairy cattle (130 kg $N \cdot animal^{-1} \cdot year^{-1}$: matching an annual milk production of 10 tons and urea content of 21 $mg \cdot 100g^{-1}$, i.e. the regional average), suckler cows, yearlings and meadow sheep (7.7 kg $N \cdot animal^{-1} \cdot year^{-1}$ for extensive grazing) (Blanken et al., 2021; Remmelink et al., 2020). Pasturing duration was usually 7 $hours \cdot day^{-1}$ for dairy cows and full-day for suckler cows, yearlings and sheep; exceptions are specified per field. Livestock excretion is hereafter regarded as slurry.
- Effective nitrogen inputs from manure and slurry (including livestock excretion) were derived by calculating its organic and mineral fractions [$kg \cdot tonne^{-1}$], multiplied by fraction-specific working coefficients (Blanken et al., 2021; Remmelink et al., 2020). These inputs give the organic nitrogen input and combined with artificial fertilization (predominantly containing 27% effective nitrogen), the total effective nitrogen input [kg $N_{eff} \cdot ha^{-1} \cdot year^{-1}$]. This quantifies the total fertilization inputs, not regarding losses after application on the field.

Forage yields:

- Grazed quantities (DM) were derived from grazing duration (expressed in days or hours for dairy cattle) and grazing estimates for dairy cattle (approximately 1 $kg \cdot hour^{-1}$) (Schils et al., 2019), yearlings (Remmelink et al., 2020) and sheep (Blanken et al., 2021), or annual feed requirements for suckler cows (Corporaal & Van Os, 2002). Losses during cattle grazing occur due to grazing efficiency and forage residue left on the field, and are estimated at 15% (Remmelink et al., 2020).
- Total dry weight (DM) as brought onto the farmyard (i.e. including field and harvesting losses, but excluding storage and feeding losses) was given by the sum of cut harvests (silage and hay) and grazed quantities. However, forage quality differs per forage type. Therefore, we distinguished the yields of different silage, hay and fresh grass (grazed) types based on field management as indicated by the farmer. Next, forage quality was assessed by energy and protein content.
- Metabolic energy production was assessed by multiplying harvest weights with standard estimates of feed units for dairy cattle ('Voeder Eenheid Melk' or VEM, a Dutch standard measure of forage quality: 1 kVEM is the reference energy content of 1 kg DM barley). We distinguished kVEM for conventional fresh grass (0.96 $kVEM \cdot kg^{-1}$ full-season average); conventional silage, first cut; conventional silage, remaining cuts; alternative (organic or beef cattle) silage, both cut or permanently grazed (and including after-grazing on hay meadows); high-quality hay (mown prior to June 20th or permanent extensive grazing); or low-quality hay (mown after June 20th: 0.6 $kVEM \cdot kg^{-1}$) (Blanken et al., 2021; CVB, 2022; Schippers et al., 2012). Estimates for fresh grass and silage refer to sandy soils. Low-quality hay was corrected for its increased fill unit (1.2) which limits nutrient uptake by the animals (Andrieu et al., 1988).

- The total energy production (all yields combined) for each field was converted from kVEM to gigajoule (GJ) (Rompelberg et al., 1984) to facilitate international comparison.
- Protein production was assessed by multiplying harvest weights with standard estimates of digestible protein (DP, or DVE in Dutch). We distinguished DP for conventional fresh grass (89 DP·kg^{-1}); conventional silage (all cuts combined); alternative grazing (organic or beef cattle); alternative silage, high quality hay and hay grazing combined; and low-quality hay (35 DP·kg^{-1}: again corrected for fill unit) (CVB, 2022; Schippers et al., 2012).

Fertilization costs:

- Slurry application costs were estimated at 4.54 euro·m^{-3} (standard contractor rate for slurry injection: KWIN) and were accounted for all organic nitrogen inputs.
- Mineral fertilizer application costs were estimated at 56.5 euro·ha^{-1} (standard contractor rates for a pneumatic fertilizer spreader) for each operation (Blanken et al., 2021). The number of operations was estimated assuming a standard quantity of 50 kg N per operation. In this way, effects of individual farmer decisions on application frequency were avoided.
- Mineral fertilizer product costs were estimated at 0.76 euro·kg N^{-1} for standard product (Blanken et al., 2021). Organic product costs were however not included since farmers typically use their own products. Moreover, slurry market prices in the Netherlands fluctuate widely, even to negative values.

Harvesting costs:

- The number of silage cuts was estimated assuming a standard yield of 2500 kg per cut (dry weight). In this way, the effects of individual farmer decisions or weather circumstances on the number of cuts was avoided. Hay cuts occurred once or twice a year as indicated by the landowners as this is standard management, but weights can differ strongly.
- Mowing costs per cut comprised standard contractor rates for a 9-meter mower combination, 8.5-meter circle gatherer (both given in euro·ha^{-1}) and bale wrapper (11.68 euro·bale^{-1} for 400-kg bales including wrapping plastic) (Blanken et al., 2021). The circle gatherer was included twice to account for both swirling and gathering of the cut.

Gross margin:

- Yield revenues were estimated for both energy and protein production using on standard market values of energy (0.17 euro·kVEM^{-1}) and protein (0.97 euro·DP^{-1}) (Blanken et al., 2021), with protein representing 25-32% of total revenues.
- The gross margin, indicating farmer income, was calculated by subtracting all fertilization and harvesting costs from the combined yield revenue.

7.2 Appendix B

Supplement to chapter 3, "Land use intensification transforms grassland arthropod communities: a few winners expand but most species disappear"

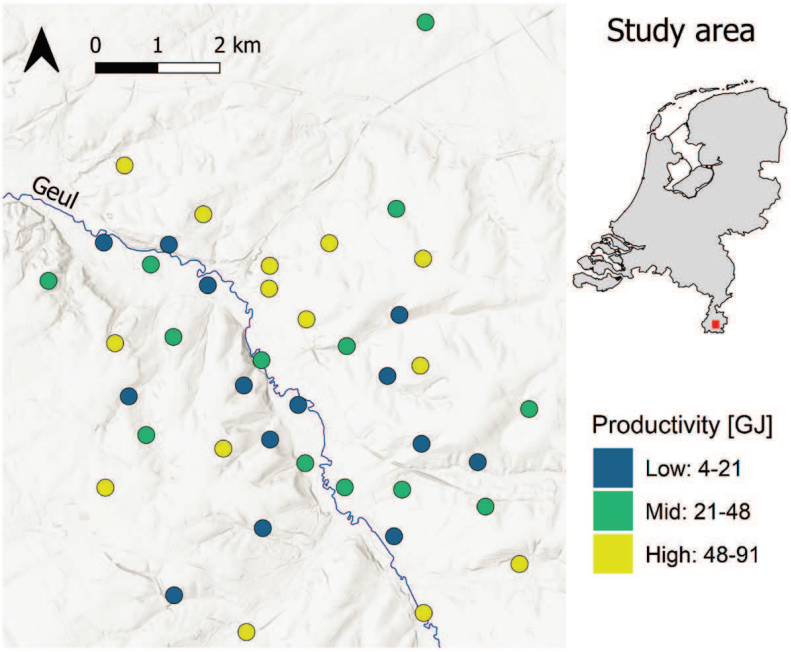

Figure 7B.1 This study was performed on 41 grasslands in a study area of approximately ten by ten kilometres, situated around the river Geul in the South of the Netherlands. The sampled grasslands are indicated by dots and coloured by annual productivity in terms of net metabolic energy (GJ·ha^{-1}·yr^{-1}).

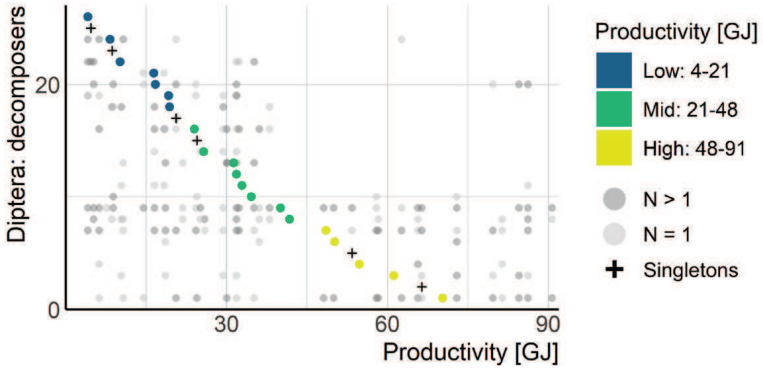

Figure 7B.3 Species distributions along the land use intensity gradient (measured by productivity [GJ·ha^{-1}·yr^{-1}]) for Diptera with larvae living as decomposers (26 species). Species are ordered on the y-axis by their center points (colored dots) which represent the abundance-weighed mean productivity, and were classified in low, medium or high productivity levels. Grey dots show all sites where a species was recorded (single records in light grey, higher numbers in dark grey).

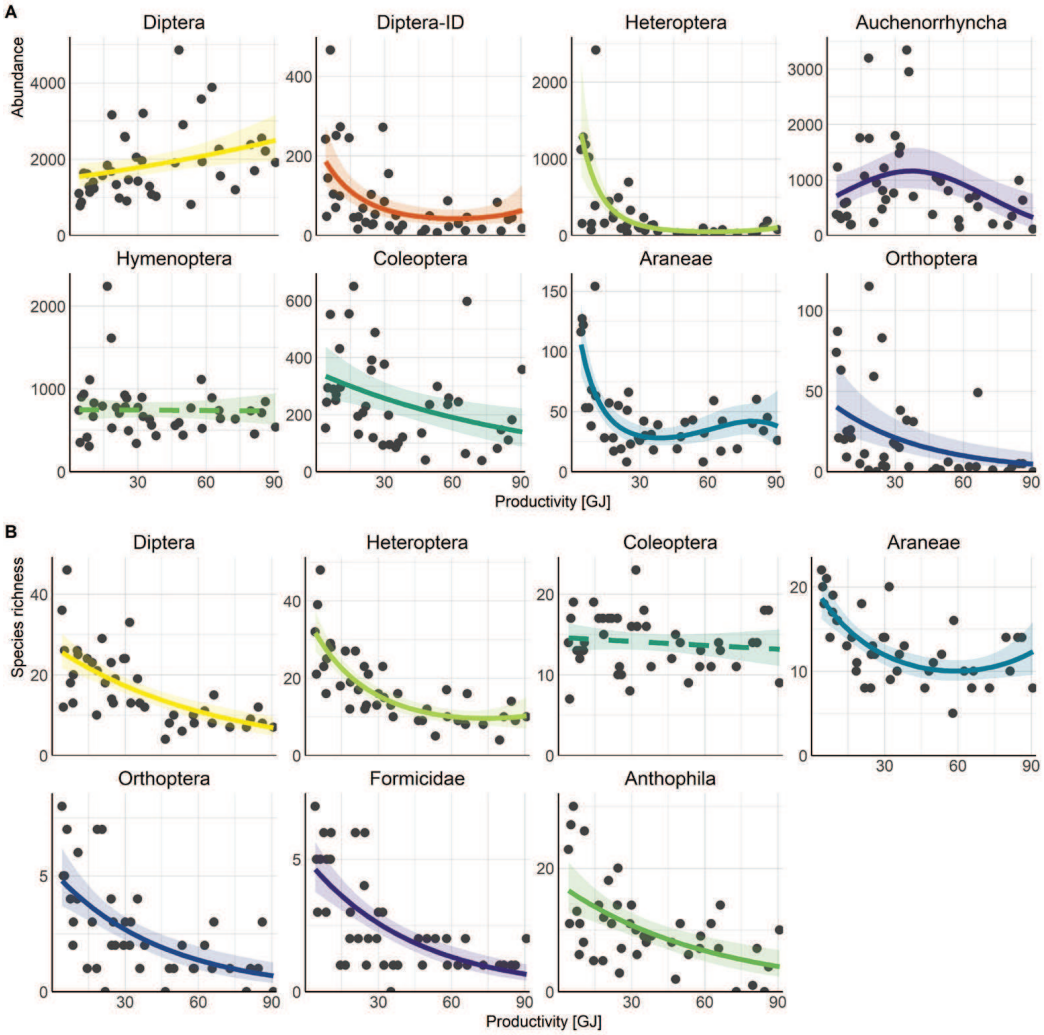

Figure 7B.2 Relations of arthropod abundance (A) and observed species richness (B) with grassland productivity [GJ·ha^{-1}·yr^{-1}] per individual arthropod group. Significant relations are shown in solid lines with 95% confidence intervals (ribbons). Arthropod abundance was measured at order level whereas species richness data represent subgroups within each order (for Diptera, the abundance of the identified subgroups is shown separately). Exponential terms were supported ($\Delta AIC_c > 2$) for abundance trends of Heteroptera, Auchenorrhyncha, Araneae and the species-identified Diptera, and for species richness trends of Heteroptera and Araneae.

Table 7B.1 Specifications of the sampling sites

Site	Area [ha]	Land Use	Grass : Forb Ratio	Fertilization [kg N·ha^{-1}·yr^{-1}]	Dry Yield [t·ha^{-1}·yr^{-1}]	Productivity [GJ·ha^{-1}·yr^{-1}]
1	1.3	hay, mown	0.8	0.0	1.2	4.1
2	5.1	hay, mown	0.7	0.0	1.4	4.7
3	0.4	hay, mown	0.7	0.0	1.5	5.2
4	0.4	hay, mown	0.2	0.0	1.8	6.2
5	6.9	hay, mown	0.8	0.0	2.2	7.6
6	0.8	hay, mown	2.8	0.0	2.5	8.6
7	5.3	hay, grazed	1.3	35.0	1.7	8.8
8	4.6	hay, mown	1.0	0.0	2.0	10.4
9	1.6	hay, mown	0.3	0.0	3.1	10.7
10	2.2	hay, mown	3.3	0.0	4.2	14.5
11	0.6	hay, mown	0.4	0.0	4.8	16.5
12	3.4	hay, mown	2.2	0.0	3.5	18.4
13	6.0	hay, grazed	1.0	23.4	3.6	18.6
14	1.5	hay, grazed	1.4	20.5	4.0	20.6
15	3.1	hay, mown	0.6	0.0	4.2	21.8
16	1.8	hay, grazed	1.0	41.9	4.7	24.3
17	1.0	hay, grazed	0.7	30.8	4.7	24.5
18	3.0	hay, mown	2.7	0.0	4.8	25.1
19	1.4	hay, mown	0.9	0.0	5.0	25.9
20	2.0	hay, grazed	1.5	36.9	5.7	29.4
21	1.3	hay, mown	1.0	0.0	5.8	30.0
22	1.3	hay, grazed	2.6	40.0	6.1	31.8
23	1.5	hay, grazed	2.6	40.6	6.2	32.3
24	1.1	hay, grazed	2.4	32.9	6.3	35.1
25	8.4	hay, mown	3.1	21.8	6.6	36.1
26	3.4	hay, mown	1.5	30.3	6.9	38.0
27	6.9	hay, grazed	1.6	53.8	8.3	46.5
28	1.3	silage, mown	17.5	144.0	7.7	48.1
29	2.8	silage, grazed	2.0	132.4	8.5	50.0
30	8.6	hay, grazed	0.8	52.3	9.1	53.4
31	3.6	silage, grazed	1.7	121.9	9.9	58.0
32	4.7	silage, mown	2.9	191.0	9.3	58.3
33	3.9	silage, grazed	2.9	189.9	10.7	62.6
34	6.2	silage, grazed	58.3	265.4	10.1	65.7
35	1.9	silage, mown	0.8	115.8	11.3	66.4
36	3.8	silage, mown	116.5	318.8	11.5	73.0
37	6.4	silage, mown	44.0	326.4	12.5	79.7
38	2.3	silage, mown	2.2	253.7	13.0	81.4
39	3.6	silage, mown	37.1	264.2	13.5	84.6
40	19.2	silage, mown	13.8	314.4	13.8	86.2
41	7.9	silage, mown	2.3	253.4	14.5	90.7

Land use lists the dominant fodder and management types. The grass:forb ratio (i.e. the cover of grass species relative to the cover of forb species) is an indicator of floral composition. Fertilization was measured by Nitrogen inputs (both mineral & organic). Productivity was measured by metabolic energy production.

Table 7B.2 Total numbers of species and records, and identification references per family

(Sub)order	Family	Species	Records	References
All species	-	520	26583	1, 2
Diptera	Asilidae	7	75	3
	Bibionidae	4	169	4
	Conopidae	3	13	5
	Opomyzidae	5	392	2
	Platystomatidae	2	34	2
	Rhagionidae	2	16	6
	Sciomyzidae	7	559	7
	Stratiomyidae	7	326	6
	Syrphidae	59	1341	8
	Tabanidae	4	25	6
	Tephritidae	16	1081	9
	Tipulidae	6	53	10
	Ulidiidae	3	36	2
Heteroptera	Anthocoridae	4	381	2
	Berytidae	4	31	
	Coreidae	3	8	
	Lygaeidae	12	49	
	Miridae	57	11734	
	Nabidae	6	175	
	Pentatomidae	9	72	
	Pyrrhocoridae	1	2	
	Rhopalidae	6	33	
	Saldidae	2	6	
	Scutelleridae	1	2	
	Tingidae	4	33	
Anthophila	Andrenidae	27	169	11, 12, 13, 14
	Apidae	21	1598	
	Colletidae	4	10	
	Halictidae	20	413	
	Megachilidae	15	34	
	Melittidae	1	15	
Coleoptera	Cantharidae	9	330	15
	Chrysomelidae	41	2217	16
	Coccinellidae	14	951	16
	Elateridae	21	830	17
Araneae	Araneidae	7	649	18, 19
	Clubionidae	2	3	
	Dictynidae	6	12	
	Hahniidae	1	1	
	Linyphiidae	27	877	

	Lycosidae	7	41	
	Mimetidae	1	1	
	Phalangiidae	1	56	
	Philodromidae	5	10	
	Pisauridae	1	2	
	Salticidae	1	34	
	Tetragnathidae	4	102	
	Theridiidae	9	244	
	Thomisidae	7	63	
Orthoptera	Acrididae	7	667	20
	Gryllidae	1	1	
	Tetrigidae	3	37	
	Tettigonidae	7	168	
Formicidae	Formicidae	16	2059	21

[1]Krediet, Buesink & Heijerman (eds.), 2022; [2]Waarneming.nl, 2024; [3]Van den Broek & Schulten, 2017; [4]Zeegers, 1997; [5]Van Veen, 2004; [6]Zeegers & Schulten, 2021; [7]Barendregt, 2021;[8]Bot & Van de Meutter, 2019; [9]Smit, 2010; [10]Peeters & Oosterbroek, 2013; [11]Falk & Lewington, 2017; [12]Nieuwenhuijsen & Peeters (eds.), 2016; [13]Nieuwenhuijsen, Peeters & Dijkshoorn (eds.), 2020; [14]Wood, 2023; [15]Verhoogt, 2020; [16]Lompe, 2024; [17]Krediet & Verhoogt, 2017; [18]Roberts, 1998; [19]Nentwig et al., 2024; [20]Bakker et al., 2015; [21]Boer, 2023.

Table 7B.3 Abundance and species richness per arthropod group related to productivity

Group	**Abundance**		**Productivity effect**	**Species**	**Productivity effect**
Total	169.913	%	-0.002; p=0.3	520	P: -1.7, p=$6e^{-12}$; P^2: 0.6, p=0.01
Diptera	76.698	46	0.005; p=0.008		
Identified	*3475*		P: -2.6, p=$6e^{-5}$; P^2: 1.7, p=0.005	125	-0.02, p=$5e^{-9}$
Auchenorr-hyncha	36.920	22	P: -1.1, p=0.1; P^2: -1.7, p=0.01		
Heteroptera	*12.386*	*8*	P: -5.8, p=$7e^{-15}$; P^2: 3.7, p=$1e^{-6}$	109	P: -2.4, p=$1e^{-12}$; P^2: 0.9, p=0.004
Hymenoptera	30.478	18	$-2e^{-4}$, p=0.9		
Anthophila	*2089*		-0.02; p=0.002	88	-0.02, p=$3e^{-5}$
Formicidae	*1318*		-0.04; p=$1e^{-7}$	16	-0.02, p=$2e^{-11}$
Coleoptera	10.189	6	-0.007; p=0.04		
Identified	*3357*		-0.005; p=0.2	85	-0.001, p=0.4
Araneae	*1874*	*1*	P: -1.2, p=0.004; P^2: 1.9, p=$3e^{-15}$; P^3: -1.0, p=0.02	79	P: -1.0, p=$3e^{-5}$; P^2: 0.8, p=$9e^{-4}$
Orthoptera	*871*	*1*	-0.02; p=0.0001	18	-0.02; p=$6e^{-7}$

Abundance per (sub)order is given in exact counts and as percentages of the total abundance, counts of the 7 identified subgroups are marked in italic. 'Productivity effect' gives the relations of abundance and observed richness with grassland productivity: linear and if present exponential (P^2, P^3) coefficients with significances (p-values) are specified.

Table 7B.4 Community dissimilarity given by abundance-based and incidence-based beta-diversity

	Differences in abundance-based beta-diversity					Differences in incidence-based beta-diversity				
		class 1 : class 2		class 2 : class 3			class 1 : class 2		class 2 : class 3	
Group	*av.*	*statistic*	*p-adj.*	*statistic*	*p-adj.*	*av.*	*statistic*	*p-adj.*	*statistic*	*p-adj.*
		Total beta-diversity					*Total beta-diversity*			
All species	0.8	-4.12	1.16E-04	-0.76	1.00	0.7	-2.84	0.013	-3.84	3.72E-04
Diptera	0.9	0.46	1.00	-3.95	2.30E-04	0.8	-2.08	0.11	-2.83	0.014
Heteroptera	0.8	-4.62	1.17E-05	-1.02	0.92	0.6	-4.49	2.17E-05	-0.52	1.00
Anthophila	0.8	-2.43	0.046	6.06	4.00E-09	0.8	-4.75	6.25E-06	6.06	4.12E-09
Coleoptera	0.8	-3.51	0.0013	2.38	0.053	0.7	-4.10	1.22E-04	-3.72	6.01E-04
Araneae	0.8	0.49	1.00	-2.34	0.058	0.7	4.17	9.05E-05	-5.49	1.24E-07
Orthoptera	0.8	1.59	0.33	0.48	1.00	0.7	0.63	1.00	-0.16	1.00
Formicidae	0.8	-0.99	0.97	-6.08	3.58E-09	0.5	0.42	1.00	-7.56	1.17E-13
		Replacement					*Replacement*			
All species	0.5	1.88	0.18	-2.02	0.13	0.5	0.71	1.00	-0.44	1.00
Diptera	0.4	-0.87	1.00	1.22	0.67	0.5	-1.77	0.23	2.28	0.068
Heteroptera	0.4	0.22	1.00	1.51	0.39	0.4	-1.54	0.37	-2.84	0.013
Anthophila	0.2	-0.64	1.00	-5.93	8.83E-09	0.3	-0.36	1.00	-3.49	0.0014
Coleoptera	0.5	-1.52	0.39	-1.25	0.63	0.5	-5.06	1.23E-06	-0.46	1.00
Araneae	0.4	2.23	0.078	0.15	1.00	0.5	2.42	0.046	-5.28	3.98E-07
Orthoptera	0.1	-2.57	0.030	-1.38	0.50	0.2	-1.96	0.15	-1.48	0.42
Formicidae	0.1	-2.97	0.0090	-1.89	0.18	0.2	-3.79	4.60E-04	-2.05	0.12
		Abundance difference					*Richness difference*			
All species	0.3	-2.48	0.040	1.35	0.53	0.2	-1.95	0.16	-1.43	0.45
Diptera	0.5	0.88	1.00	-2.22	0.078	0.2	0.39	1.00	-3.61	9.15E-04
Heteroptera	0.5	-1.76	0.23	-1.59	0.34	0.3	-0.91	1.00	1.67	0.29
Anthophila	0.6	-0.42	1.00	6.05	4.33E-09	0.4	-2.03	0.13	4.86	3.44E-06
Coleoptera	0.4	0.19	1.00	2.05	0.12	0.2	3.00	0.0080	-2.19	0.086
Araneae	0.4	-1.57	0.35	-1.37	0.52	0.2	0.59	1.00	1.25	0.64
Orthoptera	0.6	2.70	0.021	-1.21	0.68	0.5	0.91	1.00	-0.23	1.00
Formicidae	0.7	0.35	1.00	-4.04	1.58E-04	0.4	2.16	0.092	-5.32	3.08E-07

Beta-diversity was partitioned into replacement (turnover) and abundance or richness differences between sites. All unique pairwise comparisons of sites within – but not across – three productivity classes (0-21, 21-48 and 48-91 GJ: see Figure 2) were derived (column 'av.' gives the averages over the entire land-use intensity gradient). The differences in dissimilarity metrics between classes 1 and 2 and between classes 2 and 3 were compared using Dunn's tests. The test statistic and adjusted p-value are given are given for every comparison, with negative statistics reflecting a decreasing dissimilarity from class 1 to class 2 (or from 2 to 3) which indicates biotic homogenization, and with p-values <0.01 (accounting for the large number of comparisons) indicated in grey.

7.3 Appendix C

Supplement to chapter 4, "Flower richness is an effective indicator of grassland arthropod biodiversity"

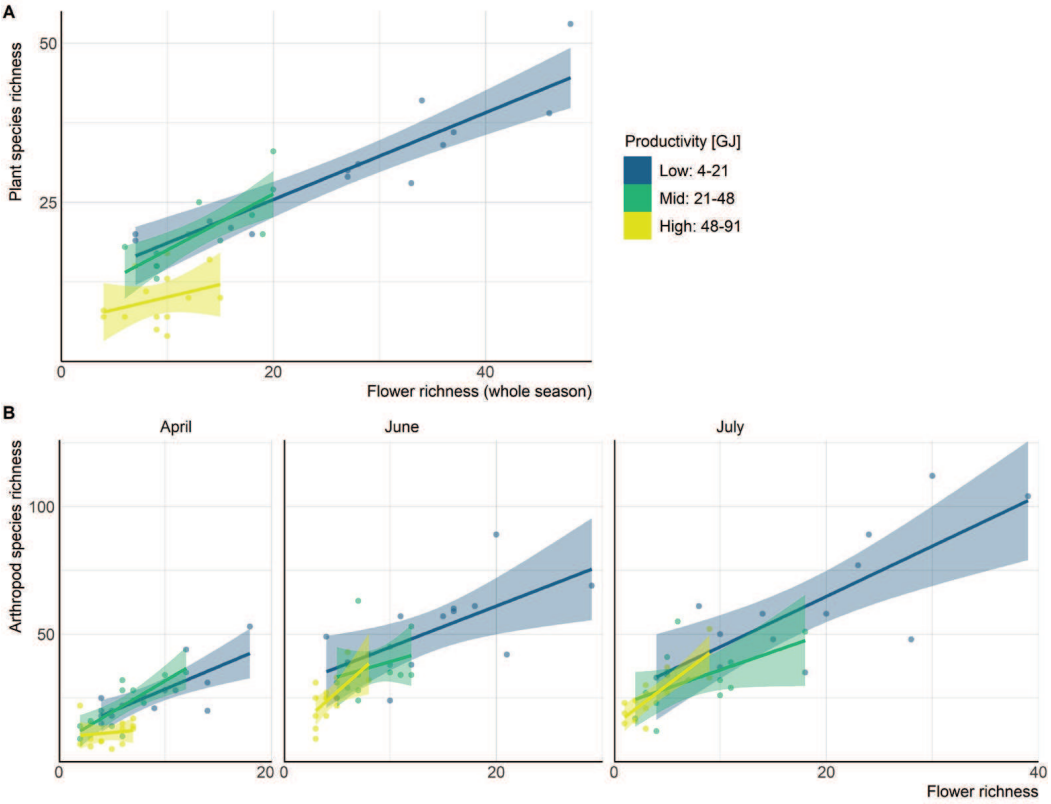

Figure 7C.1 Effects of productivity (reflecting land-use intensity) on the linear relations of flower richness with plant species richness (A: aggregated over the whole season) and arthropod species richness (B: separate for April, June and July). Productivity was measured in $GJ \cdot ha^{-1} \cdot yr^{-1}$ and classified into classes of low, medium and high productivity (reflecting 14, 13 and 14 sites respectively).

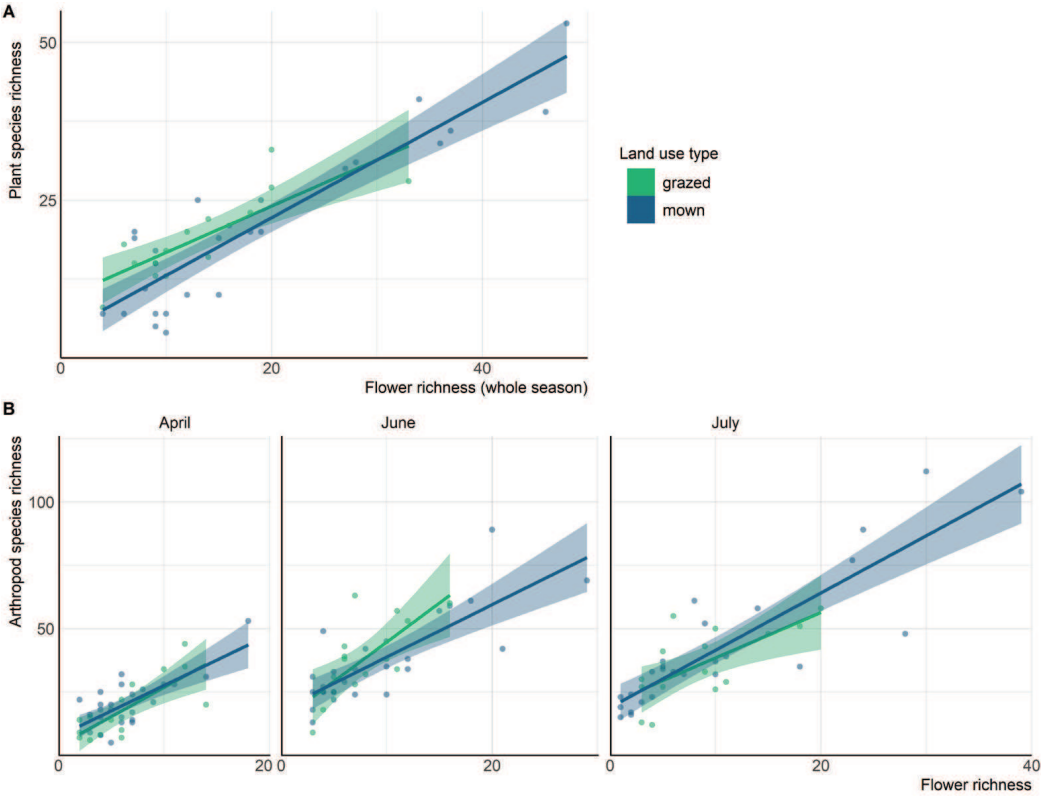

Figure 7C.2 Effects of land use type (predominantly grazed or mown) on the linear relations of flower richness with plant species richness (A: aggregated over the whole season) and arthropod species richness (B: separate for April, June and July). When land use was mixed (for example, some mown fields were grazed in autumn), the dominant type in terms of annual production was selected, which was in all cases also in place during data collection. The data includes 15 grazed and 26 mown fields.

Table 7C.1 Relations of flower richness and flower cover with the species richness of plants and arthropods.

Flower metric	Species group	April			June			July		
		slope	S. E.	p-value	slope	S. E.	p-value	slope	S. E.	p-value
Flower richness	*Plants*				*0.88*	*0.07*	***1.10E-14***			
	All arthropods	0.75	0.11	**1.84E-08**	0.76	0.10	**1.17E-08**	0.85	0.08	**1.45E-12**
	Diptera	0.69	0.12	**5.02E-07**	0.50	0.14	**9.20E-04**	0.83	0.09	**1.43E-11**
	Heteroptera	0.56	0.13	**1.42E-04**	0.73	0.11	**6.68E-08**	0.70	0.11	**2.83E-07**
	Anthophila	0.53	0.14	**3.33E-04**	0.54	0.13	**2.32E-04**	0.85	0.08	**2.70E-12**
	Coleoptera	0.29	0.15	0.068	0.02	0.16	0.91	0.02	0.16	0.92
	Araneae	0.43	0.14	**0.0046**	0.45	0.14	**0.0032**	0.72	0.11	**8.51E-08**
	Formicidae	0.51	0.14	**7.10E-04**	0.68	0.12	**9.35E-07**	0.87	0.08	**1.17E-13**
	Orthoptera							0.80	0.10	**2.63E-10**
Flower cover	*Plants*				*2.33*	*0.87*	***0.011***			
	P^2				*-2.36*		***0.010***			
	All arthropods	2.17	0.86	**0.0163**	0.49	0.14	**0.0011**	0.69	0.12	**7.50E-07**
	P^2	-2.63		**0.0041**						
	Diptera	1.93	0.82	**0.0242**	0.24	0.16	0.12	0.61	0.13	**2.34E-05**
	P^2	-3.28		**2.88E-04**						
	Heteroptera	0.27	0.15	0.088	0.53	0.14	**4.10E-04**	4.06	0.70	**1.30E-06**
	P^2							-0.15		0.83
	P^3							-2.26		**0.0028**
	Anthophila	0.42	0.15	**0.0066**	0.67	0.12	**2.01E-06**	0.76	0.10	**1.14E-08**
	Coleoptera	0.18	0.16	0.25	-0.01	0.16	0.96	0.20	0.16	0.21
	Araneae	0.05	0.16	0.75	0.09	0.16	0.56	0.45	0.14	**0.0035**
	Formicidae	0.08	0.16	0.62	0.25	0.15	0.11	0.56	0.13	**1.41E-04**
	Orthoptera							0.42	0.15	**0.0061**

For comparison with plant richness, flower cover and flower species richness were both aggregated over 3 months. Relations of both flower metrics with arthropod richness (all arthropods and per arthropod group) were modelled separately for April, June and July, using single linear models with scaled variables. Quadratic predictor terms (P^2, P^3) were included when statistically supported ($\Delta AIC_c < 2$).

Table 7C.2 Results of multiple linear models.

Species group	Flower metric	April			June			July		
		slope	p-value	R^2_{adj}	slope	p-value	R^2_{adj}	slope	p-value	R^2_{adj}
Plants	Richness				0.87	**3.57E-13**	0.78			
	Cover				0.04	**0.65**	0.00			
All arthropods	Richness	0.72	**2.32E-07**	0.55	0.67	**1.33E-07**	0.56	0.70	**3.58E-08**	0.72
	Cover	0.09	0.43	0.00	0.28	**0.011**	0.06	0.25	**0.020**	0.03
Diptera	Richness	0.67	**4.04E-06**	0.47	0.47	**0.0030**	0.23	0.74	**9.37E-08**	0.69
	Cover	0.07	0.59	-0.01	0.09	0.53	-0.01	0.14	0.22	0.00
Heteroptera	Richness	0.53	**6.62E-04**	0.30	0.62	**6.77E-07**	0.52	0.50	**9.37E-04**	0.48
	Cover	0.08	0.57	-0.01	0.32	**0.0037**	0.09	0.33	**0.022**	0.06
Anthophila	Richness	0.44	**0.0033**	0.27	0.37	**0.0024**	0.28	0.62	**8.47E-08**	0.71
	Cover	0.26	0.070	0.04	0.55	**2.18E-05**	0.26	0.37	**3.42E-04**	0.08
Coleoptera	Richness	0.26	0.13	0.06	0.02	0.89	-0.03	-0.18	0.38	-0.03
	Cover	0.09	0.58	-0.02	-0.02	0.93	-0.03	0.31	0.13	0.03
Araneae	Richness	0.48	**0.0040**	0.17	0.47	**0.0040**	0.18	0.74	**9.43E-06**	0.51
	Cover	-0.12	0.46	-0.01	-0.06	0.71	-0.02	-0.02	0.91	-0.01
Formicidae	Richness	0.55	**6.98E-04**	0.24	0.67	**4.55E-06**	0.45	0.86	**3.24E-10**	0.75
	Cover	-0.11	0.45	-0.01	0.04	0.76	-0.01	0.02	0.86	-0.01
Orthoptera	Richness							0.89	**1.01E-08**	0.64
	Cover							-0.14	0.26	0.00

Flower cover was included as a second explanatory variable next to flower richness. R^2_{adj} indicates the contribution of each metric to the model's explanatory power. Variables were scaled and exponential terms were not included.

Table 7C.3 Relations of flower richness and flower cover with annual productivity [$GJ \cdot ha^{-1} \cdot yr^{-1}$].

Metric	**Month**	slope	S. E.	p-value	R^2_{adj}
Flower richness	April	-0.06	0.02	**0.0081**	0.15
	June	-25.69	3.44	**6.73E-09**	0.65
	P^2	14.22		**1.95E-04**	0.65
	P^3	-7.53		**0.035**	0.65
	July	-36.13	5.19	**3.26E-08**	0.65
	P^2	23.83		**5.02E-05**	0.65
	P^3	-15.50		**0.0050**	0.65
Flower cover	April	-85.06	69.43	0.23	0.11
	P^2	-163.25		**0.024**	0.11
	June	-0.93	0.43	**0.035**	0.09
	July	-118.34	43.85	**0.010**	0.27
	P^2	136.21		**0.0036**	0.27

Relations were modelled separately for April, June and July using linear models with exponential terms (P^2, P^3) if statistically supported ($\Delta AIC_c < 2$).

Table 7C.4 All flower species recorded, with the cover [%] and number of sites per species

Species	cover	sites	Species	cover	sites	Species	cover	sites
Taraxacum officinale	25.2	39	*Agrimonia eupatoria*	0.1	7	*Vicia cracca*	<0.1	1
Trifolium repens	20.9	36	*Plantago media*	0.1	8	*Rosa arvensis*	<0.1	3
Trifolium pratense	10.3	33	*Lathyrus pratensis*	0.1	3	*Lythrum salicaria*	<0.1	1
Leucanthemum vulgare	6.9	15	*Lamium purpureum*	<0.1	7	*Bryonia dioica*	<0.1	1
Bellis perennis	3.9	25	*Cerastium glomeratum*	<0.1	5	*Thymus pulegioides*	<0.1	1
Medicago lupulina	3.9	15	*Crepis vesicaria*	<0.1	4	*Valeriana officinalis*	<0.1	2
Ranunculus repens	3.8	27	*Cirsium palustre*	<0.1	5	*Salvia verticillata*	<0.1	1
Centaurea jacea	3.8	9	*Pimpinella major*	<0.1	4	*Matricaria chamomilla*	<0.1	2
Ranunculus acris	3.7	22	*Capsella bursa-pastoris*	<0.1	11	*Silene vulgaris*	<0.1	1
Rhinanthus alectorolophus	3.3	9	*Linum catharticum*	<0.1	4	*Euphrasia stricta*	<0.1	1
Ranunculus bulbosus	2.6	8	*Lotus pedunculatus*	<0.1	2	*Veronica filiformis*	<0.1	3
Jacobaea vulgaris	1.4	13	*Platanthera sp.*	<0.1	3	*Campanula rotundifolia*	<0.1	3
Cardamine pratensis	1.0	10	*Vicia sativa*	<0.1	6	*Sonchus asper*	<0.1	4
Lotus corniculatus	0.9	15	*Prunella vulgaris*	<0.1	11	*Clematis vitalba*	<0.1	1
Leontodon hispidus	0.7	8	*Sanguisorba minor*	<0.1	1	*Ajuga reptans*	<0.1	2
Hypochaeris radicata	0.7	8	*Aquilegia vulgaris*	<0.1	1	*Polygala comosa*	<0.1	2
Crepis biennis	0.7	18	*Sambucus nigra*	<0.1	1	*Sherardia arvensis*	<0.1	1
Origanum vulgare	0.6	9	*Cichorium intybus*	<0.1	2	*Hypericum humifusum*	<0.1	1
Crepis capillaris	0.4	15	*Jasione montana*	<0.1	1	*Viola riviniana*	<0.1	1
Galium mollugo	0.4	6	*Glechoma hederacea*	<0.1	7	*Galium pumilum*	<0.1	1
Silene flos-cuculi	0.4	2	*Heracleum sphondylium*	<0.1	2	*Helianthemum nummularium*	<0.1	1
Knautia arvensis	0.3	8	*Campanula trachelium*	<0.1	1			
Daucus carota	0.3	13	*Melilotus altissimus*	<0.1	2	*Myosotis arvensis*	<0.1	1
Medicago sativa	0.3	1	*Campanula persicifolia*	<0.1	1	*Polygala vulgaris*	<0.1	3
Centaurea scabiosa	0.3	3	*Clinopodium vulgare*	<0.1	5	*Verbena officinalis*	<0.1	3
Trifolium dubium	0.3	5	*Sisymbrium officinale*	<0.1	2	*Melilotus officinalis*	<0.1	1
Cerastium fontanum	0.2	27	*Cardamine hirsuta*	<0.1	6	*Vicia sepium*	<0.1	2
Primula veris	0.2	5	*Echium vulgare*	<0.1	1	*Allium scorodoprasum*	<0.1	1
Dactylorhiza fuchsii	0.2	3	*Cytisus scoparius*	<0.1	1	*Astragalus glycyphyllos*	<0.1	1
Stellaria media	0.2	12	*Veronica arvensis*	<0.1	13	*Stellaria aquatica*	<0.1	1
Scabiosa columbaria	0.2	2	*Veronica serpyllifolia*	<0.1	5	*Hieracium pilosella*	<0.1	1
Gymnadenia conopsea	0.1	3	*Genista tinctoria*	<0.1	1	*Anthyllis vulneraria*	<0.1	1
Ononis spinosa	0.1	3	*Geranium molle*	<0.1	3	*Fragaria vesca*	<0.1	1
Rhinanthus minor	0.1	5	*Filipendula ulmaria*	<0.1	1	*Orchis purpurea*	<0.1	1
Galium verum	0.1	3	*Rubus sp.*	<0.1	4	*Neottia ovata*	<0.1	1
Convolvulus arvensis	0.1	8	*Cirsium vulgare*	<0.1	5	*Polygonum aviculare*	<0.1	1
Anthriscus sylvestris	0.1	6	*Veronica persica*	<0.1	5	*Allium vineale*	<0.1	1
Hypericum perforatum	0.1	5	*Tragopogon pratensis*	<0.1	2	*Polygonatum multiflorum*	<0.1	1
Trifolium hybridum	0.1	3	*Cirsium arvense*	<0.1	2	*Hypericum hirsutum*	<0.1	1
Achillea millefolium	0.1	5	*Lamium album*	<0.1	1	*Geranium dissectum*	<0.1	1
Veronica chamaedrys	0.1	7	*Malva moschata*	<0.1	1	*Geranium pusillum*	<0.1	1

Table 7C.5 All plant species recorded with the number of sites per species

Species	sites	Species	sites	Species	sites
Acer Platanoides	1	*Eleocharis palustris*	1	*Plantago media*	4
Acer campestre	2	*Elymus repens*	4	*Platanthera chlorantha*	1
Achillea millefolium	8	*Epilobium tetragonum*	1	*Poa annua*	3
Agrimonia eupatoria	3	*Equisetum arvense*	5	*Poa pratensis*	18
Ajuga reptans	2	*Festuca rubra*	10	*Poa trivialis*	33
Alopecurus pratensis	9	*Ficaria verna*	1	*Polygala comosa*	2
Angelica sylvestris	1	*Fraxinus excelsior*	3	*Populus sp.*	1
Anisantha sterilis	4	*Galium aparine*	1	*Poterium sanguisorba*	2
Anthoxanthum odoratum	5	*Galium mollugo*	3	*Primula veris*	4
		Galium pumilum	1	*Prunella vulgaris*	3
Anthriscus sylvestris	3	*Galium verum*	3	*Quercus robur*	2
Aquilegia vulgaris	1	*Genista tinctoria*	1	*Ranunculus acris*	16
Arrhenatherum elatius	15	*Geranium dissectum*	3	*Ranunculus bulbosus*	10
Avenula pubescens	7	*Geranium molle*	2	*Ranunculus repens*	22
Bellis perennis	16	*Glechoma hederacea*	11	*Rhinanthus alectorolophus*	8
Betula pendula	1	*Glyceria fluitans*	4		
Brachypodium pinnatum	1	*Gymnadenia conopsea*	1	*Rhinanthus minor*	2
Briza media	4	*Heracleum sphondylium*	10	*Rosa arvensis*	1
Bromopsis erecta	5	*Hieracium sp.*	2	*Rosa canina*	1
Bromus hordeaceus	29	*Holcus lanatus*	28	*Rubus fruticosus*	5
Bryonia dioica	1	*Hypochaeris radicata*	1	*Rumex acetosa*	14
Campanula trachelium	1	*Jacobaea vulgaris*	8	*Rumex acetosella*	1
Capsella bursa-pastoris	5	*Juncus effusus*	4	*Rumex obtusifolius*	8
Cardamine pratensis	7	*Juncus inflexus*	3	*Salvia verticillata*	1
Carex acuta	1	*Knautia arvensis*	6	*Scabiosa columbaria*	1
Carex flacca	4	*Lathyrus pratensis*	3	*Schedonorus arundinaceus*	7
Carex hirta	4	*Leontodon hispidus*	3		
Carex obtusa	1	*Leucanthemum vulgare*	10	*Schoenoplectus sp.*	1
Carex rostrata	1	*Linum catharticum*	3	*Silene flos-cuculi*	1
Centaurea jacea	12	*Lolium multiflorum*	3	*Sisymbrium officinale*	1
Centaurea scabiosa	3	*Lolium perenne*	33	*Sonchus asper*	5
Cerastium fontanum	22	*Lotus corniculatus*	8	*Stellaria media*	7
Cerastium glomeratum	1	*Lotus pedunculatus*	1	*Succisa pratensis*	3
Cichorium intybus	1	*Luzula campestris*	1	*Taraxacum agg.*	38
Cirsium arvense	8	*Matricaria discoidea*	1	*Tragopogon pratensis*	4
Cirsium oleraceum	1	*Medicago lupulina*	14	*Trifolium dubium*	1
Cirsium palustre	1	*Medicago sativa*	1	*Trifolium pratense*	28
Cirsium vulgare	5	*Ononis spinosa*	3	*Trifolium repens*	30
Convolvulus arvensis	2	*Orchis militaris*	1	*Trisetum flavescens*	4
Convolvulus sepium	1	*Origanum vulgare*	5	*Urtica dioica*	3
Cornus sanguinea	1	*Orobanche minor*	1	*Veronica arvensis*	7
Crataegus monogyna	5	*Persicaria amphibia*	1	*Veronica chamaedrys*	4
Crepis biennis	6	*Persicaria hydropiper*	1	*Veronica filiformis*	1
Crepis vesicaria	8	*Phleum pratense*	1	*Veronica serpyllifolia*	5
Cynosurus cristatus	3	*Pimpinella major*	6	*Vicia cracca*	1
Dactylis glomerata	20	*Pimpinella saxifraga*	4	*Vicia hirsuta*	3
Dactylorhiza fuchsii	2	*Plantago lanceolata*	24	*Vicia sativa*	10
Daucus carota	11	*Plantago major*	2	*Viola odorata*	1

Table 7C.6 All arthropod species recorded with the number of sites per species

Species	sites
Anthophila	
Andrena afzeliella	1
Andrena argentata	1
Andrena aurulenta	1
Andrena bicolor	1
Andrena chrysosceles	4
Andrena cineraria	11
Andrena dorsata	4
Andrena flavipes	12
Andrena gravida	7
Andrena haemorrhoa	16
Andrena hattorfiana	5
Andrena helvola	1
Andrena humilis	1
Andrena labialis	4
Andrena labiata	1
Andrena lathyri	1
Andrena minutula	7
Andrena minutuloides	3
Andrena nitida	5
Andrena nitidiuscula	1
Andrena ovatula	2
Andrena proxima	1
Andrena subopaca	4
Andrena vaga	2
Andrena viridescens	1
Andrena wilkella	9
Anthidium manicatum	1
Anthidium oblongatum	1
Anthidium punctatum	1
Apis mellifera	33
Bombus campestris	1
Bombus hortorum	15
Bombus hypnorum	4
Bombus lapidarius	37
Bombus lucorum	1
Bombus pascuorum	31
Bombus pratorum	5
Bombus rupestris	1
Bombus terrestris-group	19
Bombus vestalis	12
Ceratina cyanea	1
Chelostoma campanularum	1
Chelostoma distinctum	1
Chelostoma florisomne	1
Eucera nigrescens	1
Halictus quadricinctus	7
Halictus scabiosae	10
Halictus tumulorum	8
Heriades truncorum	3
Hoplitis adunca	1
Hylaeus brevicornis	1
Hylaeus dilatatus	4
Hylaeus gredleri	1
Hylaeus styriacus	1
Lasioglossum albipes	2
Lasioglossum calceatum	8
Lasioglossum fulvicorne	3
Lasioglossum laticeps	7
Lasioglossum lativentre	2
Lasioglossum leucozonium	3
Lasioglossum malachurum	14
Lasioglossum morio	6
Lasioglossum pallens	1
Lasioglossum pauxillum	22
Lasioglossum punctatissimum	2
Lasioglossum quadrinotatum	1
Lasioglossum sexnotatum	1
Lasioglossum villosulum	5
Megachile centuncularis	2
Megachile ericetorum	1
Megachile versicolor	1
Megachile willughbiella	2
Melitta leporina	8
Nomada bifasciata	3
Nomada conjungens	1
Nomada fabriciana	3
Nomada flava	1
Nomada flavoguttata	1
Nomada flavopicta	2
Nomada sheppardana	1
Nomada spec.	1
Osmia bicornis	4
Osmia cornuta	1
Osmia spinulosa	2
Panurgus calcaratus	3
Sphecodes ephippius	1
Sphecodes puncticeps	1
Sphecodes rubicundus	2
Araneae	
Agalenatea redii	1
Agyneta decora	1
Agyneta rurestris	9
Alopecosa pulverulenta	1
Anelosimus spec.	1
Anelosimus vittatus	25
Araeoncus humilis	11
Araniella cucurbitina	3
Argenna subnigra	1
Argiope bruennichi	14
Bathyphantes gracilis	22
Bathyphantes spec.	1
Centromerus spec.	1
Cercidia prominens	1
Cicurina cicur	1
Clubiona reclusa	1
Clubiona terrestris	2
Cnephalocotes obscurus	1
Collinsia inerrans	2
Dictyna latens	3
Dictyna pusilla	2
Dictyna uncinata	1
Dicymbium tibiale	1
Diplocephalus graecus	1
Diplostyla concolor	3
Dipoena melanogaster	1
Enoplognatha latimana	10
Enoplognatha ovata	3
Enoplognatha thoracica	1
Erigone atra	29
Erigone dentipalpis	37
Ero aphana	1
Gnathonarium dentatum	1
Heliophanus flavipes	9
Hypsosinga sanguinea	1
Lathys humilis	2
Lepthyphantes tenuis	24
Mangora acalypha	36
Maso sundevalli	2
Meioneta rurestris	19
Mermessus trilobatus	8
Metellina mengei	1
Microlinyphia pusilla	26
Milleriana inerrans	2
Misumena vatia	6
Neottiura bimaculata	12
Neriene peltata	1
Nigma flavescens	2
Oedothorax apicatus	2
Oedothorax fuscus	7
Oedothorax retusus	1
Ozyptila praticola	1
Pachygnatha clercki	1
Pachygnatha degeeri	24
Panamomops sulcifrons	1
Pardosa amentata	1
Pardosa palustris	12
Pardosa prativaga	2
Pardosa proxima	4
Pardosa pullata	2
Pardosa tenuipes	4
Phalangium opilio	5
Philodromus buxi	1
Philodromus cespitum	2
Philodromus praedatus	1
Philodromus rufus	1
Phylloneta impressa	10
Phylloneta sisyphia	2
Pisaura mirabilis	2
Porrhomma microphthalmum	5
Tenuiphantes tenuis	39
Tetragnatha extensa	5
Theridion pallens	8
Tibellus oblongus	3
Tiso vagans	15
Xysticus acerbus	3
Xysticus bifasciatus	1
Xysticus cristatus	10
Xysticus kochi	9
Xysticus lanio	2
Zilla diodia	2
Coleoptera	
Adalia bipunctata	1
Adalia decimpunctata	1
Adrastus limbatus	10
Adrastus pallens	2
Adrastus rachifer	5
Agelastica alni	6

Species	sites
Agriotes gallicus	31
Agriotes lineatus	5
Agriotes obscurus	11
Agriotes pallidulus	1
Agriotes sputator	2
Agriotes ustulatus	11
Agrypnus murinus	9
Altica spec.	15
Ampedus pomorum	1
Aphthona atrovirens	1
Aphthona nonstriata	2
Aphthona spec.	1
Athous bicolor	16
Athous haemorrhoidalis	2
Athous subfuscus	22
Athous vittatus	1
Bruchidius varius	13
Calomicrus circumfusus	1
Cantharis flavilabris	1
Cantharis fusca	6
Cantharis lateralis	7
Cantharis nigra	8
Cantharis nigricans	2
Cantharis rufa	9
Cantharis rustica	1
Cassida rubiginosa	2
Cassida sanguinolenta	1
Cassida vibex	1
Chaetocnema hortensis	27
Chaetocnema picipes	3
Chaetocnema spec.	3
Chrysolina polita	1
Cidnopus pilosus	5
Coccidula rufa	1
Coccinella septempunctata	40
Crepidodera aurata	2
Cryptocephalus aureolus	4
Cryptocephalus moraei	2
Cryptocephalus pygmaeus	5
Cryptocephalus vittatus	4
Derocrepis rufipes	1
Epitrix pubescens	2
Harmonia axyridis	3
Hemicrepidius hirtus	13
Hemicrepidius niger	1
Hippodamia variegata	7
Hippuriphila modeeri	1
Hispa atra	4
Labidostomis longimana	2
Longitarsus dorsalis	8
Longitarsus spec.	25
Luperus luperus	3
Malthinus balteatus	1
Melanotus villosus	14
Neocrepidodera ferruginea	1
Neocrepidodera spec.	1
Neocrepidodera transversa	13
Oulema melanopus	1
Oulema obscura	7
Oulema spec.	6
Phaedon cochleariae	1
Phratora vitellinae	2
Phyllotreta atra	1
Phyllotreta exclamationis	2
Phyllotreta undulata	1
Phyllotreta vittula	34
Plagiodera versicolora	1
Podagrica fuscicornis	1
Prasocuris glabra	2
Procraerus tibialis	1
Propylea quatuordecimpunctata	29
Psylliodes picina	1
Psylliodes spec.	2
Psyllobora vigintiduopunctata	4
Rhagonycha fulva	19
Rhyzobius chrysomeloides	3
Rhyzobius litura	2
Scymnus apetzi	1
Scymnus haemorrhoidalis	1
Scymnus interruptus	3
Scymnus spec.	7
Selatosomus aeneus	1
Sphaeroderma rubidum	1
Sphaeroderma testaceum	3
Synaptus filiformis	1
Tytthaspis sedecimpunctata	33
Diptera	
Acanthiophilus helianthi	3
Bibio johannis	15
Bibio lanigerus	1
Campiglossa misella	1
Campiglossa producta	2
Chaetorellia jaceae	8
Cheilosia aerea	1
Cheilosia albitarsis	2
Cheilosia bergenstammi	2
Cheilosia caerulescens	1
Cheilosia cynocephala	1
Cheilosia pagana	4
Cheilosia proxima	3
Cheilosia spec.	2
Cheilosia vernalis	4
Chloromyia formosa	22
Chorisops tibialis	1
Chrysopilus cristatus	3
Chrysotoxum bicinctum	2
Chrysotoxum festivum	2
Coremacera marginata	3
Dilophus febrilis	10
Dilophus humeralis	1
Dioctria atricapilla	1
Dioctria hyalipennis	3
Dioctria lateralis	1
Dioctria rufipes	2
Dithryca guttularis	1
Epeolus variegatus	1
Epistrophe eligans	1
Episyrphus balteatus	24
Eristalis arbustorum	1
Eristalis intricaria	3
Eristalis nemorum	9
Eristalis tenax	16
Euleia heraclei	1
Eumerus ornatus	2
Eumerus strigatus	2
Eumerus tricolor	4
Eupeodes corollae	22
Eupeodes latifasciatus	3
Eupeodes luniger	8
Geomyza balachowskyi	4
Geomyza tripunctata	21
Geomyza venusta	1
Haematopota crassicornis	1
Haematopota italica	1
Haematopota pluvialis	7
Helophilus pendulus	2
Helophilus trivittatus	2
Herina nigrina	6
Herina palustris	1
Hydromya dorsalis	1
Lejogaster metallina	1
Leptogaster cylindrica	11
Limnia unguicornis	20
Machimus rusticus	1
Melanogaster hirtella	4
Melanogaster nuda	5
Melanostoma mellinum	31
Melanostoma scalare	10
Meliscaeva auricollis	1
Merodon equestris	2
Microchrysa flavicornis	4
Microchrysa polita	3
Myathropa florea	3
Nemotelus pantherinus	9
Nephrotoma analis	1
Nephrotoma appendiculata	9
Nephrotoma cornicina	1
Nephrotoma flavescens	5
Oplodontha viridula	1
Opomyza florum	4
Opomyza germinationis	28
Orthonevra brevicornis	1
Orthonevra nobilis	2
Pachygaster atra	3
Paragus albifrons	1
Paragus haemorrhous	2
Paragus pecchiolii	1
Pherbellia cinerella	18
Pherbellia griseola	1
Pherbellia schoenherri	4
Physiphora alceae	1
Pipiza lugubris	1
Pipiza noctiluca	1
Pipizella annulata	4
Pipizella spec.	2
Pipizella viduata	11
Pipizella virens	1
Platycheirus albimanus	11

Species	sites
Platycheirus clypeatus	5
Platycheirus fulviventris	1
Platycheirus ocultus	1
Platycheirus peltatus	1
Platystoma seminationis	1
Pyrophaena rosarum	1
Rhagio scolopaceus	4
Rhingia campestris	11
Rivellia syngenesiae	6
Scaeva pyrastri	3
Scaeva selenitica	2
Sicus ferrugineus	2
Sphaerophoria scripta	32
Sphaerophoria spec.	2
Sphaerophoria taeniata	17
Sphenella marginata	3
Syritta pipiens	5
Syrphus ribesii	16
Syrphus torvus	5
Syrphus vitripennis	9
Tabanus bromius	9
Tephritis crepidis	11
Tephritis formosa	1
Tephritis matricariae	11
Tephritis neesii	10
Tephritis spec.	1
Tephritis vespertina	5
Terellia longicauda	1
Terellia winthemi	1
Tetanocera arrogans	4
Tetanocera spec.	1
Thecophora cinarescens	4
Thecophora jakutica	2
Thecophora spec.	1
Tipula luteipennis	2
Tipula vernalis	6
Tolmerus cingulatus	4
Urophora quadrifasciata	9
Urophora stylata	6
Xanthogramma citrofasciatum	2
Xanthogramma pedissequum	2
Formicidae	
Dolichoderus quadripunctatus	1
Formica cunicularia	13
Formica fusca	1
Formica rufa	1
Formica rufibarbis	6
Lasius flavus	6
Lasius niger	40
Lasius platythorax	5
Lasius umbratus	1
Myrmica rubra	10
Myrmica ruginodis	1
Myrmica sabuleti	8
Myrmica scabrinodis	8
Myrmica schencki	2
Tapinoma erraticum	1

Species	sites
Tetramorium caespitum	1
Heteroptera	
Acetropis carinata	1
Acetropis gimmerthalii	3
Adelphocoris lineolatus	14
Adelphocoris quadripunctatus	3
Adelphocoris seticornis	10
Aelia acuminata	3
Agramma laetum	2
Amblytylus nasutus	24
Anthocoris spec.	3
Atractotomus mali	1
Berytinus clavipes	2
Berytinus minor	10
Brachycarenus tigrinus	2
Capsus ater	26
Carpocoris fuscispinus	1
Carpocoris purpureipennis	7
Charagochilus gyllenhalii	1
Chartoscirta cocksii	1
Chlamydatus pulicarius	1
Closterotomus fulvomaculatus	2
Closterotomus norwegicus	28
Coreus marginatus	4
Coriomeris denticulatus	2
Corizus hyoscyami	2
Criocoris crassicornis	1
Cymus claviculus	1
Cymus melanocephalus	5
Deraeocoris flavilinea	1
Deraeocoris ruber	5
Derephysia sinuatocollis	1
Dicyphus annulatus	3
Dicyphus errans	1
Dolycoris baccarum	13
Drymus ryeii	6
Drymus sylvaticus	4
Eurydema oleracea	1
Eurygaster testudinaria	2
Gampsocoris punctipes	1
Globiceps fulvicollis-flavomaculatus	9
Halticus apterus	5
Halticus luteicollis	1
Heterocordylus genistae	1
Heterocordylus tibialis	2
Heterocordylus tumidicornis	1
Heterotoma planicornis	1
Himacerus major	1
Himacerus mirmicoides	2
Kalama tricornis	6
Kleidocerys resedae	1
Leptopterna dolabrata	29
Leptopterna ferrugata	1
Liocoris tripustulatus	1
Lopus decolor	4
Lygocoris pabulinus	1
Lygus maritimus	18

Species	sites
Lygus pratensis	32
Lygus rugulipennis	36
Macrodema microptera	1
Macrotylus paykullii	2
Megaloceroea recticornis	12
Megalocoleus molliculus	1
Megalonotus antennatus	1
Metopoplax ditomoides	1
Miridius quadrivirgatus	3
Nabis ericetorum	3
Nabis ferus-pseudoferus	35
Nabis limbatus	1
Nabis rugosus	6
Neides tipularius	1
Notostira elongata	40
Nysius huttoni	3
Nysius senecionis	1
Oncotylus viridiflavus	6
Orius spec.	35
Orius vicinus	1
Orthocephalus coriaceus	8
Orthocephalus saltator	7
Orthonotus rufifrons	2
Orthops basalis	4
Orthops campestris	5
Pachytomella parallela	4
Peribalus strictus	3
Peritrechus geniculatus	1
Phytocoris varipes	7
Picromerus bidens	1
Piezodorus lituratus	1
Pinalitus cervinus	1
Pithanus maerkelii	2
Plagiognathus arbustorum	8
Plagiognathus chrysanthemi	24
Podops inuncta	2
Polymerus nigrita	1
Polymerus unifasciatus	1
Psallus spec.	2
Pyrrhocoris apterus	2
Rhopalus parumpunctatus	1
Rhopalus subrufus	2
Salduda saltatoria	4
Scolopostethus decoratus	1
Stenodema calcarata	24
Stenodema laevigata	16
Stenotus binotatus	18
Stictopleurus abutilon	3
Stictopleurus punctatonervosus	4
Syromastus rhombeus	1
Temnostethus pusillus	1
Tingis cardui	2
Trigonotylus caelestialium	29
Trigonotylus ruficornis	11
Orthoptera	
Chorthippus albomarginatus	3
Chorthippus biguttulus	17
Chorthippus brunneus	5
Chorthippus spec.	1

Species	sites
Chrysochraon dispar	2
Conocephalus dorsalis	1
Conocephalus fuscus	10
Leptophyes punctatissima	1
Oecanthus pellucens	1
Phaneroptera falcata	2
Pholidoptera griseoaptera	2
Pseudochorthippus parallelus	34
Roeseliana roeselii	12
Stenobothrus lineatus	1
Stethophyma grossum	2
Tetrix subulata	3
Tetrix tenuicornis	4
Tetrix undulata	4
Tettigonia viridissima	4

7.4 Appendix D

Supplement to chapter 5, "Productivity and plant species identity shape the effects of mowing on the flowering of grassland forbs"

Table 7D.1 Characteristics of the 12 sampled grasslands.

Site	**Area** [ha]	**Cuts** [year^{-1}]	**Land use**	**Flower diversity**	**Productivity** [g·m^{-2}]	**Fertilization** [kg N·ha^{-1}·yr^{-1}]	**Manual input** [g·m^{-2}]
1	1.9	2	Hay, conservation	21	298	0	0
2	4.0	2	Hay, conservation	35	342	0	0
3	6.9	2	Hay, conservation	18	378	0	0
4	1.0	2	Hay, conservation	8	400	0	0
5	1.6	2	Hay, AES	14	417	0	0
6	3.1	2	Hay, AES	15	459	0	0
7	3.4	2	Hay, AES	11	474	0	0
8	1.4	2	Hay, AES	15	591	0	0
9	1.9	5	Silage, organic	15	657	84.7	72.4
10	6.0	5	Silage, conventional	7	689	302.9	268.3
11	2.0	5	Silage, conventional	10	899	241.5	178.0
12	1.0	5	Silage, conventional	9	971	229.0	140.3

Land use ranged from unfertilized hay meadows under nature conservation or agri-environmental schemes (AES), that were cut twice a year, to fertilized meadows for silage production that were typically cut five times per year. Flower diversity gives the total number of species recorded at each site. Productivity represents the summed dry weight collected upon the first cuts of treatment 1-3 (excluding the unmown controls) at each site. Manual inputs were applied to the plots in order to mimic slurry inputs that were applied by the farmer during the experiment (grams of Culterra 10-4-6 organic fertilizer pellets).

Table 7D.2 Overview of the main flowering species with responses to mowing and productivity.

Species	Percentual cover [%]	Mean date [m-d]	Productivity range & center point	Relative recovery after mowing		
				1 cut	2 cuts	3 cuts
Odontites vulgaris	0.1	8-11		0.092	0.059	0
Daucus carota	4.7	8-3		0.23	0.12	0.037
Medicago lupulina	1.4	6-19		0.20	0.25	0.34
Prunella vulgaris	0.1	7-28		0.29	0.22	0.59
Pimpinella saxifraga	< 0.1	8-8		2.8	0	0
Primula veris	0.7	4-26		-	-	-
Centaurea jacea	1.2	7-11		0.0035	0.0039	0.0010
Leucanthemum vulgare	7.9	6-8		0.014	0.0035	4.6E-04
Galium mollugo	0.5	6-9		0.32	0.037	4.2E-04
Orobanche minor	0.1	6-5		Inf	1.8	0.87
Lotus corniculatus	0.7	7-23		0.83	0.61	0.19
Rhinantus alectorolophus	20.0	5-24		0	0	0.0072
Ranunculus bulbosus	5.9	5-11		-	0	0.0082
Crepis capillaris	0.1	7-8		0	1.2	0.54
Plantago lanceolata	1.6	6-22		6.5	1.8	0.92
Crepis biennis	3.2	6-7		1.0	0.25	0.10
Ranunculus repens	0.4	5-26		0	0.029	0.10
Veronica arvensis	< 0.1	5-3		-	0	0
Trifolium dubium	0.7	5-31		0.33	0.14	0.18
Vicia hirsuta	0.1	5-26		-	0	0.0070
Bellis perennis	7.3	5-11		7.8	3.0	1.1
Trifolium repens	7.5	7-7		5.4	4.7	6.3
Trifolium pratense	6.1	6-15		3.4	0.21	0.10
Vicia sativa	0.3	5-23		-	0.012	0.013
Glechoma hederacea	< 0.1	4-30		-	0	0
Cerastium fontanum	0.5	5-27		0.12	0.18	0.12
Heracleum sphondylium	0.1	8-10		1.1	0.40	0
Taraxacum agg.	26.4	4-27		Inf	-	9.6
Ranunculus acris	0.8	5-24		4.9	0	0
Geranium dissectum	< 0.1	6-13		0.75	0	0.29
Lamium purpureum	0.4	5-12		Inf	5.1	0.7
Cardamine hirsuta	0.1	4-24		-	-	-
Stellaria media	0.3	5-14		54.0	0.10	0.18
Capsella bursa-pastoris	< 0.1	7-9		Inf	2.0	3.6

Species-specific percentual cover over all sites, mean date of flowering (month-day: weighted by the numbers of flowers), distribution on the sampled productivity gradient, and extent of flower recovery after mowing under three mowing regimes are given. The 34 species listed here were recorded in sufficient detail to assess recovery after mowing (>10 records of >200 individual flower heads in total). Distributions on the productivity gradient indicate species' ranges and center points (green dots) relative to the mean productivity of the sampling sites (dashed line: 548 $g \cdot m^{-2}$). For each species, the range indicates the minimum and maximum productivity and the center point indicates the mean productivity (weighted by the numbers of flowers) at which it was recorded. Relative recovery after mowing was quantified by dividing the AUC over the recovery period (i.e. past the first cut for each mowing regime) by the AUC of the unmown plots over the same period (i.e. 1 represents full recovery). Poor recovery (<0.05) was colored orange, partial recovery (0.05-1) was colored yellow and full recovery (>1) was colored green. Hyphens indicate that the species flowered neither in the mown plots nor the unmown plots during the recovery period, 'Inf' indicates that the species flowered only in the mown plots (usually only marginally).

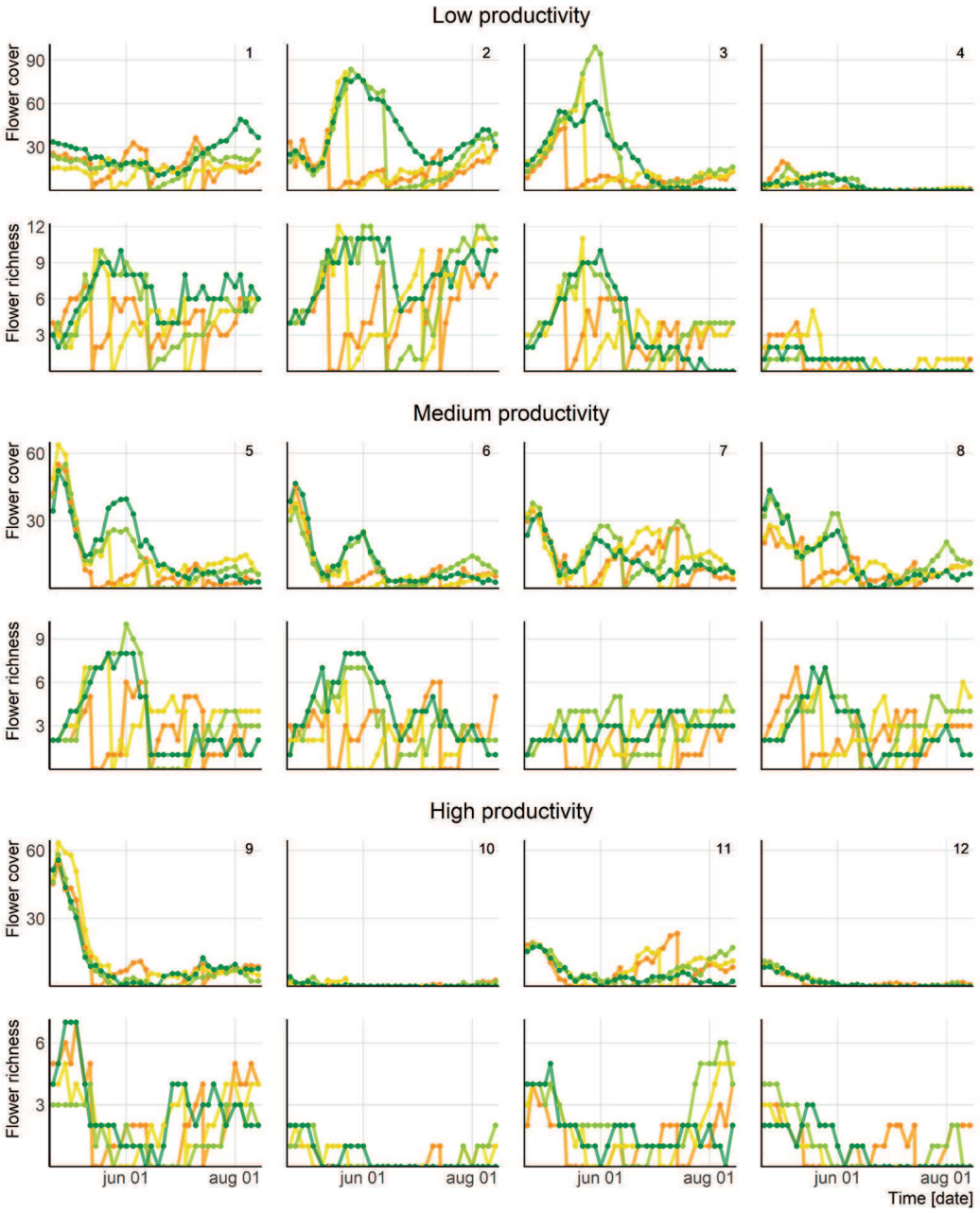

Fig. 7D.1 Curves of flower cover (square root transformed) and flower species richness for each site during the full sampling period (April 20th until August 15th). Sites are numbered 1-12 and are arranged by productivity level from left to right, and from top to bottom in classes of low productivity (300-400 g·cm^{-2}), medium productivity (420-590 g·cm^{-2}) and high productivity (660-970 g·cm^{-2}). Colors indicate the four mowing regimes with zero (dark green), one (light green), two (yellow) and three (orange) cuts during the sampling period. These curves were used to determine the summed daily flower richness or flower cover (area under the curve) and the recovery rates of flower richness and flower cover (slope of the curve over 21 days after mowing).

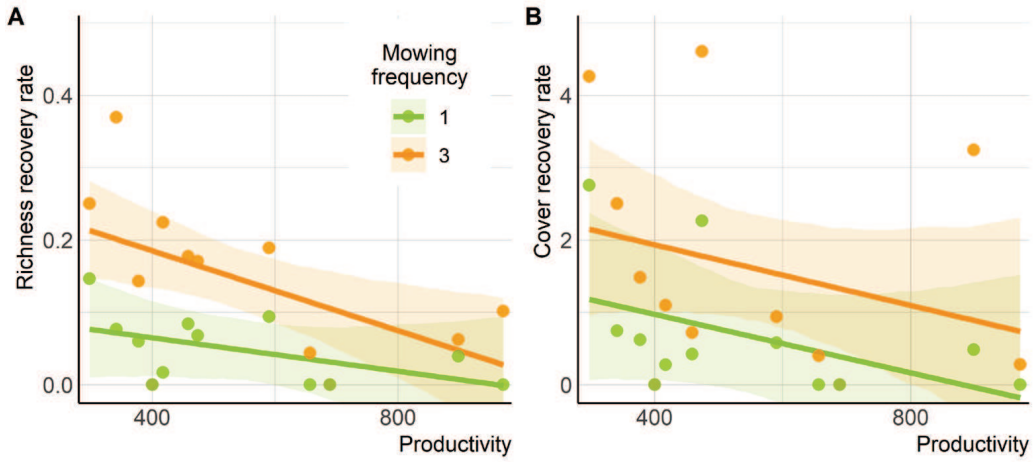

Fig. 7D.2 Recovery rates of flower richness [species·day^{-1}] (A) and flower cover [cm^2·day^{-1}] (B) after mowing for the two cuts that were timed during June 13th-15th, in relation to productivity [g·cm^{-2}] and mowing frequency. These models evaluated whether the patterns shown in Fig. 4 persisted in June, or whether they were influenced by the timing of the one-cut regime during prolonged dry weather. Flower richness recovery was significantly related to mowing regime (p=0.002; partial R^2_m=0.25) and productivity (p=0.03; partial R^2_m=0.20) without significant interaction (p=0.16; partial R^2_m=0.03); Flower cover recovery was significantly related to mowing regime (p=0.002; partial R^2_m=0.14) but not to productivity (p=0.2; partial R^2_m=0.09) nor the interaction term (p=0.8; partial R^2_m=0). Model R^2_m was 0.45 resp. 0.23.



EIGHT

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A

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9 Summary

Agriculture has become the leading cause of global environmental change and biodiversity loss, threatening the resilience of ecosystems around the globe. Grassland ecosystems, most of which are nowadays maintained by humans for livestock keeping, have suffered particularly severe habitat and biodiversity declines. This also threatens the delivery of a wide range of ecosystem services that underpin human well-being and agriculture itself. Therefore, governments and public organizations aim to restore degraded grassland ecosystems, but their actions have so far not resolved the main causes of degradation. For example, Europe's agri-environmental policies already exist for decades but the intensive land use practices that erode the continent's rich grassland biodiversity, including high fertilization inputs, stocking rates and harvesting frequencies, are still expanding. Despite substantial research emphasis on the advantages of biodiversity for agriculture, farmers remain reluctant to adopt biodiversity-friendly practices at a larger scale. In this thesis, I investigated socio-economic and management-related constraints to more effective restoration of biodiversity and ecosystem service delivery on managed grasslands. All chapters are based on data collected in a study area in the south of the Netherlands where land use ranges from very extensively used semi-natural grasslands to highly intensive production grasslands. This gradient reflects the land use intensification trend that takes place in managed grasslands across the world's temperate regions.

Starting from a broad socio-economic perspective, this thesis evaluated whether restoring biodiversity-based ecosystem services creates win-wins or trade-offs between grassland farmers and society (chapter 2). A broad range of ecosystem service indicators was measured in the field, and interviews with farmers were conducted to assess each grasslands' management and annual production. Next, its contribution to the income of farmers was estimated by the gross margin of forage production at field level. Of all investigated ecosystem services, only nitrogen fixation by legumes contributed significantly to grassland productivity, and this contribution was minor compared to the effect of fertilization. Farmer income was largely determined by productivity and traded off strongly with biodiversity, nutrient retention and carbon sequestration, all of which are public goods. Multiple public goods increased in parallel with biodiversity. This implies that the restoration of grassland ecosystems benefits society but not farmers. Therefore, ecological restoration programs require societal support that makes the delivery of public goods economically rewarding.

Biodiversity underpins the supply of multiple public goods, but the impacts of land use intensification on many taxonomic groups remain understudied, especially among arthropods. Therefore, chapter 3 investigated the effects of land use intensification on grassland arthropods in a space-for-time study. Land use intensity

was measured by annual productivity, and arthropods were surveyed in May, June and July along fixed transects by sweep-netting and pollinator counts. All specimens were counted per order and a broad selection of groups was identified to species level. From low to high intensity levels, Diptera numbers increased and stabilized overall arthropod abundance, while most other orders declined sharply in abundance and overall species richness halved. Further insight was obtained by examining the distributions of individual species along the sampled land use intensity gradient. At high intensity levels, most species declined or disappeared completely (85% resp. 64% of all identified species), but a small group of widespread species (9%) increased. It is probable that such 'winners' cause the stability of overall abundance levels. Furthermore, these species-level analyses revealed stronger biodiversity losses than more widely used diversity metrics. The highest losses occurred between low and medium levels of land use intensity. This means that low-intensity grasslands, which are nearly lost in many agricultural landscapes, are crucial for most arthropod species.

The laboriousness of biodiversity inventories severely constrains the scale of current biodiversity evaluations. Therefore, chapter 4 examined whether flower metrics can be used as general biodiversity indicators for arthropods and plants in grasslands. In parallel to the arthropod surveys presented in chapter 3, plant and flower species richness and total flower cover were surveyed along the same fixed transects. Flower richness showed consistent linear relations with plant and arthropod species richness. Flower cover showed more variable relations with plant and arthropod richness, and if linear these relations were largely explained by flower richness as well. Flower richness also reflected the increase of arthropod richness from spring to summer and its exponential decline with increasing land-use intensity. Therefore, flower richness qualifies as a broadly representative indicator of grassland biodiversity. This can facilitate the evaluation of restoration outcomes because flower richness can be measured efficiently across large areas, but is also directly relatable to site-level management decisions.

When relevant indicators are measured at site level, they can also be used to tailor restoration measures at a local basis. This thesis tested whether the effect of reduced mowing on grassland flowers depends on productivity and floral composition (chapter 5). In twelve grasslands with varying productivity levels, four test plots were set up in which each forb species' flower cover was recorded every few days during the main growing season (April-August), while the plots were mown zero to three times. Hence, both the cover and richness of flowering forbs could be traced over time in each plot. The results showed that reduced mowing only enhanced flowering at lower productivity levels, but flower recovery after mowing also went faster at lower productivity levels. These responses are probably both driven by the increased competition for light at high productivity levels, which suppresses flowering but also enhances the impact of mowing. Furthermore, effects of mowing were strongly dependent on the phenology and recovery potential of local forb species. Only a few species recovered fully under frequent mowing

regimes, but half of all species recovered fully after a single spring cut. Restoration outcomes can therefore be improved by tailoring mowing regimes to the site-specific floral composition. Possible adjustments include to retain uncut refuges that preserve late-flowering species in low-productive habitats, and partial spring cuttings to promote flower regrowth from July onwards.

The restoration of biodiversity-rich grassland ecosystems requires a drastic extensification of modern land use practices. Financial rewards for public goods can enable farmers to do so. Society, not individual farmers, must therefore take responsibility for the public goods that these ecosystems provide. In most modern agricultural landscapes, safeguarding public goods requires increased areas of restored grassland habitats, especially of high-quality habitats that sustain the majority of grassland biodiversity. However, most current restoration efforts do not succeed to restore desirable habitat qualities. Adverse influences from surrounding land use, but also knowledge gaps and suboptimal management strategies impair the effectiveness of current restoration schemes, such as Europe's agri-environment schemes. These schemes can be improved by tailoring their management to site-specific conditions, and result-based payments can motivate farmers for this, provided that restoration outcomes are measured across contracted fields. This requires a more thorough understanding of understudied taxa as well as large-scale evaluation of broadly applicable biodiversity indicators. Furthermore, ecosystem restoration needs to be integrated with sustainable food production systems in landscape-level management plans that optimize the allocation of the different functions that landscapes provide. With appropriate spatial planning, locally tailored management and fair financial support, managed grasslands can support both food security, ecosystem functions and biodiversity in accordance.

10 Samenvatting

De landbouw is wereldwijd de hoofdoorzaak van milieuverandering en biodiversiteitsverlies, waardoor de veerkracht van ecosystemen bedreigd wordt. Graslanden, die tegenwoordig grotendeels worden gebruikt voor de veehouderij, kennen een bijzonder ernstige achteruitgang van natuurlijke habitats en biodiversiteit. Deze achteruitgang bedreigt ook een breed scala aan ecosysteemdiensten die essentieel zijn voor het menselijk welzijn en de landbouw zelf. Overheden en publieke organisaties streven daarom naar herstel van gedegradeerde graslandecosystemen. Hun inspanningen hebben de belangrijkste oorzaken van degradatie tot nog toe echter niet verholpen. Zo bestaat er in Europa al decennialang beleid voor natuurvriendelijke landbouw, maar de intensieve landbouwpraktijken die Europa's rijke graslandbiodiversiteit aantasten – met name intensieve bemesting en hoge begrazingsdruk en maaifrequenties – nemen nog steeds toe. Ondanks de grote aandacht in de wetenschap voor de voordelen van biodiversiteit in de landbouw, blijven boeren terughoudend om natuurvriendelijk beheer op grotere schaal toe te passen. In dit proefschrift onderzocht ik sociaaleconomische en beheergerelateerde beperkingen voor een effectiever herstel van biodiversiteit en ecosysteemdiensten in door de mens beheerde graslanden. Alle hoofdstukken zijn gebaseerd op gegevens die zijn verzameld in een studiegebied in het zuiden van Nederland, waar het landgebruik varieert van zeer extensief beheerde, half-natuurlijke graslanden tot zeer intensieve productiegraslanden. Deze gradiënt weerspiegelt de intensivering van het gebruik van graslanden die wereldwijd plaatsvindt in regio's met een gematigd klimaat.

Dit proefschrift beoordeelde vanuit een breed sociaaleconomisch perspectief of het herstellen van ecosysteemdiensten leidt tot win-winsituaties of trade-offs tussen graslandboeren en de samenleving (hoofdstuk 2). Een breed scala aan indicatoren van ecosysteemdiensten werd in het veld gemeten, en er werden interviews met boeren gehouden om het beheer en de jaarlijkse productie van elk grasland te beoordelen. Vervolgens werd de bijdrage van het perceel aan het inkomen van boeren geschat op basis van de bruto marge van de grasproductie. Van alle onderzochte ecosysteemdiensten droeg alleen de stikstoffixatie door vlinderbloemigen significant bij aan de productiviteit van de graslanden en deze bijdrage was gering vergeleken met het effect van bemesting. Het inkomen van boeren werd grotendeels bepaald door productiviteit en vertoonde dan ook een sterke trade-off met de biodiversiteit, vastlegging van nutriënten en koolstofopslag – wat allemaal publieke diensten zijn. Diverse publieke diensten namen proportioneel toe met de biodiversiteit. Dit impliceert dat het herstel van graslandecosystemen vooral de samenleving ten goede komt, en niet zozeer de boeren zelf. Ecologische herstelprogramma's hebben daarom maatschappelijke

steun nodig die het voor boeren economisch lonend maakt om publieke diensten te leveren.

De biodiversiteit vormt de basis voor de levering van veel publieke diensten, maar voor veel soortgroepen, vooral voor ongewervelden, blijven de effecten van intensiever landgebruik onderbelicht. Hoofdstuk 3 onderzocht daarom de effecten van intensivering in graslanden op insecten en spinnen, gebruik makend van een ruimte-voor-tijd opzet. De intensiteit van het landgebruik werd gemeten aan de hand van de jaarlijkse productiviteit. Insecten en spinnen werden bemonsterd langs vaste transecten in mei, juni en juli, met behulp van sleepnetten en tellingen van bestuivers. De aantallen werden per orde geteld en een brede selectie van soortgroepen werd gedetermineerd tot soortniveau. Van lage naar hoge intensiteit namen de aantallen vliegen (Diptera) toe, wat de totale abundantie van geleedpotigen stabiliseerde, terwijl de meeste andere ordes sterk in aantal afnamen en de totale soortenrijkdom halveerde. Diepgaander inzicht werd verkregen door de verspreiding van individuele soorten langs het intensiteitsgradiënt te analyseren. Bij intensief landgebruik namen de meeste soorten af of verdwenen zelfs volledig (respectievelijk 85% en 64% van alle geïdentificeerde soorten), maar een kleine groep wijdverspreide soorten (9%) nam toe. Waarschijnlijk zorgen dergelijke 'winnaars' voor de stabiliteit van de totale abundantie. Bovendien toonden deze soort-specifieke analyses een sterker verlies van biodiversiteit dan de meer gangbare indicatoren. De grootste verliezen traden op tijdens de overgang van laag naar matig intensief beheer. Dit betekent dat zeer extensieve graslanden, die in de meeste agrarische landschappen vrijwel verdwenen zijn, cruciaal zijn voor de meeste soorten geleedpotigen.

Soortinventarisaties zijn zo tijdrovend dat dit de schaal van huidige biodiversiteitsevaluaties sterk beperkt. Daarom onderzocht hoofdstuk 4 of bloemen kunnen worden gebruikt als algemene biodiversiteitsindicatoren voor geleedpotigen en planten in graslanden. Parallel aan de inventarisaties uit hoofdstuk 3 werden de soortenrijkdom van planten en bloemen en de totale bloembedekking gemeten langs dezelfde transecten. Bloemrijkdom vertoonde consistente lineaire relaties met de soortenrijkdom van planten en geleedpotigen. Bloembedekking vertoonde meer variabele relaties met de soortenrijkdom van deze groepen, en indien lineair werden deze relaties veelal ook verklaard door bloemrijkdom. Bloemrijkdom weerspiegelde ook de toename in geleedpotigenrijkdom van voorjaar tot zomer, evenals de exponentiële afname bij toenemende intensiteit van het landgebruik. Bloemrijkdom vormt daarom een breed toepasbare indicator van graslandbiodiversiteit. Dit kan de evaluatie van herstelresultaten vergemakkelijken, want bloemrijkdom is efficiënt te meten over grote gebieden en is direct gerelateerd aan het lokale beheer.

Als relevante indicatoren op locatieniveau worden gemeten, kunnen ze ook worden gebruikt om herstelmaatregelen lokaal af te stemmen. Dit proefschrift heeft getest of het effect van minder maaien op bloemen afhangt van productiviteit en soortsamenstelling van graslanden (hoofdstuk 5). In twaalf graslanden met een

verschillende productiviteit werden steeds vier proefplots opgezet, waarin om de paar dagen de bloembedekking van elke kruidachtige soort werd geregistreerd gedurende het groeiseizoen (april–augustus), terwijl de plots nul tot drie keer werden gemaaid. Zo konden zowel de bedekking als de soortenrijkdom van bloeiende kruiden in elk plot worden gevolgd. De resultaten toonden aan dat minder maaien alleen bij een lagere productiviteit tot meer bloei leidde, terwijl de herbloei na het maaien ook sneller ging bij een lagere productiviteit. Deze effecten worden waarschijnlijk veroorzaakt door de verhoogde concurrentie om licht bij een hoge productiviteit, waardoor bloemen verdrongen worden, maar maaien ook meer impact heeft. Bovendien was het effect van maaien sterk afhankelijk van de fenologie en het vermogen tot herbloei van de lokale kruidachtigen. Slechts enkele soorten herstelden volledig onder frequente maairegimes, maar de helft van alle soorten herstelde volledig na één maaibeurt in het voorjaar. De resultaten van herstelmaatregelen kunnen daarom worden verbeterd door het maaibeheer per locatie af te stemmen op de soortsamenstelling. Mogelijke aanpassingen zijn om ongemaaide delen te behouden voor laatbloeiende soorten in laagproductieve habitats, en om juist gedeeltelijk te maaien in het voorjaar ter bevordering van de herbloei vanaf juli.

Het herstel van biodiverse graslandecosystemen vereist een drastische extensivering van moderne landbouwpraktijken. Het financieel belonen van publieke diensten kan boeren in staat stellen om dit te doen. De samenleving, niet individuele boeren, moet daarom verantwoordelijkheid nemen voor de publieke diensten die deze ecosystemen leveren. In de meeste agrarische landschappen is een toename van natuurherstel in graslanden nodig om publieke diensten te waarborgen, met name van hoogwaardige habitats die het grootste deel van de graslandbiodiversiteit herbergen. Huidige inspanningen slagen er echter meestal niet in om deze habitatkwaliteit te herstellen. De nadelige invloed van omliggend landgebruik, maar ook kennislacunes en suboptimaal beheer beperken de effectiviteit van huidige herstelprogramma's, zoals het Europees beleid voor natuurvriendelijke landbouw. Deze programma's kunnen worden verbeterd door hun beheer af te stemmen op locatie-specifieke omstandigheden, en resultaatsgerichte vergoedingen kunnen boeren hiervoor motiveren, mits de resultaten op alle betrokken percelen worden gemeten. Dit vereist een grondiger begrip van onderbelichte taxa en een grootschalige evaluatie van breed toepasbare biodiversiteitsindicatoren. Bovendien moet ecosysteemherstel worden geïntegreerd met duurzame methoden voor voedselproductie in beheerplannen op landschapsschaal, waarin de verschillende functies van een landschap op optimale locaties worden vervuld. Met een passende ruimtelijke planning, lokaal aangepast beheer en eerlijke financiële steun kunnen beheerde graslanden bijdragen aan voedselzekerheid, ecosysteemfuncties en biodiversiteitsherstel.

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12 List of publications

This thesis

De Vries, J. P. R., van Paassen, J. G., Ploeg, R., Noordam, A., Verhoogt, K., & Kleijn, D. (2026). Land use intensification transforms grassland arthropod communities: A few winners expand but most species disappear. *Biological Conservation*, *313*, 111522.

De Vries, J. P. R., Ploeg, R., van Paassen, J. G., Noordam, A., Verhoogt, K., & Kleijn, D. (2026). Flower species richness is an effective indicator of aboveground grassland arthropod biodiversity. *Ecological Indicators*, *186*, 114898.

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Chieffallo, L., Torresani, M., Zannini, P., **de Vries, J. P. R.**, Blaha, M., Monacchia, A., Kleijn, D. & Rocchini, D. (2025). Machine learning for biodiversity: UAV-based flower detection as an indirect proxy for bee abundance. *Ecological Informatics*, *91*, 103346.

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Torresani, M., Kleijn, D., **de Vries, J. P. R.**, Bartholomeus, H., Chieffallo, L., Gatti, R. C., Moudrý, V., Da Re, D., Tomelleri, E. & Rocchini, D. (2023). A novel approach for surveying flowers as a proxy for bee pollinators using drone images. *Ecological Indicators*, *149*, 110123.

De Vries, J. P. R., van Loon, E., & Borges, P. A. (2021). A small-scale analysis of elevational species richness and beta diversity patterns of arthropods on an oceanic island (Terceira, Azores). *Insects*, *12*(10), 936.

De Vries, J. P. R., Koma, Z., WallisDeVries, M. F., & Kissling, W. D. (2021). Identifying fine-scale habitat preferences of threatened butterflies using airborne laser scanning. *Diversity and Distributions*, *27*(7), 1251-1264.

Tuinenburg, O. A., & **de Vries, J. P. R.** (2017). Irrigation patterns resemble ERA-Interim reanalysis soil moisture additions. *Geophysical Research Letters*, *44*(20), 10341-10348.



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At last, my deepest gratitude goes to my family for carrying endless patience and trust in me. My **father**, thank you for learning me to take a deep breath when feeling frustrated, to love and care for the world and the people around us, to work with care and precision whatever time it takes, and to appreciate and enjoy each day that we live. I wished to follow your footsteps in working for a sustainable future. Today, I can only imagine how proud your smile would have been when you would have hold this book in your hands. Life is too short, but you live on in us. To my **mother** and my **sister**, you showed me what it really means to look after each other, and this has meant the world. You are two immensely strong women whom I can trust and rely on. Thank you for your continuous support and love you deeply.

14 About the author



Reinier de Vries grew up in Deventer, the Netherlands. At young age he was already in love with the world outdoors where he climbed trees and built hides in the woods. His parents took him on adventurous camping trips across Europe, where they showed him the continent's nature and allowed him to expand his collections of minerals, shells and lichens. But it was at the age of twelve, when he joined a camp of the Dutch youth nature association JNM, that he got truly hooked by nature and birdwatching. The JNM was a place where he looked up to knowledgeable excursion leads and where he deeply felt at home. Later he learned to lead excursions himself, made friends for life and broadened his interest to other terrestrial and marine life, including insects.

Inspired by his father's work for a sustainable future, Reinier studied Environmental Sciences in Utrecht. His first steps in the world of scientific research were set here in the domain of climate science. However, when volunteering on a research station in Namibia Reinier decided to follow his passion for nature professionally. He proceeded his master studies at the University of Amsterdam and started a PhD position at Wageningen University. Meanwhile, Reinier still finds time for his friends, sports and for excursions in- and outside the Netherlands, in search of large and small wildlife.

PE&RC Training and Education Statement

With the training and education activities listed below the PhD candidate has complied with the requirements set by the Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 30 ECTS (= 22 weeks of activities)

Review/project proposal

- Project proposal: Management of grassland biotopes on farmland and effects on the delivery of multiple ecosystem services | 6 ECTS

In-depth / Topical / On-site Postgraduate Courses

- What's bugging you | PE&RC | 2023 | 1.5 ECTS
- Linking Community and Ecosystem Dynamics | PE&RC | 2024 | 2 ECTS

Methodological / Statistical Postgraduate Courses

- Introduction to zero-inflated models with R | PE&RC | 2021 | 2.5 ECTS
- Mixed linear models | PE&RC | 2022 | 0.6 ECTS
- Structural equation modelling | PE&RC | 2022 | 1.5 ECTS

Competence, skills and career-oriented activities

- Start to teach | WGS | 2024 | 1 ECTS
- Presenting with impact | WGS | 2025 | 1 ECTS
- Writing propositions for your PhD | WGS | 2023 | 0 ECTS

Scientific Integrity/Ethics in science activities

- Ethics in plant and environmental sciences | WGS | 2025 | 0.3 ECTS

PE&RC Retreat, PE&RC Day, and other PE&RC events

- PE&RC First year weekend | 2022 | 0.9 ECTS
- PE&RC Last year weekend | 2024 | 0.6 ECTS

National/local scientific meetings, seminars, and discussion groups

- Showcase annual project meetings (oral presentations) | 2021-2024 | 4 ECTS
- Field trip with German & Austrian research groups (excursions and a presentation) | 2022 | 1 ECTS
- Masterclass & symposium by Carl Folke | 2022 | 0.2 ECTS
- WEES workshop & seminar by Tim Newbold | 2023 | 0.2 ECTS
- NAEM (poster) | 2024 | 1.6 ECTS
- Ecology Seminar at University of Göttingen (lecture) | 2025 | 1 ECTS

International symposia, workshops and conferences

- ECCB (oral presentation) | Prague, Czech Republic | 2022 | 2.5 ECTS
- SCAPE (oral presentation) | Namur, Belgium | 2023 | 1.9 ECTS
- ESP (oral presentation) | Wageningen, the Netherlands | 2024 | 2.5 ECTS
- Future for Butterflies (poster) | Wageningen, the Netherlands | 2025 | 1.9 ECTS

Societally relevant exposure

- Newspaper article featuring research on insect declines; De Volkskrant, wetenschapsbijlage | 2022 | 1 ECTS
- Guest excursions on grassland arthropods for youth nature organisation (JNM) | 2022, 2023 | 1 ECTS
- Guest lectures about PhD research for WUR study associations; Biologica, Sylvatica | 2023 | 1 ECTS
- Visit of the Dutch ministry for Agriculture's pollinator expert to PEN (oral presentation) | 2025 | 0.2 ECTS

- Article on popular science platform Nature today | 2025 | 1 ECTS

Committee work
- Dutch dragonfly association (NVL), research coordinator & editorial member for Brachytron (Dutch-Flemish journal on Odonata research) | 2021-2025 | 4 ECTS

Lecturing/Supervision of practicals/tutorials
- ENT30306: Ecol. Aspects of Bio-Interactions | 2024 | 5 days | 1 ECTS
- Ecology 1 | 2022-2024 | 12 days | 3 ECTS
- PEN22303: Ecology - Field Excursions | 2022-2025 | 12 days | 3 ECTS
- Restoration Ecology | 2024-2025 | 6 days | 1 ECTS
- PEN21803: Ecological Theory | 2024-2025 | 6 days | 1 ECTS
- Field Practicum 2 | 2024 | 20 days | 6 ECTS

BSc/MSc thesis supervision
- Research topic 1: Effects of nitrogen on grassland bee & plant diversity (MSc) | 3 ECTS
- Research topic 2: Relations between soil biota & nitrogen leaching (MSc) | 2 ECTS
- Research topic 3: Flowers as an indicators of arthropod diversity (MSc) | 1 ECTS
- Research topic 4-7: How arthropod respond to land use intensification (BSc, 4 different students) | 0 ECTS

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