Unravelling the pollinator economy

How floral resource availability shapes pollinator communities



Constant Swinkels

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Constant Swinkels
geboren op 9 april 1995
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Promotoren:

Prof. dr. J.C.J.M. de Kroon

Dr. ir. E. Jongejans

Manuscriptcommissie:

Prof. dr. D.C.E. Maes

Prof. dr. J.C. Biesmeijer (Universiteit Leiden)

Dr. A. Ebeling (Friedrich-Schiller-Universität Jena, Duitsland)

Paranimfen:

Ivanka Spruijt

Nick Hofland

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by

Constant Swinkels
born on April 9, 1995
in Nijmegen (the Netherlands)

PhD Supervisors:

Prof. dr. J.C.J.M. de Kroon

Dr. ir. E. Jongejans

Manuscript Committee:

Prof. dr. D.C.E. Maes

Prof. dr. J.C. Biesmeijer (Leiden University)

Dr. A. Ebeling (Friedrich Schiller University Jena, Germany)

Paranymphs:

Ivanka Spruijt

Nick Hofland

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1

General Introduction

GENERAL INTRODUCTION

1.1 Pollinator diversity

Flower-visiting insects, collectively referred to as pollinators, comprise a vast and taxonomically diverse group of species. In north-western Europe, bees are among the most well-known and widely appreciated representatives of this group (Sumner et al., 2018). Other important pollinators include syrphid flies, moths, butterflies, beetles and various other insects (e.g. Orford et al., 2015). Consequently, pollinator communities encompass a wide range of life-history strategies. For instance, many syrphid flies can deposit their eggs at suitable locations across the wider landscape (Reemer et al., 2009), whereas bees are central-place foragers that must return to a nest after each foraging bout (Peeters et al., 2012). Despite this diversity in strategies, adult pollinators share a common dependence on flowers, which they visit primarily to collect nectar and pollen.

Through their interactions with flowers, pollinators provide crucial ecosystem functions and services. It is estimated that over three-quarters of plant species in north-western Europe are visited by flower-visiting insects (Ollerton et al., 2011), indicating that most of them rely on pollinators for reproduction to at least some extent. Likewise, pollinators contribute substantially to agricultural production, providing ecosystem services valued at approximately billion €153 globally each year (Gallai et al., 2009). Research shows that, rather than a few key species (but see Kleijn et al., 2015), it is the total diversity of pollinator species that enhances the pollination of the wide variety of plants present in both natural and agricultural ecosystems (Garibaldi et al., 2013; Rader et al., 2016; Lundgren et al., 2016; Artamendi et al., 2024). Consequently, the conservation of pollinator diversity is of key importance.

1.2 Pollinator conservation

Alarmingly, evidence of widespread pollinator decline has accumulated across north-western Europe (Potts et al., 2010; Goulson et al., 2015; Powney et al., 2019). Although the underlying causes are diverse, pollinator declines are most often linked to habitat degradation and the loss of floral resources. For example, semi-natural grasslands, which represent important hotspots of both plant and pollinator diversity in north-western Europe (Steffan-Dewenter et al., 2002; Öckinger and Smith, 2007; Wilson et al., 2012), are among the most threatened ecosystems in Europe today (Cousins et al., 2015). Moreover, declines of individual pollinator species have been associated with the loss of their preferred floral resources (Biesmeijer et al., 2006; Scheper et al., 2014).

In response to these observations, and because vegetation composition is considered a key driver of pollinator community structure (e.g. Potts et al., 2003; Fründ et al., 2010), most pollinator conservation initiatives focus on increasing the availability of flower-rich habitat. Well-known examples include the establishment of flower strips in agricultural

landscapes (e.g. Ouvrard et al., 2018; Geppert et al., 2020) and the promotion of pollinator-friendly plants in gardens (e.g. Baldock et al., 2015, 2019; Tew et al., 2022; Timberlake et al., 2024). In general, such efforts seem to promote pollinator abundance and species richness, although conservation success does vary to some extent (Haaland et al., 2011; Sexton and Emery, 2020; Kral-O'Brien et al., 2021).

1.3 Flower limitation

An implicit assumption underlying these pollinator conservation initiatives is that a shortage of floral resources is the primary factor limiting pollinator communities. Although this assumption may hold at large spatial scales, floral resources may not always be the main limiting factor at local scales (Sponsler et al., 2023). Despite their dependence on flowers, pollinators also require a variety of non-floral resources, including suitable nesting sites and larval habitats (Requier and Leonhardt, 2020). Moreover, anthropogenic pressures, such as pesticide use, may constrain pollinator populations even where floral resources are abundant (Guzman et al., 2024). The wider landscape context can therefore strongly influence local pollinator community composition (Scheper et al., 2013, 2015), and in some cases may obscure the relationship between flower richness and bee abundance or species richness (e.g. Wood et al., 2015; Uyttenbroeck et al., 2017). Consequently, while pollinator communities may be limited by floral resource availability in flower-poor habitats, increasing flower availability beyond a certain point may yield diminishing benefits if other ecological constraints become limiting.

In this thesis, I examine how pollinator communities respond to variation in floral resource availability, combining large-scale surveys and field experiments to evaluate the extent to which floral resources structure pollinator communities in the field. In the first part of the thesis, I investigate pollinator community richness and resource collection patterns (the composition of floral resources that pollinator species collect) across a wide range of sites, from flower-poor to flower-rich. In the second part, I examine how pollinators respond to floral resources in management interventions through field experiments, and conversely, how conservation outcomes can inform our understanding of the relationship between pollinators and floral resources. Together, these approaches provide a complementary framework for assessing when and how increase in floral resources is likely to benefit pollinator conservation.

1.4 Pollinator communities along a flower richness gradient

Studying populations along ecological gradients provides a valuable way to detect potential saturating responses and to relate these patterns to specific ecological factors (Whittaker, 1967; Begon et al., 2006). For example, analysing pollinator abundance along a gradient from flower-poor to flower-rich habitats can reveal whether increases in floral resources consistently promote pollinator abundance and species richness, or whether responses saturate once other ecological constraints become limiting (Figure 1.1).

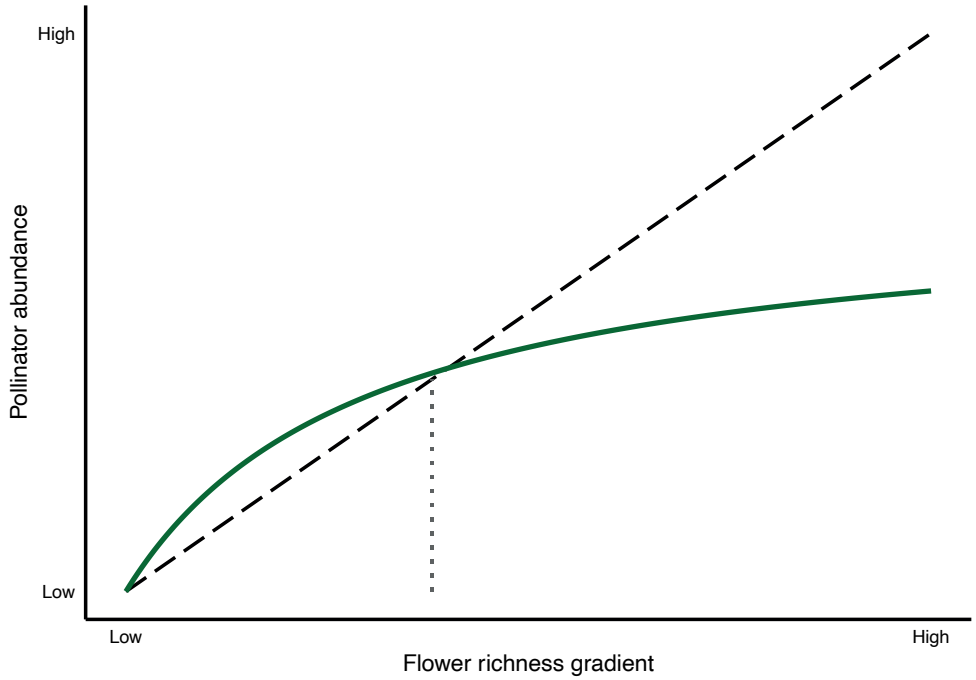


Figure 1.1: Hypothetical relationship between pollinator abundance and flower richness. The dashed line represents a linear 1:1 relationship, whereas the green line depicts a saturating response. The point where the green line begins to plateau indicates where floral resources start to become less limiting.

1.4.1 Pollinator community richness

Although such saturating patterns could be hypothesised for pollinator abundance and species richness along a flower richness gradient (Sponsler et al., 2023), not many studies assess these relationships in the field. A clear example that comes to mind is from the Jena experiment, where Anna Ebeling and colleagues show that the number of visiting pollinator species quickly plateaus with increasing blossom cover (Ebeling et al., 2008). Nevertheless, in this experiment visitation frequency increased linearly with blossom cover, suggesting pollinator abundance and pollinator species richness can show diverging results. Meanwhile, different outcomes could also be expected for different pollinator groups, since their resource collection strategies can vary substantially.

A key requirement for such analyses is the use of reliable measures of floral resource availability. Most studies quantify floral resources using flower abundance or flower species richness. However, these metrics represent only indirect proxies for the actual rewards available to pollinators, namely nectar and pollen. Because plant species vary strongly in their nectar and pollen production, similar values of flower abundance or species richness may correspond to very different levels of floral reward availability. For nectar pro-

duction, recent trait databases reporting nectar sugar production now make it possible to estimate vegetation-level nectar production as a direct expression of floral reward availability (Baude et al., 2016; Hicks et al., 2016; Tew et al., 2021, 2023). Such metrics may therefore improve predictions of pollinator community richness, but to my knowledge no study has so far tested whether estimating and incorporating vegetation-level nectar production improves predictions on wild bee abundance and species richness.

1.4.2 Pollinator resource collection

While patterns in pollinator abundance and species richness along gradients of floral resources can indicate whether communities saturate, they do not reveal the underlying ecological mechanisms that structure these communities. Analysing how individual pollinator species use floral resources across such gradients provides a complementary perspective, helping to explain how pollinator coexistence and community stability are maintained or enhanced when overall flower availability is high.

Crucially, increased flower availability might allow pollinators to reduce their resource use overlap, potentially lowering interspecific competition, especially as many pollinator communities in temperate regions are dominated by generalist species capable of adjusting their foraging behaviour in response to resource availability. Models show that when floral resource diversity increases, generalists may shift their foraging patterns in ways that reduce resource-use overlap with other pollinators (Ponisio et al., 2019; Valdovinos and Marsland, 2021). Such behavioural flexibility may reduce interspecific competition and enhance the stability and coexistence of pollinator communities (Valdovinos et al., 2013, 2016).

Despite these theoretical insights, empirical evidence for these mechanisms in natural field settings remains relatively limited. Controlled experiments provide some support for these ideas. For example, Fründ et al. (2013) show pollinator species competing for the same floral resource reduced their resource-use overlap more than expected from their individual foraging preferences alone. Similarly, a semi-controlled biodiversity experiment in Jena demonstrated that pollinators interacted with fewer plant species than expected when local flower availability increased, suggesting increased specialization (Ebeling et al., 2011). However, how these patterns translate to natural communities remains unclear (Levine et al., 2017). One of the few field-based studies addressing this question found that pollinator communities in Mallorca exhibited greater specialization and modularity in areas with higher flower richness (Gómez-Martínez et al., 2022).

A major challenge in studying pollinator resource use in natural systems is that pollinators often forage across spatial scales larger than the local sampling sites used in ecological studies. Consequently, visitation observations provide an incomplete picture of pollinator diets, particularly in habitats where local floral resources are scarce and

pollinators depend on resources from the surrounding landscape (Pornon et al., 2016). Recent advances in DNA-based pollen identification provide promising opportunities to overcome this limitation. These methods can accurately identify pollen grains to the species level and thus reveal the plant species from which pollinators have collected resources (Tommasi et al., 2021; Bell et al., 2022; Lowe et al., 2022a, 2022b). In addition to detecting rare interactions that may be missed during visual surveys, DNA-based pollen analysis can also identify plant species that occur outside the focal study sites (Pornon et al., 2016; Bell et al., 2017).

1.5 Management interventions for pollinator conservation

Examining how pollinator communities respond to management interventions provides a practical perspective on the extent to which floral resources limit pollinators in human-managed landscapes. One widely applied practice in grassland systems is mowing (Milberg et al., 2017; Bochniak et al., 2024). Traditionally, all vegetation is mown simultaneously during mowing events, leaving no refuges for insects and causing high mortality (Steidle et al., 2022). To mitigate these effects, managers increasingly experiment with partial mowing regimes, where only part of a grassland is mown at a given time while other sections remain uncut (Révész et al., 2025). Such approaches may prolong the seasonal availability of floral resources, effectively creating temporal and spatial heterogeneity in resource distribution. At the same time, unmown patches may concentrate pollinators locally, potentially intensifying competition for floral resources (Lebeau et al., 2015). Observing pollinator responses to these interventions therefore provides insight into how communities react when resources are temporarily limited or redistributed, linking directly back to the question of flower limitation in natural and semi-natural habitats.

Meanwhile, conservation practice is increasingly shifting from targeted, species-specific interventions toward ecosystem restoration, which emphasizes the recovery of natural processes rather than the direct provision of resources for particular species groups (Bouma et al., 2025). This process-oriented approach has proven effective for many taxa, yet pollinators are often overlooked in such schemes. Studying pollinator responses in these settings is particularly informative, as it can reveal the extent to which floral resources constrain pollinator communities when management does not directly manipulate flower availability.

A third key management consideration concerns the choice of plant species in restoration efforts or sown flower mixtures. Previous work has shown that plant species composition strongly influences the success of pollinator conservation measures (Warzecha et al., 2018). Nevertheless, the conservation value of ornamental plant species remains debated. Ornamental flowers are widely available and frequently planted in gardens, road verges and flower strips, yet their suitability as resources for pollinators is still uncertain. Several studies suggest that ornamental flowers are primarily visited by generalist pol-

linators (Garbuzov et al., 2015; Erickson et al., 2020), while more specialized species may rely more strongly on native plant species (Chrobock et al., 2013). However, relatively little is known about how pollinators choose between different floral resources when multiple options are available simultaneously.

1.6 Linear landscape elements

Most of the work presented in this thesis stems from dike grasslands, that are a potential high-value habitat for pollinators. Human-made linear landscape elements (LLEs), such as road verges, railway lines, power lines, ditches, and embankments, have been shown to support flower-rich vegetation and valuable pollinator communities (Noordijk et al., 2009; Phillips et al., 2019, 2020). In addition, LLEs form extensive networks across landscapes, connecting natural, rural, and urban areas (Villemey et al., 2018; Fischer et al., 2022). A key conservation advantage of LLEs is that they exist within current land-use systems, often requiring little additional land conversion, whereas interventions such as flower strips typically involve repurposing agricultural land.

Dike grasslands in the Netherlands represent a particularly promising but understudied LLE (Slikboer and Godijn, 2020; Swinkels et al., 2020). The country contains more than 17,000 km of dikes (Unie van Waterschappen, 2015), forming a dense network that connects diverse landscapes and may function as migration corridors for pollinators (Villemey et al., 2018). The grasslands covering dike slopes, when biodiversity-oriented management is applied, harbour diverse and flower-rich vegetation (Liebrand, 1999a). Such biodiverse vegetation might even contribute to dike stability (Berendse et al., 2015). South-facing slopes create warm microclimates that could benefit thermophilous insects and influence larval development in many pollinator species. Despite these characteristics, a comprehensive assessment of the ecological value of dike grasslands for pollinators is lacking.

1.7 Goals and outline of this thesis

This thesis is roughly divided into two parts. The first three research chapters explore the ecological value of dike grasslands for wild pollinators. These chapters assess pollinator diversity on dikes and subsequently study the relationship between pollinator community richness and vegetation characteristics and pollinator resource collection along a flower richness gradient. The following three chapters examine the effects of different management interventions. While some of these chapters focus directly on dike grasslands, others extend the analysis to different ecosystems. Together, these chapters provide a basis for critically evaluating pollinator community responses to floral resources and their implications for conservation.

To assess the value of dike grasslands for pollinators, **Chapter 2** synthesizes surveys of wild bees conducted on dike grasslands along the major rivers and in the Dutch river

delta. The chapter describes patterns in wild bee species richness and compares these findings with studies from other linear landscape elements. In addition, the bee community is characterized in terms of phenology and functional traits, and relationships between bee abundance, species richness and flower species richness are examined.

Chapter 3 further investigates the relationship between bee communities and floral resources using a subset of the data from chapter 2. Because surveying wild bees requires considerable expertise and time, identifying vegetation-level indicators of habitat suitability could provide a valuable tool for nature managers. This chapter therefore evaluates how well different vegetation metrics, including flower species richness, floral unit abundance and estimated vegetation-level nectar sugar production, predict wild bee abundance and species richness.

To explore how increased flower availability may facilitate pollinator coexistence, **Chapter 4** investigates plant–pollinator interactions on dike grasslands using pollen carried by pollinators collected along gradients of floral availability. This chapter introduces multi-species genotyping-by-sequencing (msGBS) as a novel approach to identify and quantify pollen carried by pollinators from both locally available plants and those from the wider landscape. Using these data, we analyse pollinator diet breadth, niche overlap and foraging patterns across gradients of flower richness and abundance, thereby examining how increases in floral resources influence pollinator coexistence.

Chapter 5 investigates short-term pollinator responses to mosaic mowing on dike grasslands. Mosaic mowing, in which small patches of vegetation are left unmown during mowing events, has been proposed as a promising management strategy for promoting insect diversity by providing refuges. However, its effects on pollinator communities remain relatively understudied. In this chapter, a field experiment compares pollinator communities and flower visitation in unmown refuge patches with those in fully unmown control sites, allowing us to assess how mowing regimes influence pollinator community dynamics.

Chapter 6 and 7 expand beyond dike grasslands to examine pollinator responses to alternative management approaches. **Chapter 6** presents a contrasting perspective on pollinator conservation by examining long-term pollinator data from the Bargerveen, a bog reserve in the north-east of the Netherlands. In this system, management focuses primarily on restoring hydrological conditions that promote bog formation rather than directly increasing floral resources. This approach, often associated with the concept of rewilding, aims to restore ecosystem processes. By analysing pollinator trends under this management regime, the chapter contributes to a broader discussion on the role of floral resources in pollinator conservation.

Finally, **Chapter 7** investigates pollinator visitation to wild-type cornflowers and its commonly planted garden varieties. Although the conservation value of non-native plants is frequently debated, relatively little attention has been given to cultivated varieties of native species. In a cafeteria experiment conducted in both urban and rural settings, pollinators were offered a choice between wild-type cornflowers and three garden varieties. By quantifying floral morphology, spectral characteristics and floral rewards, this chapter explores which plant traits influence pollinator preferences.

Chapter 8 concludes the thesis by synthesizing the main findings of the previous chapters. It discusses the results in light of the proposition that floral resource limitation in pollinator communities can be alleviated, and links these findings back to pollinator management.



2

Phenology and flower species availability define wild bee communities on river embankments

Constant Swinkels, Linde Slikboer, Ivo Raemakers,
Niels Godijn, Eelke Jongejans & Hans de Kroon

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ABSTRACT

Linear Landscape Elements contribute to pollinator conservation, with enhancing floral resources as most common restoration practice. However, theory predicts that floral resource availability is not always the limiting factor as other, non-floral resources can become more limiting once enough flowers are available. We currently lack large-scale studies covering a vegetation richness gradient that could reveal the predicted saturation that should occur with floral resource limitation relief. Here we present a comprehensive analysis of bee communities from 157 dike grasslands covering a flower richness gradient in the Netherlands in relation to vegetation composition and landscape characteristics. We show that wild bee abundance and species richness increased with more flowering plant species present, but saturated at low flower species richness. This early saturation suggests that even modest conservation efforts could effectively alleviate floral resource limitation for pollinators, but that further floral resource increase could lead to diminishing returns. Nevertheless, red-listed species occurrence increased with flower species richness without saturating effects and correlated stronger with landscape level factors. Additionally, our results highlight the unique conservational value of river embankments for wild bees, as we encountered nearly half (156) of all Dutch bee species, with nearly 10% of individuals belonging to red listed species.

2.1 INTRODUCTION

Evidence of flower visiting insect decline in North-Western Europe is mounting (Biesmeijer et al., 2006; Scheper et al., 2014; Powney et al., 2019; Hallmann et al., 2021; Barendregt et al., 2022). These pollinators are crucial for ecosystem functioning through the pollination of wild flower species (Ollerton et al., 2011; Koski et al., 2018), and some species provide additional ecosystem services such as crop pollination (Garibaldi et al., 2013; Rader et al., 2016). Wild bees are amongst the most important pollinators, both for their efficiency (Page et al., 2021) and ubiquity (Winfree et al., 2011). Suffering from a range of anthropogenic influences (Potts et al., 2010; Vanbergen et al., 2013), decrease in habitat availability and quality with subsequent loss of floral resources is generally seen as the major contributor to this decline (Biesmeijer et al., 2006; Scheper et al., 2014). Consequently, restoration practices aim to restore high-quality habitats, primarily through the promotion of local floral resource abundance and diversity.

Although nature reserves provide suitable habitat, in Western Europe they are often small and isolated. Hence, it is essential to create habitat at the landscape level to promote wild bees (Kremen and Merenlender, 2018). In this context, linear landscape elements (LLE), such as road verges, railway lines, power lines, ditches and embankments, can contribute to bee conservation (Phillips et al., 2020). LLEs form an extensive network of semi-natural grassland across countries, interweaving natural, rural and urban areas (Fischer et al., 2022). Studies show that well-managed LLEs can promote both flowers and bees (e.g. Noordijk et al., 2009; Heneberg et al., 2017; Phillips et al., 2019), including red listed and endangered species of specific conservation interest (Helldin et al., 2015; Heneberg et al., 2017).

However, although the potential of LLEs for bee conservation is evident (Villemey et al., 2018; Phillips et al., 2020), we lack an overview of the conditions associated with bee community richness. Currently, most efforts aim to promote wild bees in LLE's by increasing floral resource availability (e.g. Scheper et al., 2013; Requier and Leonhardt, 2020), with mostly small-scale studies presenting positive outcomes of increased resource availability (Haaland et al., 2011). However, theory predicts that bee communities are not always resource limited and that resource limitation can be relieved once other factors become more limiting (Sponsler et al., 2023). This could explain why some studies report no effect of agricultural schemes (Wood et al., 2015), suggesting that landscape setting can be equally important (Scheper et al., 2015) or that nesting availability is primarily limiting for wild bees (Requier and Leonhardt, 2020). We could thus hypothesize a saturating pattern, where initial floral resource increase leads to positive responses in wild bee communities but subsequent increases lead to diminishing returns. However, to our knowledge, there are currently no comprehensive studies on bee communities covering a flower richness gradient to determine whether and when resource limitation is relieved.

In addition, most knowledge that we have stems from flower strips in agricultural landscapes, while for many LLE's the context (e.g. soil, landscape setting, bee communities) is different. This is particularly true for dike grasslands where we currently lack an overview of the bee communities they harbour. In lowland regions, dikes can cover a considerable area, signified by the more than 17,000 kilometres of dikes found in the Netherlands (Unie van Waterschappen, 2015). Dikes are notably different from other LLEs for a number of reasons. By definition these embankments along water bodies are raised above the surrounding flat landscape, with warm, sun facing slopes as potential hotspots for bee nesting (Antoine and Forrest, 2021). In addition, they are often larger in surface area and relatively old compared to many other linear landscape elements. Both grassland age and size have been related to bee community richness (Sexton and Emery, 2020). Finally, vegetation on dikes contributes to their flood protection services, with studies suggesting that forb-rich grasslands could benefit dike stability due to increased rooting densities (Berendse et al., 2015). With increasing efforts to extend the area of forb-rich dike communities for flood protection, dikes have a high potential to effectively contribute to bee conservation as additional benefit.

Here we present a comprehensive analysis of dike grassland bee communities along the lower branches of the Meuse and Rhine rivers in the Netherlands. We collected and analysed multi-year data on bee community and vegetation composition from 157 locations on dike grasslands. The aims of this study were (1) to characterise the current dike grassland wild bee community composition in relation to the wild bees of the Netherlands, (2) to analyse the relationship between wild bee species richness and abundance with local flower species richness in space and time, and (3) to examine how the presence of specific bee species relates to their food sources. Herewith, we reveal the conservation potential of river embankments for wild bees in a West-European lower estuary, and present relevant relationships between bee and wild plant communities informing wild bee conservation efforts.

2.2 MATERIALS AND METHODS

Location

Samples were collected at 157 locations from dikes in the southern half of the Netherlands, essentially covering the entire Dutch lowland river and Delta area (figure 2.1). Sites were selected to always be more than 300 meters apart (mean value 1272 meters), thus exceeding the maximum foraging range of most local small bee species (Zurbuchen et al., 2010). Data were collected from a range of different dike grasslands, including monotone grasslands devoid of flowers and grasslands with high flower abundance and more structural diversity including shrubs and small trees. The study locations include primary dikes, currently functioning as flood protection barrier, and secondary dikes, no

longer in use as flood protection barrier. Primary dikes are nowadays constructed from heavy clay, often with a top soil layer of more sandy substrate, and are mown twice a year (June and September) when managed with the intent to facilitate biodiversity (Liebrand, 1999). Many of these primary dikes were 'strengthened', meaning that the vegetation was stripped to add uniform, more erosion resistant clay to enlarge the dikes, about 30 years ago after the highwaters of 1993 and 1995, meaning vegetation has had time to develop since. Secondary dike grasslands are not strengthened (sometimes 100+ years old grasslands), with diverse soil types and subjected to a variety of management practices (e.g. infrequent mowing or grazing by cattle and sheep).

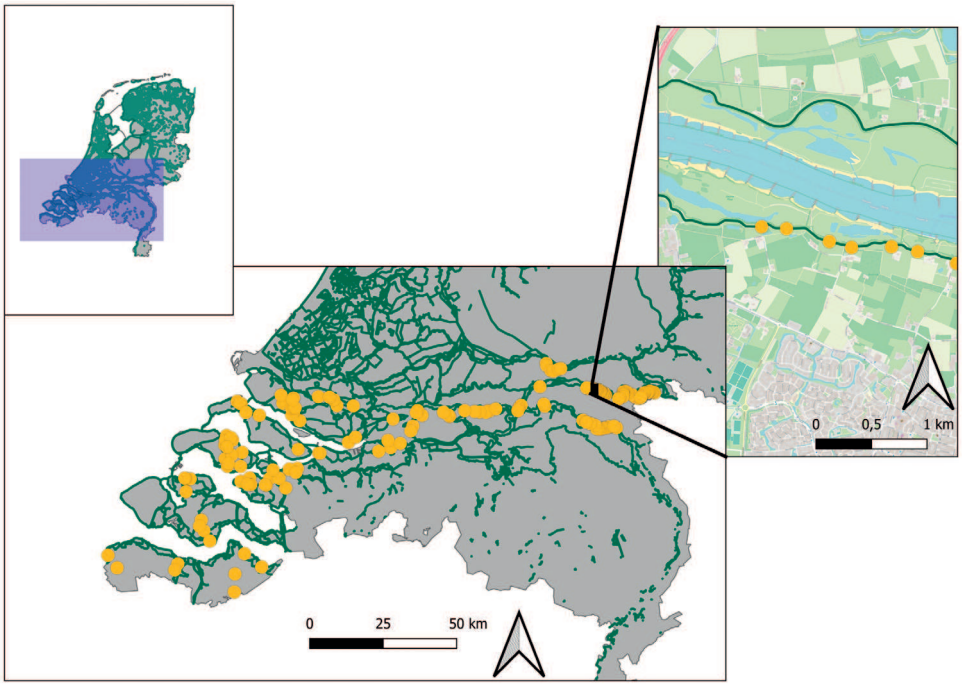


Figure 2.1: Sampling region within the Netherlands (A) with specific locations (B) and an example of how these locations are found in the landscape (C). In green all dikes in the Netherlands, in yellow the sampling locations.

Sampling strategy

Samples were collected by experienced observers; Constant Swinkels (CS) in the east of the Netherlands, Ivo Raemakers (IR) in central and east NL, and Linde Slikboer and Niels Godijn (LS) in the South-Western delta. All observers visited locations multiple times per year to account for phenology of bees and plants. Data were collected from 2018 up until 2022 and in total 654 transects surveys were collected from the 157 locations (median 3 visits per location, mean 4), with a total sampling time of 181.5 hours.

Bee Sampling

Bees were sampled along 150m long transects, running through representative vegetation for that dike grassland. Transects were sampled for 15 minutes of active searching time (time was paused while tracking, handling and identifying individuals) and all bees found within 1.5m on either side of the transect were recorded. Species that could not be identified in the field were collected and transferred to the lab for identification. The *Bombus terrestris* species complex was treated as one species due to the difficulties involved in correct identification of these species (Williams et al., 2012). Honeybees were counted, but not included in further analysis.

For 81 transects, sampling time was longer than 15 minutes. For these, we corrected for sampling effort by randomly removing a percentage of individuals equal to the percentual time increase, assuming that bee individuals were evenly distributed over the transect. Chances of removal were equal for all individuals. Species were eliminated from the sample if their abundance reached zero.

After identification, we recorded information on the status of species from the Dutch red list of bees (Reemer, 2018). In addition, we recorded species pollen preference from the German bee atlas (Westrich, 2019) supplemented with information from the Dutch field guide on bees (Falk and Lewington, 2017).

Vegetation sampling

For each transect count local flower species richness and abundance was recorded, with all open flowers identified to the species level. Grass inflorescences were not included as these are not used by bees in our study area. The exact survey method differed for observers. CS counted all flowering plants per species within a 5×5m quadrat selected to represent local vegetation (following a small upscale compared to standardized size for vegetation surveys in grasslands (Chytrý and Otýpková, 2003) as this size has been long standing practice on dike grasslands (Liebrand and Sýkora, 1996)), IR counted floral units per species along the 150m netting transect (see bee sampling) and LS scored flower abundance on a modified cover-abundance scale derived from the Tansley scale, where a value (1 - 9) is given based on the visual abundance of a species along the transect (Tansley, 1939). As such, the methods are standardised and give an accurate and comparable indication of flower species richness (which is known to be a good predictor for bee diversity (Kral-O'Brien et al., 2021)), but flower abundance could not be compared between datasets (we present analysis along a flower abundance gradient per observer in appendix A.1 – A.3, finding similar patterns as our main analysis). For 33 transects flower data were missing, resulting in their exclusion from model analysis.

Environmental factors

We collected information on landscape elements in a 250m and 1000m radius surrounding each location from the open access Dutch national Basic Registration Topography database. Land use types were divided in broad categories; agricultural area, semi-natural grassland, forest, fruit crops and a rest group (water, roads etc). Specific land use types within each category (e.g. crop type) are expected to influence bee communities in largely similar ways. Next to this we calculated the area of 'NatuurNetwerk Nederland' (NNN), designated natural area, in a 250m and 1000m radius and the distance to the closest NNN area. We collected weather data from all 50 Dutch weather stations from the KNMI database and interpolated measurements to our locations, where measurement weight was scaled inversely with distance. We collected information on daily average temperature, daily average windspeed, total daily rain and the percentage of sunshine during daylight hours.

Analysis

All data were analysed in R version 4.2.2 (R Core Team, 2022). For analysis and graphics, packages lme4 (Bates et al., 2015) and ggplot2 (Wickham, 2016) were used. For each section we describe what data we used, a flowchart can be found in Appendix B.1.

Community composition

Using all available data, we calculated median number of individuals encountered per transect, that we deemed more informative than the average since abundance data was negative binomially distributed (Appendix B.2). As species abundances were skewed with few abundant species and many species occurring in low numbers (Appendix C.1), a common occurrence in wild bee communities (Potts et al., 2003), we identified a 'core community' consisting of species detected on at least 15 out of 157 locations (~10% of all locations). A species accumulation curve was constructed for visual analysis by taking the total number of unique species encountered with increasing number of monitoring surveys. We randomly reordered surveys 1000 times, after which the mean curve and 95% confidence interval was plotted. We extrapolated species richness to estimate total species richness using the Chao estimator (Chao, 1987; Chiu et al., 2014), as it has been found to perform best among competing estimators (Palmer, 1990).

Phenological patterns

To study when different groups of bees were most encountered on dike grasslands, we visually inspected abundance per survey for the most abundant genera (*Andrena, Nomada*, *Bombus*, and a combination of the closely related *Lasioglossum* and *Halictus*, both Halictidae) and a group including all other genera (which separately had too few observations to produce meaningful patterns) during the year. The number of individuals observed within each genus for each transect count, including zeros, were plotted on a log scale. For the analysis of red listed species phenology, Halictidae were added to the

'other' genera as they did not include many red listed individuals. We fitted a loess curve smoother to aid visual interpretation of the plots.

Bee abundance and diversity

For all abundance and species richness analyses, four different (sub)sets of the data were used. Firstly, we included all available data. In addition, we split our dataset between bumblebees and all other wild bees. Bumblebees are eusocial and live in colonies, have large foraging ranges and are highly generalist. Their responses to local vegetation are well studied, with articles showing strong relationships between increases in flower availability and bumblebee abundance (e.g. Pywell et al., 2006; Carvell et al., 2007). Other wild bee responses, however, are relatively less studied, while they make up for most bee diversity and often have specific resource and nesting requirements. Finally, we selected only red-listed species to study what factors steered the occurrence of vulnerable species in our dataset.

We analysed bee abundance (negative binomial distribution, Appendix B.2) and species richness (Poisson distributed) using Generalised Linear Mixed Effect Models (GLMMs). Explanatory variables were selected based on ecological relevance. We include local flower species richness as this was the primary interest of our study. We studied phenological patterns by including the Julian date. We accounted for weather effects by including the percentage hours of sunshine during the day (calculated from the maximum possible hours of sunshine given the date) as most other weather variables are correlated with Julian date. As we repeated surveys at locations, sampling site was included as random factor. To this base model, we stepwise included one of seven different landscape level factors; area covered by agriculture in a 250m and 1km radius, grassland in 250m and 1km radius, area of NatuurNetwerk Nederland (NNN) in a 250m and 1km radius and distance to the closest NNN area. NNN is a network of areas designated for nature protection in the Netherland. In addition, we ran a model without any landscape factors added. All explanatory variables were standardised (scaled) to allow comparison of model parameter estimates.

Initial models did not converge when including observer/region effect. To check whether excluding this effect could be expected to change model outcome, we compared model residuals for observers using a Kruskal-Wallis test. Only for models on bumblebee abundance and species richness we observed a significant relationship between the model residuals and observer/region (appendices D.1 and D.2), indicating dropping observer/region in these models was not justified. To study whether accounting for observer/region would change model outcomes, we constructed an alternative GLM including observers as fixed factor and dropping the location random factor, that explained limited variance (<0.1) compared to other fixed factors (differences between models presented in appendix D.3). This GLM model is presented in the main text.

For each model, we analysed different polynomial levels for flower species richness to determine what curve best described bee abundance and diversity along a flower-richness gradient. As overall third polynomial models were most parsimonious (appendices D.4 and D.5), we report significance values and model predictions from third polynomials in the results. As models described non-linear relationships, we performed additional breakpoint analysis on the simple linear relationship between bee abundance/richness and flower richness to find support for breakpoint values from visual inspection of the models.

Red-listed species abundance data were zero-inflated with few high abundance values (when nest aggregations were present) and red-listed species richness was low. As such, we present presence/absence data (binomial) for red-listed individuals, constructing a GLM further using the same approach as described above. For all models we report marginal pseudo-R^2 following (Nakagawa and Schielzeth, 2013).

Predicting species occurrence based on resource preference

To analyse whether resource availability (i.e. presence of suitable flower host species as pollen source) could predict the occurrence of specific species, species specific resource preferences (see under 2.2.1) were matched with available flower species at each location to indicate the potential number of resources species could use per survey. We built presence absence models for all non-kleptoparasitic species that occurred sufficiently within our data set (the core community) using binomial GLMM's with location as a random effect. We excluded kleptoparasites, as they do not depend on specific floral resources. For each species we only selected transect counts within their flight period, as retrieved from (Falk and Lewington, 2017), to prevent including 'meaningless' 0's. Model structure was similar to the models described above.

2.3 RESULTS

Community composition

The median number of individuals caught per transects was 8, with totals varying between 0 and 384 (Appendix B.2). In total 12178 bees were recorded, of which 10503 were wild bees and 1675 honeybees. In total we found 154 species (Appendix C.2), with an estimated 199 occurring (Chao estimator, SE ± 21.68, see figure 2.2). Of these, the core community consisted of 39 species (89.4% total abundance) that occurred on 10% of all locations (Appendix C.3). This included five red-listed species (*Andrena gravida, A. labialis, A. wilkella, Nomada bifasciata* and *N. fulvicornis*), demonstrating that dikes can support vulnerable species. For 56 species, only 5 or fewer individuals were caught, with 25 species only caught once.

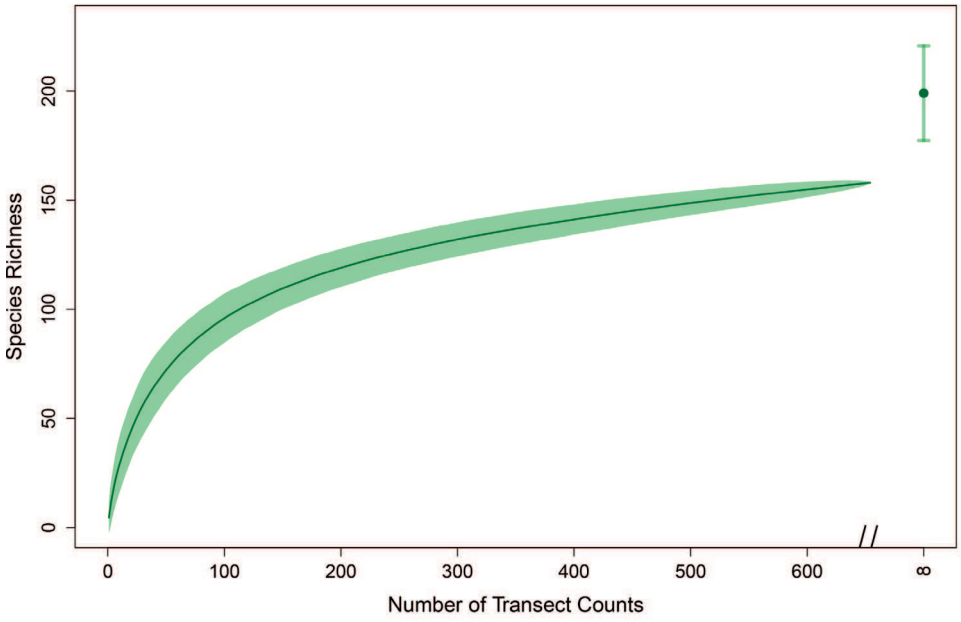


Figure 2.2: Species accumulation curve from all surveys. The dark green line represents the mean species accumulation curve from 1000 curves with randomised survey order, the light green area the 95% confidence interval. The point represents the Chao estimator with standard error.

Most species belonged to the genera *Andrena* (2508 individuals), *Nomada* (1017 individuals), *Lasioglossum* + *Halictus* (1694 individuals, henceforth Halictidae) and *Bombus* (4534 individuals) (table 2.1, Appendix C.4 for all genera). The genus *Andrena* and Halictidae family consists of species that nest underground. *Nomada* and *Sphecodes* are kleptoparasitic bees, laying their eggs in nests of other bees and respectively having *Andrena* and Halictidae species as their main hosts. The omnipresence of kleptoparasites suggests that dikes are important nesting ground for wild bees. Concomitantly we only observed 25 above-ground nesting species (327 individuals), a low number compared to the soil nesting species (4441 individuals, *Bombus* excluded) representing percentage wise fewer species (table 2.1). Finally, 942 individuals (8.96% of the total) belonging to 37 species (23.72% of the total) are red-listed in the Netherlands (Appendix C.5).

Phenology

Species phenology was not distributed equally over the year (Figure 2.3, Appendix E.1 for other genera). The two most species-rich genera *Andrena* and *Nomada* were mostly active early during the year (Figure 2.3A and 2.4D), while *Bombus* is mostly active during summer (Figure 2.3B). The Halictidae group followed no clear pattern through time (Figure 2.3C). For each group, species richness followed a similar phenological pattern (Appendix E.2). Red-listed species abundance clearly peaked early in the year, with only 59 of the total 942 observations after the 1st of June (Appendix E.3).

Table 2.1: Most species-rich bee genera in the Netherlands, their total number of species occurring in the Netherlands and the number of species found in our surveys translated to the percentage of the total number of species. Their general nesting strategy is given in the fifth column.

Taxon	#Species in the Netherlands	#Species on our dikes	Share of Dutch species found on dikes in this study (%)	Nesting
Andrena	75	37	49	Below Ground
Halictidae	52	22	42	Below Ground
Bombus	29	17	59	Both
Hoplites* + *Osmia	20	5	25	Above Ground
Megachile	13	5	38	Above Ground
Hylaeus	25	9	36	Above Ground
Nomada	48	22	46	Parasitic
Sphecodes	20	12	60	Parasitic
Total Anthophila	282	124	44	

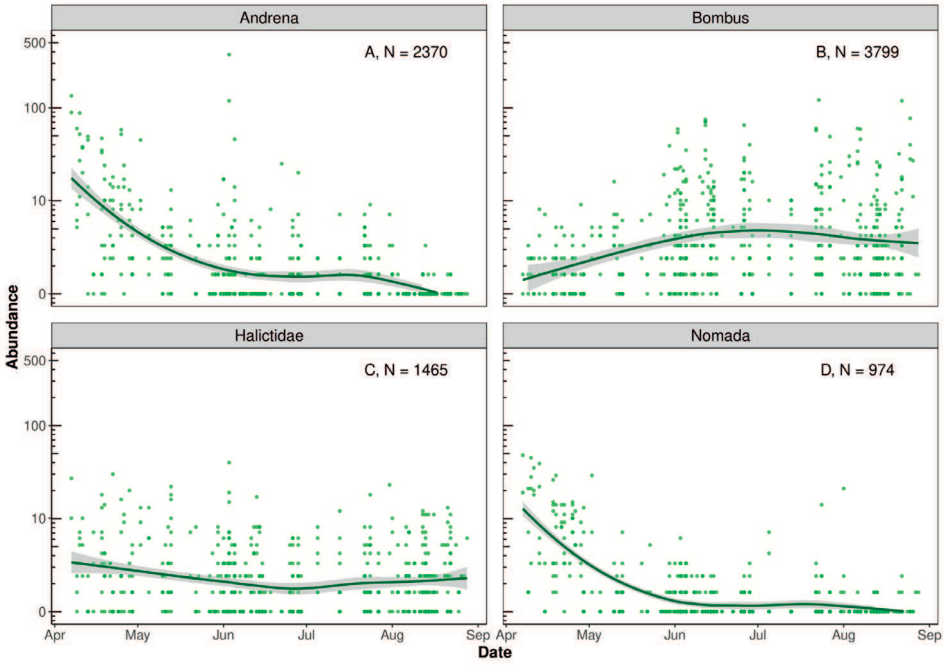


Figure 2.3: Abundance (log scale) of Andrena (A), Bombus (B), Halictidae (C)) and Nomada (D) per transect during the year. N gives the total number of individuals observed within each group, with each dot representing number of observed individuals during a single transect count. We fitted a loess curve (dark green) with 95% confidence interval to aid interpretation.

Relation Bee – Vegetation

Bee abundance and species richness in our dataset increased significantly with flower species richness in all considered subsets (figure 2.4, Appendix D.6, marginal R^2 presented in D.7 and D.8). This relationship is non-linear; third or fourth polynomial models describing flattening curves provided the best fit in all cases (figure 2.4, Appendix D.4 and D.5). Bee abundance and diversity increase rapidly at low flower species richness, after which curves flatten at around eight flower species. This is further supported by breakpoint analysis (Appendix A.4 and A.5).

The breakpoint was stronger for non-*Bombus* bees ($P < 0.001$) than bumblebees (NS) in our dataset, with slope for non-*Bombus* abundance and diversity changing from 0.15 and 0.33 before the breakpoint to 0.004 and 0.06 after respectively, compared to 0.14 and 0.16 to 0.09 and 0.05 respectively for bumblebees (figure 2.4, Appendix A.4 and A.5). This is consistent with the idea that generalist and highly mobile bumblebees keep increasing with floral resources, whereas other wild bees are limited by other factors after initial resource limitation is relieved.

Julian date showed a negative relationship with non-*Bombus* abundance and diversity, a positive effect on bumblebee abundance and no significant relationship with bumblebee diversity (Appendix D.6), in line with the phenological patterns described in 3.2. From the seven landscape factors, most parsimonious models for both abundance and diversity of all bees and non-*Bombus* bees included the area of NNN in a 1km radius (appendices D.4 and D.5). In these models a significant positive effects of more area NNN was found, although the model estimates were three to five times lower than the model estimated for local flower richness (Table 2.2). In addition, we observe a positive effect of area NNN in a 250m radius on total bee diversity. For bumblebees, model AIC's were closer together and after correcting for the observer effect (Methods 2.3.3) we found no significant effects of landscape on bumblebee abundance (Table 2.2), and a small positive significant effect of area NNN in a 1km and 250m radius and a negative effect of increasing distance to these areas (Table 2.2).

Analysis of the presence of red-listed species shows that the chance of red listed individuals being present increases with increasing flower species richness (Appendix D.9 and D.10). Opposing overall patterns, we see that red-listed species presence increases without saturating effects. In addition, Julian date correlated negatively with red-listed bee presence, suggesting that red-listed species in our system are primarily active in early spring. At the landscape level (Appendix D.11 for AIC values), there was a strong positive effect of area NNN in a 1km radius, and smaller significant effect of grassland area in a 1km radius and area NNN in a 250m radius (Table 2.2).

Predicting species occurrence

For 20 of 25 species in the core community, we found a significant increase in their presence with increase of the number of their preferred flower species (figure 2.5, Appendix F.1). Five species form an exception to this. *Andrena vaga* had no food sources on dikes (therefore not included in figure 2.5), and four showed non-significant relationships (*Andrena gravida, A.* nitida, *Lasioglossum malachurum* and *L. xanthopus*). Another two had low marginal R-square values (*A. labialis* and *A. wilkella*), indicating a poor fit. These species are ground-nesting bees that we also observed nesting on our dikes.

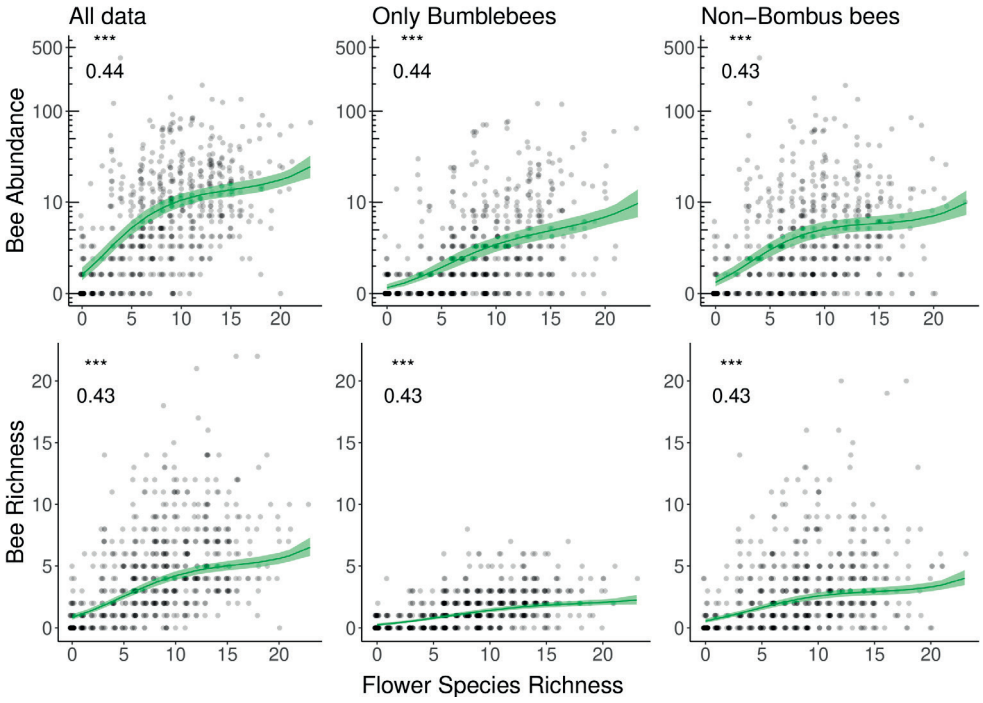


Figure 2.4: Correlations between abundance (upper row) and diversity (lower row) and local flower species richness from different subsets of the bee community; first including all available bee observation, second for only bumblebees and third for all non-Bombus bee species. Dark green lines present model predictions, the green area the 95% confidence interval.

Table 2.2: P-values (P > 0.05 = NS, P < 0.05 = *, P < 0.01 = **, P < 0.001 = ***) and model estimates with standard error from models on different subsets of wild bees (in rows) for different landscape variables (columns). NNN stands for 'NatuurNetwerk Nederland', a network that includes green infrastructure and natural areas in the Netherlands. In grey the most parsimonious models (lowest AIC values). [1]) Values for bumblebee models stem from GLM models correcting for observer.

	NNN in 1km	NNN in 250m	Shortest distance to NNN	Agricultural area in 250m	Agricultural area in 1000m	Grassland area in 250m	Grassland area in 1000m
All data Abundance	0.15 ± 0.07, *	0.09 ± 0.07, NS	0.06 ± 0.06, NS	0.09 ± 0.06, NS	0.12 ± 0.06, NS	-0.02 ± 0.07, NS	-0.04 ± 0.07, NS
Bumblebee Abudance[1]	0.08 ± 0.06, NS	0.09 ± 0.06, NS	-0.02 ± 0.06, NS	-0.05 ± 0.08, NS	0.11 ± 0.07, NS	0.002 ± 0.09, NS	-0.08 ± 0.07, NS
Non-*Bombus* bees Abudance	0.20 ± 0.08, *	0.08 ± 0.08, NS	0.09 ± 0.07, NS	0.12, NS	0.14 ± 0.08, NS	-0.08 ± 0.08, NS	-0.03 ± 0.08, NS
All data Diversity	0.11 ± 0.03, ***	0.09 ± 0.03, **	-0.04 ± 0.03, NS	-0.05 ± 0.03, NS	-0.03 ± 0.03, NS	0.02 ± 0.03, NS	0.03 ± 0.03, NS
Bumblebees Diversity[1]	0.07 ± 0.03, *	0.08 ± 0.03, *	-0.11 ± 0.04, **	-0.09 ± 0.05, NS	-0.07 ± 0.06, NS	0.06 ± 0.04, NS	0.01 ± 0.04, NS
Non-*Bombus* bees Diversity	0.13 ± 0.04, **	0.08 ± 0.04, NS	-0.001 ± 0.04, NS	-0.02 ± 0.04, NS	-0.01 ± 0.04, NS	-0.01 ± 0.04, NS	0.02 ± 0.04, NS
Red-listed presence	0.41, ***	0.27, *	-0.09, NS	-0.18, NS	-0.17, NS	0.22, NS	0.27, *

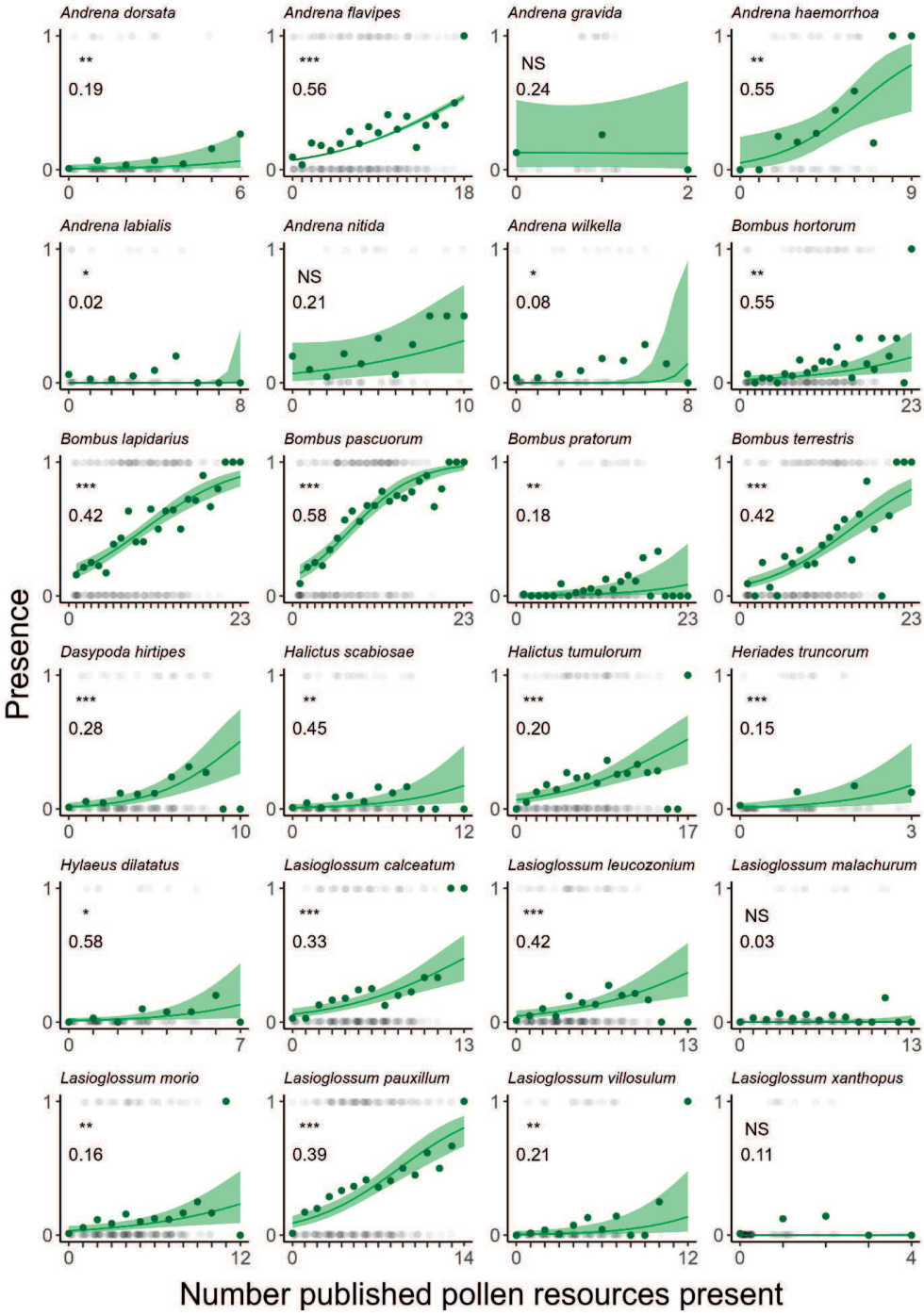


Figure 2.5: Presence of species from the core community (Y-axis), excluding *Andrena vaga* that did not have food sources present on dikes, with the number of their resource flower species (X-axis). The green line shows the model prediction, with 95% confidence intervals in light green. Green dots indicate the mean presence at the given number of floral resources present.

2.4 DISCUSSION

Previous studies have shown that dikes can harbour rich plant, true bug and grasshopper communities (Liebrand and Sýkora, 1996; Torma and Császár, 2013; Bátori et al., 2016; Torma and Bozsó, 2016). By analysing an extensive dataset on bee occurrence on semi-natural dike grasslands in the Netherlands, we show that dikes support bee communities of large conservation interest. We encountered nearly half of all Dutch bee species, with nearly 10% of all individuals and over 20% of all species on the national red list. Local conditions on dike grasslands were the strongest predictor of bee diversity and abundance, underscoring that dike grasslands provide valuable bee habitat with both a nesting and resource function, even without the presence of natural areas nearby. Increase in flower-richness increased bee richness and abundance, but this effect saturated around eight flowering plant species present. This suggests that even modest increases in plant species richness can rapidly benefit wild bees. Nevertheless, the presence of red-listed species increased most after this saturation point, and the effect of natural area surrounding the location was stronger for these bees. This suggests that red-listed species rely on both landscape-level habitat presence and high local habitat quality, thus requiring conservation efforts that consider both landscape context and local needs of these rare species.

Benchmarking wild bee communities on dikes

Comparison with other studies from North-Western Europe on linear landscape elements further emphasises the value of dike grasslands. Firstly, an encountered 156 bee species (and an estimated 199) occurring on dikes seems high. Other inventories of bees in agricultural landscapes mostly report well below a 100 species even in countries that harbour more bee species in total (e.g. Holzschuh et al., 2008; Le Féon et al., 2013; Borchardt et al., 2023). In addition, we encountered high numbers of non-*Bombus* bees versus bumblebees (4969 vs. 4525 respectively) and red listed species (942 individuals). For instance, in flower strips in rural areas in the Netherlands, Scheper et al. (2015) found 5768 bumblebees compared to 1405 other wild bees, and only 13 individuals belonging to red listed species. Another study from Wood et al., (2015) found comparable species numbers and abundance proportions, but a lower number of individuals of conservation interest (114 individuals). Although we do not have a direct explanation, we do note that many of our grasslands are older compared to the systems referred to above, and meta-analysis has shown that pollinator community richness increases with restoration age (Sexton and Emery, 2020). In addition, the warm microclimate on sun-facing dike slopes is most likely favoured by bees. While comparisons between studies should be done with caution as sampling effort, sampling method and local context differ, dike grasslands do line up as habitat worth of special conservation interest for wild bees.

Early saturation of bee species richness and abundance with increasing flower richness

Bee abundance and diversity in our dataset increased with flower species richness and abundance, a relationship described in previous studies (Kral-O'Brien et al., 2021). This relationship was only apparent at low flower species richness, with bee abundance and diversity saturating around eight flower species. This saturating effect was much stronger for non-*Bombus* wild bees (comprising the majority of all bee diversity) compared to bumblebees. Whereas bumblebees are most represented in literature (Haaland et al., 2011), our results plea for a separate consideration of non-*Bombus* wild bees for effective conservation. This finding implies that conservation efforts aimed at increasing floral resources could quickly benefit wild bee communities as a whole on flower poor locations, although after being relieved of initial floral resource limitation other factors become limiting for non-*Bombus* wild bees.

Saturating relationships between flower species richness and pollinator community richness could be theorised as pollinators are not always resource limited (Sponsler et al., 2023), and saturating patterns in bee species richness have been reported from the Jena experiment, where plant species richness is controlled in eighty 400m^2 plots (Ebeling et al., 2008). Nevertheless, to our knowledge our study is the first to report them from LLE's. In addition, we were surprised to also describe it for wild bee abundance. When increased flower species richness and abundance does not lead to an increase in pollinator abundance, this will essentially lead to fewer pollinating individuals per flowering plant. This relationship has been described by Fantinato et al (2021), who observed a humped-shaped response of pollinator visitation to floral resource availability. These results are consistent with a recent study linking declines in insect-pollinated plant species in the Netherlands to widespread pollinator decline (Pan et al., 2024). Follow-up research on the effects of pollinator saturation on pollination success of flowers would be valuable evidence for this idea.

In contrast to the overall saturating relationships, the occurrence of red-listed species in our dataset increased most at higher flower richness. Red-listed species are known to show a more selective response to habitat characteristics (Moens et al., 2023). An increase in flower species richness could hence increase the chance of host flower presence and subsequently red-listed bee species occurrence. Nevertheless, specialist bees in our dataset mostly rely on more common flower species, a trait commonly reported as nested interaction patterns in scientific literature (Bascompte et al., 2003). An additional mechanism through which increased flower species richness could promote red-listed bee species occurrence can be found in niche partitioning. Computational models suggest that an increase in flower diversity allows bees to partition their resource niches, benefiting species with weaker competitive strength and/or more specific resource preferences as generalist species shift their collection patterns to other flower species (Valdovinos et al.,

2016). Although study of the exact mechanism behind this requires further analysis of interaction patterns at our dikes, our results suggest that red-listed species conservation requires a different approach from the general bee community.

Further analysis on the occurrence of individual species revealed generally strong relationships with the occurrence of their known pollen host flowers. These relationships are based on international knowledge on pollen collection patterns, and might become even more precise with increased knowledge of local interactions. Hence, not only flower species richness, but also the identity of the flowering species determines the success of conservation efforts (Ghazoul, 2006; Warzecha et al., 2018; Filipiak, 2019; Losapio et al., 2019). Our results thus open the possibility that in addition to general community richness, conservation effort may steer towards the conservation of specific bee species through measures aimed at promoting specific host flower species.

Available nesting habitat as a limiting resource for wild bees on dike grasslands?

Nesting habitat availability has been coined as an alternative limiting factor for wild bee populations (Wood et al., 2015a ; Requier and Leonhardt, 2020). In this study, several observations suggest that dike grasslands also function as nesting location for ground-nesting bee species. Firstly, we observed especially large numbers of ground-nesting bees and their associated kleptoparasites, while aboveground nesting species were remarkably scarce. The high abundance and diversity of kleptoparasites would likely not occur without stable nesting communities of their host species. In addition, we find several diverse and abundant bee communities at low flower richness, where we also observed bee nesting colonies in the field. Finally, although most species show strong relationships with their host plant species presence in the dike grassland, several ground nesting bee species did not. *Andrena vaga* is a clear example, being found at more than 10% of all locations, suggesting that the species has its nesting location on dikes and its food source (*Salix* spp, willows) nearby. Their role as valued nesting habitat could be an additional reason as to why dikes harbour such rich wild bee communities.

This raises the question how increases in flower species richness and vegetation structure (including open spots for nesting) are connected. Higher plant diversity has been linked to more vegetation structure complexity, but this relationship has been suggested to saturate at modest plant diversity (Coverdale and Davies, 2023). This could link to the saturating patterns observed in our study. At our nutrient-rich dike grasslands, we see that that not only flower species poor but also flower species rich locations are often fully covered with vegetation leaving little bare soil. The disappearance of bare soil has been shown to have a negative relationship with bee nesting in an experiment with artificially created bare soil plots (Tsiolis et al., 2022). Thus, nesting resource could become the limiting factor under these conditions. To our knowledge, direct studies on

the relationship between VSC and bee nesting do not exist, making this an important topic for future studies that can inform nature management on how nesting and resource functions can best be combined.

Landscape setting

Previous studies have shown the importance of landscape setting for local bee community composition (e.g. Scheper et al., 2015; Griffin et al., 2021). Wild bees use partial habitats, with nesting locations being separate from foraging locations. In addition, more natural area can function as reservoirs from which species can find their way to the studied location (Leibold et al., 2004) or as buffer when local conditions are unfavourable (e.g. after mowing). While our data did not allow investigating how detailed landscape structure (e.g. availability of above-ground nesting places) was related to local bee communities, analysis of separate landscape elements revealed a small but consistent positive effect of more landscape level natural area, primarily on non-*Bombus* bees. In our dataset we find a number of above-ground breeding species (e.g. *Chelostoma florisomne* and *Hylaeus dilatatus*) that must depend on surrounding areas as there is limited to no suitable vegetation growing on dikes. In addition, for red-listed species the positive effect of natural area was only slightly smaller than that of flower species richness. However, at the community level the positive effect of natural area in the surroundings was three to five times smaller than the effect of local flower richness. In addition, the occurrence of most of the common species could accurately be predicted through the presence of their preferred resources. This suggests that dike grasslands can sustain bee communities even in otherwise heavily altered landscapes. We thus conclude that local conservation efforts on dikes are worthwhile regardless of landscape context.

Temporal differences between solitary bees and bumblebees

Phenology of most wild bee species on our grasslands, and especially both species richness and abundance of red-listed bee species, was skewed towards early spring, notably dropping after mid-June (figure 2.3). These results indicate that dike grasslands are specifically valuable early spring habitats. This is contradicting the pattern that most bee species in the Netherlands are active during June through August (Peeters et al., 2012). We hypothesize that the warm sun facing dike slopes are likely ideal nesting locations especially in early spring when average temperatures are still low. In addition, local bee communities on dikes might adapt to long term stable management of dike grasslands, where mowing typically happens in June. In contrast, we observed inversed temporal trends for bumblebees. Bumblebee colonies usually grow during the year and as such higher numbers can be expected in summer. In addition, bumblebees depend less on local conditions due to their long flight ranges. As such, bumblebees might be able to temporarily relocate their foraging grounds until flowers regrow on dike grasslands. This could be an example of temporal niche differentiation, where species avoid each other in time to reduce competition (Schoener, 1974). Literature does indeed

suggest that competition for floral resources plays an important role in bee community formation, making this explanation plausible (Ponisio et al., 2019a).

2.5 CONCLUSIONS

Linear landscape elements are known as valuable area for pollinator conservation (Öckinger and Smith, 2007; Schaffers et al., 2012). Our analysis highlights the unique potential of dike grasslands for wild bee conservation, with rich early-spring bee communities and many red-listed species that distinguishes them from many other linear landscape elements. The saturating patterns that we report indicate that, at poor dikes, modest conservation efforts can quickly benefit wild bee communities, but also that subsequent increases could lead to diminishing returns, potentially as floral resources are no longer limiting. Future research should aim to study how nesting and resource functions can best be combined.

2.6 ACKNOWLEDGEMENTS

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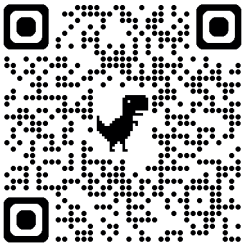
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Key floral metrics shaping local pollinator communities: a comparison between flower species richness, floral unit abundance and nectar sugar production

Thomas H. Schuurman, Wilco C.E.P. Verberk, Ivo P. Raemakers,
Eric J.W. Visser, Constant Swinkels

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Supporting information available at: https://constantswinkels.com/103-2/



ABSTRACT

1. Because pollinators provide key ecosystem services, there is interest in gauging habitat suitability for pollinators. Widely used floral metrics for habitat suitability include flower species richness and flower abundance. In contrast, nectar sugar production of the vegetation, targeting a primary food resource for pollinators, has received much less attention**.** Key barriers to using data on nectar as a metric for habitat suitability include lack of data for species-level nectar values and their transferability across countries. Here we address both barriers and test the performance of nectar supply in explaining species richness and abundance of bee communities of dike grassland transects in the Netherlands.
2. We collected nectar samples from 1,007 individual flowers belonging to 15 different plant species. For ten of these species, values for nectar sugar production are reported in the literature and we demonstrate that our measurements are broadly consistent. The remaining five species included species that were abundant on the dike grasslands and expanded the data coverage, allowing us to calculate nectar supply at the vegetation level (including 98.1% of all floral units) across 333 wild bee monitoring transects.
3. Both bee species richness and bee abundance significantly increased with nectar sugar production. Although transect flower species richness was the primary driver of wild bee response, adding nectar supply yielded better explanatory models. Nectar sugar production was a particularly strong predictor for *Bombus* bees, which likely reflects their reproductive and foraging biology.
4. Our results demonstrate that nectar sugar production of habitats provides an informative community-level floral metric for wild bees, especially bumblebees, whereas its importance in gauging habitat suitability for other, *non-Bombus* wild bees should be used with caution.

3.1 INTRODUCTION

Flower visiting insects, or pollinators, are experiencing substantial population declines (Potts et al., 2010; Goulson et al., 2015; Senapathi et al., 2015; Powney et al., 2019). It is becoming increasingly evident that this decline is closely associated with the loss of floral resources on which pollinators depend, i.e., nectar and pollen (Biesmeijer et al., 2006; Scheper et al., 2014). The decrease in floral resources is, in turn, driven by habitat degradation and changes in land use. Understanding the relationship between vegetation characteristics and pollinators is, therefore, essential, given the importance of pollinators for ecosystem functioning and agricultural yield (Ollerton et al., 2011; Garibaldi et al., 2013; Potts et al., 2016; Michez et al., 2026).

Traditionally, studies have focussed on metrics such as flower species richness and floral unit abundance for assessing pollinator habitat suitability. These floral metrics are often linked to higher pollinator numbers and more diverse communities, as they reflect greater and more varied resource availability (Potts et al., 2003; Kral-O'Brien et al., 2021; Swinkels et al., 2025). While widely used, metrics based on floral abundance and diversity serve only as indirect proxies for the amount, quality and accessibility of floral rewards (Sponsler et al., 2023). Consequently, there is a growing need to evaluate how direct measures of floral rewards can predict pollinator diversity and abundance.

Nectar, together with pollen, is widely regarded as an important currency in plant-pollinator interactions (Jones and Little, 1983; Parachnowitsch et al., 2019). At the pollinator species level, there is strong support linking their foraging choices to nectar availability (Cnaani et al., 2006; Mallinger and Prasifka, 2017). However, to what extent vegetation level nectar sugar production values derived from existing nectar datasets have direct effects and predictive strength for explaining local pollinator assemblages remains largely unexplored. Recent studies from the UK report nectar sugar production values for a wide variety of plant species (Baude et al., 2016; Hicks et al., 2016; Timberlake et al., 2019; Tew et al., 2021). These datasets enable us to move beyond traditional floral metrics and quantify nectar supply at the habitat or landscape vegetation level (Timberlake et al., 2019; Tew et al., 2021, 2023). Nevertheless, two barriers to testing the role of nectar sugar production in explaining pollinator communities remain, namely (i) it remains unknown whether nectar sugar production values can reliably be extrapolated across countries, and (ii) datasets are still incomplete for local context, especially in different countries.

In this study, we aim to overcome these barriers and test whether including vegetation level nectar sugar production improves predictions on wild bee abundance and species richness on dike grasslands in the Netherlands. Specifically, we ask three questions: (1) *How comparable are nectar sugar production values across studies?* While intraspecific nectar sugar production can vary by both temporal and environmental factors (Ryniewicz

et al., 2020; Venjakob et al., 2022; Barberis et al., 2023), we hypothesise that nectar sugar production values will be broadly comparable across studies, given that nectar production is a conservative trait linked to plant reproduction (Cane and Schiffhauer, 1997; Phillips et al., 2018). (2) *Does vegetation level nectar sugar production improve predictions on wild bee abundance and species richness compared to traditional metrics (flower species richness and floral unit abundance)?* Because nectar represents a direct measure of the energetic resources available for pollinators, rather than an indirect proxy such as floral unit abundance, nectar supply is expected to be a stronger predictor for bee species richness and abundance. (3) Does the predictive strength of nectar sugar production differ between *Bombus* bees and non-*Bombus* bees? We expected *Bombus* bees to react more strongly to nectar, compared to non-*Bombus*, because of their more generalist foraging behaviour and eusocial biology (Goulson et al., 2008).

3.2 MATERIAL AND METHODS

Location

Samples were collected at 68 dike grasslands on primary dikes, that function as active flood protection barrier, in the central and eastern parts of the Netherlands. The distance between sites exceeded 300 m, which is greater than the maximum foraging distance of most local small bee species (Zurbuchen et al., 2010). Grasslands ranged from vegetation with few flowers to high floral diversity and abundance. The soil on these dikes is characterised by heavy clay with a sandier top layer. The dike grasslands are mown yearly in mid-June and September with the specific aim to retain an erosion resistant sward height while simultaneously facilitating local biodiversity (Liebrand, 1999a). Most primary dikes were strengthened 30 years ago, meaning that the vegetation was stripped to add uniform, more erosion-resistant clay to enlarge the dikes. The current vegetation has since had time to re-establish. Nectar sampling occurred in a subset of the locations, notably five locations situated near Nijmegen.

Bee sampling

Data were collected from 2018 up to 2022, with a total of 333 transect surveys conducted. Locations were visited multiple times per year to account for the phenology of bees and plants. All sampling was done between 09:00 and 17:00. Days with temperature below 10°C, strong winds or rain were avoided. Bees were sampled along 150 m long transects, located in vegetation that provided an accurate representation of the respective dike grassland. Each transect typically took 15 minutes, during which the observer actively searched for and recorded all bees found within 1.5 m on either side of the transect. Time spent on tracking, handling and identifying bees was not included in the 15 min transect search time. Unidentifiable species were collected and taken to the laboratory for identification. Being notoriously difficult to identify, species belonging to the *Bombus*

terrestris species complex were regarded as one species (Williams et al., 2012). Honeybees were counted but not included in further analysis as they are managed pollinators. For 98 transects, the sampling time exceeded 15 min. To make the data compatible, we corrected it by randomly removing a proportion of individuals corresponding to the relative increase in sampling time, under the assumption that bee individuals were distributed evenly along the transect. Each individual had an equal probability of being removed. Species were excluded from the sample if their abundance reached zero.

Vegetation sampling

Local flower species richness and floral unit abundance were recorded along each transect, with all floral units identified to species level. Grass inflorescences were excluded, as bees in the study area did not utilize them. We counted the number of floral units per species along the 150 m netting transects (see bee sampling). In our study we followed (Baude et al., 2016) and (Carvalheiro et al., 2008) in defining floral units to facilitate comparison. Floral units comprised single capitula (number of open flowers per capitulum, e.g. *Centaurea scabiosa*), single flowers (e.g. *Rhinanthus alectorolophus*), secondary umbellets (e.g. *Heracleum sphondylium*) and single racemes (e.g. *Trifolium pratense*).

For four species (*Galium mollugo, Origanum vulgare, Lotus corniculatus* and *Lotus peduncularis*) Baude et al. (2016) considered single flowers as floral unit, whereas we considered flower stalks and flower heads respectively as floral unit. To check whether this affected model outcomes, we constructed an alternative analysis where, based on pictures, we multiplied floral unit counts for these species by 100 (*Galium mollugo*), 10 (*Origanum vulgare*) and 5 (*Lotus corniculatus* and *Lotus peduncularis*). As these species were relatively uncommon this did not affect model outcomes. Furthermore, *Centaurea jacea* and *Centaurea nigra* were regarded as a single species, as the species complex is highly polymorphic in Northwestern Europe (Hardy et al., 2000).

Nectar sampling

To construct a nectar index from data on flower-level nectar sugar production values, we needed to (1) assess whether nectar values reported in databases are comparable with local nectar sugar production values, and (2) collect additional data on nectar production values for species missing in current databases, but which were expected to be high-nectar plants in our dike transects. We selected 15 commonly occurring species on dike grasslands (Supporting Information S1), of which eleven were reported in Baude et al. (2016), whereas four were missing from current databases. For all selected species, we determined daily nectar sugar production (µg of sugars per 24 h) using microcapillaries and handheld refractometers. In addition to field sampling, we conducted greenhouse measurements of nectar sugar production on *Achillea millefolium*, *Crepis capillaris*, *Medicago lupulina* and *Trifolium pratense* in the greenhouse of the Radboud University

Nectar sampling was conducted between the end of April and mid-June 2025. Field samples were collected from multiple locations along the dikes, with at least five floral units per species sampled across multiple sampling events, where possible. Nectar was sampled using similar methods to those of Baude et al. (2016) to facilitate comparison. To prevent depletion by pollinators, floral units were covered with fine-meshed bags for 24 hours prior to extraction. Nectar was extracted using glass microcapillaries (Drummond Scientific; 0.5, 1 and 2 µL volume). Microcapillaries were inserted into fertile flowers, close to the nectar-producing glands. To quantify the total amount of nectar produced, the capillaries were left in place until no further accumulation of nectar occurred. If nectar volumes were too small or sugar concentrations too high, flowers were rinsed twice with 1–2 µL of distilled water added to the nectaries with a pipette for 1 min (see Supporting Information S2 for a detailed overview of the nectar extraction method per species). The diluted nectar solution was then collected. Nectar volume was estimated by measuring the length of the capillary that was filled using a ruler. The sugar concentration was measured by transferring the collected nectar from the microcapillaries to a handheld refractometer (Bellingham + Stanley™ Eclipse Handheld Refractometers, models 45-81 and 45-82), which provides sugar concentration as % sucrose equivalents (w/w) based on light refraction (Corbet, 2003).

To facilitate comparison between species, the nectar volume and sugar concentration were used to calculate the total mass of sugar produced (*s*; µg of sugars per 24 h), with the following formula:

$$s = 10\, d\, v\, C$$

Where v the volume of nectar collected (µl), and d the density of a sucrose solution at a concentration C (g sucrose per 100 g solution) given by $d = 0.0037921C + 0.0000178C^2 + 0.9988603$ (Corbet et al., 2001).

Calculating nectar index

Several studies quantifying nectar sugar production provide valuable data (Table 3.1), but the empirical nectar measurements differ in their scale of reporting. Baude et al. (2016) and Timberlake et al. (2019) present their nectar sugar production values at the level of individual flowers, while also providing information on the number of open flowers per floral unit. In contrast, Hicks et al. (2016) and Tew et al. (2021) report nectar values only at the floral unit level (for Asteraceae in Hicks et al. (2016)). Because our data did not overlap with species studied by Timberlake et al. (2019), and because Hicks et al. (2016) reported nectar data only as summary statistics (mean ± SE), only data from Baude et al. (2016) were suitable for flower-level species comparisons in this study. The values reported by Hicks et al. (2016) and Tew et al. (2021), however, were useful for assessing nectar production at the transect level.

Table 3.1: Overview of published nectar datasets, indicating the number of empirically measure plant species and the level of nectar sugar production quantification (individual flower vs. floral unit)

Study	Number of species	Level of quantification
Baude et al. (2016)	161	Individual flowers
Hicks et al. (2016)	64	Individual flowers, except Asteraceae (floral unit)
Tew et al. (2021)	192	Floral unit
Timberlake et al. (2019)	8	Individual flowers and floral unit

To translate species-specific, mean single-flower nectar sugar production values into site-specific estimates of local nectar supply, we followed five steps: (1) We supplemented our data with species not measured in our study using data from Baude et al. (2016). For species sampled in both studies, we calculated a weighted average. (2) To ensure compatibility between flower abundance and nectar data, some species were grouped at the genus level (e.g. *Valerianella locusta* to *Valerianella* spp.). (3) Nectar values at the floral unit level were estimated by multiplying the sampled nectar sugar content from a single flower by the number of open flowers in a floral unit. (4) To further complete the dataset, we incorporated nectar values from Tew et al. (2021), who estimated nectar sugar production at the floral unit level using both their own measurements and published data from Baude et al. (2016) and Hicks et al. (2016). (5) Nectar sugar production per transect (g per 24h) was calculated by multiplying floral unit nectar values by the number of corresponding floral units per transect.

Environmental factors

We collected data on landscape elements within a 250 m and 1000 m radius of our sampling locations from the Dutch National Basic Registration Topography database. Specifically, we recorded information on land use types and classified them into broad categories (e.g., semi-natural grassland, forest and fruit crops), with each category assumed to have a similar effect on local bee communities. Agricultural land is generally associated with lower bee abundance and species richness, whereas natural and semi-natural grasslands typically support higher bee diversity and abundance (Shackelford et al., 2013; Ekroos et al., 2020). Consequently, surrounding landscape composition may confound relationships between local floral metrics and bee species richness and abundance. To account for this potential confounding effect, we additionally quantified the presence, size and distance to areas designated as part of the National Ecological Network (NEN), as proximity to these natural areas may influence local bee communities. These variables were not included in the final models, as they did not improve their strength. We also recorded general weather conditions, including temperature, precipitation and percentage of sunshine during daylight hours, using data from Dutch meteorological stations provided by the KNMI database.

Analysis

All data were analysed in R v. 4.5.1 (R Core Team, 2025a). For analysis and graphics, packages lme4 (Bates et al., 2015), ggplot2 (Wickham, 2016) and visreg (Breheny and Burchett, 2017) were used.

Comparing nectar production

First, we assessed intraspecific differences in nectar sugar production among studies. The nectar sugar production values for each species–study combination were not normally distributed (Shapiro–Wilk test, $p < 0.05$). Therefore, we used a non-parametric Mann–Whitney U test to evaluate differences in nectar production between studies. To further evaluate the overall relationship between the nectar production values reported across studies, we included average nectar production values from both studies in a linear model. We report the model's significance and coefficient of determination (R^2). This analysis was conducted to evaluate the extent to which nectar sugar values derived from non-local studies can reliably inform the construction of an overall nectar index. In addition, we performed a simple Spearman's rank correlation test to determine whether differences were consistent among studies; that is, whether species retained their relative position on the nectar sugar production spectrum.

Predicting bee abundance and species richness

To assess how well different floral resource availability metrics (floral unit abundance, flower species richness, and nectar sugar production) predicted bee species richness and abundance, we used an information-theoretic model comparison approach. We fitted generalized linear mixed-effects models (GLMMs), specifying a negative binomial error distribution for bee abundance and species richness to account for overdispersion (using the glmer.nb function in the lme4 package in R)

For each response variable (bee species richness and bee abundance), we constructed six candidate models. Three models included a single floral resource metric, and the remaining three models included all possible pairwise combinations of the three floral metrics. All these metrics were scaled in the model to facilitate comparison of estimates. Both floral unit abundance and nectar sugar production were log-transformed, following (Swinkels et al., 2025) and as not log-transforming resulted in convergence issues. In addition, models included the Julian date (the day of the year) to account for seasonal changes and transect location as a random variable to account for nested observation (transects were sampled multiple times per year). The resulting six candidate models were ranked based on their Akaike Information Criterion values corrected for small sample size (AICc) (Burnham et al., 2011). Akaike model weights (ω), which reflect the probability that a model is the best approximating model in the candidate set, were calculated for each model in the candidate set.

We performed additional robustness tests. First, we included the longitude of our locations in the models, as east-west gradient could potentially interfere with floral richness and abundance. Secondly, we incorporated landscape variables, specifically the area of grassland within 250 m and a 1 km radius, the area of NEN within 250 m and a 1 km radius and the distance to the nearest NEN area. In addition, we tested the influence of the temperature and percentage of sunshine during daylight hours. To account for potential incongruence in floral unit counts between Baude et al. (2016) and our dataset, specifically for *Galium mollugo, Origanum vulgare, Lotus corniculatus and Lotus peduncularis* (see above), we multiplied floral units for these species by 100, 10, 5 and 5 respectively. These robustness tests demonstrated that none of these additional factors changed the model outcomes regarding the effects of floral metrics, explaining variation in bee assemblages unrelated to local floral resources.

Finally, we repeated the process described above for subsets of only bumblebees and non-*Bombus* wild bees. These groups represent different survival strategies, bumblebees generally living in large colonies and being generalist foragers, whereas wild bees are mostly solitary with more specialized resource collection patterns.

3.3 RESULTS

In total, we collected nectar samples from 1,007 individual flowers belonging to 484 floral units and 15 different plant species. We sampled four species in the controlled setting of the greenhouse and 13 species in natural conditions on the Ooijpolder dikes. By supplementing our data with data from Baude et al. (2016) and Tew et al. (2021), we were able to convert 98.1% of recorded floral unit abundance along the transects into nectar sugar production values, covering 84 of the 125 flower species (67.2 %). Along our 333 transects, we captured a total of 3,022 wild bees, of which 1,743 were *Bombus* bees and 1,279 were non-*Bombus* bees (excluding honeybees). The highest species richness of bees was 14 species on a single transect, with bee abundances ranging from 0 to 125 individuals. Floral species richness varied widely across transects, spanning 1 to 32 species (median 13), while the number of floral units reached up to 208,295 units (median 865).

Nectar sugar production

Within plant species, we found no significant differences between our measurements taken in the greenhouse and those from the field (Supporting Information S3; $p > 0.05$). Therefore, greenhouse and field measurements were grouped together in subsequent analyses. Across all ten species for which we had our own measurements and data from the literature, nectar sugar production values strongly covaried for both sources (Figure 3.1; adjusted R^2-value: 0.786, $p < 0.001$). This similarity was confirmed by a Spearman's rank correlation which revealed a strong relationship between interspecific

nectar sugar production values across the two studies ($\rho = 0.87$, $S = 28$, $p < 0.001$), indicating that species also largely maintained their relative positions in the nectar sugar production spectrum. We did find significant differences in nectar sugar production for four plant species when comparing our measurements with published values (Supporting Information S3), but these differences within species were small relative to the differences across species.

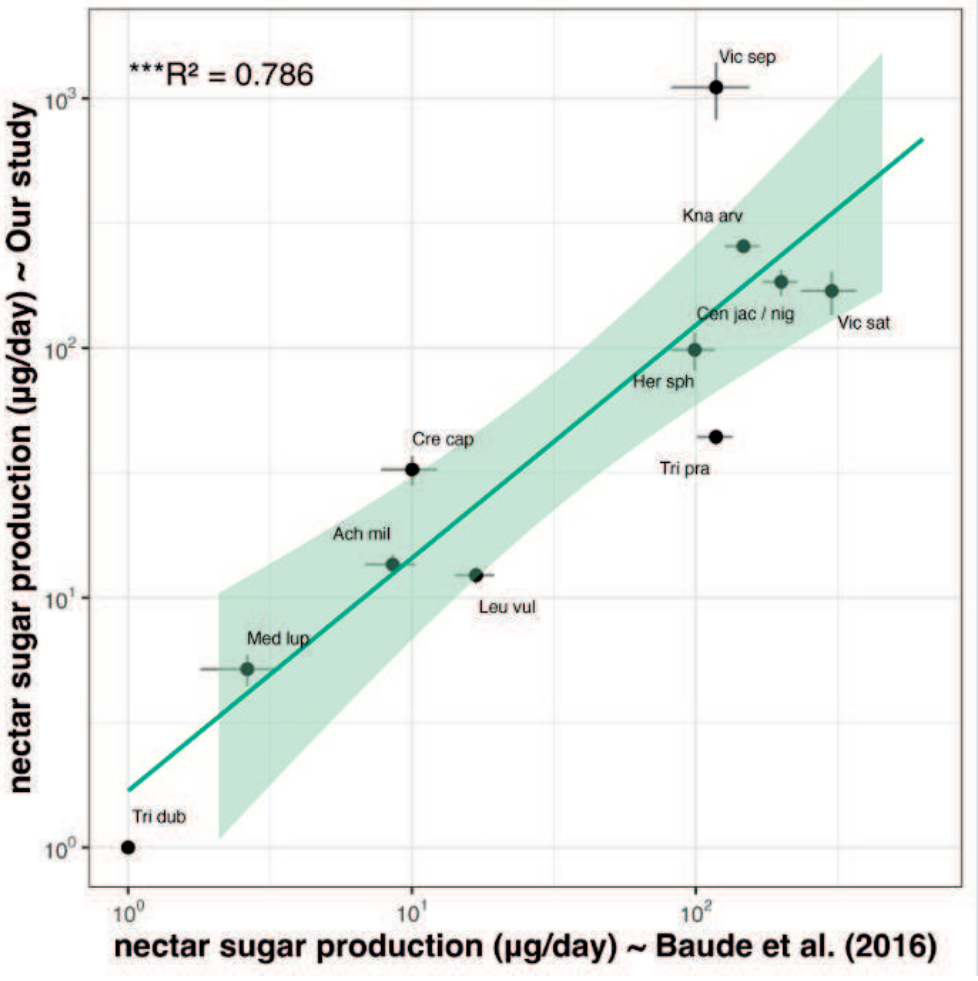


Figure 3.1: Linear relationship between the $\log_{10}(x+1)$ nectar sugar production values (µg of sugars per day) between Baude et al. (2016) and our own measurements. Points and lines represent mean nectar sugar production values and their standard errors. R^2 represents the adjusted R-squared value, $p < 0.05$. Species are denoted by abbreviations of their scientific names. A full list of these species can be found in supporting information S1.

Thus, nectar sugar production values from different studies provide a reasonably accurate characterisation of a given species allowing us to calculate nectar sugar production at the level of our surveyed grasslands using the combined data. Thus, the vegetation could be characterized by three floral metrics. (i) nectar sugar production values, (ii) number of plant species, (iii) number of floral units. Not surprisingly, these metrics are somewhat colinear, all reflecting different aspects of flowers in the vegetation. Nevertheless, they carry unique variation: the adjusted R^2 value of 0.46 ($p < 0.001$) between nectar sugar production and floral unit abundance adds nuance, showing that, while the two variables share substantial explanatory power, roughly 54% of the variance in nectar sugar production is not explained by floral unit abundance (Supporting Information S4).

Bee-vegetation relationship

Both total bee abundance and species richness significantly increased with flower species richness, floral unit abundance and nectar sugar production (Figure 3.2; Supporting Information S5). For bee abundance, the two most parsimonious models included flower species richness in combination with either nectar sugar production or floral unit abundance (ΔAICc = 0.15, model weights ω = 0.52 and 0.48 respectively). In contrast, the combined model with flower species richness and floral unit abundance (and not nectar sugar production) was most parsimonious for bee species richness (ΔAICc = 7.27, model weight ω = 0.97) (Table 3.2).

Analysis at the group level revealed clear differences between groups. For *Bombus* bees, a model combining flower species richness and nectar sugar production was most parsimonious for both bee abundance and species richness (ΔAICc = 17.24 and 11.53, respectively; model weights ω = 1; Table 3.2). When comparing single metric models, the most supported model predicting bumblebee abundance included nectar availability (ΔAICc = 4.3).

In contrast, non-*Bombus* bees responded strongest to flower species richness (Table 3.4). In the single metric models, the flower species richness model best supported for both bee variables (ΔAICc = 10.1 and 8.5). In the combined models, adding floral unit abundance or nectar sugar production did not improve model parsimony (ΔAICc < 2) and flower species richness remained a significant predictor, whereas the other metrics were generally non-significant.

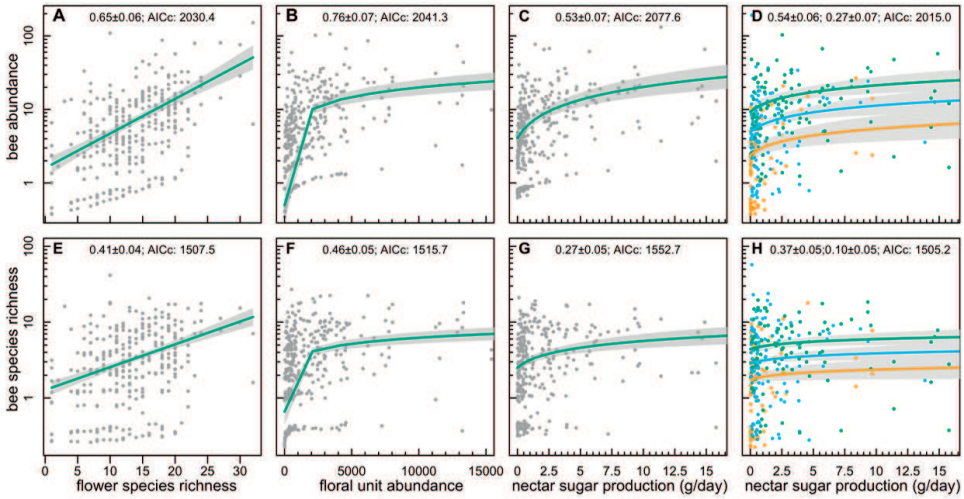


Figure 3.2: Relationship between bee abundance and species richness along flower species richness (A, E), floral unit abundance (B, F) and nectar sugar production (g/d; C, G) and their interaction (D, H), with 95% confidence intervals. Graphs weremade using the r package visreg, displaying partial residual plots that illustrate the relationship between the response variables and the independent variables, while also accounting for the effects of other independent variables (Julian date and sample location) in the models. Note the log10 transformation for the y-axis. For each model, the estimate ± SE and AICc values are given. In panels D and F, the lines give the predicted bee abundance and species richness along nectar sugar production for three different levels of flower species richness: 5 (orange), 13 (blue) and 20 (green). In panel B, C, D, F, G and H the x-axis is cropped to clarify the data distribution by omitting a small number of the highest values to make the data distribution clearer (unchanged plots, see Supporting Information S5)

Table 3.2: All data models for total bee abundance and richness.

	Total bee abundance					**Total bee richness**				
Model	*Estimate ± SE*	*pval*	*R2mar*	*R2con*	*AIC*	*Estimate ± SE*	*pval*	*R2mar*	*R2con*	*AIC*
single models										
Flower species richness	0.65 ± 0.06	***	0.33	0.33	2030.4	0.41 ± 0.04	***	0.29	0.30	1507.5
Floral unit abundance (log10)	0.76 ± 0.07	***	0.34	0.37	2041.3	0.46 ± 0.05	***	0.29	0.34	1515.7
Nectar sugar production (log10)	0.53 ± 0.07	***	0.21	0.28	2077.6	0.27 ± 0.05	***	0.15	0.25	1552.7
combined models										
Flower species richness	0.43 ± 0.08	***	0.39	0.39	2015.2	0.27 ± 0.06	***	0.33	0.34	1497.9
Floral unit abundance (log10)	0.40 ± 0.09	***				0.24 ± 0.07	***			
Flower species richness	0.54 ± 0.06	***	0.37	0.37	2015.0	0.37 ± 0.05	***	0.30	0.30	1505.2
Nectar sugar production (log10)	0.27 ± 0.07	***				0.10 ± 0.05	*			
Floral unit abundance (log10)	0.63 ± 0.09	***	0.34	0.37	2038.6	0.43 ± 0.07	***	0.29	0.34	1517.4
Nectar sugar production (log10)	0.18 ± 0.08	*				0.04 ± 0.06	ns			

Model estimates with standard error, p-values (NS, $p > 0.05$; · $p < 0.1$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$), marginal and conditional R2-values and AICc-values from single and combined models. Log_{10} indicates that data has been log_{10}-transformed: $log_{10}(x+1)$

Table 3.3: Bombus models for bee abundance and richness.

	Bee abundance (only bumblebees)					Bee richness (only bumblebees)				
Model	***Estimate ± SE***	***pval***	***R2mar***	***R2con***	***AIC***	***Estimate ± SE***	***pval***	***R2mar***	***R2con***	***AIC***
single models										
Flower species richness	0.73 ± 0.08	***	0.26	0.30	1654.8	0.41 ± 0.05	***	0.23	0.25	1033.6
Floral unit abundance (log10)	0.94 ± 0.10	***	0.32	0.35	1652.5	0.48 ± 0.06	***	0.24	0.28	1035.8
Nectar sugar production (log10)	0.81 ± 0.08	***	0.26	0.36	1648.2	0.37 ± 0.04	***	0.18	0.24	1034.9
combined models										
Flower species richness	0.43 ± 0.10	***	0.35	0.36	1636.1	0.25 ± 0.07	***	0.26	0.28	1024.2
Floral unit abundance (log10)	0.57 ± 0.12	***				0.27 ± 0.08	***			
Flower species richness	0.51 ± 0.08	***	0.36	0.38	1614.0	0.28 ± 0.05	***	0.26	0.27	1009.2
Nectar sugar production (log10)	0.54 ± 0.08	***				0.25 ± 0.05	***			
Floral unit abundance (log10)	0.55 ± 0.11	***	0.34	0.37	1631.2	0.29 ± 0.07	***	0.25	0.28	1020.7
Nectar sugar production (log10)	0.49 ± 0.10	***				0.24 ± 0.05	***			

Model estimates with standard error, p-values (NS, $p > 0.05$; · $p < 0.1$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$), marginal and conditional R2-values and AICc-values from single and combined models. Log_{10} indicates that data has been log_{10}-transformed: $log_{10}(x+1)$

Table 3.4: Non-Bombus models for bee abundance and richness.

	Bee abundance (no bumblebees)					Bee richness (no bumblebees)				
Model	***Estimate ± SE***	***pval***	***R2mar***	***R2con***	***AIC***	***Estimate ± SE***		***R2mar***	***R2con***	***AIC***
single models										
Flower species richness	0.51 ± 0.07	***	0.24	0.30	1546.3	0.40 ± 0.06	***	0.21	0.26	1254.6
Floral unit abundance (log10)	0.53 ± 0.09	***	0.21	0.33	1556.4	0.42 ± 0.07	***	0.19	0.28	1263.0
Nectar sugar production (log10)	0.22 ± 0.08	***	0.10	0.26	1582.0	0.17 ± 0.07	**	0.08	0.20	1290.8
combined models										
Flower species richness	0.39 ± 0.10	***	0.25	0.33	1545.3	0.29 ± 0.08	***	0.22	0.28	1252.8
Floral unit abundance (log10)	0.22 ± 0.12	·				0.19 ± 0.10	*			
Flower species richness	0.53 ± 0.08	***	0.24	0.30	1548.2	0.41 ± 0.07	***	0.21	0.26	1256.5
Nectar sugar production (log10)	0.03 ± 0.08	ns				0.03 ± 0.06	ns			
Floral unit abundance (log10)	0.64 ± 0.11	***	0.22	0.34	1556.5	0.51 ± 0.09	***	0.20	0.29	1263.1
Nectar sugar production (log10)	0.15 ± 0.10	ns				0.12 ± 0.06	ns			

Model estimates with standard error, p-values (NS, $p > 0.05$; · $p < 0.1$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$), marginal and conditional R2-values and AICc-values from single and combined models. Log_{10} indicates that data has been log_{10}-transformed: $log_{10}(x+1)$

3.4 DISCUSSION

Our results reveal that nectar sugar production values reported in literature can be used to calculate the nectar sugar production at the vegetation-level for pollinating insects. Nectar supply proved to be an important floral metric, especially for bumblebees (*Bombus* spp.). *Bombus* abundance and diversity were best explained by models that included flower species richness and nectar sugar production. In contrast, non-*Bombus* species were primarily influenced by local flower species richness, showing a weaker response to nectar supply. These group-specific responses highlight different ecological requirements and the relative importance of floral resources among bee taxa.

Nectar comparability

In line with our hypothesis, nectar sugar production values of flower species were highly comparable between our study system and those sampled by Baude et al. (2016) in the UK. Across species, nectar sugar production values were strongly correlated between studies, with species maintaining similar relative positions along the nectar sugar production spectrum. This pattern is consistent with the idea that nectar production is a relatively conserved floral trait, likely because it is closely linked to plant reproductive success (Cane and Schiffhauer, 1997; Phillips et al., 2018). It also validates our approach of combining published nectar sugar production values with our measurements to calculate vegetation level nectar sugar production along transects.

Despite these findings, we note that, although nectar extraction is often conducted following published methods (Baude et al., 2016), we still encountered cases where nectar sugar production values reported across studies were partly incomparable or incomplete. For instance, Hicks et al. (2016) and Tew et al. (2021) do follow standardised nectar extraction protocols, but reported summarized (mean ± SE) nectar sugar production values at floral unit level, without providing information on the individual flower measurements used to calculate them. As demonstrated by Phillips et al. (2018), plants may not show changes in nectar sugar production values in response to changed environmental conditions, but may instead produce fewer flowers per floral unit or fewer nectar-producing flowers within each unit. Hence, we emphasize the importance of reporting nectar values at both the individual flower and floral unit level, combined with the number of open flowers per floral unit. In addition, nectar sugar production values remain unavailable for many plant species. Although we were able to estimate vegetation-level nectar sugar production for 98.1 % of all floral units recorded in our study, these belonged to only 67% of the species in our dataset. This highlights the continued need to report nectar sugar production values for plant species using standardized protocols.

Finally, despite the overall strong intra- and interspecific correlations in nectar sugar production values between studies, we observed significant intraspecific differences for

four species. Such variation in nectar sugar production within species across locations has been reported previously and has been linked to differences in environmental conditions and phenology (Ryniewicz et al., 2020; Venjakob et al., 2022; Barberis et al., 2023). Although our results suggest that these intraspecific differences do not substantially affect estimates of vegetation-level nectar sugar production at the landscape scale, they do indicate that studies focusing on individual plant species, such as those examining pollinator visitation, should ideally measure nectar sugar production locally rather than relying solely on published values (Cnaani et al., 2006; Mallinger and Prasifka, 2017).

Nectar as floral metric

Our findings revealed that including nectar sugar production improved the explanatory power of our models for bee assemblages. For both abundance and species richness, the model that included nectar sugar production in addition to flower species richness outperformed the single predictor model. Nectar was an especially strong predictor for bumblebees, which differ from other wild bees in being more opportunistic foragers that live in large colonies and concentrate foraging efforts to resource-rich patches (Goulson et al., 2008; Osborne et al., 2008). Together, this explains why they respond strongly to nectar sugar production, preferentially foraging in nectar-rich vegetation (Pleasants, 1981). Our findings are consistent with this ecological explanation, suggesting that incorporating nectar production can improve predictions of bumblebee diversity and abundance.

In contrast, for other wild bees, abundance and species richness were driven by flower species richness and floral unit abundance, with flower species richness explaining most of the variation. This group comprises species with diverse life histories and often narrow resource preferences, where larval development is primarily restricted through the need for specific pollen and thus flower species (López-Uribe, 2021). Greater flower species richness increases the range of foraging niches, thereby promoting higher wild bee diversity. In addition, resource partitioning facilitated by floral diversity is considered an important mechanism underlying pollinator coexistence (Blüthgen and Klein, 2011). Empirical studies have shown that wild bees aim to reduce direct resource overlap (Fründ et al., 2013), and theoretical models demonstrate that adaptive foraging behaviour can stabilize pollinator communities (Valdovinos et al., 2013, 2016). Similarly, from the plant perspective the attraction of specialist pollinators may enhance pollination efficiency through greater pollination fidelity (Fenster et al., 2004; Larsson, 2005). As such, flower species richness might best predict non-*Bombus* wild bee abundance and species richness as a proxy for both pollen availability and increased opportunity for resource partitioning, whereas nectar sugar is less limiting. In any way, these results illustrate the difference in resource ecology between bumblebees and other wild bees, emphasizing the need to distinguish between both groups in both pollinator research and conservation.

Future outlook

Despite nectar improving predictions of bumblebee abundance and species richness, wild bees responded strongest to flower species richness. We argue this is linked to their high dependence on pollen, which is collected by adults and serves as the primary food source for larvae (Wäckers et al., 2007; Vaudo et al., 2015). As such, pollen traits play an important role in structuring plant-bee interactions and shaping bee foraging patterns (Vaudo et al., 2024). However, pollen data are even more sparse than nectar sugar production data, limiting the evaluation of the role of pollen as a floral metric. Pollen, both in terms of quality and quantity, may therefore represent an important metric explaining the strong response of non-*Bombus* wild bees to flower species richness. This gap further emphasizes the need for coordinated data collection efforts, with datasets such as those compiled by Hicks et al., (2016) offering a promising starting point for integrating pollen resources.

Furthermore, as our research focussed on bee communities, extending this framework to other pollinator groups, such as hoverflies and butterflies, would be a valuable next step. Such comparison would help assess the generality of nectar sugar production as a predictor of pollinator communities and evaluate its relevance across taxa with differing ecological requirements. Our study sites, located on Dutch dikes, are characterized by rather nutrient-rich soils with high water retention, typically consisting of clay-rich substrates. Flower species with high nectar sugar production are common in this system, such as *Centaurea jacea* and *scabiosa*, *Knautia arvensis*, *Crepis biennis* and *Trifolium pratense*. Consequently, our dike grasslands are particularly well suited to generalist bee species, such as bumblebees (Pleasants, 1981). It remains, however, unclear whether nectar sugar production plays an equally important role in different ecosystems, such as those strongly limited by soil moisture or nutrients. Because pollinator community composition differs between such habitats, the accuracy of nectar sugar production in predicting bee communities may also vary, emphasizing the need to test its applicability across different habitat types.

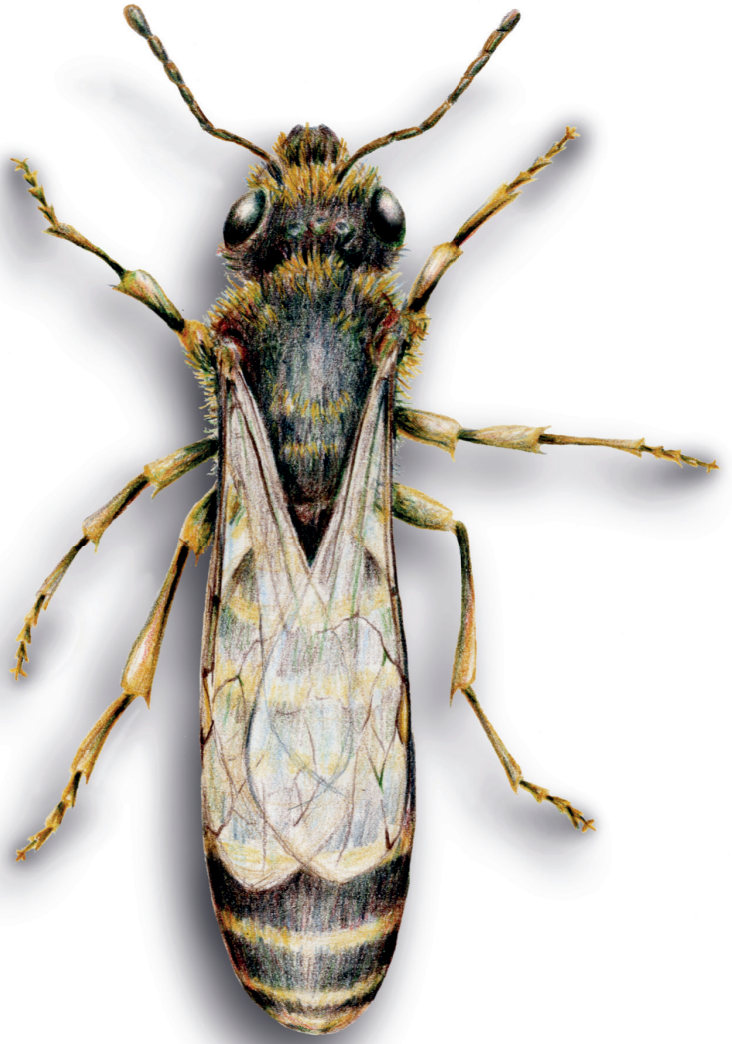
3.5 CONCLUSION

Our results show that nectar sugar production values are broadly comparable across countries, enabling the calculation of an aggregate nectar sugar production for transects. Applying this approach to dike grasslands in the Netherlands revealed that including vegetation-level nectar sugar production improves model predictions. Nectar production appeared to be more important for predicting bee abundance, whereas flower species richness was a stronger predictor of bee species richness. Furthermore, communities dominated by social, generalist species may respond more strongly to nectar sugar availability, whereas communities composed primarily of solitary or more specialized species

may depend more heavily on flower species richness. Overall, our findings highlight vegetation-level nectar sugar production as a promising metric to gauge bee communities from vegetation data, while underscoring the need to expand existing databases with standardized nectar sugar and pollen production values.

3.6 ACKNOWLEDGEMENTS

We are grateful to co-workers that helped to collect the data throughout this project: Miriam Scherpenisse, Jochem Macaré, Jeroen Willems (Natuurbalans) and Cyril Liebrand. In addition, the authors extend their gratitude to the waterboards Waterschap Rivierenland and Aa en Maas for allowing the collection of the data on their dike grasslands.

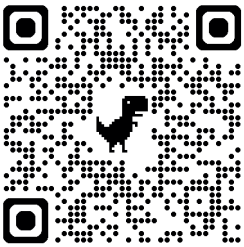


4

How Pollinators Reduce Resource Use Overlap: Diet Narrowing and Landscape-Level Foraging Revealed by Molecular Pollen Analysis

Constant Swinkels, Cornelis A. M. Wagemaker, Maarten Postuma, Annemiek E. Smit-Tiekstra, Eelke Jongejans & Hans de Kroon

Supplementary materials available at: https://constantswinkels.com/109-2/



ABSTRACT

1. Floral resource diversity is widely considered a key driver of pollinator coexistence. Higher floral resource availability should allow pollinators to forage more selectively on preferred resources while facilitating interspecific niche partitioning. Although these mechanisms are well described in conceptual and theoretical models, empirical evidence from field systems remains limited. This gap is further compounded by the reliance on visual observations of local interactions, despite the fact that many pollinators potentially forage beyond plot boundaries and incorporate landscape-level resources into their diets.
2. Here, we use a novel molecular approach, multispecies genotyping by sequencing, to quantify pollen collection patterns of pollinators along gradients of flower abundance and species richness to study (1) how local resource availability influences local foraging efforts, (2) how local resource availability and landscape level foraging influence diet breadth and (3) how this translates to interspecific resource use overlap.
3. We show that pollinators collected a higher proportion of pollen locally when both local richness and abundance of flower species increased. With increased local flower richness, pollinators also collected resources from fewer plant species, i.e. narrowed their diet breadth — a pattern driven by within-species niche narrowing rather than species turnover. This increased specialisation reduced resource use overlap between pollinator species. The ability of pollinator species to forage adaptively and through this process reduce resource use overlap provides field-based evidence to conceptual models on pollinator coexistence.
4. However, patterns at flower-poor locations were substantially altered when including landscape-level foraging. Under low local floral resource availability, pollinators obtain a large proportion of their resources from the surrounding landscape. This accounted for the observed broader diets and markedly reduced estimates of total resource use overlap. This highlights the need to consider fine-grained, cross-habitat foraging dynamics in pollinator conservation and the study of plant-pollinator interaction networks.

4.1 INTRODUCTION

How diverse groups of species can coexist has long fascinated ecologists. The question is fundamentally interesting and understanding the mechanisms that facilitate coexistence is crucial for effective biodiversity conservation. While these mechanisms are relatively well studied for plants and larger animals, the question of how pollinators coexist in diverse communities has only recently received comparable attention. This is especially relevant in light of concerns about widespread pollinator decline (Biesmeijer et al., 2006; Potts et al., 2010; Scheper et al., 2014; Goulson et al., 2015). Because pollinators share a strong dependence on floral resources, vegetation composition is a key driver of their community structure (Potts et al., 2003; Fründ et al., 2010). Consequently, much of the research on pollinator coexistence has focused on how species partition floral resources.

Increased resource availability may facilitate pollinator coexistence in two ways. First, greater resource diversity generally supports more pollinator species as plant-pollinator interactions are mediated by trait matching (Vázquez et al., 2009; Blüthgen and Klein, 2011; Schwarz et al., 2020). Diverse floral resources offer pollinators greater opportunity to select resources according to species-specific preferences (Cusser et al., 2019; Kelly and Elle, 2021), while higher flower abundance allows pollinators to collect more resources from abundant plant species (Vázquez et al., 2009; Fort et al., 2016). Second, central to theories on pollinator species coexistence is the idea that increased floral resource diversity enables generalist pollinators, often dominant in communities in temperate climates, to adjust their foraging patterns in ways that reduce interspecific resource use overlap (Brosi, 2016; Ponisio et al., 2019a; Valdovinos and Marsland, 2021). This adaptive foraging capacity is thought to increase pollinator community stability (Valdovinos et al., 2013, 2016). Consistent with these predictions, controlled experiments find that pollinators, on average, interact with fewer flower species than expected with increased local flower availability (Ebeling et al., 2011), while their collection patterns are more segregated than could be expected from individual preferences (Fründ et al., 2013).

Despite these insights, few field studies have examined how pollinator diets and community-level interaction patterns change across natural gradients of floral richness. The most direct evidence, to our knowledge, comes from a study in Mallorca (Spain), where pollinator communities exhibited greater specialization and modularity in areas with higher flower richness (Gómez-Martínez et al., 2022). However, this study did not explicitly quantify pollinators' use of resources beyond the focal locations. In field settings, such landscape-level foraging may strongly influence observed patterns, especially in flower-poor habitats where pollinators are likely to depend more heavily on surrounding resources (Pornon et al., 2016). Understanding how pollinators exploit floral resources across both local and landscape scales is therefore essential for identifying the mechanisms that sustain diverse pollinator communities under real-world conditions

and for designing conservation measures that remain effective across heterogeneous, human-modified landscapes.

Tracking landscape-level resource collection in natural settings remains challenging because visitation observations are inherently restricted to local sampling sites. Advances in DNA-based pollen identification, that can accurately identify pollen to the species level, provide a promising approach (Tommasi et al., 2021; Lowe et al., 2022b). These methods not only reveal rare local interactions missed by visual surveys, but also detect pollen collected from plant species outside the focal area (Pornon et al., 2016; Bell et al., 2017). As such, applying these molecular techniques to pollen carried by pollinators along gradients of resource availability could reveal non-local resource collection, potentially substantially altering estimates of resource overlap and diet breadth that are based solely on local resource use.

We here apply multispecies genotyping by sequencing (henceforth msGBS), a recent method that allows to identify multiple species within mixed plant species samples with high accuracy (Wagemaker et al., 2021), to pollen loads of pollinator species. We analyse their collection patterns along a flower richness gradient, separating flower resources from inside and outside the focal study habitat. Specifically, we test three hypotheses; 1) Pollinators will incorporate a greater proportion of locally available floral resources into their diets as local flower abundance and richness increase, 2) generalist pollinator species will narrow their diet breadth in flower-rich sites, reflecting increased opportunities for selective foraging, and 3) this increased specialization will lead to reduced resource-use overlap among pollinator species. We examine how the tests of these hypotheses are modified by including pollen resources from outside the local study area.

4.2 METHODS

Location

Data were collected from 15 grasslands located on primary dikes that currently function as flood protection barrier near Nijmegen, the Netherlands. These dikes are constructed from heavy clay, typically overlain by a sandier topsoil layer. All grasslands were found on the south facing, inland slope of the dike and supported semi-natural *Arrhenaterion* grasslands managed by biannual mowing (end of June and September). In contrast, the river-facing slopes typically experienced different management regimes due to their role as the primary flood barrier and consequently supported poorer vegetation.

Study sites were selected to represent a gradient of monotone, flower-poor dike grasslands (minimum of six flower species present) to well developed, flower-rich locations (up

to 22 flowering species). In addition, sites were separated by at least 400 meters (mean 1435 m), exceeding the foraging range of most small bee species (Zurbuchen et al., 2010).

Sampling strategy

All sampling was completed in May and early June, as this period is the peak flowering and bee activity time in our system while being before the first mowing event by half June (Swinkels et al., 2025). Locations were sampled once in 2021 and twice in 2022.

Vegetation sampling

For each pollinator survey, local flower species richness and abundance was recorded, with all flowering plants identified to the species level. Grass inflorescences were not included as these are not used by pollinators in our study area. For each survey, we counted the number of flowering plants per species within a 5 × 5 m quadrat selected to represent local vegetation and flower species richness. This quadrat size is slightly larger than the minimum recommended for vegetation surveys in species rich grasslands (Chytrý and Otýpková, 2003). In addition, vegetation composition of dike grasslands is rather uniform owing to their water protection function, making this size a long-standing practice on dike grasslands (Liebrand, 1999). If flowering species along the survey transect were absent from the vegetation quadrat, they were added to the species list to ensure inclusion as locally present species during analyses.

A similar approach was used to determine flower richness and abundance on the grassland on the other side of the dike and in habitat types within 250m from the transect. Quadrat size in these habitats ranged from 5 × 5 m to 10 × 10 m, depending on the vegetation structure and the area needed to capture most local flowering species. To standardize across samples, flowering plant abundance for all surveys was converted to flower density expressed as the number of flowering plants per square meter.

Leaf samples from all flowering species, both on the dike grasslands and in the surrounding landscape, were collected to create the msGBS reference database (methods 2.3). Samples were collected using sterilised scissors and tweezers while wearing gloves to minimize DNA contamination, stored in sterile zip-lock bags with silica gel in the field and transported to the freezer until further processing. Although we were not always able to access private gardens, common garden species were included in the msGBS reference dataset (see Methods 2.3).

Pollinator sampling

Pollinators were sampled along 150m long transects, running through representative vegetation for the dike grassland. Transects were sampled for 15 minutes of active searching time (time was paused while tracking, handling and identifying individuals) and all pollinators found within 1.5m on either side of the transect were recorded. Species that

could not be identified in the field were collected and transferred to the lab for identification (but see 2.2.2). The *Bombus terrestris* species complex was treated as one species due to the difficulties involved in correct identification of these species (Williams et al., 2012).

Pollen sampling, pooling and gDNA extraction

For each pollinator species observed during the surveys, individuals were collected for pollen sampling with a maximum of ten individuals per species. Specimens were caught using an insect net, which was cleaned after every successful sweep by removing all plant material and vigorously shaking to dislodge any remaining pollen. Captured individuals were transported into sterile 15 mL Eppendorf tubes containing 75% ethanol to preserve their pollen.

In the lab, tubes with pollinators were sonicated for 30 minutes and subsequently vortexed to dislodge their pollen. Remaining pollen (for bees only from the pollen collection apparatus) were carefully removed from pollinators under a microscope in sterile Petri dishes, after which 75% ethanol was added and the pollen were added back to the sample. The 15 ml tubes were then centrifuged using a swingout rotor (5 minutes, 4700rpm) after which the ethanol was carefully decanted until less than 0.5 ml ethanol remained. The rest of the ethanol was evaporated at room temperature. Pollen samples were then resuspended in 0.5ml nuclease free ultra pure water, after which they were pooled per location, date and species. Pooled samples were again centrifuged for five minutes, after which the supernatant was carefully removed until roughly 0.5ml remained. Samples were freeze dried for 16 hours.

gDNA extraction was performed resuspending the freeze-dried samples in 0.5ml P1 CTAB based lysis buffer (NucleoSpin Plant II mini kit, Marchery Nagel, Germany). To each sample a small spoon of sterile zirconia sand and 4 steel bullets (2.3 mm) were added after which the pollen were disrupted by two cycles of grinding with a dwelling time of five minutes (TissueLyzer, s=2500, t=2:00, QIAGEN, Germany). The gDNA extraction was continued according to the manual instructions of the NucleoSpin Plant II mini kit. gDNA was eluted in 50 mL Elution buffer. 1 mL was used for quantification using a Qubit fluorometer. gDNA was stored at -20 °C until further processing.

msGBS analysis

For a detailed description of molecular part of the pollen DNA analysis, we refer to Wagemaker et al. (2023). In short, the extracted gDNA was digested using the restriction enzyms *Pac*I and *Nsi*I (NEB, USA), and ligated with two indexed adapters each containing 3 unique molecule identifier (UMI) bases using T4 DNA ligase (NEB, USA). The resulting indiced products were pooled per approximate 96 individual samples, after which the pool was first concentrated to 50 mL using NucleoSpin Gel and PCR Clean-up kit (Marchery Nagel, Germany) and second, size selected by a 0.8x bead to DNA ratio NucleoMag bead

clean up step. The resulting DNA fragments were PCR amplified using a KAPA Hifi HotStart readyMix and primers indiced for the Illumina Novaseq sequencing platform. To reduce PCR bias, we performed 10 replicate PCRs. The 10 replicate PCR products of 10 mL were pooled and concentrated and size selected again. The resulting sequencing libraries were send for 150 bp paired-end sequencing at Novogene (Munich, Germany).

Read processing followed the steps described in Wagemaker et al. (2020) with some adjustments to improve performance. First, PCR duplicates were removed based on the UMI in the adapters, any adapter traces at the end of the reads were removed, and low-quality reads were filtered using fastp (0.23.4) (Chen et al., 2018). Next, the individual samples were demultiplexed using the process_radtags script from the stacks (2.68) (Rochette et al., 2019). In order to create the reference for each flowering species observed, the leaf samples were then processed separately. First, the reads were merged using NGmerge (0.3) (Gaspar, 2018). These assembled reads were subsequently dereplicated and clustered with 95% identity. These clusters were then blasted against a local blastn database in order to remove any identifiable non-eukaryote and fungi DNA using blast 2.16.0 (Altschul et al., 1990). The cleaned clusters for each species were then combined in one meta reference. On this meta reference both the reads from the pollen and the leaf samples were mapped using bowtie2 (2.5.4) (Langmead and Salzberg, 2012). From the resulting alignment files, the number of reads mapping on each fragment in the meta reference were extracted. Finally, any fragments from the meta-reference on which reads from another species mapped, were excluded from the analysis.

As duplication rate of amplified regions and samples can differ and gDNA yield typically differs per plant species we expected biomass independent, species-specific variation in the number of reads within samples. This means that read numbers could not be interpreted quantitatively, nor compared across species. To account for differences in duplication rate between samples we transformed the number of reads per species to the relative number of reads (species level reads divided by total reads in the sample), after removing all wind dispersing species from the data as these are not actively collected by pollinators. Although relative reads still do not allow for cross-species comparisons, they have shown strong correlations ($R^2 > 0.8$) with biomass within species over samples (Wagemaker et al., 2021). Further filtering choices during the analyses are discussed under methods 2.4.1.

Analysis

All analysis was performed in R version 4.5.1 (R Core Team, 2025a). All models were constructed using the *glmmTMB* function in R (Brooks et al., 2017).

Filtering msGBS data

Following (Wagemaker et al., (2021), we applied a cluster filtering to the msGBS data following default setting for the taxonomic filtering (the f2=15 setting in the msGBS protocol). This filtering removes reference clusters that could result in false positive mapping, thus increasing the taxonomic resolution of the msGBS analysis. The false positives mainly result from the presence of homologous regions in the genome, but also from potential absence of clusters in the meta reference due to incomplete sequencing. Less stringent filter settings were evaluated and did not influence the overall results of the analysis but did increase the congener signals.

To minimise artefacts from low sequencing depth and trace pollen, msGBS data were further filtered prior to analysis. Samples with low read depth can yield unreliable proportional estimates, while very low proportions assigned to flower species may reflect contamination or ecologically negligible amounts. As a conservative measure, all samples with fewer than 12,500 total reads were not included in the analysis. In addition, species with less reads than 0.5% of a sample's total read count were considered ecologically irrelevant and removed as we know these low proportions always represent low real-world quantities (Wagemaker et al., 2021).

To test the robustness of these thresholds, we re-ran all parsimonious models across a range of thresholds: total minimal read counts between 1000 and 25000 (intervals of 1000) and minimal proportion between 0 and 0.01 (intervals of 0.001).

Proportion local flowers

To examine how the proportion of pollen collected locally by pollinators depended on local floral richness, we used an information-theoretic model comparison approach. For each pollen sample (representing a pollinator species recorded during a survey), we calculated the proportion of sequencing reads that mapped to flowering plant species occurring in the local vegetation at the time of sampling. We then constructed generalized linear mixed-effects models (GLMMs) with the proportion of local reads as the response variable. Although these proportions are derived from discrete read counts and should formally be modelled using a beta-binomial distribution (Warton and Hui, 2011), this approach implicitly weights samples by their total read number. Because the absolute numbers of reads are ecologically meaningless in our data (methods 2.3), and since all retained samples contained more than 12,500 reads (ensuring a wide, nearly continuous range of possible proportions) we instead modelled the data as continuous proportions using a beta distribution with a logit link function and a zero-inflation term (Douma and Weedon, 2019). Model selection did not differ when using the beta-binomial approach (Appendix 1).

Explanatory variables of interest were local flower species richness and flowering plant abundance. Additionally, we included the number of pollinator individuals per species sample as a covariate as more individuals in one sample potentially have visited more flower species. Sampling site was included as a random effect to account for the nested data structure. We first constructed a set of models with (1) only one explanatory variable of interest, (2) both variables, and (3) also their interaction. Because locally recorded flower species occasionally occurred in surrounding habitats, and this probability increases with the number of flower species present locally, we tested whether including the landscape-level abundance of these locally collected flower species improved model fit. We note that correlation between landscape level abundance of plant species that also occur locally (and could therefor erroneously count towards local) showed low correlation with local flower diversity (-0.13) and local abundance (0.12). We created a second set of candidate models, where we added this variable to each of the candidate models described above.

The resulting eight candidate models were ranked based on their Akaike Information Criterion values corrected for small sample size (AICc) (Burnham et al., 2011). Akaike model weights (ω), which reflects the probability that a model is the best approximating model in the candidate set, were calculated for each model in the candidate set. Using the most parsimonious model (which included an interaction term), we predicted the proportion of locally collected pollen across 50 evenly spaced values of flower species richness and flowering plant abundance, and visualized the resulting surface as a two-dimensional heatmap.

Total flower species collected.

To assess whether pollinators collected pollen more selectively at higher flower availability, for each pollen sample we calculated the number of flower species contributing more than 0.5% of the total reads. We then used an information-theoretic model comparison framework with model structure similar to that described in methods 2.4.2, with the total number of flower species collected by a pollinator as the response variable. Because all samples contained pollen from at least one plant species, the data were modelled using a truncated Poisson distribution. In text, we present results from the most parsimonious model. To determine how landscape-level floral resource collection, particularly regarding non-local species, influenced the observed pattern, we reran the most parsimonious model while only including collected flower species that were locally available in the response variable.

To determine whether diet breadth changes at the community level resulted from within-species niche narrowing along the floral richness gradient (i.e. adaptive foraging) or from pollinator species turnover (i.e. a higher prevalence of specialist species at flower-rich sites), we used a stepwise modeling approach. We first fitted the most parsimonious

model using data only from pollinator species that occurred at the most flower-poor site (note that these species could occur across the entire gradient, and all of their occurrences were included). We then progressively added pollinator species present at sites of increasing floral richness and compared model estimates to those obtained from the full dataset. If model outcomes remained constant across subsets, this would indicate that pollinator species occurring throughout the gradient narrow their realized resource niche as flower availability increases. In contrast, divergent outcomes, where pollinator species present at low flower richness do not collect more selectively at high flower richness, would suggest that community-level patterns primarily arise through pollinator species turnover.

Resource niche overlap

To assess whether changes in pollen collection patterns were associated with changes in resource niche overlap between pollinator species, we calculated Pianka's niche overlap index between all pairs of pollinator species within each survey (Pianka, 1973). As niche overlap could not be sensibly calculated from surveys with very few pollinators, we only included surveys for which we had pollen samples from at least four different pollinator species. For each pair of pollinator species within the survey, here j and k, Pianka's index O_{jk} was calculated as:

$$O_{jk} = \frac{\sum_i p_{ij} p_{ik}}{\sqrt{\left(\sum_i p_{ij}^2\right)\left(\sum_i p_{ik}^2\right)}}$$

Where p_{ij} and p_{ik} represent the proportion of pollen reads from plant species i in the pollen loads of pollinator species j and k respectively. This is then repeated for all plant species i detected in the dataset. The index ranges from 0 (no shared resource use) to 1 (complete overlap). Since the index is based on proportional resource use within each plant species, it is well-suited for our pollen read data, where proportional comparisons within species are valid but absolute read numbers are not.

To avoid pseudoreplication and inflation of the sample size, we calculated the mean overlap per pollinator species with all other species in the same survey. The per-species means were used as the response variable in our statistical models, that followed the same structure as in methods 2.4.3 to facilitate linking species specialisation to resource use overlap. However, as the number of species in a community can influence average overlap, we included community species richness as covariate in the model. Overlap values were modelled using a beta distribution with a logit link function and a zero-inflation term, as values were continuous between 0 and 1 (Douma and Weedon, 2019).

To determine how non-local resource use influenced niche overlap along gradients of flower abundance and species richness, we ran the analysis twice: first calculating average

overlap using all interactions in the dataset and second only interactions between pollinators and flower species that were locally present.

4.3 RESULTS

We analysed a total of 523 pollen samples collected from 1330 individuals of 135 pollinator species, resulting in more than a billion (1,398,135,179) reads. Of these, 286 samples (from 72 species and 869 individuals) met the minimum threshold of 12,500 total reads. Samples not meeting this threshold were roughly equally divided over pollinator groups (between 40-50% of the total number of samples), except for bumblebees (18%) and non-syrphid flies (68%) (for the complete account, see Appendix 2). Across all samples, we detected 125 different plant species in the pollen loads.

Proportion local flowers

The most parsimonious model explaining variation in the proportion of pollen collected from local flower species by pollinator species along the floral resource availability gradient included an interaction between local flower species richness and flowering plant abundance per m^2 (ΔAICc = -1.31, model weight ω = 0.44; Appendix 1). This model revealed a significant positive interaction effect (0.08 ± 0.03, P = 0.013, Figure 4.1), indicating higher proportions of locally collected resources with increasing local floral resource abundance and species richness. This supports our hypothesis that local floral resource collection increases with local resource availability. Interestingly, the model predicts a negative (though non-significant) effect of high flowering plant abundance at low flower species richness (-0.75 ± 0.41, P = 0.07).

Models including landscape-level availability of local resources did not improve model fit (ΔAICc > 0), suggesting that the observed pattern is driven by local resource availability rather than by broader landscape-level resources being counted as local. Model outcomes were robust across all tested pollen read thresholds (Appendix 3) and remained significant when removing both the most flower species rich and flower abundant locations, or the most flower abundant location alone. When removing only the most flower species rich location, the relationship was not significant anymore by a small margin (P = 0.052).

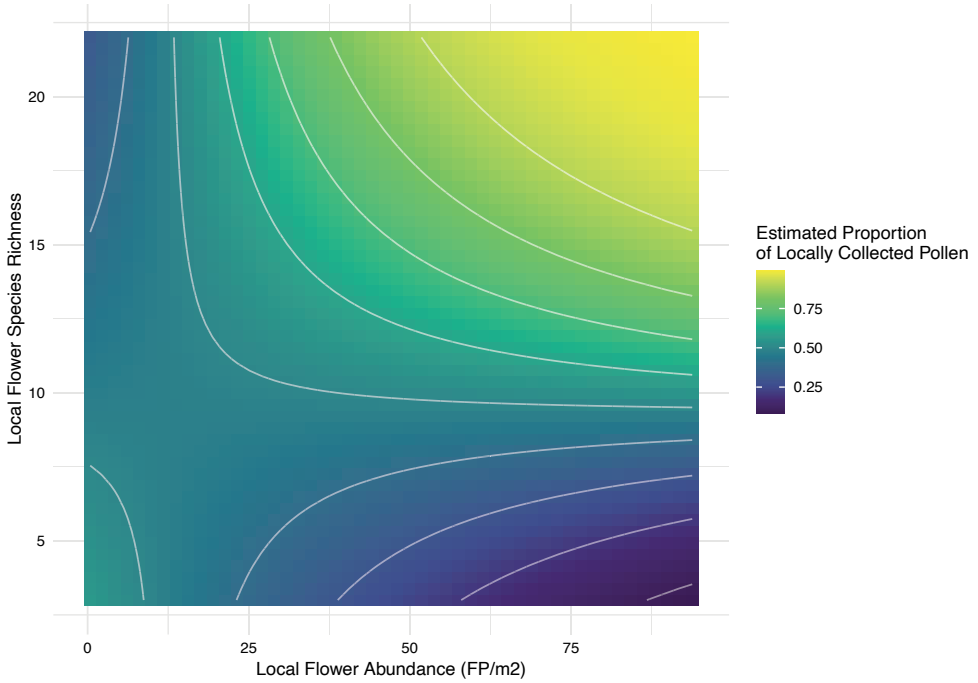


Figure 4.1: Estimated proportion of pollen collected from locally available plant species across gradients of local flower species richness and local flowering plant abundance, based on the most parsimonious model. The 2D visual representation shows the predicted proportion of locally collected pollen (dark blue = low, yellow = high) as a function of local flowering plant abundance (plants m^{-2}; x-axis) and flower species richness (y-axis). The interaction between flower species richness and flowering plant abundance is significant.

Number of flower species collected

The most parsimonious model explaining the number of flower species collected by pollinators included flower species richness and flower abundance (but not their interaction), and landscape-level abundance of locally collected flower species (ΔAICc = -1.84, ω = 0.67; Appendix 4). Both flower species richness and flowering plant abundance significantly reduced the total number of flower species, including those from the wider landscape, collected by pollinators (-0.14 ± 0.03 and -0.11 ± 0.03 respectively, both $P < 0.001$, Figure 4.2A,B), indicating that species foraged more selectively with increasing local flower richness and availability. Selective foraging was further enhanced by landscape level availability of collected resources (-0.09 ± 0.03, $P = 0.002$). When modelling diet breadth from only local flowers, the pattern reversed and pollinators carried pollen from significantly more flower species with increasing flower richness (Figure 4.2C,D). This illustrates that collection of non-local flower species accounts for of the overall reduction in diet breadth and considerably changes the outcomes.

Model outcomes were generally robust, but showed some sensitivity to low total read threshold values and to not filtering out low-proportion (pollution) reads (Appendix 5). This can be explained as very low proportions still lead to inclusion of the species being included in the tally of collected resources making the analysis sensitive to trace amounts of pollen. The results of the model considering all species collected remained significant when removing the sites with the highest flower species richness and floral abundance, or when removing each of those sites individually. The increase in the number of local flower species collected (Figure 4.2C) was no longer significant when removing the most flower rich location, although the overall relationship remained positive (scaled estimate 0.15).

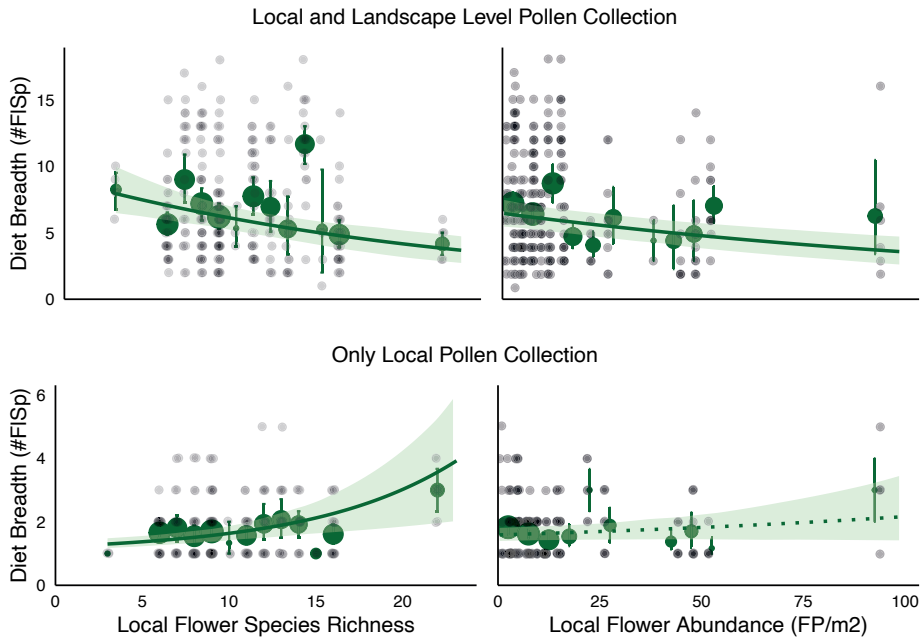


Figure 4.2: Pollinator diet breadth (number of flower species collected) in relation to (A) local flower species richness and (B) total local flower abundance (plants m^{-2}), and the same relationship when considering only locally available flower species (C, D). Green lines show predictions from the most parsimonious model, with solid lines indicating significant interactions and dotted lines non-significant interactions. Light green ribbons indicate 95% confidence intervals. Grey points represent raw data. Dark green points show mean numbers of flower species collected for each level of flower species richness or abundance, with error bars indicating standard errors. Point size is scaled by the number of samples used to calculate each mean.

The negative relationships remained prevalent in the progressive inclusion analysis (table 4.1). Only when considering species that occurred exclusively at the poorest location did the model outcomes differ, but this outcome was based on only 24 total observations. In all other cases, including analyses restricted to species present at low

flower species richness, the negative relationships persisted. This suggests that the observed patterns are not primarily driven by species turnover (i.e., the replacement of generalists with specialists), but rather reflect that individual species forage more selectively when floral resources increase. Nevertheless, among the seven species excluded at the 13-species flower richness threshold, two are known specialists (*Andrena wilkella* and *Andrena labiata*), while *Lasioglossum malachurum* is known to show floral consistency during foraging bouts (Polidori et al., 2010).

Table 4.1: The relationship between diet breadth (number of collected flower species) and local flower species and local flowering plant availability as species from progressively less flower-poor locations are included. Flower richness cut-off defines which bee species pollen samples were included, with the number of species and total samples in the analysis in the Species count and Sample count columns. Model estimates (± SE) are given in the Estimate columns for flower species richness and flowering plant abundance respectively, with P-values in the following columns.

Flower richness cut-off	Estimate Flower Sp. Richness	P-value Flower Sp. Richness	Estimate Flowering plant Abundance	P-value Flowering plant Abundance	Species count	Sample count
3-5	0.008 ± 0.03	0.76	-0.07 ± 0.1	0.58	4	24
6	-0.033 ± 0.01	0.005	-0.13 ± 0.04	<0.001	31	185
7	-0.037 ± 0.01	<0.001	-0.13 ± 0.04	<0.001	45	231
8	-0.042 ± 0.01	<0.001	-0.13 ± 0.04	<0.001	52	250
9	-0.038 ± 0.01	<0.001	-0.14 ± 0.04	<0.001	65	271
10	-0.038 ± 0.01	<0.001	-0.14 ± 0.04	<0.001	66	272
11	-0.041 ± 0.01	<0.001	-0.09 ± 0.03	<0.001	69	276
12	-0.039 ± 0.01	<0.001	-0.09 ± 0.03	<0.001	71	278
13	-0.038 ± 0.01	<0.001	-0.10 ± 0.03	<0.001	72	279
Total model	-0.026 ± 0.01	<0.001	-0.11 ± 0.03	<0.001	79	286

Niche overlap

Models on niche overlap revealed that interspecific pollinator resource use overlap decreased with increasing flower species richness ($P < 0.05$, Figure 4.3A; $P < 0.001$, Figure 4.3A, C), with no significant interaction with flower abundance in either case (both $P > 0.1$; Figure 4.3B, D). This decrease prevailed despite a positive effect of pollinator community richness on resource use overlap ($P < 0.001$ in both models). Full model outcomes are given in Appendix 6.

The model using only interactions with locally present flower species (Figure 4.3C) produced an effect size four times larger than the model using all observed interactions (Figure 4.3A; -0.71 ± 0.10 vs. -0.18 ± 0.07), particularly due to higher overlap at flower-poor locations. Hence, resources collected by pollinators from flower species that were not occurring locally reduced estimated resource use overlap compared to calculations only including local flowers, especially at flower poor locations.

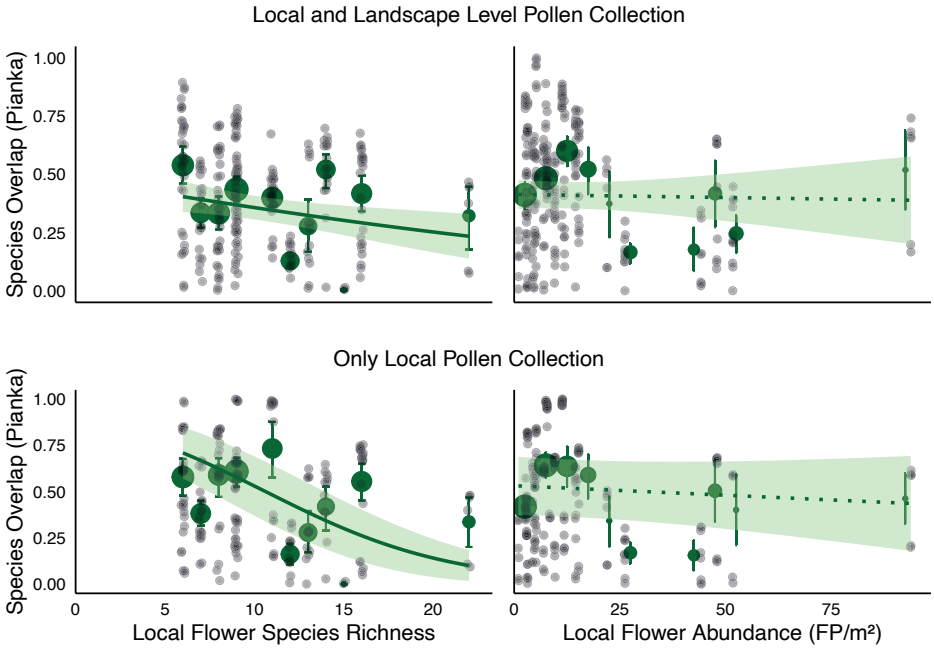


Figure 4.3: The average resource use overlap, calculated as Pianka's overlap, between species and their pollinator community (y-axes) in relation to (A) local flower species richness and (B) total local flower abundance (plants m^{-2}), and the same relationship when considering only locally available flower species (C, D). Green lines show model predictions, with solid lines indicating significant interactions and dotted lines non-significant interactions. Light green ribbons indicate 95% confidence intervals. Grey points represent raw data. Dark green points show mean numbers of flower species collected for each level of flower species richness or abundance, with error bars indicating standard errors. Point size is scaled by the number of samples used to calculate each mean.

4.4 DISCUSSION

Conceptual and theoretical models suggest that pollinator coexistence is jeopardized under low floral resource availability by increased competition. By including pollen collected from outside the sampling location, our results show that pollinators relied strongly on landscape-level resources, particularly under low local resource availability. Estimates of diet breadth and resource use overlap were thus substantially altered compared to values inferred from local resources alone. Here we discuss the consequences of our findings for selective resource foraging, niche partitioning, and pollinator persistent in fragmented landscapes.

Local resource collection

Our results show that pollinators increasingly collect resources from local flowers with increasing local resource availability, including both increased flower abundance and flower species richness. Although studies have shown how landscape level factors can influence local plant-pollinator interaction networks (Peralta et al., 2023; Parreno et al., 2024), few have directly quantified the proportion of locally and non-locally collected pollen. One of the few direct quantifications we are aware of stems from an urban setting, where O'Connell et al. (2021) show that the bumblebee *Bombus vosnesenskii* collected more pollen from focal gardens with increasing flower richness and surrounding urbanisation. Our findings align with these findings and extend them by demonstrating that this pattern also emerges at the pollinator community level in rural landscapes.

This pattern is also consistent with the expectation that pollinators preferentially exploit nearby resources when available, although they are capable of collecting sources from a wider area (Zurbuchen et al., 2010; Pyke, 2016). In flower-poor locations, pollinators may persist by increasing landscape-level foraging effort. Nevertheless, such foraging behavior does not necessarily indicate sustainable population dynamics. For example, females of *Osmia lignaria* failed to produce sufficient offspring to maintain populations when floral resources were too distant (Williams and Kremen, 2007a), and females of *Megachile rotundata* completed 75% fewer brood cells when foraging patches were located more than 150 m away (Peterson and Roitberg, 2006a). Linking observed foraging patterns to energetic expenditure and subsequent population dynamics is an important topic for future research.

Selective foraging

Our results indicate that pollinator species include fewer flower species in their diets with increasing local flower species richness and abundance, further enhanced by the landscape level availability of the collected resources. This supports our hypothesis that pollinators will forage more selectively when more resources are available to them and is consistent with previous work showing increased foraging specialization of pollinators with higher local flower diversity (Ebeling et al., 2011; Lázaro et al., 2015) and increased foraging effort on abundant floral resources (Vázquez et al., 2009; Fort et al., 2016). Importantly, we demonstrate that the observed community-wide decrease in diet breadth with increasing local resource availability arises from behavioral changes within pollinator species rather than from species turnover leading to a more specialized community. Such adaptive foraging in response to resource availability and species-specific preferences is a central assumption of theoretical models of pollinator coexistence (Valdovinos et al., 2013, 2016). While increased foraging selectivity with greater resource availability has previously been demonstrated within individual species (Cusser et al., 2019; Kelly & Elle, 2021), our results provide field-based evidence that these behavioral responses also scale up to shape community-wide resource collection patterns.

Previous studies have reported that, although pollinators forage more selectively with increasing local resource availability, this nevertheless results in a higher absolute number of flower species included in their diets (Gómez-Martínez et al., 2022). In this context, the strong reduction in the absolute number of collected resources with increasing local resource availability observed in our study is striking. We show that this apparent discrepancy can be explained by landscape-level resource collection at flower-poor locations, which is typically not considered in studies of pollinator diet breadth. When landscape-level resource collection is excluded, we recover a pattern similar to previous work, with diet breadth increasing alongside local resource availability. Although landscape-level foraging by pollinators has been documented previously (Pornon et al., 2016), our results demonstrate that its quantitative contribution can fundamentally alter inferred patterns of resource use and specialization.

Niche partitioning

The increased selectivity in pollinator foraging at higher floral resource availability translated into reduced resource use overlap between pollinator species, as reflected by lower Pianka's index values. This provides field-based support for conceptual and theoretical models predicting that increased floral resource availability promotes pollinator coexistence by enabling niche differentiation and reducing interspecific resource use overlap (Brosi, 2016; Valdovinos et al., 2016; Ponisio et al., 2019). While such mechanisms have primarily been demonstrated in experimental systems (Fründ et al., 2013), our results indicate that they also operate at the community level under natural field conditions.

Notably, this process only occurred with increasing flower species richness, and not increasing flower abundance. Conceptually, this makes sense as more abundant flower species could likely be exploited by more pollinators, expanding shared niche space rather than partitioning it. This is commonly observed in plant-pollinator interaction networks for 'hub species' (Olesen et al., 2007), flower species that attract a disproportionately large number of pollinators often because of their abundance (Fort et al., 2016). Nevertheless, our finding underscores the importance of flower species richness in structuring plant-pollinator interaction networks, as it provides the niche diversity necessary for pollinator to reduce resource use overlap.

Although interspecific floral resource use overlap decreased both when considering total and only local floral resource collection, we show that non-local resources collected at flower poor locations decrease total resource use overlap when compared to only the local collection patterns. To our knowledge, no studies have so far quantitively demonstrated this effect. This pattern suggests that access to landscape-level floral resources allows pollinators to partition their diets more effectively when local options are limited, thereby reducing direct competition within the local assemblage. As our earlier results revealed that at intermediate flower richness levels roughly 40% of pollen was collected else-

where, this mechanism can likely influence plant-pollinator interaction network structure in many cases. It therefore underscores the importance of considering landscape-scale floral availability when evaluating pollinator community structure and niche dynamics.

Implications of landscape-level floral resource collection

Together, our results also have implications for understanding pollinator persistence in degrading landscapes, where floral resources become increasingly scarce and species-poor. Previous work has shown that generalist pollinators are more likely to persist under such conditions (Goulson et al., 2008; Winfree et al., 2011), while in our own system rare and specialised species mostly occurred at flower rich locations (Swinkels et al., 2025). By demonstrating that pollinators at flower-poor locations rely heavily on landscape-level floral resources, collecting a broad range of plant species beyond the local assemblage, our results provide a mechanistic explanation for this pattern. Such opportunistic landscape-level foraging reduces local resource use overlap and is likely only feasible for generalist species capable of exploiting a wide range of floral resources.

Importantly, the ability to benefit from landscape-level resource collection is likely constrained by pollinator traits. More mobile pollinators can access a larger spatial extent of resources, which may help explain why syrphid flies, free-ranging foragers without a central nesting location, have shown higher persistence than wild bees, which are central-place foragers (Biesmeijer et al., 2006). However, mobility alone may not confer resilience: although larger bee species generally have greater foraging ranges, larger body size has been associated with higher vulnerability to decline in the Netherlands, potentially due to higher absolute resource requirements (Scheper et al., 2014). Together, these findings suggest that landscape-level floral resource availability interacts with pollinator traits to shape patterns of persistence under resource-limited conditions.

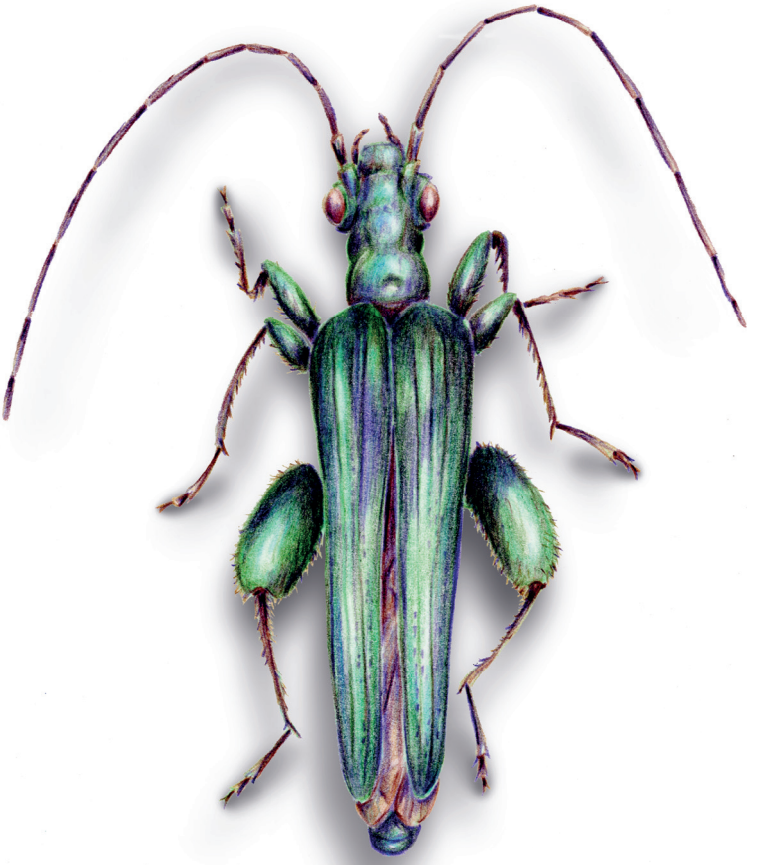
4.5 CONCLUSION

Our findings show that local flower species richness and abundance strongly shape pollinator resource collection patterns. At flower-rich sites, high floral diversity facilitates resource niche partitioning and leads to more selective foraging, providing field-based support for conceptual models of pollinator resource use complementarity and coexistence. In contrast, pollen-load analyses revealed that at flower-poor sites, pollinators increasingly rely on landscape-level resources. Accounting for this landscape-level collection substantially changed estimates of diet breadth and resource-use overlap. Whereas previous studies reported narrow diets at flower-poor locations, we show that including landscape-level foraging greatly increases diet breadth and reduces apparent resource overlap. These patterns help explain why generalist pollinators are better able to persist in flower-limited environments, and why their persistence is jeopardized in isolated and

sub-optimal habitat. Together, our results highlight the need to consider fine-grained, cross-habitat foraging dynamics in pollinator conservation, especially in linear, resource-limited habitats such as road verges and dike grasslands.

4.6 ACKNOWLEDGEMENTS

We thank Waterschap Rivierenland and dike managers Marc Büchner and de Ploegdriever (Karina Hendriks) for allowing us to collect samples from their dike grasslands. We are grateful to Maarten van Emmerik for his help in developing the msGBS method for pollen and to Lisa van den Dries and Else Dieks for their help during fieldwork.



5

Unequal pollinator benefits from partial mowing regimes in a large-scale field experiment

Constant Swinkels, Ilona de Weert, Paolo Biella,
Eelke Jongejans & Hans de Kroon

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Supplementary materials available at: https://constantswinkels.com/113-2/

SUMMARY

1. Studies suggest that partial mowing, where unmown refuges are left for insects after mowing, promotes arthropods in semi-natural grasslands. However, studies comparing community development in unmown controls to unmown vegetation are scarce, particularly for insect pollinators, while increased arthropod density in unmown refuges is likely to filter ecological communities.
2. We here present a partial mowing field experiment on dike grasslands to study how pollinator communities develop in unmown strips (refuges) within mown dike locations compared to similar strips (controls) in locations that were left unmown. We collected data on flower visitation frequency (collecting 28553 unique visitation events) and community composition from transect counts (identifying 4530 pollinators to the species level) in three periods; before, directly after and later after mowing.
3. Pollinator visitation frequency (+85%) and abundance (+25%) increased in unmown refuges directly after mowing, but 2.5 weeks later pollinators had abandoned refuges resulting in lower numbers than in control vegetation. These declines were not equally divided over species, with marked non-*Bombus* wild bee abundance and species richness decline (-82% and -70% respectively) not observed at control locations, whereas honeybees maintained high abundance. Subsequently, rank-abundance curves reveal a disproportionate decline of intermediately common and rare species at partially mown sites, with no compensatory appearance of later-season species which we did observe at unmown controls.
4. *Synthesis and applications:* We conclude that, although partial mowing can be a worthwhile alternative to traditional mowing, unmown refuges do not substitute unmown vegetation and primarily benefit common pollinators, such as honeybees, and might not sustain pollinator diversity as a whole.

5.1 INTRODUCTION

Native grasslands are biodiverse habitats that can harbour rich arthropod communities (Ghazoul, 2006; Veen et al., 2009; Sexton and Emery, 2020). Although fully natural grasslands are rare in the Western Palearctic, semi-natural grasslands, that are maintained through human activity, are widespread. Examples of these include road verges and dike grasslands that, just like natural grasslands, can harbour rich arthropod communities (e.g. Bátori et al., 2016; Phillips et al., 2020). To prevent succession, both in interest of sustaining open grassland and their anthropogenic functions, mowing management is applied (Milberg et al., 2017; Bochniak et al., 2024). This mowing management, which results in the sudden removal of all vegetation, conflicts with the needs of arthropods that require year-round vegetation (Steidle et al., 2022).

Studies show that alternative ways of mowing (e.g. using different material or delaying the first cut) can benefit arthropods (Humbert et al., 2010b, 2012; Berger et al., 2024). Nevertheless, these don't mitigate the sudden loss of vegetation. As such, more recent work suggests adopting partial (or mosaic) mowing regimes, where unmown refuge patches are left after mowing (Révész et al., 2025). The core idea is to spread mowing events over the year, while leaving unmown vegetation every time that can function as refuge to arthropods. Studies report increased abundance and species richness of many arthropod groups (e.g. orthopterans, butterflies, true bugs, spiders and beetles) in unmown refuges compared to mown vegetation and different mowing regimes, suggesting partial mowing can aid conservation of different arthropod groups (Bruppacher et al., 2016; Meyer et al., 2017; Wintergerst et al., 2021; Biella et al., 2025).

Nevertheless, comparing arthropod order level abundance and species richness in unmown refuges to completely mown controls runs the risk of oversimplifying conservation outcomes as community changes in these refuges may be overlooked. Just like traditional mowing regimes, partial mowing can filter arthropod communities (Buri et al., 2013; van Klink et al., 2019), but short-term community dynamics in unmown refuges after mowing are understudied. Nevertheless, the aggregation of individuals in unmown refuges after mowing might well result in community level changes. For instance, Lebeau et al., (2015) show that density increases in unmown refuges of *Maniola jurtina,* a common grassland butterfly, were followed by partial refuge abandonment and changes in foraging behaviour of this species. Likewise, increased arthropod density could lead to increased predation (Emery and Mills, 2020) and resource competition (see below). Comparing community development in unmown refuges at different stages after partial mowing to developments in unmown controls is thus important to further our understand of how partial mowing filters communities.

Flower visiting insects (or pollinators) are an especially relevant but understudied group in this context, that show varying responses in studies on partial mowing (Révész et al., 2025). While these (generally) mobile insects suffer relatively few casualties through direct mowing (Fluri et al., 2001) , pollinator community formation is thought to be driven by competition for available resources and subsequent niche partitioning (Fründ et al., 2013; Brosi, 2016; Valdovinos et al., 2016). In this dynamic game, generalist species seek less visited flowers allowing specialists to use their preferred resources (Valdovinos et al., 2013; Brosi, 2016). However, the division of resources could be disrupted when resources suddenly decline (Biella et al., 2019, 2020) as is the case in partial mowing. Some species within pollinator communities might thus respond differently to partial mowing than other species, explaining the varying responses observed so far. However, to our knowledge, no studies have looked at short-term community-wide changes in a well-established pollinator community when switching to a partial mowing regime.

Here, we set up a field experiment to study changes in visitation frequency and community composition of well-established pollinator communities in unmown strips (refuges) within mown vegetation. We selected experimental locations on semi-natural dike grasslands and compared to control locations where the entire vegetation was left unmown which allowed us to isolate the effects of partial mowing from other phenological changes. Specifically, we ask three questions; 1) How does pollinator visitation frequency, abundance and species richness develop in unmown refuges directly and later after partial mowing? 2) Are changes in visitation frequency, abundance and diversity evenly distributed over different phylogenetic pollinator groups? and 3) How do changes translate to pollinator species abundance distribution? We expect that directly after mowing pollinators will aggregate in unmown refuges (as recently reviewed for other arthropods (Révész et al., 2025)), leading to increased visitation frequency and abundance of the species present. Further, we hypothesize that remaining vegetation at partially mown sites is unable to sustain this higher pollinator abundance for a prolonged time as pollinators are generally suggested to be resource limited (Sponsler et al., 2023) resulting in declines later after partial mowing not observed in control sites. These declines will likely not be equal for all groups, as species with higher competitive strength are more likely to persist in resource limited conditions.

5.2 MATERIALS AND METHODS

Location

Five dike sections, that shared management practice and vegetation type (namely *Arrhenaterion* grasslands, a typical flower-rich dike grassland vegetation in the Netherlands) were selected along the southern Waal dike near Nijmegen (see appendix 1). These locations were all south-facing and, over the past couple decades, mown twice each year

(mid/late-June and September), with the intent to facilitate biodiversity while ensuring dike functioning (Liebrand, 1999). From previous monitoring work we know these sites host rich solitary bee communities adapted to early availability of floral resources (Swinkels et al., 2025). Locations were at least 300m apart with no direct sight lines towards each other, making them as independent as possible (i.e. separate from the flight ranges of most pollinating insects (Zurbuchen et al., 2010)). Both flower and pollinator community composition showed no significant differences between experimental and control locations before mowing (see Appendix 3 and 4).

Experimental set-up

The experiment took place from the 30th of May until the 28th of June, 2023. It consisted of three periods; 4 days *Before* mowing (30th of May until the 2nd of June), 4 days *After* mowing (4th until the 7th of June) and a *Later* period (from the 8th until the 28th of June) where visits were spread over a longer time depending on favourable weather conditions (at least 18 ˚C, max 3 BFT and at least 50% clear skies). At each location, we marked five 1.5m×1.5m plots in the middle section of the dike, with a 75m long transect running above and below the plots so that the area between the two transects was about 33% of the total vegetation (Figure 5.1). The five quadrants were representative for the dike grassland vegetation.

To study pollinator community dynamics in unmown refuges we adopted a Before-After Control-Impact (BACI) design, with the control consisting of unmown vegetation (Green, 1979). Grassland was mown at three of the five locations on the 3rd of June, using a bar mower. Bar mowers are generally considered to cause the least number of insect casualties, with results suggesting around 5% loss of honeybees (Fluri et al., 2001) and 20% of more sedentary arthropods (Humbert et al., 2010a). Mowing occurred between 9 AM and 3 PM with good weather conditions, as most pollinators are active at that time providing them the opportunity to escape. We mowed roughly 66% of the vegetation, both at the top and bottom of the dike, leaving an unmown strip in the middle (33%). These percentages are representative, but on the larger end of the spectrum, for partial mowing practices (Révész et al., 2025). This choice was thus conservative, leaving more vegetation for remaining arthropods. Cuttings were not collected after mowing so that pollinators that got trapped between the cuttings had the opportunity to escape.

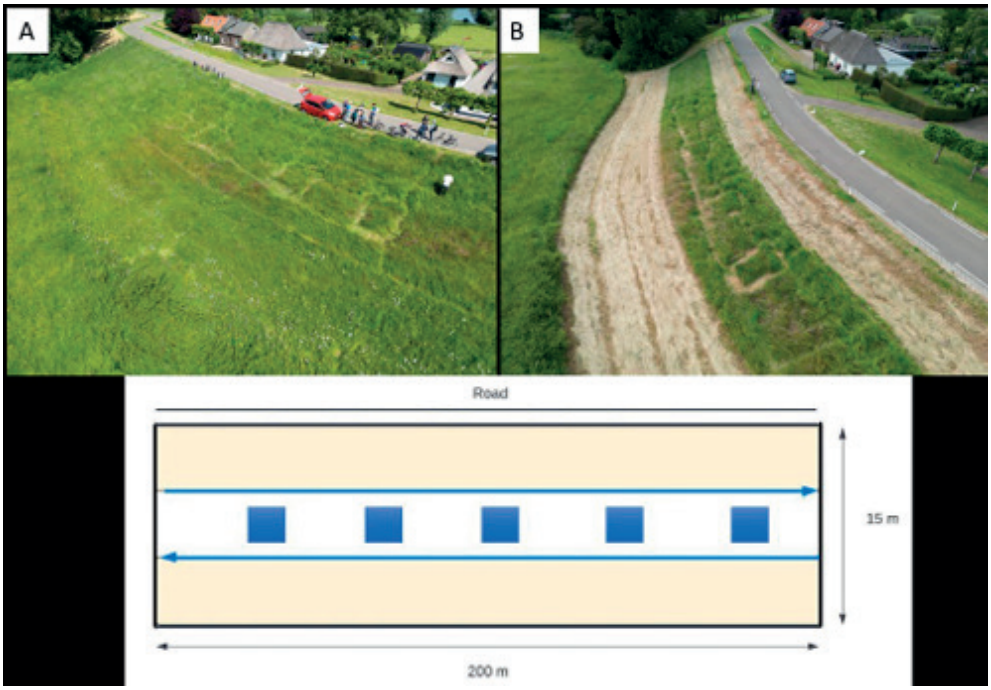


Figure 5.1: example of an experimental location before (A) and after (B) mowing. Below the pictures the schematic set-up, with blue squares indicating the plots for visitation counts, blue arrows the transect lines and the white area representing the unmown area.

Vegetation sampling

Within each of the established quadrants, flowering floral units per species, a flower or set of flowers that a pollinator can reach without having to fly, were counted at the first and last day of the Before and After periods, and quantities were interpolated between the two counts (see appendix 2 for a list of flower species and considered floral units). In the later period, floral units were counted during each visitation survey as these surveys were more irregular. As counts were partly performed by trained students, the similar looking and closely related *Centaurea jacea* and *Centaurea scabiosa* were treated as one group, as well as *Trifolium dubium* and *Medicago lupulina*.

Pollinator visitations

Between 9 AM and 5 PM, pollinator visitations were counted by experts and trained students. Students always performed surveys in pairs to minimize misidentifications. On sampling days, each quadrant at a location was observed for 20 minutes in randomised order, both in the morning and afternoon (40 mins per quadrant total, 200 minutes per location total per day). In the four days 'before' and 'after' mowing periods, all locations were monitored simultaneously every day to account for weather and insect activity effects. In the 'later' period observations were spread out over time, but each location

was at least visited on three separate days. As fewer observers were available, only three quadrants per location were observed in the later period.

During the surveys, each pollinator – floral unit interaction was registered. Pollinators were assigned to one of ten groups; honeybees, bumblebees, other wild bees, syrphid flies, other flies, ants, wasps, beetles, bee flies and butterflies, or recorded as unidentified without certain identification. The groups share similar life strategies and are at the same time easy to identify for trained volunteers. Flowers were identified to the species level (but see Methods – *vegetation sampling*).

Transects counts

Pollinator species were counted along a 150m long and 2m wide transect (following the upper edge and lower edge of the unmown strip for 75m each) with 15 minutes of active searching time - while identifying, chasing or handling pollinators, time was paused. These counts were always done by the same two people. Pollinators that could not be identified by wing were caught and transferred to the lab. Transects were surveyed four times per period, in the morning and afternoon on two separate days. We chose two days rather than all four to reduce the chance that collecting individuals would lead to local depletion of populations.

Environmental data

In addition to data on vegetation and pollinators, we recorded the time, temperature, wind speed and the percentage of clouds for each survey.

Analysis of floral visitation data

All statistical analysis were performed in R version 4.2.2 (R Core Team, 2022). To study how floral unit availability and visitation frequency changed over time we used the total number of floral units and visitations per survey. We then constructed GLMM (Generalized linear mixed models) with number of floral units or visitations as dependent variable following a Negative binomial error distribution. We included the interaction effect of the period (before mowing, after mowing or later) and treatment (experimental or control) as primary interest and corrected for cloud coverage as a proxy for weather conditions in visitation models. As baseline floral unit counts and visitation frequency differed between quadrants, we included the 'before period' average value per quadrant as an offset in our models. Finally, we accounted for nested observations by including location as a random variable. We then constructed pollinator group level models, leaving out the offset as the number of observations per group frequently included zero's, and thus low baselines, inflating model expectations. We present the outcomes for bumblebees, honeybees, beetles and wild bees as other groups had insufficient observations per survey.

The *emmeans* package (Lenth et al., 2025) was used to compute estimated marginal means (Searle et al., 1980) for between-treatment and between-periods effects within treatment, with pairwise comparisons assessed using t-tests. P-values were obtained from a post-hoc Tukey test.

Analysis of transect data

To study pollinator abundance and species richness, we constructed a similar model to the ones described above with pollinator abundance or species richness (Poisson distributed) per transect survey as dependent variable. We then constructed models at the group level to calculate group-level contributions to the larger patterns (without the offset). Groups with low abundance or few species (e.g. 'honeybees' is only one species) were excluded from the group-level analysis. We plot the estimated change in abundance or species richness per group as a proportion of that group, since there are large differences in abundance between groups.

To study species abundance distribution we constructed rank-abundance curves per period of the experiment. To correct for the different number of surveys among treatments (i.e., 3 vs 2 locations), we constructed rank-abundance curves per location and show the average curve by fitting a loess curve with 95% confidence interval. To gain insight in the patterns behind changes in rank-abundance curves between different periods of the experiment, we report changes in average species abundance per location for species that show notable changes in abundance.

5.3 RESULTS

In total we counted 28553 visitation events during 167 observation hours, and identified 4570 pollinator individuals to the species level (94 species) from transect counts. In both the visitation and transect datasets, honeybees (38.7% and 46.7% respectively) and bumblebees (42.7% and 31.2%) were the most abundant, followed by beetles (6.9% and 7.2%) and wild bees (6.3% and 9.0%). A full overview of the data is given in appendices 5 and 6.

Floral unit availability

Floral unit availability in the plots decreased significantly over time (Figure 5.2a, Appendix 7). This decline was stronger at the sites with partial mowing, resulting in a significant difference in floral unit availability in the later period of the experiment ($P < 0.001$).

Visitation frequency

In the four days before the partial mowing was applied, experimental and control plots were visited on average 40.4 and 42.1 times per 20-minute survey respectively

(Figure 5.2b, Appendix 7). In the four days after mowing, visitation frequency increased nearly twofold in unmown refuges (75.91, $P < 0.001$), whereas increase at control locations was modest (47.0, NS). Both the average number of visitations and the relative increase were significantly higher in experimental locations ($P < 0.01$ and $P < 0.001$, respectively). In the later period (on average 16 days after partial mowing), results were inversed as the number of visitations in control plots was significantly higher than in experimental plots (57.4 versus 38,5, $P < 0.01$) with an increase observed in control locations ($P < 0.001$) and twofold decrease in experimental locations ($P < 0.001$) compared to immediately after mowing. Model outcomes corrected for flower availability are shown in appendix 8, but resulted in a bimodal distribution of model predictions in the later period due to very low flower availability values.

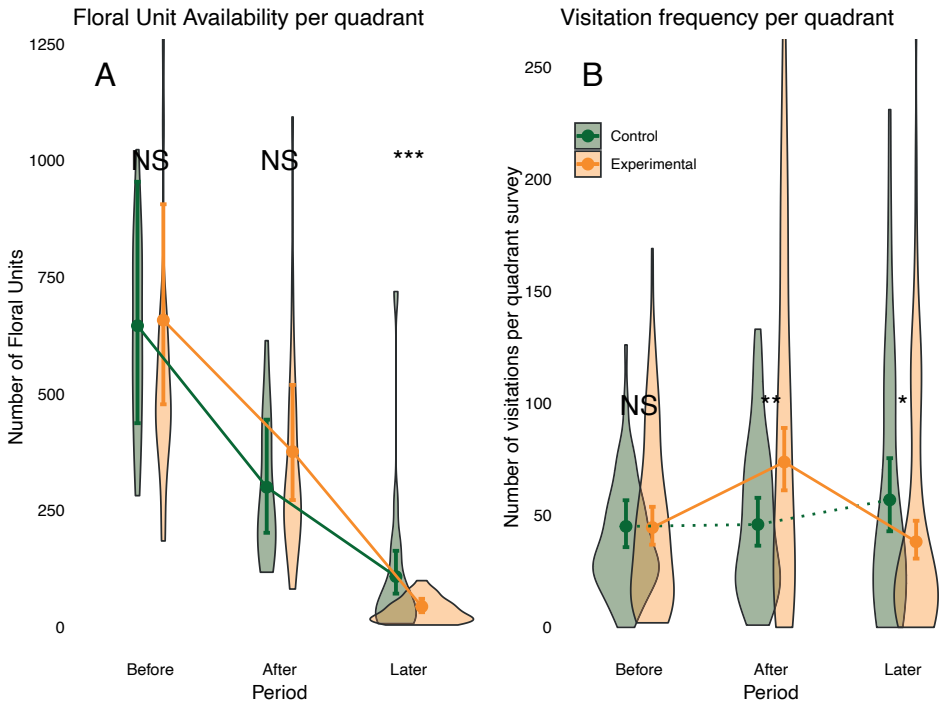


Figure 5.2: Model estimates of floral unit availability (2a) and visitation frequency (2b) per period of the experiment (x-axis). Controls are shown in green, experimental locations in orange. Violins represent the raw data distribution, points the model estimate and error bars the 95% confidence interval. Between treatment differences per period are indicated in text ($P > 0.05$ = NS, $0.01 < P < 0.05$ = *, $0.001 < P < 0.01$ = **, $P < 0.001$ = ***), changes between periods per treatment are indicated by lines (solid = significant, dotted = insignificant).

At the group level, visitation frequency of all four major groups (honeybees, bumblebees, non-*Bombus* wild bees and beetles) followed the pattern of initial increase and later decrease at partially mown locations (Figure 5.3a-d, Appendix 9). However, visitation frequency of bumblebees and non-*Bombus* wild bees decline resulted in significance changes in the later period compared to controls, whereas visitation frequency of beetles remained higher compared to the pre-mowing average. At control locations, bumblebee visitation frequency shows a reversed pattern and increased beyond averages in unmown refuges ($P < 0.05$).

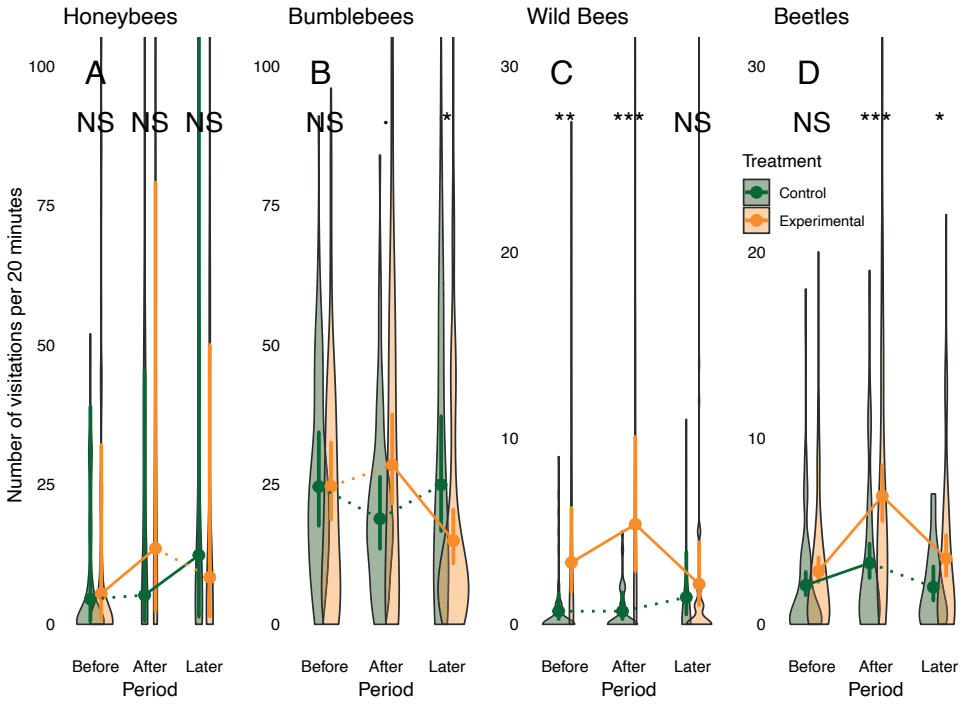


Figure 5.3: Visitation frequency per experimental period from the four largest groups; Honeybees (A), Bumblebees (B), Non-*Bombus* Wild Bees (C) and Beetles (D). Control locations are shown in green, experimental locations in orange with points indicating the model average estimate and bars the 95% confidence interval. Between treatment differences are indicated in text ($P > 0.05$ = NS, $0.01 < P < 0.05$ = *, $0.001 < P < 0.01$ = **, $P < 0.001$ = ***), whereas solid lines depict significant within treatment differences between periods and dotted lines non-significant differences.

Transect counts

Pollinator abundance at partially mown locations followed a similar pattern as visitation frequency, with an increase directly after mowing ($P < 0.05$) and later decrease ($P < 0.001$, Figure 5.4a, Appendix 10). Nevertheless, initial increase in visitation frequency (1.85 times) was larger than pollinator abundance increase (1.25 times). The initial abundance increase was, as hypothesized, not paired with an increase in species richness, but species richness did decline in unmown refuges later on ($P < 0.001$, Figure 5.4b). At control locations trends initially follow a similar pattern (albeit non-significant), but show further increase in abundance ($P < 0.05$) and species richness (NS) towards the later period, resulting in significantly higher pollinator abundance and species richness at control locations compared to unmown refuges (both $P < 0.001$). This suggests that later on, unmown refuges are at least partially abandoned by pollinators, which is in line with our hypothesis that unmown refuges cannot sustain similar pollinator numbers as unmown vegetation.

Abundance and richness changes were not equally divided over pollinator taxonomical groups. In unmown refuges, the abundance increase directly after partial mowing is mostly explained by increase in honeybee and beetle abundance (+111% and +100% respectively, NS and $P < 0.001$), whereas other groups showed no significant changes (Figure 5.4c). Later on, we observe abundance declines across all groups in unmown refuges, but especially in non-*Bombus* wild bees (-81.8%, $P < 0.001$). Bumblebee and beetle declines were less pronounced (Figure 5.4e) and final numbers did not significantly deviate from pre-mowing conditions (Appendix 11). At control locations, we also observe an initial increase in honeybee abundance (+241.7%, $P < 0.001$), here paired with a decline in bumblebee and syrphid abundance (-39.4% and -75.4% respectively, both $P < 0.001$). Nevertheless, towards the later period, no groups showed significant abundance declines and bumblebees ($P < 0.05$) and syrphids (NS) increased again. Overall, group-level abundance changes were smaller at control locations (Appendix 7).

The abundance patterns were largely mimicked in terms of group-level species richness, where especially the strong non-*Bombus* wild bee species richness decline at experimental locations stood out (-70.7%, $P < 0.001$, Figure 5.4d,f).

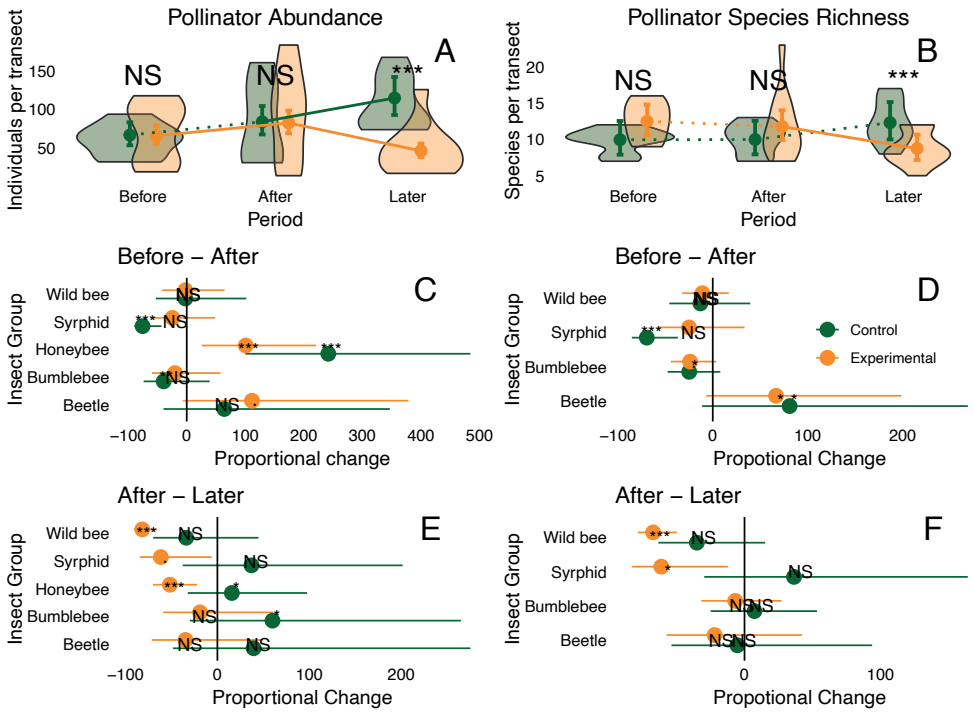


Figure 5.4: Abundance (A) and species richness (B) for different periods of the experiment on the x-axis, with proportional group-level responses in abundance (C,E) and species richness (D, F) for the *Before* versus *After* and *After* versus *Later* periods. Control locations are shown in green, experimental locations in orange with points indicating the model average estimate and bars the 95% confidence interval. Between treatment differences are indicated in text (P > 0.05 = NS, 0.01 < P < 0.05 = *, 0.001 < P < 0.01 = **, P < 0.001 = ***), whereas solid lines depict significant within treatment differences between periods and dotted lines non-significant differences.

Community composition

Rank-abundance curves reveal that the abundance distribution (log-scale) was similar in the before and after periods at both experimental and control sites, with overlapping 95% confidence intervals (Figure 5.5). In the later period we observed contrasting developments at control and experimental sites: in control vegetation the abundance and number of species increased significantly (resulting in a higher, more gradual rank-abundance curve), whereas at experimental locations the curve decreased significantly more steeply than in the earlier periods.

These shifts in the later period occurred due to three different developments (Table 5.1). Firstly, the abundance of common species in refuge vegetation declined and, secondly, we observed that semi-abundant species disappeared. For some species this decline was tied to phenology and shared by experimental and control locations. An example of this is *Halictus scabiosae,* that has two flight phases with a low activity period in June

(Peeters et al., 2012). For other species, we only observed declines in unmown refuges. For instance, the in June active *Andrena hattorfiana*, a national red listed species in the Netherlands, disappeared from experimental locations but not controls. Finally, a number of species appeared at control locations, whereas this was less the case at experimental locations. For instance, *Maniola jurtina* that is most active during July occurred commonly at control in the later period, but not experimental ones. The full table, including all species abundances during each period, is shown in appendix 6.

Table 5.1: The average number of individuals counted for selected species per location in the *Before, After* and *Later* periods of the experiment for both experimental and control locations.

	Experimental			Control		
Species	**Before**	**After**	**Later**	**Before**	**After**	**Later**
Abundance decline of abundant species						
Apis mellifera	101.3	185.3	86.3	57.0	209.0	241.0
Bombus lapidarius	67.0	59.7	37.7	44.0	37.5	53.0
Halictus scabiosae	35.7	42.0	5.3	8.0	5.0	1.0
Bombus terrestris	16.3	15.0	4.7	62.5	25.5	13.5
Oedemera nobilis	9.0	17.3	13.0	13.5	17.0	17.0
Oedemera lurida	2.0	7.3	2.3	7.5	13.0	12.5
Disappearance of semi-abundant species						
Andrena hattorfiana	1.0	3.0			2.5	2.0
Bombus hypnorum	1.7	2.0		2.0	1.5	1.0
Halictus tumulorum	3.7	1.3		1.5	1.5	0.5
Polyommatus icarus	3.0	2.7			1.0	
Helophilus trivittatus	2.7	1.3		14.5	4.0	
Occurrence of new species						
Maniola jurtina			0.3			12.5
Bombus vestalis						10.5
Volucella bombylans	1.3		0.3			2.5
Andrena ovatula	0.7		0.3			1.0
Rhagonycha fulva			0.3			1.0
Sphaerophoria scripta	0.3	0.3	0.7			1.0
Stenurella melanura		0.7				1.0
Zygaena filipendulae		1.7	8.7			1.5
Dasypoda hirtipes			0.7			

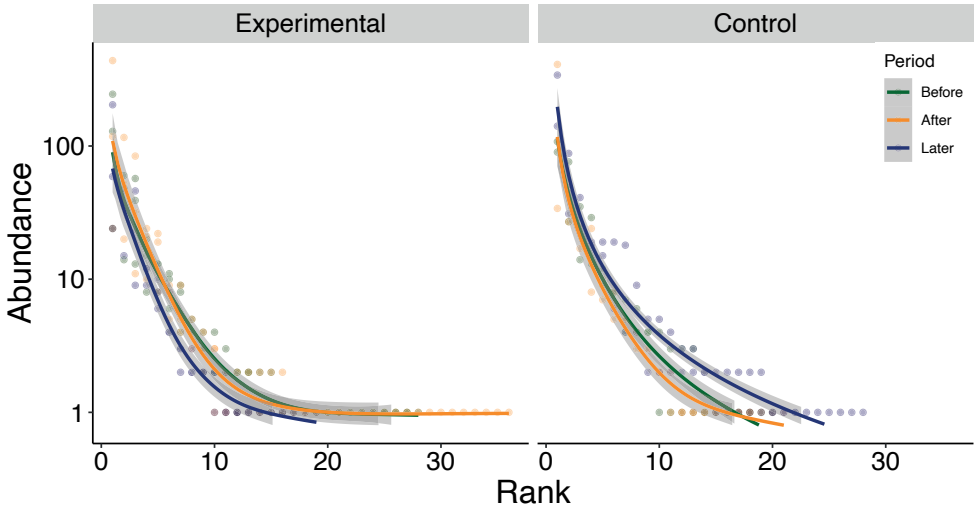


Figure 5.5: Averaged rank-abundance curves (visualised with a loess curve) of the pollinator communities during the before (dark green), after (orange) and later (dark blue) periods from experimental treatments and controls. Grey areas give the 95% confidence interval.

5.4 DISCUSSION

Partial mowing, where unmown refuge vegetation remains available to arthropods, could be a valuable alternative to traditional mowing, where all vegetation is mown at once (Révész et al., 2025). Nevertheless, studies on community development in refuge vegetation compared to unmown vegetation are scarce, whereas these are crucial to understand how partial mowing affects arthropod communities. Our study shows that, for pollinators, initial aggregation in refuge vegetation is followed by a decline in abundance and species richness only a few weeks later. These developments were not visible in unmown controls, where communities largely stayed the same. This points out that, despite positive effects of partial mowing compared to fully mown vegetation, partial mowing can still filter arthropod communities.

Total density and activity

In remaining vegetation strips on mown locations we observed that pollinator abundance and activity significantly increased after mowing, but later on declined to roughly pre-mowing conditions. On the one hand this is consistent with the broad consensus that partial mowing can benefit arthropods, on the other it shows that unmown refuges do not sustain all pollinator individuals previously present at the location. This contrasts with other arthropod groups such as spiders, arthropods, true bugs and beetles, which did maintain higher abundance and species richness (Révész et al., 2025). Despite a different setup and goals, specifically for bees the equal abundance in unmown refuges before

and multiple weeks after mowing has also been reported, but not further discussed, in two other studies (Buri et al., 2014; Meyer et al., 2017). We did not observe these increases and decreases in unmown controls, where visitation frequency and pollinator abundance were significantly higher than at partially mown sites in the later period. Together, this suggests that vegetation in unmown refuges is unable to sustain all pollinators previously present at the location as unmown refuge strips are partially abandoned.

Group-level responses

The initial increases and later decreases in unmown refuges were not divided equally over pollinator groups. Compared to pre-mowing conditions, only honeybees and beetles maintained similar numbers, whereas groups often targeted by management (non-*Bombus* wild bees, bumblebees) show abundance and species richness declines not observed at control locations. This shows that, just like with other types of management (e.g. Larkin and Stanley, 2021; Bergholz et al., 2022), partial mowing can alter pollinator community composition. Unequal responses of groups within arthropod communities to partial mowing has been shown over a 5-year period (van Klink et al., 2019). Our fine-grained experiment suggests that, for pollinators, this filtering mainly occurs in response to increased pollinator density, as abandonment of refuge strips only occurred after initial pollinator aggregation. In addition, it is unlikely that these differences result from mortality through mowing, as (1) literature for our groups does not suggest between-group differences in mortality by mowing, and (2) expected mortality lies between 5-20%, not balancing out the threefold increase expected with 1/3 vegetation remaining (Fluri et al., 2001; Humbert et al., 2010a).

What limits pollinator communities is subject of ongoing debate (Sponsler et al., 2023). While floral resource availability has traditionally been seen as a primary driver (e.g. Scheper et al., 2014; Hyjazie and Sargent, 2022; Bishop et al., 2024), other studies propose factors such as nesting availability (Requier and Leonhardt, 2020) or other anthropogenic disturbances (Potts et al., 2010). Although Swinkels et al., (2025) suggest that floral resource limitation on dike grasslands is quickly relieved, our results indicate that increased post-mowing competition for floral resources in refuge strips may still drive the observed patterns. First, visitation frequency increased roughly twofold more than pollinator abundance directly after mowing, suggesting pollinators move faster between flowers. Disproportionate visitation frequency increase has been proposed as a proxy for increased competition for floral resources (Forster et al., 2023). Second, the persistence of honeybees, that displayed high patch fidelity (Fragoso and Brunet, 2023) and can outcompete other pollinators (Henry and Rodet, 2018; Valido et al., 2019a), supports the idea that floral resources become limiting is refuge strips and thus that only stronger competitors persist. The high abundance of honeybees present in our study may also explain the contrast with others that observe stable numbers of wild bees and syrphids in refuge strips but report lower numbers of honeybees (Buri et al., 2014; Meyer et al., 2017).

Species richness and community composition

The group-level changes resulted in an overall decline in species richness at experimental locations, as opposed to unmown controls where we observed an (non-significant) increase. This finding conflicts with other studies, that generally show a smaller response of species richness in unmown refuges (Révész et al., 2025) and with studies on wild bees (Buri et al., 2014) and hoverflies (Meyer et al., 2017) specifically that show no changes in species richness. This difference might partially result from the inclusion of the whole pollinator community, where small group-level changes cumulate to an overall significant effect. In addition, it might be explained by the higher number of honeybees in our study as, proportionally, disturbance sensitive non-*Bombus* wild bee species richness declined most.

Further study of rank-abundance curves provides support for the cumulative effect of small changes as at experimental locations not only rare species disappear, but also common species become less abundant. This results in a decreased detection rate, lowering the number of species encountered per survey. Steeply declining rank abundance curves, where both rare and semi-common species decline, have been described by Habel and Schmitt (2018) to explain wide-spread insect decline (Hallmann et al., 2017). That we observe it here in miniature tied to the loss of suitable habitat is in line with Habel and Schmitt's contention connecting steeper rank-abundance curves to smaller and isolated nature areas. In addition, we observed no compensatory appearance of later-season species at partially mown locations. So far unmown refuges were thought to specifically benefit those species with a later phenology. Of course, recovery of communities can take multiple decades and it could well be that species with later phenology did not find refuges within one year (Hirayama et al., 2025). Nevertheless, van Klink et al. (2019) report that, after five years of partially mowing in Swiss meadows, species richness of species with later phenology did not increase. In addition, we do observe the appearance of species with later phenology in control vegetation, suggesting that species with later phenology are potentially limited in unmown refuges.

Conservation outlook

Our results show that unmown refuges, despite facilitating more individuals than fully mown meadows, act as an ecological filter. For conservation, this implies that unmown refuges after partial mowing are no substitute for the entire vegetation, and thus that deliberate management decisions need to be made just like with other mowing regimes. We know that delayed mowing generally benefits arthropods (Humbert et al., 2012), and this could be combined with partial mowing. In addition, Révész et al. (2024) show that unmown vegetation proportion and width of unmown areas interact and influence conservation outcomes, indicating the significance of the size and shape of the refuge. Nevertheless, generally speaking the factors that influence the carrying capacity of unmown refuges are understudied and thus important topic for future research.

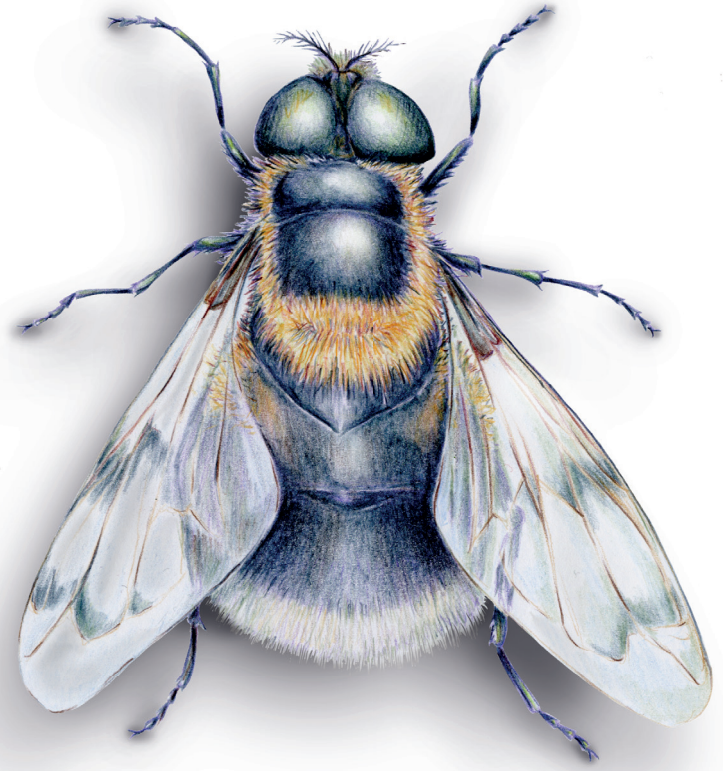
In addition to local management choices, the abandonment of refuge patches observed in our study highlights the importance of a landscape scale approach as pollinators need suitable habitat to escape towards. This has also been suggested by other studies (e.g. Schmidt et al., 2008; Meyer et al., 2017). Although, to our knowledge, there are no studies on the implementation of landscape scale partial mowing, Johansen et al., (2019) show that in traditional mowing agricultural management in Romania, heterogenous mowing times of meadows dictated where pollinators foraged at the landscape scale. How pollinators use the landscape after partial mowing, and how a landscape-level partial mowing regime can be implemented are thus important avenues for future research.

5.5 CONCLUSION

We conclude that partial mowing, although it is a promising management regime that allows a wide variety of arthropods to benefit from remaining vegetation, in our experiment did not sustain pollinator diversity as a whole. In grasslands dominated by generalists (and especially honeybees) such as at our dikes, partial mowing led to a loss of pollinator species richness, especially for (vulnerable) wild bees that are often a conservation target. While preferable above full vegetation mowing, conservation authorities should realize that partial mowing does significantly modify the pollinator community. Experiments with leaving larger areas unmown for a year are called for with examining the effects on the flowering plant community and pollinating insects alike.

5.6 ACKNOWLEDGEMENTS

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6

Keeping Raised Bog Remnants Wet Stabilizes Characteristic Pollinator Communities

Tia l'Amie, Jan Kuper, Marijn Nijssen, David Scarse,
Eelke Jongejans, Constant Swinkels

Supplementary materials available at: https://constantswinkels.com/117-2/

ABSTRACT

Recent studies report declines in abundance and species richness of pollinator communities. In response, nature managers aim to promote pollinators primarily through vegetation manipulation. However, long-term studies that evaluate pollinator community development in restored areas under active management are scarce. To assess whether landscape-level conservation efforts are able to sustain a characteristic pollinator community, we study abundance and richness trends of hoverflies (Diptera: Syrphidae), bees (Hymenoptera: Apidae s.l.), and butterflies/diurnal moths (Lepidoptera), as well as their characteristic species over 30 years within the restored and intensively managed Dutch raised bog system Bargerveen. We describe positive and stable trends in the overall abundance and species richness of pollinators, primarily Apidae and Syrphidae. These trends contrast with nation-wide declines. The effects of recent dry years were evident in declining butterfly abundance trends, although not as pronounced as in national trends. In addition, abundance of species characteristic of raised bog systems remained stable, suggesting that benefits also applied to these generally more sensitive species.

Implications for insect conservation: Results from this case study show that conservation efforts in raised bog systems can support and improve pollinator abundance and richness, as well as populations of characteristic and vulnerable species. We argue that the positive and stable population trends of pollinators in Bargerveen are primarily a result of large-scale water management, and that landscape-level hydrological management has the potential to act as a buffer against drivers of insect decline even within predominantly agricultural landscapes.

6.1 INTRODUCTION

Abundance and species richness have declined in pollinator communities in recent decades (Biesmeijer et al., 2006; Hallmann et al., 2017; Barendregt et al., 2022), even within natural areas (Hallmann et al., 2017). While pollinator decline is worrisome in and of itself, the loss of pollinators is considered especially alarming due to their crucial role in pollination of both crop and wild plant species (Kremen et al., 2002; Vanbergen and the Insect Pollinators Initiative, 2013) estimated that roughly 78% of the world's wild flowering plants rely on pollinators for reproduction. Habitat degradation, fragmentation, climate change and the increased abundance of alien species and pathogens are generally hypothesized to be the main drivers behind pollinator decline (Kearns et al., 1998; Kremen et al., 2002; Potts et al., 2010). Overall, there is a clear need for effective conservation and restoration strategies for pollinators.

Protected nature areas serve as an important refuge for both native and managed pollinator species (Garibaldi et al., 2011; Cooke et al., 2023). While many studies show how local measures, such as increasing floral richness, leads to short-term benefits for pollinator communities, this effect generally does not apply to vulnerable insect communities within natural areas. It is known that within natural areas landscape-level nature conservation can promote these communities (Sexton and Emery, 2020; Larkin and Stanley, 2021; Uhl et al., 2021). However, to our knowledge, the long-term benefits of landscape-level conservation efforts on pollinator communities are rarely assessed. Given the many landscape level threats on natural areas in North-Western Europe, it is essential to assess these long-term effects, as positive effects could well be undone over larger timescales.

Raised bog systems in the Netherlands are an excellent example of such a vulnerable natural system. They harbour characteristic pollinator communities that are not found anywhere else in the Netherlands (Van Duinen et al., 2013; Wallis de Vries et al., 2022; Speelman and Kalkman, 2023). Although raised bogs were once widespread, currently only small remnants remain in an otherwise primarily agricultural landscape. Restoration and conservation efforts within these remnants are therefore crucial for maintaining these characteristic pollinator communities.

Two major landscape-level threats for raised bog plant and insect communities in the Netherlands are nitrogen deposition and desiccation (Casparie, 1993; Tomassen et al., 2004). Whereas nitrogen deposition is an ongoing process caused by landscape level drivers beyond the control of local managers, hydrological regimes can be effectively managed at the local scale via the installation of weirs, dams, and buffers (Smolders et al., 2002; Brown et al., 2017). This in turn has been shown to promote vulnerable plant communities of raised bog systems, despite the context of nitrogen deposition (Haapalehto et al., 2017; Renou-Wilson et al., 2019). Although it has been shown that restoring dry

grassland vegetation can promote both pollinator abundance and richness (Sexton and Emery, 2020), to our knowledge the response of pollinator communities from wet systems to hydrological management, especially in the long term, is understudied.

Here we analyse two long-term (1994-2024) datasets documenting pollinator and detailed butterfly counts in Dutch raised bog reserve Bargerveen. During the study period several landscape-level hydrological interventions occurred, which gave us the opportunity to study changes in pollinator abundance and richness within the context of restoration efforts. Specifically, we aim to answer the following research questions: 1) Has the abundance of pollinators in Bargerveen changed over the past three decades?; 2) Has pollinator species richness changed?; 3) What are the population trends of selected vulnerable and characteristic species? 4) Do hoverfly abundance trends differ between species with contrasting larval strategies?

6.2 MATERIALS AND METHODS

Brief Area Description and Management

The study was conducted in the Natura2000 area Bargerveen, currently the largest raised bog in the Netherlands. Having been subject to peat extraction until 1992, the area is now actively managed to promote peat formation. It hosts a number of rare and red-listed species typical for raised bogs (van Guldener et al., 2016; Speelman and Kalkman, 2023). Management in Bargerveen includes area-wide mowing and grazing. In addition, significant system-level interventions have been taken to restore wet bog conditions and the natural hydrological regime. These include the infilling of the Noordersloot watershed in 1997 (van Guldener et al., 2016), restructuring and placement of additional weirs and dams which primarily took place between 2001 and 2006, and the placement of hydrological buffers in 2014, 2017, 2018 and 2020 (Figure 6.1A). These measures have rewetted the system and led to more stable water levels in the area, thereby facilitating the recovery of characteristic raised bog vegetation (Bijkerk et al., 2015). Nevertheless, the nature reserve is still subjected to eutrophication, acidification, drainage, and climate change that threaten the naturally nutrient-poor system (Adema et al., 2017; van Guldener et al., 2016), which are often linked to pollinator declines. In this study, we analyse transect data from two characteristic habitat types found in raised bog systems (Figure S1); *Nardus* grassland (H6230, Figure 6.1B) and Northern Atlantic wet heath with *Erica tetralix* (H4010_A) (Figure 6.1C).

Nardus Grasslands

The *Nardus* grasslands of Bargerveen are semi-natural, and developed from old agricultural fields. A well-developed *Nardus* grassland can be recognized by the presence of plant species such as *Platanthera bifolia*, *Dactylorhiza maculata*, *Galium saxatile* and

Potentilla erecta (Bijkerk et al. 2015). To maintain the preferred low to medium nutrient availability in the grasslands, management focuses on soil impoverishment, which is realized via yearly mowing and removal of the clippings. Acidification, primarily due to high N-deposition in the area, poses a significant threat to the ideally weakly buffered grasslands (Adema et al., 2017). The *Nardus* grasslands in Bargerveen have their own apparent water table, dependent on precipitation, evaporation and seepage. Maintaining a high water level is essential for maintenance of a characteristic vegetation community (Van Duinen et al., 2013). Likely as a result of hydrological interventions within the area, the water table in the *Nardus* grasslands of Bargerveen increased between 2006 and 2007, and remained relatively stable up to 2018, after which a slight drop in the surface water level was observed (Figure S2).

The *Nardus* grasslands of Bargerveen house a relatively high number of characteristic butterfly species (Van Duinen et al., 2013), including the grizzled skipper (*Pyrgus malvae*) and the sooty copper (*Lycaena tityrus*). Both butterfly species are sensitive to decline due to their life-history traits, and are closely associated with *Nardus* grasslands, making them important targets for management in the area.

Wet Heathlands

The second area is classified as a Northern Atlantic heath with *Erica tetralix*, found on acidic, nutrient-poor soils. This habitat is characterized by the presence of *Erica tetralix, Calluna vulgaris*, grasses such as *Molinia caerulea*, sedges such as *Rhynchospora alba*, and *Sphagnum* mosses. Hydrology plays an important role in wet heathland systems, as most characteristic vegetation and insect species of this habitat type rely on high water tables. Within the wet heathlands of Bargerveen, no significant long-term developments in surface water table level were identified (Figure S2).

A major challenge in the wet heathlands of Bargerveen is preventing encroachment of grasses and other vegetation due to high N-deposition and acidification. To counter this, non-heath vegetation is removed via grazing by sheep and cattle, mowing with clipping removal, and controlled burning (Bijkerk et al., 2015; Adema et al., 2017). These measures aim to promote wet heathland vegetation, but also create open patches which benefit nesting wild bee species (Wallis de Vries et al., 2022).

The pollinator communities of wet heaths are not very diverse, but contain a high proportion of characteristic and rare species. One such species is the vulnerable silver-studded blue (*Plebejus argus*), which is locally abundant in wet heaths of Bargerveen (Van Duinen et al., 2013). The critically endangered brown-banded carder bee (*Bombus humilis*) is also commonly found in the wet heaths of Bargerveen. While once widespread in the Netherlands, its distribution is limited to a few sites in Drenthe (Speelman and Kalkman, 2023), with Bargerveen likely supporting the largest *B. humilis* population in the Netherlands,

making it an important target species for management. *B. humilis* is also a valuable indicator species due to its close association with wet heathlands and sensitivity to competition pressure by other pollinating species (Speelman and Kalkman, 2023).

Pollinator Transects

Hoverflies (Diptera: Syrphidae), bees (Hymenoptera: Apidae s.l.), and butterflies/diurnal moths (Lepidoptera) were counted and identified up to species-level during nine years: 1994-1995, 1997-2001, 2017 and 2024. Sampling dates varied between the years, but always took place between May and October, with 93.7% of sampling events taking place between June and August. Transect distance was fixed with permanent poles in the field, and transects were sampled while walking at a constant pace. All individuals were counted and identified to species-level in the field if possible. In case of uncertainty, the specimen was collected and preserved for later identification. Other pollinators passing during this handling time were not included in the counts. Specimens that could not be identified at the species-level were identified to the lowest possible taxonomic rank. For species richness analyses, we included only individuals identified to the species-level, treating additional genera or families as a single species. The *Bombus terrestris* species complex was treated as one species as reliable identification based on field characteristics is not possible (Williams et al., 2012).

The *Nardus* grassland pollinator transect (NG), was located on the east end of Bargerveen (Figure 6.1), and was sampled a total of 75 times. Transect length of NG was 250m from 1994-2001 and 150 m in 2017 and 2024. Transect width remained constant at 5 m (Figure 6.1B). The wet heath pollinator transect (WH), is located in a wet heath area on the west-side of Bargerveen (Figure 6.1C), and was sampled a total of 67 times. The length of 200 meters and width of 5 meters remained constant during all sampling dates before 2024. In 2024 half of the original transect was inaccessible due to the high water level. Therefore, another nearby transect (100 x 5m) within the same habitat type was sampled in addition to the accessible half of the original transect (100 x 5m) (Figure 6.1C). During the first year (1994) sampling in WH was focused on specific species. This year was excluded from abundance and species richness analyses, but included for species-specific analyses of those species.

Butterfly Transects

Butterfly counts were consistently performed in accordance with the guidelines set by "*Handleiding Landelijke Meetnetten Vlinders en Libellen*" (van Swaay et al., 2011). This data was collected in the framework of the Dutch Butterfly Monitoring Scheme. The butterfly transects overlapped partially with the pollinator transects in both sites. The *Nardus* grassland butterfly transect (NG_B) had a length of 250 meters and width of 5 meters (Figure 6.1B). In the NG_B transect all butterfly species were counted and identified to the

species-level where possible. Sampling took place between April and October during 13 years: in 1995, 1999-2017, 2019, 2021, and 2023. NG_B was sampled a total of 198 times.

The wet heathland butterfly transect (WH_B) had a length of 200 and width of 5 meters (Figure 6.1C). Butterfly counts in WH_B focused solely on *P. argus*, and took place between June and September, during peak activity of the species. Sampling in WH_B took place a total of 96 times over the course of 20 years: in 1999, 2001-2009, 2011-2017, 2019, 2021 and 2023.

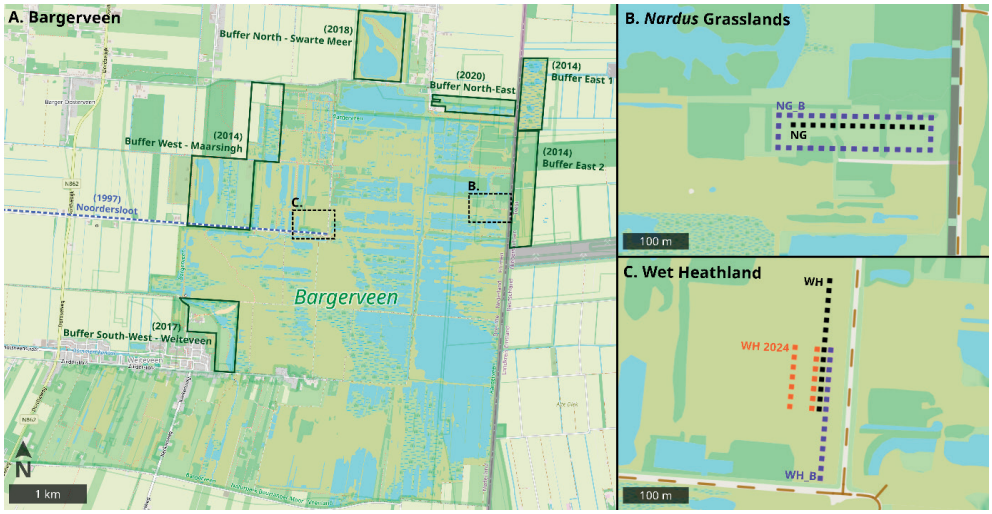


Figure 6.1: Overview of sampling sites and buffer zones within Bargerveen. Buffers installed during the course of the study are shown as solid green lines: Buffer West - Maarsingh and Buffer East 1, Buffer East 2, Buffer South-West - Weiteveen, Buffer North - Swarte Meer, and Buffer North-East. The Noordersloot which was infilled is indicated with a dashed blue line. The two sampling sites, the wet heathland and the Nardus grasslands are indicated by the dashed black lines (A). A more detailed view of the Nardus grassland (pollinator transect NG and butterfly transect NG_B), and wet heathland (pollinator transect WH and butterfly transect WH_B) sites are provided in 1B and 1C respectively. Dashed black lines represent pollinator transects, dashed purple lines indicate butterfly transects, and dashed orange lines show the alternative wet heathland transect from 2024 (the high water table in 2024, prevented access to the original transect)

Weather Data

To account for the influence of bioclimatic circumstances on pollinator abundance trends, data on temperature, irradiance, humidity, and wind speed were collected from the Royal Netherlands Meteorological Institute (Koninklijk Nederlands Meteorologisch Instituut: KNMI). Since sampling dates were chosen based on favorable weather, no hourly data on precipitation were included as precipitation was assumed to have been absent. Weather data were collected from the nearest KNMI meteorological station in Hoogeveen (approximately 30 km from Bargerveen). For the WH, WH_B and NG_B transects the starting

time of the transect counts was consistently recorded, and hourly data corresponding to the starting hour, as well as averaged daily meteorological data were used for analysis (Table S1-2). For the NG transect averaged daily meteorological data were used since start time was not always recorded.

Hydrological Data

Hydrological data describing surface water levels for the *Nardus* grasslands (ID = P23A0058 and P23A0087) and wet heath (ID= P23A0102 and P23A0103) were retrieved from Dinoloket, a public Dutch national database of groundwater head observations.

Data Analysis

All analyses and visualizations were conducted in R V4.3.2 (R Core Team, 2023). Prior to analysis, counts from NG were corrected for transect length by adjusting species counts to a standardized transect length of 150 meters, by removing individuals randomly based on percentual increase in transect length. As transect length remained constant, this was not necessary for WH, WH_B and NG_B. The western honeybee (*Apis mellifera*) is a managed species and was therefore excluded from the abundance analyses, but included in the richness analyses.

Pollinator Abundance Trends

To test whether the abundance of pollinators has changed within the transects the daily total pollinator counts and species-group specific (Syrphidae, Apidae and Butterflies) daily counts were analysed. To correct for seasonality a similar approach to Barendregt et al. (2022) was taken. A generalized additive model (GAM) was fitted to daily abundance counts irrespective of year. This model was then used to predict relative day-of-the-year pollinator abundance, resulting in a so-called season score. The season score was normalized and ranges from zero to one, with values close to one representing abundance measures taken during the peak of the season. Then, to assess changes in pollinator abundance over the years separate generalized linear mixed-effect models (GLMM) were fitted over total daily pollinator counts and species-group specific counts in WH and NG. The basic structure of the models included the season score and a continuous year variable as fixed effects, as well as year as a random categorical variable to correct for nestedness within years. Models were fitted over daily abundances over the entire study period (1994 - 2024) to analyse overall changes in abundance, as well as a subset encompassing 1994 - 2001, to assess pollinator abundance trends prior to the installation of hydrological buffers. Models including weather variables were explored, but did not significantly improve model AIC (Table S1-S2). Hence, in the main text we present the results from the basic model.

A similar approach was followed to analyse the daily count of butterfly abundances in NG_B and WH_B. However, visual inspection of the data distribution revealed that the

daily abundance of butterflies did not follow a linear trend. Therefore, in addition to GLMMs, GAMs including date and season score were fitted to assess non-linear abundance changes over the years in the butterfly transects.

Species Richness Trends

In order to gain insight into species richness trends, species accumulation curves (SAC) were generated using the R package vegan V2.6.4 (Oksanen et al., 2018). The function specpool was used to calculate Chao-estimates, a measure used to estimate the extrapolated species richness within a species-pool based on the observed species accumulation. The calculated Chao-estimates were plotted and visually inspected to assess changes in species richness over the years.

Abundance Trends Characteristic Species

The characteristic butterfly species *Pyrgus malvae*, *Lycaena tityrus*, *Plebejus argus*, and bumblebee species *Bombus humilis* were selected for species-specific analysis. GLMMs including year and season score as well as GAMs including date and season score were fitted to analyse *P. malvae* (NG_B), *L. tityrus* (NG_B) and *P. argus* (WH_B) abundance trends. To analyse *B. humilis* abundance (WH), GLMMs including year and season scores were fitted.

Abundance Trends Larval Strategies Syrphidae

In order to assess whether abundance trends of hoverflies differed per larval strategy, GLMMs including year and season score were used to analyse trends of subsets of hoverfly species. Syrphidae species were classified as either aquatic saprophagous, terrestrial saprophagous, phytophagous or zoophagous based on classification as described by Reemer et al. (2009). Due to the low abundances of Syrphidae in the wet heath transect, the larval-stage specific model failed to converge, and no significant trends were observed in the abundances of the various Syrphidae larval types in the wet heath.

6.3 RESULTS

Within the pollinator transects (WH and NG) a total of 15,284 butterfly, 3,956 hoverfly and 3,385 bee individuals (1,897 excluding *A. mellifera*) were counted, representing 30, 42 and 19 species respectively. In the pollinator grassland transect, a total of 3,625 individuals from 42 hoverfly species, 682 individuals (313 excluding *A. mellifera*) from 17 bee species, and 5,645 individuals from 27 butterfly species were recorded. In comparison, in the wet heath transect 331 individuals from 21 hoverfly species, 2,703 individuals (1,584 excluding *A. mellifera*) from 13 bee species, and 9,639 individuals representing 20 butterfly species were recorded.

A total of 47,584 butterflies were counted within the butterfly transects (NG_B and WH_B). In the butterfly grassland transect NG_B 20,774 butterflies representing 31 species were counted. In butterfly wet heathland transect WH_B 26,691 *Plebejus argus* individuals were sampled. For a more detailed species list, refer to table S3 in the supplementary information.

Pollinator Transects Abundance Trends

Total pollinator abundance within pollinator *Nardus* grassland transect NG increased significantly (0.93% per year, CI 95% [0.53%, 1.33%] Figure 6.2A) over the course of the entire study (1994 - 2024). This significant increase in abundance in NG translated to the increased abundance of Apidae (3.28% per year, CI 95% [1.82%, 4.76%], Figure 6.2C) and Syrphidae (2.90% per year, 95% CI [1.40%, 4.42%], Fig 2B). The abundance of butterflies on the other hand declined significantly between 1994 and 2024 (-2.16% per year, CI [-3.33%, -1.09%], Figure 6.2D). Analyses using separate GLMMs on smaller data subsets identified no significant changes in total pollinator abundance or group-level abundances in NG between 1995 and 2001 (Figs. 2A-D).

In contrast, no significant changes were found in pollinator abundance in the wet heathlands over the course of the entire study period (1994 - 2024), either in total pollinator abundance or at the group level (Figs. 2E-H). However, total pollinator abundance in the wet heathland pollinator transect WH decreased significantly between 1995 and 2001 (-4.96% per year, CI [-5.72%, -4.19%], Figure 6.2E), primarily due to a drop in butterfly abundance (-5.80% per year, CI [-5.95%, -5.66%], Figure 6.2H). No significant pollinator abundance trends were identified for either Syrphidae or Apidae in WH.

The majority of the Syrphidae encountered in the *Nardus* grasslands have (semi-) aquatic saprophagous and terrestrial zoophagous larval stages. The significant increase in Syrphidae mainly was mainly due to an increase in zoophagous species, which saw a significant increase in abundance (4.51% per year, 95% CI [0.11%, 9.10%], Figure 6.3B). A significant increase in phytophagous species was identified as well (2.55% per year, 95% CI [2.51%, 2.59%], Figure 6.3C), though these species were only present in very low abundance in all years except 2017. The observed increase in phytophagous syrphids is mainly a result of the remarkably high number of *Eumerus* in 2017, which accounted for 58 of the 59 phytophagous hoverflies found that year. No significant trends were found for the other larval types in the *Nardus* grasslands.

Similar to in the *Nardus* grasslands, the larval types of Syrphidae in the wet heath consisted primarily of (semi-) aquatic saprophagous and terrestrial zoophagous species. No terrestrial phytophagous species were observed in the wet heath throughout the entire study period. Terrestrial saprophagous species were recorded in the wet heath only in 1998 and 2001.

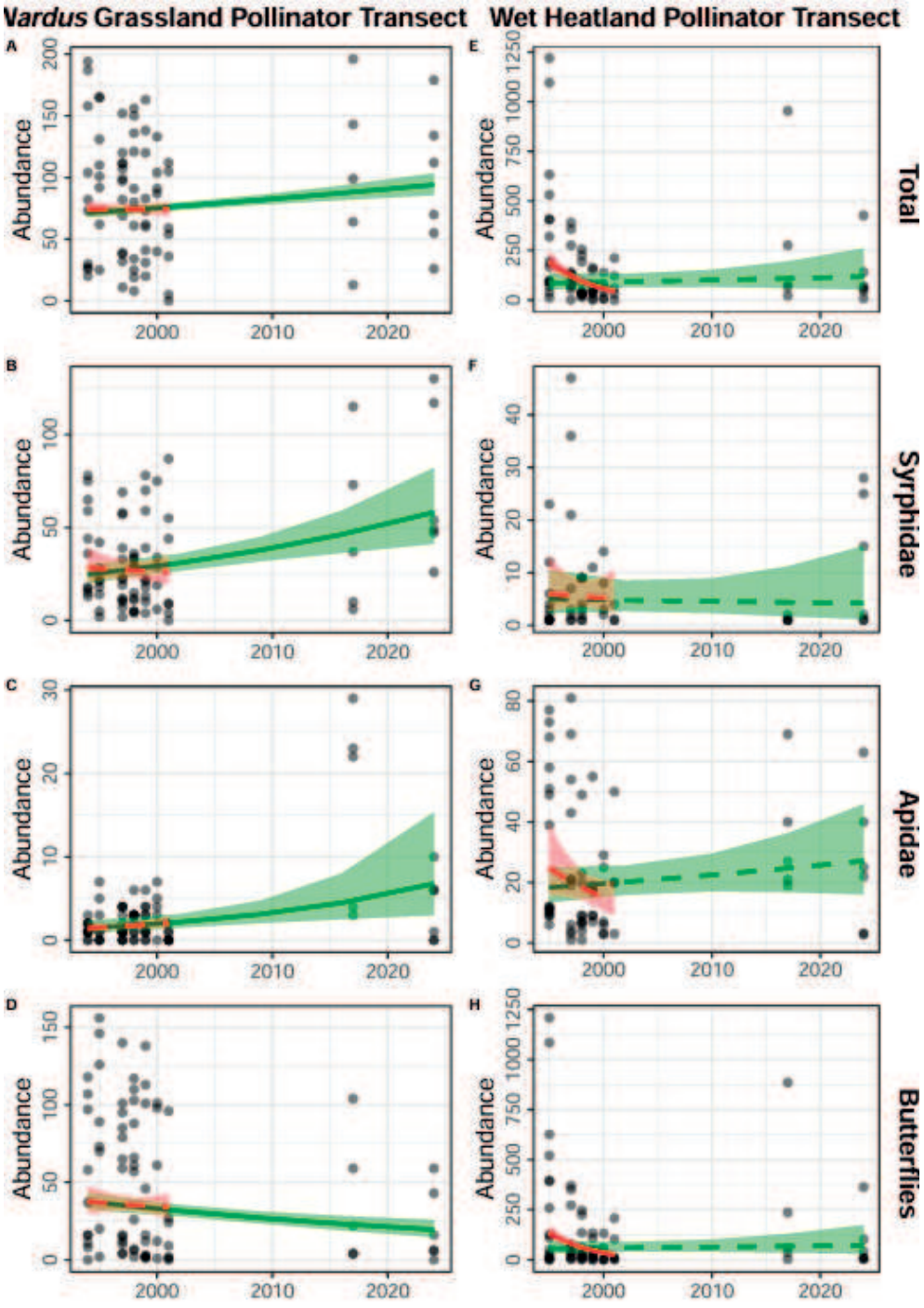


Figure 6.2: Multiyear abundance trends of pollinators in the Nardus grassland transect (GL, left column) and the wet heathland pollinator transect (WH, right column). GLMM's including year and season score as fixed effects were fitted to analyse NG total pollinator daily abundance (A),

NG Syrphidae daily abundance (B), WH Apidae daily abundance (C), NG butterfly daily abundance (D), WH total pollinator daily abundance (E), WH Syrphidae daily abundance (F), WH Apidae daily abundance (G), and WH butterfly daily abundance (H). GLMM's were fitted over the entire study period (depicted in blue), as well as a smaller subset of the data encompassing 1994-2001 in GL, and 1995-2001 in WH (depicted in red). Significant relationships are represented by solid lines, and non-significant relationships are represented by dashed lines. The managed species Apis mellifera is not included in this graph

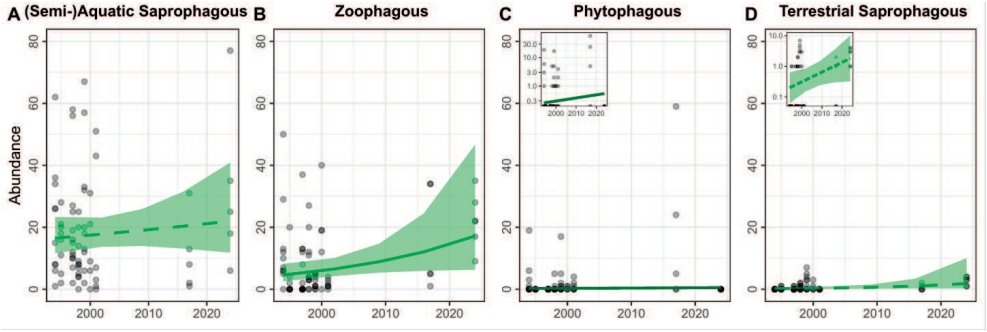


Figure 6.3: Multiyear abundance trends of hoverflies with varying larval stages in the Nardus grassland pollinator transect (NG). The coloured lines and surrounding shaded area indicate the fitted GLMM model including confidence intervals, which account for random effects of year and season score. Solid lines indicate a significant relationship, whereas dashed lines indicate an insignificant relationship. The trends of phytophagous © and terrestrial saprophagous species also were plotted on a log-scale, shown in the small upper-left panels in C and D)

Within the wet heathland pollinator transect the characteristic bumblebee *B. humilis* was found in relatively high abundance, accounting for over a quarter of all recorded Apidae individuals. *B. humilis* abundance in WH showed a near-significant decline (p = 0.061) between 1995 and 2001 of -6.21% per year, CI 95% [-9.20%, -3.11%] (Figure 6.4). However, no significant change in *B. humilis* abundance over the course of the entire study (1995-2024) was found.

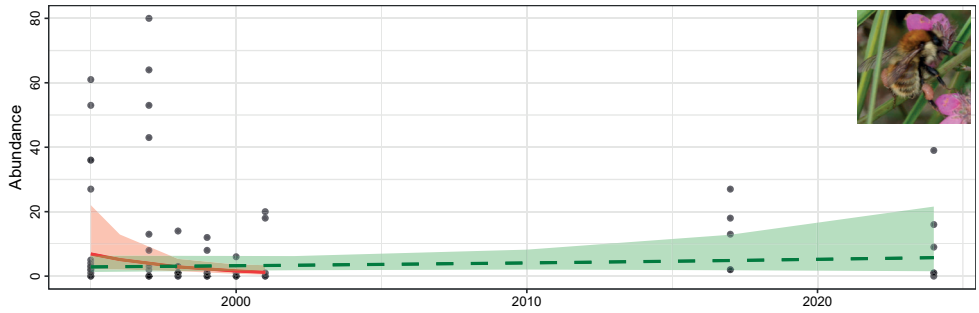


Figure 6.4: Multiyear Bombus humilis abundance trend in the wet heathland pollinator transect (WH). The colored lines and surrounding shaded area indicate the fitted GLMM including confidence intervals, which account for random effects of year and season score. Solid lines indicate a significant relationship, whereas dashed lines indicate an insignificant relationship. GLMM's were fitted over the entire study period (depicted in blue), as well as a smaller subset of the data encompassing 1995-2001 (depicted in red). Significant relationships are represented by solid lines, and non-significant relationships are represented by dashed lines

Butterfly Transects Abundance Trends

A GLMM including year and season score as fixed effects fitted to the daily count of butterfly abundance in the butterfly *Nardus* grassland transect NG_B showed a significant yearly increase of 4.29%, CI 95% [1.88%, 6.47%]. A statistically significant non-linear relationship between sampling date and daily NG_B butterfly abundance was identified (Figure 6.5A). NG_B butterfly abundance remained relatively stable at the start of the study between 1995 and 2006, and then showed an increase up to roughly 2016. In the past decade butterfly abundance in NG_B gradually declined.

Species-specific analyses using GLMM of *L. tityrus* and *P. malvae* in NG_B also found a significant increase in abundance for both butterfly species of 8.80%, CI [1.17% - 16.48%] and 5.79%, CI [1.23% - 10.60%] respectively. However, further analysis using GAMs reveals that abundance does not increase linearly, but instead follows a roughly hump-shaped pattern (Figure 6.5). A similar increasing period as seen in NG_B total butterfly abundance between 2006 and 2016 for both species. *P. malvae* abundance remains roughly stable after this increasing period (Figure 6.5C), whereas *L. tityrus* abundance steeply declines (Figure 6.5B).

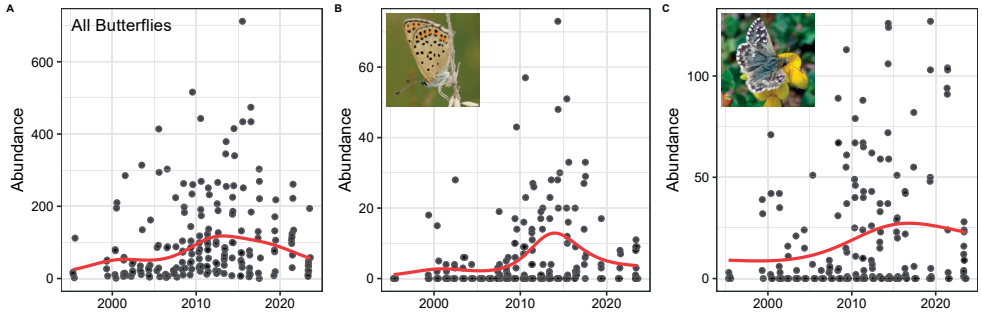


Figure 6.5: Multiyear butterfly abundance trends in the Nardus grassland butterfly transect (NG_B). GAMs were fitted over NG_B daily butterfly abundance (A), NG_B L. tityrus abundance (B), and NG_B P. malvae abundance (C), represented by the red line

No significant change in *P. argus* abundance within the wet heathland butterfly transect WH_B was found over the course of the entire study period. Further analysis using GAM found that abundance trends of *P. argus* were variable over the years. *P. argus* daily abundance in WH_B showed an initial increasing trend from 1999 to 2008, after which abundance declined. From 2014 onwards, coinciding with the installation of nearby buffer systems, *P. argus* daily abundances showed a steady increase (Figure 6.6). *P. argus* abundances did not increase during the most recent sampling years.

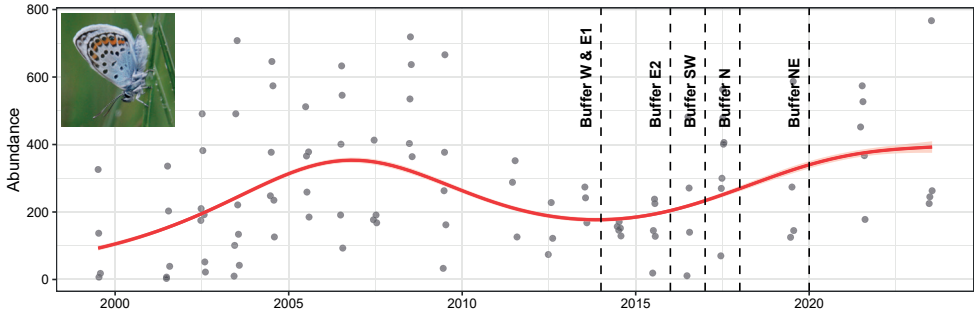


Figure 6.6: Multiyear Plebejus argus abundance trend in the wet heathland butterfly transect (WH_B). Buffers were installed during the study period in 2014 (W = Buffer West – Maarsingh, and E1 = Buffer East 1), 2016 (E2 = Buffer East 2), 2017 (SW = Buffer South-West – Weiteveen), 2018 (N = Buffer North – Swarte Meer), and 2020 (NE = Buffer North-East), and are represented with vertical black dashed lines

Pollinator Transects Species Richness Trends

Pollinator species richness in the pollinator grassland transect NG fluctuated notably more (Figure 6.7A) compared to species richness within the wet heathland pollinator transect WH (Figure 6.7B), but was consistently higher than species richness in WH. Both transects seem to have been subject to a decline in species richness prior to 2001. However, chao estimates in 2017 and 2024 are relatively similar, or even high, compared to richness estimates during the start of the study. Apidae species richness remains relatively low and stable over the course of the study in both pollinator transects (Figure S3). Species richness in the wet heathland was particularly low in 2017, primarily due to low butterfly and hoverfly richness. In the same year however, species richness within the *Nardus* grassland pollinator transect was estimated to be relatively high, especially the species richness of Apidae.

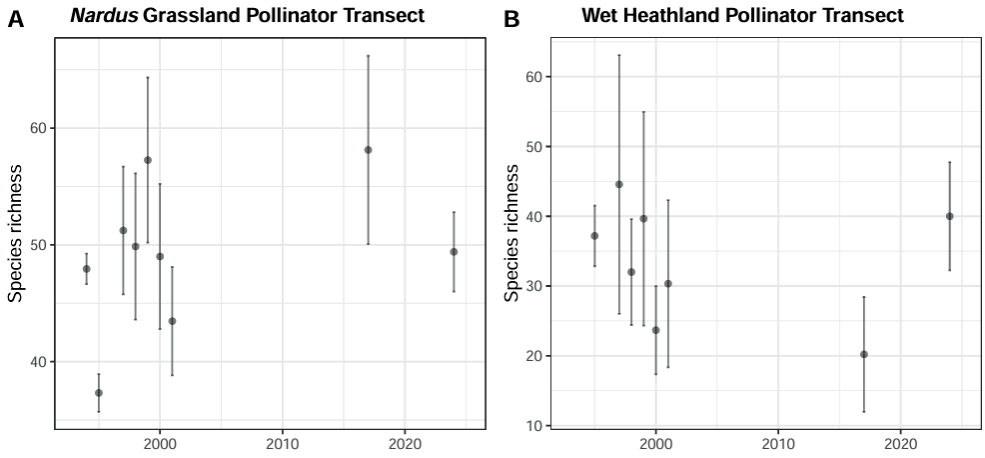


Figure 6.7: Species richness of pollinators in the Nardus grassland pollinator transect (NG) and the wet heathland pollinator transect (WH). Chao-estimates are depicted including standard deviation of NG total pollinator richness (A) and WH total pollinator richness (B)

Butterfly Transect Species Richness Trends

The species richness of butterflies in NG_B generally ranged between an estimated 15-30 species. The estimates fluctuated over the years, but an overall increase in species richness was observed (Figure 6.8). Richness was estimated to be the highest in 2017 (39.75 ± 20.72) and 2023 (33.67 ± 15.16), though both estimates have a large standard deviation. During the peak of butterfly abundance in NG_B between 2010 and 2015 (Figure 6.5A) species richness in NG_B remains very stable.

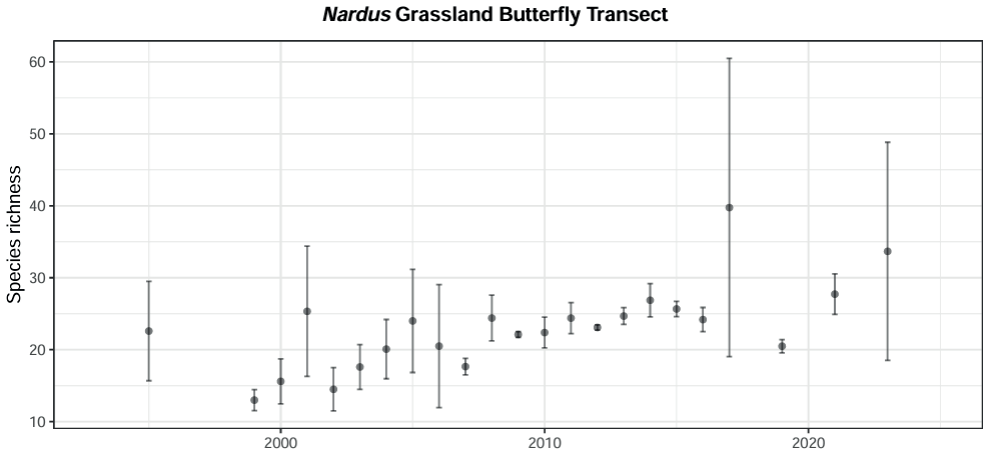


Figure 6.8: Species richness in the *Nardus* grassland butterfly transect (NG_B). Chao-estimates including standard deviation of NG_B butterfly species richness

6.4 DISCUSSION

Pollinators are declining in North-Western Europe (Biesmeijer et al., 2006; Warren et al., 2021; Barendregt et al., 2022), even within natural areas (Hallmann et al., 2017). Interestingly, our study shows that pollinator populations of two typical raised bog habitats within the natural area of Bargerveen remained stable or increased over a thirty-year long period. We argue that this is most likely a result of landscape-level nature management, including the intensive large-scale hydrological interventions in Bargerveen which were previously shown to restore typical bog vegetation (Bijkerk et al., 2015) . The same pattern was observed in selected characteristic species of the studied bog habitats, which depend on specific host plants and open habitat structure (preventing shrub or grass encroachment) that in bog-systems are typically linked to moist conditions (Speelman and Kalkman, 2023). This further suggests that landscape-level management has the potential to support characteristic pollinator species, and to contribute to the long-term conservation of pollinator communities in raised bog systems.

Abundance and Species-Richness

In both the *Nardus* grasslands and the wet heathlands we observed stable to increasing abundance and species richness of pollinators. This finding contrasts with studies describing long-term arthropod biomass and species decline that describe declines even within natural areas. For instance, Hallmann et al. (2017) studied arthropod biomass within German natural areas during the same time period. They described a 75% decline over 25 years. In later work, they scale this to hoverfly species richness decline (Hallmann et al., 2021). The natural areas studied by Hallmann et al. (2017) were often mown or grazed, but were rarely subjected to land-scape level hydrological management. Therefore, even

though management in Bargerveen is not limited to hydrological interventions, we hypothesize that the land-scape level hydrological interventions could explain the differences in pollinator trends.

This hypothesis is further supported by the fact that a lot of species that reside in raised bog systems rely on high water tables and are sensitive to drought (Wallis de Vries et al., 2022). In addition, drought has been identified as a major contributor to butterfly decline both nationally and internationally (Warren et al., 2021; Van Swaay et al., 2022). This sensitivity to drought was also reflected by our results, where the effects of dry years after 2017 (Figure S2) were evident in the butterfly abundance in the *Nardus* grassland pollinator transect, which showed a small but significant decline. In spite of this, the declines in butterfly abundance in our study seem less strong than the nationwide pattern (Van Swaay and Borkent, 2024), suggesting that although hydrological measures were not able to fully compensate for the adverse effects of exceptionally dry years, they were able to buffer them.

Abundance Trends Characteristic Wet Heathland Species

In spite of declines of characteristic bumblebees and butterflies in north-western Europe (Goulson et al., 2008; Warren et al., 2021), and their decline on a national level (Speelman and Kalkman, 2023), no overall decline in abundance was observed in either *P. argus* or *B. humilis*. It has been described that the hydrological interventions in Bargerveen have led to the recovery of characteristic heathland flora (Van Duinen et al., 2013; Bijkerk et al., 2015). Our results illustrate that this vegetation recovery also benefits the vulnerable pollinating species of wet heathland systems, further suggesting that the focus on hydrological management in the Bargerveen area is an important reason for pollinator community conservation.

Nevertheless, population trends of both species did fluctuate throughout the study period. Notably, both *B. humilis* and *P. argus* show particularly low abundance at the beginning of the monitoring period. This may have been a result of habitat disturbances resulting from the infilling of the nearby watershed Noordersloot in 1997, one of the early important hydrological interventions in Bargerveen (van Guldener et al., 2016). As Bargerveen is a relatively large area, it is likely that suitable habitat was available elsewhere in the reserve, and these species survived these local interventions and populations later recovered along the transect. However, this does illustrate that hydrological interventions can have significant adverse effects during implementation that should be considered when dealing with small, isolated and fragile populations.

Another decline in *P. argus* abundance was observed between 2007 and 2014. This may have been a result of encroachment of grasses like *Molinia caerulea* in Bargerveen. The grass reportedly occurred in high abundance during this time at the expense of typical

heathland vegetation like *E. tetralix*, an important host plant (Bijkerk et al., 2015). The increase in *P. argus* abundance after 2014 coincides with the installation of hydrological buffers. Together with the partially stabilized encroachment of *M. caerulea*, these conditions support typical heathland vegetation (Bijkerk et al., 2015). This again suggests that abundance trends are linked to improved hydrological conditions.

Overall, these findings suggest that the stable population trends of the characteristic species *P. argus* and *B. humilis* observed in Bargerveen are a result of continuous management efforts. In addition, these results highlight the need to track population trends over time. Positive effects of management interventions, such as the stable population trends we observed in spite of national declining trends, may only become clear in the longer term.

Abundance Trends Characteristic Nardus Grassland Species

Both *P. malvae* and *L. tityrus* are known to be sensitive to drought (Wallis de Vries and Oteman, 2019). Despite *P. malvae* remaining more abundant than at the start of national monitoring in 1990, the effect of dry years can clearly be seen in recent national abundance trends, with declines in abundance seen after 2017 in both the Netherlands and Belgium (Van Swaay and Borkent, 2024). We found that the *P. malvae* population in Bargerveen experienced no significant decline during this period. This stable population trend of is likely a result of the combined effect of the large population size (Wallis de Vries and Oteman, 2019), high abundance of its host plant tormentil *Potentilla erecta* (Bijkerk et al., 2015), and hydrological interventions, which likely helped mitigate the negative impacts of dry years. Though the *L. tityrus* population in Bargerveen was thought to be stable (van Duinen 2013), our results suggest a recent decline, potentially because of several dry years between 2017 and 2023.

A report by Wallis de Vries and Oteman (2019) provides a possible explanation as to why the effect of the dry years is seen in *L. tityrus*, but not *P. malvae*. They found that *L. tityrus* abundance is primarily driven by high spring precipitation, whereas *P. malvae* primarily depends on high soil moisture, with spring precipitation the year prior actually reducing its abundance. Combined with our results, this suggests that the hydrological management implemented in Bargerveen is effective in maintaining favourable soil hydrological conditions, even during extended periods of unfavourable weather.

Study Limitations and Implications

Our results are in line with our hypothesis that the nature conservation efforts within Bargerveen would aid in sustaining pollinator abundance and richness long-term. They align with short-term studies showing that system-level conservation efforts, e.g. via improving local conditions for vegetation, can lead to pollinator increases (Sexton and Emery, 2020; Larkin and Stanley, 2021; Uhl et al., 2021). Where these studies focus on dry

grassland or forest systems, our results indicate that this positive effect is also seen in raised bog habitats. In addition, most studies on pollinator restoration outcomes focus on short-term effects, whereas our analysis reveals that system-level restoration can have long lasting, stabilising effects for pollinator populations.

Although the benefits of both species-specific and system-level conservation approaches are a long-standing debate in ecology (Harvey et al., 2017; Kremen and Merenlender, 2018), this distinction has received less attention in pollinator conservation, where most measures remain group-focused (e.g., flower strips) (Albrecht et al., 2020; Pérez-Sánchez et al., 2023). Our results contribute to this debate by showing that pollinator communities, including characteristic species, can benefit from restoring system-wide abiotic conditions, particularly over longer time scales. This likely reflects the fact that most pollinators are partial habitat users that rely on a mosaic of resources such as different foraging and nesting sites. While targeted interventions can alleviate specific limitations, more recent work describes that they rarely recreate the full habitat complexity required to support diverse pollinator assemblages (Wood et al., 2015a; Requier and Leonhardt, 2020). In contrast, bottom-up restoration of entire systems appears to support this complexity. Our findings therefore suggest that landscape-level restoration may yield broader benefits for pollinators. Nevertheless, specifically for restoring hydrological conditions, our study provides only an initial indication that rewetting positively affects pollinator communities. Further research linking hydrological data to pollinator trends is needed to confirm this finding, and to better understand the mechanisms through which hydrology influences pollinators, such as through host plant recovery, changes in vegetation structure, or moisture buffering during dry periods.

Our results indicate a positive long-term impact of hydrological interventions. However, nature managers should be aware that such interventions may also lead to an increase in (temporary) disturbances as well as substantial changes within the landscape. Large-scale hydrological interventions may therefore also result in habitat loss in certain locations, with possible adverse effects on characteristic species (Verberk et al., 2010; Van Duinen et al., 2013). For instance, the increased water table of Bargerveen is likely to lead to the disappearance of *Nardus* grasslands in the center of the nature area, a conscious decision which was made to favor the development of active peat-forming raised bog habitats (Bijkerk et al., 2015; van Guldener et al., 2016) . Therefore, in order to preserve the characteristic species which reside in these *Nardus* grasslands, it is important to compensate for local habitat losses by developing and supporting suitable alternative sites elsewhere within the nature reserve.

6.5 CONCLUSIONS

Although declines in pollinator populations have been reported in North-West Europe, even within protected natural areas, we show that pollinator communities in Bargerveen are relatively stable. This suggests that landscape-level conservation efforts, and in this case hydrological buffering specifically, are able to act as a buffer against drivers of insect decline. As we observe positive and improving trends, both at the community and species-level, we conclude that management in Bargerveen is effective in supporting pollinator communities. Though much of the management in Bargerveen is focussed on restoring the natural hydrological regime to promote typical raised bog vegetation, we argue that this also benefits pollinator communities.

6.6 ACKNOWLEDGEMENTS

We are grateful to Klaas van den Berg and Piet Ursem from Staatsbosbeheer for granting access to the sites. A sincere thanks to all the volunteers, especially Jan Rocks, who have collected transect data over the years. We are also grateful to Jos Mensen for sharing his expertise on hydrological data. Thanks go to Marten Geertsma and Lars Willighagen for field assistance. The butterfly transect data used in this study was collected as a part of a larger monitoring scheme, namely the Dutch Butterfly Monitoring Scheme. The Dutch Butterfly Monitoring Scheme is a co-operation between Dutch Butterfly Conservation (De Vlinderstichting) and Statistics Netherlands (CBS), in the context of the Network Ecological Monitoring (NEM), and financed by the Ministry of Agriculture, Nature and Food Quality.



7

Floral rewards cannot explain pollinator preference for a native plant species over its cultivars

Constant Swinkels, Sophie Paquin, Casper van der Kooi, Thimo Peters, Barbara Gravendeel, Hans de Kroon & Nils van Rooijen

Supplementary materials available at: https://constantswinkels.com/121-2/

ABSTRACT

1. The planting of wildflowers is central to pollinator conservation strategies in urban and agricultural landscapes. Widely used seed mixtures often include cultivars, whose value for pollinators remains debated. Although exotic cultivars may provide floral resources and aesthetic value, altered floral architecture may reduce access to rewards. Cultivars of native species represent a special case because they share species identity with wildtype flowers and retain much of their ancestral floral architecture, making them a useful system for studying factors that drive pollinator preferences. Nevertheless, most studies focus on non-native cultivars.

2. Here, we use four varieties of cornflower (*Centaurea cyanus*), the native wildtype and the cultivars Blue Ball, Black Ball, and White Ball, as a model system. Cornflower is frequently included in seed mixtures in north-western Europe, both the wildtype and as cultivar. We examine (1) how the floral units of cultivars differ from the native form in morphological traits, spectral characteristics, and floral rewards; (2) whether pollinators show preferences among varieties in visitation frequency and duration; and (3) whether these responses are consistent across rural and urban settings.

3. In a choice experiment, where pollinators had simultaneous access to all varieties, wildtype flowers received more and longer visits than cultivars. This pattern was consistent across pollinator groups and across rural and urban sites. These differences could not be explained by floral rewards: wildtype flowers provided less pollen and similar nectar sugar content. Although White Ball and Black Ball differed in visible display colour, Blue Ball and the wildtype form did not significantly differ in reflectance patterns. Moreover, small morphological differences did not explain the higher visitation to wildtype flowers compared with Blue Ball.

4. We conclude that pollinators prefer wildtype cornflowers over cultivars, but that differences in commonly used floral signals and floral rewards cannot not explain this pattern. While these hidden cues are to be deciphered, our study demonstrates their effectiveness in pollinator attraction.

7.1 INTRODUCTION

Increasing evidence of widespread pollinator declines (e.g. Biesmeijer et al., 2006; Powney et al., 2019; Hallmann et al., 2021), largely linked to floral resource loss and habitat decline (Potts et al., 2010; Scheper et al., 2014a), has stimulated the implementation of pollinator conservation strategies. The planting of wildflowers is central to many of these initiatives, particularly in anthropogenic landscapes. Overall, such plantings can positively affect pollinator communities (Sexton and Emery, 2020), and human-made habitats like gardens, road verges and dikes are increasingly recognised as valuable conservation areas (e.g. Baldock et al., 2019; Phillips et al., 2020; Timberlake et al., 2024; Swinkels et al., 2025). However, most pollinator species exploit a limited range of plant species and are adapted to specific floral traits (Erickson et al., 2022), making plant species identity a key determinant of conservation success (Warzecha et al., 2018).

Given pollinator resource preferences, the use of exotic cultivars for pollinators remains debated. On the one hand, flowers of exotic cultivars may provide reliable nectar and pollen resources top pollinators while being aesthetically appealing to humans and requiring relatively low maintenance (Garbuzov and Ratnieks, 2015; Erickson et al., 2020). Surveys indicate that many exotic cultivars are visited by pollinators (Salisbury et al., 2025) and that these flowers may even help reduce seasonal resource gaps (Staab et al., 2020; Timberlake et al., 2024). This suggests that pollinators are capable of foraging opportunistically from novel floral resources in anthropogenic habitats.

On the other hand, wild pollinators have co-evolved with native plant species, with morphological and phenological trait matching mediating interaction success (e.g. Fenster et al., 2004; van der Kooi et al., 2021; Adedoja and Mallinger, 2024). Given that many flowers of cultivars differ markedly from native species in morphology, phenology and/or reward presentation, they may provide limited or lower-quality resources for specialist taxa, which comprise a large proportion of pollinator diversity (Garbuzov et al., 2017). In addition, trait mismatches might also affect generalist pollinators that, despite visiting exotic cultivars, might experience less efficient floral reward uptake (Klumpers et al., 2019). Moreover, studies that document pollinator visits to non-native cultivars are frequently assessed in the absence of native wildtype alternatives, making it unclear whether pollinators actively prefer these cultivars when given a choice (Chrobock et al., 2013). Importantly, responses to exotic cultivars may also depend on landscape context. Urban pollinator communities are often dominated by more generalist species compared to rural communities (Buchholz and Egerer, 2020; Ferrari and Polidori, 2022; Silva et al., 2023), yet it remains poorly understood whether responses to exotic cultivars differ between urban and rural settings.

Meanwhile, interspecific comparisons often confound multiple flower trait differences, hence making it challenging to isolate the mechanisms underlying pollinator choice (Vanparys et al., 2008). In this context, cultivars of native plant species provide a particularly informative system to move toward a more mechanistic understanding of pollinator choice. Unlike non-native ones, cultivars of native species retain species identity and much of their ancestral floral architecture, while differing in specific, selectively bred traits such as colour, floral display size or reward accessibility (Hayes et al., 2025b). This allows the effects of individual signalling or reward-related traits to be examined within the same species. Concomitantly, this system is highly relevant as garden cultivars are overrepresented in the market and are widely applied in urban and semi-natural landscapes. If selective plant breeding enhances visual signals without proportionally increasing reward quantity or accessibility for pollinators, this may create a mismatch between signal and reward (van der Kooi et al., 2023), potentially creating ecological traps. Thus, cultivars of native species offer a unique opportunity to disentangle the relative importance of floral signals and rewards in shaping pollinator foraging decisions while maintaining ecological realism.

In this study we use cornflower (*Centaurea cyanus*) as a model system. Once widespread in Dutch arable fields but now endangered in the wild due to agricultural intensification (Beringen, 2025), cornflowers are frequently included in putatively pollinator-friendly seed mixtures (Hicks et al., 2016). In addition to the native wildtype blue form, several horticultural varieties differing markedly in flower colour and morphology are commercially available and widely planted. We compared pollinator visitation among native wildtype cornflower and three cultivars to address three questions: (1) How do cultivars differ from the native wildtype in morphological traits, spectral characteristics, and floral rewards? (2) Do pollinators exhibit preferences, both in visitation frequency and time, among these varieties? (3) Are pollinator responses consistent across rural and urban settings?

7.2 MATERIALS AND METHODS

Research Species

Cornflower (*Centaurea cyanus* L.; Asteraceae) is an annual herbaceous plant species native to southeastern Europe and long established in the Netherlands. Wildtype individuals are characterized by bright blue capitula (henceforth floral units) consisting of a central cluster of fertile disc florets surrounded by several larger sterile ray florets (Figure 7.1). Cultivars of cornflower commonly sold in garden centres often exhibit increased numbers of sterile ray flowers and altered colours. In ornamental plants, such double-flower phenotypes frequently arise from reduced function of C-class MADS-box genes (AGAMOUS-like genes), which specify stamen and carpel identity; loss of this function converts reproductive organs into petaloid structures and can reduce floral resource production (Schilling

et al., 2018). In this study, we used the widely commercially available cultivars 'Black Ball', 'Blue Ball', and 'White Ball' (Figure 7.1). Seeds for native cornflower were purchased from native plant breeder Cruydt-Hoeck as "Korenbloem - *Centaurea cyanus*". Seeds of the cultivars were obtained from Vreeken's Zaden as "Black Ball", "Blue Boy / Blue Ball", and "Tom Pouce White".

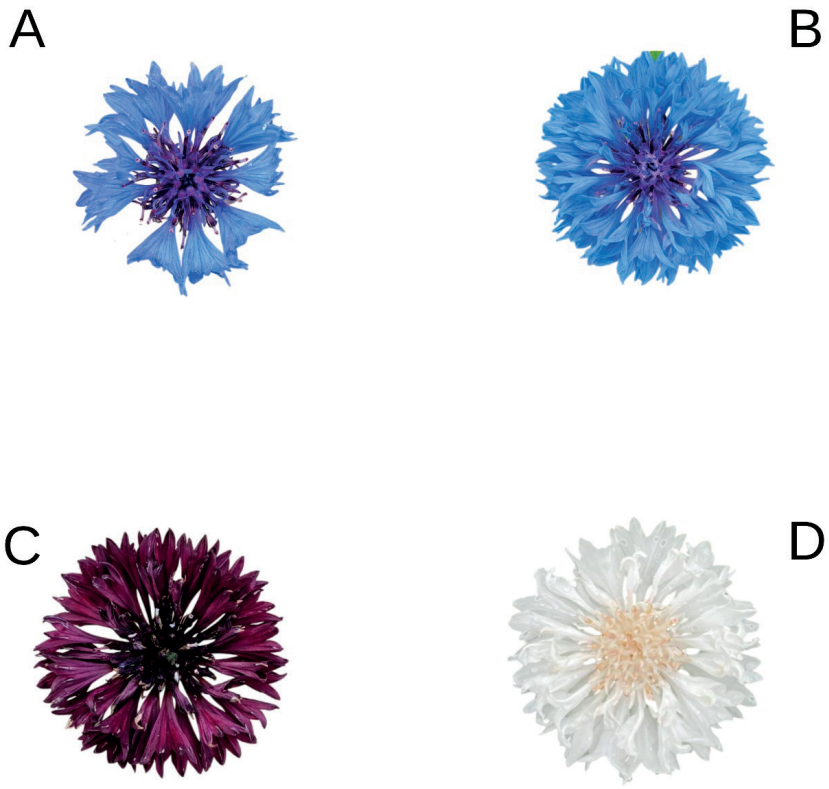


Figure 7.1: Native wildtype cornflower (*Centaurea cyanus,*A) and three different cultivars of cornflower ('Blue ball' (B), 'Black ball' (C) and 'White ball' (D)) analyzed in this study. Photographs made by Sophie Paquin.

Seed Germination and Plant Growth

Seeds of each variety were germinated in Petri dishes in a climate chamber (12 h light at 25°C; 12 h dark at 10°C) for one week. Dishes were prepared with two layers of tap water moistened 90-mm filter paper, and seeds were evenly spaced in a 50-square grid. Petri dishes were sealed with parafilm.

After germination, seedlings were transferred to trays containing potting soil and maintained under greenhouse conditions for 12 days. Individuals with developed true leaves and seminal roots were subsequently transplanted into larger pots containing a

1:1 mixture of potting soil and sand to ensure well-drained conditions. Two individuals of the same variety were planted per pot to facilitate transport during the field experiment (methods 2.4). The pots were placed on plastic saucers and kept in an exterior polytunnel (ambient temperature) to acclimatize plants prior to field deployment. The plants were watered with rain water from below, with the pots placed on saucers filled with water. A random selection of these plants was transferred to the field for the visitation experiment early on (methods 2.4), other plants remained in these conditions until flowering.

Morphology

At peak flowering, inflorescence morphological traits were measured on 15 floral units that were opened for two days (to prevent age differences from influencing results) from randomly selected plants, with each floral unit belonging to a different individual plant within each variety. The traits were selected based on their relevance for floral signalling and resource acquisition by pollinators. Floral unit diameter was measured as a proxy for floral display size, as larger floral displays are generally more conspicuous and tend to receive higher pollinator visitation rates (Conner and Rush, 1996). Assuming circular shape, floral area was calculated as $A = \pi r^2$. We counted the number of fertile disc flowers and sterile ray flowers, representing rewarding and non-rewarding floral structures, respectively. For fertile disc flowers, we measured the corolla tube (bell) diameter, corolla tube depth and the total flower length with digital calipers. In cornflowers, nectar is produced at the base of the flower and flows into the corolla tube, where it is collected by pollinators. The corolla tube length has been identified as an important regulator of resource access by pollinators (Klumpers et al., 2019). Finally, we recorded the number of floral units per plant during the field experiment.

Floral Reward

To quantify nectar and pollen availability, 25 newly opened floral units per variety were selected and enclosed in fine-mesh exclusion bags for 24 h to prevent pollinator visitation (following e.g. (Baude et al., 2016; Hicks et al., 2016). Of these floral units, 15 were used for nectar measurements and 10 for pollen quantification. For all sampled floral units, the number of fertile disc flowers per floral unit were recorded to allow scaling to floral unit level.

Nectar was collected from two open fertile disc florets per floral unit using 0.5 µL glass microcapillary tubes. Capillaries remained in place until nectar accumulation ceased, and nectar volume was estimated by measuring the length of the nectar column and converting this value to µL. Sucrose concentration (% Brix) was determined using handheld refractometers (Bellingham + Stanley™, model 45-81 (range of 0-50 °Brix) and model 45-82 (range of 45-80 °Brix)). Sugar availability per flower was calculated by multiplying the nectar quantity with the sucrose percentage and extrapolated to the floral unit level

by multiplying per-flower values by the number of open fertile disc florets. No nectar was detected from sterile ray florets.

For pollen measurements, floral units were collected, ray florets were removed and fertile florets were placed in test tubes. Fertile florets were agitated to dislodge ripe pollen grains, suspended in buffer solution, filtered through a 100 µm sieve, and an aliquot was mounted on a microscope slide. High-resolution images were obtained using LAS X software and pollen grains were quantified using ImageJ.

Spectral Measurements and Vision Modelling

To assess colour differences among four cornflower varieties, floral units from nine different plants were randomly chosen for spectral analysis. Reflectance spectra were obtained using a bifurcated probe (measurement diameter about 1 mm; for details see (Ausma et al., 2021). Absorbance spectra of florets immersed in water were obtained with a microspectrophotometer (measurement diameter 10 mm; for details, see l measurements were performed on the inner surface of the ray florets. Reflectance patterns are given in appendix 1.

To interpret the differences in colour with a "bee-subjective view", we analysed the reflectance spectra using the hexagon vision model (Chittka, 1992). The hexagon model, an established vision model for bees (Kelber et al., 2003; Kemp et al., 2015), yields a measure for perceived colour contrast of a flower to a (green) background, which corresponds to visual conspicuousness of the flower to bees (van der Kooi and Spaethe, 2025). We used the standard D65 as illuminant, honeybee spectral sensitivity (Peitsch et al., 1992) and an average green spectrum as background. Achromatic contrast, an intensity-based contrast that is more relevant for (long-range) detection, was calculated as the absolute difference in excitation of the green photoreceptor between the stimulus and background (Giurfa et al., 1995; Spaethe et al., 2001; van der Kooi and Kelber, 2022).

Pollinator Visitations

To study the visitation patterns of pollinators to the different cornflower varieties, we conducted a field experiment. We selected eight sites equally divided over both urban and rural areas in Nijmegen (NL) and its surroundings (Appendix 2). At each location, vegetation was cleared from four 1.5 m x 1.5 m plots, spaced 0.5 m apart. This layout follows the concept of a "cafeteria experiment", enabling the observation of foraging decisions by providing multiple floral resource options to wild pollinator assemblages. In each plot, 12 plants of a cornflower variety were planted alongside four rows of wheat to provide better stability to the cornflowers while mimicking traditional growing conditions of cornflowers. Plot configuration was random at each site, to make sure that visitations are linked to floral traits rather than plot placement.

Weekly surveys were conducted between May 31, 2024, and July 10, 2024. During each survey, all floral unit visitations by pollinators (i.e., pollinators trying to collect nectar and pollen by dipping their head or scopa in the flower) to each cornflower variety were recorded for 60 minutes. Surveys were conducted on days on sunny days with absence of strong winds and rain, and at temperatures exceeding 15°C. The surveys took place during daytime between 9:00 and 17:00. Surveys with insufficient observations or shorter than 20 minutes (in rare cases surveys were cut short) were excluded from the data. Visiting insects were classified at the group level (bumblebee, honey bee, wild bee, hoverfly, muscoid fly, butterfly, dagger fly, beetle, and wasp). The number of available floral units for each cornflower variety was noted during each survey.

For bumblebees and honeybees, the most abundant groups in our dataset, we collected additional data on the duration of their visits to floral units of each variety. These data were collected directly after each regular survey was finished, and comprised of following one individual and timing the duration of their foraging visits.

Statistical Analyses

All analyses were conducted in R v4.5.2 (R Core Team, 2025b). Model choice was based on the distribution and structure of the response variables, as described below. Post-hoc comparisons were performed using the *emmeans* package (Lenth et al., 2025).

Floral Display and Reward Analysis

To assess differences in morphological traits, floral rewards, and spectral measurements among cornflower varieties, we fitted linear models for all normally distributed response variables, with cornflower variety included as a fixed effect. Response variables included floral unit diameter, the number of fertile and sterile flowers per floral unit, flower bell depth and diameter, total flower length, nectar volume, total sugar availability, both spectral measures (colour contrast and achromatic contrast). As each measurement was obtained from a different plant and no hierarchical or repeated-measures structure was present in the data, models included only cornflower variety as a fixed effect. Pairwise differences between varieties were assessed using Tukey-adjusted comparisons of estimated marginal means.

Several response variables deviated from normality and were analysed using generalized linear models. Sucrose proportions (continuous values between 0 and 1) were modelled using a beta distribution with a logit link function (Douma and Weedon, 2019). Proportions of fertile disc flowers relative to sterile ray flowers were derived from count data and analysed using a quasi-binomial distribution to account for overdispersion (Warton and Hui, 2011). Nectar volume was measured from two individual flowers per floral unit. To account for the nested structure of these data, floral unit identity was included as a random effect in a linear mixed-effects model. The number of floral units available to pollinators

during the field experiments was recorded across multiple days and locations. To account for temporal and spatial variation, day and location were included as random effects in a linear mixed-effects model.

Pollinator Visitations Analysis

Visitation counts were analysed using generalized linear mixed-effects models fitted with the glmer function in the *lme4* package (Bates et al., 2015) with a Poisson distribution. Cornflower variety was included as a fixed effect. Survey time was incorporated as a log-transformed offset to account for differences in observation effort. A second model additionally included a log-transformed offset for floral unit availability per species. The base model therefore estimates total visitation at the plant level, whereas the floral unit–corrected model estimates visitation rates per floral unit. Site identity was included as a random effect to account for potential spatial clustering. Pairwise differences between cornflower varieties were assessed using Tukey-adjusted comparisons of estimated marginal means derived from the fitted models using the emmeans package. Model assumptions were evaluated using simulated residual diagnostics in the DHARMa package (Hartig, 2022). No significant overdispersion was detected (base model: dispersion = 1.28, $p = 0.38$; floral unit–corrected model: dispersion = 1.87, $p = 0.18$). To test whether wildtype and ornamental cornflowers experienced different visitation rates across rural and urban landscapes, we added an interaction between cornflower type and landscape setting (urban or rural) to both models.

Floral unit visitation times were analysed using a similar approach. As visitation times were recorded by following individual pollinators, individual identity was included as a random effect. Because individual identity was fully confounded with sampling date, inclusion of date as an additional random effect resulted in non-convergent models and was therefore not retained. Simulated residual diagnostics in DHARMa indicated slight overdispersion (dispersion = 2.17, $p = 0.064$). To account for this, models were also fitted using a negative binomial distribution, which produced qualitatively similar results. Because the Poisson assumption was not formally violated, results presented in the main text are based on the Poisson model.

Analyses were repeated separately for subsets of the visitation data corresponding to the most common pollinator groups: bumblebees, honeybees, non-Bombus wild bees, and syrphid flies (for visitation counts) and bumblebees and honeybees (for visitation times).

7.3 RESULTS

Morphology

Floral unit diameter differed significantly among varieties (ANOVA: $F_{3,56} = 10.18$, $p < 0.001$; Figure 7.2A). White Ball flowers (mean 4.4 cm) had a larger diameter than Native (3.6 cm), Blue Ball (3.8 cm), and Black Ball flowers (4.0 cm) (Tukey post hoc tests). Calculating floral unit area from diameter did not change these results (Appendix 3A). The ray flowers of White Ball were also slightly, but not significantly, longer than those of the other varieties and native cornflowers (Appendix 3B).

Wildtype cornflowers had significantly more flowering floral units per plot during the field experiment than any of the cultivars ($P < 0.001$ for all pairwise comparisons, Figure 7.2B). On average, wildtype cornflowers had 29.48 flowering floral units per plot, compared to 17.81, 14.02 and 18.29 for Black Ball, Blue Ball and White Ball, respectively.

The number of sterile ray flowers differed significantly among cornflower varieties (ANOVA: $F_{3,93} = 68.87$, $p < 0.001$; Figure 7.2C), with wildtype cornflowers displaying roughly three times fewer ray flowers than the cultivars (Native: 8.9; Black Ball: 29.6; Blue Ball: 25.8; White Ball: 28.2). No significant differences were detected among the three garden varieties (Tukey post hoc tests). In contrast, the number of fertile disc flowers varied only slightly among varieties (ANOVA: $F_{3,96} = 2.88$, $p = 0.04$; Figure 7.2D), driven by a significant difference between Black Ball and White Ball (Tukey post hoc test, $p = 0.04$). Consequently, wildtype cornflowers exhibited a significantly higher ratio of fertile disc flowers to sterile ray flowers compared with the cultivars (Appendix 3C).

Both disc flower length and bell length differed significantly among varieties (ANOVA: disc flower length: $F_{3,116} = 7.57$, $p < 0.001$; bell length: $F_{3,116} = 17.40$, $p < 0.001$; Figure 7.2E-F). These differences were primarily driven by the White Ball cultivar, which had longer disc flowers and bells than the other varieties, while Black Ball also exhibited a longer bell length. Bell diameter did not differ among varieties (ANOVA: $F_{3,116} = 7.57$, $p = 0.18$, Appendix 3D).

Floral Reward

Despite some small but significant differences between the nectar quantity per individual flower of wildtype and varieties (Appendix 4B), we found no significant differences in sugar availability per flower nor per floral unit between wildtype and cultivars of cornflower (Figure 7.3A, C). Similarly, average sucrose concentration did not differ among varieties (Appendix 4A).

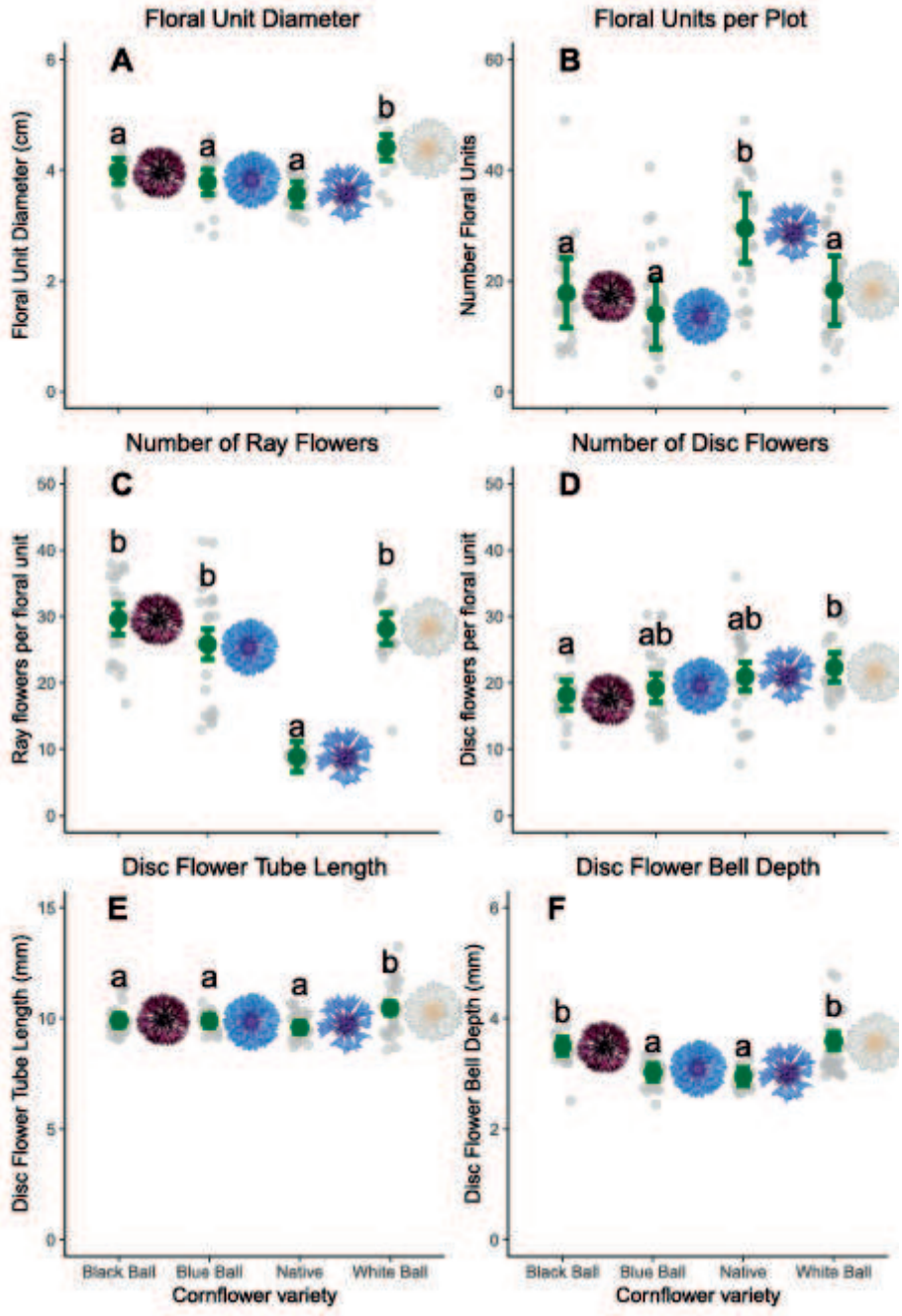


Figure 7.2: Differences among four cornflower varieties in (A) floral unit diameter, (B) the number of floral units in experimental plots, (C) the number of sterile ray flowers per floral unit, (D) the number fertile disc flowers per floral unit, (E) disc flower tube length and (F) disc flower bell depth. Green points represent mean values and error bars indicate 95% confidence intervals. Different letters denote statistically significant differences among varieties (post hoc Tukey pairwise comparisons).

In contrast, pollen availability did differ among varieties. Black Ball had the highest pollen counts per flower (356.4) and per floral unit (6828.5). White Ball did not differ significantly from any other variety, with 239.4 pollen per flower and 5521.5 per floral unit. Blue Ball had fewer pollen per flower (205.9) but not per floral unit (3769.5), while the native variant had the lowest pollen counts per flower (124.5) and per floral unit (3129.0) (Figure 7.3B, D).

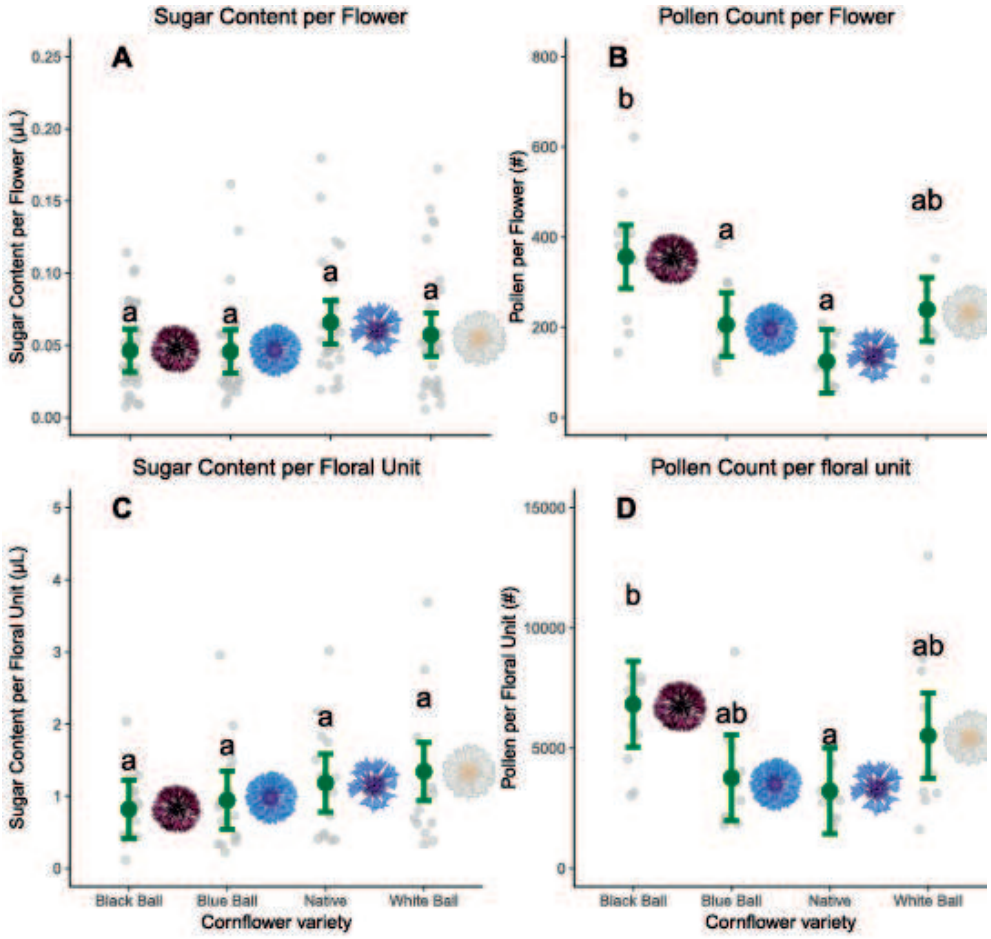


Figure 7.3: Differences among four cornflower varieties in (A) sugar content per flower (µl), (B) the number of available pollen per flower, (C) the sugar content per floral unit (µl) and (D) the number of available pollen per floral unit. Green points represent mean values and error bars indicate 95% confidence intervals. Different letters denote statistically significant differences among varieties (post hoc Tukey pairwise comparisons).

Visual modelling

When modelling visual contrasts to a green background through a "bee-subjective view", both the 'Black Ball' and 'White Ball' cultivars differed markedly from the 'Blue Ball' cultivar and wildtype flowers (that did not differ from each other). Colour contrast, which is

particularly relevant for short-distance discrimination of flowers to a green background, was similar between Blue Ball and wildtype flowers but differed significantly for White Ball and Black Ball ($P < 0.001$, Figure 7.4A). Achromatic contrast, important for long-range detection of flowers, was significantly higher in White Ball compared to the other two cultivars and wildtype ($P < 0.001$, Figure 7.5B). Despite these clear inter-cultivar differences in visual contrast, all calculated values exceed detection thresholds.

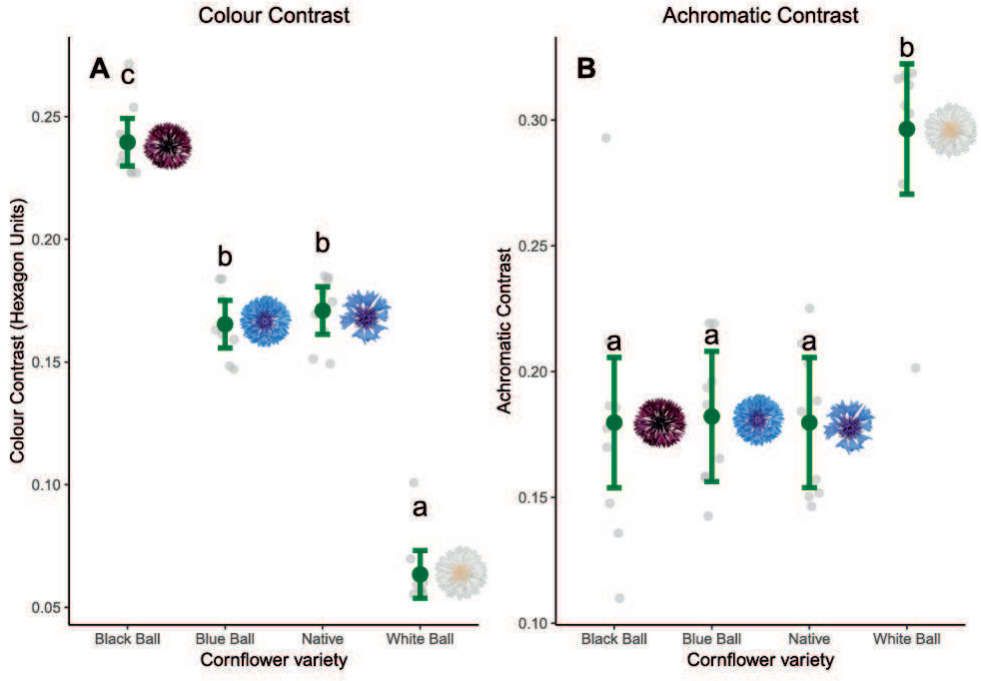


Figure 7.4: Colour contrast (A) and Achromatic contrast (B) of among four cornflower varieties. Green points indicate mean values, and error bars represent 95% confidence intervals. Different letters denote statistically significant differences among varieties based on post hoc Tukey pairwise comparisons.

Pollinator Visitation Patterns

For the field experiment, we completed 34 visits across all sites between May 31 and July 10, 2024 during which we observed 2,376 visitation events. Honeybee (920) and bumblebee (570) visits were most common, followed by syrphid flies (521) and non-Bombus wild bees (208) (for the full list, see Appendix 5). In addition, we collected 373 visitation times, of which 223 were collected from honeybee visits and 142 visits from bumblebee visits.

Wildtype cornflowers received more frequent and longer pollinator visits than cultivars (Figure 7.5). Visitation frequency was substantially higher at wildtype cornflowers both when considering the absolute number of visits per plot (Figure 7.5A, $P < 0.001$),

averaging 35.6 visits per plot compared to a maximum of 11.4 for the cultivars, and when correcting for the number of available floral units (Figure 7.5B, $P < 0.001$), with wildtypes receiving on average 24.1 visits compared to at most 13.5 for the cultivars. Cornflower variety explained a substantial proportion of the variation in visitation frequency, accounting for approximately 55% of the variation in the models (marginal $R^2 = 0.54$ and 0.56, respectively). Differences in baseline visitation rates among plots explained additional variation, resulting in conditional R^2 values of 0.94 and 0.89. Pollinators also spent more time foraging on wildtype cornflowers: visits lasted on average 15 seconds compared to less than 10 seconds for the cultivars (Figure 7.5C, $P < 0.001$). These patterns were largely consistent across urban and rural settings. In both landscapes, wildtype cornflowers received the highest and similar numbers of visits (Appendix 6). However, White Ball received significantly fewer visits in urban sites, both in terms of absolute visits per plot ($P < 0.05$) and when corrected for floral unit availability ($P < 0.001$). Similarly, Blue Ball received fewer visits per plot in urban settings ($P < 0.05$). Patterns in visitation frequency were also consistent across the most common pollinator groups (bumblebees, honeybees, non-Bombus wild bees and syrphid flies; Appendix 7), as were patterns in visitation duration for bumblebees and honeybees (Appendix 8). Notably, hoverflies visited the White Ball, Blue Ball and wildtypes equally when correcting for floral unit availability.

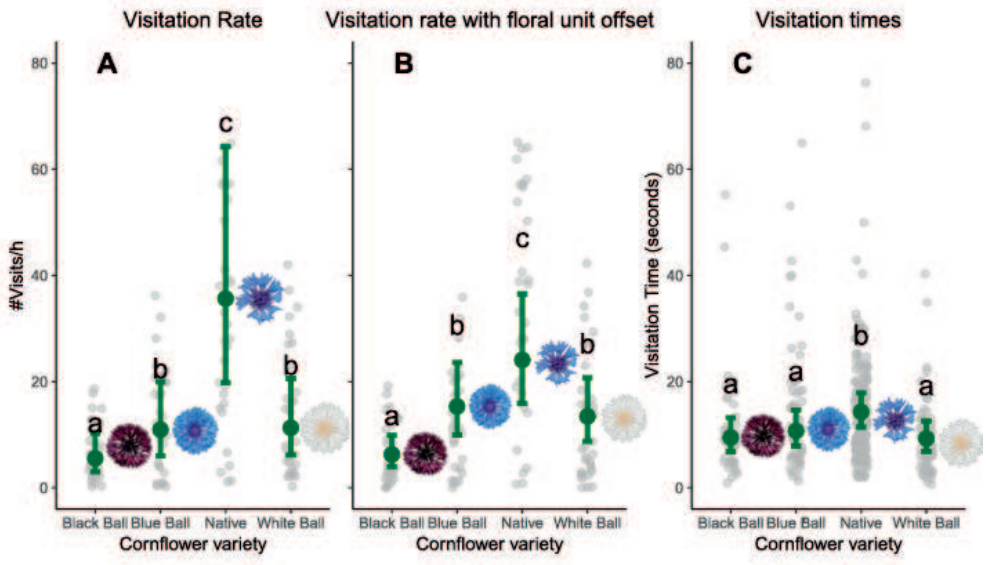


Figure 7.5: Pollinator visitations per hour to four cornflower varieties from (A) a model including a correction for the number of available floral units, (B) a model on only the total number of observations. (C) Gives the average visitation time to floral units for the four different cornflower varieties. Green points represent mean values and error bars indicate 95% confidence intervals. Different letters denote statistically significant differences among varieties (post hoc Tukey pairwise comparisons).

7.4 DISCUSSION

Whether or not pollinators prefer native wildtype flowers over cultivars is an ongoing debate. Our results show that, when given the choice, pollinators prefer wildtype cornflower over its cultivars, and that this pattern is consistent across rural and urban landscapes and among different pollinator groups. We here discuss these findings in the light of factors driving pollinator visitation decisions.

Visitation Patterns

We found that pollinators, when given the choice, preferred foraging on wildtype cornflowers over cultivars. At the plot level, wildtype received more than three times as many visits as the most visited cultivar. When correcting for the number of available floral units during each survey, wildtype floral units still received nearly twice as many visits. These findings appear to contrast with a number of studies reporting that cultivars can be actively visited by pollinators (e.g. Erickson et al., 2021, 2022b; Salisbury et al., 2025). However, many of these studies do not assess visitation when pollinators are given a direct choice between cultivars and native wildtype plants. In studies where such direct comparisons are made, they found that pollinators prefer native wildtypes over exotic cultivars (e.g. Chrobock et al., 2013; Hayes et al., 2025a). This is consistent with our study and shows the importance of choice experiments when assessing the value of ornamentals for pollinators.

In addition to receiving more visits, floral units of wildtype cornflowers were also visited for longer periods. Increased handling time has previously been associated with trait mismatches that reduce foraging efficiency (Klumpers et al., 2019). In our experiment, however, only small and mostly non-significant differences were observed in the bell and tube length of fertile disc flowers among varieties. The differences that were present (primarily deeper disc flowers in White Ball) were modest and do not match the magnitude of the differences observed in visitation times. We therefore suggest that the longer visitation times at native wildtype cornflowers reflect increased foraging effort (Jones et al., 1998), rather than morphological mismatch. Pollinators may exploit multiple disc flowers within a single cornflower floral unit, increasing the time spent per visit. Consequently, faster movement between flowers is unlikely to explain the observed differences in visitation frequency in our study.

Interestingly, these patterns were largely consistent across habitat types and pollinator groups. Urban environments are often reported to host pollinator communities dominated by generalist species quency (Buchholz and Egerer, 2020; Ferrari and Polidori, 2022; Silva et al., 2023) that can forage opportunistically on ornamentals (Erickson et al., 2020). Contrary to this expectation, both generalist honeybees and bumblebees that are known to forage on cultivars (Aslan et al., 2016; Valido et al., 2019a; Urbanowicz et al., 2020)

showed a clear preference for wildtype cornflowers, and these received similar visitation frequencies in both urban and rural settings. Hoverflies were the only group that did not show a strong preference for either wildtype cornflowers or cultivars at the floral unit level.

Floral Rewards

We did not observe differences in nectar sugar availability at either the flower or floral unit level between wildtype cornflowers and the cultivars. This result is noteworthy, as it is sometimes thought that selection for sterile ray flowers in cultivars of cornflowers is associated with reduced nectar availability (e.g. Verbeek et al., 2021). In addition, wildtype cornflowers generally provided more pollen than the cultivars. Floral rewards are commonly considered an important predictor of pollinator visitation (e.g. Makino and Sakai, 2007; Lun et al., 2025), and floral resource availability is therefore often used as an indicator of the value of ornamental flowers for pollinators (Rivière et al., 2022; Tew et al., 2023). However, our results do not support this expectation. Although cultivars in our study provided equal or even greater rewards than the wildtype flowers, pollinators still preferred the wildtypes.

Flower Morphology and Visual Models

Morphological traits of flowers can have important effects on pollinator visitation frequency (Fornoff et al., 2017; van der Kooi et al., 2023). However, morphological differences between cornflower varieties in our experiment were small. The most notable difference was the significantly higher number of sterile ray flowers in the cultivars, while the number of fertile disc flowers did not differ among varieties. Although the increased number of ray flowers could potentially make floral units of cultivars more visually conspicuous to pollinators (e.g. Makino and Sakai, 2007; Delgado et al., 2023), the observed visitation patterns do not support this explanation. Alternatively, the resulting lower ratio of rewarding to non-rewarding flowers might reduce foraging efficiency at cultivars. We were unable to quantify how often pollinators attempted to collect resources from sterile ray flowers, but such behaviour was not observed frequently. Moreover, pollinators are often well equipped to detect unrewarding flowers, making this explanation less likely.

Visual models simulating a bee-subjective view (*Apis mellifera*, D65 illuminant, average green leaf background) differed markedly between White Ball and Black Ball cultivars compared to Blue Ball and wildtype cornflowers. This was true for both colour contrast, that reflects how visible flowers are to pollinators against a green background, and for achromatic contrast, that show how visible flowers are from far away. Differences in detectability of flowers can strongly influence pollinator visitations, and as such this could explain why the 'White Ball' and 'Black Ball' cultivars are less visited than the blue wildtype cornflowers (Fornoff et al., 2017; van der Kooi et al., 2023). In contrast, 'Blue Ball' and wildtype cornflowers displayed very similar bee-perceived colours, yet visitation frequency

differed substantially, indicating that factors beyond colour, such as subtle morphological traits or other unmeasured cues, likely drive pollinator preference.

Future Directions

Although we observed some differences in floral traits, these do not explain the clear preference for wildtype cornflowers over cultivars. As such, our results suggest that commonly measured floral traits, such as floral rewards or morphology, may not fully explain pollinator visitation patterns. This emphasises the need for further research into the cues that pollinators use when making foraging decisions. One possible explanation is variation in floral volatile compounds, which we did not measure in this study but which have been shown in other systems to influence pollinator attraction (Raguso, 2004). Future work comparing the scent profiles of wildtype and cultivars of cornflowers could therefore help clarify the mechanisms underlying the observed visitation patterns.

Another potential factor is pesticide exposure. In contrast to native seeds, many seeds of garden varieties are not sourced from organic producers, as was the case in our study. This raises the possibility that seeds may have been treated with pesticide coatings, which could leave residues in plant tissues (Tarano et al., 2025) and potentially influence pollinator behaviour. Although pollinator populations are known to be affected by pesticide use (Guzman et al., 2024), to our knowledge no cafeteria experiments have tested whether pollinators can distinguish between flowers grown from pesticide-coated seeds and those grown from organic seeds.

7.5 CONCLUSIONS

Our results show that, when given the choice, pollinators prefer wildtype cornflower over its cultivars, visiting wildtype flowers substantially more often both at the plot level and after correcting for the number of available floral units. This pattern was consistent across rural and urban landscapes and among different pollinator groups. Differences in key floral signals and rewards only partially explained the observed visitation patterns, indicating that commonly measured floral traits alone may not fully predict the value of flowers for pollinators. Further research is needed to better understand the mechanisms underlying pollinator foraging choices.



8

Evaluating the importance of flowers for pollinators (Synthesis)

8.1 INTRODUCTION

Pollinators are a diverse group of organisms, which in north-western Europe consist mainly of flower-visiting insects. They are essential to ecosystem functioning, for example through the pollination of over three-quarters of all plant species (Ollerton et al., 2011). In addition, they provide valuable ecosystem services through crop pollination (Gallai et al., 2009). Because these services are enhanced by high pollinator abundance and diversity (Garibaldi et al., 2013; Lundgren et al., 2016; Rader et al., 2016; Artamendi et al., 2024), the growing body of evidence documenting pollinator declines is alarming (Potts et al., 2010; Goulson et al., 2015; Powney et al., 2019).

These declines are often linked to loss of suitable habitat and floral resource availability (Biesmeijer et al., 2006; Scheper et al., 2014; Cousins et al., 2015). Consequently, most pollinator conservation initiatives focus on the increase of floral resource availability (e.g. Ouvrard et al., 2018; Geppert et al., 2020). In general, such management interventions have positive effects on pollinator abundance and diversity (Haaland et al., 2011; Sexton and Emery, 2020; Kral-O'Brien et al., 2021). Nevertheless, in some cases studies did not find significant relationships between flower richness and pollinator abundance and species richness (Wood et al., 2015; Uyttenbroeck et al., 2017). Other studies emphasize the importance of landscape setting (Scheper et al., 2013, 2015), alternative (non-floral) resource requirements such as nesting sites (Requier and Leonhardt, 2020) and constraints resulting from anthropogenic pressures such as pesticide use (Guzman et al., 2024). Consequently, floral resource availability may not always be the primary limiting factor at local scales (Sponsler et al., 2023).

In this context, the general aim of this thesis was to evaluate the responses of pollinator communities to floral resources in light of resource limitation. It provides insights into the potential relief of flower limitation by studying pollinator communities along gradients of flower richness (chapter 2 – 4) and links these patterns to nature management by assessing the outcomes of field experiments (chapter 5 – 7). This synthesis first discusses the value of dike grasslands, the focal system in this thesis, for pollinators. It then proceeds to discuss the main findings in relation to the potential saturation of floral resources. Finally, it discusses the topic of pollinator management in linear landscape elements and gives an outlook on future research avenues.

8.2 BENCHMARKING DIKE GRASSLANDS AS VALUABLE POLLINATOR HABITAT

Although the conservation value of linear landscape elements (LLEs) for pollinators is evident (Villemey et al., 2018; Phillips et al., 2019, 2020), there is currently no comprehen-

sive overview of bee communities on dike grasslands. **Chapter 2** presents a large-scale analysis of dike grassland bee communities from 157 locations along the lower branches of the Meuse and Rhine rivers in the Netherlands. It showed that dike grasslands harbour high richness of wild bee species (154 observed, 199 estimated) and abundance (10,503 individuals observed). Noteworthy is the high share of red-listed bees (37 species, 942 individuals), species that are threatened in the Netherlands and hence are of conservation interest. These numbers are high compared to those reported from other studies on LLEs such as flower strips and hedgerows. These often report fewer species (e.g. Holzschuh et al., 2008; Le Féon et al., 2013; Borchardt et al., 2023), a lower proportion of non-*Bombus* wild bee species (e.g. Scheper et al., 2015; 80.0%, chapter 2: 43.2%) and fewer red-listed species and individuals (e.g. Scheper et al., 2015; Wood et al., 2015; 13 and 114 individuals respectively, chapter 2 942 individuals) despite broadly comparable sampling efforts. Although comparisons between studies should be interpreted with caution, this reveals that dike grasslands line up as habitat of special conservation interest for wild bees.

Further analysis of these communities revealed that, in addition to generalist bumblebees, dike grasslands typically harbour a high proportion of ground-nesting species (e.g. of the genera *Andrena, Halictus* and *Lasioglossum*) and their associated kleptoparasites (*Nomada* and *Sphecodes*). Species richness and bee abundance peaked in spring, coinciding with the known peak activity periods of these genera (especially *Andrena* and *Nomada*, Peeters et al., 2012). Similarly, red-listed species were predominantly active early in the season, with 883 out of the total 942 observations occurring before the 1st of June.

This pattern overlaps with temporal dynamics of floral resource availability, which peaks in May on dike grasslands, typically followed by mowing in mid-June (Liebrand, 1999). **Chapter 4** showed that at flower-rich locations during this period, nearly 100% of the pollen carried by pollinators was collected from flower species growing on the local dike grasslands. This illustrates the importance of flower-rich dike grasslands as foraging habitat. In addition, findings supported the notion that dikes also function as nesting habitat for bees. The high abundance of ground-nesting bees, including species specialised on willows (*Salix* sp.) that do not grow on dikes, together with the abundance of their associated kleptoparasites (that would not occur without stable breeding colonies) are indications that bees make their nests on dikes. Furthermore, the warm, south-facing dike slopes are likely to favour ground-breeding species early in the season, when they warm faster than the surrounding habitats. The combined functioning as both foraging and nesting location could explain why dike grasslands can harbour rich communities even in otherwise agricultural landscapes, as observed in **chapters 2 and 3**, and explain the high conservation value of flower-rich dike grasslands even in agricultural settings.

8.3 FLORAL RESOURCE LIMITATION

In 1840, Justus von Liebig proposed that plant growth is constrained by the resource in shortest supply relative to demand. Although originally developed in context of plant production in agriculture, Liebig's law of the minimum states can be broadly applied to other organisms and systems (de Baar, 1994). As current pollinator conservation primarily focuses on creating flower-rich habitats, it is possible that other resources, such as nesting sites, become limiting. If floral resource limitation can be effectively alleviated, this raises the question whether further increases in flower-rich habitat are worthwhile. Although pollinators are generally considered to be limited by floral resources (Roulston and Goodell, 2011), results from conservation initiatives suggest that this is not always the case (Scheper et al., 2015; Wood et al., 2015; Requier and Leonhardt, 2020). The key question therefore becomes when and to what extent floral resources limit pollinator populations (Sponsler et al., 2023).

8.3.1 Saturating bee abundance and species richness

A first step in addressing this proposition is to examine pollinator abundance and species richness along gradients of flower abundance and species richness (Ebeling et al., 2008). Studying populations along ecological gradients provides a valuable approach to detect potential saturating responses, and to relate these patterns to specific ecological factors (Whittaker, 1967; Begon et al., 2006). A saturating response of pollinator richness and abundance to floral resource availability as such may indicate that resource limitation is gradually alleviated at higher resource levels, reflecting a shift in potential limiting factor (Tilman, 1982).

Accordingly, **Chapter 2** showed that both bee abundance and species richness increased with flower species richness but saturated, irrespective of surrounding landscape context. This saturation occurred at a remarkably low flower species richness, with breakpoint analysis identifying significant change in the relationship at approximately nine flower species (within $25m^2$ vegetation surveys that represent total dike vegetation) for both wild bee abundance and species richness. Building on this, **Chapter 3** further examined changes in bee community composition using a subset of the data presented in **Chapter 2**, and revealed similar saturating patterns when floral unit abundance and vegetation-level nectar sugar production are considered. Together, these chapters thus suggest that floral resource limitation can be alleviated at flower-rich locations for a large part of the pollinator community.

Although overall community richness and abundance saturate with increasing resource availability, resource limitation may still persist for specific groups and species (Sponsler et al., 2023). Such limitations could occur due to species-specific resource preferences (e.g. specialist species that depend on specific flowers), life-history traits and foraging

ecology. **Chapters 2 and 3** explored this by distinguishing between bumblebees, non-*Bombus* wild bees and vulnerable, red-listed species (according to the Dutch Red List for bees; Reemer, 2018). Bumblebees are opportunistic foragers that live in colonies, which grow with increasing resource availability and concentrate foraging efforts to resource-rich patches (Goulson et al., 2008). In contrast, most non-*Bombus* wild bees, particularly red-listed species, are more specialised in their nesting locations and resource preferences, and are often limited by the specific pollen required for larval development rather than overall flower and nectar availability (Roulston and Goodell, 2011).

This divide revealed clear differences in responses to increase in floral resource availability. Compared to the overall community pattern, non-*Bombus* wild bee abundance and species richness saturated more strongly, suggesting they are more susceptible to other limiting factors, such as nesting availability (Requier and Leonhardt, 2020). In contrast, bumblebees showed no clear saturation (breakpoint analysis did not detect significant breakpoints in the relationship). This suggests that their foraging effort (and potentially colony growth) remains strongly linked to resource availability, even when resources are abundant. Finally, contrasting both patterns, red-listed species occurrence increased most at the highest levels of floral resource availability (Figure 8.1).

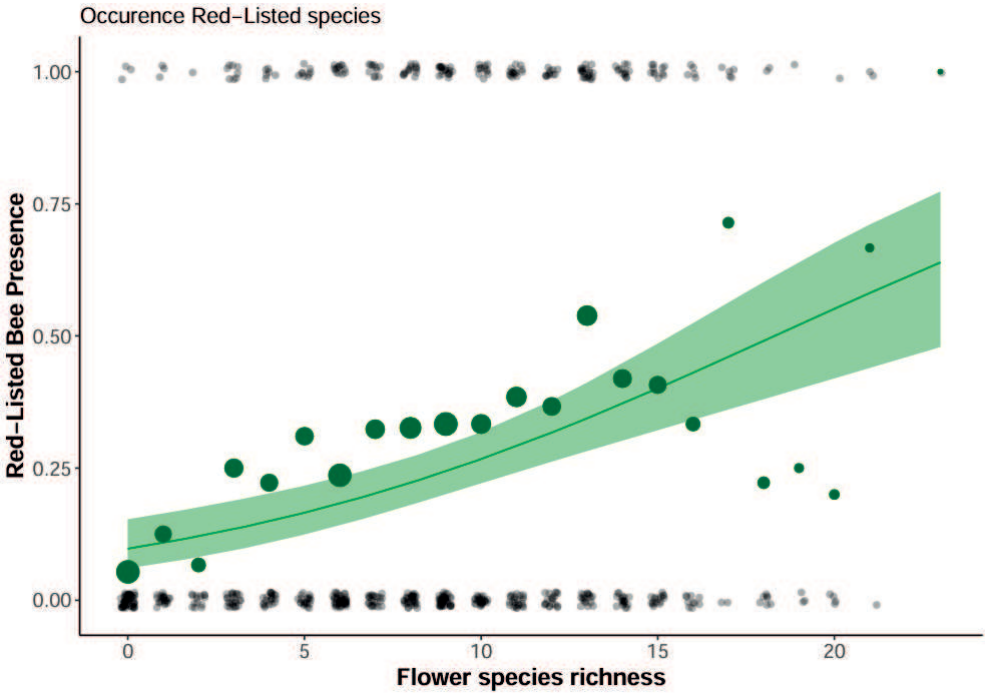


Figure 8.1: Occurrence of Red-Listed bees along a flower species richness gradient. The green line shows model predictions, the light green area the 95% confidence interval. Green points give the average presence per flower richness level, while size is scaled to the number of observations in that level. Raw data points are shown in black.

While I here link the observed saturating patterns to the alleviation of resource limitation, it is worth noting that saturation can also occur for other reasons. Pollinator species richness could, for instance, also saturate if regional species pools are limited, even under general resource-limiting conditions (Zobel, 1997). In such a case, increased niche space would not attract more species simply because there are no candidates in the regional species pool to occupy it. However, under these conditions, local populations should still be able to expand into available niche space, increasing their abundance (Tilman, 1982). **Chapters 2 and 3** revealed that both overall bee species richness and abundance saturate around the same point, suggesting increased niche space is also not occupied by the (generalist) species present. Moreover, when examining bumblebees and non-*Bombus* bumblebees separately, we find that bumblebee abundance does not saturate whereas other wild bees saturate strongly. This pattern suggests that, at least for the latter group, floral resource limitation is alleviated and something else is constraining their populations.

8.3.2 Resource specialisation and reduced niche overlap

While pollinator abundance and species richness saturate with increasing flower richness (**chapters 2 and 3**), community-wide and species-specific foraging patterns may still change with increased resource availability. Such changes are important because they reflect the mechanisms structuring pollinator communities (Okuyama and Holland, 2008; Thébault and Fontaine, 2010; Rohr et al., 2014; Landi et al., 2018). For example, the ability of generalist pollinators to adjust their collection patterns to avoid resource use overlap has frequently been linked to pollinator community coexistence and stability, and for instance promote the presence of specialist foragers (Valdovinos et al., 2013, 2016; Ponisio et al., 2019; Valdovinos and Marsland, 2021;). Increasing floral resource availability may therefore promote greater specialisation and reduced resource use overlap among pollinators, even beyond the point at which abundance and species richness saturate. However, empirical field studies examining such dynamics remain scarce.

In **chapter 4**, multi-species genotyping-by-sequencing (msGBS; Wagemaker et al., 2021)) was used to analyse pollen carried by pollinators across a gradient from flower-poor to flower-rich locations. Pollen composition revealed three key relationships along this gradient. First, increases in flower species richness and floral unit abundance led to a strong increase in the proportion of pollen collected from locally available plant species (up to nearly 100%), suggesting that increased resource availability facilitates more localised foraging. Second, pollinator species included fewer plant species in their diet with increasing local flower species richness and abundance, indicating greater diet specialisation. Finally, resource use overlap between pollinator species decreased with increasing flower species richness, indicating reduced niche overlap among co-occurring species.

Interestingly, these relationships (except for local foraging when approaching 100%) did not saturate with increasing floral resource availability. This suggests that even beyond the point at which pollinator abundance and species richness level off, increasing floral resources change foraging behaviour, promoting specialisation and reduced resource-use overlap. These patterns are likely driven by an expansion of available niche space with increasing resources. Importantly, flower species richness and abundance contribute to this process in different ways. Flower species richness enables pollinators to reduce niche overlap with other species (Fründ et al., 2010a; Fornoff et al., 2017), while floral unit abundance expands intraspecific niche space which facilitates more selective use of a particular flower species (Vázquez et al., 2009; Fort et al., 2016). Although the studied sites did not include conditions with exclusively high floral unit abundance or high flower species richness, the results from Chapter 4 are consistent with this hypothesis. While both variables correlated with increased specialisation, only flower species richness decreased floral resource use overlap. This could also explain why red-listed species, that are often specialist foragers, have a higher chance of occurring at the most flower-rich locations (**chapter 2**).

In addition, these patterns are likely to increase pollinator population and community stability. Foraging over large distances has been linked to population declines (Peterson and Roitberg, 2006; Williams and Kremen, 2007). As such, more localised foraging may promote population stability, particularly when bees can nest near or between floral resources (likely in our context; chapter 2 and 8.2). Meanwhile, greater dietary specialisation combined with reduced resource use overlap is central to theories on pollinator coexistence, which predict that such dynamics enhance community stability (Valdovinos et al., 2013, 2016).

8.3.3 Saturating communities but stable interactions

Taken together, **Chapters 2 – 4** indicate that floral resource limitation for community-level abundance and species richness may be alleviated, while additional increases in flower richness beyond this threshold allow pollinators to forage more selectively, decreasing interspecific resource use overlap (Figure 8.2). As reduced resource use overlap has been connected to increased community stability and ecosystem functioning (Brosi, 2016), this suggests that even when bee community abundance and species richness saturate, additional floral resources may increase their stability. Meanwhile, these structural changes could benefit rarer species, consistent with the observation that red-listed species occurrence peaked at the flower-rich end of the gradient. Increased resource niche space (more floral resources and/or more flower species) could allow generalist pollinators to adjust foraging efforts to unexploited resources, creating space for specialised pollinators (Valdovinos et al., 2013, 2016). The observation that resource overlap and diet breadth decreased with increasing resource availability supports this hypothesis.

These overall findings further inform the debate surrounding the potential contrast between managing for ecosystem services versus broader biodiversity conservation. Studies suggest that pollination services to crops rely on few, common pollinator species that can often be restored relatively quickly, whereas promoting total bee diversity is more challenging and requires targeted interventions (Kleijn et al., 2015; Senapathi et al., 2015a). Consistent with this proposition, **chapters 2 – 4** showed that overall pollinator abundance and species richness could indeed be promoted with relatively modest effort, while red-listed species occurrence continues to increase far beyond this point. This can be explained as additional resource increase facilitated more selective foraging, which benefits red-listed species that are often specialised on specific flowers (Reemer, 2018). In addition, more specialised foraging and decreased resource use overlap has been linked to pollinator community stability. As such, additional conservation efforts might not only promote rarer species, but also increase species persistence within communities. This is particularly important in anthropogenic habitats and under climate change, where disturbances are more frequent (Foley et al., 2005, Oliver et al., 2015).

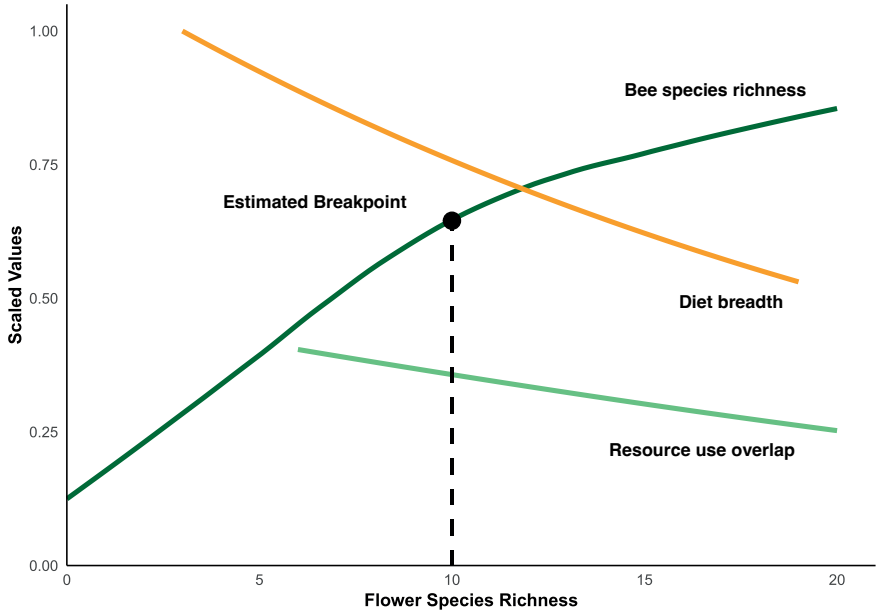


Figure 8.2: Results from **chapter 2** (figure 2.4D) and **chapter 4** (figure 4.2A and 4.3A) on the relationships between flower species richness and bee species richness (dark green), diet breadth (orange), and resource use overlap (light green). Predicted values for bee species richness and diet breadth were scaled by dividing model predictions by their respective maximum predicted values to allow direct comparison of the shapes of all relationships within a single figure. Resource use overlap was proportional data between 0 – 1 and as such did not need to be scaled. The black point indicates the estimated breakpoint (by breakpoint analysis) at which bee species richness begins to saturate.

8.4 LIMITATIONS IN POLLINATOR MANAGEMENT

In the second part of this dissertation (**chapter 5 – 7**), three case studies investigated different pollinator management interventions. While section 8.5 will discuss their broader implications for pollinator management in linear landscape elements, here I focus on how the lessons from these interventions deepen the insights revealed in the first half of the thesis.

8.4.1 Partial mowing

Chapter 5 explored the effects of partial mowing on flower-rich dike grasslands on pollinator communities. Such mowing management regimes are increasingly used in conservation management because they provide year-round vegetation for arthropods (Révész et al., 2025). Beyond management implications, they provide a useful experimental system to examine how pollinator communities respond to resource limitation, as unmown refuges can concentrate pollinators and potentially increase competition for remaining resources (Lebeau et al., 2015). Indeed, **chapter 5** showed that pollinator visitation frequency (+85%) and abundance (+25%) increased significantly in unmown refuges the first four days after mowing, both compared to the situation before mowing and unmown controls in the same period. After these initial increases, we observed strong declines in visitation frequency, pollinator abundance and species richness in unmown refuges, which were not observed in unmown controls. Notably, decreases were not equally divided over pollinator taxa, with especially honeybees maintaining their populations while non-*Bombus* wild bee populations decreased.

Increased visitation frequency has been proposed as a proxy for elevated competition for floral resources (Forster et al., 2023). As such, findings from **chapter 5** are consistent with the notion that floral resource limitation, through competition for resources, can limit pollinator communities. This idea is further supported as specifically honeybees, that are known to be strong competitors, persisted while non-*Bombus* wild bees declined (Henry and Rodet, 2018; Valido et al., 2019). Meanwhile, it shows that smaller refuges, even under flower-rich conditions, cannot substitute the total vegetation. This contrasts the saturating pollinator abundance and species richness relationships observed in **chapters 2 and 3**, that suggest a surplus of floral resources under flower-rich conditions which could limited impact of partial habitat loss.

8.4.2 Niche space

In niche theory, niche space refers to the range of resources and environmental conditions that a species can use (Hutchinson, 1957). While section 8.3 primarily addressed alleviation of floral resource limitation at the community level, resource limitation might still persist at the species level when suitable niche space for a particular species is restricted (Sponsler et al., 2023). Although **Chapter 7** focused on differences in pollinator

visitation between wild-type and cultivated cornflower, it also provides insight into how niche space influences pollinators. Wild-type cornflowers received higher pollinator visitation compared to cultivars, suggesting that they provide a broader or more suitable resource niche for the pollinator community. As such, this example illustrates that not all floral resources contribute equally to pollinator communities (Ghazoul, 2006; Warzecha et al., 2018; Filipiak, 2019; Losapio et al., 2019). Consequently, the selection of plant species in pollinator conservation measures should consider not only the quantity of floral resources, but also their suitability for specific (groups of) pollinator species.

8.4.3 An ecosystem approach

Chapter 6 provided a different perspective on pollinator conservation. Rather than following pollinator responses to interventions that increase local floral resources, it assessed pollinator populations over 30 years from the Bargerveen, a bog reserve in the north-east of the Netherlands, in response to rewetting management. Despite substantial changes in water tables and vegetation across the area during the study period, pollinator communities along the transects remained stable and characteristic species persisted. Although this ecosystem differs strongly from dikes, these findings do suggest that restoring ecosystem processes and landscape integrity, rather than focusing solely on floral resources, can conserve pollinators while simultaneously supporting broader ecosystem functioning and biodiversity (Kaiser-Bunbury et al., 2017).

Such thinking might also be relevant to dike grasslands. Both **chapters 4 and 5** showed that pollinators can forage beyond the local habitat, especially when local conditions are unfavourable. Although management of dike grasslands primarily focusses on creating flower-rich vegetation at the local scale (**chapter 2**), landscape scale restoration could provide refuges for pollinators when local conditions (temporarily) deteriorate. In addition, heterogenous landscapes will harbour higher species diversity (Parreño et al., 2024) and provide resources more steadily through the year (Olliff-Yang and Ackerly, 2020). Consequently, landscape-level management may reduce the need of high-intensity local interventions while still safeguarding pollinator communities.

8.5 A VIEW ON NATURE MANAGEMENT IN LINEAR LANDSCAPE ELEMENTS

As many ecological processes operate at large scales and many species move freely across habitat boundaries, promoting biodiversity in narrow linear landscape elements presents an inherent challenge (Phillips et al., 2020). Managing these systems is akin to walking a tightrope, balancing local interventions in a broader landscape setting. Likewise, the limited area available presents managers with many trade-offs. Nevertheless, this thesis highlights the considerable potential of LLEs (section 8.2) to support diverse and abun-

dant pollinator communities. Although much has been published on LLE management, both in the scientific literature and local reports, combined findings from this thesis add to two considerations particularly applicable to pollinator conservation, as discussed below.

8.5.1 Consistent management

Recovery of ecosystem functioning and species community assembly takes place over long time periods (Moreno-Mateos et al., 2020). Recent work by Hirayama et al. (2025), for example, shows that recovery of plant-pollinator interaction networks and associated pollination functions can take more than 75 years, and recommends maintaining similar grassland management, including mowing, over similar time scales. Victor Westhoff expressed a comparable idea. He famously stated "everywhere something else, but (locally) always the same", emphasizing that landscape-scale heterogeneity combined with local management consistency promotes overall biodiversity and community stability (Schaminée and Stortelder, 2006).

On the most flower-rich dike grasslands studied in this thesis, management has remained unchanged for decades. **Chapter 2** showed that these grasslands harbour species-rich bee communities, including many characteristic and red-listed species. Phenological patterns also revealed that these communities appear well adapted to mowing regimes, with many species completing their life cycle before the first mowing event. The vegetation itself reflects this pattern, being dominated by plant species that flower in May, distinguishing these grasslands from many surrounding habitats.

This dissertation therefore shows that well-developed habitats with long-term, consistent management have high conservation value. As such, changes to management at these sites should be made with caution. However, many nature managers are currently switching to partial mowing regimes, in which sections of vegetation are left unmown to promote year-round habitat availability. While such approaches can benefit a range of arthropod groups (Révész et al., 2025), they can also alter the temporal availability of floral resources (Lebeau et al., 2015). **Chapter 5** showed that, for pollinators, this may increase competition for floral resources during peak flowering periods and, at least in the short term, lead to declines in species characteristic of dike grassland communities. Together, these findings suggest that while partial mowing regimes may benefit some arthropod groups by providing year-round vegetation, management consistency remains a key factor in maintaining high-value pollinator communities that through time adapt to management regimes. Changes in management should therefore be implemented with caution.

8.5.2 Improving local conditions

While the previous section highlights the importance of maintaining consistent management where high-value communities already exist, many linear landscape elements remain comparatively species-poor (Swinkels et al., 2020). **Chapter 2** showed that dike grasslands have high potential for pollinators, indicating that restoring these flower-poor grasslands can effectively promote pollinators. In addition, these grasslands provide opportunities to apply Victor Westhoff's principle of "something else" at the landscape scale. They are not yet characterised by long-term, consistent management, and hence could be used to introduce alternative management regimes, such as different mowing practices (e.g. delayed or partial mowing) or grazing regimes, that ultimately increase habitat heterogeneity across the landscape.

While vegetation would ideally recover through spontaneous succession at these locations, such recovery is not always feasible. Sites could, for instance, be isolated in species-poor landscapes, strongly restricting natural establishment of diverse species communities. Even when source populations are nearby, recovery can take a long time (Ozinga, 2008). Given ongoing pollinator declines, actively introducing wildflower species through seeding may therefore be necessary to accelerate habitat development and provide resources in the short term.

However, the choice of plant species is critical. Results from **Chapter 7** showed that wild-type plant varieties are consistently more attractive to pollinators than cultivated varieties. In addition, other work indicates that even plant provenance can significantly influence pollinator visitation, with locally adapted genotypes often performing better than non-local ones (Bucharova et al., 2021). Together, these findings suggest that restoration efforts should prioritise the use of regional, wild-type plant material. Approaches such as hay transfer from nearby species-rich grasslands are particularly promising, as they introduce a diverse assemblage of locally adapted species while maintaining ecological integrity.

8.6 FUTURE RESEARCH AVENUES

While every thesis answers but a few questions, it inevitably raises many more. This dissertation is no exception. As many emerging questions have already been addressed within individual chapters, I here focus on two urgent knowledge gaps.

8.6.1 Spatio-temporal dynamics

While this thesis primarily focussed on local factors influencing bee communities and their interactions, these communities are influenced by the surrounding landscape (e.g. Kennedy et al., 2013; Scheper et al., 2013, 2015; Hass et al., 2018; Larkin and Stanley,

2021). However, while numerous studies explore how landscape level factors correlate with local community composition, empirical studies that directly quantify pollinator movement and landscape use remain comparatively limited. Yet, such dynamics are fundamental to understanding pollinator coexistence and resource use. This is illustrated by **chapter 4**, that showed that pollinators forage beyond local vegetation to decrease resource use overlap with other pollinators. Similarly, **chapter 5** demonstrated that changing management resulted in partial abandonment of remaining vegetation. Together, this illustrates that pollinators redistribute into the surrounding landscape when local conditions become unfavourable, highlighting the importance of alternative suitable habitats (Lexmond et al., 2026). A heterogeneous patchwork of suitable pollinator habitat could therefore enhance community resilience, with patches functioning as refuge when others (temporarily) become unsuitable.

In addition to these spatial dynamics, pollinators might also use different habitats through time. **Chapter 2** showed that dike grasslands support particularly species-rich pollinator communities in early spring, suggesting that these habitats are especially important during this period. In contrast, surrounding habitats such as floodplains reach peak flowering later in the season. This temporal complementarity suggests that different habitats may fulfil distinct roles throughout the year (Olliff-Yang and Ackerly, 2020), collectively supporting pollinator communities over time (Ammann et al., 2024). Understanding how such spatio-temporal habitat mosaics facilitate pollinator coexistence therefore remains an important challenge for landscape-scale conservation.

8.6.2 Pollination and plant community dynamics

Although this thesis, like most existing literature, has focussed on how vegetation facilitates pollinator coexistence, pollinators can in turn influence plant community dynamics (e.g. Brosi, 2016; Loy and Brosi, 2022; Pan et al., 2024). Such feedbacks are central to theoretical work on mutualistic networks and species coexistence (Vázquez et al., 2009; Rohr et al., 2014; Valdovinos, 2019). However, empirical evidence linking pollinator community structure to plant community dynamics in natural systems remains limited, despite its relevance in light of pollinator declines and changes in pollinator community composition.

For instance, saturating pollinator abundance and species richness, such as observed in **chapter 2 and 3,** could reduce pollinator visitation per flower, potentially decreasing pollination success for some plant species (Fantinato et al., 2021). Meanwhile, pollinator communities are changing under climate change (Hofmann et al., 2018). For example, data from this thesis reveal that 'southern species', such as *Halictus scabiosae* and *H. quadricinctus*, increased strongly on dikes over the study period, while typical species, such as *Andrena flavipes*, decreased strongly likely due to summer drought (data from **chapter 2**). Because more mobile pollinator communities might react faster than plant communities, such turnover may alter plant–pollinator interactions (Zoller et al., 2023; Trunschke et

al., 2024). Given that pollinator species differ in their foraging preferences and pollination efficiency, pollinator species turnover could impact pollination success of different plant species. This makes climate-driven changes in pollinator communities a potentially important pathway through which climate change influences plant community composition. While such processes are generally challenging to study 'in the field', space-for-time substitutions offer a promising approach to approximate the effect of climate change on pollinator communities (but see Evans et al., 2025). Potential substitutions include south-facing slopes, that generally experience increased warming effect (Bakker et al., 2024), as well as latitudinal gradients. Molecular methods (such as msGBS in **chapter 4**) and emerging AI-based applications (e.g. automated camera systems for species identification (Hogeweg et al., 2019)) can then be used to efficiently quantify insect visitation across flower species. These data can subsequently be related to plant reproductive outcomes, such as seed production and germination success, and/or population dynamics from permanent quadrants.

LITERATURE

Adedoja, O.A., Mallinger, R.E., 2024. Can trait matching inform the design of pollinator-friendly urban green spaces? A review and synthesis of the literature. Ecosphere 15, 1–17. https://doi.org/10.1002/ecs2.4734

Adema, E., Molenaar, W., Krap, S., Stroo, A., 2017. PAS-Gebiedsanalyse Natura 2000-gebied Bargerveen.

Albrecht, M., Kleijn, D., Williams, N., Laidlaw, H.H.Jr., Tschumi, M., Blaauw, B., Campbell, A., Dainese, M., Entling, M., Ganser, D., De Groot, A., Goulson, D., Grab, H., Hamilton, H., Herzog, F., Isaacs, R., Jacot, K., Jonsson, M., Knop, E., Kremen, C., Landis, D., Loeb, G., Marini, L., Mckerchar, M., Morandin, L., Pfister, S., Potts, S., Rundlof, M., Sardiñas, H., Sciligo, A., Thies, C., Tscharntke, T., Venturini, E., Veromann, E., Vollhardt, I., Wackers, F., Ward, K., Wilby, A., Woltz, M., Wratten, S., Sutter, L., 2020. Global synthesis of the effectiveness of flower strips and hedgerows on pest control, pollination services and crop yield. Ecol. Lett. 6–82. https://doi.org/10.1111/ele.13576

Altschul, S.F., Gish, W., Miller, W., Myers, E.W., Lipman, D.J., 1990. Basic Local Alignment Search Tool. J. Mol. Biol. 215, 403–410. https://doi.org/https://doi.org/10.1016/S0022-2836(05)80360-2

Ammann, L., Bosem-Baillod, A., Herzog, F., Frey, D., Entling, M.H., Albrecht, M., 2024. Spatio-temporal complementarity of floral resources sustains wild bee pollinators in agricultural landscapes. Agric. Ecosyst. Environ. 359, 1–11. https://doi.org/10.1016/j.agee.2023.108754

Antoine, C.M., Forrest, J.R.K., 2021. Nesting habitat of ground-nesting bees: a review. Ecol. Entomol. 46, 143–159. https://doi.org/10.1111/een.12986

Artamendi, M., Martin, P.A., Bartomeus, I., Magrach, A., 2024. Loss of pollinator diversity consistently reduces reproductive success for wild and cultivated plants. Nat. Ecol. Evol. 9. https://doi.org/10.1038/s41559-024-02595-2

Aslan, C.E., Liang, C.T., Galindo, B., Hill, K., Topete, W., 2016. The Role of Honey Bees as Pollinators in Natural Areas. Natural Areas Journal 36, 478–488. https://doi.org/10.3375/043.036.0413

Ausma, T., Bansal, V., Kraaij, M., Verloop, A.C.M., Gasperl, A., Müller, M., Kopriva, S., De Kok, L.J., van der Kooi, C.J., 2021. Floral displays suffer from sulphur deprivation. Environ. Exp. Bot. 192, 104656. https://doi.org/10.1016/j.envexpbot.2021.104656

Baldock, K.C.R., Goddard, M.A., Hicks, D.M., Kunin, W.E., Mitschunas, N., Morse, H., Osgathorpe, L.M., Potts, S.G., Robertson, K.M., Scott, A. V., Staniczenko, P.P.A., Stone, G.N., Vaughan, I.P., Memmott, J., 2019. A systems approach reveals urban pollinator hotspots and conservation opportunities. Nat. Ecol. Evol. 3, 363–373. https://doi.org/10.1038/s41559-018-0769-y

Baldock, K.C.R., Goddard, M.A., Hicks, D.M., Kunin, W.E., Mitschunas, N., Osgathorpe, L.M., Potts, S.G., Robertson, K.M., Scott, A. V., Stone, G.N., Vaughan, I.P., Memmott, J., 2015. Where Is the UK's Pollinator Biodiversity? The Importance of Urban Areas for Flower-Visiting Insects. Proceedings of the Royal Society B: Biological Sciences 282, 149–172. https://doi.org/10.1201/9781315366098-17

Barberis, M., Bogo, G., Bortolotti, L., Flaminio, S., Giordano, E., Nepi, M., Galloni, M., 2023. Floral nectar and insect flower handling time change over the flowering season: Results from an exploratory study. Acta Oecologica 120, 103937. https://doi.org/10.1016/j.actao.2023.103937

Barendregt, A., Zeegers, T., van Steenis, W., Jongejans, E., 2022. Forest hoverfly community collapse: Abundance and species richness drop over four decades. Insect Conserv. Divers. 15, 510–521. https://doi.org/10.1111/icad.12577

Bascompte, J., Jordano, P., Melián, C.J., Olesen, J.M., 2003. The nested assembly of plant-animal mutualistic networks. Proceedings of the National Academy of Sciences USA 100, 9383–9387. https://doi.org/10.1073/pnas.1633576100

Bates, D., Mächler, M., Bolker, B.M., Walker, S.C., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67. https://doi.org/10.18637/jss.v067.i01

Bátori, Z., Körmöczi, L., Zalatnai, M., Erdős, L., Ódor, P., Tölgyesi, C., Margóczi, K., Torma, A., Gallé, R., Cseh, V., Török, P., 2016. River Dikes in Agricultural Landscapes: The Importance of Secondary Habitats in Maintaining Landscape-Scale Diversity. Wetlands 36, 251–264. https://doi.org/10.1007/s13157-016-0734-y

Baude, M., Kunin, W.E., Boatman, N.D., Conyers, S., Davies, N., Gillespie, M.A.K., Morton, R.D., Smart, S.M., Memmott, J., 2016. Historical nectar assessment reveals the fall and rise of floral resources in Britain. Nature 530, 85–88. https://doi.org/10.1038/nature16532

Begon, Michael., Townsend, C.R.., Harper, J.L.., 2006. Ecology: from individuals to ecosystems. Blackwell Publishing.

Bell, K.L., Fowler, J., Burgess, K.S., Dobbs, E.K., Gruenewald, D., Lawley, B., Morozumi, C., Brosi, B.J., 2017. Applying Pollen DNA Metabarcoding to the Study of Plant–Pollinator Interactions. Appl. Plant Sci. 5, 1600124. https://doi.org/10.3732/apps.1600124

Bell, K.L., Turo, K.J., Lowe, A., Nota, K., Keller, A., Encinas-Viso, F., Parducci, L., Richardson, R.T., Leggett, R.M., Brosi, B.J., Burgess, K.S., Suyama, Y., de Vere, N., 2022. Plants, pollinators and their interactions under global ecological change: The role of pollen DNA metabarcoding. Mol. Ecol. 1–18. https://doi.org/10.1111/mec.16689

Berendse, F., van Ruijven, J., Jongejans, E., Keesstra, S., 2015. Loss of plant species diversity reduces soil erosion resistance. Ecosystems 18, 881–888. https://doi.org/10.1007/s10021-015-9869-6

Berger, J.L., Staab, M., Hartlieb, M., Simons, N.K., Wells, K., Gossner, M.M., Vogt, J., Achury, R., Seibold, S., Hemp, A., Weisser, W.W., Blüthgen, N., 2024. The day after mowing: Time and type of mowing influence grassland arthropods. Ecological Applications 1–16. https://doi.org/10.1002/eap.3022

Bergholz, K., Sittel, L.P., Ristow, M., Jeltsch, F., Weiss, L., 2022. Pollinator guilds respond contrastingly at different scales to landscape parameters of land-use intensity. Ecol. Evol. 12, 1–11. https://doi.org/10.1002/ece3.8708

Beringen, R., 2025. Veranderingen in de akkerflora op de zandgronden. Florabalans 3, 12–13.

Biella, P., Akter, A., Ollerton, J., Tarrant, S., Janeček, Š., Jersáková, J., Klecka, J., 2019. Experimental loss of generalist plants reveals alterations in plant-pollinator interactions and a constrained flexibility of foraging. Sci. Rep. 9, 1–13. https://doi.org/10.1038/s41598-019-43553-4

Biella, P., Borghesan, S., Colombo, B., Galimberti, A., Guzzetti, L., Maggioni, D., Pioltelli, E., Ramazzotti, F., Ranalli, R., Tommasi, N., Labra, M., 2025. Lawn management promoting tall herbs, flowering species and urban park attributes enhance insect biodiversity in urban green areas. Urban For. Urban Green. 104, 128650. https://doi.org/10.1016/j.ufug.2024.128650

Biella, P., Klecka, J., Akter, A., Ollerton, J., Nielsen, A., 2020. An empirical attack tolerance test alters the structure and species richness of plant–pollinator networks. Funct. Ecol. 00, 1–13. https://doi.org/10.1111/1365-2435.13642

Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J., Kunin, W.E., 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science (1979). 313, 351–354. https://doi.org/10.1126/science.1127863

Bijkerk, W., Bakker, R., Adema, E.B., 2015. Vegetatie-en plantensoortenkartering Bergerveen 2014. Feanwalden.

Bishop, G.A., Fijen, T.P.M., Raemakers, I., van Kats, R.J.M., Kleijn, D., 2024. Bees go up, flowers go down: Increased resource limitation from late spring to summer in agricultural landscapes. Journal of Applied Ecology 61, 431–441. https://doi.org/10.1111/1365-2664.14576

Blüthgen, N., Klein, A.M., 2011. Functional complementarity and specialisation: The role of biodiversity in plant-pollinator interactions. Basic Appl. Ecol. 12, 282–291. https://doi.org/10.1016/j.baae.2010.11.001

Bochniak, A., Kulik, M., Jaźwa, M., Sender, J., Ścibior, R., 2024. Evaluation of the mowing frequency effect on floristic diversity of seminatural meadows using generalized diversity indices. Ecol. Indic. 159. https://doi.org/10.1016/j.ecolind.2024.111719

Borchardt, K.E., Kadelka, C., Schulte, L.A., Toth, A.L., 2023. An ecological networks approach reveals restored native vegetation benefits wild bees in agroecosystems. Biol. Conserv. 287, 110300. https://doi.org/10.1016/j.biocon.2023.110300

Bouma, K., Villalva Aguilar, P., Haugum, S.V., Madsen, B., Treier, U.A., Normand, S., Rahbek, C., Heilmann-Clausen, J., 2025. What evidence exists for the impact of restoration of natural processes on biodiversity in temperate ecosystems: a systematic map protocol. Environ. Evid. 14. https://doi.org/10.1186/s13750-025-00373-6

Breheny, P., Burchett, W., 2017. Visualization of Regression Models Using visreg. R J. 9, 56. https://doi.org/10.32614/RJ-2017-046

Brooks, M.E., Kristensen, K., Benthem, K.J., van, Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Mächler, M., Bolker, B.M., 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. R J. 9, 378–400. https://doi.org/10.32614/RJ-2017-066

Brosi, B.J., 2016. Pollinator specialization: From the individual to the community. New Phytologist 210, 1190–1194. https://doi.org/10.1111/nph.13951

Brown, C.M., Strack, M., Price, J.S., 2017. The effects of water management on the CO2 uptake of Sphagnum moss in a reclaimed peatland. Mires and Peat 20, 05. https://doi.org/10.19189/MAP.2016.OMB.258

Bruppacher, L., Pellet, J., Arlettaz, R., Humbert, J.Y., 2016. Simple modifications of mowing regime promote butterflies in extensively managed meadows: Evidence from field-scale experiments. Biol. Conserv. 196, 196–202. https://doi.org/10.1016/j.biocon.2016.02.018

Bucharova, A., Lampei, C., Conrady, M., May, E., Matheja, J., Meyer, M., Ott, D., 2021. Plant provenance affects pollinator network: Implications for ecological restoration. Journal of Applied Ecology 1–11. https://doi.org/10.1111/1365-2664.13866

Buchholz, S., Egerer, M.H., 2020. Functional ecology of wild bees in cities: towards a better understanding of trait-urbanization relationships. Biodivers. Conserv. 29, 2779–2801. https://doi.org/10.1007/s10531-020-02003-8

Buri, P., Arlettaz, R., Humbert, J.Y., 2013. Delaying mowing and leaving uncut refuges boosts orthopterans in extensively managed meadows: Evidence drawn from field-scale experimentation. Agric. Ecosyst. Environ. 181, 22–30. https://doi.org/10.1016/j.agee.2013.09.003

Buri, P., Humbert, J.Y., Arlettaz, R., 2014. Promoting pollinating insects in intensive agricultural matrices: Field-scale experimental manipulation of hay-meadow mowing regimes and its effects on bees. PLoS One 9. https://doi.org/10.1371/journal.pone.0085635

Burnham, K.P., Anderson, D.R., Huyvaert, K.P., 2011. AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. Behav. Ecol. Sociobiol. 65, 23–35. https://doi.org/10.1007/s00265-010-1029-6

Cane, J.H., Schiffhauer, D., 1997. Nectar Production of Cranberries: Genotypic Differences and Insensitivity to Soil Fertility. Journal of the American Society for Horticultural Science 122, 665–667. https://doi.org/10.21273/JASHS.122.5.665

Carvalheiro, L.G., Barbosa, E.R.M., Memmott, J., 2008. Pollinator networks, alien species and the conservation of rare plants: Trinia glauca as a case study. Journal of Applied Ecology 45, 1419–1427. https://doi.org/10.1111/j.1365-2664.2008.01518.x

Carvell, C., Meek, W.R., Pywell, R.F., Goulson, D., Nowakowski, M., 2007. Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. Journal of Applied Ecology 44, 29–40. https://doi.org/10.1111/j.1365-2664.2006.01249.x

Casparie, W.A., 1993. The Bourtanger Moor: endurance and vulnerability of a raised bog system. Hydrobiologia 265, 203–215. https://doi.org/10.1007/BF00007269

Chao, A., 1987. Estimating the Population Size for Capture-Recapture Data with Unequal Catchability. Biometrics 43, 783–791. https://doi.org/https://doi.org/10.2307/2531532

Chen, S., Zhou, Y., Chen, Y., Gu, J., 2018. Fastp: An ultra-fast all-in-one FASTQ preprocessor. Bioinformatics 34, 884–890. https://doi.org/10.1093/bioinformatics/bty560

Chittka, L., 1992. The colour hexagon: a chromaticity diagram based on photoreceptor excitations as a generalized representation of colour opponency. Journal of Comparative Physiology A 170. https://doi.org/10.1007/BF00199331

Chiu, C.H., Wang, Y.T., Walther, B.A., Chao, A., 2014. An improved nonparametric lower bound of species richness via a modified good-turing frequency formula. Biometrics 70, 671–682. https://doi.org/10.1111/biom.12200

Chrobock, T., Winiger, P., Fischer, M., van Kleunen, M., 2013. The cobblers stick to their lasts: Pollinators prefer native over alien plant species in a multi-species experiment. Biol. Invasions 15, 2577–2588. https://doi.org/10.1007/s10530-013-0474-3

Chytrý, M., Otýpková, Z., 2003. Plot sizes used for phytosociological sampling of European vegetation. Journal of Vegetation Science 14, 563–570. https://doi.org/10.1111/j.1654-1103.2003.tb02183.x

Cnaani, J., Thomson, J.D., Papaj, D.R., 2006. Flower Choice and Learning in Foraging Bumblebees: Effects of Variation in Nectar Volume and Concentration. Ethology 112, 278–285. https://doi.org/10.1111/j.1439-0310.2006.01174.x

Conner, J.K., Rush, S., 1996. Effects of flower size and number on pollinator visitation to wild radish, Raphanus raphanistrum. Oecologia 105, 509–516. https://doi.org/https://doi.org/10.1007/BF00330014

Cooke, R., Mancini, F., Boyd, R.J., Evans, K.L., Shaw, A., Webb, T.J., Isaac, N.J.B., 2023. Protected areas support more species than unprotected areas in Great Britain, but lose them equally rapidly. Biol. Conserv. 278, 109884. https://doi.org/10.1016/j.biocon.2022.109884

Corbet, S.A., Bee, J., Dasmahapatra, K., Gale, S., Gorringe, E., La Ferla, B., Moorhouse, T., Trevail, A., Van Bergen, Y., Vorontsova, M., 2001. Native or Exotic? Double or Single? Evaluating Plants for Pollinator-friendly Gardens. Ann. Bot. 87, 219–232. https://doi.org/10.1006/anbo.2000.1322

Cousins, S.A.O., Auffret, A.G., Lindgren, J., Tränk, L., 2015. Regional-scale land-cover change during the 20th century and its consequences for biodiversity. Ambio 44, 17–27. https://doi.org/10.1007/s13280-014-0585-9

Coverdale, T.C., Davies, A.B., 2023. Unravelling the relationship between plant diversity and vegetation structural complexity: A review and theoretical framework. Journal of Ecology 111, 1378–1395. https://doi.org/10.1111/1365-2745.14068

Cusser, S., Neff, J.L., Jha, S., 2019. Landscape context differentially drives diet breadth for two key pollinator species. Oecologia 191, 873–886. https://doi.org/10.1007/s00442-019-04543-5

de Baar, H.J.W., 1994. von Liebig's law of the minimum and plankton ecology (1899–1991). Prog. Oceanogr. 33, 347–386. https://doi.org/10.1016/0079-6611(94)90022-1

Delgado, T., Leal, L.C., El Ottra, J.H.L., Brito, V.L.G., Nogueira, A., 2023. Flower size affects bee species visitation pattern on flowers with poricidal anthers across pollination studies. Flora 299, 1–10. https://doi.org/10.1016/j.flora.2022.152198

Douma, J.C., Weedon, J.T., 2019. Analysing continuous proportions in ecology and evolution: A practical introduction to beta and Dirichlet regression. Methods Ecol. Evol. 10, 1412–1430. https://doi.org/10.1111/2041-210X.13234

Ebeling, A., Klein, A.M., Schumacher, J., Weisser, W.W., Tscharntke, T., 2008. How does plant richness affect pollinator richness and temporal stability of flower visits? Oikos 117, 1808–1815. https://doi.org/10.1111/j.1600-0706.2008.16819.x

Ebeling, A., Klein, A.M., Tscharntke, T., 2011. Plant-flower visitor interaction webs: Temporal stability and pollinator specialization increases along an experimental plant diversity gradient. Basic Appl. Ecol. 12, 300–309. https://doi.org/10.1016/j.baae.2011.04.005

Ekroos, J., Kleijn, D., Batáry, P., Albrecht, M., Báldi, A., Blüthgen, N., Knop, E., Kovács-Hostyánszki, A., Smith, H.G., 2020. High land-use intensity in grasslands constrains wild bee species richness in Europe. Biol. Conserv. 241, 108255. https://doi.org/10.1016/j.biocon.2019.108255

Emery, S.E., Mills, N.J., 2020. Effects of predation pressure and prey density on short-term indirect interactions between two prey species that share a common predator. Ecol. Entomol. 45, 821–830. https://doi.org/10.1111/een.12855

Erickson, E., Adam, S., Russo, L., Wojcik, V., Patch, H.M., Grozinger, C.M., 2020. More Than Meets the Eye? the Role of Annual Ornamental Flowers in Supporting Pollinators. Environ. Entomol. 49, 178–188. https://doi.org/10.1093/ee/nvz133

Erickson, E., Junker, R.R., Ali, J.G., McCartney, N., Patch, H.M., Grozinger, C.M., 2022. Complex floral traits shape pollinator attraction to ornamental plants. Ann. Bot. 130, 561–577. https://doi.org/10.1093/aob/mcac082

Erickson, E., Patch, H.M., Grozinger, C.M., 2021. Herbaceous perennial ornamental plants can support complex pollinator communities. Sci. Rep. 11, 1–12. https://doi.org/10.1038/s41598-021-95892-w

Evans, M.E.K., Adler, P.B., Angert, A.L., Dey, S.M.N., Girardin, M.P., Heilman, K.A., Klesse, S., Perret, D.L., Sax, D.F., Sheth, S.N., Stemkovski, M., Williams, J.L., 2025. Reconsidering space-for-time substitution in climate change ecology. Nat. Clim. Chang. 15, 809–812. https://doi.org/10.1038/s41558-025-02392-0

Falk, S., Lewington, R., 2017. Bijen veldgids voor Nederland en Vlaanderen. Kosmos Uitgeverij.

Fantinato, E., Sonkoly, J., Török, P., Buffa, G., 2021. Patterns of pollination interactions at the community level are related to the type and quantity of floral resources. Funct. Ecol. 35, 2461–2471. https://doi.org/10.1111/1365-2435.13915

Fenster, C.B., Armbruster, W.S., Wilson, P., Dudash, M.R., Thomson, J.D., 2004. Pollination syndromes and floral specialization. Annu. Rev. Ecol. Evol. Syst. 35, 375–403. https://doi.org/10.1146/annurev.ecolsys.34.011802.132347

Ferrari, A., Polidori, C., 2022. How city traits affect taxonomic and functional diversity of urban wild bee communities: insights from a worldwide analysis. Apidologie 53, 1–23. https://doi.org/10.1007/s13592-022-00950-5

Filipiak, M., 2019. Key pollen host plants provide balanced diets for wild bee larvae: A lesson for planting flower strips and hedgerows. Journal of Applied Ecology 56, 1410–1418. https://doi.org/10.1111/1365-2664.13383

Fischer, C., Hanslin, H.M., Hovstad, K.A., D'Amico, M., Kollmann, J., Kroeger, S.B., Bastianelli, G., Habel, J.C., Rygne, H., Lennartsson, T., 2022. The contribution of roadsides to connect grassland habitat patches for butterflies in landscapes of contrasting permeability. J. Environ. Manage. 311, 114846. https://doi.org/10.1016/j.jenvman.2022.114846

Fluri, P., Frick, R., Jaun, A., 2001. Bienenverluste beim Mähen mit Rotationsmähwerken. Agrarforschung 8, 196–201.

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Stuart Chapin, F., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Colin Prentice, I., Ramankutty, N., Snyder, P.K., 2005. Global Consequences of Land Use. Science (1979). 309, 570–574. https://doi.org/10.1126/science.1111772

Fornoff, F., Klein, A.M., Hartig, F., Benadi, G., Venjakob, C., Schaefer, H.M., Ebeling, A., 2017. Functional flower traits and their diversity drive pollinator visitation. Oikos 126, 1020–1030. https://doi.org/10.1111/oik.03869

Forster, C.Y., Middleton, E.J.T., Gloag, R., Hochuli, D.F., White, T.E., Latty, T., 2023. Impact of empty flowers on foraging choice and movement within floral patches by the honey bee, Apis mellifera. Insectes Soc. 70, 413–422. https://doi.org/10.1007/s00040-023-00934-3

Fort, H., Vázquez, D.P., Lan, B.L., 2016. Abundance and generalisation in mutualistic networks: Solving the chicken-and-egg dilemma. Ecol. Lett. 19, 4–11. https://doi.org/10.1111/ele.12535

Fragoso, F.P., Brunet, J., 2023. Honey bees exhibit greater patch fidelity than bumble bees when foraging in a common environment. Ecosphere 14, 1–10. https://doi.org/10.1002/ecs2.4606

Fründ, J., Dormann, C.F., Holzschuh, A., Tscharntke, T., 2013. Bee diversity effects on pollination depend on functional complementarity and niche shifts. Ecology 94, 2042–2054. https://doi.org/10.1890/12-1620.1

Fründ, J., Linsenmair, K.E., Blüthgen, N., 2010. Pollinator diversity and specialization in relation to flower diversity. Oikos 119, 1581–1590. https://doi.org/10.1111/j.1600-0706.2010.18450.x

Gallai, N., Salles, J.M., Settele, J., Vaissière, B.E., 2009. Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. Ecological Economics 68, 810–821. https://doi.org/10.1016/j.ecolecon.2008.06.014

Garbuzov, M., Alton, K., Ratnieks, F.L.W., 2017. Most ornamental plants on sale in garden centres are unattractive to flower-visiting insects. PeerJ 2017. https://doi.org/10.7717/peerj.3066

Garbuzov, M., Ratnieks, F.L.W., 2015. Using the British national collection of asters to compare the attractiveness of 228 varieties to flower-visiting insects. Environ. Entomol. 44, 638–646. https://doi.org/10.1093/ee/nvv037

Garbuzov, M., Samuelson, E.E.W., Ratnieks, F.L.W., 2015. Survey of insect visitation of ornamental flowers in Southover Grange garden, Lewes, UK. Insect Sci. 22, 700–705. https://doi.org/10.1111/1744-7917.12162

Garibaldi, L.A., Steffan-Dewenter, I., Kremen, C., Morales, J.M., Bommarco, R., Cunningham, S.A., Carvalheiro, L.G., Chacoff, N.P., Dudenhöffer, J.H., Greenleaf, S.S., Holzschuh, A., Isaacs, R., Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L.A., Potts, S.G., Ricketts, T.H., Szentgyörgyi, H., Viana, B.F., Westphal, C., Winfree, R., Klein, A.M., 2011. Stability of pollination services decreases with isolation from natural areas despite honey bee visits. Ecol. Lett. https://doi.org/10.1111/j.1461-0248.2011.01669.x

Garibaldi, L.A., Steffan-Dewenter, I., Winfree, R., Aizen, M.A., Bommarco, R., Cunningham, S.A., Kremen, C., Carvalheiro, L.G., Harder, L.D., Afik, O., Bartomeus, I., Benjamin, F., Boreux, V., Cariveau, D., Chacoff, N.P., Dudenhöffer, J.H., Freitas, B.M., Ghazoul, J., Greenleaf, S., Hipólito, J., Holzschuh, A., Howlett, B., Isaacs, R., Javorek, S.K., Kennedy, C.M., Krewenka, K.M., Krishnan, S., Mandelik, Y., Mayfield, M.M., Motzke, I., Munyuli, T., Nault, B.A., Otieno, M., Petersen, J., Pisanty, G., Potts, S.G., Rader, R., Ricketts, T.H., Rundlöf, M., Seymour, C.L., Schüepp, C., Szentgyörgyi, H., Taki, H., Tscharntke, T., Vergara, C.H., Viana, B.F., Wanger, T.C., Westphal, C., Williams, N., Klein, A.M., 2013. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. Science (1979). 340, 1608–1611. https://doi.org/10.1126/science.1230200

Gaspar, J.M., 2018. NGmerge: Merging paired-end reads via novel empirically-derived models of sequencing errors. BMC Bioinformatics 19. https://doi.org/10.1186/s12859-018-2579-2

Geppert, C., Hass, A., Földesi, R., Donkó, B., Akter, A., Tscharntke, T., Batáry, P., 2020. Agri-environment schemes enhance pollinator richness and abundance but bumblebee reproduction depends on field size. Journal of Applied Ecology 1–11. https://doi.org/10.1111/1365-2664.13682

Ghazoul, J., 2006. Floral diversity and the facilitation of pollination. Journal of Ecology 94, 295–304. https://doi.org/10.1111/j.1365-2745.2006.01098.x

Giurfa, M., Núñez, J., Chittka, L., Menzel, R., 1995. Colour preferences of flower-naive honeybees. Journal of Comparative Physiology A 177. https://doi.org/10.1007/BF00192415

Gómez-Martínez, C., González-Estévez, M.A., Cursach, J., Lázaro, A., 2022. Pollinator richness, pollination networks, and diet adjustment along local and landscape gradients of resource diversity. Ecological Applications 32, 1–18. https://doi.org/10.1002/eap.2634

Goulson, D., Lye, G.C., Darvill, B., 2008. Decline and conservation of bumble bees. Annu. Rev. Entomol. https://doi.org/10.1146/annurev.ento.53.103106.093454

Goulson, D., Nicholls, E., Botías, C., Rotheray, E.L., 2015. Bee declines driven by combined Stress from parasites, pesticides, and lack of flowers. Science (1979). 347. https://doi.org/10.1126/science.1255957

Green, R.H., 1979. Sampling Design and Statistical Methods for Environmental Biologists. Wiley.

Griffin, S.R., Bruninga-Socolar, B., Gibbs, J., 2021. Bee communities in restored prairies are structured by landscape and management, not local floral resources. Basic Appl. Ecol. 50, 144–154. https://doi.org/10.1016/j.baae.2020.12.004

Guzman, L.M., Elle, E., Morandin, L.A., Cobb, N.S., Chesshire, P.R., McCabe, L.M., Hughes, A., Orr, M., M'Gonigle, L.K., 2024. Impact of pesticide use on wild bee distributions across the United States. Nat. Sustain. 7, 1324–1334. https://doi.org/10.1038/s41893-024-01413-8

Haaland, C., Naisbit, R.E., Bersier, L.F., 2011. Sown wildflower strips for insect conservation: A review. Insect Conserv. Divers. 4, 60–80. https://doi.org/10.1111/j.1752-4598.2010.00098.x

Haapalehto, T., Juutinen, R., Kareksela, S., Kuitunen, M., Tahvanainen, T., Vuori, H., Kotiaho, J.S., 2017. Recovery of plant communities after ecological restoration of forestry-drained peatlands. Ecol. Evol. 7, 7848–7858. https://doi.org/10.1002/ece3.3243

Habel, J.C., Schmitt, T., 2018. Vanishing of the common species: Empty habitats and the role of genetic diversity. Biol. Conserv. 218, 211–216. https://doi.org/10.1016/j.biocon.2017.12.018

Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D., De Kroon, H., 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PLoS One 12, e0185809. https://doi.org/10.1371/journal.pone.0185809

Hallmann, C.A., Ssymank, A., Sorg, M., de Kroon, H., Jongejans, E., 2021. Insect biomass decline scaled to species diversity: general patterns derived from a hoverfly community. Proceedings of the National Academy of Sciences USA 118, 1–8. https://doi.org/10.1073/pnas.2002554117

Hardy, O.J., Vanderhoeven, S., de Loose, M., Meerts, P., 2000. Ecological, morphological and allozymic differentiation between diploid and tetraploid knapweeds (Centaurea jacea) from a contact zone in the Belgian Ardennes. New Phytologist 146, 281–290. https://doi.org/10.1046/j.1469-8137.2000.00631.x

Hartig, F., 2022. DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. [WWW Document]. https://CRAN.R-project.org/ package=DHARMa.

Harvey, E., Gounand, I., Ward, C.L., Altermatt, F., 2017. Bridging ecology and conservation: from ecological networks to ecosystem function. Journal of Applied Ecology. https://doi.org/10.1111/1365-2664.12769

Hass, A.L., Kormann, U.G., Tscharntke, T., Clough, Y., Baillod, A.B., Sirami, C., Fahrig, L., Martin, J.L., Baudry, J., Bertrand, C., Bosch, J., Brotons, L., Bure, F., Georges, R., Giralt, D., Marcos-García, M., Ricarte, A., Siriwardena, G., Batáry, P., 2018. Landscape configurational heterogeneity by small-scale agriculture, not crop diversity, maintains pollinators and plant reproduction in western Europe. Proceedings of the Royal Society B: Biological Sciences 285. https://doi.org/10.1098/rspb.2017.2242

Hayes, J.J.M., Bell, N.C., Best, L.R., Bruslind, S.R., Johnson, D.O., Mead, M.E., Spofford, T.S., Langellotto, G.A., 2025a. Pacific Northwest native plants and native cultivars, part I: pollinator visitation. Environ. Entomol. 54, 199–214. https://doi.org/10.1093/ee/nvae126

Hayes, J.J.M., Bell, N.C.S., Best, L.R., Bruslind, S.R., Case, L.A., Johnson, D.O., Legier, K.N., Mead, M.E., Spofford, T.S., Chakrabarti, P., Baugus, L.N., Langellotto, G.A., 2025b. Pacific Northwest native plants and native cultivars part II: plant and pollinator traits. Environ. Entomol. 54, 1386–1402. https://doi.org/10.1093/ee/nvaf105

Helldin, J.O., Wissman, J., Lennartsson, T., 2015. Abundance of red-listed species in infrastructure habitats - "responsibility species" as a priority-setting tool for transportation agencies' conservation action. Nat. Conserv. 11, 143–158. https://doi.org/10.3897/natureconservation.11.4433

Heneberg, P., Bogusch, P., Řezáč, M., 2017. Roadside verges can support spontaneous establishment of steppe-like habitats hosting diverse assemblages of bees and wasps (Hymenoptera: Aculeata) in an intensively cultivated central European landscape. Biodivers. Conserv. 26, 843–864. https://doi.org/10.1007/s10531-016-1275-7

Henry, M., Rodet, G., 2018. Controlling the impact of the managed honeybee on wild bees in protected areas. Sci. Rep. 8, 1–10. https://doi.org/10.1038/s41598-018-27591-y

Hicks, D.M., Ouvrard, P., Baldock, K.C.R., Baude, M., Goddard, M.A., Kunin, W.E., Mitschunas, N., Memmott, J., Morse, H., Nikolitsi, M., Osgathorpe, L.M., Potts, S.G., Robertson, K.M., Scott, A. V., Sinclair, F., Westbury, D.B., Stone, G.N., 2016. Food for pollinators: Quantifying the nectar and pollen resources of urban flower meadows. PLoS One 11, 1–37. https://doi.org/10.1371/journal.pone.0158117

Hirayama, G.S., Inoue, T., Kenta, T., Ishii, H.S., Ushimaru, A., 2025. Long-term management is required for the recovery of pollination networks and function in restored grasslands. Journal of Applied Ecology 1–10. https://doi.org/10.1111/1365-2664.70017

Hofmann, M.M., Fleischmann, A., Renner, S.S., 2018. Changes in the bee fauna of a German botanical garden between 1997 and 2017, attributable to climate warming, not other parameters. Oecologia 187, 701–706. https://doi.org/10.1007/s00442-018-4110-x

Hogeweg, L., Zeegers, T., Katramados, I., Jongejans, E., 2019. Smart Insect Cameras. Biodiversity Information Science and Standards 3. https://doi.org/10.3897/biss.3.39241

Holzschuh, A., Steffan-Dewenter, I., Tscharntke, T., 2008. Agricultural landscapes with organic crops support higher pollinator diversity. Oikos 117, 354–361. https://doi.org/10.1111/j.2007.0030-1299.16303.x

Humbert, J.-Y., Ghazoul, J., Richner, N., Walter, T., 2010a. Hay harvesting causes high orthopteran mortality. Agric. Ecosyst. Environ. 139, 522–527. https://doi.org/10.1016/j.agee.2010.09.012

Humbert, J.-Y., Ghazoul, J., Sauter, G.J., Walter, T., 2010b. Impact of different meadow mowing techniques on field invertebrates. Journal of Applied Entomology 134, 592–599. https://doi.org/10.1111/j.1439-0418.2009.01503.x

Humbert, J.-Y., Pellet, J., Buri, P., Arlettaz, R., 2012. Does delaying the first mowing date benefit biodiversity in meadowland? Environ. Evid. 1, 1–13.

Hutchinson, G.E., 1957. Concluding Remarks. Cold Spring Harb. Symp. Quant. Biol. 22, 415–427. https://doi.org/10.1101/SQB.1957.022.01.039

Hyjazie, B.F., Sargent, R.D., 2022. Floral resources predict the local bee community: Implications for conservation. Biol. Conserv. 273, 109679. https://doi.org/10.1016/j.biocon.2022.109679

Johansen, L., Westin, A., Wehn, S., Iuga, A., Ivascu, C.M., Kallioniemi, E., Lennartsson, T., 2019. Traditional semi-natural grassland management with heterogeneous mowing times enhances flower resources for pollinators in agricultural landscapes. Glob. Ecol. Conserv. 18, e00619. https://doi.org/10.1016/j.gecco.2019.e00619

Jones, C.Eugene., Little, R.John., 1983. Handbook of experimental pollination biology. Scientific and Academic Editions.

Jones, K.N., Reithel, J.S., Irwin, R.E., 1998. A trade-off between the frequency and duration of bumblebee visits to flowers. Oecologia 117, 161–168.

Kaiser-Bunbury, C.N., Mougal, J., Whittington, A.E., Valentin, T., Gabriel, R., Olesen, J.M., Blüthgen, N., 2017. Ecosystem restoration strengthens pollination network resilience and function. Nature 542, 223–227. https://doi.org/10.1038/nature21071

Kearns, C.A., Inouye, D.W., Waser, N.M., 1998. ENDANGERED MUTUALISMS: The Conservation of Plant-Pollinator Interactions. Annu. Rev. Ecol. Syst. 29, 83–112. https://doi.org/10.1146/annurev.ecolsys.29.1.83

Kelber, A., Vorobyev, M., Osorio, D., 2003. Animal colour vision — behavioural tests and physiological concepts. Biological Reviews 78, 81–118. https://doi.org/10.1017/S1464793102005985

Kelly, T.T., Elle, E., 2021. Investigating bee dietary preferences along a gradient of floral resources: how does resource use align with resource availability? Insect Sci. 28, 555–565. https://doi.org/10.1111/1744-7917.12785

Kemp, D.J., Herberstein, M.E., Fleishman, L.J., Endler, J.A., Bennett, A.T.D., Dyer, A.G., Hart, N.S., Marshall, J., Whiting, M.J., 2015. An Integrative Framework for the Appraisal of Coloration in Nature. Am. Nat. 185, 705–724. https://doi.org/10.1086/681021

Kennedy, C.M., Lonsdorf, E., Neel, M.C., Williams, N.M., Ricketts, T.H., Winfree, R., Bommarco, R., Brittain, C., Burley, A.L., Cariveau, D., Carvalheiro, L.G., Chacoff, N.P., Cunningham, S.A., Danforth, B.N., Dudenhöffer, J.H., Elle, E., Gaines, H.R., Garibaldi, L.A., Gratton, C., Holzschuh, A., Isaacs, R., Javorek, S.K., Jha, S., Klein, A.M., Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L., Neame, L.A., Otieno, M., Park, M., Potts, S.G., Rundlöf, M., Saez, A., Steffan-Dewenter, I., Taki, H., Viana, B.F., Westphal, C., Wilson, J.K., Greenleaf, S.S., Kremen, C., 2013. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. Ecol. Lett. 16, 584–599. https://doi.org/10.1111/ele.12082

Kleijn, D., Winfree, R., Bartomeus, I., Carvalheiro, L.G., Henry, M., Isaacs, R., Klein, A.M., Kremen, C., M'Gonigle, L.K., Rader, R., Ricketts, T.H., Williams, N.M., Lee Adamson, N., Ascher, J.S., Báldi, A., Batáry, P., Benjamin, F., Biesmeijer, J.C., Blitzer, E.J., Bommarco, R., Brand, M.R., Bretagnolle, V., Button, L., Cariveau, D.P., Chifflet, R., Colville, J.F., Danforth, B.N., Elle, E., Garratt, M.P.D., Herzog, F., Holzschuh, A., Howlett, B.G., Jauker, F., Jha, S., Knop, E., Krewenka, K.M., Le Féon, V., Mandelik, Y., May, E.A., Park, M.G., Pisanty, G., Reemer, M., Riedinger, V., Rollin, O., Rundlöf, M., Sardiñas, H.S., Scheper, J., Sciligo, A.R., Smith, H.G., Steffan-Dewenter, I., Thorp, R., Tscharntke, T., Verhulst, J., Viana, B.F., Vaissière, B.E., Veldtman, R., Westphal, C., Potts, S.G., 2015. Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. Nat. Commun. 6. https://doi.org/10.1038/ncomms8414

Klumpers, S.G.T., Stang, M., Klinkhamer, P.G.L., 2019. Foraging efficiency and size matching in a plant–pollinator community: the importance of sugar content and tongue length. Ecol. Lett. 22, 469–479. https://doi.org/10.1111/ele.13204

Koski, M.H., Ison, J.L., Padilla, A., Pham, A.Q., Galloway, L.F., 2018. Linking pollinator efficiency to patterns of pollen limitation: Small bees exploit the plant-pollinator mutualism. Proceedings of the Royal Society B: Biological Sciences 285. https://doi.org/10.1098/rspb.2018.0635

Kral-O'Brien, K.C., O'Brien, P.L., Hovick, T.J., Harmon, J.P., 2021. Meta-analysis: Higher Plant Richness Supports Higher Pollinator Richness across Many Land Use Types. Ann. Entomol. Soc. Am. 114, 267–275. https://doi.org/10.1093/aesa/saaa061

Kremen, C., Merenlender, A.M., 2018. Landscapes that work for biodiversity and people. Science (1979). https://doi.org/10.1126/science.aau6020

Kremen, C., Williams, N.M., Thorp, R.W., 2002. Crop pollination from native bees at risk from agricultural intensification. Proceedings of the National Academy of Sciences 99, 16812–16816. https://doi.org/10.1073/pnas.262413599

Landi, P., Minoarivelo, H.O., Brännström, Å., Hui, C., Dieckmann, U., 2018. Complexity and stability of ecological networks: a review of the theory. Popul. Ecol. 60, 319–345. https://doi.org/10.1007/s10144-018-0628-3

Langmead, B., Salzberg, S.L., 2012. Fast gapped-read alignment with Bowtie 2. Nat. Methods 9, 357–359. https://doi.org/10.1038/nmeth.1923

Larkin, M., Stanley, D.A., 2021. Impacts of management at a local and landscape scale on pollinators in semi-natural grasslands. Journal of Applied Ecology 58, 2505–2514. https://doi.org/10.1111/1365-2664.13990

Larsson, M., 2005. Higher pollinator effectiveness by specialist than generalist flower-visitors of unspecialized Knautia arvensis (Dipsacaceae). Oecologia 146, 394–403. https://doi.org/10.1007/s00442-005-0217-y

Lázaro, A., Tscheulin, T., Devalez, J., Nakas, G., Stefanaki, A., Hanlidou, E., Petanidou, T., 2015. Moderation is best: effects of grazing intensity on plant-flower visitor networks in Mediterranean communities. Ecological Applications 26, 150903033531005. https://doi.org/10.1890/15-0202.1

Le Féon, V., Burel, F., Chifflet, R., Henry, M., Vaissière, A.R., Vaissière, B.E., Baudry, J., 2013. Solitary bee abundance and species richness in dynamic agricultural landscapes. Agric. Ecosyst. Environ. 166, 94–101. https://doi.org/10.1016/j.agee.2011.06.020

Lebeau, J., Wesselingh, R.A., Van Dyck, H., 2015. Butterfly density and behaviour in uncut hay meadow strips: Behavioural ecological consequences of an agri-environmental scheme. PLoS One 10, 1–17. https://doi.org/10.1371/journal.pone.0134945

Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M., Gonzalez, A., 2004. The metacommunity concept: A framework for multi-scale community ecology. Ecol. Lett. 7, 601–613. https://doi.org/10.1111/j.1461-0248.2004.00608.x

Lenth, R. V., Banfai, B., Bolker, B., Buerkner, P., Giné-vázquez, I., Herve, M., Jung, M., Love, J., Miguez, F., Piaskowski, J., Riebl, H., Singmann, H., 2025. Package ' emmeans '. https://doi.org/10.32614/CRAN.package.emmeans

Levine, J.M., Bascompte, J., Adler, P.B., Allesina, S., 2017. Beyond pairwise mechanisms of species coexistence in complex communities. Nature 546, 56–64. https://doi.org/10.1038/nature22898

Lexmond, R.E., Jongejans, E., Zeegers, T., Climo, J.D., van der Putten, W.H., de Kroon, H., 2026. Local landscape elements enhance flying insect biomass in a complex agricultural landscape. Basic Appl. Ecol. 92, 29–36. https://doi.org/10.1016/j.baae.2026.03.004

Liebrand, C.I.J.M., 1999. Restoration of species-rich grasslands on reconstructed river dikes. (PhD Thesis). Landbouwuniversiteit Wageningen.

Liebrand, C.I.J.M., Sýkora, K. V, 1996. Restoration of semi-natural, species-rich grasslands on river dikes after reconstruction. Ecol. Eng. 7, 315–326. https://doi.org/10.1016/S0925-8574(96)00023-7

López-Uribe, M.M., 2021. Wild bees: diversity, ecology, and stressors of non-Apis bees, in: Honey Bee Medicine for the Veterinary Practitioner. Wiley, pp. 81–91. https://doi.org/10.1002/9781119583417.ch7

Losapio, G., Fortuna, M.A., Bascompte, J., Schmid, B., Michalet, R., Neumeyer, R., Castro, L., Cerretti, P., Germann, C., Haenni, J.P., Klopfstein, S., Ortiz-Sanchez, F.J., Pont, A.C., Rousse, P., Schmid, J., Sommaggio, D., Schöb, C., 2019. Plant interactions shape pollination networks via nonadditive effects. Ecology 100, 1–9. https://doi.org/10.1002/ecy.2619

Lowe, A., Jones, L., Brennan, G., Creer, S., de Vere, N., 2022a. Seasonal progression and differences in major floral resource use by bees and hoverflies in a diverse horticultural and agricultural landscape revealed by DNA metabarcoding. Journal of Applied Ecology 1–12. https://doi.org/10.1111/1365-2664.14144

Lowe, A., Jones, L., Witter, L., Creer, S., de Vere, N., 2022b. Using DNA Metabarcoding to Identify Floral Visitation by Pollinators. Diversity (Basel). 14, 236. https://doi.org/10.3390/d14040236

Loy, X., Brosi, B.J., 2022. The effects of pollinator diversity on pollination function. Ecology 103, 1–14. https://doi.org/10.1002/ecy.3631

Lun, H.N., Inouye, D.W., Yang, C.F., 2025. Nectar sugar concentration contributes to structuring bumblebee and plant interactions. Journal of Ecology 113, 2744–2757. https://doi.org/10.1111/1365-2745.70136

Lundgren, R., Totland, Ø., Lázaro, A., 2016. Experimental simulation of pollinator decline causes community-wide reductions in seedling diversity and abundance. Ecology 97, 1420–1430. https://doi.org/10.1890/15-0787.1

Makino, T.T., Sakai, S., 2007. Experience changes pollinator responses to floral display size: From size-based to reward-based foraging. Funct. Ecol. 21, 854–863. https://doi.org/10.1111/j.1365-2435.2007.01293.x

Mallinger, R.E., Prasifka, J.R., 2017. Bee visitation rates to cultivated sunflowers increase with the amount and accessibility of nectar sugars. Journal of Applied Entomology 141, 561–573. https://doi.org/10.1111/jen.12375

Meyer, S., Unternährer, D., Arlettaz, R., Humbert, J.Y., Menz, M.H.M., 2017. Promoting diverse communities of wild bees and hoverflies requires a landscape approach to managing meadows. Agric. Ecosyst. Environ. 239, 376–384. https://doi.org/10.1016/j.agee.2017.01.037

Michez, D., Boustani, M., Sentil, A., Benrezkallah, J., de Manincor, N., Wood, T.J., Álvarez Fidalgo, P., Aubert, M., Bellotto, V., Biella, P., Bogusch, P., Bosch, J., Brau, T., Browne, K., Carion, F., Castro, L., Cederberg, B., Clay, J., Debont, T., Bila Dubaić, J., Dall'Olio, R., Dellicour, S., Devalez, J., Devorsine, R., Dufrêne, E., De la Rúa, P., De Tandt, B., Evrard, D., Flaminio, S., Fiordaliso, W., Fontana, P., Gadoum, S., Galbany Casals, M., Gaspar, H., Gekière, A., Gérard, M., Geslin, B., Kasparek, M., Kierat, J., Kohl, P.L., Kuhlmann, M., Kryger, P., Leclercq, N., Le Divelec, R., Lemaire, S., Lescot, S., Lhomme, P., Litman, J., Marshall, L., McCormack, G.P., Moro, A., Mudri Stojnić, S., Ockermueller, E., Oleksa, A., Ortiz-Sánchez, F.J., Patiny, S., Paukkunen, J., Perrard, A., Petanidou, T., Pinto, M.A., Potts, S.G., Praz, C., Put, S.C., Radchenko, V.G., Rasmont, P., Requier, F., Reverté, S., Risch, S., Rogenstein, S., Rosa, P., Ruiz, C., Rutschmann, B., Santerre, R., Smit, J., Straka, J., Thulier, J., Tourbez, C., Trottet, A., Vereecken, N.J., Williams, P.H., Winter, E., Zimmermann, D., Ghisbain, G., 2026. European red list of bees – Measuring the pulse of European biodiversity. Publications Office of the European Union. https://doi.org/doi/10.2779/521877

Milberg, P., Tälle, M., Fogelfors, H., Westerberg, L., 2017. The biodiversity cost of reducing management intensity in species-rich grasslands: Mowing annually vs. every third year. Basic Appl. Ecol. 22, 61–74. https://doi.org/10.1016/j.baae.2017.07.004

Moens, M., Biesmeijer, J.C., Klumpers, S.G.T., Marshall, L., 2023. Are threatened species special? An assessment of Dutch bees in relation to land use and climate. Ecol. Evol. 13, 1–13. https://doi.org/10.1002/ece3.10326

Moreno-Mateos, D., Alberdi, A., Morriën, E., van der Putten, W.H., Rodríguez-Uña, A., Montoya, D., 2020. The long-term restoration of ecosystem complexity. Nat. Ecol. Evol. 4, 676–685. https://doi.org/10.1038/s41559-020-1154-1

Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods Ecol. Evol. 4, 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x

Noordijk, J., Delille, K., Schaffers, A.P., Sýkora, K. V., 2009. Optimizing grassland management for flower-visiting insects in roadside verges. Biol. Conserv. 142, 2097–2103. https://doi.org/10.1016/j.biocon.2009.04.009

Öckinger, E., Smith, H.G., 2007. Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. Journal of Applied Ecology 44, 50–59. https://doi.org/10.1111/j.1365-2664.2006.01250.x

O'Connell, M., Jordan, Z., McGilvray, E., Cohen, H., Liere, H., Lin, B.B., Philpott, S.M., Jha, S., 2021. Reap what you sow: local plant composition mediates bumblebee foraging patterns within urban garden landscapes. Urban Ecosyst. 24, 391–404. https://doi.org/10.1007/s11252-020-01043-w

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., Mcglinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H., Szoecs, E., Wagner, H., 2018. vegan: Community Ecology Package. R package version 2.5-3.

Okuyama, T., Holland, J.N., 2008. Network structural properties mediate the stability of mutualistic communities. Ecol. Lett. 11, 208–216. https://doi.org/10.1111/j.1461-0248.2007.01137.x

Olesen, J.M., Bascompte, J., Dupont, Y.L., Jordano, P., 2007. The modularity of pollination networks. Proc. Natl. Acad. Sci. U. S. A. 104, 19891–19896. https://doi.org/10.1073/pnas.0706375104

Oliver, T.H., Heard, M.S., Isaac, N.J.B., Roy, D.B., Procter, D., Eigenbrod, F., Freckleton, R., Hector, A., Orme, C.D.L., Petchey, O.L., Proença, V., Raffaelli, D., Suttle, K.B., Mace, G.M., Martín-López, B., Woodcock, B.A., Bullock, J.M., 2015. Biodiversity and Resilience of Ecosystem Functions. Trends Ecol. Evol. https://doi.org/10.1016/j.tree.2015.08.009

Ollerton, J., Winfree, R., Tarrant, S., 2011. How many flowering plants are pollinated by animals? Oikos 120, 321–326. https://doi.org/10.1111/j.1600-0706.2010.18644.x

Olliff-Yang, R.L., Ackerly, D.D., 2020. Topographic heterogeneity lengthens the duration of pollinator resources. Ecol. Evol. 10, 9301–9312. https://doi.org/10.1002/ece3.6617

Orford, K.A., Vaughan, I.P., Memmott, J., 2015. The forgotten flies: The importance of non-syrphid Diptera as pollinators. Proceedings of the Royal Society B: Biological Sciences 282. https://doi.org/10.1098/rspb.2014.2934

Osborne, J.L., Martin, A.P., Carreck, N.L., Swain, J.L., Knight, M.E., Goulson, D., Hale, R.J., Sanderson, R.A., 2008. Bumblebee flight distances in relation to the forage landscape. Journal of Animal Ecology 77, 406–415. https://doi.org/10.1111/j.1365-2656.2007.01333.x

Ouvrard, P., Transon, J., Jacquemart, A.L., 2018. Flower-strip agri-environment schemes provide diverse and valuable summer flower resources for pollinating insects. Biodivers. Conserv. 27, 2193–2216. https://doi.org/10.1007/s10531-018-1531-0

Ozinga, W.A., 2008. Assembly of plant communities in fragmented landscapes: the role of dispersal. Radboud University Nijmegen.

Page, M.L., Nicholson, C.C., Brennan, R.M., Britzman, A.T., Greer, J., Hemberger, J., Kahl, H., Müller, U., Peng, Y., Rosenberger, N.M., Stuligross, C., Wang, L., Yang, L.H., Williams, N.M., 2021. A meta-analysis of single visit pollination effectiveness comparing honeybees and other floral visitors. Am. J. Bot. 108, 2196–2207. https://doi.org/10.1002/ajb2.1764

Palmer, M.W., 1990. The Estimation of Species Richness by Extrapolation. Ecology 71, 1195–1198. https://doi.org/https://doi.org/10.2307/1937387

Pan, K., Marshall, L., de Snoo, G.R., Biesmeijer, J.C., 2024. Dutch landscapes have lost insect-pollinated plants over the past 87 years. Journal of Applied Ecology 1–11. https://doi.org/10.1111/1365-2664.14649

Parachnowitsch, A.L., Manson, J.S., Sletvold, N., 2019. Evolutionary ecology of nectar. Ann. Bot. 123, 247–261. https://doi.org/10.1093/aob/mcy132

Parreno, M.A., Werle, S., Buydens, L., Leroy, C., Roberts, S., Koirala, S., Filipiak, M., Kuhlmann, M., Brunet, J.L., Henry, M., Alaux, C., Requier, F., Piot, N., Meeus, I., Klein, A.M., Keller, A., Leonhardt, S.D., 2024. Landscape heterogeneity correlates with bee and pollen diversity while size and specialization degree explain species-specific responses of wild bees to the environment. Science of the Total Environment 954. https://doi.org/10.1016/j.scitotenv.2024.176595

Parreño, M.A., Werle, S., Buydens, L., Leroy, C., Roberts, S., Koirala, S., Filipiak, M., Kuhlmann, M., Brunet, J.L., Henry, M., Alaux, C., Requier, F., Piot, N., Meeus, I., Klein, A.M., Keller, A., Leonhardt, S.D., 2024. Landscape heterogeneity correlates with bee and pollen diversity while size and specialization degree explain species-specific responses of wild bees to the environment. Science of the Total Environment 954. https://doi.org/10.1016/j.scitotenv.2024.176595

Peeters, T.M.J., Nieuwenhuijsen, H., Smit, J., Meer, F. van der, Raemakers, I.P., Heitmans, W.R.B., Achterberg, K. van, Kwak, M., Loonstra, A.J., Rond, J. de, Roos, M., Reemer, M., 2012. De Nederlandse bijen (Hymenoptera: Apidae s.l.). – Natuur van Nederland 11, Naturalis Biodiversity Center & European Invertebrate Survey. Leiden, the Netherlands.

Peitsch, D., Fietz, A., Hertel, H., de Souza, J., Ventura, D.F., Menzel, R., 1992. The spectral input systems of hymenopteran insects and their receptor-based colour vision. Journal of Comparative Physiology A 170, 23–40. https://doi.org/10.1007/BF00190398

Peralta, G., Webber, C.J., Perry, G.L.W., Stouffer, D.B., Vázquez, D.P., Tylianakis, J.M., 2023. Scale-dependent effects of landscape structure on pollinator traits, species interactions and pollination success. Ecography 2023, 1–12. https://doi.org/10.1111/ecog.06453

Pérez-Sánchez, A.J., Schröder, B., Dauber, J., Hellwig, N., 2023. Flower strip effectiveness for pollinating insects in agricultural landscapes depends on established contrast in habitat quality: A meta-analysis. Ecological Solutions and Evidence 4. https://doi.org/10.1002/2688-8319.12261

Peterson, J.H., Roitberg, B.D., 2006a. Impacts of flight distance on sex ratio and resource allocation to offspring in the leafcutter bee, Megachile rotundata. Behav. Ecol. Sociobiol. 59, 589–596. https://doi.org/10.1007/s00265-005-0085-9

Peterson, J.H., Roitberg, B.D., 2006b. Impacts of flight distance on sex ratio and resource allocation to offspring in the leafcutter bee, Megachile rotundata. Behav. Ecol. Sociobiol. 59, 589–596. https://doi.org/10.1007/s00265-005-0085-9

Phillips, B.B., Gaston, K.J., Bullock, J.M., Osborne, J.L., 2019. Road verges support pollinators in agricultural landscapes, but are diminished by heavy traffic and summer cutting. Journal of Applied Ecology 56, 2316–2327. https://doi.org/10.1111/1365-2664.13470

Phillips, B.B., Shaw, R.F., Holland, M.J., Fry, E.L., Bardgett, R.D., Bullock, J.M., Osborne, J.L., 2018. Drought reduces floral resources for pollinators. Glob. Chang. Biol. 24, 3226–3235. https://doi.org/10.1111/gcb.14130

Phillips, B.B., Wallace, C., Roberts, B.R., Whitehouse, A.T., Gaston, K.J., Bullock, J.M., Dicks, L. V., Osborne, J.L., 2020. Enhancing road verges to aid pollinator conservation: A review. Biol. Conserv. 250, 108687. https://doi.org/10.1016/j.biocon.2020.108687

Pianka, E.R., 1973. The Structure of Lizard Communities. Annual Reviews 3, 53–74. https://doi.org/https://doi.org/10.1146/annurev.es.04.110173.000413

Pleasants, J.M., 1981. Bumblebee Response to Variation in Nectar Availability. Ecology 62, 1648–1661. https://doi.org/10.2307/1941519

Polidori, C., Rubichi, A., Barbieri, V., Trombino, L., Donegana, M., 2010. Floral resources and nesting requirements of the ground-nesting social bee, Lasioglossum malachurum (hymenoptera: Halictidae), in a Mediterranean semiagricultural landscape. Psyche (London) 2010. https://doi.org/10.1155/2010/851947

Ponisio, L.C., Valdovinos, F.S., Allhoff, K.T., Gaiarsa, M.P., Barner, A., Guimarães, P.R., Hembry, D.H., Morrison, B., Gillespie, R., 2019a. A network perspective for community assembly. Front. Ecol. Evol. 7. https://doi.org/10.3389/fevo.2019.00103

Ponisio, L.C., Valdovinos, F.S., Allhoff, K.T., Gaiarsa, M.P., Barner, A., Guimarães, P.R., Hembry, D.H., Morrison, B., Gillespie, R., 2019b. A network perspective for community assembly. Front. Ecol. Evol. 7. https://doi.org/10.3389/fevo.2019.00103

Pornon, A., Escaravage, N., Burrus, M., Holota, H., Khimoun, A., Mariette, J., Pellizzari, C., Iribar, A., Etienne, R., Taberlet, P., Vidal, M., Winterton, P., Zinger, L., Andalo, C., 2016. Using metabarcoding to reveal and quantify plant-pollinator interactions. Sci. Rep. 6, 1–12. https://doi.org/10.1038/srep27282

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: Trends, impacts and drivers. Trends Ecol. Evol. 25, 345–353. https://doi.org/10.1016/j.tree.2010.01.007

Potts, S.G., Imperatriz-Fonseca, V., Ngo, H.T., Aizen, M.A., Biesmeijer, J.C., Breeze, T.D., Dicks, L. V., Garibaldi, L.A., Hill, R., Settele, J., Vanbergen, A.J., 2016. Safeguarding pollinators and their values to human well-being. Nature. https://doi.org/10.1038/nature20588

Potts, S.G., Vulliamy, B., Dafni, A., Ne'eman, G., Willmer, P., 2003. Linking bees and flowers: How do floral communities structure pollinator communities? Ecology 84, 2628–2642. https://doi.org/10.1890/02-0136

Powney, G.D., Carvell, C., Edwards, M., Morris, R.K.A., Roy, H.E., Woodcock, B.A., Isaac, N.J.B., 2019. Widespread losses of pollinating insects in Britain. Nat. Commun. 10, 1–6. https://doi.org/10.1038/s41467-019-08974-9

Pyke, G.H., 2016. Plant-pollinator co-evolution: It's time to reconnect with Optimal Foraging Theory and Evolutionarily Stable Strategies. Perspect. Plant Ecol. Evol. Syst. 19, 70–76. https://doi.org/10.1016/j.ppees.2016.02.004

Pywell, R.F., Warman, E.A., Hulmes, L., Hulmes, S., Nuttall, P., Sparks, T.H., Critchley, C.N.R., Sherwood, A., 2006. Effectiveness of new agri-environment schemes in providing foraging resources for bumblebees in intensively farmed landscapes. Biol. Conserv. 129, 192–206. https://doi.org/10.1016/j.biocon.2005.10.034

R Core Team, 2025a. R: A language and environment for statistical computing.

R Core Team, 2025b. R: A language and environment for statistical computing.

R Core Team, 2023. R: A language and environment for statistical computing.

R Core Team, 2022. R: A language and environment for statistical computing.

Rader, R., Bartomeus, I., Garibaldi, L.A., Garratt, M.P.D., Howlett, B.G., Winfree, R., Cunningham, S.A., Mayfield, M.M., Arthur, A.D., Andersson, G.K.S., Bommarco, R., Brittain, C., Carvalheiro, L.G., Chacoff, N.P., Entling, M.H., Foully, B., Freitas, B.M., Gemmill-Herren, B., Ghazoul, J., Griffin, S.R., Gross, C.L., Herbertsson, L., Herzog, F., Hipólito, J., Jaggar, S., Jauker, F., Klein, A.M., Kleijn, D., Krishnan, S., Lemos, C.Q., Lindström, S.A.M., Mandelik, Y., Monteiro, V.M., Nelson, W., Nilsson, L., Pattemore, D.E., Pereira, N.D.O., Pisanty, G., Potts, S.G., Reemer, M., Rundlöf, M., Sheffield, C.S., Scheper, J., Schüepp, C., Smith, H.G., Stanley, D.A., Stout, J.C., Szentgyörgyi, H., Taki, H., Vergara, C.H., Viana, B.F., Woyciechowski, M., 2016. Non-bee insects are important contributors to global crop pollination. Proceedings of the National Academy of Sciences USA 113, 146–151. https://doi.org/10.1073/pnas.1517092112

Raguso, R.A., 2004. Why are some floral nectars scented? Ecology 85, 1486–1494. https://doi.org/10.1890/03-0410

Reemer, M., 2018. Basisrapport voor de Rode Lijst Bijen.

Reemer, M., Renema, W., van Steenis, W., Zeegers, T., Barendregt, A., Smit, J.T., Veen, M. van, van Steenis, J., Van Der Leij, L., 2009. De Nederlandse Zweefvliegen, Nederlandse Fauna 8. https://doi.org/10.1017/CBO9781107415324.004

Renou-Wilson, F., Moser, G., Fallon, D., Farrell, C.A., Müller, C., Wilson, D., 2019. Rewetting degraded peatlands for climate and biodiversity benefits: Results from two raised bogs. Ecol. Eng. 127, 547–560. https://doi.org/10.1016/j.ecoleng.2018.02.014

Requier, F., Leonhardt, S.D., 2020. Beyond flowers: including non-floral resources in bee conservation schemes. J. Insect Conserv. 24, 5–16. https://doi.org/10.1007/s10841-019-00206-1

Révész, K., Gallé, R., Humbert, J.Y., Batáry, P., 2025. Effects of uncut refuge management on grassland arthropods – A systematic review. Glob. Ecol. Conserv. 57. https://doi.org/10.1016/j.gecco.2024.e03381

Révész, K., Torma, A., Szabó, M., Korsoveczky, L., Gallé-Szpisjak, N., Batáry, P., Gallé, R., 2024. Supportive effect of uncut refuge strips on grassland arthropods may depends on the amount and width of strips. Journal of Applied Ecology 61, 1894–1904. https://doi.org/10.1111/1365-2664.14699

Rivière, S., Provendier, D., Malaval, S., Sanson, B., Gourvil, J., Albert, A., Millet, J., 2022. Structuring supply chains of native plant material of wild and local provenance in France: A contribution to ecological restoration and Nature-based solutions. Nature-Based Solutions 2, 100035. https://doi.org/10.1016/j.nbsj.2022.100035

Rochette, N.C., Rivera-Colón, A.G., Catchen, J.M., 2019. Stacks 2: Analytical methods for paired-end sequencing improve RADseq-based population genomics. Mol. Ecol. 28, 4737–4754. https://doi.org/10.1111/mec.15253

Rohr, R.P., Saavedra, S., Bascompte, J., 2014. On the structural stability of mutualistic systems. Science (1979). 345. https://doi.org/10.1126/science.1253497

Roulston, T.H., Goodell, K., 2011. The role of resources and risks in regulating wild bee populations. Annu. Rev. Entomol. 56, 293–312. https://doi.org/10.1146/annurev-ento-120709-144802

Ryniewicz, J., Skłodowski, M., Chmur, M., Bajguz, A., Roguz, K., Roguz, A., Zych, M., 2020. Intraspecific Variation in Nectar Chemistry and Its Implications for Insect Visitors: The Case of the Medicinal Plant, Polemonium Caeruleum L. Plants 9, 1297. https://doi.org/10.3390/plants9101297

Salisbury, A., Bird, S., Bostock, H., Barrie, C., Harris, S., Marshall, R., Sanford, R., Tuson, M., Tew, N., 2025. Choosing to be picky: an evidence-based system for selecting pollinator-friendly garden plants to support biodiversity. Bioscience. https://doi.org/10.1093/biosci/biaf090

Schaffers, A.P., Raemakers, I.P., Sýkora, K. V., 2012. Successful overwintering of arthropods in roadside verges. J. Insect Conserv. 16, 511–522. https://doi.org/10.1007/s10841-011-9437-0

Schaminée, J.H.J., Stortelder, A.H.F., 2006. De natuur van het paradijs; het landschap van de Hof van Eden als voorbeeld voor natuurbeheer. Kunst en Wetenschap 15, 5–6.

Scheper, J., Bommarco, R., Holzschuh, A., Potts, S.G., Riedinger, V., Roberts, S.P.M., Rundlöf, M., Smith, H.G., Steffan-Dewenter, I., Wickens, J.B., Wickens, V.J., Kleijn, D., 2015. Local and landscape-level floral resources explain effects of wildflower strips on wild bees across four European countries. Journal of Applied Ecology 52, 1165–1175. https://doi.org/10.1111/1365-2664.12479

Scheper, J., Holzschuh, A., Kuussaari, M., Potts, S.G., Rundlöf, M., Smith, H.G., Kleijn, D., 2013. Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss - a meta-analysis. Ecol. Lett. 16, 912–920. https://doi.org/10.1111/ele.12128

Scheper, J., Reemer, M., Van Kats, R., Ozinga, W.A., Van Der Linden, G.T.J., Schaminée, J.H.J., Siepel, H., Kleijn, D., 2014. Museum specimens reveal loss of pollen host plants as key factor driving wild bee decline in the Netherlands. Proceedings of the National Academy of Sciences USA 111, 17552–17557. https://doi.org/10.1073/pnas.1412973111

Schilling, S., Pan, S., Kennedy, A., Melzer, R., 2018. MADS-box genes and crop domestication: The jack of all traits. J. Exp. Bot. https://doi.org/10.1093/jxb/erx479

Schmidt, M.H., Rocker, S., Hanafi, J., Gigon, A., 2008. Rotational fallows as overwintering habitat for grassland arthropods: The case of spiders in fen meadows. Biodivers. Conserv. 17, 3003–3012. https://doi.org/10.1007/s10531-008-9412-6

Schoener, T.W., 1974. Resource partitioning in ecological communities. Science (1979). 185, 27–39. https://doi.org/10.1126/science.185.4145.27

Schwarz, B., Vázquez, D.P., CaraDonna, P.J., Knight, T.M., Benadi, G., Dormann, C.F., Gauzens, B., Motivans, E., Resasco, J., Blüthgen, N., Burkle, L.A., Fang, Q., Kaiser-Bunbury, C.N., Alarcón, R., Bain, J.A., Chacoff, N.P., Huang, S.Q., LeBuhn, G., MacLeod, M., Petanidou, T., Rasmussen, C., Simanonok, M.P., Thompson, A.H., Fründ, J., 2020. Temporal scale-dependence of plant–pollinator networks. Oikos oik.07303. https://doi.org/10.1111/oik.07303

Searle, S.R., Speed, F.M., Milliken, G.A., 1980. Population marginal means in the linear model: An alternative to least squares means. American Statistician 34, 216–221. https://doi.org/10.1080/00031305.1980.10483031

Senapathi, D., Biesmeijer, J.C., Breeze, T.D., Kleijn, D., Potts, S.G., Carvalheiro, L.G., 2015a. Pollinator conservation - The difference between managing for pollination services and preserving pollinator diversity. Curr. Opin. Insect Sci. 12, 93–101. https://doi.org/10.1016/j.cois.2015.11.002

Senapathi, D., Carvalheiro, L.G., Biesmeijer, J.C., Evans, R.L., Mckerchar, M., Morton, R.D., Moss, E.D., Stuart, P., Roberts, M., Kunin, W.E., Potts, S.G., 2015b. The impact of over 80 years of land cover changes on bee and wasp pollinator communities in England. Proceedings of the Royal Society B: Biological Sciences 282.

Sexton, A.N., Emery, S.M., 2020. Grassland restorations improve pollinator communities: a meta-analysis. J. Insect Conserv. 24, 719–726. https://doi.org/10.1007/s10841-020-00247-x

Shackelford, G., Steward, P.R., Benton, T.G., Kunin, W.E., Potts, S.G., Biesmeijer, J.C., Sait, S.M., 2013. Comparison of pollinators and natural enemies: a meta-analysis of landscape and local effects on abundance and richness in crops. Biological Reviews 88, 1002–1021. https://doi.org/10.1111/brv.12040

Silva, V.H.D., Gomes, I.N., Cardoso, J.C.F., Bosenbecker, C., Silva, J.L.S., Cruz-Neto, O., Oliveira, W., Stewart, A.B., Lopes, A. V., Maruyama, P.K., 2023. Diverse urban pollinators and where to find them. Biol. Conserv. https://doi.org/10.1016/j.biocon.2023.110036

Slikboer, L., Godijn, N., 2020. Bijen op Zuid-Hollandse dijken. Hymenovaria 21, 67–69.

Smolders, A.J.P., Tomassen, H.B.M., Lamers, L.P.M., Lomans, B.P., Roelofs, J.G.M., 2002. Peat bog restoration by floating raft formation: the effects of groundwater and peat quality. Journal of Applied Ecology 39, 391–401. https://doi.org/10.1046/j.1365-2664.2002.00724.x

Spaethe, J., Tautz, J., Chittka, L., 2001. Visual constraints in foraging bumblebees: Flower size and color affect search time and flight behavior. Proceedings of the National Academy of Sciences 98, 3898–3903. https://doi.org/10.1073/pnas.071053098

Speelman, M., Kalkman, V., 2023. Verspreiding en ecologie van de heidehommel Bombus humilis in Nederland (Hymenoptera: Apidae). Entomolog. Ber. 83, 156–161.

Sponsler, D., Iverson, A., Steffan-Dewenter, I., 2023. Pollinator competition and the structure of floral resources. Ecography 2023, 1–16. https://doi.org/10.1111/ecog.06651

Staab, M., Pereira-Peixoto, M.H., Klein, A.M., 2020. Exotic garden plants partly substitute for native plants as resources for pollinators when native plants become seasonally scarce. Oecologia 194, 465–480. https://doi.org/10.1007/s00442-020-04785-8

Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C., Tscharntke, T., 2002. Scale-dependent effects of landscape context on three pollinator guilds. Ecology 83, 1421–1432.

Steidle, J.L.M., Kimmich, T., Csader, M., Betz, O., 2022. Negative impact of roadside mowing on arthropod fauna and its reduction with 'arthropod-friendly' mowing technique. Journal of Applied Entomology 146, 465–472. https://doi.org/10.1111/jen.12976

Sumner, S., Law, G., Cini, A., 2018. Why we love bees and hate wasps. Ecol. Entomol. 43, 836–845. https://doi.org/10.1111/een.12676

Swinkels, C., Liebrand, C., van Rooijen, N., Visser, E., De Kroon, H., 2020. De dijk als habitat voor bloemen en wilde bijen. De Levende Natuur 3, 96–101.

Swinkels, C., Slikboer, L., Raemakers, I., Godijn, N., Jongejans, E., Kroon, H. de, 2025. Phenology and flower species availability define wild bee communities on river embankments. Proceedings of the Royal Society B: Biological Sciences 292.

Tansley, A.G., 1939. The British Islands and Their Vegetation. Cambridge University Press.

Tarano, I.G., Boumal, T., De Toffoli, M., Buron, M., Kiljanek, T., Martel, A.C., Jacquemart, A.L., Agnan, Y., 2025. Are cover crops a potential threat for pollinators due to clothianidin residues in floral resources? Environ. Monit. Assess. 197, 1–13. https://doi.org/10.1007/s10661-025-14741-9

Tew, N.E., Baldock, K.C.R., Morten, J.M., Bird, S., Vaughan, I.P., Memmott, J., 2023. A dataset of nectar sugar production for flowering plants found in urban green spaces. Ecological Solutions and Evidence 4. https://doi.org/10.1002/2688-8319.12248

Tew, N.E., Baldock, K.C.R., Vaughan, I.P., Bird, S., Memmott, J., 2022. Turnover in floral composition explains species diversity and temporal stability in the nectar supply of urban residential gardens. Journal of Applied Ecology 59, 801–811. https://doi.org/10.1111/1365-2664.14094

Tew, N.E., Memmott, J., Vaughan, I.P., Bird, S., Stone, G.N., Potts, S.G., Baldock, K.C.R., 2021. Quantifying nectar production by flowering plants in urban and rural landscapes. Journal of Ecology 109, 1747–1757. https://doi.org/10.1111/1365-2745.13598

Thébault, E., Fontaine, C., 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. Science (1979). 329, 853–856. https://doi.org/10.1126/science.1188321

Tilman, David., 1982. Resource competition and community structure. Princeton University Press.

Timberlake, T.P., Tew, N.E., Memmott, J., 2024. Gardens reduce seasonal hunger gaps for farmland pollinators. Proceedings of the Royal Society B: Biological Sciences 291. https://doi.org/10.1098/rspb.2024.1523

Timberlake, T.P., Vaughan, I.P., Memmott, J., 2019. Phenology of farmland floral resources reveals seasonal gaps in nectar availability for bumblebees. Journal of Applied Ecology 56, 1585–1596. https://doi.org/10.1111/1365-2664.13403

Tomassen, H.B.M., Smolders, A.J.P., Limpens, J., Lamers, L.P.M., Roelofs, J.G.M., 2004. Expansion of invasive species on ombrotrophic bogs: desiccation or high N deposition? Journal of Applied Ecology 41, 139–150. https://doi.org/10.1111/j.1365-2664.2004.00870.x

Tommasi, N., Ferrari, A., Labra, M., Galimberti, A., Biella, P., 2021. Harnessing the power of metabarcoding in the ecological interpretation of plant—pollinator DNA data: Strategies and consequences of filtering approaches. Diversity (Basel). 13. https://doi.org/10.3390/d13090437

Torma, A., Bozsó, M., 2016. Effects of habitat and landscape features on grassland Orthoptera on floodplains in the lower reaches of the Tisza River Basin. Eur. J. Entomol. 113, 60–69. https://doi.org/10.14411/eje.2016.007

Torma, A., Császár, P., 2013. Species richness and composition patterns across trophic levels of true bugs (Heteroptera) in the agricultural landscape of the lower reach of the Tisza River Basin. J. Insect Conserv. 17, 35–51. https://doi.org/10.1007/s10841-012-9484-1

Trunschke, J., Junker, R.R., Kudo, G., Alexander, J.M., Richman, S.K., Till-Bottraud, I., 2024. Effects of climate change on plant-pollinator interactions and its multitrophic consequences. Alp. Bot. https://doi.org/10.1007/s00035-024-00316-w

Tsiolis, K., Potts, S.G., Garratt, M., Tilston, E.L., Burman, J., Rintoul-Hynes, N.L.J., Fountain, M.T., 2022. The importance of soil and vegetation characteristics for establishing ground-nesting bee aggregations. J. Pollinat. Ecol. 31, 186–200. https://doi.org/10.26786/1920-7603(2022)682

Uhl, B., Wölfling, M., Fiedler, K., 2021. Qualitative and Quantitative Loss of Habitat at Different Spatial Scales Affects Functional Moth Diversity. Front. Ecol. Evol. 9. https://doi.org/10.3389/fevo.2021.637371

Unie van Waterschappen, 2015. Kerngegevens Waterschappen. Den Haag.

Urbanowicz, C., Muñiz, P.A., McArt, S.H., 2020. Honey bees and wild pollinators differ in their preference for and use of introduced floral resources. Ecol. Evol. 10, 6741–6751. https://doi.org/10.1002/ece3.6417

Uyttenbroeck, R., Piqueray, J., Hatt, S., Mahy, G., Monty, A., 2017. Increasing plant functional diversity is not the key for supporting pollinators in wildflower strips. Agric. Ecosyst. Environ. 249, 144–155. https://doi.org/10.1016/j.agee.2017.08.014

Valdovinos, F.S., 2019. Mutualistic networks: moving closer to a predictive theory. Ecol. Lett. 22, 1517–1534. https://doi.org/10.1111/ele.13279

Valdovinos, F.S., Brosi, B.J., Briggs, H.M., Moisset de Espanés, P., Ramos-Jiliberto, R., Martinez, N.D., 2016. Niche partitioning due to adaptive foraging reverses effects of nestedness and connectance on pollination network stability. Ecol. Lett. 19, 1277–1286. https://doi.org/10.1111/ele.12664

Valdovinos, F.S., Marsland, R., 2021. Niche theory for mutualism: A graphical approach to plant-pollinator network dynamics. American Naturalist 197, 393–404. https://doi.org/10.1086/712831

Valdovinos, F.S., Moisset de Espanés, P., Flores, J.D., Ramos-Jiliberto, R., 2013. Adaptive foraging allows the maintenance of biodiversity of pollination networks. Oikos 122, 907–917. https://doi.org/10.1111/j.1600-0706.2012.20830.x

Valido, A., Rodríguez-Rodríguez, M.C., Jordano, P., 2019a. Honeybees disrupt the structure and functionality of plant-pollinator networks. Sci. Rep. 9, 1–11. https://doi.org/10.1038/s41598-019-41271-5

Valido, A., Rodríguez-Rodríguez, M.C., Jordano, P., 2019b. Honeybees disrupt the structure and functionality of plant-pollinator networks. Sci. Rep. 9. https://doi.org/10.1038/s41598-019-41271-5

van der Kooi, C.J., Kelber, A., 2022. Achromatic Cues Are Important for Flower Visibility to Hawkmoths and Other Insects. Front. Ecol. Evol. 10. https://doi.org/10.3389/fevo.2022.819436

van der Kooi, C.J., Reuvers, L., Spaethe, J., 2023. Honesty, reliability, and information content of floral signals. iScience 26, 1–9. https://doi.org/10.1016/j.isci

van der Kooi, C.J., Spaethe, J., 2025. Flower colour contrast, 'spectral purity' and a red herring. Plant Biol. 27, 189–194. https://doi.org/10.1111/plb.13767

van der Kooi, C.J., Stavenga, D.G., Arikawa, K., Belušič, G., Kelber, A., 2021. Evolution of Insect Color Vision: From Spectral Sensitivity to Visual Ecology. Annual Review of Entomology Downloaded from www.annualreviews.org. Guest 66, 435–461. https://doi.org/10.1146/annurev-ento-061720

Van Duinen, G.-J., Klimkowska, A., De Hullu, E., Van Swaay, C., Eysink, F., Bouwman, J., Jansen, A., 2013. Duurzaam behoud en ontwikkeling van bovenveengraslanden in het Bargerveen. Nijmegen.

van Guldener, A., Hofman, J., Roelevink, B., Rossenaar, A.J., Logemann, D., 2016. Natura 2000-beheerplan Bargerveen.

van Klink, R., Menz, M.H.M., Baur, H., Dosch, O., Kühne, I., Lischer, L., Luka, H., Meyer, S., Szikora, T., Unternährer, D., Arlettaz, R., Humbert, J.Y., 2019. Larval and phenological traits predict insect community response to mowing regime manipulations. Ecological Applications 29. https://doi.org/10.1002/eap.1900

Van Swaay, C., Borkent, B., 2024. Vlinderbalans 2024 met het jaarverslag van de meetnetten vlinders, libellen en hommels 2023. Wageningen.

van Swaay, C., Termaat, T., Plate, C., 2011. Handleiding Landelijke Meetnetten Vlinders en Libellen. Wageningen.

Van Swaay, C.A.M., Dennis, E.B., Schmucki, R., Sevilleja, C.G., Åström, S., Balalaikins, M., Barea-Azcón, J.M., Bonelli, S., Botham, M., Cancela, J.P., Collins, S., De Flores, M., Dapporto, L., Dopagne, C., Dziekanska, I., Escobés, R., Faltynek Fric, Z., Fernández-García, J.M., Fontaine, B., Glogovčan, P., Gracianteparaluceta, A., Harpke, A., Harrower, C., Heliölä, J., Houard, X., Judge, M., Kolev, Z., Komac, B., Kühn, E., Kuussaari, M., Lang, A., Lysaght, L., Maes, D., McGowan, D., Mestdagh, X., Middlebrook, I., Monasterio, Y., Monteiro, E., Munguira, M.L., Musche, M., Olivares, F.J., Õunap, E., Ozden, O., Pavlíčko, A., Pendl, M., Pettersson, L.B., Rákosy, L., Roth, T., Rüdisser, J., Šašić, M., Scalercio, S., Settele, J., Sielezniew, M., Sobczyk-Moran, G., Stefanescu, C., Švitra, G., Szabadfalvi, A., Tiitsaar, A., Titeux, N., Tzirkalli, E., Ubach, A., Verovnik, R., Vray, S., Warren, M.S., Wynhoff, I., Roy, D.B., 2022. European Grassland Butterfly Indicator 1990-2020 Technical report.

Vanbergen, A.J., Garratt, M. P., Vanbergen, A.J., Baude, M., Biesmeijer, J.C., Britton, N.F., Brown, M.J.F., Brown, M., Bryden, J., Budge, G.E., Bull, J.C., Carvell, C., Challinor, A.J., Connolly, C.N., Evans, D.J., Feil, E.J., Garratt, Mike P., Greco, M.K., Heard, M.S., Jansen, V.A.A., Keeling, M.J., Kunin, W.E., Marris, G.C., Memmott, J., Murray, J.T., Nicolson, S.W., Osborne, J.L., Paxton, R.J., Pirk, C.W.W., Polce, C., Potts, S.G., Priest, N.K., Raine, N.E., Roberts, S., Ryabov, E. V., Shafir, S., Shirley, M.D.F., Simpson, S.J., Stevenson, P.C., Stone, G.N., Termansen, M., Wright, G.A., 2013. Threats to an ecosystem service: Pressures on pollinators. Front. Ecol. Environ. 11, 251–259. https://doi.org/10.1890/120126

Vanbergen, A.J., the Insect Pollinators Initiative, 2013. Threats to an ecosystem service: pressures on pollinators. Front. Ecol. Environ. 11, 251–259. https://doi.org/10.1890/120126

Vanparys, V., Meerts, P., Jacquemart, A.L., 2008. Plant-pollinator interactions: comparison between an invasive and a native congeneric species. Acta Oecologica 34, 361–369. https://doi.org/10.1016/j.actao.2008.06.008

Vaudo, A.D., Dyer, L.A., Leonard, A.S., 2024. Pollen nutrition structures bee and plant community interactions. Proc. Natl. Acad. Sci. U. S. A. 121. https://doi.org/10.1073/pnas.2317228120

Vaudo, A.D., Tooker, J.F., Grozinger, C.M., Patch, H.M., 2015. Bee nutrition and floral resource restoration. Curr. Opin. Insect Sci. 10, 133–141. https://doi.org/10.1016/j.cois.2015.05.008

Vázquez, D.P., Bluthgen, N., Cagnolo, L., Chacoff, N.P., 2009. Uniting pattern and process in plant-animal mutualistic networks: A review. Ann. Bot. 103, 1445–1457. https://doi.org/10.1093/aob/mcp057

Veen, P., Jefferson, R., de Smidt, J., van der Straaten, J., 2009. Grasslands in Europe of high nature value.

Venjakob, C., Ruedenauer, F.A., Klein, A.M., Leonhardt, S.D., 2022. Variation in nectar quality across 34 grassland plant species. Plant Biol. 24, 134–144. https://doi.org/10.1111/plb.13343

Verbeek, P., Prins, U., Ketelaar, R., Eichorn, K., Brouwer, E., 2021. Het Akkerboek. KNNV Uitgeverij, Zeist, the Netherlands.

Verberk, W.C.E.P., Leuven, R.S.E.W., van Duinen, G.A., Esselink, H., 2010. Loss of environmental heterogeneity and aquatic macroinvertebrate diversity following large-scale restoration management. Basic Appl. Ecol. 11, 440–449. https://doi.org/10.1016/j.baae.2010.04.001

Villemey, A., Jeusset, A., Vargac, M., Bertheau, Y., Coulon, A., Touroult, J., Vanpeene, S., Castagneyrol, B., Jactel, H., Witte, I., Deniaud, N., Flamerie De Lachapelle, F., Jaslier, E., Roy, V., Guinard, E., Le Mitouard, E., Rauel, V., Sordello, R., 2018. Can linear transportation infrastructure verges constitute a habitat and/or a corridor for insects in temperate landscapes? A systematic review. Environ. Evid. 7, 1–33. https://doi.org/10.1186/s13750-018-0117-3

Wäckers, F.L., Romeis, J., van Rijn, P., 2007. Nectar and Pollen Feeding by Insect Herbivores and Implications for Multitrophic Interactions. Annu. Rev. Entomol. 52, 301–323. https://doi.org/10.1146/annurev.ento.52.110405.091352

Wagemaker, C.A.M., Mommer, L., Visser, E.J.W., Weigelt, A., van Gurp, T.P., Postuma, M., Smit-Tiekstra, A.E., de Kroon, H., 2021. msGBS: A new high-throughput approach to quantify the relative species abundance in root samples of multispecies plant communities. Mol. Ecol. Resour. 21, 1021–1036. https://doi.org/10.1111/1755-0998.13278

Wallis de Vries, M., Nijssen, M., Smit, J., Noordijk, J., Zollinger, R., 2022. Optimalisatie van begrazing voor de heidefauna - Resultaten Fase 2. Wageningen.

Wallis de Vries, M., Oteman, B., 2019. Klimaatstresstest voor Dagvlinders in Drenthe. Wageningen.

Warren, M.S., Maes, D., van Swaay, C.A.M., Goffart, P., Van Dyck, H., Bourn, N.A.D., Wynhoff, I., Hoare, D., Ellis, S., 2021. The decline of butterflies in Europe: Problems, significance, and possible solutions. Proceedings of the National Academy of Sciences 118. https://doi.org/10.1073/pnas.2002551117

Warton, D.I., Hui, F.K.C., 2011. The arcsine is asinine: The analysis of proportions in ecology. Ecology 92, 3–10. https://doi.org/10.1890/10-0340.1

Warzecha, D., Diekötter, T., Wolters, V., Jauker, F., 2018. Attractiveness of wildflower mixtures for wild bees and hoverflies depends on some key plant species. Insect Conserv. Divers. 11, 32–41. https://doi.org/10.1111/icad.12264

Westrich, P., 2019. Die Wildbienen Deutschlands. Verlag Eugen Ulmer.

Whittaker, R.H., 1967. Gradient Analysis of Vegetation. Biological Reviews 42, 207–264. https://doi.org/10.1111/j.1469-185X.1967.tb01419.x

Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis.

Williams, N.M., Kremen, C., 2007a. Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape. Ecological Applications 17, 910–921. https://doi.org/10.1890/06-0269

Williams, N.M., Kremen, C., 2007b. Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape. Ecological Applications 17, 910–921. https://doi.org/10.1890/06-0269

Williams, P.H., Brown, M.J.F., Carolan, J.C., An, J., Goulson, D., Aytekin, A.M., Best, L.R., Byvaltsev, A.M., Cederberg, B., Dawson, R., Huang, J., Ito, M., Monfared, A., Raina, R.H., Schmid-Hempel, P., Sheffield, C.S., Šima, P., Xie, Z., 2012. Unveiling cryptic species of the bumblebee subgenus Bombus s. str. worldwide with COI barcodes (Hymenoptera: Apidae). Syst. Biodivers. https://doi.org/10.1080/14772000.2012.664574

Wilson, J.B., Peet, R.K., Dengler, J., Pärtel, M., 2012. Plant species richness: The world records. Journal of Vegetation Science 23, 796–802. https://doi.org/10.1111/j.1654-1103.2012.01400.x

Winfree, R., Bartomeus, I., Cariveau, D.P., 2011. Native pollinators in anthropogenic habitats. Annu. Rev. Ecol. Evol. Syst. 42. https://doi.org/10.1146/annurev-ecolsys-102710-145042

Wintergerst, J., Kästner, T., Bartel, M., Schmidt, C., Nuss, M., 2021. Partial mowing of urban lawns supports higher abundances and diversities of insects. J. Insect Conserv. 25, 797–808. https://doi.org/10.1007/s10841-021-00331-w

Wood, T.J., Holland, J.M., Goulson, D., 2015. Pollinator-friendly management does not increase the diversity of farmland bees and wasps. Biol. Conserv. 187, 120–126. https://doi.org/10.1016/j.biocon.2015.04.022

Zobel, M., 1997. The relative role of species pools in determining plant species richness. An alternative explanation of species coexistence? Trends Ecol. Evol. 12, 266–269. https://doi.org/10.1016/S0169-5347(97)01096-3

Zoller, L., Bennett, J., Knight, T.M., 2023. Plant–pollinator network change across a century in the subarctic. Nat. Ecol. Evol. 7. https://doi.org/10.1038/s41559-022-01928-3

Zurbuchen, A., Landert, L., Klaiber, J., Müller, A., Hein, S., Dorn, S., 2010. Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. Biol. Conserv. 143, 669–676. https://doi.org/10.1016/j.biocon.2009.12.003



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SUMMARY

Introduction

In recent decades, it has become clear that flower-visiting insects, or pollinators, are declining in abundance. This is concerning, as pollinators are essential for ecosystem functioning. Approximately three-quarters of all plant species depend on insect pollination for their reproduction, and many agricultural crops also benefit from their activities. A major driver of pollinator decline is the loss of suitable habitats and the reduction of floral resources in the landscape, making food sources increasingly scarce.

To protect pollinators, many conservationists and landscape managers therefore focus on increasing the availability of flowers. Well-known examples include flower strips in agricultural landscapes and flower-rich roadside verges. A large body of research shows that such measures can be effective, leading to higher pollinator abundance and increased species richness.

However, there are important caveats. Although pollinators often benefit from increased floral resources, not all species respond in the same way. From an ecological theory perspective, this is not surprising. Populations are constrained by limiting factors. For pollinators, flowers can be such a limiting factor, but once sufficient floral resources are available, other factors may become more important. These include a lack of suitable nesting sites, exposure to pesticides, or the quality of the surrounding landscape. This thesis therefore addresses the question of to what extent pollinator communities are actually limited by floral resource availability.

Pollinators on dikes

To address this question, the first part of this thesis examines how pollinator communities change along gradients of floral richness. By comparing sites ranging from flower-poor to highly flower-rich, it is possible to assess how pollinators respond to increasing floral availability. This research was conducted in dike grasslands. The Netherlands has almost 18,000 kilometres of dikes, making these grasslands an extensive and potentially important habitat for pollinators.

Chapter 2 shows that dike grasslands harbour surprisingly rich bee communities. More than 150 wild bee species were recorded across the studied sites, including many species listed on the Dutch Red List. Moreover, flower-rich dike grasslands appear to be important not only as foraging habitat, but likely also as nesting habitat for many species.

Pollinators and floral richness

Chapters 2, 3 and 4 of this thesis together show that the response of pollinator communities to floral richness is complex. On the one hand, both pollinator abundance and spe-

cies richness increased strongly with increasing numbers of flowers and flower species. However, this increase is not unlimited: at relatively low levels of floral richness, a clear saturation occurs, after which additional flowers contribute only marginally to higher abundance or species richness. This suggests that floral limitation is alleviated for a large part of the pollinator community relatively quickly, and that other factors subsequently become more important in shaping community composition.

At the same time, not all pollinators respond in the same way. Rare and threatened species, in particular, are more frequently found at the most flower-rich sites. In addition, the way pollinators use floral resources also changes. As more flower species become available, pollinators collect resources from a smaller number of plant species, and niche overlap between species decreases. As a result, different pollinators appear to interfere less with one another. Thus, additional flowers do not necessarily lead to larger communities, but may contribute to more stable and more specialised pollinator communities.

Pollinators and management

In the second part of this thesis, the question of floral limitation is addressed from a management perspective. This involves examining how pollinators respond to different management interventions, which together provide insight into the role of floral resources in restoration practices.

Mosaic mowing

Chapter 5 presents the results of an experiment on the effects of mosaic mowing in dike grasslands. In the experimental sites, part of the vegetation remained unmown while the rest was mown. Changes in these strips were compared to the situation before mowing and to unmown control plots.

This shows that a sudden reduction in floral resources was associated with an increased concentration of pollinators in the remaining refuges, indicating increased competition for limited resources. Subsequently, both pollinator abundance and species richness in these refuges declined to below the level of the unmown controls. This underlines that, despite the relatively rapid saturation of floral richness observed in Chapters 2 and 3, pollinator communities remain strongly dependent on sufficient floral resources at the right time of the season.

Ecosystem restoration

Another increasingly common form of management focuses on steering ecosystem processes rather than targeting individual taxonomic groups. It is therefore relevant to ask whether this approach can also support pollinator communities, even without directly increasing floral resources. Chapter 6 presents the results of an analysis of two long-term monitoring datasets from the Bargerveen nature reserve. In recent decades, extensive

measures have been taken there to restore hydrological conditions. The analysis shows that, in contrast to many national trends, pollinator abundance and species richness remained remarkably stable. Even trends in rare species showed no decline. This suggests that restoring ecosystem processes as a whole can be an effective strategy for conserving pollinators.

Garden varieties

In restoration and sowing projects, seed mixes often include non-native plant species or cultivated varieties of native species. Although these may appear visually attractive, it remains unclear to what extent pollinators actually use these novel floral resources. Chapter 7 examines flower visitation on different cornflower types: the native form and three cultivated varieties. Pollinators were given a choice between these four options in field experiments.

The results show that wild-type plants are significantly more attractive to pollinators than cultivated ornamental varieties. This pattern was consistent in both urban and rural environments and across different pollinator groups, indicating a robust effect. This highlights that not only the quantity of flowers matters, but also which plant species are used.

Conclusions

The studies in this thesis show that the relationship between pollinators and flowers is not linear. Pollinators are undeniably dependent on flowers as a food resource, but this dependence appears to saturate quickly: beyond a certain level of floral richness, community size and species richness increase only marginally. At the same time, interactions within communities change, with reduced niche overlap and increased specialisation.

These complex relationships are also reflected in the management experiments. The sudden reduction in floral resources through mosaic mowing was associated with a decline in pollinator abundance in the remaining vegetation. This suggests that pollinators in dike grasslands are adapted to a high and seasonal availability of flowers, and that disruption of established management can lead to temporary negative effects on community composition. In contrast, management focused on restoring ecosystem processes, as in Chapter 6, may contribute to the long-term stability and persistence of pollinator communities.

Together, these results show that pollinator communities benefit from a high availability of flowers, but are at the same time strongly dependent on the context in which these flowers occur. Communities appear to adapt over time to local and consistent management, highlighting the importance of stable management regimes. In addition, landscape context plays an important role: pollinators require more than flowers alone to persist in the long term.

SAMENVATTING

Inleiding

De afgelopen decennia is duidelijk geworden dat bloembezoekende insecten, oftewel bestuivers, sterk in aantal afnemen. Dit is zorgwekkend, omdat bestuivers essentieel zijn voor het functioneren van ecosystemen. Ongeveer driekwart van alle plantensoorten is voor hun voortplanting afhankelijk van bestuiving door insecten, en ook veel landbouwgewassen profiteren van hun activiteiten. Een belangrijke oorzaak van de achteruitgang van bestuivers is het verlies van geschikte leefgebieden en de afname van bloemen in het landschap, waardoor voedselbronnen schaarser worden.

Om bestuivers te beschermen richten veel natuur- en landschapsbeheerders zich daarom op het vergroten van de beschikbaarheid van bloemen. Bekende voorbeelden hiervan zijn bloemstroken in agrarische gebieden en bloemrijke bermen. Veel onderzoek laat zien dat dergelijke maatregelen effectief kunnen zijn en leiden tot hogere aantallen bestuivers en meer soorten.

Toch zijn hier kanttekeningen bij te plaatsen. Hoewel bestuivers vaak profiteren van een toename van bloemen, blijken niet alle soorten hier in dezelfde mate op te reageren. Vanuit de ecologische theorie is dit niet verrassend. Populaties worden begrensd door factoren die hun groei beperken. Voor bestuivers kunnen bloemen zo'n beperkende factor zijn, maar wanneer voldoende bloemen aanwezig zijn, kunnen andere factoren belangrijker worden. Denk bijvoorbeeld aan een tekort aan geschikte nestplaatsen, de invloed van pesticiden of de kwaliteit van het omliggende landschap. Daarom staat in dit proefschrift de vraag centraal in hoeverre bestuivergemeenschappen daadwerkelijk worden beperkt door de beschikbaarheid van bloemen.

Bestuivers op dijken

Om deze vraag te beantwoorden heb ik in het eerste deel van dit proefschrift onderzocht hoe bestuivergemeenschappen veranderen langs gradiënten van bloemrijkdom. Door locaties te vergelijken die uiteenlopen van bloemarm tot zeer bloemrijk kan worden vastgesteld hoe bestuivers reageren op toenemende beschikbaarheid van bloemen. Dit onderzoek vond plaats op dijkgraslanden. Nederland telt bijna 18.000 kilometer aan dijken, waardoor deze graslanden een omvangrijk en potentieel belangrijk leefgebied vormen voor bestuivers.

In hoofdstuk 2 laat ik zien dat dijkgraslanden verrassend rijke bijengemeenschappen herbergen. Op de onderzochte locaties werden meer dan 150 soorten wilde bijen aangetroffen, waaronder veel soorten die op de Nederlandse Rode Lijst staan. Bovendien blijken bloemrijke dijkgraslanden niet alleen belangrijk als foerageergebied, maar waarschijnlijk ook als nesthabitat voor veel soorten.

Bestuivers en bloemrijkdom

Hoofdstukken 2, 3 en 4 van dit proefschrift laten samen zien dat de reactie van bestuivergemeenschappen op bloemrijkdom complex is. Enerzijds namen zowel het aantal bestuivers als het aantal soorten sterk toe bij toenemende hoeveelheid bloemen en bloemsoorten. Deze toename verloopt echter niet onbeperkt: al bij relatief lage niveaus van bloemrijkdom treedt een duidelijke verzadiging op, waarna extra bloemen nog maar beperkt bijdragen aan hogere aantallen of meer soorten. Dit suggereert dat bloembeperking voor een groot deel van de bestuivergemeenschap snel afneemt, en dat andere factoren vervolgens belangrijker worden in het bepalen van gemeenschapssamenstelling.

Tegelijkertijd blijkt dat niet alle bestuivers hetzelfde reageren. Vooral zeldzame en bedreigde soorten komen vaker voor op de meest bloemrijke locaties. Daarnaast veranderen ook de manieren waarop bestuivers gebruikmaken van bloemen. Naarmate meer bloemsoorten beschikbaar zijn, verzamelen bestuivers hun voedsel van een kleiner aantal plantensoorten en neemt de overlap tussen soorten af. Hierdoor lijken verschillende bestuivers elkaar minder in de weg te zitten. Extra bloemen leiden dus niet noodzakelijk tot grotere gemeenschappen, maar kunnen wel bijdragen aan stabielere en meer gespecialiseerde bestuivergemeenschappen.

Bestuivers en beheer

In het tweede deel van dit proefschrift benader ik de vraag naar bloembeperking vanuit natuurbeheer. Daarbij onderzoek ik hoe bestuivers reageren op verschillende beheermaatregelen, die samen een beeld geven van het belang van bloemen in herstelprojecten.

Gefaseerd maaien

In hoofdstuk 5 presenteer ik de resultaten van een experiment naar de effecten van gefaseerd maaien op dijkgraslanden. Op de experimentele locaties bleef een deel van de vegetatie ongemaaid staan terwijl de rest werd gemaaid. De ontwikkelingen in deze stroken werd vergeleken met de situatie voor het maaien, en de ontwikkelingen in ongemaaide controle vlakken.

Dit laat zien dat een plotselinge vermindering van de beschikbaarheid van bloemen gepaard kan gaan met een toename in concentratie van bestuivers in resterende refugia, wat wijst op verhoogde concurrentie om beperkte middelen. Vervolgens nemen zowel de abundantie als het aantal soorten in deze refugia af tot onder het niveau van ongemaaide controles. Dit onderstreept dat, ondanks de relatief snelle verzadiging van bloemrijkdom in hoofdstukken 2 en 3, bestuivergemeenschappen sterk afhankelijk blijven van voldoende bloemen op het juiste moment in het seizoen.

Ecosysteem herstel

Een andere vorm van beheer die steeds meer opkomt is die van sturing op ecosysteem processen, in plaats van interventies gericht op een enkele soortgroep. Het is interessant of deze aanpak ook bestuivergemeenschappen kan ondersteunen, ondanks dat het aantal bloemen niet hoeft toe te nemen. In hoofdstuk 6 presenteer ik de uitkomsten van de analyse van twee langlopende monitoringsdatasets uit het Bargerveen. In het Bargerveen zijn de laatste decennia veel maatregelen genomen om de hydrologische condities op orde te krijgen. De analyse laat zien dat, tegen veel landelijke trends in, bestuiver aantallen en soortenrijkdom verrassend gelijk bleef. Ook als we kijken naar de trend van specifieke, zeldzame soorten zien we geen afname. Dit laat zien dat ook herstel van ecosystemen als geheel een effectieve strategie kan zijn voor het behoud van bestuivers.

Tuinvarianten

In inzaaiprojecten worden vaak zaden van niet inheemse planten gebruikt, of tuinvarianten van inheemse planten. Hoewel dit er mooi uitziet, is het maar de vraag in welke mate bestuivers gebruik kunnen maken van deze nieuwe introducties. In hoofdstuk 7 kijk ik naar het bloembezoek op verschillende korenbloemen, de inheemse variant en drie tuinvarianten. Bestuivers kregen in het veld de mogelijkheid om te kiezen tussen de vier varianten.

Uit het experiment bleek dat wilde vormen aanzienlijk aantrekkelijker zijn voor bestuivers dan gekweekte siervariëteiten. Dit was het geval zowel in de stad als in het buitengebied, en voor verschillende groepen bestuivers. Daarmee is deze keuze duidelijk robuust. Dit onderstreept dat niet alleen de hoeveelheid bloemen van belang is, maar ook welke plantensoorten worden gebruikt.

Conclusies

De studies in dit proefschrift laten zien dat de relatie tussen bestuivers en bloemen niet lineair is. Bestuivers zijn onmiskenbaar afhankelijk van bloemen als voedselbron, maar deze afhankelijkheid lijkt snel te verzadigen: boven een bepaald niveau van bloemrijkdom nemen gemeenschapsgrootte en soortenrijkdom nog maar beperkt toe. Tegelijkertijd veranderen wel de interacties binnen de gemeenschap, met minder niche-overlap en meer specialisatie.

Deze complexe relaties komen ook naar voren in de beheersexperimenten. Het plotseling verminderen van het beschikbare voedselaanbod door gefaseerd maaien ging gepaard met een afname van het aantal bestuivers in de overgebleven vegetatie. Dit suggereert dat bestuivers op dijken zijn aangepast aan een hoge en seizoensgebonden beschikbaarheid van bloemen, en dat verstoring van dit beheer kan leiden tot tijdelijke negatieve effecten op de samenstelling van de gemeenschap. Anderzijds lijkt beheer gericht op

herstel van ecosysteemprocessen, zoals in hoofdstuk 6, juist te kunnen bijdragen aan het behoud en de stabiliteit van bestuivergemeenschappen.

Gezamenlijk laten deze resultaten zien dat bestuivergemeenschappen profiteren van een hoge beschikbaarheid van bloemen, maar tegelijkertijd sterk afhankelijk zijn van de context waarin deze bloemen voorkomen. Gemeenschappen lijken zich over tijd aan te passen aan lokaal en consistent beheer, wat het belang van stabiele beheerregimes onderstreept. Daarnaast speelt ook de landschappelijke context een belangrijke rol: bestuivers hebben meer nodig dan bloemen alleen om duurzaam te kunnen voortbestaan.

DANKWOORD

Eureka! De befaamde kreet van Archimedes tekent nog steeds hoe we over wetenschappers denken; het eenzame genie dat na lang nadenken plotsklaps met een doorbraak komt. Niets is natuurlijk minder waar. Een idee in een vacuüm is zelden een goed idee, en een eenzame denker komt evenzo niet ver. Als er al een genius bestaat, dan bestaat die enkel bij de gratie van een scenius: de mensen om haar of hem heen. Tijdens mijn promotietraject heb ik, zeker geen genius, het geluk gehad omringd te zijn door veel lieve en inspirerende mensen die ik hier graag wil bedanken. En dat moet uiteraard met te weinig woorden.

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ABOUT THE AUTHOR



Constant Swinkels was born on 9 April 1995. Throughout his youth, he was fascinated by nature. He started out as a birdwatcher but soon broadened his interests to plants and insects. This early fascination shaped his later work in two important ways. First, it sparked a lasting interest in the question of how so many different species can coexist. Second, it led him to realize that nature conservation is often constrained not by a lack of knowledge, but by the choices society makes.

These interests motivated him to pursue both a Bachelor's and a Master's degree in Biology at Radboud University, specializing in community ecology. After graduating, he taught courses on plant biodiversity and soon began the research that forms the basis of this thesis.

While this thesis highlights the research side of his six years at Radboud University, his contributions extended beyond research alone. He taught numerous courses and engaged a broad public audience through science communication. In recognition of his work, he received the Hermesdorf Talent Award and the PhD Teaching Award, and was selected as one of the Faces of Science of the KNAW.

PUBLICATIONS

Peer-reviewed journals

Published

- **Swinkels, C.,** Slikboer, L., Raemakers, I., Godijn, N., Jongejans, E. & de Kroon, H. Phenology and flower species availability define wild bee communities on river embankments. Proceedings of the Royal Society B. Volume 292, 137-145. (2025)
- **Swinkels, C.,** van der Wal, J.E.M., Stinn, C., Monteza-Moreno, C. & Jansen, P.A. Dynamic interactions between ocelots and prey in a Neotropical moist forest. Journal of Mammalogy. Volume 147, Issue 1, 137-145. (2023)
- Bergmeier, E., Sakellarakis, F.-N., Strid, A. & **Swinkels, C**. New additions to the flora of Prespa, Greece. Phytologia Balcanica 26(1): 103–130, Sofia, 2020 (2020)

Submitted

- **Swinkels, C**., de Weert, I., Biella, P., Jongejans, E., & de Kroon, H. Unequal pollinator benefits from partial mowing regimes in a large-scale field experiment. In review at *journal of insect diversity and conservation*
- Schuurman, T. H., Verberk, W. C. E. P., Raemakers, I. P., Visser, E. J. W. & **Swinkels, C**. Key floral metrics shaping local pollinator communities: a comparison between flower species richness, floral unit abundance and nectar sugar production. *Journal of Animal Ecology*

National Journals

- **Swinkels, C.,** Liebrand, C., van Rooijen, N., Visser, E. & de Kroon, H. De dijk als habitat voor bloemen en wilde bijen. De Levende Natuur. Issue 3, pp 96-101. (2020)

Books & book chapters

- Hilbers, D. & **Swinkels, C**. Crossbill Guides Nederland (2-parts). KNNV publishing, Zeist, the Netherlands. (2025)
- Hilbers, D., Wouterse, K & **Swinkels, C**., A. Crossbill Guides – Lanzarote & Fuerteventura Spain. KNNV publishing, Zeist, the Netherlands. (2023)
- Hilbers, D., Wouterse, K & **Swinkels, C**., A. Crossbill Guides – Tenerife & La Gomera Spain. KNNV publishing, Zeist, the Netherlands. (2023)
- Hilbers, D., **Swinkels, C**. & Vliegenthart, A. Crossbill Guides – Provence and Camargue. France. KNNV publishing, Zeist, the Netherlands. (2020)
- **Swinkels, C** & van Rooijen N.M. 'Vegetatiekundige Monografieën - buigen of barsten' (Vegetation Monographs – Bend or break). Chapter 3; 'vasthouden of loslaten: duinbeheer onder veranderende klimaatomstandigheden' (Hold on or let go: dune conservation in a changing climate). pp 69-95. KNNV. (2017)

Popular publications and reports

- **Swinkels, C.** Opinion - Radboudbeleid vooral groen achter de oren: biodiversiteit geef je geen impuls met een paar bomen (Radboud Biodiversity Policy mostly 'green behind the ears'). Vox, Nijmegen, the Netherlands. (2025)
- Van juridische fictie naar ecologische realiteit: Een multidisciplinaire analyse van de Hatertse en Overasseltse Vennen op ecologisch, juridisch en governancevlak. Rapport uit transdisciplinaire cursus 'Governance of Nature Conservation'.(2025)
- **Swinkels, C.** & Meessen, M.S. Fascinatie voor beesten van de duivel. Blog on NEMO Kennislink. (2024)
- **Swinkels, C.** Waarom iedere wetenschapper een mediatraining zou moeten doen. For Radboud in'to Languages. (2024)
- Board ComeniusNetwork. 'Toekomstige minister, geef docenten ruimte voor onderwijsinnovatie'. Science Guide. (2023)
- **Swinkels, C.** Een prijs voor biodiversiteit. Blog on NEMO Kennislink. (2021)
- **Swinkels, C.** Lang leve 'de biodiversiteit'. Blog on NEMO Kennislink. (2021)
- Runhaar, J., R.C.M. Verdonschot, **C. Swinkels**, E.C.H.E.T. Lucassen, R. Loeb & A.J.P. Smolders. Ontwikkeling broekbossen OBN227-BE, VBNE, Driebergen. (2019)

RESEARCH DATA MANAGEMENT

The research in this thesis has been carried out under the RDM policy of the Radboud Institute for Biological and Environmental Sciences, version 25-Mar-2026 accessed at www.ru.nl/ribes.

List of archived data per chapter:

Chapter 1 & 8: no code or data has been produced

Chapter 2: data and code available at https://datadryad.org/dataset/doi:10.5061/dryad.ffbg79d5b

Chapter 3 - 7: data and code available at https://10.5281/zenodo.19218578. Code and data will be made publicly available with the publication of associated chapters and are available upon request from the author before that time.



