SPATIO-TEMPORAL EFFECTS OF FLORAL RESOURCES ON POLLINATORS AND THEIR FUNCTIONS IN AGRICULTURAL LANDSCAPES

by

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„Die Welt erobern und behandeln wollen,
ich habe erlebt, dass das misslingt.
Die Welt ist ein geistiges Ding,
das man nicht behandeln darf.
Wer sie behandelt, verdirbt sie,
wer sie festhalten will, verliert sie.
Die Dinge gehen bald voran, bald folgen sie,
bald hauchen sie warm, bald blasen sie kalt,
bald sind sie stark, bald sind sie dünn,
bald schwimmen sie oben, bald stürzen sie.
Darum meidet der Berufene
das Zusehr, das Zuviel, das Zugroß."

— *Lao Tse*

DÀODÉ JĪNG (KAPITEL 29)

Übersetzt von *Richard Wilhelm*

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SUMMARY

Wild bees are essential for the pollination of wild and cultivated plants. However, within the last decades, the increasing intensification of modern agriculture has led to both a reduction and fragmentation as well as a degradation of the habitats wild bees need. The resulting loss of pollinators and their pollination poses an immense challenge to global food production. To support wild bees, the availability of flowering resources is essential. However, the flowering period of each resource is temporally limited and has different effects on pollinators and their pollination, depending on the time of their flowering.

Therefore, to efficiently promote and manage wild bee pollinators in agricultural landscapes, we identified species-specific key floral resources of three selected wild bee species and their spatial and temporal availability (**CHAPTERS 2, 3 & 4**). We examined, which habitat types predominantly provide these resources (**CHAPTERS 3 & 4**). We also investigated whether floral resource maps based on the use of these key resources and their spatial and temporal availability explain the abundance and development of the selected wild bees (**CHAPTERS 3 & 4**) and pollination (**CHAPTER 5**) better than habitat maps, that only indirectly account for the availability of floral resources.

For each of the species studied, we were able to identify different key pollen sources, predominantly woody plants in the early season (April/May) and increasingly herbaceous plants in the later season (June/July; **CHAPTERS 2, 3 & 4**). The open woody semi-natural habitats of our agricultural landscapes provided about 75% of the floral resources for the buff-tailed bumblebees, 60% for the red mason bees, and 55% for the horned mason bees studied, although they accounted for only 3% of the area (**CHAPTERS 3 & 4**). In addition, fruit orchards provided about 35% of the floral resources for the horned mason bees on 4% of the landscape area (**CHAPTER 3**). We showed that both mason bee species benefited from the resource availability in the surrounding landscapes (**CHAPTER 3**). Yet this was not the case for the bumblebees (**CHAPTER 4**). Instead, the weight gain of their colonies, the number of developed queen cells and their colony survival were higher with increasing proximity to forests. The proximity to forests also had a positive effect on the mason bees studied (**CHAPTER 3**). In addition, the red mason bees benefited from herbaceous semi-natural habitats. The proportion of built-up areas had a negative effect on the horned mason bees, and the proportion of arable land on the red mason bees. The habitat maps explained horned mason bee abundances equally well as the floral resource maps, but red mason bee abundances were distinctly better explained by key floral resources. The pollination of field bean increased with higher proportions of early floral resources, whereas synchronous floral resources showed no measurable reduction in their pollination (**CHAPTER 5**). Habitat maps also explained field bean pollination better than floral resource maps. Here, pollination increased with increasing proportions of built-up areas in the landscapes and decreased with increasing proportions of arable land.

Our results highlight the importance of the spatio-temporal availability of certain key species as resource plants of wild bees in agricultural landscapes. They show that habitat maps are ahead of, or at least equal to, spatio-temporally resolved floral resource maps in predicting wild bee development and pollination. Nevertheless, floral resource maps allow us to draw more accurate conclusions between key floral resources and the organisms studied. The proximity to forest edges had a positive effect on each of the three wild bee species studied. However, besides pure food availability, other factors seem to co-determine the occurrence of wild bees in agricultural landscapes.

ZUSAMMENFASSUNG

Wildbienen sind unerlässlich für die Bestäubung von Wild- und Kulturpflanzen. Die zunehmende Intensivierung der Landwirtschaft führte jedoch sowohl zu einer Verringerung und Fragmentierung als auch zu einer Wertminderung der von ihnen benötigten Lebensräume innerhalb der letzten Jahrzehnte. Die damit einhergehenden Verluste von Bestäubern und ihrer Bestäubung stellt die weltweite Nahrungsmittelproduktion vor eine immense Herausforderung. Zur Förderung von Wildbienen ist die Verfügbarkeit von Blüteressourcen essentiell. Die Blühdauer einzelner Ressourcen ist jedoch zeitlich begrenzt und hat, je nach Blütezeitpunkt, unterschiedliche Effekte auf Bestäuber und deren Bestäubung.

Um Wildbienen als Bestäuber in Agrarlandschaften effizient fördern und nutzen zu können, identifizierten wir deshalb die artspezifischen Schlüsselressourcen dreier ausgewählter Wildbienen und deren räumliche und zeitliche Verfügbarkeit (**KAPITEL 2, 3 & 4**). Wir untersuchten, welche Habitatstypen diese Ressourcen überwiegend bereitstellen (**KAPITEL 3 & 4**). Wir untersuchten zudem, ob Blütenressourcenkarten, die auf der Nutzung dieser Schlüsselressourcen und deren räumlich zeitlicher Verfügbarkeit basieren, die Abundanzen und die Entwicklung der ausgewählten Wildbienen (**KAPITEL 3 & 4**) und die Bestäubung (**KAPITEL 5**) besser erklären als Habitatkarten, die die Verfügbarkeit von Blüteressourcen nur indirekt beschreiben.

Für jede der untersuchten Arten konnten wir unterschiedliche, im frühen Saisonverlauf (April/Mai) überwiegend holzige im späteren Verlauf (Juni/Juli) auch zunehmend krautige, Schlüsselarten identifizieren (**KAPITEL 2, 3 & 4**). Die Wildobst- und Wildheckengehölze unserer Agrarlandschaften stellten rund 75% der Blütenressourcen für Erdhummeln, 60% für Rote Mauerbienen und 55% für Gehörnte Mauerbienen bereit, obwohl sie einen Flächenanteil von nur 3% ausmachten (**KAPITEL 3 & 4**). Obstplantagen stellten zusätzlich rund 35% des Blütenangebots für Gehörnte Mauerbienen auf 4% der Fläche bereit (**KAPITEL 3**). Wir konnten zeigen, dass beide Mauerbienenarten von der Ressourcenverfügbarkeit in den umliegenden Landschaften profitierten (**KAPITEL 3**). Bei Erdhummeln zeigte sich dieser Zusammenhang jedoch nicht (**KAPITEL 4**). Stattdessen waren die Gewichtszunahme ihrer Kolonien, die Anzahlen der darin ausgebildeten Königinnenzellen und die Überlebensdauer der Kolonie mit zunehmender Nähe zum Wald höher. Ebenfalls auf die beiden Mauerbienenarten wirkte sich die Waldnähe positiv aus (**KAPITEL 3**). Daneben profitierten Rote Mauerbienen durch krautige halbnatürliche Habitate. Nachteilig wirkten sich Siedlungsflächen auf die Gehörnten Mauerbienen, und Ackerland auf die Roten Mauerbienen aus. Habitatkarten erklärten die Abundanzen der Gehörnten Mauerbienen gleich gut wie Blütenressourcenkarten, jedoch wurden die Abundanzen der Roten Mauerbienen deutlich besser durch Schlüsselressourcen erklärt. Die Bestäubung der Ackerbohne erhöhte sich mit höheren Anteilen früher Blütenressourcen (**KAPITEL 5**). Dabei zeigte sich keine messbare Reduktion der Bestäubung durch gleichzeitig blühende Ressourcen. Habitatkarten erklärten die Bestäubung der Ackerbohne auch besser als Blütenressourcenkarten. Dabei nahm die Bestäubung mit zunehmenden Anteilen an Siedlungsflächen in den Landschaften zu und reduzierte sich mit zunehmenden Anteilen von Ackerland.

Unsere Ergebnisse verdeutlichen die Wichtigkeit der räumlich-zeitlichen Verfügbarkeit bestimmter Schlüsselarten als Ressourcenpflanzen von Wildbienen in Agrarlandschaften. Sie zeigen, dass Habitatkarten detaillierten Blütenressourcenkarten in der Vorhersage der Entwicklung von Wildbienen und deren Bestäubung voraus oder zumindest ebenbürtig sind. Dennoch ermöglichen es Blütenressourcenkarten, genauere Schlüsse zwischen den einzelnen Ressourcen und den untersuchten Organismen zu ziehen. Die Nähe zu Waldrändern wirkte sich positiv auf jede der drei untersuchten Wildbienenarten aus. Neben der reinen Nahrungsverfügbarkeit scheinen jedoch weitere Faktoren das Vorkommen von Wildbienen in Agrarlandschaften mitzubestimmen.

CONTENTS

1

GENERAL INTRODUCTION

Philipp W. Eckerter

CHALLENGES IN MODERN AGRICULTURE

During the last decades, human actions evolved into a geological force that dominates Earth's ecosystems with humankind altering the global environment from Earth's major biogeochemical cycles to the evolution of life (Chapin III et al., 2000; Crutzen, 2002; Crutzen & Stoermer, 2000; Lewis & Maslin, 2015; Ramankutty et al., 2008; Steffen et al., 2011; Vitousek et al., 1997; Zalasiewicz et al., 2008). To ensure the global food supply of an increasing human population, nowadays, about 11% of the global land surface is used for crops and around 30% for grazing (Raven & Wagner, 2021). The global demand for crops is expected to continue growing by 70-100% over the next three decades (Kastner et al., 2012; Tilman et al., 2011; Zabel et al., 2019). Modern intensive agriculture maximizes its productivity per unit area by simplifying traditional agroecosystems (Bommarco et al., 2013; Foley, 2005; Tilman, 2001). This is mainly achieved by creating large and productive monocultures that replace the natural vegetation and biological functions of former landscapes by, e.g., expanding agricultural fields accompanied by high external inputs of agrochemicals (Bommarco et al., 2013; Lewis & Maslin, 2015; Raven & Wagner, 2021).

However, the expansion of cropland and the landscape simplification has led to the destruction and fragmentation of natural habitats as well as their degradation and a decrease in their diversity (Foley, 2005; IPBES, 2016; Primack, 2014; Tscharntke, Tylianakis, et al., 2012). As a consequence, the intrinsic capability of ecosystems to maintain services like, e.g., pollination, pest control, regulation of climate or air quality and infectious diseases critically decreased making agricultural systems less efficient (Foley, 2005; IPBES, 2016; Potts, Roberts, et al., 2010; Potts et al., 2016; Pretty, 2018; Primack, 2014; Tscharntke, Clough, et al., 2012; Zabel et al., 2019). It is therefore assumed that agricultural intensification is one of the main drivers of global diversity loss which is about to take on the dimension of a Sixth Mass Extinction event (Ceballos et al., 2015; Habel et al., 2019; Raven & Wagner, 2021; Wake & Vredenburg, 2008). For example, total flying insect biomass in protected areas in Germany decreased by over 75% within the last three decades and across Europe, and especially in North America, similar negative trends for insects have been recorded (Habel et al., 2019; Hallmann et al., 2017; van Klink et al., 2020). This is problematic because approximately 85% of crops and 80% of wild plants rely on insect pollination (Klein et al., 2007; Potts, Biesmeijer, et al., 2010). The global market value of pollination in 2015 was estimated as 235-577 Billion US $ (IPBES, 2016). Continued and further simplification of natural ecosystems through intensive agriculture is therefore going to result in severe ecological and economic costs that may far outweigh the benefits of the simplification.

Sustainable agriculture aims to manage agricultural landscapes in a way that benefits agricultural production by promoting service providing organisms for e.g. pollination or pest control and reducing the effort, costs and negative consequences to ecosystems of anthropogenic inputs (Bommarco et al., 2013; Cassman, 1999; Pretty, 2018). Of the world's ~20,000 described bee species 785 species are known to visit crops and 12 are managed for crop pollination (IPBES, 2016; Potts et al., 2016). Although the major part of crop pollination depends only on a few managed pollinators a high diversity that also includes rare pollinators is vital for maintaining adequate pollination in ecosystems (Dainese et al., 2019; Hoehn et al., 2008; Kleijn et al., 2015; Kremen, 2018). In addition, relying on a few dominant species as pollinators is getting more and more riskful because of observed pollinator losses driven by increasing stresses like, e.g., parasites, pests, diseases, chemicals, resource scarcity or changes in plant phenology actuated by climate change (Goulson et al., 2015; Kremen, 2018). On top of that, bees are declining worldwide (IPBES, 2016; Ollerton, 2017). Wild bees can not only compensate for losses in managed pollinators but are often even more effective in pollinating wild and cultivated plants (Garibaldi et al., 2013; Hoehn et al., 2008; MacInnis & Forrest, 2019; Pfister, Eckerter, et al., 2017; Rader et al., 2016; Winfree et al., 2007). Therefore, it is critical for future agriculture to (1) reduce environmental damage and economic costs resulting from landscape simplification and agrochemicals, and (2) sustainably manage landscapes in a way that their inherent potential for ecosystem services can be developed and employed as far as possible (e.g. Tscharntke, Clough, et al., 2012; FIGURE 1.1).

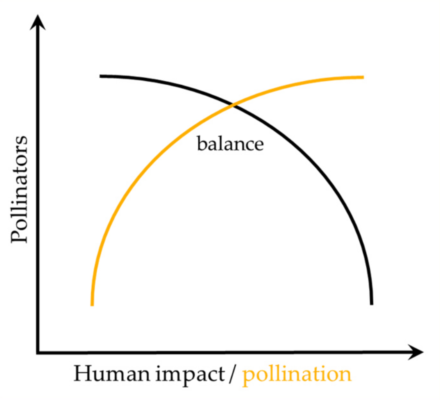

FIGURE 1.1 The relationships in between wild pollinator abundance and their diversity with human impact and their pollination of crops and wild plants in agroecosystems. Pollination quantity, quality and stability increases with the abundance and diversity of pollinators (yellow line). With increasing human impact, abundance and diversity of pollinators (black line) and their pollination decreases (yellow line) decrease. Efficient and sustainable agricultural management aims at a balance in between human impact in natural ecosystems (e.g. considered landscape modification) and enhancement of the integrity and functionality of natural ecosystems.

PROMOTING WILD POLLINATORS IN AGROECOSYSTEMS

Various methods to shape agricultural landscapes exist to promote wild pollinators (Garibaldi et al., 2014). For example, flowering perennial hedgerows and annual or perennial wild flower strips can offer suitable and less disturbed nesting and foraging resources. Hedgerows may additionally facilitate migration of species through enhanced habitat connectivity or act as refuge from pesticides or adverse weather conditions (Forrest et al., 2015; Garibaldi et al., 2014; Kremen et al., 2019; M'Gonigle et al., 2015; Vanneste et al., 2020). The availability of floral resources is assumed to be the major driver limiting bee populations (Roulston & Goodell, 2011). Bees visit flowers to collect pollen and nectar throughout their whole life cycle (Nicolson, 2011; Westrich, 2018). While pollen contains proteins, lipids, vitamins and minerals that bee larvae need for their development, nectar mainly contains sugar and water and is needed by adult bees as their main energy source (Nicolson, 2011). Aside from that bees also need the nectar to enable the transport of pollen of different sizes and structures (Thorp, 1979). Suitable foraging habitats offering floral resources are therefore vital to maintain and enhance wild bees (Dramstad & Fry, 1995; Fussell & Corbet, 1992; Holzschuh et al., 2013; Roulston & Goodell, 2011; Sutter et al., 2017, 2018; Venturini et al., 2017; Westphal et al., 2003, 2009; Williams et al., 2012). In cropland floral resources are mainly provided by mass-flowering crops like e.g. strawberries, oilseed rape or fruit trees that, mainly during spring, offer pulses of mass flowering resources followed by a severe reduction of resource availability after the flower (Holzschuh et al., 2013; Kremen et al., 2019; Westphal et al., 2003, 2009; Williams et al., 2012). Certain mass flowering-crops increase the abundance, development and reproduction of wild pollinators as well as their pollination (Grab et al., 2017; Holzschuh et al., 2013; Westphal et al., 2003, 2009). Certain types of semi-natural habitats like, e.g., hedgerows, forest edges and grasslands in the remaining part of agricultural landscapes offer a continuous availability of less disturbed habitats with a high diversity of floral resources (Dramstad & Fry, 1995; Fussell & Corbet, 1992). However, as the flowering of resource plants is temporally restricted and plants differ in their morphological and physiological traits bee foraging activity needs to overlap with the phenology of flowering plants to be efficient, and bees have to be morphologically, physiologically and behaviorally adapted to them (Bertrand et al., 2019; Corbet et al., 1979; Hoehn et al., 2008; Larsson, 2005; Miller-Struttmann et al., 2015; Nilson, 1988; Roulston & Goodell, 2011). In addition, suitable resources have to be in the flight range of the pollinators (Gathmann & Tscharntke, 2002; Walther-Hellwig & Frankl, 2000; Westrich, 1996, 2018). The species-specific temporal floral resource availability drives organisms from one habitat into another and determines their movements and activities in the landscapes (Holzschuh et al., 2011; Tscharntke, Tylianakis, et al., 2012). Although generalist species are able to forage on a broader range of resource plants, specific key species may be more often used by them (Sutter et al., 2017). Promotion of wild pollinator groups in agricultural landscapes therefore depends on conserving sets of certain key plant species with different, mutually complementary phenologies (Sutter et al., 2017). However, the identification and the landscape-wide mapping of key plants used by pollinators in agricultural landscapes across their foraging season represents a significant amount of work, and therefore, research that builds up on such data is largely lacking. In addition to the spatio-temporal availability of flowering plants, their spatio-temporal availabilities relative to each other may affect the interaction within ecological networks. For example, floral resources that flower early in the season may enhance pollinator abundances and increase pollination in later flowering crops (facilitation; Grab et al., 2017; Holzschuh et al., 2013; Westphal et al., 2003, 2009). Conversely, attractive co-flowering resources may distract pollinators away from a crop and thus reduce crop pollination or attract pollinators from the wider landscape into an area and consequently increasing pollination (competition alone or combined with facilitation; Bartomeus & Winfree, 2011; Häussler et al., 2017; Herbertsson et al., 2017; Lander et al., 2011; Morandin & Kremen, 2013; Schüepp et al., 2014). In addition, the availability of floral resources may affect the abundances, activities and interactions between pollinators within different years (Rundlöf et al., 2014; Thomson, 2016). However, the responses of wild bees in relation to the species-specific spatio-temporal availability of floral resources in the surrounding landscapes and the relating pollination are still surprisingly poorly studied.

MAPPING APPROACHES IN LANDSCAPE ECOLOGY

To model landscapes and predict organisms and their activity within them, landscape ecologists use different mapping approaches. To simplify landscapes of different complexity, they mainly use so called "land use/land cover maps" ("LULC maps") or habitat maps that account for similar land-use characteristics inside each of the different land-use types (Anderson, 1976; Fahrig, 2013; Forman, 1995; Goulson et al., 2002; Pfister et al., 2018). Different species within functional groups may use specific key floral resources that differ in their spatio-temporal availability, even inside the same habitat. These resources and their temporal availability are only indirectly considered in habitat maps (Roulston & Goodell, 2011; Vanreusel & Van Dyck, 2007). During the last decade, several studies were conducted to fill knowledge gaps related to that (e.g. Cole et al., 2017; Crone & Williams, 2016; Häussler et al., 2017; Lonsdorf et al., 2009; Nicholson et al., 2019; Olsson et al., 2015; Olsson & Bolin, 2014). However, links between the spatio-temporal availabilities of species-specific and landscape-scale resource availability and their effects on wild insect pollinators is still largely lacking. Due to the importance of floral resources and their different availabilities to pollinators, detailed species-specific and temporally resolved floral resource maps should perform better in predicting pollinator responses in agricultural landscapes than the simplified habitat maps (Dennis et al., 2006; B. D. Moore et al., 2010).

RESEARCH QUESTIONS

In order to contribute to filling the knowledge gaps mentioned above, the following main research questions were addressed in this thesis:

1. What are the key floral resources used by selected wild bee pollinators across their foraging season in European agricultural landscapes and in which habitats are they located?
2. Do the abundance of and distances to key floral resources and/or certain habitat types effect wild pollinator development, fitness and/or functions?
3. Does the spatio-temporal availability of species-specific alternative floral resources used by pollinators affect the pollination of crops?
4. Do temporally resolved floral resource maps predict the abundance, development and fitness of the selected pollinators and ecosystem delivery in agricultural landscapes better than habitat maps?

CHAPTER OUTLINE

CHAPTER 2: SEASONAL SHIFTS AND COMPLEMENTARY USE OF POLLEN SOURCES BY TWO BEES, A LACEWING AND A LADYBEETLE SPECIES IN EUROPEAN AGRICULTURAL LANDSCAPES

In this chapter, we identified the key floral resources used by *Bombus terrestris* and *Osmia bicornis* in European agricultural landscapes across their foraging seasons using visual pollen analysis of pollen from homecoming bumblebee foragers and out of mason bee nests. The findings of this chapter highlight the importance of mainly woody, non-agricultural plants as pollen sources for wild bees.

CHAPTER 3: FLORAL RESOURCE USE AND FITNESS CONSEQUENCES FOR TWO SOLITARY BEE SPECIES IN AGRICULTURAL LANDSCAPES

We released populations of *Osmia cornuta* and *Osmia bicornis* in agricultural landscapes and identified their floral resource use across their foraging periods using visual pollen analysis. We quantified the availability of these resources at the landscape scale and described the habitat types that mainly contributed to the floral resource availability for these species of wild bees. Additionally, we followed colony development of the two *Osmia* species We compared the power of floral resource and habitat maps in predicting the reproduction and fitness of these species. This chapter highlights the importance of floral resources and forests in agricultural landscapes for the reproduction of wild bee populations and the advantage of combining different mapping approaches into one study.

CHAPTER 4: USING TEMPORALLY RESOLVED FLORAL RESOURCE MAPS TO EXPLAIN BUMBLEBEE COLONY PERFORMANCE IN AGRICULTURAL LANDSCAPES

Analogous to chapter 3, we placed colonies of *Bombus terrestris* into agricultural landscapes and identified the key floral resources used by homecoming foragers across the season using visual pollen analysis. We quantified the floral resource availability at the landscape scale and identified the contributions of different habitat types to floral resource availability. We followed colony development and compared floral resource and habitat maps in predicting the development and fitness of *B. terrestris*. The findings of chapter 4 underline that other factors than pure floral resource availability may determine the occurrence of *B. terrestris* and that forests play an important role in sustaining these wild bee pollinators in agricultural landscapes.

CHAPTER 5: EFFECTS OF TEMPORAL FLORAL RESOURCE AVAILABILITY AND NON-CROP HABITATS ON BROAD BEAN POLLINATION

We set up flowering broad bean sentinels in agricultural landscapes that differed in the gradients of floral resources flowering before and synchronous to the beans. In this chapter, we describe the bee pollinators and the pollination of the broad beans in relation to the spatio-temporal availability of alternative key floral resources. The results suggest that the timing of alternative floral resources is important for crop pollination and that habitat maps may explain the pollination of crops better than spatio-temporally resolved floral resource maps.

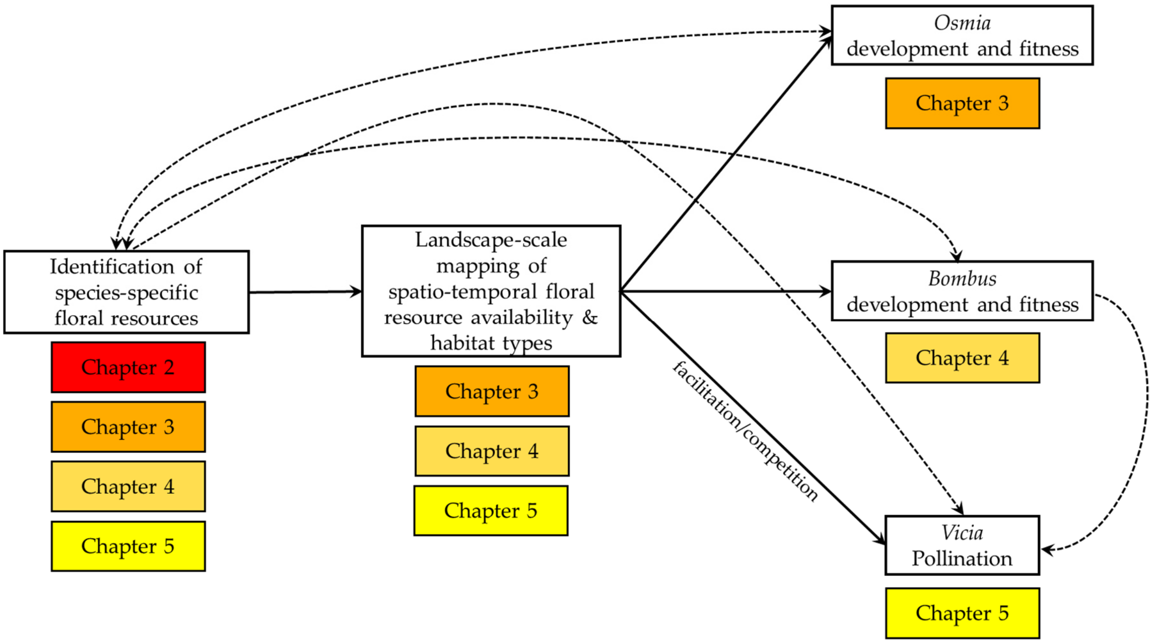

FIGURE 1.2 Conceptual overview of the approaches used, the observations made and their relations to each other inside the single chapters of this thesis. The individual colors indicate the assignment of the approaches and observations to the chapters.

2

SEASONAL SHIFTS AND COMPLEMENTARY USE OF POLLEN SOURCES BY TWO BEES, A LACEWING AND A LADYBEETLE SPECIES IN EUROPEAN AGRICULTURAL LANDSCAPES

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2.1 ABSTRACT

Continuous availability of food resources, such as pollen, is vital for many insects that provide pollination and pest control services to agriculture. However, there is a lack of knowledge about the shared or complementary use of floral resources by such species, which hampers more effective landscape management to simultaneously promote them in agroecosystems. Here, we simultaneously quantified pollen use by a bumblebee (*Bombus terrestris*) and a mason bee (*Osmia bicornis*), two bee species recognized as important crop pollinators, as well as a lacewing (*Chrysoperla carnea*) and a ladybeetle species (*Harmonia axyridis*), both common predators of crop aphids, throughout the season in 23 agricultural landscapes in Germany and Switzerland. Pollen diets were more diverse and similar among *C. carnea* and *H. axyridis* compared to the two bee species, but all four species shared key pollen types early in the season such as *Acer*, *Quercus*, *Salix* and *Prunus*. All species exhibited a pronounced shift in pollen sources from primarily woody plants (mainly trees) in spring to primarily herbaceous plants in summer. The majority of pollen (overall ≥64%) came from non-agricultural plants even in crop-dominated landscapes. Our results highlight the importance of trees as pollen sources for many insect species, particularly early in the season. Our findings support incentives that promote heterogeneous agricultural landscapes including both woody and herbaceous semi-natural habitats, ensuring phenological complementarity of floral resources for insect species that can provide pollination and pest control services to agriculture. The identified key plant species can help to design and optimize agri-environment schemes to promote these functionally important insects.

2

KEYWORDS

bumblebee, floral resources, foraging habitat, landscape resources, mason bee, pollen diet, resource specialization

2.2 INRODUCTION

Insects critically contribute to biodiversity in agroecosystems and provide ecosystem services sustaining crop production, such as crop pollination and pest control. Those services are of paramount economic and non-monetary value for human well-being (IPBES, 2016; Losey & Vaughan, 2006). Bees and other crop pollinators, as well as many natural enemies of crop pests such as syrphids, lacewings and ladybeetles, feed on nectar or pollen provided by flowering plants. Floral resources dominate the diet of bees, regardless of their development stage. The larvae of natural enemies, on the other hand, are predators primarily feeding on animal prey including major agricultural pests such as aphids, whilst adults regularly consume nectar and pollen as a sole food source (e.g. most lacewings) or to supplement their diet with key nutrients lacking in insect-only diets, in particular during periods of prey scarcity (e.g. ladybeetles; Lundgren, 2009). Hence, adequate floral resources may enhance these functionally important insects in agricultural landscapes (e.g. Carvell et al., 2017; Isaacs et al., 2009; Wäckers & van Rijn, 2012; Williams et al., 2012). The loss and degradation of semi-natural vegetation – and the concomitant loss of floral resources – is considered a principal cause of the decline of pollinators and pest enemies and the services they provide (Benton et al., 2003; IPBES, 2016; Scheper et al., 2014). Therefore, promoting adequate floral resources at the right place and time is critical for successful habitat management (Isaacs et al., 2009; M'Gonigle et al., 2015; Sutter et al., 2017) and can be highly effective to promote pest control (Tschumi et al., 2015; Wäckers & van Rijn, 2012) and pollination services (Blaauw & Isaacs, 2014) provided by insects.

Most common crop pollinators and pests' natural enemies consuming floral resources are dietary generalists; that is, they collect floral resources from multiple plant taxa from both crop and noncrop habitats (e.g. Villenave et al., 2005; Walther-Hellwig & Frankl, 2000). However, even the diets of generalist flower visitors are usually dominated by certain floral resource types (e.g. Sutter et al., 2017; Wäckers & van Rijn, 2012). Only a subset of resources offered by the flowering plant community in agroecosystems is accessible, available at the right time, of adequate chemical composition and attractive to different insect species. For instance, spatial resource use and accessibility depend on species' mobility and foraging ranges (e.g. Walther-Hellwig & Frankl, 2000). Furthermore, mass-flowering crops may offer abundant floral resources, but are ephemeral and only available during short periods. Spatio-temporal complementarity and thus continuous provisioning of floral resources by non-crop vegetation is, therefore, vital to ensure population persistence of pollinators and many important pest enemies, and the ecosystem services they provide (Schellhorn et al., 2015).

Yet, there is a lack of knowledge about the spatio-temporal dynamics of floral resource use (but see e.g. Grab et al., 2017) by co-occurring pollinators and pest enemies, which hampers more effective landscape management to simultaneously promote them in agroecosystems. Regarding pollen – a main source of protein for many functionally important insects – it remains unclear what proportions of pollen consumed by different species come from crop and non-crop plants or from different vegetation types such as woody (e.g. woodlots or hedgerows) or herbaceous (e.g. grasslands, herbaceous field margins) habitats. Information regarding the extent of overlap or divergence in pollen use by multiple species over time is also missing. Thus, to increase the effectiveness of measures to concomitantly promote service providing insects, we need to simultaneously examine how different plant resources contribute to their requirements, and how similar or complementary their use of floral resources is (Rollin et al., 2013; Shackelford et al., 2013). Such knowledge is a prerequisite to better assess and predict the distribution of these functionally important insect taxa in agricultural landscapes, and to guide scientists and land managers in identifying and promoting habitats and specific floral resources that are vital to sustain them.

The main objective of this study was to compare the spatiotemporal use of pollen resources between two pollinator and two aphid enemy insect species commonly found in Central European agricultural landscapes and that rely on pollen for at least part of their life cycle. The bumblebee *Bombus terrestris* and the mason bee *Osmia bicornis* were used as pollinator model taxa. These two species rely on pollen for development and adult survival, and are among the most abundant wild bees in the studied agroecosystems (e.g. Kleijn et al., 2015; Westphal et al., 2008) that provide pollination services in a wide range of crops, such as pumpkin (Pfister, Eckerter, et al., 2017) field beans and oilseed rape (Garratt et al., 2014), or fruit trees and strawberries (Gruber et al., 2011; Klatt et al., 2014). Aphid enemies that rely on pollen include hoverflies, ladybeetles and lacewings. We selected the lacewing *Chrysoperla carnea* s.l. due to its high abundance in annual cropping systems (McEwen et al., 2007; Pfister, Schirmel, et al., 2017). The ladybeetle *Harmonia axyridis*, despite being invasive in Europe (Roy et al., 2012), was also included as a model taxon since it became one of the most dominant aphid predators in European agroecosystems in the past years (e.g. Pfister, Schirmel, et al., 2017; Stutz & Entling, 2011). For *C. carnea* and *H. axyridis* adults, pollen is either an obligatory (*Chrysoperla*) or complementary (*Harmonia*) part of their diet, which can be vital in particular during periods of prey scarcity (Berkvens et al., 2010; Lundgren, 2009).

We addressed the following questions: (1) What are the main pollen types used by the studied bee, lacewing and ladybeetle species? (2) To what extent does pollen use overlap among the four species? Do they share important pollen taxa that could be targeted by habitat management schemes? (3) What is the relative importance of different pollen sources (i.e. woody/herbaceous plants, crop/non-agricultural plants)? How does the use of pollen sources change over the season and does the pollen use of the four insect species show similar temporal dynamics? (4) How does the landscape context influence the use of different pollen sources?

2.3 MATERIALS AND METHODS

STUDY REGIONS AND POLLEN SAMPLING DESIGN

The study was conducted in 2016 in southwestern Germany and northeastern Switzerland (see SUPPLEMENTARY INFORMATION S2.1A). In each region, 11 (Germany) to 12 (Switzerland) landscape sectors of 500 m radius were selected. The selected landscapes represent the typical range in the proportion of the two major land-use types characteristic for the study regions: agricultural land (e.g. arable crops, managed grassland, some horticulture; 38%–90%, mean = 68%, SD = 16%) and woody habitat (woodlots and hedgerows; 0%–51%, mean = 11%, SD = 12%; see S2.1A & FIGURE S2.1). In each landscape sector three (Germany) to five (Switzerland) sampling points were selected: one central sampling point, as well as 2 to 4 further ones randomly spread across the landscape (see S2.1B). Samples of insects and pollen were collected approximately every 2 weeks from beginning of April–mid-July (see TABLE S2.2). At each sampling point, adults of *C. carnea* and *H. axyridis* were sampled using sticky traps. For each species, up to five individuals per sampling round and landscape sector were randomly selected for pollen analysis. Pollen collected by *B. terrestris* was obtained from the pollen sacs of up to 10 worker bees per sampling round and landscape sector upon return to colonies experimentally established at each landscapes' central sampling point ("Mini hive"; purchased from BIOBEST and containing 30–40 workers). Pollen collected by *O. bicornis* was obtained from up to five brood cell provisions per sampling round of experimentally established trap nests at each sampling point (Switzerland) or central sampling point (Germany; see S2.1B; FIGURE S2.2).

POLLEN SAMPLES PROCESSING AND ANALYSIS

Elytra and/or wings of sampled *C. carnea* and *H. axyridis* individuals were removed, and insects were thoroughly rinsed with ETOH to remove pollen from the exoskeleton to minimize the potential of including in the analysis pollen grains that were not consumed by the insects. Subsequently, insects were crushed and acetolysis was performed following Jones (2012). All pollen samples belonging to the four insect species were treated chemically with acetolysis and KOH, and mounted in glycerin following standard palynological methods (P. D. Moore et al., 1991). Pollen grains were identified under a light microscope (400× magnification) based on palynological keys (Beug, 2004; P. D. Moore et al., 1991) and a photo atlas (Reille, 1992), as well as using the reference collection of the Institute of Plant Sciences of the University of Bern. Pollen grains were identified at species whenever possible, or at subgenus, genus, or family level (hereafter pollen types (=t.); see TABLE S2.1). About 1,070 samples were available for analysis (see TABLE S2.2). For each sample, we identified and counted up to 100 pollen grains whenever possible (i.e. between 30 and 100 grains).

DATA ANALYSIS

All statistical analyses were conducted using *R 3.4.1* (R Core Team, 2017). To account for unequal numbers of pollen grains between samples or insect species, and as we were interested in pollen composition comparisons, data were always standardized to proportions (i.e. relative contributions with total 100), and analyses were performed using pollen types percentages. For analyses of temporal dynamics and to facilitate comparisons across the two study regions, four sampling periods were defined based on accumulated Growing Degree Days (GDD; see TABLE S2.3).

To describe samples' pollen types diversity, we used pollen type richness (number of pollen types), as well as the Simpson diversity index, which represents the probability that two grains randomly selected from a sample will belong to different types ($1 - D$, with $D = \Sigma p^2$, p being the proportion of pollen grains belonging to one pollen type). Mean pollen type richness and mean Simpson diversity were compared for the four insect species with Kruskal–Wallis and Dunn tests.

To assess the degree of exclusiveness or overlap in pollen use among the four studied insect species, complementary specialization d' (Blüthgen et al., 2006) was calculated for each species for each sampling period (*R* package *'bipartite 2.08'*; Dormann et al., 2009). The index d' measures how strongly the pollen types collected by a species deviate from that of other species (Kämper et al., 2016). The measure ranges from 0 (complete overlap in pollen types use, i.e. "opportunistic" species sharing all their pollen types with other species) to 1 (exclusive pollen types use, i.e. "specialized" species; Blüthgen et al., 2008; Junker et al., 2013). Mean d' along the season was compared for the four species with Student *t* test. We also calculated $H2'$ which describes the average degree of complementary specialization for the four insect species (i.e. network specialization; Blüthgen et al., 2006). Network specialization equals the weighted sum of the specialization of its nodes (i.e. weighted sum of d' of all species). It also ranges from 0 (pollen types used by the four species completely overlap; "maximum niche overlap"; Schleuning et al., 2012) to 1 (each species uses a unique set of pollen types; "maximum exclusiveness" or "maximum niche divergence"; Blüthgen et al., 2008; Schleuning et al., 2012). The species-level index d' was used to compare the specialization levels of the four studied species within networks, while $H2'$ index was used for comparing the different networks across the season. The two study regions were analyzed together, and for each sampling period all samples belonging to one insect species were pooled. Only pollen types that accounted for more than 1% of the total number of pollen grains were considered for the analyses.

To examine the importance of pollen from woody plants, pollen types were classified as "woody" or "herbaceous" (see TABLE S2.1). Pollen types that could not be identified at the species level potentially including both woody and herbaceous plants (5% ± 10% of the data) were excluded from these analyses. For each insect species and sampling period, samples within a landscape were pooled. We used generalized linear mixed models (GLMMs) with a binomial error distribution to test the impacts of the fixed factors sampling period, species (*B. terrestris*, *O. bicornis*, *C. carnea*, *H. axyridis*), study region

(Germany/Switzerland) and their interactions and the random factor landscape sector, on the proportion of pollen from woody plants used by the insects. An observation level term was added as a second nested random effect to account for overdispersion (Lee & Nelder, 2000). Models were fitted with the *R* package *'lme4 1.1-13'* (Bates et al., 2015). As there was no significant three-way interaction in the full model (p = 0.64), indicating consistent temporal patterns of pollen use across species in both regions, data of both regions were finally analyzed together. Predictors' significance was tested with Wald chi-square tests. We also examined the importance of nonagricultural plants by classifying pollen types as "non-agricultural" (i.e. associated plant taxa can be unambiguously classified as nonagricultural plants, which includes plants from semi-natural habitats and crop weeds) and "potential crop" (i.e. associated plant taxa could potentially include crop or sown grassland plant species; see TABLE S2.1). We used similar GLMMs to those previously described, with the proportion of pollen from non-agricultural plants as the response variable, and sampling period, insect species and their interactions as fixed factors. In this case, as the significant three-way interaction of the full model indicated distinct patterns among the two study regions, they were analyzed separately.

To examine the influence of the landscape context on pollen use, we calculated landscape metrics using *ArcGIS 10.5* (ESRI) based on 2016 land-cover maps of the study regions. Maps were digitalized based on photo interpretation and were completed and validated with ground surveys. Land use was classified into five categories: woody semi-natural habitats (e.g. woodlands, hedgerows), woody crops (including vines and orchards), herbaceous crops (e.g. cereals), grasslands and "other land use" (including settlements). We calculated two metrics within each landscape sector of 500 m radius: the surface of woody semi-natural habitats and the total surface of woody land-use types (including woody semi-natural habitats and woody crops). We used as a basis the GLMMs previously described, including pollen proportion from woody plants or from non-agricultural plants used by insects as the response variable, sampling period, insect species and their interactions as fixed factors, and landscape sector and observation-level term as random effects. We complexified those models by adding a landscape metric and interactions with sampling period and insect species as additional fixed factors. The total surface of woody habitat was used as a landscape metric for the first model including the pollen proportion from woody plants as the response variable, whereas the surface of woody seminatural habitat was used for the second model including the pollen proportion from non-agricultural plants as the response variable. We confirmed that we had no remaining spatial autocorrelation in the models by checking residuals against spatial coordinates with correlogram plots using the *'ncf'* package in *R* (Bjornstad & Cai, 2020).

2.4 RESULTS

MAIN TYPES AND DIVERSITY OF POLLEN USED

A total of 140 different pollen types were identified: 91 types were used by *B. terrestris*, 54 by *O. bicornis*, 99 by *C. carnea* and 82 by *H. axyridis* (see TABLE S2.1). Most individual samples contained at least two different pollen types (see FIGURE S2.3). Individual samples of pollen used by *C. carnea* and *H. axyridis* had a roughly three times higher pollen type richness than those of the two bee species (Dunn test, $p < 0.001$), and this pattern was consistent across the season (FIGURE 2.1).

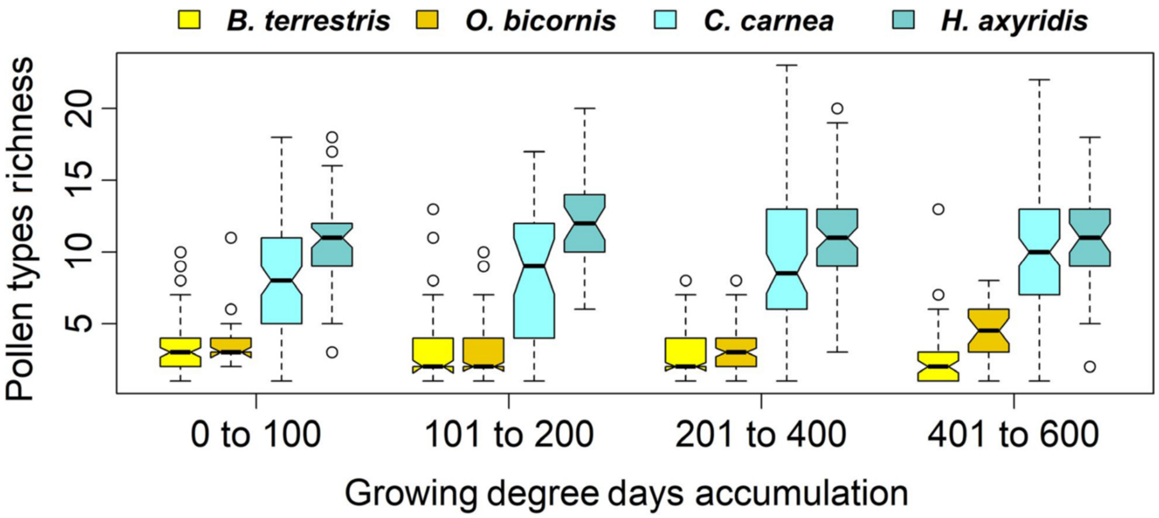


FIGURE 2.1. Changes in pollen type richness across the season for the pollen samples of *Bombus terrestris*, *Osmia bicornis*, *Chrysoperla carnea* s.l. and *Harmonia axyridis*. The notches indicate a 95% confidence interval of the median; if notches of two boxes do not overlap, this is a strong evidence that the medians differ. The four sampling periods (expressed in Growing Degree Days) correspond roughly to the months of April, May, June and July (see TABLE S2.3).

Simpson diversity of pollen types was also higher in samples from *C. carnea* and *H. axyridis* (0.54 ± 0.24 and 0.66 ± 0.18, respectively) than in those from *O. bicornis* (0.27 ± 0.22) and *B. terrestris* (0.17 ± 0.22; Dunn test: $p < 0.001$). Results were similar when pooling samples at the landscape level (see FIGURE S2.4). *Bombus terrestris* collected mainly pollen from insect-pollinated plants (83% ± 25%) in contrast to *H. axyridis* which was mainly using pollen from wind-pollinated plants (67% ± 19%), whereas *O. bicornis* and *C. carnea* used pollen from both, insect- and wind-pollinated plants (see TABLE S2.4). More precisely, early in the season, *B. terrestris* collected *Salix*, *Prunus* t. (=type), *Acer* and Brassicaceae pollen (presumably oilseed rape; see TABLE S2.5), accounting for more than 80% of the pollen collected. Later in the season, mainly *Rubus*, *Papaver rhoeas* t., *Trifolium* (mainly *Trifolium repens* t.) and *Tilia* pollen were collected by this species (FIGURE 2.2). *Osmia bicornis* collected mainly *Acer* and *Quercus* pollen early in the season, accounting for more than 65% of the pollen collected, whereas *Acer* and *Ranunculus acris* t. (probably *Ranunculus* sp.) dominated in summer samples. *Prunus* t., *Betula*, *Salix*, *Carpinus*, *Acer*, *Fagus*, *Quercus* and Brassicaceae pollen covered more than 60% of the pollen diet of *C. carnea* early in the season, whereas *Poaceae* species dominated the pollen diet during the summer months. Finally, *H. axyridis* consumed mainly *Betula*, *Fagus*, *Carpinus*, *Quercus*, *Acer* and *Pinus* pollen early in the season, covering almost 60% of the pollen diet, whereas half of the pollen consumed in summer belonged to *Urtica* and *Poaceae* species (FIGURE 2.2).

OVERLAP IN POLLEN USE AMONG INSECT SPECIES

Complementary specialization at the species level was on average twice as high in the two bee species compared to *C. carnea* and *H. axyridis* (FIGURE 2.3; mean *d'* of 0.65 and 0.30 for the two bees and the two aphid enemy species, respectively; Student t test: $p < 0.001$). At the network level, the degree of complementary specialization (*H2'*; i.e. mean complementary specialization of all four insect species) was low to intermediate, ranging from 0.33 to 0.53 across the sampling season (mean = 0.46; FIGURE 2.3). Overlap in pollen use between the four insect species was highest in May (GDD 100–200; *H2'* = 0.33, i.e. less pronounced niche complementarity), primarily due to a relatively high proportion of shared pollen types from woody plants such as *Acer*, *Quercus*, *Fagus*, *Prunus* t. and *Salix*, as well as a fairly general use of Brassicaceae pollen (FIGURE 2.3). Further key pollen types shared by at least two species included *Betula* early in the season (April, GDD 0–100), and *Poaceae*, *Tilia*, *Papaver rhoeas* t. and *Ranunculus acris* t. later in the season (June to mid-July, GDD 201–600).

RELATIVE IMPORTANCE OF DIFFERENT POLLEN SOURCES, TEMPORAL SHIFTS AND LANDSCAPE EFFECTS

For all insect species, the proportion of pollen from woody plants (collected from trees and shrubs) was high early in the year (April and May, GDD 0–200), but decreased significantly later in the season (June, GDD 201–400), indicating a shift from woody to herbaceous pollen sources (TABLE 2.1; FIGURES 2.2–2.4). The proportion of pollen from woody plants remained low until mid-July (GDD 401–600) for most species, but tended to increase again for *B. terrestris* because of the importance of *Tilia* pollen for this species in the late season. There was no significant relationship between the proportion of woody habitats in the landscapes and the proportion of pollen from woody plants collected by the insects ($p > 0.05$; see TABLE S2.6).

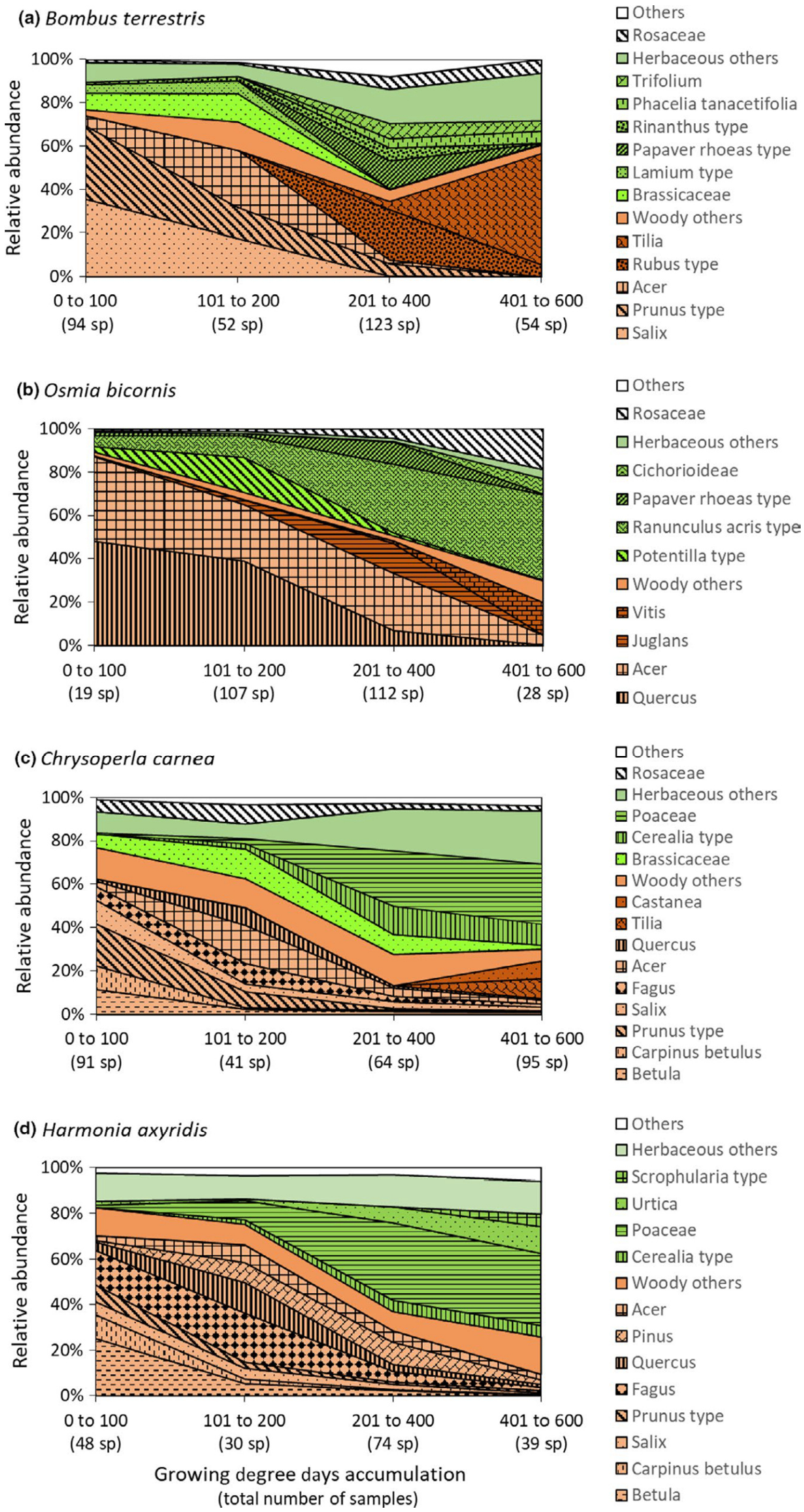
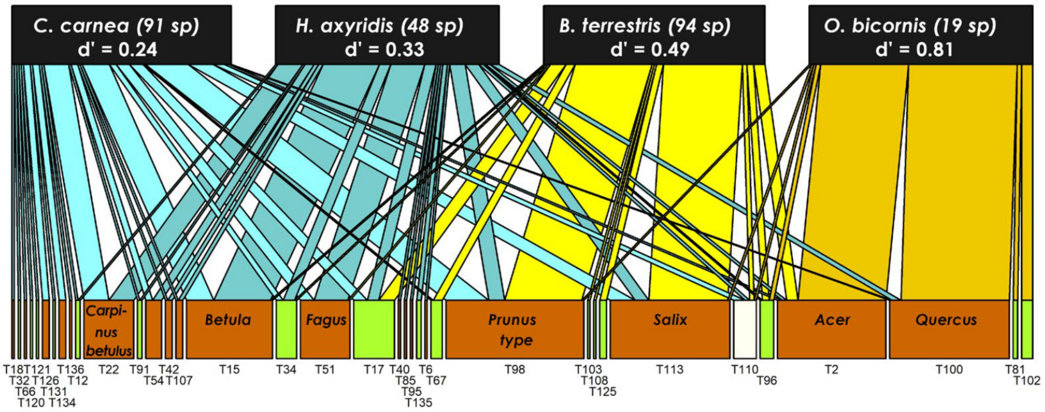
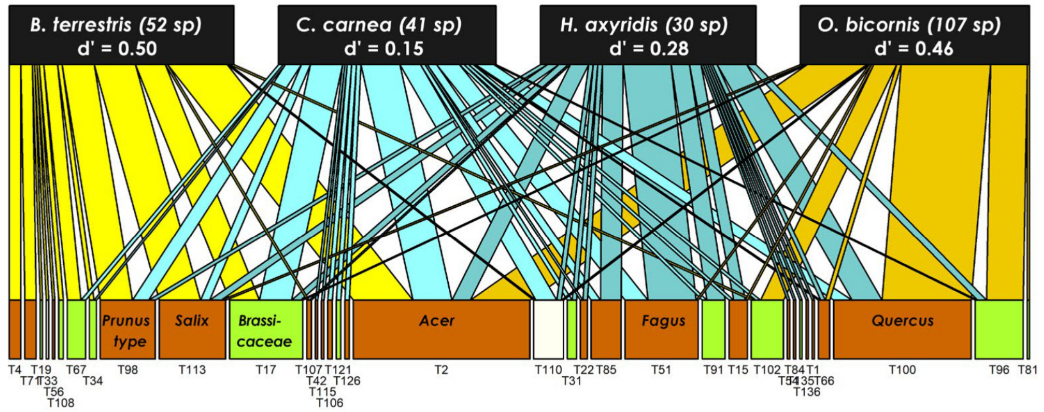


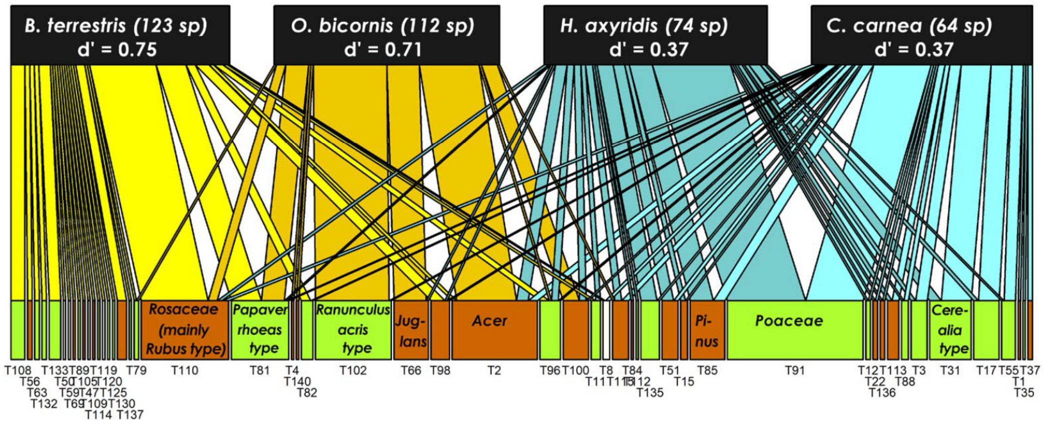
FIGURE 2.2. Relative abundance (%) of the main pollen types used across the season by (a) *Bombus terrestris*, (b) *Osmia bicornis*, (c) *Chrysoperla carnea* s.l., and (d) *Harmonia axyridis*. The four sampling periods (expressed in Growing Degree Days) correspond roughly to the months of April, May, June and July (see TABLE S2.3). Number of samples is given in brackets next to sampling periods. Only pollen types accounting for more than 5% of the total number of pollen grains used by an insect species are detailed. Brown colors represent pollen from woody plants, green colors those from herbaceous plants and white those for which this information was not available or which comprise both woody and herbaceous plants (see TABLE S2.1).



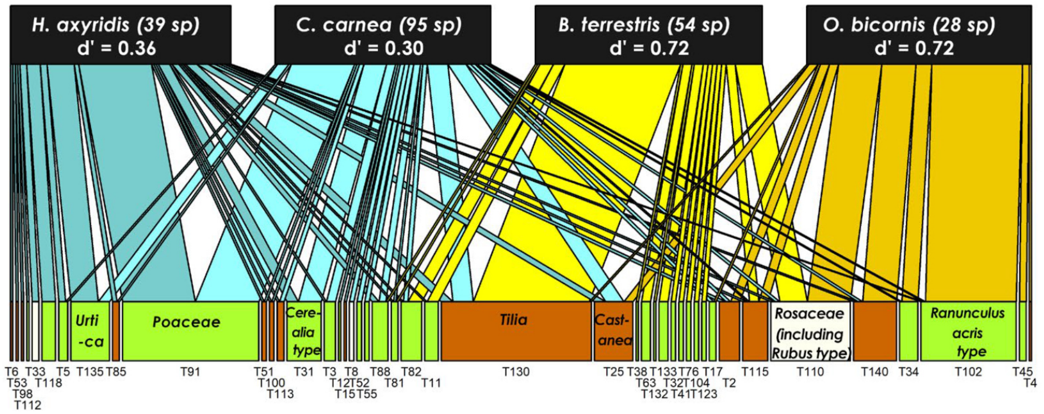
(a) GDD 0 to 100 ; H2' = 0.45



(b) GDD 101 to 200 ; H2' = 0.33



(c) GDD 201 to 400 ; H2' = 0.53



(d) GDD 401 to 600 ; H2' = 0.52

FIGURE 2.3. Pollen use network of the four insect species at each sampling period. Growing Degree Days (GDD) 0–100 correspond approximately to the month of April, 101–200 to May, 201–400 to June and 401–600 to end of June to mid-July (see TABLE S2.3). *H2'* measures network specialization; it ranges from 0 for the most generalized (i.e. maximum niche overlap) to 1 for the most specialized network (i.e. high exclusiveness, or maximum niche divergence). Upper bars represent insect species and lower bars the average proportion of pollen types used across all insect species (see TABLE S2.1 for more information on pollen types). Brown colors represent pollen from woody plants, green colors those from herbaceous plants, and white those for which this information was not available or which comprise both woody and herbaceous plants. The width of the arrows between upper and lower bars represents the proportion of a pollen type used by an insect species. Number of samples is given in brackets next to species names, and values of species-level complementary specialization (*d'*) are shown below. A high *d'* value indicates a high degree of specialization in pollen use of an insect species (high "exclusiveness"), whereas insect species sharing many pollen types with other taxa receive small *d'* values (i.e. "opportunistic" species).

TABLE 2.1. Analysis of deviance table (Type II Wald chi-square tests) of a generalized linear mixed model with binomial error structure testing for the effects of sampling period, insect species and their interaction on the proportion of pollen from woody plants used by insects.

Predictor	**χ^2**	**df**	**p (>χ2)**
Insect species	3.85	3	0.279
Sampling period	**143.91**	**3**	**< 0.001**
Insect species:Sampling period	15.59	9	0.076

Note: Pollen use by *Bombus terrestris*, *Osmia bicornis*, *Chrysoperla carnea* and *Harmonia axyridis* was assessed during four sampling periods (roughly April, May, June and July; see TABLE S2.3). Significant values are highlighted in bold.

There was no clear temporal trend in the proportion of pollen from non-agricultural plants used by studied insect species. Throughout the season, *O. bicornis* used higher percentages (82 ± 17%) of pollen from non-agricultural plants than *H. axyridis* (63 ± 15%), *B. terrestris* (57 ± 14%) or *C. carnea* (56 ± 9%; TABLE 2.2). At any time of the season and across all insect species, however, a significant part of the pollen diet was from non-agricultural plants (min≥40%, mean≥64%; TABLE 2.2). There was no significant relationship between the proportion of woody semi-natural habitats in the landscapes and the proportions of pollen from non-agricultural plants collected by the insects ($p > 0.05$; see TABLE S2.6).

TABLE 2.2. Percentages of pollen used from non-agricultural plants

	GDD 0-100	**GDD 101-200**	**GDD 201-400**	**GDD 401-600**	**Whole sampling season (mean ± *SD*)**
Bombus terrestris	52%	68%	40%	69%	57% (±14%)
Osmia bicornis	95%	82%	92%	58%	82% (± 17%)
Chrysoperla carnea	63%	63%	46%	51%	56% (± 9%)
Harmonia axyridis	77%	74%	50%	51%	63% (± 15%)
Mean	72%	72%	57%	57%	64% (± 16%)

Note: Numbers represent percentages of pollen types that can be unambiguously classified as from non-agricultural plants (i.e. pollen types potentially including crops and sown grassland plants are not included; see TABLE S2.1). The four sampling periods (expressed in Growing Degree Days) correspond roughly to the months of April, May, June and July (see TABLE S2.3).

2.5 DISCUSSION

Our findings reveal: (a) a higher diversity and lower pollen diet specialization of the two potential aphid enemies *Chrysoperla carnea* and *Harmonia axyridis* compared to the two studied bee species; (b) some important pollen plant taxa (e.g. *Acer*) shared by all four species, in particular early in the season; (c) the importance of woody plants (primarily trees) as pollen sources early in the season and a pronounced shift from woody to herbaceous pollen sources during the season for all studied insect species; (d) a generally high proportion of pollen from weeds and non-agricultural sources used by all four species.

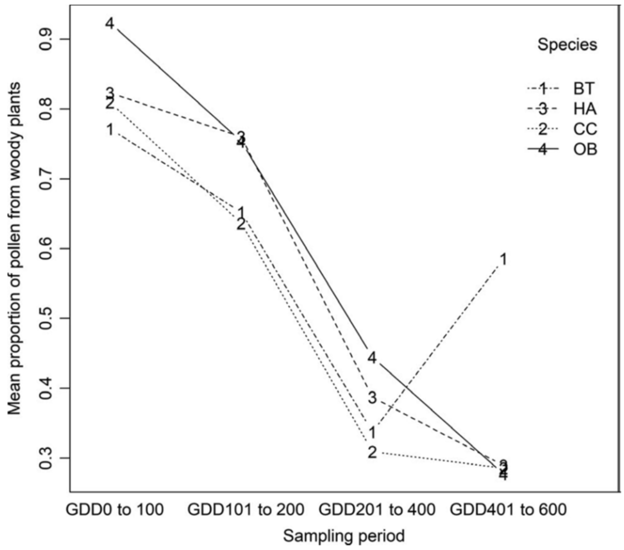


FIGURE 2.4. Mean proportion of pollen from woody plant taxa collected per landscape sector for each insect species and sampling period. The four sampling periods (expressed in Growing Degree Days) correspond roughly to the months of April, May, June and July (see TABLE S2.3). Abbreviations: BT, *Bombus terrestris*; OB, *Osmia bicornis*; CC, *Chrysoperla carnea*; HA, *Harmonia axyridis*.

COMPOSITION AND DIVERSITY OF POLLEN USED

Our findings are in agreement with the general expectation that bees (*O. bicornis* and *B. terrestris*) – exclusively relying on pollen as protein source for offspring provisioning – more selectively use pollen taxa of high nutritional quality that can be collected at relative low energy costs (e.g. mass-flowering plants), while natural enemies (*C. carnea* and *H. axyridis*) are more opportunistic in their pollen use. In spring as well as in summer, *Osmia bicornis* collected pollen mainly from a very limited number of plants: *Acer* and *Quercus* early in the year, and *Ranunculus acris* type (probably *Ranunculus* sp.), *Acer*, *Juglans* and *Papaver* in summer. The similar pollen use of *O. bicornis* in different years and regions (Coudrain et al., 2016; Radmacher & Strohm, 2010) indicates clear preferences among plants. These plants include mass-flowering trees such as *Quercus*, which is wind-pollinated but provides abundant and high-quality pollen for bees (Roulston et al., 2000), and some abundantly flowering, pollen-rich herbaceous plants including *Ranunculus*, which has been shown to be toxic to other bee species but not for *O. bicornis* (Sedivy et al., 2011).

Bombus terrestris foraged mainly on *Salix*, *Prunus* type, *Acer* and Brassicaceae (probably *Brassica* sp.) pollen in spring, and on *Rubus*, *Papaver*, *Trifolium* and *Tilia* pollen in summer (Kämper et al., 2016; Kleijn & Raemakers, 2008). Most of these plants are insect-pollinated and offer pollen of high protein content (Roulston et al., 2000), and except for *Papaver*, also relatively large amounts of nectar. In particular for the social *B. terrestris*, nectar availability may play a role in their preference for mainly insect-pollinated plants. Similar to *O. bicornis*, *B. terrestris* seems to primarily collect pollen of mass-flowering plants offering pollen of high nutritional quality (Kriesell et al., 2017). In fact, both quantity and quality of pollen collected by bumblebee workers are known to influence colony fitness (Genissel et al., 2002; Kämper et al., 2016).

Although the total number of pollen types collected at the taxa level was similarly high between bumblebees, lacewings and ladybeetles (91, 99 and 82 types, respectively), individuals of *Chrysoperla carnea* and *Harmonia axyridis* were more generalistic in their pollen diet (i.e. using more diverse pollen spectra), suggesting that they are opportunistic pollen feeders when compared to the studied bee species (Berkvens et al., 2010; Villenave et al., 2005). This is also reflected by the higher proportions of pollen from wind-pollinated plants with relatively low nutritional quality such as *Betula*, *Carpinus betulus*, *Fagus* or *Poaceae* (Berkvens et al., 2010).

RELATIVE IMPORTANCE OF POLLEN SOURCES

Despite the observed differences in pollen use among the studied insect species, our results reveal several general patterns. First, all four species used high proportions of pollen from non-agricultural plants (overall ≥64%), despite the fact that most of the studied landscapes were dominated by agricultural land (ranging from 38% to 90%; mean = 68%). The percentage of pollen from non-agricultural plants could exceed 90% in the case of *O. bicornis* and was generally high early in the year, underpinning the crucial role of floral resources offered by weeds and non-crop vegetation to sustain functionally important insect populations outside crops' flowering periods (Requier et al., 2015). These percentages should be interpreted as conservative estimates since all pollen types that potentially include crop or sown grassland species were not considered. Evidence from North American agroecosystems support these findings for generalist pollinators (e.g. Russo & Danforth, 2017; Williams & Kremen, 2007).

Another important finding is that woody plant species play a crucial role in providing the studied insect species with pollen resources early in the season (Kämper et al., 2016; Russo & Danforth, 2017; Villenave et al., 2005). The early season has been identified as a critical period during the life history of many important crop pollinators and pest enemies (e.g. Carvell et al., 2017; Kämper et al., 2016; Williams et al., 2012). This highlights the importance of maintaining woody habitats such as forest patches and hedgerows in agricultural landscapes. However, although we sampled 23 different agricultural landscapes spread over two countries and representing a high variability in landscape composition in terms of habitat and vegetation types, a rather low number of pollen types (2–8) represented more than 70% of the pollen collected by each insect species during the early season stage – in particular pollen types from flowering trees such as *Acer*, *Quercus*, *Salix*, *Fagus* or *Prunus*. These plants may also be important resources for other pollinator and natural enemy taxa such as honeybees (Requier et al., 2015) and hoverflies (Haslett, 1989). Moreover, the proportion of pollen collected from woody plants was not contingent on landscapes with high proportions of woody habitats (which ranged from 0% to 51%; mean: 11%).

Thus, maintaining even small amounts of woody habitats should receive high priority in landscape management. Key woody pollen types identified in our study (e.g. *Acer*, *Quercus*, *Salix*), which are of high nutritional value for insects (Roulston et al., 2000), are promising species for landscape management measures to simultaneously promote different pollinator and natural enemy species. Further research should focus on how the amount and spatio-temporal availability of the identified key resources may affect the distribution and dynamics of multiple insect assemblages. Maps that provide information on the spatial and temporal distribution of those specific resource plants (rather than broad land-use categories), at the right spatial scale (considering the foraging ranges of the target species), could significantly improve predictions of ecosystem service providing insects across agricultural landscapes. However, these predictions must also account for other factors such as intraguild predation (e.g. *H. axyridis* may prey upon *C. carnea* and conversely; Pell et al., 2008) which may lead to potential management conflicts. It should also be noted here that the invasive ladybeetle *H. axyridis*, despite being an effective aphid enemy, should not be specifically promoted by landscape management, because it threatens native biodiversity (and native ladybeetles in particular; Roy et al., 2012). However, our data show that due to its broad range of pollen use, and the strong dietary overlap with *C. carnea*, there appears to be little scope to selectively enhance either species by pollen resource provision. We hypothesize that the dominance of *H. axyridis* over native aphid predators can neither be countered nor exacerbated through pollen resource provisioning, but this topic requires further investigation.

SEASONAL SHIFTS IN POLLEN SOURCES USED

The four studied insect species exhibited similar temporal dynamics of pollen use during the season, characterized by a pronounced shift from woody to herbaceous pollen sources. This corroborates evidence of previous single-taxon studies focusing for example, on honeybees (Requier et al., 2015) or lacewings (*Chrysoperla* ssp.; Villenave et al., 2005). This pattern is likely at least partly driven by plant phenology: in most European agricultural landscapes, many dominant flowering trees and shrubs bloom relatively early and contribute more to floral resource availability early rather than later in the season (Williams et al., 2012; but see e.g. *Tilia* as an important exception). Yet, our results highlight the critical role of phenological complementarity among habitat types in providing food resources for multiple functionally important insect species throughout the year, and thus the importance of maintaining heterogeneous agricultural landscapes (Benton et al., 2003; Mallinger et al., 2016), including both species-rich woody and herbaceous habitats.

However, the high diversity of insects inhabiting agricultural landscapes that we could not investigate points to some limitations of our study. Further research is needed to confirm to what extent our findings could be generalized to natural bumblebee colonies and other important taxonomic groups of pollinators and crop pest enemies. Different functional groups such as parasitic wasps may show contrasting patterns of floral resource use (Patt et al., 1997). Finally, monitoring over several years may help identify potential inter-annual variation in the observed pollen use patterns (e.g. due to varying phenologies of flowering plants and insects).

2.6 CONCLUSIONS

Our findings have several important implications for the promotion of multiple key insect species that can provide crop pollination and pest control services in agroecosystems. Among the most important findings is that pollen use overlapped only little among the four studied species, with the exception of *Chrysoperla carnea* and *Harmonia axyridis*. Nevertheless, the diet generally shifted from woody to herbaceous pollen collected from mostly weeds and non-agricultural vegetation sources. This strongly supports incentives to maintain or restore heterogeneous agricultural landscapes (Benton et al., 2003; Martin et al., 2019). Heterogeneous landscapes should be characterized by a high diversity of plants and vegetation types, including both woody and herbaceous vegetation providing complementary floral resources throughout the year (phenological completeness), a factor proposed to be critical for effective provision of pollination and pest control services in agroecosystems (Schellhorn et al., 2015). Such incentives may include floral enhancement measures, such as the establishment of flower-rich hedgerows or sown flower strips promoted through agri-environmental schemes, which mitigate the isolation of semi-natural areas, and have a high potential to enhance floral-resource consuming insects and the ecosystem services they provide (e.g. Blaauw & Isaacs, 2014; M'Gonigle et al., 2015; Sutter et al., 2017; Tschumi et al., 2015). Our results, however, highlight an important role of trees for the nutrition of all four studied insect species in the early (*Acer*, *Quercus*, *Salix*, *Fagus* or *Prunus*) or late (*Tilia*) season, questioning whether schemes based on herbaceous plants alone can always provide enough adequate pollen resources to meet the pollen dietary requirements of multiple functionally important insect species (see also Wood et al., 2017). The identified early flowering trees are promising targets for habitat management measures to simultaneously promote both crop pollinators and pest enemies and the multiple ecosystem services they can provide in European agroecosystems.

DATA AVAILABILITY

Data are available from the *Dryad Digital Repository*.
DOI:10.5061/dryad.6836p06org/10.5061/dryad.6836p0

3

FLORAL RESOURCE USE AND FITNESS CONSEQUENCES FOR TWO SOLITARY BEE SPECIES IN AGRICULTURAL LANDSCAPES

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In preparation

3.1 ABSTRACT

The availability of key floral resources is crucial for wild pollinators. Identifying the spatio-temporal floral resource use and its effects on the development and fitness of wild crop pollinators might help to promote them and their pollination in agricultural landscapes. We established populations of *Osmia cornuta* Latreille and *Osmia bicornis* L., two solitary wild bee species and important crop pollinators in Southern and Central Europe, in 24 agricultural landscapes with varying floral resource availability. Based on their pollen use across their foraging period and the availability and landscape-scale availability of the visited plants in the landscapes, we estimated the total potential floral resource availability for each species. We used different mapping approaches to explain the development and fitness of the *Osmia* populations. The reproduction of both bee species increased with the total floral resource availability in the surrounding landscapes. More specifically, the reproduction of *Osmia cornuta* increased with increasing cover of plants that offer *Prunus* pollen, that of *Osmia bicornis* with increasing cover of *Papaver rhoeas*, *Ranunculus acris* and *Quercus* spec. as well as in proximity to oilseed rape. Using habitat maps, the reproduction of both species decreased with increasing distance to forest. Additionally, *Osmia cornuta* reproduction decreased with increasing proportions of built-up areas and that of *Osmia bicornis* increased with increasing proportion of herbaceous semi-natural habitats and decreased with proportion of arable land. Total pollen availability did not significantly explain the population fitness of the *Osmia*. A combination of non-agriculturally managed woody and semi-natural habitats as well as forests should be conserved and enhanced to maintain and support *O. cornuta*, *O. bicornis* and other wild bee populations and their pollination in agricultural landscapes. The combination of different mapping approaches gives a deeper understanding into the population processes of solitary bees.

KEYWORDS

agricultural landscapes; ecosystem services; landscape composition; landscape mapping; Megachilidae; wild bees; pollen diet; parasitism

3.2 INTRODUCTION

Around 88% of flowering plants and roughly 75% of crops at least partly rely on insect pollination (Klein et al., 2007; Ollerton et al., 2011). During the last decades, though, agricultural intensification has led to declines in the abundances and diversity of wild and managed insect pollinators that threaten the global productivity of agriculture, especially as the dependence from crop pollination is increasing (Aizen et al., 2019; IPBES, 2016; Potts, Biesmeijer, et al., 2010).

The availability of floral resources can be a driver of bee populations (Roulston & Goodell, 2011). However, studies that directly quantify floral resources at the landscape scale are scarce (Ammann et al., 2020; Eckerter et al., 2020). Instead, most studies indirectly infer flower availability from the cover of land-use types with different vegetation composition (Roulston & Goodell, 2011). The ecological modification of agricultural landscapes (e.g. planting flower strips and hedgerows as foraging and nesting habitats) may enhance the abundances and diversity of insect pollinators (Sutter et al., 2018; Venturini et al., 2017). Still, for the effective conservation of wild bee species and their pollination in agricultural landscapes, further research is needed to better understand the relationships between landscape-scale availability of floral resources, their use by pollinators and the consequences on pollinator abundance, reproductive success and fitness as major drivers of population growth and persistence in agricultural landscapes (Bertrand et al., 2019; Eckerter et al., 2021; Ganser et al., 2020; Gathmann & Tscharntke, 2002; Lawson et al., 2021; Schellhorn et al., 2015; Venturini et al., 2017; Woodard, 2017).

The mason bees *Osmia cornuta* Latreille and *Osmia bicornis* L. (former: *Osmia rufa* L., both Apoidea: Megachilidae) are solitary and polylectic wild bee species with a univoltine life cycle (Westrich, 2018). As all bees, next to species-specific nesting habitat and nesting material, adults depend on nectar as their main energy source and pollen for rearing their brood (Westrich, 2018). The nesting phenology and foraging of *O. cornuta* is in synchrony with the flowering of rosaceous (fruit) trees (Bosch, 1994b; Márquez et al., 1994; Tasei & Picart, 1973). Consequently, *Prunus* type (i.e. the pollen offered by these plants) is usually the dominant pollen in its diet (Márquez et al., 1994; Tasei & Picart, 1973) and *O. cornuta* is managed as an effective fruit tree pollinator in Southern and Central Europe (Bosch, 1994b, 1994a; Bosch et al., 2021; Vicens & Bosch, 2000). In strong contrast to *O. cornuta*, *O. bicornis* uses mainly pollen from non-agricultural tree species as well as from herbaceous plants. Its pollen provisions are often dominated by *Acer*, *Papaver rhoeas* type, *Quercus*, *Ranunculus acris* type, *Salix* and *Rubus* (Bertrand et al., 2019; Coudrain et al., 2016; Free & Williams, 1970; Hansted et al., 2014; Radmacher & Strohm, 2010; Tasei & Picart, 1973). We used *O. cornuta* and *O. bicornis* as species with similar lifestyle but with different hypothesized pollen use preferences to explore the relationships between species specific and landscape-scale floral resource availability and the consequences on their reproductive success and fitness.

The different use of pollen plant species suggests, that both solitary bees, although they are generalists, show a more oligolectic foraging behavior in agricultural landscapes and prefer and forage on a different set of key floral resource plants if they are available (Bertrand et al., 2019; Sutter et al., 2017; Tasei & Picart, 1973). In temperate agricultural landscapes, pollen from woody plants are highly used by wild bees and, due to their higher cover, entomophilous trees and shrubs can offer a higher amount of pollen than herbaceous plants (Ammann et al., 2020; Eckerter et al., 2020). We therefore expect that a different set of woody plants contribute most to pollen resource availability in these agricultural landscapes, and that both solitary bee species will predominantly use these pollen plants in landscapes where they are available in high amounts within their foraging ranges. In addition, as the majority of floral resources for wild bees is predicted to be offered by non-agricultural plants out of semi-natural habitats (Bertrand et al., 2019; Eckerter et al., 2020; Williams & Kremen, 2007), we expect a high contribution of land-use types other than arable lands and permanent crops to floral resource availability for those bees. Pollen contains proteins, lipids, vitamins and minerals that are crucial for the larval development (Nicolson, 2011; Westrich, 2018). A higher availability and proximity to the preferred floral resources should lead into an increased offspring provision efficiency and thus higher offspring produced and higher reproductive success via e.g. shorter and more efficient foraging trips of females (Ganser et al., 2020; Pitts-Singer & Bosch, 2010; Zurbuchen et al., 2010). Increased pollen provision of larvae by higher availability of and proximity to key floral resources might also result in heavier (i.e. larger) offspring (Bosch & Vicens, 2002, 2006; Ganser et al., 2020; J. -y. Kim, 1999; Peterson et al., 2006; Radmacher & Strohm, 2010, 2010). As the females of both *Osmia* species studied are larger than the males and their development requires a higher availability of food, we also expect increasing proportions of females with increasing availability of floral resources (Bosch & Vicens, 2002, 2005, 2006; Bukovinszky et al., 2017; J. -y. Kim, 1999; Kratschmer et al., 2020; Westrich, 2018). A larger body size was shown to enhance e.g. the foraging efficiency, fertility and survival in megachilid bees and on the long run the pollination efficiency of populations (Bosch & Kemp, 2004; Bosch & Vicens, 2006; J.-Y. Kim, 1997; Torchio & Tepedino, 1980). The cocoon weight and the proportion of produced females are therefore positively correlated to the fitness of *O. cornuta* and *O. bicornis* populations.

Different mapping approaches are used to assess landscape characteristics as predictors of wild bee abundances and populations in agricultural landscapes. The commonly used land use/land cover maps (LULC maps, hereafter “habitat maps”) does typically not account for species-specific floral resource occurrences or their temporal availability (Ammann et al., 2020; Crone & Williams, 2016; Eckerter et al., 2020, 2021; Fahrig, 2013; Forman, 1995; Roulston & Goodell, 2011). However, we expect that floral resource maps that provide quantitative information about the availability of pollen resource plants used by wild bees and their temporal dynamics across bee-specific foraging periods to be better predictors of wild bee fitness and population dynamics than habitat maps. Antagonists of nest-constructing bees mainly enter the nest when the foraging female is absent and harm *Osmia* populations by e.g. feeding on its pollen provisions or feeding and destroying the brood (Goodell, 2003; Krunic et al., 2005; Seidelmann, 2006). They are more diverse and abundant with increasing abundances in bee populations (Krunic et al., 2005). As the *Osmia* studied are hypothesized to mainly use pollen out of woody semi-natural habitats, parasitism should also increase with increasing proportions of and proximity to those habitats.

In this study, we established populations of *O. cornuta* and *O. bicornis* in 24 agricultural landscapes varying in the gradient of early and late floral resources in southwest Germany, quantified their pollen use throughout their foraging periods and mapped the most used plant species. Combining the data on their pollen use and the availability of plants that offer the used pollen in our landscapes, we calculated quantitative indices of pollen availability for each species in each landscape across their activity period. We tested how well floral resource maps explain the reproduction of the mason bee species studied in comparison to habitat maps. We additionally quantified the antagonists in the nests of the *Osmia* and tested for relationships between parasitism and the proportions of woody semi-natural habitats and the distance to them. We tested the following hypotheses: (1) Both solitary bee species studied use a different set of key pollen resources; (2) the reproduction of the two *Osmia* species studied increases with the landscape scale potential availability of pollen resources; (3) floral resource maps explain the reproduction of the *Osmia* better than habitat maps; (4) the weight of the offspring and the proportion of female cocoons of both of the *Osmia* species increase with the availability of pollen resources; (5) the abundance of antagonists in the nests of the *Osmia* increases with the availability and proximity to woody habitats.

3.3 MATERIALS AND METHODS

STUDY LANDSCAPES

We selected 24 agricultural landscapes of 500 m radius in the surroundings of Landau, Rhineland-Palatinate, Germany (SUPPLEMENTARY INFORMATION, FIGURE S3.1). The mean nearest neighbor distance between landscapes was 1993 ± 183 m (average ± standard error). The landscapes represented a gradient in the amounts of pollen resource availability. We established populations of *Osmia cornuta* and *Osmia bicornis* inside grassy field margins in the centers of each landscape (see below). As the landscapes were located in the same region and had similar altitude, there were no major differences in the flowering phenology and weather conditions between them. We mapped the major habitat types and the cover (in m^2) of all woody plants and those herbaceous plant taxa which pollen is used by either *O. bicornis*, *O. cornuta* or both species inside of Central European agricultural landscapes across the landscape areas (Bertrand et al., 2019, own data, not published; Coudrain et al., 2016). We mapped the woody plants between June and November 2017, the annual herbaceous plants during their flowering period and the land use between April and July 2019. A more detailed description of the floral resource mapping methodology is provided in S3.1. For the orientation during the mapping process and ground truthing of each landscape element, we used optical satellite imagery (Copernicus: Sentinel-2, L2A-L2C, 2018, 10 m resolution) processed by the Federal Agency for Cartography and Geodesy (BKG). We accounted for every change between the satellite imagery and a landscape element during our field inspection (Eckerter et al., 2020, 2021).

CREATION OF FLORAL RESOURCE MAPS

TOTAL POTENTIAL POLLEN AVAILABILITY

We studied the pollen use of the established *Osmia* populations throughout their foraging periods. With the obtained data on their pollen diet and the landscape-scale availability of plant taxa that contributed to more than 1% to the pollen diet of the respective species, we created floral resource maps for each *Osmia* species. For this, we considered 16,500 pollen grains out of 165 cells from 101 nests for *Osmia cornuta* and 28,100 pollen grains out of 281 cells from 223 nests *Osmia bicornis*, taken at 10 sampling days across the foraging period of both species. We ensured that multiple pollen samples out of the same nest were collected at different days. This way, the floral resource maps comprised the plant taxa that together offered around 95% of pollen diet of each species (TABLE S3.1). To describe the potentially pollen resource availability in each landscape and specifically for each of the two *Osmia* species studied, we calculated floral resource availability indices that are based on the spatial availability of visited plants (i.e. the relative cover of the plants offering the collected pollen types) multiplied by their utilization (i.e. the percentage of the relative collected pollen volume) of each species across the foraging season (Eckerter et al., 2020, 2021). We calculated one index value that accounts for the pollen availability in each landscape and for each species (i.e. 24 values per species). The average pollen availability is denoted by an index value of 1, while larger or smaller values indicate the proportional difference of the resource availability in a given landscape relative to the average. We excluded *Muscari* (accounting for 1.2 % of the diet of *O. cornuta*) from the floral resource maps because we did not detect it in our landscapes during the mapping. For a complete list of the plant taxa that were excluded from the floral resource maps see TABLE S3.2. Whenever we use the term "total pollen availability" in the remainder of this paper, we are referring to the pollen availability calculated with the indices.

KEY POLLEN TYPES

We identified the pollen types contributing to more than 3% to the studied bee's pollen diet as key pollen types. These were *Acer*, *Prunus* and *Salix* for *O. cornuta* and *Juglans*, *Papaver*, *Quercus*, *Ranunculus* and *Rubus* for *O. bicornis* (TABLE S3.1). For *O. bicornis*, we additionally included oilseed rape because it is an important nectar source for this species and one of the most important mass-flowering crops for wild pollinators in European agroecosystems (Holzschuh et al., 2013; Westphal et al., 2003, 2009).

CREATION OF HABITAT MAPS

Additionally, for comparison, we created habitat maps using polygon and point layers in QGIS 3.6.2 (QGIS Development Team, 2019). We distinguished the following habitat types: arable land, permanent crops, forest edges (i.e. the first ten meters into forest), woody semi-natural habitats (i.e. hedgerows and single standing trees including those of semi-natural orchards), herbaceous semi-natural habitats (i.e. intensively and extensively managed meadows and pastures) and built-up areas (i.e. rural settlements).

We additionally included the distances to forests into our analysis and divided the forest edges from semi-natural habitats because forests can be important predictors of pollinator richness and visitation rates (Ricketts et al., 2008) and colony development of *Bombus terrestris* (Eckerter et al., 2020), and may serve as indicator for habitat connectivity (Tscharntke, Tylianakis, et al., 2012).

ESTABLISHMENT AND MONITORING OF THE *OSMIA* POPULATIONS

At each landscape center, we placed one nesting block attached on wooden pales 1 m above the ground in mid-February 2019 (FIGURE 3.1A). The nesting blocks consisted of ten MDF nesting boards each providing ten cavities of 145 mm length, open at one side (WAB-MAUERBIENENZUCHT, Konstanz, Germany). Boards in nesting blocks were alternating in nesting cavity diameter of 8 mm, preferred by *O. bicornis*, and 9 mm, preferred by *O. cornuta*. We oriented the openings of the nesting holes in south-east direction. As rain protection, we attached an additional MDF board without nesting holes and a plate of phenolic resin coated plywood (31 x 31 cm) on top of the nesting blocks (FIGURE 3.1B). To protect the nesting blocks from climbing arthropods that could prey on the *Osmia* brood or feed on their nesting provisions, we added repellant glue around each pole. To ensure standardized starting populations, we released 30 cocoons of each *Osmia* species at each nesting block at the end of February (S3.3). Given the very low natural colonization of nests at the same sites in the previous year (1.38 ± 0.8 *O. cornuta* cells and 7.42 ± 6.5 *O. bicornis* cells on average), the nests constructed in the study year should largely represent the reproduction of the released starting populations.

FIGURE 3.1 Experimental set up of nesting blocks inside the center of an example landscape (**a** & **b**) and monitoring example of a nesting plate (**c**).

We monitored the nesting of the *Osmia* weekly across the activity period of both species. This resulted in eleven sampling dates between mid-February and early July 2019. To follow brood cell construction in nests, we controlled every nesting plate and marked either the closing position of the last brood cell (containing either stored pollen, or pollen with egg or a larvae) or the position of the last collected pollen in a not yet completed brood cell (FIGURE 3.1C).

ASSESSMENT OF REPRODUCTIVE SUCCESS, FITNESS AND PARASITISM

At the beginning of July, when nesting activity was over (i.e. no newly constructed brood cells were detected any more), we collected the nesting blocks and stored them, entrances closed by placing the plates close to a shelf wall, at room temperature. We used the number of cocoons as a measure for the reproductive success of each species. We weighted the cocoons from late September until mid-October and hibernated them at 3 °C. We transferred the hibernated cocoons to room temperature in late February (cocoons preliminary assigned to *O. cornuta,* FIGURE S4) or mid-March, respectively (cocoons preliminary assigned to *O. bicornis,* FIGURE S4), and visually identified the hatching species and their sex. We manually opened the cocoons of non-hatched individuals by mid-May. Detected parasites were determined to the highest possible taxonomic level (Krunic et al., 2005). For statistical analysis, we used the number of cocoons per landscape as a proxy for the reproductive success of the *Osmia* species. The reproductive success (i.e. number of cocoons) was highly correlated to the numbers of produced offspring (i.e. number of brood cells) and the survival (i.e. number of hatching bees after hibernation; Pearson correlation tests: $n = 24$, $r = 0.99$, $p < 0.001$ and $n = 24$, $r = 0.88$, $p < 0.001$, respectively). As a proxy for fitness, we calculated the mean cocoon weight per species and sex and the proportion of hatching female offspring for each landscape. We used the proportion of parasitized brood cells (i.e. the number of parasitized brood cells/total number of brood cells) as a proxy for parasitism (Coudrain et al., 2013). In each sampling round, up to three pollen samples per landscape and species were taken. We stored the samples in water and froze them at -18 °C until further acetolysis (Jones 2012). We mounted the acetolysed pollen in glycerin and counted and identified 100 pollen grains per sample to the highest possible taxonomic level using a light microscope (400 x magnification), a palynological key (Beug 2007) and own reference slides with pollen collected by *B. terrestris* in the same region (Eckerter et al., 2020).

STATISTICAL ANALYSIS

To determine the contribution of different habitat types to floral resource availability, we divided the cover of plant taxa that offered the used pollen types per habitat type per landscape by the total cover of that plant taxon across all habitats and landscapes. We then multiplied these values with the proportion of each pollen type in the diet of the respective *Osmia* species. We used the sum of these values across all plant species per habitat type to estimate its contribution to pollen availability (Eckerter et al., 2020). We tested the relations between the reproduction (i.e. number of cocoons) of each *Osmia* species and the mean cocoon weight per species and the landscape using the landscape variables as response variables via generalized linear models (GLMs) using a negative binomial error structure, to account for overdispersion present in the data. Explanatory variables were the habitat types as well as distances to forests and built-up areas (see "creation of habitat maps" above). We tested the proportions of hatched females and parasitized brood cells using GLMs with binomial error distributions. In the case of overdispersion (dispersion parameter >1.5), we used quasi-distributions. We pooled response variables to obtain one value for each species and for each landscape and z-transformed explanatory variables (Field, 2017). In a first set of models, the floral resource availability index was the sole explanatory variable (see above). In a second set, we constructed models based on the cover of and the minimum distances to the key pollen resource plants (see above). In a third set of models, we used the cover of habitat types as explanatory variables. For the models out of the second and third set (i.e. single pollen type resource plants and habitat types), we started with full models containing all explanatory variables and simplified them through model selection via an information criterion approach using AICc (QAICc in the case of overdispersion) using the *dredge* function of the '*MuMin*' package (Bartón, 2020) and a cutoff rule (Δ(Q)AICc < 2; Burnham et al. 2011; Symonds and Moussalli 2011). To avoid multicollinearity, we excluded models with highly correlated variables (r > 0.6) out of the selection of the most parsimonious models. For the model validation, we used the '*DHARMa*' package (Hartig, 2020). We additionally calculated the Simpson's diversity of pollen used by each of the *Osmia* species in each landscape across their foraging periods using the 'vegan' package (Oksanen et al., 2019). We calculated H_2' to describe the level of complementarity specialization of the network of different pollen types used by the two *Osmia* species (Blüthgen et al., 2006). This index ranges from 0 to 1 with larger values indicating higher selectiveness (i.e. higher niche divergence) of the species inside a food web (Blüthgen et al., 2006). For the calculation of H_2' and the creation of a pollen network graph, we used the package '*bipartite*' (Dormann et al., 2009). We used the package '*ggplot2*' for the plotting of bar plots and scatter plots (Wickham, 2016). All analyses were done in R 4.0 (R Core Team, 2020). In the text, figures and tables, means ± standard errors are given.

3.4 RESULTS

POLLEN DIET

We found 25 pollen types among 16,600 analyzed pollen grains from 102 nests of *O. cornuta*. As expected, *O. cornuta* collected mainly *Prunus* type pollen (46.2%, pooled across its whole foraging period). Further main contributors to its pollen diet were *Salix* (38.0%) and *Acer* (5.1%). Each of the remaining pollen types contributed less than 2.5% to their pollen diet. We found 40 pollen types among 28,000 analyzed pollen grains from 222 nests of *O. bicornis.* The main pollen types collected across its foraging period were *Juglans* (28.0%), *Quercus* (25.7%), *Rubus* (16.7%), *Papaver rhoeas* type (11.4%) and *Ranunculus acris* type (7.0%). Each of the remaining pollen types contributed 1.5% or less to the diet of *O. bicornis*. The pollen provisions in a brood cell of the two *Osmia* species contained similar numbers of pollen types (*O. cornuta* 2.21 ± 0.08 pollen types, min = 1, max = 6; *O. bicornis* 2.35 ± 0.07 pollen types, min = 1, max = 6). However, the Simpson's diversity of pollen collected per landscape across the season was significantly higher in *O. bicornis* than in *O. cornuta* (0.67 ± 0.01 and 0.45 ± 0.01, respectively, Mann-Whitney-U-Test: $p < 0.001$).

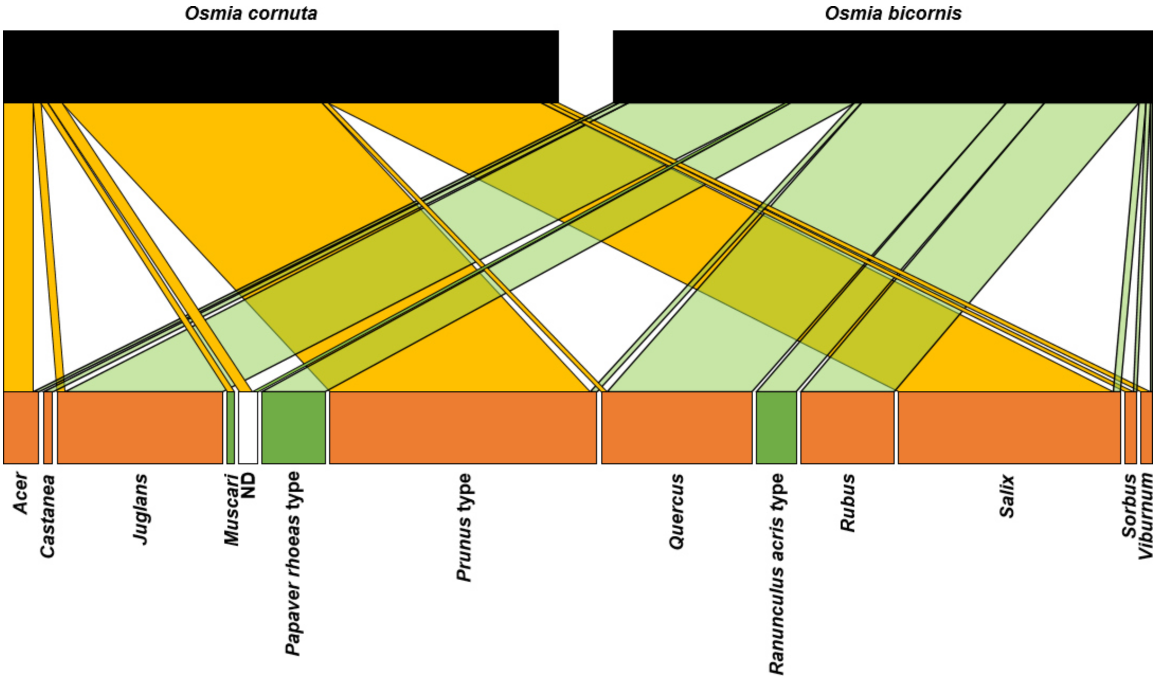

FIGURE 3.2 Pollen collection network out of 101 nests of *O. cornuta* (indicated in light orange) and 223 nests of *O. bicornis* (light green) in 24 agricultural landscapes in Rhineland-Palatinate (south-west Germany) across the activity period of both species in 2019. Lower bar width indicates the proportional number of pollen grains collected per pollen type across both species. The pollen types collected from woody plants are indicated in brown, pollen from herbaceous plants in dark green. Only the pollen types that constituted > 1% of the pollen diet of at least one species are shown, accounting for 98.6 and 96.1% of the diet of *O. cornuta* and *O. bicornis*, respectively. We abbreviate the pollen grains that could not be identified with "ND". See TABLE S3.1 and TABLE S3.2 for a complete list with all the pollen types collected.

The overlap in the pollen use between the two species was low (H_2' = 0.77, FIGURE 3.2). Across their foraging periods, both species mainly used the pollen from woody plant species (*O. cornuta*: 95.7%, *O bicornis*: 79.3%; FIGURE 3.2). *Osmia cornuta* collected pollen almost exclusively on woody plant species across its foraging season. In contrast to that, *Osmia bicornis* collected increasing amounts of pollen on herbaceous plants species during its late foraging season FIGURE S3.2A and FIGURE S3.2B.

LANDSCAPE COMPOSITION AND POLLEN AVAILABILITY

The landscapes consisted mainly of arable land (69.8% ± 0.047), followed by herbaceous semi-natural habitats (11.3% ± 0.024), forest (5.8% ± 0.024), permanent crops (3.9% ± 0.012), woody semi-natural habitats (2.9% ± 0.004), built-up areas (2.5% ± 0.011), and forest edges (1.3% ± 0.004). The contribution to the pollen availability of each habitat type deviated strongly from their relative cover in the landscape (FIGURE 3.3). The woody semi-natural habitats accounted for more than half of the pollen use in spite of covering only 2.9% ± 0.004% of the landscapes (FIGURE 3.3). Moreover, the permanent crops and the forest edges contributed in disproportionately high amounts of pollen to the diet of both bees (FIGURE 3.3). On the other hand, arable land was a minor pollen source (0% in *O. cornuta*, 3.5% in *O. bicornis*), in spite of dominating the landscapes. Similarly, the herbaceous semi-natural habitats provided little pollen used by the two *Osmia* species relative to their area (0.004% in *O. cornuta*, 3.3% in *O. bicornis*). This similar contribution of the habitat types to the diet of both bees was, however, based on largely different plant species. The main contributor to pollen availability for *O. cornuta* in the woody semi-natural habitats was *Prunus* type (37.5%), while *Juglans* was the main contributor for *O. bicornis* (45.8%). These two pollen types were also the most important contributors in the permanent crops (*O. cornuta*: *Prunus* type, 33.6%; *O. bicornis*: *Juglans*, 11.0%). See TABLE S3.3 for the proportions of habitat types in each of the studied landscapes and TABLE S3.4 for the contributions of the single pollen types to the pollen availability in each habitat type.

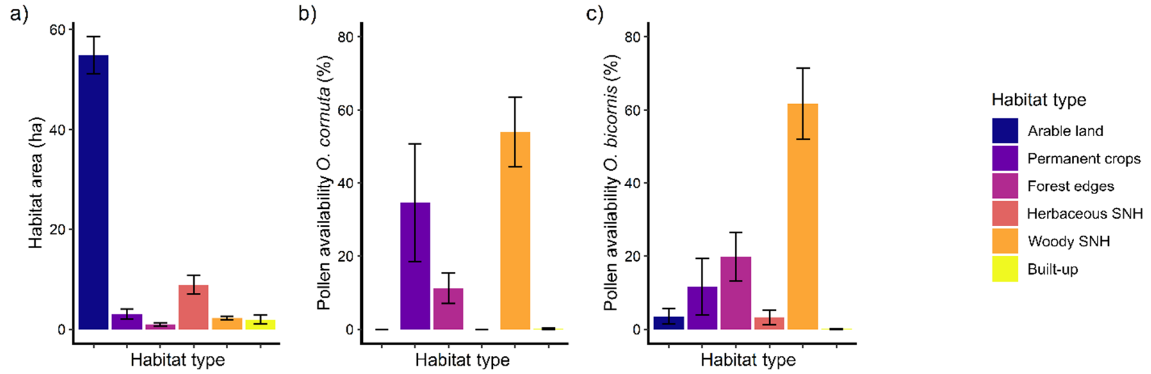

FIGURE 3.3 Mean area of habitat type in the studied landscapes (**a**) and their mean contributions to pollen availability to *O. cornuta* (**b**) and *O. bicornis* (**c**). We based pollen availability in a respective habitat on the relative area covered by plants offering a pollen type multiplied by their relative collection volume.

In *Osmia cornuta*, the use of the three dominant pollen types did not increase with their cover in the landscapes in that it was collected (Pearson correlation test, n = 66, r = 0.17, p = 0.17). In contrast, the use of the six dominant pollen types used by *Osmia bicornis* increased with their cover (n = 115, r = 0.31, *p* < 0.001). As indicated by its position towards the upper left of the regression line, in average, *Salix* pollen was disproportionally more used by *O. cornuta* in relation to its availability, while *Acer* pollen was disproportionally less used (FIGURE 3.4). In the diet of *O. bicornis,* in average, *Juglans, Quercus* and *Papaver rhoeas* type pollen were overrepresented relative to their availability, while *Ranunculus acris* type *and Rubus* pollen were underrepresented (FIGURE 3.4).

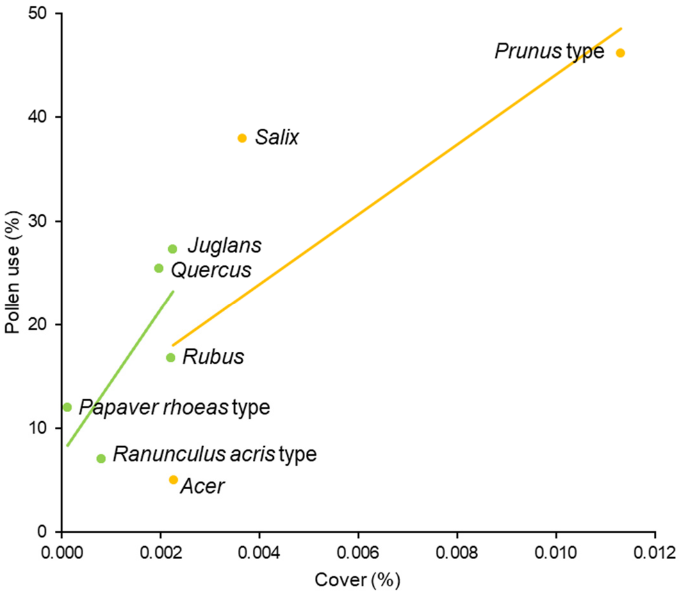

FIGURE 3.4 Average pollen use versus average resource availability based on the pollen diet of *O. cornuta* (orange) and *O. bicornis* (green). Pollen use is expressed as the average proportion of total collected pollen grains of the respective bee species, while resource availability is expressed as the average proportional landscape cover of the plant species providing the respective pollen.

OSMIA REPRODUCTION AND PARASITISM

Inside a total of 913 (38 ± 10) produced offspring (i.e. brood cells) from 213 nests (9 ± 2) of *O. cornuta,* 634 (26 ± 6) offspring reached the cocoon stage, and inside a total of 3,585 produced offspring (149 ± 29) from 609 nests (25 ± 4) of *O. bicornis* 2,954 (123 ± 25) reached the cocoon stage. The weight of female cocoons was 68.8% higher than that of male cocoons in *O. cornuta* (135 ± 8 mg versus 80 ± 5 mg), and 67.2% more in *O. bicornis* (97 ± 6 mg versus 58 ± 3 mg). The average parasitism rate was 10.4 ± 2.6% for *O. cornuta* and 11.3 ± 1.9% for *O. bicornis*. For an overview of the detected antagonists in brood cells of the *Osmia* see TABLE S3.5.

For *O. cornuta*, the reproduction increased with the total pollen availability (calculated with indices) in the agricultural landscapes (TABLE 3.1, FIGURE 3.5A). Furthermore, reproduction was positively related to the cover of plants that offer *Prunus* type pollen, the dominantly used pollen source (TABLE 3.1). The habitat maps revealed that the reproduction of *O. cornuta* decreased with distances to forest (FIGURE S3.3A) and the proportions of built-up areas in the landscapes (TABLE 3.1). For *O. cornuta*, the habitat maps explained the reproduction with similar reliability as the maps based on the total pollen availability or the dominant used single pollen type resources ($\Delta_i = 0.73$ and 0.55, respectively; TABLE 3.1). For *O. bicornis*, the reproduction increased with the total pollen availability in the landscapes as well (TABLE 3.2, FIGURE 3.2), and also decreased with increasing distances to forest (TABLE 3.2, FIGURE S3.3A). In addition, it increased with the proportion of herbaceous semi-natural habitats and decreased with the proportion of arable land in the surrounding landscape. In contrast to *O. cornuta*, the single pollen type resources maps explained reproduction of *O. bicornis* distinctly better than the total pollen availability and habitat maps ($\Delta_i = 22.40$ and $\Delta_i = 18.77$, respectively, TABLE 3.2). The reproduction of *O. bicornis* increased with the cover of *Papaver rhoeas* type, *Quercus* and *Ranunculus acris* type pollen in the landscape, and decreased with increasing distance to Brassicaceae pollen sources (TABLE 3.2, FIGURES 3.5B-E). See TABLE S3.6 for a summary of all results of the relationships of important single pollen resources and the reproduction of the two *Osmia* species.

The weight of the *Osmia* cocoons and the proportion of developed females showed no significant relation to the pollen availability in the surrounding landscapes (TABLES 3.1-TABLE 3.3, FIGURE S3.3B). The parasitism rates of the nests of both species decreased with increasing distances from forests, built-up areas and the proportions of permanent crops (TABLE 3.3, FIGURE S3.3C). They increased with the proportions of woody semi-natural habitats (TABLE 3.3). The parasitism rate did not significantly negatively affect the reproduction of the *Osmia* (TABLE 3.3)

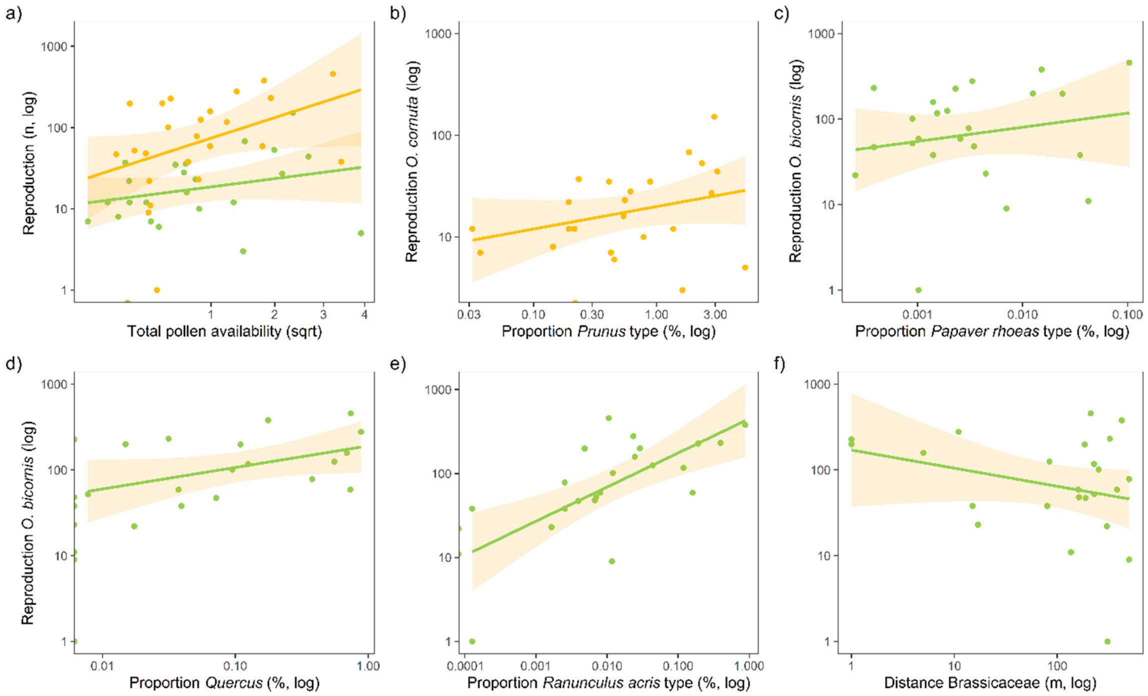

FIGURE 3.5 The reproduction (i.e. number of cocoons) of the two *Osmia* species studied (orange: *O. cornuta*, green: *O. bicornis*) in relation to (**a**) the total pollen availability (calculated with indices) present in the surrounding landscapes and to (**b**-**f**) the proportional cover of and minimum distance to the plant taxa that provided important pollen types for each species. Predicted significant linear relationships and 95 % confidence intervals are shown.

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TABLE 3.1 Comparison of models to test for variation in the reproduction and proportion of female offspring of *Osmia cornuta* explained by landscape-level total potential pollen availability (indices), cover of and distance to plant taxa that offer the important pollen types and habitat maps. We use the Akaike second-order Information Criterion (AICc) for count data and its quasi-version (QAICc) for proportional data and the *dredge* function from the *MuMin* package to select the best models ($\Delta_i < 2$). Delta weight (Δ_i) is the difference between the AICc of a particular model compared with that of the best model. We z-transformed variables and highlight significant effects (i.e., $p \leq 0.05$) in bold. “SNH” stands for “Semi-natural habitat”.

Model type	Response	Model description	df	(Q)AICc	Δ_i	Predictor	Estimate	SE	*z*-value	*p* value
Total pollen availability	Reproduction	Total pollen availability	22	205.57	0.00	**Total pollen availability**	**0.56**	**0.18**	**3.13**	**0.002**
	Proportion females	Total pollen availability	21	96.74	0.00	Total pollen availability	0.10	0.09	1.20	0.231
Important single pollen resources cover and distance	Reproduction	Cover *Prunus* type	22	205.32	0.00	**Cover *Prunus***	**0.54**	**0.18**	**2.99**	**0.003**
		Cover *Prunus* type + distance *Prunus* type	21	206.62	1.20	**Cover *Prunus***	**-0.22**	**0.18**	**-1.24**	**0.216**
						Distance *Prunus*	0.55	0.18	3.12	0.002
Habitat type cover and distance	Reproduction	Distance forest + Built-up	21	204.84	0.00	**Distance forest**	**-0.55**	**0.17**	**-3.32**	**< 0.001**
						Proportion built-up	**-0.40**	**0.18**	**-2.15**	**0.032**
		Distance forest	22	205.29	0.45	**Distance forest**	**-0.54**	**0.18**	**-3.05**	**0.002**
		Distance forest + distance built-up	21	205.42	0.58	**Distance forest**	**-0.63**	**0.17**	**-3.70**	**< 0.001**
						Distance built-up	0.30	0.17	1.73	0.084

TABLE 3.2 Comparison of models to test for variation in the reproduction and proportion of female offspring of *Osmia bicornis* explained by landscape-level total potential pollen availability (indices), cover of and distance to plant taxa that offer the important pollen types and habitat maps. We use the Akaike second-order Information Criterion (AICc) for count data and its quasi-version (QAICc) for proportional data and the *dredge* function from the *MuMin* package to select the best models ($\Delta_i < 2$). Delta weight (Δ_i) is the difference between the AICc of a particular model compared with that of the best model. We z-transformed variables and highlight significant effects (i.e., $p \leq 0.05$) in bold. “SNH” stands for “Semi-natural habitat”.

Model type	Response	Model description	df	(Q)AICc	Δ_i	Predictor	Estimate	SE	*z*-value	*p* value
Total pollen availability	Reproduction	Total pollen availability	22	281.14	0.00	**Total pollen availability**	**0.46**	**0.19**	**2.35**	**0.019**
	Proportion females	Total pollen availability	22	140.16	0.00	Total pollen availability	-0.04	0.04	-0.87	0.385
Important single pollen resources cover and distance	Reproduction	Distance Brassicaceae + cover *Papaver* + cover *Quercus* + cover *Ranunculus*	19	258.74	0.00	**Distance Brassicaceae**	**-0.24**	**0.10**	**-2.33**	**0.020**
						Cover *Papaver*	**0.29**	**0.11**	**2.69**	**0.007**
						Cover *Quercus*	**0.54**	**0.11**	**4.77**	**< 0.001**
						Cover *Ranunculus*	**0.71**	**0.11**	**6.26**	**< 0.001**

TABLE 3.2 *Cont.*

Model type	Response	Model description	df	(Q)AICc	Δ_i	Predictor	Estimate	SE	*z*-value	*p* value
		Cover *Papaver* + cover *Quercus* + cover *Ranunculus*	20	259.73	1.00	**Cover Papaver**	**0.33**	**0.12**	**2.79**	**0.005**
						Cover Quercus	**0.45**	**0.12**	**3.70**	**< 0.001**
						Cover *Ranunculus*	**0.79**	**0.12**	**6.36**	**< 0.001**
		Distance *Juglans* + cover *Papaver* + cover *Quercus* + cover *Ranunculus*	19	260.34	1.60	Distance Juglans	0.21	0.11	1.85	0.065
						Cover *Papaver*	**0.32**	**0.11**	**2.88**	**0.004**
						Cover *Quercus*	**0.43**	**0.12**	**3.73**	**< 0.001**
						Cover *Ranunculus*	**0.77**	**0.12**	**6.56**	**< 0.001**
Habitat type cover and distance	Reproduction	Distance forest + herbaceous SNH	21	277.50	0.00	**Distance forest**	**-0.49**	**0.18**	**-2.70**	**0.007**
						Proportion herbaceous SNH	0.32	0.18	1.77	0.077
		Distance forest	22	278.20	0.69	**Distance forest**	**-0.61**	**0.18**	**-3.30**	**< 0.001**
		Distance forest + Distance built-up + Herbaceous SNH	20	278.70	1.19	**Distance forest**	**-0.54**	**0.17**	**-3.09**	**0.002**
						Distance built-up	0.25	0.19	1.34	0.182
						Proportion herbaceous SNH	**0.45**	**0.19**	**2.31**	**0.021**
		Arable land	22	279.25	1.75	**Proportion arable land**	**-0.55**	**0.19**	**-2.92**	**0.004**

TABLE 3.3 Comparison of models to test for variation in the cocoon weight explained by landscape-level total potential pollen availability (indices), as well as parasitism rate with habitat maps and the effects of parasitism on the reproduction of the *Osmia*. We use the Akaike second-order Information Criterion (AICc) for count data and its quasi-version (QAICc) for proportional data and the *dredge* function from the *MuMin* package to select the best models ($\Delta_i < 2$). Delta weight (Δ_i) is the difference between the AICc of a particular model compared with that of the best model. We z-transformed variables and highlight significant effects (i.e., $p \leq 0.05$) in bold. "Sex" is the average cocoon weight that were preliminary assigned to either "male" or "female" individuals (see FIGURE S3.4). Species "Cornuta" stands for the produced cocoons of *Osmia cornuta*. "SNH" stands for "Semi-natural habitat".

Model type	Response	Model description	df	(Q)AICc	Δ_i	Predictor	Estimate	SE	*z*-value	*p* value
Total pollen availability	Weight	Total pollen availability + Sex	88	766.91	0.00	Total pollen availability	-0.01	0.02	-0.51	0.613
						Male	**-0.52**	**0.04**	**-12.62**	**< 0.001**
Habitat type cover and distance	Parasitism rate	Permanent crops + distance forest + distance built-up + woody SNH	42	100.96	0.00	Proportion permanent crops	-0.25	0.13	-1.84	0.072
						Distance forest	**-0.42**	**0.11**	**-3.87**	**< 0.001**
						Distance built-up	-0.20	0.12	-1.65	0.108
						Proportion woody SNH	0.27	0.15	1.80	0.078

TABLE 3.3 *Cont.*

Model type	Response	Model description	df	(Q)AICc	Δ_i	Predictor	Estimate	SE	*z*-value	*p* value
		Permanent crops + distance forest + woody SNH	43	102.04	1.08	**Proportion permanent crops**	**-0.32**	**0.13**	**-2.49**	**0.017**
						Distance forest	**-0.43**	**0.11**	**-3.85**	**< 0.001**
						Proportion woody SNH	**0.33**	**0.15**	**2.27**	**0.029**
		Permanent crops + distance forest + woody SNH + built-up	42	102.63	1.67	Proportion permanent crops	-0.26	0.14	-1.91	0.063
						Distance forest	**-0.46**	**0.12**	**-3.95**	**< 0.001**
						Proportion woody SNH	0.28	0.16	1.76	0.085
						Proportion built-up	0.16	0.13	1.22	0.228
		Permanent crops + distance forest + distance built-up	43	102.73	1.76	Proportion permanent crops	-0.20	0.14	-1.47	0.148
						Distance forest	**-0.44**	**0.11**	**-3.98**	**< 0.001**
						Distance built-up	**-0.27**	**0.12**	**-2.18**	**0.035**
Parasitism rate	Reproduction	Reproduction + species	44	500.00	0.00	Reproduction	-0.16	0.14	-1.14	0.256
						Cornuta	**-1.53**	**0.27**	**-5.60**	**< 0.001**

3.5 DISCUSSION

As predicted, the reproduction of both *Osmia* species significantly increased with the total availability of floral resources expressed as indices and with the cover or proximity of important key pollen plants present in the surrounding landscapes. The main contributors to floral resource availability for both species were woody semi-natural habitats, however, later in the season, *Osmia bicornis* also used pollen out of the herbaceous semi-natural habitats. The used pollen taxa differed strongly between both *Osmia* species. Our findings highlight the importance of preserving diverse non-agricultural woody and herbaceous key pollen plants as floral resources to sustain and enhance populations of these solitary bee crop pollinators in agricultural landscapes.

Surprisingly, the single resources explained the reproduction of *O. bicornis* distinctly better than the floral resource maps although the floral resource maps captured 94% of its pollen diet across the foraging period. *Juglans* and *Rubus* were highly used by *O. bicornis* and *Juglans* made up a large share of the mapped floral resources (TABLE S3.1). However, the single resource maps revealed, that the reproduction of *O. bicornis* were neither significantly positively related to the cover nor to the distance of *Juglans* and *Rubus* (TABLE S3.5). Thus, the power of floral resource maps in predicting the reproduction of *O. bicornis* decreases by including plants offering these two pollen types. The high amounts of *Juglans* used by *O. bicornis* in our study are surprising because we are not aware of any other study that indicates a comparably high use of that pollen type by this wild bee species, although *O. bicornis* is known to collect pollen on anemophilous plants (Coudrain et al., 2016; Haider et al., 2013). In this context it is surprising that the reproduction of *O. bicornis* increased with the use of *Quercus*, which is also wind pollinated, but not with *Juglans*, although both pollen types are equally used. Next to the availability and distance to preferred pollen sources in the landscapes, the provisioning of the cells with pollen depends on the availability of nectar. Foraging females are dependent on close-by nectar resources as energy source during their foraging trips and for managing to carry the poorly cohering pollen of anemophilous plants like *Juglans* and *Quercus,* as their nectar availability in is highly limited (Chambers, 1945; Nicolson, 2011). In our landscapes, *Juglans* occurs mainly as isolated individual high-stem trees in the open farmland, where nectar offering resource plants are sparser compared to the hedgerows and the forest edges, where the majority of *Quercus* trees were located close-by nectar-rich rosaceous trees and shrubs. Foraging flights to *Juglans regia* therefore seem to be less profitable due to the nectar scarcity of this plant and its direct surroundings. This might also be reflected by the significantly lesser use of *Quercus* pollen *O. bicornis* with increasing distance from plants offering *Prunus* type pollen (r = -0.50), that are highly attractive in terms of pollen as well as nectar early in the season (McGregor, 1976). We did not map forest interiors (i.e. the forest area besides of 10 m of forest edges) as the reproduction of bees are generally lower in closed woody habitats than in the open land (e.g. Bartual et al. 2019). However, it is still possible that *O. bicornis* collected on *Rubus* located inside of forests and that the mapped *Rubus* does not fully reflect the amount that was actually used by it. Observing fluctuations in the pollen diets of the *Osmia* (especially for *O. bicornis*, related to the high use of *Juglans* in this study) across several years could better account for the varying pollen use of this species related to varying weather conditions and phenologies of plants.

Also, it is surprising that the single resource maps performed distinctly better than the floral resource and the habitat maps in predicting the reproduction of *O. bicornis*, whereas, in predicting the reproduction of *O. cornuta*, the different mapping approaches performed equally well. The reproduction of *O. cornuta* was best explained by only one pollen resource across its whole foraging period, *Prunus* type and this type contributed to around 80% the potential total pollen availability for *O. cornuta*. In addition, plants offering this pollen type are important pollen and nectar resources for pollinators. In contrast, the reproduction of *O. bicornis* was best explained by a combination of different key pollen resources during different periods of the season (Brassicaceae and *Quercus* as well as *Papaver rhoeas* type and *Ranunculus acris* type in its early only contributed to around 25% to the potential pollen availability if this species.

Besides these resources, *Osmia bicornis* might have additionally collected on other nectar offering resources that, if accounted for, enhance the predictive power of floral resource maps for this species (see below). In addition, during our study, different plant species offered *Prunus* type pollen during the foraging period of *O. cornuta* (i.e. mainly *P. spinosa, P. avium, P. domestica, P. armeniaca, P. persica, Malus* spec., *Pyrus* spec., *Crataegus spec.*), with different availabilities across the landscapes and with different attractiveness for this species relating to pollen and nectar availability and its nutritional quality. In contrast, for *O. bicornis*, collected pollen types were offered by mainly one (for *Brassicaceae, Papaver rhoeas* type) to a maximum of three plant species (for *Quercus*). Thus, the higher power of the key pollen types in predicting the reproduction of *O. bicornis* compared to the reproduction of *O. cornuta* might be related to the slightly better representation of the used key plant species of *O. bicornis* via the plant taxa that offer these pollen types.

The weight of the *Osmia* cocoons and the proportion of developed females could not be explained by the floral resources present in the surrounding landscapes. We base the specific indices that represent the floral resources available to the *Osmia* on the pollen availability (i.e. quantity) and their use during the foraging periods. For their development, bee larvae need a balance in nutritional composition rich in body-building nutrients (Bukovinszky et al., 2017; Filipiak, 2018, 2019; Lawson et al., 2021). *Osmia* are able to adapt the quality of pollen needed for rearing their larvae to the offspring's sex. *Osmia bicornis* provides its offspring of different sexes with different pollen mixtures that account for sex-specific demand in nutrients, with a high proportion of phosphorus being particularly related to a higher fitness in females (Filipiak, 2019). The pollen use during the foraging periods of *Osmia* reflect the particular nutritional needs and pollen offered by some plant species may indirectly provide sufficient levels of nutrient classes (Woodard, 2017). In addition, the key pollen types the *Osmia* collected in our study is rich in proteins (Roulston et al., 2000). However, the nutritional composition provided by the different pollen types and their ideal balance is only partially reflected by the indices we used to calculate the floral resource availability as the nutritional quality of the pollen diet was not evaluated. Thus, accounting for ecological stoichiometry in the pollen diet (i.e. a balanced larval diet needed for maximal fitness of the adults; e.g. Filipiak 2018) could further enhance the predictability of floral resource maps, that combine different resources.

The high use of pollen types offered by different key woody and herbaceous plant taxa, especially *Prunus* for *O. cornuta* and *Juglans*, *Papaver*, *Quercus*, *Ranunculus* for *Osmia bicornis* and the increasing use of herbaceous pollen plants by *Osmia bicornis* later in the season is in accordance with other studies (Bertrand et al., 2019; Coudrain et al., 2016; Free & Williams, 1970; Márquez et al., 1994; Radmacher & Strohm, 2010; Tasei & Picart, 1973). In addition, both species used a different set of key pollen plants during their foraging seasons. The fact that these species also lead to a higher reproductive success of both species, highlights the importance of preserving non-agricultural woody and herbaceous semi-natural habitats with a diverse availability of floral resources across the season to foster these solitary bee crop pollinators and their pollination in agricultural landscapes (Bertrand et al., 2019; Kämper et al., 2016; Requier et al., 2015; Sutter et al., 2017; e.g. Westphal et al., 2009). Oilseed rape was cultivated in eight of the landscapes studied and we found Brassicaceae pollen (i.e. the pollen type it provides) in the nests of *Osmia bicornis* in each of these landscapes, albeit in quantities of <1%. In addition, the number of produced offspring and the reproduction of *Osmia bicornis* increase with increasing distances to oilseed rape. This supports that oilseed rape is used for its nectar rather than its pollen supply (Coudrain et al., 2016; Eckerter et al., 2020; Holzschuh et al., 2013; Kämper et al., 2016). The same applies for *Aesculus hippocastanum*, that was collected in amounts below <1% in each of the landscape where it was present. Both plants may therefore be key nectar plant for this species. Identifying important nectar resources (i.e. especially those plants that are mainly or solely visited for its nectar) and considering them in floral resource maps might further increase their predictive power.

HABITAT MAPS

In this study, we mapped floral resources at an unprecedented level of detail and spatial and temporal resolution. Yet, also the "classical" habitat maps yielded useful information for explaining the development of the two bee taxa. In fact, distance to forest was the most important factor for explaining the reproduction of both *Osmia* species in our landscapes. It also had been the most important predictor for the development of colonies of the buff-tailed bumblebee (*Bombus terrestris* L.) in the same landscapes and this effect was stronger than the availability of floral resources (Eckerter et al., 2020). It is possible, that foraging bees might have benefited from factors provided in proximity to forests as for example beneficial microclimatic conditions during their foraging flights like decreased wind speed or air temperature (Bentrup et al., 2019; e.g. Chen et al., 1999). Bees might also have benefited from the non-mapped resources present in the forest interiors. For example, *Prunus avium, Acer* spec. and partially *Salix* spec. as well as *Quercus* and *Rubus* are commonly found in the interiors of forests in our region and may have served as additional pollen sources for the *Osmia*. However, data on the pollen use and the foraging behavior of wild bees present in agricultural landscapes inside forests is largely lacking. The decrease in the reproduction of *O. bicornis* with the proportion of arable land is likely to be related to its scarcity of floral resources. Our findings using the habitat maps underline the importance of maintaining a combination of woody as well as herbaceous semi-natural habitats in agricultural landscapes to support wild bee pollinators (Bartual et al., 2019; Eckerter et al., 2020; Holland et al., 2017; Schirmel et al., 2018). Yet, also rural urban areas provide resources for wild bees, such as nesting places like wooden fences, barns, walls or bee hotels, *O. cornuta* and *O. bicornis* are ubiquitous in urban areas (Everaars et al., 2011; Fortel et al., 2016; Hernandez et al., 2009). Thus, foraging *O. cornuta* might have migrated from the nesting plates into the built-up areas. *Osmia* populations inside built-up areas might also harbor different antagonists and partially explain the decreasing parasitism with decreasing distance to built-up areas (Krunic et al., 2005). Accordingly, the decrease in the parasitism rate with increasing distances to forests and increase with proportions of open woody semi-natural habitats could also be related to the higher host abundances associated with these variables. This fact also supports the trophic rank and the specialist consumer hypothesis, with species of higher trophic levels like antagonists being more vulnerable to landscape changes than species of lower trophic levels, like e.g. their hosts (Albrecht et al., 2007; Davies et al., 2000; Tscharntke, Tylianakis, et al., 2012). Although also antagonists benefited from forest proximity and woody semi-natural habitats, these land-use characteristics had an overall positive effect on the *Osmia* populations, either via e.g. increasing their reproduction and/or offering a high abundance of key pollen types.

3.6 CONCLUSIONS

Our findings suggest that generalist solitary crop pollinators can be quite selective in their floral resource use and that the availability of certain key floral resources is crucial for their reproduction in agricultural landscapes. Despite the abundant floral resources provided by commercial orchards and their small area inside the landscapes, woody and herbaceous non-agriculturally managed semi-natural habitats offer high amounts of floral resources for the bee species studied. In addition, the reproduction of both species increased with proximity to forest. These habitats should therefore be conserved and enhanced to maintain and support *O. cornuta*, *O. bicornis* and other wild bee populations in agricultural landscapes. However, more research is needed in relating the floral resources used by the bee species studied to their fitness. Our findings also highlight the importance of combining different mapping approaches to complement each other in predicting and understanding solitary bee population processes in agricultural landscapes.

4

USING TEMPORALLY RESOLVED FLORAL RESOURCE MAPS TO EXPLAIN BUMBLEBEE COLONY PERFORMANCE IN AGRICULTURAL LANDSCAPES

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4.1 ABSTRACT

4

Wild bumblebees are key pollinators of crops and wild plants that rely on the continuous availability of floral resources. A better understanding of the spatio-temporal availability and use of floral food resources may help to promote bumblebees and their pollination services in agricultural landscapes. We placed colonies of *Bombus terrestris* L. in 24 agricultural landscapes with various degrees of floral resource availability and assessed different parameters of colony growth and fitness. We estimated pollen availability during different periods of colony development based on detailed information of the bumblebee pollen diet and the spatial distribution of the visited plant species. Total pollen availability did not significantly explain colony growth or fitness. However, when using habitat maps, the weight gain of colonies, the number of queen cells, and colony survival decreased with increasing distance from the forest. The better explanation of bumblebee performance by forest proximity than by (plant-inferred) pollen availability indicates that other functions of forests than pollen provision were important. The conservation of forests next to agricultural land might help to sustain high populations of these important wild pollinators and enhance their crop pollination services. Combining different mapping approaches might help to further disentangle complex relationships between *B. terrestris* and their environment in agricultural landscapes.

KEYWORDS

agricultural landscapes; *Bombus terrestris*; colony development; landscape composition; wild bees

4.2 INTRODUCTION

Animal pollination is crucial for around one third of worldwide food production, with 85% of leading global crop types relying to varying degrees on pollination (Klein et al., 2007). In addition to domestic honeybees (*Apis mellifera L.*), wild bees greatly enhance and stabilize crop pollination, and they are often the most effective pollinators (Garibaldi et al., 2011, 2013; Greenleaf & Kremen, 2006; Hoehn et al., 2008; Mallinger et al., 2017). However, habitat loss and intensive agricultural practices contribute to pollinator declines in different regions of the world (IPBES, 2016), while the dependency of global agriculture on pollinators is increasing (Aizen et al., 2019). Hence, supporting wild bees in agricultural landscapes is crucial to future economic and environmental stability (Schellhorn et al., 2015; Venturini et al., 2017).

Bumblebees are important wild pollinators that increase the yield of many crops, e.g., fruit trees, pepper, pumpkin, strawberries, and tomatoes (Pfister, Eckerter, et al., 2017; Velthuis & van Doorn, 2006). The buff-tailed bumblebee (*Bombus terrestris* L.) is one of the dominant crop pollinators in Europe (Kleijn et al., 2015). Like all wild bees, wild bumblebees rely on foraging and nesting resources provided by the surrounding landscape (Goulson et al., 2015; Westrich, 1996). Thus, favorable foraging habitats can enhance pollinator populations and crop pollination at the landscape scale (Nicholson et al., 2019; Sutter et al., 2017, 2018; Venturini et al., 2017). As habitat types differ in resource availability, habitat maps using broad land use categories are commonly used to predict wild bee development and the service they provide (Garibaldi et al., 2013). For example, habitat maps explained faster growing and heavier colonies of *B. terrestris* in suburban gardens than elsewhere (Goulson et al., 2002). In different studies, the pollen deposition of *B. terrestris* was higher with a decreasing proportion of cropland in the surrounding landscape (Pfister et al., 2018), and *B. terrestris* colonies had higher reproductive success and survived longer in urban areas than agricultural areas (Samuelson et al., 2018). In intensively managed agricultural landscapes, floral resources are mainly offered by small fragments of semi-natural habitats (Garibaldi et al., 2011; Kremen et al., 2007; Ricketts et al., 2008) or single mass flowering crops. Consequently, in addition to habitat maps, maps of single mass flowering species, e.g., apple, oilseed rape, and strawberry, have been found to explain colony development of *B. terrestris* (Grab et al., 2017; Holzschuh et al., 2013; Westphal et al., 2009). *Bombus terrestris* mainly collects pollen on woody plants (Bertrand et al., 2019; Kämper et al., 2016). No single plant accounts for >15% of the total pollen diet of *B. terrestris* (Bertrand et al., 2019). Furthermore, the flowering of single plant species is temporally restricted, and most pollinators use a sequence of specific plant species during their flight season (Bertrand et al., 2019). Resources may be limited, especially during early stages of colony development (Herrmann et al., 2017; Rotheray et al., 2017; Westphal et al., 2009; Williams et al., 2012). Hence, comprehensive floral resource maps at the landscape scale that give information on temporal resource availability may further improve our ability to predict the growth and reproductive success of bumblebee colonies (Crone & Williams, 2016).

Here, we placed colonies of *B. terrestris* in 24 agricultural landscapes in southwest Germany, quantified their pollen use, mapped the most commonly used plants (71 species derived from 30 pollen types, offering 95% of the total pollen diet), and calculated a weighed pollen availability index for the early and late flight period of the species in each landscape. We tested the effects of detailed plant-inferred pollen availability versus classical land use maps (i.e., distances from and proportions of land use categories in the landscapes) on colony development (i.e., colony growth and longevity).

We tested the following hypotheses: (1) pollen resources for bumblebees are mostly provided by woody semi-natural habitats; (2) a high availability of pollen resources in the landscape enhances colony development; (3) early pollen resources have stronger effects on the weight gain of colonies than late pollen resources; and (4) floral resource maps predict colony development better than habitat maps.

4.3 MATERIALS AND METHODS

STUDY LANDSCAPES AND THE CREATION OF FLORAL RESOURCE MAPS

The study was conducted in the surroundings of Landau in the Upper Rhine Valley, Rhineland-Palatinate, Germany (Supplementary Information, FIGURE S4.1). A total of 24 agricultural landscapes of 500 m radius were selected to represent gradients of the amounts of early and late pollen resources for *B. terrestris* (Eckerter et al., 2021). Landscape centers were at least 800 m away from each other and were placed in grassy field margins. The cover of plants offering selected pollen types and the major land use types were mapped according to field inspections between June and November 2017 (woody plants) and between April and June 2018 (land use and annual herbaceous plants; for further details see SUPPLEMENTARY INFORMATION S4.1). We used Copernicus (Sentinel-2; L2A–L2C) optical satellite imagery (2016; 10 m resolution), processed by the Federal Agency for Cartography and Geodesy (BKG), as orientation in the field during mapping. We ground-truthed each landscape element via field inspection during our mapping process in 2018 and noted every change if necessary. Obtained data were later digitized as polygon (land use classes) and point layers (single resources), and they were analyzed with QGIS 3.6.2 (QGIS Development Team, 2019) using the above-mentioned satellite imagery as a base map. To create land use/land cover (LULC) maps (hereafter: "habitat maps"), the following habitat types were distinguished: arable land, permanent crops, forest edges (i.e., the first ten meter into forests), forest (i.e., forest interiors without its edges), open woody semi-natural habitat (i.e., hedgerows and single standing trees including those of semi-natural orchards), herbaceous semi-natural habitat (i.e., intensively and extensively managed meadows and pastures), and built-up area (i.e., rural settlements). The proportions of habitat types across the landscapes are shown in TABLE S4.1. We also measured the Euclidean distances of colonies to forests because these were important predictors of wild bee development or performance in previous studies (Bailey et al., 2014; Holzschuh et al., 2013; Mitchell et al., 2014; Osborne et al., 2007). To analyze single resources, the cover of and distance to dominant pollen types were used: *Brassica* *napus* L. (hereafter: oilseed rape), because it has been an important predictor of bumblebee densities and colony development in earlier studies (Kleijn et al., 2015; Westphal et al., 2003, 2009), and *Cornus*, *Lonicera*, *Prunus*, *Rubus*, and *Tilia* because each of these plant taxa contributed more than 10% of pollen availability to *B. terrestris* in at least one season during our study (TABLE S4.2). To create floral resource maps, the area covered by plant species offering pollen types that constitute at least 5% of the pollen diet of *B. terrestris* in our study region in at least one season, and all remaining woody plant species were mapped (Bertrand et al., 2019). These maps accounted for the area covered by 71 plant species derived from 30 pollen types. Plants in forest interiors (i.e., deeper than ten meters into a forest) were not mapped because most bees (Hanula et al., 2015), and *B. terrestris* in particular, prefer open habitat for foraging (Dramstad & Fry, 1995; Kreyer et al., 2004; Marja et al., 2018). Floral resource indices were used as described in (Eckerter et al., 2021). Indices considered the relative cover of plants offering pollen types multiplied by their utilization (i.e., percentage of the total collected pollen volume) by *B. terrestris* during a specific period, summed up over all pollen types. An index value of 1 denotes the average pollen availability of all studied landscapes, while larger or smaller values describe the proportional difference of resource availability in a given landscape relative to the average. Pollen availability was calculated over the whole duration of *B. terrestris* colony field placement (from mid-April to mid-June) and separately for the early and late phase of colony development. The early season started with the placement of colonies in the field (mid-April) and ended when they reached their maximum weight (end of May). The late season was from when the colonies had their maximum weight until colony termination (i.e., when no evidence of living bumblebees could be detected at the nest boxes during measurements; mid-June). Floral resource maps accounted for 96.3% of early, 83.2% of late, and 94,9% of the total pollen diet of *B. terrestris* according to the analysis of pollen diets from the 48 colonies when considering 45,900 pollen grains out of 306 samples (TABLE S4.2). See TABLE S4.3 for the composition of pollen diet of returning foragers that was excluded from the index calculations.

PLACEMENT OF *BOMBUS TERRESTRIS* COLONIES

Two commercially bred *B. terrestris* colonies (STB CONTROL, Aarbergen, Germany) were established in the center of each of the 24 landscapes (48 colonies in total) on a grassy field margin in mid-April 2018. Colonies were even-aged, consisted of one queen and approximately 50–60 workers, and were embedded in a nest box. For acclimatization, a tank filled with sugar water was provided for each colony. Nesting box and tank were enclosed by a cardboard box to protect colonies against unfavorable weather conditions. To protect colonies from soil moisture, boxes were placed on wooden plates that were 10 cm above ground level. Colony entrances were facing south-east. The day after placement, colonies were weighted and colony entrances were opened. After one week of acclimatization, sugar tanks were closed. The weight of nest boxes containing colonies was measured every second week until colony termination. After that, colonies were harvested and frozen at −18 °C for later dissection in the laboratory. Weight gain was obtained by subtracting the maximum colony weight by its initial weight. After colony dissection, cells were counted and assigned to two classes: queen cells (diameter ≥11 mm or length ≥19 mm if diameter was not measurable because cells were fragmented) and other cells (i.e., male/worker cells with diameter <11 mm and length <19 mm; Inoue et al., 2010). Male and worker cells could not be consistently differentiated and were therefore grouped together (Goulson et al., 2002; Herrmann et al., 2017; Williams et al., 2012). Days of survival were measured from the day of colony placement until colony termination. Weight gain, the number of cells, and the survival of the two colonies in each landscape were averaged.

POLLEN COLLECTION, PREPARATION AND DETERMINATION

The pollen diet of *B. terrestris* was recorded at up to four sampling dates between 24 April and 16 June 2018. At each nest, pollen loads were collected from up to four workers returning from foraging trips per sampling date. The start of the sampling period coincided with the peak flowering of oilseed rape and *Crataegus* spec., while at the end, *Rubus fruticosus* L. and *Tilia* spec. were flowering, which are dominant flowering resources of *B. terrestris* in the respective seasons (Bertrand et al., 2019). Pollen was stored in water, frozen at −18 °C, and then acetolysed (Jones, 2012). Acetolysed pollen was mounted on permanent slides in glycerin, and 150 pollen grains per sample were counted starting at a random position of the slide and identified to the highest possible taxonomic resolution using a light microscope (400 × magnification), a palynological key (Beug, 2004), a photo atlas (Reille, 1992), and the reference pollen collection of the Institute of Plant Sciences of the University of Bern. Pollen types that contributed more than 3% of the diet of *B. terrestris* colonies in any period (i.e., before colonies reached their maximum weight or from this moment until colony termination) were classified as key pollen types. Deformed pollen grains that could not be assigned to pollen types (2.2% of detected pollen) and pollen fragments were excluded from the analysis. The pollen type Brassicaceae could not be identified to the species level. However, oilseed rape accounted for 98.3% of the cover of Brassicaceae in the landscapes.

STATISTICAL ANALYSIS

Correlations between colony response (i.e., weight gain, queen cells, and survival) and explanatory variables (i.e., variables used to describe floral resource maps, habitat maps, or single resources) were tested with linear regression. To visualize the interaction among variables, a correlation matrix among all variables was drawn (FIGURE S4.3). All variables were standardized before the analysis using the *standardize* function of the *'arm'* package (Gelman, 2008) in order to allow for a comparison between effect sizes between models. To compare the predictive power of the mapping approaches, three different sets of linear candidate models were set up for each colony response variable. The explanatory variables of the candidate models were either the pollen availability indices, the parameters derived from habitat maps, or the single pollen resources. The correlations of variables in models were below $|r| \leq 0.7$ (FIGURE S4.3). Models were compared via the

Akaike second-order Information Criterion (AICc) (Akaike, 1987; Burnham et al., 2011; Hurvich & Tsai, 1989; Symonds & Moussalli, 2011) using the *dredge* function from the *'MuMin'* package (Bartón, 2020). We compared the overall best model(s) using $\Delta_i < 2$ as a cutoff rule (Burnham et al., 2011; Symonds & Moussalli, 2011). In addition to this statistically based model comparison, models with single explanatory variables that contain either one of the focal predictors of this study (resource availability and dominant single pollen resources) or key variables reported in the literature (distance to forests, cover of arable land and built-up area, see introduction) are displayed. To compare the predictive power of the different mapping approaches, the best models of each approach were compared to each other. Data analyses were conducted in *R 4.0* (R Core Team, 2020). Model diagnostic plots were visually checked (residuals vs. fitted values and normal Quantile–Quantile plots). A pollen network graph was created using the package *'bipartite'* (Dormann et al., 2009). The plotting of bar plots and linear models was done using the package *'ggplot2'* (Wickham, 2016), and the correlation matrix was drawn using the *'corrplot'* package (Wei & Simko, 2017).

4.4 RESULTS

POLLEN DIET

We identified 45,900 pollen grains collected from 306 returning foragers of *B. terrestris*. The key pollen types collected in the early season were *Prunus* (16.2%), *Rubus* (15.5%), and *Rosaceae* other than *Prunus* (12.3%); these were followed by *Cornus sanguinea* (8.5%), Brassicaceae (8.4%), *Acer* (7.3%), *Papaver rhoeas* type (5.5%), *Lonicera xylosteum* type (4.8%), *Sorbus* (4.0%), and *Lamium album* type (3.5%; TABLE S4.2). Key pollen types in the late season were *Rubus* (28.6%), *Tilia* (26.8%), *Phacelia tanacetifolia* (10.3%), *Vitis* (3.6%), and *Rosaceae* (3.5%; TABLE S4.2). During both periods, the majority of pollen was collected on woody plants (74.1% in the early season and 67.4% in the late season; FIGURE S4.2).

LANDSCAPE AND POLLEN AVAILABILITY

The studied landscapes were dominated by arable land (69.0% ± 0.047—average ± standard error), followed by the herbaceous semi-natural habitat (10.7% ± 0.024), forest (5.7% ± 0.024), permanent crops (4.0% ± 0.012), woody semi-natural habitat (3.2% ± 0.006), built-up area (2.1% ± 0.010), and forest edges (0.8% ± 0.003).

After giving each pollen type a weight proportional to its use by bumblebees, open woody semi-natural habitats (woody semi-natural habitat excluding forests and forest edges) provided 75.2% of the total pollen availability (expressed with indices) in the 24 studied landscapes (FIGURE 4.1). In open, woody semi-natural habitats, plants offering *Cornus sanguinea*, *Lonicera xylosteum* type, and *Prunus* type pollen were the most important contributors to pollen availability in the early season (39.8%, 15.4%, and 6.8%, respectively). In the late season, *Tilia*, *L. xylosteum* type and *Rubus* were the most important contributors (25.2%, 23.2%, and 17.4%, respectively). Forest edges contributed to 11.3% of total pollen availability. Additionally, in the early season, *C. sanguinea* and *L. xylosteum* type were most important contributors (5.0% and 1.6%, respectively); and in the late season *Rubus*, *Tilia*, and *L. xylosteum* type (9.7%, 4.2%, and 2.4%, respectively). The herbaceous semi-natural habitat contributed 3.5% to early pollen availability and 8.5% to late pollen availability. Here, the main contributors in the early season were *Papaver rhoeas* type, *Lamium album* type, and *Trifolium pratense* type (1.4%, 1.3%, and 0.6%, respectively), and the main contributors in the late season were *T. pratense* type and *Phacelia tanacetifolia* (5.3% and 2.8%, respectively). In permanent crops (average cover: 4.0%), the most important contributors were fruit trees in the early season (5.2%) and *Vitis* in the late season (1.8%). Though arable land covered the major part of the landscapes, its contribution to pollen availability over the seasons did not exceed 3.2%. The most important crop pollen resources were oilseed rape in the early season (2.5%) and *Asparagus officinalis* type in the late season (1.1%). The contributions of built-up area to pollen availability were low (<2.1% in any season). FIGURE 4.1 shows the average area of habitat categories in the studied landscapes, as well as their average contributions to pollen availability (indices) during different periods. For a list of the plant species detected in the landscapes offering collected pollen types and their contributions to pollen availability during different time periods, see TABLE S4.2.

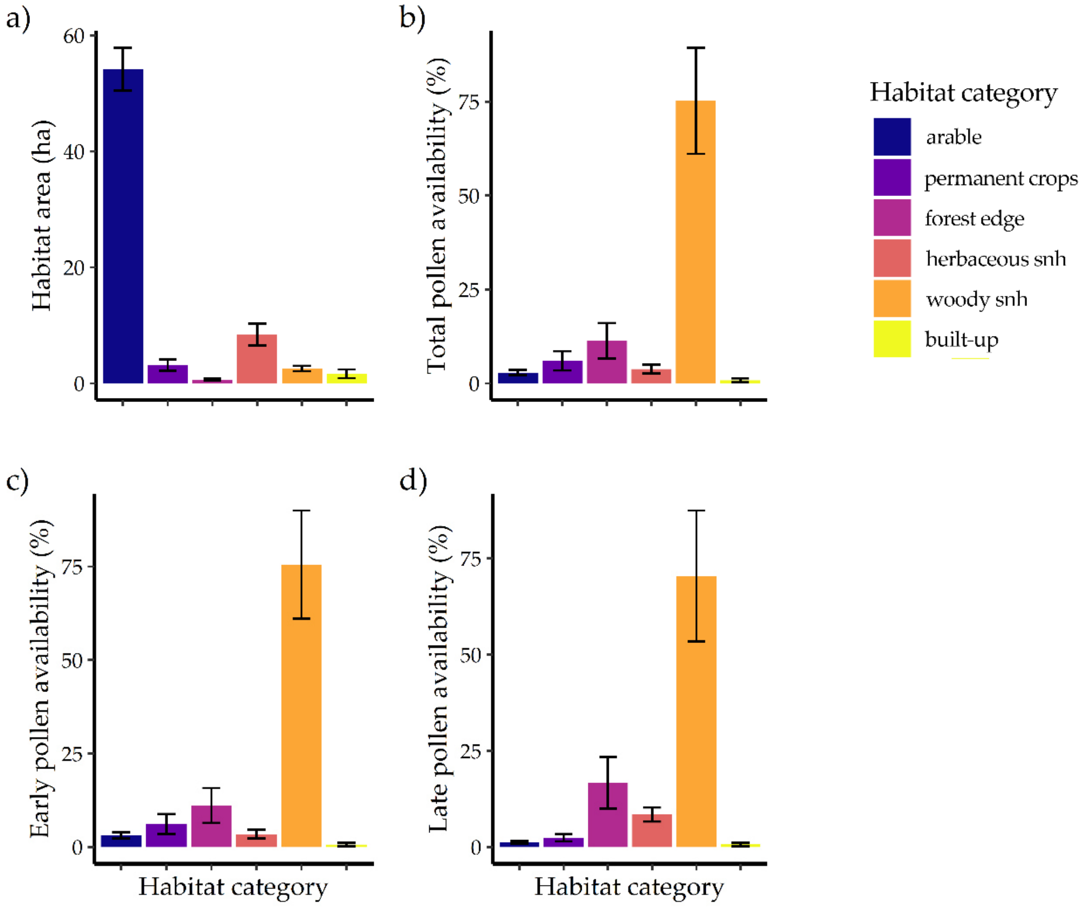

FIGURE 4.1 Average (±1 standard error) area of habitat categories (arable, permanent crops, forest edges, herbaceous semi-natural habitats, and woody semi-natural habitats but excluding forests and built-up area)

in the studied landscapes (**a**), their average contribution to pollen availability per landscape (**b**), in the early season (**c**), and in the late season (**d**). Pollen availability is based on the relative area covered by plant species offering a pollen type in the respective habitat type across all landscapes multiplied by the relative collected pollen volume of each type over the whole season.

COLONY DEVELOPMENT AND SURVIVAL

On average, each colony contained 675 ± 218 male/worker cells (minimum: 177; maximum: 1206), contained 88 ± 64 queen cells (min: 2; max: 245), gained 648 ± 202 g of weight (min: 146; max: 1076), and survived for 68 ± 9 days (min: 50; max: 84). The maximum weight gain increased with the number of total cells (i.e., male/worker and queen cells; $t_{1,22} = 3.15$, $R^2_{mult} = 0.311$, and $p < 0.01$) and with the number of queen cells ($t_{1,22} = 4.54$, $R^2_{mult} = 0.484$, and $p < 0.001$). Colony survival and the number of queen cells were positively correlated ($t_{1,22} = 4.07$, $R^2_{mult} = 0.430$, and $p < 0.001$). Correlations between other colony variables were non-significant (i.e., $p \geq 0.05$; FIGURE S4.3).

POLLEN AVAILABILITY AND COLONIES

The total pollen availability in the landscapes during any time did not significantly affect colony weight gain, survival, or the number of queen cells ($p > 0.35$; TABLE 4.1 and FIGURE S4.3). Using habitat maps, we found that the weight gain of colonies, queen cells, and survival decreased with distance to forests (FIGURE 4.2). In addition to the distance from forests, the best models contained either increases of survival with distance to built-up area or decreased survival with an increasing proportion of it in the landscapes (TABLE 4.1). Using important predictors from previous studies, we found that the number of queen cells tended to decrease with the proportion of arable land (TABLE 4.1). However, this model was distinctly worse than models containing distance to forests ($\Delta_i \geq 2$; TABLE 4.1).

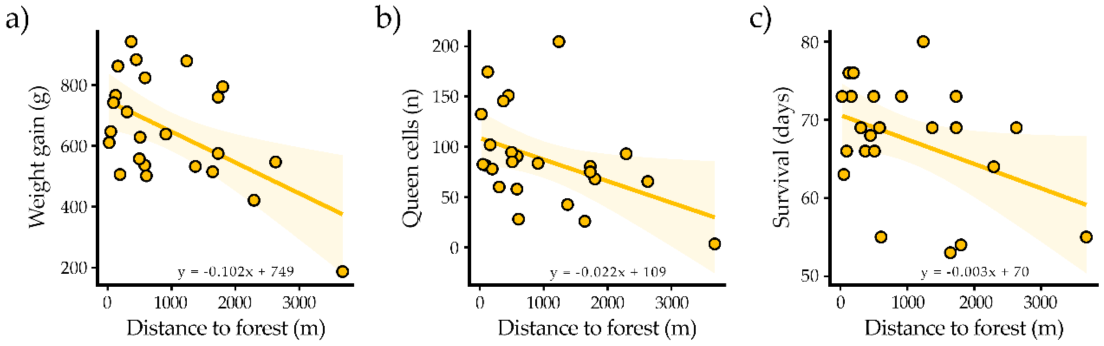

FIGURE 4.2 Relations of (**a**) weight gain ($t_{1,22} = -2.28$, $R^2_{mult} = 0.191$, and $p = 0.033$), (**b**) number of queen cells ($t_{1,22} = -3.09$, $R^2_{mult} = 0.302$, and $p < 0.01$), and (**c**) survival and distance to forests ($t_{1,22} = -2.67$, $R^2_{adj} = 0.286$, and $p = 0.015$). Predicted linear relations (regression lines) and 95% confidence intervals (shaded area) are drawn for significant relations.

Regarding single pollen resources, weight gain decreased with increasing distance to oilseed rape, and no significant relationship was found with any other variable (TABLE 4.1). The number of queen cells showed no significant relationship with any of the single pollen resources. Colony survival decreased with increasing distance to *Cornus sanguinea* in all of the best-ranking models (TABLE 4.1). Alternatively, a negative correlation also existed between colony survival and the distance to *Rubus* (Δ_i = 2.11). For correlations among all observed variables, see FIGURE S4.3.

TABLE 4.1 Comparison of models explaining bumblebee colony response variables with pollen availability indices, classical habitat maps, and single resources (see main text for description of mapping approaches). The abbreviation "SNH" is used for "Semi-natural habitat". The Akaike second-order Information Criterion (AICc) and the dredge function from the *'MuMin'* package (Bartón, 2020) were used to select the best models ($\Delta_i < 2$). Delta weight (Δ_i) is the difference between the AICc of the model and the best model. Best models containing pollen availability and important predictors using habitat maps or single pollen resources are displayed regardless of AICc values (see main text). Models listed below a dashed line are not included in the best model set ($\Delta_i < 2$). Variables were standardized (Gelman, 2008). Significant effects (i.e., $p \leq 0.05$) are shown in bold.

Explanation	Response	Model description	df	R^2_{mult}	AICc	Δ_i	Predictor	Estimate	SE	*t*-value	*p* value
Pollen availability indices	Weight gain		23		319.70	0.00	(Intercept)	648.90	35.85	18.10	< 0.001
		Early pollen availability	22	0.001	322.30	2.60	Early	12.55	74.84	0.17	0.868
		Total pollen availability	22	0.000	322.40	2.62	Total	7.29	74.87	0.10	0.923
		Late pollen availability	22	0.000	322.40	2.63	Late	0.72	74.89	0.01	0.992
	Queen cells		23		256.20	0.00	(Intercept)	87.73	9.54	9.20	< 0.001
		Late pollen availability	22	0.007	258.70	2.46	Late	7.85	19.86	0.40	0.697
		Total pollen availability	22	0.006	258.70	2.47	Total	-7.49	19.87	-0.38	0.710
		Early pollen availability	22	0.005	258.70	2.51	Early	-6.64	19.88	-0.33	0.741
	Colony survival		23		166.80	0.00	(Intercept)	67.54	1.48	45.62	< 0.001
		Early pollen availability	22	0.040	168.40	1.66	Early	2.89	3.03	0.95	0.350
		Total pollen availability	22	0.033	168.60	1.82	Total	2.63	3.04	0.87	0.396
		Late pollen availability	22	0.027	168.70	1.97	Late	2.39	3.05	0.78	0.442
Habitat distance and cover	Weight gain	Distance forest	22	0.302	313.70	0.00	**Distance forest**	**-193.12**	**62.55**	**-3.09**	**0.005**
		Distance forest and built-up	21	0.342	315.20	1.51	**Distance forest**	**-208.73**	**63.74**	**-3.28**	**0.004**
							Built-up	-71.38	63.74	-1.12	0.275
		Distance forest and woody SNH	21	0.339	315.30	1.59	**Distance forest**	**-210.35**	**64.29**	**-3.27**	**0.004**
							Woody SNH	-69.82	64.29	-1.09	0.290
		Distance forest and distance built-up	21	0.333	315.60	1.83	**Distance forest**	**-202.71**	**63.37**	**-3.20**	**0.004**
							Distance built-up	62.11	63.37	0.98	0.338
		Arable	22	0.035	321.50	7.80	Arable	-65.42	73.58	-0.89	0.384
		Built-up	22	0.005	322.24	8.54	Built-up	-25.73	74.68	-0.35	0.734
	Queen cells	Distance forest	22	0.191	253.80	0.00	**Distance forest**	**-40.82**	**17.93**	**-2.28**	**0.033**
		Distance forest, herbaceous SNH and built-up	20	0.344	254.90	1.10	Distance forest	-36.07	18.22	-1.98	0.062
							Herbaceous SNH	34.03	19.62	1.73	0.098
							Built-up	-34.66	18.74	-1.85	0.079
		Distance forest and built-up	21	0.245	255.00	1.23	**Distance forest**	**-45.71**	**18.16**	**-2.52**	**0.020**
							Built-up	-22.37	18.16	-1.23	0.232
		Arable	22	0.142	255.20	1.41	Arable	-35.20	18.46	-1.91	0.070
		Forest edge	22	0.135	255.40	1.60	Forest edge	34.31	18.54	1.85	0.078
		Distance forest and herbaceous SNH	21	0.232	255.40	1.66	Distance forest	-33.46	19.19	-1.74	0.096
							Herbaceous SNH	20.31	19.19	1.06	0.302

TABLE 4.1 *Cont.*

Explanation	Response	Model description	df	R^2_{mult}	AICc	Δ_i	Predictor	Estimate	SE	*t*-value	*p* value
		Permanent crops and distance forest	21	0.227	255.50	1.79	Permanent crops	17.97	18.02	1.00	0.330
							Distance forest	**-42.59**	**18.02**	**-2.36**	**0.028**
		Arable and distance forest	21	0.225	255.60	1.87	Arable	-19.86	20.67	-0.96	0.348
							Distance forest	-30.98	20.67	-1.50	0.149
		Built-up	22	0.018	258.41	4.61	Built-up	-12.38	19.75	-0.63	0.537
	Colony survival	Distance forest and distance built-up	21	0.348	162.00	0.00	**Distance forest**	**-6.90**	**2.59**	**-2.67**	**0.015**
							Distance built-up	**6.23**	**2.59**	**2.41**	**0.025**
		Distance forest and built-up	21	0.337	162.40	0.40	**Distance forest**	**-7.27**	**2.64**	**-2.75**	**0.012**
							Built-up	**-6.12**	**2.64**	**-2.32**	**0.031**
		Distance forest, distance built-up and permanent crops	20	0.401	163.20	1.20	**Distance forest**	**-7.23**	**2.55**	**-2.83**	**0.010**
							Distance built-up	**6.25**	**2.54**	**2.46**	**0.023**
							Permanent crops	3.35	2.52	1.33	0.199
		Distance forest, distance built-up and built-up	20	0.396	163.40	1.38	**Distance forest**	**-7.43**	**2.59**	**-2.87**	**0.009**
							Distance built-up	4.22	3.01	1.40	0.177
							Built-up	-3.85	3.05	-1.26	0.221
		Built-up	22	0.026	168.75	6.75	Built-up	2.36	3.05	0.77	0.448
		Arable	22	0.016	169.02	7.02	Arable	-1.81	3.07	-0.59	0.561
Single resource distance and cover	Weight gain	Distance Brassicaceae	22	0.209	316.70	0.00	**Distance Brassicaceae**	**-160.60**	**66.60**	**-2.41**	**0.025**
		Distance Brassicaceae and distance *Lonicera*	21	0.258	318.10	1.37	**Distance Brassicaceae**	**-193.91**	**71.82**	**-2.70**	**0.013**
							Distance *Lonicera*	-84.62	71.82	-1.18	0.252
		Distance Brassicaceae and cover *Prunus*	21	0.243	318.60	1.86	**Distance Brassicaceae**	**-181.46**	**70.08**	**-2.59**	**0.017**
							Prunus	-67.92	70.08	-0.97	0.344
		Distance Brassicaceae and cover *Lonicera*	21	0.243	318.60	1.86	**Distance Brassicaceae**	**-184.22**	**71.04**	**-2.59**	**0.017**
							Lonicera	68.63	71.04	0.97	0.345
		Cover Brassicaceae	22	0.136	318.86	2.16	Brassicaceae	129.50	69.61	1.86	0.076
		Distance *Prunus*	22	0.016	321.98	5.28	Distance *Prunus*	44.26	74.29	0.60	0.557
		Cover *Rubus*	22	0.007	322.21	5.51	*Rubus*	28.43	74.64	0.38	0.707
		Distance *Cornus*	22	0.003	322.29	5.59	Distance *Cornus*	20.06	74.76	0.27	0.791
		Cover *Tilia*	22	0.002	322.33	5.63	*Tilia*	-14.02	74.83	-0.19	0.853
		Cover *Prunus*	22	0.001	322.34	5.64	*Prunus*	-12.17	74.84	-0.16	0.872
		Cover *Cornus*	22	0.001	322.35	5.65	*Cornus*	10.06	74.85	0.13	0.894
		Distance *Lonicera*	22	0.001	322.35	5.65	Distance *Lonicera*	-8.28	74.87	-0.11	0.913
		Distance *Rubus*	22	0.001	322.36	5.66	Distance *Rubus*	-8.07	74.87	-0.11	0.915

TABLE 4.1 *Cont.*

Explanation	Response	Model description	df	R^2_{mult}	AICc	Δ_i	Predictor	Estimate	SE	*t*-value	*p* value
		Distance *Tilia*	22	0.000	322.36	5.66	Distance *Tilia*	-7.50	74.87	-0.10	0.921
		Cover *Lonicera*	22	0.000	322.36	5.66	*Lonicera*	5.23	74.88	0.07	0.945
	Queen cells	(empty)	23		256.20	0.00	(Intercept)	87.73	9.54	9.20	< 0.001
		Distance *Prunus*	22	0.066	257.20	1.00	Distance *Prunus*	23.95	19.27	1.24	0.227
		Distance *Rubus*	22	0.026	258.20	1.99	Distance *Rubus*	-15.19	19.67	-0.77	0.448
		Distance *Tilia*	22	0.015	258.50	2.28	Distance *Tilia*	11.28	19.79	0.57	0.574
		Cover *Prunus*	22	0.013	258.50	2.32	Cover *Prunus*	-10.58	19.80	-0.53	0.598
		Cover *Rubus*	22	0.011	258.60	2.37	Cover *Rubus*	9.72	19.82	0.49	0.629
		Distance *Cornus*	22	0.007	258.70	2.46	Distance *Cornus*	-7.87	19.86	-0.40	0.696
		Cover *Tilia*	22	0.005	258.70	2.51	Cover *Tilia*	6.56	19.88	0.33	0.744
		Distance *Lonicera*	22	0.004	258.70	2.52	Distance *Lonicera*	-6.27	19.89	-0.32	0.756
		Cover *Cornus*	22	0.003	258.70	2.55	Cover *Cornus*	-5.44	19.90	-0.27	0.787
		Distance Brassicaceae	22	0.001	258.80	2.59	Distance Brassicaceae	3.60	19.92	0.18	0.858
		Cover *Lonicera*	22	0.000	258.80	2.63	Cover *Lonicera*	0.55	19.93	0.03	0.978
		Cover Brassicaceae	22	0.000	258.80	2.63	Cover Brassicaceae	0.22	19.93	0.01	0.991
	Colony survival	Distance *Cornus*	22	0.253	162.40	0.00	**Distance *Cornus***	**-7.29**	**2.67**	**-2.73**	**0.012**
		Distance *Cornus* and cover *Tilia*	21	0.301	163.70	1.29	**Distance *Cornus***	**-7.40**	**2.65**	**-2.80**	**0.011**
							Cover *Tilia*	3.21	2.65	1.21	0.239
		Distance *Cornus* and distance *Lonicera*	21	0.294	164.00	1.55	**Distance *Cornus***	**-9.15**	**3.15**	**-2.91**	**0.008**
							Distance *Lonicera*	3.48	3.15	1.10	0.282
		Distance Brassicaceae and distance *Cornus*	21	0.289	164.10	1.71	Distance Brassicaceae	-2.80	2.70	-1.04	0.311
							Distance *Cornus*	**-7.69**	**2.70**	**-2.85**	**0.010**
		Distance *Cornus*, distance *Lonicera* and cover *Tilia*	20	0.376	164.20	1.81	**Distance *Cornus***	**-10.04**	**3.08**	**-3.26**	**0.004**
							Distance *Lonicera*	4.87	3.15	1.55	0.138
							Cover *Tilia*	4.33	2.67	1.62	0.120
		Distance *Cornus* and distance *Prunus*	21	0.281	164.40	1.97	**Distance *Cornus***	**-8.10**	**2.83**	**-2.87**	**0.009**
							Distance *Prunus*	2.58	2.83	0.91	0.373
		Distance *Rubus*	22	0.184	164.51	2.11	**Distance *Rubus***	**-6.23**	**2.79**	**-2.23**	**0.036**
		Distance *Tilia*	22	0.102	166.82	4.42	Distance *Tilia*	4.63	2.93	1.58	0.129
		Cover *Cornus*	22	0.047	168.24	5.84	Cover *Cornus*	3.15	3.02	1.04	0.308
		Cover *Tilia*	22	0.041	168.38	5.98	Cover *Tilia*	2.95	3.03	0.98	0.340
		Cover *Prunus*	22	0.030	168.67	6.27	Cover *Prunus*	2.50	3.05	0.82	0.421
		Distance Brassicaceae	22	0.014	169.06	6.66	Distance Brassicaceae	-1.70	3.07	-0.55	0.585
		Distance *Lonicera*	22	0.010	169.17	6.77	Distance *Lonicera*	-1.42	3.08	-0.46	0.650
		Cover Brassicaceae	22	0.010	169.17	6.77	Cover Brassicaceae	1.42	3.08	0.46	0.650
		Cover *Rubus*	22	0.002	169.34	6.94	Cover *Rubus*	0.67	3.09	0.22	0.830
		Cover *Lonicera*	22	0.000	169.39	6.99	Cover *Lonicera*	0.31	3.09	0.10	0.922
		Distance *Prunus*	22	0.000	169.40	7.00	Distance *Prunus*	0.02	3.09	0.01	0.994

4.5 DISCUSSION

As expected, *B. terrestris* mostly used pollen from woody semi-natural habitats. Surprisingly, however, species-specific floral resource maps at the landscape level did not explain the colony development of *B. terrestris*, although they accounted for the vast part of their pollen diet. Instead, all three parameters of colony performance declined with the distance to forests. This suggests that forest edges had other important functions for bumblebees than pollen provision, such as protection from adverse weather or nectar provision. Alternatively, our results could indicate that the proximity to floral resources is more important than their amount in the landscape, which was expressed by the pollen availability index. In line with a high importance of proximity rather than amount, colony survival decreased with increasing distance to major pollen sources like *Cornus sanguinea* and *Rubus*. In turn, the cover of *Rubus* and *Tilia* declined with distance from the forest (see SUPPLEMENTARY INFORMATION, FIGURE S4.3). Our findings therefore suggest that, in addition to pollination (Mitchell et al., 2014), pollinator species richness and flower visitation rate of pollinators (Ricketts et al., 2008), bumble bee colony growth and fitness might be positively affected by proximity to forests. Positive effects of forests on *B. terrestris* may be surprising, because the species is considered an inhabitant of open landscapes (Dramstad & Fry, 1995; Kreyer et al., 2004; Marja et al., 2018). Following the literature on *B. terrestris* habitat use, we only mapped pollen resources in open habitats and in the first 10 m of forests ("forest edge"). We still cannot fully exclude, that bumblebees were exploiting floral resources, e.g., *Acer* spec., *Castanea sativa* Mill., *Tilia* spec., and *Rubus fruticosus*, within forests and that our floral resource index is thus incomplete. Flower use by pollinators in the forest canopy is difficult to quantify, and we are unaware of studies that have comprehensively described pollinator communities of trees growing in European forest interiors. Furthermore, other pollen resource plants commonly used by *B. terrestris* such as *Asparagus officinalis* L., *Brassica napus*, *Cornus sanguinea* L., *Papaver rhoeas* L., *Phacelia tanacetifolia* Benth., and *Trifolium pratense* L. are absent or rare in forest interiors. Of the most important pollen resource plants collected by bumblebees in our study, only *Lonicera xylosteum* L. and *Rubus fruticosus* can be commonly found in forest interiors, but they are equally found along forest edges, in hedgerows, and in gardens. Typically, forests are semi-natural habitats that often have positive effects on pollinator richness, visitation rate, or pollination service (Ammann et al., 2020; Garibaldi et al., 2013; Kremen et al., 2004; Ricketts et al., 2008). Apart from food availability, possible benefits of forests for pollinators were summarized in (Bentrup et al., 2019): already established bumblebee colonies may benefit from the reduced daytime temperature in forest interiors in comparison to open habitats during summers (e.g., Chen et al., 1999), and *B. terrestris* might have benefited from microclimatic conditions along and inside forests during its foraging flights. Other benefits of forests include the reduction of air movement, which leads to reduced energetic costs of foraging flights compared to open habitats (e.g., Bentrup et al., 2019; Chen et al., 1999). In addition, in the same study year, *B. terrestris* was found collecting honeydew from a colony of the giant willow aphid in England, probably due to an increase of nectar sugar concentration while floral nectar resources were simultaneously restricted, followed by exceptional hot and dry weather (Cameron et al., 2019). Our study year was extremely hot, with the highest average temperature ever recorded in Germany along with drought due to low summer rainfall in combination with a high sunshine duration (Zscheischler & Fischer, 2020). These extreme weather conditions could have caused a shift in limitations from pollen towards nectar resources and potentially enhanced the collection of honeydew in forest interiors. Weather conditions that exceed the thermal tolerance limits of species are likely to increase with climate change (Soroye et al., 2020; Sunday et al., 2014).

Bombus terrestris tend to forage on close-by patches with high resource densities (Kallioniemi et al., 2017; Kämper et al., 2016; Kreyer et al., 2004), and their average flight distances lie below or close to 500 m if rewarding resources are available (Darvill et al., 2004; Wolf & Moritz, 2008). However, they were also found foraging up to several kilometers from their nests (Kreyer et al., 2004; Osborne et al., 2008). Hence, although bumblebees prefer patches of abundant floral resources close to their colonies, the unexpected low effect of local floral resource availability on colony development might partly be explained by the potentially long foraging distances of *B. terrestris*. On the other hand, during early phases of colony development, the number of workers is still low and every lack of resources is detrimental to colony development (Goulson, 2009; Rotheray et al., 2017). In addition, long distance flights are more energy-consuming than short distance flights, making close resources more valuable than resources further away from the nest (Goulson, 2009). Further, a mean foraging range of 275.3 ± 18.5 m with a range of 70–631 m was observed for *B. terrestris*, indicating that the major part of their foraging may occur at that scale (Osborne et al., 1999). Thus, we believe that our landscape radius of 500 m is still appropriate.

The negative effect of built-up area on colony termination contrasts with findings of increased weight gain, higher numbers of males and queens, higher queen survival, and more food stores in colonies of *B. terrestris* in suburban areas and sites with varying degrees of urbanization (Goulson et al., 2002; Kremen et al., 2007). Bumblebees can profit from large proportions of beneficial habitats at the outskirts of urban areas related to urban sprawl (Wenzel et al., 2020). In our landscapes, built-up areas had a minor role in providing pollen resources compared to some previous studies (Kaluza et al., 2016), probably because landscapes were selected to be dominated by agricultural land use.

The increasing amount of arable land in the landscape provides an alternative explanation for the decreased colony performance with increasing distance to forests. The negative effects of arable land on pollinators have commonly been observed (e.g. Pfister et al., 2018) and can be explained by, e.g., the negative effects of pesticides or the scarcity of floral resources in intensive agriculture. Pollen availability in our study was lowest in arable land. In addition, longer foraging trips and foraging on scarce, widely distributed, and distant pollen resources (thus less efficient foraging flights) might have had a negative influence on colony development. Large fields in arable land largely lack the beneficial microclimate offered by rural settlements or woody semi-natural habitats (Chen et al., 1999; Wenzel et al., 2020). The decreasing number of queen cells with arable land was in accordance with the decrease of seed set in *Vicia faba* L. with arable land observed in (Eckerter et al., 2021). When we excluded forest distance from our models, weight gain increased with the proximity to oilseed rape fields in the landscape. This resembled the results of (Westphal et al., 2003, 2009), the authors of which found increasing abundance and weight gain in colonies of *B. terrestris* with larger amounts of oilseed rape in the landscape. The less strong effect on weight gain on *B. terrestris* observed in our study may be explained by the lower amounts of oilseed rape in our study (the mean proportion of oilseed rape was 1.8%, compared to 7.0% in Westphal et al., 2009). In addition, weight gain during the early season does not account for differences in colony growth during the different phases of early colony development. In our study, pollen from *Cornus sanguinea* and from oilseed rape were collected in similar amounts, despite oilseed rape, as a mass flowering crop, theoretically being highly attractive for *B. terrestris*. In addition, Brassicaceae pollen has a lower mean pollen grain volume than *Cornus sanguinea* pollen. Thus, despite its benefits for colony development, oilseed rape has a rather low contribution to early pollen availability indices. The high effect of oilseed rape on colony growth despite low pollen use indicates that *B. terrestris* might visit oilseed rape mostly for nectar rather than for its pollen (Kämper et al., 2016). Thus, the true effect of oilseed rape and of plants visited for nectar rather than for pollen might also be underestimated when using the pollen diet as base for floral resource indices.

The high importance of pollen from woody plants in the diet of *B. terrestris*, especially in the early season (mid-March to end of May) is in line with other studies (Bertrand et al., 2019; Kämper et al., 2016). A positive effect of woody floral resources on the development on wild pollinators might be stronger in the beginning of the early season, with the full flowering of *Salix*, *Acer*, and *Prunus* (especially *Prunus spinosa*, *Prunus domestica* and *Prunus avium*), which are important floral resource plants of *B. terrestris* in the early season (Bertrand et al., 2019).

4.6 CONCLUSIONS

Classical habitat maps predicted the colony development of *B. terrestris* better than detailed landscape-scale floral resource maps based on pollen use. This indicates that high amounts of attractive pollen food resources in the landscape alone are not sufficient to ensure a high fitness of bumblebee colonies. Still, the floral resource maps and diet analyses provided information that was not accessible only through classical habitat maps, e.g., that hedgerows play an overriding role in pollen availability to bumblebees in our study region despite their very small cover. More knowledge of floral resource use by *B. terrestris* inside forest areas is needed to better understand its effects on colony development. Microclimatic conditions in or along forests may help bumblebees to better survive hot and dry weather periods and counteract possible stressors like pesticide exposure in arable land. Overall, our study demonstrates how predictors created by different mapping approaches are needed to complement each other and help to explain their complex relationships between *B. terrestris* colonies and their development in agricultural landscapes. Using a combination of predictors created by different mapping approaches might help to clearly identify dominant drivers of wild pollinator development and their service in crop pollination in agricultural landscapes.

DATA AVAILABILITY

The data that support the findings of this study is available in *figshare.*
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5

EFFECTS OF TEMPORAL FLORAL RESOURCE AVALABILITY AND NON-CROP HABITATS ON BROAD BEAN POLLINATION

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5.1 ABSTRACT

CONTEXT

Flowering plants can enhance wild insect populations and their pollination services to crops in agricultural landscapes, especially when they flower before the focal crop. However, characterizing the temporal availability of specific floral resources is a challenge.

OBJECTIVES

Developing an index for the availability of floral resources at the landscape scale according to the specific use by a pollinator. Investigating whether detailed- and temporally-resolved floral resource maps predict pollination success of broad bean better than habitat maps.

METHODS

We mapped plant species used as pollen source by *Bombus terrestris* in 24 agricultural landscapes and developed an index of floral resource availability for different times of the flowering season. To measure pollination success, patches of broad bean (*Vicia faba*), a plant typically pollinated by bumblebees, were exposed in the center of selected landscapes.

RESULTS

Higher floral resource availability before bean flowering led to enhanced seed set. Floral resource availability synchronous to broad bean flowering had no effect. Seed set was somewhat better explained by habitat maps than by floral resource availability, increasing with urban area and declining with the cover of arable land.

CONCLUSIONS

The timing of alternative floral resource availability is important for crop pollination. The higher explanation of pollination success by habitat maps than by floral resource availability indicates that additional factors such as habitat disturbance and nesting sites play a role in pollination. Enhancing non-crop woody plants in agricultural landscapes as pollen sources may ensure higher levels of crop pollination by wild pollinators such as bumblebees.

KEYWORDS

Bombus terrestris; ecosystem services; landscape composition; crop pollination; *Vicia faba*; wild bees

5.2 INTRODUCTION

Pollination by insects is crucial to reproduction for many plants. Animal pollination benefits 88% of wild flowering plants (Ollerton et al., 2011) and 35% of global crop production (Klein et al., 2007). The worldwide economic value of crop pollination in 2015 was estimated as 153 billion € (Gallai et al., 2009). During the last few decades, the dependency of global agriculture on pollinators has increased (Aizen et al., 2019). Wild insects greatly contribute to pollination in addition to managed bees (Garibaldi et al., 2013; Mallinger & Gratton, 2015). Globally, roughly half of the economic value of crop pollination has been attributed to wild pollinators (Kleijn et al., 2015).

Agricultural intensification has led to declines in pollinator populations (IPBES, 2016). Aside from pesticides and diseases, the scarcity of floral and nesting resources in agricultural landscapes are major causes of the decline in bee populations (IPBES, 2016). Thus, the addition of flowering crop or non-crop plants to agricultural landscapes can enhance wild pollinators and their pollination of agricultural crops (Blaauw & Isaacs, 2014; Ganser et al., 2018; Nicholson et al., 2019; Sutter et al., 2017, 2018; Venturini et al., 2017). The timing of the flowering of these alternative floral resources relative to the flowering period of crops may also be an important factor in their effect on crop pollination (Grab et al., 2017; Kremen et al., 2019). Availability of early flowering plants is expected to enhance pollinator populations and thus to benefit pollination of later flowering crops. For example, mass flowering oilseed rape (*Brassica napus*) facilitated later colony development of *Bombus terrestris* (Westphal et al., 2003, 2009) as well as later abundance of *Osmia bicornis* (Holzschuh et al., 2013). Mass flowering oilseed rape also enhanced bumblebee densities in later flowering sunflower crops (Riedinger et al., 2014) and pollination of wild shrubs in adjacent hedgerows (Kovács-Hostyánszki et al., 2013). Furthermore, mass-flowering apple trees successively led to higher pollination and yield of strawberries, most likely due to the increased abundance and diversity of bees present in the landscapes (Grab et al., 2017). Similarly, mass-flowering oilseed rape also led to higher yield in the later-flowering strawberry crop, given low proportions of semi-natural grassland in the surrounding landscape (Herbertsson et al., 2017). In contrast, plant species that produce high amounts of pollen and/or nectar synchronously with the focal crop may reduce crop pollination by competition (Bartomeus & Winfree, 2011; Lander et al., 2011). For example, synchronous mass flowering oilseed rape reduced pollination of *Primula veris* in nearby calcareous grasslands due to shared bumblebee pollinators (Holzschuh et al., 2011) as well as reducing pollination of nearby wild shrubs hedgerows (Kovács-Hostyánszki et al., 2013). Likewise, synchronous mass-flowering apple trees reduced pollinator activity and yield in strawberries (Grab et al., 2017). Visitation rate of pollinators for wild flowers and oilseed rape decreased when flower strips flowered synchronously in late June-late August (Häussler et al., 2017).

To account for the effects of alternative floral resources, it is necessary to characterize the availability of resources at different times of the season. However, this requires the mapping of the available floral resources across habitat types at the landscape level, which is a major challenge, and in the context of crop pollination such data has rarely been recorded. So far, studies of pollinators in agricultural landscapes distinguish only a small number of habitat types with different suitability for pollinators (Fahrig, 2013; Forman, 1995). Other studies included foraging distances to explain relative abundance of pollinators in nesting habitats (Lonsdorf et al., 2009) or combined foraging distances and resource quality to explain distribution of foraging bees (Olsson et al., 2015). Further, habitat classes and floral resources were used to explain colony growth and queen production of *Bombus vosnesenskii* (Crone & Williams, 2016). Only recently, the temporal dynamics of focal and alternative floral resources were taken into account to explain crop visitation rates of wild pollinators (Häussler et al., 2017) or to explain the effects of a preceding versus a synchronous single mass flowering resource on crop pollination success (Grab et al., 2017).

In the present study, we combine a new method to quantify floral resource availability with a crop pollination experiment using broad bean (*Vicia faba* L.). The work was conducted in 24 landscapes selected along a gradient in the availability of preceding and synchronous alternative floral resources. We quantified floral resource availability at the species level across all major habitat types in the landscapes in combination with specific floral resource use information of crop pollinators. The broad bean is an insect-pollinated crop mostly pollinated by bumblebees (Garratt et al., 2014; Kendall & Smith, 1975; Stoddard & Bond, 1987). We inferred detailed information on floral resources from pollen types used by *Bombus terrestris*, one of the dominant bumblebee species, in different periods of the year and used an index to describe the availability of preceding and synchronous floral resources (Eckerter et al., 2020). In addition, we explored whether such temporally-resolved floral resource maps predict pollination better than habitat maps built on landscape characteristics such as the proportion of crops, forest, other semi-natural habitats or urban area.

We tested the following hypotheses: (1) High availability of floral resources preceding crop flowering enhances pollination success; (2) High availability of alternative floral resources synchronous to crop flowering reduces pollination success; (3) Detailed floral resource maps predict crop pollination better than habitat maps.

5.3 MATERIALS AND METHODS

STUDY DESIGN EXPERIMENTAL SET UP

The study was conducted around the city of Landau in the Upper Rhine Valley, Rhineland-Palatinate, Germany. Broad bean (*Vicia faba* L. Var. Sutton Dwarf; KINGS SEEDS, Essex, UK) phytometers were exposed in the centre of 24 study landscapes of 500 m radius (SUPPLEMENTARY INFORMATION, FIGURE S5.1). Landscapes were selected along gradients of dominant preceding (i.e. *Prunus* type, *Acer*, *Aesculus*, *Fragaria* and *Brassicaceae*) and synchronous (i.e. *Tilia*, *Rubus* and *Asparagus*) pollen resources used by the bumblebee *Bombus terrestris* L. during the foraging season in the same region (Bertrand et al., 2019).

While the broad bean is self-fertile, pollination from bees improves seed set (Aouar-sadli et al., 2008; Bartomeus et al., 2014; Marzinzig et al., 2018; Nayak et al., 2015), and bumblebees are among the main and most effective pollinators of this plant (Bartomeus et al., 2014; Garratt et al., 2014; Marzinzig et al., 2018).

For floral resource maps, we distinguished plant species flowering (1) preceding and (2) synchronous to broad beans. We considered 32 key pollen types that included all woody plants found to be used by *Bombus terrestris*, plus herbaceous plants representing more than 5% of pollen grains collected by the bumblebee at any point in time (i.e. either preceding or synchronous to broad bean flowering; data from Bertrand et al., 2019; TABLE S5.1). We mapped the cover (m^2) of all 69 plant species offering these 32 key pollen types in our study region between late May and November 2017 (TABLE S5.1). Annuals (*Papaver rhoeas, Phacelia tanacetifolia* and *Trifolium* spec.) were mapped during their flowering period (late-May until mid-July) in all landscapes. The pollen collected from all of the mapped plant species accounted for 84% of the pollen diet of *Bombus terrestris* across the season (Bertrand et al., 2019). The unmapped plant species, which made up the 39 remaining pollen types identified as part of bumblebees' diets in Bertrand et al., 2019 but were not included in this study, were mostly herbaceous plants with relatively low floral abundances (TABLE S5.2). For habitat maps (also land use / land cover maps or LULC maps), the habitat types arable land, permanent crops, forest, other woody semi-natural habitat, herbaceous semi-natural habitat and urban areas were mapped in all landscapes according to field inspection and aerial photographs. Landscapes consisted mainly of crops (average: 70%, standard error: 0.05, range: 29-97%) and herbaceous semi-natural habitat (average: 11%, range: 1-51%). Main crops were cereals, maize and sugar beet.

Bombus terrestris forages mostly within a radius of 500 m around its colony, although longer foraging flights are possible (Kreyer et al., 2004; Osborne et al., 1999; Wolf & Moritz, 2008). In order to keep landscape gradients as independent as possible from each other, landscape centres were separated from each other by at least 800 m (average: 10,391 m, standard error: 252 m). All landscape centres were located in grassy field margins. Twenty pots with one plant of broad bean *Vicia faba* L. var. Sutton Dwarf each were exposed in each landscape centre (FIGURE S5.2). The plants were grown in greenhouses and net cages with no pollinator access before or after field exposure. When sowing the beans, we applied 1000 g of NPK 6-17-27 fertilizer per m^3 of soil. The pots with full flowering plants (BBCH65; Lancashire et al., 1991) were watered regularly and placed in two rows with a distance of 0.3 m between pots and 0.5 m between rows. The segments of plants that only flowered during field exposure were marked with cable ties and later evaluation of pollination success was restricted to flowers of these segments. Two independent sets of plants were exposed in the field, one from 25th May to 9th June and the other from 13th to 28th June 2017. Both exposure periods occurred after the flowering of the major early pollen sources in the study region such as *Acer*, *Aesculus*, Brassicaceae (mainly oilseed rape), *Crataegus*, *Fragaria*, *Prunus* and *Salix* but simultaneous to major late-flowering pollen resources such as *Papaver*, *Phacelia*, *Rubus* and *Tilia* in order to reflect the typical flowering time of *Vicia faba* in the study region. To verify the general role of insect pollination on seed set of the used variety, we placed one additional plant per landscape centre into a gauze cage ("Aerarium Size L", AERARIUM NETS GMBH, Switzerland, 155 meshes per cm^2) next to the other sentinels. To obtain an overview of flower visitors, we employed camcorders (SONY HDR-CX115E) once during the morning (in between 8.45 and 11.30 am) and once during the afternoon (in between 3.30 and 5.30 pm), for 1:50 h each and a total of 3:40 h of video observation in each landscape. After returning all plants to the greenhouse, they were watered every two days until early August, when pods were fully ripe (BBCH89; Lancashire et al., 1991). Two weeks later, the dried pods were harvested. Pods and seeds were counted in the lab.

DATA ANALYSIS

To test our hypotheses, we used the number of seeds per pod as an indicator of pollination success as open pollination led to higher seed set in other studies (Aouar-sadli et al., 2008; Free, 1966; Ishag, 1973; Nayak et al., 2015; Suso et al., 1996).

The cover of different land use types and the distribution of plant species providing pollen resources were digitized as vector layers and analysed with the geographic information system QGIS V. 3.6 (QGIS Development Team, 2019; Table S5.S2).

The availability of different floral resources in each landscape during a time period was combined into a floral resource availability index (*fai*) that weighed the relative cover of each flowering plant species in a landscape ($cr_{p,l}$) by its quantitative utilization by workers of *B. terrestris* in our study region ($vr_{p,t}$; Eq. 1; see below for details; Bertrand et al., 2019). These indices were calculated for each landscape *l* for three time periods *t*: (1) preceding broad bean exposure (i.e. start of flowering season in mid-March until late May), (2) synchronous to broad bean exposure (i.e. late May to late June) and (3) pooled across the whole study period. To account for the range in preference of different pollen sources to *B. terrestris*, we used pollen volume collected by multiple colonies across multiple landscapes in our study region (Bertrand et al., 2019) as a proxy of preference. The total cover of plants providing each pollen type across all landscapes was, thus, weighted proportionally to the total pollen volume of each time period. This ensured that the contribution of each plant type to the pollen availability index was proportional to the preference of this plant type for bumblebees (e.g. a plant type accounting for 20% of pollen use by *B. terrestris* counts ten times more than a plant type accounting for 2% of pollen use).

$$fai_{l,t} = n \cdot \sum_{p=1}^{P} cr_{p,l} \cdot vr_{p,t} \qquad \text{(EQ. 1)}$$

In this equation, *n* represents the number of landscapes, *P* is the number of key pollen types flowering in the respective time period, $cr_{p,l}$ is the cover of plants providing pollen type *p* in the respective landscape *l* divided by their total cover across all landscapes and $vr_{p,t}$ is the volume of pollen type *p* in the diet of *Bombus terrestris* divided by the volume of all pollen recorded in their diet during the respective time period *t*. This index returns a positive decimal value, whereby a value of 1 corresponds to the average pollen availability across all landscapes at the respective time. Values below 1 indicate below-average pollen availability, whereas values higher than 1 reveal an above-average pollen availability. For more details on the index see S5.2. Whenever we use the term "floral resources" in the remainder of this paper, we are referring to the resource availability index *fai*.

For the habitat maps approach, landscape context was expressed as the proportion of arable land, permanent crops, forest, other woody semi-natural habitat, herbaceous semi-natural habitat and urban areas in the landscape. Euclidean distances from the broad bean sentinels in the landscape centres to the nearest forest or urban land use were also calculated.

To test and compare predictability of seed set by the two mapping approaches, a model containing all explanatory variables was set up for each approach. To facilitate interpretation of parameter estimates, input variables were standardized by dividing by two standard deviations using the standardize function from the *'arm'* package (Gelman, 2008). Models of each mapping approach were compared based on Akaikes second-order information criterion for small sample sizes (AICc; Akaike, 1987; Burnham et al., 2011; Hurvich & Tsai, 1989; Symonds & Moussalli, 2011) using the dredge function from the '*MuMin*' package (Bartón, 2020) and a cutoff rule ($\Delta_i < 2$; Burnham & Anderson, 2002; Symonds & Moussalli, 2011). For comparison of seed set predictability of both mapping approaches, R^2_{mult} and R^2_{adj} values for the most parsimonious models were compared. Effects of landscape context on seed set were assessed using models from the subset of models best explaining seed set (i.e. all models with ($\Delta_i < 2$). Contributions of landscape context to floral resource availability were assessed with linear regression models. Linear models were plotted using the package '*ggplot2*'(Wickham, 2016). In order to determine whether habitat maps would be more effective when using finer categories (i.e. division of crops into the classes of arable land and permanent crops as well as semi-natural habitat into the classes forest, other woody and herbaceous semi-natural habitats), their performance in predicting seed set and contributions of landscape context to floral resource availability were compared using linear regression. All statistical analyses were conducted using *R 4.0* (R Core Team, 2020). Diagnostic plots (residuals vs. fitted values and normal Q-Q plots) were visually checked. We further assessed correlations among explanatory variables and created a correlation plot using the *'corrplot'* package in *R* (Wei & Simko, 2017).

5.4 RESULTS

The pollen use by *Bombus terrestris* during the various time periods is shown in TABLE S5.1. From 55,099 broad bean flowers, we harvested 1,328 pods (mean per landscape = 55.3 ± 14.3) with at least one developed seed and 3,269 (mean = 136.2 ± 37.2) developed seeds in total. The mean number of developed seeds per pod per landscape ranged from 2 to 2.8 (mean = 2.5 ± 0.2). The caged plants developed no seeds. The video observations recorded the bumblebee species *B. terrestris* agg. (*B. terrestris, B. lucorum, B. cryptarum* and *B. magnus*, n = 25), *B. hortorum* (n = 11) and *B. lapidarius* (n = 1) as well as the honeybee *A. mellifera* (n = 34) as pollinators of the sentinel plants.

FLORAL RESOURCE MAPS

As expected, broad bean seed set increased in landscapes with preceding floral resource availability ($t_{1,22}$ = 2.19, R^2_{mult} = 0.18, p = 0.039, FIGURE 5.1A). In contrast, synchronous floral resources had no significant influence on seed set ($t_{1,22}$ = -0.26, R^2_{mult} < 0.01, p = 0.797, FIGURE 5.1B). Floral resources pooled across the whole season had no significant influence on seed set of broad beans ($t_{1,22}$ = 0.74, R^2_{mult} = 0.02, p = 0.466).

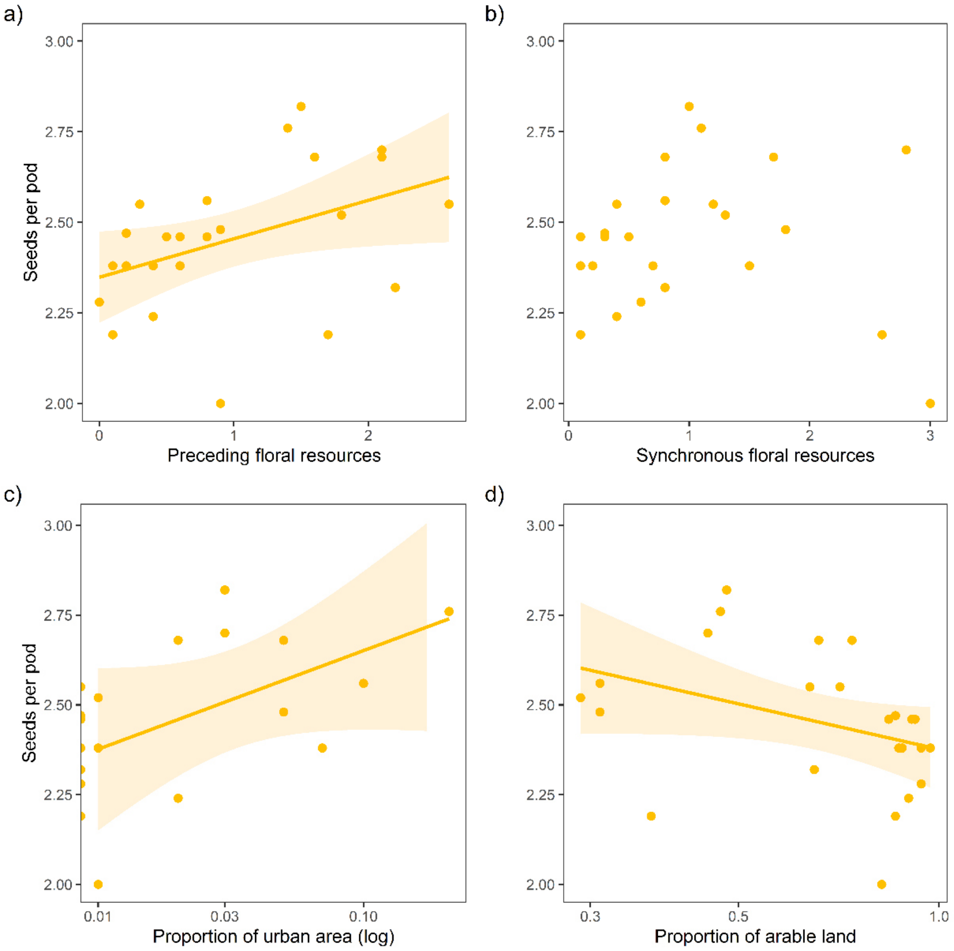


FIGURE 5.1 The relationships between seed set and floral resource availability (**a**) preceding broad bean (*Vicia faba* L.) flowering, (**b**) synchronous to broad bean flowering as well as relationships with proportions of (**c**) urban area and (**d**) arable land. Predicted linear relationships and 95 % confidence intervals are shown for statistically significant results (a, c and d).

TABLE 5.1 Comparison of selected models best explaining seed set of broad beans with linear regression using the mapping approaches of floral resource maps and habitat maps. Model selection is based on Akaikes second-order Information Criterion (AICc). Only models considered to be as good as the most parsimonious model (i. e. $\Delta_i < 2$) are shown. R^2_{mult} and R^2_{adj} are the proportions of variances explained by models using one or more variables, respectively. Delta weight Δ_i is the difference between the AICc for a model and the most parsimonious model, and Akaike weight ω_i is the probability that the model *i* is the most parsimonious model of models given. To make estimates and standard errors comparable between the models, variables were standardized by dividing by two standard deviations. Significant relations ($p < 0.05$) are printed in bold.

Method	**Model description**	**df**	R^2_{mult}	R^2_{adj}	**AICc**	Δ_i	ω_i	**Predictor**	**Estimate**	**SE**	***t*-value**	***p* value**
Floral resources	Preceding	22	0.179	0.142	-8.6	0.00	0.62	**Preceding**	**0.1661**	**0.0759**	**2.19**	**0.039**
	Preceding + Synchronous	21	0.241	0.169	-7.6	1.01	0.38	**Preceding**	**0.2099**	**0.0818**	**2.57**	**0.018**
								Synchronous	-0.1074	0.0818	-1.31	0.203
Habitat maps	Crop permanent + Urban	21	0.324	0.259	-10.3	0.00	0.25	Crop permanent	0.1394	0.0723	1.93	0.068
								Urban	**0.2088**	**0.0723**	**2.89**	**0.009**
	Crop permanent + Forest + Urban	20	0.390	0.299	-9.6	0.73	0.18	Crop permanent	0.1415	0.0704	2.01	0.058
								Forest	0.1015	0.0686	1.48	0.154
								Urban	**0.2080**	**0.0704**	**2.96**	**0.008**
	Urban	22	0.204	0.168	-9.3	1.00	0.15	**Urban**	**0.1774**	**0.0747**	**2.37**	**0.027**
	Arable + Herbaceous SNH + Urban	20	0.366	0.271	-8.6	1.69	0.11	**Arable**	**-0.2382**	**0.1061**	**-2.25**	**0.036**
								Herbaceous SNH	-0.1812	0.1054	-1.72	0.101
								Urban	0.1513	0.0777	1.95	0.066
	Arable	22	0.179	0.142	-8.6	1.73	0.11	**Arable**	**-0.1664**	**0.0758**	**-2.19**	**0.039**
	Arable + Urban	21	0.272	0.203	-8.6	1.77	0.11	Arable	-0.1123	0.0803	-1.40	0.176
								Urban	0.1310	0.0803	1.63	0.118
	Forest + Urban	21	0.267	0.198	-8.4	1.92	0.10	Forest	0.0988	0.0734	1.35	0.192
								Urban	**0.1761**	**0.0734**	**2.40**	**0.026**

HABITAT MAPS

In the best models based on habitat cover, seed set increased with urban area in the landscape ($t_{1,21} = 2.89$, $R^2_{adj} = 0.26$, $p < 0.01$; FIGURE 5.1C. In alternative models containing the proportion of arable land ($\Delta_i \geq 1.7$), seed set decreased with increasing proportion of arable land ($t_{1,20} = 2.25$, $R^2_{adj} = 0.27$, $p = 0.036$, FIGURE 5.1D). Correlations of seed set and other landscape variables contained in these models were non-significant ($p > 0.05$; TABLE 5.1).

Seed set was somewhat better predicted using habitat maps ($R^2_{adj} = 0.26$) compared to floral resource maps ($R^2_{mult} = 0.18$) according to the respective most parsimonious model of each mapping approach ($\Delta_i = 1.7$; TABLE 5.1).

CONTRIBUTION OF HABITAT TYPES TO RESOURCE AVAILABILITY

Floral resources preceding crop flowering were negatively correlated with the proportion of arable land in the landscape ($t_{1,22} = -3.55$, $R^2_{mult} = 0.364$, $p < 0.01$). They increased with the proportion of permanent crops ($t_{1,22} = 2.20$, $R^2_{mult} = 0.181$, $p = 0.038$) and woody semi-natural habitat other than forest ($t_{1,22} = 2.11$, $R^2_{mult} = 0.168$, $p = 0.047$).

Synchronous floral resources were negatively correlated with the proportion of arable land ($t_{1,22} = -2.88$, $R^2_{mult} = 0.274$, $p < 0.01$) and distance to forest ($t_{1,22} = -3.08$, $R^2_{mult} = 0.301$, $p = 0.006$). They increased with the proportion of forest habitats ($t_{1,22} = 3.12$, $R^2_{mult} = 0.307$, $p = 0.005$). For complete correlations among variables see TABLE S5.3 and FIGURE S5.3. For a complete list of regression models between seed set and landscape context see TABLE S5.4. When using habitat maps, the division of broad habitat categories (crop and semi-natural habitat) into the finer categories of arable land and permanent crops as well as forest, other woody and herbaceous semi-natural habitat improved predictability of seed set ($R^2_{mult} = 0.140$ compared to $R^2_{mult} = 0.179$ for broad and fine resolution, respectively; TABLE S5.5).

Wild plants contributed more to floral resource availability preceding and synchronous to broad bean flowering (72% and 95%, respectively) than cultivated plants. Regarding their vegetation type (i.e. either herbaceous or woody), woody plant types contributed more to floral resource availability (preceding: 94%, synchronous: 76%) than herbaceous plants.

5.5 DISCUSSION

TEMPORAL FLORAL RESOURCE MAPS

As predicted, pollination success of broad bean increased with the availability of preceding floral resources in the landscapes. This confirms our first hypothesis that increasing pollinator populations early in the year lead to higher pollinator visitation of subsequently flowering crops. These findings are similar to Grab et al., 2017, who observed that preceding mass-flowering apple enhanced successive strawberry pollination. Our results show that the timing of alternative floral resources is also crucial in more diverse landscapes, where a high number of plant species provide alternative resources to key pollinators. By accounting for the varied pollen usage of *Bombus terrestris* in our study region (Bertrand et al., 2019), we could show that the presence of fruit trees (*Prunus* spec.), maple (*Acer* spec.) and willow (*Salix* spec.) contribute to this higher flower availability for *B. terrestris* in the early season. The combined contribution of these three groups of trees to floral resource availability for *Bombus terrestris* preceding broad bean flowering was 75 %.

In contrast, the availability of synchronous alternative resources during broad bean flowering had neither a positive nor a negative effect on pollination success. This contrasts with the decline of early-flowering strawberry pollination with increasing synchronous mass-flowering apple observed by (Grab et al., 2017). This difference could be explained by contrasting attractiveness of the focal crop versus the alternative resources to pollinators between the two studies. According to (Abrol, 1990, 1992), strawberry plants have a comparatively low attractivity for pollinators in contrast to mass-flowering apple based on higher total daily energy reward per apple flower compared to that of strawberry. Additionally, flower density is higher in apple orchards than in strawberry fields. Therefore, it is not surprising that apple attracts pollinators away from strawberry crops during simultaneous flowering. Conversely, broad bean is highly attractive, especially in terms of nectar, which could explain why its visitation did not significantly decline with increasing availability of synchronous alternative flowers such as *Papaver*, *Phacelia* and *Rubus*. Negative effects of synchronous flowering resources on yield due to competition in the late season might also be mitigated by positive carry-over effects of flowering resources from the preceding year. For example, production of queens and males of bumblebees increased in the same year, density and species richness and foragers of bumblebees in the following years increased with late flowering resources in the landscapes (Häussler et al., 2017; Kallioniemi et al., 2017; Rundlöf et al., 2014). Thus, even if late alternative resources attract pollinators away from the focal crop, they may facilitate higher overall pollinator populations over time, which could lead to a net neutral effect on crop pollination. In addition, attractive synchronous flowering plants may have led to pollinator attraction from the wider landscape into the area where the broad beans were placed and, therefore, facilitated pollination (Morandin & Kremen, 2013). This effect might have been higher for the smaller number of floral resources provided by phytometer plants compared to that provided by mass-flowering cultures. Hence, positive and negative effects of late floral resources may level each other out, which could explain why neither a positive nor a negative effect of synchronous floral resources on pollination was observed in our study. Of course, the dominance of either the negative effect via competition for pollinators or the positive effect of pollinator enhancement may also depend on the design and location of the study. We hypothesize that positive carry-over effects are more likely in landscapes in which other resources for pollinators such as nesting sites are not limited. In contrast, competition for pollinators is more likely in highly simplified landscapes, in which there are generally fewer pollinators and the alternative floral resources are highly attractive relative to the crop.

HABITAT MAPS

Seed set increased with the proportion of urban area and decreased with arable land recorded in habitat maps. Indeed, pollinators can benefit from urban sprawl in city margins due to higher amounts of floral or nesting resources or benefits by intermediate levels of disturbance (Wenzel et al., 2020). Furthermore, urbanization leads to an increase of pollinator diversity compared to intensified agricultural areas, although diversity decreases in urban areas compared to natural or semi-natural areas (Wenzel et al., 2020). Colonies of *Bombus terrestris* were found to have developed more in suburban than agricultural areas due to a higher diversity and density of floral resources provided by gardens compared to farmland (Goulson et al., 2002). However, in our study, urban area was not significantly associated with flower availability (preceding, synchronous and total: r = 0.13, 0.08, 0.11, respectively). Nevertheless, pollinators may have benefited from other factors provided by urban areas such as nesting sites or reduced disturbance (i.e. offering shelter during adverse weather conditions or reduced application of agrochemicals), which were not documented in our study. Negative effects of intensive agriculture on pollinators are consistent with literature (Goulson et al., 2015; Kovács-Hostyánszki et al., 2017; Pfister et al., 2018). The lack of a better predictive power of our detailed floral resource availability information suggests that floral resources alone are not the dominant factor limiting broad bean pollination in our study region but that other factors such as availability of nesting habitat, disturbance of agricultural soils or pesticide applications are also relevant. The effect of floral resource availability cannot clearly be distinguished from the effects of landscape composition because the statistical strength of the predictors was similar and the availability of preceding floral resources declined with the proportion of arable land (r = -0.60) but not with the proportion of urban areas (r = 0.13).

Semi-natural habitat can positively affect wild bees and their performance in agricultural landscapes (Crone & Williams, 2016; Rollin et al., 2013, 2015). Loss of semi-natural habitats or increasing distance between these habitats can have direct negative consequences on pollinators (Ricketts et al., 2008; Winfree et al., 2011) and, thus, on crop pollination as well (Greenleaf & Kremen, 2006; Klein et al., 2012; Kremen et al., 2004). In our study, although pooled floral resources increased with proportion of herbaceous (r = 0.45) and woody semi-natural habitat other than forest (r = 0.42) in the landscapes, semi-natural habitats did not explain seed set. Additionally, Westphal et al. (2003) found densities of *Bombus terrestris* to be explained by the amount of mass-flowering oilseed rape rather than by semi-natural habitat. However, this crop is comparatively rare in the region where our study was conducted. There, woody semi-natural habitat included patches offering high amounts of floral resources, especially hedgerows and semi-natural orchards. Herbaceous semi-natural habitat, in contrast, contained wide areas of grassland under various management schemes with a rather low flower availability to *Bombus* *terrestris*. Nevertheless, herbaceous semi-natural habitats could have provided nesting sites to bumblebees in the form of vole burrows, which were recently suggested to increase bee populations and crop visitation (Nicholson et al., 2019). In order to be beneficial for pollinators, semi-natural habitat may need to offer a minimum number of floral resources (Rollin et al., 2013, 2019). The dominance of pollen collected from woody plants in the diet of *Bombus terrestris* seen in our study aligns with earlier studies highlighting the importance of early-flowering trees and shrubs for bumblebees (e.g. Kämper et al., 2016). We observed higher floral availability synchronous to broad bean flowering and pooled across the whole season with increased amount and proximity to forest habitat. This is partially explained by availability of wild-growing *Rubus*, contributing 31.7% to synchronous and 19% to pooled pollen use (Table S5.S1), which increased with forest (r = 0.65) and its proximity (r = 0.51) to the landscape centers. Pollination and bee abundance are shown to benefit from proximity to forest patches that also offer mating and nesting sites as well as nesting material (Bailey et al., 2014, and references therein). Proximity to other fields of *Vicia faba* in the surrounding landscape may increase cross-fertilization of plants thus leading to higher seed set. Considering the mean foraging range of *B. terrestris*, which mostly lies below 500 m (Osborne et al., 1999; Wolf & Moritz, 2008), we inspected the 1,000 m radius around our landscape centers for close-by fields of *V. faba*. We recorded one single field of *V. faba* 880 m from one of our study sites. Seed set in that site was below average across all landscapes, with plants in 19 out of the 24 landscapes developing a higher seed set. We, therefore, assume that surrounding fields of *V. faba* did not critically lead to a higher cross-fertilization in our sentinels.

COMPARISON OF MAPPING APPROACHES

In our study, seed set was somewhat better predicted by habitat maps than by floral resource maps. Similarly, habitat maps explained abundance of aphid predators and related aphid pest control on broad bean better than temporal floral resource maps in Switzerland (Ammann et al., 2020). This may be due to other above-mentioned parameters that were not assessed in this study (e.g. availability of nesting habitat) but which were likely important for pollinator activity. In addition, the floral resources were closely related to the habitat categories used in this study. The predictive power of habitat maps improved when using finer habitat categories. Hence, connecting resources to finer habitat categories might help to further improve the prediction of pollinators with habitat maps and the use of habitat maps in conservation planning. Woody non-crop plants in the agricultural landscape such as hedgerows, woodlots and tree rows have been found to provide the highest densities of floral resources to bumblebees (Eckerter et al., 2020). In this study, exposed colonies of *B. terrestris* showed increased weight gain, queen production and survival with proximity to forest, although species-specific floral resource availability did not show significant effects on colonies. Beneficial effects of woody structures next to resource availability such as protection from adverse weather conditions or nectar provision may also play a role in directing pollinator activities in agricultural landscapes. As woody structures are also key for the conservation of farmland birds and predatory arthropods (e.g. Mestre et al., 2018), addition of woody structures to agricultural landscapes would likely benefit overall biodiversity and other ecosystem services in addition to pollinators (e.g. Bartual et al., 2019; Holland et al., 2017; Schirmel et al., 2018). Further studies are needed to address other responses of *Vicia faba* to pollinators (e.g. seed size) in relation with the spatio-temporal availability of floral resources in the surrounding landscape. Additional investigations are also needed to transfer our findings to the crop level.

5.6 CONCLUSIONS

Our study underlines the key role of early flowering resources for crop pollination in agricultural landscapes. However, the detailed examination of pollen types and their spatial and temporal availability in the landscapes did not allow for a clearer explanation of pollination success than simple landscape metrics such as the proportion of arable land. Further research may help to disentangle the effects that are combined in these simplified predictors. As most of the early-flowering resources were provided by wild trees and shrubs, flower-rich woody structures such as hedgerows and forest edges should be conserved in agricultural landscapes to ensure high levels of crop pollination by wild pollinators such as bumblebees.

DATA AVAILABILITY

The data that support the findings of this study is available in *figshare.*
DOI: 10.6084/m9.figshare.12444707

6

SYNTHESIS AND OUTLOOK

Philipp W. Eckerter

6

In addition to the inestimably valuable, aesthetic, scientific, educational and spiritual aspects of ecosystems, human actions also reduce the economic value of ecosystems and the direct and indirect benefits for humanity they provide (e.g. Primack, 2014). Identifying, maintaining and guiding the factors, relationships and processes that underlie natural ecosystem services allows us to reduce the negative impact of human actions on worldwide ecosystems and to stabilize and increase beneficial ecosystem functions. As modern agriculture is thought to be one of the main causes of global damage caused by human actions, sustainably altering its function also has great potential to counteract and avert this damage (e.g. Bommarco et al., 2013). Pollination is a highly valuable ecosystem service and is directly linked to human wellbeing by providing and enhancing food quantity, quality and its security (IPBES, 2016; Porto et al., 2020). Efficiently managing floral resources inside agricultural landscapes may enhance ecological intensification and thus increase ecosystem service provision (Albrecht et al., 2021; Bommarco et al., 2013; Cassman, 1999). However, knowledge gaps exist in the species-specific and spatio-temporal floral resource requirements of wild crop pollinators and their resource-related services in agricultural landscapes. Also, to predict pollinator responses and pollination in agricultural landscapes, it is not yet clear if landscape ecologists should further rely on simplified habitat maps or if they should rather refine their mapping by including information on the spatio-temporal availability and species-specific use of floral resources by the organisms studied. This thesis aimed at (1) identifying and landscape-scale mapping of the spatio-temporal availability of key floral resources used by three wild crop pollinators, (2) measuring the spatio-temporal effects of these resources on the selected pollinators and their pollination of a target crop species, and (3) comparing the power of detailed floral resource and simplified habitat maps in predicting the floral resource-related wild pollinator abundances, their fitness and pollination in agricultural landscapes.

IMPORTANCE OF SPATIO-TEMPORAL AND STRUCTURAL COMPLEXITY

The findings of this thesis underline that even generalist wild bee species can be selective in the use of floral resources and that the use varies in the course of the season (**CHAPTERS 2, 3 & 4**). Even in crop-dominated landscapes the majority of the floral resources that were used by the three wild bee crop pollinators studied is offered by plants of semi-open woody semi-natural habitats on small and non-agriculturally managed parts of the landscapes. Early in the season these key resources consist of mainly woody species, later in the season additionally of a set of herbaceous plants (especially for *Osmia bicornis*, **CHAPTER 4**). The findings suggest that promoting certain sets of key floral resources may foster wild bee pollinators like mason bees in agricultural landscapes (e.g. Kämper et al., 2016; Sutter et al., 2017; Westphal et al., 2009). As especially non-cultivated and woody plants were offering the major part of floral resources we encourage future researchers in refining their maps and, for example, consider specific vegetational subtypes to gain further insights into the structure and dynamics of ecological communities in agroecosystems (Bartual et al., 2019; Kämper et al., 2016). In agricultural landscapes, a diversity of pollinators is likely to compete for floral resources and this is also likely to influence the pollinator-specific behavior and their pollination within a year and also over the years. For example, local bumblebee abundances decreased in years with increasing foraging activity of honeybees in the previous years (Thomson, 2016). This might further affect the responses of single wild pollinators in agricultural landscapes and probably needs further research. As also *Ranunculus acris*, a non-cultivated herbaceous plant mainly offered by grasslands, was used by *Osmia bicornis* later in the season (**CHAPTER 3**), our results also indicate that crop pollinators are likely to benefit from an increased spatio- and temporal connectivity and continuity of non-cultivated resources out of different types of semi-natural habitats, including extensively managed meadows, in addition to the short pulses of mass flowering crops in the early season (e.g. Grab et al., 2017; Holzschuh et al., 2013; Schellhorn et al., 2015; Westphal et al., 2003, 2009). *Papaver rhoeas* typically is considered as a weed in agricultural landscapes (e.g. Stankiewicz-Kosyl et al., 2020). As it is a key resource plant for *Osmia bicornis*, management options that reduce this plant in agroecosystems are simultaneously reducing the development and pollination of this wild bee species. General reduction of weeds might thus be a factor leading to a decrease of wild pollinators and their pollination in agricultural landscapes and should therefore be applied in a balanced manner. Beneficial effects of habitat connectivity and woody landscape elements on organisms in agricultural landscapes are well studied and the adding of woody elements or flower strips are likely to increase overall abundances, species richness of insects and their (pollination) services in agricultural landscapes (Albrecht et al., 2021; Campbell et al., 2017; Damschen et al., 2019; Primack, 2014; Ricketts et al., 2008; Rundlöf et al., 2018). During our studies, forests played a crucial role for the wild bees studied as forest proximity was the best explanation for the increasing abundances of *Osmia cornuta* and *Osmia bicornis* as well as the increasing weight gain, queen production and survival of *Bombus terrestris* (**CHAPTERS 3 & 4**). Colony responses of *Bombus terrestris* and *Osmia cornuta* were explained better by forest proximity than by floral resources. Hence, conserving and managing forest remnants in agricultural landscapes is likely to foster these wild bees and their pollination. This also indicates that these wild bees might benefit from other functions provided by forests in agricultural landscapes apart from the floral resources they offer, such as beneficial microclimatic conditions or the reduced application of agrochemicals compared to the surrounding arable land (Bentrup et al., 2019; Jose, 2009). Most bees and especially Bombus *terrestris* usually prefer open habitats for foraging (Dramstad & Fry, 1995; Hanula et al., 2015; Kreyer et al., 2004; Marja et al., 2018). However, the wild bees studied might have partially foraged on readily accessible floral resources within forests like, e.g., *Acer* spec., *Prunus avium*, *Rubus fruticosus* and *Quercus* spec. Wild pollinators within forests, especially in forest remnants within agricultural landscapes, are poorly studied. Therefore, the importance of floral resources within forests in agroecosystems by wild pollinators might be underestimated. Further research into the resource use of wild pollinators within forest fragments inside agricultural landscapes might give further insights into how wild pollinators may be supported from these resources.

USING DIFFERENT MAPPING APPROACHES FOR A HOLISTICAL VIEW

The species-specific, spatio-temporally and landscape-scale resolved floral resources maps showed contrasting results in predicting wild bee development and their fitness in agricultural landscapes. Despite accounting for around 95% of the used floral resources of each species they predominantly lagged behind the simplified habitat maps in their predictive power (**CHAPTERS 3 & 4**). However, finer habitat categories performed better than broader ones and the detailed floral resource maps were able to disentangle the spatio-temporal effects of floral resources on crop pollination by identifying early floral resources as the main driver of increased pollination in the late-flowering faba bean (**CHAPTER 5**). The combination of detailed floral resource and simplified habitat maps provided a more holistic insight into the relationships between the wild bees studied and their environment. Detailed resource maps might be used by landscape ecologists to gain further insights into the complex relationships between organisms and their environment. This also supports recent studies that suggest refining simplified habitat maps by using finer categories and considering, e.g., floral resources as well as vegetation traits within different habitat types (e.g. Bartual et al., 2019). As floral resource maps based on the species-specific spatio-temporally pollen availability alone failed to predict wild bee fitness, future studies might also consider the dietary stoichiometric balance for the bee larvae provided by the pollen provided by the landscapes which is crucial for larval development albeit from pure floral abundances and their diversity (Filipiak, 2018, 2019; Vaudo et al., 2015). As early floral resources were shown to boost pollinator populations (Grab et al., 2017; Holzschuh et al., 2013; Kämper et al., 2016; Moquet et al., 2015; Ostaff et al., 2015; Westphal et al., 2003, 2009), we encourage further researchers to consider especially the effects of non-cultivated woody key plant species that flower early in the season on target organisms in agricultural landscapes.

CONCLUSION

In conclusion, the findings of this thesis mainly suggest, that (1) the availability of certain key floral resources, especially those provided by woody semi-natural habitats of small surface, have the potential to promote at least two of the three wild crop pollinators studied within agricultural landscapes; (2) crop pollination in agricultural landscapes benefits from preceding woody and non-agriculturally used, floral resources in the surrounding landscapes; (3) conserving and managing woody structures like hedgerows, forest remnants and single trees but also semi-natural and commercial orchards as well as extensively used grasslands within agricultural landscapes might help to sustain and enhance wild bee pollinators and lead to higher pollination; (4) simplified habitat maps were appropriate for predicting wild bee responses in agricultural landscapes. However, the complementary use of more detailed floral resource maps provides further and more holistic insights into the use of specific key resources and the importance of timing of floral resources.

Heterogeneous landscapes that include extensively managed meadows, forests and woody structures harboring a combination of early and late key floral resources for wild pollinator guilds should therefore be conserved in agricultural landscapes to sustain the wild bee pollinators studied and enhance their services to crop pollination. As they also offer a higher diversity of floral and nesting resources for, e.g., less dominant and rare pollinators, they will likely also increase overall insect diversity, the service they provide, and the inter-annual stability in pollinator communities and the resilience of ecosystems (Perović et al., 2015; Senapathi et al., 2015, 2021; Sutter et al., 2017). In the long run they may thus offer an important link between efficiently maintaining, managing and conserving natural ecosystems and their services, food production and food stability.

7

SUPPLEMENTARY INFORMATION

S2

SEASONAL SHIFTS AND COMPLEMENTARY USE OF POLLEN SOURCES BY TWO BEES, A LACEWING AND A LADYBEETLE SPECIES IN EUROPEAN AGRICULTURAL LANDSCAPES

S2.1A DETAILED INFORMATION REGARDING STUDY SITES

The study was carried out in 2016 in two agricultural regions: in southwestern Germany (49°11′N, 8°20′E) and northeastern Switzerland (47°29′N, 8°39′E) (see Figure S2.1). In each region, we selected 11 (Germany) and 12 (Switzerland) landscape sectors of 500 m radius. Landscape sectors were selected based on available aerial photographs along gradients of the proportion of the two major land use types (see FIGURE S2.1) in order to cover different landscape contexts commonly encountered in the study regions: the percentage of agricultural land ranged from 38 to 90% (mean=68%, SD=16%), whereas the percentage of woody habitat ranged from 0 to 51% (mean=11%, SD=12%).

The sites in the German region were distributed over an area of 465 km² in the vicinity of Landau. The minimum distance between two landscape sectors was of 820 m. The region is characterized by intensively used farmland with a high share of specialized crop (vegetables, vineyards), woody habitats (e.g. woodlots and hedgerows), interspersed with some rural settlements. It has a temperate climate with an annual mean temperature of 10.5 °C and precipitation of 667 mm (GERMAN WEATHER SERVICE, station Landau). The elevation ranges from 90 to 150 m a.s.l.

The sites in the Swiss region were distributed over an area of 1760 km² in the cantons of Aargau, Zürich and Thurgau. The minimum distance between two landscape sectors was 3600 m. The region is characterized by a relatively small-scaled mosaic mainly of arable and permanent horticultural crops, grasslands, forest remnants and hedgerows, interspersed with some settlements or urban areas. The climate is warm temperate with warm summers, fully humid and with a mean temperature of 9.4°C and average annual precipitation of 1053 mm (Kottek et al., 2006). Elevation ranges from 340 to 690 m a.s.l.

S2.1B DETAILED INFORMATION ON SAMPLING METHODS

Sampling methods used to obtain pollen samples from the bees *Bombus terrestris* (Hymenoptera: Apidae) and *Osmia bicornis* (Hymenoptera: Megachilidae), and from the lacewing *Chrysoperla carnea* s.l. (Neuroptera: Chrysopidae) and the ladybeetle *Harmonia* *axyridis* (Coleoptera: Coccinellidae). In each landscape sector, 3 (Germany) to 5 (Switzerland) insect (and/or pollen) sampling points were selected at least 100 m apart from each other: one central sampling point and 2 (Germany) to 4 (Switzerland) further sampling points randomly spread across each landscape sector.

SAMPLING OF POLLEN COLLECTED BY *B. TERRESTRIS*

In the first week of April 2016, a purchased colony of *B. terrestris* ("Mini hives", BIOBEST) was placed in each landscape sector (see FIGURE S2.2). Due to the relatively large potential foraging radius of *B. terrestris*, colonies were placed only at the central sampling point of each landscape. Colonies contains 30-40 workers. To encourage foraging activity, the sugar solution provided with the colonies was removed. Colonies were covered with a lid to protect them from rain and colony entrance was oriented to the south. After 6-8 weeks most of the colonies were senescing, so they were replaced by new ones. Each colony was visited on average every 15 days (see TABLE S2.2). Up to 10 pollen-collecting worker bees were caught at the colony entrance upon return from foraging trips. Each captured bee was placed in a plastic vial filled halfway with water. The bottle was gently shaken to dislodge the pollen pellets from the bee's corbiculae into the water. All bees recovered quickly from the procedure and were able to fly away within a few minutes. Pollen samples were taken to the lab and were frozen until they were analyzed.

SAMPLING OF POLLEN COLLECTED BY *O. BICORNIS*

In the first week of April 2016, trap nests for aboveground nesting bees were established in each landscape sector. A trap nest consisted of either a plastic pipe filled with approximately 40 hollow paper straws (Swiss region; 7.5mm diameter; purchased from WAB-MAUERBIENENZUCHT, Konstanz, Germany) or wooden blocks with 40 drilled holes (German region; 7.5mm diameter; "mdf nesting plates" purchased from WAB-MAUERBIENENZUCHT, Konstanz, Germany, see FIGURE S2.2). Trap nests were attached to a wooden post at a height of roughly 1.5 m, protected against rain, and cavity openings were exposed to east. To encourage nests colonization, each trap nest was provisioned with 6 female and 6 male *O. bicornis* cocoons (purchased from WAB-MAUERBIENENZUCHT, Konstanz, Germany). Trap nests were regularly visited (see TABLE S2.2) and at each visit pollen provisions from up to five recently constructed brood cells of *O. bicornis* were randomly selected per landscape (see details below). Pollen samples were frozen until they were analyzed.

— In the German region, a trap nest was placed at the central sampling point of each landscape sector. Trap nests were inspected for newly constructed brood cells and pollen provision were taken at each visit. A photo of each drilled plate was taken and the total number of brood cells per nest and per drilled plate was recorded. This allowed us to identify newly constructed brood cells within a sampling period.

— In the Swiss region, trap nests were placed at each sampling point of each landscape sector. Paper straws containing brood cells were collected and replaced by new empty ones at each visit. In the lab, paper straws were dissected and the pollen provisions from one or two randomly selected brood cells were obtained. Paper straws selection was done in order to balance as much as possible the different sampling points within a landscape. After pollen collection, paper straws were closed again to allow the normal development of offspring of the other brood cells in a straw. To ensure, that all sampled pollen was from brood cells constructed by *O. bicornis*, trap nests were collected at the end of the field season, and all, together with the earlier collected paper straws, kept in the laboratory at ambient temperature (c. 23°C) until mid-October and then put in a cool chamber (4°C) to allow hibernation of bee offspring. In March, adult bees emerged at ambient temperature and emerged bees of each nest from which pollen was sampled were identified.

SAMPLING OF *C. CARNEA* S.L. AND *H. AXYRIDIS* INDIVIDUALS

In the first week of April 2016, sticky traps were placed at each sampling point of each landscape sector. Sticky traps were attached to wooden boards with yellow, blue and white painting to increase attractiveness, and mounted on wooden posts. When activating the traps, transparent films were attached to the trap and sprayed with insect glue (Soveurode, WITASEK, see FIGURE S2.2). The traps were activated on average every 15 days (see TABLE S2.2) and the insects were collected after 4 trapping days. All potential *C. carnea* and *H. axyridis* individuals were collected and stored in 70% ethanol prior to species identification under a binocular magnifier. For each species, up to five individuals per landscape per sampling period were selected for pollen analyses, and this was done in a way to balance as much as possible the different sampling points within a landscape.

TABLE S2.1 Detailed information on the complete list of different pollen types used by *Bombus terrestris*, *Osmia bicornis*, *Chrysoperla carnea* s.l. and *Harmonia axyridis*. Pollen identification units are 'pollen types'. Pollen type names are based on Beug (2004) and Moore et al. (1991) nomenclatures. A pollen type may be equivalent to different plant taxonomic groups (e.g. family, genus, species) or groups of two or more species or genera (or families) with similar pollen morphology (e.g. '*Achillea* type', '*Prunus* type'). For the family Rosaceae, pollen was classified into 6 pollen types (*Aruncus* type (=t.), *Filipendula* t., *Potentilla* t., *Prunus* t., *Sanguisorba minor* t. and Rosaceae type – the last type including Rosaceae pollen not attributable to any of the other five types). For pollen collected by *B. terrestris*, the species collecting most Rosaceae pollen, additional identification efforts allowed the separation of a seventh Rosaceae pollen type: *Rubus* type. Deformed pollen grains ("NB") or grain fragments that could not be identified were excluded from the analyses. Pollen types used by insects that could potentially include crop species (arable crops and horticultural crops blooming during their cultivation, e.g. fruit trees) or sown grassland plant species, are indicated with asterisk. In the "Pollen sources" column information is provided (*i*) regarding whether the plant taxa associated with the pollen type are woody or herbaceous plants; and (*ii*) regarding the assumed primary pollen dispersal mode (vectored by wind, insect, both or none – the latter group corresponding to plants that are considered to mainly autogamously self-pollinate). Information on pollen dispersal mode is based on the main species associated with a particular pollen type occurring in the study regions (e.g. https://www.infoflora.ch/) and according to information given in the '*BiolFlor*' database. We used "NA" when (*i*) the information was not available, (*ii*) both woody and herbaceous taxa are potentially associated with a pollen type, or (*iii*) different dispersal modes are associated to a pollen type. "Bt" stands for *Bombus terrestris*, "Ob" for *Osmia bicornis*, "Cc" for *Chrysoperla carnea* s.l. and "Ha" for *Harmina axyridis*.

					Used by			
ID	**Pollen type**	**Description**	**Comments**	**Pollen sources**	**Bt**	**Ob**	**Cc**	**Ha**
1	*Abies*	Family: Pinaceae Genus: *Abies*		Woody Wind	X	X	X	X
2	*Acer*	Family: Sapindaceae Genus: *Acer*		Woody Insect	X	X	X	X
3	*Achillea* type	Family: Asteraceae Genera: *Achillea, Anthemis, Chrysanthemum, Cotula, Leucanthemopsis, Leucanthemum, Matricaria, Tanacetum, Tripleurospermum*	idem *Matricaria* type	Herbaceous Insect	X	X	X	X
4	*Aesculus hippocastanum*	Family: Sapindaceae Genus: *Aesculus*		Woody Insect	X	X	X	X
5	*Allium* type	Family: Amaryllidaceae Genus: *Allium, Narcissus, Ruscus*		Herbaceous Insect	X	X	X	X
6	*Alnus*	Family: Betulaceae Genus: *Alnus*		Woody Wind	X		X	X
7	*Anagallis* type	Family: Primulaceae Genus: *Anagallis, Glaux, Lysimachia* (*L. neumorum, L. thyrsiflora*)		Herbaceous NA (None vector or insect)			X	
8	Apiaceae	Family: Apiacea		NA NA	X		X	X
9	*Artemisia*	Family: Asteraceae Genus: *Artemisia*		NA Wind			X	X
10	*Aruncus* type	Family: Rosaceae Genus: *Aruncus, Spiraea, Physocarpus*		NA Insect	X			X
11*	*Asparagus*	Family: Asparagaceae Genus: *Asparagus*		Herbaceous NA	X		X	X

TABLE S2.1 *Cont.*

					Used by			
ID	**Pollen type**	**Description**	**Comments**	**Pollen sources**	**Bt**	**Ob**	**Cc**	**Ha**
12	*Aster* type	Family: Asteraceae Genus: *Adenostyles, Antennaria, Arnica, Aster, Bellis, Bindens, Bombycilaena, Buphthalmum, Calendula, Carpesium, Conyza, Doronicum, Erechthites, Eupatorium, Filago, Galinsoga, Gnaphalium, Helichrysum, Homogyne, Inula, Ligularia, Leontopodium, Petasites, Pseudognaphalium, Pulicaria, Rudbeckia, Silphium, Solidago, Senecio, Telekia, Tephroseris, Tussilag*		Herbaceous NA	X		X	X
13*	Asteraceae	Family: Asteraceae		Herbaceous NA			X	X
14	Asteroideae	Family: Asteraceae Subfamily: Asteroidea		Herbaceous NA			X	
15	*Betula*	Family: Betulaceae Genus: *Betula*		Woody Wind	X	X	X	X
16	Boraginaceae	Family: Boraginacea		NA NA		X		
17*	Brassicaceae	Family: Brassicaceae	Probably *Brassica* for *B. terrestris* (see Table S2.5)	Herbaceous NA	X	X	X	X
18	Buxus	Family: Buxaceae Genus: *Buxus*		Woody Insect			X	
19	*Campanula* type			Woody Insect			X	
20	Campanulaceae	Family: Campanulacea		NA NA	X	X		
21	*Carduus* type	Family: Asteraceae Genera: *Carduus, Cynara, Silybum*		Herbaceous Insect				X
22	*Carpinus betulus*	Family: Betulaceae Genus: *Carpinus* Species: *C. betulus*		Woody Wind	X		X	X
23	*Carya*	Family: Juglandaceae Genus: *Carya*		Woody Wind				X
24	Caryophyllaceae	Family: Caryophyllacea		Herbaceus Insect	X	X	X	X
25	*Castanea*	Family: Fagaceae Genus: *Castanea*		Woody Wind	X	X	X	X
26	*Celtis*	Family: Cannabaceae Genus: *Celtis*		Woody Wind				X
27	*Centaurea cyanus* type	Family: Asteraceae Genus: *Centaurea* Species: *C. cyanus, C. montana*		Herbaceous Insect	X		X	X

TABLE S2.1 *Cont.*

ID	Pollen type	Description	Comments	Pollen sources	Used by			
					Bt	Ob	Cc	Ha
28	*Centaurea jacea* type	Family: Asteraceae Genus: *Centaurea* Species: *C. alba, C. calcitrapa, C. diffusa, C. jacea, C. nervosa, C. nigra, C. nigrescens, C. phrygia, C. pseudophrygia, C. solstitiales, C. spinosociliata, C. stoebe, C. vallesiaca, C. benedictus*		Herbaceous Insect	X		X	X
29	*Centaurea scabiosa* type	Family: Asteraceae Genus: *Centaurea* Species: *C. scabiosa, C. dichroantha, C. rupestris*		Herbacaceous Insect	X		X	
30	*Cerastium* type	Family: Caryophyllaceae Genus: *Cerastium, Holosteum, Moehringia, Moenchia, Minuartia* (except from *M. austriaca, M. hybrida, M. recurva, M. sedioides, M. setacea and M. verna*), *Sagina* (except from *S. apetala, S. glabra* and *S. maritima*), *Stellaria* (except from *S. holostea*)		Herbaceous NA (None vector or insect)			X	X
31*	Cerealia	Family: Poaceae Genus: *Avena, Hordeum, Triticum, Secale*		Herbaceous Wind	X	X	X	X
32	*Chelidonium majus*	Family: Papaveraceae Genus: *Chelidonium* Species: *C. majus*		Herbaceous Insect	X		X	X
33*	Chenopidoaceae	Family: Chenopodiaceae		NA NA	X		X	X
34	Cichorioideae	Family: Asteraceae Subfamily: Cichorioideae		Herbaceous NA	X	X	X	X
35	*Convolvulus arvensis* type	Family: Convolvulaceae Genus: *Convolvulus* Species: *C. arvensis, C. antabrica*		Herbaceous Insect			X	
36	*Cornus mas* type	Family: Cornaceae Genus: *Cornus* Species: *C. mas, C. suecica, C. canadensi*		Woody Insect			X	
37	*Cornus sanguinea* type	Family: *Cornaceae* Genus: *Cornus* Species *C. sanguinea, C. alba, C. sericea, C. amomum, C. racemosa, C. alternifolia, C. rugosa. C. stolonifera. C. drummondii, C. florida*		Woody Insect			X	
38	*Coronilla* type	Family: Fabaceae Genera: *Coronilla, Hippocrepis, Securigera*		Herbaceous Insect	X			
39	*Corydalis*	Family: Papaveraceae Genus: *Corydalis*		Herbaceous Insect	X			
40	*Corylus*	Family: Betulaceae Genus: *Corylus*		Woody Wind	X		X	X
41*	*Cucurbita*	Family: Cucurbitaceae Genus: *Cucurbita*		Herbaceous Insect	X			
42	Cupressacea	Family: Cupressacea		Woody Wind	X		X	X

TABLE S2.1 *Cont.*

					Used by			
ID	**Pollen type**	**Description**	**Comments**	**Pollen sources**	**Bt**	**Ob**	**Cc**	**Ha**
43	*Cynoglossum*	Family: Boraginaceae Genus: *Cynoglossum*		Herbaceous Insect			X	
44	Cyperaceae	Family: Cyperaceae		Herbaceous Wind		X	X	X
45	*Echium*	Family: Boraginaceae Genus: *Echium*		Herbaceous Insect	X	X	X	X
46	Epilobium	Family: Onagraceae Genus: *Epilobium*		Herbaceous NA (None vector or insect			X	
47*	Ericaceae	Family: Ericaceae		NA NA	X			
48	*Euonymus*	Family: Celastraceae Genus: *Euonymus*		Woody Insect				X
49	*Euphorbia*	Family: Euphorbiaceae Genus: *Euphorbia*		NA Insect			X	
50*	Fabaceae	Family: Fabaceae		NA Insect	X	X	X	X
51	*Fagus*	Family: Fagaceae Genus: *Fagus*		Woody Wind	X	X	X	X
52	*Filipendula*	Family: Rosaceae Genus: *Filipendula*		Herbaceous Insect	X		X	X
53	*Frangula alnus*	Family: Rhamnaceae Genus: *Frangula* Species: *F. alnus*	idem *Rhamnus frangula*	Woody Insect			X	X
54	*Fraxinus excelsior*	Family: Oleaceae Genus: *Fraxinus* Species: *F. excelsior*		Woody Wind	X		X	X
55	*Galium* type	Family: Rubiaceae Genera: *Asperula, Cruciata, Galium, Rubia, Sherardia*	idem Rubiaceae	Herbaceous NA (None vector or insect)	X		X	X
56	*Genista* type	Family: Fabaceae Genera: *Genista, Cytisus* (*C. scoparius*), *Ulex, Calicotom*		Woody Insect	X	X		
57	*Gentiana pneumonanthe* type	Family: Gentianaceae Genus: *Gentiana* Species: *G. cruciata, G. lutea, G. pneumonanthe, G. purpurea*		Herbaceous Insect				X
58	*Hedera helix*	Family: Araliaceae Genus: *Hedera* Species: *H. helix*		Woody Insect			X	X
59	*Helianthemum*	Family: Cistaceae Genus: *Helianthemum*		NA NA	X		X	
60*	*Helianthus annuus*	Family: Asteraceae Genus: *Helianthus* Species: *H. annuus*		Herbaceous Insect	X		X	
61	*Heracleum sphondylium* type	Family: Apiaceae Genus: *Heracleum* Species: *H. mantegazzianum, H. sphondylium*		Herbaceous Insect			X	
62*	*Humulus* type	Family: Cannabaceae Genera: *Humulus, Cannabis*		Herbaceous Wind		X		
63	*Hypericum perforatum* type	Family: Hypericaceae Genus: *Hypericum* (except from *H. elodes*)		Herbaceous Insect	X	X	X	
64	*Ilex aquifolium*	Family: Aquifoliaceae Genus: *Ilex* Species: *I. aquifolium*		Woody Insect	X	X	X	
65	*Impatiens*	Family: Balsaminaceae Genus:*Impatiens*		Herbaceous Insect				X

TABLE S2.1 *Cont.*

					Used by			
ID	**Pollen type**	**Description**	**Comments**	**Pollen sources**	**Bt**	**Ob**	**Cc**	**Ha**
66	*Juglans*	Family: Juglandaceae Genus: *Juglans*		Woody Wind	X	X	X	X
67	*Lamium*	Families: Lamiaceae, Orobanchaceae, Plantaginaceae Genera: *Lamium* (*L. album, L. galeobdolon, L. maculatum, L. orvala*), *Odontites, Veronica*	idem *Veronica* type	Woody NA (None vector or insect)	X	X	X	X
68	*Larix*	Family: Pinaceae Genus: *Larix*		Woody Wind			X	X
69	*Ligustrum* type	Family: Oleaceae Genera: *Ligustrum, Syringa*		Woody NA (None vector or insect)	X	X	X	
70	*Liliaceae*	Family: *Liliaceae*		NA NA		X		
71	*Lonicera periclymenum* type	Family: Caprifoliaceae Genus: *Lonicera* Species: *L. alpigena, L. caprifolium, L. etrusca, L. implexa, L. periclymenum*		Woody Insect		X		X
72	*Lonicera xylosteum* type	Family: Caprifoliaceae Genus: *Lonicera* Species: *L. caerulea, L. nigra, L. xylosteum*		Woody Insect	X		X	X
73*	*Lotus*	Family: Fabaceae Genus: *Lotus*		Herbaceous Insect	X			X
74	*Lysimachia vulgaris* type	Family: Primulaceae Genera: *Lysimachia* Species: *L. nummularia, L. punctata, L. vulgaris*		Herbaceous Insect			X	
75	Malvaceae	Family: Malvaceae		NA NA	X			
76	*Mentha* type	Family: Lamiaceae Genera: *Acinos, Calamintha, Clinopodium, Horminum,Lycopus, Mentha, Origanum, Satureja, Thymus*		Herbaceous Insect	X	X	X	
77	*Mercurialis annua*	Family: Euphorbiaceae Genus: *Mercurialis* Species: *M. annua*		Herbaceous Wind			X	
78	Oleaceae	Family: Oleacea		Woody NA	X		X	X
79*	*Onobrychis* type	Family: Fabaceae Genus: *Onobrychis*		Herbaceous Insect	X	X	X	
80	*Papaver argemone*	Family: Papaveraceae Genus: *Papaver* Species: *P. argemone*		Herbaceous Insect	X			
81	*Papaver rhoeas* type	Family: Papaveraceae Genus: *Papaver* Species: all *Papaver* species except from *P. argemone*		Herbaceous NA (None vector or insect)	X	X	X	X
82*	*Phacelia tanacetifolia*	Family: Boraginaceae Genus: *Phacelia* Species: *P. tanacetifolia*		Herbaceous Insect	X	X	X	X

TABLE S2.1 *Cont.*

					Used by			
ID	**Pollen type**	**Description**	**Comments**	**Pollen sources**	**Bt**	**Ob**	**Cc**	**Ha**
83	*Phyteuma* type	Family: Campanulaceae Genera: Phyteuma, Campanula, Jasione Species: *P. betonicifolium, P. comosum, P. globulariifolium, P. hedraianthifolium, P. hemisphaericum, P. humile, P. nanum, P. nigrum, P. orbiculare, P. ovatum, P. scheuchzeri, P. scorzonerifolium, P. spicatum, P. sieberi, P. tenerum, P. zahlbruckneri, C. baumgartenii, C. bononiensis, C. cenisia, C. cervicaria, C. glomerata, C. patula, C. persicifolia, C. pulla, C. rapunculus, C. rhomboidalis, C. rotundifolia, C. spicata, C. uniflora, J. laevis*		Herbaceous Insect		X		
84	Picea	Family: Pinaceae Genus: *Picea*		Woody Wind	X	X	X	X
85	Pinus	Family: Pinaceae Genus: *Pinus*		Woody Wind	X	X	X	X
86	*Plantago*	Family: Plantaginaceae Genus: *Plantago*		Herbaceous Wind			X	
87	*Plantago alpina* type	Family: Plantaginaceae Genus: *Plantago* Species: *P. alpina, P. maritima*		Herbaceous Wind				X
88	*Plantago lanceolata* type	Family: Plantaginaceae Genus: *Plantago* Species: *P. lanceolata, P. altissima, P. argentea, P. lagopus*		Herbaceous Wind	X		X	X
89	*Plantago major-media* type	Family: Plantaginaceae Genus: *Plantago* Species: *P. major, P. media, P. sempervirens, P. reniformis, P. indica*		Herbaceous Wind	X		X	X
90	*Platanus*	Family: Platanaceae Genus: *Platanus*		Woody Wind		X	X	
91*	Poaceae	Family: Poaceae		Herbaceous Wind	X	X	X	X
92	*Polygonatum*	Family: Asparagaceae Genus: *Polygonatum*		Herbaceous Insect	X			
93	*Polygonum aviculare* type	Family: Polygonaceae Genus: *Polygonum* Species: *P. arenarium, P. aviculare, P. bellardii, P. maritimum*		Herbaceous None vector			X	
94	*Polygonum bistorta* type	Family: Polygonaceae Genus: *Bistorta* Species: *B. officinalis, B. vivipara*		Herbaceous NA (None vector or insect)			X	
95	*Populus*	Family: Salicaceae Genus: *Populus*					X	X
96*	*Potentilla* type	Family: Rosaceae Genus: *Fragaria, Potentilla*		Herbaceous Insect	X	X	X	X

TABLE S2.1 *Cont.*

					Used by			
ID	**Pollen type**	**Description**	**Comments**	**Pollen sources**	**Bt**	**Ob**	**Cc**	**Ha**
97	*Prunella* type	Family: Lamiaceae Genera: *Dracocephalum, Glechoma, Hyssopus, Melissa, Nepeta, Prunella*		Herbaceous Insect	X			
98*	*Prunus* type	Family: Rosaceae Genera: *Prunus, Amelanchier, Crataegus, Cydonia, Eriobotrya, Malus, Mespilus, Pyrus, Pyracantha*		Woody Insect	X	X	X	X
99	*Pterocarya*	Family: Juglandaceae Genus: *Pterocarya*		Woody Wind	X			
100	*Quercus*	Family: Fagaceae Genus: *Quercus*		Woody Wind	X	X	X	X
101	Ranunculaceae	Family: Ranunculaceae		Herbaceous Insect		X		
102	*Ranunculus acris* type	Family: Ranunculaceae Genera: *Actaea, Anemone, Callianthemum, Ceratocephala, Clematis, Myosurus, Pulsatilla* (except *P. alpina*), *Ranunculus* (except *R. arvensis* and *R. parviflorus*)	Probably *Ranunculus* for *O. bicornis*	Herbaceous Insect	X	X	X	X
103	*Ranunculus ficaria*	Family: Ranunculaceae Genus: *Ranunculus* Species: *R. ficaria*		Herbaeous Insect	X			
104	*Reseda*	Family: Resedaceae Genus: *Reseda*		Herbaceous Insect	X			
105	*Rhamnus* type	Family: Rhamnaceae Genera: *Rhamnus, Paliurus, Ceanothus, Berchemia, Koelreuteria*		Woody Insect	X		X	X
106	*Rhus* type	Family: Amaryllidaceae Genera: *Rhus, Cotinus, Ailanthus*		Woody Insect			X	
107*	*Ribes*	Family: Grossulariaceae Genus: *Ribes*		Woody Insect	X		X	X
108	*Rinanthus* type	Family: Orobanchaceae Genera: *Rinanthus, Bartsia, Pedicularis (P. acaulis, P. sceptrum-carolinum), Lathraea, Euphrasia*		Herbaceous Insect	X	X	X	
109	*Robinia pseudoacacia*	Family: Fabaceae Genus: *Robinia* Species: *R. pseudoacacia*		Woody Insect	X			
110*	Rosaceae	Family: Rosaceae		NA NA	X	X	X	X
111*	*Rubus* type	Family: Rosaceae Genus: *Rubus*		Woody Insect	X			
112	Rumex acetosa *type*	Family: Polygonaceae Genera: *Oxyria, Rumex* Species: *R. acetosa, R. acetosella, R. arifolius, R. conglomeratus, R. crispus, R. maritimus, R. nivalis, R. obtusifolius, R. palustris, R. pseudoalpinus, R. pulcher, R. sanguineus, R. thyrsiflorus*	Identification of this type was done just for *B. terrestris*	Herbaceous Wind			X	X
113	*Salix*	Family: Salicaceae Genus: *Salix*		Woody Insect	X	X	X	X

TABLE S2.1 *Cont.*

ID	Pollen type	Description	Comments	Pollen sources	Used by			
					Bt	**Ob**	**Cc**	**Ha**
114	*Salvia* type	Family: Lamiaceae Genus: *Salvia, Rosmarinus*		Herbaceous Insect	X		X	
115	*Sambucus nigra* type	Family: Adoxaceae Genus: *Sambucus* Species: *S. nigra, S. racemosa*		Woody Insect	X	X	X	X
116	*Sanguisorba minor* type	Family: Rosaceae Genera: *Sanguisorba, Sarcopoterium* Species: *S. minor, S. spinosum*		Herbaceous Insect			X	X
117	*Saxifraga*	Family: Saxifragaceae Genus: *Saxifraga*		Herbaceous Insect			X	
118	Scrophulariaceae	Family: Scrophulariacea		Herbaceous Insect				X
119	*Scutellaria*	Family: Lamiaceae Genus: *Scutellaria*		NA NA	X			
120	*Sedum* type	Family: Crassulaceae Genera: *Sedum, Rhodiola, Crassula, Sempervivum, Cotyledon*		Herbaceous Insect	X	X	X	X
121	*Silene* type	Family: Caryophyllaceae Genera: *Silene, Arenaria, Cucubalus, Heliosperma, Lychnis, Petrorhagia, Saponaria, Viscaria*		Herbaceous Insect	X	X	X	X
122	*Solanum dulcamara*	Family: Solanaceae Genus: *Solanum* Species: *S. dulcamara*		Herbaceous Insect	X			
123*	*Solanum nigrum* type	Family: Solanaceae Genus: *Solanum* Species: All *Solanum* except from *S. dulcamara*		Herbaceous Insect	X			
124	*Stachys sylvatica* type	Family: Lamiaceae Genera: *Stachys, Galeopsis, Lamium, Melittis, Leonurus* Species: *S. sylvatica, S. palustris, S. arvensis, S. annua, S. germanica. S. alpine, S. recta, L. amplexicaule, L. hybridum, M. melissophyllum, L. cardiaca*		Herbaceous Insect	X			
125	*Symphytum*	Family: Boraginaceae Genus: *Symphytum*		Herbaceous Insect	X		X	
126	*Syringa*	Family: Oleaceae Genus: *Syringa*		Woody Insect			X	X
127	*Taxus*	Family: Taxaceae Genus: *Taxus*		Woody Wind			X	
128	*Thalictrum*	Family: Ranunculaceae Genus: *Thalictrum*		Woody Wind	X			
129	*Thymelaea*	Family: Thymelaeaceae Genus: *Thymelaea*		Woody Insect			X	
130	*Tilia*	Family: Malvaceae Genus: *Tilia*		Woody Insect	X	X	X	X
131*	*Trifolium*	Family: Fabaceae Genus: *Trifolium*		Herbaceous Insect			X	
132*	*Trifolium pratense* type	Family: Fabaceae Genera: *Trifolium* Species: *T. incarnatum, T. medium, T. ochroleucum, T. pratense, T. subterraneum*		Herbaceous Insect	X	X		X

TABLE S2.1 *Cont.*

ID	Pollen type	Description	Comments	Pollen sources	Used by			
					Bt	**Ob**	**Cc**	**Ha**
133*	*Trifolium repens* type	Family: Fabaceae Genus: *Trifolium* Species: *T. alpinum, T. arvense, T. aureum, T. bocconei, T. campestre, T. dubium, T. fragiferum, T. hybridum, T. lupinaster, T. ornithopodioides, T. pallescens, T. patens, T. repens, T. resupinatum, T. retusum, T. saxatile, T. scabrum, T. striatum, T. caerulea, T. monspeliaca*		Herbaceous Insect	X		X	X
134	*Ulmus*	Family: Ulmaceae Genus: *Ulmus*		Woody Wind			X	X
135	*Urtica*	Family: Urticaceae Genus: *Urtica*		Herbaceous Wind	X	X	X	X
136	*Viburnum*	Family: Adoxaceae Genus: *Viburnum*		Woody Insect	X	X	X	X
137*	*Vicia* type	Family: Fabaceae Genera: *Vicia* (except from *V. sepium*), *Pisum*		Herbaceous Insect	X	X	X	X
138	*Viola tricolor* type	Family: Violaceae Genus: *Viola* Species: *V. alpina, V. arvensis, V. calcarata, V. cornuta, V. dubyana, V. lutea, V. tricolor*		Herbaceous Insect				X
139	*Viscum album*	Family: Santalaceae Genus: *Viscum* Species: *V. album*		Woody Insect			X	
140*	*Vitis*	Family: Vitaceae Genus: *Vitis*		Woody None		X	X	X

TABLE S2.2 Sampling dates, number of landscape sectors we obtained pollen samples from, and total number of samples included in the analyses. Samples with less than 30 grains were not considered for the analyses. The number of samples included in the final analyses therefore correspond to the total number of samples after removing (1) the samples with insufficient pollen (<30 grains) and (2) the *Osmia* samples belonging to other Osmia species (see `S2.1.B`).

	Landscape sectors (n)		**Samples analyzed (n)**	
Sampling dates	**Switzerland**	**Germany**	**Switzerland**	**Germany**
Bombus terrestris				
12 to 22 April	10	9	46	47
02 to 15 May	8	4	34	15
19 to 27 May	4	3	17	12
01 to 17 June	4	10	14	59
20 to 30 June	7	6	20	31
01 to 10 July	5	2	11	16
Total	***12***	***11***	***142***	***180***
Osmia bicornis				
04 to 30 April	0	3	0	0
01 to 17 May	12	8	44	58
18 to 31 May	12	6	36	25
01 to 10 June	11	5	32	15
11 to 20 June	10	0	28	0
21 to 30 June	6	1	26	2
Total	***12***	***8***	***166***	***100***
***Chryspoerla carnea* s.l.**				
04 to 15 April	10	8	25	16
15 to 22 April	7	7	21	22
03 to 10 May	11	9	23	20
18 to 31 May	7	6	10	12
06 to 15 June	7	9	29	17
20 to 28 June	12	7	32	12
06 to 12 July	12	11	23	29
Total	***12***	***11***	***163***	***128***
Harmonia axyridis				
04 to 15 April	7	2	15	3
15 to 22 April	9	6	17	10
03 to 10 May	9	7	14	12
18 to 31 May	12	10	21	18
06 to 15 June	12	10	16	22
20 to 28 June	11	10	10	12
06 to 12 July	9	9	12	9
Total	***12***	***11***	***105***	***86***

TABLE S2.3 Sampling equivalence of GROWING DEGREE DAYS (GDD) and sampling dates in each study region. To facilitate comparisons between study regions, sampling periods were redefined based on accumulated GDD. GDD were calculated based on daily temperature data (max,min) from a weather station in the German study region (AGRARMETEOROLOGIE RLP) and a wheater station in the Swiss region (METEOSWISS, Zürich Affoltern). For each day, GDD are defined as the number of degrees the average daily temperature exceeds a base temperature (T_{base}, here taken as 10°C), and are calculated as $((T_{max}+ T_{min}) / 2) - T_{base}$ (McMaster & Wilhelm, 1997). The GDD value should always be positive; therefore, if the mean daily temperature is lower than the base temperature, then GDD = 0. The lower developmental threshold temperature (or base temperature; 10°C in our calculations) is the temperature below which we consider that most plants and insects development stops. Any temperature (max or min) below 10°C was therefore set to 10°C before calculating the average. In a similar way, an upper developmental threshold (i.e. temperature above which the rate of growth or development begins to decrease or stop) was fixed at 30°C (Dixon et al., 2009), and temperatures (max and min) values were capped at 30°C before calculating the average. Growing Degrees were accumulated daily, starting on January 1st, by adding each day's GDD to all previous days' totals. For the analyses, accumulated GDD were pooled in four categories: 0 to 100 corresponding approximatively to the month of April, 101 to 200 to May, 201 to 400 to end of May to end of June, and 401 to 600 to end of June to mid-July.

	2016 dates equivalence	
Accumulated GDD	**Zürich**	**Landau**
0 to 100	01.01. to 21.04.	01.01. to 05.05.
101 to 200	22.04. to 21.05.	06.05. to 26.05.
201 to 400	22.05. to 22.06.	27.05. to 24.06.
401 to 600	23.06. to 13.07.	25.06. to 18.07.

TABLE S2.4 Proportion of pollen types collected by each insect species classified according to the principal assumed pollen dispersal mode ("vector", wind-pollinated or insect-pollinated; see TABLE S2.1)."NA" indicates pollen types for which either no information on principal pollen dispersal mode was found or because the pollen type contains both insect-and wind-pollinated plant taxa.

		0 to 100		**101 to 200**		**201 to 400**		**401 to 600**		**Total**	
Species	**Vector**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**
B. terrestris	Wind	0.05	0.18	0.01	0.02	0.03	0.11	0.03	0.07	0.03	0.12
	Insect	0.83	0.21	0.76	0.37	0.85	0.19	0.91	0.15	0.83	0.05
	NA	0.12	0.16	0.23	0.37	0.13	0.12	0.07	0.15	0.14	0.22
O. bicornis	Wind	0.46	0.17	0.50	0.31	0.20	0.20	0.03	0.05	0.32	0.30
	Insect	0.53	0.16	0.48	0.32	0.74	0.20	0.53	0.28	0.58	0.29
	NA	0.01	0.01	0.02	0.05	0.06	0.08	0.45	0.28	0.10	0.19
***C. carnea* s.l.**	Wind	0.44	0.23	0.33	0.27	0.05	0.26	0.59	0.15	0.47	0.25
	Insect	0.42	0.24	0.45	0.28	0.34	0.28	0.29	0.17	0.37	0.25
	NA	0.15	0.15	0.22	0.27	0.17	0.13	0.12	0.10	0.16	0.18
H. axyridis	Wind	0.68	0.16	0.65	0.22	0.72	0.16	0.62	0.20	0.67	0.19
	Insect	0.19	0.14	0.28	0.22	0.22	0.12	0.30	0.19	0.25	0.18
	NA	0.13	0.14	0.06	0.10	0.07	0.06	0.08	0.11	0.09	0.11

TABLE S2.5 Relationship between the area of oilseed rape (OSR) in the landscape sectors and the proportion of Brassicaceae pollen collected by *Bombus terrestris*. Analysis of Deviance Table (Type II Wald chi square tests) of a generalized linear mixed model of the effects of the area of oilseed rape (OSR) in a landscape sector, the study region, the sampling period and their interactions on the proportion of Brassicaceae pollen used by *B. terrestris*. A landscape sector random factor was included in the model fitted with a Binomial error distribution. An observation level term was added as a second nested random effect to account for overdispersion. Akaike Information Criterion (AIC) was used to identify the best model, i.e. the best combination of explanatory variables. Consistently across regions, results show a positive relationship between the area of OSR in the landscape on the proportion of Brassicaceae pollen collected by bumblebees. The proportion of Brassicaceae pollen was higher early in the season during OSR flowering (GDD 0-200).

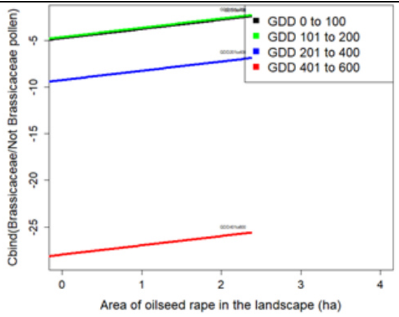
Pedictor	Chisq	Df	*p* value	Plot of the effect
Area OSR	4.98	1	0.025	
Period	17.31	3	< 0.001	

TABLE S2.6 Analysis of deviance tables (Type II Wald chi square tests) of generalized linear mixed models with binomial error structure testing for the effects of sampling period, insect species, a landscape metric (surface of woody semi-natural habitats or total surface of woody habitats in the landscape) and their interactions on (model A) the proportion of pollen from woody plant taxa or (models B1 and B2) the proportion of pollen from non-agricultural plants used by the insects studied. The pollen use by four insect species *Bombus terrestris*, *Osmia bicornis*, *Chrysoperla carnea* and *Harmonia axyridis*, was assessed during four sampling periods (roughly April, May, June and July; see TABLE S2.3). The surface of woody semi-natural habitats (WSNH), as well as the total surface of woody habitats (S_WH; including WSNH and woody crops), were calculated within each landscape sector of 500 m radius based on 2016 land cover maps of the study regions.

Model	Predictor	Chisq	Df	*p* value
Model A	Species	4.15	3	0.246
Response variable: % pollen from woody plants	Period	149.78	3	< 0.001
Dataset: both regions	S_WH	1.50	1	0.227
	Species:Period	15.64	9	0.075
	Species:S_WH	3.43	3	0.330
	Period:S_WH	6.72	3	0.082
	Species:Period:S_WH	6.92	9	0.645
Model B1	Species	5.54	3	0.136
Response variable: % pollen from non-agricultural plants	Period	10.79	3	0.013
Dataset: both regions	WSNH	0.90	1	0.342
	Species:Period	37.88	9	< 0.001
	Species:WSNH	4.49	3	0.214
	Period:WSNH	6.79	3	0.079
	Species:Period:WSNH	2.30	8	0.934
Model B1	Species	66.05	3	< 0.001
Response variable: % pollen from non-agricultural plants	Period	6.86	3	0.077
Dataset: Swiss region	WSNH	2.50	1	0.115
	Species:Period	42.70	8	< 0.001
	Species:WSNH	1.06	3	0.786
	Period:WSNH	3.87	3	0.276
	Species:Period:WSNH	11.65	8	0.167

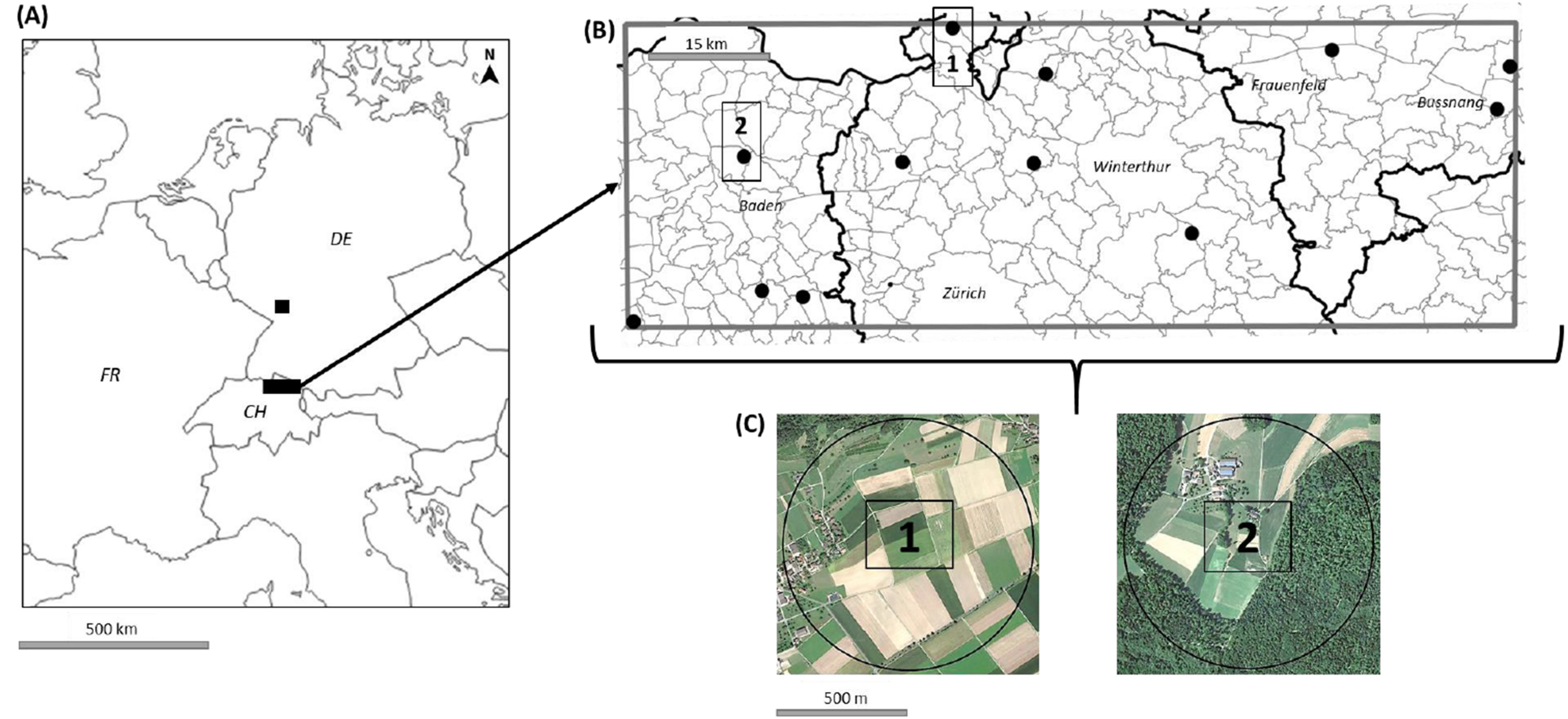


FIGURE S2.1 (A) Location of the two study regions (black squares); (B) location of the 12 landscape sectors sampled in northeastern Switzerland (black dots); (C) aerial photographs of two example landscape sectors (500 m radius) in Switzerland covering different landscape contexts (i.e. variation in the proportion of agricultural land and woody habitat covering representative gradients). See the map (B) for the geographic location of landscape sectors illustrated in (C).

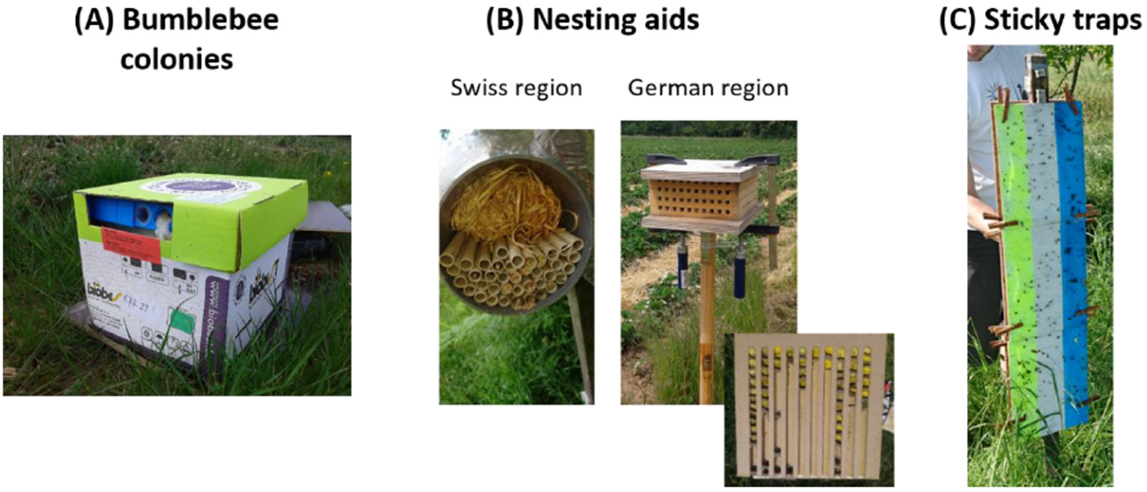


FIGURE S2.2 Pictures of the different sampling methods used for: (A) obtaining pollen from pollen sacs of *Bombus terrestris* workers upon return to purchased colonies; (B) obtaining pollen from nest provisions of *Osmia bicornis* nesting in established nesting aids (trap nests); (C) sampling adults of *Chrysoperla carnea* s.l. and *Harmonia axyridis* using sticky traps to obtain pollen consumed by sampled individuals.

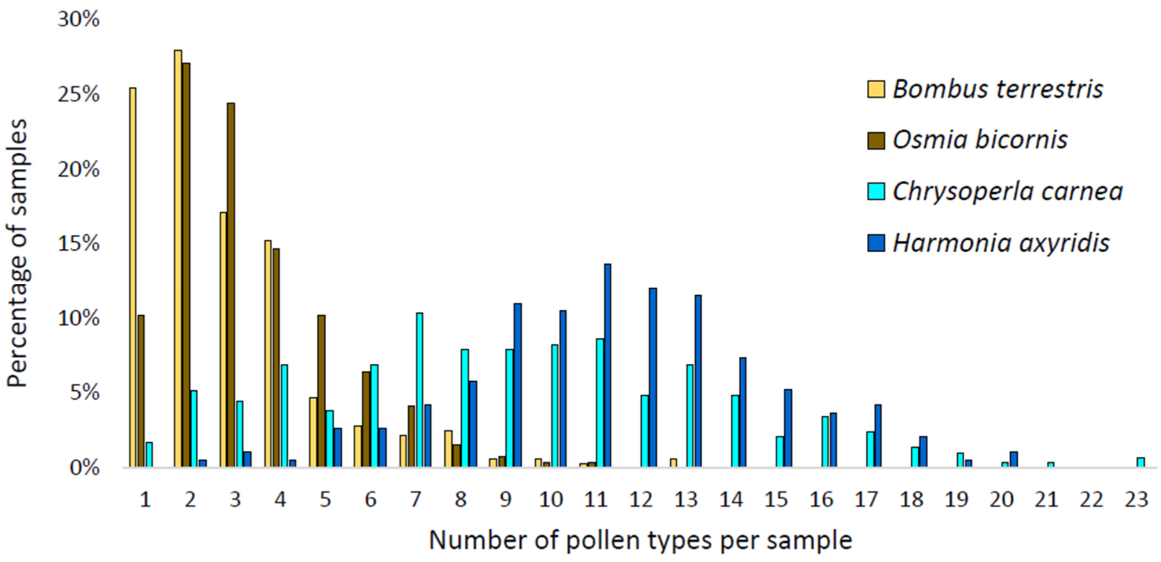


FIGURE S2.3 Sample distribution (percentage of samples) according to the number of different pollen types per sample. Most samples contained at least two different pollen types (75%, 90%, 98% and 100% of *Bombus terrestris, Osmia bicornis, Chrysoperla carnea* s.l. and *Harmonia axyridis* samples, respectively).

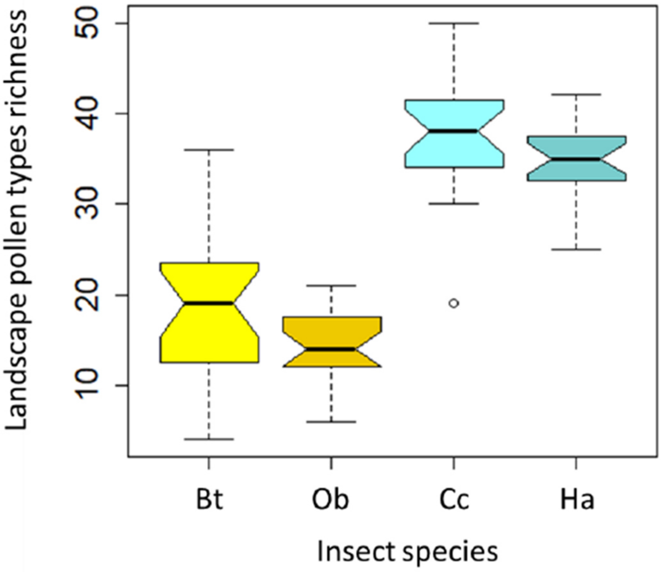


FIGURE S2.4 Mean landscape pollen type richness for *Bombus terrestris, Osmia bicornis, Chrysoperla carnea* s.l. and *Harmonia axyridis*. For each species, samples (from all sampling periods) were pooled at the landscape level. Bt stands for *B. terrestris*, Ob for *O. bicornis*, Cc for *C. carnea* s.l. and Ha for *H. axyridis*. The notches indicate a 95% confidence interval of the median; if the notches of two boxes do not overlap this is strong evidence that the medians differ.

S3

FLORAL RESOURCE USE AND FITNESS CONSEQUENCES FOR TWO SOLITARY BEE SPECIES IN AGRICULTURAL LANDSCAPES

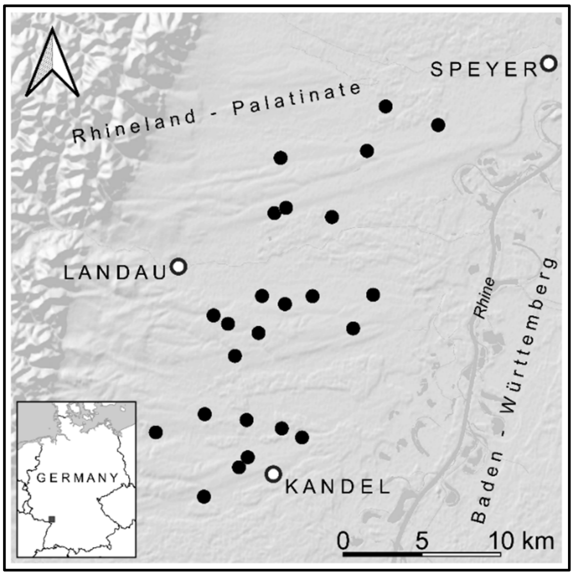


FIGURE S3.1 Location of the studied landscapes in Rhineland-Palatinate, south-west Germany

S3.1 MAPPING DETAILS ON THE FLORAL RESOURCE MAPS

We use the cover (i.e. the projection of the crown to the ground in m²) of plants as a proxy for the pollen amount that they offer. Assuming that the height of the canopies does not systematically differ between landscapes (averaged over hundreds to thousands of tree and shrub individuals), the cover is proportional to the volume.

Inside radii of 500 m surrounding the landscape centers (further referred to as "landscapes"), we obtained the cover of floral resources offering around 95% of the pollen diet of each of the *Osmia* (TABLE S3.1).

We mapped the woody plants in the landscapes from mid-July till mid-November 2017 and as follows. For the mapping of woody plants in woody landscape elements like forest edges (i.e. the first 10 m into forests) and in hedgerows we used plots of 10 m², placed every 10 m along the woody elements. Inside these plots, we identified every plant species that offered a used pollen type by one of the *Osmia* (TABLE S3.1) to the highest possible taxonomic level and measured its cover using a measure band. Also, the cover of single standing trees was measured. We calculated the tree cover inside commercial orchards by multiplying the number of rows by their mean width, a mean density factor for rows, which we measured and assessed in the field, by their mean length, which we obtained in QGIS 3.6.2. In total, we mapped around 75 ha of woody plant species (Eckerter et al., 2020, 2021).

We visited each landscape twice from end-April till end-July 2019 to map the cover of target herbaceous (i.e. annual) plants during their flowering. We mapped the single herbaceous resource patches as a projection of their combined crown to the ground using a measure band. We mapped patchy herbaceous resources flowering on wider homogeneous areas (e.g. patchy *Ranunculus* stands distributed over a certain area of herbaceous semi-natural habitat) by measuring their cover within ten 1m^2-subplots and by later extrapolating the obtained cover over the whole field area, which we calculated in QGIS.

TABLE S3.1 Use and availability of key pollen types included in the study and used for calculating the resource availability indices for *O. cornuta* and *O. bicornis*. For the index calculation, for each *Osmia* species, we included plants that offered morphologically distinguishable pollen types that constituted > 1% of the pollen diet across the season. Use of pollen types is given as % in the diet of respective species. Index % gives the contribution of each pollen type to the resource availability index of respective species which is defined by the relative cover of plants offering a pollen type proportional to the use of the respective pollen type times its relative volume (Eckerter et al., 2020, 2021). Number of landscapes ("Ls (n)") indicates the number of landscapes in which a pollen type was collected. "Plant type" is the type of plant species associated to one pollen type, "Flower class" is the flower class and "Pollen vector" is the type of pollen transfer (Beug 2004; Kühn et al. 2004; see notes below the table for further explanations). In total, 44 detected plant species with the respective morphology of 11 pollen types were mapped.

		O. cornuta			*O. bicornis*					
Pollen type	**Plant species**	**Use (%)**	**Index (%)**	**Ls (n)**	**Use (%)**	**Index (%)**	**Ls (n)**	**Plant type**	**Flower class**	**Pollen vector**
Acer	*A. campestre*, *A. platanoides*, *A. pseudoplatanus*	5.102	6.776	13	1.196	1.050	11	W	A	I
Castanea	*C. sativa*	-	-	0	1.506	0.056	5	W	W	W/(I)
Juglans	*J. regia*	1.577	5.308	6	27.971	61.179	22	W	W	W
Papaver rhoeas type	*P. rhoeas*	-	-	0	11.367	5.206	20	H	Po	I
Prunus type	*Amelanchier ovalis*, *Crataegus* spec., *Cydonia oblonga*, *Malus domestica*, *Malus sylvestris*, *Malus* spec., *Mespilus germanica*, *Prunus armeniaca*, *P. avium*, *P. cerasus*, *P. domestica*, *P. domestica* subsp. *syriaca*, *P. dulcis*, *P. laurocerasus*, *P. padus*, *P. persica*, *P. serotina*, *P. spinosa*, *P.* spec., *Pyrus communis*, *Pyrus domestica*, *Pyrus pyraster*, *Pyrus* spec.	46.232	78.979	22	1.228	1.356	7	W	AB	I
Quercus	*Q. petraea*, *Q. robur*, *Q. rubra*, *Q.* spec.	1.077	1.125	12	25.717	17.883	21	W	W	W
Ranunculus acris type	*R. acris*, *R. repens*, *R. reptans*	(*)	-	(*)	7.030	3.872	18	H	AB	I/(S)
Rubus	*R. fruticosus*, *R. idaeus*	-	-	0	16.676	9.259	23	W	BH	S/I
Salix	*S. alba*, *S. babylonica*, *S. caprea*, *S. fragilis*, *S. matsudana* 'Tortuosa', *S.* spec.	37.987	5.776	22	1.373	0.139	9	W	AB	I
Sorbus	*S. aucuparia*, *S. domestica*, *S.* spec.	1.379	1.144	4	(*)	-	2	W	AB	I/(S)
Viburnum	*V. lantana*, *V. opulus*	1.629	6.776	13	(*)	-	(*)	W	ADe	I
7 (*O. cornuta*) / 9 (*O. bicornis*)	38 (*O. cornuta*) / 41 (*O. bicornis*)	**94.98**	**100**	**22**	**94.07**	**100**	**23**			

Notes: (*): Excluded from index calculations, see TABLE S3.2. **Plant type: H:** Herbaceous / **W:** Woody. **Flower classes: A:** Flowers with open accessible nectar. Typical pollinators: beetles, flies, syrphids, wasps, middle-tongued bees / **AB:** Flowers with partly hidden nectar. Typical pollinators: syrphids, bees / **Ade:** Transition type flowers with open nectar - nasty flowers. Typical pollinators: flies, beetles / **BH:** Transition type flowers with totally hidden nectar - bee flowers. Typical pollinators: Hymenoptera / **Po:** Pollen flowers. Typical pollinators: short tongued bees, syrphids, flies, beetles / **W:** Wind flowers. **Pollen vector: I:** Insects, **W:** Wind, **S:** Selfing. Abbreviations in brackets indicate rare events.

TABLE S3.2 Composition of the pollen diet of the *Osmia* species that was excluded from the index calculations. We excluded the pollen types that constituted that either constituted ≤1% of pollen diet across the season or that were not detected in the landscapes during the mapping. The use of the pollen types is given as % in the diet of the respective species. The number of landscapes ("LS") indicates the number of landscapes in which the pollen type was collected. "Plant type" is the type of the plant species that is associated to the pollen type (Kühn et al. 2004; see the notes below the table for further explanations).

	O. cornuta		***O. bicornis***		
Pollen type	**Use (%)**	**LS (n)**	**Use (%)**	**LS (n)**	**Plant type**
Achillea type	0.014	3	-	1	H
Aesculus hippocastanum	-	-	0.259	10	W
Asparagus	0.004	1	0.071	3	H
Betula	0.041	7	0.035	6	W
Brassicaceae	0.394	1	0.565	8	H
Carpinus betulus	0.011	1	-	-	W
Cerealia type	-	-	0.006	2	H
Chenopodiaceae	-	-	0.003	1	H
Cichorioideae	0.188	7	0.068	6	H
Cornus sanguinea type	-	-	0.020	5	W
Corylus	0.011	2	0.004	1	W
Cucurbitaceae	-	-	0.006	1	H
Epilobium	0.008	1	-	-	H/W
Ericaceae	0.015	1	-	-	(H)/W
Fabaceae	-	-	0.003	1	H/W
Fagus	0.012	2	-	-	W
Fraxinus	0.006	1	0.006	1	W
Humulus	0.010	1	-	-	H
Hypericum perforatum type	-	-	0.261	1	H
Ligustrum type	0.092	4	0.306	10	W
Lonicera xylosteum type	-	-	0.037	4	W
Muscari	1.187	4	-	-	H
ND	2.435	6	0.880	9	-
Phacelia tanacetifolia	-	-	0.005	1	H
Picea	-	-	0.009	2	W
Pinus	-	-	0.004	1	W
Poaceae	-	-	0.012	2	H
Potentilla	0.076	2	0.092	2	H
Ranunculus acris type	0.003	1	(*)	(*)	H
Rosaceae	0.504	3	0.446	4	H/W
Sambucus nigra type	-	-	0.503	5	W
Senecio	0.006	1	0.035	7	H
Silene type	-	-	0.003	1	H
Sorbus	-	-	0.774	2	W
Symphytum	-	-	0.003	1	H
Trifolium	-	-	0.125	1	H
Ulmus	-	-	0.040	3	W
Urtica	-	-	0.134	2	H
Viburnum	-	-	0.371	4	W
Vitis	-	-	0.858	2	W
Total	**5.02**		**5.93**		

Notes: (*): Included into the index calculations, see TABLE S3.1. **Plant type: H:** Herbaceous / **W:** Woody. Abbreviations in brackets indicate rare occurrences.

S3.3 ESTABLISHMENT OF THE OSMIA POPULATIONS

Of each species, one starter population was released at each landscape centre at end of February. Populations consisted of 30 cocoons (sex ratio *O. cornuta*: 0.4; *O. bicornis*: 0.3, calculated as female cocoons/total cocoons). We preliminary assignment sex according to colour, shape and size of cocoons, see FIGURE S3.3). To minimize dispersal of hatching females compared to a release in their natal straws or inserting the individual cocoons in new straws (Bosch, 1994c), cocoons were placed in an emergence box (cardboard cryobox, 13.5 x 13.5 x 5 cm) with two pencil sized openings. We attached the boxes with their openings facing south-east between the nesting blocks (southern side) and a tension belt. After hatching of the *Osmia*, empty cocoons and boxes were removed.

TABLE S3.3 Proportions of habitat classes in each of the studied landscapes ("ls"). Habitat classes "other" gives the proportion of remaining habitat area without terrestrial vegetation (i.e. asphaltic streets and water bodies).

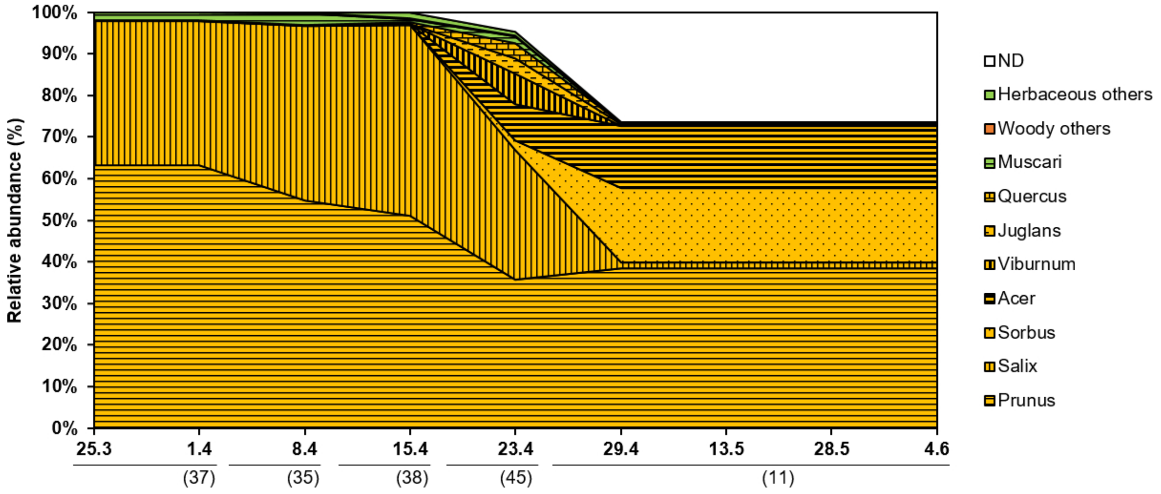
	Habitat classes							
ls	**Arable**	**Perm. Crops**	**Forest interior**	**Forest edge**	**Herb. SNH**	**Woody SNH**	**Built-up**	**Other**
1	0.97	0.00	0.00	0.00	0.01	0.00	0.00	0.02
2	0.25	0.00	0.29	0.05	0.33	0.07	0.01	0.01
3	0.29	0.00	0.02	0.01	0.53	0.04	0.10	0.01
4	0.92	0.01	0.00	0.00	0.05	0.01	0.00	0.02
5	0.74	0.04	0.00	0.00	0.09	0.03	0.05	0.04
6	0.81	0.00	0.07	0.01	0.10	0.00	0.00	0.01
7	0.46	0.10	0.10	0.04	0.25	0.03	0.00	0.03
8	0.88	0.01	0.00	0.00	0.06	0.03	0.00	0.01
9	0.47	0.17	0.05	0.06	0.12	0.04	0.04	0.06
10	0.65	0.15	0.00	0.00	0.07	0.07	0.00	0.06
11	0.66	0.02	0.10	0.06	0.08	0.03	0.01	0.04
12	0.82	0.00	0.01	0.01	0.09	0.04	0.01	0.01
13	0.63	0.14	0.00	0.00	0.16	0.06	0.00	0.02
14	0.92	0.00	0.00	0.00	0.04	0.02	0.00	0.02
15	0.97	0.00	0.00	0.00	0.01	0.00	0.00	0.01
16	0.87	0.03	0.00	0.00	0.05	0.02	0.00	0.04
17	0.82	0.03	0.00	0.00	0.09	0.03	0.00	0.03
18	0.92	0.01	0.00	0.00	0.04	0.00	0.01	0.02
19	0.91	0.00	0.00	0.00	0.05	0.02	0.00	0.01
20	0.33	0.00	0.43	0.04	0.10	0.04	0.04	0.02
21	0.86	0.00	0.00	0.00	0.04	0.00	0.08	0.02
22	0.43	0.05	0.33	0.04	0.09	0.01	0.00	0.05
23	0.72	0.19	0.00	0.00	0.04	0.03	0.00	0.02
24	0.46	0.00	0.00	0.00	0.21	0.05	0.24	0.04
mean	0.70	0.04	0.06	0.01	0.11	0.03	0.02	0.03
min	0.25	0.00	0.00	0.00	0.01	0.00	0.00	0.01
max	0.97	0.19	0.43	0.06	0.53	0.07	0.24	0.06
se	0.05	0.01	0.02	0.00	0.02	0.00	0.01	0.00

TABLE S3.4 Contributions of the collected pollen types to the pollen availability for *O. cornuta* and *O. bicornis* within each habitat class. The pollen availability is defined by the relative cover of the plants offering a pollen type proportional to the use of the respective pollen type times its relative volume (Eckerter et al., 2020, 2021).

O. cornuta		***O. bicornis***	
Arable land			
(None)		*Papaver rhoeas* type	3.54%
		Ranunculus acris type	< 0.01%
	0.00%		**3.54%**
Built-up			
Prunus type	0.20%	*Papaver rhoeas* type	0.09%
		Prunus type	< 0.01%
		Ranunculus acris type	< 0.01%
	0.20%		**0.09%**
Forest edges			
Prunus type	7.71%	*Quercus*	10.61%
Acer	1.63%	*Juglans*	4.38%
Salix	0.68%	*Rubus*	3.67%
Quercus	0.67%	*Ranunculus acris* type	0.73%
Juglans	0.38%	*Acer*	0.25%
Viburnum	0.10%	*Prunus* type	0.13%
Sorbus	0.09%	*Castanea*	0.02%
		Salix	0.02%
		Papaver rhoeas type	< 0.01%
	11.20%		**19.81%**
Herbaceous SNH			
(None)		*Ranunculus acris* type	1.78%
		Papaver rhoeas type	1.52%
	0.00%		**3.30%**
Permanent crops			
Prunus type	33.60%	*Juglans*	11.02%
Juglans	0.96%	*Prunus* type	0.58%
		Papaver rhoeas type	< 0.01%
		Ranunculus acris type	< 0.01%
	34.60%		**11.60%**
Woody SNH			
Prunus type	37.51%	*Juglans*	45.78%
Acer	5.15%	*Quercus*	7.27%
Salix	5.10%	*Rubus*	5.59%
Juglans	3.97%	*Ranunculus acris* type	1.36%
Sorbus	1.06%	*Acer*	0.80%
Viburnum	0.79%	*Prunus* type	0.64%
Quercus	0.46%	*Salix*	0.12%
		Papaver rhoeas type	0.05%
		Castanea	0.04%
	54.00%		**61.65%**

S3.4 TEMPORAL SHIFTS IN THE POLLEN DIETS OF THE *OSMIA*

a) *Osmia cornuta*



b) *Osmia bicornis*

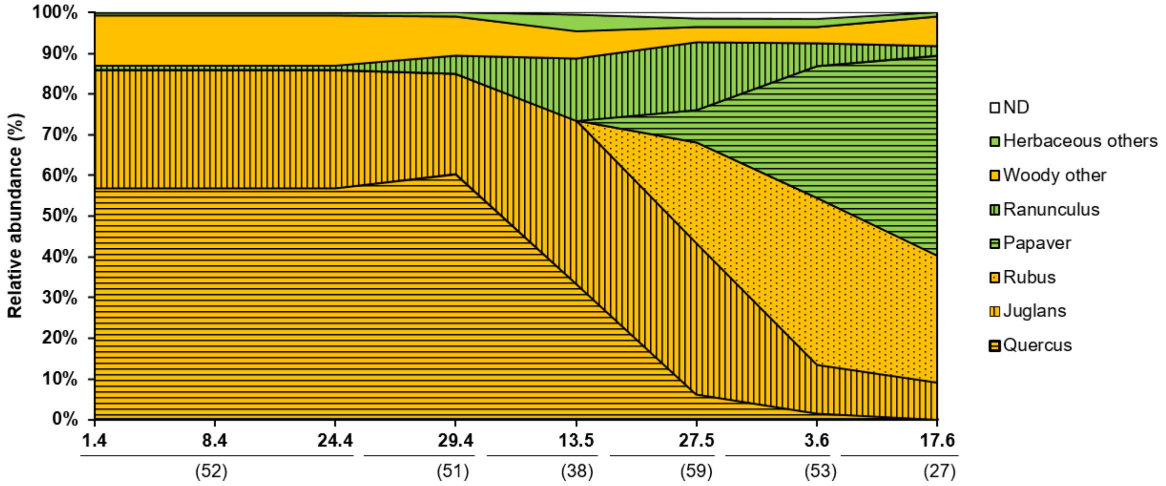


FIGURE S3.2 Relative abundances (%) of the main pollen types used across the season by (**a**) *O. cornuta* and (**b**) *O. bicornis*. The lines below the dates indicate the periods, into which the samples of the respective species were categorized. The number of samples included into each period is given in brackets below the lines that indicate the range of the analysis periods. We detail only pollen types that account for >3% of the pollen grains used by a species. The pollen types collected below <3% are summarized as either "Herbaceous other" or "Woody other", depending on the vegetation type of the plants that offer the respective pollen types. The pollen types collected from woody plants are indicated in orange colour, those ones collected on herbaceous plants are indicated in green. Pollen types that could not be identified ("ND") are indicated in white. See TABLE S3.1 and TABLE S3.2 for details on the use and availability of the pollen types used by the Osmia pooled across the whole season.

During its early foraging period (i.e. from late March till mid-April; FIGURE S3.2A), *O. cornuta* mainly used *Prunus* type and *Salix*. In its mid foraging period (i.e. from mid to end April, average accumulated GDD across landscapes: 2-25), in addition to *Prunus* type and *Salix*, it used *Viburnum*, *Juglans* and *Quercus*, which were collected mainly during this period. In addition, it started to use *Acer* and *Sorbus*. During its late foraging period (i.e. from end-April till early June) *O. cornuta* mainly used *Prunus* type, *Sorbus* and *Acer*. It collected *Prunus* type in high amounts (62% in its early season to 39% in its late season) during its whole foraging period. During its early foraging period (i.e. from beginning till end-April; FIGURE S3.2B), *O. bicornis* mainly used *Quercus* and *Juglans*. In its mid foraging period (i.e. from late April till mid-May, average accumulated GDD across landscapes: 25-26) it started to use *Ranunculus acris* type and the amounts of *Quercus* and *Juglans* started to decrease. During its late foraging period (from mid-May till mid-June), *O. bicornis* used mainly *Rubus* and *Papaver rhoeas* type.

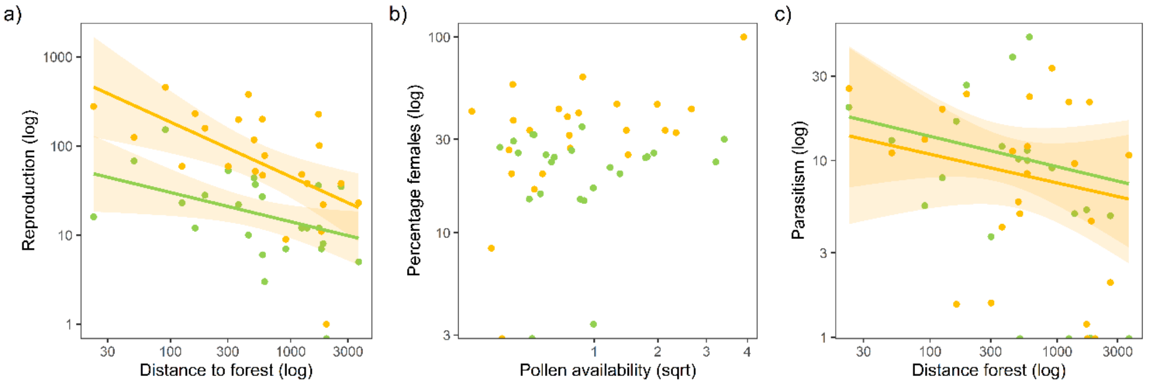


FIGURE S3.3 Relations between (**a**) the reproduction of the *Osmia* species (orange: *O. cornuta*, green: *O. bicornis*) and the distances to forests, (**b**) the percentage of female cocoons and the pollen availability in the landscapes and (**c**) the parasitism and the distances to forest. Predicted linear relations and the 95 % confidence intervals for the significant relations are shown.

TABLE S3.5 Antagonists detected in the cells of *O. cornuta* and *O. bicornis* as well as the number and proportion of parasitized cells

Target *Osmia* species	**Family**	**Species**	**Cells (n)**	**Proportion**
O. cornuta	Drosophilidae	*Cacoxenus indagator*	34	0.52
	Dermestidae	undet.	13	0.20
	Cleridae	*Trichodes* spec.	9	0.14
	Chalcidoidea	*Mellitobia acasta*	5	0.08
	Chalcidoidea	*Monodontomerus* spec.	4	0.06
O. bicornis	Drosophilidae	*Cacoxenus indagator*	247	0.65
	Cleridae	*Trichodes* spec.	48	0.13
	Dermestidae	undet.	40	0.10
	Chalcidoidea	*Mellitobia acasta*	29	0.08
	Chalcidoidea	*Monodontomerus* spec.	10	0.03
	Bombyliidae	*Anthrax anthrax*	8	0.02

TABLE S3.6 Comparison of the models explaining the reproduction (i.e. the number of cocoons) of *O. cornuta* and *O. bicornis* with important single predictors resources (see description in the manuscript). We use the Akaike second-order Information Criterion (AICc) and the QAICc to model count data and proportional data, respectively, and the *dredge* function from the MUMIN package to select the best models ($\Delta_i < 2$). Delta weight (Δ_i) is the difference between the AICc of the model and the best model. We use "SNH" as abbreviation for "semi-natural habitat". We z-transformed variables and highlight significant effects (i.e., $p \leq 0.05$) in bold.

Species	**Response**	**Model description**	**df**	**AICc**	**Δ_i**	**Predictor**	**Estimate**	**SE**	***z*-value**	***p* value**
O. cornuta	Reproduction	Cover *Salix*	22	211.52	6.20	Cover *Salix*	0.29	0.20	1.45	0.147
		Cover *Acer*	22	211.66	6.34	Cover *Acer*	0.27	0.20	1.34	0.181
		Distance *Prunus*	22	212.00	6.68	Distance *Prunus*	-0.23	0.20	-1.16	0.246
		Distance *Acer*	22	212.74	7.42	Distance *Acer*	-0.18	0.20	-0.90	0.370
		Distance *Salix*	22	213.19	7.87	Distance *Salix*	0.01	0.21	0.07	0.948
O. bicornis	Reproduction	Cover *Ranunculus*	22	272.66	67.34	**Cover *Ranunculus***	**0.84**	**0.17**	**4.96**	**< 0.001**
		Cover *Quercus*	22	279.20	73.88	**Cover *Quercus***	**0.56**	**0.19**	**2.95**	**0.003**
		Distance *Quercus*	22	283.14	77.83	Distance *Quercus*	-0.39	0.20	-1.92	0.055
		Cover *Rubus*	22	283.47	78.15	Cover *Rubus*	0.31	0.20	1.53	0.127
		Cover *Papaver*	22	283.47	78.15	Cover *Papaver*	0.33	0.20	1.63	0.103
		Distance *Ranunculus*	22	283.48	78.16	**Distance *Ranunculus***	**-0.40**	**0.20**	**-1.97**	**0.048**
		Distance *Rubus*	22	284.02	78.70	Distance *Rubus*	-0.35	0.20	-1.69	0.091
		Cover Brassicaceae	22	284.85	79.53	Cover Brassicaceae	0.26	0.21	1.26	0.209
		Distance *Juglans*	22	285.48	80.16	Distance *Juglans*	0.23	0.21	1.09	0.275
		Distance Brassicaceae	22	285.89	80.57	Distance Brassicaceae	-0.14	0.21	-0.65	0.516
		Distance *Papaver*	22	286.20	80.88	Distance *Papaver*	0.10	0.21	0.49	0.623
		Cover *Juglans*	22	286.34	81.02	Cover *Juglans*	0.04	0.21	0.21	0.837

FIGURE S3.4 Preliminary assignment of the *Osmia* cocoons to species and sex (examples). From top to bottom row: *O. cornuta* (female), *O. cornuta* (male), *O. bicornis* (female), *O. bicornis* (male). Picture: Philipp Wolfgang Eckerter

S4

USING TEMPORALLY RESOLVED FLORAL RESOURCE MAPS TO EXPLAIN BUMBLEBEE COLONY PERFORMANCE IN AGRICULTURAL LANDSCAPES

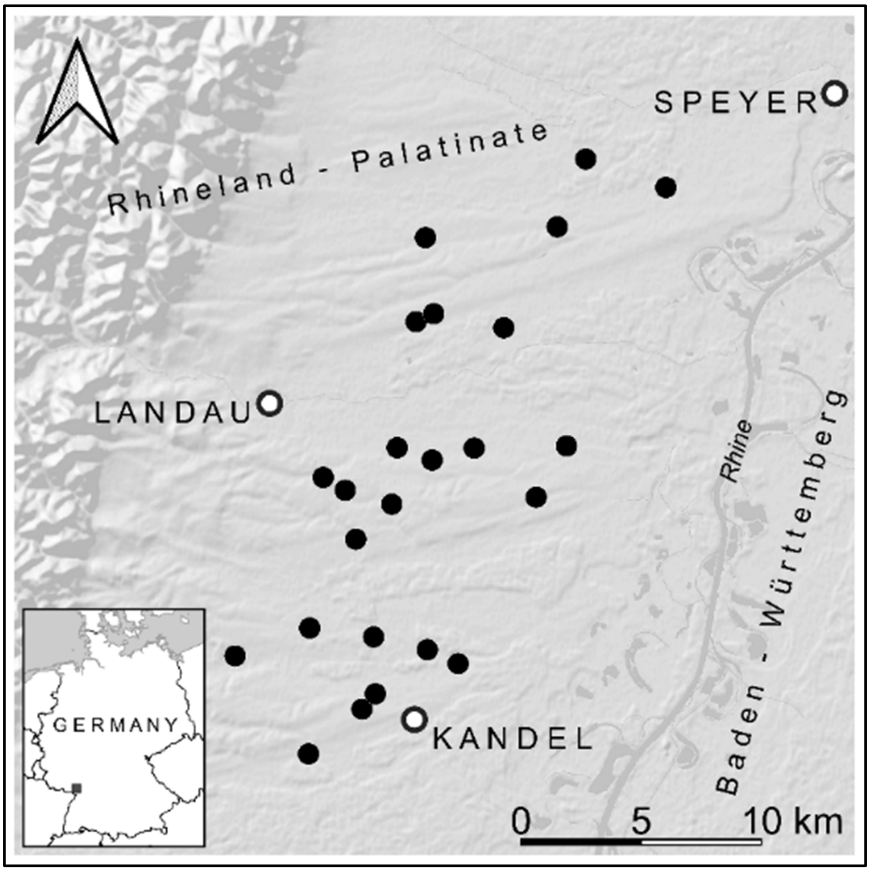


FIGURE S4.1 Location of the studied landscapes in Rhineland-Palatinate, south-west Germany

TABLE S4.1 Proportions of habitat types across the landscapes

	Habitat type							
Site	**Arable**	**Perm. Crops**	**Forest interior**	**Forest edge**	**Other**	**Herb. SNH**	**Woody SNH**	**Rural**
1	0.89	0.00	0.00	0.00	0.04	0.04	0.01	0.02
2	0.26	0.00	0.26	0.03	0.03	0.31	0.10	0.01
3	0.29	0.00	0.02	0.01	0.04	0.50	0.04	0.10
4	0.91	0.01	0.00	0.00	0.04	0.04	0.01	0.00
5	0.75	0.03	0.00	0.00	0.05	0.09	0.04	0.05
6	0.77	0.00	0.07	0.01	0.02	0.14	0.00	0.00
7	0.39	0.10	0.09	0.02	0.03	0.32	0.05	0.00
8	0.86	0.01	0.00	0.00	0.05	0.05	0.03	0.00
9	0.47	0.17	0.04	0.03	0.07	0.12	0.07	0.02
10	0.65	0.14	0.00	0.00	0.09	0.05	0.07	0.00
11	0.62	0.06	0.10	0.02	0.07	0.06	0.07	0.00
12	0.80	0.00	0.02	0.01	0.04	0.09	0.04	0.01
13	0.62	0.14	0.00	0.00	0.06	0.12	0.06	0.00
14	0.89	0.00	0.00	0.00	0.06	0.04	0.02	0.00
15	0.97	0.00	0.00	0.00	0.01	0.01	0.00	0.00
16	0.86	0.03	0.00	0.00	0.06	0.04	0.00	0.00
17	0.87	0.03	0.00	0.00	0.04	0.02	0.03	0.00
18	0.94	0.01	0.00	0.00	0.04	0.01	0.00	0.00
19	0.91	0.00	0.00	0.00	0.02	0.07	0.00	0.00
20	0.32	0.00	0.44	0.03	0.04	0.12	0.03	0.03
21	0.89	0.00	0.00	0.00	0.02	0.04	0.00	0.05
22	0.44	0.05	0.33	0.03	0.05	0.08	0.01	0.00
23	0.71	0.19	0.00	0.00	0.04	0.03	0.03	0.00
24	0.48	0.00	0.00	0.00	0.07	0.19	0.05	0.21
mean	0.69	0.04	0.06	0.01	0.04	0.11	0.03	0.02
min	0.26	0.00	0.00	0.00	0.01	0.01	0.00	0.00
max	0.97	0.19	0.44	0.03	0.09	0.50	0.10	0.21
se	0.05	0.01	0.02	0.00	0.00	0.02	0.01	0.01

S4.1 FLORAL RESOURCE MAPPING

Herbaceous plants selected for mapping offered morphologically distinguishable pollen types that constituted > 5% of the collected pollen either from April to Mai and/or from June to July (Bertrand et al., 2019). Flower cover of herbaceous plants representative for a field (e.g., one specific meadow inside a landscape) was assessed in ten 1m²-subplots and extrapolated over the whole area, which was calculated in QGIS 3.6.2 (QGIS Development Team, 2019). Cover of all woody plants (along hedgerows, semi-natural orchards, isolated trees and the first ten meters into forest along forest edges) in the landscape was measured in the field. Tree cover in commercial orchards was calculated by multiplying the mean length of tree rows contained in the orchard, which were obtained from QGIS, with the number of rows, their mean width and a mean density factor for rows, which were measured and assessed in the field.

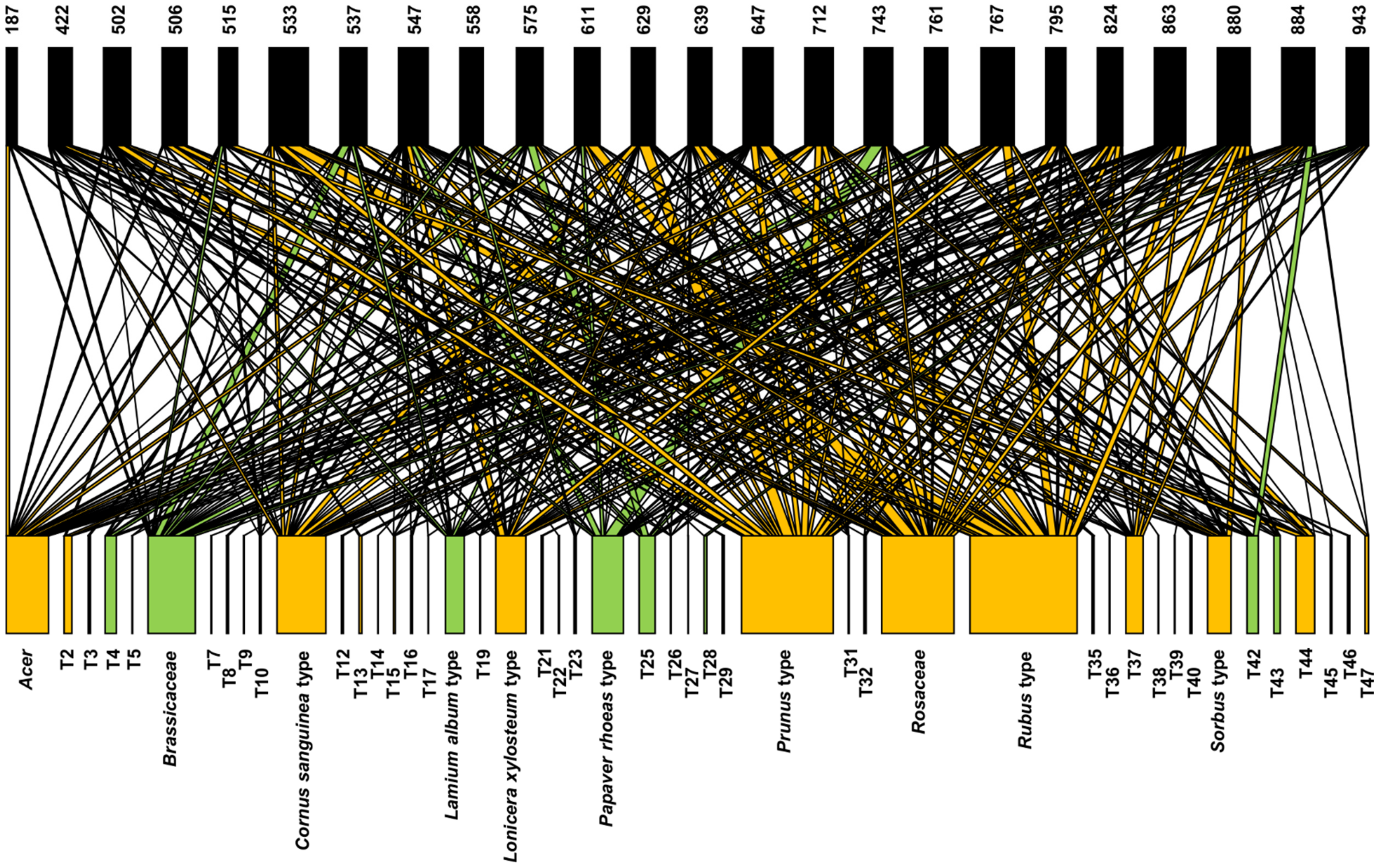


FIGURE S4.2 Pollen collection network of 657 returning foragers of 48 *Bombus terrestris* colonies in 24 agricultural landscapes in Rhineland-Palatinate (south-west Germany) across their lifecycle (from end-April till mid-July 2018). Numbers above upper bars indicate average weight gain (in g) of two colonies per landscape. Width of upper bars indicate the number of pollen grains sampled from two colonies in the landscape. Width of lower bars is proportional to the number of pollen grains collected per pollen type across all colonies. Herbaceous plants are shown in green, woody plants in yellow. Pollen types that constituted < 3% of the collected pollen are abbreviated (see TABLE S4.2 and TABLE S4.3).

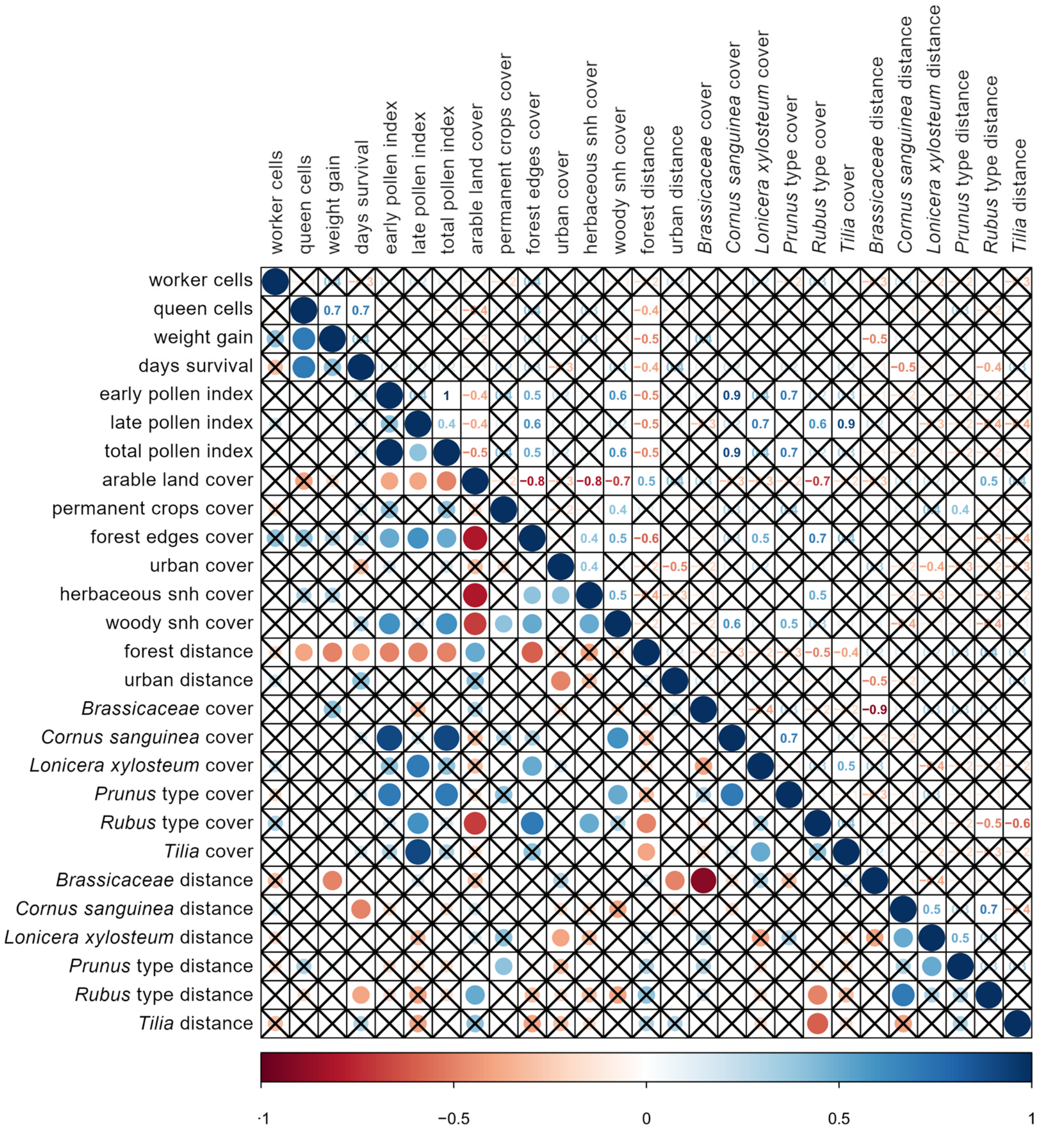


FIGURE S4.3 Pearson correlation matrix between observed parameters. Colony fitness parameter of *Bombus terrestris* colonies (number of worker and queen cells, weight gain of colonies and days of survival of colonies) and predictors using different mapping approaches. Floral resource maps are represented by floral resource availability early in the foraging season until colonies reached their maximum weight ("early", from late April until late May), from there on till colony collapse ("late", late May till mid-June) and during the whole period ("total"). Classical habitat maps represented by landscape variables (proportions of arable land, permanent crops, forest edges, other woody and herbaceous semi-natural habitat and urban, as well as Euclidean distances to forest and urban). We also included cover and distance to oilseed rape (Brassicaceae), *Cornus sanguinea, Lonicera xylosteum* type, *Prunus* type, *Rubus* and *Tilia*, important floral resources for *B. terrestris* (Westphal et al., 2003, 2009, Table S4.1). An "X" was plotted over non-significant relations (i.e. $p \geq 0.05$). The matrix was drawn using the *'corrplot'* package in *R* (R Core Team, 2020; Wei & Simko, 2017).

TABLE S4.2 Use and availability of key pollen types included in the study and used for calculating the resource availability index for *B. terrestris*. Plants selected for mapping were plants offering morphologically distinguishable pollen types that constituted > 5% of the collected pollen either from April to Mai and/or from June to July or across the whole season from April to July (Bertrand et al., 2019). Use of pollen types is given as % in the diet of *B. terrestris* during the time periods until colonies reached their maximum weight ("Early", from late April till end of May), after that until colony collapse ("Late", end of May till mid-June) and pooled across the whole season. Pollen types used for calculating the resource availability indices are mapped plants that were collected during the respective time period. Index % gives the contribution of each pollen type to the resource availability index which is defined by relative cover of a pollen type proportional to the use times the relative volume (Eckerter et al., 2021). "Plant type" is the type of plant species associated to one pollen type (Beug, 2004; w = woody, h = herbaceous), "Flower class" is the flower class (Kühn et al., 2004; see notes below the table for further explanations and typical pollinators). "Colonies" is the number of bumblebee colonies who foraged on respective pollen types across the season. In total, 71 detected plant species with the respective morphology of 30 pollen types were mapped.

			***B. terrestris* use (%)**			**Index (%)**					
Pollen type		**Plant species**	**Early**	**Late**	**Total**	**Early**	**Late**	**Total**	**Plant type**	**Flower class**	**Colonies**
T1	*Acer*	*A. campestre, A. platanoides, A. pseudoplatanus*	7.338	0.000	6.571	4.571	0.000	4.368	w	A	28
T2	*Aesculus*	*A. hippocastanum*	1.484	0.000	1.329	0.335	0.000	0.320	w	B	6
T4	*Asparagus*	*A. officinalis*	1.455	2.396	1.553	0.269	1.120	0.307	h	B	10
T5	*Betula*	*B. pendula*	0.005	0.000	0.004	0.002	0.000	0.002	w	W	2
T6	*Brassicaceae*	*Brassica napus*	8.387	0.063	7.516	2.538	0.143	2.427	h	AB	35
T8	*Castanea*	*C. sativa*	0.185	0.000	0.166	0.005	0.000	0.005	w	W	1
T10	*Cichorioideae*	*Hypochaeris radicata*	0.377	0.000	0.338	0.690	0.000	0.659	h	B	5
T11	*Cornus sanguinea*	*C. sanguinea*	8.470	0.000	7.584	45.10	0.000	43.09	w	A	33
T14	*Fagus*	*F. sylvatica*	0.002	0.000	0.002	0.002	0.000	0.002	w	W	1
T15	*Fraxinus excelsior*	*F. excelsior*	0.144	0.125	0.142	0.037	0.081	0.078	w	W	6
T17	*Juglans*	*J. regia*	0.010	0.000	0.009	0.015	0.000	0.015	w	W	2
T18	*Lamium album* type	*L. album*	3.465	0.021	3.105	1.333	0.020	1.274	h	H	18
T19	*Ligustrum* type	*Ligustrum vulgare, Syringa vulgaris*	0.019	0.521	0.072	0.011	0.776	0.045	w	B	5
T20	*Lonicera xylosteum* type	*L. xylosteum*	4.791	2.854	4.588	17.13	25.80	17.55	w	Hh	24
T24	*Papaver rhoeas* type	*P. rhoeas*	5.506	0.438	4.976	1.672	0.335	1.610	h	Po	18
T25	*Phacelia tanacetifolia*	*P. tanacetifolia*	1.584	10.25	2.490	0.174	2.834	0.291	h	H	12
T26	*Picea*	*Picea* spec.	0.029	0.000	0.026	0.641	0.000	0.612	w	W	9
T29	*Potentilla* type	*Fragaria* spec. only	0.367	0.000	0.329	0.053	0.000	0.051	h	AB	2
T30	*Prunus* type	*Amelanchier ovalis, Crataegus* spec., *Cydonia oblonga, Malus domestica, Malus sylvestris, Malus* spec., *Mespilus germanica, Prunus armeniaca, P. avium, P. cerasus, P. domestica, P. domestica* subsp. *syriaca, P. dulcis, P. laurocerasus, P. padus, P. persica, P. serotina, P. spinosa, P.* spec., *Pyrus communis, Pyrus domestica, Pyrus pyraster, Pyrus* spec.	16.19	0.000	14.50	12.83	0.000	12.26	w	AB	38

TABLE S4.2 *Cont.*

Pollen type		Plant species	*B. terrestris* use (%)			Index (%)					
			Early	Late	Total	Early	Late	Total	Plant type	Flower class	Colonies
T31	*Quercus*	*Q. alba, Q. petraea, Q. robur, Q. rubra, Q. spec.*	0.012	0.000	0.011	0.006	0.000	0.006	w	W	38
T32	*Ranunculus acris* type	*R. acris, R. repens, R. reptans*	0.290	0.000	0.259	0.111	0.000	0.106	h	AB	5
T33	*Rosaceae*	*R. agrestis, R. canina*	12.30	3.542	11.39	4.109	2.990	4.058	w	Po	5
T34	*Rubus*	*R. fruticosus, R. idaeus*	15.51	28.56	16.88	5.984	27.86	6.947	w	BH	36
T36	*Salix*	*S. alba, S. babylonica, S. caprea, S. fragilis, S. matsudana 'Tortuosa', S.* spec.	0.002	0.000	0.002	0.000	0.000	0.000	w	AB	40
T37	*Sambucus nigra* type	*S. nigra, S. racemosa, S.* spec.	2.895	0.000	2.593	0.232	0.000	0.221	w	Po	2
T41	*Sorbus* type	*S. aucuparia, S. domestica, S.* spec.	4.005	1.396	3.732	1.362	1.200	1.354	w	AB	2
T43	*Trifolium pratense* type	*T. pratense*	0.808	2.667	1.002	0.636	5.320	0.843	h	Hh	15
T44	*Tilia*	*T. chordata, T. platyphyllos*	0.007	26.77	2.806	0.003	29.71	1.354	w	A	4
T45	*Viburnum*	*V. lantana, V. opulus*	0.423	0.000	0.379	0.108	0.000	0.103	w	ADe	13
T47	*Vitis*	*V. vinifera, V. vinifera* subsp. *Sylvestris*	0.243	3.625	0.597	0.048	1.819	0.126	w	A	3
	30 pollen types	**71 plant species**	**96.3**	**83.2**	**94.9**	**100**	**100**	**100**			

Notes: **Flower classes**: **A:** Flowers with open accessible nectar. Typical pollinators: beetles, flies, syrphids, wasps, middle-tongued bees / **AB:** Flowers with partly hidden nectar. Typical pollinators: syrphids, bees / **Ade:** Transition type flowers with open nectar - nasty flowers. Typical pollinators: flies, beetles / **B:** Flowers with hidden nectar. Typical pollinators: bees, bumblebees, wasps, Bombyliidae, syrphids / **BH:** Transition type flowers with totally hidden nectar - bee flowers. Typical pollinators: Hymenoptera / **H:** Flowers for Hymenoptera. Typical pollinators: Hymenoptera / **Hh:** Flowers for bumblebees. Typical pollinators: bumblebees / **Po:** Pollen flowers. Typical pollinators: short tongued bees, syrphids, flies, beetles.

TABLE S4.3 Composition of pollen diet of returning foragers of *B. terrestris* excluded from index calculations. Use of pollen types is given as % in the diet of *B. terrestris* during the time periods until colonies reached their maximum weight (“Early”, from late April until end of May), after that until colony collapse (“Late”, end of May till mid-June) and pooled across the whole season. Plant type is the type of plant species associated to one pollen type (Beug, 2004; w = woody, h = herbaceous). Pollen types were excluded from index calculations because they constituted < 5% of pollen diet of *B. terrestris* in our study region in 2016 (Bertrand et al., 2019). Cucurbitaceae were excluded because they were not found flowering in our landscapes during sampling rounds.

		***B. terrestris* use (%)**			
Pollen type		**Early**	**Late**	**Total**	**Vegetation type**
T3	*Apiaceae*	0.000	2.063	0.216	h
T7	*Calystegia* type	0.000	0.063	0.007	h
T9	*Cerealia*	0.000	0.375	0.039	h
T12	*Cucurbitaceae*	0.000	2.667	0.279	h
T13	*Ericaceae*	0.467	0.000	0.418	w/h
T16	*Hypericum perforatum* type	0.000	4.167	0.436	h
T21	*Lotus* type	0.178	0.000	0.159	h
T22	*Oenothera biennis*	0.000	0.313	0.033	h
T23	*Onobrychis*	0.370	0.000	0.331	h
T27	*Poaceae*	0.007	0.000	0.007	h
T28	*Polygala comosa*	0.000	5.938	0.621	h
T35	*Rumex* type	0.384	0.000	0.344	h
T38	*Scrophulariaceae*	0.063	0.000	0.057	h
T39	*Aster* type	0.002	0.000	0.002	h
T40	*Solanum nigrum* type	0.000	1.188	0.124	h
T42	*Symphytum*	2.015	0.000	1.804	h
T46	*Vicia* type	0.197	0.000	0.176	h
		3.7	**16.8**	**5.1**	

S5

EFFECTS OF TEMPORAL FLORAL RESOURCE AVAILABILITY AND NON-CROP HABITATS ON BROAD BEAN POLLINATION

S5.1 MAPPING DETAILS ON THE FLORAL RESOURCE MAPS

We use the cover (the projection of the crown to the ground) of plants as a proxy for the pollen amount that they offer. Assuming that the height of the canopies does not systematically differ between landscapes (averaged over hundreds to thousands of tree and shrub individuals), the cover is proportional to the volume.

We scanned each woody plant in forest edges (i.e. the first 10 m into forests) and other woody landscape elements (i.e. single standing trees, hedgerows) inside the 500 m of each landscape for its cover in m^2 from mid-July till mid-November 2017. We calculated the tree cover inside commercial orchards by multiplying the number of rows by their mean width, a mean density factor for rows, which we measured and assessed in the field, by their mean length, which was obtained in QGIS 3.6.2. In total, we mapped around 75 ha of woody plant species.

For mapping of respective herbaceous (i.e. annual) synchronous flowering plants (*Papaver rhoeas, Phacelia tanacetifolia* and *Trifolium* spec.), each landscape was visited once from end-Mai till mid-July 2017. During mapping, each of these species was flowering in our study region. We obtained cover of single patchy herbaceous resources flowering on wider homogeneous areas by assessing their cover within ten $1m^2$-subplots and by extrapolating the obtained cover over the whole field area, which we calculated in QGIS.

S5.2 CALCULATIONS OF FLORAL RESOURCE AVAILABILITY INDICES

Relative pollen type cover in a landscape

Cover c of pollen type p in landscape l relative to cover C of pollen type p summed up across all landscapes:

$$cr_{p,l} = c_{p,l}/C_p \qquad \text{(EQ. 1)}$$

Single mean pollen type grain volume

Single mean pollen type grain volume v_p of pollen type p with ae (length equatorial axis) und ap (length polar axis; formula of spheroid):

$$v_p = 4\pi/3 \ \cdot ae^2/2 \cdot ap_p/2 \qquad \text{(EQ. 2)}$$

Measurements were taken from Beug (2004). Missing values of either ae_p or ap_p were calculated by PFormI (relation of length of value for available axis and highest transverse dimension of a pollen type).

Single pollen type collection volume during time period

Single mean pollen type collection volume cv of a single pollen type p with n pollen grains of pollen type p during period t:

$$cv_{p,t} = n_{p,t} \cdot v_p \qquad \text{(EQ. 3)}$$

Total pollen type collection volume during a time period

Total collection volume CV of all pollen types pooled across all landscapes during period t:

$$CV_{p,t} = \sum_{p=1}^{P} cv_{p,t} \qquad \text{(EQ. 4)}$$

Relative pollen type collection volume during a time period

Collection volume cv of pollen type p during period t relative to collection volume CV of all pollen types during period t:

$$vr_{p,t} = cv_{p,t}/CV_t \qquad \text{(EQ. 5)}$$

Floral resource availability index

$$fai_{l,t} = n \cdot \sum_{p=1}^{P} cr_{p,l} \cdot vr_{p,t} \qquad \text{(EQ. 6)}$$

The floral resource availability index fai in landscape l during time period t is calculated by the number of landscapes n multiplied by the sum of the relative pollen type cover cr_p in landscape l multiplied by its relative collected pollen volume vr of the respective pollen type p during time period t and P gives the total number of relevant pollen types in the respective time period.

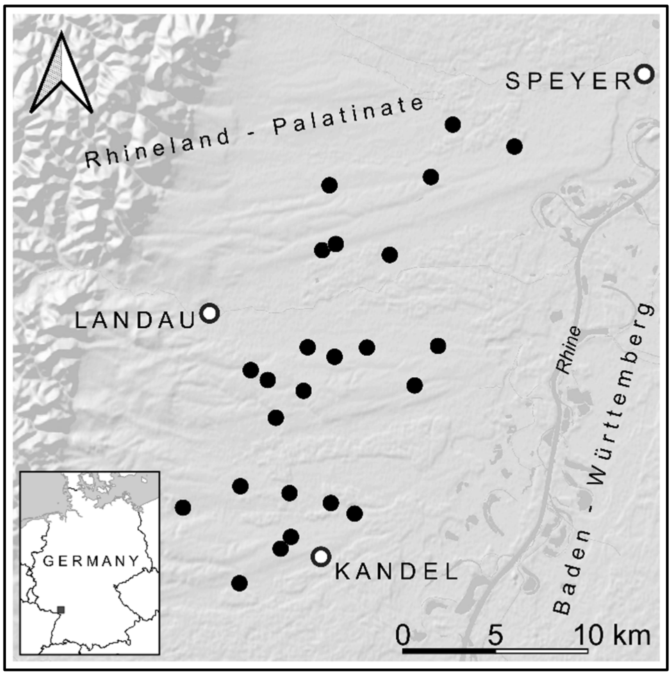


FIGURE S5.1 Location of landscapes in Rhineland-Palatinate, south-west Germany

FIGURE S5.2 Example set up of broad bean phytometers in a grassy field margin in the center of landscape Insheim_3. Photograph by Philipp Wolfgang Eckerter

TABLE S5.1 Use and availability of key pollen types included in the study and used for calculating the resource availability index for *Bombus terrestris*. Key pollen types are morphologically distinguishable pollen types that constitute > 5% of the collected pollen in at least one season (i.e. preceding, synchronous to broad bean flowering or across the whole season from April to July; Bertrand et al., 2019) and pollen types collected on woody plants. Plant species are species mapped in the studied landscapes that have the respective pollen morphology. Use of pollen types is given as % in the diet of *Bombus terrestris* during the time periods preceding and synchronous to broad bean flowering as well as pooled across the whole season. Volumes are estimated for single grains using measurements of Beug (2004) assuming spheroidal shapes of pollen grains. Index % gives the contribution of each pollen type to the resource availability index which is defined by relative cover of a pollen type proportional to the use times the relative volume (S5.1, Equation 6). Vegetation type is the type of plant species associated to one pollen type (Beug 2004; w = woody, h = herbaceous), and cover is the total area of the respective plant species in the studied landscapes. Three key pollen types were excluded from the calculations: Cucurbitaceae because they were not flowering during field work of the current study, and *Pterocarya* and *Rhamnus* because they were not found in our landscapes. In total, 69 detected plant species with the respective morphology of 32 pollen types were mapped.

		***B. terrestris* use (%)**				**Index (%)**				
Key pollen type	**Plant species**	**prec.**	**sync.**	**total**	**Volume (μm^3)**	**prec.**	**sync.**	**total**	**Vegetation type**	**Cover (ha)**
Abies	*A. alba, Abies* spec.	0.08	0.01	0.08	803 368	6.1	0.8	3.0	w	0.382
Acer	*A. campestre, A. platanoides, A. pseudoplatanus, A.* spec.	9.15	0.00	9.15	18 729	17.0	0.0	6.8	w	4.355
Aesculus hippocastanum	*A. hippocastanum*	4.11	0.00	4.11	6 790	2.8	0.0	1.1	w	0.107
Alnus	*A. glutinosa, A.* spec.	0.05	0.00	0.05	9 194	0.0	0.0	0.0	w	3.649
Asparagus	*A. officinalis*	0.00	5.30	0.00	5 560	0.0	3.4	2.0	h	19.539
Betula	*B. pendula*	1.12	0.00	1.12	9 795	1.1	0.0	0.4	w	0.944
Brassicaceae	*Brassica napus*	4.15	0.06	4.15	9 098	3.7	0.1	1.5	h	28.895
Carpinus betulus	*C. betulus*	0.25	0.00	0.25	32 788	0.8	0.0	0.3	w	2.290
Castanea	*C. sativa*	0.00	0.55	0.00	786	0.0	0.0	0.0	w	0.176
Cornus sanguinea	*C. sanguinea*	0.00	0.13	0.00	160 100	0.0	2.3	1.4	w	2.232
Corylus	*C. avellana, C.* spec.	0.02	0.00	0.02	12 452	0.0	0.0	0.0	w	1.545
Fagus	*F. sylvatica*	1.05	0.03	1.05	28 099	2.9	0.1	1.2	w	1.275
Ilex aquifolium	*I. aquifolium*	0.05	0.00	0.05	14 910	0.1	0.0	0.0	w	0.001
Juglans	*J. regia*	0.09	0.00	0.09	47 182	0.4	0.0	0.2	w	4.275
Ligustrum type	*Ligustrum vulgare, Syringa vulgaris*	0.00	0.07	0.00	17 726	0.0	0.1	0.1	w	0.961
Lonicera xylosteum type	*L. xylosteum*	0.03	0.00	0.03	107 493	0.3	0.0	0.1	w	0.062
Oleaceae (other)	*Forsythia × intermedia*	0.69	0.00	0.69	12 331	0.8	0.0	0.3	w	0.003
Papaver rhoeas type	*P. rhoeas*	0.00	13.0	0.00	9 120	0.0	13.6	8.1	h	0.012
Phacelia tanacetifolia	*P. tanacetifolia*	0.02	6.46	0.02	3 292	0.0	2.4	1.5	h	0.070
Picea	*Picea* spec.	0.00	0.02	0.00	659 710	0.0	1.4	0.8	w	0.601
Pinus	*Pinus* spec.	0.09	0.00	0.09	118 024	1.1	0.0	0.4	w	0.574

TABLE S5.1 *Cont.*

		***B. terrestris* use (%)**				**Index (%)**				
Key pollen type	**Plant species**	**prec.**	**sync.**	**total**	**Volume (μm^3)**	**prec.**	**sync.**	**total**	**Vegetation type**	**Cover (ha)**
Potentilla type	*Fragaria* spec. only	4.54	0.00	4.54	4 374	2.0	0.0	0.8	h	2.082
Prunus type	*Amelanchier ovalis, Crataegus* spec., *Cydonia oblonga, Malus domestica, Malus sylvestris, Malus* spec., *Mespilus germanica, Prunus armeniaca, P. avium, P. cerasus, P. domestica, P. domestica* subsp. *Syriaca, P. dulcis, P. laurocerasus, P. padus, P. persica, P. serotina, P. spinosa, P.* spec., *Pyrus communis, Pyrus domestica, Pyrus pyraster, Pyrus* spec.	21.2	0.00	21.2	23 810	50.1	0.0	20.2	w	21.565
Quercus	*Q. alba, Q. petraea, Q. robur, Q. rubra, Q. spec.*	0.69	0.00	0.69	14 796	1.0	0.0	0.4	w	3.727
Robinia pseudoacacia	*R. pseudoacacia*	0.00	1.10	0.00	15 862	0.0	2.0	1.2	w	1.634
Rosaceae	*R. agrestis, R. canina, R.* spec., *Sorbus aucuparia, Sorbus domestica, Sorbus* spec.	1.66	5.14	1.66	10 114	1.7	6.0	4.2	w	0.967
Rubus type	*R. fruticosus, R. idaeus*	0.00	23.8	0.00	11 599	0.0	31.7	19.0	w	4.262
Salix	*S. alba, S. babylonica, S. caprea, S. fragilis, S. matsudana 'Tortuosa', S.* spec.	37.1	0.35	37.1	2 157	7.9	0.1	3.2	w	6.870
Sambucus nigra type	*S. nigra, S. racemosa, S.* spec.	0.11	0.13	0.11	2 405	0.0	0.0	0.0	w	1.808
Tilia	*T. chordata, T. platyphyllos*	0.02	20.5	0.02	13 196	0.0	4.9	2.9	w	0.146
Trifolium repens type	*T. repens*	0.03	5.04	0.03	8 476	0.0	31.0	18.5	h	0.554
Viburnum	*V. lantana, V. opulus*	0.00	0.04	0.00	7 645	0.0	0.0	0.0	w	0.220
32 pollen types	**69 plant species**	**86.3**	**81.7**	**83.7**		**100**	**100**	**100**		**115.8**

TABLE S5.2 Pollen types other than key pollen types are morphologically distinguishable pollen types that constitute <5% of the collected pollen in at least one season (i.e. preceding, synchronous to broad bean flowering or across the whole season from April to July; Bertrand et al., 2019). Use of pollen types is given as % in the diet of *Bombus terrestris* during the time periods preceding and synchronous to broad bean flowering as well as pooled across the whole season. Vegetation type is the type of plant species associated to one pollen type (Beug, 2004; w = woody, h = herbaceous).

	B. terrestris **use (%)**			
Pollen type	**prec.**	**sync.**	**total**	**Vegetation type**
Achillea type	0.00	0.07	0.0	h
Allium type	0.00	0.01	0.0	h
Apiaceae	0.00	0.79	0.5	h
Campanula type	0.78	0.00	0.3	h
Campanulaceae	0.00	0.01	0.0	h
Caryophyllaceae	0.09	0.00	0.0	h
Centaurea cyanus type	0.00	0.04	0.0	h
Centaurea jacea type	0.00	0.10	0.1	h
Cerealia type	0.38	0.00	0.1	h
Chelidonium majus	0.26	0.00	0.1	h
Chenopodiaceae	1.17	0.00	0.4	h
Cichorioideae	1.74	0.04	0.7	h
Corydalis	0.02	0.00	0.0	h
Cucurbita	0.00	0.74	0.5	h
Echium	0.26	0.00	0.1	h
Galium type	0.00	0.02	0.0	h
Genista type	1.11	0.04	0.4	h
Helianthemum	0.00	0.74	0.5	h
Hypericum perforatum type	0.00	3.51	2.2	h
Lamium type	4.65	0.00	1.7	h
Malvaceae	0.00	0.01	0.0	h
Mentha type	0.22	1.00	0.7	h
ND (pollen grains could not be identified)	0.00	3.08	1.9	NA
Plantago lanceolata type	0.00	0.01	0.0	h
Poaceae	0.34	0.15	0.2	h
Potentilla type (other than *Fragaria* spec.)	0.00	2.23	1.1	h
Pterocarya	0.02	0.00	0.0	w
Ranunculus acris type	0.12	0.15	0.1	h
Reseda	0.00	0.84	0.5	h
Rhamnus type	0.00	1.04	0.7	w
Ribes	0.98	0.05	0.4	h
Rinanthus type	1.26	0.04	0.5	h
Sedum type	0.00	1.61	1.0	h
Silene type	0.23	0.00	0.1	h
Solanum dulcamara	0.00	0.04	0.0	h
Stachys sylvatica type	0.02	0.00	0.0	h
Thalictrum	0.00	0.04	0.0	h
Trifolium pratense type	0.02	0.89	0.6	h
Urtica	0.00	0.09	0.1	h
Vicia type	0.00	0.90	0.6	h
39 pollen types + ND	**13.7**	**18.3**	**16.3**	

TABLE S5.3 Pearson correlation matrix between seed set (seeds per pod) and predictors using different mapping approaches. Floral resource maps are represented by floral resource availability preceding and synchronous to broad bean flowering as well as pooled across the whole season from April to July (total), classical habitat maps by landscape variables (proportions of arable land, permanent crops, forest, other woody and herbaceous semi-natural habitat and urban, as well as its Euclidean distances). "SNH" stands for semi-natural habitat. For visualisation of the correlation matrix see FIGURE S5.3.

	seed set	**floral resource maps**			**classical habitat maps**								
	sp	**prec.**	**sync.**	**total**	**arable**	**crop permanent**	**forest**	**snh herb**	**snh woody**	**urban**	**dist forest**	**dist snh herb**	**dist snh woody**
Preceding pollen resources	0.42[c]												
Sychronous pollen resources	-0.06	0.41[c]											
Total pollen resources	0.16	0.76[a]	0.90[a]										
Arable land	-0.42[c]	-0.60[b]	-0.52[b]	-0.65[a]									
Permanent crops	0.24	0.43[c]	0.11	0.27	-0.26								
Forest	0.26	0.40[d]	0.55[b]	0.59[b]	-0.70[a]	-0.02							
Herbaceous SNH	0.14	0.32	0.23	0.45[c]	-0.74[a]	0.01	0.20						
Woody SNH	0.34	0.41	0.35[d]	0.42[c]	-0.78[a]	0.12	0.37	0.65[a]					
Urban area	0.46[c]	0.13	0.08	0.11	-0.41[c]	-0.23	0.01	0.40[d]	0.51[c]				
Distance forest	-0.19	-0.23	-0.55[b]	-0.50[c]	0.49[c]	0.11	-0.45[c]	-0.28	-0.56[b]	-0.29			
Distance herbaceous SNH	-0.03	-0.15	-0.26	-0.24	0.31	-0.17	-0.20	-0.19	-0.29	-0.09	0.10		
Distance woody SNH	0.05	-0.03	-0.29	-0.18	0.29	0.06	0.04	-0.33	-0.58[b]	-0.27	0.41[c]	-0.08	
Distance urban area	-0.20	-0.17	0.12	0.01	0.38[d]	-0.01	-0.07	-0.37[d]	-0.35[d]	-0.54[b]	0.15	0.16	0.26

Notes: correlation is significant at the [a] 0.001-level; [b] 0.01-level; [c] 0.05-level; [d] 0.10-level.

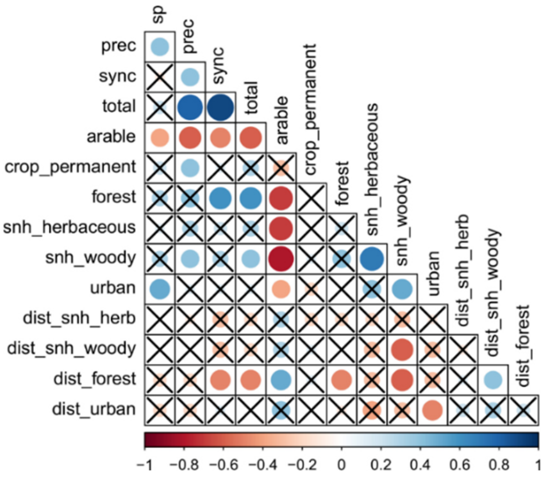


FIGURE S5.3 Pearson correlation matrix between seed set (seeds per pod) and predictors using different mapping approaches. Floral resource maps are represented by floral resource availability preceding and synchronous to broad bean flowering as well as pooled across the whole season from April to July (total), classical habitat maps by landscape variables (proportions of arable land, permanent crops, forest, other woody and herbaceous semi-natural habitat and urban, as well as its Euclidean distances). An “X” was plotted over circles representing non-significant correlations (i.e. $p \geq 0.05$). For relating r values see TABLE S5.3. The matrix was drawn using the *‘corrplot’* package in *R* (Wei & Simko, 2017).

TABLE S5.4 Contribution of landscape context to floral resource availability in the landscapes during time periods preceding and synchronous to broad bean flowering and across the whole season from April to July using linear regression.

Floral resources	**Predictor**	**df**	**t-value**	**R^2_{mult}**	***p* value**
Preceding	**Arable**	**22**	**-2.05**	**0.364**	**0.002**
	Permanent crop	**22**	**2.20**	**0.181**	**0.038**
	Forest	22	2.04	0.159	0.054
	Herbaceous SNH	22	1.57	0.101	0.130
	Woody SNH	**22**	**2.11**	**0.168**	**0.047**
	Urban	22	0.62	0.017	0.540
	Distance forest	22	-1.11	0.053	0.281
	Distance herbaceous SNH	22	-0.69	0.021	0.495
	Distance woody SNH	22	0.13	0.001	0.900
	Distance urban	22	-0.80	0.028	0.433
Synchronous	**Arable**	**22**	**-2.88**	**0.274**	**0.009**
	Permanent crop	22	0.52	0.012	0.605
	Forest	**22**	**3.12**	**0.307**	**0.005**
	Herbaceous SNH	22	1.10	0.052	0.285
	Woody SNH	22	1.73	0.120	0.097
	Urban	22	0.39	0.007	0.698
	Distance forest	**22**	**-3.08**	**0.301**	**0.006**
	Distance herbaceous SNH	22	-1.26	0.067	0.222
	Distance woody SNH	22	-1.43	0.085	0.168
	Distance urban	22	0.58	0.015	0.571
Total	**Arable**	**22**	**-4.01**	**0.422**	**0.001**
	Permanent crop	22	1.33	0.074	0.198
	Forest	**22**	**3.43**	**0.349**	**0.002**
	Herbaceous SNH	22	1.48	0.090	0.154
	Woody SNH	**22**	**2.19**	**0.180**	**0.039**
	Urban	22	0.52	0.012	0.606
	Distance forest	**22**	**-2.69**	**0.248**	**0.013**
	Distance herbaceous SNH	22	-1.19	0.060	0.247
	Distance woody SNH	22	-0.84	0.031	0.413
	Distance urban	22	0.07	0.000	0.947

TABLE S5.5 Comparison of seed set predictability and contributions of landscape context to floral resource availability preceding, synchronous to broad bean flowering and across the whole season from April to July using broader and finer classifications of classical habitat maps and linear regression. Significant relations (i.e. $p < 0.05$) are printed in bold.

Response	Classification type	Predictor	df	*t-value*	R^2_{mult}	*p*
Seed set	Broad	Crop	22	-1.89	0.140	0.072
		SNH	22	1.34	0.076	0.193
	Fine	**Arable**	**22**	**-2.19**	**0.179**	**0.039**
		Permanent crops	22	1.14	0.055	0.269
		Forest	22	1.25	0.066	0.225
		Herbaceous SNH	22	0.67	0.020	0.509
		Woody SNH	22	1.71	0.117	0.102
Preceding floral resources	Broad	Crop	22	-2.77	0.259	0.011
		SNH	22	2.52	0.224	0.020
	Fine	**Arable**	**22**	**-3.55**	**0.364**	**0.002**
		Permanent crops	**22**	**2.20**	**0.181**	**0.038**
		Forest	22	2.04	0.159	0.054
		Herbaceous SNH	22	1.57	0.101	0.130
		Woody SNH	**22**	**2.11**	**0.168**	**0.047**
Synchronous floral resources	Broad	**Crop**	**22**	**-2.79**	**0.261**	**0.011**
		SNH	**22**	**2.82**	**0.266**	**0.010**
	Fine	**Arable**	**22**	**-2.88**	**0.274**	**0.009**
		Permanent crops	22	0.52	0.012	0.605
		Forest	**22**	**3.12**	**0.307**	**0.005**
		Herbaceous SNH	22	1.10	0.052	0.285
		Woody SNH	22	1.73	0.120	0.097
Total floral resources	Broad	**Crop**	**22**	**-3.50**	**0.357**	**0.002**
		SNH	**22**	**3.40**	**0.345**	**0.003**
	Fine	**Arable**	**22**	**-4.01**	**0.422**	**0.001**
		Permanent crops	22	1.33	0.074	0.198
		Forest	**22**	**3.43**	**0.349**	**0.002**
		Herbaceous SNH	22	1.48	0.090	0.154
		Woody SNH	**22**	**2.19**	**0.180**	**0.039**

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REFERENCES

Abrol, D. P. (1990). Energetics of nectar production in some apple cultivars as a predictor of floral choice by honeybees. *Tropical Ecology*, *31*(1), 116–122.

Abrol, D. P. (1992). Energetics of nectar production in some strawberry cultivars as a predictor of floral choice by honeybees. *Journal of Biosciences*, *17*(1), 41–44. https://doi.org/10.1007/BF02716772

Aizen, M. A., Aguiar, S., Biesmeijer, J. C., Garibaldi, L. A., Inouye, D. W., Jung, C., Martins, D. J., Medel, R., Morales, C. L., Ngo, H., Pauw, A., Paxton, R. J., Sáez, A., & Seymour, C. L. (2019). Global agricultural productivity is threatened by increasing pollinator dependence without a parallel increase in crop diversification. *Global Change Biology*, *25*(10), 3516–3527. https://doi.org/10.1111/gcb.14736

Akaike, H. (1987). Factor analysis and AIC. *Psychometrika*, *52*(3), 317–332.

Albrecht, M., Duelli, P., Schmid, B., & Müller, C. B. (2007). Interaction diversity within quantified insect food webs in restored and adjacent intensively managed meadows. *Journal of Animal Ecology*, *76*(5), 1015–1025. https://doi.org/10.1111/j.1365-2656.2007.01264.x

Albrecht, M., Kleijn, D., Williams, N. M., Tschumi, M., Blaauw, B. R., Bommarco, R., Campbell, A. J., Dainese, M., Drummond, F. A., Entling, M. H., Ganser, D., Arjen de Groot, G., Goulson, D., Grab, H., Hamilton, H., Herzog, F., Isaacs, R., Jacot, K., Jeanneret, P., … Sutter, L. (2021). The effectiveness of flower strips and hedgerows on pest control, pollination services and crop yield: A quantitative synthesis. *Ecology Letters*, *23*, 1488–1498. https://doi.org/10.1111/ele.13576

Ammann, L., Bosem-Baillod, A., Eckerter, P. W., Entling, M. H., Albrecht, M., & Herzog, F. (2020). Aphid predators reduce pest aphids and are better predicted by classical habitat maps than floral resource maps. *Unpublished Manuscript, Last Modified June 17. Microsoft Word File*.

Anderson, J. R. (1976). *A Land Use and Land Cover Classification System for Use with Remote Sensor Data*. U.S. Government Printing Office.

Aouar-sadli, M., Louadi, K., & Doumandji, S.-E. (2008). Pollination of the broad bean (Vicia faba L. var. Major) (Fabaceae) by wild bees and honey bees (Hymenoptera: Apoidea) and its impact on the seed production in the Tizi-Ouzou area (Algeria). *African Journal of Agricultural Research*, *3(4)*, 266–272.

Bailey, S., Requier, F., Nusillard, B., Roberts, S. P. M., Potts, S. G., & Bouget, C. (2014). Distance from forest edge affects bee pollinators in oilseed rape fields. *Ecology and Evolution*, *4*(4), 370–380. https://doi.org/10.1002/ece3.924

Bartomeus, I., Potts, S. G., Steffan-Dewenter, I., Vaissière, B. E., Woyciechowski, M., Krewenka, K. M., Tscheulin, T., Roberts, S. P. M., Szentgyörgyi, H., Westphal, C., & Bommarco, R. (2014). Contribution of insect pollinators to crop yield and quality varies with agricultural intensification. *PeerJ*, *2*, e328. https://doi.org/10.7717/peerj.328

Bartomeus, I., & Winfree, R. (2011). The Circe Principle: Are pollinators waylaid by attractive habitats? *Current Biology*, *21*(17), R652–R654. https://doi.org/10.1016/j.cub.2011.07.010

Bartón, K. (2020). *MuMIn: Multi-Model Inference* (R package version 1.43.17) [Computer software]. https://CRAN.R-project.org/package=MuMIn

Bartual, A. M., Sutter, L., Bocci, G., Moonen, A.-C., Cresswell, J., Entling, M., Giffard, B., Jacot, K., Jeanneret, P., Holland, J., Pfister, S., Pintér, O., Veromann, E., Winkler, K., & Albrecht, M. (2019). The potential of different semi-natural habitats to sustain pollinators and natural enemies in European agricultural landscapes. *Agriculture, Ecosystems & Environment*, *279*, 43–52. https://doi.org/10.1016/j.agee.2019.04.009

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*(1). https://doi.org/10.18637/jss.v067.i01

Benton, T. G., Vickery, J. A., & Wilson, J. D. (2003). Farmland biodiversity: Is habitat heterogeneity the key? *Trends in Ecology & Evolution*, *18*(4), 182–188. https://doi.org/10.1016/S0169-5347(03)00011-9

Bentrup, G., Hopwood, J., Adamson, N. L., & Vaughan, M. (2019). Temperate Agroforestry Systems and Insect Pollinators: A Review. *Forests*, *10*(11), 981. https://doi.org/10.3390/f10110981

Berkvens, N., Landuyt, C., Deforce, K., Berkvens, D., Tirry, L., & De Clercq, P. (2010). Alternative foods for the multicoloured Asian lady beetle Harmonia axyridis (Coleoptera: Coccinellidae). *European Journal of Entomology*, *107*(2), 189–195. https://doi.org/10.14411/eje.2010.025

Bertrand, C., Eckerter, P. W., Ammann, L., Entling, M. H., Gobet, E., Herzog, F., Mestre, L., Tinner, W., & Albrecht, M. (2019). Seasonal shifts and complementary use of pollen sources by two bees, a lacewing and a ladybeetle species in European agricultural landscapes. *Journal of Applied Ecology*, *56*(11), 2431–2442. https://doi.org/10.1111/1365-2664.13483

Beug, H.-J. (2004). *Leitfaden der Pollenbestimmung für Mitteleuropa und angrenzende Gebiete*. Verlag Dr. Friedrich Pfeil.

Bjornstad, O. N., & Cai, J. (2020). *ncf: Spatial Covariance Functions* (1.2-9) [Computer software]. https://CRAN.R-project.org/package=ncf

Blaauw, B. R., & Isaacs, R. (2014). Flower plantings increase wild bee abundance and the pollination services provided to a pollination-dependent crop. *Journal of Applied Ecology*, *51*(4), 890–898. https://doi.org/10.1111/1365-2664.12257

Blüthgen, N., Fründ, J., Vázquez, D. P., & Menzel, F. (2008). What do interaction network metrics tell us about specialization and biological traits? *Ecology*, *89*(12), 3387–3399. https://doi.org/10.1890/07-2121.1

Blüthgen, N., Menzel, F., & Blüthgen, N. (2006). Measuring specialization in species interaction networks. *BMC Ecology*, *6*(1), 9. https://doi.org/10.1186/1472-6785-6-9

Bommarco, R., Kleijn, D., & Potts, S. G. (2013). Ecological intensification: Harnessing ecosystem services for food security. *Trends in Ecology & Evolution*, *28*(4), 230–238. https://doi.org/10.1016/j.tree.2012.10.012

Bosch, J. (1994a). Improvement of field management of Osmia cornuta (Latreille) (Hymenoptera, Megachilidae) to pollinate almond. *Apidologie*, *25*(1), 71–83. https://doi.org/10.1051/apido:19940108

Bosch, J. (1994b). The nesting behaviour of the mason bee Osmia cornuta (Latr) with special reference to its pollinating potential (Hymenoptera, Megachilidae). *Apidologie*, *25*, 84–93.

Bosch, J. (1994c). Osmia cornuta Latr. (Hym., Megachilidae) as a potential pollinator in almond orchards. *Journal of Applied Entomology*, *117*(1–5), 151–157. https://doi.org/10.1111/j.1439-0418.1994.tb00720.x

Bosch, J., & Kemp, W. P. (2004). Effect of pre-wintering and wintering temperature regimes on weight loss, survival, and emergence time in the mason bee *Osmia cornuta* (Hymenoptera: Megachilidae). *Apidologie*, *35*(5), 469–479. https://doi.org/10.1051/apido:2004035

Bosch, J., Osorio-Canadas, S., Sgolastra, F., & Vicens, N. (2021). Use of a Managed Solitary Bee to Pollinate Almonds: Population Sustainability and Increased Fruit Set. *Insects*, *12*(1), 56. https://doi.org/10.3390/insects12010056

Bosch, J., & Vicens, N. (2002). Body size as an estimator of production costs in a solitary bee: Body size in a solitary bee. *Ecological Entomology*, *27*(2), 129–137. https://doi.org/10.1046/j.1365-2311.2002.00406.x

Bosch, J., & Vicens, N. (2005). Sex allocation in the solitary bee Osmia cornuta: Do females behave in agreement with Fisher's theory? *Behavioral Ecology and Sociobiology*, *59*(1), 124–132. https://doi.org/10.1007/s00265-005-0017-8

Bosch, J., & Vicens, N. (2006). Relationship between body size, provisioning rate, longevity and reproductive success in females of the solitary bee Osmia cornuta. *Behavioral Ecology and Sociobiology*, *60*(1), 26–33. https://doi.org/10.1007/s00265-005-0134-4

Bukovinszky, T., Rikken, I., Evers, S., Wäckers, F. L., Biesmeijer, J. C., Prins, H. H. T., & Kleijn, D. (2017). Effects of pollen species composition on the foraging behaviour and offspring performance of the mason bee Osmia bicornis (L.). *Basic and Applied Ecology*, *18*, 21–30. https://doi.org/10.1016/j.baae.2016.11.001

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (2nd ed.). Springer.

Burnham, K. P., Anderson, D. R., & Huyvaert, K. P. (2011). AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. *Behavioral Ecology and Sociobiology*, *65*(1), 23–35. https://doi.org/10.1007/s00265-010-1029-6

Cameron, S. A., Corbet, S. A., & Whitfield, J. B. (2019). Bumble bees (Hymenoptera: Apidae: Bombus terrestris) collecting honeydew from the giant willow aphid (Hemiptera: Aphididae). *Journal of Hymenoptera Research*, *68*, 75–83. https://doi.org/10.3897/jhr.68.30495

Campbell, A. J., Wilby, A., Sutton, P., & Wäckers, F. L. (2017). Do sown flower strips boost wild pollinator abundance and pollination services in a spring-flowering crop? A case study from UK cider apple orchards. *Agriculture, Ecosystems & Environment*, *239*, 20–29. https://doi.org/10.1016/j.agee.2017.01.005

Carvell, C., Bourke, A. F. G., Dreier, S., Freeman, S. N., Hulmes, S., Jordan, W. C., Redhead, J. W., Sumner, S., Wang, J., & Heard, M. S. (2017). Bumblebee family lineage survival is enhanced in high-quality landscapes. *Nature*, *543*(7646), 547–549. https://doi.org/10.1038/nature21709

Cassman, K. G. (1999). Ecological intensification of cereal production systems: Yield potential, soil quality, and precision agriculture. *Proceedings of the National Academy of Sciences*, *96*(11), 5952–5959. https://doi.org/10.1073/pnas.96.11.5952

Ceballos, G., Ehrlich, P. R., Barnosky, A. D., García, A., Pringle, R. M., & Palmer, T. M. (2015). Accelerated modern human–induced species losses: Entering the sixth mass extinction. *Science Advances*, *1*(5), e1400253. https://doi.org/10.1126/sciadv.1400253

Chambers, V. H. (1945). British bees and wind-borne pollen. *Nature*, *3927*, 145.

Chapin III, F. S., Zavaleta, E. S., Eviner, V. T., Naylor, R. L., Vitousek, P. M., Reynolds, H. L., Hooper, D. U., Lavorel, S., Sala, O. E., Hobbie, S. E., Mack, M. C., & Díaz, S. (2000). Consequences of changing biodiversity. *Nature*, *405*(6783), 234–242. https://doi.org/10.1038/35012241

Chen, J., Saunders, S. C., Crow, T. R., Naiman, R. J., Brosofske, K. D., Mroz, G. D., Brookshire, B. L., & Franklin, J. F. (1999). Microclimate in Forest Ecosystem and Landscape Ecology: Variations in local climate can be used to monitor and compare the effects of different management regimes. *BioScience*, *49*(4), 288–297. https://doi.org/ttps://doi.org/10.2307/1313612

Cole, L. J., Brocklehurst, S., Robertson, D., Harrison, W., & McCracken, D. I. (2017). Exploring the interactions between resource availability and the utilisation of semi-natural habitats by insect pollinators in an intensive agricultural landscape. *Agriculture, Ecosystems & Environment*, *246*, 157–167. https://doi.org/10.1016/j.agee.2017.05.007

Corbet, S. A., Unwin, D. M., & PRŷS-JONES, O. E. (1979). Humidity, nectar and insect visits to flowers, with special reference to Crataegus, Tilia and Echium. *Ecological Entomology*, *4*(1), 9–22. https://doi.org/10.1111/j.1365-2311.1979.tb00557.x

Coudrain, V., Herzog, F., & Entling, M. H. (2013). Effects of Habitat Fragmentation on Abundance, Larval Food and Parasitism of a Spider-Hunting Wasp. *PLoS ONE*, *8*(3), e59286. https://doi.org/10.1371/journal.pone.0059286

Coudrain, V., Rittiner, S., Herzog, F., Tinner, W., & Entling, M. H. (2016). Landscape distribution of food and nesting sites affect larval diet and nest size, but not abundance of *Osmia bicornis*: Fragmentation impacts on a multiple-habitat user. *Insect Science*, *23*(5), 746–753. https://doi.org/10.1111/1744-7917.12238

Crone, E. E., & Williams, N. M. (2016). Bumble bee colony dynamics: Quantifying the importance of land use and floral resources for colony growth and queen production. *Ecology Letters*, *19*(4), 460–468. https://doi.org/10.1111/ele.12581

Crutzen, P. J. (2002). Geology of mankind—The Anthropocene. *Nature*, *415*, 23.

Crutzen, P. J., & Stoermer, E. F. (2000). The "Anthropocene." *IGBP Global Change Newsletter*, *41*, 17–18.

Dainese, M., Martin, E. A., Aizen, M. A., Albrecht, M., Bartomeus, I., Bommarco, R., Carvalheiro, L. G., Chaplin-Kramer, R., Gagic, V., Garibaldi, L. A., Ghazoul, J., Grab, H., Jonsson, M., Karp, D. S., Kennedy, C. M., Kleijn, D., Kremen, C., Landis, D. A., Letourneau, D. K., … Steffan-Dewenter, I. (2019). A global synthesis reveals biodiversity-mediated benefits for crop production. *SCIENCE ADVANCES*, 14.

Damschen, E. I., Brudvig, L. A., Burt, M. A., Fletcher, R. J., Haddad, N. M., Levey, D. J., Orrock, J. L., Resasco, J., & Tewksbury, J. J. (2019). Ongoing accumulation of plant diversity through habitat connectivity in an 18-year experiment. *Science*, *365*(6460), 1478–1480. https://doi.org/10.1126/science.aax8992

Darvill, B., Knight, M. E., & Goulson, D. (2004). Use of genetic markers to quantify bumblebee foraging range and nest density. *Oikos*, *107*(3), 471–478. https://doi.org/10.1111/j.0030-1299.2004.13510.x

Davies, K. F., Margules, C. R., & Lawrence, J. F. (2000). Which traits of species predict population declines in experimental forest fragments? *Ecology*, *81*(5), 1450–1461. https://doi.org/10.1890/0012-9658(2000)081[1450:WTOSPP]2.0.CO;2

Dennis, R. L. H., Shreeve, T. G., & Van Dyck, H. (2006). Habitats and resources: The need for a resource-based definition to conserve butterflies. *Biodiversity and Conservation*, *15*(6), 1943–1966. https://doi.org/10.1007/s10531-005-4314-3

Dixon, A. F. G., Honěk, A., Keil, P., Kotela, M. A. A., Šizling, A. L., & Jarošík, V. (2009). Relationship between the minimum and maximum temperature thresholds for development in insects. *Functional Ecology*, *23*(2), 257–264. https://doi.org/10.1111/j.1365-2435.2008.01489.x

Dormann, C. F., Fruend, J., Gruber, B., & Bluethgen, N. (2009). Indices, graphs and null models: Analyzing bipartite ecological networks. *The Open Ecology Journal*, *2*, 7–24.

Dramstad, W., & Fry, G. (1995). Foraging activity of bumblebees (Bombus) in relation to flower resources on arable land. *Agriculture, Ecosystems & Environment*, *53*(2), 123–135. https://doi.org/10.1016/0167-8809(94)00561-R

Eckerter, P. W., Albrecht, M., Bertrand, C., Gobet, E., Herzog, F., Pfister, S. C., Tinner, W., & Entling, M. H. (2021). Effects of temporal floral resource availability and non-crop habitats on broad bean pollination. *Unpublished Manuscript, Last Modified April 4. Microsoft Word File*.

Eckerter, P. W., Albus, L., Natarajan, S., Albrecht, M., Ammann, L., Gobet, E., Herzog, F., Tinner, W., & Entling, M. H. (2020). Using temporally resolved floral resource maps to explain bumblebee colony performance in agricultural landscapes. *Agronomy*, *10*(12), 1993. https://doi.org/10.3390/agronomy10121993

Everaars, J., Strohbach, M. W., Gruber, B., & Dormann, C. F. (2011). Microsite conditions dominate habitat selection of the red mason bee (Osmia bicornis, Hymenoptera: Megachilidae) in an urban environment: A case study from Leipzig, Germany. *Landscape and Urban Planning*, *103*(1), 15–23. https://doi.org/10.1016/j.landurbplan.2011.05.008

Fahrig, L. (2013). Rethinking patch size and isolation effects: The habitat amount hypothesis. *Journal of Biogeography*, *40*(9), 1649–1663. https://doi.org/10.1111/jbi.12130

Field, A. (2017). *Discovering Statistics Using IBM SPSS Statistics: North American Edition*. SAGE Publications.

Filipiak, M. (2018). A Better Understanding of Bee Nutritional Ecology Is Needed to Optimize Conservation Strategies for Wild Bees—The Application of Ecological Stoichiometry. *Insects*, *9*(3), 85. https://doi.org/10.3390/insects9030085

Filipiak, M. (2019). Key pollen host plants provide balanced diets for wild bee larvae: A lesson for planting flower strips and hedgerows. *Journal of Applied Ecology*, *56*(6), 1410–1418. https://doi.org/10.1111/1365-2664.13383

Foley, J. A. (2005). Global Consequences of Land Use. *Science*, *309*(5734), 570–574. https://doi.org/10.1126/science.1111772

Forman, R. T. T. (1995). *Land Mosaics: The Ecology of Landscapes and Regions* (1st ed.). Cambridge University Press.

Forrest, J. R. K., Thorp, R. W., Kremen, C., & Williams, N. M. (2015). Contrasting patterns in species and functional-trait diversity of bees in an agricultural landscape. *Journal of Applied Ecology*, *52*(3), 706–715. https://doi.org/10.1111/1365-2664.12433

Fortel, L., Henry, M., Guilbaud, L., Mouret, H., & Vaissière, B. E. (2016). Use of human-made nesting structures by wild bees in an urban environment. *Journal of Insect Conservation*, *20*(2), 239–253. https://doi.org/10.1007/s10841-016-9857-y

Free, J. B. (1966). The pollination requirements of broad beans and field beans (Vicia faba). *The Journal of Agricultural Science*, *66*(3), 395–397. https://doi.org/10.1017/S002185960006370X

Free, J. B., & Williams, I. H. (1970). Preliminary Investigations on the Occupation of Artificial Nests by Osmia rufa L. (Hymenoptera, Megachilidae). *The Journal of Applied Ecology*, *7*(3), 559. https://doi.org/10.2307/2401978

Fussell, M., & Corbet, S. A. (1992). Flower usage by bumble-bees: A basis for forage plant management. *Journal of Applied Ecology*, *29(2)*, 451–465.

Gallai, N., Salles, J.-M., Settele, J., & Vaissière, B. E. (2009). Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecological Economics*, *68*(3), 810–821. https://doi.org/10.1016/j.ecolecon.2008.06.014

Ganser, D., Albrecht, M., & Knop, E. (2020). Wildflower strips enhance wild bee reproductive success. *Journal of Applied Ecology*, 1365-2664.13778. https://doi.org/10.1111/1365-2664.13778

Ganser, D., Mayr, B., Albrecht, M., & Knop, E. (2018). Wildflower strips enhance pollination in adjacent strawberry crops at the small scale. *Ecology and Evolution*, *8*(23), 11775–11784. https://doi.org/10.1002/ece3.4631

Garibaldi, L. A., Carvalheiro, L. G., Leonhardt, S. D., Aizen, M. A., Blaauw, B. R., Isaacs, R., Kuhlmann, M., Kleijn, D., Klein, A. M., Kremen, C., Morandin, L., Scheper, J., & Winfree, R. (2014). From research to action: Enhancing crop yield through wild pollinators. *Frontiers in Ecology and the Environment*, *12*(8), 439–447. https://doi.org/10.1890/130330

Garibaldi, L. A., Steffan-Dewenter, I., Kremen, C., Morales, J. M., Bommarco, R., Cunningham, S. A., Carvalheiro, L. G., Chacoff, N. P., Dudenhöffer, J. H., Greenleaf, S. S., Holzschuh, A., Isaacs, R., Krewenka, K., Mandelik, Y., Mayfield, M. M., Morandin, L. A., Potts, S. G., Ricketts, T. H., Szentgyörgyi, H., … Klein, A. M. (2011). Stability of pollination services decreases with isolation from natural areas despite honey bee visits: Habitat isolation and pollination stability. *Ecology Letters*, *14*(10), 1062–1072. https://doi.org/10.1111/j.1461-0248.2011.01669.x

Garibaldi, L. A., Steffan-Dewenter, I., Winfree, R., Aizen, M. A., Bommarco, R., Cunningham, S. A., Kremen, C., Carvalheiro, L. G., Harder, L. D., Afik, O., Bartomeus, I., Benjamin, F., Boreux, V., Cariveau, D., Chacoff, N. P., Dudenhoffer, J. H., Freitas, B. M., Ghazoul, J., Greenleaf, S., … Klein, A. M. (2013). Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science*, *339*(6127), 1608–1611. https://doi.org/10.1126/science.1230200

Garratt, M. P. D., Coston, D. J., Truslove, C. L., Lappage, M. G., Polce, C., Dean, R., Biesmeijer, J. C., & Potts, S. G. (2014). The identity of crop pollinators helps target conservation for improved ecosystem services. *Biological Conservation*, *169*, 128–135. https://doi.org/10.1016/j.biocon.2013.11.001

Gathmann, A., & Tscharntke, T. (2002). Foraging ranges of solitary bees. *Journal of Animal Ecology*, *71*, 757–764.

Gelman, A. (2008). Scaling regression inputs by dividing by two standard deviations. *Statistics in Medicine*, *27*(15), 2865–2873. https://doi.org/10.1002/sim.3107

Genissel, A., Aupinel, P., Bressac, C., Tasei, J.-N., & Chevrier, C. (2002). Influence of pollen origin on performance of Bombus terrestris micro-colonies. *Entomologia Experimentalis et Applicata*, *104*(2–3), 329–336. https://doi.org/10.1046/j.1570-7458.2002.01019.x

Goodell, K. (2003). Food availability affects Osmia pumila (Hymenoptera: Megachilidae) foraging, reproduction, and brood parasitism. *Oecologia*, *134*(4), 518–527. https://doi.org/10.1007/s00442-002-1159-2

Goulson, D. (2009). *Bumblebees: Behaviour, Ecology, and Conservation* (2 Revised edition). Oxford University Press, USA.

Goulson, D., Hughes, W., Derwent, L., & Stout, J. (2002). Colony growth of the bumblebee, Bombus terrestris, in improved and conventional agricultural and suburban habitats. *Oecologia*, *130*(2), 267–273. https://doi.org/10.1007/s004420100803

Goulson, D., Nicholls, E., Botias, C., & Rotheray, E. L. (2015). Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science*, *347*(6229), 1255957–1255957. https://doi.org/10.1126/science.1255957

Grab, H., Blitzer, E. J., Danforth, B., Loeb, G., & Poveda, K. (2017). Temporally dependent pollinator competition and facilitation with mass flowering crops affects yield in co-blooming crops. *Scientific Reports*, *7*(1), 45296. https://doi.org/10.1038/srep45296

Greenleaf, S. S., & Kremen, C. (2006). Wild bees enhance honey bees' pollination of hybrid sunflower. *Proceedings of the National Academy of Sciences*, *103*(37), 13890–13895. https://doi.org/10.1073/pnas.0600929103

Gruber, B., Eckel, K., Everaars, J., & Dormann, C. F. (2011). On managing the red mason bee (Osmia bicornis) in apple orchards. *Apidologie*, *42*(5), 564–576. https://doi.org/10.1007/s13592-011-0059-z

Habel, J. C., Samways, M. J., & Schmitt, T. (2019). Mitigating the precipitous decline of terrestrial European insects: Requirements for a new strategy. *Biodiversity and Conservation*, *28*(6), 1343–1360. https://doi.org/10.1007/s10531-019-01741-8

Haider, M., Dorn, S., Sedivy, C., & Müller, A. (2013). Phylogeny and floral hosts of a predominantly pollen generalist group of mason bees (Megachilidae: Osmiini). *Biological Journal of the Linnean Society*, 14.

Hallmann, C. A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D., & de Kroon, H. (2017). More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLOS ONE*, *12*(10), e0185809. https://doi.org/10.1371/journal.pone.0185809

Hansted, L., Grout, B. W. W., & Toldam-Andersen, T. B. (2014). An assessment of Osmia rufa (syn. Bicornis) as a pollinator of the sour cherry (Prunus cerasus) cv. *Journal of Apicultural Research*, *53*(1), 177–182.

Hanula, J. L., Horn, S., & O'Brien, J. J. (2015). Have changing forests conditions contributed to pollinator decline in the southeastern United States? *Forest Ecology and Management*, *348*, 142–152. https://doi.org/10.1016/j.foreco.2015.03.044

Hartig, F. (2020). *DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models* (0.3.3.0) [Computer software]. https://CRAN.R-project.org/package=DHARMa

Haslett, J. R. (1989). Interpreting patterns of resource utilization: Randomness and selectivity in pollen feeding by adult hoverflies. *Oecologia*, *78*(4), 433–442. https://doi.org/10.1007/BF00378732

Häussler, J., Sahlin, U., Baey, C., Smith, H. G., & Clough, Y. (2017). Pollinator population size and pollination ecosystem service responses to enhancing floral and nesting resources. *Ecology and Evolution*, *7*(6), 1898–1908. https://doi.org/10.1002/ece3.2765

Herbertsson, L., Rundlöf, M., & Smith, H. G. (2017). The relation between oilseed rape and pollination of later flowering plants varies across plant species and landscape contexts. *Basic and Applied Ecology*, *24*, 77–85. https://doi.org/10.1016/j.baae.2017.08.001

Hernandez, J. L., Frankie, G. W., & Thorp, R. W. (2009). Ecology of Urban Bees: A Review of Current Knowledge and Directions for Future Study. *Cities and the Environment*, *2*(1), 1–15. https://doi.org/10.15365/cate.2132009

Herrmann, J. D., Haddad, N. M., & Levey, D. J. (2017). Testing the relative importance of local resources and landscape connectivity on Bombus impatiens (Hymenoptera, Apidae) colonies. *Apidologie*, *48*(4), 545–555. https://doi.org/10.1007/s13592-017-0499-1

Hoehn, P., Tscharntke, T., Tylianakis, J. M., & Steffan-Dewenter, I. (2008). Functional group diversity of bee pollinators increases crop yield. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1648), 2283–2291. https://doi.org/10.1098/rspb.2008.0405

Holland, J. M., Douma, J. C., Crowley, L., James, L., Kor, L., Stevenson, D. R. W., & Smith, B. M. (2017). Semi-natural habitats support biological control, pollination and soil conservation in Europe. A review. *Agronomy for Sustainable Development*, *37*(4), 31. https://doi.org/10.1007/s13593-017-0434-x

Holzschuh, A., Dormann, C. F., Tscharntke, T., & Steffan-Dewenter, I. (2011). Expansion of mass-flowering crops leads to transient pollinator dilution and reduced wild plant pollination. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1723), 3444–3451. https://doi.org/10.1098/rspb.2011.0268

Holzschuh, A., Dormann, C. F., Tscharntke, T., & Steffan-Dewenter, I. (2013). Mass-flowering crops enhance wild bee abundance. *Oecologia*, *172*(2), 477–484. https://doi.org/10.1007/s00442-012-2515-5

Hurvich, C. M., & Tsai, C.-L. (1989). Regression and time series model selection in small samples. *Biometrika*, 297–307.

Inoue, M. N., Yokoyama, J., & Tsuchida, K. (2010). Colony growth and reproductive ability of feral nests of the introduced bumblebee Bombus terrestris in northern Japan. *Insectes Sociaux*, *57*(1), 29–38. https://doi.org/10.1007/s00040-009-0047-8

IPBES. (2016). *The assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on pollinators, pollination and food production* (p. 552). Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. https://ipbes.net/sites/default/files/downloads/pdf/2017_pollination_full_report_book_v12_pages.pdf

Isaacs, R., Tuell, J., Fiedler, A., Gardiner, M., & Landis, D. (2009). Maximizing arthropod-mediated ecosystem services in agricultural landscapes: The role of native plants. *Frontiers in Ecology and the Environment*, *7*(4), 196–203. https://doi.org/10.1890/080035

Ishag, H. M. (1973). Physiology of seed yield in field beans (Vicia faba L.): I. Yield and yield components. *The Journal of Agricultural Science*, *80*(2), 181–189. https://doi.org/10.1017/S0021859600057622

Jones, G. D. (2012). Pollen extraction from insects. *Palynology*, *36*(1), 86–109. https://doi.org/10.1080/01916122.2011.629523

Jose, S. (2009). Agroforestry for ecosystem services and environmental benefits: An overview. *Agroforestry Systems*, *76*(1), 1–10. https://doi.org/10.1007/s10457-009-9229-7

Junker, R. R., Blüthgen, N., Brehm, T., Binkenstein, J., Paulus, J., Martin Schaefer, H., & Stang, M. (2013). Specialization on traits as basis for the niche-breadth of flower visitors and as structuring mechanism of ecological networks. *Functional Ecology*, *27*(2), 329–341. https://doi.org/10.1111/1365-2435.12005

Kallioniemi, E., Åström, J., Rusch, G. M., Dahle, S., Åström, S., & Gjershaug, J. O. (2017). Local resources, linear elements and mass-flowering crops determine bumblebee occurrences in moderately intensified farmlands. *Agriculture, Ecosystems & Environment*, *239*, 90–100. https://doi.org/10.1016/j.agee.2016.12.039

Kaluza, B. F., Wallace, H., Heard, T. A., Klein, A.-M., & Leonhardt, S. D. (2016). Urban gardens promote bee foraging over natural habitats and plantations. *Ecology and Evolution*, *6*(5), 1304–1316. https://doi.org/10.1002/ece3.1941

Kämper, W., Werner, P. K., Hilpert, A., Westphal, C., Blüthgen, N., Eltz, T., & Leonhardt, S. D. (2016). How landscape, pollen intake and pollen quality affect colony growth in Bombus terrestris. *Landscape Ecology*, *31*(10), 2245–2258. https://doi.org/10.1007/s10980-016-0395-5

Kastner, T., Rivas, M. J. I., Koch, W., & Nonhebel, S. (2012). Global changes in diets and the consequences for land requirements for food. *Proceedings of the National Academy of Sciences*, *109*(18), 6868–6872. https://doi.org/10.1073/pnas.1117054109

Kendall, D. A., & Smith, B. D. (1975). The pollinating efficiency of honeybee and bumblebee visits to field bean flowers (Vicia faba L.). *Journal of Applied Ecology*, *12*(3), 709. https://doi.org/10.2307/2402083

Kim, J. -y. (1999). Influence of resource level on maternal investment in a leaf-cutter bee (Hymenoptera: Megachilidae). *Behavioral Ecology*, *10*(5), 552–556. https://doi.org/10.1093/beheco/10.5.552

Kim, J.-Y. (1997). Female size and fitness in the leaf-cutter bee Megachile apicalis. *Ecological Entomology*, *22*(3), 275–282. https://doi.org/10.1046/j.1365-2311.1997.00062.x

Klatt, B. K., Holzschuh, A., Westphal, C., Clough, Y., Smit, I., Pawelzik, E., & Tscharntke, T. (2014). Bee pollination improves crop quality, shelf life and commercial value. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1775), 20132440. https://doi.org/10.1098/rspb.2013.2440

Kleijn, D., & Raemakers, I. (2008). A retrospective analysis of pollen host plant use by stable and declining bumble bee species. *Ecology*, *89*(7), 1811–1823. https://doi.org/10.1890/07-1275.1

Kleijn, D., Winfree, R., Bartomeus, I., Carvalheiro, L. G., Henry, M., Isaacs, R., Klein, A.-M., Kremen, C., M'Gonigle, L. K., Rader, R., Ricketts, T. H., Williams, N. M., Lee Adamson, N., Ascher, J. S., Báldi, A., Batáry, P., Benjamin, F., Biesmeijer, J. C., Blitzer, E. J., … Potts, S. G. (2015). Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nature Communications*, *6*(1), 7414. https://doi.org/10.1038/ncomms8414

Klein, A.-M., Brittain, C., Hendrix, S. D., Thorp, R., Williams, N., & Kremen, C. (2012). Wild pollination services to California almond rely on semi-natural habitat: Wild pollination services to California almond. *Journal of Applied Ecology*, *49*, 723–732. https://doi.org/10.1111/j.1365-2664.2012.02144.x

Klein, A.-M., Vaissière, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., & Tscharntke, T. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1608), 303–313. https://doi.org/10.1098/rspb.2006.3721

Kottek, M., Grieser, J., Beck, C., Rudolf, B., & Rubel, F. (2006). World Map of the Köppen-Geiger climate classification updated. *Meteorologische Zeitschrift*, *15*(3), 259–263. https://doi.org/10.1127/0941-2948/2006/0130

Kovács-Hostyánszki, A., Espíndola, A., Vanbergen, A. J., Settele, J., Kremen, C., & Dicks, L. V. (2017). Ecological intensification to mitigate impacts of conventional intensive land use on pollinators and pollination. *Ecology Letters*, *20*(5), 673–689. https://doi.org/10.1111/ele.12762

Kovács-Hostyánszki, A., Haenke, S., Batáry, P., Jauker, B., Báldi, A., Tscharntke, T., & Holzschuh, A. (2013). Contrasting effects of mass-flowering crops on bee pollination of hedge plants at different spatial and temporal scales. *Ecological Applications*, *23*(8), 1938–1946. https://doi.org/10.1890/12-2012.1

Kratschmer, S., Petrović, B., Curto, M., Meimberg, H., & Pachinger, B. (2020). Pollen availability for the Horned mason bee (Osmia cornuta) in regions of different land use and landscape structures. *Ecological Entomology*, *45*(3), 525–537. https://doi.org/10.1111/een.12823

Kremen, C. (2018). The value of pollinator species diversity. *Science*, *359*(6377), 741–742. https://doi.org/10.1126/science.aar7614

Kremen, C., Albrecht, M., & Ponisio, L. C. (2019). Restoring pollinator communities and pollination services in hedgerows in intensively-managed agricultural landscapes. In J. W. Dover (Ed.), *The Ecology of Hedgerows and Field Margins* (pp. 163–185). Routledge. https://books.google.de/books?hl=de&lr=&id=h8yGDwAAQBAJ&oi=fnd&pg=PA163&dq=Restoring+pollinator+communities+and+pollination+services+in+hedgerows+in+intensively-managed+agricultural+landscapes&ots=JrKiMgun18&sig=AIPWgWhIbSi_8qOLUoGGncaznqg#v=onepage&q&f=false

Kremen, C., Williams, N. M., Aizen, M. A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., Packer, L., Potts, S. G., Roulston, T., Steffan-Dewenter, I., Vázquez, D. P., Winfree, R., Adams, L., Crone, E. E., Greenleaf, S. S., Keitt, T. H., Klein, A.-M., Regetz, J., & Ricketts, T. H. (2007). Pollination and other ecosystem services produced by mobile organisms: A conceptual framework for the effects of land-use change. *Ecology Letters*, *10*(4), 299–314. https://doi.org/10.1111/j.1461-0248.2007.01018.x

Kremen, C., Williams, N. M., Bugg, R. L., Fay, J. P., & Thorp, R. W. (2004). The area requirements of an ecosystem service: Crop pollination by native bee communities in California: Area requirements for pollination services to crops. *Ecology Letters*, *7*(11), 1109–1119. https://doi.org/10.1111/j.1461-0248.2004.00662.x

Kreyer, D., Oed, A., Walther-Hellwig, K., & Frankl, R. (2004). Are forests potential landscape barriers for foraging bumblebees? Landscape scale experiments with Bombus terrestris agg. and Bombus pascuorum (Hymenoptera, Apidae). *Biological Conservation*, *116*(1), 111–118. https://doi.org/10.1016/S0006-3207(03)00182-4

Kriesell, L., Hilpert, A., & Leonhardt, S. D. (2017). Different but the same: Bumblebee species collect pollen of different plant sources but similar amino acid profiles. *Apidologie*, *48*(1), 102–116. https://doi.org/10.1007/s13592-016-0454-6

Krunic, M., Stanisavljevi, L., Pinzauti, M., & Felicioli, A. (2005). The accompanying fauna of Osmia cornuta and Osmia rufa and effective measures of protection. *Bulletin of Insectology*, *58*(2), 141–152.

Kühn, I., Durka, W., & Klotz, S. (2004). BiolFlor - a new plant-trait database as a tool for plant invasion ecology: BiolFlor - a plant-trait database. *Diversity and Distributions*, *10*(5–6), 363–365. https://doi.org/10.1111/j.1366-9516.2004.00106.x

Lancashire, P. D., Bleiholder, H., Boom, T. V. D., Langelüddeke, P., Stauss, R., Weber, E., & Witzenberger, A. (1991). A uniform decimal code for growth stages of crops and weeds. *Annals of Applied Biology*, *119*(3), 561–601. https://doi.org/10.1111/j.1744-7348.1991.tb04895.x

Lander, T. A., Bebber, D. P., Choy, C. T. L., Harris, S. A., & Boshier, D. H. (2011). The Circe Principle explains how resource-rich land can waylay pollinators in fragmented landscapes. *Current Biology*, *21*(15), 1302–1307. https://doi.org/10.1016/j.cub.2011.06.045

Larsson, M. (2005). Higher pollinator effectiveness by specialist than generalist flower-visitors of unspecialized Knautia arvensis (Dipsacaceae). *Oecologia*, *146*(3), 394–403. https://doi.org/10.1007/s00442-005-0217-y

Lawson, S. P., Kennedy, K. B., & Rehan, S. M. (2021). Pollen composition significantly impacts the development and survival of the native small carpenter bee, CERATINA CALCARATA . *Ecological Entomology*, *46*(2), 232–239. https://doi.org/10.1111/een.12955

Lee, Y., & Nelder, J. A. (2000). Two ways of modelling overdispersion in non-normal data. *Journal of the Royal Statistical Society: Series C (Applied Statistics)*, *49*(4), 591–598. https://doi.org/10.1111/1467-9876.00214

Lewis, S. L., & Maslin, M. A. (2015). Defining the Anthropocene. *Nature*, *519*, 171–180. https://doi.org/doi:10.1038/nature14258

Lonsdorf, E., Kremen, C., Ricketts, T., Winfree, R., Williams, N., & Greenleaf, S. (2009). Modelling pollination services across agricultural landscapes. *Annals of Botany*, *103*(9), 1589–1600. https://doi.org/10.1093/aob/mcp069

Losey, J. E., & Vaughan, M. (2006). The Economic Value of Ecological Services Provided by Insects. *BioScience*, *56*(4), 311. https://doi.org/10.1641/0006-3568(2006)56[311:TEVOES]2.0.CO;2

Lundgren, J. G. (2009). Nutritional aspects of non-prey foods in the life histories of predaceous Coccinellidae. *Biological Control*, *51*(2), 294–305. https://doi.org/10.1016/j.biocontrol.2009.05.016

MacInnis, G., & Forrest, J. R. K. (2019). Pollination by wild bees yields larger strawberries than pollination by honey bees. *Journal of Applied Ecology*, *56*(4), 824–832. https://doi.org/10.1111/1365-2664.13344

Mallinger, R. E., Gaines-Day, H. R., & Gratton, C. (2017). Do managed bees have negative effects on wild bees? A systematic review of the literature. *PLOS ONE*, *12*(12), e0189268. https://doi.org/10.1371/journal.pone.0189268

Mallinger, R. E., Gibbs, J., & Gratton, C. (2016). Diverse landscapes have a higher abundance and species richness of spring wild bees by providing complementary floral resources over bees' foraging periods. *Landscape Ecology*, *31*(7), 1523–1535. https://doi.org/10.1007/s10980-015-0332-z

Mallinger, R. E., & Gratton, C. (2015). Species richness of wild bees, but not the use of managed honeybees, increases fruit set of a pollinator-dependent crop. *Journal of Applied Ecology*, *52*(2), 323–330. https://doi.org/10.1111/1365-2664.12377

Marja, R., Viik, E., Mänd, M., Phillips, J., Klein, A.-M., & Batáry, P. (2018). Crop rotation and agri-environment schemes determine bumblebee communities via flower resources. *Journal of Applied Ecology*, *55*(4), 1714–1724. https://doi.org/10.1111/1365-2664.13119

Márquez, J., Bosch, J., & Vicens, N. (1994). Pollens collected by wild and managed populations of the potential orchard pollinator Osmia cornuta (Latr.) (Hym., Megachilidae). *Journal of Applied Entomology*, *117*, 353–359.

Martin, E. A., Dainese, M., Clough, Y., Báldi, A., Bommarco, R., Gagic, V., Garratt, M. P. D., Holzschuh, A., Kleijn, D., Kovács-Hostyánszki, A., Marini, L., Potts, S. G., Smith, H. G., Al Hassan, D., Albrecht, M., Andersson, G. K. S., Asís, J. D., Aviron, S., Balzan, M. V., … Steffan-Dewenter, I. (2019). The interplay of landscape composition and configuration: New pathways to manage functional biodiversity and agroecosystem services across Europe. *Ecology Letters*, *22*(7), 1083–1094. https://doi.org/10.1111/ele.13265

Marzinzig, B., Brünjes, L., Biagioni, S., Behling, H., Link, W., & Westphal, C. (2018). Bee pollinators of faba bean (Vicia faba L.) differ in their foraging behaviour and pollination efficiency. *Agriculture, Ecosystems & Environment*, *264*, 24–33. https://doi.org/10.1016/j.agee.2018.05.003

McEwen, P. K., New, T. R., & Whittington, A. E. (Eds.). (2007). *Lacewings in the crop environment*. Cambridge University Press.

McGregor, S. E. (1976). Insect pollination of cultivated crop plants. *US Department of Agriculture*, *496*, 849.

McMaster, G. S., & Wilhelm, W. W. (1997). Growing degree-days: One equation, two interpretations. *Agricultural and Forest Meteorology*, *87*(4), 291–300. https://doi.org/10.1016/S0168-1923(97)00027-0

Mestre, L., Schirmel, J., Hetz, J., Kolb, S., Pfister, S. C., Amato, M., Sutter, L., Jeanneret, P., Albrecht, M., & Entling, M. H. (2018). Both woody and herbaceous semi-natural habitats are essential for spider overwintering in European farmland. *Agriculture, Ecosystems & Environment*, *267*, 141–146. https://doi.org/10.1016/j.agee.2018.08.018

M'Gonigle, L. K., Ponisio, L. C., Cutler, K., & Kremen, C. (2015). Habitat restoration promotes pollinator persistence and colonization in intensively managed agriculture. *Ecological Applications*, *25*(6), 1557–1565. https://doi.org/10.1890/14-1863.1

Miller-Struttmann, N. E., Geib, J. C., Franklin, J. D., Kevan, P. G., Holdo, R. M., Ebert-May, D., Lynn, A. M., Kettenbach, J. A., Hedrick, E., & Galen, C. (2015). Functional mismatch in a bumble bee pollination mutualism under climate change. *Science*, *349*(6255), 1541–1544. https://doi.org/10.1126/science.aab0868

Mitchell, M. G. E., Bennett, E. M., & Gonzalez, A. (2014). Forest fragments modulate the provision of multiple ecosystem services. *Journal of Applied Ecology*, *51*(4), 909–918. https://doi.org/10.1111/1365-2664.12241

Moore, B. D., Lawler, I. R., Wallis, I. R., Beale, C. M., & Foley, W. J. (2010). Palatability mapping: A koala's eye view of spatial variation in habitat quality. *Ecology*, *91*(11), 3165–3176. https://doi.org/10.1890/09-1714.1

Moore, P. D., Webb, J. A., & Collinson, M. E. (1991). *Pollen Analysis*. Blackwell Scientific Publications.

Moquet, L., Mayer, C., Michez, D., Wathelet, B., & Jacquemart, A.-L. (2015). Early spring floral foraging resources for pollinators in wet heathlands in Belgium. *Journal of Insect Conservation*, *19*(5), 837–848. https://doi.org/10.1007/s10841-015-9802-5

Morandin, L. A., & Kremen, C. (2013). Hedgerow restoration promotes pollinator populations and exports native bees to adjacent fields. *Ecological Applications*, *23*(4), 829–839. https://doi.org/10.1890/12-1051.1

Nayak, G. K., Roberts, S. P. M., Garratt, M., Breeze, T. D., Tscheulin, T., Harrison-Cripps, J., Vogiatzakis, I. N., Stirpe, M. T., & Potts, S. G. (2015). Interactive effect of floral abundance and semi-natural habitats on pollinators in field beans (Vicia faba). *Agriculture, Ecosystems & Environment*, *199*, 58–66. https://doi.org/10.1016/j.agee.2014.08.016

Nicholson, C. C., Ricketts, T. H., Koh, I., Smith, H. G., Lonsdorf, E. V., & Olsson, O. (2019). Flowering resources distract pollinators from crops: Model predictions from landscape simulations. *Journal of Applied Ecology*, *56*(3), 618–628. https://doi.org/10.1111/1365-2664.13333

Nicolson, S. W. (2011). *Bee food: The chemistry and nutritional value of nectar, pollen and mixtures of the two*. *46*(2), 8.

Nilson, L. A. (1988). The evolution of flowers with deep corolla tubes. *Nature*, *334*(6178), 147–149.

Oksanen, J., Blanchet, F. G., Friendly, M., Roeland, K., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2019). *vegan: Community Ecology Package* (2.5-6) [Computer software]. https://CRAN.R-project.org/package=vegan

Ollerton, J. (2017). Pollinator Diversity: Distribution, Ecological Function, and Conservation. *Annual Review of Ecology, Evolution, and Systematics*, *48*(1), 353–376. https://doi.org/10.1146/annurev-ecolsys-110316-022919

Ollerton, J., Winfree, R., & Tarrant, S. (2011). How many flowering plants are pollinated by animals? *Oikos*, *120*(3), 321–326. https://doi.org/10.1111/j.1600-0706.2010.18644.x

Olsson, O., & Bolin, A. (2014). A model for habitat selection and species distribution derived from central place foraging theory. *Oecologia*, *175*(2), 537–548. https://doi.org/10.1007/s00442-014-2931-9

Olsson, O., Bolin, A., Smith, H. G., & Lonsdorf, E. V. (2015). Modeling pollinating bee visitation rates in heterogeneous landscapes from foraging theory. *Ecological Modelling*, *316*, 133–143. https://doi.org/10.1016/j.ecolmodel.2015.08.009

Osborne, J. L., Clark, S. J., Morris, R. J., Williams, I. H., Riley, J. R., Smith, A. D., Reynolds, D. R., & Edwards, A. S. (1999). A landscape-scale study of bumble bee foraging range and constancy, using harmonic radar. *Journal of Applied Ecology*, *36*(4), 519–533. https://doi.org/10.1046/j.1365-2664.1999.00428.x

Osborne, J. L., Martin, A. P., Carreck, N. L., Swain, J. L., Knight, M. E., Goulson, D., Hale, R. J., & Sanderson, R. A. (2008). Bumblebee flight distances in relation to the forage landscape. *Journal of Animal Ecology*, *77*(2), 406–415. https://doi.org/10.1111/j.1365-2656.2007.01333.x

Osborne, J. L., Martin, A. P., Shortall, C. R., Todd, A. D., Goulson, D., Knight, M. E., Hale, R. J., & Sanderson, R. A. (2007). Quantifying and comparing bumblebee nest densities in gardens and countryside habitats: Bumblebee nest survey in gardens and countryside. *Journal of Applied Ecology*, *45*(3), 784–792. https://doi.org/10.1111/j.1365-2664.2007.01359.x

Ostaff, D. P., Mosseler, A., Johns, R. C., Javorek, S., Klymko, J., & Ascher, J. S. (2015). Willows (Salix spp.) as pollen and nectar sources for sustaining fruit and berry pollinating insects. *Canadian Journal of Plant Science*, *95*(3), 505–516. https://doi.org/10.4141/cjps-2014-339

Patt, J. M., Hamilton, G. C., & Lashomb, J. H. (1997). Foraging success of parasitoid wasps on flowers: Interplay of insect morphology, floral architecture and searching behavior. *Entomologia Experimentalis et Applicata*, *83*(1), 21–30. https://doi.org/10.1046/j.1570-7458.1997.00153.x

Pell, J. K., Baverstock, J., Roy, H. E., Ware, R. L., & Majerus, M. E. N. (2008). Intraguild predation involving Harmonia axyridis: A review of current knowledge and future perspectives. *BioControl*, *53*(1), 147–168. https://doi.org/10.1007/s10526-007-9125-x

Perović, D., Gámez-Virués, S., Börschig, C., Klein, A.-M., Krauss, J., Steckel, J., Rothenwöhrer, C., Erasmi, S., Tscharntke, T., & Westphal, C. (2015). Configurational landscape heterogeneity shapes functional community composition of grassland butterflies. *Journal of Applied Ecology*, *52*(2), 505–513. https://doi.org/10.1111/1365-2664.12394

Peterson, J. H., Roitberg, B. D., & Peterson, J. H. (2006). Impacts of flight distance on sex ratio and resource allocation to offspring in the leafcutter bee, Megachile rotundata. *Behavioral Ecology and Sociobiology*, *59*(5), 589–596. https://doi.org/10.1007/s00265-005-0085-9

Pfister, S. C., Eckerter, P. W., Krebs, J., Cresswell, J. E., Schirmel, J., & Entling, M. H. (2018). Dominance of cropland reduces the pollen deposition from bumble bees. *Scientific Reports*, *8*(1), 13873. https://doi.org/10.1038/s41598-018-31826-3

Pfister, S. C., Eckerter, P. W., Schirmel, J., Cresswell, J. E., & Entling, M. H. (2017). Sensitivity of commercial pumpkin yield to potential decline among different groups of pollinating bees. *Royal Society Open Science*, *4*(5), 170102. https://doi.org/10.1098/rsos.170102

Pfister, S. C., Schirmel, J., & Entling, M. H. (2017). Aphids and their enemies in pumpkin respond differently to management, local and landscape features. *Biological Control*, *115*, 37–45. https://doi.org/10.1016/j.biocontrol.2017.09.005

Pitts-Singer, T. L., & Bosch, J. (2010). Nest Establishment, Pollination Efficiency, and Reproductive Success of *Megachile rotundata* (Hymenoptera: Megachilidae) in Relation to Resource Availability in Field Enclosures. *Environmental Entomology*, *39*(1), 149–158. https://doi.org/10.1603/EN09077

Porto, R. G., de Almeida, R. F., Cruz-Neto, O., Tabarelli, M., Viana, B. F., Peres, C. A., & Lopes, A. V. (2020). Pollination ecosystem services: A comprehensive review of economic values, research funding and policy actions. *Food Security*, *12*(6), 1425–1442. https://doi.org/10.1007/s12571-020-01043-w

Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global pollinator declines: Trends, impacts and drivers. *Trends in Ecology & Evolution*, *25*(6), 345–353. https://doi.org/10.1016/j.tree.2010.01.007

Potts, S. G., Imperatriz-Fonseca, V., Ngo, H. T., Aizen, M. A., Biesmeijer, J. C., Breeze, T. D., Dicks, L. V., Garibaldi, L. A., Hill, R., Settele, J., & Vanbergen, A. J. (2016). Safeguarding pollinators and their values to human well-being. *Nature*, *540*(7632), 220–229. https://doi.org/10.1038/nature20588

Potts, S. G., Roberts, S. P. M., Dean, R., Marris, G., Brown, M. A., Jones, R., Neumann, P., & Settele, J. (2010). Declines of managed honey bees and beekeepers in Europe. *Journal of Apicultural Research*, *49*(1), 15–22. https://doi.org/10.3896/IBRA.1.49.1.02

Pretty, J. (2018). Intensification for redesigned and sustainable agricultural systems. *Science*, *362*(6417), eaav0294. https://doi.org/10.1126/science.aav0294

Primack, R. B. (2014). *Essentials of Conservation Biology* (6th ed. 2014 Edition). Sinauer.

QGIS Development Team. (2019). *QGIS Geographic Information System* (3.6) [Computer software]. Open Source Geospatial Foundation Project. https://www.qgis.org

R Core Team. (2020). *R. A language and environment for statistical computing* (4.0) [Computer software]. R Foundation for Statistical Computing.

Rader, R., Bartomeus, I., Garibaldi, L. A., Garratt, M. P. D., Howlett, B. G., Winfree, R., Cunningham, S. A., Mayfield, M. M., Arthur, A. D., Andersson, G. K. S., Bommarco, R., Brittain, C., Carvalheiro, L. G., Chacoff, N. P., Entling, M. H., Foully, B., Freitas, B. M., Gemmill-Herren, B., Ghazoul, J., …

Woyciechowski, M. (2016). Non-bee insects are important contributors to global crop pollination. *Proceedings of the National Academy of Sciences*, *113*(1), 146–151. https://doi.org/10.1073/pnas.1517092112

Radmacher, S., & Strohm, E. (2010). Factors affecting offspring body size in the solitary bee Osmia bicornis (Hymenoptera, Megachilidae)*. *Apidologie*, *41*, 169–177.

Ramankutty, N., Evan, A. T., Monfreda, C., & Foley, J. A. (2008). Farming the planet: 1. Geographic distribution of global agricultural lands in the year 2000: GLOBAL AGRICULTURAL LANDS IN 2000. *Global Biogeochemical Cycles*, *22*(1), n/a-n/a. https://doi.org/10.1029/2007GB002952

Raven, P. H., & Wagner, D. L. (2021). Agricultural intensification and climate change are rapidly decreasing insect biodiversity. *Proceedings of the National Academy of Sciences*, *118*(2), e2002548117. https://doi.org/10.1073/pnas.2002548117

Reille, M. (1992). *Pollen et spores d'Europe et d'Afrique du Nord*. Laboratoire de Botanique historique et Palynologie.

Requier, F., Odoux, J.-F., Tamic, T., Moreau, N., Henry, M., Decourtye, A., & Bretagnolle, V. (2015). Honey bee diet in intensive farmland habitats reveals an unexpectedly high flower richness and a major role of weeds. *Ecological Applications*, *25*(4), 881–890. https://doi.org/10.1890/14-1011.1

Ricketts, T. H., Regetz, J., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., Bogdanski, A., Gemmill-Herren, B., Greenleaf, S. S., Klein, A. M., Mayfield, M. M., Morandin, L. A., Ochieng', A., & Viana, B. F. (2008). Landscape effects on crop pollination services: Are there general patterns? *Ecology Letters*, *11*(5), 499–515. https://doi.org/10.1111/j.1461-0248.2008.01157.x

Riedinger, V., Renner, M., Rundlöf, M., Steffan-Dewenter, I., & Holzschuh, A. (2014). Early mass-flowering crops mitigate pollinator dilution in late-flowering crops. *Landscape Ecology*, *29*(3), 425–435. https://doi.org/10.1007/s10980-013-9973-y

Rollin, O., Bretagnolle, V., Decourtye, A., Aptel, J., Michel, N., Vaissière, B. E., & Henry, M. (2013). Differences of floral resource use between honey bees and wild bees in an intensive farming system. *Agriculture, Ecosystems & Environment*, *179*, 78–86. https://doi.org/10.1016/j.agee.2013.07.007

Rollin, O., Bretagnolle, V., Fortel, L., Guilbaud, L., & Henry, M. (2015). Habitat, spatial and temporal drivers of diversity patterns in a wild bee assemblage. *Biodiversity and Conservation*, *24*(5), 1195–1214. https://doi.org/10.1007/s10531-014-0852-x

Rollin, O., Pérez-Méndez, N., Bretagnolle, V., & Henry, M. (2019). Preserving habitat quality at local and landscape scales increases wild bee diversity in intensive farming systems. *Agriculture, Ecosystems & Environment*, *275*, 73–80. https://doi.org/10.1016/j.agee.2019.01.012

Rotheray, E. L., Osborne, J. L., & Goulson, D. (2017). Quantifying the food requirements and effects of food stress on bumble bee colony development. *Journal of Apicultural Research*, *56*(3), 288–299. https://doi.org/10.1080/00218839.2017.1307712

Roulston, T. H., Cane, J. H., & Buchmann, S. L. (2000). What governs protein content of pollen: Pollinator preferences, pollen-pistil interactions, or phylogeny? *Ecological Monographs*, *70*(4), 617–643. https://doi.org/10.1890/0012-9615(2000)070[0617:WGPCOP]2.0.CO;2

Roulston, T. H., & Goodell, K. (2011). The Role of Resources and Risks in Regulating Wild Bee Populations. *Annual Review of Entomology*, *56*(1), 293–312. https://doi.org/10.1146/annurev-ento-120709-144802

Roy, H. E., Adriaens, T., Isaac, N. J. B., Kenis, M., Onkelinx, T., Martin, G. S., Brown, P. M. J., Hautier, L., Poland, R., Roy, D. B., Comont, R., Eschen, R., Frost, R., Zindel, R., Van Vlaenderen, J., Nedvěd, O., Ravn, H. P., Grégoire, J.-C., de Biseau, J.-C., & Maes, D. (2012). Invasive alien predator causes rapid declines of native European ladybirds: Alien predator causes declines of native ladybirds. *Diversity and Distributions*, *18*(7), 717–725. https://doi.org/10.1111/j.1472-4642.2012.00883.x

Rundlöf, M., Lundin, O., & Bommarco, R. (2018). Annual flower strips support pollinators and potentially enhance red clover seed yield. *Ecology and Evolution*, *8*(16), 7974–7985. https://doi.org/10.1002/ece3.4330

Rundlöf, M., Persson, A. S., Smith, H. G., & Bommarco, R. (2014). Late-season mass-flowering red clover increases bumble bee queen and male densities. *Biological Conservation*, *172*, 138–145. https://doi.org/10.1016/j.biocon.2014.02.027

Russo, L., & Danforth, B. (2017). Pollen preferences among the bee species visiting apple (Malus pumila) in New York. *Apidologie*, *48*(6), 806–820. https://doi.org/10.1007/s13592-017-0525-3

Samuelson, A. E., Gill, R. J., Brown, M. J. F., & Leadbeater, E. (2018). Lower bumblebee colony reproductive success in agricultural compared with urban environments. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1881), 20180807. https://doi.org/10.1098/rspb.2018.0807

Schellhorn, N. A., Gagic, V., & Bommarco, R. (2015). Time will tell: Resource continuity bolsters ecosystem services. *Trends in Ecology & Evolution*, *30*(9), 524–530. https://doi.org/10.1016/j.tree.2015.06.007

Scheper, J., Reemer, M., van Kats, R., Ozinga, W. A., van der Linden, G. T. J., Schaminée, J. H. J., Siepel, H., & Kleijn, D. (2014). Museum specimens reveal loss of pollen host plants as key factor driving wild bee decline in The Netherlands. *Proceedings of the National Academy of Sciences*, *111*(49), 17552–17557. https://doi.org/10.1073/pnas.1412973111

Schirmel, J., Albrecht, M., Bauer, P.-M., Sutter, L., Pfister, S. C., & Entling, M. H. (2018). Landscape complexity promotes hoverflies across different types of semi-natural habitats in farmland. *Journal of Applied Ecology*, *55*(4), 1747–1758. https://doi.org/10.1111/1365-2664.13095

Schleuning, M., Fründ, J., Klein, A.-M., Abrahamczyk, S., Alarcón, R., Albrecht, M., Andersson, G. K. S., Bazarian, S., Böhning-Gaese, K., Bommarco, R., Dalsgaard, B., Dehling, D. M., Gotlieb, A., Hagen, M., Hickler, T., Holzschuh, A., Kaiser-Bunbury, C. N., Kreft, H., Morris, R. J., … Blüthgen, N. (2012). Specialization of Mutualistic Interaction Networks Decreases toward Tropical Latitudes. *Current Biology*, *22*(20), 1925–1931. https://doi.org/10.1016/j.cub.2012.08.015

Schüepp, C., Herzog, F., & Entling, M. H. (2014). Disentangling multiple drivers of pollination in a landscape-scale experiment. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1774), 20132667. https://doi.org/10.1098/rspb.2013.2667

Sedivy, C., Müller, A., & Dorn, S. (2011). Closely related pollen generalist bees differ in their ability to develop on the same pollen diet: Evidence for physiological adaptations to digest pollen: Pollen digestion ability of bees. *Functional Ecology*, *25*(3), 718–725. https://doi.org/10.1111/j.1365-2435.2010.01828.x

Seidelmann, K. (2006). Open-cell parasitism shapes maternal investment patterns in the Red Mason bee Osmia rufa. *Behavioral Ecology*, *17*(5), 839–848. https://doi.org/10.1093/beheco/arl017

Senapathi, D., Biesmeijer, J. C., Breeze, T. D., Kleijn, D., Potts, S. G., & Carvalheiro, L. G. (2015). Pollinator conservation—The difference between managing for pollination services and preserving pollinator diversity. *Current Opinion in Insect Science*, *12*, 93–101. https://doi.org/10.1016/j.cois.2015.11.002

Senapathi, D., Fründ, J., Albrecht, M., Garratt, M. P. D., Kleijn, D., Pickles, B. J., Potts, S. G., An, J., Andersson, G. K. S., Bänsch, S., Basu, P., Benjamin, F., Bezerra, A. D. M., Bhattacharya, R., Biesmeijer, J. C., Blaauw, B., Blitzer, E. J., Brittain, C. A., Carvalheiro, L. G., … Klein, A.-M. (2021). Wild insect diversity increases inter-annual stability in global crop pollinator communities. *Proceedings of the Royal Society B: Biological Sciences*, *288*(1947), rspb.2021.0212, 20210212. https://doi.org/10.1098/rspb.2021.0212

Shackelford, G., Steward, P. R., Benton, T. G., Kunin, W. E., Potts, S. G., Biesmeijer, J. C., & Sait, S. M. (2013). Comparison of pollinators and natural enemies: A meta-analysis of landscape and local effects on abundance and richness in crops: Comparison of pollinators and natural enemies. *Biological Reviews*, *88*(4), 1002–1021. https://doi.org/10.1111/brv.12040

Soroye, P., Newbold, T., & Kerr, J. (2020). Climate change contributes to widespread declines among bumble bees across continents. *Science*, *367*(6478), 685–688. https://doi.org/10.1126/science.aax8591

Stankiewicz-Kosyl, M., Synowiec, A., Haliniarz, M., Wenda-Piesik, A., Domaradzki, K., Parylak, D., Wrochna, M., Pytlarz, E., Gala-Czekaj, D., Marczewska-Kolasa, K., Marcinkowska, K., & Praczyk, T. (2020). Herbicide Resistance and Management Options of Papaver rhoeas L. and Centaurea cyanus L. in Europe: A Review. *Agronomy*, *10*(6), 874. https://doi.org/10.3390/agronomy10060874

Steffen, W., Grinevald, J., Crutzen, P., & McNeill, J. (2011). The Anthropocene: Conceptual and historical perspectives. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, *369*(1938), 842–867. https://doi.org/10.1098/rsta.2010.0327

Stoddard, F. L., & Bond, D. A. (1987). The pollination requirements of the faba bean. *Bee World*, *68*(3), 144–152. https://doi.org/10.1080/0005772X.1987.11098923

Stutz, S., & Entling, M. H. (2011). Effects of the landscape context on aphid-ant-predator interactions on cherry trees. *Biological Control*, *57*(1), 37–43. https://doi.org/10.1016/j.biocontrol.2011.01.001

Sunday, J. M., Bates, A. E., Kearney, M. R., Colwell, R. K., Dulvy, N. K., Longino, J. T., & Huey, R. B. (2014). Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proceedings of the National Academy of Sciences*, *111*(15), 5610–5615. https://doi.org/10.1073/pnas.1316145111

Suso, M. J., Moreno, M. T., Mondragao-Rodrigues, F., & Cubero, J. I. (1996). Reproductive biology of Vicia faba: Role of pollination conditions. *Field Crops Research*, *46*(1–3), 81–91. https://doi.org/10.1016/0378-4290(95)00089-5

Sutter, L., Albrecht, M., & Jeanneret, P. (2018). Landscape greening and local creation of wildflower strips and hedgerows promote multiple ecosystem services. *Journal of Applied Ecology*, *55*(2), 612–620. https://doi.org/10.1111/1365-2664.12977

Sutter, L., Jeanneret, P., Bartual, A. M., Bocci, G., & Albrecht, M. (2017). Enhancing plant diversity in agricultural landscapes promotes both rare bees and dominant crop-pollinating bees through complementary increase in key floral resources. *Journal of Applied Ecology*, *54*(6), 1856–1864. https://doi.org/10.1111/1365-2664.12907

Symonds, M. R. E., & Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology*, *65*(1), 13–21. https://doi.org/10.1007/s00265-010-1037-6

Tasei, J.-N., & Picart, M. (1973). Le comportement de nidification chez Osmia (Osmia) cornuta Latr. Et Osmia (Osmia) rufa L. (Hymenoptera Megachilidae). *Apidologie*, *4*(3), 195–225. https://doi.org/10.1051/apido:19730301

Thomson, D. M. (2016). Local bumble bee decline linked to recovery of honey bees, drought effects on floral resources. *Ecology Letters*, *19*(10), 1247–1255. https://doi.org/10.1111/ele.12659

Thorp, R. W. (1979). Structural, Behavioral, and Physiological Adaptations of Bees (Apoidea) for Collecting Pollen. *Annals of the Missouri Botanical Garden*, *66*(4), 788–812. https://doi.org/10.2307/2398919

Tilman, D. (2001). Forecasting Agriculturally Driven Global Environmental Change. *Science*, *292*(5515), 281–284. https://doi.org/10.1126/science.1057544

Tilman, D., Balzer, C., Hill, J., & Befort, B. L. (2011). Global food demand and the sustainable intensification of agriculture. *Proceedings of the National Academy of Sciences*, *108*(50), 20260–20264. https://doi.org/10.1073/pnas.1116437108

Torchio, P. F., & Tepedino, V. J. (1980). Sex ratio, body size and seasonality in a solitary bee, Osmia lignaria propinqua Cresson (Hymenoptera: Megachilidae). *Evolution*, *34*(5), 993–1003. https://doi.org/10.1111/j.1558-5646.1980.tb04037.x

Tscharntke, T., Clough, Y., Wanger, T. C., Jackson, L., Motzke, I., Perfecto, I., Vandermeer, J., & Whitbread, A. (2012). Global food security, biodiversity conservation and the future of agricultural intensification. *Biological Conservation*, 8.

Tscharntke, T., Tylianakis, J. M., Rand, T. A., Didham, R. K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T. O., Dormann, C. F., Ewers, R. M., Fründ, J., Holt, R. D., Holzschuh, A., Klein, A. M., Kleijn, D., Kremen, C., Landis, D. A., Laurance, W., … Westphal, C. (2012). Landscape moderation of biodiversity patterns and processes—Eight hypotheses. *Biological Reviews*, *87*(3), 661–685. https://doi.org/10.1111/j.1469-185X.2011.00216.x

Tschumi, M., Albrecht, M., Entling, M. H., & Jacot, K. (2015). High effectiveness of tailored flower strips in reducing pests and crop plant damage. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1814), 20151369. https://doi.org/10.1098/rspb.2015.1369

van Klink, R., Bowler, D. E., Gongalsky, K. B., Swengel, A. B., Gentile, A., & Chase, J. M. (2020). Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. *Science*, *368*(6489), 417–420. https://doi.org/10.1126/science.aax9931

Vanneste, T., Govaert, S., Spicher, F., Brunet, J., Cousins, S. A. O., Decocq, G., Diekmann, M., Graae, B. J., Hedwall, P.-O., Kapás, R. E., Lenoir, J., Liira, J., Lindmo, S., Litza, K., Naaf, T., Orczewska, A., Plue, J., Wulf, M., Verheyen, K., & De Frenne, P. (2020). Contrasting microclimates among hedgerows and woodlands across temperate Europe. *Agricultural and Forest Meteorology*, *281*, 107818. https://doi.org/10.1016/j.agrformet.2019.107818

Vanreusel, W., & Van Dyck, H. (2007). When functional habitat does not match vegetation types: A resource-based approach to map butterfly habitat. *Biological Conservation*, *135*(2), 202–211. https://doi.org/10.1016/j.biocon.2006.10.035

Vaudo, A. D., Tooker, J. F., Grozinger, C. M., & Patch, H. M. (2015). Bee nutrition and floral resource restoration. *Current Opinion in Insect Science*, *10*, 133–141. https://doi.org/10.1016/j.cois.2015.05.008

Velthuis, H. H. W., & van Doorn, A. (2006). A century of advances in bumblebee domestication and the economic and environmental aspects of its commercialization for pollination. *Apidologie*, *37*(4), 421–451. https://doi.org/10.1051/apido:2006019

Venturini, E. M., Drummond, F. A., Hoshide, A. K., Dibble, A. C., & Stack, L. B. (2017). Pollination reservoirs for wild bee habitat enhancement in cropping systems: A review. *Agroecology and Sustainable Food Systems*, *41*(2), 101–142. https://doi.org/10.1080/21683565.2016.1258377

Vicens, N., & Bosch, J. (2000). Pollinating Efficacy of Osmia cornuta and Apis mellifera (Hymenoptera: Megachilidae, Apidae) on 'Red Delicious' Apple. *Environmental Entomology*, *29*(2), 235–240.

Villenave, J., Thierry, D., Al Mamun, A., Lodé, T., & Rat-Morris, E. (2005). The pollens consumed by common green lacewings Chrysoperla spp. (Neuroptera: Chrysopidae) in cabbage crop environment in western France. *European Journal of Entomology*, *102*(3), 547–552. https://doi.org/10.14411/eje.2005.078

Vitousek, P. M., Mooney, H. A., Lubchenco, J., & Melillo, J. M. (1997). Human Domination of Earth's Ecosystems. *Science*, *277*, 494–499.

Wäckers, F. L., & van Rijn, P. C. J. (2012). Pick and Mix: Selecting Flowering Plants to Meet the Requirements of Target Biological Control Insects. In G. M. Gurr, S. D. Wratten, W. E. Snyder, & D. M. Y. Read (Eds.), *Biodiversity and Insect Pests* (pp. 139–165). John Wiley & Sons, Ltd. https://doi.org/10.1002/9781118231838.ch9

Wake, D. B., & Vredenburg, V. T. (2008). Are we in the midst of the sixth mass extinction? A view from the world of amphibians. *Proceedings of the National Academy of Sciences*, *105*(Supplement 1), 11466–11473. https://doi.org/10.1073/pnas.0801921105

Walther-Hellwig, K., & Frankl, R. (2000). Foraging habitats and foraging distances of bumblebees, Bombus spp. (Hym., Apidae), in an agricultural landscape. *Journal of Applied Entomology*, *124*(7–8), 299–306. https://doi.org/10.1046/j.1439-0418.2000.00484.x

Wei, T., & Simko, V. (2017). *R package "corrplot": Visualization of a Correlation Matrix* (0.84) [Computer software]. https://github.com/taiyun/corrplot

Wenzel, A., Grass, I., Belavadi, V. V., & Tscharntke, T. (2020). How urbanization is driving pollinator diversity and pollination – A systematic review. *Biological Conservation*, *241*, 108321. https://doi.org/10.1016/j.biocon.2019.108321

Westphal, C., Bommarco, R., Carré, G., Lamborn, E., Morison, N., Petanidou, T., Potts, S. G., Roberts, S. P. M., Szentgyörgyi, H., Tscheulin, T., Vaissière, B. E., Woyciechowski, M., Biesmeijer, J. C., Kunin, W. E., Settele, J., & Steffan-Dewenter, I. (2008). Measuring bee diversity in different european habitats and biogeographical regions. *Ecological Monographs*, *78*(4), 653–671. https://doi.org/10.1890/07-1292.1

Westphal, C., Steffan-Dewenter, I., & Tscharntke, T. (2003). Mass flowering crops enhance pollinator densities at a landscape scale: Flowering crops enhance pollinator densities. *Ecology Letters*, *6*(11), 961–965. https://doi.org/10.1046/j.1461-0248.2003.00523.x

Westphal, C., Steffan-Dewenter, I., & Tscharntke, T. (2009). Mass flowering oilseed rape improves early colony growth but not sexual reproduction of bumblebees. *Journal of Applied Ecology*, *46*(1), 187–193. https://doi.org/10.1111/j.1365-2664.2008.01580.x

Westrich, P. (1996). Habitat requirements of central European bees and the problems of partial habitats. In *The conservation of bees* (Vol. 18, pp. 1–16). Academic Press.

Westrich, P. (2018). *Die Wildbienen Deutschlands*. Eugen Ulmer KG.

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis* (2nd ed.). Springer International Publishing. https://doi.org/10.1007/978-3-319-24277-4

Williams, N. M., & Kremen, C. (2007). Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape. *Ecological Applications*, *17*(3), 910–921. https://doi.org/10.1890/06-0269

Williams, N. M., Regetz, J., & Kremen, C. (2012). Landscape-scale resources promote colony growth but not reproductive performance of bumble bees. *Ecology*, *93*(5), 1049–1058. https://doi.org/10.1890/11-1006.1

Winfree, R., Bartomeus, I., & Cariveau, D. P. (2011). Native pollinators in anthropogenic habitats. *Annual Review of Ecology, Evolution, and Systematics*, *42*(1), 1–22. https://doi.org/10.1146/annurev-ecolsys-102710-145042

Winfree, R., Williams, N. M., Dushoff, J., & Kremen, C. (2007). Native bees provide insurance against ongoing honey bee losses. *Ecology Letters*, *10*(11), 1105–1113. https://doi.org/10.1111/j.1461-0248.2007.01110.x

Wolf, S., & Moritz, R. F. A. (2008). Foraging distance in Bombus terrestris L. (Hymenoptera: Apidae). *Apidologie*, *39*(4), 419–427. https://doi.org/10.1051/apido:2008020

Wood, T. J., Holland, J. M., & Goulson, D. (2017). Providing foraging resources for solitary bees on farmland: Current schemes for pollinators benefit a limited suite of species. *Journal of Applied Ecology*, *54*(1), 323–333. https://doi.org/10.1111/1365-2664.12718

Woodard, S. H. (2017). Wild bee nutritional ecology: Predicting pollinator population dynamics, movement, and services from floral resources. *Current Opinion in Insect Science*, 8.

Zabel, F., Delzeit, R., Schneider, J. M., Seppelt, R., Mauser, W., & Václavík, T. (2019). Global impacts of future cropland expansion and intensification on agricultural markets and biodiversity. *Nature Communications*, *10*(1), 2844. https://doi.org/10.1038/s41467-019-10775-z

Zalasiewicz, J., Williams, M., Smith, A., Barry, T. L., Coe, A. L., Bown, P. R., Brenchley, P., Cantrill, D., Gale, A., Gibbard, P., Gregory, F. J., Hounslow, M. W., Kerr, A. C., Pearson, P., Knox, R., Powell, J., Waters, C., Marshall, J., Oates, M., … Stone, P. (2008). Are we now living in the Anthropocene. *GSA Today*, *18*(2), 4. https://doi.org/10.1130/GSAT01802A.1

Zscheischler, J., & Fischer, E. M. (2020). The record-breaking compound hot and dry 2018 growing season in Germany. *Weather and Climate Extremes*, *29*, 100270. https://doi.org/10.1016/j.wace.2020.100270

Zurbuchen, A., Cheesman, S., Klaiber, J., Müller, A., Hein, S., & Dorn, S. (2010). Long foraging distances impose high costs on offspring production in solitary bees. *Journal of Animal Ecology*, *79*(3), 674–681. https://doi.org/10.1111/j.1365-2656.2010.01675.x

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APPENDIX

A. STATUS AND AUTHOR CONTRIBUTIONS OF PUBLICATIONS

B. AUTHOR AFFILIATIONS

C. FUNDING

D. CURRICULUM VITAE

E. DECLARATION ACCORDING TO §8 OF THE „PROMOTIONSORDNUNG DES FACHBEREICHS 7: NATUR- UND UMWELTWISSENSCHAFTEN DER UNIVERSITÄT KOBLENZ-LANDAU, CAMPUS LANDAU VOM 14.6.2013“

APPENDIX A

STATUS AND AUTHOR CONTRIBUTIONS OF PUBLICATIONS

CHAPTER 2

Colette Bertrand, Philipp W. Eckerter, Lolita Ammann, Martin H. Entling, Erika Gobet, Felix Herzog, Laia Mestre, Willy Tinner & Matthias Albrecht (*published*). Seasonal shifts and complementary use of pollen sources by two bees, a lacewing and a ladybeetle species in European agricultural landscapes. *Journal of Applied Ecology*, 56(11): 2431-2442 (2019).

> C.B., M.A., L.A., M.H.E., L.M. and F.H. conceived and designed the experiment. C.B., L.A. and L.M. performed the field surveys. C.B., P.E., E.G. and W.T. contributed to pollen sample preparation and identification. C.B. and M.A. performed the analysis. C.B. wrote the first draft of the manuscript, and all authors contributed substantially to writing. All authors gave final approval for publication.

CHAPTER 3

Philipp W. Eckerter, Matthias Albrecht, Felix Herzog, Martin H. Entling (*in preparation*). Floral resource use and fitness consequences for two solitary bee species in agricultural landscapes

> P.E., M.A., F.H. and M.H.E. conceived and designed the experiment. P.E. performed the field surveys. P.E. contributed to pollen sample preparation and identification. P.E. performed the analysis. P.E. wrote the first draft of the manuscript, and all authors contributed substantially to writing.

CHAPTER 4

Philipp W. Eckerter, Lars Albus, Sharumathi Natarajan, Matthias Albrecht, Lolita Ammann, Erika Gobet, Felix Herzog, Willy Tinner & Martin H. Entling (*published*). Using temporally resolved floral resource maps to explain bumblebee colony performance in agricultural landscapes. *Agronomy*, 10, 1993 (2020).

> Conceptualization, M.H.E., M.A., and F.H.; methodology, M.H.E., F.H., M.A., and P.W.E.; software, P.W.E.; validation, P.W.E., L.A. (Lars Albus), and S.N.; formal analysis, P.W.E.; investigation, P.W.E., L.A. (Lars Albus), S.N., and E.G.; resources, M.H.E. and W.T.; data curation, P.W.E.; writing—original draft preparation, P.W.E.; writing—review and editing, P.W.E., M.H.E., L.A. (Lars Albus), S.N., M.A., L.A. (Lolita Ammann), E.G., F.H., and W.T.; visualization, P.W.E.; supervision, M.H.E., M.A., and F.H.; project administration, M.H.E. and F.H.; funding acquisition, M.H.E., F.H. All authors have read and agreed to the published version of the manuscript.

CHAPTER 5

Philipp W. Eckerter, Matthias Albrecht, Colette Bertrand, Erika Gobet, Felix Herzog, Sonja C. Pfister, Willy Tinner, Martin H. Entling (*under review*). Effects of temporal floral resource availability and non-crop habitats on broad bean pollination. *Landscape Ecology.*

> P.E., M.A., F.H. and M.H.E. conceived and designed the experiment. P.E. and S.C.P. performed the field surveys. C.B., P.E., E.G. and W.T. contributed to pollen sample preparation and identification. P.E. and M.H.E. performed the analysis. P.E. wrote the first draft of the manuscript, and all authors contributed substantially to writing. All authors gave final approval for publication.

APPENDIX B

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In alphabetical order:

Matthias Albrecht[a]
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Martin H. Entling[c]
Erika Gobet[d],
Felix Herzog[a]
Laia Mestre[c]
Sharumathi Natarajan[a]
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APPENDIX C

FUNDING

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APPENDIX D – CURRICULUM VITAE

PHILIPP WOLFGANG ECKERTER

ENVIRONMENTAL SCIENTIST

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EDUCATION

09/2016 – present	**UNIVERSITY OF KOBLENZ-LANDAU, CAMPUS LANDAU** PhD Student. Project: „Effects of spatio-temporal resource availability on pollinators and pest-natural enemies in fragmented agricultural landscapes (FRAGMENT III)“
10/2006 – 03/2016	**UNIVERSITY OF KOBLENZ-LANDAU, CAMPUS LANDAU** Diploma in Environmental Sciences. Mark: 1.2 (equivalent to A-) Major subject: Biodiversity and sustainability. Mark: 1.0 (equivalent to A) Minor subjects: Applied Ecology (mark: 1.0) and Geoecology (mark: 1,7; equivalent to B+)
19/2004 – 09/2005	**RUPRECHT-KARLS-UNIVERSITY OF HEIDELBERG** Philosophy and theology (both Magister; without degrees)
1996 – 2004	**HUMANISTIC ACADEMIC HIGH SCHOOL HOHENBADEN IN BADEN-BADEN** Higher education entrance qualification (Mark 2.6, equivalent to C+)

RESEARCH EXPERIENCE

09/2016 – Present	**UNIVERSITY OF KOBLENZ-LANDAU, CAMPUS LANDAU** PhD-Student
03/2015 – 02/2016	**UNIVERSITY OF KOBLENZ-LANDAU, CAMPUS LANDAU** Diploma thesis: „Effects of natural habitats on pollinators and pollination of Red kuri squash (*C. maxima*)“. Fieldwork and data acquisition from grown Red kuri squash after hand pollination, pollination from honeybees, bumblebees and halictid bees. Literature research, pollen extraction via acetolysis, pollen analysis, data acquisition, data analysis. Mark: 1.0
11/2014 – 01/2015	**UNIVERSITY OF KOBLENZ-LANDAU, CAMPUS LANDAU** Case study: „Measurement of pollination performance on Red kuri squash in dependance of surrounding landscape, adjacent habitats and management“. Literature research, pollen extraction via acetolysis, pollen analysis data acquisition and data analysis. Mark: 1.0
04/2013	**DEMETER-IMKEREI GÜNTER FRIEDMANN** Research into varroa tolerance of *Apis mellifera lamarckii*. Literature research, research planning, implementation and data acquisition in Sekem, Egypt

RELATED WORK EXPERIENCE, INTERNSHIPS AND CIVIL SERVICE

08/2016	**GÄRTNERMEISTER ANDREAS FRETZ** Employee. Getting to know standard tasks, conceptions on bee friendly gardening

04/2014 – 2017	**KREISIMKERVEREIN BADEN-BADEN E.V.** Scientific talks, practical and ecological exchange, website creation and maintenance
06/2012 – 09/2012	**DEMETER-IMKEREI GÜNTER FRIEDMANN** Intern. Beekeeping work during the course of the year
03/2012	**MUNICIPALIDAD DISTRITAL DE YANQUE** Assistance. Cultivation of organic quinoa and work in current agriculture in Yanque, Peru
12/2011	**ORGANIC FARM OF CECILIA CANCHO ROSS AND ELVIS ROSS-BIER** Assistance. Cultivation of organic fruits and vegetables near to Ancud on Chiloé Island, Chile

PUBLICATIONS

IN PROGRESS

Eckerter, P. W., Albrecht, M., Bertrand, C., Gobet, E., Herzog, F., Pfister, S. C., Tinner, W. & Entling, M. H. (resubmitted to *Landscape Ecology*). Effects of temporal floral resource availability and non-crop habitats on broad bean pollination.

Ammann, L., Bosem-Baillod, A., Eckerter, P. W., Entling, M. H., Albrecht, M., Herzog, F. (resubmitted to *Landscape Ecology*). Aphid predators reduce pest aphids and are better predicted by classical habitat maps than floral resource maps

González, E.; Bianchi, F.J.J.A.; Eckerter, P.W.; Pfaff, V.; Weiler, S.; Entling, M.H. (resubmitted to *Journal of Applied Ecology*). Ecological requirements drive the variable responses of wheat pests and natural enemies to the landscape context.

Eckerter, P. W., Albrecht, M., Herzog, F., Entling, M. H. (in prep.) Floral resource use and fitness consequences for two solitary bee species in agricultural landscapes with contrasting resource availability.

PUBLISHED

Eckerter P. W., Albus L., Natarajan N., Albrecht M., Ammann L., Gobet E., Herzog F., Tinner, W. & Entling, M. H. (2020). Using temporally resolved floral resource maps to explain bumblebee colony performance in agricultural landscapes. *Agronomy*, 10, 1993

Schirmel, J., Entling, M. H., Eckerter, P.W. (2020). Eichenschrecken als Hauptbeute des neozoischen Stahlblauen Grillenjägers *Isodontia mexicana* (Hymenoptera: Sphecidae) in der südpfälzischen Agrarlandschaft. *Articulata*, 35: 149–160

Bertrand C., Eckerter, P. W., Ammann, L., Entling, M. H., Gobet, E., Herzog, F., Mestre, L., Tinner, W., Albrecht, M. (2019). Seasonal shifts and complementary use of pollen sources by two bees, a lacewing and a ladybeetle species in European agricultural landscapes. *Journal of Applied Ecology*, 00:1–12.

Pfister, Sonja C., Eckerter, P. W., Krebs, J., Cresswell, J. E., Schirmel, J., Entling, M. H. (2018). Dominance of cropland reduces the pollen deposition from bumble bees. *Scientific Reports* 8: 13873

Pfister, S. C., Eckerter, P. W., Schirmel, J., Cresswell, J. E., Entling, M. H. (2017): Sensitivity of commercial pumpkin yield to potentional decline among different groups of pollinating bees. *R Soc Open Sci*. 4(5): 170102

CONFERENCE CONTRIBUTIONS

TALKS

Eckerter, P. W., Lars Albus, Farnaz Faramarzi, Sharumathi Natarajan, Erika Gobet, Willy Tinner, Christopher Bause, Thomas Eltz, Matthias Albrecht, Felix Herzog, Martin H. Entling (2019). Effects of spatio-temporal resource availability on pollinators in agricultural landscapes. SCAPE 2019 24-27 October, Höör (Sweden)

POSTERS

Eckerter, P. W., Bosem-Baillod, A., Ammann, L., Sandau, N., Macheda, D., Bertrand, C., Albrecht, M., Mestre, L., Pfister, S. C., Eltz, T., Gobet, E., Tinner, W., Herzog, F., Entling, M. H. (2017). Effectiveness of functional resource maps in predicting pollination and natural pest control on broad bean *Vicia faba*. Joint annual meeting: Ecology across borders with BES, GFÖ, NECOV & EEF, 11-14 December 2017 Ghent (Belgium)

MENTORING

2018	**UNIVERSITY OF KOBLENZ-LANDAU, CAMPUS LANDAU** Joint supervision of two M.Sc. students and one B.Sc. student

APPENDIX E

Declaration according to §8 of the ‚Promotionsordnung des Fachbereichs 7: Natur- und Umweltwissenschaften der Universität Koblenz-Landau, Campus Landau vom 14.06.2013'

Erklärung des Doktoranden darüber,

— dass er die eingereichte Dissertation selbstständig verfasst hat und alle von ihm für die Arbeit benutzten Hilfsmittel und Quellen in der Arbeit angegeben sowie die Anteile etwaig beteiligter Mitarbeiterinnen oder Mitarbeiter sowie anderer Autorinnen oder Autoren klar gekennzeichnet sind;
— dass er nicht die entgeltliche Hilfe von Vermittlungs- oder Beratungsdiensten (Promotionsberater oder andere Personen) in Anspruch genommen hat;
— dass er die Dissertation nicht in gleicher oder ähnlicher Form als Prüfungsarbeit für eine staatliche oder andere wissenschaftliche Prüfung im In- oder Ausland eingereicht hat;
— ob er die gleiche oder eine andere Abhandlung in einem anderen Fachbereich oder einer anderen wissenschaftlichen Hochschule als Dissertation eingereicht hat, ggf. mit welchem Erfolg; - *nicht zutreffend*
— dass ihm bewusst ist, dass ein Verstoß gegen einen der vorgenannten Punkte den Entzug des Doktortitels bedeuten und ggf. auch weitere rechtliche Konsequenzen haben kann;

Karlsruhe, 30. Juli 2021

P. Eckerter

Philipp Wolfgang Eckerter

COLOPHON

The typeset and the layout of this document are inspired by the '*classicthesis*' typography
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