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Sampling Pollinator Communities and Interactions Across Changing Landscapes: Insights from a German Case Study

Dissertation

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"We should preserve every scrap of biodiversity as priceless while we learn to use it and come to understand what it means to humanity" - E. O. Wilson

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Chapters 2 and 3 have been published and Chapter 4 is in the process of being published in international journals as open access articles distributed under the terms and conditions of the Creative Commons Attribution license which permits and use, distribution, and reproduction in any medium, provided the original authors and sources are credited. For the other parts of this dissertation, reprint of the presented material requires the author's permissions. Copyright is with the authors.

Summary

Land use change is a process in which human activity changes the natural environment, whether it be from natural to artificial (i.e. urbanization) or a transfer to cultivated land use (i.e. agricultural). This turnover continues to transform the landscape at an increasing rate and is known to be a global threat to pollinator and plant communities. Therefore, it is important to understand how land use change influences these communities, as over 90% of plant species require pollinators for reproduction, including 35% of crop plants. Urban sprawl is also decreasing semi-natural habitats, which are important for supporting diverse communities of plants and pollinators. Some research has shown that urban environments provide sufficient resources for wide variety of different species. However, syntheses of this research are difficult as individual studies vary in methods, landuse gradients, and taxon-level identification.

This thesis adds to resolving this difficulty and is composed of five chapters that contribute to our understanding of community-level patterns of pollinators and plant-pollinator interactions in response to changes in land use. The **first chapter** serves as an introduction to the broad topic of pollination in the context of different land uses by looking at pollination as an ecosystem service and the importance of non-bee pollinators. I also explore different methods, scales, functional traits, and land use gradients used in the following chapters. Finally, I look at how I can use plant-pollinator interactions and network structure to understand the impact of land use on plant and pollinator communities.

The second and third chapter have been published in international peer-reviewed journals and the fourth chapter is in submission. All three are data-based chapters and can serve as standalone studies. The **second chapter** looks at two commonly used methods for observing pollinator species richness, abundance and composition in the field— yellow combined flight traps and net sampling. I focused on two important and diverse groups of pollinators, wild bees (Hymenoptera: Anthophila) and hoverflies (Diptera: Syrphidae). I was interested if differences in these methods were potentially biased towards individuals or species with specific traits. I captured more individuals and more species of bees with the traps and more individuals and more species of hoverflies with the nets, finding that the traps captured more small-sized bees and hoverflies. However, differences in rarefied richness was less dramatic between the sampling methods for bees and there was no difference for hoverflies. Therefore, the differences in species richness between the sampling methods was mainly driven by the differences in the number of individuals captured between the two methods.

The **third chapter** looks at what pollinators share plants in semi-natural habitats with the mass-flowering crop, Oilseed Rape (OSR). I was interested in if OSR was attracting more pollinators than the other flowering plants nearby and if the plants that share interactions with OSR also shared

similar floral traits or roles in a network. I found that OSR shared most of its pollinators with four common plants. OSR's role in the network was as module hub and primarily influenced the other plants in its module that had similar functional traits. However, the plants that most influenced the pollination of OSR had different functional traits and were part of different modules.

In the **fourth chapter**, I looked at how plant-pollinator community composition and network structure change across two gradients of land use—urban and agricultural. I found the community composition of plants and pollinators changed significantly across the land use gradients, however the presence of keystone pollinator taxa results in minimal changes to network structure (Syrphidaehoverflies, Halictidae- sweat bees). Yet species composition of these families did not vary across the land use gradients. These families, however, are important for maintaining structure within the network.

The final and **fifth chapter** is a synthesis of how the findings from the three data chapters contribute to our general understanding of different land uses on plant-pollinator communities and interactions and how they can be used to help create meaningful and successful conservation measures.

Zusammenfassung

Landnutzungsänderung ist ein Prozess, bei dem menschliche Aktivitäten die natürliche Umwelt verändern, sei es von der natürlichen zur künstlichen (z. B. Urbanisierung) oder zur kultivierten Landnutzung (z. B. Landwirtschaft). Dieser Wandel verändert die Landschaft immer schneller und stellt bekanntermaßen eine globale Bedrohung für Bestäuber- und Pflanzengemeinschaften dar. Daher ist es wichtig zu verstehen, wie sich die veränderte Landnutzung auf diese Gemeinschaften auswirkt, da über 90 % der Pflanzenarten zur Fortpflanzung Bestäuber benötigen, darunter 35 % der Nutzpflanzen. Die Zersiedelung der Landschaft führt zu einer Verringerung naturnaher Lebensräume, die für die Erhaltung vielfältiger Pflanzen- und Bestäubergemeinschaften wichtig sind. Einige Forschungsarbeiten haben gezeigt, dass städtische Umgebungen ausreichende Ressourcen für eine Vielzahl verschiedener Arten bieten. Eine Synthese dieser Forschungsarbeiten ist jedoch schwierig, da sie sich in Bezug auf Methoden, Landnutzungsgradienten und Ebene der taxonomischen Identifikation unterscheiden.

Die vorliegende Doktorarbeit trägt zur Lösung dieses Problems bei und besteht aus fünf Kapiteln, die zu unserem Verständnis der Muster von Bestäubern auf Gemeinschaftsebene und der Interaktionen zwischen Pflanzen und Bestäubern als Reaktion auf Landnutzungsänderungen beitragen. **Das erste Kapitel** dient als Einführung in das breite Thema der Bestäubung im Zusammenhang mit Landnutzungsänderungen, indem es die Bestäubung als Ökosystemdienstleistung und die Bedeutung von Nicht-Bienen-Bestäubern betrachtet. Ich erkunde verschiedene Methoden, Maßstäbe, funktionelle Merkmale und Landnutzungsgradienten, die in den folgenden Kapiteln verwendet werden. Schließlich beschäftige ich mich damit, wie ich die Interaktionen zwischen Pflanzen und Bestäubern und die Netzwerkstruktur nutzen kann, um die Auswirkungen von Landnutzungsänderungen auf Pflanzen- und Bestäuber Gemeinschaften zu verstehen.

Das zweite und dritte Kapitel wurden in internationalen, von Experten begutachteten Fachzeitschriften veröffentlicht, und das vierte Kapitel ist in Vorbereitung. Alle drei Kapitel sind Datenkapitel und können als eigenständige Studien dienen. **Das zweite Kapitel** befasst sich mit zwei häufig verwendeten Methoden zur Beobachtung des Artenreichtums, der Abundanz und der Zusammensetzung von Bestäubern im Feld - gelbe kombinierte Flugfallen und Netzproben. Ich konzentrierte mich auf zwei wichtige und vielfältige Gruppen von Bestäubern, Wildbienen (Hymenoptera: Anthophila) und Schwebfliegen (Diptera: Syrphidae). Ich wollte herausfinden, ob die Unterschiede zwischen diesen Methoden möglicherweise zu einer Verzerrung in Bezug auf Individuen oder Arten mit bestimmten Merkmalen führen. Mit den Fallen fingen wir mehr Individuen und Arten von Bienen, mit den Netzen mehr Individuen und Arten von Schwebfliegen. Ich stellte fest, dass ich mit Fallen mehr kleine Bienen und Schwebfliegen gefangen haben. Der Unterschied in Artenreichtum war jedoch bei den Bienen weniger dramatisch, und bei den Schwebfliegen gab es keinen Unterschied. Die Unterschiede im Artenreichtum zwischen den Beprobungsmethoden waren also hauptsächlich auf die unterschiedliche Anzahl der gefangenen Individuen zurückzuführen.

Das dritte Kapitel befasst sich mit Bestäubern, die sowohl Pflanzen in naturnahen Lebensräumen sowie Raps (englisch: oilseed rape, OSR) bestäuben. Ich wollte herausfinden, ob sich Pflanzen die zur selben Zeit wie OSR Bestäuber mit selbigen teilen und ob dies mehr ist als Zufall. Außerdem untersuchte ich, ob die Modularität des Netzwerks auf Artenmerkmalen beruht und welche Pflanzen Knotenpunkte und Verbindungsglieder des Netzwerks sind. Ich fand heraus, dass OSR die meisten seiner Bestäuber mit vier generalisierten Pflanzen teilte und dass die gemeinsame Nutzung somit nicht mehr als durch Zufall zu erwarten war. OSR fungierte als Knotenpunkt des Moduls und beeinflusste in erster Linie die anderen Pflanzen in demselben Modul, die ähnliche funktionale Merkmale aufwiesen. Die Pflanzen, die die Bestäubung von OSR am stärksten beeinflussten, haben jedoch unterschiedliche funktionale Merkmale und sind Teil verschiedener Module.

Im vierten Kapitel untersuche ich, wie sich die Pflanzen-Bestäuber-Gemeinschaft und ihre Zusammensetzung und Netzwerkstruktur über zwei Gradienten der Landnutzungsänderung - städtisch und landwirtschaftlich - verändern. Ich fand heraus, dass sich die Zusammensetzung der Pflanzenund Bestäubergemeinschaften über die Landnutzungsgradienten hinweg erheblich verändert, jedoch verändert sich die Netzwerkstruktur aufgrund des Vorhandenseins von Schlüsselbestäuber-Taxa (Syrphidae-Schwebfliegen, Halictidae- Schmal- / Furchenbienen) nur minimal. Die Artenzusammensetzung dieser Familien variierte jedoch nicht über die Landnutzungsgradienten hinweg. Diese Familien sind jedoch wichtig für die Aufrechterhaltung der Verschachtelung, Verallgemeinerung und Gleichmäßigkeit innerhalb des Netzwerks.

Im letzten und fünften Kapitel fasse ich zusammen, wie die Erkenntnisse aus den drei Datenkapiteln zu unserem allgemeinen Verständnis der Auswirkungen von Landnutzungsänderungen auf Pflanzen-Bestäuber-Gemeinschaften und -Interaktionen beitragen und wie sie genutzt werden können, um sinnvolle und erfolgreiche Schutzmaßnahmen zu entwickeln.

General Introduction

1. Importance of pollinating insects in changing landscapes

Pollination is when pollen, the male gametes of flowering plants, is transferred to the stigma, the female receptor of a flower. Typically pollen must be transferred from one plant to another plant of the same species in order for successful fertilization to occur, which is typically transported by insects. Pollinating animals are important for the reproductive success of up to 87 % of flowering plants (Ollerton *et al.* 2011). Thus, they play a role in maintaining plant biodiversity (Memmott *et al.* 2004; Klein *et al.* 2007; Garibaldi *et al.* 2013; Carrié *et al.* 2017), improving crop yield (Garibaldi *et al.* 2014), and in the stability and resilience of ecosystems (Bai *et al.* 2004; Tilman *et al.* 2014). Economically, pollinators contribute globally \$235–\$577 billion (in 2009, United States dollars) in ecosystem services (Lautenbach *et al.* 2012) as they provide services for approximately 35% of global crop production (Klein *et al.* 2007) and can contribute on average over \$3,000 per hectare towards crop production (Kleijn *et al.* 2015).

There are several factors that influence the contribution of pollinators to crop production. These include habitat structure and heterogeneity, suitable food and nesting resources, and the abundance of functional groups of pollinators. Services provided by pollinators towards crop production are influenced by the surrounding landscape structure and its heterogeneity. Historically, the cultural landscape in Europe was comprised of a mosaic landscape with small-scale cultivation areas of orchards, meadows, pastures and forests (Fig 1). This type of landscape is still present in Eastern Europe, although it is slowly disappearing with the intensification of the landscapes to large-scale farms (Kuemmerle *et al.* 2016).



Fig 1: Respresentation of extensive, mosaic landscape (left) vs. intensive, monoculture landscape (right). Drawing credit: Demetra Rakosy

This conversion from one habitat type to another due to human activity is the process of land use change. A third of global land has been affected by land use change in the last six decades (Winkler *et al.* 2021) and is one of the main agents negatively affecting pollinator and plant communities (González-Varo *et al.* 2013; Vanbergen & The Insect Pollinators Initiative 2013). Several studies have demonstrated that habitat alteration is associated with changes in diversity, abundance and composition of pollinator (Winfree *et al.* 2009; Potts *et al.* 2010; Senapathi *et al.* 2017; Seibold *et al.* 2019) and plant communities (Laliberté *et al.* 2010; Nicholson *et al.* 2017). For example, conversion from a mosaic landscape to a large-scale arable field reduces the number and diversity of feeding and nesting habitats for pollinators (Kline & Joshi 2020).

Sites surrounded by more semi-natural areas or sites that are better connected to these areas have increased crop yield compared to those embedded in more human-altered landscapes (Raderschall *et al.* 2021). Semi-natural areas are ecosystems that are human altered, but with most of their processes of biodiversity intact (IPBES 2019), which can include hedgerows, meadows, or flower strips along field margins. These areas are highly diverse (Kennedy *et al.* 2013), are important for providing shelter and nesting sites for insect pollinators (Holzschuh *et al.* 2013; Simba *et al.* 2018), and offer consistent and diverse food resources for pollinators that are not always available in agricultural landscapes (Kennedy *et al.* 2013; Burkle *et al.* 2017; Cole *et al.* 2017), thus contributing to the survival of pollinators.

The necessary food and nesting resources differ across pollinator taxa. These different pollinator taxa also vary significantly in their contributions to pollination across plant species and habitats, and both bee and non-bee species are known to contribute significantly to global crop pollination (Rader et al. 2016, 2020). Some pollinating taxa are specialized, providing pollinator services to a limited number of species or genera of plants (i.e. specialists, Minckley & Roulston 2006); whereas others are generalized and provide pollinator service to a large number of plant species (i.e. generalists). The main orders of flower visitors in Europe are butterflies (Lepidoptera), flies (Diptera), bees (Hymenoptera), and some species of beetles (Coleoptera). Beetles are the most numerous and diverse order and therefore represent about 40 percent of known insects (Fig 2c-d). Most beetle species are not direct pollinators; however, some species will eat the flowers or rest on them, inadvertently carrying pollen from one flower to the next (Fallon 2020). Similarly, butterflies land on flowers mainly for feeding on nectar and will inadvertely spread pollen that sticks to their probosics (mouth part), body or legs. They specialize on brightly-colored and highly scented flowers that contain nectar and are usually in clusters (Fig 2a-b). Although butterflies are thought of as a main group of pollinators by the general public, they are less efficient in moving pollen between plants as bees (Jennersten 1984).



Fig 2: Pictures of common groups of flower visitors: Butterflies (Lepidoptera, a-b), beetles (Coleoptera, c-d), flies (Diptera, e-h), and bees (Hymenoptera, i-l). a) an orange skipper (Ochlodes sylvanus) on cream pincushions (Scabiosa ochroleuca), b) a garden whites butterfly (Pieres sp.) on black hornhound (Ballota nigra), c) a common red soldier beetle (Rhagonycha fulva) on wild chamomile (Tripleurospermum inodorum), d) a chrysomelid leaf beetle (Cryptocephalus hypochaeridis) on alfalfa (Medicago sativa), e) a Death's Head hoverfly (Myanthropa florea) on hogweed (Heracleum sphondylium), f) the long hoverfly (Sphaerophora scripta) on a dandilion (Taraxicum officinale), g) a bee-fly (Villa hottentotta.) on a Tansy (Tanacetum vulgare), h) thickheaded fly (Cnopidae) and a green bottle fly (Calliphoridae) on a Tansy (Tanacetum vulgare), i) a honeybee (Apis mellifera) on oilseed rape (Brassica napus), j) a buff-tailed bumblebee (Bombus terrestris) on a Norway maple (Acer platanoides), k) a cuckoo-bee (Sphecodes sp.) on a common hawthorn flower (Crataegus monogyna), l) great banded furrow-bee (Halictus subauratus) on Yarrow (Achillea millefolium). Photo credits: A. Thompson.

Bees vary in their body shape and functionality as pollinators (Fig 2i-l). They are often the focus of pollinator research because of their dominance in both abundance and diversity as flower visitors (Potts *et al.* 2003; Garibaldi *et al.* 2013; Kleijn *et al.* 2015; Winfree *et al.* 2018). Managed bee species, such as honeybees (*Apis mellifera*, Fig 2i) and bumble bees (*Bombus terrestris/ impatiens*, Fig 2j), are important for crop pollination (Velthuis & Doorn 2006; Rollin & Garibaldi 2019). Honeybees are one of the most common managed bee species, due to the fact that their colonies can easily be managed (semi-domestication) and transported. They are used for crop pollination with thousands of colonies being imported for certain crops, such as apple orchards (Somerville 1999).

They are generalist pollinators, visiting most flowering plants that contain pollen or nectar, and are effective pollinators due to their large numbers (Hung *et al.* 2018). However, they have been shown to be less efficient at delivering pollen per visit than wild bee species and can have negative affects on wild bee communities (Rader *et al.* 2009; Lindström *et al.* 2016; Mallinger *et al.* 2017). Some crop species, such as tomatoes are specifically pollinated by bumble bees, because of a special mechanism called "buzz pollination," where the vibrations from the buzzing of the bee are necessary to release the pollen (Vallejo-Marín 2019). Wild bees contain species such as mason bees (*Osmia sp.*), carpenter bees (*Xylocopa sp.*), leaf-cutter bees (*Megachile sp.*), and sweat bees (*Lassioglossum sp./Halictus sp.*), all of which differ in their traits and foraging habits (Westrich 2018; Querejeta *et al.* 2023). These bees can be specialists, such as *Osmia adunca* (Natternkopf-Mauerbiene (DE)), which visits mainly *Echium vulgare* (Gewöhnliche Natternkopf (DE)) or oil-collecting bees, such as *Macropis fulvipes*, which forages for floral oils such as on *Lysimachia* sp. (Rasmussen *et al.* 2020).

Similarly to bees, flies also have several different groups that vary in their traits and contribution to pollination (Fig 2e-h). Flies usually specialize on white or yellow flowers. Hoverflies (Syrphidae) are the most common family of pollinating flies, but other families such as the Tachinid flies (Tachinidae) or Bee-flies (Bombylidae) also contribute. For example, in some habitats, flies are the most abundant pollinators, and might be more important than bees, even if they are not as efficient in delivering pollen (Rader *et al.* 2016; Zoller *et al.* 2023). Non-bee pollinators can provide over 50% of the pollination service in some areas (Cusser *et al.* 2021), so it is critical for a broad group of pollinators to be the focus of ecological monitoring and research. To date, less is known about how non-bee pollinators respond to land use changes.

2. Methods for comparing pollinator communities

Pollinator monitoring is accomplished through a variety of methods, including visual observations and counts, sweep netting, net sampling of floral visitors, light or bait traps for nocturnal pollinators, and using passive insect traps (e.g., flight, pan, vane, or malaise traps). Visual observations and counts work well for taxa that are identifiable in the field. For example, transect walks have been successfully employed for butterfly monitoring across the world (Pollard 1977; Caldas & Robbins 2003; Nowicki *et al.* 2008; Van Swaay *et al.* 2008; Habel *et al.* 2019). The other methods are more suitable for monitoring taxa that require laboratory methods (e.g., microscopy or genetics) for identification to species level (Roulston *et al.* 2007; Westphal *et al.* 2008; Wilson *et al.* 2008; Nielsen *et al.* 2011; Popic *et al.* 2013). Two commonly employed methods are flight traps and net sampling. Traps are simple to construct and can quickly capture the flying insect community by attracting insects with specific colors. The traps, however, collect species that are not always pollinators. In addition, traps can document the presence and abundance of pollinating species, but not their roles (i.e., which plant species they are visiting, Roulston *et al.* 2007; Tuell & Isaacs 2009;

Gonçalves & Oliveira 2013; Popic *et al.* 2013; Joshi *et al.* 2015). Net sampling captures insects that are interacting with flowers, and thus provides information on both insect presence and the insect role in the community. However, net sampling is more time consuming in the field, and may capture fewer individuals compared to traps that can be set out for several weeks.

Previous research comparing the diversity and/or composition of pollinating insects captured in flight traps versus net sampling find that the methods differ in their results (Popic *et al.* 2013; O'Connor *et al.* 2019). Popic and colleagues sampled the entire insect community using the two methods across three different sampling periods. They found that net sampling captured more species number and richness and that species composition differed between the different sampling methods and sampling periods. O'Connor and colleagues found the opposite to be true—that flight traps collected more species, although the abundance differed between species groups.

To fully evaluate and understand biodiversity differences between sampling methods, it is necessary to consider multiple components of biodiversity (i.e. abundance, richness, evenness) and more than one spatial grain (Chase et al. 2018; McGlinn et al. 2019). Components include the abundance of individuals, species richness and species evenness. All else being equal, species richness of a sample will be higher when there are more individuals in the sample and when those individuals are sampled from more even communities. Species accumulation curves can be used to understand the relationship between the number of individuals sampled and species richness (Thompson & Withers 2003). If the shapes of species accumulation curves differ between sampling methods, this means that the effect size of method on biodiversity could change in magnitude or even direction across different spatial grains because the number of species observed increases non-linearly with spatial scale. For the case of comparing sampling methods, the diversity can be measured at one trap or site (alpha) and across all traps or sites (gamma). Effect sizes, the difference in biodiversity components across a factor (e.g., sampling method), can change in magnitude or even direction depending on the spatial sampling grain (Chase et al. 2018). Evaluation of multiple components of biodiversity allows a more complete understanding of whether methods alter biodiversity by capturing different abundance of individuals or by capturing a more even or uneven distribution of individuals of different species. Understanding the biases between different sampling methods can help us when interpreting and comparing different measures of biodiversity across different scales.

Different sampling methods can also help us in understanding the functional distributions of pollinators across different land uses. For example, the color, height, size, or shape of the traps and different netting methods (i.e. sampling only flower plants or all vegetation) are known to collect a different compositon of species (Tuell & Isaacs 2009; Joshi *et al.* 2015; Shrestha *et al.* 2019). Different species have different functional traits, that can help in determining their role or efficiencey as pollinator (Rosas-Guerrero *et al.* 2014). Common functional traits considered for pollinators are

body size, nesting preferences, life history, and habitat preference. It is predicted and often (but not always) observed, that plants and pollinators that interact share matching traits (Buchholz *et al.* 2020; Peralta *et al.* 2020; Van der Kooi *et al.* 2021). Land use change is known to filter out species with certain traits, reducing the functional diversity of the community (Forrest *et al.* 2015; Bartomeus *et al.* 2018). Conversion of land can affect pollinators directly, by reducing the availability of nesting habitats, which varies between different species, for example, materials needed for cavity nesters or open, sandy pits for ground nesting species.

Currently different methods are employed to determine how land use change influences the species and functional diversity of pollinators. However, studies focus on different pollinator groups and employ different methods. In order to synthesize results across studies, we must first understand how sampling methods influence the species and functional diversity of pollinators, and how the results depend on the spatial grain of investigation. **Chapter 2** of my thesis aims to advance our understanding of the differences in diversity and composition of insects sampled using two methods, yellow combined flight traps and net sampling, by considering multiple components of biodiversity, multiple spatial grains and functional traits of insects. Two pollinator groups were considered, wild bees (Hymenoptera: Anthophila) and hoverflies (Diptera: Syrphidae). These two groups were chosen as they are abundant, diverse and are important for providing pollination services in the study region as well as globally (Ssymank *et al.* 2008; Jauker *et al.* 2012; Rader *et al.* 2016).

3. Importance of plant-pollinator network structure

It is not enough to just record pollinator diversity. Pollinator diversity is linked to ecosystem services such as pollination through the interaction with plants. Thus understanding the impact of land-use change on the functioning of ecosystems (such as pollination) requires considering the community of plant-pollinator interactions as a network across multiple sites, as change in land use is also known to impact the structure of these plant-pollinator interaction networks (Devoto *et al.* 2012; Doré *et al.* 2021a). A plant-pollinator interaction network is a bipartite network, where every member of one trophic level only interacts with members of the other (i.e. plants and pollinators, Dormann *et al.* 2008). The links between nodes of plants and pollinators reflect either the presence of an interaction (qualitative networks) or the frequency of the interaction (i.e. number of times an pollinator species has visited a certain plant species; quantitative networks).

Metrics have been developed to quantify the topology of networks, and these metric values provide information about the robustness of a network to perturbation (Kaiser-Bunbury *et al.* 2010; Bascompte & Scheffer 2023). Metrics can thus reveal the richness and evenness of interactions, their compartmentalization (nestedness, modularity) as well as patterns of resource partitioning (specialization). The diversity or interaction richness of a network is calculated as the number of

different interactions within the network, whereas interaction evenness evaluates the homogeneity of links in the network. Higher evenness indicates more uniformity in interactions between nodes (Fisogni *et al.* 2021), whereas evenness approaches zero as relative abundances varies (Pyron 2010). Nestedness is a community-wide pattern in which generalist taxa tend to interact with specialists and vice versa (Bascompte *et al.* 2003). Nested networks are more robust to the loss of a node, as the loss of specialists will not result in cascading extinctions to their interaction partners (Memmott *et al.* 2004; Fortuna & Bascompte 2006). Modularity measures the structure of the network, dividing the network into modules (or compartments). Species within the modules interact with each other stronger than other species in the network, thus showing the strength and frequency of interactions between species (Newman 2006). Specialization evaluates the degree to which species in the network restrict their partners to a subset of those that are available (Blüthgen *et al.* 2006). More generalized networks are more robust to perturbations due to the redundancy of interactions (Zografou *et al.* 2020; Fisogni *et al.* 2021), but specialized pollinators are likely to offer better pollination services to plants (Minckley & Roulston 2006).

Network stuctures and meterics have not only been used to identify pollinator functions within the network, but have also been used to link functional traits for both plants and pollinators. For example, flower traits, such as flower size or shape, can help determine the identity and frequency of polliantors (Stang *et al.* 2007; Klumpers *et al.* 2019) and can also influence the structure of plant–pollinator interaction networks (Fantinato *et al.* 2019). Flower shapes and rewards can also determine interactions with pollinators (Koski *et al.* 2015; Lázaro *et al.* 2020), whereas pollinator traits can determine dispersal distance, energy requirement, and ability to access a flower (Hall *et al.* 2019). Functional traits and network structures can also be used to determine the effect of different management types on the plant and pollinator communties (Motivans Švara *et al.* 2021).

Management types can have differing effects on the plant and pollinator communities. Agriculturally managed landscapes make over 50 % of German's area and almost 40 % of the European and global landscape (FAO 2020; eurostat 2021; Bundesministerium für Ernährung und Landwirtschaft (BMEL) 2022), making it an important habitat to study. In agroecosystems, mass flowering crops provide a large but homogenous food resource to pollinators (Ferreira *et al.* 2013). However, this occurs in pulses, whereas semi-natural areas can offer consistent floral resources over a long period of time and supplement their feeding after the flowering of the crop (Mandelik *et al.* 2012). In Germany, Oilseed Rape (OSR) was planted on over 1.1 million hectares in 2022, making it the fourth most produced crop (BMEL 2022). OSR can self-pollinate but insect pollination is known to increase its seed set (Langridge & Goodman 1982; Manning *et al.* 2005; Bommarco *et al.* 2012). The plants in the surrounding landscape provide important ecosystem functions by providing shared food resources to pollinators of OSR. However, most pollination research on OSR has considered

only the pollinators that visit this crop plants (Langridge & Goodman 1982; Jauker & Wolters 2008), or how the crop presence affects pollinator communities and not the surrounding plant community (Diekötter *et al.* 2010). Despite abundant research on OSR and its effect on the pollinator community, less is known about its role in the plant-pollinator network. It is also not known which of the co-flowering plants share more pollinators that would be expected by chance, and have strong indirect effects on pollination of OSR. In **Chapter 3**, I quantified a plant-pollinator interaction network in order to determine the co-flowering plants that are most similar in their visiting pollinator compositions to OSR, and if this similarity was higher than expected by chance. I tested this by creating a null model that considers the plants that are visited by the most abundant pollinators in the community are likely to share pollinators by chance. Another goal was to quantify the module that OSR is a part of, and if the other plants in this module have similar floral traits. Finally, I identified the species that act as keystones in the network, by providing many interactions within their modules and/or by connecting modules. Lastly, I used Müller's index to determine the indirect effect the plants and pollinators have on each other, due to their shared interactions.

4. Communities and network structure across land use gradients

Modern agricultural areas are dominated by large-scale farms, which are characteristic for Western Europe (Lowder et al. 2016). In such landscapes, little semi-natural habitats have remained and studies have shown that these intensively managed landscapes are often no longer able to sustain the necessary pollinator services (Kremen et al. 2002; Bartomeus et al. 2014; Deguines et al. 2014). Although urban areas make up a small proportion of land use globally (2 %, Liu et al. 2014), it is predicted that this area will triple by 2030 in response to the growing population (Seto *et al.* 2012). This expansion can have devastating effects on the biodiversity of some groups, but cities are known to be "biodiverstiy hotspots" for other groups (Elmqvist et al. 2013). While there has been separate research on the effects of agricultural intensification and urbanization on pollinator biodiversity, few studies consider both simultaneously. Thus, it is currently unclear if these two highly anthroporgenic land uses have similar or differing effects on biodiversity. Most studies show that semi-natural habitats have higher diversity of plants and pollinators compared to agricultural habitats (Carvalheiro et al. 2010; Laliberté et al. 2010; Le Féon et al. 2010; Nicholson et al. 2017) and urban habitats (Ahrné et al. 2009; Bates et al. 2011; Geslin et al. 2013). However, this is not always the case, with some studies showing similar diversity of pollinators in semi-natural habitats compared to urban habitats (Fitch 2017; Ellis & Wilkinson 2020), which could be due to the differences in resolution and scales of the studies.

In accordance with community assembly theory, the composition and relative abundance of species in a community is determined through environmental filtering, i.e. species with traits better suited for an agricultural environment thrive in that environment. Thus it could be predicted that agricultural and

urban landscapes select for different species. However, both land uses could have similar effects on the community, negatively effecting specialist species and therefore creating an environment where generalist thrive. To date, few studies have compared these multiple land use variables (agricultural, urban, and semi-natural) simultaneously, but those that have, found differences in taxonomic responses (e.g. hoverflies and wild bees) and species preferences between the different land uses (Verboven et al. 2014; Baldock et al. 2015; Collado et al. 2019). Most research has only looked at how composition of plants or pollinators are affected by the land use change. Both agricultural and urban habitats can act as strong filters to plants and pollinators, but they may filter for different taxa or even for a different range of taxa (i.e. urban habitats may be more heterogeneous and thus support more taxa, urban habitats also harbor much more species which are not of local origin). While previous studies did not consider whether multiple land use variables had similar or different effects on network structure, I hypothesized that both types of land use change will filter for plant and pollinator species that are flexible in their resource use, and thus shift the network structure to be less specialized, more nested, and more even in both urban and agricultural areas (Weiner et al. 2014; Takemoto & Kajihara 2016; Doré et al. 2021b). Chapter 4 examined how agricultural and urban areas compare to each other and to semi-natural habitats in terms of diversity, composition and network structure. I additionally quantified which pollinator families have important connector roles in the networks.

5. Thesis scope

In this thesis, I investigated how pollinator communities and their interactions with plant changes across different land use categories. First, I was interested in understanding how different sampling methods compare in their ability to capture bee and syrphid communities and if this was related to the functional traits of these pollinator groups (Chapter 2). Second, I applied net sampling to determine how the pollinator and plant communities and their interactions were influenced by the mass flowering crop, OSR (Chapter 3). Finally, I assessed how different anthropogenically altered habitat types (e.g. agricultural and urban) compare to semi-natural habitats to determine the impact of land use change on plant and pollinator communities and network structure (Chapter 4).



Fig 3: Graphical abstract of thesis' research chapters. Chapter 2 focused on comparing different methods, pan traps and netting, to detect community change. Chapter 3 focused on how interactions are influenced by a mass flowering crop and if functional traits play a role in determining interactions. Chapter 4 focused on how communities and networks for plants and pollinators change across different land uses, from highly agricultural to highly urban.

Fieldwork for all three research chapters was conducted over the course of three summers (2017-2019) at six different agricultural sites that are a part of the Terrestrial Environmental Observatories Network (TERENO, www.tereno.net, Zacharias et al. 2011) and of the German and European LTER (Long-Term Ecological Research) network (Müller et al. 2010) in Sachsen-Anhalt, Germany (Fig 4). The sites have been monitored since 2008 and are 4 km by 4 km. These sites all have varying degree of agricultural intensity—from a moderate to high percentage and different type of land management practices—livestock grazing, hay production, or agricultural production. They also vary in their altitude, slope, soil properties and climatic conditions, (e.g., mean annual precipitation and temperature; Frenzel et al. 2016; Papanikolaou et al. 2017; Slabbert et al. 2022). An additional eight sites were sampled within Sachsen-Anhalt and Sachsen in 2019 and 2020. These sites had a higher percentage of semi-natural or urban land use and were used in Chapter 4's analyses. The most urban sites include the cities of Halle (Saale) and Leipzig, both of which have pollinator friendly initiatives (i.e. Leipzig Summt, Blühwiese Halle). For the network analyses, all individuals from the orders of Hymenoptera, Diptera, Lepidoptera, and Coleoptera that were observed visiting a flowering plant were considered pollinators. I found it important to observed all plant-visiting pollinators and not just bees.



Fig 4: Map of sampled locations with in Sachsen-Anhalt und Sachsen, Germany. Black points indicated TERENO sites, where data was used in all three research chapters. Grey points indicate additional sampling sites used for Chapter 4.

In **Chapter 5**, I synthesize the key findings of the thesis and discuss (1) the broader applicability of the results, (2) the potential application of my results to inform conservation of plant-pollinator interactions and their services to wild and agriculturally important plants, and (3) the limitations of my approach and specific needs for future studies.

6. References

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Pollinator sampling methods influence community patterns assessments by capturing species with different traits and at different abundances

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ABSTRACT

In order to synthesize changes in pollinating insect communities across space and time, it is necessary to understand whether, and how, sampling methods influence assessments of community patterns. We compared how two common sampling methods-yellow combined flight traps and net samplinginfluence our understanding of the species richness, abundance and composition of wild bees and hoverflies, and addressed whether these patterns resulted from potentially biased sampling of individuals or species with different types of functional traits. We sampled bee and hoverfly communities in six sites over three seasons in Saxony-Anhalt, Germany. We captured more species and individuals of bees with traps and more species and individuals of hoverflies with net sampling. However, rarefied richness results were less dramatic between the sampling methods for bees and were not different between the sampling methods for hoverflies. Thus, differences in species richness across sampling methods were mostly due to differences in the number of individuals captured in the different methods. We captured more small-sized bees and hoverflies with traps. We tested if the different methods collected individuals and species with different functional traits, such as nesting preferences, sociality and flower specialization for bees and floral preference, migratory status and habitat preference for hoverflies. For most traits, we collected more individuals but not more species with a certain trait in the different methods. This was mainly due to a high abundance of one species being collected in the different methods. These results suggest that the best methodology depends on the aim of the survey, and that the methods cannot be easily combined into synthesis research. Our results have implications for the development of monitoring schemes for pollinators and for synthesis of trends that can identify threats to pollinators and inform research of pollinator conservation strategies.

1. Introduction

Recent research has shown declines in the abundance and species richness of insect communities and shifts in community composition in response to global change (Habel et al. 2016, 2019a; Hallmann et al. 2017; Rada et al. 2019; van Klink et al. 2020; Warren et al. 2021). Included in this decline are pollinating insects, which are important for the reproductive success of up to 94% of flowering plants (Ollerton et al. 2011). Pollinating insects therefore play a role in maintaining plant biodiversity (Memmott et al. 2004; Klein et al. 2007; Garibaldi et al. 2013; Carrie et al. 2017), and in the stability and resilience of ecosystems (Bai et al. 2004; Tilman et al. 2014). Pollinators have high economic value, providing globally \$235–\$577 billion (in 2009, United States dollars) in ecosystem services (Lautenbach et al. 2012). It is critical that insect pollinators are monitored so that trends in their diversity can be detected, and these trends can motivate research aimed at identifying threats to

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pollinators and developing pollinator conservation strategies (Wagner et al. 2021). The urgent need to protect pollinators is reflected by national and international pollinator initiatives (European Commission 2018) and corresponding current developments of pollinator monitoring schemes (Potts et al. 2020; Breeze et al. 2021).

Global syntheses on trends for pollinating insect communities are difficult due to differences in the methods employed and taxonomic foci across monitoring schemes, and due to geographic biases in monitoring (Aizen and Feinsinger 1994; Aizen and Feinsinger 2003; Bartomeus and Dicks 2018; Ollerton 2017; Winfree et al. 2009, van Klink et al. 2020). Pollinator monitoring is accomplished through a variety of methods, including visual observations and counts, sweep netting, net sampling of floral visitors, light or bait traps for nocturnal pollinators, and using passive insect traps (e.g., flight, pan, vane, or malaise traps). Visual observations and counts work well for taxa that are identifiable in the field. For example, transect walks have been successfully employed for butterfly monitoring across the world (Pollard 1977; Caldas and Robbins 2003; Nowicki et al. 2008; van Swaay et al. 2008; Habel et al. 2019b). The other methods are more suitable for monitoring taxa that require laboratory methods (e.g., microscopy or genetics) for identification to species level (Roulston et al. 2007; Westphal et al. 2008; Wilson et al. 2008; Nielsen et al. 2011; Popic et al. 2013).

Traps and net sampling are commonly employed methods for pollinator monitoring, each with advantages and disadvantages. Traps represent a simple and quick method to capture the flying insect community by taking advantage of the attractiveness of specific colors for insects. However, the species collected are not always pollinators, and for flower visiting insects, their potential roles and importance as pollinators will not be recorded by this method (Roulston et al. 2007; Tuell and Isaacs 2009; Gonçalves and Oliveira 2013; Popic et al. 2013; Joshi et al. 2015). Net sampling, in which insects are collected on flowers, offers the opportunity to obtain information on the presence of interactions between insect and plant species and potential pollination. However, this method is typically more laborintensive as it is smaller in its temporal extent compared to traps, which can sample for days or weeks. These methods may have different biases towards the types of insects that are collected, with traps capturing insects that are more likely to be attracted to or accidently fall into traps and net sampling capturing insects that the collector is able to spot and successfully capture. Previous research

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that compares the diversity and/or composition of pollinating insects captured in pan traps versus net sampling find that the sampling methods yield considerably different compositions of insects (Popic et al. 2013; O'Connor et al., 2019). For example, Popic et al. (2013) found that only 25% of the morphospecies of pollinators overlapped between both methods.

To fully evaluate and understand biodiversity differences between sampling methods, it is necessary to consider multiple components of biodiversity and more than one spatial grain (Chase et al. 2018; McGlinn et al. 2019). Biodiversity increases non-linearly with spatial scale, and if the shapes of species accumulation curves differ between sampling methods this will result in biodiversity responses that change in magnitude or even direction at different spatial grains of investigation. Thus, biodiversity responses to sampling methods are best understood if they are evaluated at multiple scales. Sampling methods can influence the assessment of the number of individuals and/or the species abundance distribution (i.e., evenness) of the community, and both of these components determine biodiversity at a given spatial grain. Evaluation of multiple components of biodiversity allows a more complete understanding of whether sampling methods alter biodiversity by capturing different abundance of individuals or by capturing a more even or uneven distribution of individuals of different species.

In this study, we focused on two important and diverse groups of pollinators in European agroecosystems, wild bees (Hymenoptera: Anthophila) and hoverflies (Diptera: Syrphidae) (Doyle et al. 2020). These two groups are considered the pollinator "power-houses" and are important for providing most of the pollination services in agroecosystems (Fontaine et al. 2011; Jauker et al. 2012; Rader et al. 2016). Bees, especially wild bees, can be used as bio-indicators for assessing a range of environmental stressors such as pesticide or heavy metal exposure, introduced competitors, diseases, parasites, and predators (Kevan 1999; Ghini et al. 2004; Potts et al. 2010; Zhelyazkova 2012). Bees are central-place foragers that can travel up to several kilometers for large species (Greenleaf et al. 2007; Zurbuchen et al. 2010b; Zurbuchen et al., 2010a). Common and generalist hoverfly species that dominate agricultural landscapes are important in providing pollination services and are mobile species that are more robust to habitat fragmentation and can disperse over great distance (Schweiger et al. 2007; Jauker et al. 2009; Raymond et al. 2013; Rader et al. 2016).



Fig. 1. Distribution of the six study sites (squares) within the region of Harz/Central German Lowland Observatory in Saxony-Anhalt, Germany. The locations (small colored circles) where netting occurred are highlighted in red whereas trap locations are highlighted in blue. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

To date, few studies have examined how methods might be biased towards sampling species with different types of functional traits (Carri'e et al. 2017; Prendergast et al. 2020; Prendergast and Hogendoorn 2021). We expect such a bias for traps and net sampling. For example, body size, generalization, and species guilds of the bees may play a role since differences are associated with flying height, foraging behavior, and floral preference (Cane et al. 2000; Gonzalez et al. 2016; Carrie et al. 2017; Wood et al. 2017). Larger, noisier, more conspicuous species are easier for net samplers to observe and might be more difficult to collect in pan traps. Furthermore, other studies have found that bees tend to forage in a horizontal stratum, which can influence the species collected in pan traps (Ortiz-Sanchez and Aguirre-Segura 1992). The flower visitation of hoverflies may also be affected by body size, flower preference, migratory status, or habitat preference (Klecka et al. 2018; Luder et al. 2018). Larger hoverflies are likewise easier to spot and catch with nets, while certain species may be more attracted by particular colors of the traps.

The aim of our study was to compare the diversity (abundance and species richness) and composition of wild bees and hoverflies between yellow combined flight trap and net sampling methods. First, we quantified the abundance (number of individuals), evenness and diversity of species for each method at two spatial scales (local and regional). Second, we compared species composition between the two methods. Third, to understand observed differences in species composition, we assessed whether methods differ in the size distribution or the frequencies of individuals and species in different functional groups.

2. Methods

2.1. Site description

The data were collected at six sites in Saxony-Anhalt, Germany. They are part of the Terrestrial Environmental Observatories network (Fig. 1; TERENO www.tereno.net, Zacharias et al., 2011) and of the German and European LTER (Long-Term Ecological Research) network (Müller et al. 2010). Each site is 4 km \times 4 km and is divided into 16 squares of 1 km². Sites are separated by a distance of 20–35 km. The six sites (Friedeburg (FRI), Greifenhagen (GRE), Harsleben (HAR), Siptenfelde (SIP), Schafstadt (SST), Wanzleben (WAN), Fig. 1 and Supplementary Table 1) are all embedded in agricultural landscapes. Net sampling took place in semi-natural grasslands in close proximity to established traps.

We consider each site to be the local (α) scale, and all sites pooled together to be the regional (γ) scale. Data for each sampling method (i.e., all traps in a site, all transects for net sampling in a site) were pooled for each site (α -scale).

2.2. Data collection

Data were collected over two consecutive years, divided into three seasons: spring of 2017 (2017), spring of 2018 (2018a) and late summer of 2018 (2018b). Yellow combined flight traps, a combination of a yellow funnel (25 cm diameter) and window panel (24x40 cm) mounted on poles at about 1.30 m height (Fig. 2, Duelli et al. 1999), were placed within each of the 16 squares at a transition area between semi-natural habitat and agricultural fields. This type of trap was chosen because it was proven as highly efficient for a rapid biodiversity assessment (Duelli et al. 1999) and as part of a longterm monitoring scheme at the TERENO sites. We relied on the color yellow for the funnel since it was shown to catch more species compared to other colors (Laubertie et al. 2006; Vrdoljak and Samways 2012), particularly in our landscapes which are dominated by yellow flowers, e.g. mass flowering crops such as oilseed rape. Furthermore, this design was selected for comparative



Fig. 2. Picture of combined yellow flight trap made from a yellow funnel and window trap used in the field (cf. Duelli et al. 1999). Picture provided by M. Frenzel. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

biodiversity studies (e.g. Papanikolaou et al., 2017a; Papanikolaou et al., 2017b) and was not meant for full faunistic assessments. The traps were set out for two-week intervals (Supplementary Table 2). At the end of two weeks, the contents of the traps were collected and stored in 70% ethanol. In total, we sampled 8–10 traps per site, totaling to 54 traps across all 6 sites in the region. Difference in trap number across sites was due to differences in habitat quality and structure (Supplementary Table 3).

During the same time periods (Supplementary Table 2), we used net sampling by focusing on flowering plant species and collecting visiting insects targeting flowering plants during sunny days between 9.00 and 15.00 when insects were most active (see also Bennett et al. 2018; Thompson and Knight 2018). Overall, we collected insect visitors on 150 different plant species across all sites. Net sampling was conducted in semi-natural grasslands in proximity (10 m to 760 m) to the traps, and net sampling locations were 350 m to 3 km away from each other (average 1.8 km). In 2017, we sampled 3-4 plots (plots were 100 m radius and were separated from each other by at least 100 m) for each of the six sites in the region. In 2018, we sampled along a 30 m by 2 m transect for 15 min and stopped the timer during the processing of insects. Transects were separated from each other by at least 100 m. During our sampling period in 2017, the average temperature in April was 9 °C and in May 15.3 °C with around 45 mm of precipitation. In 2018, the average temperature in May was 16.8 °C and 37.10 mm of precipitation and in August 20.7 °C and 54.80 mm of precipitation. Insects that could be identified in the field (e.g. Bombus spp. (to lucorum- agg and terrestris-complex)) were recorded and released. Honeybees (Apis mellifera) were not included in any analyses since they are managed by beekeepers. Other insects were collected in vials and labeled with the site and date of collection. The insects were frozen, pinned, and later identified to species level (or, less commonly, to species complex level) using published taxonomic guides (Amiet 1996; Amiet et al. 1999, 2001, 2004, 2007, 2010; Bartsch 2009; van Veen 2009; Oosterbroek 2015) and assistance from a local expert (Frank Creutzburg, Jena, Germany). At one site (FRI in 2017), no hoverfly individuals were collected in the traps.

Bee functional traits came from a data set provided by Simon Potts (University of Reading), and our co-authors (Roberts and Kuhlmann). This data set provided 1) the average bee body size (measured as inter- tegular distance, ITD), 2) nesting preference, 3) sociality, and 4) flower specialization (Supplementary Table 4a). For hoverflies, we used a data set provided by the database Syrph the Net (Speight and Sarthou 2017). Here, the body size of adult hoverflies was measured from the anterior extremity of the head (excluding the antennae) to the posterior extremity of the abdomen (Speight and Sarthou 2017). The size data is reported as a range given in 0.5 mm increments per species. We used the mean of the size range for our analyses. We compared the number of individuals and species in each method to 1) their preference to feed on nectarbearing flowers and pollen-only flowers, 2) whether or not they migrate, and 3) their preference for habitat types (rural, crop, or field- edge/hedgerows) (Supplementary Table 4b). Data from Syrph the Net is categorical data that is given in number codes that indicate the extent a species associates with each trait (Speight and Sarthou 2017). Our translation of these codes to categories can be found in Supplementary Table 4b.

2.3. Statistical analysis

For net sampling, we attempted to sample insects until we reached saturation of the species richness observed on each plant species. We used a Chao Estimator (Colwell and Coddington 1994; Chao and Chiu 2016) to extrapolate 'true' species richness for our plant species, pollinator species, and pollinator interaction during each season based on methods by Fantinato et al. 2018 (R-package: vegan, Oksanen et al. 2018; Supplementary Table 7). As there was variation in the distance between netting plots and its nearest traps (ranging from 10 m to 760 m), we tested whether this distance predicted the difference between methods in insect density, species richness, or species composition. We ran a linear model with difference of insect abundance or species richness between the two methods as our response variable and distance between the methods as our explanatory variable. Difference in species composition was tested with an analysis of variance using distance matrices (ADONIS, R-package: vegan::adonis). We did not find any significant relationships. There was also variation in the number of traps and transects sampled at each site, however, we made sure that it was a paired-design, sampling equal numbers of each method at each individual site (Supplementary Table 3).

We quantified the number of individuals (N), observed species richness (S), rarefied richness (S_n), and effective numbers of species (S_{PIE}) at two scales (site α and region γ) using the "mobr" R-package (Chase et al. 2018; McGlinn et al. 2019). PIE is the probability of intraspecific encounter (also known as 1- Simpson's evenness index or Gini-Simpson index), which is a measure of species evenness. It is calculated as the slope at the base of the individualbased rarefaction curves. PIE is converted into an effective number of species (S_{PIE}), which is the number of equally abundant species needed to yield PIE (1/ Simpson's index). S_{PIE} comparisons are

robust to differences across treatments in sample sizes (Jost 2007). To test whether the methods differ in any of these metrics, we used a non-parametric, randomized test where the null expectation of each metric is established by randomly shuffling the sites between the two methods, and recalculating the metrics for each shuffle. The null expectation was created using the differences between the methods and comparing it to the actually observed test statistic, to find significant differences between the methods. An ANOVA F-statistic was used to compare metrics across methods at the site scale (α scale), whereas the absolute difference between methods (D) was used to compare metrics across methods at the region scale (γ scale). At both scales, *D* is reported as a measure of effect size. The pvalues are based on 999 permutations of the methods category (netting vs. trap). We visualize species richness results using individual-based rarefaction curves

We visualized species composition across sites and methods using nonmetric multidimensional scaling analysis based on Bray-Curtis dissimilarity distances (NMDS, R-package: vegan::metaMDS) for both species abundance and identity. An Analysis of Similarities (ANOSIM, R- package: vegan::anosim) was employed to test for a statistical difference in species composition between the two methods at the α scale (sites) using the Bray-Curtis dissimilarity distance. A Similarity Percentages analysis (SIMPER, R-package: vegan::simper) quantified the percentage by which each species contributed to dissimilarity between the methods also using Bray-Curtis dissimilarities.

At the regional scale, we tested for differences in functional traits of bee and hoverfly individuals and species collected with the different methods in each season. Using bee size (measured as inter-tegular distance, ITD) and average adult hoverfly body size, we ran a Welch Two Sample *t*-test to test for differences in sizes of individuals between methods. For bees, functional groups included sociality categories, nesting preference, and flower specialization categories (polylectic vs. oligolectic). For hoverflies, functional groups included floral preference (nectar-bearing or pollen only flowers), migratory status (non- or migratory), and preferred habitat (rural, crop, or field-edge/hedgerow). We used χ^2 to test whether methods differed in the proportion of individuals and species observed across all sites of the functional traits. With a bar graph, we visualized the proportion of individuals of each species collected to see what species was driving the difference between the χ^2 test of individuals and

Table 1

Bee and hoverfly abundance and species richness in each collection season (20	017, 2018a, 2018b) for each method (Net, Trap).
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	Bees				Hoverflies			
Collection	Individual	Species	Individual	Species	Individual	Species	Individual	Species
Season	Net	Net	Trap	Trap	Net	Net	Trap	Trap
2017	1170	70	2387	98	154	28	81	22
2018a	335	71	2143	108	191	34	42	20
2018b	466	50	839	72	122	22	122	23



Fig. 3. Box-plots comparing abundance (N), species richness (S), and rarefied richness (Sn) between netting (red) and trap sampling (blue) for each season (2017, 2018a, 2018b) at the local (α)-scale for wild bees (a) and hoverflies (b). Lower and upper box boundaries are the 25th and 75th percentiles; lines inside the box are the medians; the whiskers are the 10th and 90th percentiles; circles are the data that fall outside of the 10th or 90th percentile; * indicates significant difference between methods in the season (* p < 0.05, ** p < 0.01). Regional (y)-scale results can be found in the supplementary materials, Fig. 1. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

species. All statistical operations were performed in R version 3.5.2 (RStudio Team 2016).

3. Results

3.1. Biodiversity

Across all sites and seasons, we collected 175 different species of wild bees (Supplementary Table 5) and 76 species of hoverflies (Supplementary Table 6). The number of individuals or species collected between the two methods varied between the seasons (Table 1). From the total of 175 wild bee species, 50 were exclusively sampled with traps, while 29 were exclusively sampled with netting. Of the 76 hoverfly species, 16 were sampled only in the traps and 33 only found by netting.

The choice of sampling method (net vs. trap) resulted in different estimates for abundance and species richness of wild bees at both local and regional scales in the spring (2017 and 2018a), but not in the late summer (2018b). In the spring of 2017 and 2018(a), we collected significantly more individuals (N) of bees in the traps, and observed higher species richness (S) (Fig. 3a, Table 2a).

However, differences in species richness disappeared with rarefaction (except at the regional scale in 2017). In the late summer of 2018(b), we found no significant difference between the methods for abundance and species richness. Across all seasons, both methods showed similar patterns of effective numbers of species (S_{PIE}) (Table 2a, Supplementary Fig. 1a). Individual- based rarefaction curves used to calculate rarefied richness are found in Supplementary Fig. 2a.

For hoverflies, we found significantly more in abundance and species richness from netting in the spring of 2018(a) (Fig. 3b, Table 2b). This difference in species richness disappeared with rarefaction. For the other seasons (2017 and 2018b), there was no significant difference between the methods in abundance or species richness. Across all seasons, both methods showed similar patterns of effective numbers of species (S_{PIE}) (Table 2b, Supplementary Fig. 1b).

Table 2

Differences TD in the biodiversity metrics of Abundance (N), Species richness (S), Rarefied richness (Sn), and Effective numbers of species (SPIE) between trap and net sampling for a) wild bees and b) hoverflies during the three different collection periods (2017, 2018a, 2018b) at the site level (α scale) and the regional level (γ scale). Significant results are in bold.

a)						
	2017		2018a		2018b	
	Bee Local	Bee Regional	Bee Local	Bee Regional	Bee Local	Bee Regional
	(a scale)	(y scale)	(a scale)	(y scale)	(a scale)	(y scale)
Abundance (N)	<u>D</u> =202.83,	<u>D</u> = 1217,	<u>D</u> = 301.33,	<u>D</u> =1808,	<u>D</u> = 62.17,	<u>D</u> = 373,
	p=0.020	p=0.045	p= 0.005	p= 0.01	p= 0.345	p= 0.325
Species richness	<u>D</u> =21,	<u>D</u> =28,	<u>D</u> =28.67,	<u>D</u> =37,	<u>D</u> = 9.67,	<u>D</u> =22,
(S)	p= 0.005	p= 0.010	p= 0.005	p= 0.015	p= 0.095	p= 0.215
Rarefied richness	n= 85	n= 510	n= 26	n=156	n= 20	n= 120
(Sn)	<u>D</u> = 7.26,	<u>D</u> =16.2,	<u>D</u> = 0.37,	<u>D</u> = 5.25,	<u>D</u> =1.42,	<u>D</u> = 5.27,
	p= 0.065	p=0.03	p= 0.785	p=0.44	p= 0.450	p= 0.545
Effective	D = 4.59,	D = 6.14,	$\underline{D} = 1.67,$	D = 910.16,	$\underline{D} = 1.54,$	D = 0.3,
numbers of	p=0.080	p = 0.255	p=0.650	p=0.235	p=0.72	p=0.98
species (S _{PIE})	•	-	•	-	•	-
b)						
	2017		2018a		2018b	
	Hoverfly Local	Hoverfly	Hoverfly Local	Hoverfly	Hoverfly Local	Hoverfly
	(a scale)	Regional	(a scale)	Regional	(a scale)	Regional
		(y scale)		(y scale)		(y scale)
Abundance (N)	<u>D</u> =14.6,	<u>D</u> =73,	<u>D</u> =24.83,	<u>D</u> =149,	$\underline{D} = 0,$	$\underline{D} = 0,$
	p=0.455	p=0.485	p= 0.035	p= 0.02	p= 1	p= 1
Species richness	<u>D</u> =4,	<u>D</u> = 6,	<u>D</u> = 6.17,	<u>D</u> =14,	<u>D</u> = 0.17,	<u>D</u> =1,
(S)	p= 0.26	p= 0.525	p= 0.01	p=0.18	p= 1	p= 0.97
Rarefied richness	n= 5	n= 25	n= 5	n= 30	n= 5	n= 30
(Sn)	<u>D</u> = 0.58,	<u>D</u> = 0.75,	<u>D</u> = 0.18,	<u>D</u> = 2.22,	<u>D</u> = 0.06,	<u>D</u> = 0.51,
	p= 0.375	p=0.83	p= 0.675	p= 0.315	p= 0.905	p= 0.855
Effective	D = 0.65,	D = 5.51,	D = 0.2,	D = 7.22,	D = 0.82,	D = 0.68,
numbers of	p=0.905	p = 0.525	p=0.99	p=0.185	p=0.785	p=0.885
species (S _{PIE})	•	•	•	•	•	•



Fig. 4. NMDS visualization for bees and hoverflies species abundance in the fall 2018. The sites are labeled with three-letter codes and methods are presented in red (netting) and blue (traps). Insect species ID numbers are shown in grey (Supplementary Tables 4 and 5). Other NMDSs can be found in the supplementary material, Fig. 3.



Fig. 5. Histograms of body sizes of individuals collected by net sampling and traps in the fall of 2018. Inter-tegular distance (ITD, mm) for bee individuals and average adult size (mm) for hoverflies. Other histograms can be found in the supplementary material, Fig. 4.

3.2. Species composition

There were differences across methods in species composition based on both abundance (2017: ANOSIM statistic R = 0.7944, **P = 0.001**; 2018a: R = 0. 8185, **P** = 0.001; 2018b: R = 0.4907, **P** = 0.002) and identity of wild bees in all seasons (2017: ANOSIM statistic R = 0.6074, **P = 0.003**; 2018a: R = 0.5278, **P** = 0.003; 2018b: R = 0.4639, **P** = 0.004). There were significant differences in species composition based on hoverfly abundance in the spring and late summer of 2018 (2017: ANOSIM *statistic R* = 0.166, *P* = 0.184; 2018*a*: *R* = 0.5148, *P* = 0.001; 2018b: R = 0.3972, P = 0.006) and identity (2017: ANOSIM statistic R = 0.25, P = 0.076; 2018a: *R* = 0.4315, *P* = 0.003; 2018b: *R* = 0.3778, *P* = 0.006). An example of the species composition for fall 2018 can be seen in Fig. 4; similar patterns for other seasons can be found at Supplementary Fig. 3. The SIMPER analysis revealed the bee species most responsible for the dissimilarity between the two methods: 2017- Andrena nigroaenea (explained 10.37% of the dissimilarity between methods), 2018a-A. nigroaenea (19.90%), and 2018b-Lasioglossum politum (9.30%). These species were caught in much higher numbers in the traps than with netting (Supplementary Table 5). The hoverfly species most responsible for the dissimilarity between the two methods were: 2017- Platycheirus

albimanus (12.42%), 2018a- *Sphaerophoria scripta* (19.99%), and 2018b- *Syritta pipiens* (15.09%). *P. albimanus* was more abundant in the traps, whereas the two other species were caught more often with the netting (Supplementary Table 6).

3.3. Functional traits

Although both methods captured wild bees and hoverflies species within the same range of body sizes, we found considerable differences in the mean body size of individuals between the different methods in most of the seasons. Traps predominantly caught smaller individuals, whereas the net sampling caught more of larger individuals for both groups (Fig. 5). This difference was significant for all seasons of wild bees and hoverflies (Welch Two Sample *t*-test, $\mathbf{p} < 0.001$), except spring in 2018(a) for hoverflies ($\mathbf{p} = 0.168$).

For wild bees, the proportion of individuals found in categories of nesting preference (Supplementary Fig. 5), sociality (Supplementary Fig. 6) and flower specialization (Supplementary Fig. 7) also differed across methods. With the traps, we collected proportionally more soil nesters in all seasons and more solitary individuals in the spring. The proportion of wild bee species found in these same functional categories did not differ across methods. Some categories of the functional traits had no
individuals in the net method. However, our results were robust to the removal of these categories. For hoverflies, the proportion of individuals and species found in categories of floral preference did not differ between the methods (Supplementary Fig. 8). In spring of 2018 (a), we caught proportionally more migrating individuals with the net and non-migrating individuals with the traps, but no difference in species richness was found (Supplementary Fig. 9). For the different habitat types, we collected different proportions of individuals in all the seasons, but not of species (Supplementary Fig. 10). We captured more individuals with generalized habitat preferences (the 'all' category) in the traps and more individuals with preferences towards rural habitats with the net method. The difference between the proportion of individuals and species between the methods was usually driven by one species of a certain trait that was collected in high frequency in one method and not the other (Supplementary Figs. 5–10g).

4. Discussion

Our goal was to compare the assessment of species richness and community composition of wild bees and hoverflies between two common sampling methods, traps and net sampling, and to determine if functional traits can explain the observed differences. Both are common methods used to sample pollinators and ideally would be combined in *meta*analyses and regional trend analyses. We found that different sampling methods collect different information on richness of pollinating insects, mostly due to differences across methods in the abundance of individuals collected. This difference was consistent across both spatial scales (local and regional).

Likewise, the methods also collect a different composition of species, with a single species explaining almost 10% of the difference. Traps collected relatively smaller sized individuals for both wild bees and hoverflies, and also different proportions of individuals for several wild bee and hoverfly functional traits compared to net sampling. However, these methods sampled similar proportions of species in every functional trait category.

We collected more wild bee individuals using traps (in 2017, 2018a), and more hoverflies using net sampling (in 2018a). The higher abundance of wild bees in the traps is most likely due to the longer period of collection, since the traps were in the field for two weeks at a time and the yellow color is attractive to bees. Results on abundance will depend on the amount of effort and time employed by the methods, which is expected to vary across studies. For example, O'Connor et al. (2019) captured higher

abundances of bumblebees using net sampling and higher abundances of hoverflies using traps. These results highlight the importance of using individualbased rarefaction to compare the effects of different methods on species richness (Roulston et al. 2007; Westphal et al. 2008; Rhoades et al. 2017; O'Connor et al., 2019). On the other hand, we found significantly higher rarefied richness of wild bees in traps in 2017 at the regional scale, and considerable differences in the composition of both wild bees and hoverflies between methods in almost all of our sampling times, demonstrating that factors other than abundance can also drive differences in the assessment of diversity and composition. Species identity also differed between the methods; for example, in 2017, we found in total 111 species of wild bees, 51.35% were sampled by both methods, 11.71% were sampled only in nets, and 36.94% were sampled only in traps. Many of the unique species of wild bees found in the traps are small, such as Hylaeus angustatus, Lasioglossum morio, and L. *minutulum* (ITD < 1.26).

Our study is unique in its examination of functional traits to explain differences in the observed composition of pollinating insects between traps and net sampling. We find that smaller-sized individuals were sampled at higher frequencies by traps compared to net sampling. This may be because these smaller individuals are difficult to spot and capture by an observer with a net (see Cane, Minckley, and Kervin 2000; Roulston, Smith, and Brewster 2007), and/or because larger individuals might more readily escape from traps (Cane et al. 2000). Further, our observed differences in functional traits of bees between the methods are likely due to associations between the traits and bee size (ITD). In the traps, we collected a higher proportion of excavator individuals, and the majority of these were from small-sized species (ITD < 3). Similarly, we collected a higher proportion of solitary bees in the traps, and the majority of these individuals were also from small-sized species. We did not observe differences across methods in functional trait composition of species. This can be attributed to the strong dominance of individuals of one or a few species. For example, in the spring of 2018(a), over 34% of the solitary individuals collected in the traps were one species, Andrena nigroeanea (449 individuals). This species has a flight season from February until July (only 12 individuals were collected in the traps in the late summer). This helps to explain the shift in functional trait results in the late summer season.

For hoverflies, differences across methods in the proportion of individuals—but not species—in

different categories was also due to the high abundance of single species. However, unlike wild bees, there is not an apparent association of the hoverfly functional trait patterns being driven by individuals in a particularly small size class. For example, in the spring of 2018(a), we collected proportionally more migrating individuals with nets and non-migrating individuals in the traps; this difference can be explained by one species-Sphaerophoria scripta— that was collected in high abundance with nets. This species was collected in all the seasons and methods, but not in such high quantities as in 2018a with nets. We also saw a significant difference across methods in the proportion of individuals in different categories of habitat preference, which can be explained by a different single species that was collected in high abundance in each season. A high abundance of Syrphus torvus ("rural") was collected with netting in 2017, a high abundance of Melanostoma mellinum ("all") was collected in the traps in 2018a, and a high abundance of Syritta pipiens ("rural/field") was collected with netting in 2018b.

There is no consensus about which sampling method is best. A study by Krahner et al. (2021) found that pan traps were the most efficient method in collecting high abundance and number of bee species, whereas Portman et al. (2020) have the opinion that pan traps are inefficient in monitoring bee abundance. Advocates of trap sampling argue that this method is inexpensive to set-up, easy to monitor and also captures the diurnal activity of insects (Westphal et al. 2008; Grundel et al. 2011; Nielsen et al. 2011). However, a disadvantage of passive traps is that they can negatively affect the insect population. Although one study has found that there was not a negative impact on the bee communities (Gezon et al. 2015), another study has found that Russels yellow traps have strong negative effects as these traps can kill bumble bee queens (Kuussaari et al. 2008). These traps rely on the same attraction effect as pan and flight traps, and therefore it seems reasonable to expect a negative effect of these traps under specific circumstances. Advocates of net sampling often argue that netting is a good measure of species richness provided that sufficient time is allowed and also surveyor experience is high (Westphal et al. 2008; Popic et al. 2013). Further, net sampling also results in killing fewer individuals (because some species can be identified alive and released), and can provide information about plantpollinator interactions. For both methods, the ratelimiting step is insect identification.

The best choice depends on the length of the study, the focal habitat, and the focal insect taxa,

which is a common issue in ecology (Belovsky et al. 2004). Our results show that there are differences in the community collected depending on the methods and the time of study (spring or late summer; 2017-2018). This echoes the point that collections at one time and place is not sufficient to capture the true abundance or species richness of an area. The choice of method also does not solely depend on the target species, but on the required data type. If the goal is species richness assessment, then both methods are reliable and rarefaction should be used. This is particularly relevant for *meta*-analyses using both kinds of data. If the goal is to obtain a full species list, then a combination of both methods is best. Overall, we believe that when measuring and monitoring biodiversity, both methods should be employed, due to the differences between the methods by capturing species with different body sizes and other functional traits.

Our study highlights the importance of individualbased rarefaction. Understanding the drivers of biodiversity change, such as climate and land use change, requires analyzing community changes across broader spatial and temporal scales (Knight et al. 2018). For future meta-analyses and regional trend analysis, it is important to provide data on each individual collected or observed so that future studies can calculate appropriate metrics for biodiversity across studies (Roulston et al. 2007; Westphal et al. 2008; Rhoades et al. 2017). However, it is important to note that traps sample at a larger temporal grain, whereas netting along transects can have a larger spatial grain, and these differences cannot be as easily standardized.

Declarations

5. Authors' Contributions

AT, MF, OS, MM, and TK contributed to the study concept and design. Net data collection was performed by AT and TG. Material preparation, statistical analyses, and draft writing was done by AT. SPMR and MK provided the bee functional trait dataset. All authors commented on and approved the final manuscript.

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7. Ethical approvalss

This article does not contain any studies with human participants or vertebrate animals performed by any of the authors. We had permission to collect insects in Saxony-Anhalt granted by the Office for Environmental Protection (Bescheinigungs-Nr. RL-0503, - 0504,-0505).

CRediT authorship contribution statement

Amibeth Thompson: Conceptualization, Investigation, Writing – original draft, Writing – review & editing, Visualization. Mark Frenzel: Conceptualization, Writing – review & editing. Oliver Schweiger: Conceptualization, Writing – review & editing. Martin Musche: Conceptualization, Writing – review & editing, Data curation. Till Groth: Investigation, Writing – review & editing. Stuart P.M. Roberts: Data curation, Writing – review & editing. Michael Kuhlmann: Data curation, Writing – review & editing. Tiffany M. Knight: Supervision, Conceptualization, Methodology, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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Supplementary Materials- Thompson et al. (2021) Ecological Indicators

SUPPLEMENTARY MATERIALS

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Method	Site	Latitude	Longitude
Trap	FRI	51.3735	11.4302
Trap	GRE	51.3759	11.2645
Trap	HAR	51.5041	11.041
Trap	SIP	51.3847	11.0257
Trap	SST	51.2205	11.434
Trap	WAN	52.0521	11.2515
Net	FRI	51.3739	11.4314
Net	GRE	51.3716	11.2653
Net	HAR	51.5041	11.0401
Net	SIP	51.3845	11.0303
Net	SST	51.2207	11.4332
Net	WAN	52.0521	11.2519

Table 1: Latitudinal and longitudinal coordinates of each of the six sites.

Table 2: Details of sampling periods for 2017 and 2018. Dates highlighted in grey were not used because collection was not overlapping.

Year	Method	Season	Collection	Start date	End date
2017	Trap		1	4/18/2017	5/4/2017
			2	5/2/2017	5/17/2017
			3	5/15/2017	5/31/2017
	Net			4/20/2017	5/23/2017
2018	Trap		1	4/16/2018	5/2/2018
		a	2	4/30/2018	5/16/2018
		a	3	5/14/2018	5/30/2018
				8 week break	k
		b	4	7/30/2018	8/17/2018
		b	5	8/13/2018	8/30/2018
			б	8/27/2018	9/13/2018
	Net	a	1	5/7/2018	5/8/2018
		a	2	5/15/2018	5/25/2018
		a	3	6/4/2018	6/9/2018
			4	6/25/2018	6/30/2018
			5	7/16/2018	7/21/2018
		b	6	8/6/2018	8/9/2018
		b	7	8/21/2018	8/23/2018

	FRI	GRE	HAR	SIP	SST	WAN
2017 Trap	3	4	4	3	3	3
2017 Net	3	4	4	3	3	3
2018a Trap	7	8	6	6	7	9
2018a Net	7	8	6	6	7	9
2018b Trap	5	4	4	4	5	6
2018b Net	5	4	4	4	5	6

Table 3: Number of traps and netting transects/areas used during each collection season at each location.

 Table 4: Functional trait categories and measurements

a) Bee trait categories used in analyses. Data was provided by Simon Potts and co-authors Roberts and

Kuhlmann.

Bee Traits	Categories/Measurements		
Gender	male/female		
Body Size	Intertegular Distance (mm)		
Nesting	Ca- Carder		
	Cl- Cleptoparasite		
	Ex- Excavator		
	Ma- Mason		
	Re- Renter		
	SP- Social_parasite		
Sociality	Cl- Cleptoparasite		
	Co- Communal		
	Po- Polymorphic		
	PE- Primitively_eusocial		
	SP- Social_parasite		
	So- Solitary		
	So_co- Solitary or communal		
	So_PE- Solitary + Primitively eusocial		
	Un- Unknown		
Generalization	Oligolectic		
	Polylectic		
	none		

Supplementary Materials- Thompson et al. (2021) Ecological Indicators

b) Hoverfly trait categories used in analyses. Data was provided by the database Syrph the Net (Speight and Sarthou 2017) and was reported in fuzzy coding. Fuzzy coding uses positive scores (1-3) to describe the extent a species associates with each trait category (Chevene et al. 1994) with the scores indicating an increasing in probability of association. The coding of "blank" indicates no known association, "1" indicates that the association can occur under a very particular situation ("possible"), "2" indicates the association is predicted to occur ("predicted"), and "3" indicates the association is preferred by the species ("preferred"). Traits that are italicized in the first column are the categories used in the Syrph the Net database. The second column are the categories we used for the analyses. The third column are how we translated the fuzzy coding into the categories used for analyses.

Hoverfly Traits (Syrph the Net trait categories)	Measurements/ Categories	Fuzzy Coding description
Gender	male/female	
Average Body Size	mm	Average of given range
Floral Preference (Nectar-	Nectar-bearing flowers	number only for nectar category
bearing flowers; Pollen-only	Pollen-only flowers	number only for pollen category
<i>flowers)</i>	both	number for both categories
Migratory Status (Migratory;	both	number for both categories
Non-migratory)	migratory	number only for migratory category
	non-migratory	number only for non-migratory category
	unknown	blank for both categories
Habitat (Rural; Crop; Field	all	number for all categories
margin/Hedge)	no known	blanks for all categories
	rural	number only for rural category
	rural/crop	numbers for rural and crop categories
	rural/field	numbers for rural and field margin/hedge categories

For example, Species 1 we would categorize as floral preference of "nectar-bearing flowers" and migratory status of "both". Species 2 would be categorized as floral preference of "both" and migratory status of "non-migratory."

	Nectar-bearing flowers	Pollen-only flowers	Migratory	Non-migratory
Species 1	3		3	1
Species 2	1	2		3

Literature

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Table 5: Species list of bees and number of individuals collected in each method at each site. Relative abundance
(as percent) in brackets. Species are listed in alphabetical order with coinciding ID number used in NMDS
visualization.

ID	Species	2017	2017	2018a	2018a	2018b	2018b
#	Androng gailissing	Net	Trap	Net	Trap	Net	Trap
1	Andrena_aguissima				2 (0.09)		
2	Anarena_aijkenetia	1 (0.09)			2 (0.09)		
3	Andrena_angustior			1 (0.30)			
4	Anarena_barbareae			1 (0.30)			
5	Andrena_bicolor		1 (0.04)	1 (0.30)			
6	Andrena_chrysosceles	4 (0 34)	(0.42)				
7	Andrena_cineraria	165	174		102		
		(14.10)	(7.29)	3 (0.90)	(4.76)		1 (0.12)
8	Andrena_clarkella		2 (0.08)				
9	Andrena_combinata				2 (0.09)		
10	Andrena_denticulata						2 (0.24)
11	Andrena_dorsata	2 (0.17)	1 (0.04)	1 (0.30)	2 (0.09)		
12	Andrena_enslinella				1 (0.05)		
13	Andrena_flavipes	74	23	1 (0 20)	20		
14	Androng floricala	(6.32)	(0.96)	1 (0.30)	(0.93)		1 (0.12)
14	Andrena_fioncold	5 (0.43)	4 (0.17)		5 (0.23)		
15	Anarena_jucaia	1 (0.09)	1 (0.04)		(0.70)		
16	Andrena_fulva		59		18		
		2 (0.17)	(2.47)	1 (0.30)	(0.84)		
17	Andrena_fulvago		1 (0.04)				
18	Andrena_fuscipes						1 (0.12)
19	Andrena_gravida	9 (0 69)	67 (2.81)	1 (0.20)	20		
20	Andrena haemorrhoa	8 (0.08)	(2.81)	1 (0.50)	(0.93)		
20	That cha_haemon hou	(3.76)	(7.58)	8 (2.39)	(4.43)		
21	Andrena_helvola		159	- / / / >	123		
22	Andreag hemilia	9 (0.77)	(6.66)	5 (1.49)	(5.74)		
22	Andrena_numitis				1 (0.05)		
25	Andrena_lablalis			1 (0.30)			
24	Anarena_iabiata	1 (0.09)			3 (0.14)		
25	Anarena_latnyri				1 (0.05)		
26	Andrena_marginata			11		1 (0.21)	
27	Andrena_minutula	3 (0.26)	1 (0.04)	(3.28)	3 (0 14)		
28	Andrena_minutuloides	3 (0.20)	1 (0.01)	(3.20)	13		
		4 (0.34)	6 (0.25)	2 (0.60)	(0.61)	1 (0.21)	1 (0.12)
29	Andrena_mitis		7 (0.20)		28		
30	Andrena nigroaenea	30	7 (0.29)		(1.31)		
50	Marcha_mgrouchea	(2.56)	(18.64)	6 (1.79)	(25.15)		9 (1.07)
31	Andrena_nitida		21		19		
22		6 (0.51)	(0.88)		(0.89)		
32	Andrena_niveata		3 (0 13)		10 (0.47)		
33	Andrena_ovatula		2 (0.08)		1 (0.05)		
34	Andrena_pandellei		2 (0.00)		3(0.14)	1 (0 21)	
I	-				5 (0.17)	1 (0.41)	

35	Andrena pilipes		2 (0.12)		5 (0.28)		
36	Andrena praecox		3 (0.13)		5 (0.28)		
37	Andrena proxima		5(0.13)	1 (0.30)	1 (0.03)		
38	Andrena scotica		23	1 (0.50)	33		
		2 (0.17)	(0.96)	6 (1.79)	(1.54)		1 (0.12)
39	Andrena_semilaevis		3 (0.13)		5 (0.23)		
40	Andrena_similis			5 (1.49)			
41	Andrena_strohmella	6 (0.51)	6 (0.25)		2 (0.09)		
42	Andrena_subopaca	2 (0.17)	7 (0.29)	6 (1.79)	8 (0.37)		
43	Andrena_synadelpha	1 (0.09)	9 (0 38)		14		
44	Andrena_tibialis	1 (0.07)	1(0.04)		4 (0 19)		
45	Andrena vaga	1 (0.09)	1 (0.04)		3(014)		
46	Andrena varians	1(0.07)	4 (0.17)		$\frac{3(0.14)}{4(0.10)}$		
47	Andrena ventralis	1 (0.09)	4 (0.17)		32		
			8 (0.34)		(1.49)		
48	Andrena_viridescens	3 (0.26)					
49	Andrena_wilkella			4 (1.19)			
50	Anthidiellum_strigatum			3 (0.90)		1 (0.21)	
51	Anthophora_aestivalis				1 (0.05)		
52	Anthophora_plumipes	41			11		
52		(3.50)	6 (0.25)	2 (0.60)	(0.51)		
53	Bombus_bohemicus		(0.42)		1 (0.05)		2 (0 24)
54	Bombus_hortorum		16		1 (0.05)		2 (0.24)
		1 (0.09)	(0.67)	4 (1.19)	2 (0.09)		2 (0.24)
55	Bombus_humilis					5 (1.07)	
56	Bombus_hypnorum	1 (0.09)	1 (0.04)				
57	Bombus_lapidarius	2 (0 17)	15 (0.63)	27 (8.06)	5 (0 23)	101 (21.67)	3 (0 36)
58	Bombus_lucorum	2 (0.17)	124	(0.00)	12	(21.07)	5 (0.50)
			(5.19)	2 (0.60)	(0.56)		4 (0.48)
59	Bombus_lucorum.agg		20		2 (0.00)		
60	Bombus mucidus		(0.84)	1 (0.20)	2 (0.09)		
61	Bombus pascuorum	236	30	1 (0.30)		69	15
01	Dombas_paseroram	(20.17)	(1.26)	(4.48)	6 (0.28)	(14.81)	(1.79)
62	Bombus_pratorum	5 (0.42)	21	8 (2 20)	4 (0, 10)		1 (0 12)
63	Bombus red-tail.complex	54	(0.88)	0 (2.39)	4 (0.19)		1 (0.12)
0.5	Demous_rea lancompten	(4.62)					
64	Bombus_ruderarius		1 (0.04)				
65	Bombus_rupestris		5 (0.21)		6 (0.28)		2 (0.24)
66	Bombus_soroeensis		17		10		
67	Pombus subserve		(0.71)	10	(0.47)	40	1 (0.12)
0/	bombus_sylvarum		(0.54)	(3.58)	(1.12)	(8.58)	(1.67)
68	Bombus_sylvestris	1	2 (0.08)		1 (0.05)		1 (0.12)
69	Bombus_terrestris		123	40	32	60	15
70		4 (0.34)	(5.15)	(11.94)	(1.49)	(14.81)	(1.79)
70	Bombus_terrestris.complex	(20.43)					
71	Bombus vestalis	(20.43)	5 (0.21)		5 (0.23)		3 (0.36)
		1	J(0.21)		5 (0.25)		5 (0.50)

72	Ceratina_cyanea	2 (0.17)				1 (0.21)	
73	Chelostoma_florisomne	1 (0.09)	1 (0.04)	1 (0.30)	3 (0.14)		
74	Colletes_cunicularius	6 (0.51)	46 (1.93)		3 (0.14)		
75	Colletes_daviesanus			2 (0.60)		3 (0.64)	
76	Colletes_fodiens			, ,		3 (0.64)	3 (0.36)
77	Colletes_similis			1 (0.30)		7 (1.50)	
78	Dasypoda_argentata					1 (0.21)	
79	Eucera_longicornis			1 (0.30)			
80	Eucera_nigrescens	1 (0.09)					
81	Halictus_confusus			2 (0.60)	4 (0.19)	1 (0.21)	3 (0.36)
82	Halictus_leucaheneus			1 (0.30)			
83	Halictus_maculatus	3 (0.26)	1 (0.04)	1 (0.30)		4 (0.86)	
84	Halictus_quadricinctus		1 (0.04)		9 (0.42)		
85	Halictus_rubicundus		5 (0.21)			1 (0.21)	3 (0.36)
86	Halictus_scabiosae					44	
07	Hulidan simular	2 (0.17)			7 (0.33)	(9.44)	6 (0.72)
8/	Hauctus_simplex		5 (0 21)		(0.56)		
88	Halictus_subauratus		5 (0.21)		(0.50)	14	16
				1 (0.30)	3 (0.14)	(3.00)	(1.91)
89	Halictus_tumulorum	10	(0.46)	1 (0 20)	18		54
90	Hoplitis adunca	(0.83)	(0.40)	1(0.30)	(0.64)		(0.44)
91	Hylaeus angustatus			1 (0.50)	5 (0.14)	11	
			2 (0.08)	2 (0.60)	2 (0.09)	(2.36)	3 (0.36)
92	Hylaeus_annularis			1 (0.30)			
93	Hylaeus_brevicornis						6 (0.72)
94	Hylaeus_communis			1 (0.30)	1 (0.05)		11 (1.31)
95	Hylaeus_confusus			1 (0.30)		1 (0.21)	1 (0.12)
96	Hylaeus_dilatatus						4 (0.48)
97	Hylaeus_gredleri			7 (2.09)			1 (0.12)
98	Hylaeus_hyalinatus						1 (0.12)
99	Hylaeus_leptocephalus			1 (0.30)			
100	Hylaeus_nigritus			1 (0.30)			
101	Lasioglossum_aeratum		1 (0.04)				
102	Lasioglossum_albipes	1 (0.00)	15		()		
103	Lasioglossum calceatum	1 (0.09)	(0.63)		6 (0.28) 20	2 (0.43)	8 (0.95)
105	Lusiogrossum_curceutum	(1.54)	(8.04)		(0.93)	2 (0.43)	(13.23)
104	Lasioglossum_clypeare						1 (0.12)
105	Lasioglossum_convexiusculum		1 (0.04)		1 (0.5)		
106	Lasioglossum_fratellum			2 (0.60)		1 (0.21)	1 (0.12)
107	Lasioglossum_fulvicorne	1 (0.09)	3 (0.13)			4 (0.86)	6 (0.72)
108	Lasioglossum_interruptum		6 (0.25)		4 (0.19)	2 (0.43)	3 (0.36)
109	Lasioglossum_laevigatum	1 (0.09)	1 (0.04)		2 (0.09)		9 (1.07)
110	Lasioglossum_laterale					2 (0.43)	
111	Lasioglossum_laticeps						14
			3 (0.13)		2 (0.09)	2 (0.43)	(1.67)

112	Lasioglossum lativentre						38
	0 _	1 (0.09)	7 (0.29)	6 (1.79)	7 (0.33)		(4.53)
113	Lasioglossum_leucopus						1 (0.12)
114	Lasioglossum_leucozonium			9 (2.69)			1 (0.12)
115	Lasioglossum_lineare	1 (0.09)	5 (0.21)				5 (0.60)
116	Lasioglossum_majus						12
			1 (0.04)	2 (0.60)	20 (0.9.)		(1.43)
117	Lasioglossum_malachurum	7 (0.60)	(0.06)	(3.88)	15 (0.70)	2(0.43)	16 (1.01)
118	Lasioglossum minutulum	7 (0.00)	(0.90)	(3.88)	(0.70)	2 (0.43)	(1.91)
			4 (0.17)	1 (0.30)	4 (0.19)	1 (0.21)	(2.03)
119	Lasioglossum_morio		30		67		83
120	T		(1.26)	5 (1.49)	(3.13)	4 (0.86)	(9.89)
120	Lasiogiossum_nigripes		20	1 (0.30)			
121	Lasioglossum_nitidiusculum	2 (0 17)	(0.84)				2 (0 24)
122	Lasioglossum_nitidulum	2 (0.17)	(0.01)				1(0.12)
123	Lasioglossum pallens		16				1 (0.12)
		1 (0.09)	(0.67)		5 (0.23)		
124	Lasioglossum_parvulum	2 (0.25)	81	a (0.00)	15	4 (0.00)	2 (2 2 4)
125	Lasioglossum paurillum	3 (0.26)	(3.39)	3 (0.90)	(0.70)	4 (0.86)	2 (0.24)
123	Lasiogiossum_pauxilium	(2.05)	(0.54)	(12.84)	(2.99)	(6.01)	(3.58)
126	Lasioglossum_politum	(2:00)		11	25	(0.01)	214
		1 (0.09)	3 (0.13)	(3.28)	(1.17)	9 (1.93)	(25.51)
127	Lasioglossum_punctatissimum		1 (0.04)		1 (0.05)		
128	Lasioglossum_puncticolle					3 (0.64)	
129	Lasioglossum_pygmaeum		4 (0.45)	a (0, co)	18	0 (0 (0)	17
130	Lasioglossum quadrinotatum		4 (0.17)	2 (0.60)	(0.84)	3 (0.64)	(2.03)
121	Lasioglossum_quaarinotatum				5 (0.23)		1 (0.12)
131	Lasioglossum_rujitarse	1 (0.09)	2 (0.08)	1 (0.30)	2 (0.09)		
132	Lasioglossum_sabulosum		1 (0.04)				1 (0.12)
133	Lasioglossum_semilucens					1 (0.21)	
134	Lasioglossum_sexnotatum		8 (0.34)	2 (0.60)	5 (0.23)		1 (0.12)
135	Lasioglossum_villosulum	1 (0.09)		2 (0.60)	1 (0.05)		
136	Lasioglossum_xanthopus		16	((1, 70))	45 (2,1)	1 (0 21)	
137	Megachile alpicola		(0.07)	0(1.79)	43 (2.1)	1 (0.21)	1 (0.12)
138	Megachile centurcularis				1 (0.05)	2 (0.42)	1(0.12)
130	Megachile ligniseca				1 (0.05)	2 (0.43)	1 (0.12)
139	Megachile_ugnisecu			1 (0.00)		1 (0.21)	1 (0.12)
140	Magaahila varsioolor			1 (0.30)		1 (0.21)	1 (0.12)
141	Melasta alliforna					2 (0.43)	1 (0.12)
142	Melitta lenevius				1 (0.05)		
145	Mentia_leporina						1 (0.12)
144	Nomada_alboguttata	4.4	6 (0.25)				
145	Nomada_bifasciata	14	3 (0 13)		4 (0 10)		
146	Nomada fabriciana	(1.20)	5 (0.15)		+ (0.17)		
147	Nomada flava	5 (0.42)	8 (0.24)		4 (0.10)		
148	Nomada flavoguttata	5 (0.45)	0 (0.34)		12		
		2 (0.17)	4 (0.17)	2 (0.60)	(0.56)		
149	Nomada_fucata	2 (0.17)	1 (0.04)		2 (0.09)	1 (0.21)	

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150	Nomada_goodeniana	34	27	7 (2.00)	37		
151	Nomada_lathburiana	(2.91)	9 (0 38)	7 (2.09)	9(0.42)		
152	Nomada marshamella	1 (0.51)) (0.50)		10		
152	Nonaua_marshamena	7 (0.60)	4 (0.17)		(0.47)		
153	Nomada_panzeri	12	16		13		
		(1.03)	(0.67)		(0.61)		
154	Nomada_ruficornis		10		20		
		4 (0.34)	(0.42)	2 (0.60)	(0.93)		
155	Nomada_rufipes						1 (0.12)
156	Nomada_sheppardana				1 (0.05)		
157	Nomada_signata				2 (0.09)		
158	Nomada_succincta				28		
		5 (0.43)	7 (0.29)	2 (0.60)	(1.31)		
159	Osmia_bicolor	1 (0.00)	22				
160	Ognia hisomia	1 (0.09)	(0.92)		22		
100	Osmia_bicornis	3 (0.26)	(0.71)		(1.54)		
161	Osmia bravicornis	25	(0.71)		278		
101	Osmu_Drevicornis	(2.14)	(2.35)	1 (0.30)	(12.97)		
162	Osmia_caerulescens		4 (0.17)	2 (0.60)			
163	Sphecodes_albilabris	2 (0.17)		1 (0.30)		6 (1.29)	1 (0.12)
164	Sphecodes_crassus						16
					6 (0.28)	1 (0.21)	(1.91)
165	Sphecodes_ephippius				13		15
		2 (0.17)	5 (0.21)		(0.61)	7 (1.50)	(1.79)
166	Sphecodes_geoffrellus				1 (0.05)		1 (0.12)
167	Sphecodes_gibbus						1 (0.12)
168	Sphecodes_majalis		6 (0.25)		1 (0.05)		
169	Sphecodes_miniatus				2 (0.09)		1 (0.12)
170	Sphecodes_monilicornis				, , ,		10
			3 (0.13)		1 (0.05)	1 (0.21)	(1.19)
171	Sphecodes_pellucidus					1 (0.21)	2 (0.24)
172	Sphecodes_rubicundus			3 (0.90)		1 (0.21)	
173	Sphecodes_spinulosus	1 (0.09)			1 (0.05)		
174	Stelis_ornatula				1 (0.05)		
175	Xylocopa_violacea					1 (0.21)	
	Total	1170	2387	335	2143	466	839

Table 6: Species list of hoverflies and number of individuals collected in each method at each site. Relative abundance (as percent) in brackets. Species are listed in alphabetical order with coinciding ID number used in NMDS visualization.

ID	Species		2017	2018a	2018a	2018b	2018b
		2017 Net	Trap	Net	Trap	Net	Trap
1	Cheilosia_albitarsis/ranunculi			2 (1.05)			
2	Cheilosia_carbonaria			1 (0.52)			
3	Cheilosia_illustrata			1 (0.52)		1 (0.82)	
4	Cheilosia_latifrons	12 (7.79)					
5	Cheilosia_lenis		1 (1.23)				
6	Cheilosia_scutellata					1 (0.82)	
7	Cheilosia_soror					1 (0.82)	
8	Cheilosia_vicina	2 (1.30)					
9	Chrysogaster_solstitialis					9 (7.38)	
10	Chrysotoxum_cautum	8 (5.19)		2 (1.05)	3 (7.14)		
11	Chrysotoxum_festivum	1 (0.65)					1 (0.82)
12	Dasysyrphus_albostriatus	2 (1.30)	2 (2.47)	1 (0.52)		1 (0.82)	· · · · ·
13	Dasysyrphus_hilaris			2 (1.05)			
14	Dasysyrphus_pinastri			5 (2.62)			
15	Dasysyrphus_tricinctus	4 (2.60)		1 (0.52)			
16	Dasysyrphus_venustus	2 (1.30)	3 (3.70)	8 (4.19)			
17	Epistrophe_eligans	1 (0.65)	2 (2.47)		1 (2.38)		
18	Episyrphus_balteatus	1 (0.65)	1 (1.23)	19 (9.95)	1 (2.38)	3 (2.46)	7 (5.74)
19	Eristalinus_aeneus	1 (0100)	1 (1120)	1) ()))))	1 (2.00)	2 (1.64)	/ (01/ 1)
20	Eristalinus_sepulchralis					_ (1101)	1 (0.82)
21	Eristalis_abusiva			1 (0.52)			1 (0102)
22	Eristalis_arbustorum			22			
		1 (0.65)		(11.52)		5 (4.10)	
23	Eristalis_horticola	1 (0.65)					
24	Eristalis_intricaria			9 (4.71)			
25	Eristalis_jugorum	1 (0.65)		1 (0.52)			
26	Eristalis_nemorum			1 (0.52)			
27	Eristalis_pertinax			9 (4.71)	4 (9.52)	8 (6.56)	1 (0.82)
28	Eristalis_picea					1 (0.82)	
29	Eristalis_similis	7 (4.55)					
30	Eristalis_tenax				1 (2.38)	5 (4.10)	
31	Eumerus_strigatus						1 (0.82)
32	Eumerus_strigatus/sogdianus				1 (2.38)	4 (3.28)	3 (2.46)
33	Eupeodes_corollae	1 (0 (7)	1 (1 22)			2 (1 (1)	16
34	Eupeodes latifasciatus	1 (0.65)	1 (1.23)	11 (5.76)	2 (4.76)	2 (1.64)	(13.11)
35	Funeodes luniger	1 (0 (5)	1 (1 02)				1 (0.82)
36	Ferdinandea cunrea	1 (0.65)	1 (1.23)		1 (2.20)		1 (0.02)
37	Helophilus hybridus				1 (2.38)	2 (1 (1)	1 (0.82)
20	Helophilus nondulus					2 (1.64)	7 (5.74)
50	netophilus_pendulus	2 (1.30)		8 (4.19)	4 (9.52)	(11.48)	5 (4.10)
39	Helophilus_trivittatus		1 (1.23)	1 (0.52)	· · · /	/	1 (0.82)
40	Heringia_heringi		`, /	, <i>,</i> , ,	1 (2.38)		· · · ·
41	Mallota_fuciformis		1 (1.23)				

42	Melanogaster_hirtella	1 (0.65)					
43	Melanogaster_nuda			3 (1.57)			
44	Melanostoma_mellinum	6 (3.90)	4 (4.94)	5 (2.62)	7 (16.67)		2 (1.64)
45	Melanostoma_scalare		4 (4.94)		1 (2.38)		`
46	Melanostoma_sp		1 (1.23)				
47	Meliscaeva_cinctella		1 (1.23)				
48	Merodon_equestris				1 (2.38)		
49	Myathropa_florea				1 (2.38)	1 (0.82)	1 (0.82)
50	Neoascia_meticulosa		5 (6.17)			, , ,	, , , , , , , , , , , , , , , , , , ,
51	Orthonevra_nobilis					2 (1.64)	
52	Paragus_bicolor			1 (0.52)			
53	Parasyrphus_annulatus	1 (0.65)		1 (0.52)			
54	Pipiza_quadrimaculata			3 (1.57)			
55	Pipiza_sp		1 (1.23)				
56	Pipizella_divicoi			1 (0.52)			
57	Pipizella_virens			2 (1.05)			
58	Platycheirus_albimanus	17	36				
50		(11.04)	(44.44)				
59	Platycheirus_ambiguus	1 (0.65)	1 (1.23)				
60	Platycheirus_peltatus				2 (4.76)		3 (2.46)
61	Platycheirus_scutatus	4 (2.60)					
62	Platycheirus_sp			1 (0.52)			
63	Platycheirus_tarsalis	2 (1.30)	3 (3.70)				
64	Scaeva_pyrastri			2 (1.05)			8 (6.56)
65	Scaeva_selenitica	5 (3.25)					
66	Sphaerophoria_scripta	9 (5 10)	4 (4 0 4)	50	1 (2 29)	18	2(164)
67	Svritta pipiens	0 (3.19)	4 (4.94)	(20.18)	1 (2.36)	31	2 (1.04)
07	29 <u>_</u> p.q. co.co			2 (1.05)		(25.41)	
68	Syrphus_ribesii	21					21
60	Sumbus tomus	(13.64)	3 (3.70)			5 (4.10)	(17.21)
09	Syrphus_lorvus	(22.73)	3 (3.70)			4 (3.28)	2 (1.64)
70	Syrphus_vitripennis	6 (3.90)	2 (2.47)	7 (3.66)			4 (3.28)
71	Tropidia_scita			6 (3.14)	1 (2.38)		
72	Volucella_bombylans			1 (0.52)	1 (2.38)		
73	Volucella_pellucens				3 (7.14)		1 (0.82)
74	Volucella_zonaria			1 (0.52)			
75	Xanthogramma_pedissequum	1 (0.65)				2 (1.64)	2 (1.64)
76	Xylota_segnis						31
					5 (11.90)		(25.41)
	Total	154	81	191	42	122	122

Plant Species			Pollinator Species			Pollinator Interactions		
Observed Richness	Asymptotic Richness	Sampling Completeness (%)	Observed Richness	Asymptotic Richness	Sampling Completeness (%)	Observed Richness	Asymptotic Richness	Sampling Completeness (%)
56	75	74.67	187	292.1	64.02	555	1859.79	29.84
87	104.65	83.13	231	334.28	69.10	759	2658.95	28.55
52	61.25	84.90	149	223.32	66.72	494	1405.37	35.15

Table 7: Chao estimator (Colwell and Coddington 1994) extrapolates 'true' species richness for plant species, pollinator species, and interactions based on our abundance data to see if we've reached saturation on species richness observed (Oksanen et al. 2018). We based our methods on Fantinato 2018 calculation of sampling completeness.

Literature

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Figure 1: Differences in patterns of abundance (N), species richness (S), rarified richness (Sn), and effective numbers of species (S_{PIE}) between netting (red) and trap sampling (blue) for each season (2017, 2018a, 2018b) at site (α -scale) and regional (γ -scales) for wild bees (a) and hoverflies (b). Effect size is summarized by computing \overline{D} , which is the average absolute difference between the methods. The p-values are based on 999 permutations of the method category (netting vs. trap).





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Figure 3: NMDS visualization for bees (a) and hoverflies (b). The sites are labeled with three-letter codes and methods are presented in red (netting) and blue (traps). Insect species ID numbers are shown in grey (Supplementary Tables 4 and 5). There was a significant difference across methods in species composition for wild bees abundance in all seasons (2017: ANOSIM statistic R= 0.7944, **P= 0.001**; 2018a: R=0. 8185, **P= 0.001**; 2018b: R= 0.4907, **P= 0.002**) and identity (2017: ANOSIM statistic R= 0.6074, **P= 0.003**; 2018a: R=0.5278, **P= 0.003**; 2018b: R= 0.4639, **P= 0.004**). There is significant differences in species composition of hoverfly abundance in 2018 (2017: ANOSIM statistic R= 0.166, P=0.184; 2018a: R= 0.5148, **P= 0.001**; 2018b: R= 0.3972, **P= 0.006**) and identity (2017: ANOSIM statistic R= 0.25, P=0.076; 2018a: R= 0.4315, **P= 0.003**; 2018b: R= 0.3778, **P= 0.006**).



Figure 4: Histograms of body sizes of individuals collected by net sampling and traps. (a) Inter-tegular distance (ITD, mm) for bee individuals. (b) Average adult size (mm) for hoverflies. Differences between the methods are significant for wild bees and hoverflies in all seasons (Welch Two Sample t-test, p < 0.001), except for hoverflies in 2018a (p =0.1668).





Figure 5: Bar graph of wild bee nesting preference of individuals and species collected in the two methods, netting (red) and traps (blue). Nesting preference of the bees is carder (Ca), cleptoparasite (Cl), excavator (Ex), mason (Ma), renter (Re), or social parasite (SP). The χ^2 test was significant for individuals (**p** < **0.05**), but not for species (p> 0.05).



5g) Bar graph of wild bee nesting preferences of species' abundances collected in the two methods across the three seasons. Species with the highest abundances of individuals is highlighted in black and the name of the species is written at the top of the bar.



Figure 6: Bar graph of bee sociality of individuals and species collected in the two methods, netting (red) and traps (blue). Sociality of the bees is cleptoparasite (Cl), communal (Co), polymorphic (Po), primitively eusocial (PE), social parasite (SP), solitary (So), solitary or communal (So_Co), solitary and primitively eusocial (So_PE), or Unknown (un). The χ^2 test was significant for individuals (p < 0.05), but not for species (p > 0.05).



6g) Bar graph of wild bee sociality of species' abundances collected in the two methods across the three seasons. Species with the highest abundances of individuals is highlighted in black and the name of the species is written at the top of the bar.



Figure 7: Bar graph of wild bee flower specialization of individuals and species collected in the two methods, netting (red) and trap (blue). Polylectic are generalist and oligolectic are specialists. The χ^2 test was significant for individuals in all seasons and species in the spring 2018(a) (**p** < **0.05**); there was no significant difference for species in the other seasons (p > 0.05). Significance disappears in spring 2018(a) for species when the "none" category (parasitic species) is removed.



7g) Bar graph of wild bee flower specialization of species' abundances collected in the two methods across the three seasons. Species with the highest abundances of individuals is highlighted in black and the name of the species is written at the top of the bar.



Figure 8: Bar graph of hoverflies combined floral preference for nectar-bearing or both (nectar-bearing and pollen-only flowers) of individuals and species collected in the two methods, netting (red) and traps (blue). The χ^2 test was not significant for both individuals and species (p > 0.05).



8g) Bar graph of hoverflies floral preference of species' abundances collected in the two methods across the three seasons. Species with the highest abundances of individuals is highlighted in black and the name of the species is written at the top of the bar.



Figure 9: Bar graph of hoverfly migratory status showing the proportion of hoverflies individuals and species of each migratory status category (migratory, non-migratory, or both) for each method, netting (red) and traps (blue). The χ^2 test showed significant differences across methods for the proportion of individuals in each migratory status category in the spring 2018(a) (**p=0.001**). There was no significant differences between methods for the proportion of individuals in each migratory status category for the other season and for the proportion of species in each migratory status category for any of the seasons (all p > 0.05).



9g) Bar graph of hoverflies migratory status of species' abundances collected in the two methods across the three seasons. Species with the highest abundances of individuals is highlighted in black and the name of the species is written at the top of the bar.



Figure 10: Bar graph of hoverfly habitat preference showing the proportion of hoverfly individuals and species in each category for habitat preference (all, no known, rural, rural/crop, or rural/field(-edge/hedgerows)) for each method, netting (red) and traps (blue). The χ^2 test showed significant differences across methods for the proportion of individuals in each habitat preference category in all seasons (all **p<0.001**), but no significant differences between methods for the proportion of species in each habitat preference category in any season (all **p**<0.05). Significance disappeared in 2018a when the "rural/crop" category was removed, suggesting the significant results for individuals are most robust in the other two seasons.



10g) Bar graph of hoverflies habitat preference of species abundances collected in the two methods across the three seasons. Species with the highest abundances of individuals is highlighted in black and the name of the species is written at the top of the bar.



Supplementary Methods 1

In order to test for the variation in sampling effort between the sites, we calculated the maximum distance between the sampling areas at each site in each season and method. We then checked to see if the maximum distance between the sampling areas significantly increased with increase in the number of samples. We also calculated the percentage of different land-uses in a 100 m radius around the sampling area using the calculated from CORINE land cover (CLC, © European Union, Copernicus Land Monitoring Service 2018, European Environment Agency (EEA)). We combined the CORINE classes into "managed" and "semi-nature." We then plotted the percent of managed to the percent of forest at each sampling area and calculated the distance between the sampling areas at each site in each season and method using Pythagorean theorem. A habitat distance of "0" means that there was no difference between the samples, whereas a "1.41" there was 100% dissimilarity between two sample areas at a site. Similar to the maximum distance, we checked to see if the maximum habitat distance at each site changed significantly with increase in sampling areas.

Only in the spring 2018(a) did maximum distance between sampling areas increase significantly with increase number of traps. This difference was less than 1.3 km (Figure 11a). The difference in habitat composition did not change significantly between the traps during this season. In the fall 2018(b) the habitat distance significantly decreased for the netting sampled areas; sites became more similar with increase in sampling areas (Figure 11b). Therefore, we feel that despite different number of sampling between our sites, the spatial heterogeneity remained the same.

Figure 11: Linear relationship between number of samples at sites and the a) maximum distance (m) between samples and b) habitat maximum distance for the different seasons and methods, net (pink and circles) and traps (blue and triangles).





Chapter 3

Oilseed Rape Shares Abundant and Generalized Pollinators with Its Co-Flowering Plant Species

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Article



Oilseed Rape Shares Abundant and Generalized Pollinators with Its Co-Flowering Plant Species

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Simple Summary: Plants in semi-natural areas provide food resources for pollinators that visit pollinator-dependent crop species, such as Oilseed Rape (OSR). Here, we study the patterns of pollinator visitation on OSR and its co-flowering plants in adjacent semi-natural areas. We find that OSR is visited by pollinators that are abundant in the community and that these pollinators also visit co-flowering plant species in semi-natural areas. OSR primarily influences the pollination of plant species which have similar floral traits (i.e., other disc flowers). Plant species that attract a high abundances of bumblebees, wild bees, flies, and beetles influence the pollination of OSR the most. Our results suggest that plant species in semi-natural areas that support the high abundances of common pollinators which are generalized in their visitation are most important to the pollination of OSR, and that such plant species do not necessarily have similar floral traits to OSR.

Abstract: Mass-flowering crops, such as Oilseed Rape (OSR), provide resources for pollinators and benefit from pollination services. Studies that observe the community of interactions between plants and pollinators are critical to understanding the resource needs of pollinators. We observed pollinators on OSR and wild plants in adjacent semi-natural areas in Sachsen-Anhalt, Germany to quantify (1) the co-flowering plants that share pollinators with OSR, (2) the identity and functional traits of plants and pollinators in the network module of OSR, and (3) the identity of the plants and pollinators that act as network connectors and hubs. We found that four common plants share a high percentage of their pollinators with OSR. OSR and these plants all attract abundant pollinators in the community, and the patterns of sharing were not more than would be expected by chance sampling. OSR acts as a module hub, and primarily influences the other plants in its module that have similar functional traits and are part of different modules. Our study demonstrates that supporting the pollination of OSR requires the presence of semi-natural areas with plants that can support a high abundances of generalist pollinators.

Keywords: oilseed rape; community composition; floral functional traits; null model; plant-pollinator network; Bray-Curtis index; modularity

1. Introduction

Pollinators underpin food production, since they provide services for approximately 35% of global crop production [1]. While honeybees are traditionally thought of as being the most important pollinating agents, wild bees alone can provide the full pollination requirements of many crops [2–4] and the stability of crop pollination increases with the bee richness [2,5,6]. Non-bee insects also contribute a substantial amount to global crop

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Copyright: © 2021 by the authors. Submitted for possible open access publication under the terms and conditions of the Creative Commons Attribution (CC BY) license (http://creativecommons.org/license s/by/4.0/). pollination [7]. Wild pollinators' economical contribution towards crop production is similar to that of honeybees [8]. The abundance and diversity of these wild pollinators, and the quality of the services they provide to crops within agricultural landscapes, is influenced by the composition and quality of the surrounding landscape [3,9]. In order to continue meeting the agricultural demands that come with a growing human population, it is increasingly essential to investigate the factors that may influence pollinator abundance and diversity, and subsequently impact their service to crops [1,10].

Semi-natural areas which surround agricultural fields are important to wild pollinators because they offer a diversity of shelter and nesting sites [11,12] that are not always readily available in agricultural landscapes, and they provide more consistent or diverse food resources for pollinators [9,13–16]. Mass flowering crops provide a large, but homogenous, food resource to pollinators, which occurs in pulses [17]. Semi-natural areas offer more consistent floral resources over a longtime period [18]. There is a recognition of the importance of semi-natural areas, and practitioners aim to increase floral resources for pollinators with active management (e.g., planting hedgerows near agricultural landscapes). However, the choice of plants in these management activities is often based on pollinator syndromes, rather than on the ecological observations of pollinator activities between crop plants and plants within the semi-natural areas [19].

By observing the interactions between plants and pollinators in the community, it is possible to identify the semi-natural plant species that are highly similar to the focal agricultural plant, in regards to their composition of pollinating insects. These semi-natural plant species might be the ones that provide important resources to agriculturally important pollinators, which sustain pollinators across longer time periods. However, plant species might have a high similarity in their composition of pollinating insects by chance if, for example, the plants interact with the most common pollinator species in the community. Null models can be used to distinguish real patterns in similarity from those which are driven by neutral patterns expected from sampling [20–22]. These interactions via shared species can be either facultative (by attracting pollinators and leading to an increased chance in conspecific pollen deposition) or competitive (attracting a pollinator away or inhibiting pollination through the deposition of heterospecific pollen). We can measure the potential of one species to indirectly influence another species of the same trophic level based on the frequency of shared interactions (i.e., Müller's index, [23]).

Bipartite networks that describe observations of plant-pollinator interactions are also an important tool for understanding the community structure and roles of species [24]. Networks are modular in their structure, where species with similar interactions group together, interacting more with each other than with species in different modules [25]. Plants and pollinators often cluster in modules based on their functional traits, due to the important role of trait-matching in determining whether or not species interact. Thus, identifying the plants and pollinators that are important for sustaining the pollination of a focal crop species requires understanding the modular location of the crop, as well as the locations and roles of all other co-flowering plant species in the network. Most species are *peripheral* species; they have links that are almost exclusively with species in their module. Species that are *module hubs* are important for linking species within the module. Species that are *connectors* provide links between modules. Species that are *network* hubs are important within their module and in connecting modules. To ensure the stable and adequate pollination of a focal agricultural species, it is important to have plant species present in the community that are in its module, as well as the connector and network hub species that ensure the cohesiveness of the entire network [26,27].
Oilseed Rape (OSR, *Brassica napus*) is a highly abundant crop in Europe that mass flowers and provides resources for pollinators. Although OSR is self-compatible [28], many studies have found its yields and market value to increase significantly with insect pollination [29–32]. OSR produces many bright, yellow, entomophilic flowers that secrete high amounts of nectar, making them very attractive to pollinating insects [12,33]. Insect pollination enhances the average crop yield, but overall yield is enhanced by higher visitation rates and not by a higher pollinator richness [7,34]. Many studies have observed the identity of pollinators that provide services to OSR [33,35–37] and have examined how the pollinator community is affected by the mass-flowering plant [38–42]. The two studies that have considered OSR in a network context have demonstrated that OSR shares pollinators with plants in hedgerows and surrounding semi-natural grasslands, and attracts some of the most abundant pollinators in the network [39,43].

In this study, we observed plant–pollinator interactions in order to determine the co-flowering plants that are most similar in their visiting pollinator compositions to OSR, and to test if this similarity was higher than expected by chance. We expected to find that OSR attracts abundant pollinators, and therefore it is possible that the similarities in pollinator compositions with many co-flowering plant species are due to chance. Another goal was to quantify the module that OSR is a part of, the identity and functional traits of other plants in that module, and the identity of species that act as connectors and network hubs. We expected that OSR shares a module with co-flowering plants which have similar functional traits, and that it may play a connector or hub role in the network by attracting abundant and generalized pollinator species. Lastly, we used Müller's index to determine the indirect effect the plants and pollinators have on each other, due to their shared interactions.

2. Materials and Methods

Data were collected at six different sites that are 20-35 km away from each other, in Sachsen-Anhalt, Germany (Table S1), and that are a part of the Terrestrial Environmental Observatories Network (TERENO) [44]. Each site was 4 km × 4 km and was divided into 16 squares of 1 km². From 20 April to 23 May 2017-during the flowering of oilseed rape (OSR, *Brassica napus*)—we used net sampling to collect visiting insects on flowering plants during sunny days, between 9:00 and 15:00 when insects were most active. We sampled within 3-4 squares at each site, in areas that included flowering natural vegetation near OSR fields using a plant-based method, in which an equal amount of time observing pollinators was spent on all flowering plants within 100 m from the field edge, until the sampling saturation was reached (Table S2). Insects that could be identified in the field (e.g., Bombus spp complex, Apis mellifera, many Lepidopteran species) were recorded and released. Other insects were collected in vials and labeled with the plant species they were collected from, as well as the site and date of collection. The insects were frozen, pinned, and later identified using published taxonomic guides [45-53] and the assistance from a local expert. Insects were identified to a species level when possible, but when it was not, they were identified to genus or family levels. Data were pooled across sites and time periods.

We grouped our plant and pollinator species into functional groups. For plants, we used simplified flower types after Kugler from the BiolFlor database [54], resulting in nine different flower types (Table S3a). We grouped pollinators into eight functional groups based on taxonomic groupings that reflect their life-histories and roles as pollinators (Table S3b). For example, within Hymentopterans, functional groups included honeybees, bumblebees, wild bees, and wasps.

A plant–pollinator network, with all flower visitors and plants, was visualized using the bipartite package in R [22]. We visualized the composition of pollinators

on different plant species using nonmetric multidimensional scaling analysis (NMDS), based on Bray-Curtis dissimilarity distances. The NMDS' were created using the vegan package (function: metaMDS) in R [55]. We tested whether the pollinator composition differed between plants in different functional groups using a permutational multivariate analysis of variance using distance matrices (PERMANOVA), based on the principles of McArdle & Anderson [56].

We created a null model to calculate whether or not the plant species in the semi-natural areas share more pollinator species with OSR than expected by chance. To create the null model, first we calculated the observed Bray-Curtis dissimilarity distance of the pollinator composition for each plant species in the network, as well as for OSR. Bray-Curtis uses a scale from 0 to 1, for which 0 means 100% similarity and 1 means 100% dissimilarity in pollinator community composition. We then randomly assigned pollinators to each plant species based on the observed number of pollinator seen on each plant species and the relative abundances of each pollinator species (i.e., pollinators that were observed frequently were more likely to be chosen). We then re-calculated the Bray-Curtis dissimilarity distance of the pollinator composition for each plant species in the network, and OSR, for this null model. The null model was replicated 1000 times and the mean dissimilarity and its 95% confidence intervals were plotted, along with the observed Bray-Curtis dissimilarity.

Modularity and the modular networks were calculated using the metaComputeModules function in the bipartite package. Modularity is based on a scale from -1 to 1, in which 0 indicates that community division is not better than random, and 1 indicates a strong community structure. We visualized the number of interactions between different functional groups in each module with a bar plot, and tested whether the proportional representation of different functional groups differed between modules using a Chi-squared test. The role of a speciesperipherals, module hubs, connectors, or network hubs - can be assigned according to its interactions within its module and within the network. The among-module connectivity (c-value) and within-module degree (z-value) were calculated for both the plants and pollinators in the network using the methods from Olesen and colleagues [57]. Species with low c- and z-values are specialist peripherals, since they have few links within their module and among modules. A connector has a low z- and a high c-value, and are important for connecting several modules together. A module hub has a high z- and a low c-value, and are important for linking species together within its module. A network hub has high z- and high cvalues, and are important for the cohesion of the network and within its module. Following the methods from Dormann and colleagues [58], we calculated the 95% quantiles of the c- and z-values using 1000 null models, to objectively set the thresholds for the species roles.

We calculated the Müller Index using the PAC function in R [23]. This index calculates the potential indirect interaction of each plant species to influence all the co-flowering plant species via shared pollinators, and vice versa for pollinators [11,59]. The index is a relative measure and varies between zero (no pollinators/plants shared) to 1 (diet of all visitors depends on the acting plant/visitation to all plants depends on the acting pollinator). A higher value indicates a greater potential for the acting species to influence the target species via shared pollinators for plants, or plants for pollinators. The metric is also asymmetrical, meaning that species A could have more influence on species B than species B on species A.

3. Results

Our observed plant-pollinator interaction network consisted of 2778 interactions of 48 plant species and 189 unique pollinators from four orders

(Hymenoptera, Diptera, Lepidoptera, and Coleoptera) (Figure 1). The most visited plant was *Brassica napus* (OSR, 26.89% of all visits), followed by *Taraxacum officinale* (23.97%). The functional groups with the most visits were disk flowers with hidden nectar (46.04%), flower heads (25.23%), and lip flowers (14.32%). The most observed pollinator at the species level was *Apis mellifera* (12.99%) which visited 16 (33.33%) different plant species. The most observed functional group of pollinators were wild bees (64 species, 22.53%), followed by bumble bees (nine species, 19.44%) and other fly families (15 families, 17.93%). Percentages for all the species are in Tables S4 and S5.



Figure 1. Bipartite network of plant–insect interactions. Plant species are on top and pollinator functional groups on bottom. The thickness of the bars indicates the total number of interactions. OSR and its interactions are black; the other four plants that share a high proportion of interactions with OSR are highlighted in dark grey.

3.1. Plant-Pollinator Interactions and Composition

We observed 747 interactions with OSR from 73 different pollinators, 82.2% of which were shared with other plants in the network. The three most frequent visitors were *Apis mellifera*, Mordellidae beetles, and Empididae flies. Over half of the *A. mellifera* observations were on OSR. Likewise, a high percentage of the Mordellidae beetle and Empididae fly observations were on OSR (over 56 and 24% respectively). Unique pollinators visiting OSR, but no other plant species, accounted for only 3.6% of the interactions observed on OSR.

We found that different plant functional groups have significantly different compositions of pollinators (p < 0.01) (Figure 2). Disk flowers with hidden nectar were mainly visited by fly species, whereas flower heads were visited by wild bee species, and lip flowers by bumblebees.

OSR had a similar composition of visiting pollinators (based on the Bray-Curtis dissimilarity index) to *Taraxacum officinale*, *Crataegus monogyna*, *Lamium purpureum*, and *L. album*. OSR is a disk flower with hidden nectar and was mainly visited by common, generalist pollinators. *Taraxacum officinale* has yellow flower heads and is pollinated by a wide variety of wild bees and flies. *Crataegus monogyna* is a spring-flowering tree with disk flowers with open nectar and is typically visited by honeybees and beetles. *Lamium album* and *L. purpureum* are white and purple lip flowers that offer nectar to pollinators and are pollinated by many insects, but mainly bumblebees. While all of these species shared many pollinators was not significantly higher than that expected by chance, and for some plant species, the pollinator composition was significantly more dissimilar from OSR than expected by chance (Figure 3).

3.2. Network Modularity

The network contained 16 modules and a modularity value of 0.47 (Figure 4). OSR was in a module with six other plant species, including *C. monogyna*, and 40 pollinator taxa; the majority of which were honeybees or beetles. *T. officinale* is in a module with two other plant species and forty six pollinators, a majority being wild bees; *L. album*, and *L. purpureum* are in a module with 10 other plant species and 13 pollinators, a majority being bumblebees. The relative abundance of interactions involving different plant and pollinator functional groups significantly differed across modules (p < 0.001, Figure 5). The threshold limits for plants were c-value= 0.83 and z-value=2.27 and for pollinators, c-value= 0.83 and z-value=2.03. A percentage of 9.28% of all species had an important role in the network (10.40% of plants, 8.99% of pollinators). Three plants were module hubs (*Lamium purpureum*, *Brassica napus* (OSR), *Veronica chamaedrys*) and two plants were modular hubs, and seven were connectors (Figure 6b).



Figure 2. Non-metric multidimensional scaling (NMDS) plot based on the Bray-Curtis dissimilarity distance of insect visitations on plant species (top). Bottom is a close-up of ordination with the removal

of the outlier, plus the visualization of pollinator species. OSR is highlighted in red. Different functional groups of plants are symbols and pollinator groups are colors. Stress level = 0.13.



Figure 3. Results of the Bray-Curtis dissimilarity distance of plant species to OSR using a null model. Observed dissimilarity distances are shown in black circles and the mean and 95% confidence intervals of the dissimilarity distances from null models are in red.



Figure 4. Modular network with 16 different modules. Species are sorted according to their modular affinity, plants as rows and pollinators as columns. Darkers squares indicate more interactions. OSR is in the fifth module. Species names are listed in Tables S4 and S5.



Figure 5. Bar graph showing the abundance of interactions involving different (a) plant and (b) pollinator functional groups across modules.



Figure 6. Distribution of (**a**) plants and (**b**) pollinators according to their network role. Each point represents a species, colors and shapes represent functional groups. Species with high c- and/or z-values are named. Threshold lines (95% quartiles) are shown.

3.3. Müller Index

OSR had the highest influence mediated by shared pollinators in the network (Müller index sum = 10.73, mean= 0.22). The species that OSR had a greater effect on were different from those that had a greater effect on OSR (Figure S1). OSR had the greatest effect on *Ranunculus auricomus*, *Adonis vernalis*, *Prunus spinosa*, itself, *Sinapis arvensis*, and *Sorbus aucuparia*, all of which are in the same module. The plants that had the most effect on OSR were *Taraxacum officinale*, *Crataegus monogyna*, *Lamium purpureum*, and *L. album*, all of which shared many pollinators with OSR. The pollinators that had the highest influence on the network were *Apis mellifera* (Müller index sum = 22.2, mean = 0.11), Empididae flies (12.27, 0.06), *Andrena cineraria* (11.74, 0.06), Mordellidae beetles (11.02, 0.06), and *Bombus terrestris* complex (10.06, 0.05).

4. Discussion

Our study documents observations of plant–pollinator interactions, revealing that OSR attracts abundant pollinators in the community, and all the similarities in pollinator compositions with co-flowering plants are due to chance. OSR occurs in a module with other disc flowers and plays the role of a module hub, due to the high abundance of pollinators it attracts, which are mostly honeybees, beetles, and flies. OSR has a large influence on the other plants in its module. However, plant species, both in its module and in other modules that also attract abundant pollinators, have the largest influence on OSR. These species include: *Taraxacum officinale, Crataegus monogyna, Lamium purpureum*, and *L. album*. Our results suggest that these plant species provide the resources for pollinators that support the pollination of focal crop species.

We find that the composition of visiting pollinators differs across categories of plants with different functional traits, and that the functional traits of plants and pollinators are clustered into modules in the network. This matches the results of other studies that have found an important role for trait-matching in determining the interactions between plants and pollinators, and the structure of modules [25,60]. Surprisingly, we found that the plant species most similar to OSR in the composition of visiting pollinators were those with dissimilar functional traits that were not members of its module. This is because OSR interacts with common pollinators that are also important to plants in other modules. OSR forms a module with other disk flowers for which honeybee visitors are the most common. However, OSR is also visited by wild bees and flies, which are the predominant visitors in the module that is dominated by plants with flower heads, such as *Taraxacum officinale*. Likewise, OSR is visited by bumblebees, which are the dominant pollinator group in the module that contains lip flower plants, such as *Lamium album* and *L. purpureum*.

We found that OSR acts as a modular hub in the network, and thus is important within its module. By interacting with most of the module's pollinators (82.5%), OSR ensures stability for the other plants in the module. This is similar to the findings of Stanley and Stout, who found that OSR had a high niche overlap with other plant species in the network [43]. We found in total three module hub plant species, which corresponds with the findings from Dupont that most networks are organized around a few plant hubs [61]. These plant hubs are important for the stability of the network and for supporting a high diversity of plants and pollinators. Loss of these species would fragment the modules and cause the cascading extinction of pollinators.

Our study illustrates the importance of using null models to interpret patterns of pollinator sharing across plant species. In our study, the patterns of similarity in visiting pollinators between OSR and other co-flowering plant species are expected by chance. For example, OSR and *T. officinale* were the most visited plants in the

entire network and both were visited by the most abundant pollinators in the system. This finding is in line with another network study on OSR that also found that OSR attracts the most abundant pollinators in the system [39]. Our null model result, combined with the results of other studies that show that the number of visitors, rather than the diversity, influences the reproductive success of OSR [33,62], have implications for management. Specifically, hedgerow plantings and semi-natural areas should be managed in a manner that creates abundant floral resources and habitats to support a high density of pollinating insects. It does not seem necessary to focus on planting co-flowering plant species that share functional traits with OSR.

The plants that OSR affects the most based on the Müller index are those in its module: *Ranunculus auricomus, Adonis vernalis, Prunus spinosa, Sinapis arvensis,* and *Sorbus aucuparia.* We only observed one to three different pollinator species on each of these plants and these pollinators were all common. This suggests that OSR might have a negative effect on these plants by reducing the number of visits these wild plants receive, or lowering the quality of visits to wild plants, if pollinators deliver OSR pollen rather than conspecific pollen. However, a study by Stanly and Stout [43] found that the wild plants that share pollinators with OSR have very little OSR pollen deposited on their stigmas, suggesting that the effects OSR on the pollination of wild plants might be minimal.

Honeybees (*Apis mellifera*) are the most observed flower visitor in our system and play an important role in the network, as seen from their role as a module hub and from their high Müller index. However, less abundant groups of pollinators also have important roles in the network. Other pollinator groups with roles as network hubs and connectors and with a high Müller index included a fly family (Empididae), a beetle family (Mordellidae), and two wild bee species (*Andrena cineraria* and *Bombus terrestris* complex). Empididae flies (dagger flies) are also a known generalist species that thrives in field hedgerows [63] and will expand their foraging breadth to rare plant species when overall plant density is low [64]. Creating habitats that support the nesting, larval, and adult food resources of these pollinators is therefore an important consideration in the management of agroecosystems.

5. Conclusions

OSR is a mass flowering crop that plays an important role in plant and pollinator communities during its flowering period. Although it provides abundant floral resources and is a highly attractive plant, this attractiveness could be reducing visitation to co-flowering plants, particularly those in its module. The co-flowering plant species most important to supporting the pollinators of OSR are species that are very common in our region, such as *Taraxacum officinale* and *Lamium purpureum*. These species will naturally colonize semi-natural areas and planted hedgerows and are also found in disturbed areas, such as roadsides and forest margins. Semi-natural areas are important for supporting a high abundance and diversity of insects that provide pollinators' services to wild and agricultural plant species [16,65]. Studies such as this one, which examined the network structure and sharing of pollinators, contribute to our understanding of the plants and pollinators that are most likely to be either facilitated by or compete with OSR, and which ones most influence the pollination of OSR.

Supplementary Materials: The following are available online at www.mdpi.com/xxx/s1, Figure S1: Müller Index; Table S1: Coordinates of sites, Table S2: Extrapolated species richness, Table S3: Functional groups, Table S4: List of plant species, Table S5: List of pollinator species

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SUPPLEMENTARY MATERIALS

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Figure S1. Results from Müller's Index calculated using the PAC function in R. Index ranges from 0 to 1 with 0 indicating no shared visitors (no influence) to 1, diet of all visitors depends on the acting plant. The values for *Brassica napus*' effect on plants in the community (a) and the effect of other plant species on *Brassica napus* (b).



Site	ID	Lat	Long	Int	Pol	Pl	Time Sampled
Friedeberg	FRI1	51.62053	11.72198	108	38	13	4:38
Friedeberg	FRI2	51.62335	11.73013	86	29	10	3:54
Friedeberg	FRI3	51.63262	11.70642	141	48	16	4:30
Greifenhagen	GRE1	51.62443	11.4552	166	43	13	4:45
Greifenhagen	GRE2	51.62147	11.45708	26	12	4	0:40
Greifenhagen	GRE3	51.61945	11.43882	197	36	15	4:35
Greifenhagen	GRE4	51.64473	11.43882	172	44	15	5:12
Harsleben	HAR1	51.85657	11.07052	125	22	9	3:39
Harsleben	HAR2	51.83783	11.05842	41	6	4	0:56
Harsleben	HAR3	51.8536	11.08758	157	40	15	4:23
Harsleben	HAR4	51.8259	11.067	71	14	8	2:13
Siptenfelde	SIP1	51.6543	11.03887	195	29	7	3:43
Siptenfelde	SIP2	51.63853	11.0606	182	39	13	4:01
Siptenfelde	SIP3	51.6365	11.05487	164	22	9	3:50
Schafstädt	SST1	51.38192	11.71798	147	36	13	4:30
Schafstädt	SST2	51.37763	11.72055	94	24	11	2:55
Schafstädt	SST3	51.35478	11.73462	237	25	9	3:30
Wanzleben	WAN1	52.09462	11.4175	143	33	16	4:20
Wanzleben	WAN2	52.09283	11.4278	178	27	9	4:18
Wanzleben	WAN3	52.08375	11.41837	148	31	10	3:44

Table S1. Information of sites sampled including coordinates (WGS84), the number of interactions (Int), pollinator species (Pol), plant species (Pl) and time spent sampling (hours:minutes) at each site.

Table S2. Extrapolated species richness based on number of individuals (for pollinators) and number of interactions sampled using specpool in the vegan package. Observed richness; Estimated richness with Chao1 estimator; Standard error with Chao1 estimator; Sampling completeness (Observed richness/Estimated richness x 100 \pm Standard Error) for plant species, pollinator species and interactions of both.

	Observed Richness	Estimated Richness	Standard Error	Sampling Completeness (%)
Pollinator Species	189	281.75	27.02	61.21-74.19
Interactions	567	1836.55	202.58	27.81-34.70

Table S3. Relative abundance of functional groups for a) plants and b) pollinators used in analyses. Relative abundance was caculated as number of interactions observed for a functional group divided by total number of interactions in network; then multiplied by 100 for a percentage.

a)	Plant	functional	groups
u)	1 Iuni	runetional	Sidups

Flower Type	Relative abundance
Bell	1.80 %
Disk with Hidden Nectar (HN)	46.04 %
Disk with Open Nectar (ON)	10.44 %
Flag Blossoms	1.19 %
Flower Head	25.23 %
Funnel	0.14 %
Lip	14.33 %
Pollen	0.68 %
Stalk Disk	0.14 %

b) Pollinator functional groups

Pollinator group	Relative abundance
Bumblebee	19.44 %
Coleoptera	13.46 %
Honeybee	13.00 %
Hoverfly	5.94 %
Lepidoptera	3.42 %
Other_fly	17.93 %
Wasp	4.28 %
Wild_bee	22.53 %

Table S4. List of 48 plant species (in alphabetical order) found in our study along with information for each on
its flower type, the number of interactions with pollinators observed, and its module. Each plant is given a short
ID, and these IDs are used in Figure 4, which shows network modularity.

ID	Plant	Flower type	Interactions	(Percentage)	Module
P_01	Adonis vernalis	Pollen	19	(0.68)	5
P_02	Aesculus hippocastanum	Lip	6	(0.22)	8
P_03	Alliaria petiola	Disk_HN	32	(1.15)	12
P_04	Anthemis arvensis	FlowerHead	2	(0.07)	2
P_05	Bellis perennis	FlowerHead	21	(0.76)	2
P_06	Brassica napus	Disk_HN	747	(26.89)	5
P_07	Brassica nigra	Disk_HN	82	(2.95)	9
P_08	Capsella bursa-pastoris	Disk_HN	37	(1.33)	13
P_09	Crataegus monogyna	Disk_ON	179	(6.44)	5
P_10	Daucus carota	Disk_ON	35	(1.26)	15
P_11	Descurainia sophia	Disk_HN	13	(0.47)	9
P_12	Erodium cicutarium	Disk_HN	17	(0.61)	8
P_13	Euphorbia cyparissias	Disk_ON	40	(1.44)	16
P_14	Euphorbia helioscopia	Disk_ON	7	(0.25)	7
P_15	Fragaria vesca	Disk_HN	5	(0.18)	11
P_16	Fumaria officinalis	FlagBlossoms	12	(0.43)	4
P_17	Genista sp	FlagBlossoms	9	(0.32)	4
P_18	Heracleum sphondylium	Disk_ON	25	(0.90)	7
P 19	Lamium album	Lip	123	(4.43)	4
P 20	Lamium amplexicaule	Lip	8	(0.29)	4
P 21	Lamium purpureum	Lip	188	(6.77)	4
P_22	Lathyrus vernus	FlagBlossoms	2	(0.07)	6
P_23	Lepidium campestre	Disk_HN	79	(2.84)	10
P_24	Lycium barbarum	StalkDisk	4	(0.14)	4
P_25	Muscari botryoides	Bell	8	(0.29)	8
P_26	Prunus avium	Disk_HN	19	(0.68)	4
P_27	Prunus cerasus	Disk_HN	92	(3.31)	3
P_28	Prunus spinosa	Disk_HN	3	(0.11)	5
P_29	Ranunculus acris	Disk_HN	72	(2.59)	2
P_30	Ranunculus auricomus	Disk_HN	8	(0.29)	5
P_31	Ranunculus repens	Disk_HN	14	(0.50)	2
P_32	Ribes aureum	Bell	3	(0.11)	4
P 33	Salvia pratensis	Lip	4	(0.14)	8
P 34	Senecio jacobaea	FlowerHead	12	(0.43)	1
P 35	Sinapis arvensis	Disk_ON	4	(0.14)	5
P 36	Sorbus aucuparia	Disk_HN	10	(0.36)	5
P 37	Stellaria holostea	Disk_HN	14	(0.50)	14
P 38	Stellaria media	Disk_HN	17	(0.61)	8
P_39	Symphytum officinale	Bell	39	(1.40)	4
P_40	Taraxacum officinale	FlowerHead	666	(23.97)	1
P_41	Thlaspi arvense	Disk_HN	18	(0.65)	1

P_42	Trifolium campestre	FlagBlossoms	4	(0.14)	4
P_43	Trifolium medium	FlagBlossoms	3	(0.11)	8
P_44	Valerianella locusta	Funnel	4	(0.14)	8
P_45	Veronica chamaedrys	Lip	27	(0.97)	8
P_46	Veronica persica	Lip	17	(0.61)	8
P_47	Vicia sativa	FlagBlossoms	3	(0.11)	4
P_48	Viola arvensis	Lip	25	(0.90)	8

Table S5. List of 189 pollinators (in alphabetical order) observed in our study at the highest level of identification along with information for each on its functional group, the number of interactions with plants observed, and its module. Each pollinator is given a short ID, and these IDs are used in Figure 4, which shows network modularity.

ID	Pollinator	Pollinator Group	Interactions	(Percentage)	Module
I_01	Adelidae	Lepidoptera	34	(1.22)	12
I_02	Aglais io	Lepidoptera	11	(0.4)	1
I_03	Alocerus sp	Coleoptera	1	(0.04)	7
I_04	Altica sp	Coleoptera	2	(0.07)	16
I_05	Ampedus rufipennis	Coleoptera	1	(0.04)	15
I_06	Anatis ocellata	Coleoptera	6	(0.22)	5
I_07	Andrena alfkenella	Wild_bee	1	(0.04)	5
I_08	Andrena chrysosceles	Wild_bee	4	(0.14)	1
I_09	Andrena cineraria	Wild_bee	165	(5.94)	1
I_10	Andrena dorsata	Wild_bee	2	(0.07)	5
I_11	Andrena flavipes	Wild_bee	74	(2.66)	1
I_12	Andrena floricola	Wild_bee	5	(0.18)	10
I_13	Andrena fucata	Wild_bee	1	(0.04)	1
I_14	Andrena fulva	Wild_bee	2	(0.07)	4
I_15	Andrena gravida	Wild_bee	8	(0.29)	1
I_16	Andrena haemorrhoa	Wild_bee	44	(1.58)	1
I_17	Andrena helvola	Wild_bee	8	(0.29)	5
I_18	Andrena labiata	Wild_bee	1	(0.04)	8
I_19	Andrena minutula	Wild_bee	3	(0.11)	13
I_20	Andrena minutuloides	Wild_bee	4	(0.14)	11
I_21	Andrena nigroaenea	Wild_bee	29	(1.04)	5
I_22	Andrena nitida	Wild_bee	6	(0.22)	1
I_23	Andrena scotica	Wild_bee	2	(0.07)	3
I_24	Andrena strohmella	Wild_bee	6	(0.22)	1
I_25	Andrena subopaca	Wild_bee	2	(0.07)	8
I_26	Andrena synadelpha	Wild_bee	1	(0.04)	5
I_27	Andrena vaga	Wild_bee	1	(0.04)	1
I_28	Andrena varians	Wild_bee	1	(0.04)	3
I_29	Andrena viridescens	Wild_bee	3	(0.11)	8
I_30	Anthaxia nitidula	Coleoptera	12	(0.43)	16
I_31	Anthocharis cardamines	Lepidoptera	2	(0.07)	9
I_32	Anthomyiidae	Other_fly	60	(2.16)	5

I 33	Anthophora plumipes	Wild_bee	41	(1.48)	4
I 34	Apis mellifera	Honeybee	361	(12.99)	5
I 35	Araschnia levana	Lepidoptera	1	(0.04)	2
I_36	Asilidae	Other_fly	2	(0.07)	10
I_37	Athalia rosae	Wasp	1	(0.04)	10
I_38	Bibionidae	Other_fly	40	(1.44)	3
I_39	Bombus dark form complex	Bumblebee	9	(0.32)	5
I_40	Bombus hortorum	Bumblebee	1	(0.04)	4
I 41	Bombus hypnorum	Bumblebee	1	(0.04)	5
I_42	Bombus lapidarius	Bumblebee	1	(0.04)	5
I_43	Bombus pascuorum	Bumblebee	235	(8.46)	4
I_44	Bombus pratorum	Bumblebee	5	(0.18)	4
I_45	Bombus red-tail complex	Bumblebee	46	(1.66)	5
I_46	Bombus terrestris	Bumblebee	4	(0.14)	4
I_47	Bombus terrestris complex	Bumblebee	238	(8.57)	4
I_48	Bombylius major	Other_fly	121	(4.36)	8
I_49	Brachyderini sp 1	Coleoptera	2	(0.07)	16
I_50	Brachyderini sp 2	Coleoptera	1	(0.04)	1
I_51	Byturus ochraceus	Coleoptera	35	(1.26)	2
I_52	Calliphoridae	Other_fly	17	(0.61)	7
I_53	Cantharis fusca	Coleoptera	13	(0.47)	15
I_54	Cephus brachycerus	Wasp	32	(1.15)	2
I_55	Cephus pygmeus	Wasp	56	(2.02)	9
I_56	Ceratina cyanea	Wild_bee	2	(0.07)	2
I_57	Cetonia aurata	Coleoptera	32	(1.15)	5
I_58	Cheilosia illustrata	Hoverfly	1	(0.04)	10
I_59	Cheilosia latifrons	Hoverfly	12	(0.43)	2
I_60	Cheilosia vicina	Hoverfly	2	(0.07)	2
I_61	Chelostoma florisomne	Wild_bee	1	(0.04)	2
I_62	Chrysanthia sp	Coleoptera	1	(0.04)	1
I_63	Chrysomela aenea	Coleoptera	2	(0.07)	4
I_64	Chrysotoxum cautum	Hoverfly	9	(0.32)	10
I_65	Chrysotoxum festivum	Hoverfly	2	(0.07)	15
I_66	Cladius pectinicornis	Wasp	1	(0.04)	5
I_67	Coccinella septempunctata	Coleoptera	6	(0.22)	5
I_68	Coenonympha pamphilus	Lepidoptera	11	(0.4)	10
I_69	Colias alfacariensis	Lepidoptera	1	(0.04)	1
I_70	Colletes cunicularius	Wild_bee	6	(0.22)	3
I_71	Collyriinae	Wasp	1	(0.04)	10
I_72	Conopidae	Other_fly	5	(0.18)	3
I_73	Dasysyrphus albostriatus	Hoverfly	2	(0.07)	1
I_74	Dasysyrphus tricinctus	Hoverfly	4	(0.14)	1
I_75	Dasysyrphus venustrus	Hoverfly	2	(0.07)	3
I_76	Dasytes virens	Coleoptera	1	(0.04)	5

I_77	Dinoptera collaris	Coleoptera	2	(0.07)	10
I_78	Dixidae	Other_fly	7	(0.25)	1
I 79	Elateridae	Coleoptera	33	(1.19)	15
I_80	Elinora koehleri	Wasp	3	(0.11)	13
I_81	Ematurga atomaria	Lepidoptera	1	(0.04)	1
I_82	Empididae	Other_fly	171	(6.16)	1
I_83	Entiminae	Coleoptera	3	(0.11)	1
I_84	Epistrophe eligans	Hoverfly	1	(0.04)	5
I 85	Episyrphus balteatus	Hoverfly	1	(0.04)	5
I_86	Eristalis arbustorum	Hoverfly	1	(0.04)	13
I_87	Eristalis horticola	Hoverfly	1	(0.04)	14
I_88	Eristalis jugorum	Hoverfly	1	(0.04)	1
I_89	Eristalis similis	Hoverfly	1	(0.04)	10
I_90	Eristalis tenax	Hoverfly	6	(0.22)	5
I_91	Eucera nigrescens	Wild_bee	1	(0.04)	6
I 92	Eupeodes corollae	Hoverfly	1	(0.04)	10
I 93	Eupeodes luniger	Hoverfly	1	(0.04)	5
I 94	Gnorimus variabilis	Coleoptera	1	(0.04)	5
I 95	Gonepteryx rhamni	Lepidoptera	3	(0.11)	9
I 96	Halictus maculatus	Wild_bee	3	(0.11)	7
I 97	Halictus scabiosae	Wild_bee	2	(0.07)	10
I 98	Halictus tumulorum	Wild_bee	10	(0.36)	5
I 99	Helophilus pendulus	Hoverfly	2	(0.07)	1
I 100	Ichneumoninae	Wasp	2	(0.07)	1
I_101	Issoria lathonia	Lepidoptera	1	(0.04)	1
I_102	Lasioglossum albipes	Wild_bee	1	(0.04)	1
I_103	Lasioglossum calceatum	Wild_bee	18	(0.65)	1
I_104	Lasioglossum fulvicorne	Wild_bee	1	(0.04)	16
I 105	Lasioglossum laevigatum	Wild_bee	1	(0.04)	9
I 106	Lasioglossum lativentre	Wild_bee	1	(0.04)	1
I 107	Lasioglossum lineare	Wild_bee	1	(0.04)	8
I 108	Lasioglossum malachurum	Wild_bee	7	(0.25)	1
I 109	Lasioglossum nitidiusculum	Wild_bee	2	(0.07)	4
I 110	Lasioglossum pallens	Wild_bee	1	(0.04)	5
I 111	Lasioglossum parvulum	Wild_bee	3	(0.11)	13
I 112	Lasioglossum pauxillum	Wild_bee	20	(0.72)	9
I 113	Lasioglossum politum	Wild_bee	1	(0.04)	5
I 114	Lasioglossum rufitarse	Wild_bee	1	(0.04)	1
I 115	Lasioglossum sp	Wild_bee	4	(0.14)	5
I 116	Lasioglossum villosulum	Wild_bee	1	(0.04)	1
I 117	Leptidea sinapis	Lepidoptera	1	(0.04)	5
I 118	Longitarsus sp	Coleoptera	1	(0.04)	1
I 119	Macrophya montana	Wasp	1	(0.04)	7
I 120	Malachius bipustulatus	Coleoptera	10	(0.36)	5
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I 121	Melanogaster hirtella	Hoverfly	1	(0.04)	1
I 122	Melanostoma mellinum	Hoverfly	6	(0.22)	5
I 123	Melanostoma scalare	Hoverfly	3	(0.11)	1
I 124	Mordellidae	Coleoptera	170	(6.12)	5
I_125	Muscidae	Other_fly	11	(0.4)	9
I_126	Nomada bifasciata	Wild_bee	14	(0.5)	1
I_127	Nomada fabriciana	Wild_bee	1	(0.04)	1
I_128	Nomada flava	Wild_bee	5	(0.18)	3
I_129	Nomada flavoguttata	Wild_bee	2	(0.07)	1
I_130	Nomada fucata	Wild_bee	2	(0.07)	10
I_131	Nomada goodeniana	Wild_bee	33	(1.19)	1
I_132	Nomada lathburiana	Wild_bee	4	(0.14)	1
I_133	Nomada marshamella	Wild_bee	7	(0.25)	4
I_134	Nomada panzeri	Wild_bee	12	(0.43)	3
I_135	Nomada ruficornis	Wild_bee	4	(0.14)	1
I_136	Nomada sp	Wild_bee	1	(0.04)	8
I_137	Nomada succincta	Wild_bee	5	(0.18)	3
I_138	Oedemera lurida	Coleoptera	3	(0.11)	1
I_139	Oedemera virescens	Coleoptera	8	(0.29)	2
I_140	Osmia bicolor	Wild_bee	1	(0.04)	5
I_141	Osmia bicornis	Wild_bee	3	(0.11)	5
I_142	Osmia brevicornis	Wild_bee	25	(0.9)	9
I_143	Pachyprotasis rapae	Wasp	1	(0.04)	14
I_144	Parasyrphus annulatus	Hoverfly	1	(0.04)	14
I_145	Phloeopora sp	Coleoptera	1	(0.04)	1
I_146	Phyllobius sp	Coleoptera	4	(0.14)	5
I_147	Pieris brassicae	Lepidoptera	5	(0.18)	7
I_148	Pieris napi	Lepidoptera	7	(0.25)	9
I_149	Pipizella divicoi	Hoverfly	1	(0.04)	16
I_150	Pipizella viduata	Hoverfly	2	(0.07)	16
I_151	Pipizella zeneggenesis	Hoverfly	1	(0.04)	10
I_152	Pissodes sp	Coleoptera	3	(0.11)	3
I_153	Platycheirus albimanus	Hoverfly	18	(0.65)	8
I_154	Platycheirus scutatus	Hoverfly	3	(0.11)	7
I_155	Platycheirus sp	Hoverfly	1	(0.04)	3
I_156	Platycheirus tarsalis	Hoverfly	2	(0.07)	4
I_157	Podistra sp	Coleoptera	1	(0.04)	2
I_158	Poecilus cupreus	Coleoptera	1	(0.04)	1
I_159	Poecilus versicolor	Coleoptera	2	(0.07)	5
I_160	Polyommatus bellargus	Lepidoptera	3	(0.11)	4
I_161	Pontia edusa	Lepidoptera	3	(0.11)	4
I_162	Procraerus tiblalis	Coleoptera	1	(0.04)	10
I_163	Pyralidae	Lepidoptera	9	(0.32)	14
I_164	Pyrgus malvae	Lepidoptera	2	(0.07)	9

I_165	Rhagionidae	Other_fly	1	(0.04)	5
I_166	Sarcophagidae	Other_fly	38	(1.37)	5
I_167	Scaeva selenitica	Hoverfly	5	(0.18)	5
I_168	Sphaerophoria rueppellii	Hoverfly	1	(0.04)	1
I_169	Sphaerophoria scripta	Hoverfly	7	(0.25)	13
I_170	Sphecodes albilabris	Wild_bee	2	(0.07)	3
I_171	Sphecodes ephippius	Wild_bee	2	(0.07)	1
I_172	Sphecodes spinulosus	Wild_bee	1	(0.04)	15
I_173	Syrphus ribesii	Hoverfly	21	(0.76)	8
I_174	Syrphus torvus	Hoverfly	35	(1.26)	5
I_175	Syrphus vitripennis	Hoverfly	6	(0.22)	5
I_176	Tachina fera	Other_fly	1	(0.04)	1
I_177	Tachinidae	Other_fly	19	(0.68)	2
I_178	Tenthredo sulphuripes	Wasp	1	(0.04)	5
I_179	Tenthredo temula	Wasp	1	(0.04)	5
I_180	Tenthredo zonula	Wasp	5	(0.18)	7
I_181	Tenthredopsis sp	Wasp	5	(0.18)	10
I_182	Tipulidae	Other_fly	3	(0.11)	14
I_183	Tropinota hirta	Coleoptera	12	(0.43)	1
I_184	Tryphoninae	Wasp	8	(0.29)	7
I_185	Ulidiidae	Other_fly	2	(0.07)	10
I_186	Valgus hemipterus	Coleoptera	2	(0.07)	7
I_187	Vesperus sp	Coleoptera	1	(0.04)	3
I_188	Vespula rufa	Wasp	1	(0.04)	1
I_189	Xantogramma pedissequum	Hoverfly	1	(0.04)	13



Chapter 4

Plant-Pollinator Interactions along an Urban and Agricultural Gradient

Authors

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Under Review in Urban Ecosystems.

Abstract

The conversion of natural habitats into more urban and agricultural landscapes is one of the greatest threats to plants, pollinators and their interactions. Most studies consider the transition from semi-natural to either more urban or more agricultural landscapes, but little is known about whether these different types of land use change have similar or different effects on plant-pollinator interactions. In this study, we consider the effects of land use across a broad region containing habitats that are semi-natural, urban and agricultural on plant and pollinator richness and composition and the structure of plant-pollinator interactions. We find that although community composition changes dramatically and differently across different land use gradients, the persistent presence of keystone pollinator taxa results in minimal changes to network structure. Specifically, Syrphidae flies and Halictid bees were keystone pollinator families. Within these families, similar compositions of species persisted across all land use types. Our virtual exclusion of these families highlighted how their loss would cause the networks to become less generalized, less even and less nested. Our results demonstrate that robust plant-pollinator interactions can persist across many land use types, so long as the habitats allow persistence of keystone taxa.

Keywords

Plant-pollinator interactions, urban land use, agricultural land use, keystone taxa, virtual exclusion

Introduction

Land use change is as a global threat to plant and pollinator communities (González-Varo et al., 2013; Vanbergen et al., 2013). Several studies have demonstrated that habitat alteration is associated with changes in diversity, abundance and composition of pollinator (Potts et al., 2010; Seibold et al., 2019; Senapathi et al., 2017; Winfree et al., 2009) and plant communities (Laliberté et al., 2010; Nicholson et al., 2017) and the structure of plant-pollinator interaction networks (Devoto et al., 2012; Doré et al., 2021). Most of these studies focus on one type of land use change, typically shifting semi-natural habitats to those that are either more agricultural or more urban. Observing multiple land use types in a single region provides an opportunity to quantify the similarities and differences by which different types of land use change influence plants, pollinators and their interactions (Baldock et al., 2015; Cariveau et al., 2013). For example, shifts from semi-natural towards more agricultural land use are generally thought to degrade nesting habitats for pollinators and homogenize their food resources (Feltham et al., 2015), whereas urban environments have sometimes been found to provide sufficient nesting habitats for pollinators and urban gardens can provide diverse food resources (Lowenstein et al., 2014; Wojcik & McBride, 2012).

The effects of urbanization and agriculture on the diversity of plants and pollinators are typically studied separately and the results vary across studies. Most studies show that semi natural habitats have higher diversity of plants and pollinators compared to agricultural habitats (Carvalheiro et al., 2010; Laliberté et al., 2010; Le Féon et al., 2010; Nicholson et al., 2017) and urban habitats (Ahrné et al., 2009; Bates et al., 2011; Geslin et al., 2013). However, this is not always the case, with some studies showing similar diversity of pollinators in semi-natural habitats compared to urban habitats (Ellis & Wilkinson, 2020; Fitch, 2017). This might be because the diversity of generalist pollinators increases in urban compared to semi-natural habitats (Callaghan et al., 2021). The few studies that compared multiple land use variables (agricultural, urban, and semi-natural) simultaneously found differences across taxa (e.g. hoverflies and wild bees) in how their diversity changed across different land use types (Baldock et al., 2015; Collado et al., 2019; Verboven et al., 2014).

Urbanization and agriculture land use are also known to affect the composition of plants and pollinators. Both land use types are expected to create strong environmental filters for taxa with traits best suited for the environmental conditions. Important traits to consider are flight ability (foraging range), dietary specialization (also in the larval stage), and nesting habitat types (ground or cavity availability). For example, smaller-bodied, above-ground-nesting bees are more common in small fragmented urban environments because of their small foraging range and because their nesting type is available in the urban environment (Cane et al., 2006), whereas larger bees with larger foraging ranges are better able to utilize resources found in large fragmented agricultural environments (Grundel et al., 2010; Lonsdorf et al., 2009). Changes in plant composition are also an important consideration, as these directly influence the pollinator trophic levels (Fitch, 2017; Potts et al., 2003). For example, intensively grazed European grasslands are often dominated by disturbance tolerant Fabaceae plant species such as *Trifolium repens*, and these flag-blossom flowers with hidden rewards are accessible primarily to medium- and long-tongued Hymenopterans (Rakosy et al., 2022). Hoverflies often rely on different plant resources as larvae (e.g., aphids and decaying plant material) and adults (floral resources), which are more available in agricultural compared to urban environments (Barendregt & van de Klashorst, 1978).

Changes in the diversity and composition of plants and pollinators are expected to influence the emerging structure of their interaction networks (Tylianakis & Morris, 2017; Weiner et al., 2011), which in turn influences their robustness to perturbations (Astegiano et al., 2015; Kaiser-Bunbury et al., 2010). Network structure can be quantified using a variety of different metrics such as nestedness, specialization, and evenness (Blüthgen et al., 2008; Kaiser-Bunbury & Blüthgen, 2015; Novella-Fernandez et al., 2019). Nestedness is a community-wide pattern in which generalist taxa tend to interact with specialists and vice versa (Bascompte et al., 2003). Nested networks are more robust to the loss of a node, as the loss of specialists will not result in cascading extinctions to their interaction partners (Fortuna & Bascompte, 2006; Memmott et al., 2004). Interaction evenness evaluates the homogeneity of links in the network, with higher evenness indicating more uniformity in interactions between nodes (Fisogni et al., 2021). High evenness can occur if rare taxa become locally extinct

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(Blüthgen et al., 2006, 2008). Specialization evaluates the degree to which species in the network restrict their partners to a subset of those that are available (Blüthgen et al., 2006). More generalized networks are more robust to perturbations due to the redundancy of interactions (Fisogni et al., 2021; Zografou et al., 2020), but specialized pollinators are likely to offer better pollination services to plants (Minckley & Roulston, 2006). Evenness and specialization are important metrics for applied conservation, as they are indicators for ecosystem stability and function (Kaiser-Bunbury & Blüthgen, 2015). Land use change is generally expected to filter for plant and pollinator species that are flexible in their resource use, and thus shift the network structure to be less specialized, more nested, and more even (Doré et al., 2021; Weiner et al., 2014).

Species-level network metrics are used to assess the contributions of individual species or taxonomic groups to network structure (i.e., distinguishing keystone from peripheral taxa) and to quantify how the roles that taxa play in the network shift with land use change. Betweenness centrality (BC) can be calculated for each node in the network, and describes the number of times each node provides the shortest bridge that connects two other nodes. Taxa with high values of BC are those that are critical to the cohesiveness of the network (Martín González et al., 2010a). Identifying these taxa in a network, and how they change with land use change can help us to understand changes in network structure and create management plans that support keystone species. Anthropogenic changes can negatively impact these central species, which can lead to cascading effects on peripheral taxa and ultimately network structure. Using simulated removal of these keystone species, we can predict how the networks would respond in their absence (Chakraborty et al., 2021). In Europe and North America, most studies have found that bees, usually solitary bees, play central roles in the network (Burkle et al., 2021; Chakraborty et al., 2021; Martín González et al., 2012). Few studies have examined how the roles of species change across habitats with different land use. In the Tropical Andes, Crespo and colleagues (Crespo et al., 2021) compared old growth to second growth forests and found that shrubs with abundant flowers are critical to restoring plant-hummingbird interaction networks. The centrality of taxa is expected to change differently across different types of land use change, as these habitats support disparate compositions of taxa. Alternatively, the same taxonomic

groups (e.g., solitary bees) might play central roles across all habitat types, but the particular species involved in interactions within those groups might shift.

In this study, we quantified how agricultural and urban land use influence plant and pollinator diversity and composition, network structure, and the roles of particular pollinator taxa. Specifically, our questions were: (1) Does plant and/or pollinator diversity and composition change across gradients of land use? (2) Does network structure change across gradients of land use? (3) Which pollinator families have important connector roles in the network? For families that have important roles overall, do their roles shift across gradients of land use, and does their simulated removal from the network alter overall network structure? (4) For pollinator families that play important connector roles in the network, does the composition of species within the family shift across gradients of land use?

Methods

1. Data collection

We collected our data at 14 sites with varying degree of agriculture and urbanization in Sachsen and Sachsen-Anhalt, Germany during the summer of 2019 and 2020 on warm sunny days (Sup Figure 1). We sampled using 30m x 2m transect and sampled 7-10 transects per site, each separated by approximately 100 m. At each transect, we identified plants that were in flower to species level and recorded the percent cover of flowering plant species using the Braun-Blanquet coefficients in the classifications from (de Manincor et al., 2019). Insect visitors were sampled at transects for a total of 15 minutes. Time was stopped during the processing of the insects. Insects coming in contact with reproductive parts of flowering plants (we refer to these as pollinators) were collected with nets and placed into vials with information about site, transect, and flower it was collected on. Insects that could be identified in the field (honeybees, butterflies, bees in the genus *Bombus*, and unique hoverfly species) were recorded and released. Insects were frozen, pinned, and identified using taxonomical keys (see Supplementary Table 4 for reference list). All pollinators were identified to the family level and most analyses of pollinators are conducted at this level.

2. Land use gradient index

To calculate the land use for each site, we created a 3000m radius circle around each site, centered at the mean of the transects' coordinates. All transects fell within the circle. The proportion of land use for each site was calculated from CORINE land cover (CLC, © European Union, Copernicus Land Monitoring Service 2018, European Environment Agency). CLC has overall 44 classes; we combined classes into four land uses (Urban (artificial surfaces), Agriculture (agricultural areas), Semi-natural, and Forests). Six land use gradient indices were calculated using methods from (Theodorou et al., 2017) The scale for each land use gradient can range from -1, indicating 100% of one land use type, to +1, indicating 100% of the other type. For example, using the Agriculture-Urban gradient, 100% agriculture would be -1 and 100% urban would be +1. For more information on land use gradients, see Supplementary Table 1.

3. Statistical analyses

The number of pollinator families, plant species, interactions, unique interactions, and the total percent cover of flowering plants was calculated for each site. To check for difference in sampling effort, we extrapolated richness of pollinator families, plant species, and interactions using the Chao estimator (Chao & Chiu, 2016; Chao & Jost, 2012). Each site was sampled to a high saturation (Estimated sampling richness > 50%, Supplementary Table 2). Linear regressions were used to test whether the richness of pollinator families, plant species, interactions, and/or unique interactions and whether the total percent cover of flowering plants changed across each of the six different land use gradient indices.

We used a Canonical Correspondence Analysis (CCA) to test how community composition changed with land use (ter Braak, 1986). A CCA is a multivariate ordination analysis used to explain the relationship between species distribution and environment gradients, where the observations are assumed to be unimodally distributed along the gradients (ter Braak & Verdonschot, 1995). The abundance matrices were created with sites in n rows and pollinators or plants in m columns. Number of interactions was used as abundance for pollinators and total percent coverage was used for plants.

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Matrices were log transformed since the abundances were highly right-skewed. The percentages of land use were overlaid as environmental variables. An ANOVA was calculated for the CCA to determine if our model with the environmental variables explained more variance in the abundance matrices than would be expected by chance.

Plant-pollinator networks were calculated for each site with plant species and pollinator families as nodes connected by observations of interactions. Using the bipartite package in R, we calculated nestedness (NODF), network-level specialization (H2), and interaction evenness for each site. The relationship between each metric and each of the six different land use gradient indices was linearly compared with a Gaussian linear model. Rarefication was used in order to determine if sampling effort was what caused differences between the network metrics. Each network metric was recalculated 50 times (bootstrapped) with different network arrangements limited at 133 interactions, which was the minimum number of interactions observed in a network, using the package bootstrapnet (Stefan & Knight, 2022).

We calculated Betweenness Centrality (BC) for each pollinator node (family) in the network at each site. A pollinator with a BC value greater than zero is considered a connector in the network (Martín González et al., 2010b). We summed the BC values for all sites across the pollinator families to see which families had the highest total BC values. For those families, we calculated the linear relationship between BC and the six different land use gradient indices.

For families with a high BC, we identified the individuals to species level and calculated the change in species composition using a CCA, similarly to the community composition. Environmental variables were included in the CCA and an ANOVA was calculated, to determine if species composition changed across the land use gradients. One site (LEI_C) was removed from the Halictidae CCA as individuals could not be identified to species level at that site.

For the same families, we calculated how virtual exclusion influences the network metrics nestedness (NODF), specialization (H2), and interaction evenness, following the methods from Chakraborty and colleagues (Chakraborty et al., 2021). Virtual exclusion was calculated by excluding

the pollinator family from the network, recalculating the network metric, and calculating the deviation from the original network metric was calculated. A value of 0 indicates that the removal of the family from the network did not have any difference on the network metric. A positive value means that the removal of the family increased the network metric, whereas a negative value indicates a decrease in the metric. All statistical operations were performed in R (RStudio Team, 2016).

Results

We observed a total of 111 plant species and 61 different pollinator families from four orders (Coleoptera, Diptera, Hymenoptera, and Lepidoptera) at our sites. Number of total interactions was significantly linearly related for two of the land use gradients and plant percent cover for four of the land use gradients (Table 1). Total number of interactions increased from highly agricultural to highly urban and from highly urban to highly semi-natural. Percent cover of plants also increased along the same gradients, plus from urban to forest and from agricultural to semi-natural. We expected that the number of pollinator interactions observed would be positively correlated with plant percent cover; however, this relationship was not significant (R=0.14, p=0.63).

Numbe Pollina		of or Family	Number of Plant Species		Number of Interaction		Number of Unique Interactions		Plant Percent Cover	
Land use Gradient	Adj. R^2	P	Adj. R^2	Р	Adj. R^2	P	Adj. R^2	Р	Adj. R^2	Р
-1 Agricultural + 1 Urban	0.02	0.28	-0.06	0.64	0.27	0.03	0.05	0.21	0.35	0.02
-1 Urban +1 Semi- natural	-0.03	0.43	-0.07	0.68	0.29	0.03	0.04	0.24	0.30	0.03
-1 Urban +1 Forest	-0.08	0.80	-0.07	0.69	0.07	0.19	-0.07	0.75	0.22	0.05
-1 Agricultural +1 Semi- natural	0.06	0.20	-0.06	0.62	0.20	0.06	0.05	0.22	0.34	0.02
-1 Agricultural +1 Forest	0.09	0.16	0.03	0.27	0.20	0.06	0.14	0.11	0.15	0.10
-1 Semi- natural +1 Forest	-0.02	0.40	0.16	0.08	-0.03	0.47	0.08	0.17	-0.07	0.69

Table 1: Adjusted R^2 and p-value for linear regressions. Number of pollinator families, number of plant species, number of interactions, number of unique interactions, and total percent-cover of plants were linearly regressed with six different land use gradients. Significant p-values (<0.05) are bolded.

We found that the environmental variables explained 40.06% of variance in community composition for pollinator families (p<0.01) and 36.25% of variance (p<0.05) for plant species (Figure 1). Sites with high percentage of urban and semi-natural differed in composition of pollinator families (ANOVA, p=0.036 and 0.008, respectively) and plant species composition differed in sites with high percentage of agricultural (ANOVA, p=0.030). There were four pollinator families that were abundant across all sites (Apidae, Syrphidae, Halicidae, and Tachinidae; Supplementary Figure 2a). For plants, seven of the top 10 most abundant plant species (in percent cover) also received many interactions (Supplementary Figure 2b and c). In particular, *Achillea millefolium* and *Falcaria vulagris* were two species with high percent cover and number of interactions.





We did not observe significant relationships between any of the rarefied network metrics and land use gradient indices (Supplementary Table 2). Of the 61 pollinator families, 38 families were connectors of at least one site. Across all sites, the BC value was highest for Halictidae and Syrphidae (Figure 2). The role of these two families do not change along the land use gradients, expect Syrphidae becomes a bit more important as a connector in forested landscapes (Supplementary Figure 3). The relative distribution of Halictidae and Syrphidae species across the sites had a similar pattern to the pollinator families with several common species found at most sites (Supplementary Figure 4). However, there was no significant change in species composition across the environmental variable for both families (Supplementary Figure 5, p > 0.05). The virtual exclusion for each of the Halictidae and Syrphidae family from the networks lead to an overall increase in specialization and a decrease in evenness and nestedness (Figure 3).



Figure 2: Bar graph of Betweenness Centrality (BC) at each site for each pollinator family. Families are ordered from highest total BC to least.



Figure 3: Boxplot of deviation from virtual exclusion of pollinator families Halictidae and Syrphidae for network metrics specialization (H2), interaction evenness, and Nestedness (NODF). The deviation value of 0 (red line) indicates that the removal of the family from the network does not change the network metric. A positive value means that the removal of the family increases the network metric, whereas a negative value indicates a decrease the metric. The black line in box plot is the mean of the deviation values across all sites.

Discussion

Across our sites of varying gradients of land use, we found that dramatic changes in plant and pollinator composition with land use type, but no effect on plant or pollinator richness. Biodiversity change is a multifaceted problem, and thus is best understood by considering multiple metrics (Aggemyr et al., 2018, Chase et al., 2018). Other studies examining the effects of land use change on biodiversity have found that richness can remain similar, but that long-lived species are replaced by smaller species with faster life cycles, with consequences for ecosystem functioning (Baessler &

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Klotz, 2006). We found that insect and plant composition were driven by the different land uses, with urban and semi-natural land uses driving different compositions of pollinators and agriculture land use driving different compositions of plants. In our study, some of the plant species and pollinator families were present only in one land use type. For example, the family of Melittidae bees, which is a specialized, solitary, ground nesting family, were found almost exclusively in sites with high urban land use. Likewise, the plant species *Geranium molle* was only found in the sites with a high percentage of forested area.

Network structure was similar across the different land use types, despite their differences in plant and pollinator composition. This similarity in structure is most likely due to the consistent presence of two connector families, Hoverflies (Syrphidae) and Halictid bees (Halictidae). Hoverflies are important, cosmopolitan pollinators with large variety of traits between the species allowing for specialization on different floral resources and niche partitioning of species within and between different habitats (Klecka et al., 2018). Halictid bees are a large and cosmopolitan group of bees. They belong to the generalized group of short-tongued bees that range from solitary to social species. Species from this family have been found in all types of land use (Pesenko et al., 2000). Both families are known to be efficient pollinators and carry equal amounts of pollen compared to honeybees (Rader et al., 2009, 2011), and thus the consistent presence and strong roles that these groups play in our pollination networks suggest high pollination services.

The virtual exclusion of Hoverflies and Halictid bees demonstrated the importance of these taxa to network structure. Without these groups, the networks would become more specialized, which in the end could result in cascading extinctions in the network. Conservation of these families is important not only to maintain stability in the community, but these families can be used as bio-indicators for assessing a range of environmental stressors (Doyle et al., 2020; Kevan, 1999; Pesenko et al., 2000), as increase pressures from an increase in pesticides, lack of suitable nesting habitats, or lack of food resources (for both larvae and adults) are negatively affecting these families. Current measures, such as increasing awareness of the general public, maintaining pollinator meadows, and
installing nesting material, can help to support these families, even in highly urban or highly agricultural environments (Vaughan et al., 2015).

One reason for why we did not see much difference in plant-pollination interactions across our land use gradients could be that the environmental gradients are not as dramatic in our region as in other places. Our semi-natural areas are still highly managed, so they may be more similar to the urban and agricultural landscapes than semi-natural areas in other parts of Europe, such as Eastern and central Europe where more traditional management practices still persist (J. Fischer et al., 2012; Milberg et al., 2017). Likewise, the German urban landscapes in our study have been known to host high diversity of bee species (Buchholz et al., 2020; L. K. Fischer et al., 2016; Theodorou et al., 2017), possibly because of the presence of pollinator-friendly gardens, and thus may be more similar to semi-natural areas than other cities that have more artificial surfaces that are inhospitable to pollinators. A report in 2012 found that most of Germany's cities were ranked as the greenest cities in Europe (Stelzner, 2012). For example, the city of Leipzig, has several initiatives to increase pollinator-friendly gardens and meadows, increase pollinator nesting sites, and also increase the public awareness about how to help pollinators through workshops and exhibitions. These initiatives are not exclusive to Leipzig, but can be found in all major cities in Germany (e.g. Berlin, Bremen, Frankfurt, Hamburg, Hannover, Mannheim, Munich, Nuremberg and Stuttgart). These initiatives, combined with research on land use change us, can help us develop meaningful and impactful conservation measures.

Conclusion

In conclusion, we found that although community composition changes dramatically along different land use gradients, the persistent presence of keystone pollinator taxa results in minimal changes to network structure. However, a removal of these important families would lead to a less nested, less even, and more specialized network, which could eventually lead to cascading extinctions. Understanding how land use change affects networks and knowing the keystone species, are important when creating efficient conservation plans.

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SUPPLEMENTARY MATERIALS

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Figure 1: Map of sites with percentage of different land uses in the 3 km radius. One circle shows the geographic distribution of land use data from the Corine database at each site. Next to it, are pie charts, which show the percentage of land use at that site.



Figure 2: Abundance of a) pollinator families (number of individuals), b) plant species (percent cover) and c) interactions on plant species at the different sites. Pollinators and plants are ordered from highest to lowest abundances overall. Locations are ordered alphabetically.











Figure 4: Relative abundance of a) Syrphidae and b) Halictidae species across the sites.

Figure 5: Canonical Correspondence Analysis (CCA) of **a**) Halictidae species composition and **b**) Syrphidae species composition. Percentage of land use are plotted as environmental variable and do not significantly explain the change in composition (ANOVA, p > 0.05). Identity of the families and species are shown in red, site names are in black and environmental variables are in blue.



Table 1: Site and land use information. Mean latitude and longitude of transects at the different sites (used as center point for 3km radius), proportions of land use, and the land use gradients.

Agriculture -Urban = Proportion urban – proportion agriculture (-1= 100% agriculture; +1= 100% urban)

Urban -Semi-natural = Proportion semi-natural – proportion urban (-1= 100% urban; +1= 100% semi-natural)

Urban-Forest = Proportion forest – proportion urban (-1= 100% urban; +1= 100% forest)

Agriculture -Semi-natural = Proportion semi-natural – proportion agriculture (-1= 100% agriculture; +1= 100% semi-natural)

Agriculture -Forest = Proportion forest – proportion agriculture (-1= 100% agriculture; +1= 100% forest)

Semi-natural -Forest = proportion forest-proportion semi-natural ((-1= 100% semi-natural; +1= 100% forest

Location	Longitude	Latitude	year	Urban%	Agriculture%	Semi-	Forest%	Agriculture-	Urban-	Urban-	Agriculture-	Agriculture-	Semi-
	(mean)	(mean)				natural%		Urban	Semi-	Forest	Semi-	Forest	natural-
									natural		natural		Forest
BRA	11.9282	51.50919	2020	0.5930	0.1630	0.0508	0.1932	0.4300	-0.5423	-0.3999	-0.1122	0.0302	0.1424
FRI	11.72058	51.62372	2019	0.0329	0.9040	0.0000	0.0630	-0.8711	-0.0329	0.0301	-0.9040	-0.8410	0.0630
GRE	11.42946	51.62872	2019	0.0219	0.8418	0.0000	0.1363	-0.8198	-0.0219	0.1143	-0.8418	-0.7055	0.1363
HAL	11.94062	51.49442	2019	0.7683	0.0450	0.0216	0.1569	0.7233	-0.7467	-0.6114	-0.0234	0.1119	0.1353
HAR	11.05846	51.83682	2019	0.0276	0.7588	0.0287	0.1849	-0.7311	0.0011	0.1573	-0.7301	-0.5739	0.1562
LEI_A	12.27669	51.37611	2019	0.3273	0.4174	0.0000	0.2553	-0.0901	-0.3273	-0.0720	-0.4174	-0.1621	0.2553
LEI_C	12.39275	51.3232	2020	0.9455	0.0032	0.0000	0.0513	0.9423	-0.9455	-0.8942	-0.0032	0.0481	0.0513
LUN	11.89446	51.52992	2020	0.1908	0.6658	0.0713	0.0720	-0.4750	-0.1195	-0.1188	-0.5945	-0.5938	0.0007
NIE	11.88765	51.48546	2020	0.3815	0.3091	0.0153	0.2942	0.0724	-0.3662	-0.0873	-0.2938	-0.0149	0.2789
PFI	11.94169	51.44592	2020	0.4518	0.3848	0.0702	0.0698	0.0670	-0.3816	-0.3820	-0.3147	-0.3150	-0.0004
QUE	11.50188	51.34638	2019	0.0110	0.4570	0.0000	0.5321	-0.4460	-0.0110	0.5211	-0.4570	0.0751	0.5321
SIP	11.03608	51.64179	2019	0.0223	0.4717	0.0110	0.4950	-0.4493	-0.0113	0.4727	-0.4607	0.0234	0.4841
SST	11.71092	51.36624	2019	0.0120	0.9880	0.0000	0.0000	-0.9759	-0.0120	-0.0120	-0.9880	-0.9880	0.0000
WAN	11.41533	52.08756	2019	0.0547	0.9453	0.0000	0.0000	-0.8905	-0.0547	-0.0547	-0.9453	-0.9453	0.0000

Table 2: Extrapolated richness at each site based on visitor count of pollinator family, plant species and number of interactions sampled using estimateR in the vegan package. Observed richness; Estimated richness with Chao1 estimator; Standard error with Chao1 estimator; Sampling completeness (Observed richness/(Estimated richness \pm Standard Error) x 100).

Location	Observed	Estimated	Standard	Sampling completeness (±
	Richness	Richness	Error	Standard Error)
BRA	28	41.20	10.21	67.96 (54.47-90.35)
FRI	25	32.00	6.64	78.13 (64.7-98.58)
GRE	27	30.33	4.11	89.01 (78.38-100)
HAL	28	33.00	5.52	84.85 (72.68-100)
HAR	15	20.00	5.99	75 (57.72-100)
LEI_A	30	48.00	16.09	62.5 (46.81-94.02)
LEI_C	20	21.50	2.22	93.02 (84.3-100)
LUN	28	47.50	14.73	58.95 (45-85.43)
NIE	30	31.20	1.84	96.15 (90.81-100)
PFI	21	24.33	4.11	86.3 (73.83-100)
QUE	30	52.00	17.44	57.69 (43.2-86.81)
SIP	17	20.00	4.15	85 (70.41-100)
SST	19	21.00	2.58	90.48 (80.58-100)
WAN	17	24.50	8.11	69.39 (52.13-100)
All	63	141.46	50.64	44.53 (32.79-69.37)

A) Pollinator Family Extrapolated Richness

B) Plant Species Extrapolated Species Richness

Location	Observed	Estimated	Standard	Sampling completeness
	Richness	Richness	Error	
BRA	11	11.00	0.24	100 (97.88-100)
FRI	25	30.25	5.36	82.64 (70.2-100)
GRE	19	19.20	0.62	98.96 (95.87-100)
HAL	21	24.00	4.15	87.5 (74.59-100)
HAR	16	17.00	1.81	94.12 (85.08-100)
LEI_A	27	28.00	1.81	96.43 (90.57-100)
LEI_C	27	37.00	10.35	72.97 (57.03-100)
LUN	17	17.00	0.08	100 (99.53-100)
NIE	27	32.00	5.52	84.38 (71.96-100)
PFI	13	16.00	4.53	81.25 (63.33-100)
QUE	27	28.50	2.23	94.74 (87.87-100)
SIP	22	31.33	8.84	70.21 (54.77-97.79)
SST	14	15.00	2.29	93.33 (80.98-100)
WAN	21	23.00	2.87	91.3 (81.16-100)
All	111	202.00	34.64	54.95 (46.91-66.32)

	Extrapolated Rienness			
Location	Observed	Estimated	Standard	Sampling completeness
	Richness	Richness	Error	
BRA	57	145.00	46.15	39.31 (29.82-57.66)
FRI	85	141.40	21.87	60.11 (52.06-71.11)
GRE	99	122.38	10.56	80.9 (74.48-88.54)
HAL	106	183.21	31.48	57.86 (49.37-69.86)
HAR	41	83.00	26.00	49.4 (37.62-71.93)
LEI_A	101	153.11	20.84	65.97 (58.06-76.36)
LEI_C	97	134.71	17.60	72 (63.68-82.83)
LUN	62	132.13	34.69	46.93 (37.17-63.63)
NIE	117	170.45	20.38	68.64 (61.31-77.96)
PFI	52	98.43	25.59	52.83 (41.93-71.39)
QUE	111	233.00	45.17	47.64 (39.9-59.09)
SIP	57	127.20	40.19	44.81 (34.05-65.51)
SST	56	102.00	26.59	54.9 (43.55-74.26)
WAN	55	89.50	19.27	61.45 (50.56-78.32)
All	621	1453.31	120.91	42.73 (39.45-46.61)

C) Interaction Extrapolated Richness

Table 3: Adjusted R² and p-value

	Nestedness ((NODF)	Specializatio	on (H2)	Interaction H	Evenness
Land use Gradient	Adj R ²	Р	Adj R ²	Р	Adj R ²	Р
Agriculture -Urban	0.03	0.26	0.02	0.29	-0.08	0.90
Urban-Semi-natural	-0.04	0.50	-0.01	0.38	-0.07	0.66
Urban-Forest	-0.06	0.62	0.06	0.20	-0.07	0.75
Agriculture -Semi- natural	0.11	0.14	0.04	0.24	-0.08	0.87
Agriculture -Forest	0.05	0.21	-0.07	0.67	-0.08	0.92
Semi-natural- Forest	-0.08	0.91	0.05	0.21	-0.08	0.94

a) Adjusted R^2 and p-value for tests of linear relationships between network metrics and the six different land use gradients. There was no significant relationship (p>0.05).

b) Adjusted R^2 and p-value for tests of linear relationships between rarefied network metrics and the six different land use gradients. Network metrics were rarified to 131 interactions. There was no significant relationship (p>0.05).

	Nestedness (NODF)		Specialization (H2)		Interaction Evenness	
Land use Gradient	Adj R ²	Р	Adj R ²	Р	Adj R ²	Р
Agriculture -Urban	0.12	0.12	0.05	0.22	-0.08	0.87
Urban-Semi-natural	0.01	0.32	0.01	0.30	-0.06	0.62
Urban-Forest	-0.05	0.56	0.09	0.16	-0.07	0.75
Agriculture -Semi- natural	0.23	0.05	0.07	0.19	-0.08	0.88
Agriculture -Forest	0.18	0.07	-0.06	0.58	-0.08	0.96
Semi-natural- Forest	-0.06	0.65	0.04	0.23	-0.08	0.86

Family	Reference
Coleoptera (Beetle)	Müller/Bährmann (2015) Bestimmung wirbelloser Tiere, 7. Auflage. Springer Spektrum, Berlin.
	Stresemann (2011) Exkursionsfauna von Deutschland Wirbellose: Insekten, 11. Auflage. Springer Spektrum, Heidelberg.
Diptera (Flies)	Bartsch, Hans (2009) Tvåvingar. Blomflugor : Diptera : Syrphidae : Syrphinae (Nationalnyckeln till Sveriges flora och fauna). ArtDatabanken SLU, Uppsala.
	Oosterbroek, Pjotr (2009) The European Families of the Diptera: Identification, diagnosis, biology. KNNV Publishing, Hamburg.
	vanVeen, Mark (2010) Hoverflies of Northwest Europe: Identification keys to the Syrphidae. KNNV Publishing, Hamburg.
Hymenoptera (Bees)	Amiet F (1996) Fauna Helvetica. Apidae 1: Apis, Bombus, Psithyrus. Schweizerische Entomologische Gesellschaft, Neuch [*] atel, p. 12th edition.
	 Amiet F, Müller A, Neumeyer R (1999) Fauna Helvetica. Apidae 2: Colletes, Dufourea, Hylaeus, Nomia, Nomioides, Rhophitoides, Rophites, Sphecodes, Systropha. Centre Suisse de Cartographie de la Faune (CSCF), Neuch^atel, p. Fourth edition
	Amiet F, Herrmann M, Müller A, and Neumeyer R (2001) Fauna Helvetica. Apidae 3: Halictus, Lasioglossum. Centre Suisse de Cartographie de la Faune (CSCF), Neuch ^{atel} , p. Sixth edition.
	 Amiet F, Herrmann M, Müller A, Neumeyer R. (2004) Fauna Helvetica. Apidae 4: C. Anthidium D. Coelioxys L. Heriades O. Megachile . Stelis. Centre Suisse de Cartographie de la Faune (CSCF), Neuch^atel, p. Ninth edition
	Amiet F, Herrmann M, Müller A, and Neumeyer R (2007) Fauna Helvetica. Apidae 5: Ammobates, Ammobatoides, Anthophora, Biastes, Ceratina, Dasypoda, Epeoloides, Epeolus, Eucera, Macropis, Melecta, Melitta, Nomada, Pasites, Tetralonia, Thyreus, Xylocopa. Centre Suisse de Cartographie de la Faune (CSCF), Neuch ^{atel} , p. 20th edition.
	Amiet F, Herrmann M, Müller A, and Neumeyer R (2010) Fauna Helvetica. Apidae 6: Andrena, Melitturga, Panurginus, Panurgus. Centre Suisse de Cartographie de la Faune (CSCF), Neuch [^] atel, p. 26th edition.
	Falk, Steven (2015) Field Guide to the Bees of Great Britain and Ireland. British Wildlife Publishing, London.
	Collins, Graham (2012) Keys to the genera of British bees. BWARS bee-book.
Hymenoptera (Wasp)	Goulet H & Huber JT (1993) Hymenoptera of the world: An identification guide to families. Canada Communication Group-Publishing, Ottawa.
	Müller/Bährmann (2015) Bestimmung wirbelloser Tiere, 7. Auflage. Springer Spektrum, Berlin.
	Stresemann (2011) Exkursionsfauna von Deutschland Wirbellose: Insekten, 11. Auflage. Springer Spektrum, Heidelberg.
Lepidoptera (Butterfly, Moth)	Müller/Bährmann (2015) Bestimmung wirbelloser Tiere, 7. Auflage. Springer Spektrum, Berlin.
	Order LEPIDOPTERA (Moths & Butterflies): Key and Description of Families. Accessed 10 Oct. 2022. https://www.zoology.ubc.ca/bclepetal/Order%20Lepidoptera%20et%20al%20Text%20Fil es/order_lepidoptera.htm

Table 4: Insect Identification Keys References



Chapter 5

Synthesis

1. Key research gaps

Pollination is an important ecosystem service as a majority of our crops require pollinators for successful yields, increasing both quality and genetic diversity, while providing economic stability (Garibaldi *et al.* 2014; Woodcock *et al.* 2019). As the global human population continues to grow, pollination becomes even more critical for ensuring food security, as insufficient pollination could lead to potential food shortages. While research on agricultural pollination has made significant progress, my thesis aimed to contribute to the key gaps in our knowledge that remain.

The first gap is that it is unclear how different pollinator observation methods influence the findings and thus the comparability across studies. Different researchers often use varied methodologies, making it challenging to compare data and draw meaningful conclusions. Addressing this gap requires quantifying how sampling methods influence estimates of diversity and functional composition of pollinators and developing standardized protocols for data collection, including sampling frequency, duration, and spatial coverage, to enhance the reliability of pollinator monitoring.

The second gap is that many observation methods are biased towards larger or more conspicuous pollinators, such as bees and butterflies, often overlooking smaller or less conspicuous species. Addressing this gap requires developing techniques that can accurately assess the diversity and abundance of all pollinator groups, including flies, beetles, and native bees.

The third gap is that species diversity is often measured but few studies incorporate functional traits. Functional traits provide a framework to study pollination interactions beyond traditional taxonomic classifications, and provide insight into the environmental filtering process (Buchholz *et al.* 2020; Peralta *et al.* 2020). Further, by focusing on traits such as tongue length, body size, and floral morphology, researchers can gain insights into how specific traits facilitate pollination and influence plant-pollinator interactions. Addressing this gap is becoming possible through time as trait databased on insects become more readily available.

The fourth gap is that many studies examine the effects of agricultural intensification on pollinator diversity, but research is needed to understand how plants in the surrounding semi-natural landscape indirectly benefit crop species by providing resources for shared pollinators. Understanding the complexity of pollination networks within agricultural landscapes is crucial. Addressing this gap requires research focusing on how different pollinator species interact with various crops and wild plants, as well as how changes in pollinator diversity and abundance affect overall pollination efficiency and crop yield stability.

Finally, while some studies have explored pollinator biodiversity in agricultural and urban landscapes separately, there is a lack of comprehensive comparative research. Understanding how the diversity, abundance, and composition of pollinators differ between these types of land use change can shed light on the impact of future changes on pollinator communities.

Addressing these research gaps are essential for developing science-based strategies to enhance pollination services in agricultural landscapes, mitigate pollinator decline, and ensure sustainable food production for the future.

2. Main findings of the thesis

The aim of this thesis was to address the research gaps mentioned above. I found that sampling method and spatial grain have dramatic effects on the species diversity, functional diversity and composition of pollinators sampled, and concluded that multiple methods should be employed in future monitoring and research studies assessing pollinator biodiversity (Chapter 2). The goal of the monitoring should be clearly defined beforehand, in order to accurately choose the method that will provide the most robust data for the question being addressed. If the goal is to properly categorize the diversity and composition of the pollinator community, then multiple methods are necessary to gain a more complete sample, as different species respond differently to different methods (Tronstad *et al.* 2022). Another goal could be to synthesize pollinator community change across land use of other environmental gradients. If that is the case, consistent methodology is important, as I show that it has a large influence on the abundance, diversity and composition of pollinators collected and can also vary between different taxa-groups.

All chapters of this thesis considered bees as well as non-bee pollinators, and consistently show that the responses of these groups are variable. In Chapter 2, the most abundant hoverfly pollinators were more variable across time and across methods than the bee pollinators. In Chapter 3, honeybees were the most observed flower visitor in a network that included Oilseed Rape and co-flowering plant species in the surrounding semi-natural landscape. However, non-bee pollinators such as Empididae flies and Mordillidae beetles were abundant and played important network roles. In Chapter 4, Halictid bees and Syrphid flies were the most important pollinator families across all land use types. Observing all pollinator groups is important, as taxa can respond differently to collection methods or land use change (Bergholz *et al.* 2022).

Functional traits were helpful in understanding differences across sampling methods in pollinator biodiversity (Chapter 2) and explaining species interactions (Chapter 3). Pollinator traits, such as body size, explained the abundance of species sampled by different methods, with traps sampling smaller sized pollinators compared to netting (Chapter 2). Traits played a significant role in the formation of network modules (Chapter 3). Despite this, Oilseed Rape shared pollinators with flowering plants that have distinct functional traits and were not part of its module (Chapter 3).

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Overall, incorporating functional traits in pollination research provides a more nuanced understanding of the ecological processes underlying pollination interactions, contributing to effective conservation efforts and sustainable management of pollinator-dependent ecosystems (Cappellari *et al.* 2022; Kendall *et al.* 2022).

Modularity analyses and null models, such as those employed in Chapter 3, provide important tools for understanding how plants in the surrounding semi-natural landscape indirectly benefit crop species by providing resources for shared pollinators (Fijen *et al.* 2022; Fountain 2022). Modularity analyses can determine the degree to which trait matching vs. other processes (i.e., neutral processes based on abundance) structure interactions (Olesen *et al.* 2007). This is a growing topic in the ecological literature, but has rarely been applied to understand agriculturally important plants and their pollinators (Saunders & Rader 2019). Likewise, null models are often used in the study of plant-pollinator interaction networks to disentangle the role of abundance in explaining interactions and to understand how network size influences network indices, but have rarely been applied to understand agriculturally important plants and their pollinators. By applying these methods to an agricultural system, I found that the strong patterns of pollinator sharing of species in the same module did not reflect trait matching but instead were expected by chance due to the high interaction frequencies of the focal plant and pollinator species that made up the pattern.

By considering both agricultural and urban land use in a single study (Chapter 4), I found that the different land use types resulted in different compositions of pollinator communities. I hypothesized that both types of land use would select for more generalized pollinator networks compared to semi-natural reference sites (Deguines *et al.* 2016). However, in contrast, I discovered that the consistent presence of two groups of keystone pollinators (Halictid bees and Syrphid flies) across all land use categories resulted in minimal variability in network structure. The role of keystone species extends across multiple ecological niche dimensions, with important implications for ecosystem resilience and conservation (Timóteo *et al.* 2022).

3. Conservation implications

Assessing threats to pollinator species and prioritizing their conservation requires adequate data on the abundance and distribution of species, their required nesting and food resources, and their responses to potential threats such as land use change (Tscharntke *et al.* 2007; Gardein *et al.* 2022). For many pollinators, especially non-bee species, such data are scarce or nonexistent. The results of this thesis provide new data for many species of bee and non-bee pollinators. Further, the approaches I have taken should be a guide for future studies. Specifically, I suggest monitoring pollinators using multiple methods, as many rare species will be captured by one method but not another. Likewise, conservation of pollinators requires understanding and knowledge of their species along with

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understanding their current populations. Training of wild bee experts should focus not only on acquiring theoretical knowledge about the individual species and species groups, but also on different methods and for which purposes they are suitable (Fornoff *et al.* 2022). Second, I suggest simultaneously examining pollinator responses to multiple land use categories, to better classify the threat of land use change, as their response can also be species or taxa specific (Ganuza *et al.* 2022; Grossmann *et al.* 2023).

Regional maps of pollinator diversity are also important tools for conservation, as they identify biodiversity hotspots that should be prioritized for conservation efforts and help us to identify the factors that are important in diversity (Sydenham *et al.* 2022). The data used to create these maps are heterogeneous, and my thesis suggests that sampling effort, sampling methods and sampling spatial grain are all critical in determining the resulting biodiversity of an area. In the short term, those making regional maps should attempt to standardize the effort and spatial grain as much as possible (Graham & Hijmans 2006). In the long term, standardized sampling schemes would provide more accurate and robust regional maps of pollinator diversity.

Land use changes, such as urbanization and agriculture intensification, can significantly alter the composition and structure of plant-pollinator networks (Udy *et al.* 2020). Studying these changes allows us to understand how human activities affect the biodiversity and the functioning of ecosystems. Studying networks across various land uses can identify species that are particularly vulnerable to land use change, as well as interactions that might be disrupted (Bascompte & Scheffer 2023). Such research can inform conservation planning by identifying areas that support diverse and resilient networks that should be targeted for protection or restoration (Glenny *et al.* 2023). Much of the Earth's surface has been altered by human activities, and understanding how plant-pollinator networks function in these anthropogenic habitats is crucial for developing conservation strategies that integrate human needs and ecological sustainability.

Identifying taxa that play keystone roles in plant-pollinator interaction networks is crucial for conservation (Timóteo *et al.* 2022). Protecting and restoring these keystone taxa ensures the stability and resilience of the entire ecosystem, as these taxa often play a crucial role in pollinating a wide variety of plant species (Jordán 2009). Monitoring keystone species as ecological indicators is a useful conservation strategy, as changes in the abundance or distribution of these species provides early warning signs of ecological disruptions. Enhancing populations of keystone pollinators can accelerate ecosystem recovery and enhance pollination services (Traveset *et al.* 2017). Importantly, I identify two families of pollinators as keystone taxa: Halictid bees and Syrphid flies. Therefore, I suggest that these groups should be prioritized for monitoring and conservation.

4. Limitations

Chapter 5

I have often discussed the importance of identifying all pollinator taxa in the field, rather than focusing on certain groups. However, there are difficulties when attempting to identify all taxa to species level. Previous research focuses mainly on bees and syrphid flies, because these groups are easier to identify to the species level than other taxa due to the accessibility of identification keys and expert knowledge, which continues to erode due to lack of knowledge exchange (Hochkirsch et al. 2022). Likewise, because of the amount of research dedicated to these groups, trait information is available and accessible. Bees and hoverflies are known to be important and abundant pollinators, but Tachinid and Muscid flies are also relatively abundant and have been shown to be important (Ssymank et al. 2008). However, despite their abundance, they are difficult to identify, due to the more cryptic morphologies and the lack of identification keys for many regions. Due to the lack of research of these groups, we also do not know if the species are functionally different. For some questions, identifying these difficult groups to species might not be necessary if groups of species are playing functionally similar roles in their nesting and food requirements and in their pollination services. More research is needed to determine their functional traits and also their role as pollinators. Barcoding may help to identify these species in future, but at this time, many species of flies are not barcoded (only 20% worldwide, 30% in Germany, Ratnasingam & Herbert 2007). Contrastingly, all plant families have been extensively studied, with trait data freely available.

Currently, due to the difficulty in identifying all taxa to the species level I made compromises in how I spent my energy. In Chapter 2, I restricted my analysis to flies in a single family, *Syrphidae*. Thus, I cannot assess how the different sampling methods and spatial grains influenced the diversity patterns of other fly families. Chapter 4 attempted to consider a broad spatial scale (many sites across different land use types). As a result, I restricted most identifications and analyses to family-level identification, including all flower visiting families in the analysis. However, more detailed species level identification was prioritized for keystone families. While this represents a good compromise, it prevents the collection of more detailed data that might provide the base for some of the conservation applications discussed in the previous section. Chapter 3 occurred at a more limited spatio-temporal scale, and thus I was able to identify nearly all floral visitors to species level.

I found interesting differences in community richness and also in composition across different sampling seasons in Chapter 2. However, for the remainder of my thesis research I collected only at short temporal scales. Plant-pollinator networks are very dynamic, and known to vary not only across years, but vary also across seasons (Alarcón *et al.* 2008). It would be an important topic for future research to consider how different land use types and different seasons and years vary in their plant-pollinator network (Lázaro & Gómez-Martínez 2022). It would be reasonable to discover in future research that the findings of Chapters 3 and 4 of my thesis represents two of many possible results once larger temporal grains are considered. In particular, I think it would be interesting to understand

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which plant species are supporting the pollinators of Oilseed Rape outside of the flowering season of this focal crop plant.

Finally, while my thesis sampled the different land use types that I could find in my region, I think it would be important and interesting to expand the spatial grain to capture more dramatic land use differences in future research. The urban sites of Leipzig and Halle have many pollinator initiatives, and are home to a diversity of pollinator species and habitats. It is possible that expanding to other, larger cities with fewer pollinator initiatives could better capture the threat of urbanization. Likewise, my semi-natural sites were relatively small and fragmented, potentially not capturing the true capabilities of semi-natural habitats for plants or pollinators. It is possible that locations with larger and more connected semi-natural grasslands would have even higher abundances and diversity of pollinators than what I found in my study.

5. Conclusion

Pollination is a vital ecosystem service with significant implications for food security and ecological stability. My thesis identified several gaps in our knowledge that need to be addressed for effective conservation, such as unknown effects of different pollinator sampling methods on biodiversity estimates, lack of data for non-bee pollinators, the need to interpret changes in pollinator communities using functional traits, the need for information on the indirect effects of plants in the surrounding semi-natural landscape on crop species pollination, and the needs to simultaneously consider and compare the effects of multiple types of land use on pollinator communities and plant-pollinator networks.

The findings of the thesis contribute significantly to addressing these gaps. The use of multiple sampling methods in Chapter 2 highlighted the effects of sampling method on diversity and functional composition of pollinators, advocating for their combined use in future monitoring and research studies. The inclusion of both bee and non-bee pollinators in all chapters revealed variable responses of these groups. The incorporation of functional traits in pollination research provided valuable insights into diversity patterns and species interactions. Modularity analyses and null models highlighted the role of traits in forming modules and the plant species that indirectly benefit Oilseed Rape. I identified keystone taxa that allow for similar structures of plant-pollinator networks across land use types that contain different overall compositions of pollinator communities.

In conclusion, this thesis provides valuable insights into the optimal monitoring of pollinators, the indirect effects of wild plants on crop species through shared pollinators, and on the effects of land use on pollinator communities and network structure. The identified research gaps and conservation

implications offer a roadmap for future efforts to protect and preserve pollinator populations, ensuring the sustainability of our ecosystems.

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Appendix

Appendix

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Zusätzliches Information

Supplementary materials

Supplementary materials are included at the end of each data chapter. Additionally, for published manuscripts (Chapters 2 &3), supplementary materials can be digitally downloaded from the respective journal's website. R code and unpublished graphs and materials can be requested from the author. Text and figures can be found on the attached CD.

Curriculum vitae

Pollination Ecologist with

- Expertise in pollinator collection and identification with training in Syrphidae and Apidae
- Research interests in plant-pollinator networks in connectance with the pollen limitation and breeding system of plants
- Experience conducting research in the field, alone, or as team leader and coordinating a large-scale collaborative project

Higher Education

Feb 2018-Jan 2022	Martin Luther University Halle-Wittenberg, Halle (Saale), Germany Doctor of Science in Biology (Expected date of graduation: Dec 2023) Thesis: Sampling Pollinator Communities and Interactions Across Changing Landscapes: Insights from a German Case Study
Apr 2016-Oct 2017	Martin Luther University Halle-Wittenberg, Halle (Saale), Germany
•	Master of Science in Biology (Two-year program, Date of graduation: 26
	October 2017)
	Honors: Summa Cum Laude (Sehr gut 1,0)
	Thesis: Exotic plant species receive adequate pollinator service despite variable integration into plant-pollinator networks
Aug 2010-May 2014	Illinois College, Jacksonville, Illinois, USA
	Bachelor of Science (Four-year program, Date of graduation: 11 May 2014)
	Honors: Summa Cum Laude, Phi Beta Kappa
	Majors: Environmental Science and German
	Minors: Biology and Economics

Professional Experience

Nov 2023- Present	Albert-Ludwigs-Universität Freiburg, Freiburg, Germany Research Officer at Chair of Nature Conservation and Landscape Ecology Project manager for Horizon Europe Project "RestPoll: Restoring Pollinator habitats across European agricultural landscapes based on multi-actor participatory approaches"
	 Communicate internally with project consortium and externally with the EU Secretariat Manage the project across seven different work packages and 32 partners
Feb 2022- Oct 2023	 Albert-Ludwigs-Universität Freiburg, Freiburg, Germany Research Officer at Chair of Nature Conservation and Landscape Ecology Project coordinator for Agricultural and Open Landscape Chapter in the BfN Project "Faktencheck Artenvielfalt" Conducted literature search, Delphi survey, and coordinated writing of the chapter Organized online and in-person workshops

• Supervised student helpers and bachelor students

Feb 2018- Jan 2022	 Martin Luther University Halle-Wittenberg, Halle (Saale), Germany Research Officer at Research Group Spatial Interaction Ecology (SIE) Conducting research on project "Plant-pollinator networks across space and time in Agro-ecosystems" Mentored high school and bachelor students Organized and supervised two master student projects Assisted with the exhibition "Blütenbesucher-Beziehungsgeschichten aus der Natur" at the Leipzig Botanical Garden
July 2016-Jan 2018	 Martin Luther University Halle-Wittenberg, Halle (Saale), Germany Research Assistant at Research Group Spatial Interaction Ecology (SIE) Conducted research on plant-pollinator network at TERENO (Terrestrial Environmental Observatories) sites in Harz/Central Germany region Helped compile data for pollen limitation meta-analysis Helped lead summer school for pollen supplementation experiments and plant-pollinator network data collection Helped collect pollinators in the Swiss Alps
Apr 2015- Mar 2016 May 2014-Nov 2014	 Washington University in St. Louis, Missouri, USA Field Laboratory Technician in the Department of Biology Team leader of research and mentor to undergraduate and high school students Conducted research on demography, pollen limitation, breeding systems, and pollinator network of invasive plants at Tyson Research Centre in St. Louis, MO, USA
Jan 2015- Apr 2015	 Sophia M. Sachs Butterfly House, St. Louis, Missouri, USA Entomology Intern Conducted experiment on survival rate of damaged <i>Morpho</i> butterflies Maintained and cared for insect species including butterflies, beetles, cockroaches, ants, mantises, stick-bugs, mealworms, along with vinegaroons and arachnids

Publications

Elliot, T.*, **A.H. Thompson***, A.-M. Klein, C. Albert, N. Eisenhauer, F. Jansen, A. Schneider, M. Sommer, T. Straka, J. Settele, M. Sporbert, F. Tanneberger, A.-C. Mupepele (2023). Abandoning grassland management influences biodiversity in Europe. Conservation Science and Practice. *considered duel first authors

Thompson, A.H., A. Ilyassova, T.M. Knight (in Review). Plant-Pollinator Interactions along an Urban and Agricultural Gradient. Urban Ecosystems.

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

Bennett, J.*, **A.H. Thompson***, I. Goia, R. Feldmann, V. Stefan, A. Bogdan, D. Rakosy, M. Beloiu, I. Biro, S. Bluemel, M. Filip, A.-M. Madaj, A. Martin, S. Passonneau, D.P. Kalisch, G. Scherer, and T.M. Knight (2018). A review of European studies on pollination networks and pollen limitation, and a case study designed to fill a gap. AoB Plants. *considered duel first authors

Thompson, A.H. and T.M. Knight (2018). Exotic plant species receive adequate pollinator service despite variable integration into plant-pollinator networks. Oecologia.

Thompson, A.H (2014). Politik der erneuerbaren Energie: was wir von Deutschland lernen können. Senior Honors Thesis. (Bachelor Honors Thesis)

Conference Presentations

Thompson, A.H., A. Ilyassova, T.M. Knight (2021). Plant-Pollinator Interactions along an Urban and Agricultural Gradient. SETAC Europe 31st Annual Meeting. (Poster presentation)

Thompson, A.H., T. Groth, T.M. Knight (2019). The attractiveness of oilseed rape in a plant-pollinator network. 49th Annual Meeting of the Ecological Society of Germany, Austria, and Switzerland. (Poster presentation)

Thompson, A.H., D. Rakosy, E. Motivans, L. Zoller, T.M. Knight (2019). Addressing the Spatial and Temporal Data Gaps in Plant-Pollinator Networks in Europe. 43rd New Phytologist Symposium (Poster

presentation) and Entomology 2019 (Oral presentation)

Thompson, A.H., M. Frenzel, O. Schweiger, M. Musche, T. Groth, and T.M. Knight (2018). A comparison of sampling methods for Apidae bees and Syrphidae flies. TERENO International Conference 2018. (Oral presentation)

Thompson, A.H. and T.M. Knight (2016). Network connectance does not predict pollen limitation of exotic plant species. iDiv Annual Conference 2016, Leipzig, Germany. (Oral presentation)

Thompson, A.H. and T.M. Knight (2016). Breeding system, plant-pollinator networks and pollen limitation of exotic plant species. 9th International Conference on Biological Invasions (NEOBIOTA), Vianden, Luxemburg. (Poster presentation)

Students Mentored

Yang, Z. (2023). Bachelor student. Thesis: Der Verbindung zwischen indirekten und direkten Ursachen in Agrarund Offenlandschaften in Deutschland.

Reeh, A. (2023). Bachelor student. Thesis: Zustand der Schmetterlinge Deutschlands: Ursachen für den Rückgang und Maßnahmen zum Schutz.

Ilyassova, A. (2019). Master student. Thesis: Shifts in Plant-Pollinator Interactions along Gradients of Urban and Agricultural Landscapes.

Zeisler, H. (2019). Master student. Thesis: Quantifying Pollen Transport Effectiveness in Relation to Plant-Pollinator-Networks in Meadows in the Apuseni Mountains, Romania.

Alvarado, B. (2015). Undergraduate student. Project: Effects of Exotic Plant Species on Pollination.

Alvarado, B. (2014). High School student. Project: Pollen limitation does not decrease reproductive fitness of some exotic plant species.

Poor, E. (2015). High School student. Project: Novel functional traits aid the success of the invasive biennial *Carduus nutans*.

Workman, M. (2015). High School student. Project: Competitive release may increase the fitness of exotic plants in their novel range.

Workshops and Short Courses

Insect Taxonomy and Field Sampling Skills: 5–9 March 2018. University of Oxford Department for Continuing Education. (Short Course)

Awards

Anton-Wilhelm-Amo-Preis 2019 for the Master Thesis "Exotic plant species receive adequate pollinator service despite variable integration into plant-pollinator networks"

Additional skills and competencies

Languages English- Mother tongue

	German- Good passive and active command (B2)	
IT skills	Proficient with Microsoft Word, Excel, PowerPoint, Adobe InDesign,	
	Photoshop, and web-based communication	
Reference software	Good knowledge of Zotero, Mendeley	
Modelling and statistical	Good knowledge of R/RStudio	
analysis software	Basic knowledge of Git, GitHub, and GitLab	
Field experience	North America (temperate forest, temperate rain forest, everglades, mid-west	
	prairie, glade), Costa Rica (tropic rain forest), Germany (lichen-rich pine	
	forest, wetland, meadows), Portugal (mountain forests), Austria/Italy	
	(Alpine)	
Laboratory experience	Use of microscopes	
	Knowledge of DNA and RNA barcoding	
Peer-review and editorial	Peer-reviewed for five different journals	
skills		

Erklärung über den persönlichen Anteil and den Publikationen

Declaration of personal contribution in the publications

Chapter 2

Thompson, A.H., M. Frenzel, O. Schweiger, M. Musche, T. Groth, S.P.M. Roberts, M. Kuhlmann, and T.M. Knight (2021). *Pollinator sampling methods influence community patterns assessments by capturing species with different traits and at different abundances.* Ecological Indicators.

Fieldwork:	Thompson, A. (55%)
	Groth, T. (40%)
	Knight, T.M. (5%)
Data analysis:	Thompson, A. (80%)
	Knight, T.M. (20%)
Writing:	Thompson, A. (50%)
	Knight, T.M. (20%)
	Frenzel, M. (5%)
	Schweiger, O. (5%)
	Musche, M. (5%)
	Groth, T. (5%)
	Roberts, S.P.M. (5%)
	Kuhlmann, M. (5%)

AT, MF, OS, MM, and TK contributed to the study concept and design. Net data collection was performed by AT and TG. Material preparation, statistical analyses, and draft writing was done by AT. SPMR and MK provided the bee functional trait dataset. All authors commented on and approved the final manuscript.

Chapter 3

Thompson, A.H., V. Ștefan, T.M. Knight (2021). Oilseed Rape Shares Abundant and Generalized Pollinators with Its Co-Flowering Plant Species. Insects.

Fieldwork:	Thompson, A. (95%)
	Knight, T.M (5%)
Data analysis:	Thompson, A. (70%)
	Stefan, V. (10%)
	Knight, T.M. (20%)
Writing:	Thompson, A. (70%)
	Stefan, V. (10%)
	Knight, T.M. (20%)

Conceptualization, A.T. and T.M.K.; Data curation, A.T.; Formal analysis, A.T. and V.S; Investigation, A.T.; Supervision, T.M.K.; Visualization, A.T. and V.S.; Writing—original draft, A.T.; Writing—review & editing, V.S. and T.M.K. All authors have read and agreed to the published version of the manuscript.

Chapter 4

Thompson, A.H., A. Ilyassova, and T.M. Knight (Under Review). *Plant-Pollinator Interactions along an Urban and Agricultural Gradient*. Urban Ecosystems.

Fieldwork:	Thompson, A. (50%)
	Ilyassova, A. (45%)
	Knight, T.M. (5%)

Appendix

Data analysis:	Thompson, A. (70%)
	Ilyassova. (20%)
	Knight, T.M. (10%)
Writing:	Thompson, A. (70%)
	Ilyassova, A. (10%)
	Knight, T.M. (20%)

All authors contributed to the study concept and design. Investigation, Data curation, and Formal analysis were performed by AT and AI. Supervision of the project by TMK. Visualization was performed by AT. The first draft was written by AT and all authors commented on previous versions of the manuscript. All authors have read and approved the final manuscript.

Halle (Saale), den 20.08.2023

Amibeth Helene Thompson
Eigenständigkeitserklärung

Declaration of independence

Hiermit erkläre ich, dass die vorliegende Arbeit mit dem Titel "Sampling Pollinator Communities and Interactions Across Changing Landscapes: Insights from a German Case Study" bisher weder an der Naturwissenschaftlichen Fakultät I der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt wurde.

Ferner erkläre ich, dass ich die vorliegende Arbeit selbstständig und ohne unzulässige fremde Hilfe verfasst, sowie keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe. Die den Werken wörtlich oder inhaltlich entnommenen Stellen wurden als solche von mir kenntlich gemacht. Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe.

I hereby declare that I have written this doctoral thesis entitled " *Sampling Pollinator Communities and Interactions Across Changing Landscapes: Insights from a German Case Study* " has not previously been submitted to the Faculty of Natural Sciences I - Life Sciences of the Martin Luther University Halle-Wittenberg or to any other scientific institution for the purpose of obtaining a doctorate.

Furthermore, I declare that I have written this thesis independently and without outside help and that I have not used any sources or aids other than those indicated in the text. Text passages that have been taken over verbatim or in terms of content from works used have been marked as such by me. I further declare that I have never applied for a doctoral degree before.

Halle (Saale), den 20.08.2023

Amibeth Helene Thompson